FRONTISPIECE

Adult Bearded Vulture captured at the feeding site in the
Giant's Castle Game Reserve, Natal Drakensberg.

ABSTRACT

The Bearded Vulture Gypaetus barbatus has experienced a substantial decrease in range in southern Africa during this century. The present population, numbering about 200 pairs, is confined mainly to the highlands of Lesotho and the Natal Drakensberg. In these areas the birds breed successfully (about 0,9 young/pair/year) and non-adult birds constitute about 36% of the total population.

The food supply was found not to be responsible for the decline of Bearded Vultures on commercial farming areas in South Africa. The use of poisons by farmers for the control of mammalian predators is considered to be the most important factor leading to the extinction of Bearded Vultures and other scavenging species on farmlands.

Adult Bearded Vultures forage over an area of about 4000 km^2, but were recorded up to 75 km from the nest. They feed exclusively on carrion, at least 75% of which is derived from domestic animals. Present conservation areas are not large enough to contain the entire ranges of any pairs of these birds or to supply sufficient food to support a viable population throughout the year. The birds therefore have to forage over commercial farmlands in South Africa and communal areas in Lesotho.

This study, designed to be as broad-based as possible, covers in detail the following aspects of Bearded Vulture biology; age related characteristics, home range and movements, feeding ecology, breeding biology, behaviour away from the nest, energetics, distribution, status and population dynamics and their conservation. In conclusion, recommendations on the management and monitoring of the population are offered.

ACKNOWLEDGEMENTS

and Dave Wolhuter.

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Bearded Vulture research in the Natal and Lesotho Drakensberg

by Christopher J. Brown

Navorsing op die Lammergeyer in die Drakensberge van Natal en Lesotho

deur Christopher J. Brown

Background

Until recently, it was widely believed that only 20 pairs of Bearded Vultures still survived in the mountain massif of the Natal and Lesotho Drakensberg. Coupled with their dramatic range reduction, the continued survival of the Bearded Vulture gave conservationists considerable cause for concern. As a result, the Wildlife Society funded the building of a feeding station in the Giant's Castle Game Reserve in 1967, with the Natal Parks Board undertaking to provide offal and bones on a weekly basis. The fact that the largest breeding population of Bearded Vultures discovered to date is in the Giant's Castle area attests to the success of the feeding scheme. In addition, a research project to investigate the biology and status of the Bearded Vulture in southern Africa was promoted by the Natal Parks Board and the Wildlife Society, being funded also by the University of Natal/Natal Parks Board Research Fund, the S.A. Nature Foundation and the C.S.I.R. Research commenced in February 1980 and fieldwork was completed by March 1983. Some of the results of this work are presented in this booklet.

Amphitheatre. Basalt cliffs of the high 'Berg and sandstone cliffs of the little 'Berg; typical Bearded Vulture habitat.

Amfiteater: Basaltkranse van die Drakensbergpieke en sandsteenkranse van die voetheuwels wat tipiese lammergeyerhabitat is.
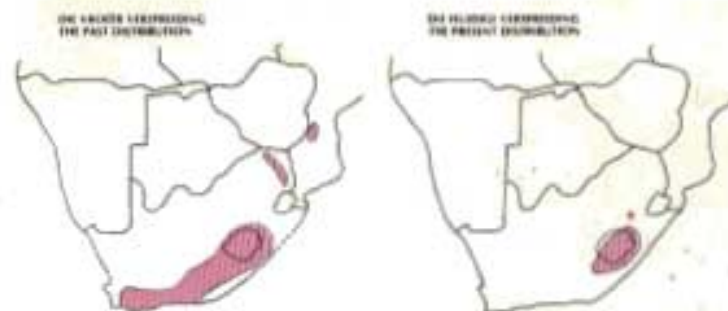
The past and present distributions of the Bearded Vulture in southern Africa.
Vroeëre en huidige verspreiding van die lammergeyer in Suider-Afrika.

Agtergrond

Tot onlangs is dit algemeen aanvaar dat daar nog net 20 broeipare lammergeyers in die bergmassief van die Drakensberg in Natal en Lesotho voorkom. Tesame met die dramatiese verkleining in hulle verspreidingsgebied, besorg die voortgesette voortbestaan van die lammergeyer natuurbewaarders eindelose hoofbrekens. Daarom het die Natuurlewevereniging in 1967 die fondse verskaf vir die daarstelling van 'n voerstasie in die Giant's Castle-wildtuin en die Natalse Parkeraad het onderneem om weekliks afval en bene te verskaf. Die feit dat die grootste lammergeyerbroeibevolking tot op hede waargeneem, juis in die Giant's Castlegebied voorkom, getuig van die sukses van die voerskema. Verder is 'n navorsingsprojek oor die biologie en status van die lammergeyer in Suider-Afrika in Februarie 1980 deur die Natalse Parkeraad en Natuurlewevereniging van stapel gestuur en die veldwerk is in Maart 1983 afgehandel. Die Universiteit van Natal/Natalse Parkeraad Navorsingsfonds, die SA Natuurstigting en die WNNR het die nodige fondse verskaf. Verskeie van die resultate van die projek word in hierdie boekie weergegee.

Research Procedure

Bearded Vultures were captured by cannon netting and by padded-jaw gin traps. A week's trapping resulted on average in the capture of one Bearded Vulture. A total of 23 Bearded Vultures were caught, measured, marked and then re-leased. All birds were marked with a numbered metal ring and coloured plastic rings, with wing "windows" for identification in flight and five birds were equipped with small radio transmitters. The birds' movements and home range sizes were obtained by resighting marked birds and by tracking birds fitted with radios, both from the ground and from an aircraft. The life of the transmitters was about 12 months, and from the air, ranges of over 100 km were obtained. Over 600 hours were spent at Bearded Vulture nest sites obtaining information on all aspects of their breeding biology. Their diet was determined by collecting and identifying prey remains from ossuaries (bone dropping sites) and from below nest sites. Finally, 6 000 questionnaires were sent to farmers in southern Africa within the range of the Bearded Vulture, requesting information on their sightings of these birds, their use of poisons and their attitudes towards Bearded Vultures. A very positive response was obtained and it says much for the enlightened attitudes of the Natal farming community that not one

Three cannons (inset) are attached to a large net, one side of which is pegged to the ground and the other side is folded back on itself. Food is placed in front of the net to attract the vultures. Once the required species is feeding on the ground the cannons are fired electronically, igniting a charge of gunpowder in each cannon. The projectiles fired by the cannons carry the net up and over the feeding birds.

Drie kannonne (inlas) word vasgemaak aan 'n groot net waarvan die eenkant aan die grond vasgepen is en die ander drie kante teruggevou. Voedsel word voor die net neergesit om die aasvoëls te lok. Sodra die gewenste spesie op die grond kom sit en vreet, word die kannonne elektries afgevuur en 'n lading kruit word in elke kannon ontbrand. Die projektiele wat deur die kannonne afgevuur word, lig die net op en oor die vretende voëls.

Padded-jaw gin traps were successfully used for capturing Bearded Vultures. The metal teeth were ground off, the spring was weakened and the jaws were padded with muslin cloth. The trap was attached to a peg in the ground by a length of speargun elastic. A similar padded-jaw gin trap is very effective for trapping jackals.

Slagysters met opgestopte klemme is suksesvol aangewend vir die vang van lammergeyers. Die metaaltande is afgevyl, die veer is verslap en die klemme is opgestop met moeseliendoek. Die slagyster is met 'n stuk pylgeweerrek aan 'n pen in die grond vasgeheg. Jakkalse word net so suksesvol met dié slagyster gevang.

farmer who reported the presence of Bearded Vultures on his/her farm considered this bird a threat to their farming programme in any way!

The Bird

Bearded Vultures are mountain specialists, found in many of the mountain ranges of the Old World. The African race occurs in southern Africa, East Africa and Ethiopia, while the North African and Eurasian races occur in the Atlas mountains, the Pyrenees, formerly in the Alps, and across to the Himalayas.

Bearded Vultures are large birds, weighing about 5,5 kg, with a wingspan of about 2,5 m; the wings are long and fairly narrow (=high aspect ratio). The tail is long (50 cm) and diamond-shaped. Compared with the weight of the bird, the combined wing and tail area is very large, giving it a favourable wing loading (ratio of weight to wing area). This allows the Bearded Vulture to be largely free of thermals, and with its high aspect ratio it is able to specialise in using slope lift, a phenomenon which results from moving air striking a hillside and being forced up. These factors make it possible for the Bearded Vulture to fly at first light, not being restricted to

Captured birds were marked with a numbered metal ring and a set of coloured plastic rings. The number and colour combination is unique to each bird.

Gevange voëls is gemerk met 'n genommerde metaalring en 'n stel gekleurde plastiekringe. Elke voël het 'n unieke nommer- en kleurkombinasie.

Radio transmitters (weighing 80 g) were attached to the backs of the Bearded Vultures by a harness consisting of nylon chord sheathed in surgical tubing. The birds soon preened their feathers over the transmitters, only the antenna being visible along the tail.

Radiosenders (wat 80 g weeg) is op die lammergeyers se rûe vasgemaak met behulp van 'n harnas bestaande uit nylontou in chirurgiese pyp. Die voëls het gou hulle vere bo-oor die senders begin kam sodat net die antenna tussen die stertvere uitgesteek het.

"Windows" were cut into the wing feathers for identification of birds in flight. The position of the window was different for each bird so that individuals could be recognised. These windows were visible for distances of up to 2 km using 8 × binoculars. In soaring and gliding birds such as the Bearded Vulture, the cutting of windows in the wings has little effect on their flying ability.

"Vensters" is in die vlerkvere geknip sodat die voëls in vlug geïdentifiseer kon word. Die posisie van elke voël se venster was uniek sodat individuele voëls uitgeken kon word. Met behulp van 8X-verkykers was hierdie vensters tot op 'n afstand van 2 km sigbaar. Die vensters in die vlerk het min effek op die vliegvermoë van voëls wat sweef soos die lammergeyer.

die lammergeyers. Die boere het baie positief reageer, wat getuig van die verligte benadering van die Natalse boeregemeenskap. Geeneen van die boere wat die teenwoordigheid van lammergeyers op hul plase aangemeld het, het die voël as 'n bedreiging vir hulle boerderyprogramme beskou nie.

Die voël

Lammergeyers is bergbewoners by uitnemendheid en word aangetref in baie van die bergreekse van die Ou Wêreld. Die Afrikaras kom voor in Suider-Afrika, Oos-Afrika en Ethiopië, terwyl die Noord-Afrikaanse en Eurasiese rasse voorkom in die Atlasgebergtes, die Pireneë, voorheen in die Alpe, en in die Himalajas.

Lammergeyers is groot voëls; hulle weeg sowat 5,5 kg en het 'n vlerkspan van sowat 2,5 m; die vlerke is lank en redelik smal (hoë aspekverhouding). Die stert is lank (50 cm) en diamantvormig. In vergelyking met die voël se gewig, is die gesamentlike oppervlak van die vlerke en stert baie groot, wat die voël 'n gunstige vlerkbelading gee (verhouding van gewig tot vlerkoppervlakte). Gevolglik is die lammergeyer in 'n groot mate onafhanklik van warm lugstrome, en met sy hoë aspekverhouding kan hy selfs enige opwaartse lugstrome benut. Hierdie faktor stel die lammergeyer in staat om vroeggoggend te vlieg, want hy hoef nie te wag vir geskikte warm

awaiting suitable thermals as are many other vulture species.

The appearance of the Bearded Vulture is unlike that of a typical vulture. The head is well feathered and bearded; a black mask adorns the side of the face and the eye is surrounded by a blood red scleral ring. In young birds the scleral ring is opaque, the head is dark brown, and the feathers of the breast and belly are mottled brown. In adult birds, the underparts are a rich rufous colour. This comes about by the birds acquiring a coating of iron oxide (rust) on their feathers, which is obtained quite passively from their everyday contact with rocks rich in this compound. The microstructure of the feathers is conducive to the adhesion of iron; birds kept in captivity have pure white underparts. Iron oxide is also present on young birds, but because of their dark coloured feather pigment, is not so visible.

Bearded Vultures also go by the name of "Lammergeier" (in Afrikaans — Lammergeyer), but due to confusion with the Afrikaans "Lammervanger" (given to any bird of prey thought to kill small livestock!) and the resulting unjustified persecution, the name has been officially changed to Bearded Vulture.

Most of the tracking was done from the ground. Continuous dawn to dusk monitoring provided details on the daily foraging patterns of the birds.

Die opsporing is meestal vanaf die grond gedoen. Ononderbroke monitering van dagbreek tot sononder het inligting verskaf oor die daglikse kossoekpatroon van die voëls.

Because of the rugged terrain and the large areas covered by Bearded Vultures, radio signals were sometimes lost to trackers on the ground. The Natal Parks Board aircraft was then used to locate and track the birds.

As gevolg van die onbegaanbare terrein en die groot afstande wat die lammergeyers aflê, het die opspoorders op die grond soms die radioseine verloor. Die Natalse Parkeraad se vliegtuig is dan gebruik om die voëls vanuit

lugstrome soos die meeste ander aasvoëlspesies nie.

'n Lammergeyer lyk anders as 'n tipiese aasvoël. Die kop is vol vere en het ook kenvere; daar is 'n swart masker oor die kante van die gesig en die oog is omring met 'n bloedrooi ronde sklera. By jong voëls is die skleraring onduidelik, die kop is donkerbruin en die bors- en maagvere is spikkelbruin. By volwasse voëls is die maag 'n ryk rooibruin kleur, wat veroorsaak word deurdat die voëls 'n lagie ysteroksied (roes) op hulle vere kry as gevolg van hulle daaglikse kontak met rotse wat ryk is aan ysteroksied. Die mikrostruktuur van die vere dra daartoe by dat die roes daaraan vassit. Voëls in aanhouding het 'n spierwit onderkant. Jong voëls het ook ysteroksied aan hulle vere, maar as gevolg van die donkerder veerpigment is die roes nie so opsigtelik nie.

Die Afrikaanse benaming "lammergeyer" is verkies in plek van "lammervanger", wat aan enige voël wat kleinvee vang toegeken is, en wat gevolglik tot onregverdige vervolging lei. Die Engelse benaming "bearded vulture" is offisieel in gebruik geneem.

Breeding and Home Range

Bearded Vultures are cliff nesters, the pairs being fairly evenly spaced out. On the Drakensberg escarpment, nests are on average 6,5 km apart and are usually built in a small cave or pothole two thirds of the way up a large cliff. The nest may be a very large structure, and old nests of over 2 m in height are not uncommon. The nest is built of branches and twigs, *Protea* species being commonly used, and thickly lined with wool, hair and even old sacks and rags. The breeding season commences in May, with nest building or repair carried out mainly by the male. The eggs (usually two, though one-egg clutches have been recorded) are laid in June and hatch about 57 days later. The first chick to hatch, usually three to five days before the second, survives at the younger chick's expense. Little sibling aggression takes place, but the first chick is physically more developed and is able to outbeg its sibling, which receives little food and steadily fades away. The surviving nestling remains in the nest for about 110 days, during the first 40 of which it is closely brooded. Food is brought to the young vulture for a further two months after its first flight, during which time it ventures farther and farther from the nest, until it accompanies its parents when foraging. When the adult birds begin

An immature Bearded Vulture. The head is dark brown and the feathers of the underparts are mottled brown.

'n Onvolwasse lammergeyer. Die kop is donkerbruin en die vere op die onderkant is spikkelbruin.

Wild adult Bearded Vultures have rufous underparts. This is caused by the adhesion of iron oxide (rust) to the feathers.

Wilde volwasse lammergeyers se onderkant is rooibruin as gevolg van die ysteroksied (roes) wat aan die

Captive adult Bearded Vultures which do not come into contact with iron-rich cliffs and rocks have pure white underparts.

Volwasse lammergeyers in aanhouding, wat nie met ysterryke kranse in aanraking kom nie, se onderkante is

Broei en tuisgebiede

Lammergeyers maak nes teen kranse en die broeipare word redelik eweredig versprei. Op die Drakensbergse eskarp is die neste gemiddeld sowat 6.5 km uit mekaar en gewoonlik gebou in 'n klein grotjie of holte sowat twee derdes van die hoogte teen die krans op. Die nes is soms 'n baie groot konstruksie, en ou neste van meer as twee meter hoog is nie ongewoon nie. Die nes word gebou van takke en twyge en *Protea*-spesies word veral hiervoor gebruik. Die nes word uitgevoer met wol, hare en selfs ou sakke en lappe. Die broeiseisoen begin in Mei met die bou of herstel van neste deur die manlike voël. Die eiers (gewoonlik twee, maar broeisels van 'n enkele eier is al waargeneem) word in Junie gelê en broei sowat 57 dae later uit. Die eerste kuiken, wat gewoonlik drie tot vyf dae voor die tweede kuiken uitbroei, oorleef ten koste van die jonger kuiken. Die kuikens is nie danig aggressief nie, maar die eerste kuiken is fisiek beter ontwikkel en kan vinniger eet as die kleintjie, wat dan minder kos ontvang en gestadiglik wegkwyn. Die oorlewende kleintjie bly sowat 110 dae in die nes. Gedurende die eerste veertig dae word hy deeglik opgepas. Kos word aangedra tot twee maande na die jong voël se eerste vlug. Gedurende hierdie tyd waag hy dit al verder en verder van

young bird has to become independent, and joins up with other young Bearded Vultures, forming groups of two or three, or joining foraging Cape Vultures.

Although Bearded Vulture pairs are fairly evenly dispersed, they do not defend large territories. The only area actively defended is that immediately around the nest site covering a radius of some 300 m. For the rest, home ranges are completely overlapping. Bearded Vultures do much of their foraging within an area of about 500 km² around the nest site. This area is usually searched from a fairly low altitude (usually below 100 m) and very small items of food such as dead rodents or small bones may be found. A high searching method may also be employed, usually above 1 000 m, with the bird searching for larger sources of food. Using this method, birds can cover much larger areas, and the largest home range recorded for a Bearded Vulture is 4 800 km², though an average home range size is about 3 000 km². The space required by these birds is thus far greater than could ever be provided by nature reserves.

A typical "pothole" nest site on a sandstone cliff.
'n Tipiese nes in 'n holte teen 'n sandsteenkrans.

A young Bearded Vulture, almost ready to fly, hordes its cache of food on the nest. Bearded Vultures take about six years to attain adult plumage.
'n Jong lammergeyer, byna gereed om te vlieg, met sy hoop opgegaarde kos in die nes. Dit duur sowat ses jaar voordat 'n lammergeyer 'n volwasse veredos

ouers vergesel op soek na kos. Sodra die ouers begin nesskop vir hulle volgende broeipoging, moet die jong voël onafhanklik raak en sluit dan by ander jong lammergeyers in groepe van twee of drie, of hy sluit aan by kransaasvoëls op soek na kos.

Alhoewel lammergeyerpare redelik eweredig versprei nesmaak, verdedig hulle nie baie groot territoriums nie. Die enigste gebied wat aktief verdedig word, is die onmiddellike omgewing van die nes in 'n radius van sowat 300 m. Verder oorvleuel die tuisgebiede heeltemal. Lammergeyers soek meestal kos in 'n gebied sowat 500 km² rondom die nes. Hierdie gebied word gefynkam terwyl die voël laag (gewoonlik laer as 100 m) oor die gebied vlieg en baie klein stukkies kos, soos dooie knaagdiere en stukkies been opspoor. Soms soek hulle ook groter bronne van voedsel vanaf 'n baie groot hoogte (gewoonlik hoër as 1 000 m). Sodoende kan die voëls baie groter gebiede dek, en die grootste tuisgebied sover aangeteken, is 4 800 km². Hierdie voëls het dus baie meer ruimte nodig as wat ooit deur natuurreservate verskaf kan word.

Food and Feeding

Bearded Vultures feed mainly on carrion, and although there are a number of records of birds carrying rodents and dassies, there is no evidence that they killed these animals rather than picking them up as carrion. Bearded Vultures feed on all parts of a carcase, including the red meat and viscera. However, they are not able to compete with the larger, gregarious Cape Vultures and so specialise on bones which the Cape Vultures are not able to swallow. Bearded Vultures have a very large gape, and can swallow bones of at least 18 cm long and 3 cm diameter. If the bone should prove to be too large, the bird flies off with it carried lengthways in the feet and tucked up against the body, until a suitable slab of rock is found. Here the bird will drop the bone, usually from a height of about 150 m, diving down rapidly to land beside the fragments, which are then eaten. Should the bone not break, the drop is repeated, and birds have been seen dropping bones 20 or more times before they break. Some of these bone dropping-sites or ossuaries, may be used regularly (daily by some pairs) and become littered with bone fragments.

Of the identifiable prey remains collected from ossuaries, almost 90% were of domestic stock. These remains were of mature to very old
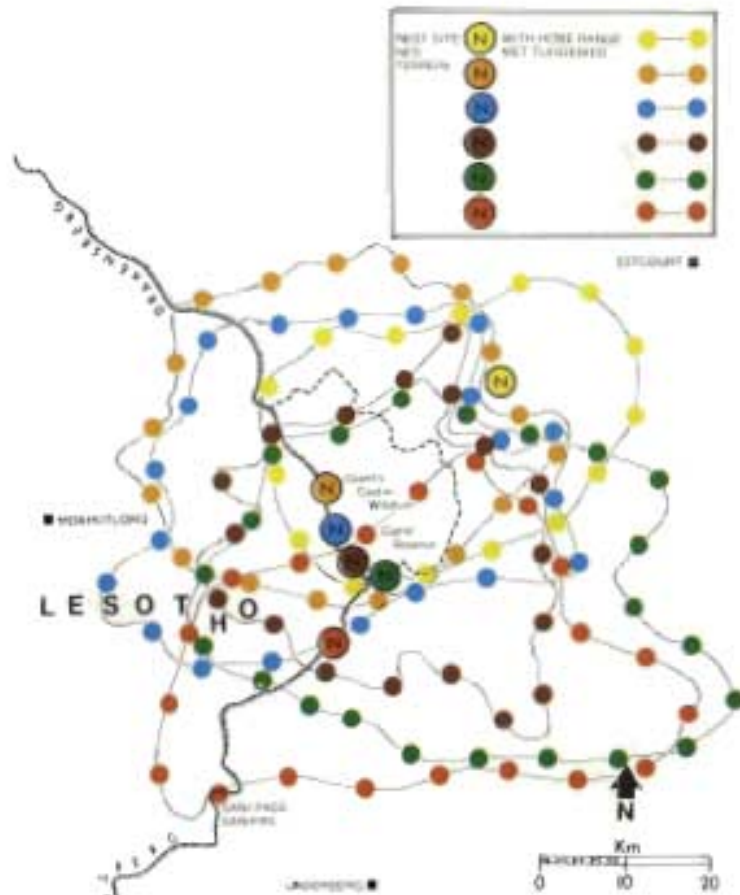
The distribution (nest sites) and home ranges of some pairs of Bearded Vultures in the Giant's Castle area. Note the extent of overlap of home ranges, with many pairs foraging over the same ground.

Die verspreiding (nesliggings) en tuisgebiede van verskeie pare lammergeyers in die Giant's Castlegebied. Let op die mate waarin tuisgebiede

Voedsel en voedingsgewoontes

Lammergeyers is hoofsaaklik aasvreters en alhoewel daar al voëls waargeneem is met knaagdiere en dassies in hulle kloue, bestaan daar geen bewyse dat die lammergeyers die diere gedood het in plaas van hulle as aas opgetel het nie. Lammergeyers vreet enige deel van die karkas, insluitend die rooivleis en ingewande. Omdat hulle nie opgewasse is teen die groter kransaasvoëls wat in groot groepe voorkom nie, vreet hulle dus eerder die bene wat die kransaasvoëls nie kan behartig nie. Lammergeyers het 'n wye keelgat en kan bene insluk wat 18 cm lank en 3 cm in diameter is. As 'n voël nie 'n been kan insluk nie, vlieg hy weg met die been in die lengte in sy pote vasgehou en opgetrek teen sy liggaam, totdat hy 'n geskikte rots kry waar hy die been laat val, gewoonlik vanaf 'n hoogte van sowat 150 m. Hy duik dan vinnig agterna, gaan sit langs die stukkies en vreet dit op. As die been nie die eerste keer breek nie, laat val die voël dit weer, en voëls is al waargeneem wat 'n been meer as twintig keer laat val voordat dit breek. Sommige van hierdie ossuariums, of plekke waar bene laat val word, word soms gereeld (daagliks deur sommige pare) gebruik en is besaai met stukkies been.

Negentig persent van die identifiseerbare prooireste wat versamel in

scavenging behaviour rather than hunting and killing. This indicates that the domestic stock on farmlands in the Natal Drakensberg provides an important source of food, and that the Drakensberg Forestry and Natal Parks Board Reserves alone may not be able to support a viable population.

Poisons

Preliminary results from the questionnaire survey show that 34% of farmers in the Natal Drakensberg used potentially lethal poisons. The distribution of this poison use is as follows: 60% of farmers bordering Forestry or Natal Parks Board reserves use poisons, mainly against jackals; 40% of farmers bordering KwaZulu areas use poisons, mainly against dogs, and in other areas, 21% of farmers poison. Strychnine is the most commonly used poison (69% of cases), but 10-80, toxaphene, "dip" and dieldrin are also used.

In a natural situation, food supply is the main limiting factor to the size of vulture populations. However, at present, the single most important mortality factor in vultures is poisons. 24% of farmers volunteered that Cape Vulture numbers in the southern and central Drakensberg had decreased dramatically over the past 20 years. This is true too for Bearded Vultures, with eight confirmed cases of poisoning having

Bearded Vultures specialise in feeding on what remains after the Cape Vultures have fed. Bones make up the major part of the Bearded Vulture's diet.

Lammergeyers vreet wat oorbly nadat die kransaasvoëls hulle honger gestil het, en hulle dieet bestaan hoofsaaklik uit bene.

Prey remains collected at an ossuary (bone dropping site). Smaller bones are swallowed whole, while larger bones are dropped onto a slab of rock until they break.

Prooireste versamel by 'n ossuarium ('n plek waar bene laat val word). Kleiner bene word heel ingesluk, terwyl groter bene op 'n rotsplaat laat val word totdat hulle breek.

Food of Bearded Vultures in the Natal Drakensberg. These were identified from prey remains collected at nests and ossuaries, and from farmers' observations of what birds fed on.

Die voedsel van die lammergeyer in die Natalse Drakensberg. Hierdie voedselbronne is geïdentifiseer uit prooireste wat by neste en ossuariums versamel is, en uit die boere se waarnemings van wat die voëls eet.

vee. Hierdie reste was afkomstig van volwasse en baie ou diere, wat daarop dui dat die voëls eerder aasvreters as jagters is. Dit dui ook daarop dat die vee op die plase in die Natalse Drakensberg 'n belangrike bron van voedsel is, en dat die Drakensbergse Bosboureservate en Natalse Parkeraadreservate alleen nie 'n lewensvatbare lammergeyer-bevolking sal kan onderhou nie.

Gifstowwe

Voorlopige resultate verkry uit die vraelysopname, toon aan dat 34% van die boere in die Natalse Drakensberg potensieel dodelike gifstowwe gebruik. Die verspreiding van die gifgebruik is soos volg: 60% van die boere langs die Bosbouge-biede en die Natalse Parkeraad-reservate gebruik gif, hoofsaaklik teen jakkalse; 40% van die boere langs KwaZulu gebruik gif, hoofsaak-lik teen honde; en in ander gebiede gebruik 21% van die boere gif-stowwe. Strignien word die meeste gebruik (69% van die gevalle), maar 10-80, toksafeen, dip en dieldrin word ook gebruik.

Gewoonlik is die voedselvoorraad die belangrikste beperkende faktor vir die grootte van 'n aasvoël-bevolking. Huidiglik hou gifstowwe egter die grootste bedreiging in vir aasvoëls. Vier en twintig persent van die boere het toegegee dat die kransaasvoëlgetalle dramaties afge-neem het die afgelope twintig jaar. Dieselfde geld ook vir lammergeyers

been reported. At present, there are some 30 pairs of Bearded Vultures nesting in the Natal Drakensberg with perhaps another 200 pairs in Lesotho, the north eastern Cape, O.F.S., Qwa Qwa and Transkei. Because of the large home ranges of this species, many of these birds also forage in Natal. Likewise, the 700 surviving Cape Vultures in the high 'Berg are largely dependent on domestic livestock carcasses for their well-being. The future of these birds depends largely, if not solely, on the farming community.

How you can help conserve vultures

1. Do not use poisons indiscriminately. Remember, even small pieces of meat can be picked up and eaten by Bearded Vultures.

   If at all possible, do not use poisons at all. A number of alternative controls for problem animals are available to you e.g. coyote getters, padded-jaw gin traps, jackal-proof fencing.

   (Please note: animals put down by barbiturates and many other compounds are lethal to vultures. Do not allow birds to feed on these carcasses.)

2. Leave the carcasses of animals which have died from non-
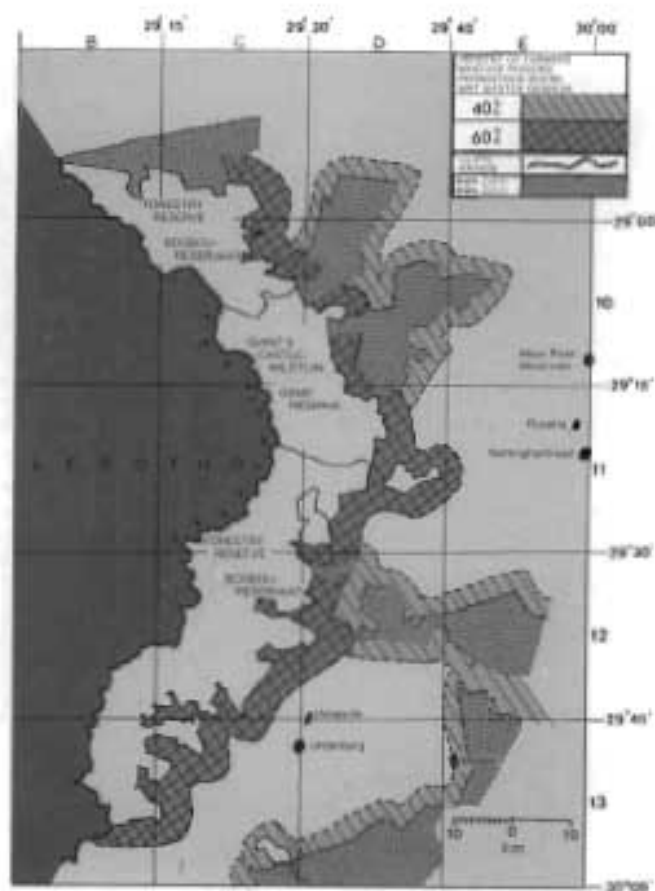
The central and southern Drakensberg, showing the distribution in the use of poisons. Poisoning is the most important factor causing mortality in vultures in the Natal Drakensberg.

Die Sentrale en Suidelike Drakensberg en die verspreiding van die gebruik van gifstowwe. Vergiftiging veroorsaak die meeste aasvoëlvrektes in die gebied.

met agt aangemelde bevestigde gevalle van vergiftiging. Tans maak sowat 30 broeipare lammergeyers nes in die Natalse Drakensberg, en daar is miskien nog 200 pare in Lesotho, die Noordoos-Kaap, die OVS, Qwa Qwa en Transkei. As gevolg van hierdie spesie se uitgestrekte tuisgebiede, soek party van hulle selfs kos in Natal. Eweneens is die 700 oorlewende kransaasvoëls in 'n groot mate aangewese op veekarkasse vir hulle voortbestaan. Hierdie voëls se toekoms is grotendeels, indien nie geheel en al nie, van die boeregemeenskap afhanklik.

Hoe u kan help om aasvoëls te bewaar

1. Moenie gifstowwe onoordeelkundig gebruik nie. Onthou dat selfs klein stukkies vleis deur lammergeyers opgetel en geëet kan word.

   Indien moontlik moet hoegenaamd geen gifstowwe gebruik word nie. 'n Aantal alternatiewe metodes bestaan vir die beheer van probleemdiere, nl. gifskieters, slagsysters met opgestopte klemme, jakkalsdraad, ens.

   (Let wel: Diere wat uitgesit is met barbiturate en heelparty ander stowwe, is dodelik vir aasvoëls; moenie die voëls toelaat om aan die karkasse te vreet nie.)

provide birds with a good healthy food supply. If you are concerned about bones littering the veld, an area can be fenced off (about 200 m × 200 m) in which all carcasses are placed. This area can be fenced with mesh if jackals or dogs are likely to be attracted.

For more information regarding the above two points, please phone or write to:

The Director
Natal Parks Board
P.O. Box 662
PIETERMARITZBURG
3200

Telephone (0331) 51221

or

Dr Andre Boshoff
Cape Department of Nature and Environmental Conservation
Private Bag 6546
GEORGE
6530

Telephone (04455) 302 or 366

2. Laat die karkasse van diere wat van nie-aansteeklike siektes gevrek het, in die veld bly lê om die voëls te voorsien van 'n gesonde voedselvoorraad. As u begaan is oor bene wat die veld kan besaai, kan 'n gebied afgegrens word (sowat 200 m × 200 m) waarin alle karkasse geplaas word. Span die gebied toe met ogiesdraad as jakkalse of honde deur die karkasse aangelok sal word.

Vir meer besonderhede oor bogenoemde maatreëls, skakel of skryf aan:

Die Direkteur
Natalse Parkeraad
Posbus 662
PIETERMARITZBURG
3200

Telefoon (0331) 51221

of

Dr Andre Boshoff
Kaapse Departement van Natuur- en Omgewingsbewaring
Privaatsak 6546
GEORGE
6530

Telefoon (04455) 302 of 366

The Cape Vulture, another endangered species, is endemic to southern Africa and could be extinct in 60 years if the present rate of mortality continues.

Die kransaasvoël, nog 'n bedreigde spesie, is endemies aan Suider-Afrika en kan binne sestig jaar heeltemal uitgestorwe wees indien die huidige sterftesyfer gehandhaaf word.

27 The Giant
28 Long Wall
29 Mt. Durnford
30 Mt. Erskine
31 Gypaetus Point
32 The Judge

∿ Drakensberg escarpment

∿ Natal-Lesotho border

Km 0 10

TRANSVAAL

ORANGE FREE STATE

NATAL

LESOTHO

Orange River

CAPE

TRANSKEI

1   Bethlehem
2   Harrismith
3   Golden Gate Highlands National Park
4   Qwa Qwa
5   Royal Natal National Park
6   Butha Butha
7   Oxbow
8   Cathedral Peak State Forest
9   Cathkin Peak State Forest
10 Giant's Castle Game Reserve
11 Ntabamhlopa mountain
12 Loteni Nature Reserve
13 Mkomaasi State Forest
14 Sani Pass
15 Cobham State Forest
16 Bushman's Nek
17 Estcourt
18 Mokhotlong
19 Thaba Tseka
20 Pietermaritzburg
21 Underberg
22 Ladybrand
23 Maseru
24 Roma
25 Aliwal North
26 Barkly East

∿ District boundaries

Land above 2500 m above sea level

N

Km 0 100

FIGURE 2.1.   The Bearded Vulture study area showing the main topographic features and place names mentioned in the text.

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Edwards (1967, 1974), Killick (1963), King (1944, 1972),
Pearse (1978), Scotcher & van Rensburg (1977), Tyson et al.
(1976) and van der Merwe (1941). Many of the meteorological
data were obtained from the weather station on the Little
Berg in the Cathedral Peak State Forestry Reserve (28° 58'S,
29° 14'E; 1860 m above sea level).

2.2 STUDY AREA

2.2.1 Topography

The area covered by this study ranges in altitude from
about 1400 m above sea level to the summit of Thabana-
Ntlenyana at 3482 m, the highest point in Africa south of
Mt. Meru in Tanzania. The area contains two major mountain
ranges, the Drakensberg and the Malutis. The Drakensberg is
made up of the High and Little Bergs, the Malutis of the
Front and Central Ranges. The Drakensberg between Mont-aux-
Sources in the north and Bushman's Nek in the south has an
average altitude of about 3000 m above sea level and
constitutes the High Berg. The watershed on the top of the
High Berg forms the boundary between Lesotho and the
province of Natal. To the north of Mont-aux-Sources the
Drakensberg is lower with an average altitude of about
2000 m and forms the boundary between Natal and the Orange
Free State before entering the eastern Transvaal. To the
south of Bushman's Nek the Drakensberg varies between 2000
and 2500 m in altitude and forms the boundary between
Lesotho and the Transkei, Lesotho and the Cape Province and
then continues south into the Cape.

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The High Berg consists of an escarpment of sheer cliffs, some over 2000 m high. Few passes through this escarpment offer access to the highlands, and only one steep roadway, at Sani Pass, provides access for four-wheel-drive vehicles. Below the High Berg a terrace consisting of finger-like spurs project into Natal, forming the Little Berg. This area is eroded into deep valleys by numerous streams and rivers which flow mainly eastwards. A similar but less dramatic projection of ridges occurs to the west of the Front Range of the Malutis in Lesotho. An east-west cross-section of the landscape illustrates this topography (Figure 2.2). The largest river in southern Africa, the Orange River (Senqu River) rises at Mont-aux-Sources and flows south and southeast through Lesotho. This river divides the Drakensberg mountain range to the east from the Malutis to the west.

2.2.2 Geology and soils

The geology of Lesotho and adjacent regions is simple, consisting of a series of horizontal layers of rock belonging to two series of the Karoo System, the Stormberg and Beaufort Series.

The uppermost layer consists of basalt lavas which can be up to 1500 m thick. This basalt layer was built up by a number of larval flows, superimposed one on the other, causing the basalt to be conspicuously stratified and forming long ledges on eroded cliffs. Sheer, dark coloured basalt cliffs occur along the escarpment of the High Berg,

15
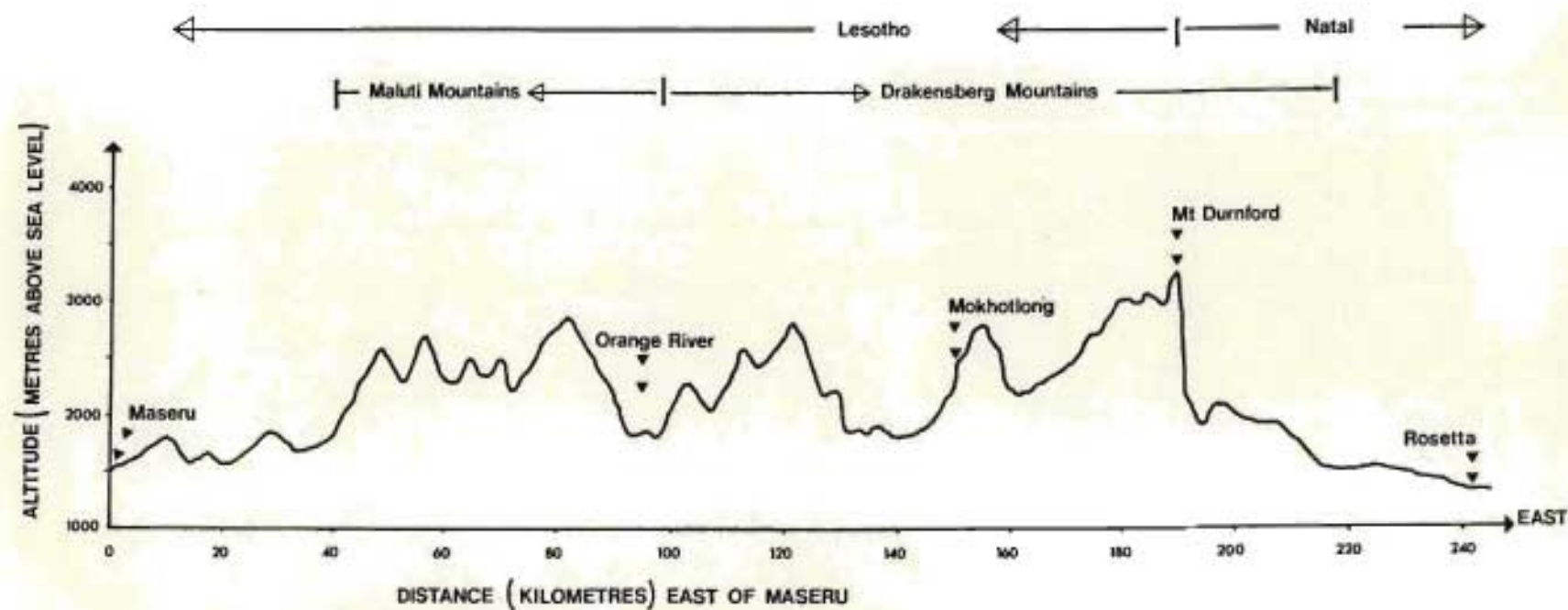
FIGURE 2.2. East-west cross-section of the study area, from Rosetta in Natal to Maseru in Lesotho, showing the mountain ranges and their altitudes.

on the peaks of mountains in Lesotho and along river gorges. The cliffs usually give way to rounded, grassy hillsides.

At about 1800 m above sea level the basalt gives way to cave sandstone, which can be up to 100 m thick. These cream to orange-coloured cliffs often contain series of potholes or small caves. Below the sandstone are the red beds, the molteno beds and the upper Beaufort beds, all of which are rarely exposed but underlie the grassy slopes below the sandstone cliffs.

Gradients from the mountain ridges to the rolling hills and plains below the montane region are steep, particularly on the eastern side of the Drakensberg. Here the altitude decreases by about 3000 m over a distance of less than 100 km. Gradients are steepest near the mountains, which has resulted in the formation of deep valleys, gorges and inselbergs and produced rugged and majestic scenery.

Soils in this area are classed as Mountain Black Clays and are derived from the basalt lavas. At high altitudes the soil is usually shallow and easily eroded by cultivation and overgrazing by domestic stock, but at lower altitudes soils are deep with high organic content. During summer soils on the summit become waterlogged and in winter they often freeze.

2.2.3 Insolation and temperature

Daylength in summer is about 14 h and in winter about 10 h. The average daily sunshine in the Natal Drakensberg (measured at Cathedral Peak) varies between 5,5 h in

17

December and 8,3 h in June. In Lesotho the average daily length of sunshine is greater, but no precise data are available. In summer clouds form almost daily against the Drakensberg escarpment and extend out over Natal for up to 15 km. These usually produce thunderstorms.

The climate below the Alpine Belt (i.e. below about 2800 m) is temperate, but at higher altitudes it can be severe. At Cathedral Peak absolute maximum monthly temperatures range from 15°C in June and July to 34°C in November. Absolute minimum monthly temperatures are below zero from March to October. There is normally a range of at least 15°C between daily maximum and minimum temperatures. Altitude has a considerable effect on temperature. At high altitudes the lower atmospheric pressure results in lower air temperatures and an increase in the intensity of insolation. This leads to high surface temperatures during the day, which cool rapidly at night. There are few weather data from high altitudes in southern Africa, but temperature data can be extrapolated as follows: an average decrease of about 0,5°C is experienced with each 100 m ascended. Absolute maximum and minimum temperatures (Stevenson screen) at 3000 m would then be about 25°C and -9°C respectively. At Letseng-la-Terae (29°01'S, 28°52'E; 3100 m above sea level) in the Lesotho highlands the mean temperature in June and July is below zero and night temperatures below -10°C are often experienced. At grass level temperatures have been found to be as much as 25°C lower than those recorded in the Stevenson screen. The lowest grass-level temperature

recorded at Cathedral Peak was -16°C while for the High Berg a conservative estimate would be -22°C.

2.2.4 Wind and precipitation

In winter a high pressure system is centred over the Orange Free State. Anti-cyclonic winds blow from the west and northwest. These "Bergwinds" (katabatic winds) are warm, dry and of high velocity. In summer the high pressure system retreats from the sub-continent and is replaced by a low pressure system over the Kalahari. Moisture-laden winds originate over the warm Indian Ocean and blow from the east and southeast. The mean hourly duration of wind per month at Cathedral Peak is shown in Figure 2.3.

The current range of the Bearded Vulture lies in the summer rainfall area of southern Africa, but historically, these birds occurred through areas of all-year rainfall to those of winter rainfall in the southwestern Cape. In their present range, about 85% of the rain falls between October and March, with about 50% being produced by thunderstorms. The seasonal occurrence and the high frequency of thunderstorms in this area are shown by the lightning-flash counter at eNjesuthi, Giant's Castle Game Reserve (Figure 2.4). The rainfall pattern across the study area from east to west is shown in Figure 2.5. The annual rainfall increases to the top of the Little Berg (2017 mm) but then decreases westwards, particularly in the rain-shadow west of the High Berg. The lowest rainfall (480 mm) is recorded in the Orange River valley at Mashai (29°40'S, 28°49'E),
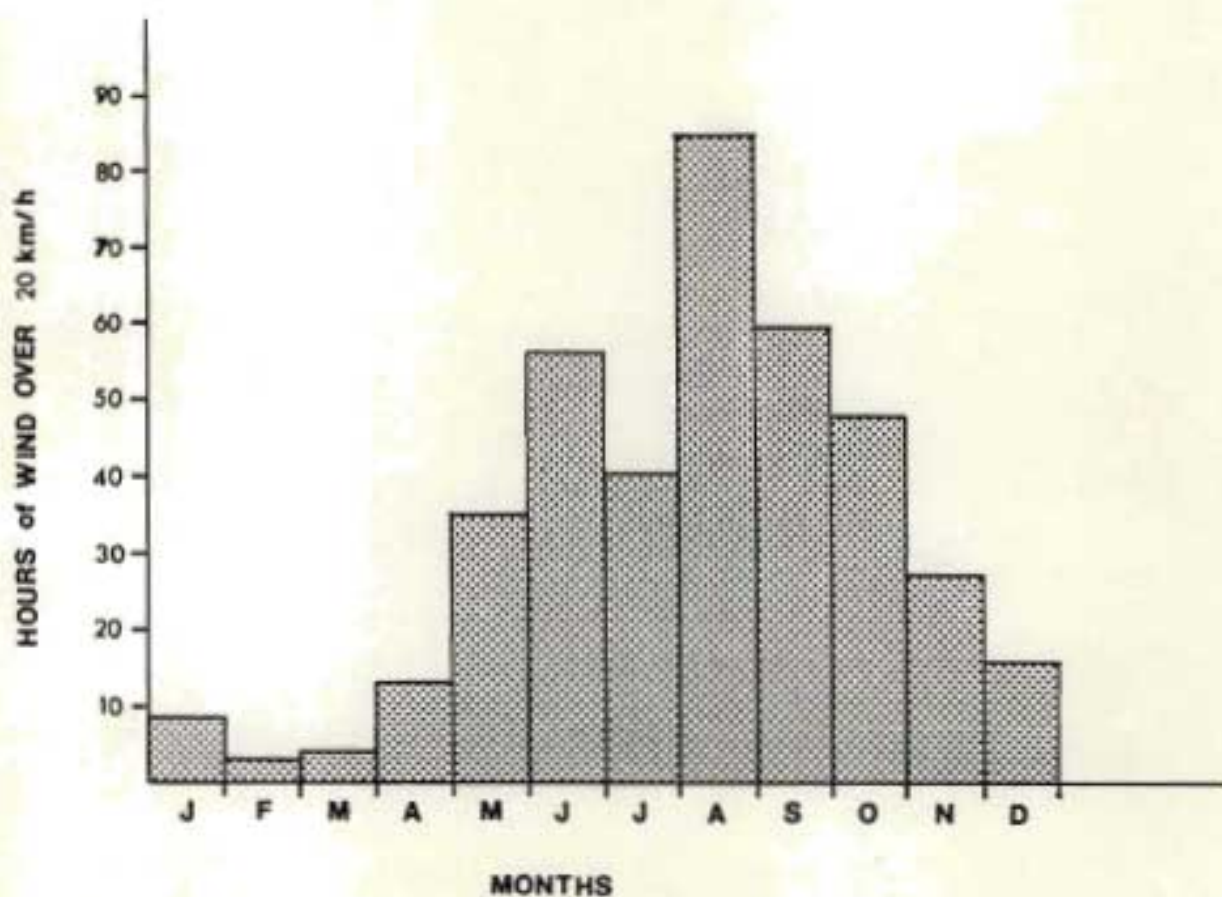
FIGURE 2.3. Mean hourly duration of wind over 20 km/h per month (1972-1982) recorded at the Cathedral Peak State Forestry meteorological station.

20
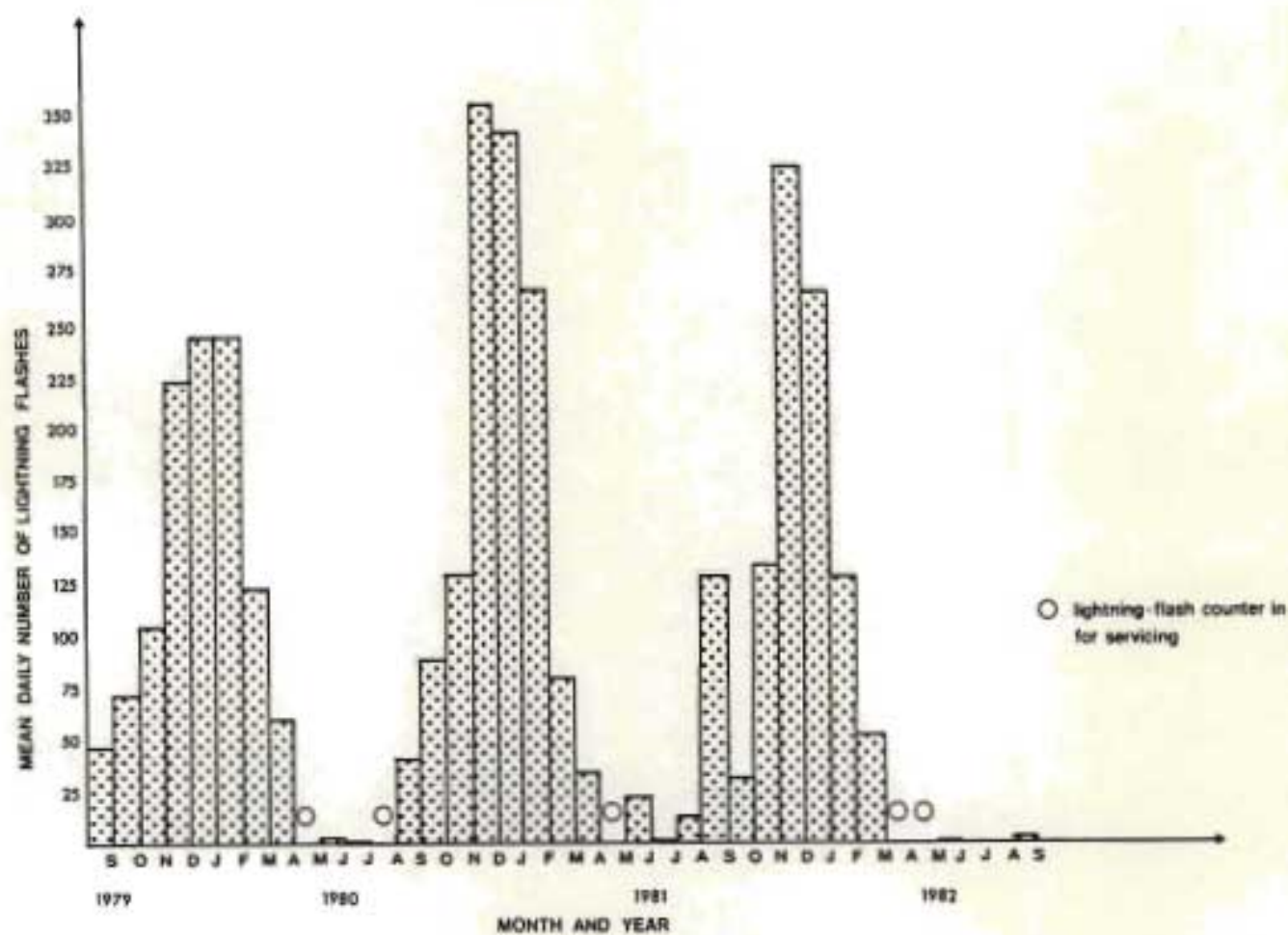
FIGURE 2.4. Mean daily number of lightning flashes per month
as an indication of thunderstorm occurrence in
the Natal Drakensberg, measured at eNjesuthi,
Giant's Castle Game Reserve.
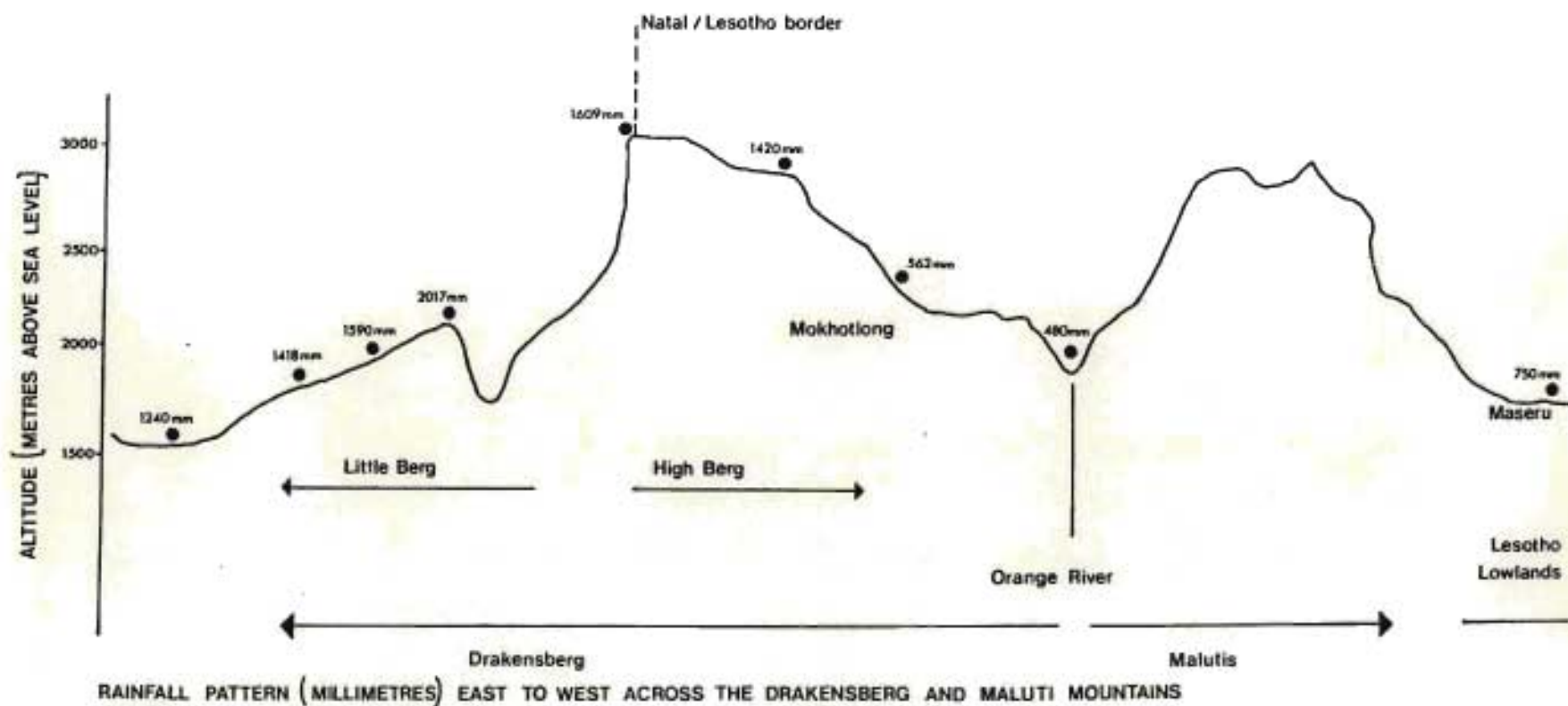
FIGURE 2.5. Rainfall pattern from east to west across the Drakensberg and Maluti mountains.

thereafter increasing to about 750 mm on the plains to the west of the Maluti mountains.

Snow has been recorded at high altitude in all months of the year, but falls mainly between April and September. Snow is usually restricted to areas above 2800 m but may occasionally fall at 1800 m. It seldom lies for longer than a few days except in protected gullies and on south faces of peaks where it may remain for weeks. Fog occurs commonly in summer, particularly along the escarpment of the High Berg. It can last for periods of up to two weeks.

The overall precipitation in this mountainous region of southern Africa is generally high and reliable. The many marshes, streams and rivers provide an abundance of water and most of the larger of these are perennial.

2.2.5 Vegetation

.The Drakensberg-Maluti region of southern Africa falls mostly within Acocks' (1953) Themeda-Festuca Alpine Veld. This is predominantly a grassland habitat and encompasses all the area in the region above about 1800 m. Killick (1963) divided the area into three belts based on the distribution of climax vegetation. These are (a) the Montane Belt (1280-1830 m), (b) the Subalpine Belt (1830-2865 m) and (c) the Alpine Belt (above 2865 m).

The vegetation of the Montane and Subalpine Belts consist chiefly of tussock grassland, dominated by Themeda triandra with species of Protea occurring mainly at lower altitudes and more commonly on the Natal side of the

Drakensberg. Small patches of montane forest survive in Natal. They are dominated by <u>Podocarpus</u> <u>latifolius</u> and are confined to sheltered gorges and valleys. <u>Leucosidea</u> <u>sericea</u>, a bush or small tree, is dominant along watercourses at altitudes below about 2400 m.

The Alpine Belt consists of climax heather communities composed mainly of low woody species of <u>Erica</u> and <u>Helichrysum</u> interspersed with alpine grasses.

The general pattern of land-use in the area covered by this study is shown in Figure 2.6. Human impact on the land has been most marked in Lesotho, where cultivation is practiced in areas more suited to stock farming and where the numbers of domestic stock far exceed the recommended carrying capacity. It is estimated that 0,2% of the arable land in Lesotho is being lost each year by erosion. In contrast, a large part of the Natal Drakensberg is under conservation (Natal Parks Board and Department of Forestry) and these areas are managed for water conservation. The maintenance of a healthy vegetation cover is considered to be a priority, and management practices are selected to further this objective.

2.2.6 <u>Fauna</u>

The highest concentrations of game species occur in the Drakensberg conservation areas, although most farms adjacent to these regions support some animals. A total of 11 large wild herbivores have been recorded in the area, of which the Eland <u>Taurotragus</u> <u>oryx</u>, Grey Rhebok <u>Pelea</u> <u>capreolus</u>,
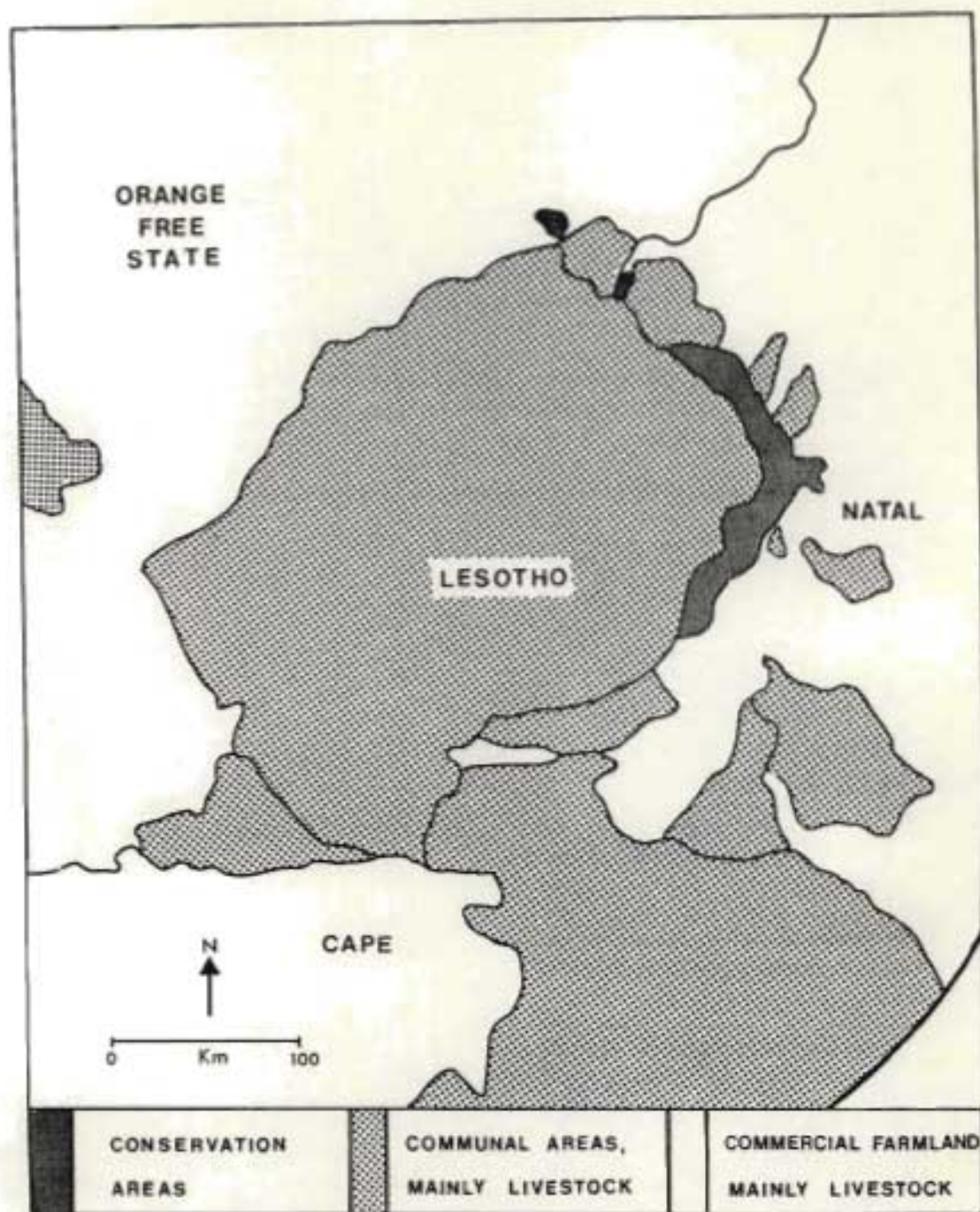
FIGURE 2.6. General pattern of land-use in the study area.

Mountain Reedbuck _Redunca fulvorufula_, Blesbok _Damaliscus dorcas phillipsi_ and Oribi _Ourebia ourebi_ are most common. In Lesotho only the Grey Rhebok is still fairly common, the other species having been eliminated many years ago. The Chacma Baboon _Papio ursinus_, Blackbacked Jackal _Canis mesomelas_ and the Rock Hyrax _Procavia capensis_ are common in the more isolated areas.

Domestic stock have replaced the indigenous herbivores in Lesotho, in the tribal areas of KwaZulu, Qwa Qwa and the Transkei, and to a large extent on the adjacent commercial farming areas. In the areas where the stocking rates are known, cattle and sheep predominate and range on average from 9 to 24 cattle/km^2 and 43 to 75 sheep/km^2.

2.3 GENERAL METHODS

This section provides an overview of the methods used which were pertinent to the overall study. Details of procedures as well as those methods relevant to only certain parts of the study are described in subsequent chapters.

Bearded Vultures were caught at a vulture feeding site in the Giant's Castle Game Reserve (29° 20'S, 29° 31'E; 2250 m above sea level). They were attracted to the site by meaty bones and were trapped by a cannon-net (Clark 1978), padded-jaw gintraps or an elasticised nylon noose (the last two methods are illustrated in Figure 2.7). Periods of 5-6 consecutive days were spent trapping, usually once a month. The average rate of capture was one bird per 4,4 days or per 24,8 h.
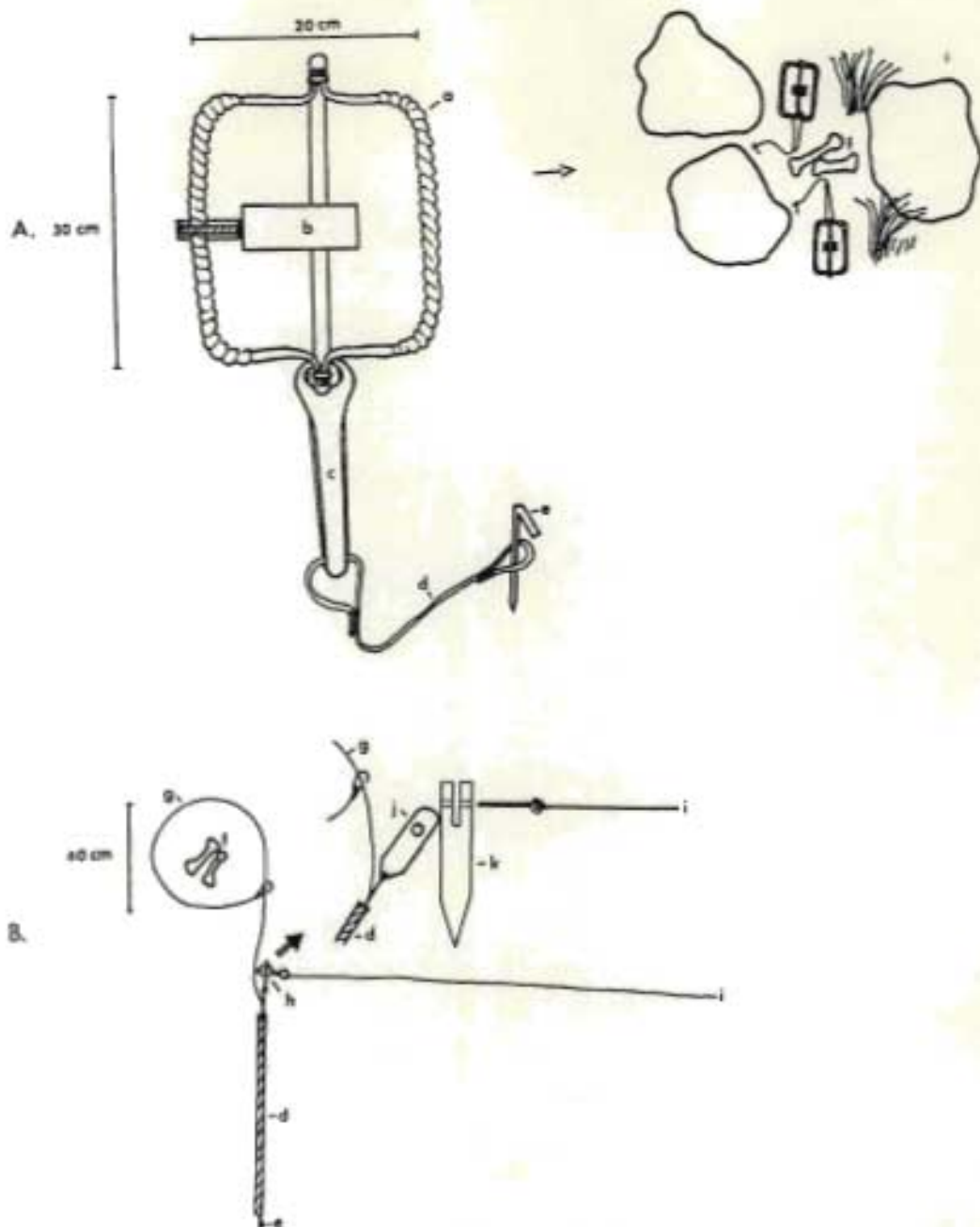
FIGURE 2.7. Methods used to capture Bearded Vultures in the Giant's Castle Game Reserve: A = padded-jaw gin trap, B = elasticised nylon noose trap.

a = jaws of gin trap, filed smooth and padded with muslin cloth, b = pressure-release plate, cut small so that most of the bird's foot is within the trap before it is sprung, c = spring, weakened to prevent injury, d = speargun elastic, 1,4 cm thick and 60 cm long, e = peg knocked into ground. The entire trap is set and lightly buried where birds are likely to walk to reach food (f). g = nylon noose (40 kg fishing line), h = release mechanism, i = release pin and cord, j = metal plate attached to elastic and nylon and with hole to secure in slotted peg (k) with release pin (i). The elastic is stretched from peg (e) to slotted pen (k) (which is securely knocked into ground) and held in place by release pin (i). The nylon noose (g) is set and food (f) is placed in the centre.

Bearded Vultures were ringed with serially numbered metal rings (supplied by the South African Bird Ringing Unit) and plastic coloured rings. Windows were cut into the remiges and/or rectrices which allowed for identification of individual birds in flight. Five birds were fitted with 80 g radiotransmitters and these birds were monitored for periods ranging from five to nine months.

Amateur involvement was encouraged throughout this study and visitors to the parks, Natal Parks Board and Forestry conservation staff and local farmers provided assistance. Data forms were made available to all interested people, and an observations book, with a set data-entry format, was placed in the public hide at the Bearded Vulture feeding site in Giant's Castle Game Reserve.

Few routes in the study area were negotiable by vehicle. Observations were made mostly from on foot and a considerable period of this study was spent back-packing and camping out in remote areas. Horses were also used to get to distant areas and in the more accessible regions observations were made from an open Land Rover, using 8 x 40 and 16 x 50 binoculars.

Every sighting of a Bearded Vulture was recorded, with the time, locality, identity and activity being noted. These records provided information on the behaviour of the birds, i.e. an "instantaneous sampling" of activity (Altmann 1974).

A questionnaire was mailed to about 4500 commercial farmers within and outside the expected range of the Bearded Vulture. The questionnaire was in English and Afrikaans

(Appendix 2.1) and consisted of a covering letter, a coloured illustration of the bird in adult and immature plumage and at perch and in flight, and a stamped addressed envelope in which to return the completed questionnaire. Farmers' addresses were obtained from the 1981 Voters Roll for magisterial districts in the Cape Province, from the individual regional Post Offices (with permission of the Postmaster General) for the Orange Free State and from the Cedara Agricultural College for magisterial districts in Natal. 6,4% of the questionnaires were returned with incorrect addresses.

TABLE 2.1

Areas visited within the range of the Bearded Vulture during the study period. Areas within about 50 km of the Giant's Castle Game Reserve, e.g. Ntabamhlope, Loteni and Kamberg Nature Reserves and adjacent Forestry Reserves are not listed.

Region	Visit	Route/area	Period
Cathedral Peak Forestry Reserve	1	via Ulundi & Loskop	10-14/11/80
	2	via Ulundi & Loskop	03-11/02/81
Royal Natal National Park	1	via Bergville	23-27/03/81
	2	via Bergville	17-19/11/82
Golden Gate Highlands National Park	1	via Oliviershoek Pass and Phuthaditjhabu, Qwa Qwa	21-27/08/83
Transkei	1	Ongeluksnek area	29-30/11/81
	2	Ongeluksnek area	07-08/12/81
Underberg & Bulwer area	1	Farms Sunset, Glengariff	28/12/82-04/01/83
	2	& Hlogoma	29/01-04/02/83
	3	as above	02-05/03/83
	4	as above	01-09/04/83
Drakensberg escarpment	1	Sani Pass-Giant's Castle	19-23/11/80
	2	Popple Peak-Langalibalele	27/02-01/03/81
	3	Giant's Castle-Langalibalele	19-22/03/81
	4	Langalibalele-Mt. Durnford	09-11/06/81
	5	Giant-The Hawk-Mt. Durnford	13-15/11/81
	6	Sani Pass area	01-02/07/81
Roma, Lesotho	1	via Oliviershoek Pass & Golden Gate Highlands National Park	23-29/04/81
	2	via Makhotlong & Thaba Tseka	02-20/07/81
	3	via Makhotlong & Oxbow	22-29/09/81
	4	via Oliviershoek Pass & Bethlehem	06-11/09/82
Northeastern Cape	1	Barkly East, Maclear, Indwe, Lady Grey, Aliwal North, Elliot & Wodehouse	01-06/12/81
	2	as above	13-16/12/82
Aerial surveys	1	Eastern & central Lesotho highlands	01/09/82
	2	Central Lesotho highlands	23/11/82
	3	Central & northern Lesotho highlands	28/12/82
	4	Central & southern Lesotho highlands	06/02/83
	5	Natal Drakensberg escarpment and eastern Lesotho	07/03/83
	6	Southern Natal Little Berg	03/04/83

APPENDIX 2.1

Questionnaire survey to commercial farmers adjacent to Lesotho in the provinces of Natal, the Orange Free State and the Cape. Included was a covering letter, the questionnaire and a coloured illustration of the Bearded Vulture.

(AFRIKAANS, KEERSY).

Tel. Add. "UNIVERSITY"

Dept. of Zoology

TELEPHONE 63320

CJB/nmc

UNIVERSITY OF NATAL

P.O. Box 375
PIETERMARITZBURG

April 1982

Dear Sir/Madam,

LAMMERGEYER RESEARCH PROGRAMME

The Lammergeyer, also known as the Bearded Vulture (Gypaetus barbatus) is listed as an endangered species in the South African Red Data Book, and until recently it was thought that their numbers had been reduced to less than 20 pairs. This bird is now the subject of an urgent study requiring information about their numbers, distribution, nesting and behaviour.

We would be grateful if you could help us by completing the attached form and returning it to us in the stamped envelope provided. The time period covered by this questionnaire is from 1970 to the present day. It is important to remember that if you do not see Lammergeyer on your farm, that information is as useful to us as a positive sighting.

Please Note:
a) You are not obliged to fill in your name and address if you would rather not, although this information would help us considerably.

b) All information will be treated as strictly confidential, and will not be revealed under any circumstances without your prior permission.

c) This questionnaire refers only to the Lammergeyer (see illustration) and NOT to the "Lammervanger", Black Eagle or any other bird.

Thank you for your help.

Yours sincerely

Christopher J. Brown

UNIVERSITY OF NATAL

Tel Add. "UNIVERSITY"

Dept. _Dierkunde_

TELEPHONE 63320

CJB/nmc

P.O. Box 375

PIETERMARITZBURG

April, 1982

Geagte Mnr./Mev./Mej..

LAMMERGEYER NAVORSINGSPROGRAM

In die Suid-Afrikaanse "Red Data Book" word die Lammergeyer (Gypaetus barbatus) as 'n bedreigde spesie gelys. Tot onlangs was daar vermoed dat hul getalle verminder het tot ongeveer 20 pare. Dit het dus nodig geword vir 'n dringende studie oor dié spesie wat inligting aangaande hul getalle, verpsreiding, broeigewoontes en gedrag vereis.

Ons sal dit hoog op prys stel indien u ons van hulp kan wees deur die aangehegte vraelys te voltooi en in die gefrankeerde koevert aan ons terug te stuur. Hierdie vraelys verwys na die tydperk 1970 tot op huidige. Dit is belangrik om te onthou dat indied u nie 'n Lammergeyer gedurende hierdie tydperk gesien het nie, hierdie inligting net so waardevol is an 'n positiewe observasie.

Nota: a) U word nie verplig om u naam en adres te verstrek nie, alhoewel dié informasie ons aansienlik van hulp sal wees.

b) Alle inligting sal as streng vertroulik beskou word en sal onder geen omstandighede bekend gemaak word sonder u toestemming nie.

c) Hierdie vraelys verwys slegs na die Lammergeyer (sien illustrasie) en NIE die Lammervanger , Witkruis-arend of ander voëlsoorte nie.

By voorbaat baie dankie.

Die uwe

Christopher J. Brown

Name and Initials:...

Name of farm(s): ....

Postal address : ....

....

Telephone:.................

A. (i) Are there Lammergeyer nesting on your farm? Yes ☐ ;   No ☐ .

     If yes, how many pairs?........................

 (ii) If you know of nesting sites elsewhere, please would you describe

     their locations: ....

     ....

     ....

B. (i) How often do you see Lammergeyer flying over your farm (approximately)?

     Never ☐ ; once or twice a year ☐ ; monthly ☐ ; weekly ☐ ; daily ☐ .

 (ii) If you have seen these birds elsewhere, please describe where:...........

     ....

     ....

C. (i) Have you ever had Lammergeyer feeding on your farm? Yes ☐ ; No ☐ .

     If yes; (ii)   How often have you seen them feeding?.....................

          (iii) How many Lammergeyer were feeding? ....

          (iv)   On what were they feeding? ....

D. (i) Have you ever found dead Lammergeyer on your farm? Yes ☐ ; No ☐ .

     If yes; (ii)   How many were adult?.........; juvenile (young birds)?.......

          (iii) Suspected reason for death?..............................

E. (i) Do you use poison baits? Yes ☐ ; No ☐ .

     If yes; (ii)   What types of poison?...............................

          (iii) In what bait? ....

          (iv)   For what vermin?.....................................

F. (i) Do you consider Lammergeyer to be harmful to your farming programme in any

     way? Yes ☐ ; No ☐ .

     If yes, please explain:...

     ....

G. Any additional information:...

....

....

....

------oOo------

—Vertroulik—

Van en Voorletters: ....

Naam van Plaas: ....

Posadres: ....

....

Telefoon: ....

A. (i) Broei die Lammergeyer op u plaas? Ja ☐ ; Nee ☐ .

Indien ja, hoeveel pare? ....

(ii) As u van enige broeiplekke elders kennis dra, dui asseblief die

lokaliteit aan: ....

....

B. (i) Hoe gereeld sien u Lammergeyers oor u plaas vlieg (naastenby)?

Nooit ☐ ; een/twee maal per jaar ☐ ; maandeliks ☐ ; wekliks ☐ ; daagliks ☐ .

(ii) As u van die Lammergeyers elders gesien het, dui asseblief aan waar :

....

....

C. (i) Het u enige Lammergeyers op u plaas sien vreet? Ja ☐ ; Nee ☐ .

Indien ja,

(ii) Hoe gereeld het u hul gesien vreet? ....

(iii) Hoeveel Lammergeyers was daar? ....

(iv) Waaraan het hulle gevreet? ....

D. (i) Het u al enige dooie Lammergeyers op u plaas gevind? Ja ☐ ; Nee ☐ .

Indien ja,

(ii) Hoeveel was volwasse? .... Jong voëls? ....

(iii) Vermoedelike rede vir vrekte ....

E. (i) Gebruik u enige vergiftigde aas? Ja ☐ ; Nee ☐ .

Indien ja,

(ii) Watter tipe gif? ....

(iii) In watter tipe aas? ....

(iv) Vir watter ongedierte? ....

F. (i) Beskou u die Lammergeyer as nadelig vir u boedery in enige opsig?

Ja ☐ ; Nee ☐ .

Indien ja, verduidelik ....

....

G. Enige addisionele inligting ....

....

....

------oOo------

Adults / Volwassenes

Immature / Jong voël

THE   BEARDED   VULTURE / DIE   LAMMERGEYER

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Chapter 3

PLUMAGES AND MEASUREMENTS

3.1 INTRODUCTION

The physical characteristics of most birds of prey have been poorly studied. The limited information available has been obtained mainly from museum specimens. The African race of the Bearded Vulture is no exception. Delibes _et_ _al._ (1984) located five specimens from southern Africa in the museums of Europe and I located 14 specimens in institutes in southern Africa during this study; I was granted access to 11 of these. Museum specimens usually provide limited information, however, and although 21 wild birds captured during this study constitute a relatively small sample, the measurements obtained from these are considered worthy of inclusion and discussion as they represent the largest (and as far as I am aware, only) sample of live wild Bearded Vultures measured to date. In addition, the morphological characteristics of this bird form an integral part of our understanding of the ecology and biology of the species.

3.2 METHODS

During this study all Bearded Vultures captured were photographed from at least four positions, (a) lateral view of head, (b) dorsal view of head, (c) dorsal view of body with wing extended and (d) ventral view of body with wing extended. Preliminary age classes were ascribed to each

captured bird based on the criteria given by Brown (1977) but these were later refined by assessing the presence or absence of the following 11 of 22 characteristics given by Delibes et al. (1984).

Head region:

1. Brown-blackish feathers in the crown (Figure 3.1.a)
2. Brown semiplumes in the crown (Figure 3.1.b)
3. White semiplumes with a variable proportion of black bristles in the crown (Figure 3.1.c & d)
4. Brown-blackish feathers in the occiput and the nape (Figure 3.1.a-c)
5. White feathers in the occiput and the nape (Figure 3.1.d)

Ventral region:

6. Brown feathers ventrally
7. White feathers ventrally

Wing:

8. Sharp second primary (Figure 3.2.a & b)

Eyebrow:

9. No differentiated eyebrow (Figure 3.1.a)
10. Incomplete dark-brown eyebrow (Figure 3.1.b)
11. Complete eyebrow, well differentiated, black (Figure 3.1.c & d)

Delibes et al. (1984) divided Bearded Vultures into four main age classes:

A. Juvenile birds, classed as birds from the time they leave the nest to the moulting of the first remiges (which are
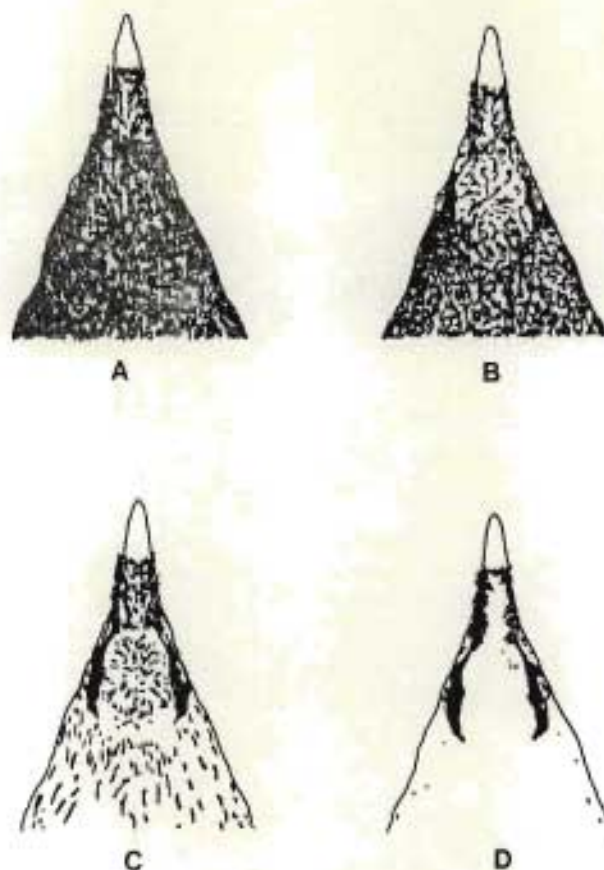
FIGURE 3.1. Age-related differences in the plumage in the head region of Bearded Vultures. After Delibes et al. (1984).

    a. Only brown-blackish feathers are present in the crown, the occiput and the nape. The "eyebrow" is not differentiated. (Juvenile)

    b. Brown semiplumes are present in the crown, as is an incomplete dark-brown "eyebrow". (Immature)

    c. Brown and white semiplumes in the crown. Brown-blackish feathers and white feathers in the occiput and nape. Well differentiated black "eyebrow". (Subadult)

    d. White semiplumes only in the crown. White feathers in the occiput and nape. "Eyebrow" as in C. (Adult)
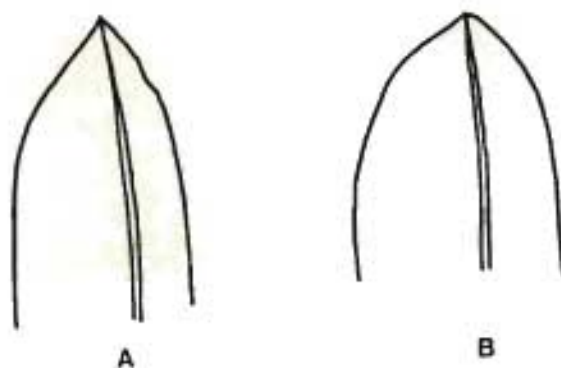
FIGURE 3.2. The second primary feather of Bearded Vultures.

a. The first remiges acquired are sharply pointed. These start to moult out at about two years. (Juvenile birds)

b. Subsequent remiges have more rounded ends. (Immature, subadult and adult birds)

sharp in this plumage). These include specimens that have not started to moult through to those which have started the contour moult. The ventral regions are brown. The head is brown-black and no eyebrow is apparent.

B. Immature birds, classed as specimens that have started, through to those that have completed the moult of their remiges, i.e. those that have at least some rounded remiges. Birds in this category include those which have completed their first contour moult through to those which have started their second. The ventral regions are brown. Brown semiplumes have appeared on the head and an incomplete dark brown eyebrow is present.

C. Subadult birds, classed as immature birds phenetically closer to adults than to juveniles. Birds in this category include those which have started their second moult of remiges and those which have finished it, but are still moulting contour feathers. The ventral regions are pale golden brown to white, overlain with varying concentrations of rufous. The head has variable proportions of black bristles in the crown and the eyebrow is complete, well differentiated and black in colour.

D. Adult birds, classed as specimens with complete adult plumage. Ventral regions are pure white, overlain with varying amounts of rufous (see Chapter 4) and the white head has no black bristles in the crown.

A photographic record of the plumage development of two

Bearded Vultures of known age, from the time of their capture at four months old to adulthood, was used to ascribe ages to the different plumage categories. The two captive birds were rescued from young Basotho herders who were attempting to kill the birds following their first flights from their nests in the Roma valley, Lesotho. Both birds were injured to the extent that they could never be released, and were raised by a medical doctor (A.C. Jaques) and his wife in Ladybrand, Orange Free State (29°09'S, 27°29'E; 1600 m above sea level), where they had the full run of the garden (about 2000 m^2). The birds were fed on meaty longbones supplemented by incidental road kills.

Measurements and mass characteristics were determined for the 21 captured wild Bearded Vultures (within their respective age classes) as well as for 11 skin specimens held in the following collections: Natal Museum, Pietermaritzburg (2), Bloemfontein Museum (7), East London Museum (1) and Giant's Castle Game Reserve (1). Up to 24 measurements were taken per bird. The sex of adult birds was determined by recording whether that bird incubated at night (female) or not (male). The following measurements were taken.

1. Bill length (to nearest 0,1 mm), from the tip of the culmen to the distal dorsal margin of the cere.

2. Bill width (to nearest 0,1 mm), from the junction of the tomium of the upper jaw and the cere on one side to the same point on the other side.

3. Bill height (to nearest 0,1 mm), from the distal dorsal

margin of the cere of the upper jaw to the distal ventral margin of the cere of the lower jaw, with the bill firmly closed.

4. Gape length (to nearest 0,1 mm), from the fold of the gape to the tip of the lower jaw.

5. Gape width (to nearest 0,1 mm), from the fold of the gape on one side, to the same point on the other, with the bill closed.

6. Standard wing length (to nearest 1 mm), from the front of the folded wrist to the tip of the longest primary, following the curvature of the wing.

7. Longest rectrix (to nearest 1 mm), from the posterior edge of the uropygial gland to the tip of the longest central rectrix.

8. Shortest rectrix (to nearest 1 mm), same as for 7 but to the tip of an outermost rectrix.

9. Tarsus length (to nearest 0,1 mm), from the depression behind the tibiotarsal-tarsometatarsal joint to the dorsal base of the hind toe, where the crease occurs when the toe is extended.

10. Toe lengths; toe I = hind, toe II = inner, toe III = middle and toe IV = outer (to nearest 0,1 mm), from the junction with the tarsometatarsus to the dorsal claw-skin junction along the dorsal surface, with the toe extended.

11. Claw lengths; claw numbers as for the toes (to nearest 0,1 mm), from the dorsal skin-claw junction to the tip of the claw, along the chord.

12. Total wing length (to nearest 1 mm), from the proximal end of the humerus to the end of the longest primary, with the wing stretched out such that the anterior margin forms as straight a line as possible, and measured on the dorsal surface across the curvature of the wing.

13. Shoulder width (to nearest 1 mm), from the proximal end of the humerus on one side to the same position on the other side.

14. Overall length (to nearest 1 mm), from the tip of the bill, over the head and following the contour of the body to the tip of the longest rectrix.

15. Wing area (to nearest 1 cm^2), measured by opening the wing so that the anterior margin forms as straight a line as possible and tracing the outline onto high quality paper. The outline was traced up to the posterior and anterior points where the wing joins the body. The traced outline was then cut out and weighed, and the area calculated from the standard g/m^2 value of the paper.

16. Tail area (to nearest 1 cm^2), measured by fanning the tail so that each feather overlapped each adjacent feather by about half its area, so that the tail was about half spread. The outline was then traced onto high quality paper, from the skin-feather junction on one side to the same point on the other side. The outline was cut out, weighed and the area calculated as in 15 above.

17. Body mass (to nearest 50 g), measured using a Pesola 10-kg spring balance. The balance was checked for accuracy before field work started and again on completion.

18. Body temperature (to nearest 0,1° C), taken with a clinical thermometer inserted 4-5 cm into the cloaca.

Wingspan, aspect ratio, wing and tail loadings were calculated from the measurements.

Although moult of the primary and secondary remiges and rectrix feathers was recorded, as were the extent of feather wear, too few birds were captured to give enough information on which generalizations could be based. Information on moult in Bearded Vultures, however, has been fairly well documented (e.g. Hiraldo et al. 1979; Cramp & Simmons 1980).

Two blood smears were taken from a leg of each bird captured, stained in Giemsa and examined for blood parasites. Birds were systematically searched for ectoparasites which, when found, were then preserved in 70% alcohol and sent to the South African Institute of Medical Research for identification.

3.3 RESULTS

3.3.1 Age classes

From photographs of two Bearded Vultures of known ages the approximate ages at which the different plumages were acquired were determined (Table 3.1). As can be seen, these age figures are very similar to those estimated by Delibes et al. (1984). Some variation in age at acquiring different plumages may be expected, because of geographic variation,

availability of food, etc.

Some additional age-related characteristics are worth mentioning. The length of the beard of Bearded Vultures varied with age, from first projecting below the lower jaw in young birds, at about 10 weeks old, to a final length of 45-55 mm long in adults. Beard lengths at intermediate ages are given in Table 3.2.

The colour of the iris and surrounding scleral ring also changed as Bearded Vultures grew older. From the nestling stage through to the end of the first year young birds had a slightly opaque pale yellow-brown iris. The scleral ring was opaque browny-red until the young vulture was about 8 months old, thereafter becoming an opaque dull red. By about 24 months old, the scleral ring was deep red, although still slightly opaque. By 36 months the iris was clear yellow, although still slightly darker than that of the adult birds. The scleral ring was no longer opaque but remained a deeper red than the blood red eyering of the adults until the subadult stage was reached.

3.3.2 Measurements

All live birds and skins measured were assigned to age classes according to the criteria given above. Results from these measurements are presented in Table 3.3.

Sexual dimorphism

There was no significant difference between adult male and female birds in any of the characteristics measured (t-

test) although females tended on average to be heavier than males. This is similar to the findings of other workers (e.g. Glutz von Blotzheim et al. 1971; Hiraldo et al. 1979; Cramp & Simmons 1980; Brown et al. 1982; Delibes et al. 1984) but the last-mentioned authors found that the bill was significantly larger in the female than the male. This was not evident in the small sample in this study, where the male actually had a slightly larger bill on average. One feature noticed towards the end of the study and not substantiated by mensural data was that adult females had slightly broader wings at the point of the primary/secondary junction than did adult males (Figure 3.3). This could not be reliably used when single birds were seen, but a pair together could be sexed if the wing shapes were clearly seen from underneath. The sexes of seven different pairs were predicted in this way, and when checked against their colour ring codes or by observing which bird incubated at night, all predictions were found to be correct.

Age-class differences

Adult and young Bearded Vultures differed in a number of characters. Statistical tests (t-test) were carried out between juvenile and adult age classes. Where these were found to be significantly different, immature and subadult measurements were invariably intermediate in value between those of juvenile and adult birds. The following measurements were significantly greater in adult than in juvenile birds: bill width, standard wing length, wingspan
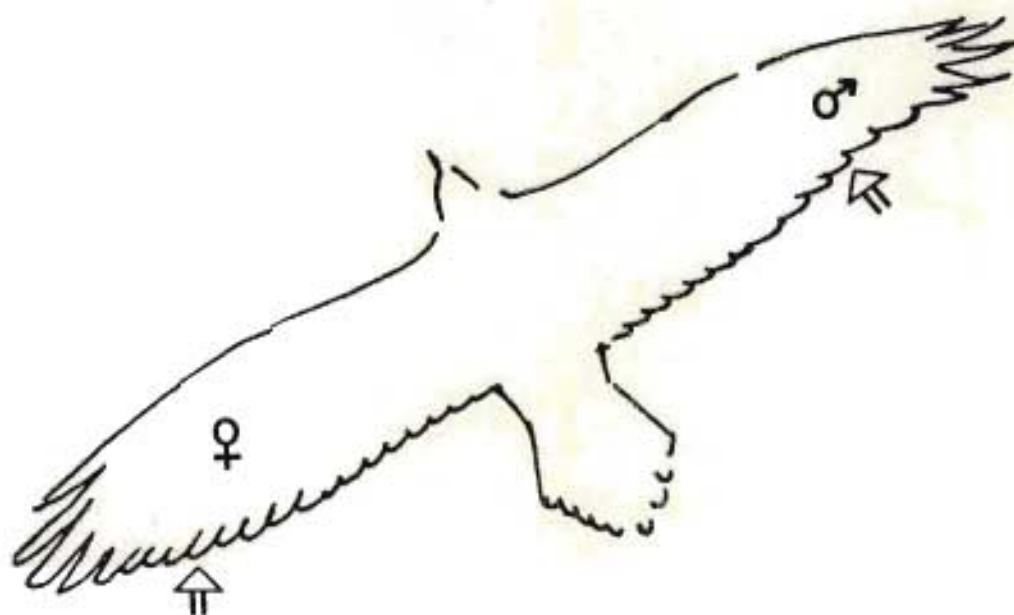
FIGURE 3.3. The wing shapes of adult male and female Bearded
Vultures. Note that the wing of the female is
slightly broader than that of the male in the
area of the first few primaries.

and mass. These characters are all associated with the normal growth of the young bird. Juvenile birds were significantly larger than adults in a number of characteristics related to flight. Their outer rectrices were 4% longer than those of adults resulting in a tail area, when half-spread, of 11% more than that of the adults. Their wings were 9% broader on average but shorter than those of adults, and they had a 7% larger wing area than that of adults. Immature birds (and the one subadult bird in the sample) were on average intermediate in size between juveniles and adults. Calculated flight characteristics were affected by the different wing and tail shapes of adult and juvenile birds. Adult birds had the highest aspect ratio (8,9:1) and juvenile birds the lowest (7,8:1) with immature and subadult birds having intermediate values. Likewise, adults had a significantly higher wing-and-tail loading (67,4 N/m^2) than juveniles (55,9 N/m^2) with immature birds (63,0 N/m^2) falling between the two.

3.3.3 Parasites

All Bearded Vultures had parasites, but levels of infestation were low. A 2-min search usually resulted in the collection of 1-3 ectoparasites, found mainly about the head and face, and in the short woolly down feathers around the cloaca. During the breeding season, however, two adult birds had noticeably more ectoparasites (six and seven respectively). Two species of feather lice were found, in almost equal numbers, on most birds examined: both male and

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female specimens of Colpocephalum barbati (Price & Beer, 1963) and female specimens only of Degeeriella punctifer (Gervais, 1844), these being insects in the order Phthirptera.

No blood parasites were found. One bird had a particularly high number of lymphocytes, about 60 times that found in the blood of the other birds examined, which might suggest that the bird had a viral infection. This bird was a juvenile and in particularly good condition, weighing just on 6 kg.

3.4 DISCUSSION

Bearded Vultures have a number of unusual features not shared with other large birds of prey.

3.4.1 Flight-related characters

Bearded Vultures have unusually long wings, a high aspect ratio and a particularly long tail (Table 3.4).

Pennycuick (1972, 1973) has suggested that the three feeding categories to which Kruuk (1967) assigned vultures may also be applied to their soaring behaviour. Category (a) contains the Gyps (= griffon) vultures, e.g. Cape Vulture Gyps coprotheres and Whitebacked Vulture Gyps africanus, gregarious in both nesting and feeding, and covering long distances from their nests in search of food. Their cross-country performance is adequate for a foraging radius of over 100 km in dry-season conditions. Category (b) contains the large, solitary-nesting species of vultures, e.g. Lappetfaced Vulture Torgos tracheliotus and Whiteheaded

Vulture *Trigonoceps occipitalis*, which are said to never gather in large numbers at a food source and have a fixed foraging territory. They have a lower wing loading than that of the griffon vultures and were never seen cross-country flying by Pennycuick (1972). Category (c) includes the small vultures, e.g. Egyptian Vulture and Hooded Vulture *Necrosyrtes monachus*, which are solitary nesters. The Hooded Vulture may gather in numbers at food and does fly across country, but the Egyptian Vulture is restricted to a small foraging range and is normally seen singly or in pairs (Pennycuick 1972).

The wing loadings of these and some other species of large birds are shown in Figure 3.4. The species can be divided into two main groups, those with a high wing loading, e.g. the griffon vultures, and those with a low wing loading, e.g. the Lappetfaced and Whiteheaded Vultures. Three scavenging raptors do not follow the predicted correlation between (a) being solitary nesters, not gathering in large numbers at food and having fairly clearly defined home ranges and (b) having a low wing loading. These are the Bearded Vulture, the Egyptian Vulture and the Bateleur *Terathopius ecaudatus*. These three species all have a particularly high aspect ratio (Figure 3.5), a feature which imparts improved gliding performance such as reduced minimum sinking speed and increased best-glide ratio, but which is a disadvantage in small thermals (Pennycuick 1971).

Both the Bearded and Egyptian Vultures are cliff-
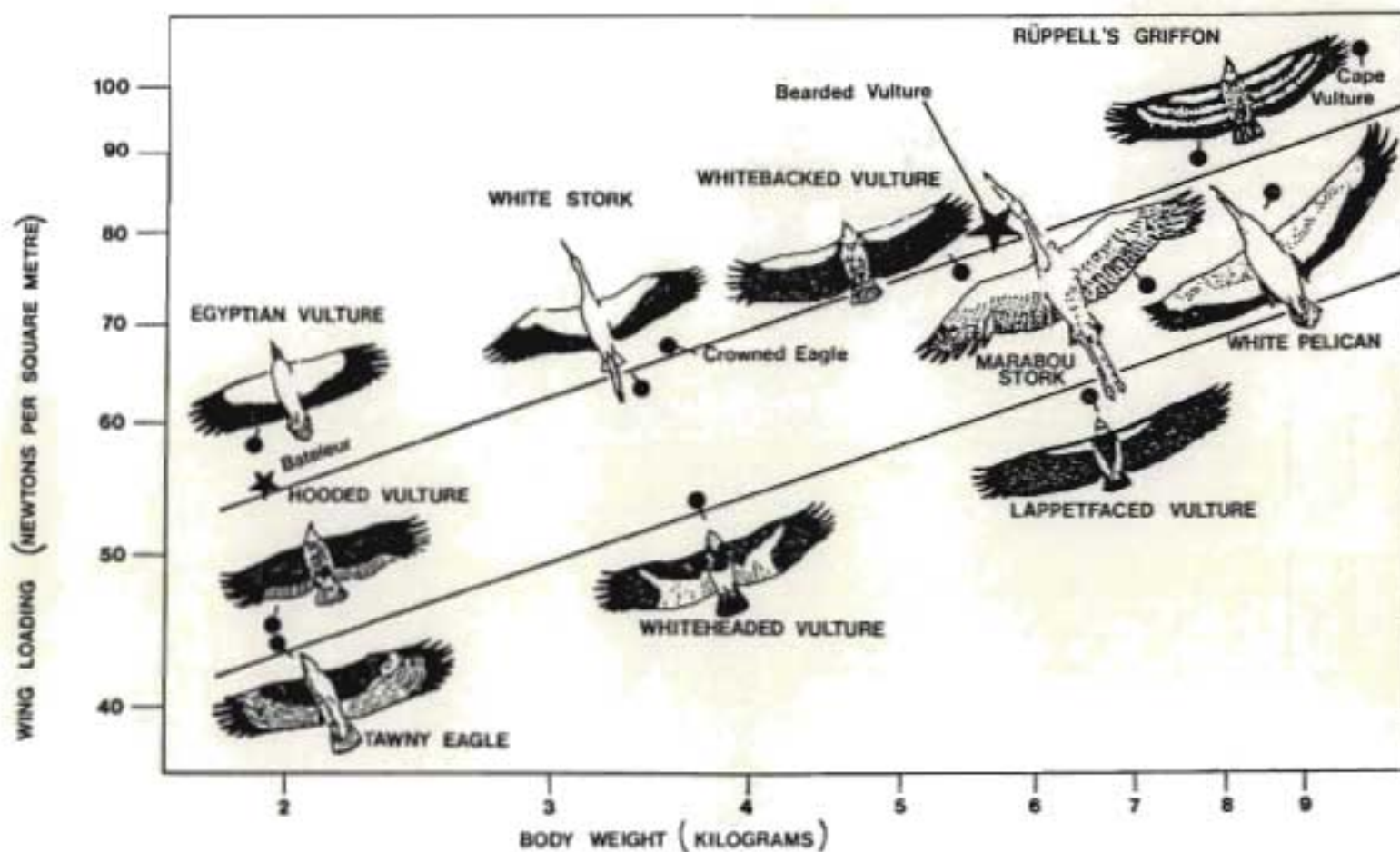
FIGURE 3.4. Soaring birds fall mainly into two groups, (a) birds with a relatively heavy wing loading (upper diagonal) and (b) birds with a relatively light wing loading (lower diagonal). From Pennycuick (1973) with a few additional species included, reproduced here with permission from W.H. Freeman & Company.
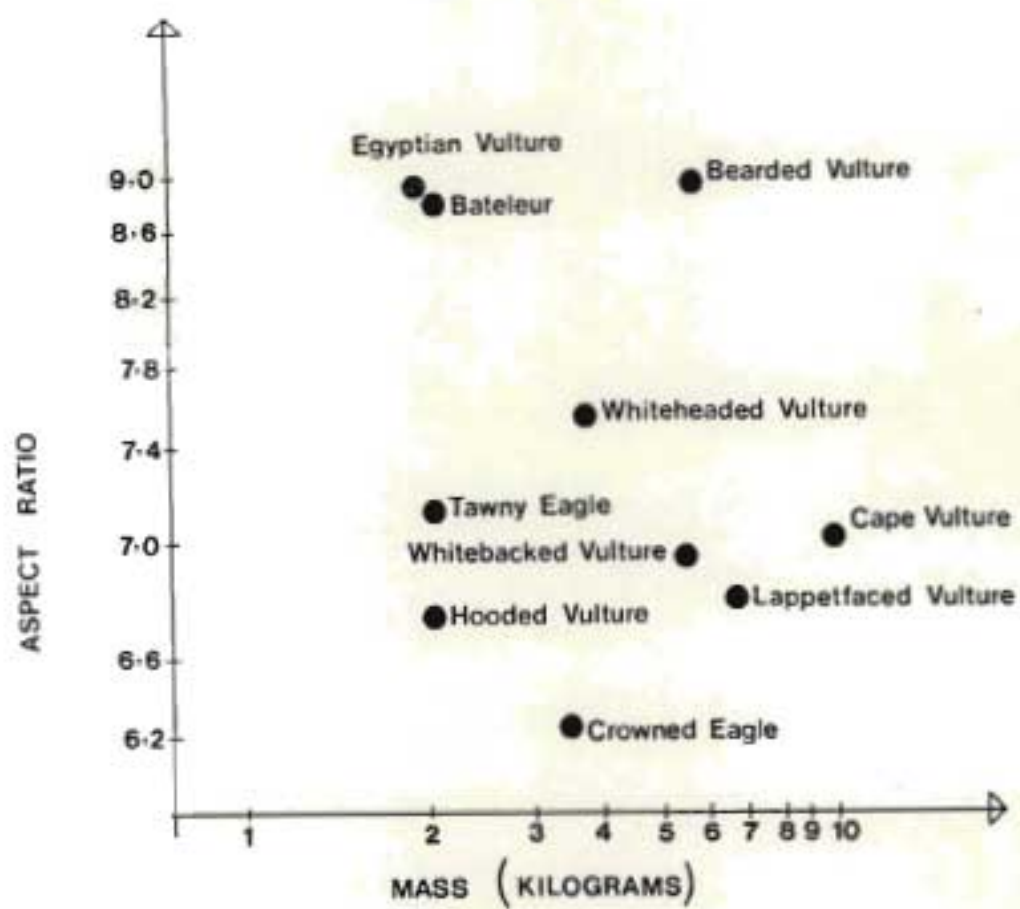
FIGURE 3.5. The aspect ratios of some large African birds of prey, plotted against their body mass.

nesting species and therefore have a height advantage over competing tree-nesting species. They can also make use of various forms of slope lift around their nesting cliffs, and Bearded Vultures, which are confined largely to mountain massifs, use mainly slope lift for foraging and rely to a lesser extent on thermals. A similar situation is found in the higher wing loading of Cape Vultures (cliff nesters) compared to Whitebacked Vultures (tree nesters) (Brown 1985a), but once away from their cliffs, Cape Vultures have to face similar conditions to those of Whitebacked Vultures. Egyptian Vultures are said to patrol small areas and not fly cross-country (Pennycuick 1972), so the use of thermals would not be such an important consideration in this species. Bateleurs differ from both the Bearded and Egyptian Vultures by having a unique foraging method. They glide upwind at low altitude above the ground in an almost straight line, banking from side to side to obtain lift by "showing the raised wing to the swell" (Klemperer 1958). Thermals are only occasionally used, to gain height to return to the point of origin (Pennycuick 1972). It can therefore be concluded that, although the wing loadings of these three species do not conform to what would be expected from their nesting distribution and home range characteristics, these discrepencies can be explained by the different flying methods employed by these birds. These differences are further emphasised by their unique wing shapes.

In contrast to the characteristics ascribed to

Lappetfaced Vultures by Pennycuick (1972), current studies on this species in the central Namib Desert of South West Africa/Namibia using radio telemetry indicate that home ranges are extremely large and overlap extensively. Birds were recorded over 200 km from their nests, covering over 370 km in a day. In addition, in these arid areas, Lappetfaced Vultures sometimes gather at a carcass or water hole in groups of over 40 birds and the same has been recorded at a feeding station in a savanna region (pers. obs.).

From this it is apparent that our understanding of foraging methods and related morphology in the large birds of prey is still incomplete, and the simplistic hypothesis referred to above is not acceptable. Detailed comparative morphological studies on birds of prey are needed together with field studies of foraging methods, home-range sizes and use. Why other large birds of prey do not have more efficient high-aspect-ratio wings, for example, is unclear. It is thought that this may be related to landing and taking off (Pennycuick 1972). Bearded Vultures, living in mountainous terrain, may be compared to seabirds which take off from a swell into the wind. In mountainous areas there is almost always some wind, the birds are usually on a slope or steep hillside and the vegetation is low.

The long tail of the Bearded Vulture may serve a number of different functions. When the tail is closed the combined wing and tail loading of an adult bird is about 73 N/m^2, but

when fully spread, this decreases to about 62 N/m^2, a difference of 15%. The difference for juvenile birds is greater still. By contrast, the equivalent figures for the Cape Vulture are 104 N/m^2 and 99,5 N/m^2, a decrease of only 4%. The tail of the Bearded Vulture can therefore alter the overall loading of the bird from fairly high to fairly low. This enables the bird to glide more slowly (Pennycuick 1975), to make better use of lift and to carry heavier food loads.

The tail is also used to correct small errors in pitch and yaw, an important consideration when flying at very low levels over rough terrain in the gusty conditions typical of mountainous habitats, especially when accuracy is needed for dropping bones and for entering small nest cavities. The tail is also used to direct the airflow vertically downwards during hovering, an activity occasionally undertaken by Bearded Vultures, mainly for bone dropping or for close inspection of possible food items, but not to my knowledge by any other vulture species. Finally, the tail is used as an air brake, and Mundy (1982) suggested that cliff nesting vultures (with the exception of the Bearded Vulture) have two more tail feathers than the other (tree-nesting) vultures because this increases the braking capacity of the bird when it approaches a cliff. The large surface area of the Bearded Vulture's tail is probably also important in this regard, especially as nests are usually built in small cavities and the birds have to swoop in, a more difficult manoeuvre than landing on a ledge.

3.4.2 Food-related characters

Some of the unusual morphological features of the Bearded Vulture are directly related to their food and method of feeding. The most obvious of these is the enormously wide gape. This is almost twice the size of that of the much larger Cape Vulture and 17% wider than that of the Lappetfaced Vulture, and is undoubtedly related to the Bearded Vultures' habit of swallowing large bones whole. Another unique feature is the beard which projects below the lower jaw of the Bearded Vulture. Unlike most other vultures the Bearded Vulture has a richly feathered head, neck and throat, and the sides and underparts of the face are covered by a thick woolly down. This dense insulation is probably important for thermoregulation in the cold mountainous habitat of the species. While they feed mainly on the remains of carcasses once Cape Vultures have eaten, Bearded Vultures also feed on fresh carcasses when they are able to. I suggest that the beard, in conjunction with the bristles which extend from the black facial mask onto the cutting edge of the upper mandible, function as tactile organs to prevent the bird from inserting its head too deeply into a fresh carcass and thereby risk matting its thickly feathered face, neck and throat with blood. Bearded Vultures were never seen with blood-stained feathers about the head and face, even when bringing fresh lumps of red meat to the nest.

Mundy (1982) has pointed out that the Cape Vulture has relatively short toes compared to those of the Whitebacked

Vulture, and this difference is even more noticeable in the claw lengths (Table 3.4). He attributed this to the cliff-nesting and roosting habits of the Cape Vulture as compared to the other vultures he studied, which nested and roosted on trees. The Bearded Vulture nests and roosts on cliffs, yet it has toes and claws of very similar proportions to those of the similar sized Whitebacked Vulture. It is suggested that, because Bearded Vultures carry food with their feet, these are larger with longer claws than would be the case for a similarly sized cliff-nesting scavenger that carried all its food in its crop. It is nevertheless apparent from Figure 3.6 that the mean total claw length of Bearded Vultures falls clearly into the zone of "scavenger" and not "predator".

3.4.3 Sexual dimorphism

Newton (1979) has shown that there is a clear relationship between the relative sizes of male and female birds of prey within a species (or even a population) and their feeding habits. The faster and more agile the prey, the larger the female tends to be in relation to the male. Those species which feed on slow-moving prey or carrion show no reversed size dimorphisms, males and females being about the same size. Mendelsohn (1981) suggested that reversed dimorphism is an adaptation to the storage of food reserves in females of species which live on large prey animals which are fast-moving and a fairly unpredictable food source. The male, which does all the hunting during much of the breeding
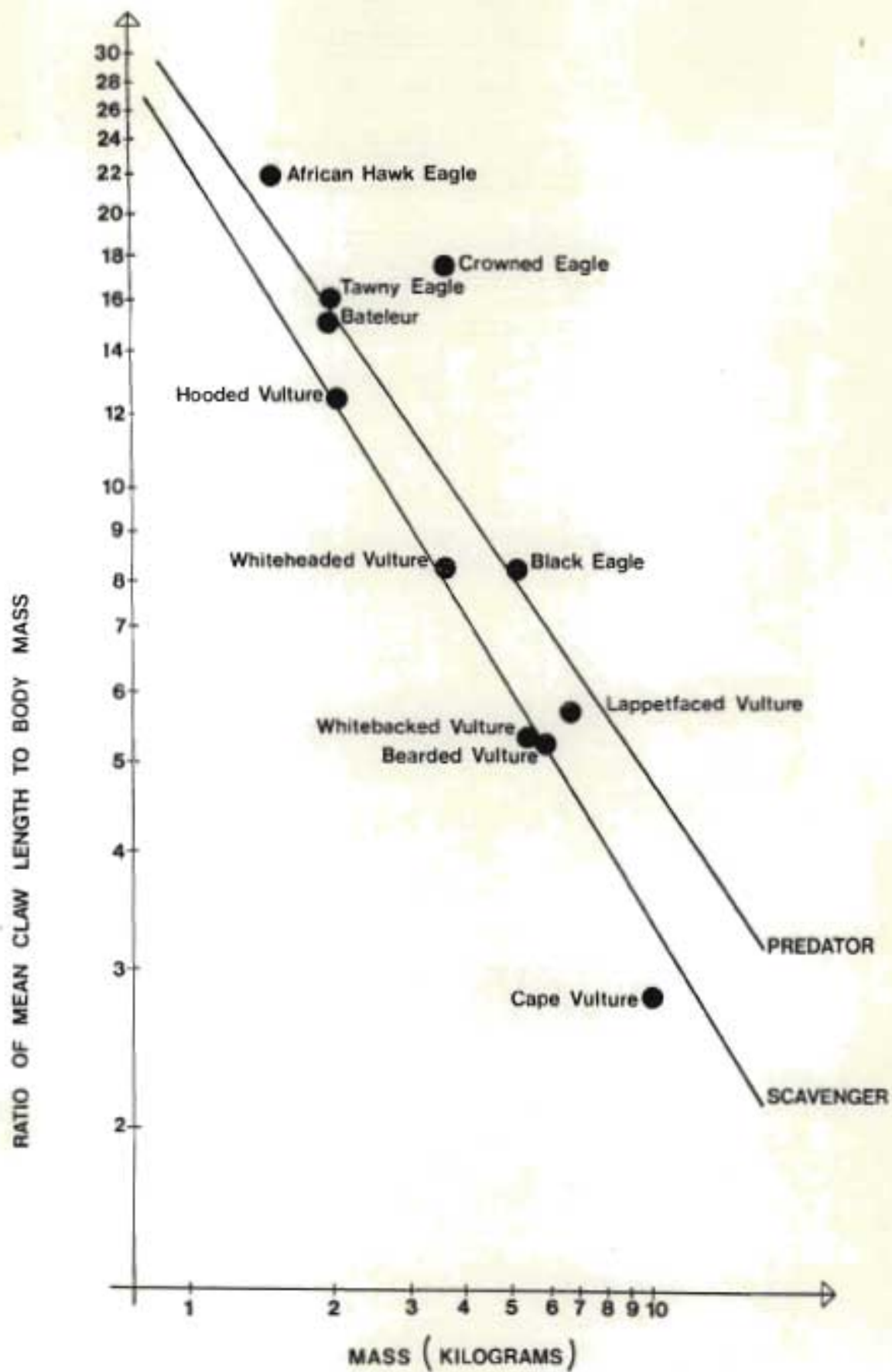
FIGURE 3.6. The mean total claw length as a ratio to body mass, plotted against body mass.

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season, would have to remain small and agile to capture this food. Vultures, by contrast, do not have the same need for manoeuvrability so both sexes can afford to be large and lay down food reserves (a condition found by Houston (1976)). Mendelsohn mentioned that females may obtain several other benefits from being large, including being better able to defend the nest.

There is generally an inverse correlation between the size and agility of prey animals and their numbers. Correspondingly, those raptors which feed on large, agile prey tend to have large home ranges, while species feeding on less active, smaller and usually more numerous prey have smaller ranges. In the event of a predator or competitor threatening the nest, the male of a species with a small range is more likely to be nearby and able to come to assist in the defence of the nest than is the case in species with larger ranges where nest defence may be left entirely to the female. Larger size of females may then be important in ensuring nesting success. In vultures, both sexes are usually so large that gaining of additional size by the female is not required. Perhaps even more importantly, particularly among the griffon vultures, a size dimorphism would place the smaller sex at a considerable disadvantage in the frenetic squabble for a place at a carcass.

3.4.4 Age-class differences

Hiraldo et al. (1979) and Delibes et al. (1984) state that, whereas adult Bearded Vultures are on average slightly

larger than young birds, this is statistically insignificant. These authors, however, looked at few characters and none of the ones that proved to be significantly different in this study. In addition, it appears from the description of their methods that all young birds were lumped into one group and the mean of this sample was tested against that of the adult sample. As can be seen from the measurements in this study, immature and subadult birds are usually intermediate in size between juvenile and adult birds and so, by grouping all the young-bird age classes, the degree of difference between juvenile and adult birds is reduced.

Differences in size between young and adult birds have been well documented for many species but their significance is not easily explained (Amadon 1980). Mendelsohn (1981) suggested that this may be related to different methods of hunting, but in the carrion-feeding Bearded Vulture no such differences were found, and yet juvenile birds were significantly larger than adults in a number of characters related to flight.

The young of short-tailed species, which are often specialist fliers, usually have considerably longer tails than the adult birds, e.g. Augur Buzzard Buteo augur (Jackson & Slater 1938), Bateleur (Brown & Amadon 1968), Martial Eagle Polemaetus bellicosus (Amadon 1980). These become progressively shorter with each moult. Likewise, all the feathers, except the longest primaries, were measurably

shorter in adult Peregrine Falcons _Falco peregrinus_ than in first year birds, amounting to "as much as half an inch on the secondaries and an inch on the tail" (Beebe 1960).

Young Bearded Vultures, during their first few months off the nest, are easily recognizable in flight by their clumsy, uncoordinated behaviour. By reducing the wing loading and increasing the tail area birds decrease their stalling speed and so are able to fly and land more slowly and manoeuvre themselves better. These features would be of considerable advantage to young, inexperienced birds, particularly for the somewhat specialized flying requirements of Bearded Vultures such as entering small cavities on cliffs, foraging at low levels above the ground and bone dropping, all these often having to take place in gusty wind conditions. These advantages are gained, however, at the expense of cross-country flying performance. Young birds, once independent, are not obliged to return to a nest site with food (as are adult birds during the breeding season) but can wander about and remain in the area where the food supply is good. They therefore do not have the same need for cross-country flying that adult birds do, and can afford to be built more for stability and manoeuvrability. In addition, there is some evidence that young birds move out of the main foraging areas used by adults during the breeding season. Adult birds nest on the highest suitable cliffs available, and the most mountainous terrain is likely to be occupied by them. Young birds tend to concentrate in areas less heavily foraged by adults, and these are likely

to be the less mountainous areas. Young birds may therefore be more dependent on thermals than adult birds, and this may also account in part for their lower aspect ratio.

It is unlikely that one single explanation accounts for the described physical characteristics of a bird, but that many ecological, biological, climatic and topographic features are constantly exerting selective pressures on each individual. Only some of the more obvious features have been mentioned in this Chapter.

TABLE 3.1

Ages at which the different plumages of Bearded Vultures are acquired, determined from two known-age birds photographed from four months old to adulthood.

Plumage type	Age (months)	
	This study	Delibes et al. 1984
A. Juvenile	3-24	3-21
B. Immature	24-45	21-43
C. Subadult	45-60	43-60
D. Adult	60+	60+

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TABLE 3.2

Length of the beard of Bearded Vultures at different ages, measured from the distal tip to where it joins the lower jaw.

Age (months)	Beard length (mm)
3,5 (on nest)	4,0
4,5	6,6
10-12	12,2
22-24	31,5
36	36,8
42-44	42,8
60+	45-55

TABLE 3.3

Some physical characteristics of Bearded Vultures of different age classes. Information is presented as mean ± standard deviation (sample size). Statistical tests were done between the means of adult and juvenile samples using the t-test, and where significant differences were found these are indicated as follows: * for P<0,05; ** for P<0,02 and *** for P<0,01.

Variables	Juvenile birds	Immature birds	Subadult birds	Adult birds	Diff.
Bill length (mm)	73,8 ±4,4 (7)	74,8 ±4,4 (5)	74,7 (1)	73,1 ±2,2 (10)	
Bill width (mm)	19,2 1,2 (7)	19,4 1,8 (5)	21,0 (1)	21,8 3,4 (12)	***
Bill height (mm)	29,7 1,6 (8)	30,4 1,1 (5)	30,4 (1)	31,0 1,3 (11)	
Gape length (mm)	92,1 (2)			95,2 7,8 (5)	
Gape width (mm)	67,4 (2)			69,6 4,0 (5)	
Std. wing length (mm)	755,0 15,1 (8)	760,4 21,6 (5)	765,0 (1)	782,4 24,4 (11)	***
Tail centre length (mm)	478,1 17,7 (8)	468,6 15,9 (8)	470,0 (2)	473,5 13,9 (11)	
Tail outer length (mm)	373,5 16,6 (4)	364,7 16,0 (7)	366,5 (2)	353,5 13,5 (7)	*
Tarsus length (mm)	95,4 7,0 (8)	96,6 4,0 (5)	97,0 (1)	94,8 6,2 (11)	
Toe length I (mm)	34,8 3,9 (8)	35,6 4,7 (5)	32,4 (1)	35,1 3,2 (11)	
II (mm)	40,6 2,0 (8)	43,0 6,8 (5)	41,5 (1)	38,1 4,2 (11)	
III (mm)	76,4 4,1 (8)	80,6 4,6 (5)	81,2 (1)	75,1 5,9 (11)	
IV (mm)	47,0 1,5 (8)	50,9 3,4 (5)	54,2 (1)	47,9 3,3 (11)	

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TABLE 3.3 continued

Variables	Juvenile birds	Immature birds	Subadult birds	Adult birds	Diff.
Claw length I (mm)	34,2 ± 5,1 (8)	38,9 ± 3,0 (5)	41,0 (1)	36,9 ± 2,2 (11)	
II (mm)	35,6 2,0 (8)	37,4 2,5 (5)	37,9 (1)	35,4 2,4 (11)	
III (mm)	25,9 1,7 (8)	29,2 3,1 (5)	29,7 (1)	26,4 1,9 (11)	
IV (mm)	23,5 2,1 (8)	25,4 2,2 (5)	26,9 (1)	23,3 2,3 (11)	
Total wing length (mm)	1183,3 13,3 (6)	1188,3 29,4 (9)	1210,0 (1)	1208,0 39,6 (5)	
Shoulder width (mm)	85,8 6,6 (6)	88,0 4,5 (5)	85,0 (1)	107,0 2,7 (5)	
Wingspan (mm)	2538,3 29,3 (6)	2566,0 36,5 (5)	2595,0 (1)	2630,0 73,8 (5)	**
Overall length (mm)	999,2 7,8 (5)	985,0 31,6 (5)	1070,0 (1)	1035,0 38,3 (6)	
Wing area (one wing; cm^2)	3835,4 163,6 (6)	3654,9 190,8 (8)	3620,0 (1)	3561,4 205,0 (5)	*
Mean wing width (mm)	324,1 13,3 (6)	306,9 10,7 (8)	299,2 (1)	294,8 10,7 (5)	***
Aspect ratio	7,8:1	8,4:1	8,7:1	8,9:1	
Tail area (cm^2)	1393,6 172,6 (6)	1297,3 130,0 (5)	1114,5 (1)	1233,8 77,4 (5)	
Wing loading (N/m^2)	66,1	74,2	79,3	79,1	***
Wing & tail loading (N/m^2)	55,9	63,0	68,0	67,4	***
Mass (kg)	5,17 0,7 (7)	5,53 0,5 (5)	5,85 (1)	5,74 0,4 (8)	*
Temperature (°C)	40,7 0,3 (7)	40,4 0,3 (4)	39,9 (1)	40,3 0,7 (5)	-

TABLE 3.4

Comparative measurements of some large African raptors. Data from: Pennycuick (1972); Brown et al (1982); Mundy (1982); Brown (1985a); Maclean (1985); C.J. Brown (unpublished data).

Species	Mass (kg)	Wingspan (m)	Wing loading (N/m^2)	Aspect ratio	Longest rectrix (mm)	Gape width (mm)	Ratio of body mass:claw length
Bearded Vulture	5,7	2,63	79	8,9:1	474	69,6	1:5,3
Cape Vulture	9,9	2,58	112	7,1:1	316	38,8	1:2,8
Whitebacked Vulture	5,4	2,18	77	6,9:1	260	35,2	1:5,4
Lappetfaced Vulture	6,6	2,64	63	6,8:1	360	59,3	1:5,8
Whiteheaded Vulture	3,7	2,23	54	7,5:1	280	50,3	1:8,4
Hooded Vulture	2,0	1,71	45	6,7:1	222	-	1:12,2
Egyptian Vulture	1,9	1,68	59	8,9:1	246	-	-
Bateleur	2,0	1,75	55	8,8:1	117	48,6	1:14,8
Tawny Eagle	2,0	1,78	44	7,1:1	262	47,9	1:16,0
Black Eagle	5,1	-	-	-	323	43,6	1:8,2
Martial Eagle	4,5	2,20	-	-	280	-	-
Crowned Eagle	3,5	2,01	67	6,0:1	330	-	1:17,2
African Hawk Eagle	1,4	-	-	-	270	37,3	1:21,7

Chapter 4

PLUMAGE COLOUR AND FEATHER STRUCTURE

4.1 INTRODUCTION

The rufous colouring in adult Bearded Vultures has been the subject of discussion and dissension for many years. Variations in colour intensity between individuals have long been recognized (for review see Berthold 1967) with new species having been erected on the basis of these differences, e.g. G. albicans, (Fatio 1899). Colour differences have been ascribed to locality (Meves 1860; von Homeyer 1883a, 1883b; Grossman & Hamlet 1965), subspecies (Fischer 1963) and age (Brodtmann 1816; Gloger 1834; Reiser 1933).

The origin of the coloration has also been a controversial topic and the following explanations have been suggested.

1) The colour is internal to the feather, or internally produced;

   a) from the bird's own blood (e.g. Gloger 1862; Stemmler 1932),

   b) from the bird's skin (e.g. von Czynk 1894; Hartert 1912/1921),

   c) from the powder down (e.g. Volker 1938),

   d) from the preen glands (e.g. Kamner 1928; Reiser 1933; Hartert 1932; Berndt & Meise 1962),

   e) from carotenoid pigment (Clancey 1963, 1964).

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2) The colour is an external deposit or stain;

    a) from the blood of animals eaten (e.g. Gloger 1862; Hodek 1879, 1883a, 1883b),

    b) from water and soil contact (e.g. Meves 1860; Fatio 1899; Dodsworth 1912; Fischer 1963).

As early as 1860, Meves showed that there was iron on Bearded Vulture feathers and eggs, and assumed that iron oxide was responsible. This was confirmed by other workers (e.g. Schuz 1927; Volker 1960), and most recently by Berthold (1967), whose detailed study showed that the colouring was external to the feathers. Fretzdorff et al. (1966) showed that Bearded Vultures have no more iron in their preen glands than do other birds, and that to obtain the colour intensity required, twice the contents of the preen gland would have to be applied to each feather.

The structure of Bearded Vulture feathers is favourable to the attachment and accumulation of iron oxide. Where barbules are short, densely packed and project from the barbs at an acute angle, iron oxide can adhere and accumulate. Iron oxide is detectable on all parts of the Bearded Vulture but only the feathers of the underparts are of suitable structure to hold appreciable amounts. The throat and belly feathers of intensely coloured birds can hold up to about 3% of the weight of the feather. These richly coloured birds have overall about 1 g of iron adhering to their plumage (Berthold 1967).

Berthold (1967) suggested that the oxide is not

produced by the bird (being free of fats, powder and "horn" particles, dried blood or carotenoid pigments), but comes from iron-oxide-stained soils and is passively assimilated by the bird and adheres to the feathers. Clancey (1968) finds this explanation "almost impossible to accept" and furnishes the following reasons.

a) Only adults have the coloration.

b) There have been no reports of Bearded Vultures dusting in red soils.

c) All adults seen and handled (i.e. by Clancey) had precisely the same colouring.

d) Siting of the rusty colouring is difficult to comprehend; presumably the whole bird would have to be saturated in red dust to achieve the distribution which is seen to occur. However, there is very little evidence of dust on other feathers.

This chapter investigates the Bearded Vulture's feather structure and colouring, and discusses the biological significance of these.

4.2 METHODS

All adult Bearded Vultures observed at close quarters in the Giant's Castle area were rated according to their colour intensity; pale, normal and dark. Subtle differences from the norm were not considered. A number of pale coloured individuals were resighted at regular intervals, and the time taken for these birds to regain "normal" colouring was

recorded. Few observations were obtained on the time taken for dark birds to lose their colour. Captured Bearded Vultures were carefully examined for colour distribution, uniformity and intensity. Feathers from the belly, breast, throat, neck and head were collected and stored in glass phials for later examination.

Some preliminary observations were made on a captive adult Bearded Vulture which had been obtained as a fully grown nestling and kept in captivity for 10 years in an outdoor enclosure about 2000 m^2 in area at Ladybrand, South Africa ($29°9'S$, $27°29'E$), but before more experimental work could be done, it was struck by lightning and died. No other Bearded Vulture was currently being held in captivity in southern Africa.

Feathers were examined macroscopically for distribution and tenacity of the rufous colouring, and chemically by trying to dissolve the colouring compound in oil solvents (ethyl alcohol, toluene, chloroform and detergents).

Feathers were then examined by light and scanning electron microscopes. Finally, X-ray diffraction was used to analyse chemicals present on feathers, and to produce line scans of the distribution of iron compounds.

4.3 RESULTS

4.3.1 Field observations

Adult Bearded Vultures were found to vary in the intensity of their rufous coloration, both between individuals and within individuals over time. A total of 465

observations were made on birds for colour, 84% of which were classified as "normal", 10% were "paler" and 6% "darker". Figure 4.1 gives the individual colour intensities of Bearded Vultures observed from March 1980 to November 1981, each month being divided into three periods of approximately 10 days each.

Observations showed that after heavy rainfall, some birds appeared to lose their colouring and become much paler, and after periods of little or no rainfall, some birds became darker. Figure 4.2 shows the total rainfall per 10-day period during the study, together with the highest maximum daily rainfall. The percentage of Bearded Vultures with different colour intensities is plotted on Figure 4.3. A visual correlation exists between rainfall and percentage of pale birds, and dry periods and percentage of dark birds.

The time taken for known birds (either marked birds or birds under observation at particular nest sites) to regain normal colouring after being "washed out" during rainfall of known date is recorded in Table 4.1. The mean time taken to regain normal colouring was 5,8 days, with over 80% of the birds having regained normal colouring within seven days.

Some pale birds were observed following long periods of little or no rainfall. Bearded Vultures are known to bathe quite frequently (pers. obs.; P.R. Barnes pers. comm.) and this may account for the colour loss. However, it also makes it difficult to determine the minimum rainfall required to produce the colour loss. From Figure 4.2 it seems that a minimum daily rainfall of at least 10 mm is required, but
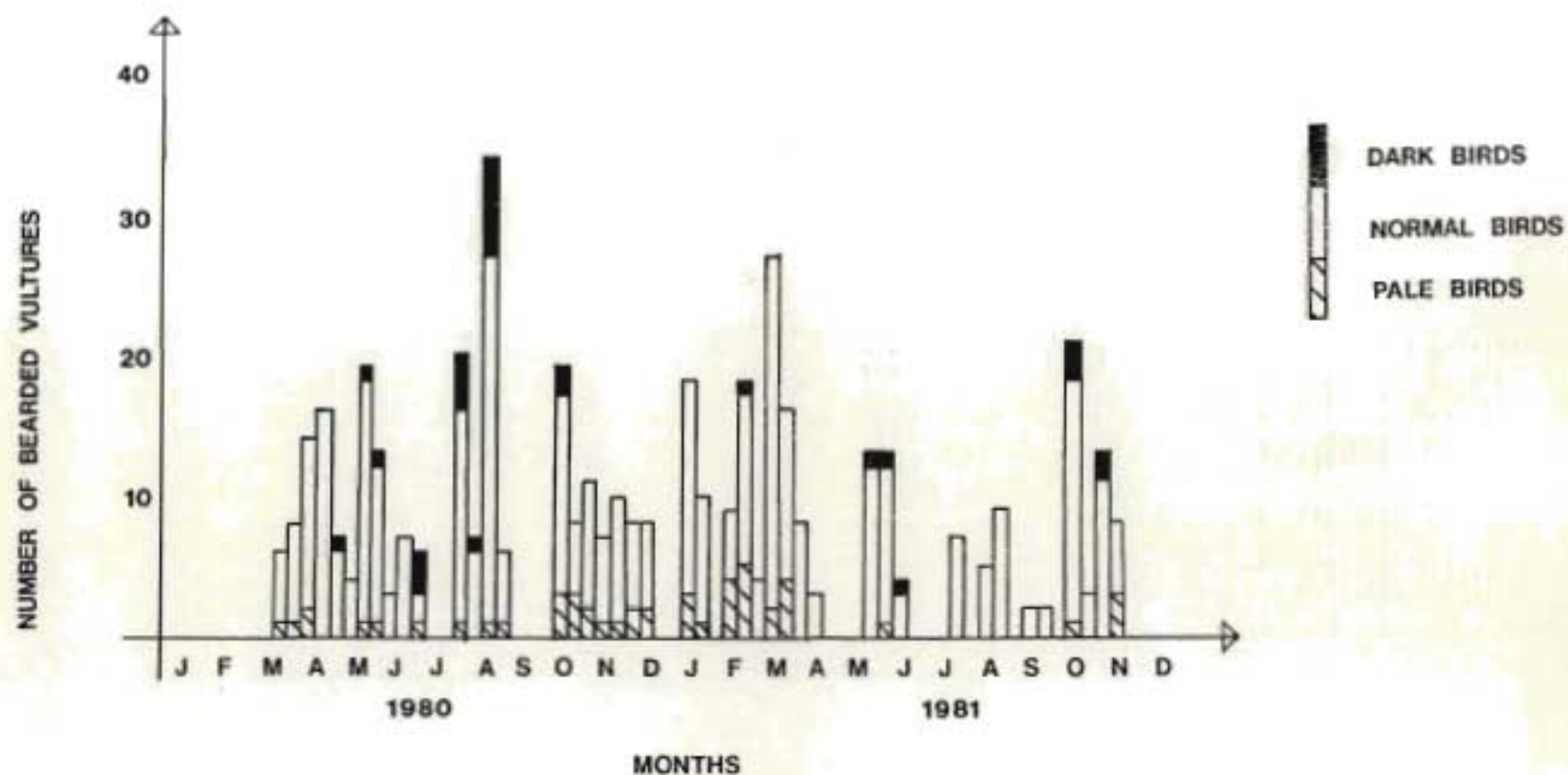
FIGURE 4.1. Colour intensity of the rufous underparts of Bearded Vultures, analysed per 10-day intervals.
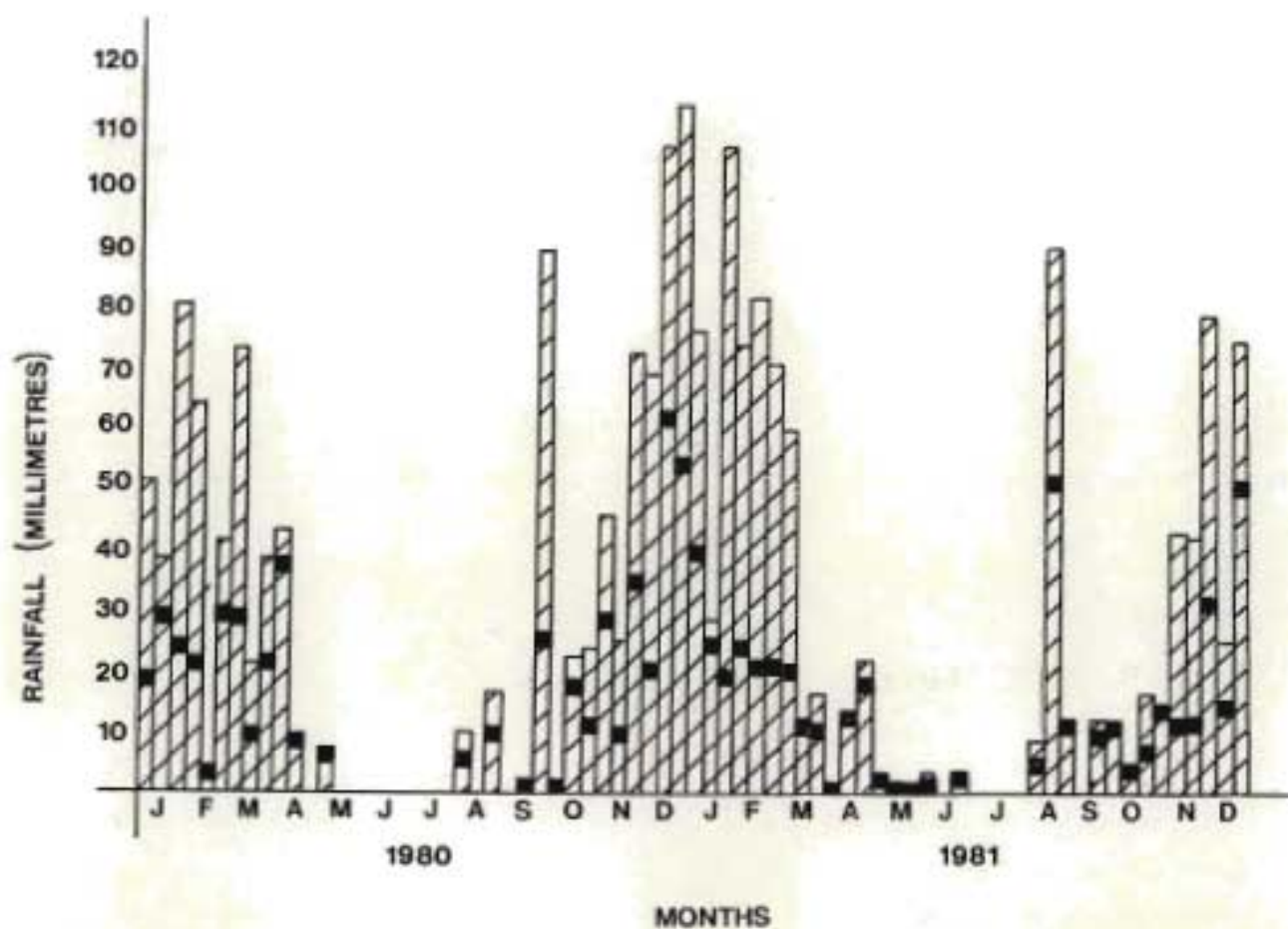
FIGURE 4.2. Rainfall during the study, recorded in the Giant's Castle Game Reserve per 10-day periods, together with the highest maximum daily rainfall.
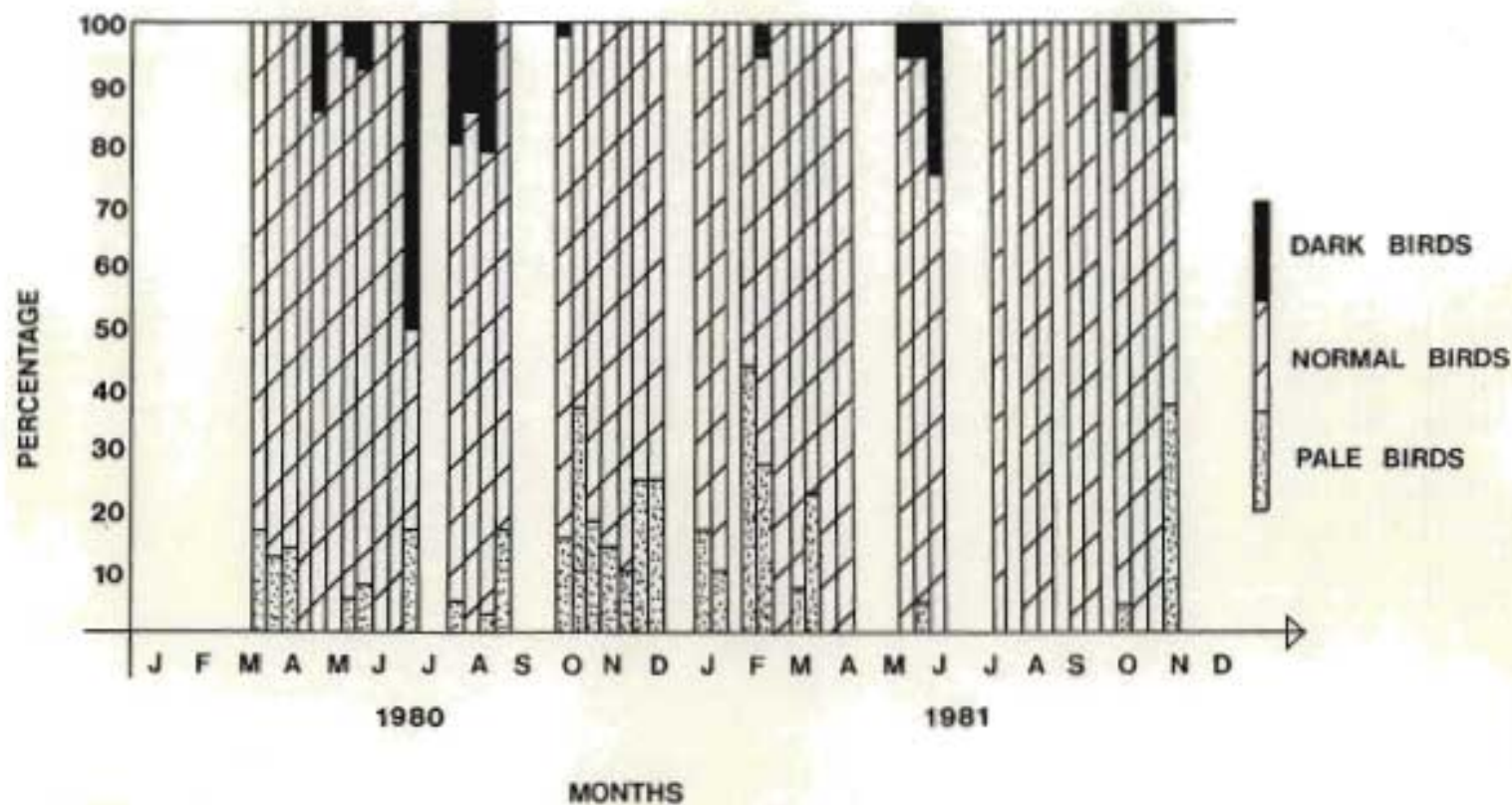
FIGURE 4.3. Percentage of Bearded Vultures with rufous underparts pale, normal and dark per 10-day period.

factors such as intensity of rain, exposure and driving force of wind would play an important part. The colour intensity counts were divided into those for which the preceding seven-day period had experienced less than 10 mm of rain per day, and those with more than 10 mm per day (Table 4.2). Pale birds were significantly more common after rain than before, the converse being true for darker birds. It should be noted however, that even following heavy rains, the percentage of pale birds rarely went above 30%. Birds usually avoid venturing out in rainy weather but may sometimes be caught out.

Observations at nest sites (Chapter 7) and data obtained from radiotelemetry indicate that on rainy days Bearded Vultures do not fly. For example, two radiotagged adults (from different pairs) remained on their cliffs for three consecutive days during rainy weather. The birds do venture out however, in damp misty conditions, light drizzle and light snowfalls. On four occasions birds were seen caught out in hard rain, twice at the feeding station and twice in the open veld. The birds settled on the ground (once on the edge of a small cliff), hunched themselves up and waited for the rain to stop before flying off. Three of these birds were observed immediately after the downpour (weather conditions precluding further observations in one instance) and only one had become appreciably paler.

4.3.2 Distribution of colour

Captive Bearded Vultures have pure white to off-white underparts (Berthold 1967; pers. obs.) (Figure 4.4). In wild adult birds, the underparts, head and neck are usually coloured a rich orange-red (Figure 4.5). The colour is generally evenly distributed over the lower breast, belly, leggings (boots), vent and head. The long narrow feathers of the neck, throat and upper chest may be darker, and the face is paler, verging on white proximally.

The extent of colouring in young birds is difficult to ascertain visually, as feathers of different background colours are replaced at different times giving the birds a mottled appearance. Until birds have acquired adult plumage, the intensity of colour and its distribution cannot be compared. Macroscopic investigations revealed, however, that the presence of the colouring occurs in the same areas on young birds as it does on adults.

The outermost feathers are most affected by the colouring, and inner layers often have just the protruding most distal parts of feathers coloured. The feathers of the throat are small and narrow and tend to stick out at right angles to the skin. These feathers do not therefore provide as much "shading" to underlying feathers, and all feathers are stained which makes this region look darker than the rest of the bird.

FIGURE 4.4. Captive adult Bearded Vulture.

FIGURE 4.5. Wild adult Bearded Vulture.

4.3.3 Macroscopic examination

The distribution of colour on feathers was most intense distally and peripherally. In older, more worn feathers the colour spreads and the whole feather may become a uniform rich rufous. The same is true of the feathers of immature birds, but in first-year birds, the background is so dark (and the feathers are new and unworn) that any rufous colour is not visible, though its presence can be detected by microscopy.

When handling live birds, both adults and immatures, a quantity of rusty coloured powder rubs off on one's hands and Clancey (1968) reports a similar phenomenon when handling skins. If a feather is wiped on a white cloth a red mark is left on the cloth (Berthold 1967; pers. obs.) and some rufous colouring can be washed off with pure water. Clancey (1963) found that when sponging the feathers of the lower neck and breast of an adult Bearded Vulture specimen (shot in the Underberg district of Natal) with water and white face soap, much of the colour was removed.

It was found that the less intensely coloured, less worn feathers lost their colouring more easily by washing than did the darker more worn feathers. Washing off the colour with water is a physical process; the colour does not dissolve in water, but if the darker, more tenacious feathers are treated with an oil solvent (ethyl alcohol, chloroform or a detergent) considerably more colour can be removed by subsequent washing with water. Although feathers can be made considerably lighter, it was never possible

using this technique to make them absolutely white.

4.3.4 Light and scanning electron microscopy

Light and scanning electron microscopic investigations of wild Bearded Vulture feathers showed rufous colouring on most feather parts, with an accumulation particularly at the ends of barbs and barbules and in the axes of shaft and barbs, barbs and barbules and barbules and hamuli (Figure 4.6). No differences between adult and immature feathers were found, but the more worn feathers were more thickly coated.

In the feathers of the captive bird, the hamuli and splintered keratin at the ends of barbules are clearly visible (Figure 4.7). In wild birds these sites are ideal for the accumulation of the rust colouring, often forming large "blobs" at the ends of the barbs (Figure 4.8) and barbules (Figure 4.9). Barbules may become so thickly coated that they are bound together in clumps of two or three (Figure 4.10), and the more worn a feather the greater the amount of colour that adheres to it. Figure 4.11 shows a section of a breast feather of an immature Bearded Vulture that received an injury resulting in the keratin partly splintering and breaking. As can be seen, this region accumulated very high levels of colouring.

4.3.5 X-ray diffraction

Results obtained from X-ray diffraction analysis are shown in Figures 4.12 to 4.15. The stub, coated with the adhesive and covered with a very thin carbon layer was

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FIGURE 4.6. Breast feather of a wild adult Bearded Vulture showing iron oxide coating the barbs and barbules and accumulating in the axes (S.E.M. x 350).

FIGURE 4.7. Breast feather of a captive adult Bearded Vulture showing hamuli and split keratin at the ends of the barbules; no iron oxide (S.E.M. x 100).
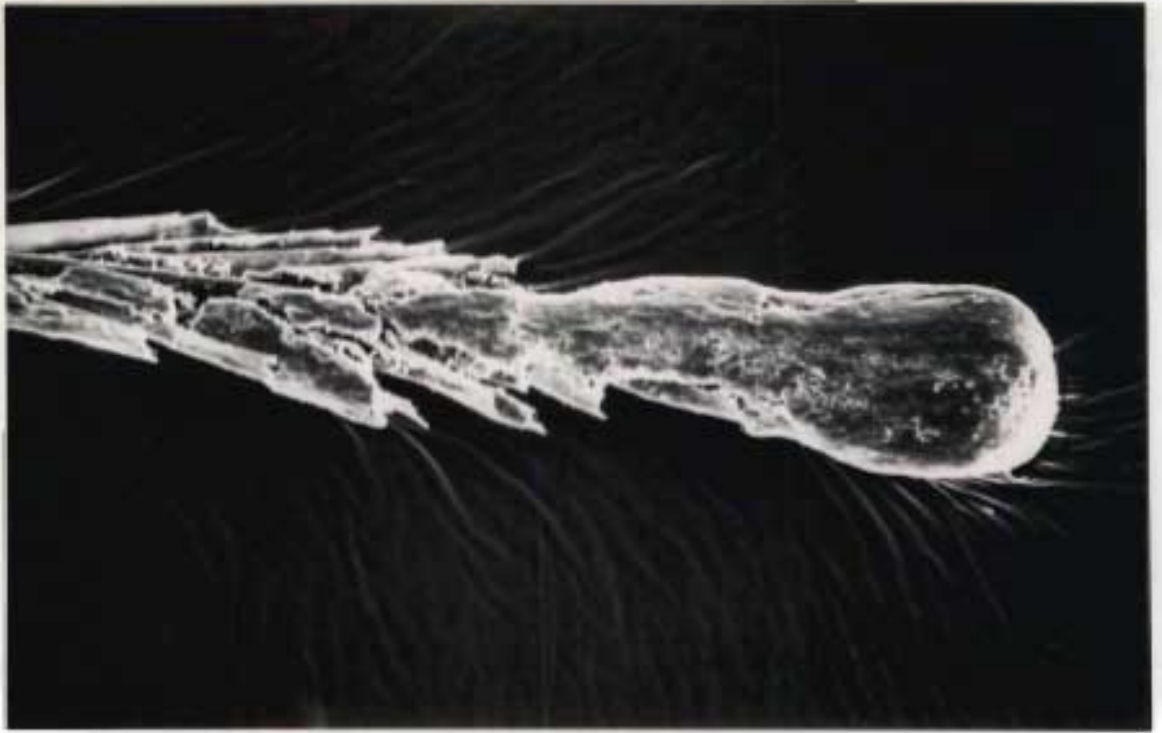
FIGURE 4.8. Iron oxide forming a "blob" on the end of a barb of a wild adult Bearded Vulture breast feather (S.E.M. x 200).

FIGURE 4.9. Iron oxide forming "blobs" at the ends of barbules of a wild adult Bearded Vulture breast feather (S.E.M. x 500).
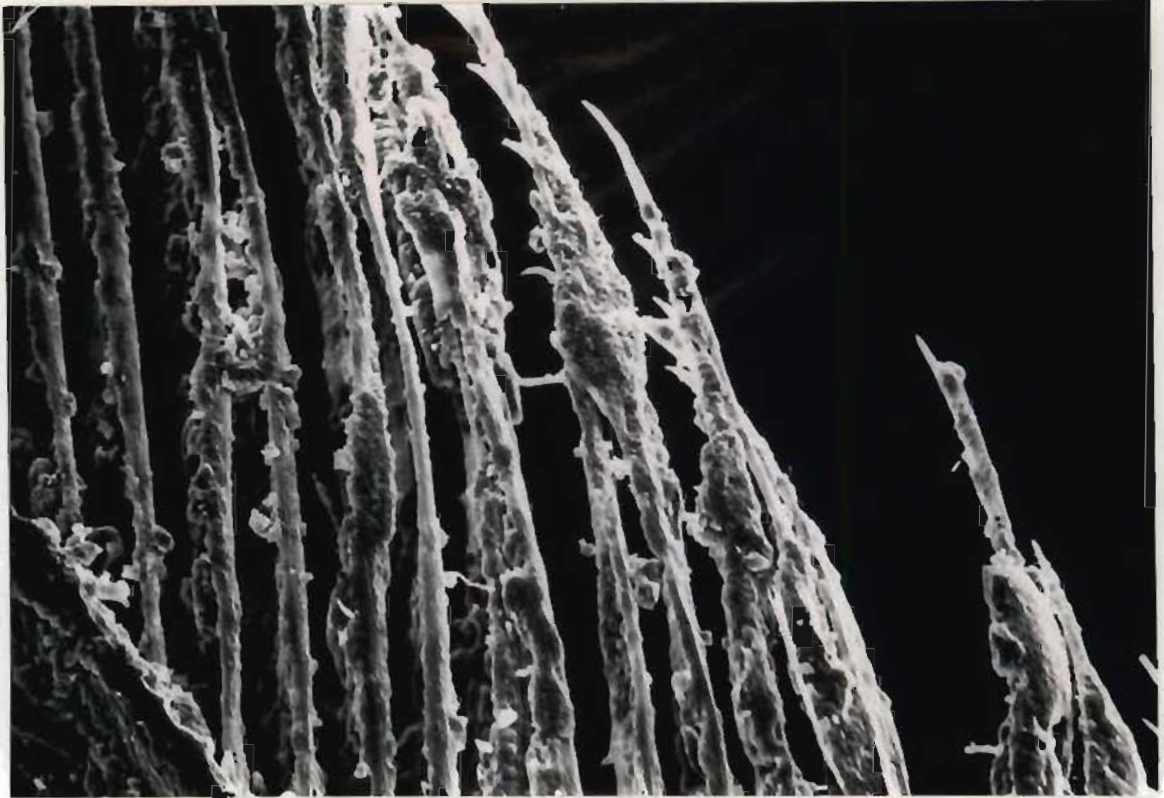
FIGURE 4.10. Barbules of a wild adult Bearded Vulture breast feather bound together in groups of two or three by iron oxide (S.E.M. x 350).

FIGURE 4.11. Section of an immature Bearded Vulture breast feather that received an injury. Iron oxide attached in high concentration in this region of keratin breakage (x 16).
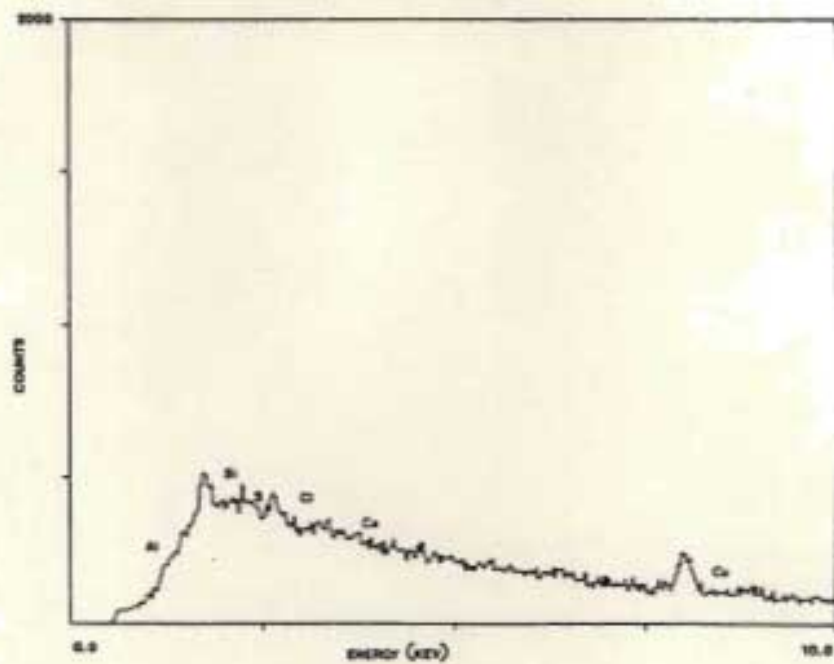
FIGURE 4.12. X-ray diffraction analysis for elements on the stub on which sections of feathers were mounted, coated with glue and covered with a thin carbon layer.
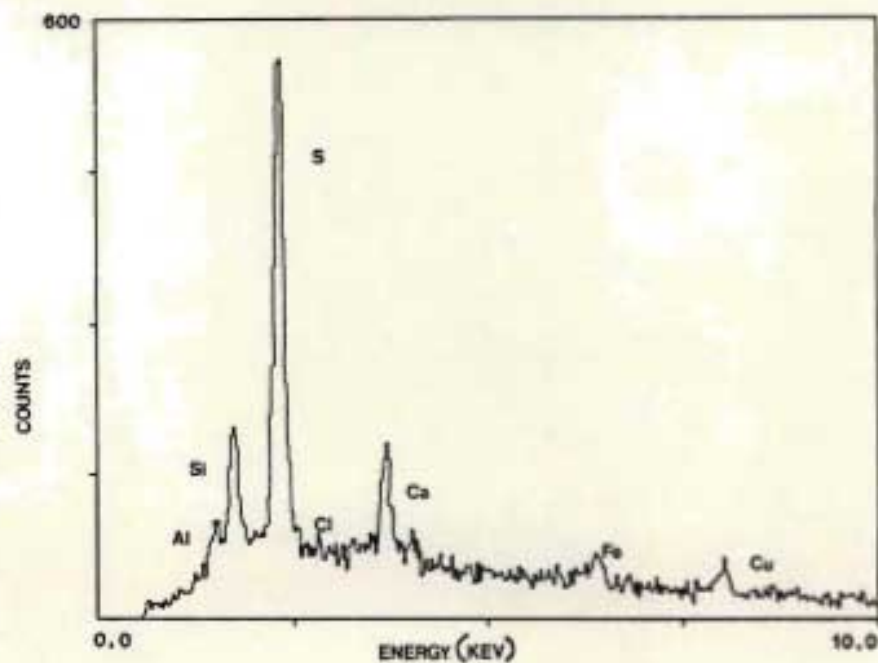
FIGURE 4.13. X-ray diffraction analysis of the breast feather of a captive adult Bearded Vulture.
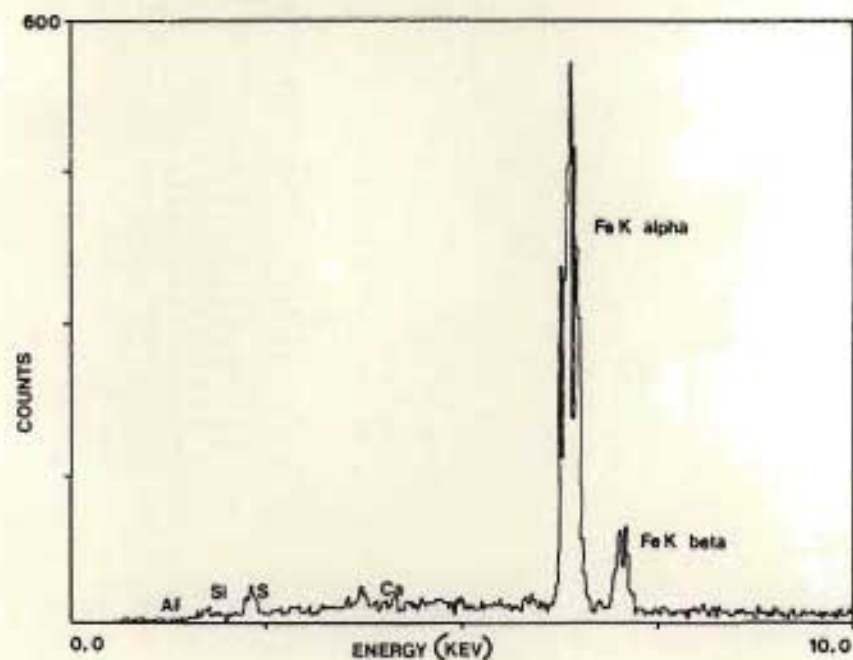
FIGURE 4.14. X-ray diffraction analysis of the breast feather of a wild adult Bearded Vulture.
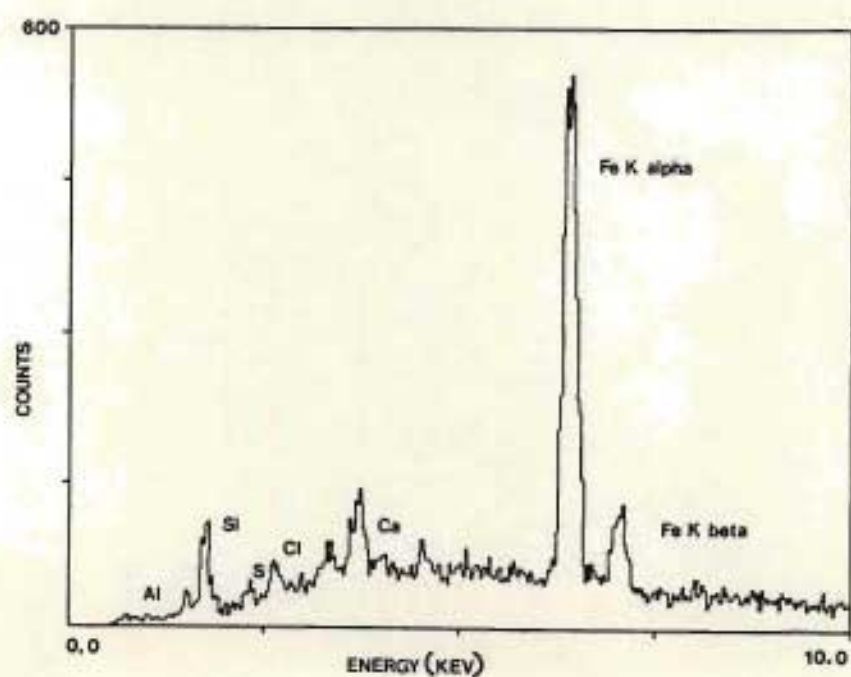
FIGURE 4.15. X-ray diffraction analysis of the breast feather of a·wild immature Bearded Vulture.

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examined first, to determine the "background noise" and any possible bias that may arise. As can be seen from Figure 4.12, very small peaks of Si (Silicone), S (Sulphur), Cl (Chlorine) and Cu (Copper) are detected, possibly being components of the adhesive material used, but these do not significantly affect the following analyses. The white feathers of the captive Bearded Vulture show high peaks of Si, S and Ca (Calcium) (Figure 4.13). These elements are components of the feather itself. The level of Fe (Iron) was extremely low. In the case of both adult and immature wild birds (Figures 4.14 & 4.15 respectively) very similar high peaks for α-Fe compounds were obtained, with lower β-Fe levels. Some Si and Ca are seen in the immature bird, these presumably being due to quartz or other mineral particles adhering to the plumage.

Line scans for iron across feathers of different colour intensities are shown in Figures 4.16 to 4.19. The white feathers of the captive bird show only background effects (Figure 4.16) a pale adult shows definite peaks as the scan crosses parts of the feather (Figure 4.17) and dark coloured adults show very large peaks (Figure 4.18). In immature birds, the same range is observed as in adults. Less worn feathers show lower levels of iron than more worn feathers. Figure 4.19 shows an immature Bearded Vulture breast feather with an intermediate amount of wear and iron attachment.

Iron removed from feathers by means of ultrasound in dilute NaOH solution proved to be amorphous to X-rays, indicating that it is probably related to ferrihydrite, a
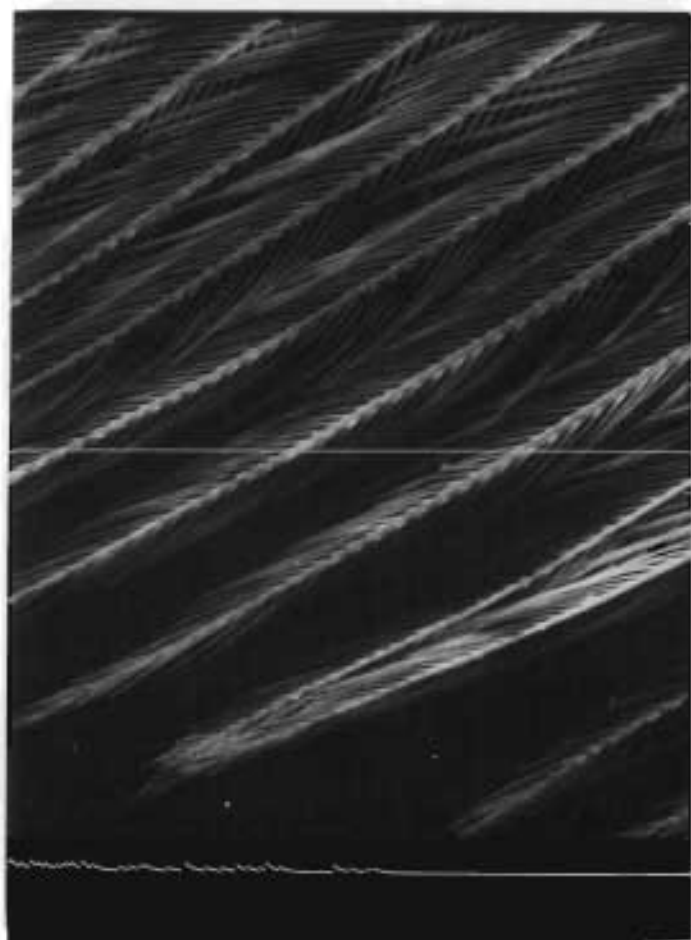
FIGURE 4.16. X-ray line scan for iron across a captive adult Bearded Vulture breast feather (x 50).
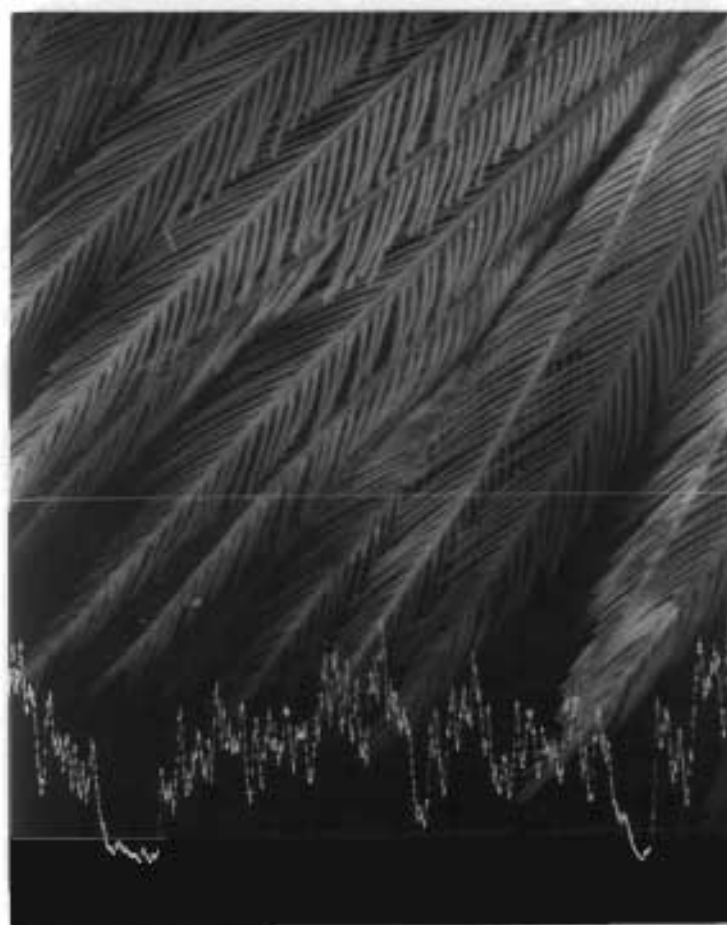
FIGURE 4.17. X-ray line scan for iron across the breast feather of a wild, pale-coloured adult Bearded Vulture (x 50).
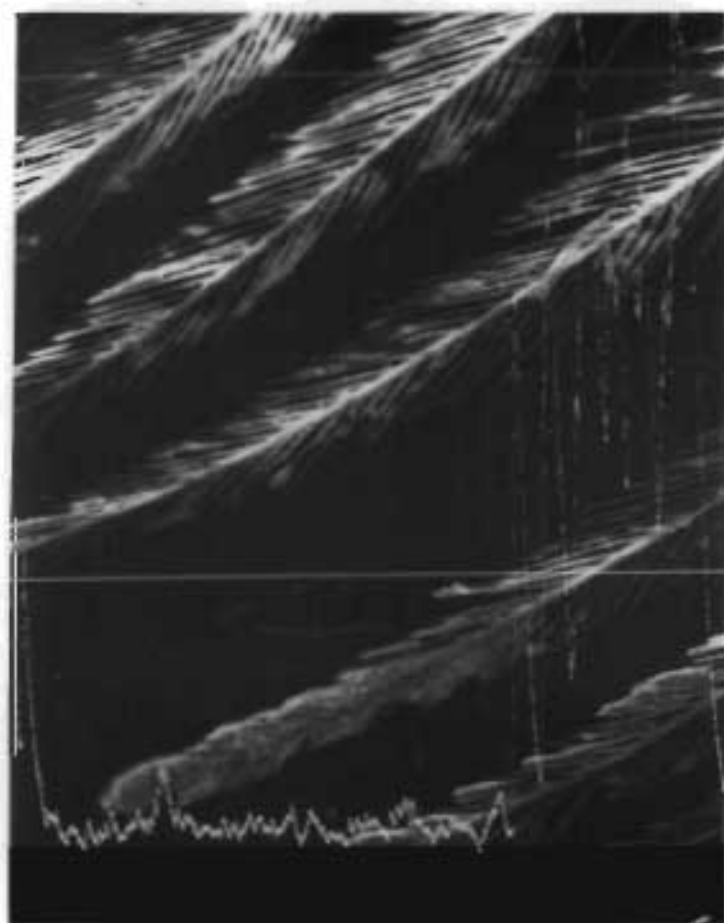
FIGURE 4.18. X-ray line scan for iron across the breast feather of a very rufous wild adult Bearded Vulture (x 50).
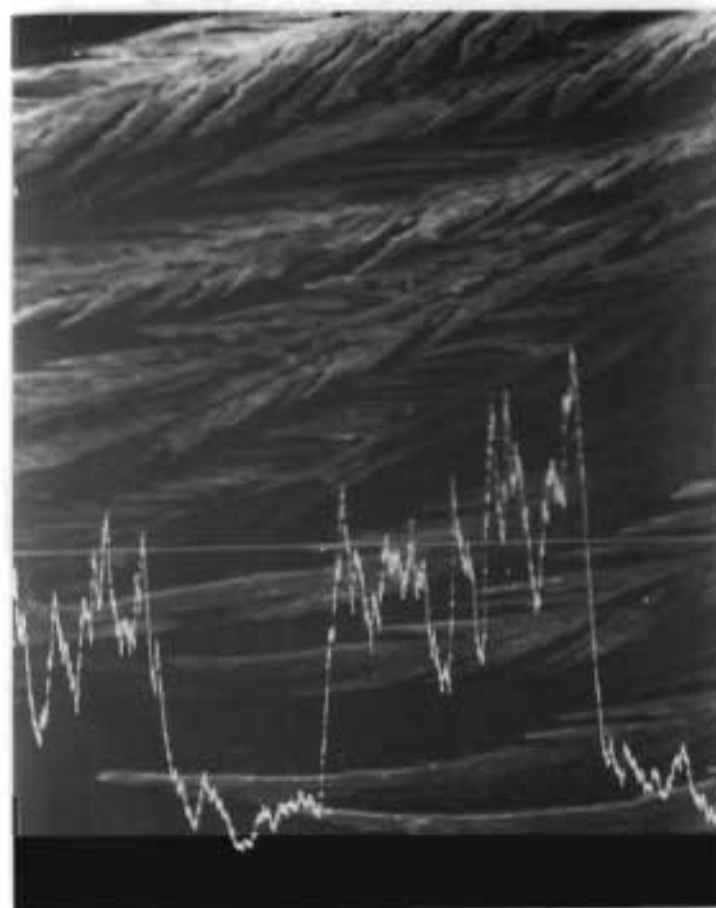
FIGURE 4.19. X-ray line scan for iron across the breast feather of an immature Bearded Vulture of intermediate colour (x 50).

poorly crystalline hydrous oxide of iron, rather than haematite (α-Fe$_2$O$_3$) which is the common crystalline oxide form. The rusty orange (as opposed to red) colour of the stained feathers also attests to this (M. Fey pers. comm.).

This type of iron compound is typically found as a gelatinous or filmy accumulation in freshly oxidized water which has emerged by seepage from more reducing subterranean sources. Typically, with ageing, it will transform to one or other of the crystalline Fe compounds (geothite, α-FeOOH or haematite). Mountainous habitats are usually rich in iron oxide; both the basalt and cave sandstone cliffs of the Drakensberg and Maluti mountains are richly coloured by iron oxide. The oxide tends to accumulate particularly in caves, potholes and ledges on these cliffs, seeping or leeching into such sites through fissures in the rock. If a hand is rubbed over the floor of these sites, many are found to be rich in iron oxide, staining the hand a rusty colour.

4.3.6 Behaviour of the birds

Bearded Vultures spend much of their time on ledges and in potholes on cliffs. They nest, roost and perch on these sites, and often, having obtained food, carry it to a cliff to feed. Just over 16% of all Bearded Vulture diurnal activity away from the nest takes place on cliffs (Chapter 8). At night birds roost either on the nest (mainly females) or on a nearby ledge or pothole. Captive European Bearded Vultures reportedly lie down on the ground at night, resting on their chest, throat and head, with wings spread (Berthold

1967). Siegfried & Frost (1973) report that the captive southern African Bearded Vulture under their observation adopted a prone position with neck retracted and ventral surfaces of the body resting flat on the ground. The legs and feet were drawn up into the ventral feathers, the head drooped sideways and the eyes were closed. Wild Bearded Vultures sleeping away from the nest rested on their bellies with feet drawn up into the ventral feathers, and head and neck hunched up and retracted. They were never observed to lie down. Only on nests were adults and young birds seen sleeping with their heads resting on the substrate (nest rim).

During the course of this study wild Bearded Vultures were never observed dust bathing and, although Steyn (1982) reports that the species does, this is probably not very common. In captivity, birds often dust and mud bath (Berthold 1967; A.C. Jaques pers. comm.; pers. obs.), particularly after bathing in water when their plumage is still wet.

The captive adult Bearded Vulture bathed regularly, usually after feeding and often more than once a day. I observed the bird bathing at 09h15 on a winter morning, when a thin layer of ice covered the pond. The bird began by dipping its bill in a number of times, sometimes lifting its head and drinking, sometimes just passing its bill through the water. It moved away from the pond and stood in the sun for about 10 min, then returned and climbed clumsily into the pond (a circular cement tub about 1,5 m in diameter and

25 cm deep, sunk into the ground). After stamping its feet a few times it began scooping its bill through the water, the scoops becoming progressively deeper until its whole head was being submerged (Figure 4.20). It then sat in the water having first fluffed up its feathers, bobbing and drenching itself by thrusting its body back and forth and up and down. From this position it continued to duck its head under the water. After about 2,5 min in the water the bird emerged, sat on a small patch of grass and commenced rubbing its breast, belly, throat, sides of face and chin up and down on the ground (Figure 4.21). This continued for just over 2 min. The bird had four more such trips to the water in which it also wetted its back and wings by leaning over to one side and lowering that wing, almost folding it beneath its belly. This would then be repeated for the other side and back again, being done five or six times per dip. The bathing lasted 34 min, by which time the bird was completely soaked. It then climbed out onto a sunny rock, fluffing up its feathers every now and again. Whenever the garden was watered the captive Bearded Vulture also rubbed itself in the mud (A.C. Jaques pers. comm.).

Wild Bearded Vultures were observed bathing at 14 different sites in southern Africa, four of which were regularly used. Two sites were temporary rainwater rock pools and the other 12 sites were small streams. These sites were all closely investigated, but no regions rich in iron oxide were found. In addition, wild Bearded Vultures were

FIGURE 4.20. Captive Bearded Vulture bathing during which it submerged its head and most of its body.

FIGURE 4.21. Captive Bearded Vulture rubbing its face, throat and breast on the ground after bathing.

never observed to rub themselves on the substrate during or after bathing. Steyn (1982) suggests that Bearded Vultures may obtain the coloration from iron oxide in the water. However, Berthold (1967) has shown that the iron oxide content in water is far too low to cause coloration of Bearded Vulture feathers (though it may in some species which have a different feather microstructure, e.g. Anatidae, which have thin hollow spaces in their barbs, barbules and hamuli). It is possible that wet birds fly up to cliffs and rub themselves on iron-rich ledges and floors of potholes to pick up the rufous coloration, but during the course of this study, despite the many hundreds of hours spent watching nesting and roosting cliffs, this activity was never recorded.

It seems far more likely that Bearded Vultures incidentally come into contact with gelatinous or filmy accumulations of iron oxide in potholes and ledges of cliffs, where they spend an appreciable amount of their time. These areas are likely to be damp, facilitating the attachment of iron oxide: Berthold (1968) noted that captive birds supplied with soil rich in iron oxide coloured very much more quickly after the soil had been dampened by rain than when the soil was dry. The colour would be rapidly spread by preening, and excess iron oxide would fall off.

4.4 DISCUSSION

How Bearded Vultures acquire the rufous colouring of
their underparts has caused much speculation, as no really
convincing behavioural activity has ever been seen. Iron is
the fourth most common element in the earth's crust (Sienko
& Plane 1966). Mountainous habitats are usually rich in iron
oxide, which tends to accumulate in caves and on ledges
after seeping through fissures in the rock. These damp,
typically gelatinous or filmy accumulations occur on the
sites where Bearded Vultures are most likely to roost and
perch. In southern Africa, many of the cave sandstone and
basalt cliffs are a rusty colour from iron oxide. I never
saw wild Bearded Vultures rubbing themselves in iron oxide-
rich soils or on cliffs. I suggest, therefore, that the
rufous colouring is obtained passively by incidental
contact.

Why should the Bearded Vulture acquire an external
coating of iron oxide on its feathers? Perhaps the most
obvious explanation is that of camouflage. Berthold (1967)
states that in a number of species (at least 120 species of
birds have been shown to have rufous colouring due to iron
oxide) the rusty coloration provides camouflage for the bird
and can thus be considered to have a protective function.
This is especially the case with birds which have light
coloured feathers and, by taking on the colour, blend in
with their surroundings. As mentioned above, where the
sandstone and basalt cliffs in southern Africa are not dark
grey or black in colour, the presence of iron oxide causes

yellow and gold through orange to red colouring of the cliffs. Adult Bearded Vultures have their upper parts (back, wings and tail) a dark slate colour matching the dark sections of cliffs, and their underparts (rufous) matching the light iron oxide coloured regions. Pure white underparts would be immediately obvious on a cliff, advertising the bird's presence. For a bird as large as the Bearded Vulture, its presence, and especially its nest site, are particularly difficult to detect. Nests are almost invariably in deep potholes hidden from sight. Very little "whitewash" is left on the cliff under the nest, and when approaching the nest, birds usually fly below the top of the cliff and so are not silhouetted. In addition, little activity takes place about the nest, particularly in the early stages until the chick is well able to defend itself, the parents arriving and departing rapidly. This is in contrast to the situation reported for the European Bearded Vulture (Brown & Amadon 1968; Cramp & Simmons 1980) (see Chapter 7). So effective is this behaviour that two farmers who had Bearded Vultures nesting on cliffs directly behind their homes were totally unaware of the presence of the birds, and a third, very interested farmer, who knew of the presence of the birds, could not locate the nest, whose cave entrance proved to be visible from his dining room window! Perhaps Bearded Vultures and other large raptors alternate between nest sites in order to enhance their inconspicuousness.

Camouflage of nest sites, however, is of a long-term

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nature. Perhaps short-term camouflage is even more important, because it is really only against man that long-term camouflage is going to be at all effective. Nesting sites are inaccessible to all other mammals (including baboons), and it is only other birds that pose a possible threat. It is unlikely that the presence of a nest could be kept hidden for very long from a pair of Black Eagles Aquila verreauxii or other raptors living in the area. Bearded Vultures often carry food to a ledge or pothole on a cliff to feed. There are a number of records of piracy from Bearded Vultures, involving both Black and Martial Eagles (Scotcher 1973; Steyn 1982). In addition, Whitenecked Ravens Corvus albicollis are a constant source of annoyance, attempting to steal food whenever possible. The short-term camouflage afforded by the rufous colouring could be important in allowing the bird sufficient unmolested time in which to feed.

An additional explanation for the dark dorsal surface of Bearded Vultures is worth considering. Desert animals, when not cryptically coloured, are most often black (Serventy 1971). In white and dyed Zebra Finches Poephila guttata exposed to artificial sunlight, the dyed black birds used about 23% less energy than did the white birds (Hamilton & Heppner 1967). Similarly, Lustick (1969) found that oxygen consumption in birds exposed to solar radiation was reduced by 26% in dark birds and by 6% in pale birds. Dark-coloured birds could therefore achieve a considerable saving in metabolic energy in low-temperature situations.

Alpine regions have, in common with deserts, a high incidence of solar radiation because of the clear atmospheric conditions. This leads to a great diurnal temperature range. Surfaces exposed to the sun heat up rapidly, but once in shade, they quickly cool off. Black colouring as a means of reducing energy expenditure is therefore most efficient in areas where solar radiation is high. The dark dorsal colouring in Bearded Vultures might therefore be important for reducing their energy expenditure in the early morning, on cold clear days and when in flight through cold alpine air with the sun shining on their dorsal surface. In the unlikely event of heat stress becoming a threat, birds could retire to the shade, turn their backs away from the sun or soar.

Other explanations for acquiring iron oxide on feathers become possible when looking at the microscopic positioning and nature of the deposits. The iron oxide concentrates at the ends of barbs and barbules, usually forming "blobs". These are the points were keratin splitting and breakage most commonly occur, and it is as a result of the initial wear that iron oxide can get a hold. These "blobs" therefore form at the sites which experience most wear, and it is suggested that they act as protective caps, thus reducing the extent of further feather wear. For a species which spends an appreciable amount of time on rocks and cliffs, and has relatively short legs, the amount of contact between the feathers of the underparts and the rock substrate must lead to considerably more wear than is usual in most birds.

Iron oxide also tends to gather in the axes of barbs & barbules, thus giving rigidity to these structures. A number of barbules may also be bound together by iron oxide at their tips. From a microscopic investigation one would assume that iron oxide imparts rigidity to the feather, perhaps making it more wind- and waterproof. However, if a heavily coated feather is compared to a lightly coloured one (i.e. an outer feather compared to a feather a few layers down), it is apparent that the barbs of the darker feather are free from one another and do not "zip up" or interlock to form a windproof surface, as do the more lightly coloured feathers. This is because the hamuli become coated with iron oxide and can no longer interlock efficiently with the ridges on the adjacent barbules. It is therefore significant that only surface feathers and exposed ends of immediately underlying feathers become heavily coated with iron oxide, the underlying feathers retaining their windproof structure. Flight feathers are structurally unsuited to accumulate iron oxide.

Finally, the iron oxide could act as an ectoparasite control. When handling wild birds (and skins) particles of iron oxide impart a dusty or powdery "feel" to the birds (Berthold 1967; Clancey 1968; pers. obs.). This may account for dust bathing in captive Bearded Vultures (which lack iron oxide) and the paucity of records of wild birds dust bathing.

TABLE 4.1

Time taken for pale Bearded Vultures to regain normal colour after rainfall.

Number of days	Number of Bearded Vultures
4	2
5	4
6	3
7	1
8	1
9	1
mean = 5,8	total = 12

TABLE 4.2

Colour intensities of Bearded Vultures observed with rainfall of preceding seven days <10 mm, and >10 mm.

Rainfall on preceding seven days (mm)	No. days	No. Bearded Vulture sightings			
		Pale	Normal	Dark	Total
<10/day	108	20 **	308	28 *	356
>10/day	46	28	80	1	109
Total	154	48	388	29	465

<u>Chi</u>-squared test; * = p<0,05, ** = p<0,001.

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Chapter 5

HOME RANGE AND MOVEMENTS

5.1 INTRODUCTION

Patterns of dispersion vary considerably between different species of birds of prey. At one end of the range are species which nest singly in exclusive territories, at the other are those that nest in closely packed colonies. The former are associated with a food source which is fairly evenly distributed both spatially and temporally, whereas the latter are dependent on a highly unpredictable and patchy food source (Newton 1979). Scavenging species of raptors may be found to correspond with all points along this range. Some scavenging species are thought to maintain largely exclusive ranges, such as the Whiteheaded Vulture and the Bateleur (Kruuk 1967; Pennycuick 1972; Watson 1984) while in the Gyps vultures, home ranges overlap totally and all the species are to some extent colonial (e.g. Kruuk 1967; Pennycuick 1972; Houston 1975; Mundy 1982). Solitary-nesting species whose ranges are partly or totally overlapping fall into intermediate categories, e.g. Lappetfaced Vultures in the Namib Desert (Sauer 1973; pers. obs.), Hooded and Egyptian Vultures (Pennycuick 1972), but the movements and ranges of these species have generally been little studied. The Bearded Vulture clearly falls into this intermediate group.

Information on the patterns of dispersion and more

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particularly, on home range sizes, use of ranges and the extent of territoriality in most large birds of prey, including the Bearded Vulture, is generally lacking. This is because these species characteristically cover vast areas daily, cumulatively forming a foraging range which may be tens or hundreds of kilometres in diameter. In addition, healthy populations of scavenging raptors are usually restricted to isolated areas where the rate of resightings of marked individuals is low, (e.g. Snelling 1970), and biased towards human access routes. It is only relatively recently, with the development of small radio transmitters, that intensive investigation of the movements of large raptors has become possible (e.g. Southern 1964; Kenward 1980; Pennycuick 1983; Boshoff et al. 1984).

In order to understand patterns of dispersion it is necessary to have some insight into the day-to-day movements of individual birds and the areas used by a single pair at different times of the year. In birds such as Bearded Vultures, which spend most of the day patrolling across country in search of food (Chapter 6), daily foraging patterns and home-range size and use are closely interrelated. This chapter describes the more important modes of flight of Bearded Vultures, investigates their home-range sizes at different times of the year, looks at range use and daily foraging patterns of adults and describes the movement patterns of a radiotagged immature bird.

5.2 METHODS

Descriptive accounts of foraging-related flight behaviour were made opportunistically. When possible, flight air speeds were timed with a stop watch, using geographic features to measure distances and allowing for wind speed. The frequency of wingbeats during flapping flight was timed for Bearded Vultures and some other species during different activities. Rates of ascent were measured using a theodolite or geographic features. Because the rate of climb is dependent largely on the amount of lift available, measurements were made only when other raptor species were present and attempting to gain height in the same thermal or hillside updraught so that comparisons could be made.

An attempt was made to determine the home-range sizes of Bearded Vultures using standard marking techniques, e.g. numbered metal leg rings, coloured plastic rings and cutting "windows" into the remiges and rectrices (Snelling 1970; Gargett 1973). Bearded Vultures' legs are almost entirely feathered. The plastic coloured rings, one per leg, were therefore placed immediately above the foot. A metal ring was attached above one of the plastic rings. A choice of three window positions on each wing and two on the tail were possible (Figure 5.1). In most cases a window on each wing and one on the tail were used (Table 5.1), but in the last three immature birds which were window-marked, two windows were cut on one wing as no other new combinations were available. Each bird obtained a unique colour code and
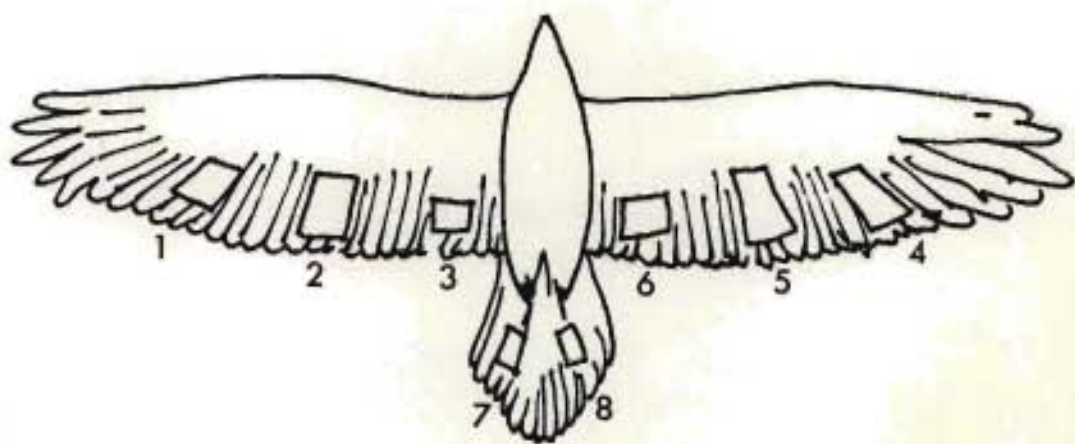
FIGURE 5.1. The wing and tail window positions used for marking Bearded Vultures captured in the Giant's Castle Game Reserve.

window combination, although window positions were sometimes duplicated between immature and adult birds.

Information on resightings of marked birds was requested from (a) Natal Parks Board and Forestry staff in all conservation areas in the Drakensberg, (b) visitors to all Drakensberg conservation areas and (c) farmers in areas adjacent to the conservation areas. Information and observation forms were supplied to these and all other interested people. I undertook twice-weekly foot and horse patrols, concentrating mainly on areas which were otherwise poorly covered. All observations of marked birds were plotted directly onto a grid map. The numbers of resightings on each marked bird are given in Table 5.1. It is clear that no useful information on young birds was obtained, with an average of only 2,5 sightings (including capture locality) per bird (range 1-4). The mean period between capture and the last sighting for young birds was 2 months (range 0-6 months). The average resighting rate of adult birds was considerably higher at 48 sightings per bird (range 36-67) over a mean period of 10,8 months (range 7-14 months) and the resultant ranges plotted from these sightings appear superficially to be adequate (Figure 5.2). However, they were suspected to not be representative of the ranges of the birds for the following reasons:

(a) the nest sites were not central to the ranges of the birds, suggesting that not all parts of the ranges were being identified;

(b) many of the sightings were in predictable localities
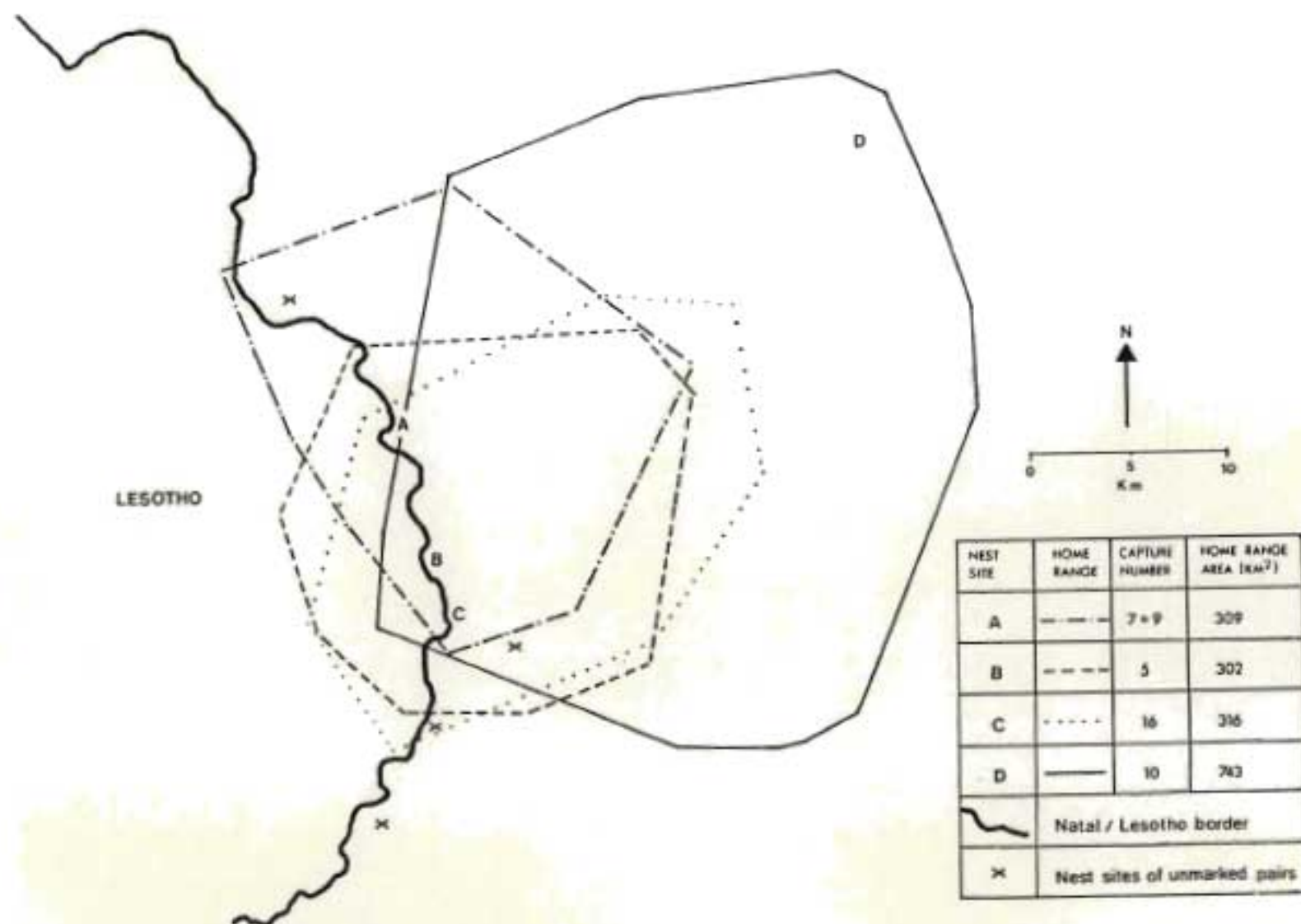
FIGURE 5.2. Dispersion pattern of five Bearded Vultures (from four pairs, A-D) marked with numbered metal and coloured plastic rings and windows in the Giant's Castle area. Home ranges were determined by plotting all resightings of these birds.

such as near the birds' nests or at the feeding sites, and few sightings were obtained at any distance from these localities;

(c) the sightings tended to indicate the distribution of the observers (mainly tourists and conservation staff) rather than the distributions of the birds (few records were obtained from Lesotho, all of which were my own);

(d) birds were often seen disappearing into areas for which their ranges had not been mapped.

When trips into these unmapped areas were made (invariably on foot, and lasting up to seven days), no marked birds were seen, presumably because they were then foraging in another part of their range. Similarly, observations made through a telescope on the movements of a pair of Bearded Vultures nesting on a large inselberg, a site that would have been ideal for the study of a species moving even up to 10 km from its nest, showed that for more than half of their foraging time they were out of visual range. The information obtained from this pair, one of which was marked (capture number 10 in Table 5.1) indicated, however, that the information obtained from the other adult birds was highly inadequate.

Other disadvantages of using these standard marking-resighting techniques were that no information on daily or seasonal movements and area utilization were obtained.

It was concluded that the home range and daily movements of Bearded Vultures were too extensive, the numbers of observers too few and unevenly distributed and

the terrain too rugged and inaccessible to provide suitable information from these marking techniques.

Once the inadequacies of these marking techniques had been recognized, radiotelemetry was introduced as a possible solution. Equipment was obtained from the A.V.M. Instrument Company, Illinois, U.S.A., consisting of two L.A. 12 receivers with sweep option, two hand-held, three-element yagi antennae and five H-module S.B.2 transmitter packs, each weighing about 80 g, inclusive of battery, antenna, ground plate and plotting material, with a current drain of about 0,35 mA. The transmitters were within the 148,000-148,275 mHz frequency range and had a theoretical life of about 14 months. In practice radio life ranged from 8-14,5 months.

The transmitters were attached to the Bearded Vultures by a harness-type back mount (Kenward 1980), constructed of 3-mm nylon cord sheathed in clear, soft PVC surgical tubing. The transmitter was mounted high on the bird's back (Figure 5.3) at a point judged to be over its centre of gravity. The harness ran from the transmitter to the base of the bird's neck, formed a loop about the neck and joined just posterior to the junction of the clavicles and sternum, thereby allowing the crop to bulge out unimpeded when full. The harness ran down the centre of the breast and belly to a point between the legs about 5 cm anterior to the cloaca and then split, a cord passing posterior to each leg and attaching on the hind edge of the transmitter. All knots were tied in the nylon cord only. The surgical tubing was

VENTRAL

DORSAL
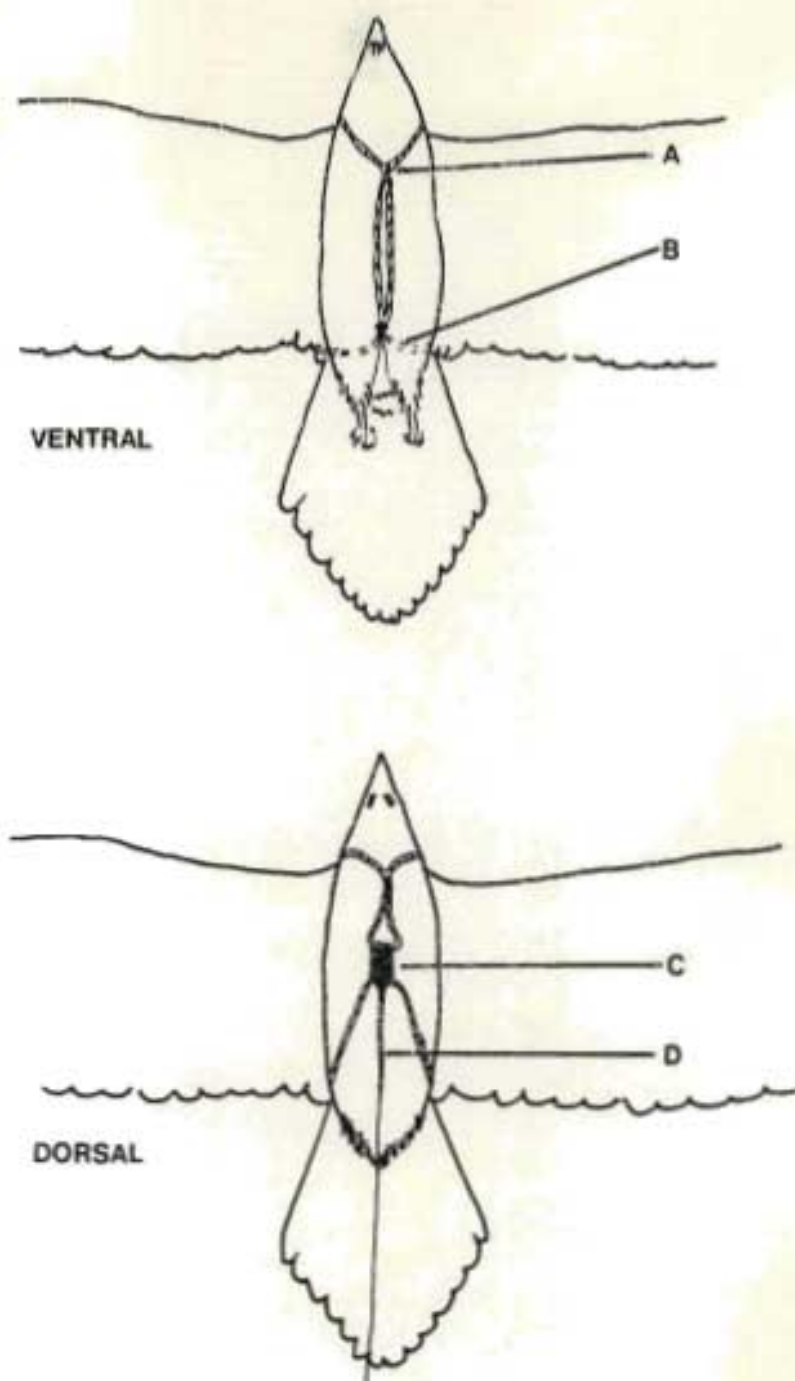
FIGURE 5.3. The 80 g radio transmitter was mounted on the bird's back by a harness made from 3-mm nylon cord sheathed in soft plastic surgical tubing. A - "V" shape to accommodate a bulging crop and the swallowing of large bones, B - harness passes behind legs, C - transmitter is attached above the bird's centre of gravity and D - antenna extends along and slightly beyond tail.

pushed up against the knot and sealed with quickset epoxy resin. Before releasing each radio-tagged bird its wings were stretched out and a number of postures were tested to ensure that the radio fitted snugly but that all movements were unimpeded.

Radiotagged birds were located by triangulation. A number of tracking points were chosen (Figure 5.4) each of which allowed reasonable line-of-sight coverage of large areas. No single set of tracking points allowed the ranges of all birds, or even the entire range of one bird, to be adequately covered. Tracking was therefore done from different sites in an attempt to include all parts of each bird's range. Although both operators of tracking equipment (trackers) were usually in contact by hand-held radios, tracking times were scheduled at 10-min intervals, starting with capture no. 17 and working through to capture no. 21, each on a different channel. Compass bearings of the "peak" signals from each bird were therefore taken at approximately the same time by each tracker. Because the distance to the radiotagged bird was often more than 30 km and up to a maximum of about 80 km when tracking from the ground, as wide a tracking base (i.e. distance between receivers) as possible was used, usually at least 20 km. This ensured that most of the crossplots were at an angle of between 50° and 130°, which resulted in more accurate fixes than could be obtained from very acute angles of intersection.

Transmitters were attached to the following birds; a juvenile about two months after its first flight (see
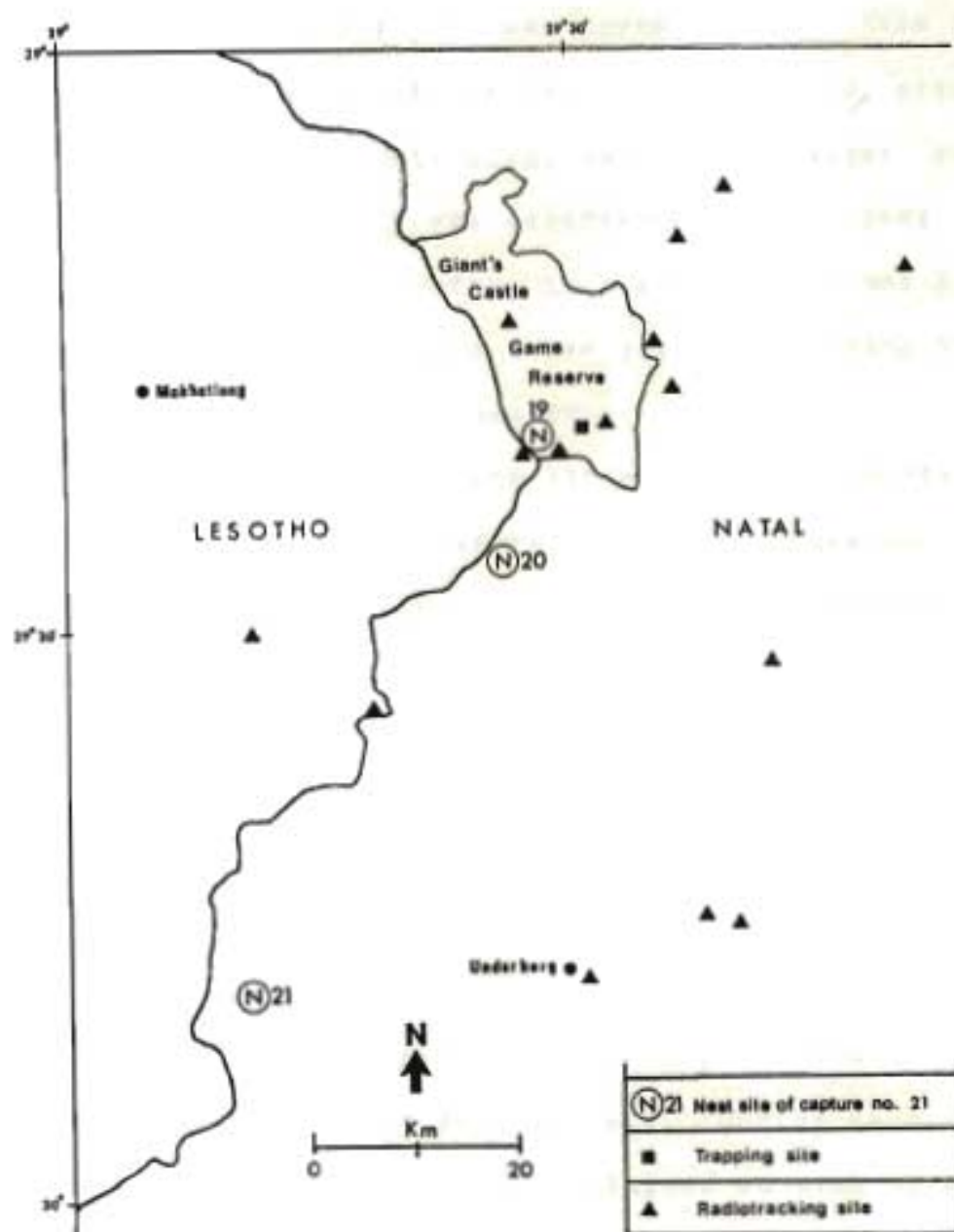
FIGURE 5.4. Localities of the nest sites of the three radiotagged adult Bearded Vultures, the trapping site and the sites from which birds were tracked.
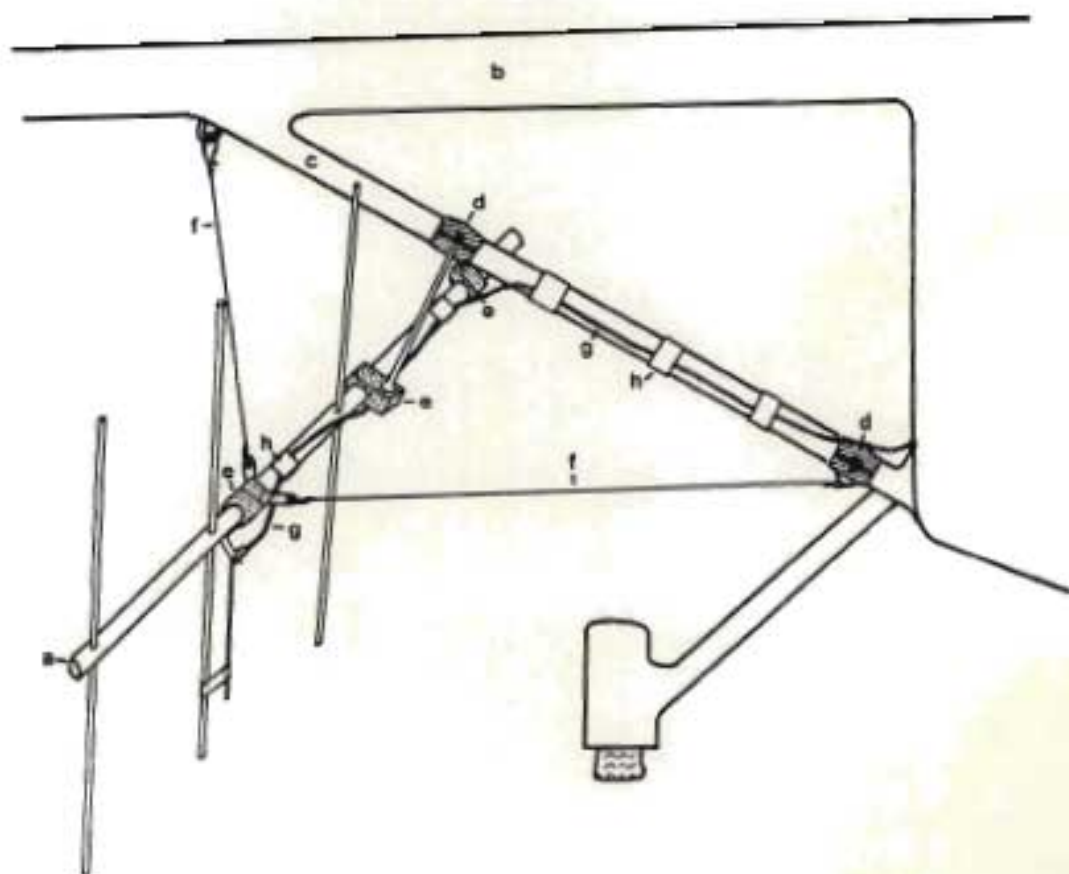
FIGURE 5.5. Method used to attach the three-element yagi antennae to the wing struts of the Cessna Skylane.

a = 3-element yagi antenna, b = aircraft wing, c = wing strut, d = metal split-clamp, felt lined, e = PVC clamp (for insulation), f = wire stays, g = antenna cable, h = plastic binding tape.

were taped to the back of the struts, up the fuselage and into the cabin, where they entered a two-way switchbox, which in turn was connected to an L.A. 12 receiver. This allowed the operator to switch between the antennae. Once a signal had been picked up, the bird was approached until the signal was strong and clear. The pilot then made a slow and level turn to locate the strongest signal. By switching back and forth between the antennae, the direction of a signal of equal strength was determined audibly through headphones. The direction to the bird was then recorded from the aircraft's compass and the position of the aircraft was recorded. By turning the volume of the reciever very low as an equal signal was approached, a more accurate bearing could be obtained. The process was then repeated with a turn from the opposite direction, and the mean compass bearing was calculated. The aircraft then flew to a point where another compass bearing could be taken, such that the two bearings would intersect at an angle near to 90°. Because the aircraft travelled at well over 200 km/h the time difference between the two sets of plots was not considered to seriously affect the accuracy of locating the birds. If birds were moving fast, subsequent plots showed this.

To determine the accuracy of tracking from the aircraft, tests were made on stationary birds, one of known position, one of unknown position (at that time), and on birds in flight. The flying birds were an adult which was soaring within its "activities area" (see section 5.3.3 below) close to the nest site, and a young bird flying

cross-country. The aircraft was flown in a wide circle about each bird, obtaining bearings from roughly every quarter. None of the birds were seen. Tracking distances varied from about 6,5-36 km. The intersections of the bearings obtained at near to right angles (four per bird) were plotted, but not the intersections of bearings taken from approximately opposite sides (Figure 5.6). The area contained within the four plots was calculated and was taken to represent the degree of precision of aerial tracking, while the distance from the centre of this area to the known (or later known) position of the nest, or the centre of the "activities area" was taken to be a measure of accuracy.

Stationary birds were plotted to within 600 m and 700 m respectively of their actual positions, and the bird soaring in its activities area was plotted to within 1,6 km of the centre of this area (Table 5.2). The reduction in accuracy in the case of the soaring bird might be partly because the bird was not in the same position when each bearing was taken, but probably more because of the varying signal intensity that is received from a circling bird, making it more difficult to match the two antennae exactly. The actual position of the bird flying across country was not known but the apparent precision was fairly low, being within an area of about 16 km^2. Considering that to obtain four bearings takes almost 30 min (about three times longer than is required for two) and that a bird can move a considerable distance in this time, the lack of precision is
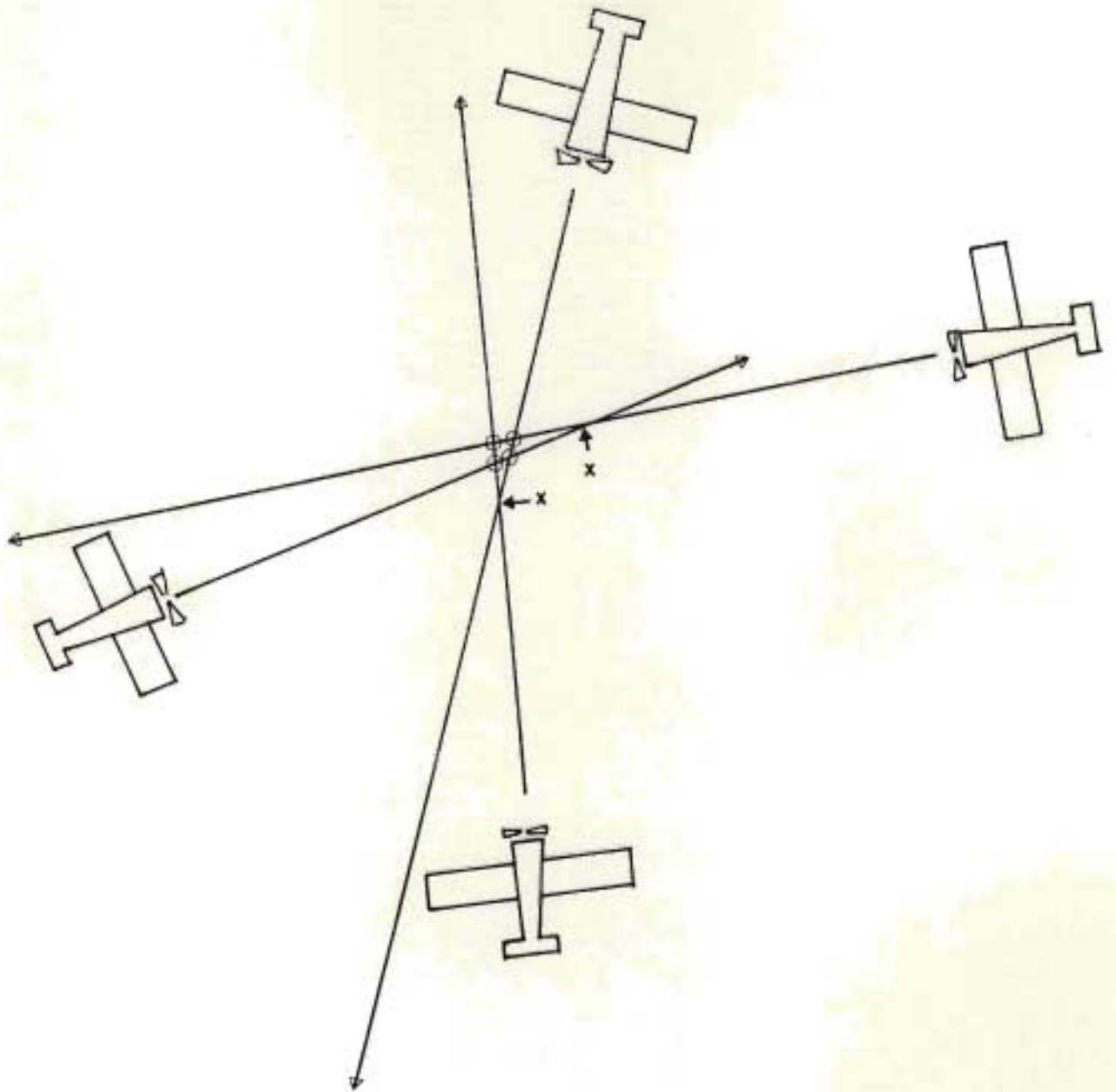
FIGURE 5.6. Method used to locate and plot the position of radiotagged birds during aerial tracking. Intersections of lines obtained from near right-angles were used (o) but not intersections of lines obtained from opposite sides (x).

understandable. In this case, the distance between the intersections of the first two and second two sets of bearings was about 7 km. This distance, rather than reflecting a lack of precision, probably reflects the movement of the bird. Aerial tracking was considered to be sufficiently accurate to augment the ground tracking data, considering the size of the Bearded Vultures' range and the distances they covered each day. Aerial tracking was particularly important for locating young birds, whose movements were unpredictable and whose localities would otherwise have remained unknown for long periods.

Data on the juvenile radiotagged bird (capture no. 17) are given in Chapter 7. Results on the other four radiotagged birds are presented in this Chapter. A total of 3323 localities were plotted for these birds, covering about 707 bird-hours, many of which, however, were tracked concurrently on a total of 44 days.

Radiotelemetry was used to (a) locate nests and roosts, (b) calculate home range sizes during different times of the year, (c) determine the degree of use of different areas within the home ranges and (d) investigate daily movements and foraging patterns.

Four methods of analysis were used to calculate the ranges of Bearded Vultures from the tracking data. The minimum-area method (Mohr 1947) is one of the most commonly used methods for determining home range size (e.g. Marquiss & Newton 1981), in which a basic assumption is that the radiotagged animal will reveal the boundaries of its home

range, a line joining the outermost points forming a convex polygon representing the minimum perimeter of the range. The polygon was formed by choosing the most northerly point, then rotating a perimeter line clockwise until it intersected another point. This new point was then taken as the point of rotation for the perimeter line, and the procedure repeated until the polygon was completed. The area of the polygon was then calculated.

The convex polygon may not always represent the minimum area of a range, however, since it may include unused areas within its boundary. A second method was therefore used, to identify those areas within the range which were not utilized, as well as those areas of intensive use. This method involves the use of grid cells (Siniff & Tester 1965; Voigt & Tinline 1980; Samuel et al. 1985), the size of which were chosen to reflect the error inherent in calculating each fix. In this study, fixes were made at widely varying distances, with different degrees of intersection of triangulation. In addition, because of the large home range sizes, it is necessary to select a manageable number of cells. A grid cell size of 2 x 2 km was adopted as appropriate for the degree of precision obtained from the telemetric data. A count of used cells then became a measure of home range as well as range use. Cells around and between used cells may be influenced in a number of ways (Voigt & Tinline 1980). In this analysis the only influence of other cells used was the "linked cell" method. Where successive

fixes were closely related in time, (defined here as less than 1 h), and bridged one or more cells, cells between the two points were linked in a straight line. Data obtained from this grid cell method were used to plot three-dimensional maps of the home ranges to show areas of concentrated use, using "Plotcall", a computer package consisting of a number of mapping programs. The information (x, y & z axes) was entered on a data file and then gridded. This in turn was transformed into three dimensions. A small smoothing factor (0,01 on a 0-1 scale) was introduced to the program so that sharp peaks and troughs were slightly evened out.

A third method, a "maximum area" range was obtained by drawing a circle about a centre point. While the longest distance between two points is often taken as the diameter of the circle (e.g. Evans & Holdenried 1943; Hayne 1949; Calhoun & Casby 1958), for this analysis the distance between the nest site (representing the centre of activity) and the furthest point was taken as the radius of the circle. This area was assumed to represent the theoretical maximum range of the bird, although within this area large regions may be seldom or never used.

Finally, a fourth method of chronologically linked fixes (Voigt & Tinline 1980) proved to be useful for representing the information obtained from the immature radio-tagged bird, because this bird did not centralize its activities about a fixed point (i.e. a nest), but moved constantly from area to area.

5.3 RESULTS

5.3.1 Flight

Bearded Vultures spend about 77% of the day in foraging-related flight (see Chapters 6 and 8). Only about 3% of flight was found to involve flapping, the rest took various forms of gliding flight. To put this chapter into perspective, the main foraging-related flight modes are summarized (Table 5.3) and some information on flying parameters is given.

Bearded Vultures are capable of a wide range of flying modes, from hovering (or even flying backwards) on the brow of a hill into strong slope lift, to sustained speeds during level flight of at least 116 km/h. The accuracy of timing of diving birds must often be questioned, but conservative estimates for the Bearded Vulture were between 170-230 km/h during fairly short dives (twice while chasing Whitenecked Ravens with food and once when pursued by a Black Eagle; timing was started only once considerable speed had been built up). It is probable that the birds never attained their maximum possible speed over the short distances, and it is estimated that this would be in the order of 300 km/h (Brown 1976a). Cross-country travel and high-level searching were done at a mean speed of about 96 km/h (but the overall speed would be slower if the time spent rising up on thermals was included). Intermediate foraging was normally at about 60-70 km/h. It was not possible to measure the speed of flight during low foraging directly because of

the highly irregular flight path. It was executed, however, at a lower speed than intermediate-height foraging, with the tail usually well spread (which not only decreased stall speed but also increased manoeuvrability) and was probably at much the same speed as flight mode E (Table 5.3), i.e. about 40 km/h.

The rate of flapping flight in Bearded Vultures was found to vary according to their activity (Table 5.4); during undisturbed flight and during play they used a low-frequency wingbeat (about 130 beats/min), which increased to about 155 beats/min when being chased, mobbed or when in pursuit of another bird, and also when flying with shallow wingbeats close to the ground. Both Cape Vultures and Black Eagles used a higher-frequency wingbeat during undisturbed flight than did Bearded Vultures. The flapping flight of immature Bearded Vultures was found on average to be slower in each set of circumstances than that of adult birds, probably because of their larger wing area, but this difference was not significant.

Few measurements of climb rate comparing Bearded Vultures to other species were obtained (Table 5.5), and comparisons were made only with Cape Vultures and Black Eagles. In all cases, Bearded Vultures gained height more quickly, being 5-9% more efficient than Black Eagles (unsexed) and 20-47% more efficient that Cape Vultures. In spiral thermals Bearded Vultures gained height about 20% faster than did Cape Vultures, but on slope lift they were even more efficient at about 40-47% faster than Cape

Vultures.

5.3.2 Home ranges

The average home range size identified for adult window-marked Bearded Vultures, monitored for an average period of 10,8 months (range 7-14 months), and using the minimum area method of calculation was found to be 418 km^2 (range 302-743 km^2). These ranges are considerably smaller than the actual areas covered by the birds, but it can nevertheless be seen (Figure 5.2) that they are totally overlapping, indicating that Bearded Vultures are not territorial in the sense that they do not exclude conspecifics from their foraging ranges, although they do defend a small area immediately about their nest (see section 5.3.3 below).

Three adult birds, two males and one female, were radiotagged and closely monitored for periods of 6, 7 and 8 months respectively (Table 5.6). An average of 998 plots were obtained per bird (range 688-1349). Where data allowed, the sizes of ranges covered were determined when (a) adults were incubating or close-brooding (early nesting period), (b) young were in the nest but not closely attended (late nesting period) and (c) the young vulture had left the nest and when adult birds wandered widely. The three methods used to obtain a measure of home range size in adult birds (i.e. radius to furthest point, minimum-area method and grid-cell method) were chosen not only because they have been widely used in other studies and therefore allow comparisons, but,

more importantly, because the radius method provides an indication of the maximum possible area over which the bird would move, the minimum-area method is probably a close representation of the actual area used during the study period and the grid-cell method provides a means of showing the actual areas in which the bird was recorded, thus identifying areas of concentrated use within the overall home range.

To evaluate the degree of completeness of the radiotracking data relative to the actual ranges of the birds, after each 50 locality plots the area enclosed in the polygon formed by using the minimum-area method was plotted (Figure 5.7). It was assumed that once the curve flattened off, *i.e*. no increase in home-range size was found despite continued tracking, that the size of the bird's range for that particular period had been reasonably identified. Data on home range sizes for the three radiotagged birds during the three periods and using the different methods are summarized in Table 5.7.

Calculations on home-range sizes were found to differ considerably depending on the method used to calculate them. The grid-cell method, defining the area in which birds were actually located, would be completely accurate only with continuous tracking over the entire study period. This was not possible in this study, and would ideally require widely distributed automatic tracking stations to cover all movements, or satellite tracking. However, the minimum-area
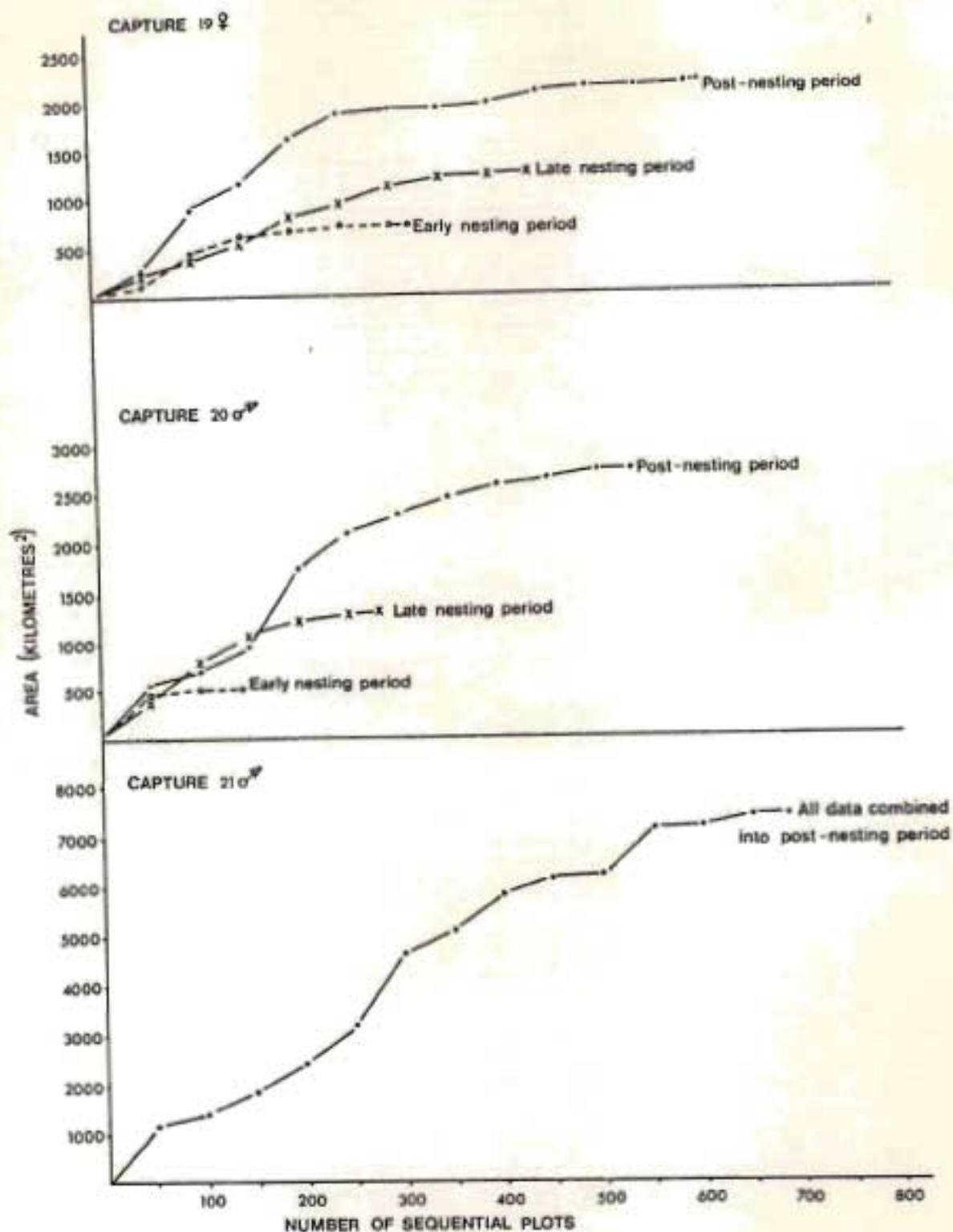
FIGURE 5.7. Range sizes, after every 50 consecutive plots
and using the minimum area methods, for three
adult radiotagged Bearded Vultures, during three
different periods.

method provided a good approximation of the area used by the birds and is adopted here as the most useful and practical method. The use of the radius to the furthest point from the nest to determine the area used by a bird is clearly an overestimation of range size, but because the habitat is fairly uniform and birds are not limited by constraints of territoriality and because they can fly in all directions, it was taken to be the maximum possible area over which they might forage, and possibly the area that would be covered over a long period of time, perhaps the life of a pair. Pairs situated on the edge of the species' distribution, however, do not always nest near the centre of the home range; capture no. 10 (bird D in Figure 5.2) ranged to the west of its nest into the mountains, while movements to the east over less mountainous terrain were very limited in distance and occurrence. The average ratio of range sizes obtained for Bearded Vultures using the three different methods (minimum-area method:grid-cell method:radius circle method) was approximately 1:0,5:2,4.

It is apparent (Table 5.7) that, during the early nesting period (when a parent bird is in close attendance at the nest), home ranges are at their smallest at about 600 km^2. This is similar to the areas obtained from the window-marked birds (300-740 km^2), suggesting that the window-marking method identified only the core foraging area about the nest. Because bird capture no. 21 was nesting so far away from the other two radio-tagged adults details of this bird's movements during the first two periods were

inadequately covered and are not included in the results.

Once a parent bird was no longer in fulltime attendance
at the nest (late nesting period) the time available for
foraging increased, hence birds foraged further from the
nest and home ranges more than doubled in size to about 1300
km^2. Birds were nevertheless obliged to return to the nest
to provide for their young. Once the nestling had left the
nest this constraint no longer applied, and the birds were
again able to expand their foraging range (often with the
young bird accompanying them). The mean post-nesting (not
post-breeding, as the young bird was still dependent on its
parents) home ranges of birds 19 and 20 was 2441 km^2 while
that of bird 21 was considerably larger at 7468 km^2, an
overall mean of 4116 km^2. Despite the very much larger
overall home range of bird capture no. 21, the actual area
utilized (grid-cell method) was not much larger than that of
the other two adult birds. It travelled considerably further
from its nest (75 km), however, than the other two
individuals (36 & 47 km respectively). Based on data from
birds 19 and 20, a theoretical annual pattern of home range
size is shown in Figure 5.8.

5.3.3 Range use

All three adult radiotagged Bearded Vultures had their
nests on the Natal Drakensberg side of the escarpment, and
all were in Forestry or Natal Parks Board conservation
areas. Two (capture nos. 19 & 20) bred on the High Berg near
Giant's Castle while one (capture no. 21) bred further
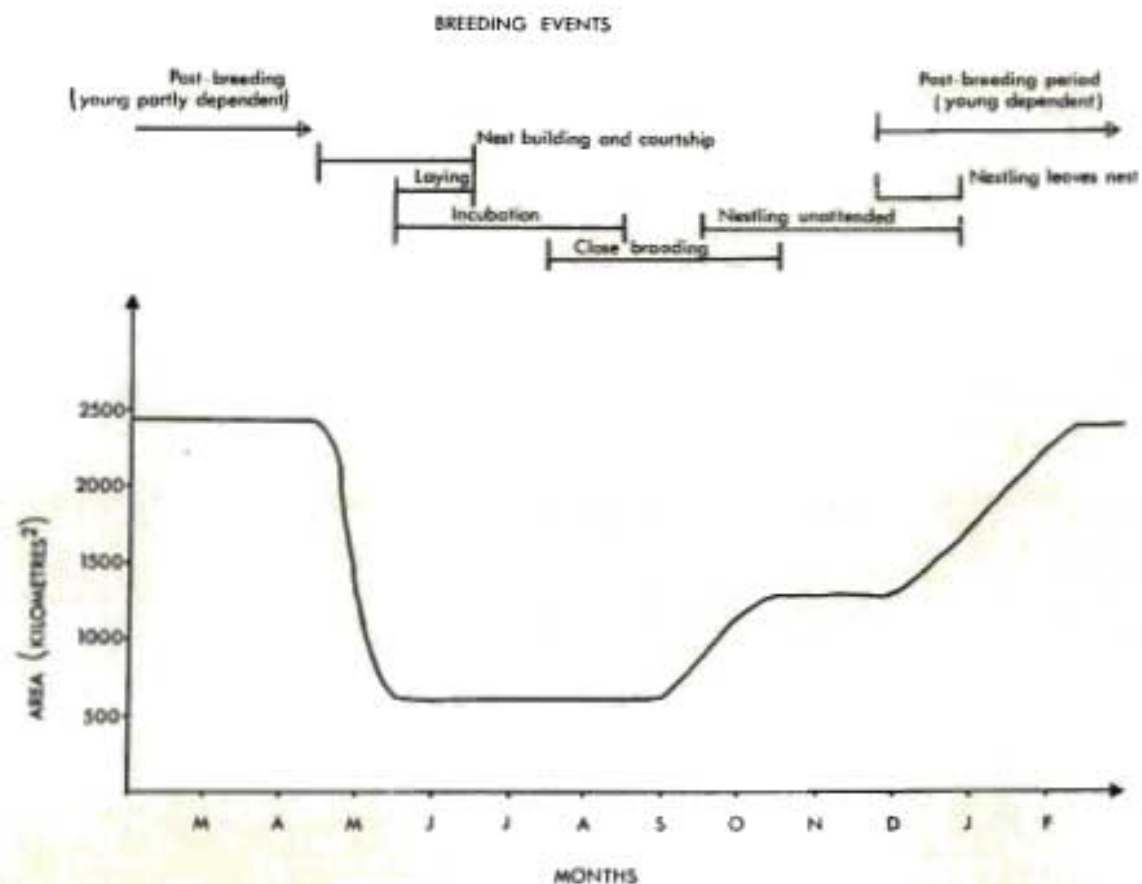
FIGURE 5.8. Theoretical home-range size during different seasons of the year for a pair of Bearded Vultures breeding in the Natal Drakensberg, based on data obtained from radiotagged birds.

south near Bushman's Nek in the cliffs of the Little Berg.

Typical distribution patterns for the three different periods, as obtained from radiotagged bird 19, are shown in Figures 5.9-5.11. Birds on nest duty were not included in the data shown in these figures, and high peaks in the position of the nest (map A in each case) therefore indicate the large amount of time that off-duty birds spent near the nest, amounting to 25% of all occurrences during the early nesting stage, 15% during the late nesting stage and 5,5% during the post-nesting stage. This clearly indicates that, as the breeding season progressed, off-duty birds spent less and less time in the nesting area. During the early stages of the breeding season the off-duty birds spent on average 75% of their time foraging within the borders of the Forestry and Natal Parks Board conservation areas, 20% foraging in Lesotho and only about 2% over farmlands (Table 5.8). By the late nesting period parent birds spent 9% of their foraging time over farmlands and by the post-nesting stage, about 25% of their foraging was over farmlands.

The montane, subalpine and alpine belts of the Drakensberg and Maluti mountains are very similar in general vegetation structure, consisting mainly of open, tussock grassland and at high altitudes (above 2900 m), low woody species interspersed with alpine grasslands (Killick 1963). Throughout the Bearded Vulture's range in southern Africa the habitat is therefore mainly open, and only in the more protected valleys and hillsides do small patches of forest
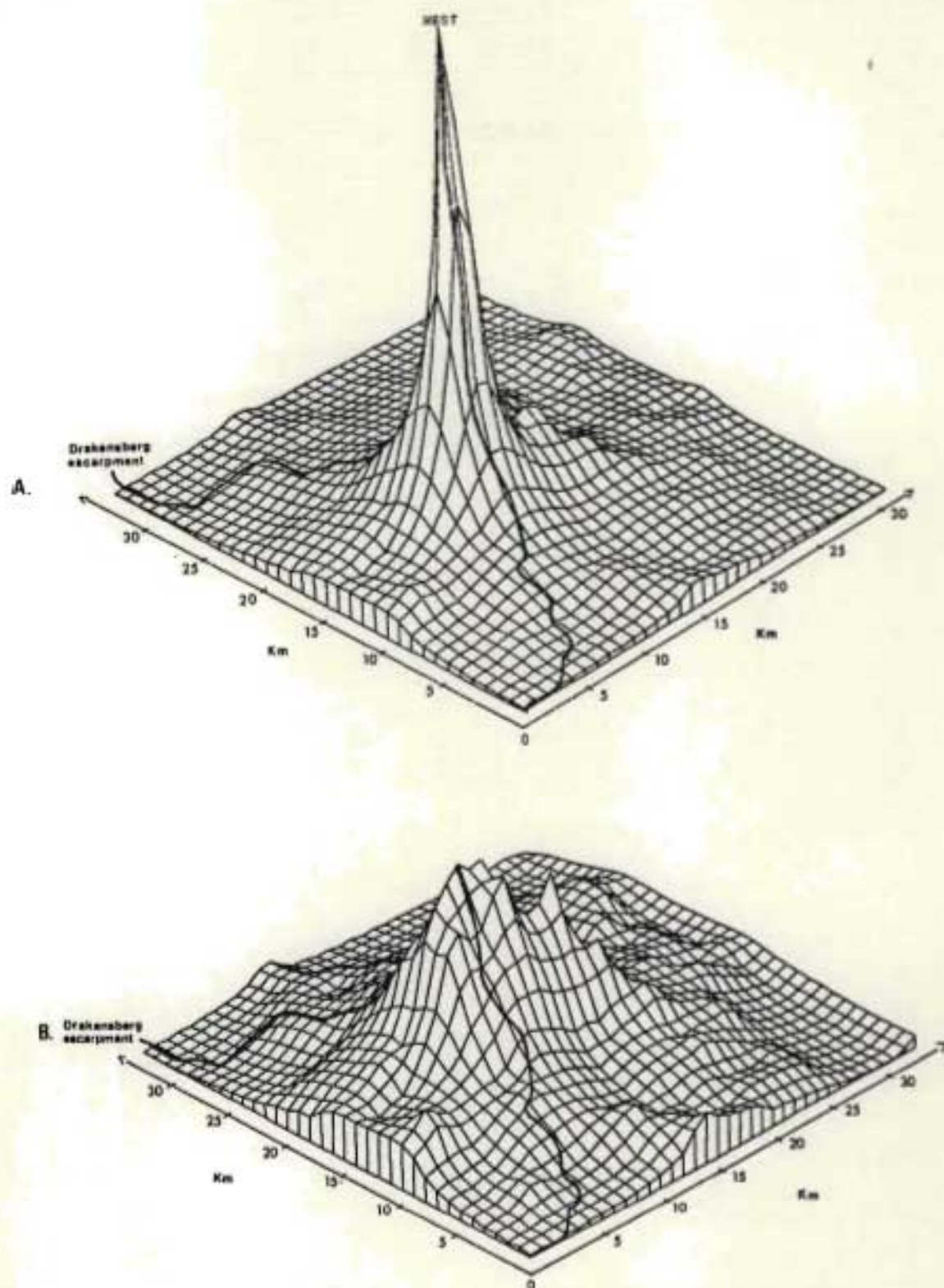
FIGURE 5.9. Home range of a radiotagged female Bearded Vulture (capture no. 19) during the early nesting period. In A. the square with the nest was included in the analysis (but data were not included when the bird was actually on the nest) while in B. this square was excluded from the analysis.
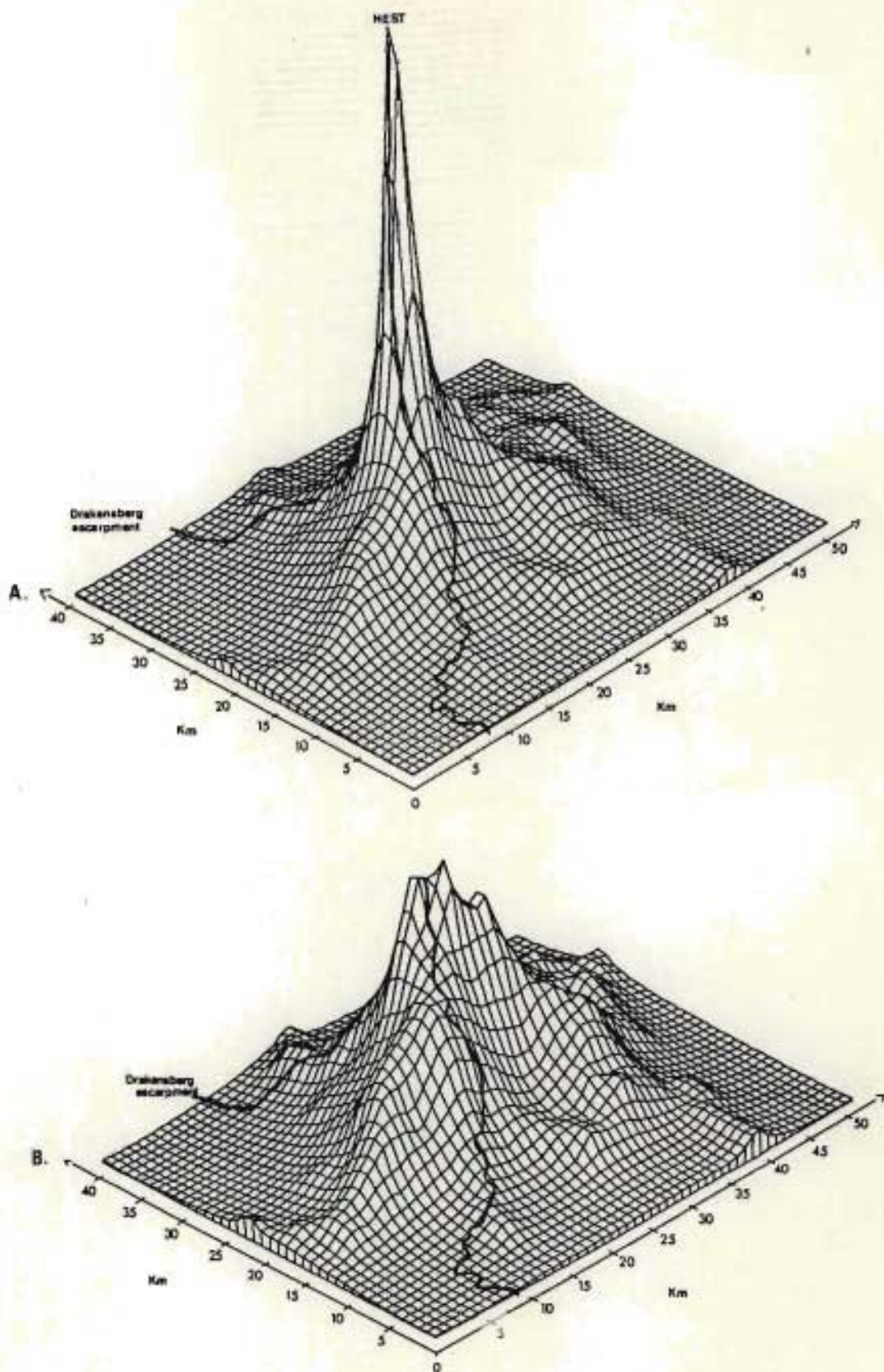
FIGURE 5.10. Home range of radiotagged bird no. 19 during the late nesting period. Maps A. and B. are as for Figure 5.9.

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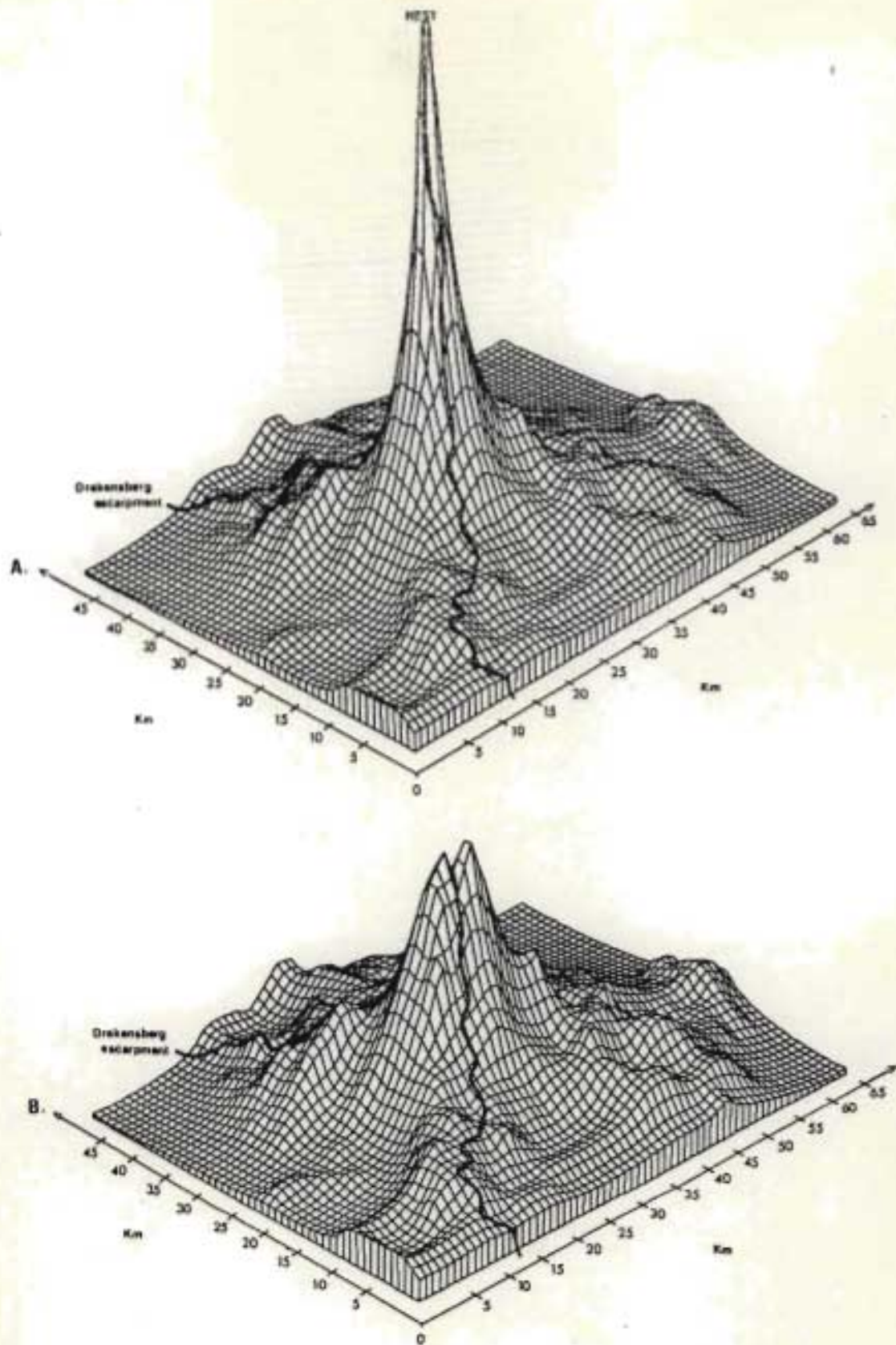
FIGURE 5.11. Home range of radiotagged bird no. 19 during the post-nesting period. Maps A. and B. are as for Figure 5.9.

and woody scrub occur. No clear-cut vegetation types can therefore be identified over which Bearded Vultures may be expected to forage more often than others. At high altitudes the carrying capacity of the environment may be expected to be lower than at lower altitudes, species richness and abundance being related to latitude, altitude and habitat complexity (Pianka 1966; Nel 1975; Rowe-Rowe & Meester 1982), but this effect is probably obscured by the pastoral practices in Lesotho, where grazing lands are heavily overstocked (Ambrose 1976; Jilbert 1979). Although the radio-tagged birds spent more time foraging over Natal than over Lesotho, their ranges over Natal were larger than those over Lesotho, possibly because less energy is needed to glide out over Natal, 1000 m below their nests, than to rise up to Lesotho. Nevertheless, when the proportion of time spent foraging in each area relative to the proportion of each area available within the home range was analysed for birds 19 & 20 (Chi-squared test), it was clear that no preference for one or other area was shown (p = 0,7 and 0,8 respectively). Physical features in the home ranges of the two birds were of far greater importance. The Drakensberg escarpment was used about three times more often than would be expected from random distribution (p < 0,001), mainly for fast cross-country travel. The birds made use of the good lift conditions which prevail.

The relative coarseness of the grid plots (2 x 2 km) does not allow for assessment of preferences of use with regard to fine topographic features. Large ridges and

valleys could be examined, however, and for radiotagged birds 19 & 20 during all seasons examined, ridges were used for foraging three times more frequently than were valleys (p < 0,001). In addition, birds were located in the areas of their nests and the feeding sites more often than would be expected from random occurrence (p < 0,001). In the case of the feeding sites this indicates that birds were at least attracted to these areas, even though they might not always be making good use of the food provided (see Chapter 10).

The frequency of location of radio-tagged birds at different distances from the nest varied in accordance with the range size (Table 5.9). For example, for birds 19 & 20, 75% of location plots were contained within a radius of about 10,5 km of the nest during the early nesting period, within 12 km during the late nesting period and within 20 km during the post-nesting period. During the early nesting period both female and male radiotagged birds 19 and 20 foraged within a radius of about 16 km of their nests (Figure 5.12). A similar situation was found during the late nesting period, except that a few forays into more distant areas were made. Once the parent birds were no longer committed to return at regular intervals to the nest, foraging extended regularly up to about 28 km from the nest, with a distinct peak between 8 and 22 km from the nest. When considering that for each flight to a distant area, birds have to overfly areas around the nest on the way out and back again, many of the plots near the nest probably do not
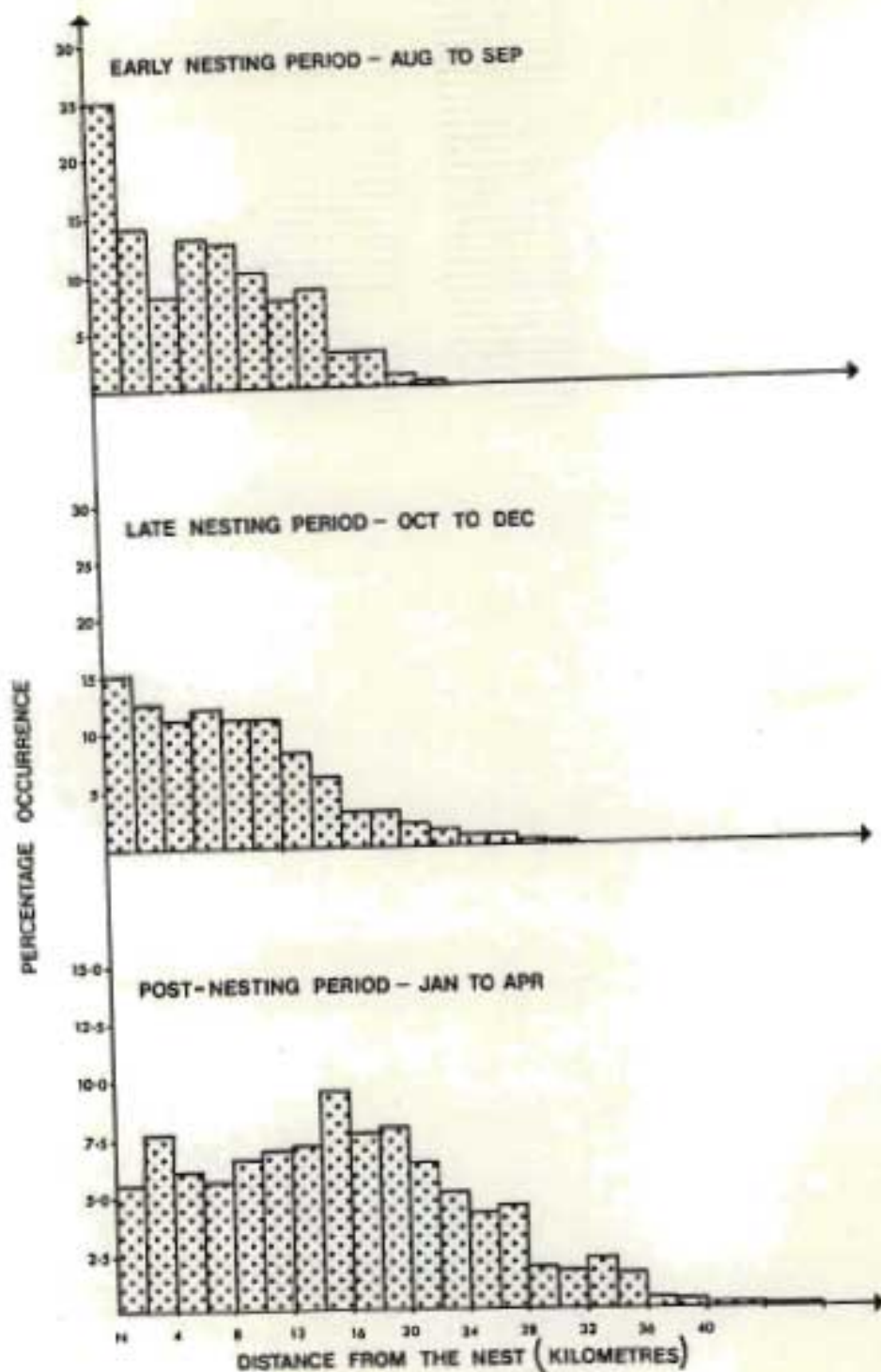
FIGURE 5.12. Mean percentage occurrence of two radiotagged Bearded Vultures (captures 19 & 20) at different distances from their nests during three periods of the year.

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reflect birds foraging but rather birds in transit. If cross-country travel could be separated from foraging, the trend suggested above, where the post-nesting birds concentrate their foraging at some distance from the nest, would probably be more greatly emphasised.

Bird 21 gave a somewhat different pattern (Figure 5.13). This bird foraged consistently at some distance from the nest and no clear pattern was evident, other than that most foraging (55%) took place within 30 km of its nest, thereafter progressively declining, except for between 50-60 km from its nest, this interval being the distance to the two feeding stations in Giant's Castle Game Reserve, where the bird was periodically located.

Based on the resightings of marked birds, radiotracking data and behaviour patterns, the home ranges of adult Bearded Vultures could be divided into four different regions (Figure 5.14) as follows.

1. The territory, defined as that area actively defended against intruding conspecifics and some other species. This area circumscribed the nest site at a variable distance, depending on the individual and species intruding, but had a maximum radius of about 500 m (Table 5.10). Immature birds and neighbouring adult Bearded Vultures were allowed to approach to within 50 m or less, while Bearded Vultures from more distant regions were sometimes attacked at up to 500 m from the nest. The behaviour of the approaching bird was also important; birds flying straight past at high speed, obviously involved in travelling across country, even if
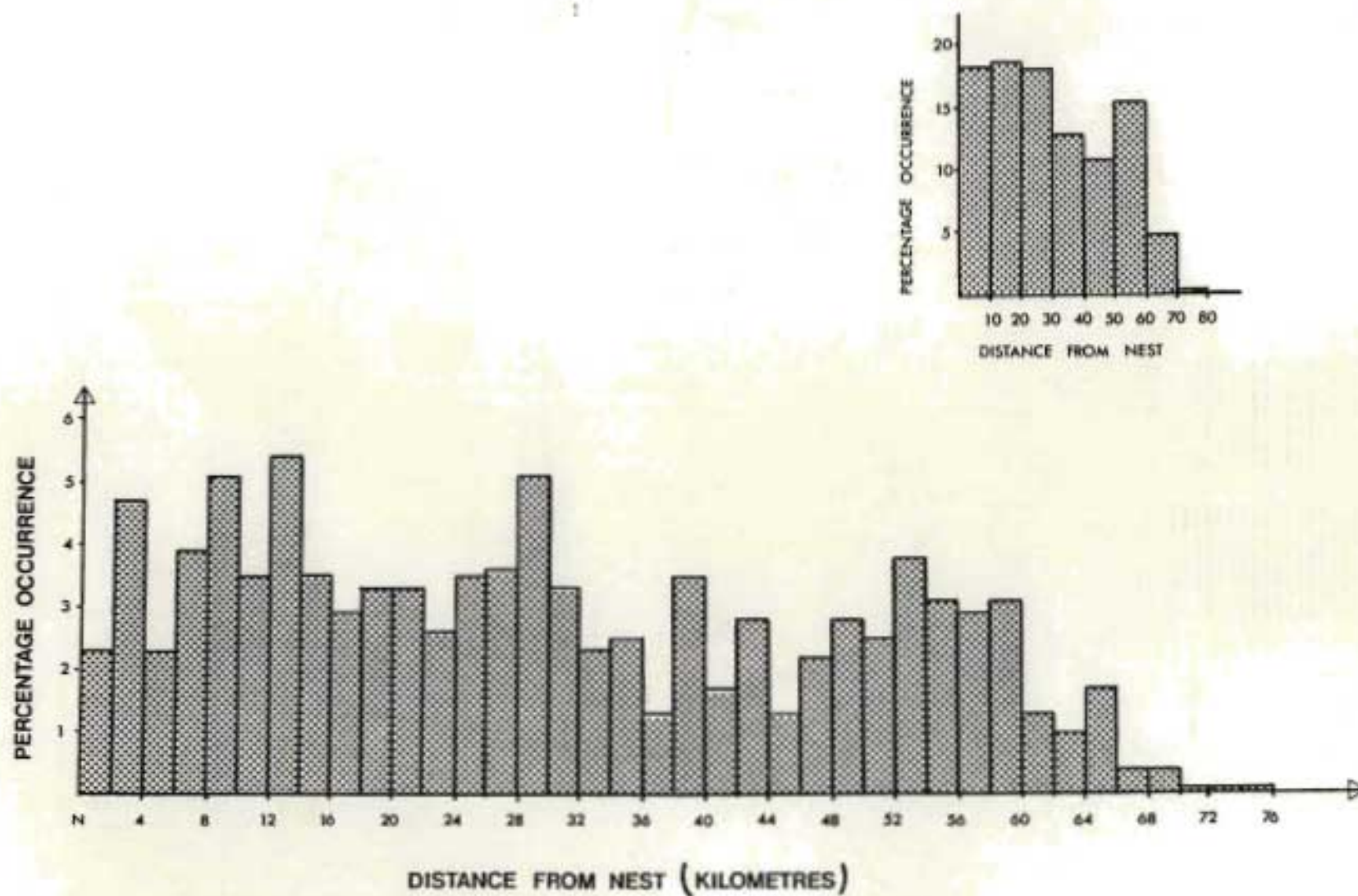
FIGURE 5.13. Percentage occurrence of radiotagged Bearded Vulture no. 21, at different distances from its nest, tracked for a period of 6 months.
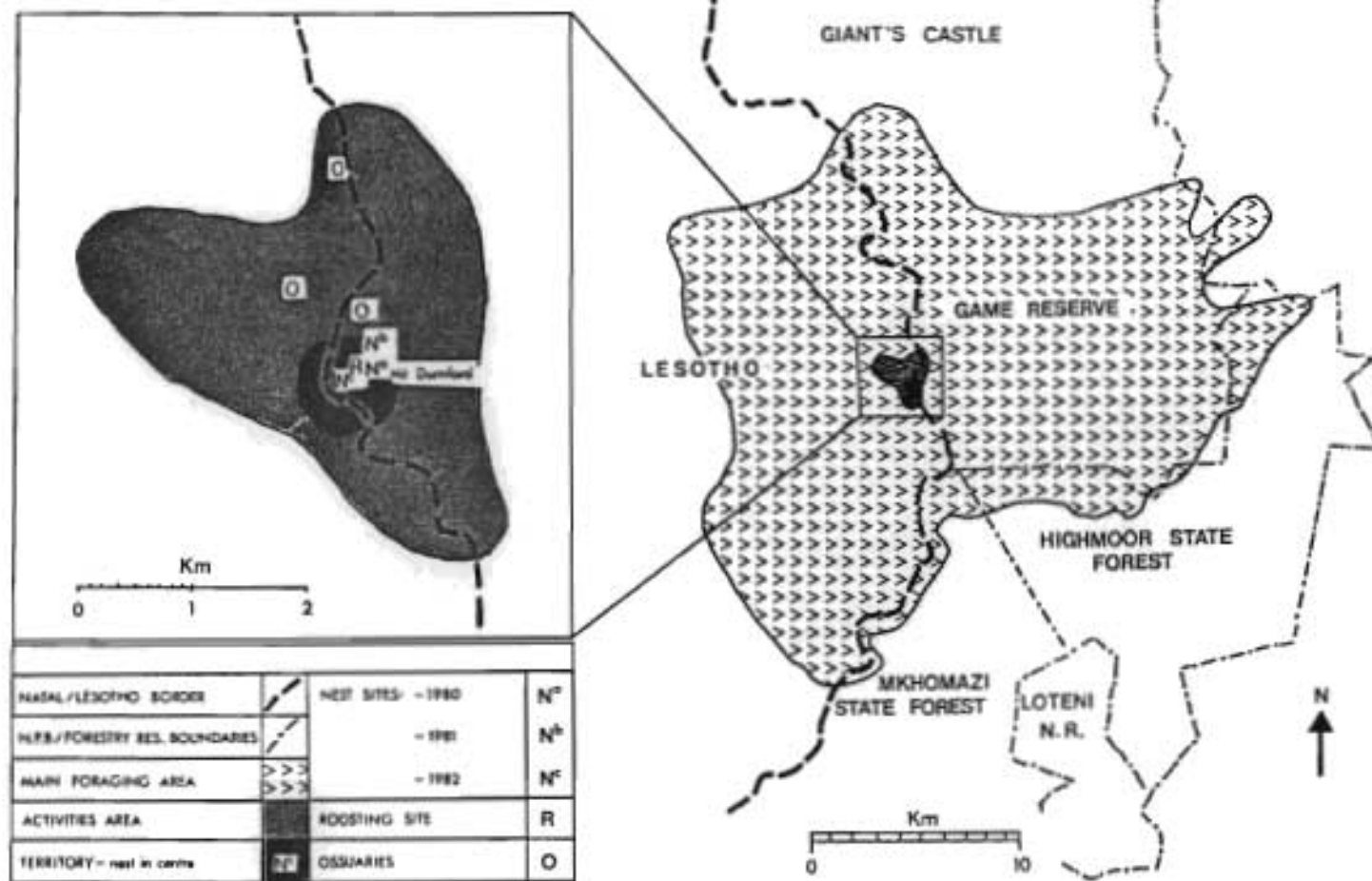
FIGURE 5.14. Home ranges of adult Bearded Vultures can be divided into four different regions, 1. the territory, 2. the activities area, 3. the main foraging area and 4. the home range.

only 100 m above an active nest, were seldom challenged. Birds circling near another bird's nest were sometimes aggressively attacked. If the off-duty bird was present it would drive the invading one away, but in the absence of a mate, the nesting bird would leave the nest and attack the intruder. Species other than Bearded Vultures were also subject to territorial aggression. Black Eagles were aggressively challenged and attacks were aimed at birds at up to 500 m from the nest. Other species were tolerated considerably closer, e.g. Cape Vultures were rarely attacked, even at 30 m from a nest, while small raptors and nonraptorial birds, e.g. Rock Kestrels Falco tinnunculus, Gymnogene Polyboroides typus, Bald Ibis Geronticus calvus, and storks, were never attacked.

2. The activities area, consisting of an area about the nest in which a pair of Bearded Vultures spent most of their non-foraging time. This area contained the active nest, alternate nests, adjacent roost sites, the main bone dropping areas (ossuaries) and usually one or more areas that provided good soaring conditions, such as part of an escarpment, large slope or gully. Depending on the topography, this area was usually 3-7 km^2 (mean = 4,6 km^2) (Table 5.11). Only the territory itself within the activities area was defended; for the rest, birds often gathered over ossuaries or areas providing good lift, and nonaggressive interactions (interpreted as "play") regularly took place, with up to seven birds taking part. Birds spent considerable time soaring about their activities area (9% of

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the day, see Chapter 8), particularly in the afternoons, and the high utilization of this area is also apparent from the radiotracking data (Figures 5.9-5.11, maps A).

3. The main foraging area, being that area in which mainly low and intermediate-height foraging usually occurred. Breeding adults were generally restricted to this area during the early nesting period. During the late nesting period and the post-nesting period radiotagged birds 19 & 20 spent about 95% and 76% of their time respectively within this area. The sizes and shapes of the main foraging areas varied between pairs, but they were usually fairly circular about the nest (except where nests were on the edge of the species' distribution) and between 300-700 km^2 in size. These main foraging areas were the approximate areas identified for birds that were resighted on ring and window markings.

4. The home range, incorporating the entire area over which a pair of adult birds ranged. The maximum area recorded during this study (using the minimum area method) was 7468 km^2, but birds 19 and 20 had ranges of under 3000 km^2, and this is probably a more representative home range size, birds foraging up to about 45 km from their nests.

5.3.4 Daily movements

The detailed foraging pattern of radiotagged bird 19 was obtained during a sortie in the late nesting period by continuous tracking (Figure 5.15). The bird was in sight for about 30% of the time by one of the two trackers. The

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Giant's Castle
Game Reserve

LESOTHO

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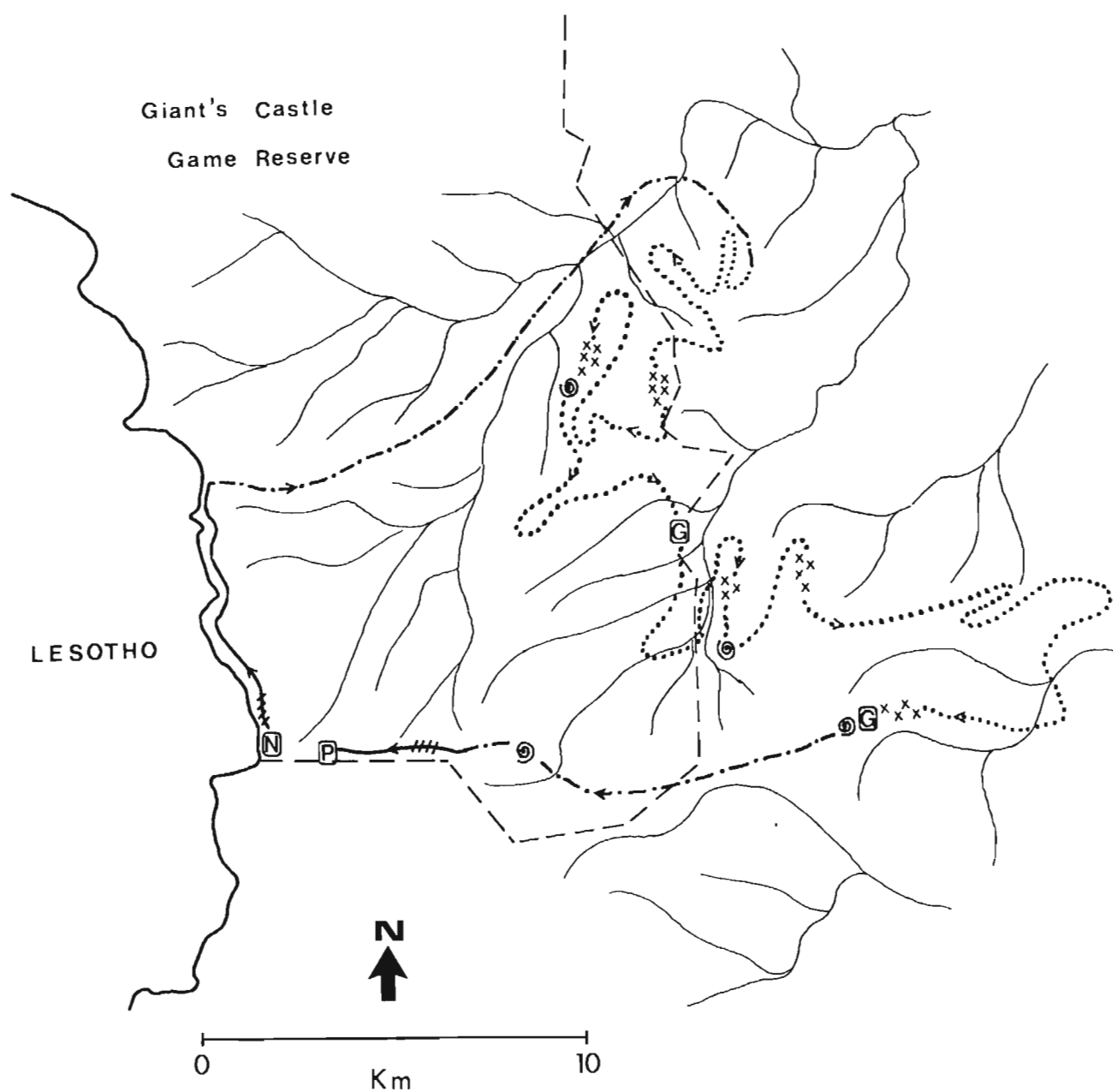
/	Natal–Lesotho border	⚡	Escarpment soaring
/	Park boundary	↗	Escarpment gliding
⋎	Rivers & streams	/	High searching / Cross-country
Ⓝ	Nest site	:	Medium–height searching
Ⓟ	Perched on cliff	xxx	Low searching
Ⓖ	On ground	☉	Thermalling

FIGURE 5.15. Detailed foraging pattern of an adult radiotagged Bearded Vulture, obtained by continuous tracking over 2,8 h in the Natal Drakensberg.

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trackers were close to the bird throughout the tracking period and the information recorded on this sortie was the most precise that was obtained. On other occasions when I had attempted to obtain these details birds foraged either totally or partly out of the range being covered by the two trackers.

The bird covered an estimated 149 km in 2,8 h giving a mean speed of 53 km/h. The speed varied considerably at different stages, however, depending on the bird's activity and ranged from stationary to 96 km/h. Because of the different speeds involved, only about 19% of the distance was covered by low foraging despite this taking up 30% of the time. The converse situation applied to the other two foraging methods. About 10,6% of time was spent exclusively in obtaining lift, about half in thermals and half against the escarpment in slope lift; the bird was of course constantly obtaining lift while foraging, this being slope lift along hillsides and ridges.

Apart from this detailed tracking exercise, birds were usually tracked at 10-min intervals. By joining the 10-min interval points in Figure 5.15 and measuring the distance travelled a figure of 94 km was obtained, about 63% of the actual distance covered. This is clearly a result of the very irregular foraging pattern of Bearded Vultures during (a) intermediate-height foraging, during which they are inclined to follow contour lines along and around hills and ridges, and (b) low foraging when they quarter (zig-zag) across hillsides. During high foraging and escarpment-

gliding flight paths are much more direct, as has been found with other high-foraging species such as the _Gyps_ vultures (Pennycuick 1972, 1973, 1983; Boshoff _et al_. 1984).

Data on 37 complete foraging sorties are presented in Table 5.12, covering the three periods. Because these data were obtained at 10-min intervals, distances travelled were multiplied by a correction factor of 1,582 as obtained from the detailed foraging sortie above. This assumes that the same proportion of time was spent in each of the activities on each sortie, and that similar types of flight paths were flown. Apart from obvious variations due to topography, when birds are foraging further from the nest they are likely to spend more time in fast, high-level flight, and this is suggested in the mean corrected speeds, with foraging during the post-nesting period being at almost 10 km/h faster on average than foraging during the early nesting period.

Despite these complications, some trends are clearly apparent. Foraging sorties varied from 16 min to 5 h, but were shortest during the early nesting period and longest during the post-nesting period, although these differences were not statistically significant because of the high degree of variance in the foraging times. Corrected distances covered varied from 11-318 km (uncorrected were 7-201 km) and, as would be expected, were on average shortest during the early nesting period (84 km) and longest during the post-nesting period (140 km). As birds might go out foraging two or more times per day, and spend about 77% of

the day (more than 9 h) in foraging-related flight, and assuming that their mean speed of flight was about 48 km/h, it is not unlikely that they were covering up to about 430 km per day, excluding non-foraging flight. While these distances may appear excessively great it should be remembered that a visit to the feeding station in Giant's Castle Game Reserve by radio-tagged bird 21 from its nest near Bushman's Nek, following the Drakensberg escarpment (which is the fastest and least energy-consuming route), involves a round trip of 182 km. A monitored one-way trip took the bird only 55 min.

The final point which should be considered under daily movements is how subsequent foraging sorties relate spatially to preceding ones. It is reasonable to expect that, if a good source of food is located, birds will return to that area in preference to exploring new areas. Good food sources do not last longer than a few days, however, after which new sources must be located. The main foraging sorties of radiotagged birds 19 & 20 were therefore monitored during two periods of five consecutive days during the post-nesting period (see example of five consecutive sorties by bird 19, Figure 5.16.a). While absolute detail was not obtained on all sorties, enough information was obtained to plot the general foraging areas (Figure 5.16.b). From this the degree of overlap of area covered during a particular sortie, with that of sorties on previous days, was calculated and the means of the daily overlap (i.e. two birds tracked for two periods of five days each) were determined (Table 5.13).
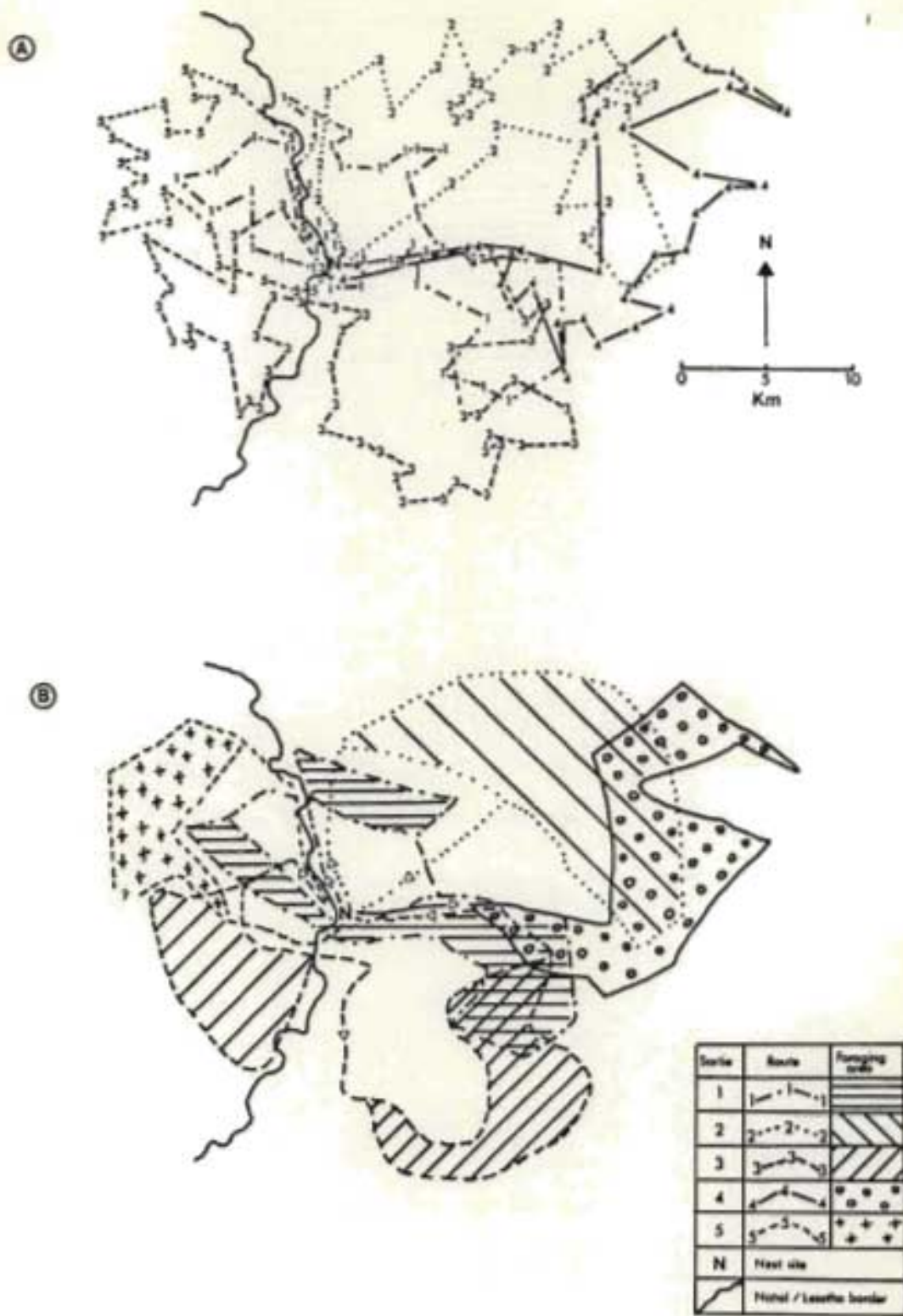
FIGURE 5.16. An example of five consecutive foraging sorties
(A) and the approximate areas searched by the
radiotagged Bearded Vultures (B).

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The foraging area covered on any one day was found to overlap very little (mean = 10%) with the area covered the previous day. The extent of overlap varied from 0-61%. It is probable that a good food supply in the area of the previous day's foraging caused the bird to return to the same area the following day, accounting for the exceptionally high overlap of 61%. As would be expected, the overlap of foraging range increased with increasing foraging sorties. By the fifth day the overlap with one or more sorties from the previous four days was 58%, but overlap with any one particular sortie was less than 30%.

5.3.5 Dispersal of young birds

Once into their second year immature birds wander widely. This fact was apparent from the relatively large number of young birds captured in the Giant's Castle Game Reserve and window-marked (70% of birds captured before radiotagging) compared to their very low resighting rate (average of 2,5 sightings per bird compared to 48 sightings per adult). No young bird was resighted more than four times and no information was therefore obtained on their pattern of movement. An immature bird aged about 22 months at time of capture was therefore radiotagged and its movements were monitored from the ground and from an aircraft over 9 months on a total of 23 days; 329 positional plots were obtained. This bird was considerably more difficult to track than the adult birds because it did not return to a particular site and its locality was therefore unpredictable. The use of

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the aircraft was essential in locating the position of the
bird, and this was then followed up by ground tracking.

The radiotagged immature bird wandered widely,
remaining in an area for periods ranging from two days to
three months (mean occupation time for six areas over 10
months was about 5 weeks) then moving to another area
(Figure 5.17). The movements were unpredictable, and because
of the inaccessibility of some of the areas, few positional
plots were obtained in these regions. These ranges are
therefore not good reflections of the sizes of the areas
occupied but rather reflect the wandering nature of the
bird, a characteristic also suggested by the few times the
roost sites were used. The bird moved an average of 31 km
(range 22-38 km) from the centre of one area to the centre
of the next, and the three areas occupied for which
reasonable data were obtained (areas I, III & V) were on
average 608 km^2 in size (range 511-785 km^2).

5.4 DISCUSSION

It is apparent from the data presented in Figure 5.7
that the larger the home range (both belonging to one
individual at different periods of the year, and between
individuals), the longer it took to establish its limits.
Assuming that the figures obtained for the respective range
sizes were the actual total ranges of the birds during
those periods, then to obtain 95% of these ranges for
birds 19 & 20 took about 100-250 plots during the early
nesting period, 250-350 plots during the late nesting period

Range	
I	June – August
II	August : 1+ week
III	August – October : 9+ weeks
IV	November – 2 days
V	November – February – 13+ weeks
VI	March – 2+days
/	Natal / Lesotho border
▲	Capture site
⊕	Some roost sites and number of times used

MOKHOTLONG ●

N

0   10   30
Km
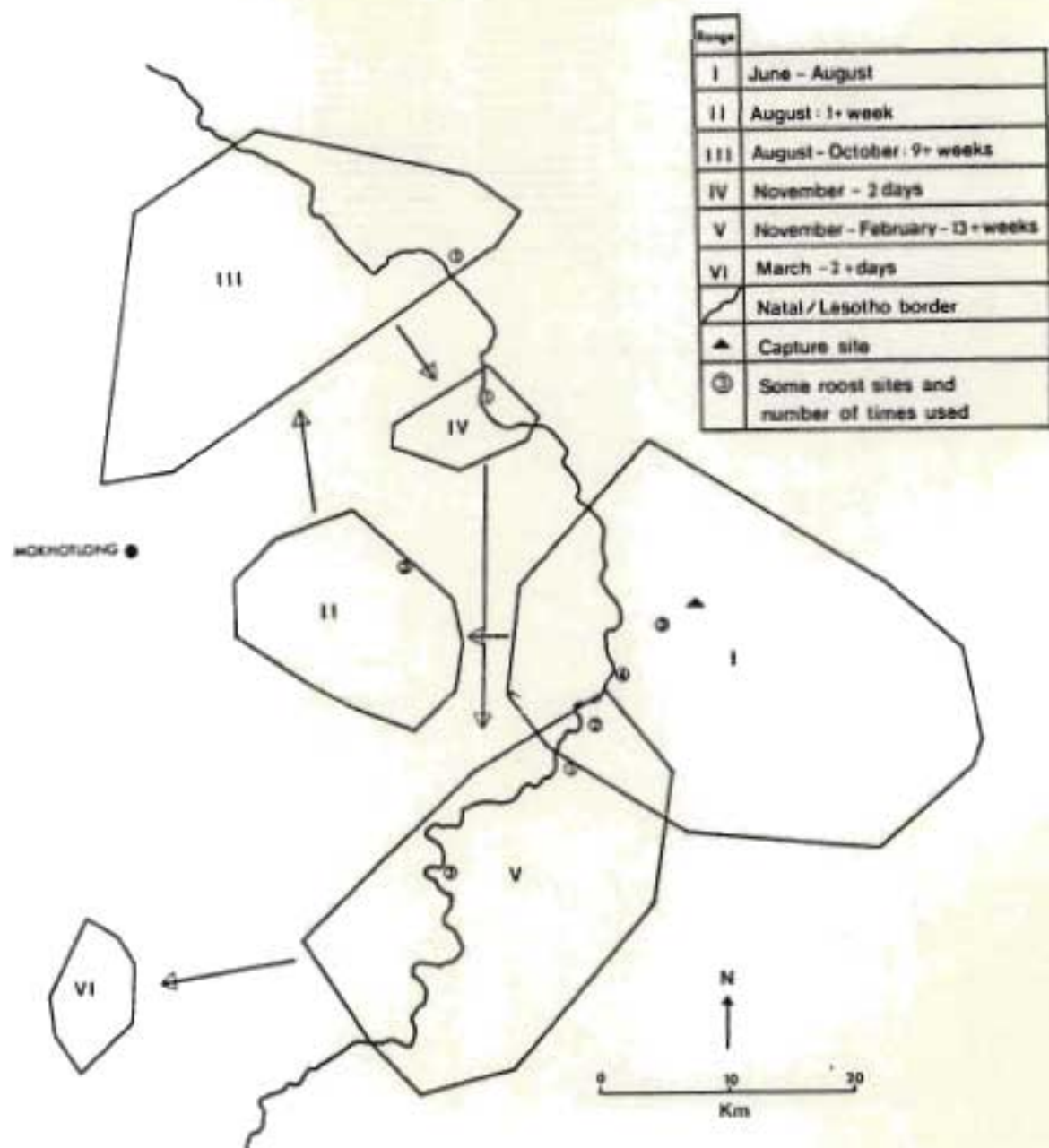
FIGURE 5.17. The movements of a radiotagged immature Bearded Vulture in the Drakensberg, monitored over a period of 10 months.

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and 450 plots (85 h of tracking over 14 days) during the post-nesting period. Bird 21, with its considerably larger post-nesting range, required 600 plots and 160 h of tracking over 26 days. This trend is supported by other studies, e.g. for European Sparrowhawks Accipiter nisus with ranges up to about 35 km², the areas used by the birds could be determined from about 20 locality plots on 4-7 days of tracking (Marquiss & Newton 1981).

5.4.1 Territoriality

The foraging ranges of Bearded Vultures have often been described as "territories" (e.g. Brown & Amadon 1968; Cramp & Simmons 1980; Steyn 1982), suggesting an exclusive right by the resident pair to a particular foraging range which is actively defended against conspecifics. This study has clearly shown that foraging ranges overlap extensively. Taking an average circular home range as extending up to about 40 km from the nest and using the mean inter-pair nesting distances for different regions given in Chapter 9, it is theoretically possible for about 50 pairs of Bearded Vultures to forage over the Giant's Castle Game Reserve and, in addition, perhaps as many young birds. The reasons why Bearded Vultures maintain the nesting dispersion pattern that they do, but do not defend a foraging territory, are discussed in some detail in Chapter 6, where it is suggested to be related to the erratic availability of their food. From a conservation point of view, these overlapping foraging ranges make the species highly vulnerable to

persecution and the irresponsible use of poisons.

5.4.2 Home range size

The sizes of home ranges in Bearded Vultures (and many other large raptors) are often calculated from the inter-pair nesting density (e.g. Brown et al. 1982; Steyn 1982). This interpretation of home-range size is meaningless in all but the most highly territorial species, and even in these there are differences from area to area, e.g. in the Matobo (formerly the Matopos) of Zimbabwe, Black Eagles were found to maintain exclusive ranges at ground level, and in the fairly uniform habitat of this area inter-pair nesting distances were a fairly accurate reflection of territory size (Gargett 1975). By contrast, in the Drakensberg, the habitat suitable for their main food source, the Rock Hyrax, is patchy and limited to scree slopes, gullies and river courses with boulders, with wide expanses of grassy hillsides and ridges between these areas. In these less suitable areas, Black Eagles were found to overlap extensively, and adult birds from three different pairs were captured at one site within 2 km of an active nest, despite the fact that these birds forage up to 9 km from their nest (pers. obs.).

The use of inter-pair nesting distances to calculate range size led Steyn (1982) to state about the Bearded Vulture that "the size of the 'territory' (= home range) does not appear to be particularly large". In the Pyrenees home ranges were estimated to be about 300 km^2 (Terrasse et

al. 1960-1961) and 160 km^2, spread over two valleys and an intersecting mountain ridge (Suetens & van Groenendael 1973). In Ethiopia, ranges of 12,5 km^2 were estimated based on inter-pair nesting distances (3,5 km) while in Lesotho ranges of 625 km^2 are given (Brown et al. 1982). These range sizes were usually estimated during the breeding season and are generally similar to those obtained in this study when resightings of marked birds were plotted, and are probably inaccurate for the same reasons. It is probable that many home-range studies based on resightings of marked birds (as opposed to continuous observations on target individuals) are equally inaccurate. For example, home ranges obtained for Martial and Tawny Eagles Aquila rapax using radiotagged birds in South West Africa/Namibia (C.J.B. unpublished data) were on average 26 and 74 times larger respectively than ranges obtained from window-marked birds of these species in the Kruger National Park (Snelling 1970). Habitat and food availability undoubtedly influence the amount of space which a pair have to cover to obtain their prey, but I do not believe that, in a species the size of a Tawny Eagle, home-range size can vary in the respective habitats as much as from 27 to 2018 km^2. I would therefore contend that the resighting method must be inaccurate for wide-ranging species where observers are few, as was found in this study.

5.4.3 Range use

From Figures 5.9-5.11 on range use it is clear that the nest site forms the centre of the range about which

activities revolve, during both the nesting and post-nesting periods. Birds forage outwards from this point in a fairly uniform fashion and foraging efforts were not concentrated in the long term in particular habitats. Food, though patchily distributed, was therefore probably equally likely to be found in any area, though concentrated foraging in one area in the short term could mean that this area subsequently has less food than an adjacent area. The energetics involved in foraging, however, appear to be of greater long-term importance in dictating utilization of an area. Areas where slope lift was best available to facilitate fast and low-cost gliding, namely along ridges and escarpments, were more heavily utilized than any other areas.

The size of the foraging range changed at different times of the year. Ranges were smallest during the nesting period. This is probably a function of the amount of foraging time available; each bird of a breeding pair had about half the normal foraging time in which to find food. The end of the early nesting period was probably the time of year when parent birds had greatest difficulty in meeting their food requirements because (a) foraging range was restricted by limitations of foraging time and (b) the nestling was demanding a substantial amount of food. At this time of year the mortality of ungulates in the Drakensberg was at its highest, and carrion was more readily available than at any other time of the year (Chapter 8).

I have argued that breeding in Bearded Vultures in

southern Africa is timed so that the period when parent birds are under most stress coincides with the period of greatest food availability (Chapter 8). Small foraging ranges can therefore be maintained during this relatively short period. During the late nesting period the nestling was left unattended for progressively longer periods and home ranges got larger during this time and, in addition, both parents were able to forage simultaneously. The main food of Bearded Vultures (i.e. bones) does not decay rapidly and birds could therefore continue to enjoy a fairly abundant supply of food, which cannot be used by other species, for a considerable length of time; thus, despite their overall ranges having expanded during this period, most foraging still took place within much the same area as was used during the early nesting period. At the end of the nesting period, the food supply in the areas near the nest had probably been depleted, and once young vultures left the nest and were able to fly sufficiently well, the range of adult birds increased considerably. On evidence presented in Figure 5.12 it would appear that, during the post-nesting period, birds concentrated their foraging effort at some distance from the nest, and mainly beyond areas intensively foraged during the nesting period. A theoretical representation of my interpretation of foraging by Bearded Vultures during the different periods is illustrated in Figure 5.18. This use of home range would achieve two purposes: (a) during the post-nesting period birds would

EARLY NESTING PERIOD

LATE NESTING PERIOD

POST-NESTING PERIOD

DISTANCE FROM NEST (KILOMETRES)
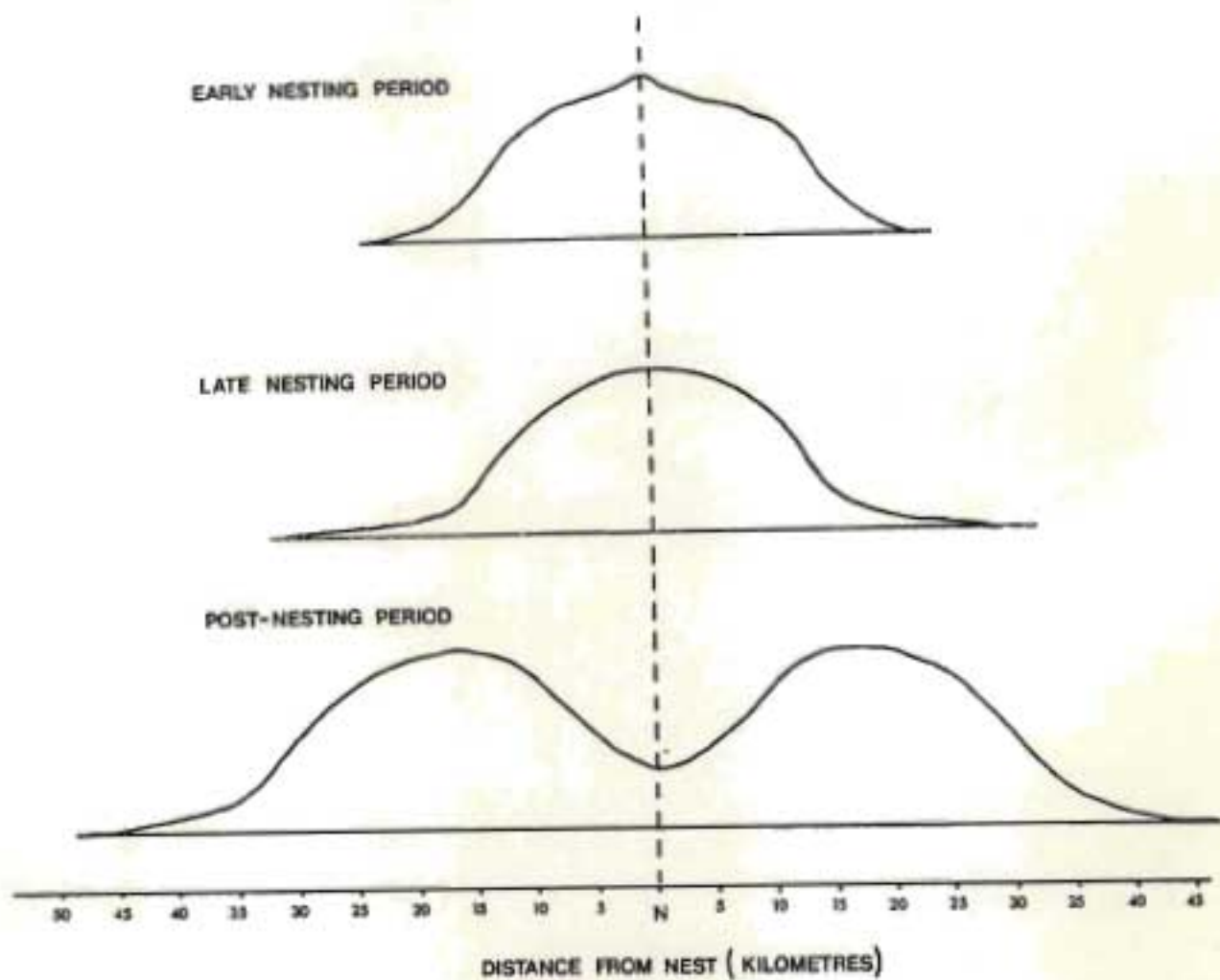
FIGURE 5.18. Theoretical illustration of the foraging use made
of the home range by Bearded Vultures in the
Drakensberg during different periods of the year.

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avoid areas intensively searched during the nesting periods and (b) a build-up of food in the main foraging area may take place before the start of the next breeding season so that, when birds were again restricted to this area and before the mortality rate of ungulates had increased (during the incubation period), a reasonable food supply would be present.

From the day-to-day foraging pattern obtained for Bearded Vultures (Table 5.13) it would appear that,

(a) overlap from one day to the next is avoided unless a good food supply would reward returning to the same area, i.e. birds move into new areas to forage,

(b) even after a number of days of foraging, overlap with areas covered on previous days is fairly low and birds identify and cover areas not recently searched and

(c) despite birds leaving and returning to their activities areas along set and predictable flight paths (i.e. along the escarpment and large ridges), once away from the activities area it is not possible to predict where they are likely to forage, except to identify recently covered areas where they are unlikely to forage.

Bearded Vultures nesting deep in the central regions of Lesotho are at present largely unaffected by modern man's activities. The birds which nested in the mountains of the Cape Province on commercial farmlands were eliminated more than 40 years ago, and the species is currently confined mainly to the highlands of Lesotho and adjacent regions (Chapters 9 & 10). It is therefore reasonable to assume that

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those individuals on the edge of the species' distribution, and which range over commercial farmlands, are most vulnerable to persecution, both direct and indirect. Bearded Vultures nesting on the Drakensberg escarpment are near the edge of their distribution, and it was therefore important to determine the extent to which they ranged beyond conservation areas. During the nesting period, because of their restricted ranges, Bearded Vultures nesting on the Drakensberg escarpment spent 2-9% of their foraging time over commercial farmlands. During the post-nesting period birds spent up to 30% of their time foraging over farmlands, despite the fact that food was provided at the feeding station in Giant's Castle Game Reserve every week throughout the year in an attempt to contain the birds within conservation areas (Chapter 10). There was no significant difference between the time spent over farmlands by the three radiotagged birds, one of whose nest virtually overlooked the feeding site, the other two nesting at distances of about 17 and 73 km respectively from the site. The sample size was undoubtedly small, but it can nevertheless be assumed that the feeding site was not effective in containing birds within the conservation areas.

5.4.4 Dispersal of immature birds

Finally, young birds were found to range extensively and unpredictably in search of suitable foraging areas. They tended to concentrate in areas where there was little competition from adults, e.g. in the northeastern Cape and

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along roadways and around villages in Lesotho, but did not settle permanently in these areas. While resident in a particular region they ranged over a relatively small area compared to the ranges of adult birds. These areas were probably searched intensively, and when they no longer provided sufficient food, the birds merely moved to new areas. This probably accounts for the very variable lengths of time spent in any one area, ranging from two days (indicating little or no food found) to three months (indicating a good source of food).

TABLE 5.1

Marking codes and number of sightings (including capture) of Bearded
Vultures trapped in Giant's Castle Game Reserve and marked with
colour rings and wing and tail windows.

Capture number	Age class	Ring number	Ring colour		Window position	Number of sightings	Period (months)
			Left	Right			
1	Juv.	G15502	Red	Red	1,6,7	4	2
2	Juv.	G15503	Black	Red	2,6,7	4	5
3	Juv.	G15504	White	Red	3,6,7	4	3
4	Juv.	G15505	Yellow	Red	1,5,7	3	1
5	Ad.	G15506	Red	Black	2,5,7	45	13
6	Juv.	G15507	Black	Black	3,5,7	2	6
7	Ad.	G15508	White	Black	1,4,7	44	9
8	Juv.	G15509	Yellow	Black	2,4,7	2	1
9	Ad.	G15510	Red	White	3,4,7	36	7
10	Ad.	G15511	Black	White	1,5,8	67	14
11	Juv.	G15512	Yellow	Blue	2,5,8	1	0
12	Juv.	G15513	Blue	Yellow	1,4,8	2	2
13	Juv.	G15514	Green	Blue	1,2,8	1	0
14	Imm.	G15515	Green	Yellow	3,4,8	3	2
15	Imm.	G15516	Blue	Blue	4,5,7	1	0
16	Ad.	G15517	Yellow	Yellow	2,4,8	46	11

TABLE 5.2

The precision and accuracy with which radio-tagged Bearded Vultures were located from a fixed-wing aircraft in the Natal-Lesotho Drakensberg. For full explanation see page 116.

Bird activity	Distance of aircraft to bird (km)		Precision (km²)	Accuracy (km)	Notes
	Mean	Range			
1) Stationary - locality known	14,7	6,5-21,5	0,9	0,6	On nest
2) Stationary - locality unknown	20,6	10,0-36,0	1,8	0,7	On nest
3) Flying - locality known	14,6	10,0-25,0	5,3	1,6	Over "activities" area
4) Flying - locality unknown	21,6	11,5-29,0	15,6	-	Foraging

TABLE 5.3. The main flight modes used by Bearded Vultures during foraging and cross-country travel.
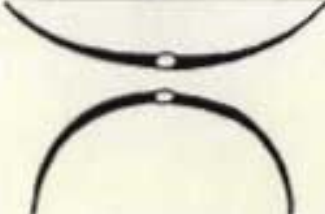
Flight mode	Flight silhouette	Description	Function	Flying speed (km/h) Mean	Range	Sample size No.	Distance (km)	Activity
A. Level gliding through calm air with sufficient lift		Wings fully extended, tail folded, talons tucked against body	Soaring along ridges foraging at "medium-height" level	70.7	51-77	3	11.3	Medium-height foraging
B. Level gliding through rising air or shallow diving		Diving posture, with wings drawn partially back and arched, tail folded and sometimes slightly raised, talons tucked against body	Fast cross-country travel, usually at high altitude, soaring along escarpments with strong updraughts or performing shallow dives	95.7	77-116	3	20.7	Cross-country travel along Drakensberg escarpment using strong slope lift; bird adopting diving posture but maintaining constant altitude
C. Descending steeply		Streamlined diving posture, wings drawn well back to almost alongside body, tail folded and often raised, talons tucked against body when diving fast but lowered for braking, bird sometimes twisting from side to side	Descending steeply, e.g. into valley, to food, pursuit of another bird or being chased	197	170-230	3	2.8	Diving after Raven with food (X2), being chased by Black Eagle
D. Ascending, or maintaining altitude when there is little lift		Wings held fully extended, tail partly to fully spread, talons tucked against body	Gaining height by thermalling or slope lift, maintaining altitude when there is little lift (early mornings, and when gliding at slow speeds, usually during low level foraging	40.3	38-44	2	4.3	Maintaining altitude on weak slope lift early on a cold morning
				For rates of ascent see Table 3.5				
E. Flapping flight		Deep, slow downward strokes of the wings	Sometimes on take-off; most usual in early mornings and late evenings, but also during interactions with other birds, e.g. courtship, play, when mobbed etc.	For frequencies of flapping flight see Table 3.4				

TABLE 5.4

The frequency of wingbeats during flapping flight by Bearded Vultures and some other species timed in the Natal-Lesotho Drakensberg.

Species	Age class	Conditions	Sample size		Frequency (beats/min)	
			No. birds timed	No. wingbeats	Mean	Range
Bearded Vulture	Ad.	Undisturbed	17	183	130,3	120-157
Bearded Vulture	Imm.	Undisturbed	6	77	129,1	120-153
Bearded Vulture	Ad.	Chasing/being chased	12	407	156,6	133-187
Bearded Vulture	Imm.	Chasing/being chased	7	103	144,2	133-162
Bearded Vulture	Ad.	Play between Bearded Vultures	4	46	136,0	124-148
Bearded Vulture	Imm.	Play between Bearded Vultures	5	69	130,1	120-133
Bearded Vulture	Ad.	Shallow flapping low over ground	2	14	158,5	144-171
Bearded Vulture	Imm.	Shallow flapping low over ground	2	37	182,2	178-183
Cape Vulture	-	Undisturbed	5	36	155,2	150-166
Cape Vulture	-	Shallow flapping low over ground	2	14	164,7	156-171
Black Eagle	Ad.	Undisturbed	4	26	156,0	150-160
Yellowbilled Kite	Ad.	Undisturbed	2	66	182,2	178-183
Lanner Falcon	Ad.	Mobbing raven	1	66	220	-
Black Crow	Ad.	Undisturbed	1	50	286	-
Pied Crow	Ad.	Undisturbed	1	80	209	-
Whitenecked Raven	Ad.	Undisturbed	9	266	207,8	171-253
Whitenecked Raven	Ad.	Chased/mobbing	5	112	241,3	211-262

TABLE 5.5

The rate of climb achieved by Bearded Vultures compared to Cape Vultures and Black Eagles ascending in the same thermal or against the same slope.

Conditions	Altitude gained (m)	Bearded Vultures' rate of ascent (m/s)	Rate of ascent (m/s) by:	Relative efficiency (%)
Weak slope lift along Drakensberg escarpment	548	0,94	Black Eagle 0,89	5,2
Good slope lift along Drakensberg escarpment	735	2,45	Cape Vulture 1,67	46,7
Good slope lift against large ridge in Lesotho	416	3,62	Cape Vulture 2,60 (X2)	39,1
Thermal	806	1,92	Cape Vulture 1,58	21,5
Thermal	839	1,68	Cape Vulture 1,40 (X3)	20,0

TABLE 5.6

Number of localities (plots) obtained for five Bearded Vultures marked with radio transmitters.

Capture number	Age class	Ring number	Ring colour		Transmitter number	Number of sightings	Period (months)
			Left	Right			
17	Juv.	G15518	Red	Blue	1	446	5
18	Imm.	G15521	Blue	Green	2	329	9
19	Ad.	G15524	Red	Green	3	1349	8
20	Ad.	G15525	Green	Green	4	957	7
21	Ad.	G15526	Blue	White	5	688	6

TABLE 5.7

The home-range sizes identified for three adult radio-tagged Bearded Vultures in the Natal-Lesotho Drakensberg, during three periods of the year and using three methods to calculate home range size. These were (A) the grid-cell method, (B) the minimum-area method and (C) the circle method where the radius is the furthest point at which the bird was located from its nest. The early nesting period comprises the incubation and brooding stages when an adult is in constant attendance on the nest; the late nesting period concerns the time when the nestling is still in the nest but is not attended constantly by an adult; the post-nesting period refers to the stage when the nestling has left the nest but is still dependent on its parents for some or all its food.

Capture number	Sex	Number of plots	Time (months)	Home range size (km^2)								
				Early nesting period			Late nesting period			Post-nesting period		
				A	B	C	A	B	C	A	B	C
19	F	1349	8	528	718	1521	732	1234	2597	1656	2162	4128
20	M	957	7	344	509	1827	816	1347	2943	1548	2719	6866
21	M	688	6	–	–	–	–	–	–	1820	7468	17671
Mean	–	998	7	436	614	1672	774	1291	2770	1675	4116	9555

TABLE 5.8

Percentage occurrence of three radiotagged adult Bearded Vultures (all nesting on the Natal side of the Drakensberg escarpment) over Lesotho, Natal Parks Board (NPB) and Department of Forestry conservation areas, KwaZulu, Transkei and commercial farming areas.

Early nesting period

Capture number	Lesotho (%)	NPB/ Forestry (%)	KwaZulu (%)	Transkei (%)	Commercial Farmlands (%)
19	19,2	75,2	3,1	–	2,5
20	21,1	76,1	1,4	–	1,4
Mean	19,8	75,4	2,6	–	2,2

Late nesting period

Capture number	Lesotho (%)	NPB/ Forestry (%)	KwaZulu (%)	Transkei (%)	Commercial Farmlands (%)
19	22,3	66,8	3,0	–	8,0
20	23,6	61,8	2,9	–	11,8
Mean	22,8	64,9	2,9	–	9,4

Post-nesting period

Capture number	Lesotho (%)	NPB/ Forestry (%)	KwaZulu (%)	Transkei (%)	Commercial Farmlands (%)
19	22,9	50,1	7,7	–	19,3
20	20,2	44,1	6,4	–	29,3
21	22,5	41,7	4,7	6,5	24,6
Mean	22,0	45,2	6,2	2,4	24,2

TABLE 5.9

The distances from their nests at which three radiotagged adult Bearded Vultures in the Natal Drakensberg could be located on 50%, 75%, 95% and 100% of occasions, during the three different periods and excluding times when the birds were on nest duty.

Capture number	Distances from the nest (km)											
	Early nesting (%)				Late nesting (%)				Post-nesting (%)			
	50	75	95	100	50	75	95	100	50	75	95	100
19	6	10	16	22	8	12	20	29	12	18	26	36
20	6	11	17	24	8	12	25	31	16	23	34	47
21	-	-	-	-	-	-	-	-	28	48	62	75

TABLE 5.10

Distance from an active nest at which other Bearded Vultures, Cape Vultures and Black Eagles were attacked by breeding Bearded Vultures in the Natal Drakensberg.

Species	Age class	Sample	Distance from nest (m)		
			Mean	±SD	Range
Bearded Vulture	Ad.	11	244	174	30-500
Bearded Vulture	Imm.	5	36	21	10-50
Black Eagle	Ad.	6	367	88	250-500
Cape Vulture	All	5	41	37	5-100

TABLE 5.11

Size of activities areas used by Bearded Vultures, and numbers of nests, roosts, ossuaries and soaring sites contained therein. Soaring site A = escarpment, B = cliffs, C = ridge/steep hillside and D = gully.

Locality	Size of activities area (km^2)	No. Nests	No. Roosts	No. Ossuaries	Soaring sites			
					A	B	C	D
Ntabamhlope	3,0	2	2	4		*	*	*
Gypaetus point	4,6	3	2	2	*	*	*	*
Mt. Durnford	6,7	3	3	3	*	*	*	*
Long Wall	4,5	3	2+	2	*	*	*	*
Giant's Castle	5,1	2+	2+	2	*	*	*	*
Redi	4,9	2+	2+	3	*	*	*	*
Roma	3,2	8	2	1		*	*	*
Mean	4,6	3,3+	2,1+	2,4				

TABLE 5.12

Distances and time periods of foraging sorties undertaken by radiotagged Bearded Vultures in the Natal-Lesotho Drakensberg. Positions of birds were plotted at 10 min intervals. Because of the irregular flight paths of these birds when foraging, distances are greater than measured along the straight line between the 10-min plots. From continuous tracking (Figure 5.15) a correction factor of 1,582 was applied. Using the corrected distances, mean speeds were calculated for the foraging sorties.

Period	Time (min)	Distance covered (km)		Corrected speed (km/h)
	Mean ± SD (range)	Measured	Corrected	Mean (range)
		Mean ± SD (range)	Mean ± SD (range)	
Early nesting (n=7)	113,4 43,6 (48-176)	53,0 20,5 (19-79)	83,9 32,4 (30-125)	44,4 (38-47)
Late nesting (n=8)	118,6 45,0 (48-192)	61,1 22,5 (27-94)	96,7 35,6 (43-149)	48,9 (41-54)
Post-nesting (n=22)	158,7 80,7 (16-309)	88,6 49,8 (7-201)	140,2 78,8 (11-318)	53,0 (41-62)

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TABLE 5.13

The extent of overlap (scale of 0-1) by radiotagged Bearded Vultures in the Natal-Lesotho Drakensberg of areas covered on foraging sorties with those areas covered on previous days. Two birds were monitored on each of two occasions for periods of five continuous days.

Day	Day 1 Mean (Range)	Day 2 Mean (Range)	Day 3 Mean (Range)	Day 4 Mean (Range)	Day 5 Mean (Range)	Totals
1	–					–
2	0,18 (0-0,61)	–				0,18
3	0,11 (0-0,20)	0,06 (0-0,20)	–			0,17
4	0,16 (0-0,32)	0,18 (0-0,49)	0,06 (0-0,12)	–		0,40
5	0,27 (0,03-0,41)	0,09 (0-0,28)	0,12 (0-0,26)	0,10 (0-0,41)	–	0,58

Chapter 6

FEEDING ECOLOGY

6.1 INTRODUCTION

While it is generally accepted that Bearded Vultures feed mainly on carrion (Brown & Amadon 1968; Glutz von Blotzheim et al. 1971; Cramp & Simmons 1980; Brown et al. 1982; Steyn 1982) little quantitative information exists on their diet apart from that gleaned from incidental records. The most detailed information previously available was that obtained from two nests in Spain where, of 35 identified items, 86% consisted of bones from large animals but Wood Pigeons Columba palumbus and Redlegged Partridges Alectoris rufa were also recorded (Suetens & van Groenendael 1973). The diet of the Bearded Vulture in southern Africa has not previously been studied, and no adequate information exists on how this species finds food or how it deals with it.

This chapter sets out to investigate the diet of the Bearded Vulture in southern Africa as broadly as possible, to determine how it obtains and handles its food, and to discuss how this species has combined a number of physiological and behavioural specializations to enable it to survive in its unique way.

6.2 METHODS

During March and April 1980 the height above ground of foraging Bearded Vultures was estimated at 1-min intervals

for the duration of time that they were in sight. As a result three foraging methods were defined, based on their height above ground. All subsequent observations were classified into these categories. Foraging activities, group sizes and age classes were determined for the entire study period from observations recorded on the field-data form described in Chapter 8. Group sizes refer to the basic foraging unit and not to numbers of units congregating at food, or in areas providing good lift. Data were grouped during the study for each calendar month (i.e. Aprils of 1980, 1981 & 1982 were grouped, etc.).

On six occasions different food items were set out at feeding sites, and the choice of Bearded Vultures and other bird species was recorded. The following food was made available: (a) fresh carcasses (four horses and two cattle) slit along the belly and with the meat from one hindlimb removed; (b) this same meat, cut into pieces about 15 cm long and 6 cm diameter; (c) sections of the lower limb-bones of pigs, the tibia having been sawn into sections about 5 cm by 8 cm including the marrow and bits of attached meat. Some of these bones, obtained on a regular weekly basis, were placed in a protected sunny area and allowed to dry out, providing a regular range of ages from fresh to five weeks old. Some bones were also placed in a sealed plastic bag for two weeks, the contents becoming partly liquid and very foul. These different items were spread over a feeding area of about 30 m x 30 m in equal numbers and evenly distributed about the carcass. The experiments ran until particular

items had been so preferentially consumed that the birds were no longer offered an equal choice of foods.

Observations were made at four carcasses away from the feeding station (all discovered by the descent of Cape Vultures) from which the selection by Bearded Vultures for various parts of the carcasses was determined. Bearded Vultures were already present at three of the four carcasses on my arrival but they did not feed until the Cape Vultures had almost completed their feeding.

The natural food of Bearded Vultures was determined from five different sources: (a) information provided by farmers on what they had seen Bearded Vultures eating on their farms, (b) my direct observations of birds feeding on "natural" prey (i.e. not provided at one of the feeding stations, but including domestic livestock), as well as birds carrying food and dropping bones, (c) food brought to nests to feed nestlings, (d) prey remains collected at bone-dropping sites (ossuaries) and (e) prey remains collected from below nest sites. All collected prey remains were sent to I. Plug of the Transvaal Museum for identification and housing. The collection was analysed according to procedures suggested by Brain (1974), Voigt & Plug (1981) and Voigt (1983).

Feeding behaviour, the preparation of food and interactions with other animals were recorded for all observations of Bearded Vultures at or in the vicinity of food. Most observations were made at the feeding sites in

Giant's Castle Game Reserve. The most important and unique form of food preparation undertaken by Bearded Vultures was bone dropping. This usually took place at regular sites. The following information concerning these sites was recorded: type of site (e.g. smooth rock slab or group of large boulders), size of dropping zone, position on hillside, aspect and slope. An attempt was made to record the following information on each bone dropped: type of bone being dropped, height of drop, direction of approach for the drop, result of each drop, method of descent by bird and direction of take-off.

In this and subsequent chapters the term "bone" refers not to a cleaned pure bone, but the scavenged item collected usually once Cape Vultures had finished feeding, and with varying amounts of skin and soft tissue still attached and containing the marrow.

6.3 RESULTS

6.3.1 Foraging

High-intensity foraging can be defined as flight for the sole purpose of searching for food. 35% of the average 13,5-h day was spent foraging in this fashion, comprising 44% of all flight activities. Foraging might also take place concurrently with other activities such as thermalling, cross-country travel or even while perched on a cliff. Thus an additional maximum of 33% of flight activities could be used for searching, but this is considered to be of a lower intensity and is not included in the following analysis.

The height above ground of 31 foraging Bearded Vultures was estimated at 1-min intervals, resulting in 149 height records being obtained (Figure 6.1). Three main foraging heights were identified, namely "low", "medium" and "high", and during the course of the study they were confirmed as representing different foraging methods or strategies. Foraging methods were defined as follows:

a. Low searching; classed as below 20 m above the ground, but in effect generally below 8 m, the most common height being 2-4 m. Heights between 8 m and the next foraging level occurred mainly when birds changed from one foraging method to another, and they rarely remained at these intermediate levels. Low searching took a number of different forms: sweeping along hillsides and ridges following the contours; quartering the ground in similar manner to that of a Black Harrier Circus maurus; and zig-zagging and circling up hillsides. Bearded Vultures also change freely from one form of low searching to another.

b. Medium-height searching; from 20-100 m above ground level, most of the records being from 20-70 m. Birds used slope lift to glide along a ridge, covering the area in a number of broad sweeps or bands. They then sailed across to the next ridge. When gliding between ridges a bird was considerably higher above the ground than while sweeping along a ridge, and went out of the normal range of medium-height searching. These "valley" records are indicated in Figure 6.1.

c. High searching; usually above 1000 m. There are few
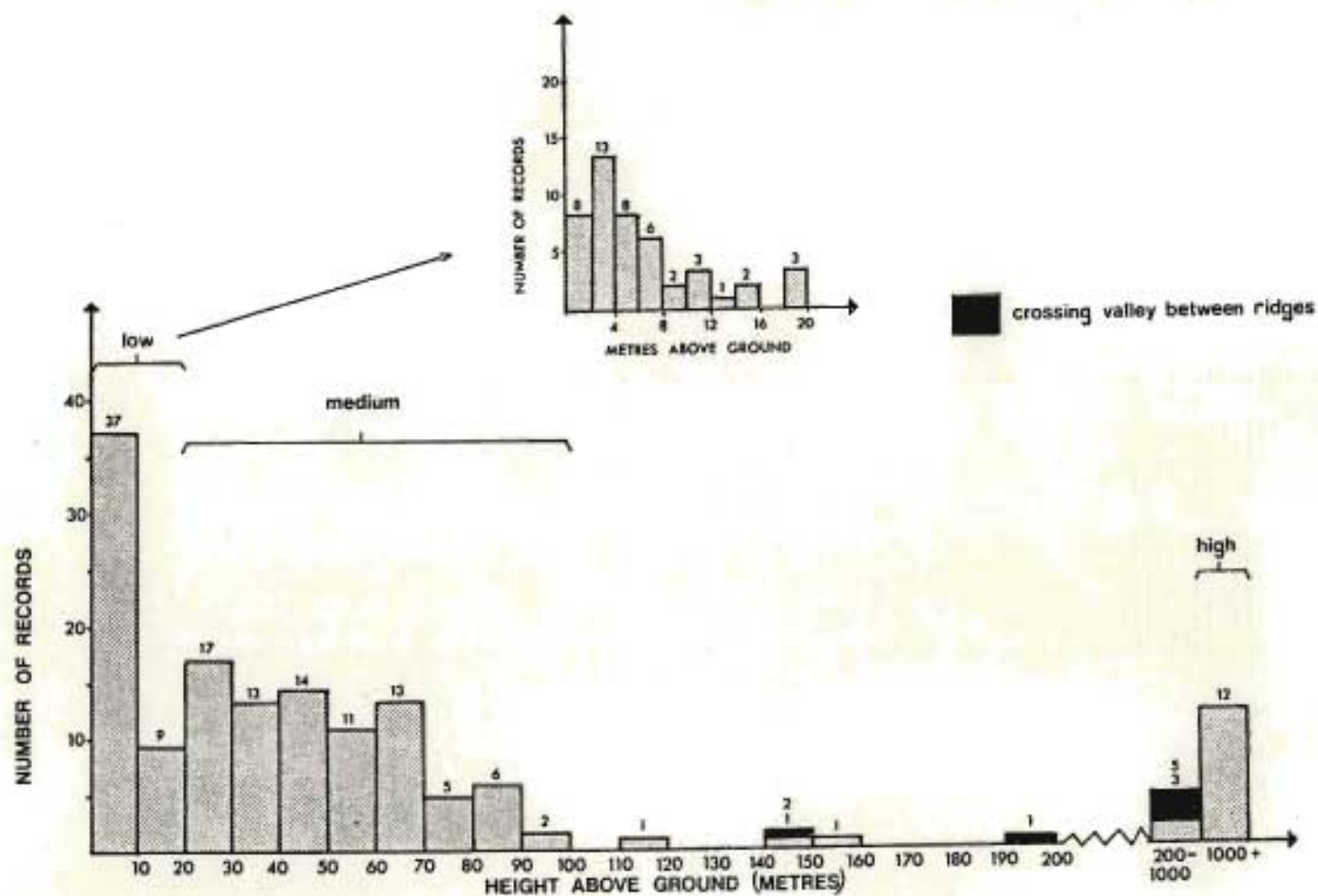
FIGURE 6.1. The height above ground of foraging Bearded Vultures in the Giant's Castle area, sampled at 1-min intervals (n = 149).

records of birds foraging at levels between 100 m and 1000 m. Although birds commonly thermalled up from medium to high altitudes, these were not included in the analysis because the activity had changed from foraging to thermalling. High searching was usually more than 1000 m above the ground and often very much higher, involving birds either using slope lift above the Drakensberg escarpment and then heading out over Natal (initially at about 1400 m above the ground), or obtaining lift in thermals, sometimes to heights at which the birds could no longer be seen through 8 x binoculars, and then travelling across country until another thermal was encountered. After having travelled some distance using high searching, birds often descended to lower altitudes and employed medium-height searching, e.g. Bearded Vultures from the Sani Pass area of the high Drakensberg were often seen approaching Bulwer Mountain (about 46 km east of Sani Pass, with relatively flat ground between) at very high altitudes. Once at Bulwer Mountain, the birds descended and began foraging at medium and low altitudes.

During the course of this study data were collected and analysed within these three categories of foraging.

Low searching amounted to 36%, medium-height searching to 58% and high searching to 6% of the total time spent foraging by Bearded Vultures (see Table 8.3). Although young birds spent 37% of their day foraging compared to 34% spent by adults, this was not significantly different (see Table

8.4.). Of the medium-height searching records, 76% were of birds foraging along ridges, the remaining 24% being of birds crossing or foraging in and over valleys.

Daily foraging patterns showed peaks at mid-morning and mid-afternoon with a decline in activity towards midday (Figure 6.2). The morning peak was slightly higher than the afternoon one (50% and 47% respectively of the total hourly activities between 09h00 and 10h00, and between 14h00 and 15h00). Both low and medium-height foraging showed similar trends, although medium-height searching increased in the afternoon to exceed the amount that took place in the morning. High searching began only at mid-morning, after 09h00.

The amount of low and medium-height searching increased from June to December while high searching showed the opposite trend, increasing in December and decreasing in April with the lowest figures being obtained during the breeding season (Figure 6.3). This can be more clearly seen in Figure 6.4 where the three foraging methods are plotted as percentages of the total foraging per month.

Bearded Vultures spent more time foraging in the breeding season than in the non-breeding season (37% and 32% of the day respectively, Chi-squared test; $p < 0,1$). Similarly, both low and medium-height searching occupied greater proportions of the day during the breeding season than the non-breeding season. For high searching, the converse was found.
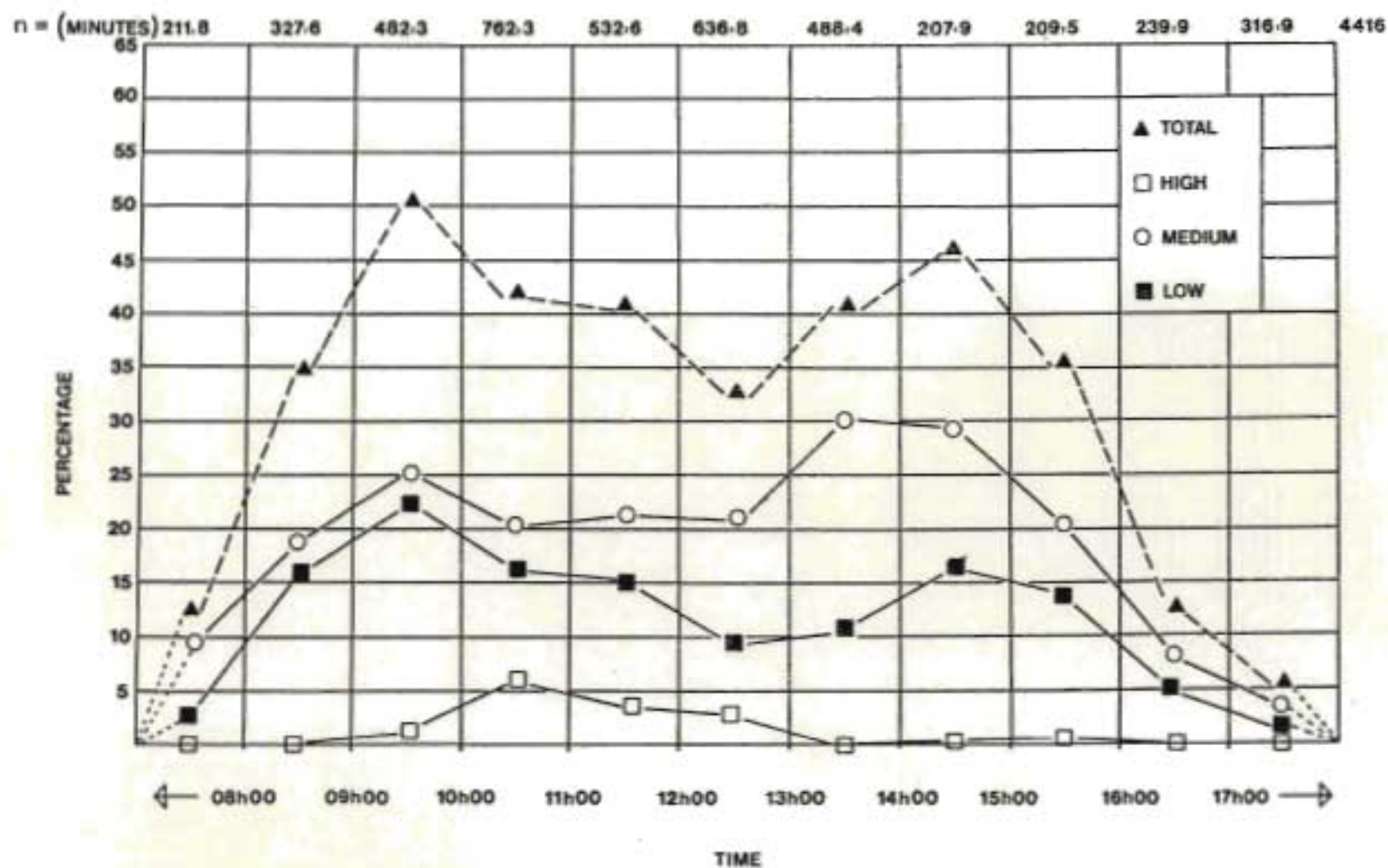
FIGURE 6.2. Daily foraging pattern in Bearded Vultures as a percentage of all activities per hour.
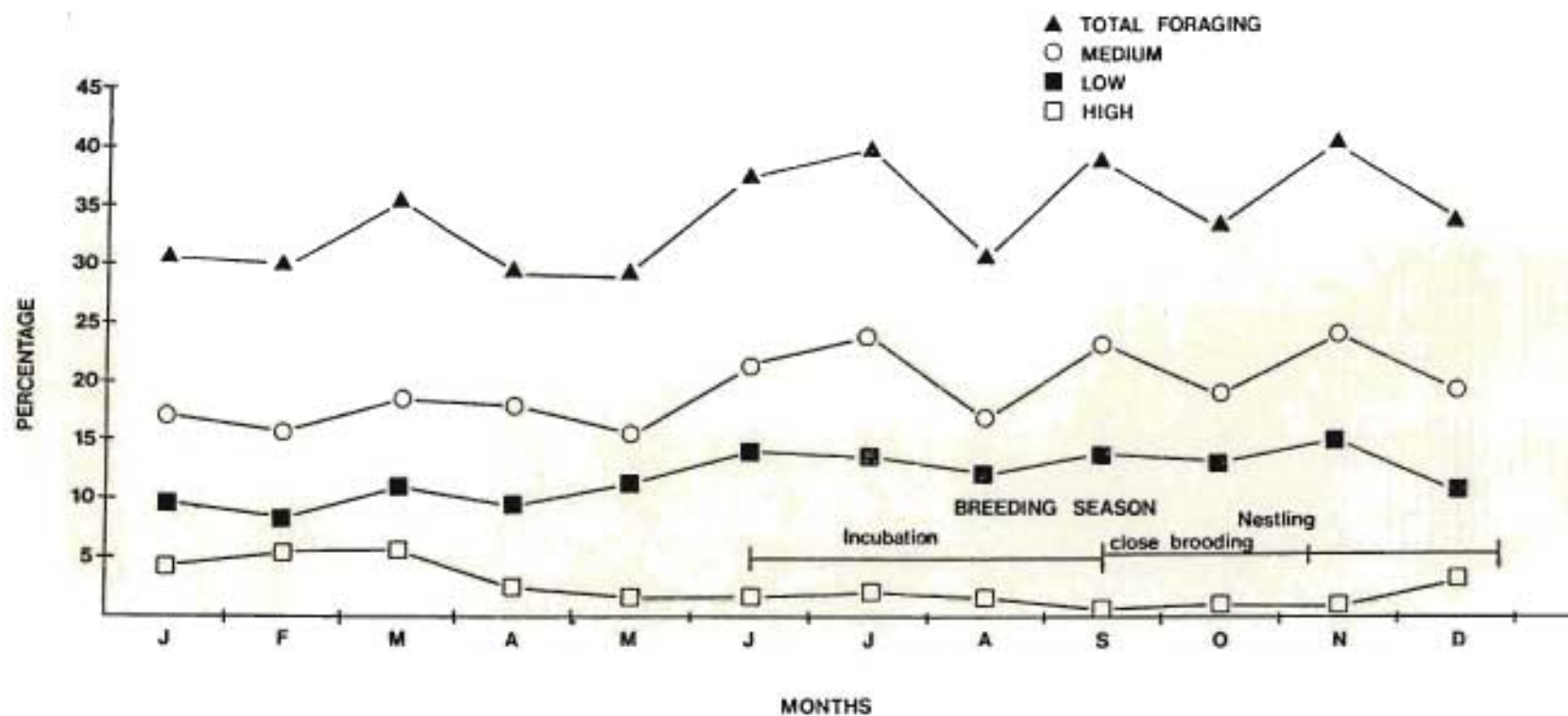
FIGURE 6.3. Yearly foraging pattern in Bearded Vultures as a percentage of all activities per month.

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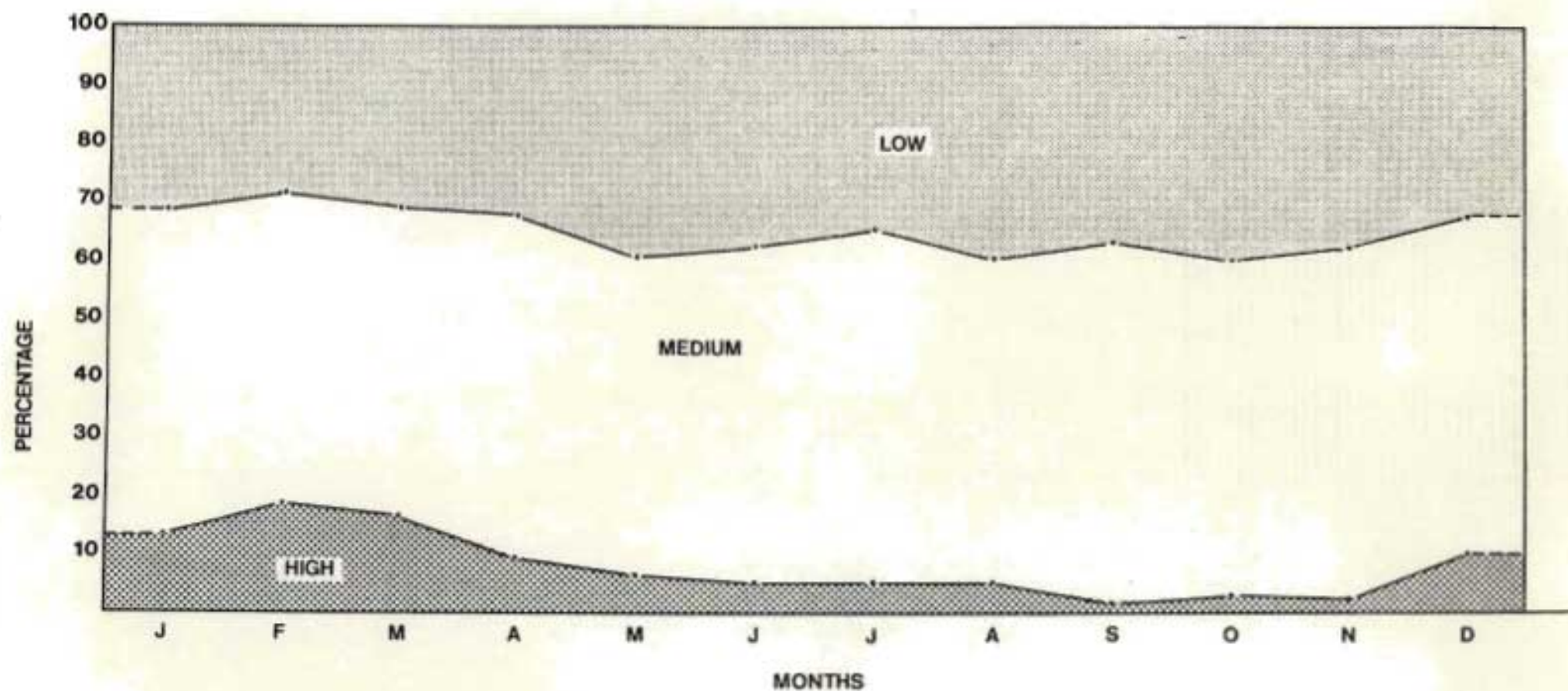
FIGURE 6.4. Yearly pattern of the three foraging methods used by Bearded Vultures, as a percentage of the total amount of foraging per month.

6.3.2 Group sizes

Young Bearded Vultures were present at 13% of all sightings of adult birds. Young birds, inexperienced in finding food, were probably accompanying adult birds to gain assistance in this regard; it is unlikely that they contributed much to the relationship as far as foraging acumen is concerned. Adult Bearded Vulture records were therefore analysed for singles, pairs and larger groups of adults per month irrespective of whether young birds were attached to the group (Table 6.1).

Adult Bearded Vultures foraged mainly either singly or in pairs. 6% of adults were observed in groups larger than two adults (four groups of three adults and two groups of four adults) and for the duration of time that these birds were under observation, they did not disperse into smaller groups.

During the non-breeding season 45% of adults sighted were single birds, the remainder being mainly in pairs. During the breeding season 56% of adult Bearded Vultures were single (significantly greater, Chi-squared test; p<0,05) while 37% were paired and 6% in larger groups (Figure 6.5). The percentage of pairs represented here would constitute the minimum pair-foraging figure as birds were often a little way apart, and particularly when low-searching in rough terrain, one of a pair could easily be overlooked.

During the breeding season, particularly during the incubation and close-brooding periods (June to the end of

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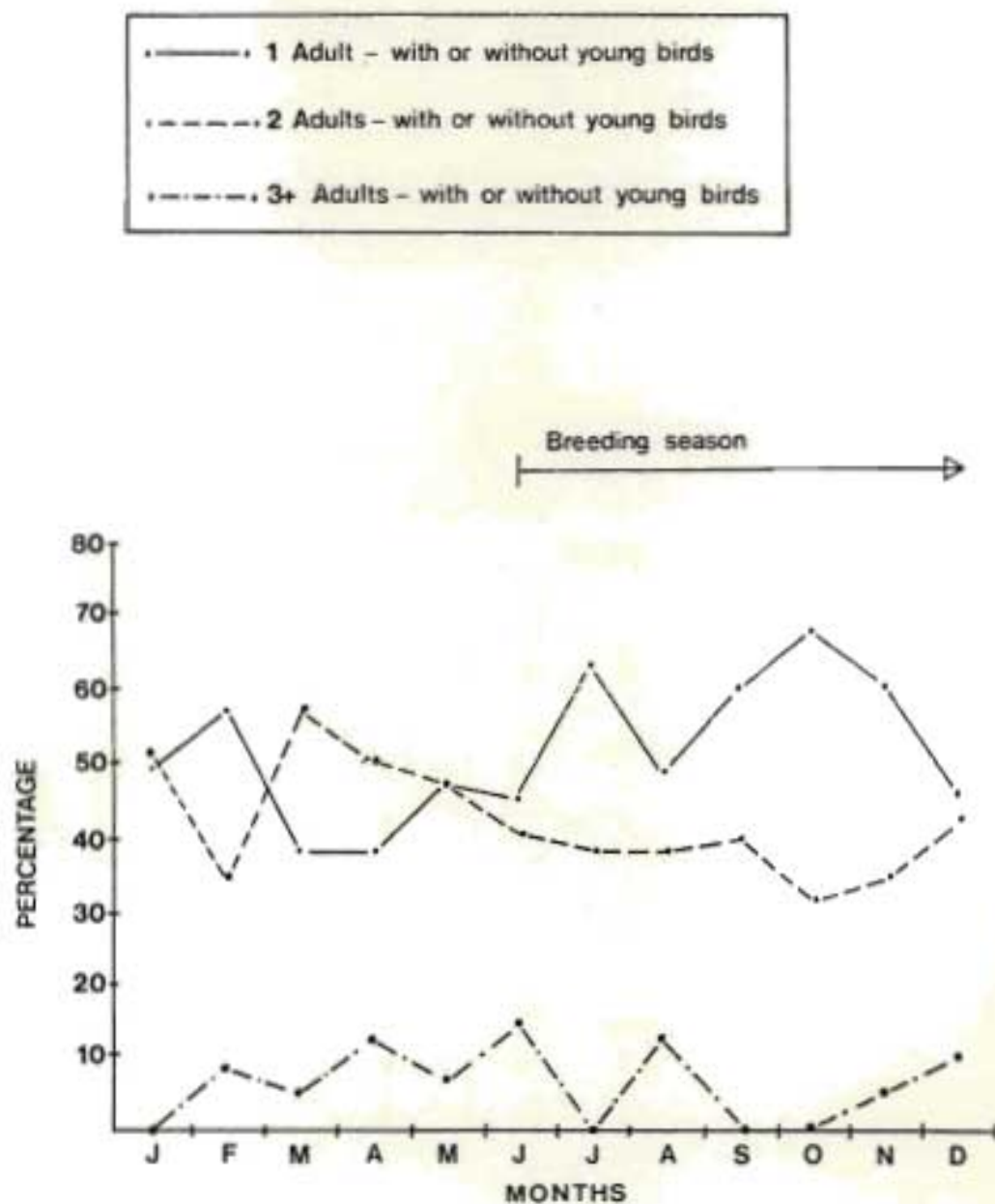
FIGURE 6.5. Group sizes in adult Bearded Vultures per month of the year.

October), one of the nesting pair of Bearded Vultures was in constant attendance at or near the nest. Because all pairs of Bearded Vultures bred every year (40 nest-years monitored) and as there was not a surplus of non-breeding adults (subadults were being recruited into the breeding population, see Chapter 7), there should have been no pairs of adults sighted during this period: yet 37% of adults were seen foraging in "pairs". From observations at nest sites and of marked birds in the Giant's Castle area it was found that "off duty" birds from neighbouring nest sites regularly came together to forage (Table 6.2). This was further substantiated at other nest sites, e.g. at the Roma nest in Lesotho, where, on five of the 16 early mornings that observations were made during the "close attendance" period, an adult Bearded Vulture came gliding in from the east and circled above the Roma nest until it was joined by the male bird of the Roma pair; thereafter the birds departed together. Birds sometimes arrived at a nest site looking for a foraging partner after the departure of the off duty bird. This was seen at Ntabamhlope, where an adult Bearded Vulture appeared and visited first the alternate nest then circled in front of the nest in use. After about 2 min, when no response was obtained, the bird went gliding off. From the few data collected, only all-male and all-female groups were positively identified. This may reflect the sequence of sharing of incubation and brooding duties rather than an avoidance of "mixed groups", or may be a result of the small sample. Many more "pairs" of unmated

birds were confirmed than is reflected in Table 6.2, but
they were either unmarked or too far away to identify.

The monthly group sizes and compositions in young
Bearded Vultures are listed in Table 6.3. Subadult birds
have been included in the adult category because they are
about five years old, have survived the high mortality of
their first few years and are therefore fairly experienced
at finding food. Between January and June about 27% of young
birds were seen in the company of adults. During the
breeding season, this figure decreased significantly to 14%
(Chi-squared test; p < 0,01). Corresponding with this
decrease was an increase in the number of groups of young
birds. Young birds in groups rose significantly from 17% in
the non-breeding season to 37% in the breeding season (Chi-
squared test; p < 0,01) (Figure 6.6). Young birds formed
groups of twos (75%) and threes. Also corresponding with the
decrease in groupings of young birds together with adults
was an increase in the association between young birds and
Cape Vultures. During the non-breeding season 8% of young
birds were seen with foraging groups of Cape Vultures. Twice
young birds arrived at carcasses with Cape Vultures. It
seems likely that young birds benefitted from this
association and used Cape Vultures to help them locate food.
During the breeding season this association increased. About
15% of young Bearded Vultures were seen in the company of
Cape Vultures during this period. A steady decrease in the
monthly percentage of single young birds from January (when
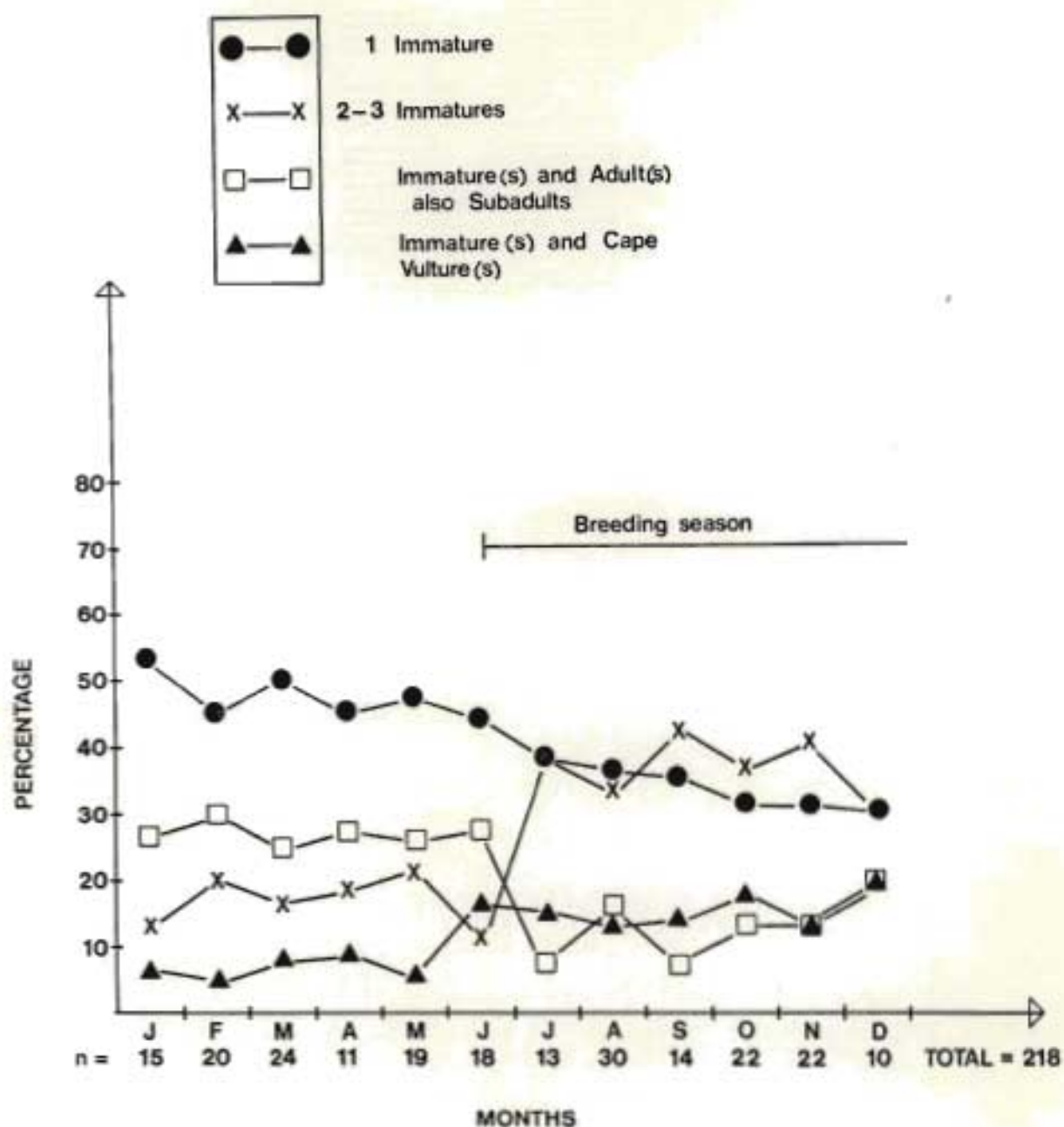
FIGURE 6.6. Group sizes in immature Bearded Vultures per month of the year.

juvenile birds join the free-flying population) to December was recorded. This trend is not properly understood but could result from (a) single birds forming groups more and more regularly, (b) mortality of immature Bearded Vultures, (c) emigration from the Giant's Castle area where most observations were made, or a combination of all three.

The group sizes of young birds near to and away from known or likely nest or roost sites was investigated (Table 6.4). Observations of foraging birds at least 2 km from known or likely roosts (i.e. outside the activities area) were considered to be "away from" roosts, those within 2 km, "near to" roosts. Despite the many possible errors inherent in this analysis (e.g. overlooking roost sites, or birds from distant roosts foraging within 2 km of another bird's roost), some trends are nevertheless clearly apparent (Figure 6.7). 69% of the single young birds recorded were near to roost sites, while 69% of young birds in groups were away from roosts. Young birds in association with adults and Cape Vultures were also more common away from their roosts (61% and 77% of records respectively). This indicates that single birds were more common near to roosts (usually the natal nest sites), but away from these sites, i.e. when going out foraging, young birds formed groups with each other or joined adult birds or Cape Vultures. On returning to their roosting cliffs, young birds separate. Immature birds may wander over large areas (Chapter 5), changing roost sites as new areas are covered. There is evidence that these birds sometimes roost together (two young birds were
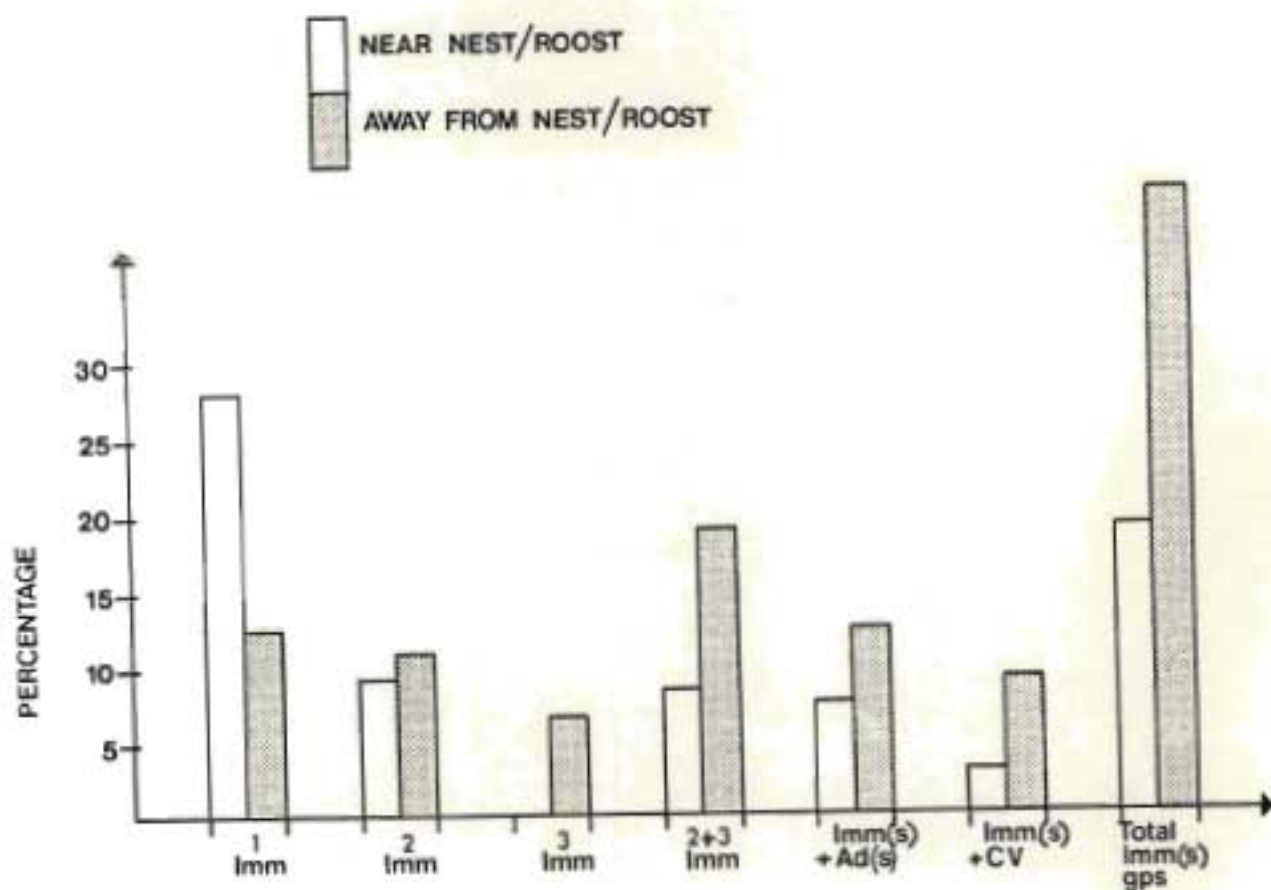
FIGURE 6.7. Group sizes of immature Bearded Vultures near to and away from nests and roosts.

seen on the same cliff ledge on two occasions at dusk), but more often they roost apart.

Observations by farmers, as revealed by the questionnaire survey, provide some data on group sizes, but no age classes were given (Table 6.5). The group sizes of Bearded Vultures foraging and feeding on farmlands were combined for the provinces of Natal, the Orange Free State and the Cape. Most sightings were of pairs of Bearded Vultures, single birds being more common than groups larger than two (Figure 6.8). These figures are likely to be somewhat biased (particularly for adult birds) in favour of the non-breeding season, as birds fly further from their nesting cliffs at this time of the year and spend more time foraging on farmlands. The large groups reported are unlikely to be the basic foraging group but rather a number of smaller groups or individuals that have congregated at a large food source.

6.3.3 Food choice

When offered a selection of foods, Bearded Vultures chose bones in preference to meat, and paid very little attention to the carcasses (Table 6.6). On four occasions birds departed with lumps of meat. These occasions were all during the breeding season when the birds were known to have nestlings and the meat was probably destined for the nestlings. Bearded Vultures selected the older drier bones, 66% of those eaten being three weeks old or more. The rotten bones aged in plastic were avoided. Cape Vultures by
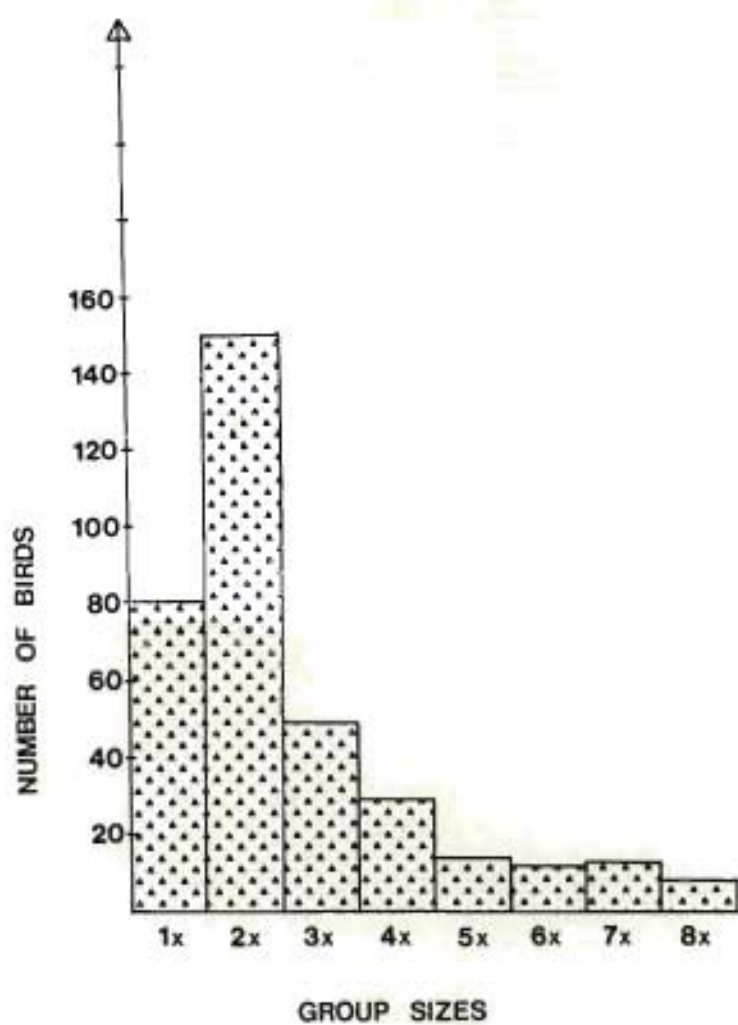
FIGURE 6.8. Group sizes in Bearded Vultures as reported by farmers in the questionnaire survey.

contrast ate mainly from the carcasses, although when approaching a carcass, pieces encountered _en_ _route_, particularly lumps of meat, were consumed. Cape Vultures had difficulty in swallowing all but the smallest pieces of bone. Birds temporarily evicted from a place at the carcass would often pounce on nearby meat before returning to the fight. Black Eagles, Jackal Buzzards _Buteo_ _rufofuscus_, Lanner Falcons _Falco_ _biarmicus_ and Black Crows _Corvus_ _capensis_ selected fresh meat and bones (although all but the Lanner Falcons would eat dried meat from three-week old bones when fresh meat was not available). Whitenecked Ravens were less selective than the other species. Although favouring fresher food, they often flew off with whatever was nearest at hand.

Being carrion-feeders, Bearded Vultures are bound to be largely opportunistic in obtaining food. Some food is obtained as single items, discovered from low or medium foraging heights. At a carcass a certain amount of selection can take place, particularly in the sequence in which different parts of the carcass are eaten. Four carcasses, an adult and a subadult sheep, a Mountain Reedbuck and a Red Hartebeest _Alcelaphus_ _buselaphus_, cleaned of most soft tissue by Cape Vultures, were monitored for food selection. Although some picking at attached flesh did take place, the Bearded Vultures preferred to remove sections of the carcass and fly off with these. Table 6.7 lists the order in which the carcasses were taken apart, observations being over a

period of two to three days; Blackbacked Jackals often removed parts of the carcasses at night. It is apparent that limbs are the first choice of Bearded Vultures, being removed whole where possible. From smaller carcasses such as the subadult sheep, a forelimb from scapula to hoof inclusive was carried off, while from larger carcasses, e.g. adult sheep, the humerus to hoof was taken. In the case of the still larger Red Hartebeest, the limbs were disarticulated into a number of sections before being removed. Ribs and vertebrae were the next to be removed, and in one case, the skull was also taken. Although detailed observations were not made after three days, Bearded Vultures revisited the sites of the carcasses for up to two weeks after the animals' deaths.

It is difficult to obtain an accurate idea of the diets of raptors that do not produce pellets of indigestible portions of food. Many studies are based on prey remains collected at nests (e.g. Boshoff & Palmer 1980; Boshoff et al. 1981; Brown 1952/1953; Plug 1978; Steyn 1964, 1965, 1973a), but it is unlikely that these remains accurately reflect the prey spectrum of the species in question. The extent of the bias varies from species to species, and would be greatest in those birds that use their nest sites only during the breeding season, in those species in which the diets of nestlings and parents differ and in those species that feed predominantly on soft material (usually carried in the crop) with most of the "hard remains" found at nests

consisting of rejected items.

The Bearded Vulture uses its nest throughout the year, but food is brought to the nest only once the first nestling hatches (see Chapter 7). Although nearby ledges used for roosting may also be used for feeding, very few prey remains were found under these sites compared to under nests. The nest site collections would therefore reflect the diet destined mainly for the nestling, covering the period from mid-August to the end of December. During this study an attempt was made to obtain as broad a coverage of prey items from other sources as was possible.

Of the 367 farmers who reported the presence of Bearded Vultures on their farms, only 40% actually saw the birds feeding (Table 6.8) and few recorded this on more than one or two occasions (Table 6.9), whereas, many farmers gave unsolicited reports of regular observations of Cape Vultures feeding. Farmers in the northeastern Cape reported the most frequent sightings of Bearded Vultures feeding. These farms are in the mountains, in some cases nest sites were on the farms, whereas in Natal and the Orange Free State most farms are some way from the mountains and birds visit these farms only to forage. Table 6.10 lists the food items reported by farmers from the three provinces covered by the questionnaire survey. At least 88% of these items were obtained as carrion. Although no farmer actually observed a Bearded Vulture make a kill, 5% claim that they take young lambs and goat kids. A further 9% of their food could have

been obtained by predation, i.e. hyraxes, hares, birds and small mammals, and while the birds would appear perfectly capable of this, no farmer actually observed a kill. As would be expected from farmlands, most of the food items consisted of domestic animals (89%), with sheep and lambs predominating.

My observations on the food of the Bearded Vulture away from the nest were made mainly in Giant's Castle Game Reserve and the adjacent Lesotho highlands, with incidental sightings from KwaZulu areas, Natal farmlands and farms in the northeastern Cape (Table 6.11). In Lesotho, the northeastern Cape, KwaZulu and Natal farmlands, all food items identified (with the exception of a Mountain Reedbuck) were of domestic animals, mainly sheep and lambs. In Giant's Castle Game Reserve 68% of the identified food was of non-domestic animals, mainly small antelopes. The domestic animal component in the Bearded Vultures' diet observed in Giant's Castle Reserve had obviously been brought in from adjacent areas.

The food items brought to nests by Bearded Vulures is given in Table 6.12. Again, domestic stock predominates. Limbs, sections of limbs and long-bones were well represented (62%). Lumps of red meat formed 12% of all food items brought to the nest, 73% of these being brought within the first three weeks of the nestling having hatched.

A total of 1034 bones and bone fragments were collected from 12 ossuaries and 460 bones were retrieved from the base

of eight nesting sites (Table 6.13). The localities of these sites are indicated in Figure 6.9. A number of bones from the ossuaries had tissue adhering, but there was tissue on most of the bones collected beneath the nests. Evidence of weathering was present on a small number of bones with tissue from both ossuaries and nest sites, suggesting that visible weathering can occur on exposed bone even before all the soft tissue disappears. Evidence of digestion or regurgitation was found on only 10 items, but scratch and peck marks were common, particularly on bones from the nest sites. Carnivore and rodent damage was present on only two bones, both from the Giant's Castle Game Reserve.

A few bones from both ossuaries and nest sites showed burn or scorch marks. While some of these could have been collected by the birds after veld fires (game deaths due to uncontrolled fires are fairly common in the Drakensberg), many of the bones collected at ossuaries were scorched when those areas were burned subsequent to the bone-dropping. No non-faunal remains were found at either nest sites or ossuaries. The collection from ossuaries consisted mainly of bone flakes and unidentifiable bone fragments, whereas the collection from nesting sites consisted mostly of identifiable fragments.

Tables 6.14 and 6.15 list the species and numbers of prey items collected at ossuaries and nest sites respectively. Domestic animals were present in almost all the samples, forming at least 67% of the bones collected at ossuaries and 65% of those from nest sites. The few wild
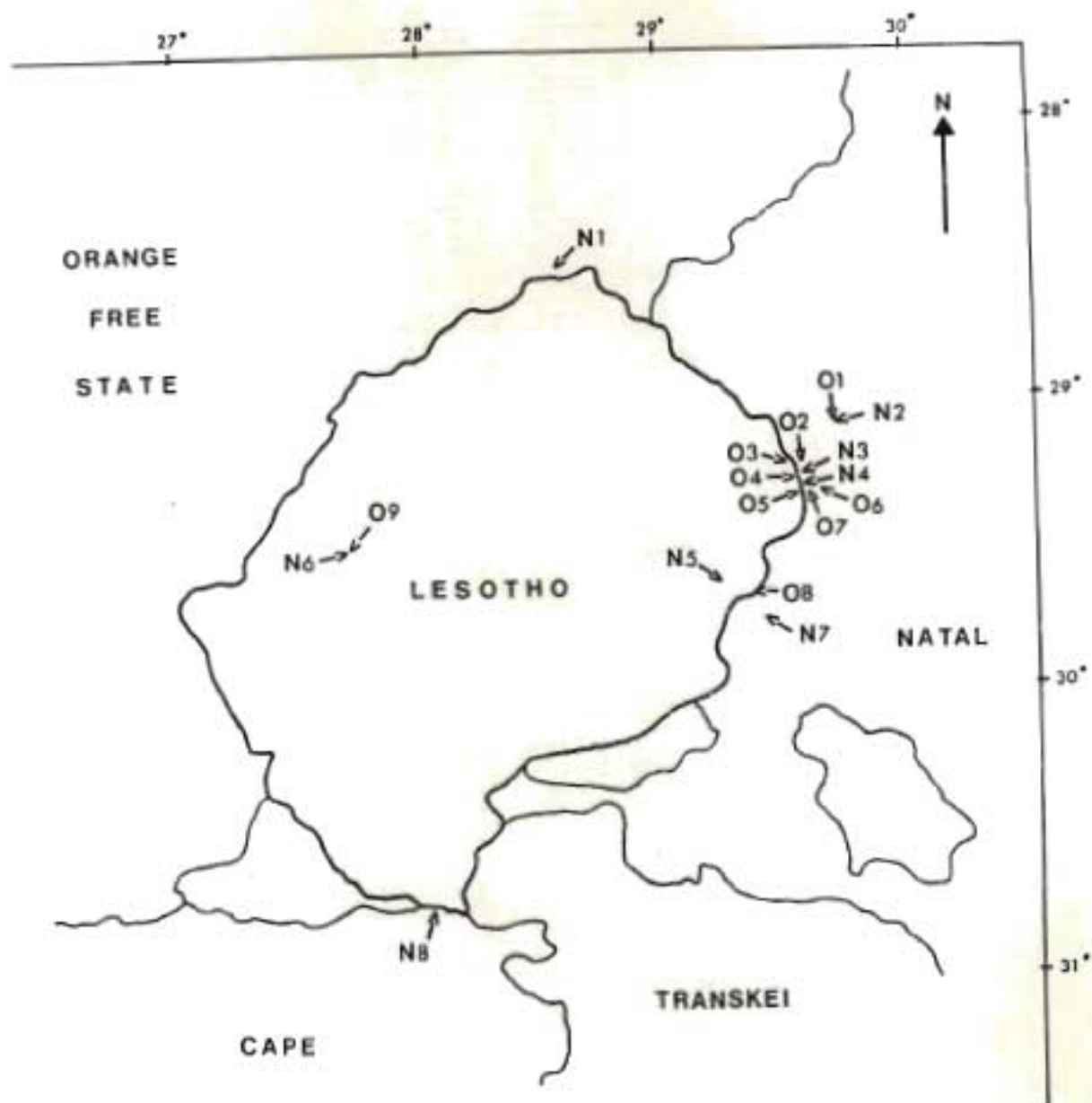
FIGURE 6.9. The localities of Bearded Vulture nests and

ossuaries at which prey remains were collected.

Nests: N1 = Golden Gates, N2 = Ntabamhlope, N3 = Long Wall north, N4 = Long Wall south, N5 = Black Mountain, N6 = Roma, N7 = Cobham State Forest and N8 = Barkly East.
Ossuaries: O1 = Ntabamhlope, O2 = Thumb Ridge, O3 = Mt. Erskine, O4 = Jarding Pass, O5 = Long Wall, O6 = Giant's Ridge, O7 = Giant's Castle, O8 = Sani Pass and O9 = Roma.

animals represented were mainly found at sites within Drakensberg reserves. Ageing of animals was based on patterns of tooth wear. Sheep/goats, wild bovids and hyrax teeth were present from nesting sites and ossuaries. Although equid remains were quite common, teeth were virtually absent from the sample. Cattle teeth were present only in the ossuary collection. Teeth from the ossuaries were mainly those of adult and old animals, but the nesting sites yielded teeth of young animals, particularly in the sheep/goat group. Post-cranial remains from juveniles were also more common from the nesting sites than from the ossuaries (11,2% and 0,3% respectively). All bone fragments were measured along the longest axis and are plotted in 10-mm categories (Figure 6.10). It is evident that the fragments from nest sites are generally larger than those found at ossuaries.

The composite picture of food eaten by Bearded Vultures as determined from the identifiable items from the five sources of data is shown in Figure 6.11. It is evident that in southern Africa, Bearded Vultures are dependent on domestic livestock throughout their range, particularly on sheep and cattle which they probably obtain solely as carrion. Non-domestic bovids constitute only 12% of the Bearded Vulture's diet in the areas studied, and probably considerably less in large regions of their range in southern Africa, while non-domestic animals from other groups, e.g. small mammals, birds, genets, contributed 7% in number, but certainly less in biomass to the Bearded
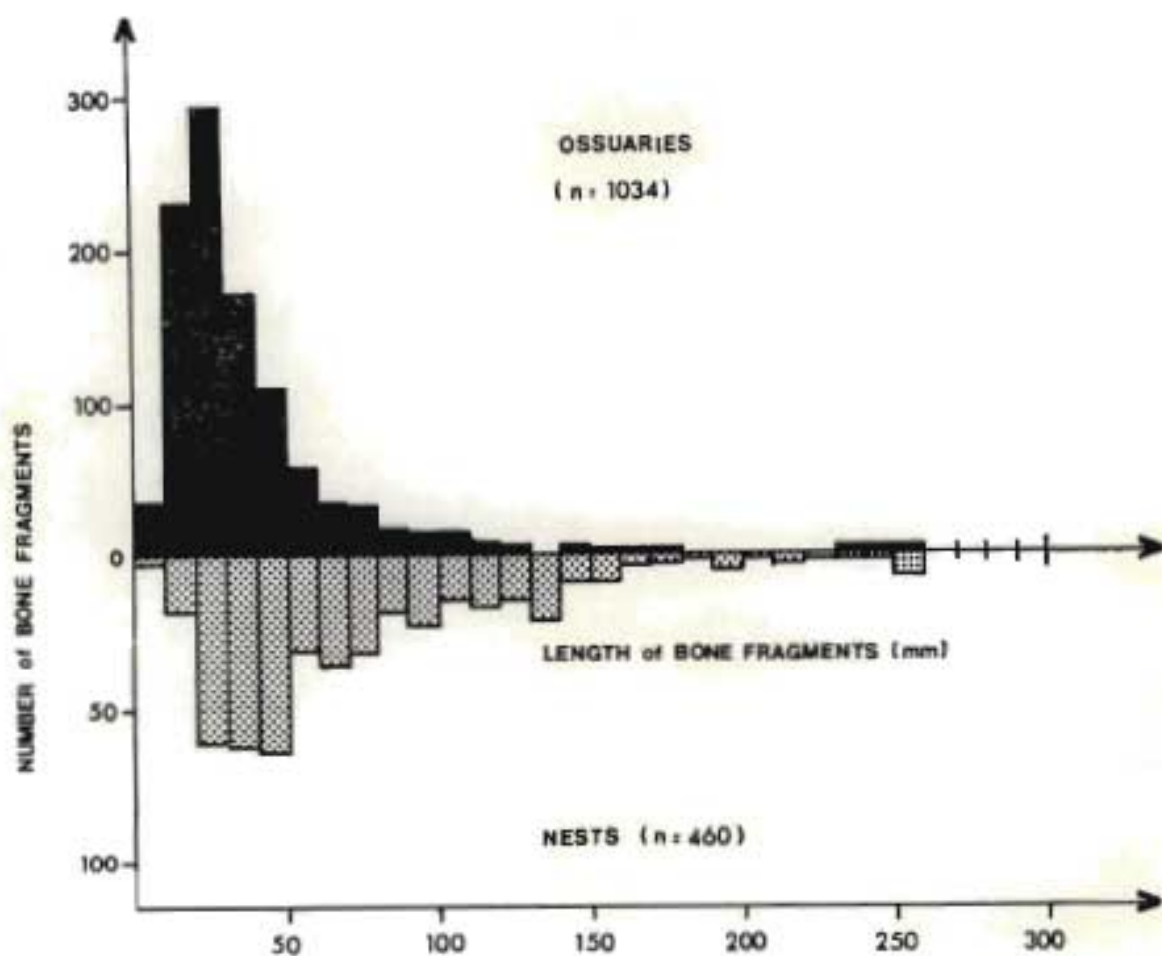
FIGURE 6.10. Lengths of bones and bone fragments (measured
along the longest axis) collected from Bearded
Vulture nests and ossuaries.
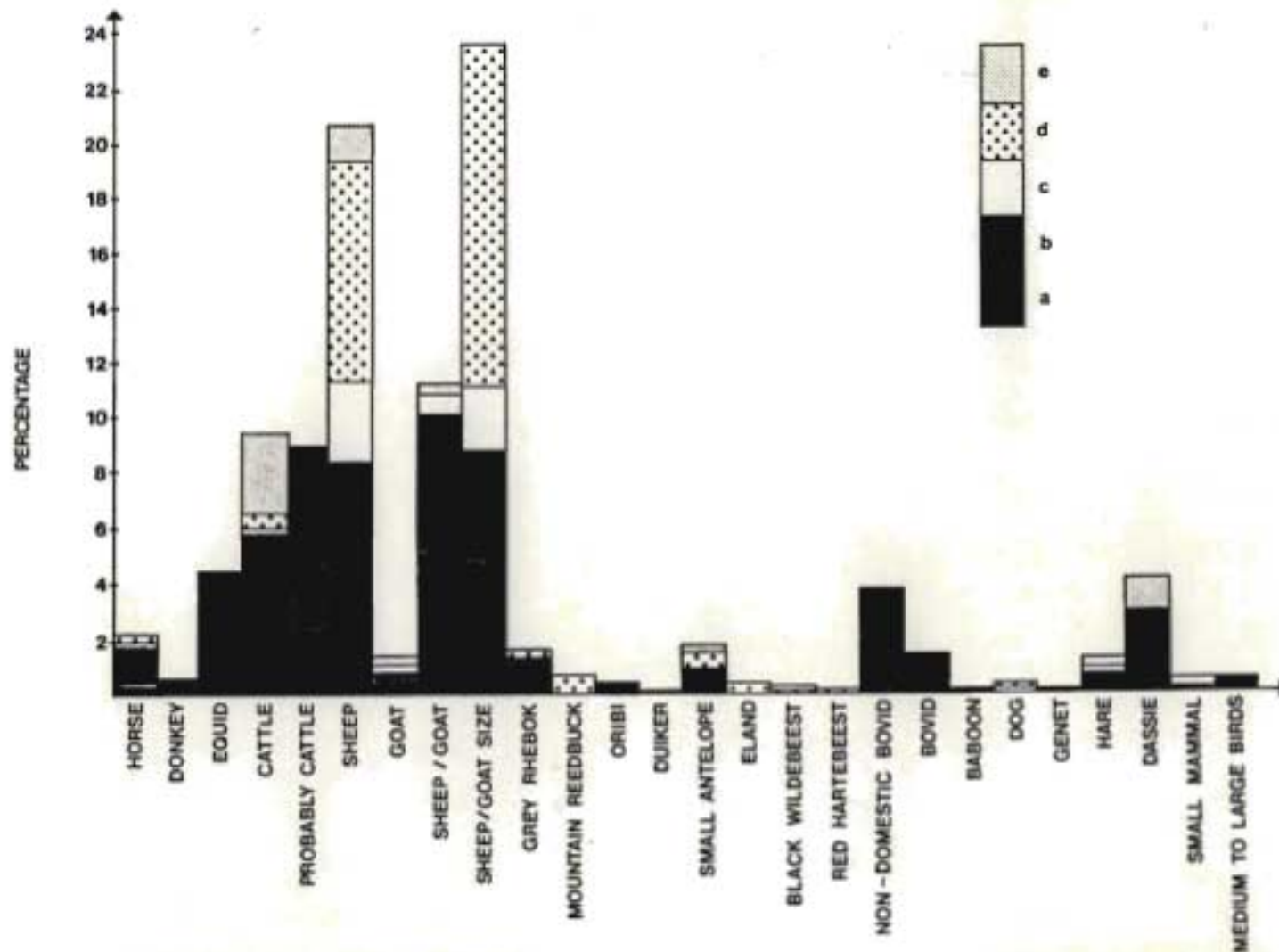
FIGURE 6.11. The diet of the Bearded Vulture in southern Africa, determined from 683 identifiable prey items (a) collected at nests, (b) collected at ossuaries, (c) seen brought to the nest, (d) seen being carried and eaten away from the nest and (e) reported by farmers in the questionnaire survey.

Vulture's diet.

Skeletal remains retrieved at nests and ossuaries are shown in Table 6.16. The high percentage of skulls, vertebrae, ribs and sterna from these sites are in contrast to the observed selection of limbs at carcasses and the high percentage of limbs and longbones seen carried and consumed by the birds.

6.3.4 Feeding behaviour

All vultures come to carrion (Mundy 1982), but the strategies in finding and dealing with food and the choice of the components of the food may vary considerably (König 1983). Vultures of the genus Gyps (griffon vultures) forage gregariously and feed almost exclusively on the carcasses of larger animals, preferring soft meat and viscera. The feeding method employed by these species has been classed as "pulling" (Kruuk 1967). They have elongated skulls and long, powerful, nearly feather-free necks with which they can reach deep into large carcasses (König 1983). Representing this group in the mountainous areas of southern Africa (and in the study area specifically) is the Cape Vulture, a large cliff-nesting griffon. The other two feeding classes of vultures, the "tearers" (e.g. Lappetfaced and Whiteheaded Vultures, but see Richardson (1984) regarding the latter species) and the "peckers" (e.g. Hooded and Egyptian Vultures), are all generally solitary species and fairly evenly dispersed, and do not occur in the study area, although the Egyptian Vulture may have done so 60 or more

years ago (Symons 1919). Neither the Palmnut Vulture Gypohierax angolensis nor the Bearded Vulture falls conveniently into any of the feeding classes of the otherwise ecologically well-defined group of Old World Vultures (König 1983).

Bearded Vultures have a stouter, more powerful version of the "pecking" class of bill. They are able to tear the hide of a moderate sized animal, at least as thick as that of a subadult sheep, while still being able delicately to peck small pieces of soft tissue from bones and areas inaccessible to the griffon vultures. They never put their heads into carcasses, although they "pull" at red meat when it is available. Like the "tearers" and "peckers", Bearded Vultures are solitary nesters, and fairly evenly dispersed. They forage singly or in pairs over an area that is regularly patrolled and presumably intimately known. They usually arrive at carrion before Cape Vultures. During the course of 72 observations at laid-out carrion, the species to arrive first was most frequently the Whitenecked Raven (43% of first arrivals). The Bearded Vulture was the next most frequently recorded species to arrive first (36% of first arrivals).

Figure 6.12 shows the percentage of occasions on which each species arrived in a particular sequence. While the Whitenecked Raven regularly arrived early in the proceedings (usually first or second) and species such as the Cape Vulture and Black Eagle arrived later (third or later), the Bearded Vulture did not fit clearly into either of these
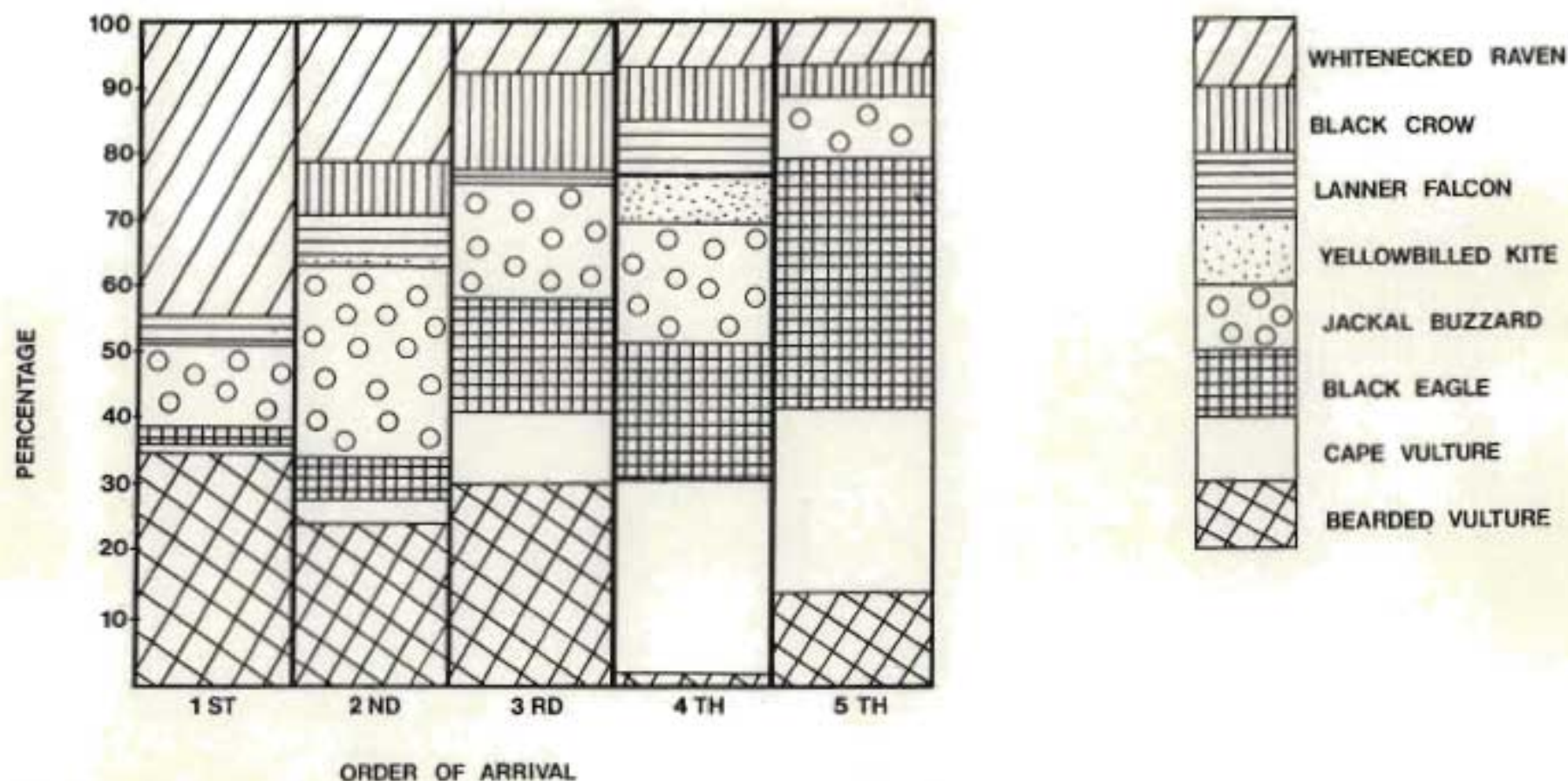
FIGURE 6.12. The percentage of occasions on which carrion-feeding birds in the Giant's Castle area arrived at carrion in a particular sequence.

patterns, but arrived from first to third in relatively high and equal proportions, with a fairly high arrival rate in fifth place! It thus appears to use components of both the early-arrival and late-arrival strategies but biased towards the former.

The first bird to arrive actually <u>finds</u> the food. Birds arriving subsequently, particularly the regular latecomers, <u>e.g.</u> Cape Vultures, may be largely dependent on the activities of other birds to indicate the source of food. This is supported by the fact that Cape Vultures often descended when small food items such as a few handfulls of bones had been laid out - enough to attract Whitenecked Ravens and Bearded Vultures, but almost impossible for Cape Vultures to use as they cannot swallow the bones and are not adept at picking off small pieces of meat. These birds passed low over the food, then usually departed. The Bearded Vulture is both an active searcher for food and a watcher of other birds (and possibly mammals), the Whitenecked Raven being a particularly attractive indicator. Bearded Vultures were often seen to deviate from their flight path to pass over a Whitenecked Raven, and Jackal Buzzards did the same. Feeding Cape Vultures sometimes bounced across to where a Whitenecked Raven was pecking at a scrap, but ignored feeding Bearded Vultures and other species.

Most of the carcasses encountered by Bearded Vultures were medium to small animals, mainly sheep and small antelopes. At two large-animal carcasses under observation (horse and cow), Bearded Vultures made no attempt to feed

although they were present with Whitenecked Ravens for 20 min and over half an hour respectively before the arrivals of the first Cape Vultures. At smaller unopened carcasses, (e.g. sheep, Mountain Reedbuck), Bearded Vultures were successfully able to tear the skin and gain access to the red meat. However, the extremely cautious approach made by Bearded Vultures when they were the first to arrive usually resulted in another species actually feeding first.

If a Bearded Vulture was the first bird present it would circle the carcass in the air, often departing for short periods, then returning to circle. After perhaps 15-20 min it might land, at least 5 m from the carcass, and stand nervously looking about. It would probably take off to circle again, then land slightly closer. It might now walk a few paces towards the carcass, continuing to peer nervously in all directions, with head and neck bobbing jerkily from side to side.

As it got nearer to the carcass it became more and more cautious, and the final approach usually involved the bird walking around the carcass. The entire procedure might take the Bearded Vulture 30 min or more before it attempted to feed.

Bearded Vultures were never seen to perch on top of carcasses as do Black Eagles (perhaps this aggressive dominant stance is partly responsible for the antagonism shown towards Black Eagles by many farmers, due to their assumption that this eagle was the predator responsible for

the stock loss) but preferred to feed standing on the ground. When Whitenecked Ravens were present and feeding, Bearded Vultures would land nearby (1-2 m) and walk across to the carcass with more confidence. They then began to feed immediately.

Bearded Vultures were never seen feeding for long before Cape Vultures arrived, but on four occasions they obtained some food. On three of these the food came from a hindlimb and on one from the rump. The food was red meat, which they tore off by walking backwards and pulling, or tearing upwards with one foot on the carcass. Once Cape Vultures began to arrive (and they often came straight in to feed if they saw Bearded Vultures busy feeding) then the Bearded Vultures retreated, usually taking off and circling to land some distance away until the feeding frenzy generated by the Cape Vultures had died down. Towards the end of the furore, when there were only pickings left for the Cape Vultures, although a few latecomers were usually still present and bouncing from one scrap to the other, the Bearded Vultures began feeding again, walking in among the Cape Vultures with little concern. They sometimes picked up scraps, often pieces of bone or skin too large for the Cape Vultures to swallow, but usually they headed straight for the carcass where they removed sections of limbs by tearing at the tendons connecting the bones, and flew off with these in their talons, carried lengthways and well tucked up against the abdomen. While disarticulating bones, small pieces of muscle or tendon were often torn off and

swallowed. On two occasions, immature birds removed limb bones from the carcass, walked a little to one side and then proceeded to swallow the bones there.

Bearded Vultures obtained a significant proportion of their diet as small items, detected from medium or low altitudes, either as scraps of bone and skin discarded by other species, or as components of carcasses that had become scattered over a larger area. The percentage of food obtained from the respective sources is not known, and it would be difficult to determine where one stopped and the other started, because the sites of carcasses are revisited for several weeks, the remaining skeletal parts becoming more and more dispersed. When a small food item was encountered the birds would land either next to or on the piece of food. This would be grasped with one foot, the other being used to push off. Once in the air, the food was held with both feet, one behind the other. Should a number of small food items be scattered about, Bearded Vultures would often pick food up and swallow it, although they usually stood clasping the item for a while before attempting to swallow. This presumably was done so that, should a quick departure be necessary during this stage, the food could still be carried away. Once the first item had been swallowed, the birds moved across to other pieces, this behaviour being more common in young birds than in adults, the latter preferring to fly off with the food and return for additional pieces. Birds were never seen feeding or

pecking at food on the wing (cf. Newman 1969).

Bearded Vultures almost invariably carried food in their feet. Of the 257 occasions when birds were seen carrying food, an item was carried in the bill only once. This was a small bone (section of small ungulate rib) with fresh meat attached. On take-off, particularly when nervous or taking off in a hurry, small food items were sometimes held in the bill. These were soon transferred to the feet and tucked up against the body. When attempting to land on narrow ledges or small entrances to nests, birds occasionally transferred food from feet to bill, freeing both feet for the landing. This was, however, unusual and birds more commonly landed with the food in one talon, the other one being free to clasp the crag.

Food items that could not immediately be swallowed were usually (in the case of adults) and often (in the case of young birds) carried away to a ledge or pothole on a cliff, where the bird could feed in relative safety. Once on the cliff the bird pinned the food down, usually with both feet, while pulling and tearing pieces off with its bill. The bird usually faced out from the pothole or ledge with feet slightly apart. The head was lowered between the legs and soft tissue was torn from the bone by the upward heave of the whole body, from legs and shoulders to neck and head. Each piece was swallowed with a forward jerk of the head. A slight pause between tearing off food and swallowing occurred, while the bird looked about. After swallowing the head was lowered immediately. Should a section prove to be

particularly tough, the bird would interrupt its tugging after 5-6 s to look about for a second or two before resuming. Sometimes slow pulling motions were executed, presumably to remove strips of muscle or connective tissue.

Bearded Vultures were very adept at pecking and tearing off the smaller soft components adhering to bones. Once most of this soft material had been removed, the bones would be disarticulated (if required) by tearing at the tendons connecting them. A bird was also seen standing on a bone and twisting another, albeit rather clumsily, by grasping the second bone in its bill and twisting its head from side to side. Disarticulation is quickly achieved, even in larger ungulates, e.g. Red Hartebeest, where birds selected the most suitable joint and cut and tore through the tendons. If small enough, the freed bone was held near one end and lifted in the bill. The head was then thrown back with the bill pointing almost vertically upwards, and the bone was caught in the mouth. A couple of flicks of the head were sometimes required to align the bone correctly. The bird then attempted to swallow the bone, with the head and neck being revolved and stretched from side to side and up and down in an effort to accommodate the bone. With a large bone, the whole throat region became dilated as the bone passed through, and the feathers on the throat and neck stood out in a ruff. Often a number of attempts were made with large bones, the bone being regurgitated and the process repeated. Up to six such attempts were sometimes

observed before a large bone was successfully swallowed. After swallowing a bone the bird would stretch its neck out forward and slightly side to side once or twice. Bearded Vultures sometimes tried to swallow absurdly large bones, but after a number of failures the bird would resume pecking at bits of tissue on the bone, or would take off in search of a bone-dropping site. Bones up to at least 250 mm long and 35 mm in diameter were swallowed and sharp splintered ends seem to cause no discomfort. Feeding periods lasted for 40 min or more, much of this time being spent in food preparation. Food was rarely abandoned except in "pantry" potholes near nests during the incubation stage. Reserves of food were built up in the nest during the nestling period, but no other form of caching was observed. Birds normally flew off with what remained of the food, even occasionally roosting overnight with a bone in their talons. After feeding, birds sometimes wiped their bills on the edge of a rock, but while this was common in some raptors, e.g. Black Eagles, Lanner Falcons (pers. obs.) it was unusual in Bearded Vultures.

6.3.5 Bone dropping

A unique form of food preparation undertaken by Bearded Vultures is the dropping of bones onto a rocky substrate to reduce them to sizes more suitable for swallowing and to gain access to the marrow. Although considered by some to be an accidental happening (Meinertzhagen 1959) or "no more than a side-line" (Ferguson-Lees 1960), bone dropping has

been shown to be a deliberate behaviour to assist feeding (North 1948; Huxley & Nicholson 1963; Brown 1970; Boudoint 1976), and a regular and important part of food preparation (Glutz von Blotzheim et al. 1971; Suetens & van Groenendael 1973; Hiraldo et al. 1979).

During the course of this study bone dropping was observed on 67 different occasions (details were recorded on 22 of these when I was sufficiently close) and, if I had wished to, I could have observed it on most days by visiting one of the bone dropping sites. In addition, bone dropping can be "encouraged" by placing suitable bones at such a site, particularly during the non-breeding season (cf. B.B.C. film "Life in the air", of the series "Planet Earth" part of which was filmed in the Natal and Lesotho Drakensberg under my guidance). During the breeding season, birds are inclined to carry the bones off to their nests.

Bone dropping sites, called ossuaries, were divided into three types:

(a) sites used regularly (often daily) within the "activity area" and used almost exclusively by the resident pair of Bearded Vultures and their offspring.

(b) sites used frequently, away from nesting areas, by any bird which happens to be in the vicinity and in need of an ossuary. These sites are used frequently because of their superior characteristics.

(c) sites used irregularly or on a once only basis, usually wherever the bird happens to be, and not used more often either because birds are rarely in the area or because

the site does not possess ideal qualities.

Altogether 18 ossuaries were found during the course of this study. These are listed in Table 6.17 together with certain physical characteristics thought to be important in their selection. All regularly used sites (n = 8) were slabs of smooth rock. Two of the three irregularly used sites consisted of areas with a high concentration of loose boulders. All sites were on slopes, varying between 10° and 30°. Most of the smooth slabs were convex in shape so the degree of slope of these was taken as the average slope measured by the drop from one side of the ossuary to the other. The Jarding Pass ossuary was divided horizontally into two sections by a 2-m rounded cliff, but all other smooth slab sites were fairly uniform in shape. The aspect of these ossuaries (Figure 6.13) was mainly northerly, but ranged through the northern sector of the compass from east to west. No sites faced in a southerly direction. Sizes of ossuaries were generally large, the regularly and frequently used sites ranging from 205-14288 m^2 (cf. Steyn (1982) who implies that bone dropping is usually carried out on a flat slab of rock no larger than 4 m^2). It was not possible to measure the size of scattered boulder type ossuaries, but the Bamboo Hollow site, used very occasionally, was considerably smaller (48 m^2) than the more frequently used sites. Of the regularly and frequently used sites, 87% were on the summit of hills, ridges and escarpments, while two of the three irregularly used sites were near the base of
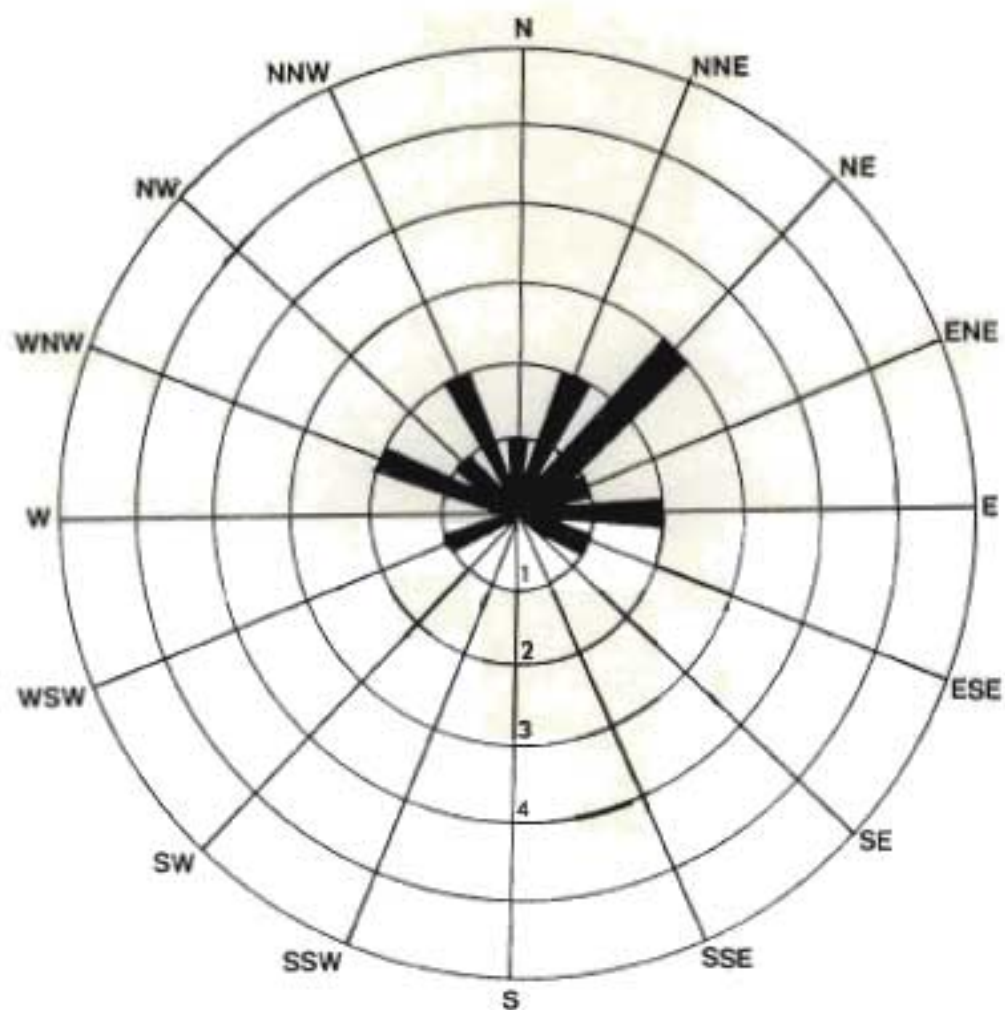
FIGURE 6.13. The orientation of ossuaries used by Bearded Vultures in southern Africa.

hills. All regularly used ossuaries afforded an unobstructed view in all directions for at least 500 m, and most sites for many kilometers, whereas two of the three occasionally used sites had visibilities of less than 100 m in some directions.

Bone dropping has been described by Brown & Amadon (1968) and Boudoint (1976) in some detail. During the course of this study, however, bone dropping was filmed at close range. Three slightly differing methods of bone dropping were recorded. The method most commonly employed by adult birds (Figure 6.14.A) was to glide down-wind towards the dropping zone in a very shallow dive, sometimes steepening the dive just before releasing the bone. A few seconds before release, the legs would be lowered, while the bone was held firmly with one talon, the other being used to steady the bone. Just before release the bird would check very slightly by lowering its tail a little and fanning its wings a little upwards. The bone would then be either passively released or pushed away from the body. The bird would then resume its normal gliding posture before commencing the descent.

In the second method (Figure 6.14.B) the bird glides in over the dropping zone in the normal shallow dive and, just before dropping, executes a sharp turn in a steeper dive. At the sharpest point of the turn the bone is vigorously pushed away, giving the impression that the bird is throwing the bone at the ossuary.

The third bone-dropping method observed (Figure 6.14.C),
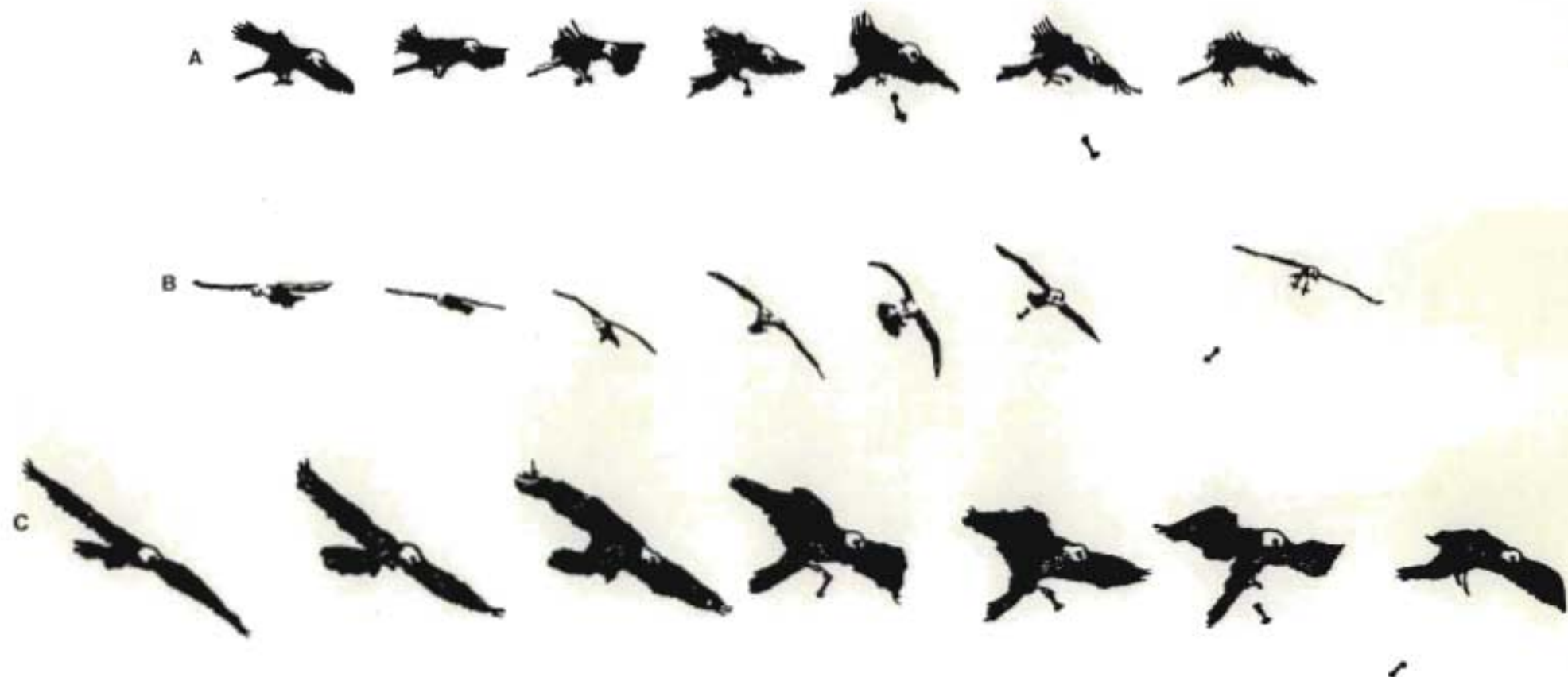
FIGURE 6.14. Three different bone-dropping methods of the Bearded Vulture, filmed at the Thumb Ridge ossuary in Giant's Castle Game Reserve.

and one usually employed by young, unpracticed birds, involves the normal approach, but when above the dropping zone the bird brakes sharply before the release. The tail is pulled well down, the wings are fanned steeply upwards and sometimes the bird hovers for a wingbeat or two before dropping the bone. After the release the bird might sometimes have to dive quite steeply to regain gliding speed.

After dropping a bone the bird would circle slowly down to land (particularly if there were no other Bearded Vultures or Whitenecked Ravens in sight) or more usually, turn sharply into the wind and descend almost vertically with fanning wings to land beside the bone or fragments. The bone rarely broke on the first drop, and the same bone could be dropped more than 20 times, although the mean number of drops per bone was 6,3 (range 1-21). Of the 17 identified bones in this sample, one was a scapula and all others (94%) were long bones of medium and large ungulates. The height from which bones were dropped was estimated visually. The mean height of 139 drops was 56 m (range 16-70 m).

In all cases observed, the ossuary was approached downwind, and take-offs were into the wind. The bone was grasped with one foot, the other being used to push off from the sloping ground. Usually one or two wingbeats would suffice and often no flapping was necessary at all. The bird would pick up slope lift, and after gaining sufficient height, would return to the dropping area. The topography and wind strength affected the rate at which bone-dropping

took place: in one case a bone was dropped six times in succession in under 2 min (over three drops per min) while in another case five drops took over 9 min (0,5 drops per min). In both cases approximately the same amount of time was spent on the ground retrieving the unbroken bone, but in the first case, strong slope lift allowed the bird to rise up rapidly whereas in the second case the bird had to travel back and forth for over 1 km along the ridge before sufficient height had been gained to approach the ossuary for another drop.

All bones dropped onto rock slabs hit the target area. Drops on scattered boulders were less successful, four of 10 drops missing the boulders and landing on grass-covered ground.

6.3.6 Competition

Much has been written on interactions between scavenging birds (e.g. Attwell 1963; Kruuk 1967; König 1974, 1983; Alvarez et al. 1976; Houston 1980; Mundy 1982; Richardson 1984) but little information exists on the behaviour and position of the Bearded Vulture in these interactions. Those accounts that do exist are mostly incidental, and indicate that Bearded Vultures are (a) generally not aggressive, (b) tend to be submissive to most other avian scavengers and (c) avoid interactions as far as possible (e.g. Meinertzhagen 1959; Cramp & Simmons 1980). The results from this study support the first and last contentions but not the second. Interactions at food

sources were divided into three parts, (i) the arrival of one species resulting in the departure of another without any interaction, (ii) interactions in the air and (iii) interactions on the ground.

On sighting the approach of a Black Eagle all other species except Cape Vultures would take off, sometimes to settle again after the Black Eagle had landed. If only one or two Cape Vultures were present at food, they would be obviously nervous on the approach of a Black Eagle and would stop feeding and watch the bird until it had landed, whereas a larger group of Cape Vultures would pay no attention to an approaching eagle. On the arrival of a Bearded Vulture, Black Eagles would sometimes take off (54% of occasions), Lanner Falcons always took off and Jackal Buzzards and Whitenecked Ravens took off on 67% and 36% of occasions respectively. Bearded Vultures at food paid little attention to the arrival of species other than Black Eagles, and it was only after the dash for food by Cape Vultures had begun that Bearded Vultures would give way; the initial arrival of Cape Vultures elicited little reaction. Bearded Vultures would, however, carefully watch the approach of Jackal Buzzards, which often dived aggressively at feeding birds.

Although the larger raptors were sometimes attacked aggressively in the air by smaller species in the vicinity of food, these attacks never succeeded in driving the larger birds away. Whitenecked Ravens and Lanner Falcons were particularly persistent in their attacks on Black Eagles and

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Jackal Buzzards, and ravens also mobbed Bearded Vultures, although far less persistently. Records of aggressive aerial pursuits by large raptors on other birds were mainly of Black Eagles chasing Whitenecked Ravens and Bearded Vultures, particularly when these latter two species were carrying food. Of nine such chases observed, the Black Eagle never succeeded in obtaining any food. On three occasions Bearded Vultures were recorded chasing Whitenecked Ravens with food, twisting and turning sharply in pursuits that commenced high on a ridge and went out of sight about 2 km downstream in a deep valley. In all cases the ravens fairly easily out-manoeuvred the Bearded Vultures and retained their food. Bearded Vultures were never seen attacking other species in the air, although twice, short aggressive flights were made by adults at immature birds, which quickly gave way.

On the ground Cape Vultures were undisputedly the dominant species and a single Cape Vulture would easily drive off a pair of Black Eagles from a small food source. Cape Vultures, although dominant, were tolerant of other species feeding nearby, and Black Crows, Whitenecked Ravens and Bearded Vultures could move and feed freely within 0,5 m of a Cape Vulture. These species never ventured so close to Black Eagles. Bearded Vultures and Black Eagles seemed to keep a mutual distance of 3-4 m between each other and no interactions on the ground were ever observed; Bearded Vultures appeared to be more alert in the presence of Black Eagles than _vice versa_, however, and on a few occasions

Bearded Vultures did not land at food until the Black Eagles
had left.

Nine interactions between Cape Vultures and Bearded
Vultures were recorded and in all cases the Bearded
Vultures immediately gave way to both adult and immature
Cape Vultures. Of 11 interactions between adult and immature
Bearded Vultures, the adult birds were always dominant.
Interactions between adult birds clearly showed the absence
of territoriality; on two of three occasions birds nesting
nearest to the feeding site (about 5 km away) were
submissive to birds nesting at least 18 km away. In all
Bearded Vulture interactions observed, physical contact
never took place. When aggression was shown towards Bearded
Vultures by dominant individuals or species they immediately
gave ground, and aggression in Bearded Vultures was
expressed simply by the bird walking purposefully towards
its opponent; no aggressive postures such as are adopted by
Gyps and some other vultures were used. When taking into
account the amount of time spent watching birds at food
(about 120 days), very few interactions indeed involving
Bearded Vultures took place. The dominance order of
scavenging birds in the Drakensberg is summarized in Figure
6.15.

6.4 DISCUSSION

6.4.1 Foraging strategies

Different searching methods have not previously been
recognized and adequately covered in general accounts of the

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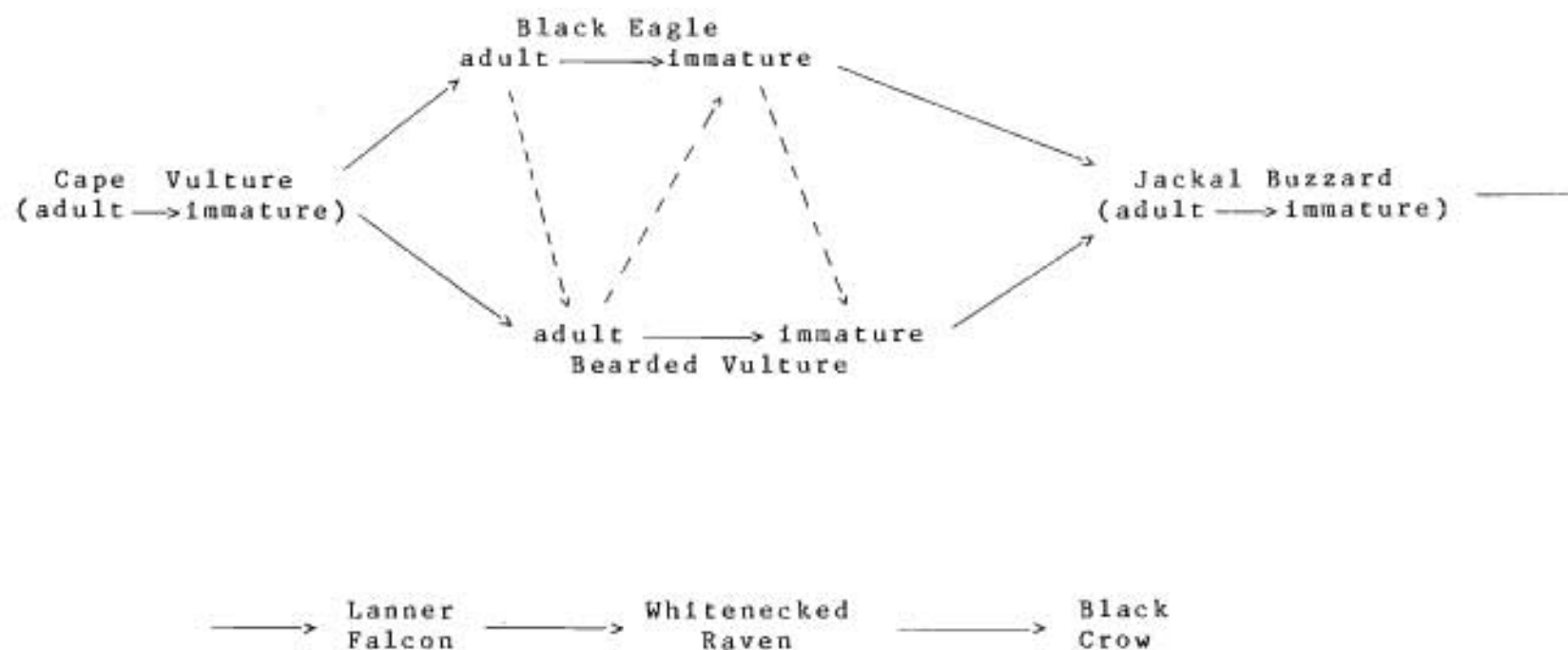
FIGURE 6.15. Dominance order of birds attracted to carrion in the Natal

Drakensberg. (Dominant ———→Submissive)

foraging of Bearded Vultures. Low and high gliding have been reported by Kelham (1909) and Berg (1931) but these were not related to different searching methods. Schaefer (1938) stated that the Bearded Vulture gets its food by methodically searching at a low, constant height above the ground, and Rudebeck (1956) described another technique where "the bird passes over at considerable speed rather high up, with wings markedly angled". He suggested that this flying manner allows the bird to inspect large areas within a short time.

Medium-height searching (at around 50 m) was found to be the most common foraging method used at all times of the day and throughout the year. The birds made use of slope lift, usually along a ridge but also along a large hillside, travelling fairly fast. Using this method, fairly large areas could be covered quite thoroughly with little energy expended, as only gliding flight was used. Birds using this foraging method were freed from the need to thermal, and any small breeze from any direction (and I have never known a totally windstill day in the Drakensberg) would make some area suitable for slope-lift foraging. From this foraging height birds descended to low searching, covering a very small area in great detail. A pair of Bearded Vultures foraging together took 16 min to cover an area on a hillside of about 800 x 900 m whereas two sweeps of the area at medium height took just under 2 min. The properties of a particular area which make it attractive to low searching are not known, but low searching is probably used to find

small items of food that would be overlooked at higher levels.

High searching combined fast cross-country travel (sometimes in excess of 100 km/h) with a more coarse level of foraging, where either large food items (carcasses) or the feeding activities of other scavengers were sought. High searching started much later in the day than did the other two methods because it was the only form of foraging that was dependent on the formation of thermal activity.

The amount of time spent foraging by adult birds increased during the breeding season (June to December) and, as would be expected, the contributing components of low-level and medium-height searching also increased. High searching, however, showed the converse trend; less high searching was recorded between May and November than during the rest of the year. Two factors are thought to be responsible for this: (a) in winter thermalling conditions are less favourable than in summer, and (b) during the breeding season parent birds are confined to a far smaller range about their nest, and foraging periods are fairly short. They therefore undertake fewer and less extensive cross-country flights because most of their foraging is concentrated in the vicinity of their nest, using mainly medium- and low-searching methods.

Although Bearded Vultures are usually reported in the literature as foraging singly (Cramp & Simmons 1980) my study shows that two birds foraging together (sometimes

three in the case of immature birds) is a more frequent group size. Newton (1979) recognizes three main patterns of dispersion of raptors in relation to food supply, ranging from solitary nesting species with individual home ranges (defended to a greater or lesser extent) which feed on an evenly distributed and predictable food supply, to colonial species which forage gregariously on unpredictable but superabundant sources of food. Bearded Vultures are solitary nesters and therefore fall most nearly into the first category, one which contains most of the raptor genera. Bearded Vultures differ from most other members in this category, however, in the following ways.

(a) They do not defend any area other than that immediately about their nest (i.e. up to about 500 m in radius) and therefore no foraging range is protected. Foraging ranges therefore overlap extensively.

(b) They do not feed on live vertebrate prey but rather on carrion and particularly on bones, but they nevertheless do show considerable stability in numbers and distribution from year to year.

(c) Individuals do not usually hunt and roost solitarily, but favour groups of two (sometimes three), even reducing nest-site aggression between neighbouring pairs to achieve this foraging group size during the breeding season.

Carcasses are sporadic, unpredictable superabundances of food that can be exploited by many birds, and the formation of a "foraging net", made up of most or all of the individuals in a colony (as occurs in the Gyps vultures),

greatly increases the likelihood of the birds finding food. Bearded Vultures, however, although they feed on carcasses when available, are rarely in a position to exploit these food sources effectively as they are usually quickly evicted by Cape Vultures. Based on some of the ecological characteristics of the Bearded Vulture (e.g. solitary nesting, even distribution, small foraging groups and apparent longterm stability of the population) it could be predicted that these birds have a fairly uniform, stable and reliable food supply. This may seem surprising since much of their food is derived from what remains of a carcass after the Cape Vultures have fed on it.

A carcass remains viable as a food source for Gyps vultures for perhaps five days after death in summer and a week in winter. Thereafter the soft tissue becomes liquid and maggots rapidly consume what remains. Therefore, if Cape Vultures do not find a carcass within the first few days they have missed out on it. The food supply of the Cape Vulture is thus not only spatially sparse but also temporally fairly transient. The remains of a carcass, whether located by Cape Vultures or not, remains viable to Bearded Vultures for many weeks or perhaps even months. In addition, large carcasses are easily located by Bearded Vultures by observation of the descent of many Cape Vultures, so that little effort is necessary to locate such a food source. Finally, Bearded Vultures are not restricted solely to bones and the remains of medium and large

carcasses, but can opportunistically exploit any form of carrion from small rodents to large fresh carcasses.

All the above factors suggest that Bearded Vultures have a somewhat more stable and predictable food supply than do many carrion-feeding birds, and particularly the Gyps vultures which feed only on carcasses of medium and large vertebrates. Nevertheless, the Bearded Vulture's food supply is probably not as uniform, stable and predictable as that of most solitary hunting and nesting eagles which feed on live vertebrate prey. I suggest that Bearded Vultures are able to compensate for this in the following ways:

(a) They spend a large part of the day (almost 11 h) in flight, up to 83% of which time may be spent in foraging or foraging-related activities. This is considerably longer than the time spent foraging by any eagle which has been studied and is even longer than the average time spent foraging by the colonial Cape Vulture (this study, Chapter 8).

(b) They are flexible in their foraging patterns, being able to search from a great height and speed over large areas in a short period of time for large items of food as well as from very low levels above the ground for small items of food. They are therefore able to locate any form of carrion within their foraging range.

(c) They are able both to locate their own food sources and to make use of other scavengers to lead them to food.

(d) They have totally overlapping foraging ranges allowing a superabundance of food to be utilized by as many Bearded

Vultures as can locate it.

(e) They have huge home ranges with no absolute boundaries, allowing them to exploit food sources many kilometres from their nests. During the non-breeding season they often remain away from their nest sites for many days and range over still larger areas (see Chapter 5).

(f) They have both physiological and behavioural adaptations which enable them to eat bones. This food source is long lasting, high in energy and is not used by any other species in that area. There is therefore no competition for this resource from other species.

(g) They store food (sometimes in large quantities) in the nest during the nestling period. This ensures that during this period when food is most in demand and when they are restricted by nest duties to the area that they can cover in the limited time available for foraging, they can make best use of super-abundances to tide them over periods when food may be in short supply.

(h) They carry food in their feet. The nature of their food means that they can remove large sections, (e.g. limbs that weigh up to at least 5 kg), and carry these away to feed at their leisure or store them in the nest during the nestling period. Cape Vultures, by comparison, can transport food only in their crop which can accommodate up to about 1 kg of meat (Richardson 1984).   Thus although a Cape Vulture population can use a   suber-abundant food source, the individuals are limited by what they can carry in their

crops.

(i) They have evolved a group-foraging strategy where two or three birds forage together, thereby covering perhaps twice the area that a single bird would cover. This implies that the food source is usually sufficient to feed at least two individuals and sometimes four, because during the breeding season birds would be foraging for their nestling as well as for themselves.

(j) They are not aggressive at large food sources, which allows many Bearded Vultures to congregate and make best use of a superabundance.

Bearded Vultures could not nest colonially as they rely on their spatial distribution to exploit a relatively small, widespread food supply. They could not be highly gregarious in their foraging because their main source of food usually comes in small quantities sufficient usually for two to four birds but probably not more. They nest solitarily and fairly evenly spaced out and the combination of all the above strategies and specializations enables them to survive a fairly spatially sparse and unpredictable food supply. This implies, however, that Bearded Vultures have a fairly narrow survival margin and that they make use of a wide range of strategies to survive. This is a situation that would be expected in a highly specialized species, and it could be predicted that Bearded Vultures would be highly vulnerable should a change take place that would substantially reduce the amount of food available or adversely affect its periodicity. The extinction of the

Egyptian Vulture in southern Africa may be a similar case (as intimated by Mundy 1978), whereas for species such as the Holarctic Golden Eagle _Aquila chrysaetos_, the average food potential within the home range is usually greatly in excess of the requirements, and in two areas where drastic reductions in food supply took place, no decline in eagle densities occurred (Brown & Watson 1964).

6.4.2 Food choice

During this study an effort was made to obtain as wide a coverage as possible of the food eaten by Bearded Vultures. Nevertheless, items such as soft tissue and small food items will have been under-represented because these are swallowed whole and no evidence remains. In addition, samples from different sources _i.e._ nests, ossuaries, farmlands, _etc._, are not of equal size, so that, while Tables 6.10-6.15 have been kept separate, the composite picture in Figure 6.11 is intended to show only very general trends. It is nevertheless obvious that Bearded Vultures are highly dependent on domestic stock for food. Even birds nesting in conservation areas, _e.g._ Giant's Castle Game Reserve, Golden Gate Highlands National Park and Cobham Forestry Reserve, were largely dependent on domestic stock from adjacent regions; 55% of bones collected below four nests (n = 121) in these conservation areas were from domestic stock. This is not surprising as the home range size of the Bearded Vulture is many times the size of the largest conservation area in the Drakensberg. This means

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that these reserves can neither adequately contain a single pair of Bearded Vultures nor provide sufficient food throughout the year to support a viable population. Bearded Vultures are therefore reliant on the adjacent farming communities of Natal and KwaZulu, and on the Basotho stockmen of Lesotho for their longterm survival.

Tooth remains found at ossuaries indicated that the bones of mainly adult and old mammals were brought for breaking, and these were mostly of larger animals (e.g. horses and cattle). This is to be expected as the bones of adult larger animals would be too large to swallow whole and would need to be broken. In addition, larger bones contain less energy per net weight and Bearded Vultures are inclined to scoop out the marrow and reject much of the calcified material. Smaller bones, which are nevertheless too large to swallow whole, are often broken into two or three pieces and these are then swallowed in their entirety, leaving no more than a few unidentifiable flakes of bone behind. Cattle and horse bones made up only 12% of the food that I saw Bearded Vultures bring to their nests, whereas sheep and goats accounted for over 84%. Conversely, of the items collected below nests, 50% were cattle, horse and donkey bones and 48% were sheep and goat bones. Much evidence of young animals in the diet of Bearded Vultures was obtained from below nests.

Bearded Vultures have a nestling in the nest from September to January. This coincides with both the period of spring lambing and the period of highest game and domestic-stock mortality (see Chapter 8). Young animals are most

vulnerable, particularly if their parents are in poor condition, and it would be expected that these would form a significant part of the diet of scavengers during this period. While smaller bones and soft parts are usually fed to young nestlings, they soon take larger bones. Bones too large for the nestlings are eaten by the adults. Bones of medium and small ungulates found below nests have therefore probably fallen or been knocked out accidentally. Birds never deliberately cleaned out old bones or other food, and never flew off with food remains. Bones of larger animals that could not be swallowed by adult birds would therefore accumulate and fall out of the nest, which probably accounts for the high percentage of larger bones found below nests.

During this study I never saw Bearded Vultures take live prey and no incident led to the speculation that this was probable. Although Rock Hyrax skulls made up over 4% of all prey remains found at nests and ossuaries this does not automatically mean that the animals were killed by Bearded Vultures. Black Eagles are common residents throughout the range of the Bearded Vulture in southern Africa, and these eagles feed almost exclusively on the Rock Hyrax (Gargett 1971; Steyn 1982). During the breeding season Rock Hyraxes are often brought to the nests of Black Eagles already beheaded (Rowe 1947; Gargett 1971, 1972). In addition, while the skull may be picked clean of external musculature, Black Eagles cannot get at the brains, and the skull usually falls off the nest or feeding perch and may then be picked up by

Bearded Vultures which would be able to feed on the brains by dropping the skull to crack it open. While a number of records exist confirming that whole Rock Hyrax carcasses were carried by Bearded Vultures (and even dropped) (Newman 1969; farmers questionnaires), these animals could well have been picked up dead. Two observations support this: (a) Bearded Vultures were never seen hunting in a manner which would be effective for capturing a hyrax, and (b) when Bearded Vultures flew over a group of sunning hyraxes they paid little attention to the bird, whereas, when a Black Eagle appeared the group scattered for shelter, some emerging cautiously to screech at the eagle. Other instances of predator avoidance have been seen, in which Mountain Reedbuck and Grey Rhebok with small young took off in haste down steep hillsides to gain the protection of patches of woody vegetation at the approach of a pair of Black Eagles. These antelope paid no attention to Bearded Vultures passing a few metres overhead. This is even more apparent in the case of domestic smallstock. During lambing in the highlands of Lesotho the presence of a Black Eagle caused sheep to huddle in small groups, protecting their lambs. Bearded Vultures, by contrast, would fly in and land between the sheep and walk to within 1 m of animals with lambs to feed on the afterbirths, causing no concern whatsoever. A similar situation has been reported by Rudebeck (1956) for domestic goats in Lesotho, and by Kelham (1909) for goats and Ibex in the Himalayas.

The record of a rodent at the Mt. Erskine ossuary in

Giant's Castle Game Reserve is probably not attributable to Bearded Vultures, as such food would have been swallowed whole. Two farmers reported small mammals in the diet of Bearded Vultures, but I viewed these records with suspicion as bal-chatri traps baited with live white mice evoked no interest in the birds. However, a Bearded Vulture was seen bringing rodents to its nest in the Cobham State Forestry Reserve (W. Small pers. comm.). While it is possible that Bearded Vultures captured these animals alive, it is more likely that they scavenged them, as these observations coincided with the burning season in the Drakensberg when rodent mortality is high (Rowe-Rowe & Lowry 1982). In Spain dead rats were also brought to a nest (Ferguson-Lees 1960) and these were obviously scavenged as they were dried out on delivery. Prey records of species such as Wood Pigeons and Redlegged Partridge recorded by Suetens & van Groenendael (1973) at nests in Spain were considered by the authors as "most probably collected as dead birds, as there are many under the snow on passes, where the Lammergeiers are frequently seen hunting on the fringe of the receding snow".

The reports by a few farmers that Bearded Vultures kill young smallstock are highly unlikely. Less than 5% of farmers who reported the birds on their farms held this opinion, whereas 28% thought that Cape Vultures attacked young and calving livestock (Brown & Piper in press). The impression that scavengers are responsible for predation is sometimes gained when the farmer arrives at a dead animal to

find a large bird of prey present and feeding. For example, at seven lamb and sheep carcasses that were reported by farmers to have been killed by Black Eagles in the southern Drakensberg areas of Natal, six had clear evidence of domestic dog, Blackbacked Jackal and Caracal *Felis* *caracal* predation before the arrival of the Black Eagle, and at only one carcass could no other evidence of predation or disease be found (pers. obs.). The behaviour of small domestic stock in the presence of Bearded Vultures suggests that these birds do not attack live animals.

Reports of attacks on other animals and even man, particularly when near the edge of a precipice, are not uncommon, but mainly from old literature, (e.g. Bree 1875; von Czynk 1890), although these have been quoted widely in modern writings. The most recent reports of this behaviour are by Meinertzhagen (1959), who, in highly emotive terms, refers to the despicable character of the Bearded Vulture, "a bird of unashamed cowardice, ready to take advantage of any animal in distress". He recounts how when in difficulty on a moving scree slope a Bearded Vulture sailed close by him until, by throwing stones, he was able to drive it away. I regard all such stories of attacks on healthy animals, and particularly man, as figments of the imagination. Bearded Vultures in flight are very confiding and inquisitive and they will glide about a person at remarkably close quarters. Their blood red scleral eyering gives them an appearance of ferocity, but on at least 20 days that I sat on the edge of the Drakensberg escarpment with a drop of many hundreds of

metres with Bearded Vultures passing close by on an average of eight times per day, never once did a bird give the impression that it might attack me. In addition, nests visited by descending a rope would have provided ideal opportunities for the bird to attack the intruder, yet this never occurred.

Although not very common in the Giant's Castle area of the Drakensberg, a pair of Klipspringers Oreotragus oreotragus were once seen high on a narrow ledge above an almost vertical cliff, when an adult Bearded Vulture came sweeping around the corner. The bird passed about 4 m above the antelopes but made no attempt to attack them. The Klipspringers in turn made no attempt to get into a more protected site. Bearded Vultures may be attracted by the sound of falling rocks. Twice I accidentally started fairly large rock slides in passes, which echoed over some considerable distance. Within minutes a Bearded Vulture was circling overhead. This may be just coincidence or inquisitiveness, or it may be a response to a sound that may well indicate the death of one or more animals.

Bearded Vultures are specialist foragers, capable of scavenging from a large carcass but also able to find very small food items. This study provides no evidence to support the statement that "in South Africa at least, it (the Bearded Vulture) is a more active predator than is generally realized" (Newman 1969) and all indications are that predation on animals other than very slow moving species

such as tortoises (which do not occur within the range of the Bearded Vulture in southern Africa) are extremely rare indeed.

Finally, while the ability of a bird as large as a Bearded Vulture to live mainly off bones may seem incredible (Newman 1969) this study supports the more recent literature (e.g. Hiraldo et al. 1979; Cramp & Simmons 1980; Steyn 1982) which states that bones are by far the most important component of their diet. Hiraldo et al. (1979) give figures of bones accounting for over 90% of stomach contents and over 80% of all food brought to the nest. In this study birds actively selected bones in preference to lumps of meat and to feeding from a carcass. Of the identifiable food items seen carried by Bearded Vultures away from their nests (n = 136), 89% (by number) were bones, 8% lumps of meat and the rest were whole or large sections of small carcasses. Of the identifiable items brought to nests (n = 53), 81% were bones, 15% meat and 4% carcasses of smaller animals. No detailed quantitative assessment of the amounts of bone, muscle and skin consumed by Bearded Vultures could be made during this study, but 70% bone (with its associated marrow), 25% muscle and 5% skin (ratio of 14:5:1) is probably a reasonably accurate estimate taking into account some feeding from fleshy carcasses. Using figures for the energy contents of these various components given in Chapter 8, 100 g of the food eaten by Bearded Vultures contains about 674 kJ of energy whereas the same mass of muscle provides about 586 kJ of energy, or 87% as much. It is

therefore not so surprising that Bearded Vultures are able
to survive mainly on bones, with older dried-out ones
providing a particularly concentrated source of energy.
Taking into account the possibly higher assimilation energy
of the more inorganic diet Bearded Vultures still get more
energy from their food, weight for weight, than do meat-
eating species.

TABLE 6.1

Group sizes in adult Bearded Vulture per month.

Month	1 Adult		2 Adults		> 2 Adults		Totals
	No.	%	No.	%	No.	%	No.
Jan	19	49	20	51	0	0	39
Feb	20	57	12	34	3	9	35
Mar	21	38	32	57	3	5	56
Apr	9	38	12	50	3	13	24
May	20	47	20	47	3	7	43
Jun	18	45	16	40	6	15	40
Jul	20	63	12	38	0	0	32
Aug	42	49	32	38	11	13	85
Sep	21	60	14	40	0	0	35
Oct	43	68	20	32	0	0	63
Nov	38	60	22	35	3	5	63
Dec	13	46	12	43	3	11	28
Totals	284	52	224	41	35	6	543

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TABLE 6.2

Some non-mated "pairs" of adult Bearded Vultures observed foraging together during the incubation and close-brooding periods of the breeding season in the Giant's Castle area of the Natal Drakensberg.

No.	Date	Time	Birds involved	Sex	Marked	Activity
1	28/07/81	09h50	Mt. Durnford Long Wall south	M M	Yes Yes	Low foraging together approx. 6 km from respective nests. Settled on rock outcrop side by side for about 2 min before resuming low foraging together.
2	20/08/81	15h20	Gypaetus Pt. ?	? ?	Not seen No	Two adults came over escarpment together from Lesotho, one diving down and swopping over at nest, the other swinging north and disappearing around corner.
3	26/08/81	13h15	Long Wall south ?	M ?	Yes No	Medium-height foraging, one behind the other along ridge approx. 8 km from Long Wall south nest site, then thermalling up together and out of sight.
4 & 5	13/10/81	12h45	Long Wall south Long Wall north	M(F) M(F)	Yes(No) *No(Yes)	Both male birds came sailing in to the Long Wall from the south together, the "south bird" swopped with mate, the "north bird" swopping with its mate and both relieved birds (i.e. both females) headed off north along the escarpment together.
6	05/07/82	07h15	Ntabamhlope ?	F ?	No No	Shortly after swopping over at nest bird was gliding along east face of Ntabamhlope when an unmarked adult bird came gliding in from the east. Both birds thermalled together for about 6 min then headed off north, where, with the aid of a telescope, they were observed low- and medium-height searching for over 15 min.

TABLE 6.2 continued

No.	Date	Time	Bird involved	Sex	Marked	Activity
7 & 8	18/07/82	07h00	Long Wall south Long Wall north	M(F) M(F)	Yes(No) *No(Yes)	Adult from L.W. south came gliding along escarpment and settled next to L.W. north male (still on roost, some 45 m from nest). After about 3 min, both took off, south bird returning to nest and swopping over, being accompanied by north bird, which circled near nest entrance, then north bird returned to its nest and swopped over, being accompanied by south bird (female) which circled above cliff. The relieved north bird thermalled up to join the other, then both headed west into Lesotho.
9	18/07/82	11h50	Long Wall south Long Wall north	F F	No Yes	Two Long Wall birds (one south, one north) returned together from Lesotho, both going to their respective nests and swopping over. L.W. north male headed due north, L.W. south male dived down to water pool to bathe and drink.
10	20/07/82	06h55	Mt. Erskine Mt. Durnford	?M M	No Yes	Mt. Erskine bird observed leaving roost site at 07h05 (presumed to be male because did not incubate at night). Mt. Durnford bird came sailing over, Erskine bird flapping to gain altitude to reach it. Both birds soared together for about 7 min, then dived down and were observed foraging along ridges in Natal. At 09h20 both birds were seen thermalling together (presumed to be Mt. Erskine bird due to very pale colour of underparts) and headed due west into Lesotho

* = subadult male paired with female, which formerly nested on Mt Durnford (1980), then moved to the north side of the Long Wall when acquiring the new mate. Not many subadult birds occurred in the area, so identification was fairly reliable.

TABLE 6.3

Group sizes in immature Bearded Vulture per month. Abbreviations are as follows: imm. = immature birds, ad. = adults and C.V. = Cape Vultures.

Month	1 imm.		2&3 imm.		imm.(s) + ad.(s)		imm.(s) + C.V.		Totals
	No.	%	No.	%	No.	%	No.	%	No.
Jan	8	53	2	13	4	27	1	7	15
Feb	9	45	4	20	6	30	1	5	20
Mar	12	50	4	17	6	25	2	8	24
Apr	5	46	2	18	3	27	1	9	11
May	9	47	4	21	5	26	1	5	19
Jun	8	44	2	11	5	28	3	17	18
Jul	5	39	5	39	1	8	2	15	13
Aug	11	37	10	33	5	17	4	13	30
Sep	5	36	6	43	1	7	2	14	14
Oct	7	32	8	36	3	14	4	18	22
Nov	7	32	9	41	3	14	3	14	22
Dec	3	30	3	30	2	20	2	20	10
Totals	89		59		44		26		218

TABLE 6.4

Group sizes of immature Bearded Vultures at and away from nest or roost sites. Abbreviations as for Figure 6.6.

Group composition	Near nest/roost		P	Away from nest/roost		Totals
	No.	%		No.	%	No.
1 imm.	61	28,0	***	28	12,8	89
2 & 3 imm.	18	8,3	**	41	18,8	59
imm.(s) + ad.(s)	17	7,8		27	12,4	44
imm.(s) + C.V.	6	2,8	*	20	9,2	26
(All imm. groups)	41	18,8	***	88	40,4	129
Totals	102	46,8		116	53,2	218

(Chi-squared test: * = P 0,05; ** = P 0,025; *** = P 0,001)

TABLE 6.5

Group sizes of Bearded Vultures recorded on farmlands by farmers in Natal, Orange Free State and the Cape. The abbreviation Gps. refers to the number of groups of birds recorded within a particular group size, and No. refers to the numbers of birds.

Province	Group sizes (No. of birds)																Total no. of birds
	1		2		3		4		5		6		7		8		
	Gps.	No.	Gps.	No.	Gps.	No.	Gps.	No.	Gps.	No.	Gps.	No.	Gps.	No.	Gps.	No.	
Natal	51	51	37	74	4	12	2	8	1	5	1	6	1	7	0	0	163
O.F.S.	10	10	11	22	3	9	1	4	0	0	0	0	0	0	0	0	45
Cape	20	20	27	54	10	30	4	16	2	10	1	6	1	7	1	8	151
Totals	81	81	75	150	17	51	7	28	3	15	2	12	2	14	1	8	359

TABLE 6.6

The food choice of scavenging birds attracted to carrion in the Giant's Castle Game Reserve.

Species	No. birds	Carcass	Meat	Bones							Totals
				Fresh	1 week	2 weeks	3 weeks	4 weeks	5 weeks	plastic	
Bearded Vulture	15	1	4	7	6	9	13	16	14	0	70
Cape Vulture	134	134	27	7	8	0	1	0	0	2	179
Black Eagle	14	1	12	5	1	0	0	0	0	0	19
Jackal Buzzard	9	0	7	4	0	1	0	0	0	0	12
Lanner Falcon	5	0	1	5	0	0	0	0	0	0	6
Whitenecked Raven	18	17	14	19	6	1	2	5	0	3	67
Black Crow	11	0	8	9	0	0	0	0	0	0	17

TABLE 6.7

The sequence of removal by Bearded Vultures of parts from four carcasses in the Giant's Castle area, after the Cape Vultures had completed their feeding.

Order of removal	Sheep (adult)	Sheep (subadult)	Red Hartebeest (adult)	Mountain Reedbuck (adult)
	Carcasses			
1	left humerus to hoof	left scapula to hoof	left metacarpals to hoof	left femur to hoof
2	left femur to hoof	right humerus to hoof	left radius/ulna	left radius/ulna
3	right tibia/fibula	ribcage	left tibia/fibula to hoof	left carpals to hoof
4	left scapula	skull	rib	left humerus
5	rib		rib	caudal vertebrae
6	right femur		rib	right humerus
7	cervical vertebrae		thoracic vertebrae	rib
8	rib		rib	
9	caudal vertebrae			

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TABLE 6.8

The number of farmers who reported sightings of Bearded Vultures, and those who observed the birds feeding on their farms.

Province	Sightings	Feeding	%
Natal	216	84	39
O.F.S	59	16	27
Cape	90	46	51
Totals	365	146	40

TABLE 6.9

The frequency of sightings by farmers of Bearded Vultures feeding on farmlands.

Province	Frequency of sightings									
	Once	Twice	Very seldom	Occas-ionally	Often	When stock is lost	Mainly summer	Winter & spring	Lambing season	Totals
Natal	22	9	15	15	7	5	2	1	0	76
O.F.S.	3	2	5	1	1	2	0	0	2	16
Cape	6	3	7	9	12	4	0	0	0	41
Totals	31	14	27	25	20	11	2	1	2	133
%	23	11	20	19	15	8	2	1	2	101

TABLE 6.10

The food preference of Bearded Vultures as recorded by farmers for birds seen on their farms.

Food	Number of food items reported				
	Natal	O.F.S	Cape	Totals	%
Carrion	9	0	5	14	8
Carcass	7	1	5	13	7
Left-overs from carcass after Cape Vultures have eaten	2	2	2	6	3
Bones	6	1	3	10	6
Dead cattle	16	2	2	20	11
Dead sheep (adult)	35	6	18	59	33
Dead lambs	18	2	4	24	14
Sheep afterbirth	1	1	1	3	2
Small stock, particularly limbs	1	0	2	3	2
Lambs killed by Bearded Vultures	3	0	1	4	2
Goat kids killed by Bearded Vultures	0	2	0	2	1
Antelope carcass	1	0	0	1	1
Black Wildebeest carcass	0	1	0	1	1
Rock Hyrax	2	0	6	8	5
Hares	0	1	2	3	2
Road kill	0	0	1	1	1
Small mammals	0	2	0	2	1
Birds	0	1	2	3	2
Totals	101	22	54	177	102

TABLE 6.11

Food items recorded for Bearded Vultures away from the nest.

Food	Number of food items					
	Lesotho highlands	Giant's Castle Game Reserve	KwaZulu and Natal farms	N.E. Cape farms	Totals	%
Horse carcass	2	0	0	0	2	1
Cattle carcass	3	0	1	0	4	2
Sheep carcass	8	0	4	1	13	6
Lamb carcass	5	0	1	0	6	3
Sheep afterbirth	2	0	0	0	2	1
Sheep limb	17	7	7	1	32	15
Sheep skull	1	0	0	0	1	0
Eland carcass	0	3	0	0	3	1
Black Wildebeest carcass	0	1	0	0	1	0
Red Hartebeest carcass	0	1	0	0	1	0
Mountain Reedbuck carcass	0	3	1	0	4	2
Mountain Reedbuck lamb	0	1	0	0	1	0
Grey Rhebok carcass	0	2	0	0	2	1
Small antelope limb	0	4	0	0	4	2
Small ungulate scapula	2	2	1	0	5	2
Bones - long	26	29	7	2	64	30
Ribs	3	5	1	0	9	4
Vertebrae	3	3	0	0	6	3
Red meat	7	4	0	0	11	5
Dog carcass	1	0	0	0	1	0
Unidentified	19	14	9	0	42	19
Totals	99	79	32	4	214	

TABLE 6.12

Food brought by Bearded Vultures to their nests.

Food	Number of food items					
	Roma	Ntabamhlope	Barkly East	Gypaetus Pt.	Total	%
Horse hoof & tarsals	1	0	0	0	1	2
Cattle hoof & tarsals/carpals	0	0	1	0	1	2
Sheep forelimb	7	1	2	1	11	17
Sheep hindlimb	2	0	1	0	3	5
Sheep hoof & tarsals/carpals	2	0	2	0	4	6
Sheep head	1	0	0	0	1	2
Unidentified sheep piece	1	0	0	0	1	2
Goat hindlimb	2	0	0	0	2	3
Smallstock hindlimb	3	2	0	0	5	8
Small ungulate ribcage	1	0	0	0	1	2
Small ungulate longbone	10	1	2	1	14	21
Dog carcass	1	0	0	0	1	2
Hare	0	0	1	0	1	2
Lumps of red meat	7	1	0	0	8	12
Unidentified	7	1	1	2	11	17
Totals	45	6	10	4	65	104

TABLE 6.13

Bones and bone fragments collected from Bearded Vulture nesting sites and ossuaries.

Skeletal parts	Nesting sites		Ossuaries	
	No.	%	No.	%
Bovid teeth and tooth rows	8	1,7	39	3,8
Bovid skeletal parts	198	43,0	64	6,2
Other identified remains	50	10,9	18	1,7
Enamel fragments	0	0,0	6	0,6
Skull fragments	22	4,8	34	3,3
Vertebral fragments	53	11,5	2	0,2
Sternum fragments	4	0,9	0	0,0
Rib fragments	56	12,2	3	0,3
Bone flakes	42	9,1	732	70,8
Miscellaneous fragments, skin	27	5,8	136	13,2
Total	460		1034	

TABLE 6.14

The identifiable prey remains collected from ossuaries of Bearded Vultures. 1 = Ntabamhlope, 2 = Thumb Ridge, 3 = Giant's Castle, 4 = Giant's Ridge, 5 = Long Wall, 6 = Mt. Erskine, 7 = Jarding Pass, 8 = Sani Pass and 9 = Roma Valley.

Species	Ossuaries									Total	%
	1	2	3	4	5	6	7	8	9		
Horse		8							2	10	6,3
Donkey									2	2	1,3
Equid	1				2					3	1,9
Cattle	3	1				1	2			7	4,4
Probably cattle	22	8		1	1		1	1	12	46	29,1
Sheep	1	1								2	1,3
Goat	1								1	2	1,3
Sheep/goat	17	2	1		2	7	4		1	34	21,5
Grey Rhebok	2									2	1,3
Oribi		3								3	1,3
Small antelope		1		1						2	1,3
Sheep/goat size	15	1		2				1	8	27	17,1
Bovid		3				3				6	3,8
Baboon		1								1	0,6
Rock Hyrax	1								5	6	3,8
Genet					1					1	0,6
Hare	2									2	1,3
Rodent						1				1	0,6
Large bird	1									1	0,6
Total	66	29	1	4	6	12	7	2	31	158	

TABLE 6.15

Prey remains collected from below the nests of Bearded Vultures. Nest site 1 = Roma Valley, 2 = Black Mountain, 3 = Barkly East, 4 = Ntabamhlope, 5 = Cobham State Forestry, 6 = Golden Gate and 7 = Giant's Castle (two nesting pairs).

Species	Nest sites							Total	%
	1	2	3	4	5	6	7		
Horse	2							2	0,7
Donkey	2							2	0,7
Equid		2		4			21	27	10,2
Cattle			3	9			21	33	12,5
Probably cattle	12			2	1			15	5,7
Sheep			35	3	1		16	55	20,7
Goat	1			1		1		3	1,1
Sheep/goat	1	2	14	15	3			35	13,2
Grey Rhebok					1	6		7	2,6
Common Duiker					1			1	0,4
Small antelope					3		1	4	1,5
Sheep/goat size			4	3	1	18		26	9,8
Non-domestic bovid	8			6	4	14		32	12,1
Bovid							4	4	1,5
Rock Hyrax	5		3	1	5			14	5,3
Hare				1		1	1	3	1,1
Medium-large bird					1	1		2	0,7
Total	31	4	59	45	21	41	64	265	

TABLE 6.16

Summary of skeletal remains of food items from Bearded Vulture ossuaries and nesting/roosting sites.

Skeletal parts	Ossuaries		Nests	
	No.	%	No.	%
Skull	79	7,6	89	19,3
Axis	1	0,1	1	0,2
Vertebra	2	0,2	53	11,5
Scapula	7	0,7	27	5,9
Humerus	11	1,1	10	2,2
Radius	4	0,4	6	1,3
Ulna	3	0,3	8	1,7
Rib and sternum	3	0,3	60	13,0
Pelvis	1	0,1	12	2,6
Femur	10	1,0	8	1,7
Tibia	3	0,3	20	4,3
Metapodial	13	1,2	32	7,0
Astragalus	1	0,1	5	1,1
Calcaneum	1	0,1	6	1,3
Patella	0	0,0	1	0,2
Sesmoid	3	0,3	3	0,7
Naviculo-cuboid	2	0,2	4	0,9
Carpal/tarsal	1	0,1	1	0,2
Phalanx 1	9	0,9	13	2,9
Phalanx 2	5	0,5	14	3,0
Terminal phalanx	7	0,7	18	3,9
Bone flakes	732	70,8	42	9,1
Miscellaneous fragments	136	13,2	27	4,8
Total	1034		460	

TABLE 6.17

Some physical parameters of bone-dropping sites (ossuaries) used by Bearded Vultures. Type of ossuary: R = used regularly, F = used frequently and O = used occasionally. Nature of ossuary: 1 = smooth rock, 2 = rocky outcrop (boulders) on ridge and 3 = scattered boulders. Visibility: Good = at least 500 m in all directions, Poor = less than 100 m in some direction.

Locality	Type of ossuary	Nature of ossuary	Slope	Aspect	Dimensions (m x m)	Area (m^2)	Visibility	Topography
Ntabamhlope Centre	R	1	20°	NNE	35x45	1575	Good	High pt. on inselberg
Ntabamhlope East	R	1	25°	NE	14x40	560	Good	Crest of cliff
Ntabamhlope South	R	1	15°	ENE	8x46	368	Good	Crest of cliff
Thumb Ridge East	F	1	15°	NNE	15x42	630	Good	Crest of ridge
Thumb Ridge West	F	1	20°	NE	19x37	703	Good	Crest of ridge
Bamboo Hollow	O	1	8°	NE	4x12	48	Poor	Lip on edge of gorge
eNjesuti jeep track	O	3	20°	E	–	–	Poor	Quarter way up hillside
Giant's Ridge	F	2	–	–	4x60	240	Good	Band of boulders across ridge running NNW-SSE
Mt Erskine	R	1	15°	NNW	16x18	288	Good	Crest of ridge
Jarding Pass	R	1	15°	NNW	26x32	832	Good	Crest of saddle
Long Wall	R	1	10°	E	63x78	4914	Good	Plateau on top of ridge
Long Wall Ridge	F	1	20°	NW	23x31	713	Good	Crest of ridge
Giant's Castle	R	1	20°	–	8x28	224	Good	Ledge near summit
Sani Pass	F	1	10°	ESE	5x41	205	Good	Edge of escarpment
Farm Edgehill	F	1	15°	N	94x152	14288	Good	Ridge on hillside
Tlohoeng village	O	3	–	WNW	–	–	Good	Base of hillside
Roma East	R	1	10°	WNW	26x58	1508	Good	Edge of gorge
Roma West	R	1	15°	WSW	29x140	4060	Good	Summit of plateau

Chapter 7

BREEDING BIOLOGY

7.1 INTRODUCTION

The breeding period is the best known part of the biology of most birds of prey, because at this time observation is facilitated by the fact that the birds must return to a particular site, their nest. Bearded Vulture nest sites, however, are particularly inaccessible. They are difficult to find and impossible to reach without mountaineering equipment. Few sites offer a vantage point from which observations can be made without disturbing the parent birds. For these reasons published accounts on the breeding biology of the Bearded Vulture are incomplete, mainly descriptive and often inaccurate. Descriptive accounts of aspects of the breeding biology have been given by Berg (1931), Lowther (1949), Ferguson-Lees (1960), Stegmann (1961), Steyn (1970), Suetens & von Groenendael (1973), Brown (1977), Boudoint (1978) and, most complete and detailed, by J.J. Guy (in manuscript). General accounts are summarised by Brown & Amadon (1968), Glutz von Blotzheim et al. (1971), Cramp & Simmons (1980), Hiraldo et al. (1979), Brown et al. (1982) and Steyn (1982).

This chapter sets out to describe and quantify the breeding biology of the Bearded Vulture from pre-laying courtship and nest building to the independence of the young vulture.

7.2 METHODS

Bearded Vulture nest sites were located (a) by direct observation, both from the ground and the air, (b) from reports by nature conservation and forestry staff, farmers and other interested people and (c) from the mail questionnaire survey. In areas where nest densities were being determined (e.g. Giant's Castle Game Reserve) consecutive sections of cliffs were watched during the breeding season, from first to last light, for up to three consecutive days or until a nest was discovered. Because nests are usually out of sight in potholes and because the rock face below nests are not heavily "whitewashed" with droppings (cf. Cape Vultures) the presence of a nest could be found usually only by observations of birds "swopping over" i.e. an adult diving down and entering a pothole, followed a few seconds later by the rapid departure of another adult. Nests were located wherever possible while traversing sections of the Drakensberg escarpment, and while driving through Bearded Vulture nesting habitat.

The following physical parameters of Bearded Vulture nesting sites were recorded: (a) cliff rock type, (b) cliff height (from the top of the scree at the base of the cliff), (c) distance from nest to top of cliff, (d) altitude, (e) aspect (of nest entrance), (f) nest type (pothole, pothole/ledge, ledge), (g) presence or absence of overhang above nest, (h) extent of protection of the nest site and the nest entrance, (i) number of alternate nests, (j) distance between alternate nests, (k) other raptor species

and large birds nesting or roosting nearby, and the distance to them, (l) vegetation type and (m) habitat description and land usage in area of nest. Estimates of the length of time that sunlight fell on nests and cliffs at nest entrances were made. When sufficient shade fell on the nest for a bird to be two-thirds out of the sun, the nest was judged to be in shade.

During the first year of the study I did not find a nest site which offered a view into the nest. Because of this a closed-circuit television monitor was placed into a side passage of a nesting pothole. Although care was taken to camouflage the equipment and to keep the bird off the nest for as short a time as possible, the parent birds did not return to incubate even though the equipment was removed the following day.

The following year my attention was drawn to a nest site near Roma, Lesotho, which was kindly shown to me by J.J. Guy, who also made some 200 h of observations available to me in manuscript. This nest, when viewed through a 40 x telescope across a gorge of about 230 m allowed for detailed observations on the breeding activities and became my main source of information. A number of other nests with less satisfactory visibility were also observed to obtain corroborative information. From the start of the breeding season to the first flight of the young vulture, 583 h were spent on direct nest observations. A further period of about 210 h was spent on the post-nestling dependence period of

the young bird, 118 h of which were devoted to radiotracking a Bearded Vulture captured in the Giant's Castle Game Reserve after it had been out of the nest about two months.

The breeding distribution and population estimate of Bearded Vultures in southern Africa is discussed in Chapter 9.

7.3 RESULTS

7.3.1 Nest sites

All Bearded Vulture nests found were on cliffs of either basalt or cave sandstone formation. As basalt overlies the sandstone, nests in sandstone were at lower altitudes than those in basalt. The breeding sites of four pairs of Bearded Vultures were found in cave sandstone cliffs and 20 pairs in basalt cliffs. Some of the information obtained from these sites is summarized in Table 7.1. In addition, 16 active nests were observed from a distance, e.g. fixed-wing aircraft, and the localities of a further seven sites were provided by reliable persons. The data from these 23 sites are not included in the analysis that follows.

The mean number of nests per pair of Bearded Vultures was 3,1 (range 2-8). Figure 7.1 shows the distribution of numbers of nests per pair of birds. Three nests per pair was most common (50% of pairs) followed by two nests per pair (29%). In some cases only one nest was found (invariably the nest in current use), but this was normally when an incomplete search of the area was made. All well-known
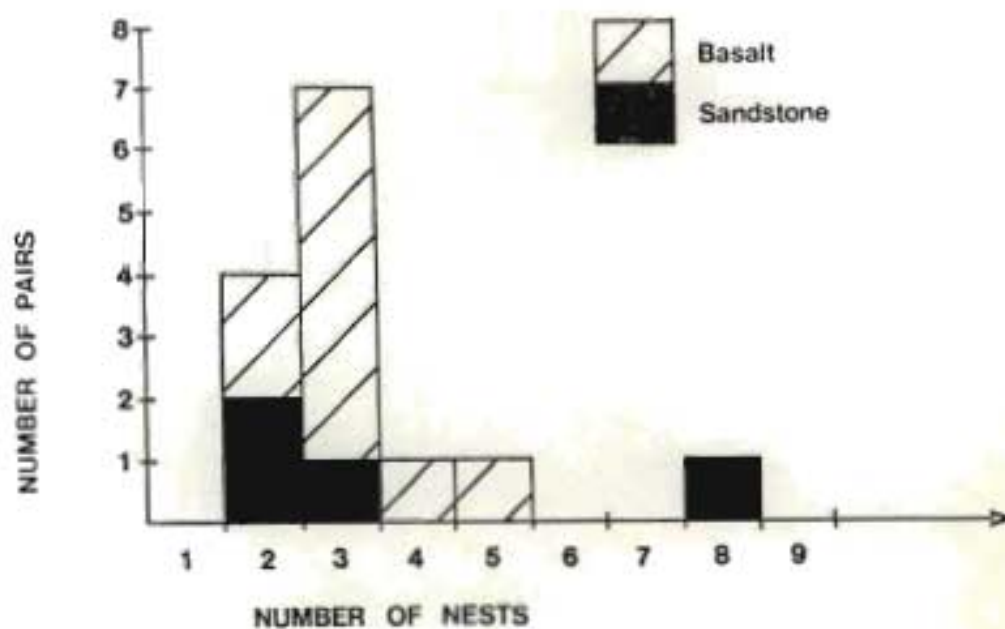
FIGURE 7.1. Number of nests per pair of Bearded Vultures in southern Africa.

breeding pairs of Bearded Vultures had two or more nests. For this reason the pairs for which only one nest was found were not included in the calculations resulting in the figures presented above. Thirteen breeding pairs of Bearded Vultures were closely monitored, six over three years and seven over two years (32 nest-years). With one exception, birds did not nest in the same nest in consecutive years. The exception was the Ntabamhlope pair (a two-nest pair) which deserted their nest during the incubation period in 1980 because of my interference with the closed circuit television. In 1981 and 1982 this pair bred successfully in their alternate nest, and were never seen to re-enter their deserted nest pothole, which was only about 80 m away. During the course of this three-year study, birds with three or more nests did not use the same nest twice. The Roma pair had eight nests, four in reasonable repair and four neglected. These birds used the four better-maintained nests and returned to the first-used in the sequence in their fifth consecutive breeding year (J.J. Guy pers. comm.).

Alternate nests belonging to one pair of birds were on average 230 m apart (range 2-2000 m) (Figure 7.2). Nests in sandstone may be very close together because of the rock structure which often forms horizontal series of potholes 2-6 m apart. Caves in basalt tend to be single formations, fewer in number and randomly spaced on a cliff. The distance between the nests belonging to a pair of Bearded Vultures was therefore greater on average for birds nesting on basalt than for those nesting on sandstone (mean = 304 m and 52 m
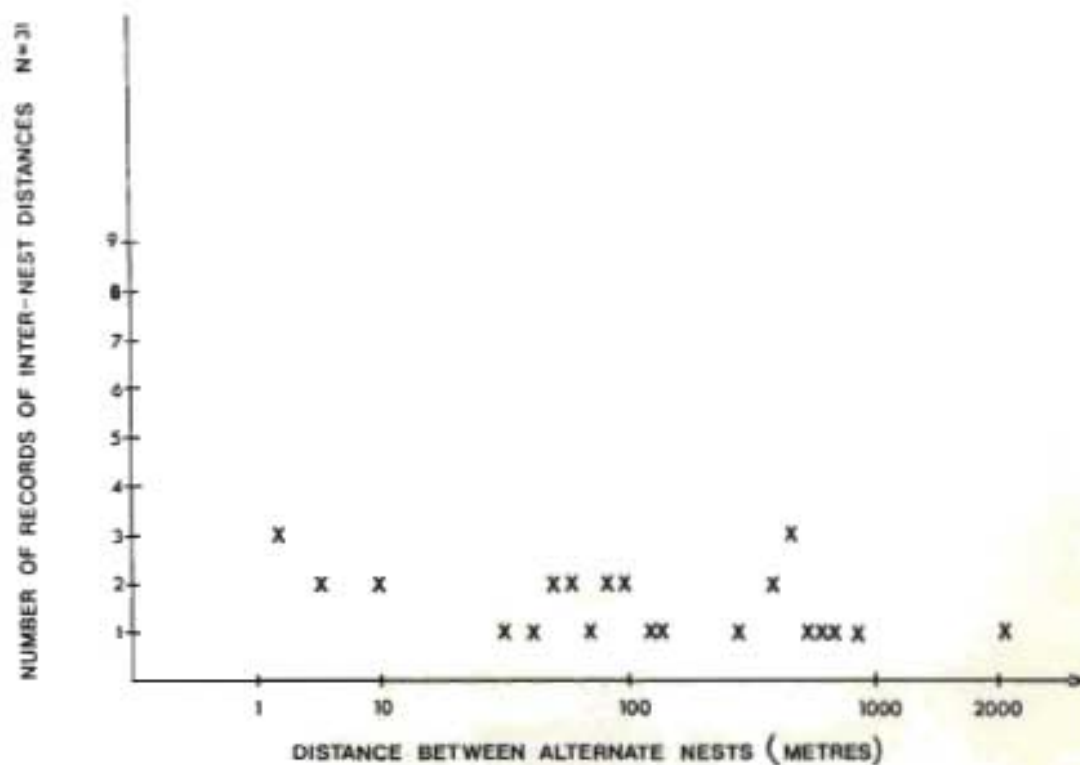
FIGURE 7.2. Distances between the nests maintained by each pair of Bearded Vultures (i.e. intra-pair nest distance).

respectively). In most cases, pairs of Bearded Vultures had all their nests on a particular peak or cliff face, so alternate nests were not very far apart. One exception was observed in the northern Long Wall pair. In 1980 they nested on Mt. Durnford only 700 m north of the Mt. Durnford pair's nest site. During the incubation period, the male bird of the northern Long Wall pair failed to return from a foraging trip into Lesotho (presumed killed) resulting in a nesting failure. The female took on a new mate in 1981, (a subadult), and they moved to what was presumed to be a new nest site about 2 km to the south and on the northern section of the Long Wall. This may not represent an alternate nest site, but rather a move to a completely new area following the acquisition of a new mate and a nesting failure. The next longest distance recorded between alternate nests was 800 m.

The orientation of nests are shown in Figure 7.3. Nests that are in protected sites (e.g. deep narrow gorges), and nests that have some protection at their entrances (e.g. large rock outcrops), are indicated. Nests faced from due north through east and south to west-southwest. No nests were found facing from west to north-northwest. 27% of all nests faced due south. All nests facing due north belonged to the Roma pair, situated in a narrow deep valley at relatively low altitude, and were classed as "protected". Half of the west-southwest facing nests and the one southwest nest were also in protected sites. The unprotected nests faced mainly between east and south-southwest (79%).
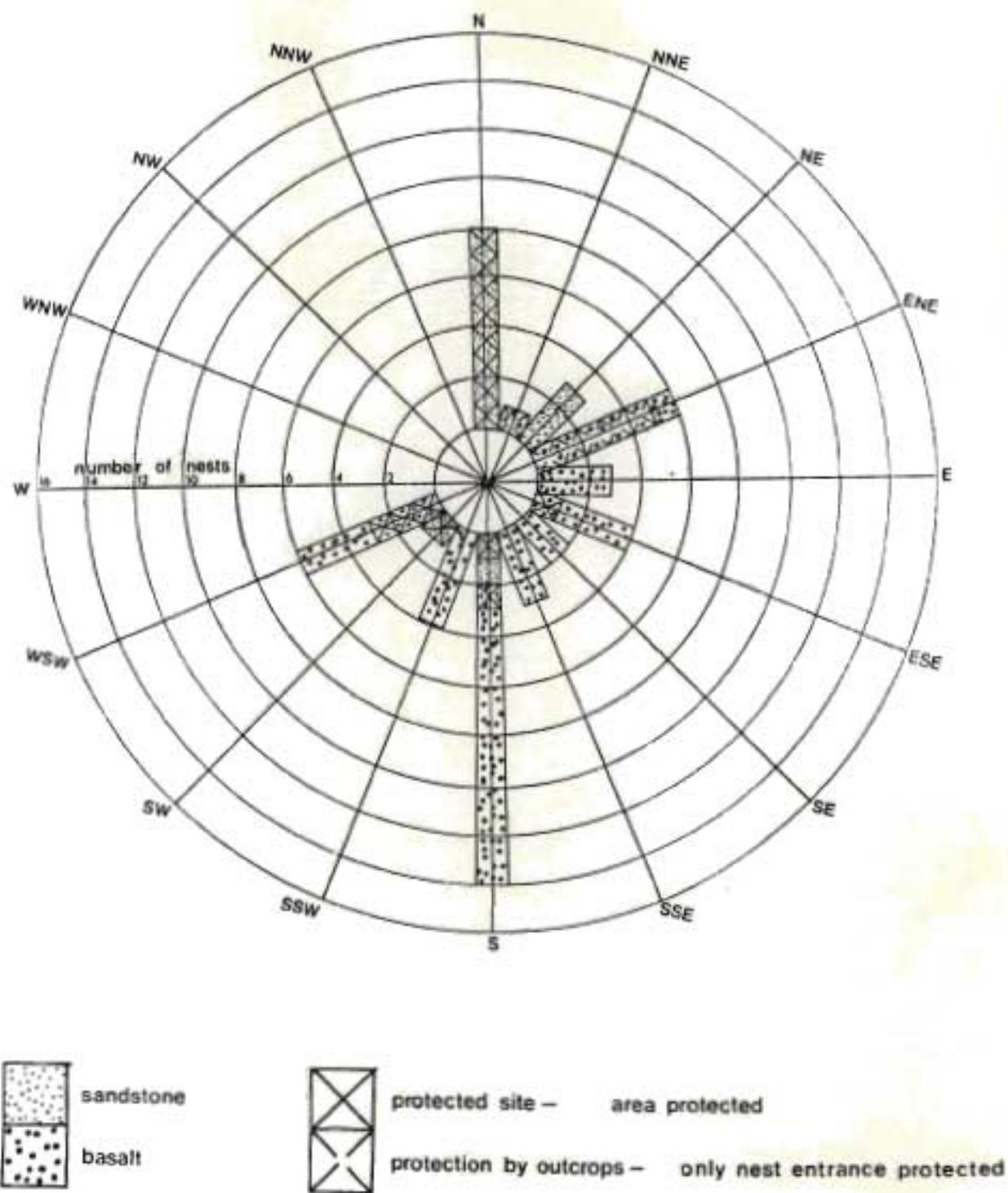
FIGURE 7.3. The orientation of Bearded Vulture nest sites in southern Africa.

Most nests (89%) were built in potholes (small caves) in the cliff face. The nest structure was usually invisible when viewed from any angle other than horizontally into the pothole. In one notable exception the nest had outgrown the pothole and extended out of the entrance and up the side of the cliff for about 1,4 m in height. Three nests (all belonging to one pair of birds) were built on ledges, and three nests were classed as pothole/ledge nests, having been built into shallow depressions on ledges. 90% of nests had overhangs or concave cliffs above the nest entrance, varying from 0,5-15 m wide. These overhangs would prevent snow settling and blocking nest entrances, although since most were in potholes, the nests themselves would be sheltered. The ledge nests were at low altitude (2286 m above sea level) where snowfalls were neither frequent nor usually severe, and all had overhangs. All the pothole/ledge nests had large overhangs.

All nests found were either in the subalpine (1829-2865 m above sea level) or alpine (>2865 m) belts (Killick 1963). The altitude of nesting cliffs ranged from 1850 m to 3201 m (Figure 7.4), the mean altitude being 2578 m. Sandstone nests were between 1850 and 2134 m and basalt nests between 2149 and 3201 m. The lower-altitude nests in basalt were on the eroded river cliffs in Lesotho and the lower Drakensberg of the northeastern Cape. The high-altitude nests were on cliffs of the Natal Drakensberg escarpment and peaks in Lesotho.

The height of nesting cliffs varied from 24-732 m (mean
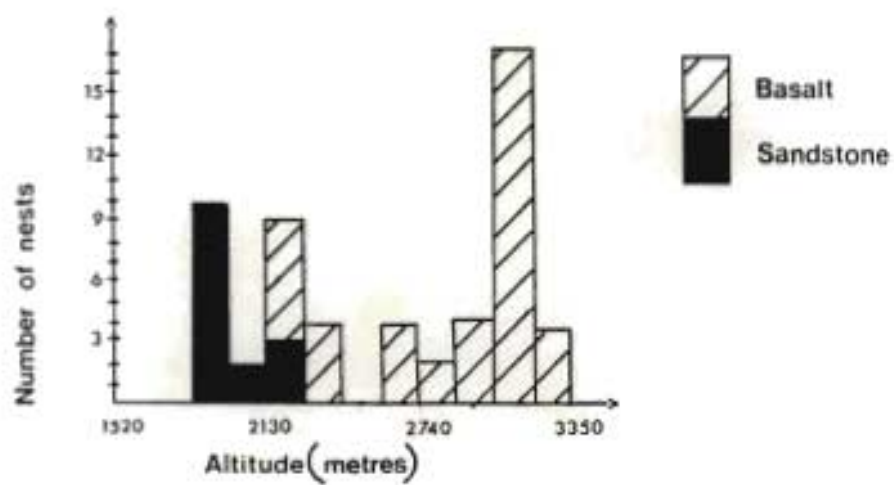
FIGURE 7.4. Altitude of Bearded Vulture nest sites.

= 212 m) (Figure 7.5). Basalt cliffs attain greater heights than do those of sandstone, and this is seen in the nesting-cliff heights. However, it is interesting that the lowest cliff on which Bearded Vultures were found breeding was of basalt. The position of a nest on a cliff was expressed as a percentage (from the base of the cliff) of the cliffs' height. The average position of nests was 72% of the cliff height (range 21-91%). The minimum height was something of an exception, the next lowest height being half way (50%) up the cliff. The distribution of positions of nests on cliffs is shown in Figure 7.6. In Figure 7.7 the positions of nests on cliffs are plotted against the respective cliff heights. Nests on high cliffs (viz. above 250 m) were significantly (Chi-squared test, P<0,001) and more consistently higher on the cliffs (average of 81% of cliff height) than were nests on lower cliffs (average of 60% of cliff height).

The habitat surrounding nests consisted mainly of subalpine and alpine grassland-fynbos and grassland-heath. The nests of two pairs had montane Podocarpus forests at the bases of the nesting cliffs and two pairs had nests directly above rivers.

Direct sunlight rarely fell for long periods on Bearded Vulture nests. Only when the sun was approximately horizontal to the pothole entrance would the rays fall on the nest. In addition, 25% of the nests were on due south-facing cliffs and received no sun at all. Table 7.2 lists some of the nests that did receive direct sunlight and the approximate lengths of time that sun was on the nest and the
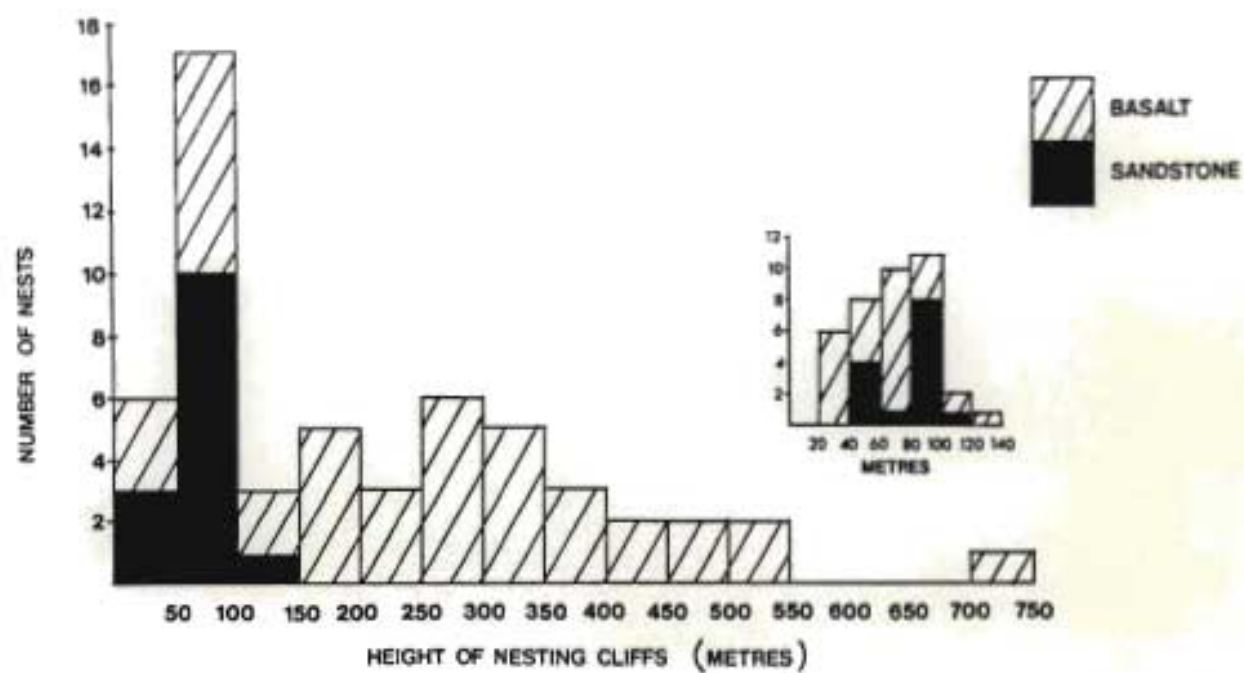
FIGURE   7.5.   Height of cliffs used by Bearded Vultures   for
nesting.
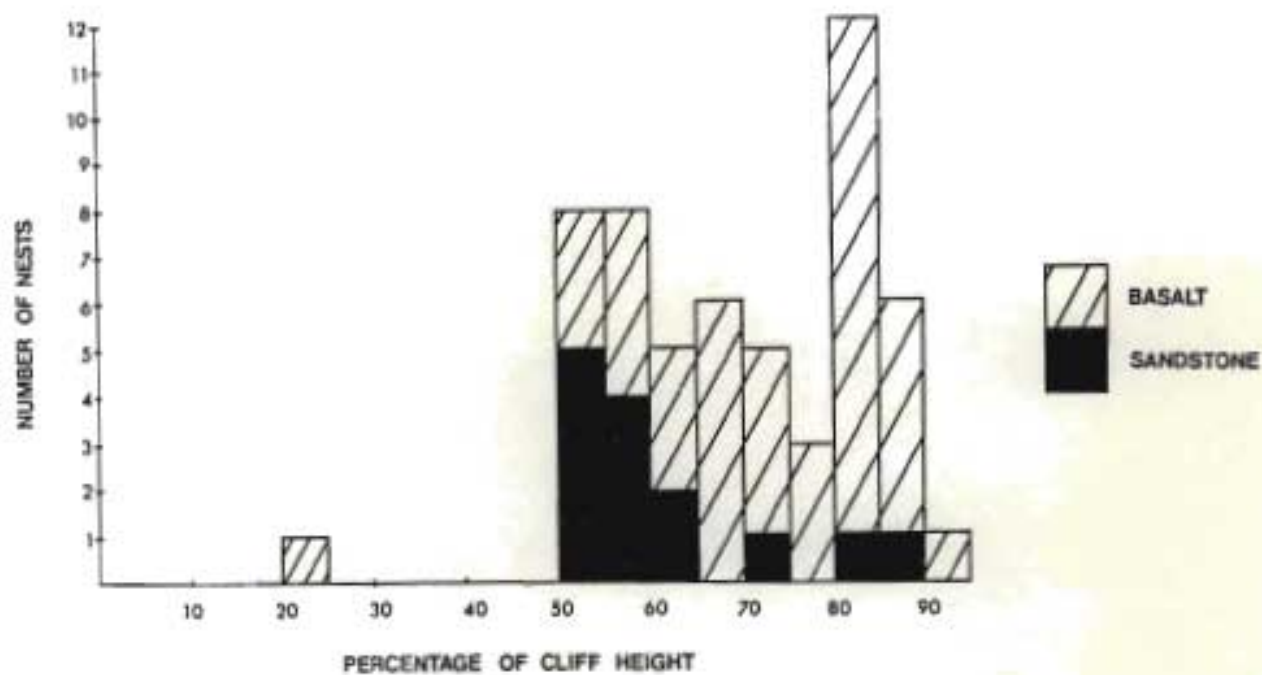
FIGURE 7.6. The position of Bearded Vulture nests on cliffs measured as a percentage of the cliff height from the base.
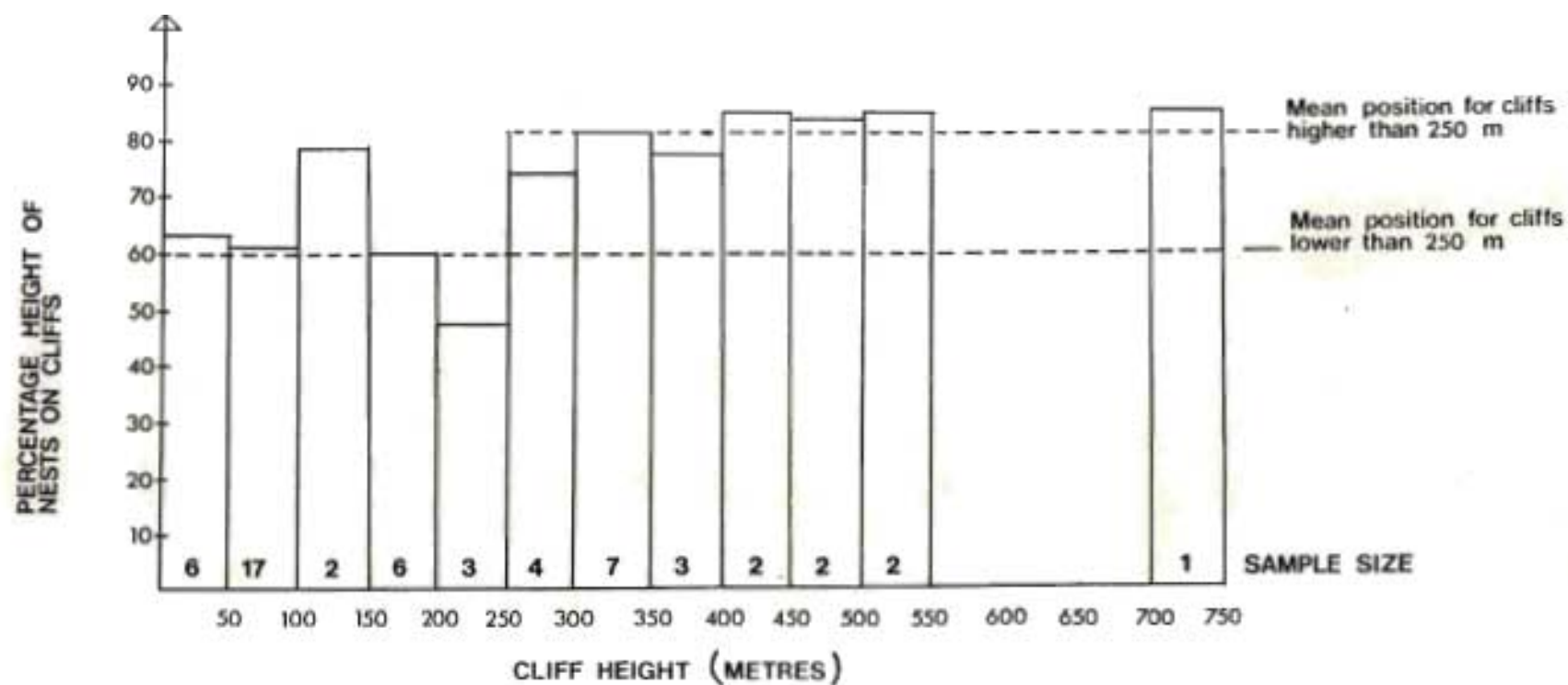
FIGURE 7.7. Position of Bearded Vulture nests on cliffs, plotted against the height of the cliff.

nest cliff around the nest entrance. The longest recorded period of sun on a nest was 4 h (mean for those nests that received direct sunlight = 2,6 h). Sun was recorded on nests only in the mornings, because of the predominantly south to east aspects of most nests. Figures for sun on cliffs at nest entrances ranged from 0-11,5 h.

Bearded Vultures were very tolerant of other birds nesting and roosting near their nest sites. Rock Pigeons Columba guinea perched within 0,5 m of nesting birds and Black Swifts Apus barbatus were seen roosting within 1 m of a Bearded Vulture nest entrance, evoking no response from the Bearded Vultures. Table 7.3 lists the larger species found nesting and roosting near nesting Bearded Vultures, and the distances involved. In the only incidence of two pairs of Bearded Vultures nesting on the same peak (about 700 m apart), no aggressive interactions between the pairs was seen. "Off-duty" birds from the different pairs would soar together, and co-operative foraging occurred (see Chapter 6), the birds separating on their return and entering their respective nests. Cape Vultures were commonly closely associated with Bearded Vultures on cliffs, colonies of up to 50 birds being located within 100 m of a Bearded Vulture nest. The closest that a Cape Vulture was recorded was 15 m. Once when a Cape Vulture attempted to land on the lip of a Bearded Vulture nesting pothole the incubating bird aggressively rushed at the Cape Vulture which departed immediately. Cape Vultures were seen roosting on the edge of Bearded Vulture nests which were not in use (in the non-

breeding season and at alternate nests), evoking no response from Bearded Vultures.

Only one record of Black Eagles nesting on the same peak as Bearded Vultures was obtained. The nests were 120 m apart on either side of a 90° corner and therefore out of sight of one another. Both species successfully reared young birds. In most cases the nearest Black Eagle was on another cliff or peak, the mean minimum distance being over 1 km. One incident of Bearded Vulture-Black Eagle nesting interaction was recorded at Ntabamhlope during the Bearded Vulture's incubation period in late July 1981. The Black Eagles which had bred successfully about 1500 m northwest of the Bearded Vulture's site the previous year and had three alternate nests in good condition in that area, started nest building about 150 m from the Bearded Vulture's nest on a ledge facing their pothole entrance. Nest building was accompanied by aerial displays (diving, looping and rolling) in front of the Bearded Vulture's nest. Any flying Bearded Vulture was vigorously attacked by both eagles, one behind the other, the Bearded Vulture being hard pressed to avoid the combined onslaught. Even when perched on the cliff or in a pothole, the eagles would attack the Bearded Vulture, forcing it to take up a defensive position with talons extended, and in one case the Bearded Vulture tumbled out of a pothole following a particularly close encounter. It then settled into a smaller, deeper pothole out of reach of the eagles, although they continued to display. Twice the

situation was reversed, with the Bearded Vulture diving aggressively at a Black Eagle. The Black Eagles attempted to establish themselves for a further three days, after which their activities in that area decreased. The eagles did not breed that year and it is unlikely that they would have, as they usually lay their eggs in May (Tarboton & Allan 1984).

Interactions between Bearded Vultures and other birds are mentioned later in this chapter, but with the exception of Whitenecked Ravens at the time of the Bearded Vulture's incubation and early nestling periods, the latter species were very tolerant of other birds nesting in close proximity; Jackal Buzzards nested within 150 m, Peregrine Falcons within 80 m and one pair of Lanner Falcons nested only 9 m from an active Bearded Vulture nest.

7.3.2 Breeding density

The breeding density of Bearded Vultures was determined for the Natal Drakensberg escarpment, for an area of the Lesotho highlands about the Mokhotlong village and for an area in the northeastern Cape in the Barkly East district. All three areas were considered to be of suitable habitat throughout. In some cases a number of adjacent nests were also found, but the areas about these were not systematically searched, and they are therefore not included in the analysis.

Eight nesting pairs of Bearded Vultures were found on the Natal Drakensberg escarpment between Sani Pass in the south and The Corner in Giant's Castle Game Reserve in the

north, a distance of about 48 km. A 21-km sample section in the Cathedral Peak State Forest yielded three nesting pairs. An average breeding density for the Drakensberg escarpment is therefore one pair of Bearded Vultures per 6,3 km.

In the Lesotho highlands all suitable nesting cliffs within an area of about 1250 km^2 were examined (both from the air and ground) and nine active nests found. Thus, for this area the breeding density was about one pair per 139 km^2 with a mean inter-nest distance of about 13 km.

In the northeastern Cape (on the Transkei/Lesotho borders) four nesting pairs were found in an area of just over 1000 km^2 giving a nesting density of 290 km^2 per pair and a mean inter-nest distance of 19 km. The breeding density drops off dramatically further south from the Transkei/Lesotho borders.

Newton (1979) states that, in any landscape, the upper limit to the number of established raptor pairs is set either by food or nesting sites, whichever is in shorter supply. Availability of nest sites as a limiting factor was investigated for a section of about 5 km of cliffs on the Natal Drakensberg escarpment. Cliffs were scanned through a 40 x telescope, and the following criteria were applied: (a) only sheer or near sheer cliffs of over 50 m in height were considered, (b) sites had to be at least above halfway up the cliff, (c) sites had to face between east and south, or be in a protected position, (d) only potholes were considered, with entrance either circular or elliptical and about 0,8-2 m wide (although sometimes difficult to assess,

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sites that did not appear to be at least 1 m in depth were not considered), (e) sites had to have overhangs or concave sections of cliff above them, (f) sites had to be dry, (g) sites had to be unoccupied, or occupied by easily displaced species, and at least 1 km from a Black Eagle's nest. In all, 11 sites were judged to be suitable. Assuming that each pair of birds has three nests, then the potential breeding is one pair/1,4 km, or 4,5 times the actual population density. Bearded Vultures do not defend large areas about their nests, though they do advertise their presence in an area by soaring. Nest site availability and territorial behaviour are therefore not responsible for setting the upper limit on their population density.

While this sort of exercise is limited in that we can apply only what we think are important criteria to the birds in the selection of a nest site, and the observations are only as good as what can be seen through a telescope from the ground, my strong impressions are that within the range of the Bearded Vulture in southern Africa, nesting sites are not limiting to the size of the breeding population.

7.3.3 The nest

The nest of the Bearded Vulture has been correctly described as a large structure of sticks and twigs lined predominantly with wool and hair, but also with a variety of other materials such as sacking, rope and animal skin (e.g. Brown & Amadon 1968; Cramp & Simmons 1980; Steyn 1982). Few quantitative data were obtained on nest dimensions because

nests were difficult to reach and Bearded Vultures are sensitive to nest interference. If they do not abandon a nest that has been disturbed, they are likely to move to a new nesting area the following season (P.R. Barnes, pers. comm.). As I wished to monitor nesting success, I decided to avoid disturbing birds at nests wherever possible.

Where possible, samples of branches and twigs used for the nest structure were collected for identification. These were generally found to represent the most abundant and easily obtainable material in the area. Branches particularly commonly used were from Protea spp., Podocarpus spp. and Leucosidea sericea, while other trees and shrubs represented were Buddleia, Erica and Helichrysum species. Branches were mainly about 10-15 mm thick and about 60 cm long, though one branch was 34 mm thick and 97 cm long.

Nests were lined mainly with sheep's wool which comprised at least 90% of the lining materials of all nests examined. Other lining material included horse hair, usually in long twisted tufts from the mane or tail, pieces of dried hide, sacking, cotton waste, a piece of hessian rope, cattle dung and, in three nests at lower altitudes, large clumps of Usnea lichen.

Nests were placed at the back of potholes, or in the case of ledge nests, at the back of the ledge against the cliff. The sizes and shapes of nests were dictated mainly by the size and shape of the ledge or pothole; a small pothole does not allow for a large nest, and two nests examined were

only 35 cm and 42 cm in height (cf. Cramp & Simmons 1980, who state that nests are rarely much less than 70-100 cm high) with 37 and 41 cm of headroom above the cups respectively. In one smallish pothole which had become filled with nest material, the nest was then built up the side of the cliff to a height of approximately 1,4 m. Sloping pothole floors resulted in nests of uneven height, one such nest being 18 cm high at the back and built up to 76 cm in front. Nests unrestricted by rock formations tended to be round, as was seen in large potholes and nests on wide ledges. Nests in restricted sites often adopted the shape of the pothole, one nest being 62 cm wide (the width of the pothole) and 108 cm long.

The mean diameter and depth of the cup during incubation and the early nestling period were about 42 and 15 cm respectively (n = 4), with incubating or brooding birds constantly pulling wool in and about themselves. As the chick began to move about the nest and was less frequently attended by an adult, so the cup became shallower and was eventually almost flat.

In contrast to the situation described by Brown & Amadon (1968), nesting cliffs in southern Africa do not become "very heavily plastered with droppings", and it is impossible, even towards the end of the breeding season, to locate with conviction the nest and roost sites of Bearded Vultures by the presence of "whitewash".

7.3.4 The pre-laying period

Courtship flights were observed on only 11 occasions, all in May and June and mostly in the late afternoon. They were performed in the nesting area but not immediately in front of the nest, and were far more restrained in nature than those described for the European birds (e.g. Glutz von Blotzheim et al. 1971) and those in the Himalayas (Ali & Ripley 1968). On four occasions when marked birds were seen in courtship flight, all were initiated by the male, which flapped up behind the female causing her to change from gliding to flapping flight. An undulating flight of gliding and flapping then followed, lasting for 2-3 min, sometimes accompanied by shrill, high-pitched calling by both birds. During this phase the birds would dive and rise in the form of a gentle sine wave and on at least three occasions the positions of birds were switched, with the female chasing the male. Then one of the birds would break off and circle up, flapping vigorously. Once sufficient height had been gained this bird would dive down on the lower bird, then rise up and dive again, usually calling a shrill "kweeeee kweeeee-eeeeee-eeeee". These dives were usually repeated 8-14 times, and as the birds came together the lower one would turn onto its back and present talons. On three occasions talons were locked and the birds cartwheeled, with heads held back and wings slightly open. On all occasions the birds disengaged after falling a few hundred metres, and well clear of the ground. Thereafter the birds would glide about together for a while before going to roost.

Although Bearded Vultures remain in the vicinity of their nesting sites to a greater or lesser extent during the non-breeding season (some birds roost almost nightly in the area while others are absent for up to five days at a time) by the beginning of May (about six weeks before egg laying) birds can be seen almost nightly at their nesting sites and pre-laying activities start to increase. Many of these activities were observed sporadically during the non-breeding season, e.g. allopreening and the bringing of an occasional stick or piece of wool to the nest, but during the six or so weeks before laying these activities took place at least daily, many increasing in frequency as the laying date approached. During the month before laying, just over 90 h of observations were made at five different nests in three seasons. The activities recorded are shown in Figures 7.8 and 7.9.

During the pre-laying period, most (77%) of the nest visits by Bearded Vultures were to bring in nesting material. Of the 37 visits with nesting material, 34 (92%) were by the male. Females brought only nest lining, and all the sticks were brought by the male. Larger sticks were brought in from some distance, and carried lengthways in the feet. The birds usually landed on a convenient site near the nest, transferred the stick to the bill and then carried it to the nest. With larger sticks, landing on the nest edge was often clumsy, and the stick was sometimes transferred back to the feet, the bird landing with one foot and
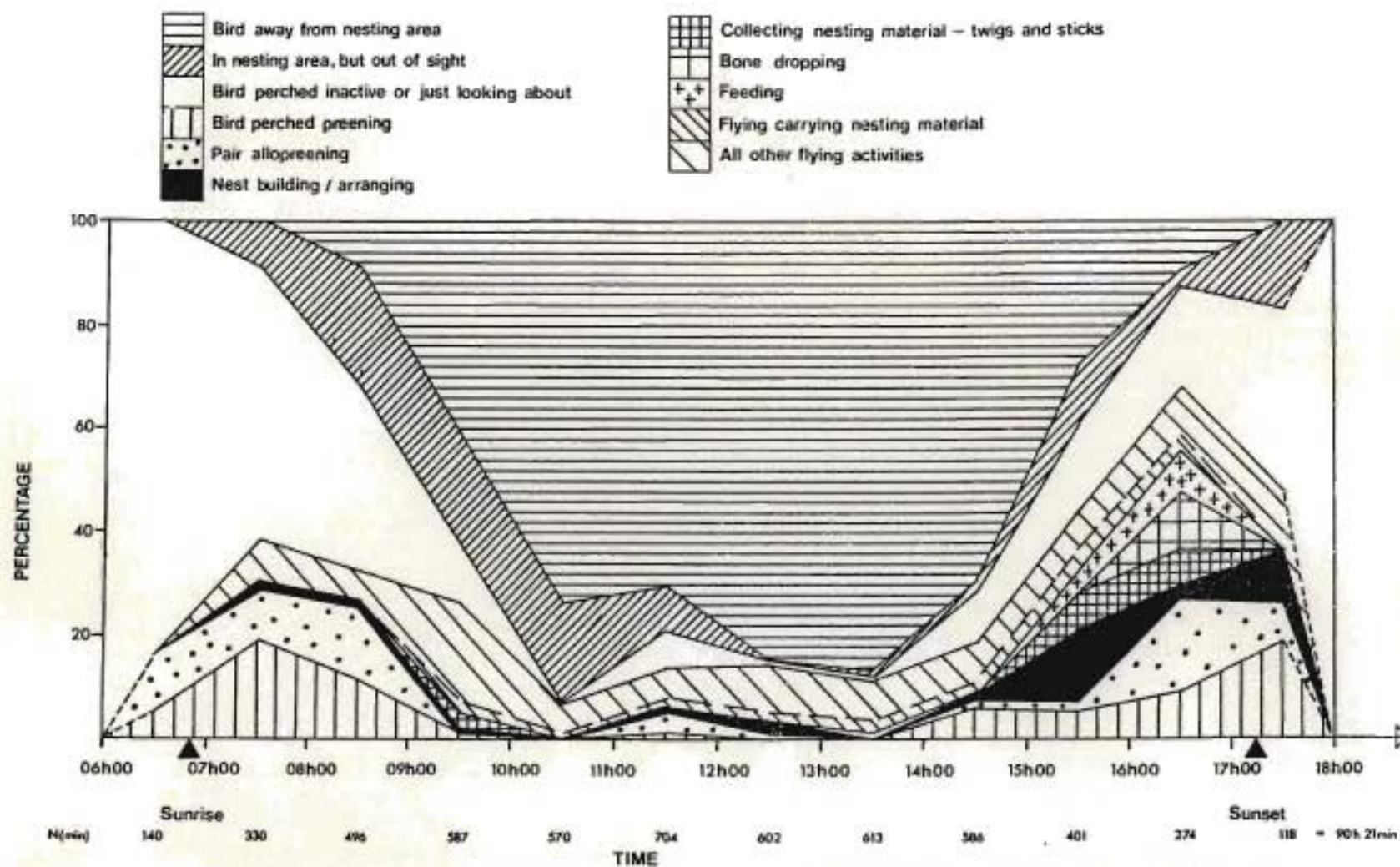
FIGURE 7.8. Activities recorded for Bearded Vultures in their nesting areas during the pre-laying period, per hour of the day.
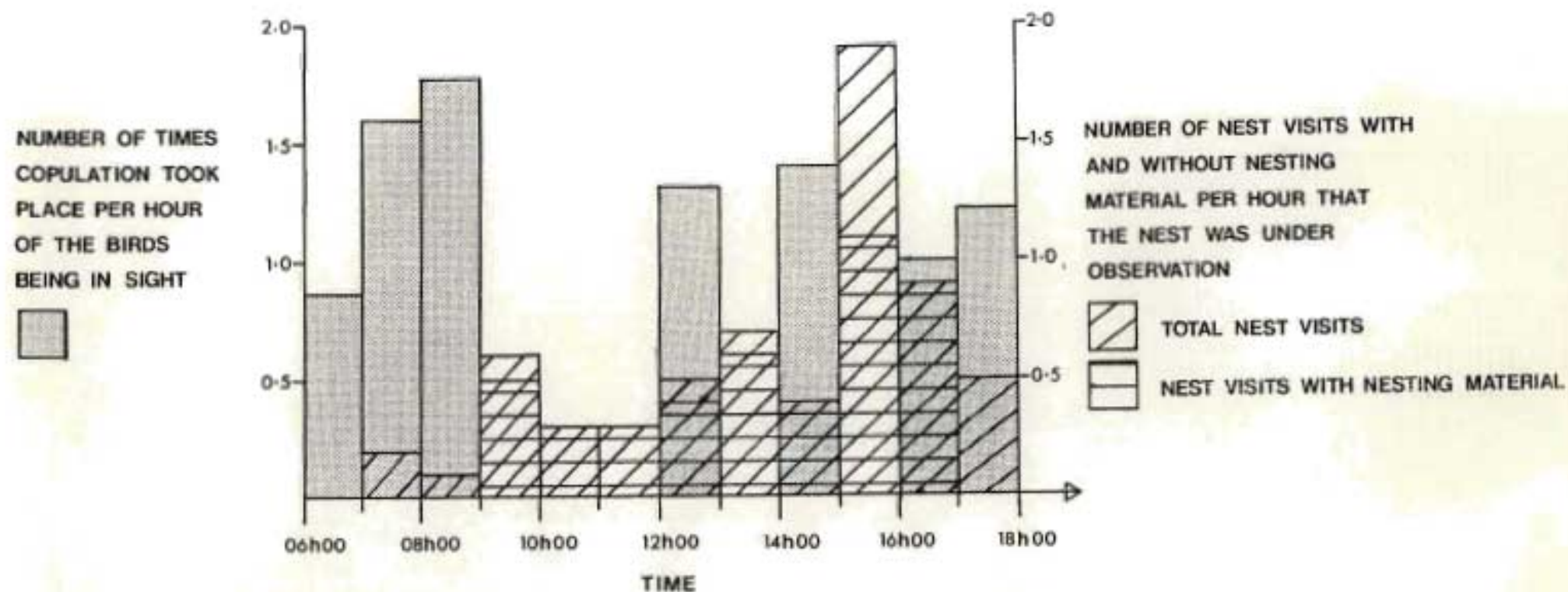
FIGURE 7.9. Number of nest visits and number of times that copulation was recorded in the nesting area by Bearded Vultures during the pre-laying period, per hour of the day.

shuffling up the edge of the nest with the other. Smaller twigs were collected in the vicinity of the nest, from shrubs and bushes growing on the scree slopes. While the larger sticks were always dead, the smaller twigs were often still green. These were broken off near their bases by a twist of the bird's head; usually five or six would be collected before the bird returned to the nest, carrying them in its bill. Lining material was carried in the bill if small, but large lumps of wool and skin were carried in the feet.

The male bird invariably just deposited the nesting material on the nest then immediately departed. At sites where a number of alternate nests were close together, e.g. the Roma site, nesting material was initially placed randomly in three different nests, as if the birds had not yet decided which nest to use that season. Arranging nesting material was done mainly by the female which spent some time in placing each stick, then sat on the nest and arranged the lining material about herself. As the pre-laying period progressed, three nests at the Roma site were developed. In the week before laying, one nest was selected, and while fresh material was still collected, much was pirated from the other two nests and transferred to the selected nest. The collection of nesting material, the subsequent nest visits and the arranging of the material took place mainly in the afternoons.

Copulation was observed on 32 occasions, always in the vicinity of the nest, but never on the nest itself.

Copulation was always preceded by allopreening; on 29 occasions (91%) this was initiated by the male, although the female sometimes assisted by walking over and standing next to and facing him. Allopreening was mainly about the face and head, the bird being preened usually turning its face one way then the other. Although allopreening was mutual, the male spent more time preening the female than vice versa (approximately 70% to 30% respectively). Sometimes both birds preened each other at the same time, and each might also preen itself while being preened. Birds also occasionally preened each other about the neck, throat and upper breast, and once on the back and wing. Allopreening pairs were seen to rub their heads and faces together on seven occasions. Allopreening lasted from 30 s to 16 min (mean = 6,4 min; n = 17) and took place mainly in the mornings and late afternoons (Figure 7.8) in the nesting area. Only twice was it seen away from nest sites. Allopreening was followed by copulation on 84% of occasions. Just before copulation the male was seen on six occasions to bow three or four times to the female, and twice, accompanying the bowing, the male stamped his feet a few times as if marching on the spot. Copulation lasted from 3,5 to 12 s (mean = 7,5 s; n = 13), and occurred most frequently in the mornings once the birds became active and before they started to soar for the day's foraging (i.e. between 06h30 and 09h00) (Figure 7.9), although it was also observed in the afternoons, and throughout the day when adverse weather

prohibited foraging. After allopreening, and once the intentions of the male were clear, the female crouched slightly; the male then jumped onto the anterior region of the female's back. Once balanced, he shuffled backwards, taking his weight on the tarsometatarsi, then lowered his abdomen and pulled his tail well across to one side. The female moved her tail to the opposite side. On a number of occasions the male swung his tail from side to side as he lowered himself, thereby brushing the female's tail out of the way. Once in position, the male then lowered his abdomen still further, bringing his tail down with it. During this last stage, lasting from 2 to 7 s, the male often had to flap vigorously to remain in position and on four occasions copulation was accompanied by a soft, high-pitched call. Loud calling was never heard to accompany copulation (cf. Glutz von Blotzheim et al. 1971). Once copulation was completed, the male jumped off the female and moved some distance away, both birds facing away from each other. The shortest interval between successive copulations was 22 min and in all but two occasions a short flight and a change of perch took place during this interval. Upon landing at the new perch, allopreening soon began. On the five occasions that adults began to allopreen at the same perch site after copulation, only two led on to copulation, i.e. a 40% success rate as opposed to a 91% success rate after a perch change.

Only one incident of the male bringing food to the nesting area during the pre-laying period could possibly be

construed as feeding the female; in this case both birds fed side by side on a ledge some 60 m from the nest. On other occasions both male and female birds brought food to their nesting area (mainly in the afternoons) and proceeded to eat it themselves (cf. in Spain the male brought food to the female three times per day during the pre-laying period (Suetens & van Groenendael 1973)). Food was never taken into the nest during this period.

7.3.5 The incubation period

A total of 287 h were spent at the nests of seven pairs of Bearded Vultures over three years, with detailed observations being made at the Ntabamhlope and Roma sites (108 and 113 h respectively). The remaining 66 h were spent opportunistically at the other sites to confirm that behaviour observed at the "focal" nests was in fact representative. Only two sites afforded views into the nest itself, one being the Roma site, viewed at a distance of about 230 m across a gorge, the other, a nest in the northeastern Cape which was found at the end of the study and not used for observation. When viewed through a 40 x 60 telescope, details and activities at the Roma nest could be clearly seen. At other nests, the nest site and nest entrance were kept under observation, and nest-relief and all activities in the nesting area were recorded.

Egg laying

Egg laying was seen only once. The female bird moved onto the nest just before 10h30, and after restlessly moving

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about for 16 min, settled down until 12h27, when she stood up and turned about. At 13h16 she stretched out her neck five or six times, partly opened her wings to rest them on the nest rim and half stood up, sank back and half stood up again. At 13h18 she stood up to reveal a damp, newly laid egg. Thus the bird began full-time occupation of the nest only about 3 h before egg laying.

Clutch size

It was formerly generally accepted that the Bearded Vulture produced a one-egg clutch (e.g. Winterbottom 1971). Steyn (1982) states that "according to a limited number of records, two eggs are laid as often as one". Eleven nesting attempts that could be checked without undue disturbance to birds indicated that nine were two-egg clutches and two were one-egg clutches (Brown & Barnes 1984). In addition, the Roma pair, monitored for seven years, produced seven two-egg clutches (J.J. Guy pers. comm.).

The laying interval between eggs was accurately determined twice as between 70 and 76 hours (3 days), and 118 and 127 hours (5 days), and less accurately on another two occasions as between 3 and 5 days and 4 and 7 days respectively. Since incubation begins with the laying of the first egg, the hatching interval may give an indication of the laying interval. Two clutches whose laying intervals were not determined hatched 2 days apart and between 9 and 10 days apart respectively, these perhaps representing the smallest and largest laying intervals recorded.

Eggs seen during this study were more variable in colour than are described in the literature (e.g. Brown & Amadon 1968; Cramp & Simmons 1980; Steyn 1982), ranging from almost pure white to dark, blotched, rusty rufous. Berthold (1967) has shown that iron oxide is responsible for the blotched rufous colouring on eggs, and when this is removed, the eggs are almost pure white. Presumably then, the eggs do not have a coating of rust when laid, and this is accumulated on the shell from the incubating birds' plumage (see Chapter 4) becoming darker (up to a certain point) with time. Four of the eggs measured fell within the ranges given by Steyn (1982), with the first-laid of each of the two clutches being larger than the second (mean of larger = 88,2 x 65,8; mean of smaller = 84,0 x 63,1). At the time of measuring the second eggs (within a week of laying) the first eggs were more heavily marked. This difference in colour intensity was still present in one clutch examined towards the end of the incubation period.

Roles of sexes

Both sexes incubate. The female incubates at night, and the daylight hours are evenly shared; males incubate for 50,7% and females for 49,3% of the time between sunrise and sunset. A parent bird is always in attendance at the nest during this period. In the course of nest relief, the incubating bird might leave the nest a short while before the relieving bird landed, but the longest unattended period recorded was just less than 2 min, during which one of the

adults circled directly in front of the nest. The mean attendant period was 2 h 27 min (excluding sunrise to first nest relief, and last nest relief to sunset which were usually fairly short periods), the maximum recorded period being just over 4 h, and the minimum 30 min. Although Steyn (1982) states that the maximum recorded attentive period lasted over 8 h this must be very unusual and was never recorded during this study, except in the case of an incubating female whose mate failed to return from a foraging trip into Lesotho, presumed killed. This bird remained on the nest for over 50 hours, interrupting this sit only for a short flight in front of her nest on the afternoon of the second day. Even once she had left her nest to forage, she returned to continue incubating for another day. Under normal circumstances, however, foraging trips are remarkably short, those of the males being on average only slightly longer than the females (2 h 35 min and 2 h 20 min respectively). The hourly percentage of incubation by the sexes is shown in Figures 7.10.a to c, first for all pairs monitored, then for the Roma and Ntabamhlope pairs respectively. From the first, a tendency can be seen for females to be off their nests in the early mornings, but thereafter no real trends are apparent. When looking at individual pairs, however, distinct patterns are evident, depicting different strategies. The Roma pair changed over at the nest near sunrise, the female remaining in the nesting area until conditions for aerodynamic lift developed
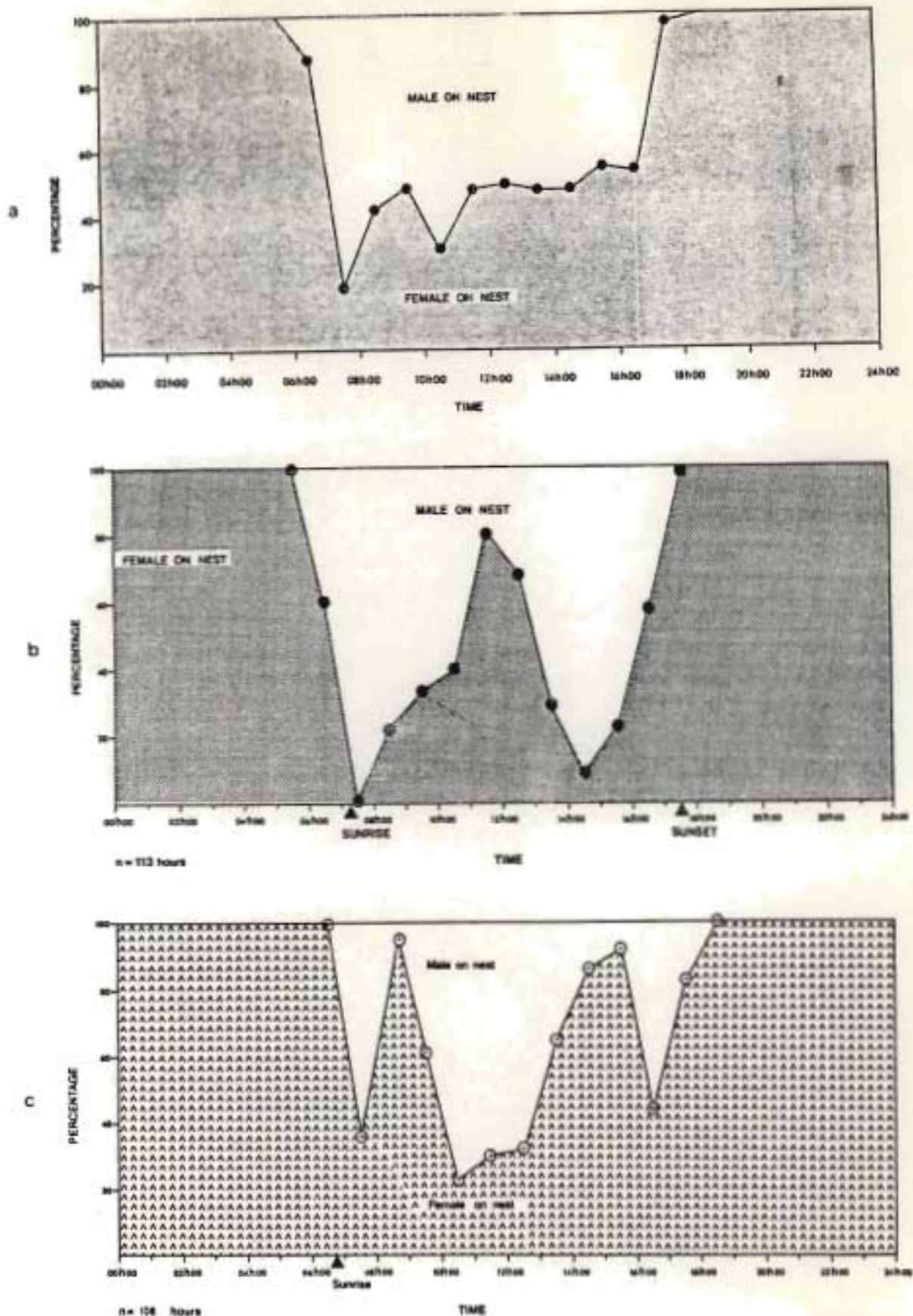
FIGURE 7.10. The roles of the sexes in Bearded Vultures during
incubation. a = all pairs monitored, b = the Roma
pair and c = the Ntabamhlope pair.

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at about 09h30. She then returned to the nest and changed over with the male who departed to forage almost immediately. The male usually returned between 12h00 and 14h00. The female then left to forage, returning to the nest in time to take over for the night shift. As can be seen from Figure 7.10.b, this pattern was remarkably consistent, there being usually four changes per day. In the case of the Ntabamhlope pair (Figure 7.10.c) the male relieved the female at about sunrise, but because the nature of the terrain and prevailing winds allow birds from this site to depart to forage much earlier than from the Roma site (about at 08h00), this first shift was very much shorter, the female returning to the nest and the male leaving the area to forage. The male returned about 2 h later and the female left for a relatively long period of 3-4 h returning usually between 13h00 and 14h00. The male went off again for about 2,5 h, thereafter relieving the female for a short period (to stretch her wings) before she settled in for the night. Thus the Ntabamhlope pair usually had six change-overs during the course of a day with the male having two shortish foraging trips and the female, one long one. As Bearded Vultures are dependent on an irregular and unevenly distributed food supply, these foraging times are not totally inflexible, as a bird may find food within a few minutes of leaving the nest or not at all. However, the rigidity with which particular pairs adhere to their specific patterns suggests that some sort of timetable is maintained to give the mate sufficient time to obtain food.

Although it was not possible to know whether a particular bird had returned to relieve at the nest without having found food, this was suspected on many occasions. During the nestling stage, birds often returned from foraging without food, and it is suggested that the "timetable" overrides the foraging urge once that bird's time is up (provided it is not itself excessively hungry). On the other hand, birds that found food very early in their foraging period did not immediately return to the nest, but perched inactive on a cliff or whiled time away by soaring.

The hourly activities of both the incubating and relieved birds in the nesting areas are shown in Figures 7.11 and 7.12. The full activities of each parent of the pair are represented as 50% on the graph. Although the photoperiod during incubation was the same or slightly shorter than during the pre-laying period, the time of departure for first foraging and the time of return after last foraging were respectively earlier and later, suggesting that the birds were making more use of their day. Less time was spent preening, and very little feeding was recorded in the nest area.

Incubating birds spent 95% of their attentive period sitting tightly on the eggs. For the remaining 5% the birds stood to turn about through 180°, roll the eggs, rearrange nesting material or defaecate over the edge of the nest. Figure 7.12 shows the frequency of some of these activities recorded at the Roma nest. "Standing" was most frequent
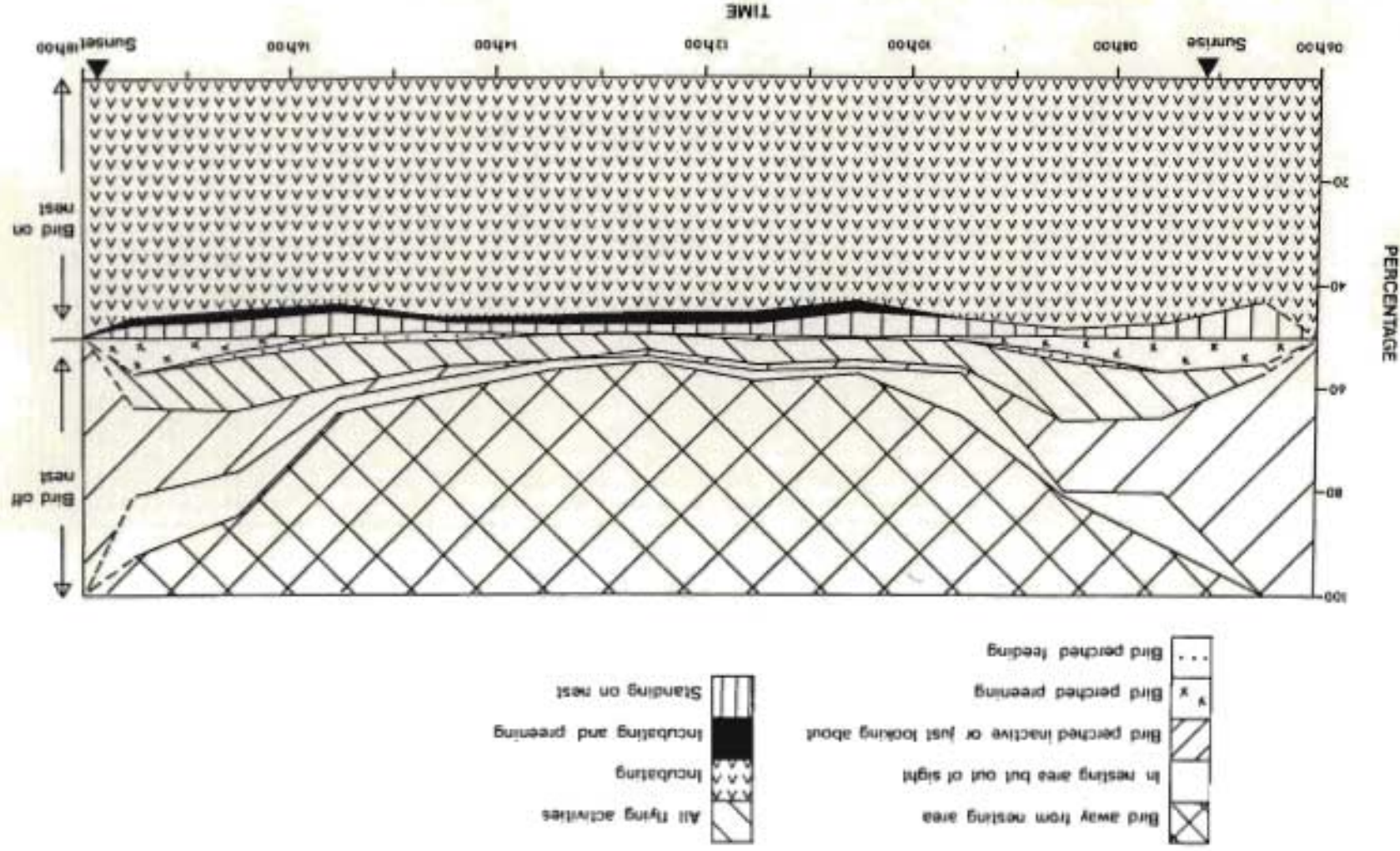
FIGURE 7.11. Activities recorded for Bearded Vultures in the nesting area and on the nest during the incubation period, per hour of the day.
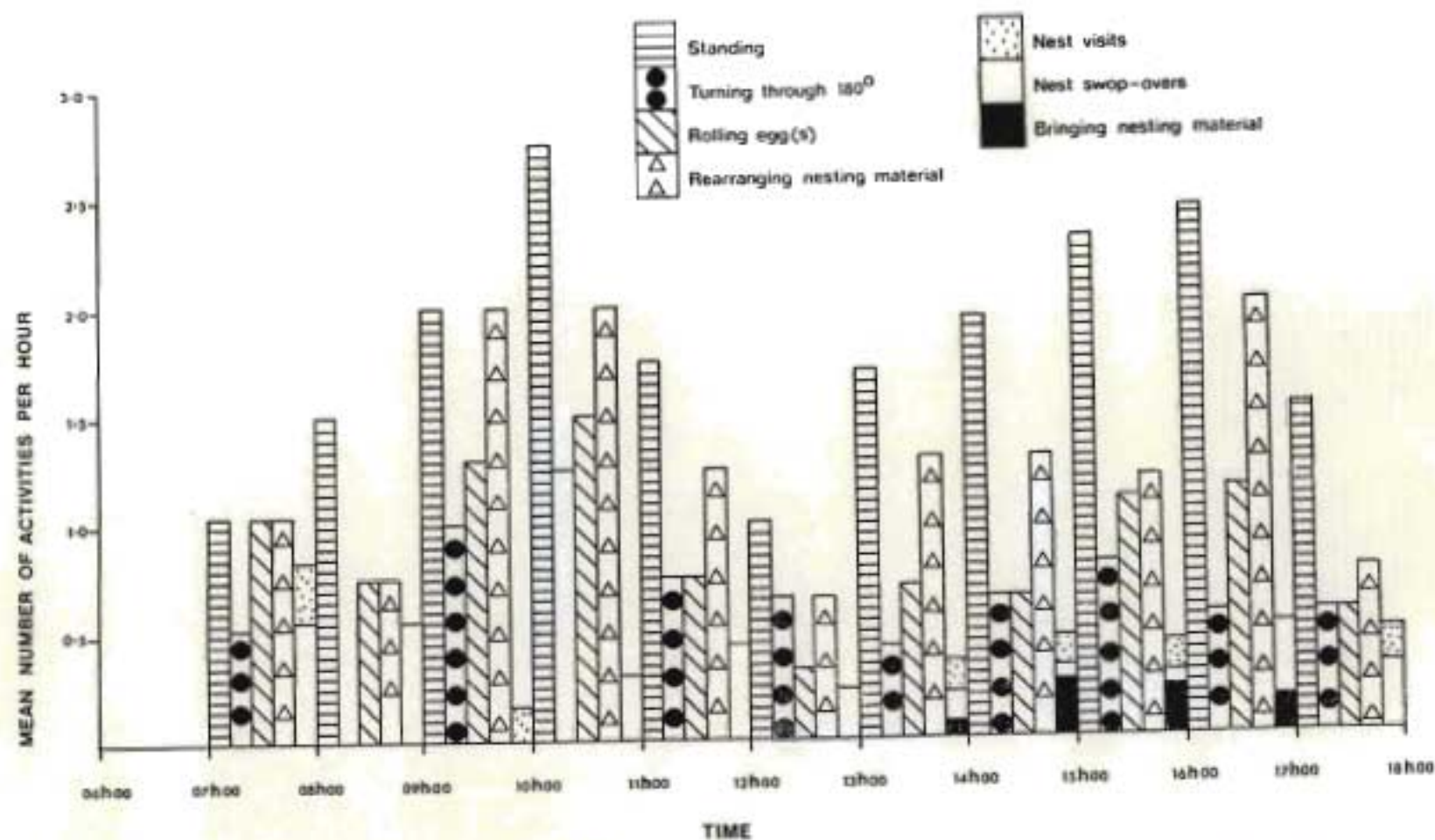
FIGURE 7.12. Mean number of times per hour that various nesting activities were recorded at the Roma nest during the incubation period.

between 10h00 and 11h00, and between 15h00 and 17h00, corresponding to the end of the attendant periods of the male, which was generally more restless on the nest than the female, particularly when about to be relieved. Birds stood once or twice per hour, turning through 180° on 35% of occasions, arranging nesting material on 70% of occasions and rolling eggs on 46% of occasions (on average 1,2 times per hour, and most frequently during mid-mornings and late afternoons).

Of 27 nest visits by off-duty birds recorded at Roma, 67% resulted in change-overs, on 33% nesting material was brought and on 11% no change-over or nesting material was brought, with the incoming bird departing again once the incubating bird showed no inclination to be relieved. As during the pre-laying period, nesting material was brought to the nest mainly in the afternoons, but this consisted of only nest-lining, and at about 45% the previous frequency.

At the Roma nest the incubating bird was seen to defaecate from the nest rim only six times, on all occasions attempting to shoot the excreta with considerable force beyond the lip of the nesting pothole. This was not always achieved, but by the end of the incubation period there was little whitewash on the edge of the nest and cliff, and it was certainly not visible from a distance. However, soon after departing from the nest after a change-over, birds defaecated in flight on 72% of occasions.

The frequency of drinking observed in the nesting area was remarkably high, one of the pair drinking every 3,8 h,

from the lip of a small waterfall across the gorge and slightly upstream from the nest. Each bird usually drank at least daily in the nesting area, and on at least four days one of the birds drank twice. This usually took place after the bird had been relieved at the nest, but sometimes on returning from foraging and before starting a spell of nest duty.

Only twice did the Roma male bring food to the nesting area, to bone-drop and then settle in a roosting pothole to feed. The Ntabamhlope pair however, as well as a number of others birds, e.g. Long Wall, Mt. Durnford, Gypaetus Point and Black Mountain pairs, often brought food to their nesting areas, but never into the nest itself. Usually this was for bone-dropping or immediate consumption, but sometimes food was also cached. At the Ntabamhlope site for example, two potholes within 20 m and 50 m of the nest were regularly used to cache food, by both male and female birds. A bird which had been relieved would fly past both sites, peering intently in, and if food was present, would land and feed before departing to forage. Also, birds would purposefully fly over their ossuaries to check for food remains, and at Ntabamhlope, the arrival of a Bearded Vulture was often heralded by the calls of a pair of Whitenecked Ravens which would fly out to intercept the Bearded Vulture, mobbing it and attempting to steal food at ossuaries or cache potholes if it was left unguarded for too long.

At nest change-overs the incoming bird sometimes bowed to the bird being relieved and on rare occasions, both birds bowed. A high-pitched call _cheek_, _acheek_, _acheek_ was occasionally uttered by the bird being relieved.

Incubatory behaviour

Bearded Vultures were particularly careful when moving onto or off their nest. Their talons were folded into a "fist" and they shuffled forwards or backwards with legs bent, taking their weight on their tarsometatarsi, rocking gently from side to side. Once off the nest the bird often stood and poked into the nest cup, giving the impression of making depressions for the eggs. The eggs were then rolled towards the depression, using the bill and pulling the eggs backwards between the legs. A similar shuffling movement was executed to get back onto the nest. The wings were often partly spread and placed on the nest rim as was the bill, thereby providing support and distributing the bird's weight. Once settled, the bird usually tucked the eggs more comfortably beneath itself by partially lifting its breast and pushing the eggs backwards with its bill. Thereafter the bird usually pulled nest-lining up onto the rim and placed this about itself.

During the incubation period, no sign of mutual preening or copulation was observed, and birds were never seen in aerial display or heard to give high screaming calls near their nests as do the birds in Europe (Brown & Amadon 1968; Glutz von Blotzheim _et al_. 1971). Birds rather

approached their nesting sites stealthily, usually below the cliff skyline, and if a person was seen in the vicinity of the nest, the bird would not enter the pothole, but glide on by so as not to give away the locality of the nest. Nest relief was usually quick, the relieving bird flying straight up to the nest and entering, and the relieved bird departing immediately.

Interspecific aggression

Interactions between nesting Bearded Vultures and other birds were generally fairly rare. Interactions between Black Eagles and Bearded Vultures at Ntabamhlope have already been mentioned, and an incubating bird on the Long Wall was seen to dive out of its pothole onto a Black Eagle that remained for a few minutes within 200 m of its nest. One of the same pair behaved similarly when an unmarked adult Bearded Vulture (presumed to have come from outside the Giant's Castle study area) circled for over 5 min in front of the nest. Bearded Vultures from neighbouring nests, when meeting a foraging partner, also circled close in front of the nest, but they were never attacked. Because many birds made use of the lift provided by the Drakensberg escarpment, different species and individuals were continually passing Bearded Vulture nests, and the birds appeared to accept this situation. However, if a bird remained in the immediate area for any length of time, it might be attacked. An exception to the statement that interactions were fairly rare was shown by the Roma pair, whose interactions with Whitenecked

Ravens were frequent. It appeared as if these birds actively sought confrontation with the ravens, and they would search for them, particularly after a nest relief. Although the ravens sometimes arrived to mob the Bearded Vultures, 80% of the conflicts were initiated by the Bearded Vultures, which often went in search of the birds even when they were out of sight.

The incubation period

The incubation period was determined by direct observation at the Roma site as 57 ± 1 days. At other sites where it was not possible to view the nest contents, the incubation period was determined from the date that full-time occupation of the nest first took place until the first food item was taken into the nest (the latter starting on the same day as the hatching of the first egg). Three such periods were determined, two being 56 ± 1 days and the other being 58 ± 2 days. Thus an incubation period of 56 to 57 days can be assumed.

No information on clutch replacement could be obtained. Only two failures during the incubation stage were recorded, one in which a male bird failed to return from foraging in Lesotho, the female remaining without a mate for the duration of the breeding season (thus not attempting to breed again that year), and the other due to my interference. The incubating bird at Ntabamhlope was kept off the nest for just under 45 min while a television camera was installed, during which time it circled in front of the

nest. It never returned to incubate, continuing to circle near the nest for the remainder of the day, and being joined twice by its mate. The following day all equipment was removed, but although both birds remained in the vicinity, they never resumed incubation and were never seen to enter that nest pothole again. Two days later the male bird was seen bringing sticks to a site about 80 m away. The rate of nest building was similar to that recorded during the pre-laying period, but soon tapered off and the nest was left only partially lined. No cases of clutch replacement were recorded during this study.

7.3.6 The nestling period

On the morning of 10 July 1981 a small bump was noticed on the larger egg in the Roma nest, and this had perceptibly increased in size by late afternoon. On three occasions when the incubating adult moved the eggs, it attempted to peck at the bump, but this was too small to afford any purchase. The bump was little larger when observations ended the next day 30 min after sunset, but the following morning at 07h05 (5 min before sunrise) the empty, shiny wet eggshell was seen on the outer edge of the nest. Final hatching presumably took place in the early hours of the morning. The nestling period was taken to commence with the hatching of the first egg (and in nests where direct observation was not possible, with the first food item carried into the nest by a parent bird).

The hatching of the second Roma egg took place two days

later. Although the actual process could not be observed over the nest rim, judging by the restless behaviour of the adult bird, it was thought to hatch between 09h30 and 10h20. Half the eggshell, wet and shiny, was deposited on the nest rim at 10h45. This was the shortest recorded interval between hatching, the longest being between nine and 10 days. Three other hatching intervals fell between four and six days.

No nest produced more than one surviving nestling. In captivity, the parents are reported to kill the second chick during hatching or within 24 hours thereof (Schumann 1929; Louman 1981). Also in captivity, sibling aggression has been demonstrated, with the injured second chick being removed and hand reared to avoid probable death (Thaler & Pechlaner 1980). Further, Newton (1979) states that the "Lammergeier" is among the group of birds in which "the older nestling repeatedly and mercilessly attacks its smaller nest mate". In the wild, two incidents of nestling mortality were observed, and a further case supplied by J.J. Guy (unpublished data, pers. comm.). In all three cases, neither sibling aggression nor adult predation were responsible. Instead, the older nestling (N1) was able to so dominate the younger nestling (N2) (even when separated by an age difference of only two days) that the latter was unable to obtain any food. N2 disappeared early from the scene, surviving in one case for only 26 hours (J.J. Guy pers. comm.). In another incident, N2 hatched at about 10h45 and by the afternoon of the next day, although still alive, was

too weak to lift its head. The next morning it was dead in the nest, and by that afternoon was no longer seen. The third case was similar, N2 being found dead in the nest on the second morning after hatching. About 27,5 h of observations were made during the period when two nestlings occupied the nest. Of 17 feeds recorded, not one morsel was obtained by the younger nestlings. The older nestling invariably positioned itself in front of its sibling, and whenever the parent lent forward with food, the older chick would raise its head, sometimes shuffling backwards more effectively to block off N2, thereby obtaining all food offered. Once satiated, N1 continued to rise up, taking food and then dropping it. The parent would retrieve the morsel and offer it again; again it would be accepted and dropped. Once this had happened five or six times the parent would terminate the feed, resulting in N2 going hungry. On two occasions (once at each of two nests) aggression by N1 towards N2 was observed. On each occasion N1 pecked three times at the head of N2. These attacks were neither purposeful nor powerful, and on both occasions N1 stopped of its own accord. No signs of injury could be detected, and the N2's in question made no attempt to move away from their siblings, as is observed in eagles in which sibling aggression is highly developed (Meyburg 1974). The dead nestlings invariably disappeared from their nests within 24 hours. They were never found below the nesting cliffs nor seen on the outer rim. While N2 may have been eaten by

parents or fed to N1 (as has been recorded in the Lesser Spotted Eagle _Aquila pomarina_ (Meyburg 1973) and a number of owl species (Steyn 1984)), this was not observed, and most probably they were trampled into the nest lining and covered over with wool. In all three cases, an abundance of food was present in the nesting pothole.

Based on the attendance patterns of the parent birds, the nestling period was divided into three stages (Figure 7.13). Nestlings were closely brooded for about the first 40 days after hatching (early nestling stage). From days 40-90 (mid-nestling stage), the percentage attendance steadily decreased until the nestling was unattended (late nestling stage), being visited only to provide food. Each of these three stages is treated separately.

7.3.6.1 Early nestling stage

A total of 137 h were spent at the nests of five pairs of Bearded Vultures during this stage, with most observations being made at the Roma and Ntabamhlope nest sites (104 and 13 h respectively), with the remaining 20 h being spent opportunistically at three other nest sites.

Both parents brood the nestling. The female brooded at night, and the daylight hours were fairly evenly shared, the female brooding on average for slightly longer (57,6%) than the male (42,4%). During my observations, the nest was left unattended for 0,4% of the daylight hours, during which time a parent was always in the immediate vicinity. Thus, for all practical purposes, an adult was always on the nest. The
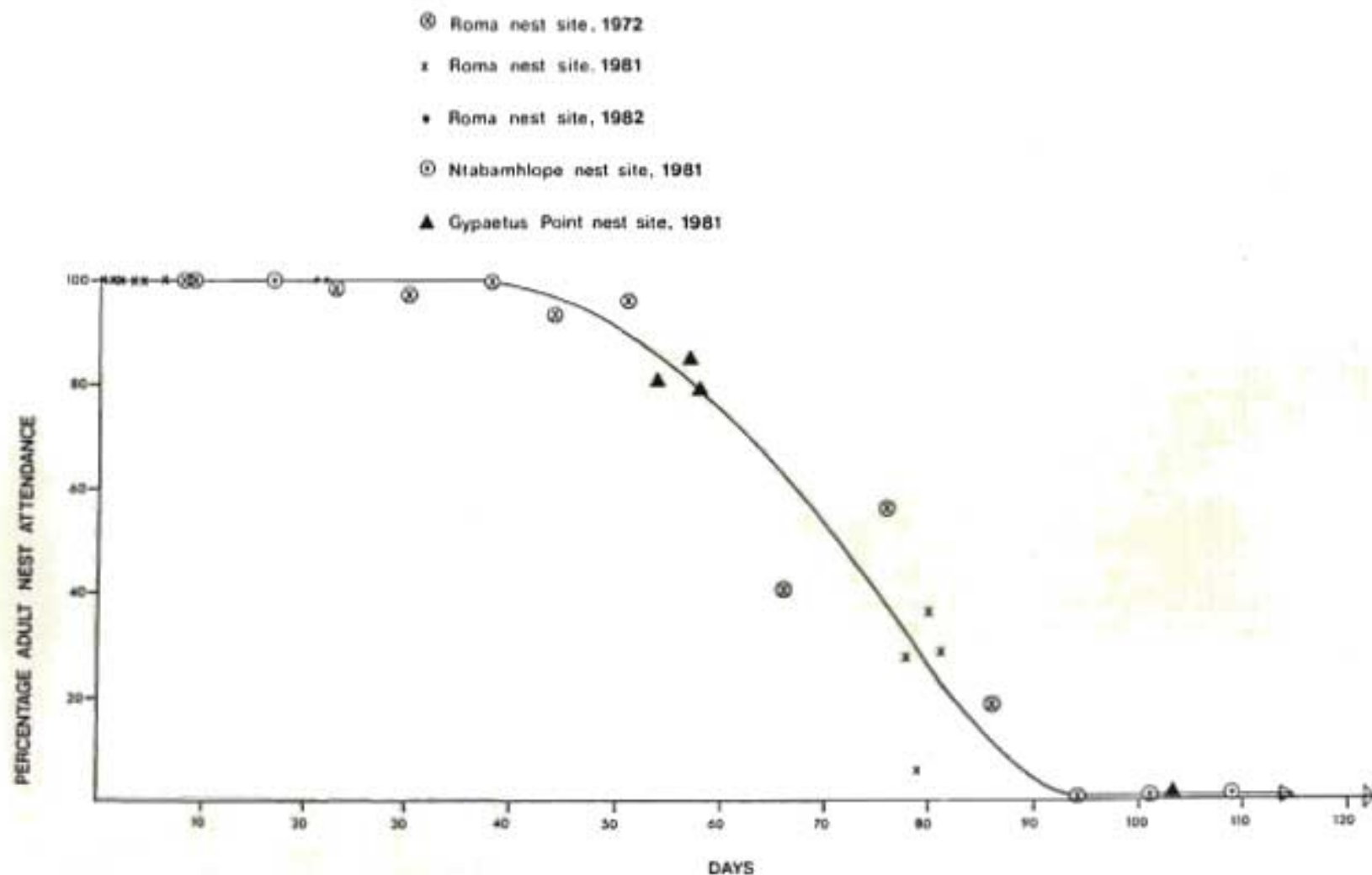
FIGURE 7.13. Percentage of time that a parent Bearded Vulture is in attendance at the nest throughout the nestling period.

mean period of nest duty (excluding sunrise to first nest-relief and last nest-relief to sunset) was 1 h 56 min. The mean male duty was slightly longer than that of the female (2 h 2 min and 1 h 52 min respectively). The maximum length of duty was 5 h 14 min (by the female - the maximum for the male being 4 h 29 min) while the minimum was 5 min. The hourly brooding percentages for both sexes is given in Figure 7.14. The clear pattern of nest duties observed during the incubation period was not carried over into the nestling period. Once the female had been relieved in the morning, nest-duty sharing fluctuated between 40% and 60%, the only trend being for the female to be off the nest between 15h00 and 16h00, before resuming duty for the night. The unregimented timetable during this stage is reflected in the more varied lengths of nest duties (from 5 min to over 5 h) and the generally shorter mean length of duty.

The hourly activities recorded in the nesting area are shown in Figures 7.15 and 7.16. The day length during the early nestling stage is slightly longer than during the incubation period. Off-duty birds spent a greater percentage of this longer day away from the nesting area, leaving earlier and returning later. The male bird departed to forage directly from his roost before relieving the female and the first nest relief was recorded only after 08h00. In addition, on two occasions males which left the nesting area late in the afternoon spent the night away, returning the next morning with food. The off-duty bird spent less time perched in the nesting area. Although more nest visits were
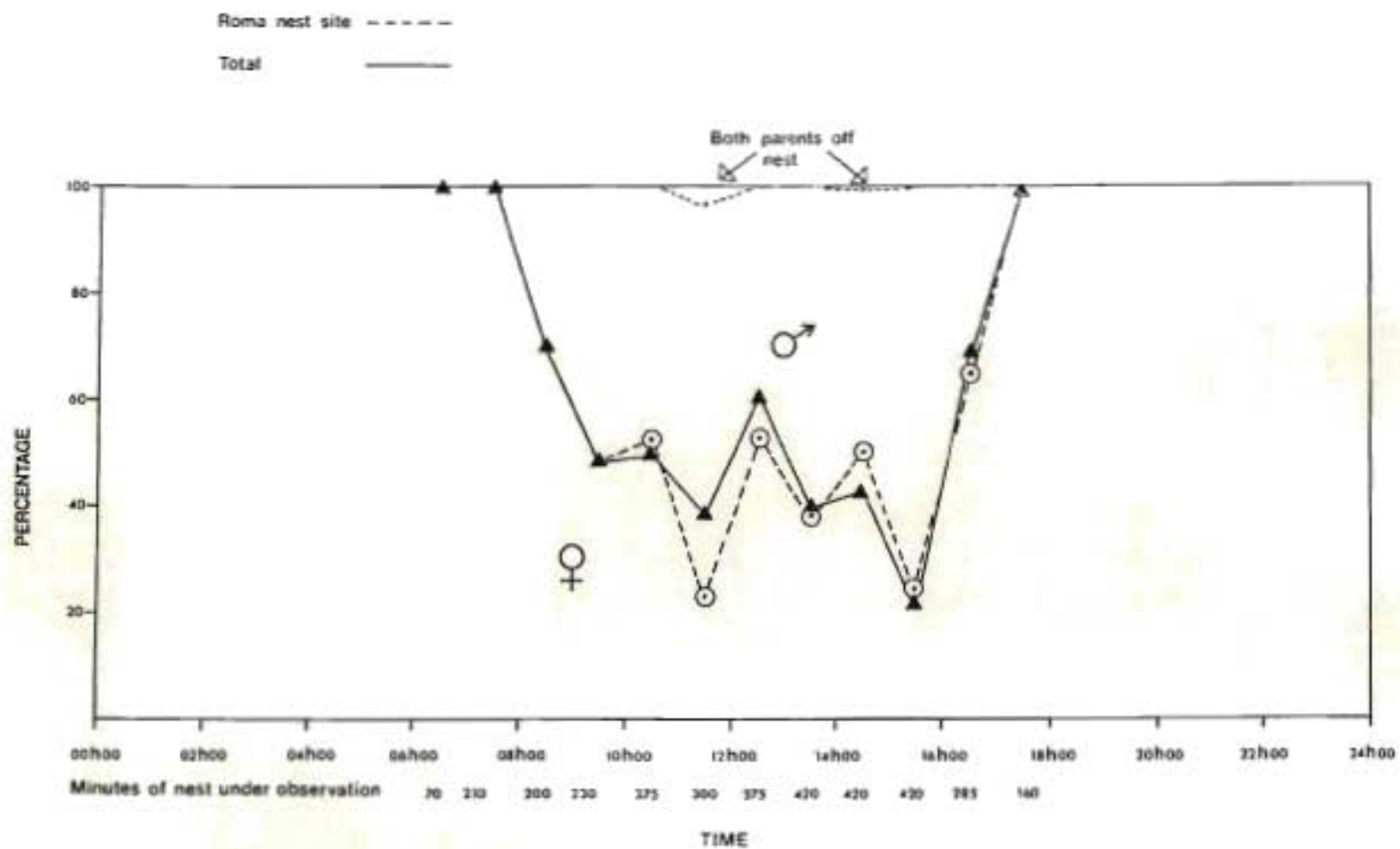
FIGURE 7.14. Role of the sexes at the nest in Bearded Vultures during the early nestling period.

Legend:
- Bird away from nesting area
- Bird in nesting area but out of sight
- Bird perched inactive or looking about
- Bird perched preening
- Bird flying
- On nest – bird standing (and . .)
- Brooding young and preening self
- Brooding young only

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FIGURE 7.15. Activities recorded for Bearded Vultures in the nesting area and on the nest during the early nestling stage, per hour of the day.

FIGURE 7.16. Mean number of times per hour that various nesting activities were recorded during the early nestling stage.

made (0,5/h as compared to 0,4/h), the amount of time recorded for birds flying in the nesting area was less. The strong impression gained was that birds were more purposeful during this stage and spent more time foraging than during the incubation period.

Of 31 nest visits by off-duty birds recorded during this stage, 90% ended in nest relief and on 45% of them food was brought to the nest. No nesting material was gathered during this stage. Nest visits and nest reliefs began after 08h00 but showed no clear pattern. Food was brought to the nest after 09h00, mainly around midday and mid- and late afternoons.

The on-duty bird spent 74% of its attentive period closely brooding the chick(s). For the remaining 26% the bird stood, either preparing food, feeding the nestling or itself, arranging nesting material, preening the chick or just looking about and occasionally preening itself. Although the number of times the bird stood up was greatest during the middle of the day (09h00 to 15h00), this does not reflect the true amount of time spent standing. As shown in Figure 7.15, the bird in attendance spent much more time standing in the morning between 07h00 and 11h00, this being the time when sunlight shone directly into the nest. Once the nest was in shade, the amount of brooding increased. On 56% of occasions that the bird in attendance stood up it arranged nesting material, on 44% it prepared food and on 33% it fed the nestling. Both food preparation and feeding of the nestling took place during all hours of the

photoperiod, but more frequently in the early mornings. Three small feeding peaks later in the day were also apparent: midday, mid-afternoon and early evening.

During this study no details of plumage development or rates of growth were obtained for nestling Bearded Vultures. Nest disturbance was avoided wherever possible, and no captive nestlings were kept. Plumage details of nestling Bearded Vultures are available for the European birds reared in captivity (e.g. Schumann 1928, 1929; Psenner 1976; Thaler & Pechlaner 1980; Louman 1981), but little is recorded for the African race. My observations, made through a 40 x 60 telescope at a distance of about 200 m, indicate that there is little difference between the subspecies. The first down is pale grey. A dark eyepatch is evident and the bill is a pale horn colour. By 21 days the nestling is a light grey-brown, and at five to six weeks is covered in thick dark brown down with wing feathers starting to grow.

Feeding the chick

Food was brought to the nest for the first time on the day that the first egg hatched. In two cases where the intervals were accurately recorded, the first food items were brought at 11h20 and 15h37, with the respective eggs having hatched sometime before sunrise. Thus, within 4,5 h and 8,5 h respectively of actual foraging time, food was obtained. First feeds began immediately. The food brought to nests and prey remains collected from below nests are recorded in Tables 6.12 and 6.15, and discussed in Chapter

6. In all observations during this and subsequent nestling stages, only once was an adult bird seen regurgitating food at the nest, this being a short, chunky, meaty bone. On all other occasions, food was carried, invariably in the feet. Both parents fed the nestling. This usually began shortly after a nest relief and then at fairly regular intervals of, on average, 86 min. This rate of feeding varied little as the chick grew, being the same in the first and fourth week. However, the average number of items fed per meal increased from 12 to 20 and the mean time spent in feeding the nestling rose from 3,8 to 7,8 min (n = 21 and 14 feeds respectively). There was considerable variation in the size of feeds, ranging from 3 to 48 items. The small feeds invariably occurred after nest relief, when the nestling had recently been fed by the previous parent in attendance. The first feed of the day was fairly large (mean of 31 items). After a long period of not receiving food (i.e. first feed of the day), the nestling would rise up as soon as the parent got off the nest, with its bill partly open, and bob up and down. At normal feeding intervals, however, the parent bird would often have to stimulate the nestling to beg by passing the food in front of the chick and sometimes rub it against its bill, thus causing the nestling to rear up and beg.

Before feeds, adults usually spent considerable time sorting, selecting and preparing food from the supply that accumulated and was stored in the back of the nesting pothole. Initially, only red meat and soft material was

accepted by the nestling, with the first small bone being swallowed on the seventh day. Sometimes ridiculously large items of meat or bone were offered, but rejected by the nestling. All feeds were bill to bill. The adult held the food in the very tip of its bill and leaned forward over the nestling, turning its head sideways so that the nestling could more easily grasp the item by reaching slightly forwards and up. Once the nestling had firmly grasped the food, it was released by the parent, which then watched until it had been swallowed before tearing off the next piece.

Occasionally, food was dropped by the nestling. This was retrieved by the parent (never the nestling) and offered again, sometimes six or seven times. If the food item proved to be too large, it was swallowed by the parent. Parents fed themselves before, during and (most often) after feeding the nestling. Parents fed mainly on the bones from which the soft material had been removed and fed to the nestling. Carrion was never cleared from the nest by Bearded Vultures, although on occasions bones were knocked out accidentally.

The frequency with which food was brought to the nest varied considerably. The normal pattern was once or twice per day but if a good source was located, birds would shuttle back and forth between the nest and the food supply. Up to seven nest visits with food were recorded in one day, these all being cached in the pothole behind the nest. During this stage, eight of the 14 visits made to the nest with food were by the male bird.

During the incubation period attendant birds lay low on the nest, often with the bill resting on the nest rim. During the early stage of the nestling period, parent birds more often sat and the nestling could sometimes be seen moving beneath the parent's breast feathers. Other activities remained very similar to those described for the incubation period. Adult birds continued to defaecate away from the nest when possible, and on one occasion what looked like a faecal sac was carefully lifted out of the nest and dropped over the rim.

Although the number of interactions initiated by parent Bearded Vultures in the nesting area against other birds had decreased to 3,3% in this stage compared to that recorded during the incubation period at 8,8% (measured by the time spent in aggressive pursuit as a percentage of the time off-duty birds were present in the nest area), the impression gained was that these attacks were far more aggressive and determined than those made during the incubation period.

One case of nestling mortality was recorded during this stage, at the Roma nest on 10 September 1982. The nestling was 23 days old. There was little food in the nest (none having been brought in that day) and when feeding the nestling at 13h04, the female spent over half an hour attempting to pull pieces of food off a largish bone. After some 29 small pieces had been fed, the parent swallowed the bone. At 13h57 the male arrived without food, the female

departing to forage. The male was very restless on the nest, getting up frequently to walk about, and by 16h45 was standing permanently at the nest entrance. Between 17h00 and 17h30 this bird took off three times to circle in front of the nest, never going more than 400 m from the nest, and twice aggressively chasing off a pair of Whitenecked Ravens. At 17h55 the adult left the nest, thermalling up and out of the gorge, and disappeared over the range of hills some 6 km away, as if departing to forage. The ravens reappeared 12 min later, circling in front of the nest, then, on seeing that both parents were absent, settling on the ledge two potholes away from the nest. Both ravens walked along this ledge and peered nervously into the nest and, on confirming that only the nestling was present, jumped onto the nest and began pecking and pulling at it, tugging it towards the edge of the pothole. The nestling lay back on its wings and struck out with its talons, but to no avail. The nestling was pulled out of the nest and over the edge, falling to the ground some 55 m below, closely followed by the ravens who pecked and tore it to pieces. The male bird returned at 18h46 without food, flying directly to the nest where, after looking at the nest contents for a few seconds, began preening and showed no sign of concern. The female did not return to the nesting area that evening (an unprecedented event), so had presumably not found food. The circumstances of this nest desertion by the male resulting in predation by ravens all seemed to indicate that the parent Bearded Vultures were having difficulty finding food, and that food

shortage was, indirectly, the cause of mortality. Predation by ravens has also been recorded on Cape Vulture nestlings (Vernon et al. 1983a), occurring when late-nesting adults were kept off their nests during ringing operations.

7.3.6.2 Mid-nestling stage

During this stage 35 h were spent at the Roma nest, from day 78 to 81, unpublished data from four days observation were made available by J.J. Guy (at nestling ages of 44, 51, 66 and 86 days); and a further 11 h were obtained at the Gypaetus Point nest on about days 54, 57 and 58.

After about 50 days of age, the nestling Bearded Vulture was no longer closely brooded, and although a parent bird spent about 90% of the day in the nest, the nestling was usually left alone on the nest at night. Both adults left the nest area for the first time when the nestling was about 58 days old. By about day 80, an adult spent only about 25% of the day in the nest (range 6-36%) (Figure 7.13), although one was in the nesting area for about 46% of the day. This duty was no longer evenly shared, the female contributing 57% of the nesting area attendance and 91% of the on-nest attendance. Both parents foraged during this stage, sometimes together, leaving the nesting area unattended for 54% of the photoperiod, and on some occasions, also at night. Nest-duty and off-duty periods were no longer clearly defined, the mean foraging period being 1 h 57 min, but the male spending longer away than the

female (2 h 19 min and 1 h 33 min respectively). The longest spell of absence from the nest (apart from overnight) was 5 h 22 min, recorded for the male. The hourly attendance of parents in the nesting area and on the nest is shown in Figure 7.17, and activities are shown in Figures 7.18 and 7.19. The male bird spent very little time on the nest, mainly visiting simply to deposit food and twice to feed. Only one of the 10 observed feeds of the nestling was by the male. The female spent considerably more time on the nest, mainly during the middle of the day, usually lying (but not brooding), standing or feeding. The nestling, no longer brooded, sat apart on the nest which had become much more flattened with no sign of a cup and larger, as it had spread laterally.

During the mid-nestling stage the activities of the parent birds became less regular and predictable. Allopreening was observed in the early mornings on two occasions, though no copulation took place. Little aggressive behaviour towards other birds was observed, and apart from the female diving half-heartedly at a Black Stork Ciconia nigra and a pair of Bald Ibises, all interactions were initiated by Whitenecked Ravens.

The number of nest visits by parent birds remained the same as during the preceding stage, though the number of visits with food increased slightly (once every 5 h to once every 3,3 h). Although the male spent more time away from the nest than the female, he brought only four of the 10 food items. The male, however, fed at the nest only twice,
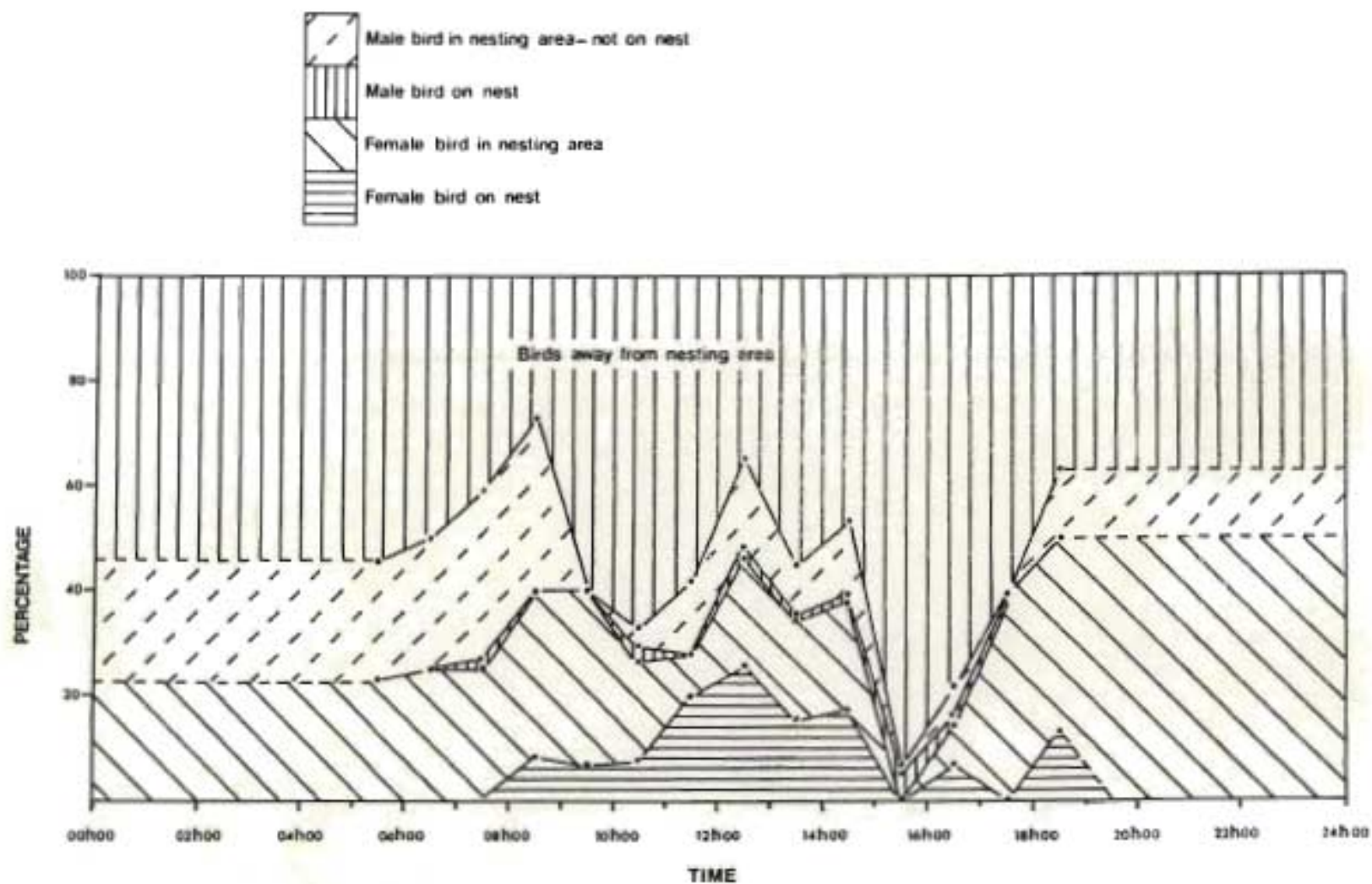
FIGURE 7.17. Role of the sexes in Bearded Vultures in the Roma nesting area and on the nest during the mid-nestling stage.
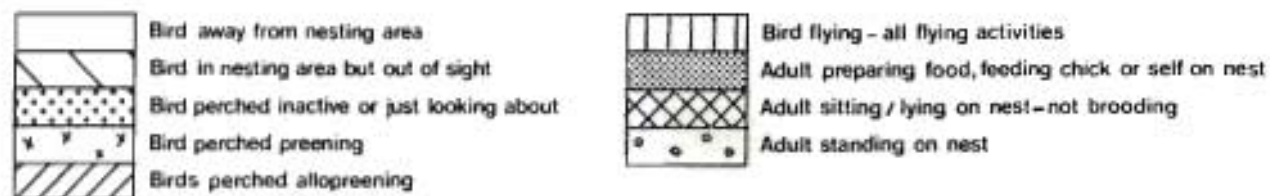
Above heavy line – bird off nest; below heavy line – bird on nest

Legend:
- Bird away from nesting area
- Bird in nesting area but out of sight
- Bird perched inactive or just looking about
- Bird perched preening
- Birds perched allopreening
- Bird flying – all flying activities
- Adult preparing food, feeding chick or self on nest
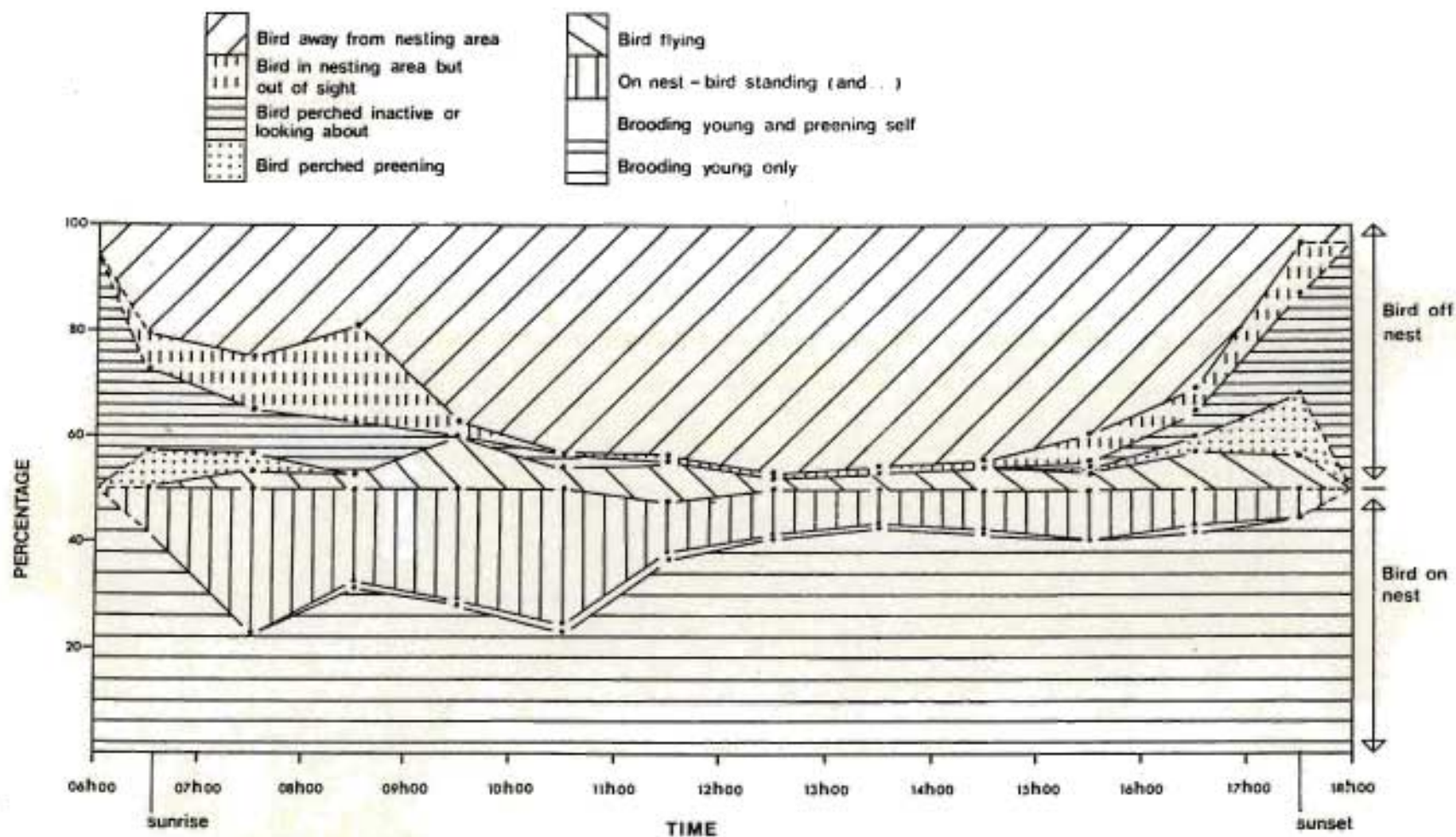- Adult sitting / lying on nest – not brooding
- Adult standing on nest
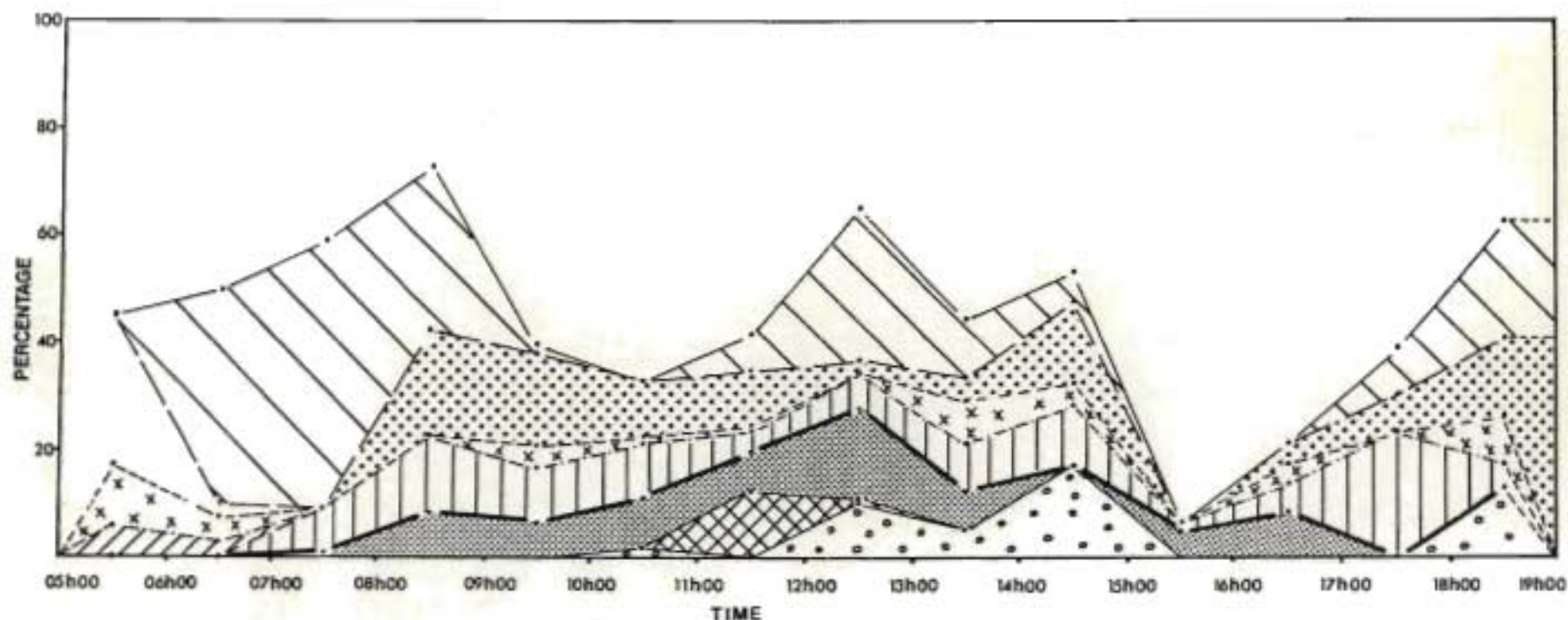
FIGURE 7.18. Activities recorded for Bearded Vultures in the nesting area and on the nest during the mid-nestling stage, per hour of the day.

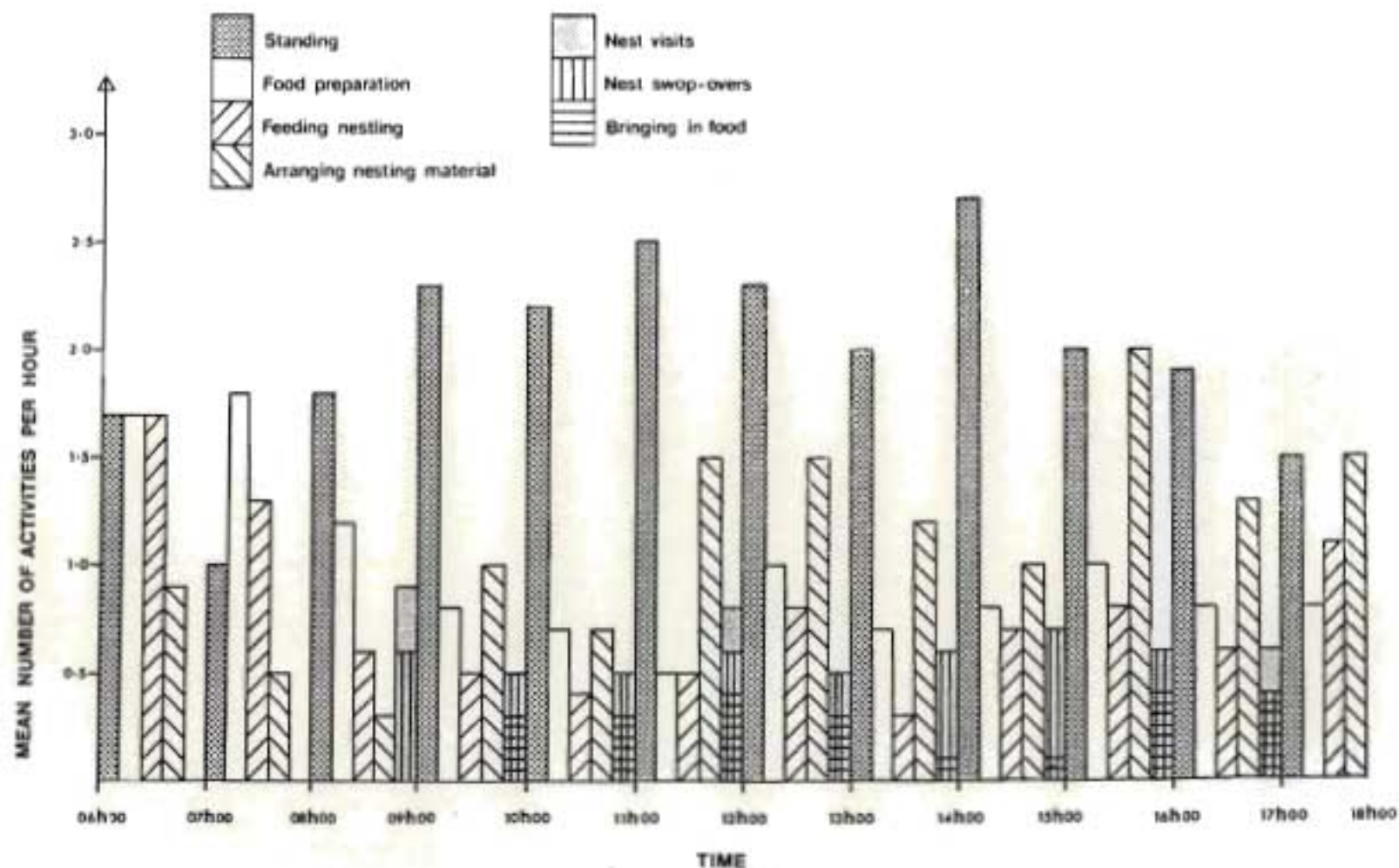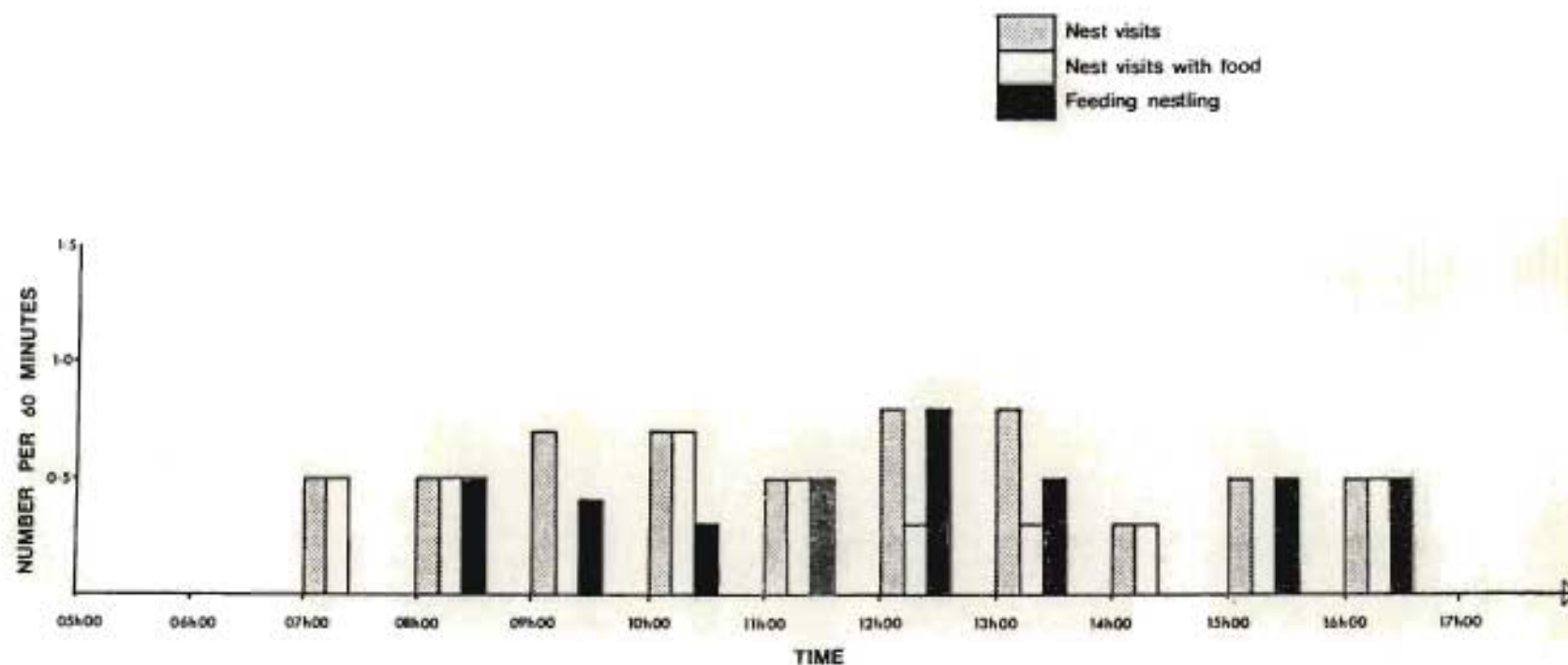FIGURE 7.19. Mean number of times that various nesting activities were recorded at the Roma nest during the mid-nestling stage.

while the female fed there regularly, suggesting that the male took most of his meals away from the nest.

The frequency with which the nestling was fed had decreased by about the 80th day from an average of once every 1,4 h to once every 3,3 h, although the size of the morsels of food offered by the parents was very much larger and the number of morsels had increased to about 70 per feed (max. 134), with each feed lasting on average 13 min and requiring an additional 6 min for food preparation. At this age the nestling was able to hold food clumsily in its talons, tear off pieces and feed itself, although it clearly preferred to be fed, coming forward towards the parent with its head held low and begging with a mewing call. If the parent did not react the nestling crouched in front of it with head and neck extended. Should there be a further delay in feeding the nestling would bounce up and down, flutter its wings slightly and squeak. Feeding was the same as during the preceding stage, i.e. bill to bill, with the parent continuing to retrieve any dropped items. Large bones, at least 15 cm in length, were being accepted and swallowed by the nestling, and on one occasion the nestling was seen to regurgitate four or five bones, sort through them and swallow them again.

By around the 80th day the nestling was dark brown, mottled with white on the wings. The tail and primaries were about 40% and 60% of their full-grown lengths respectively. While the legs were booted, these feathers were a bit sparse below the tibiotarsal joint. The talons appeared fully

grown, though lighter in colour (pale grey) than in the adult. The bill was also a lighter horn colour than that of the adults, and the sides of the face had a sparse covering of bristles, though these had not yet protruded below the bill to form a beard. The eyes were surrounded by a scleral ring which was predominantly brown, just showing a tinge of red, and the iris appeared more light brown than yellow. At this stage the nestling was fairly active on the nest, spending 16% of the photoperiod standing and looking about, 8% clumsily sorting through, preparing and feeding on food stored on the nest, 6% being fed by a parent, 5% preening itself and 2% exercising its wings. Analysis of hourly activities (Figure 7.20) show that in the early morning the nestling was fairly active and, after feeding itself, dozed off until visited by a parent sometime after 07h00. After about 11h00 the nestling became decreasingly active throughout the remainder of the day. Wing exercises took the form of flapping at the nest entrance, the nestling often coming perilously close to taking off. The nestling flapped seven or eight times, then stopped for a few seconds, resumed again and stopped etc., usually exercising for about 2 min per session and on average 2,8 times per hour, mainly in the mornings.

When overnighting in the nesting area at this stage, both parents roosted in a pothole about 6 m from the nest, the female occupying an old nest within the pothole, the male roosting on the outer lip.
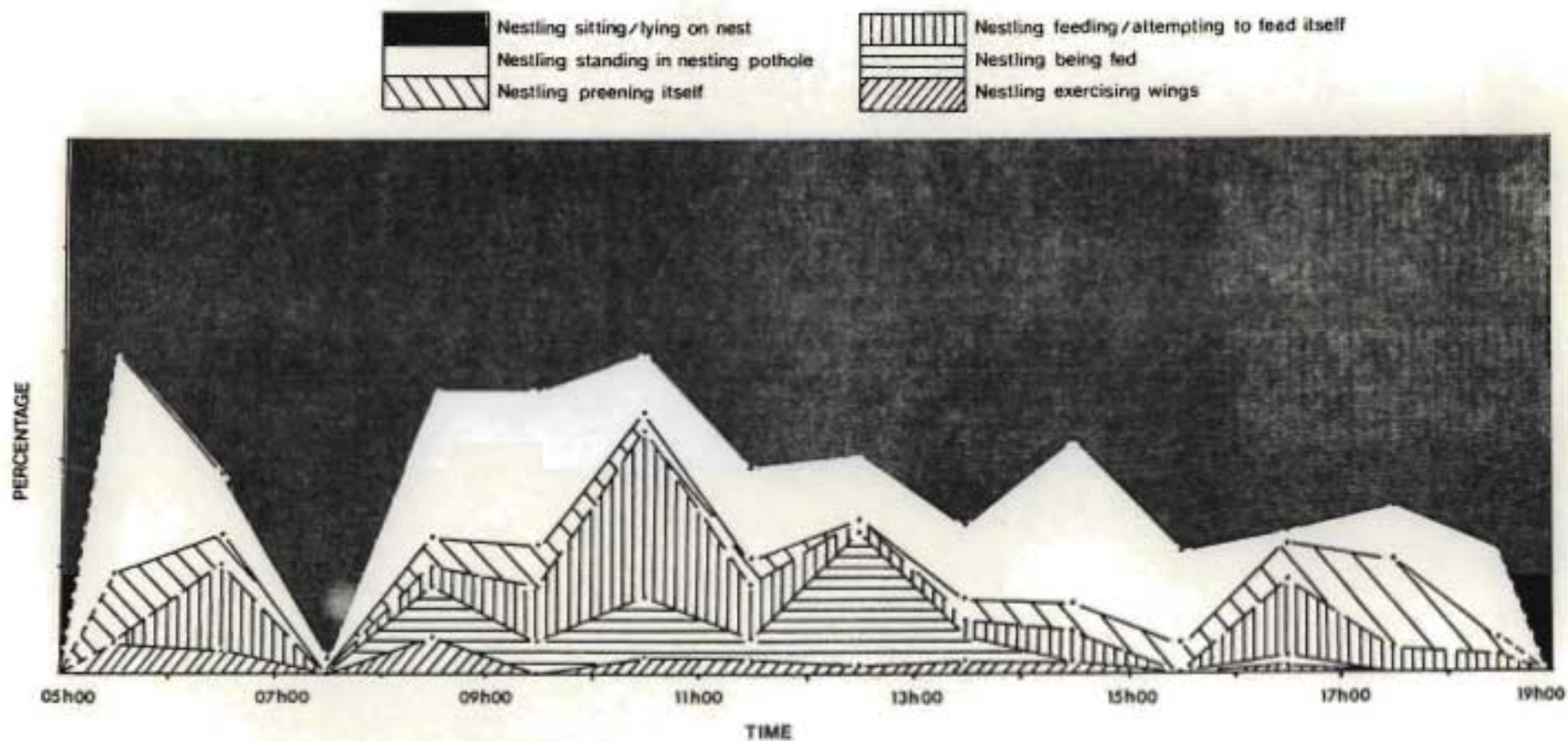
FIGURE 7.20. Activities of the nestling Bearded Vulture at the Roma nest, recorded at age 78-81 days (mid-nestling stage), per hour of the day.

7.3.6.3 Late nestling stage

Information on this stage of the nesting cycle is a little less detailed; two days were spent at the Ntabamhlope nest, one day at Gypaetus Point and data for one day was provided by J.J. Guy for the Roma nest. During this stage the parent Bearded Vultures visit the nest only to bring food, usually departing immediately, although on one occasion both parents fed in the nest pothole with the nestling. Food was brought to the nest on average once every 3,7 h, with similar frequency to the preceding stage. Parent birds did not remain in attendance in the nesting area, and on two of the four days did not overnight there either. The nestling fed itself, and food was snatched from the parents. The nestling spent considerable time sorting through the food items on the nest, and once, when a Black Eagle flew nearby, it crouched over the food with wings slightly spread.

The nestling exercised regularly during this stage, more energetically than during the preceding stage, flapping its wings vigorously and bouncing up and down on the nest, often lifting into the air and coming close to leaving the nest site. J.J. Guy (pers. comm.) observed a nestling in 1972 which did take off "by mistake", a gust of wind causing the bird to lift off at 117 days and go sailing out into the valley, landing on the bottom and being stoned by Basotho herdboys. (This bird was rescued and released later in Giant's Castle Game Reserve.) Exercise periods were longer during this stage, averaging about 8,5 min, but sometimes

lasting as long as 12 min, but interspersed with short breaks.

No new material was added to the nest, which became even flatter and more laterally enlarged. On both mornings that parent birds were in the nesting area allopreening took place, and while this did not lead to copulation then, copulation has been observed during this stage (J.J. Guy pers. comm.).

The lengths of four nestling periods were determined during this study, the most accurate of 127-129 days being at the Ntabamhlope nest. A Gypaetus Point nestling flew at 126-131 days. Assuming an incubation period of 56-57 days and calculating from the first day of full-time occupation of the nest by the female, the Mount Erskine bird was seen out of the nest on about the 125th or 126th day. At the Roma nest, under observation by R. Metcalfe, the nestling had not flown by the 117th day but was seen on a nearby perch on day 125. While the earliest recorded flight by a Bearded Vulture is 110 days (Steyn 1982), this was a captive bird and probably not typical. Two records from Lesotho of birds flying before 120 days (J.J. Guy pers. comm.) indicate that flight was not at all strong and with little flapping. Both birds glided down to the ground and were unable to escape the pursuit of herdboys. The four records here of birds surviving their first few days of flight indicate that the nestling period is usually between 120 and 130 days, and probably more accurately, between 124 and 128 days.

7.3.7 Post-nestling period

This period covers the time between the nestling's first flight and when it is no longer dependent on its parents. The movements of young independent Bearded Vultures is given in Chapter 5. The post-nestling period is a particularly difficult one to study as young birds are not easily found or followed. As a result, most studies on the breeding biology of raptors stop at or soon after their first flight. In the case of Bearded Vultures, apart from the fact that parents continue to feed the young bird for at least a few weeks to a few months (e.g. Cramp & Simmons 1980; Brown et al. 1982; Steyn 1982) no further details are known. Information on this period was obtained through periodic observations at the Ntabamhlope nest site, opportunistic observations at the Mt. Durnford and Gypaetus Point nests and by radiotracking a first-year bird, captured on what must have been one of its earlier foraging trips out of the nesting area (in the company of a parent), at about two months after its first flight.

Unlike tree-nesting raptors where young birds can venture from their nest onto adjacent branches, the first movement from the nest by young Bearded Vultures involves a flight. Early flights were usually short, the young bird settling on a ledge or pothole (on one occasion flying straight back to the nest), and spending a considerable amount of time here before attempting another flight. During 17 h of observation during the first two weeks after the first flight, young birds made six short flights, spending

the remainder of the time on the nest or a nearby perch, and never more than 200 m from the nest. On five occasions when food was brought by parent birds, it was always carried to the young vulture, on three occasions at the nest, once in a pothole about 20 m from the nest and once on a ledge 60 m from the nest. Parent birds were never seen trying to coax their young offspring to fly. Young birds always returned to the nest at night. A young bird was seen attempting to carry food (the lower foreleg of a sheep) from its perch to the nest, but on landing on the lip of the pothole the food was dropped. Flight during these first few weeks was unsteady, and birds during their first two months of flying could be easily identified.

At about the third week of flight young birds ventured further from the nest, gliding for short periods up and down the nesting cliff in front of the nest and gliding about with parents in the evening. During 13 h of observation 31 flights took place, these averaging just over 2 min, the longest lasting almost 6 min. The greatest distance from the nest that a young bird was seen was about 800 m. Food was still brought to the young bird, which during this stage made no effort to fly out to meet its parents. Roosting took place in the nest.

After a month young birds were increasingly difficult to find, since they spent longer and longer periods gliding about and ventured further from the nest. At least 40% of their day was spent in flight (n = 23 h) and during a 5,5 h

watch at Ntabamhlope, the young bird spent three periods of 57 min, 1 h 36 min and 1 h 4 min (66% of observation time) gliding about the nesting area. Young birds, however, began flying rather later in the day than their parents, usually only once the air had stabilized and the down-draughts had turned to up-draughts (about 2 h after sunrise). Young birds were found up to 3 km from their nests, often inspecting ossuaries where they would walk about picking up bits of bone overlooked by adults. A young bird was seen dropping the scapula of a small ungulate at about five to six weeks after first flight, the bone descending slowly and not breaking on the three drops observed. While these attempts appeared clumsy and awkward, with sharp braking and fluttering at the point of release, all three drops succeeded in making contact with the rocky slab. During this period young birds were often seen carrying bones in their feet, just flying about, and bone dropping was observed more and more frequently. At about this time young birds started flying along the cliffs towards the nesting sites of other pairs, meeting first-year birds from neighbouring nests and gliding about together for a while before separating and returning to their natal areas. At about six weeks a young bird was seen following a parent for at least 7 km, but as it returned alone to the nest area about 14 min later it was assumed not to have gone much further. Young birds began to accompany their parents for longer periods of time: at about 45 days out of the nest the Ntabamhlope bird left the nest area with a parent for 34 min, returning alone; at 49 days

it twice accompanied a parent for 1 h 7 min and 56 min respectively, on both occasions returning alone; and at 57 days it departed and returned with a parent, staying away for just under 3 h. Young birds, however, did not always accompany parents. During observations on days 51, 56 and 61 the young bird remained within sight of the nest area. The earliest record of a first-year Bearded Vulture at the feeding station in Giant's Castle Game Reserve was towards the end of February (i.e. about two months out of the nest), and this was in the company of an adult.

At about seven or eight weeks out of the nest first year birds, except at very close range, became increasingly difficult to recognize from two- and three-year-olds. Although they continued to roost in their natal nest, as none were marked and as they disappeared so quickly from sight once they started flying, it became impractical to follow them visually and on foot. Some insight into their dependence period can be obtained, however, from data on group-age compositions. During the nestling period, 13% of all immature birds were seen in the company of adults. In February, (corresponding to the time when first-year birds began venturing out with their parents) this increased to 25%; the mean for the non-breeding season was 27%. The situation reverted to that recorded during the nestling period again between June and July, at the start of the next breeding season (Figure 7.21). The opposite trend occurred in the groupings of immature birds, and in the numbers of
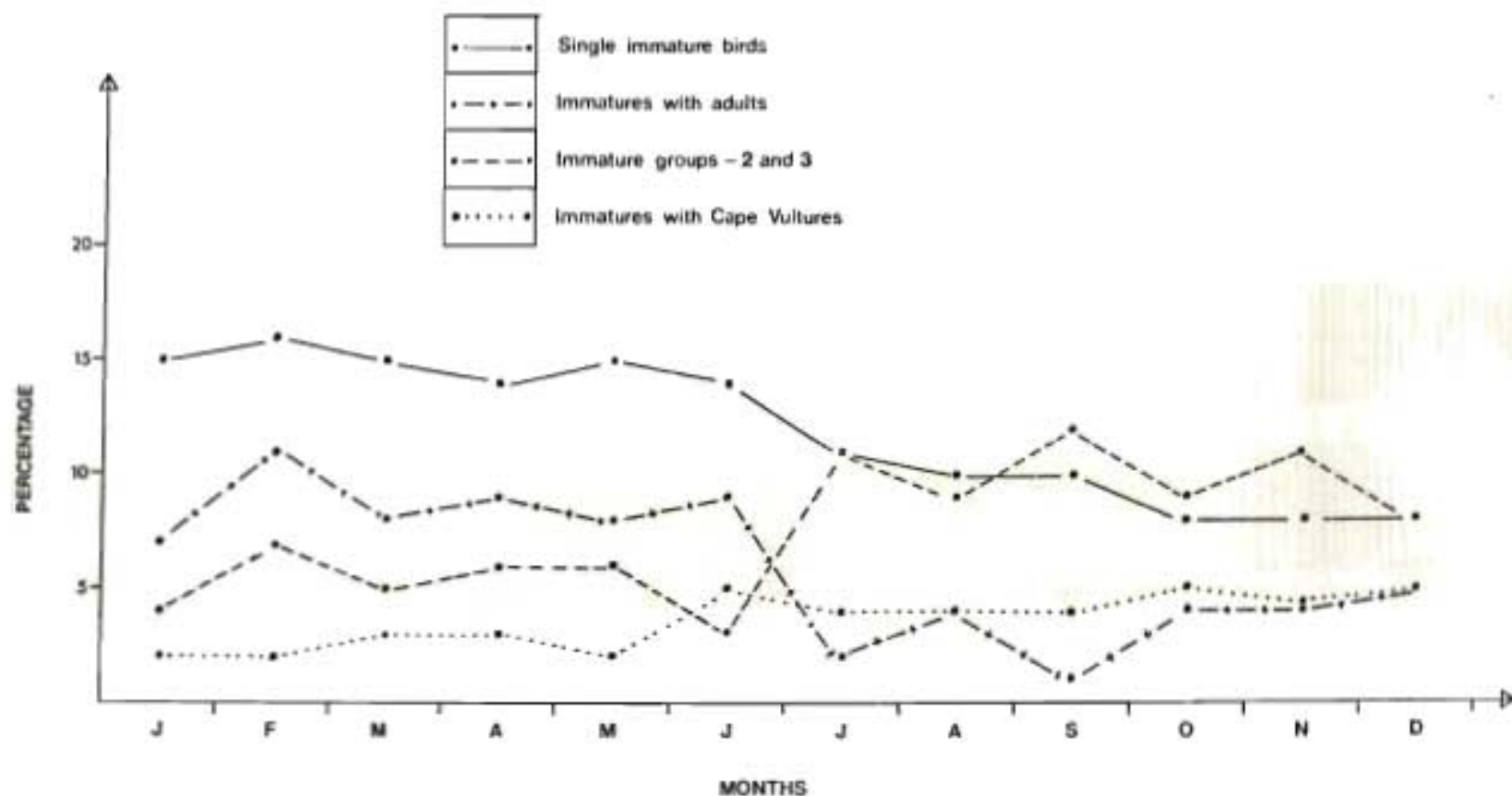
FIGURE 7.21. Immature Bearded Vulture group compositions as a percentage of all immature birds recorded per month.

immature birds seen with foraging Cape Vultures, i.e. at the time when the numbers of immature birds with adults was decreasing, the numbers of immatures forming groups together and the numbers following Cape Vultures was increasing. I interpret the situation as follows: once first-year birds had been out of the nest for about two months, they were fairly confident in their flying ability. They then began to accompany their parents on foraging trips, but on an irregular basis. As about half these groups were with one adult and half with two, on about 26% of occasions one or both parents are likely to be accompanied by a young bird. No significant change in the proportions of adults to immatures was detected through the non-breeding season. At the start of the next breeding season, adults were less often accompanied by young birds as they went about their next breeding attempt and although the small percentage of young birds accompanying adults may indicate the partial dependence of these birds, this is not consistent with the general movements observed for immature birds (Chapter 5). I would incline to the idea that single off-duty adults may opportunistically join up with older (three- to four-year-old) immatures to forage if neighbouring adults were not currently available.

Bearded Vultures usually carry food from where it is found to a cliff to feed (Chapter 6). Food is delivered to immatures and sometimes shared with them. The extent of the dependence of first-year birds on their parents for food as they get older is not known, because food is delivered to

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the young bird wherever it may be and not just deposited at the nest, and immatures may cover quite a large area. However, at the end of April (the immature being just over four months out of the nest) an adult was seen landing on a ledge with food, closely followed by the young bird. The adult then left without the food and the young bird proceeded to feed. In mid-May, an adult was observed dropping a bone at an ossuary, and circling while an immature dived down and retrieved it. The immature dropped the bone three times, then fed on the splintered pieces. I assumed that this "hand-over" was deliberate, as the immature was in full sight and the adult made no attempt to follow the bone down, something which Bearded Vultures are very quick to do if they are about to be robbed. At a food source in the veld, however, adults always dominate young birds, sometimes chasing them and causing them to take off and circle until they (the adult(s)) have fed or have taken off with food. Although enough marked individuals were never involved to give definite proof, I was fairly sure that on occasions the conflict was between parents and their offspring. In any event, in none of the cases observed did adults step back and allow young birds to feed first.

Some idea of the early movements of first year birds was obtained from a radiotracking study of a single bird, captured in late February at about 26 to 27 weeks of age and about two months out of the nest. This bird was monitored for a period of five months after which it could not be

located even though the entire southern African range of the species was covered from an aircraft. Either the radio malfunctioned or the bird was killed and the radio destroyed. One defect of this study was that neither of the radiotagged bird's parents could be captured. While the position of the radiotagged bird could be pinpointed by triangulation, it was very seldom seen, so whether it was alone or in the company of a parent could not be confirmed.

At between two and three months out of the nest, six days (comprising only about 28 h because of bad weather) were spent tracking. Two patterns emerged:

(a) 25% of the bird's activities were confined to an area of about 4 km immediately around the nest and ossuary. For a further 50% of the time it ventured out for short forays, the furthest distance from the nest being just over 6,5 km. The utilized range, in the sense of Odum & Kuenzler (1955), was elongate in shape, running northeast to southwest (Figure 7.22), and covered an area of about 42 km². To the northeast, the area extended out towards the tip of The Giant, including both north and south faces, and to the west and southwest, incorporating a large valley system and the two adjacent high ridges in Lesotho.

(b) On two occasions (making up the remaining 25% of the monitored period), two uncharacteristic, large and decisive movements were recorded (Figure 7.23). On the first, the young bird departed along the escarpment, descended into Natal and headed towards Loteni Nature Reserve, where it appeared to forage intensively in two localities (varying

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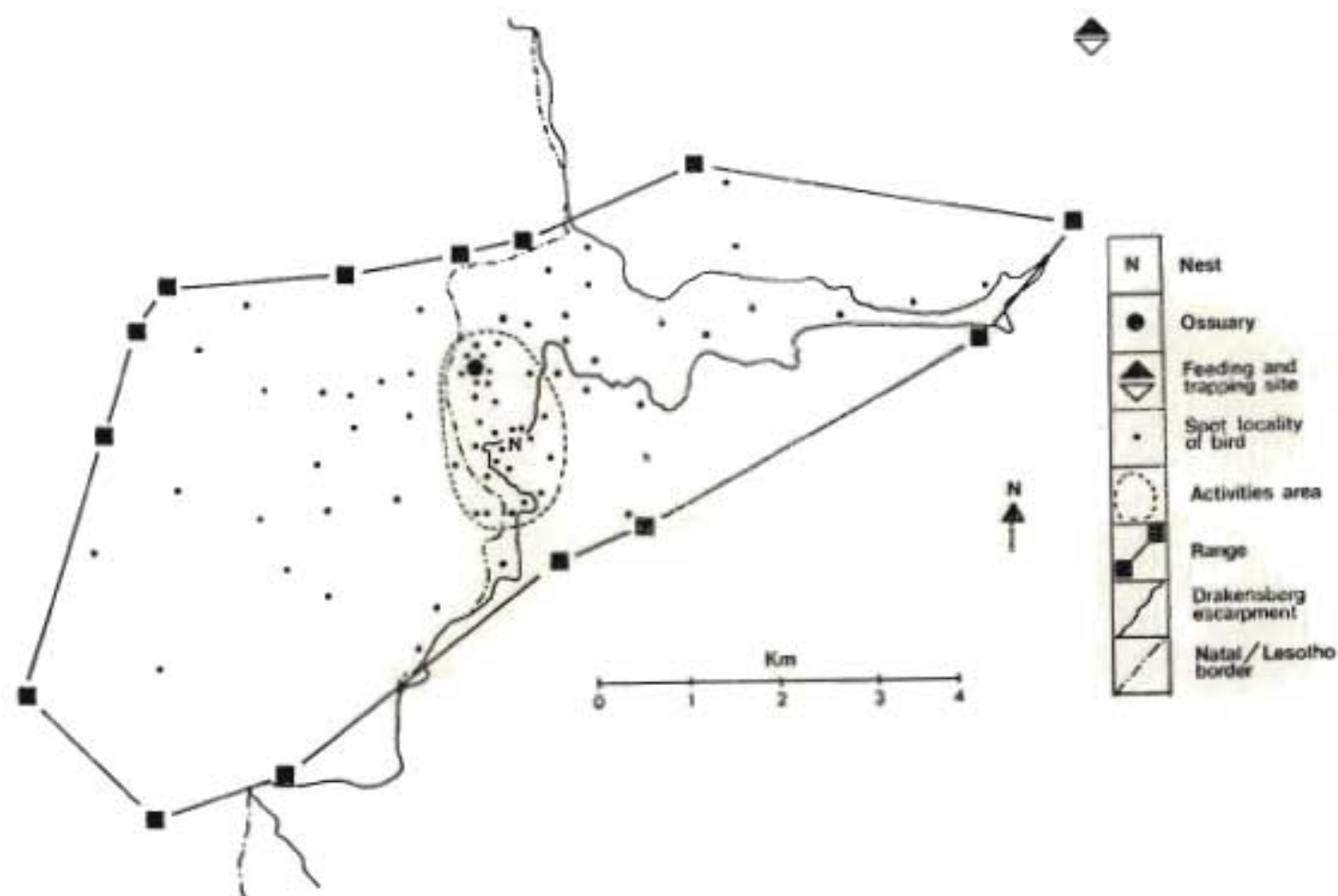
FIGURE 7.22. Range of a radiotagged juvenile Bearded Vulture between 2 and 3 months out of the nest, in the Giant's Castle area.
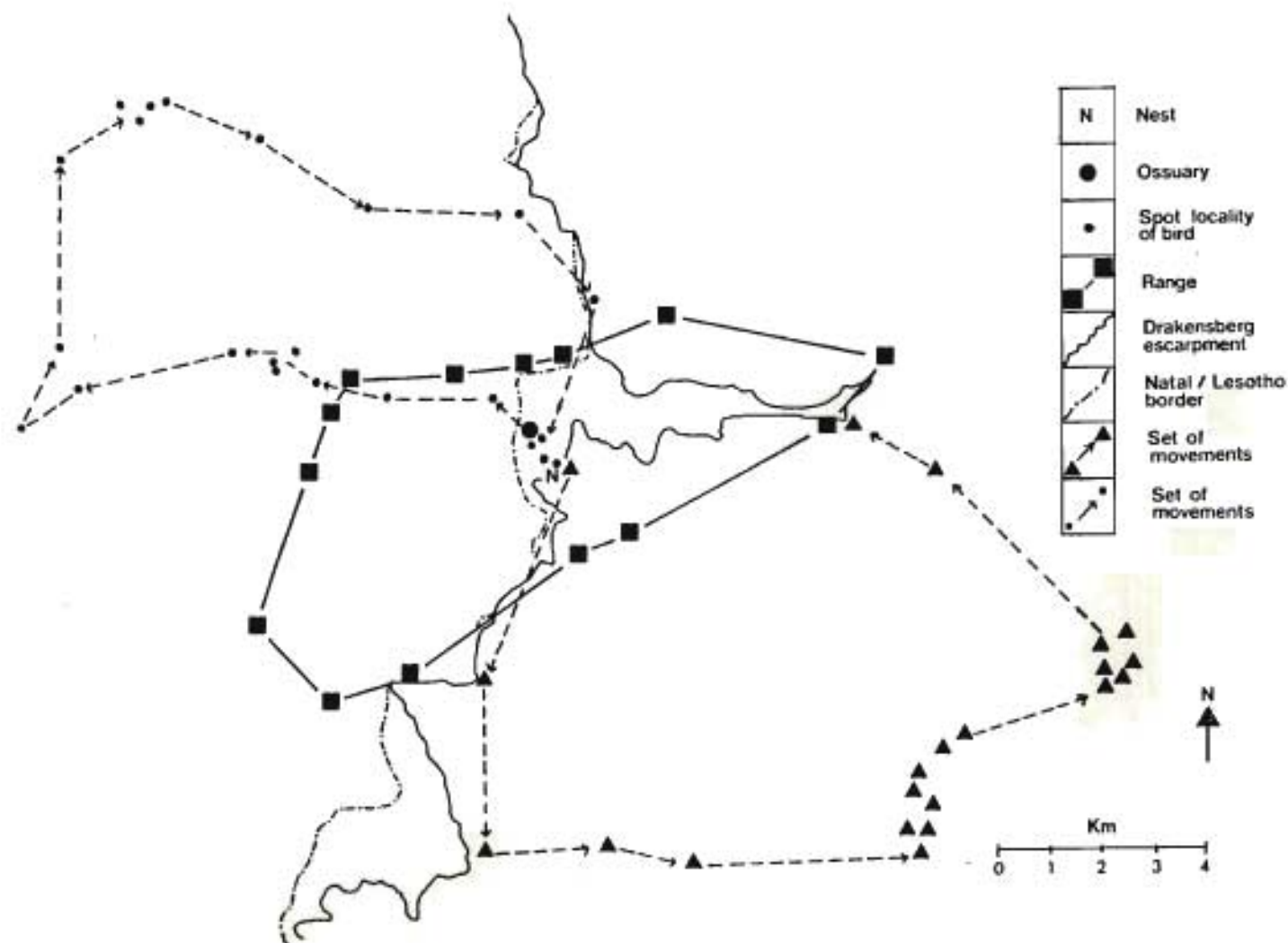
FIGURE 7.23. Superimposed on the range of the juvenile Bearded Vulture at 2-3 months out of the nest were two uncharacteristically large and decisive foraging sorties.

signal received indicated that the bird was in flight), then returned to The Giant via a high ridge to the west of Loteni, where the bird perched for over an hour. The second large movement was to the northwest, into Lesotho via a ridge, north across the headwaters of the Sanqebethu River and back to the nest via the escarpment. The first trip took 3 h 30 min and covered a distance of at least 36 km, the second took 3 h 50 min and covered at least 33 km.

At between three and four months out of the nest, four days were spent tracking, during which 29 h of information were obtained. The size of the young bird's range had increased to 78 km^2 with the bird moving up to about 9 km from the nest. The utilized range was now more uniform in shape (Figure 7.24), having expanded mainly towards the northwest and southeast, incorporating another valley and ridge system in Lesotho and ridges above Loteni in the Natal Little Berg respectively. The steep river gorges of the Loteni and Elands Rivers in the Natal Little Berg appeared to be avoided. During this period the young bird spent only about 14% of the day in the immediate nest and ossuary area.

Seven solitary outings at the Ntabamhlope nest timed during this age period indicate that the mean time that the young bird spent away from its nest was 53 min with the longest period being 1 h 37 min. On two of these occasions the young bird returned with food, but whether this was obtained by itself or from an adult is not known.

Superimposed on this range was another larger, more
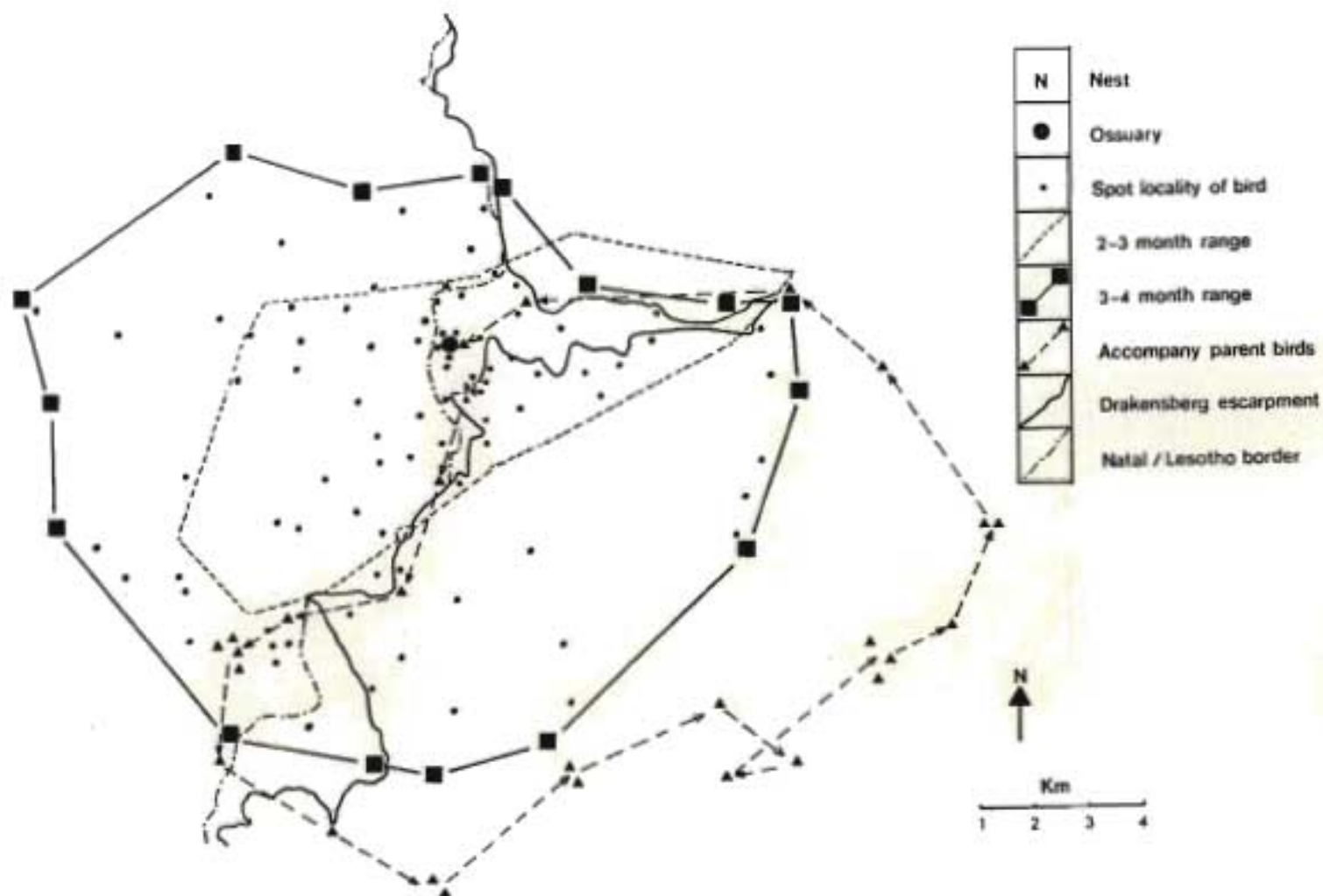
FIGURE 7.24. Range of the radiotagged juvenile Bearded Vulture at 3-4 months out of the nest and showing a foraging sortie outside of this area.

purposeful movement, very similar in route to the first described to the Loteni area (Figure 7.24). The distance covered was at least 48 km and the bird was away from the nesting area for just over 4 h.

During the period from late April to late June, with the young bird having been out of the nest from four to six months, the utilized range had again increased in size to 168 km^2 (Figure 7.25), with the young bird ranging up to about 15 km from the nest. In seven days, 53 h were spent tracking the bird. It was no longer possible to discern clearly the two different patterns in the foraging activities.

In early July when checking the cliffs for nesting activities, the radiotagged first-year bird was seen returning to roost in its natal nest, its parents meanwhile having begun their next breeding attempt and already incubating in a nest about 240 m southwest of this. Towards the end of July, during two days spent tracking, signals from the young bird were faintly detected for a short period from about 35 km north of the nest and just north of Champagne Castle. The young bird did not return on either night to roost in the nesting area, and it was never seen or heard again, even though the entire area was tracked from the air about two months later.

No activity on the part of adults was ever observed that would indicate that young birds were encouraged to leave their home range or nesting area.
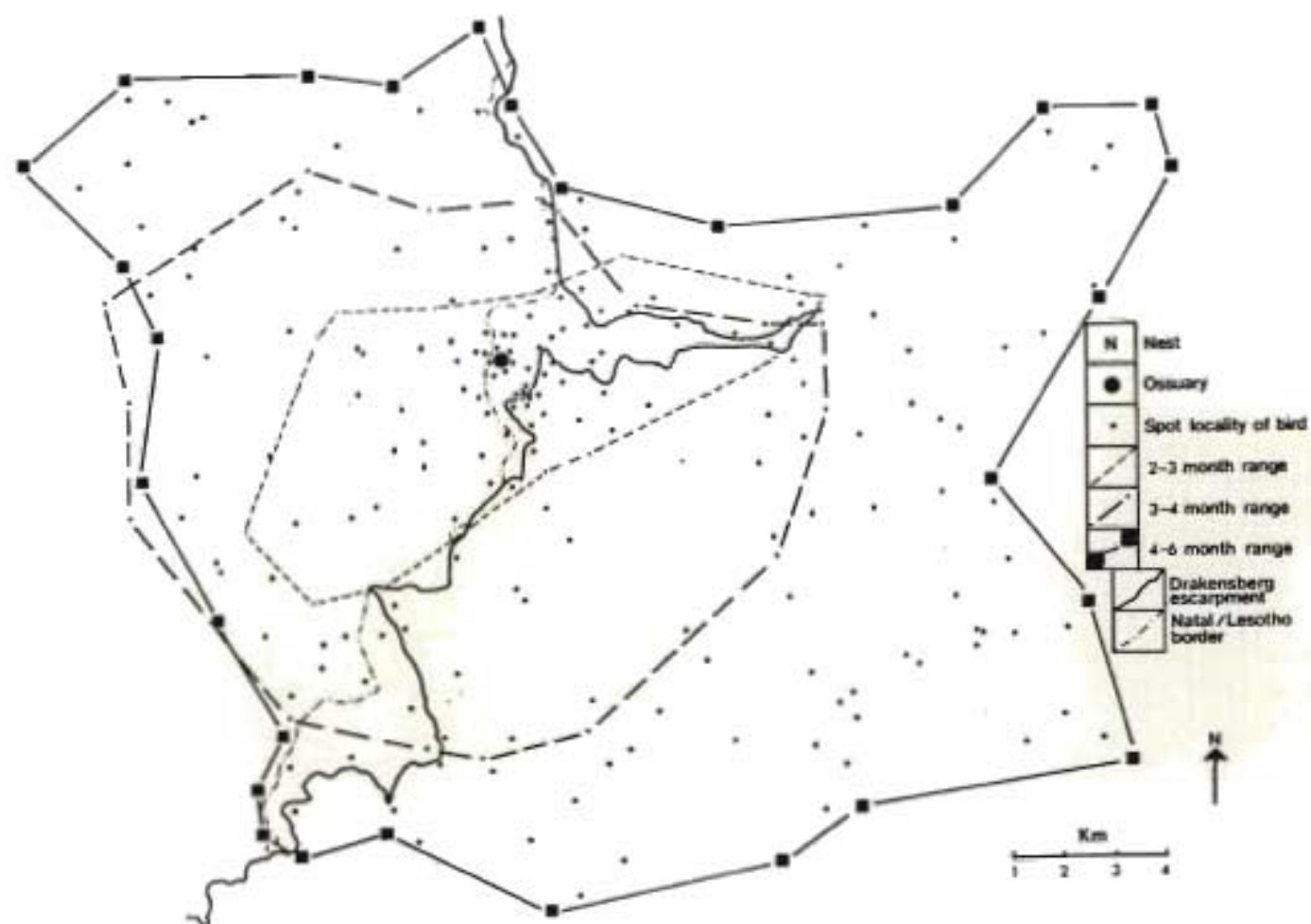
FIGURE 7.25. Range of the radiotagged juvenile Bearded Vulture at 4-6 months out of the nest.

7.4 DISCUSSION

7.4.1 Alternate nest sites

Bearded Vultures use their nests in rotation, allowing a maximum period of time between re-use of a particular site. Nests are large and their construction represents a large energy expenditure. The nature of their chosen sites, being dry, cold and in shadow, means that nesting material will remain in good condition for many years. The strategy of building onto a number of nests and then, towards the end of the pre-laying period, pirating from these for the nest finally decided upon, means that in any one year a far smaller energy expenditure is necessary than would be the case if a nest were built from scratch.

The use of alternate nests for general nest hygiene and parasite avoidance is a more acceptable hypothesis in the case of Bearded Vultures than in many other species. While many species are more inclined to move to a new nest after an unsuccessful breeding attempt than after a successful one, the Bearded Vulture invariably occupies a new site each year. With the large build-up and storage of carrion in the nest, nest hygiene and nest parasites must be an important consideration. Because nests are so thickly lined with wool and other mammal hair and because they are in such protected sites, parasites may survive far longer than in tree nests or nests in more exposed places where rain would wash through them and where they would be exposed to a far greater temperature range. In addition, in the nests of

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other species the nest lining is usually much thinner and is often trampled away by the end of the nestling period. It is possible then that Bearded Vultures use their nests on a rotational basis to starve out parasites that have accumulated in a nest before it is re-used. In addition, carrion flies are attracted, these presumably laying their eggs in suitable dead material. The resulting larvae may pose a direct threat to the nestling, or more likely, the larvae may burrow into the woollen nest lining and pupate. Because of the generally cold temperatures, the pupae may remain dormant until warmed by the parent incubating the following year. Should the birds avoid that nest for a year or more, the pupae may die.

7.4.2 Nest orientation

Nest sites, particularly those at high altitudes (i.e. in basalt) and those in more exposed situations tend to face between east and southwest. A similar situation exists for Cape Vultures in the Natal Drakensberg (Figure 7.26), with 77% of the birds and 84% of the nests (totals of 1325 and 215+ respectively) facing from east to south (Brown & Piper in press). Most of the Cape Vulture colonies documented by Mundy (1982) faced south, but as he pointed out, the large north-facing Manoutsa colony in the eastern Transvaal is equally successful. In the Natal Drakensberg and the Lesotho highlands a most striking climatic feature is the occurrence of Bergwinds, which blow from July to September and coincide with the incubation and early nestling periods of both the

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No. NESTING COLONIES & ROOSTS

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■ = NESTING COLONIES
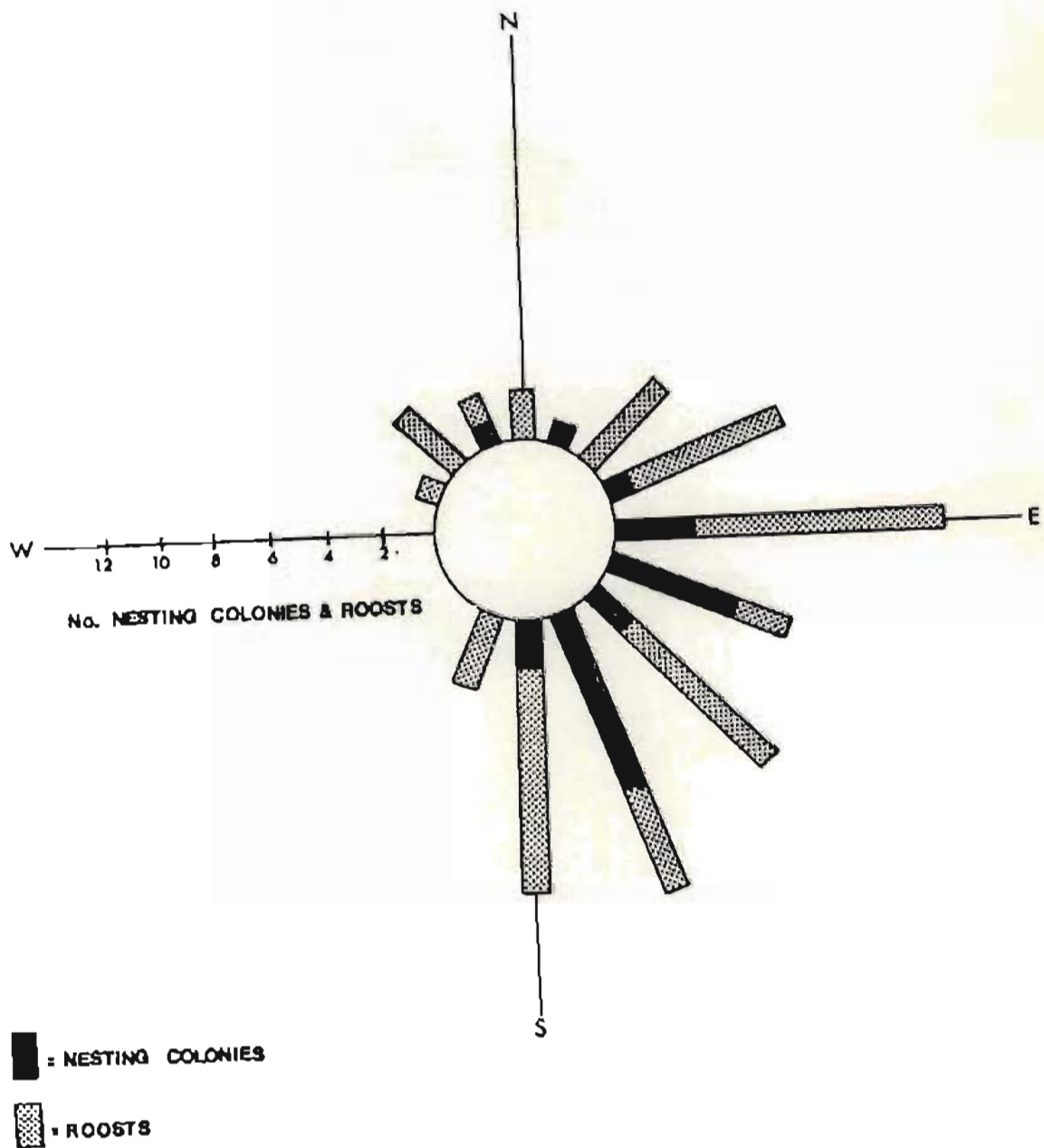
▨ = ROOSTS

FIGURE   7.26.   The   orientation   of   Cape   Vulture   nesting

colonies and roosts in the Natal Drakensberg.

Cape and Bearded Vultures, when the latter are visiting their nests five or more times per day. Wind data, recorded automatically at the Cathedral Peak State Forestry meteorological station (1860 m above sea level), were analysed for velocity, direction and duration. Late winter and early spring were the windiest months in the Natal-Lesotho highlands (Figure 2.3, p. 20). The wind direction, given here for the windiest month of August (Figure 7.27) shows that winds above 20 km/h from the west-northwest to west-southwest were by far the most frequent, blowing for a monthly average of 77 h, with about 49 h of winds over 30 km/h and 23 h of over 40 km/h. While winds in excess of 75 km/h were not infrequent, the velocities of all these winds recorded at Cathedral Peak must have been considerably higher at the altitudes of the nests, as, on the exposed ridges in the Giant's Castle area I could often not stay on my feet and had to seek the lee side. I suggest therefore that the orientation of nesting sites, both for Bearded and Cape Vultures, is chosen on the lee sides of cliffs, so that birds arriving at nests are protected from the high winds.

7.4.3 Nest altitude

The mean altitude of Bearded Vulture nests in the basalt of the High Berg was 2835 m above sea level, with those nests on higher cliffs tending to be relatively higher up the cliff. As higher cliffs are also usually longer, there is probably a bigger selection of suitable potholes than on lower cliffs. It seems likely that birds select

WIND SPEED (km/h)
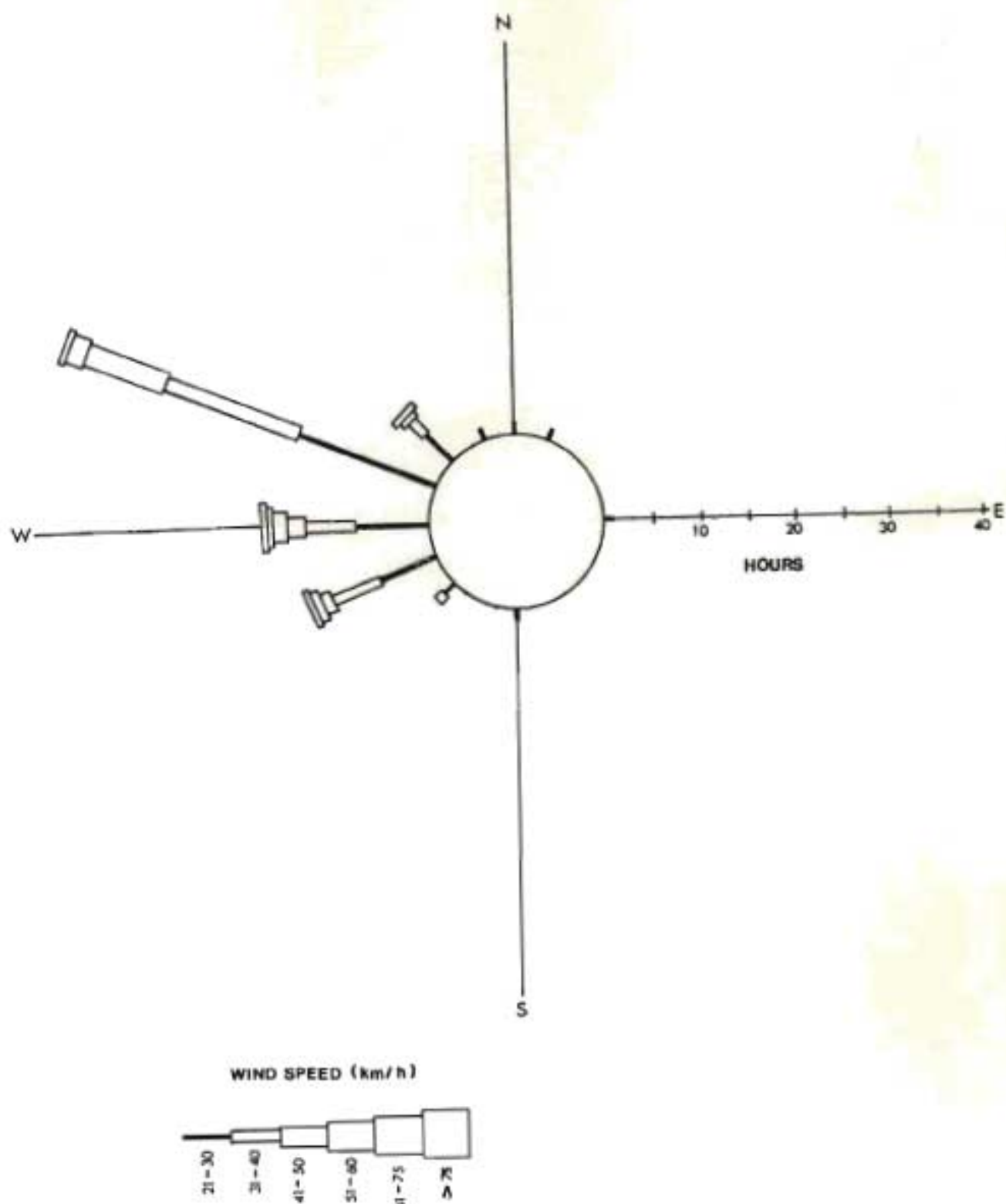
FIGURE 7.27. Wind direction, duration and velocity recorded for the windiest month of August in the Natal Drakensberg (1972-1982).

higher sites where these are available, as this provides an energetic advantage when going out foraging, particularly in the early mornings before thermals have developed. In the Cape Vulture, a different situation appears to prevail. The mean altitude of nesting colonies on the Drakensberg escarpment was 2747 m above sea level, approximately 100 m lower than Bearded Vultures' nests. Roosting colonies, however, were higher, averaging 2827 m. Cape Vultures nest mainly on open ledges and, while on the High Berg these are usually in cut-backs, they are nevertheless more exposed than are the Bearded Vultures' nests in potholes. Thus, while the advantage of height is a consideration, falls of snow in winter may dictate a lower altitude, as has been shown for Golden Eagles in Scotland (Brown 1976a). It is interesting that the roosting cliffs, which can be left for lower ledges in bad weather, are at a very similar altitude to Bearded Vulture nests.

7.4.4 Courtship display

Elaborate courtship displays have been recorded for the Egyptian Vulture and the Bearded Vulture (Brown et al. 1982; Cramp & Simmons 1980; this study), but as far as is known no obvious or spectacular courtship displays are performed by other African vultures. Many of the eagles are well known for their courtship flights, and Newton (1979) has suggested that these displays act to advertise over long distances the fact that territories are occupied. Of the species which maintain territories and nest sites for periods of many

years it could then be expected that those species with less visible nests, e.g. built within or under the canopy of a tree, on cliffs, either in potholes or on ledges, would perform more spectacularly than species nesting in more open sites, e.g. on the crown of a tree. This is in fact generally the case (Table 7.4): eagles and vultures nesting on the crown of a tree (and usually these nests are large) have poorly developed courtship displays, e.g. Tawny, Martial, Brown Snake Circaetus cinereus and Blackbreasted Snake C. gallicus Eagles, Lappetfaced and Whiteheaded Vultures, while those species nesting within or under the crown of a tree, e.g. Wahlberg's Aquila wahlbergi, African Hawk Hieraaetus fasciatus, Ayres H. ayresii, Longcrested Lophaetus occipitalis and Crowned Stephanoaetus coronatus Eagles and Bateleurs, have very spectacular displays. (Although Steyn (1982) states that spectacular chasing flights and rolls are performed by the Bateleur during courtship, this was never observed during a three-year study of the species in the Kruger National Park, Transvaal Province (R. Watson pers. comm.). This species, with its relatively small foraging range of about 45 km^2 (Watson 1984), low foraging altitude and high percentage of the day spent on the wing, is very conspicuous throughout the year in its territory and therefore constitutes a possible exception to the rule.) Cliff-nesting species, whether they breed in potholes or on ledges, all perform elaborate displays, e.g. Black and Booted Hieraaetus pennatus Eagles, Egyptian and Bearded Vultures. While the two vultures

usually build in potholes and are completely out of sight, the eagles' nests may be slightly more visible. On any cliff, however, a nest would be visible only from in front of that site and, in addition, Booted Eagles build small nests usually at the base of a tree on a ledge (Brooke et al. 1980; Brown 1985b), while Black Eagles usually build on a protected part of a cliff, in valleys, ravines and canyons (Tarboton & Allan 1984), so that their nests are relatively inconspicuous. Colonial nesting species, such as the griffon vultures, do not have any marked nuptial display. These species do not proclaim ownership of an area and defend only the area immediately about their nests.

7.4.5 General breeding biology

Newton (1979) gives a general picture of the breeding biology of raptors against which single-species studies can be compared. The breeding biology of the Bearded Vulture falls neatly into this account, although a few aspects warrant comment. Parent Bearded Vultures share incubation and nestling duties more or less equally, a characteristic of all African vultures studied, with the possible exception of the Palmnut Vulture (Mundy 1982; Pennycuick 1976; Houston 1976; Brown et al. 1982).

In the griffon vultures, self-foraging by both birds of a breeding pair is associated with the nature of their food (Houston 1976), since birds may have to travel up to 150 km from their nests to find the soft, slippery and sometimes rotten meat and viscera that cannot be carried in the feet

but in the crop, the nestling being fed by regurgitation. One bird may not be able to provide sufficient food for itself, its nestling and another adult. While the Lappetfaced and Whiteheaded Vultures also bring small animals and sections of carcasses to the nest (Mundy 1982; pers. obs.), they feed their chicks mainly on regurgitated meat which has been carried in their crops, which are smaller than the crops of griffon vultures. These birds may also cover quite large areas in search of food, e.g. Lappetfaced Vultures in the Namib Desert, South West Africa/Namibia, forage up to over 250 km from their nests during the early nestling period (pers. obs.). Bearded Vultures on the other hand, brought to the nest mainly chunks of small ungulates, mostly limbs, but also including lumps of red meat, all of which were carried in the feet. Regurgitation was seen only once, and this was of a meaty bone which could as easily have been carried in the feet.

Bearded Vultures foraged over a relatively small area during the breeding season, rarely moving much further than about 15 km from their nests. As a Bearded Vulture could presumably carry sufficient food back to the nest for itself, its nestling and its partner (an adult Bearded Vulture took off with a 4,3-kg section of Red Hartebeest leg with no effort and proceeded to rise up on slope lift), why then does it share incubation and indulge in self-foraging?

An important part of feeding in Bearded Vultures is the preparation of food, an important component of this being

bone-dropping. Adult birds always drop bones for themselves; ready-to-eat bone fragments were never seen being passed to a partner. The fact that each bird must prepare its own food for consumption may partly account for their doing their own foraging, but this is not a total explanation, as food could be dumped at the nest, and once the male had eaten, the female could depart for as long as it would take her to prepare and eat her food, then return to incubate or brood. The disadvantage of this would be that, during the nestling period, some foraging time would be lost, when one bird could be feeding and attending the nest at the same time. The self-foraging pattern could be necessary during the incubation period and carried over into the nestling period.

During the incubation period, no food is brought to the nest possibly because of carrion flies laying their eggs in the meat, which could hatch when the Bearded Vultures hatch and when the nestlings are too weak to defend themselves against the larvae. Whatever the reason, because food is not brought into the nest, it would have to be left somewhere else and the chances of having this stolen by other birds would be very high.

Finally, scavenging raptors tend to spend much more time on the wing in search of food than do other large birds of prey, such as the more predatory eagles which spend much of their day foraging from a perch or perched inactive. During the breeding season the minimum mean daily time that Bearded Vultures spent on high-intensity foraging increased from 4,3 h during the non-breeding season to 5 h and the

time spent in flight was between 10 h and 11 h of the average 13,5-h daylight period. It may be that, after a foraging sortie, the vulture is simply tired, and by taking turns at foraging, birds get an opportunity to rest. The rate of success in finding food may be increased after birds have rested.

7.4.6 Breeding success

The potential output in Bearded Vultures is one offspring per pair per breeding attempt. By removing the second nestling immediately after it has hatched and hand-rearing it, the output could be almost doubled (keeping in mind that two of 11 clutches recorded were one-egg clutches) to about 1,8 young per pair.

During this study all pairs monitored (40 pair-years) attempted to breed every year. While this may sound unlikely (and this species, like most others studied, does not breed every year in East Africa and Ethiopia (Brown et al. 1982)) I could find no evidence to indicate otherwise. The pair that previously bred in Golden Gate Highlands National Park, Orange Free State, apparently bred every year (Penzhorn 1969) and the Roma pair bred in seven successive years (J.J. Guy pers. comm.). If the food supply allows birds to accumulate sufficient body reserves of fat and protein, why should they not breed every year?

Of 18 pair-years monitored up to the nestlings' first flight, 16 breeding attempts were successful. The details of the two failures have been given, one being due probably to

food shortage (this being the ultimate factor, the proximate factor being predation) and the other possibly to human persecution. (Not long after this a number of adult Bearded Vulture skins were confiscated from a Mosotho on his way to the mines in Johannesburg, where the feathers were to be used in the making of dancing regalia. The birds (including a Cape Vulture and a Black Eagle) were captured in the central Maluti range in Lesotho (within the potential foraging range of the lost bird) in gin traps (M. van Gelden in litt.).) Thus a breeding rate of 0,89 young/pair/year was achieved, almost the potential breeding rate. Hiraldo et al. (1979) give a similar figure of about 0,9 young/pair/year. Comparing these figures with those obtained for some other large African raptors (Table 7.5), it is apparent that the Bearded Vulture has a far higher breeding rate, up to about twice that of most other large birds of prey. The reason for this is not immediately apparent, though the very secure and well-protected nest site and the close parental attendance may be contributing factors. Food supply must be an important consideration, and the fact that Bearded Vultures can feed on bones, which may have been lying in the veld for a month or more means that food from a period of abundance can be used some time later when the supply of food may be lower. In addition, the large amount of food that can be collected and stored in the nest when an abundant supply is found helps ensure against lean times. The cold environment of the nest ensures that the food cached there has a long storage life.

No evidence was found to indicate that there was a surplus of non-breeding adult birds in the population. On the contrary, the one recorded case of mate replacement was of a subadult bird entering the breeding population. This may indicate a higher mortality of adult birds than would have taken place when man's influence on the environment was less severe.

The survival rates of flying dependent young needs further investigation. I have no idea what this could be but general immature survival rates are discussed in Chapter 9.

7.4.7 The breeding season

There is little published information on the egg-laying dates of the Bearded Vulture in southern Africa. Steyn (1982) states that apart from eggs being recorded from May to August, "there are too few records to indicate a laying peak". Brown (1977) suggests "about June" as a laying peak for southern Africa. During this study a very distinct laying period was observed in mid-winter (Figure 7.28). To the east of the species' range, in the Natal/Lesotho Drakensberg (i.e. to the east of the Orange River), no laying before June was recorded. At two nests incubation began in the second week of June, nine breeding attempts began in the third week and three in the last week. One nesting attempt was recorded for the first week in July. To the west of the species' range in the foothills of the front range of the Maluti mountains, breeding started about one month earlier, laying taking place in the third (two

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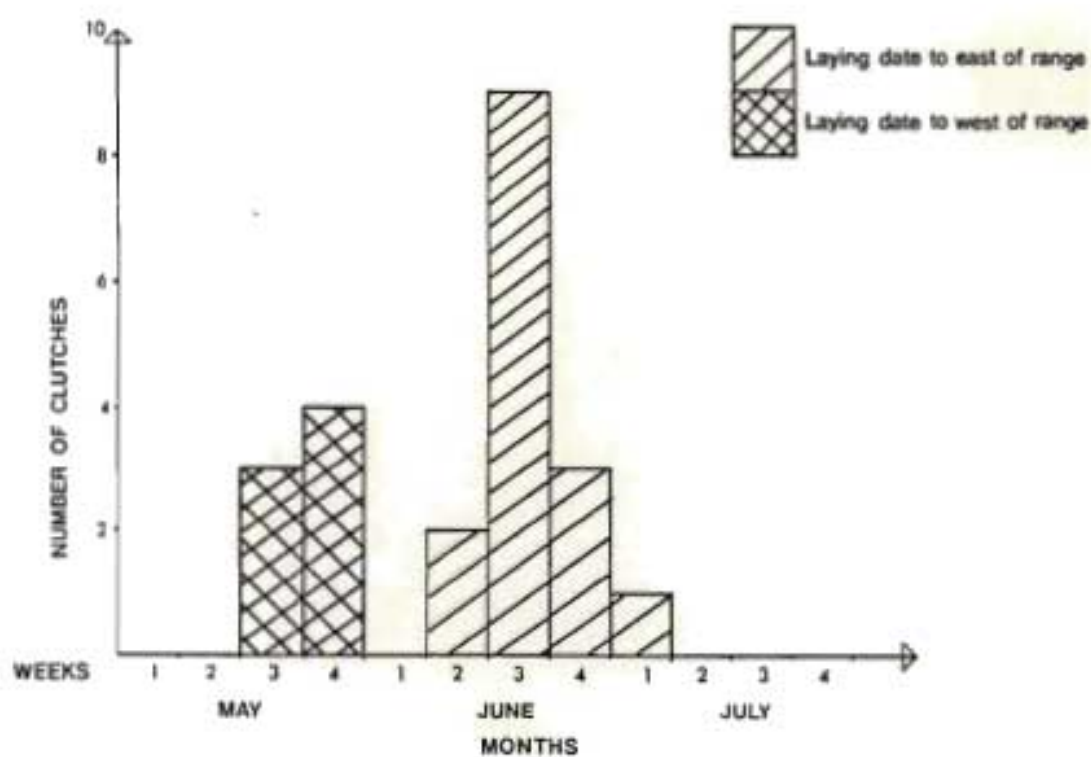
FIGURE 7.28. Months in which eggs were laid by Bearded Vultures in southern Africa.

records) and fourth (three records) weeks of May.

Laying dates for other populations of G.b. meridionalis suggest that, where the entire breeding season can be completed in dry weather (e.g. parts of Ethiopia), eggs are laid early in the dry season (October & November) while in intertropical zones where two three-month rainy and dry seasons alternate (Kenya and Uganda), eggs are laid far less seasonally (records of eggs in the nest are for January, April, May and July (Brown et al. 1982)). Eurasian birds, like those in southern Africa, breed in mid-winter. In Europe eggs are laid in December and January (Cramp & Simmons 1980) and in the Himalayas from November (Lowther 1949).

While most birds (including raptors) breed when food is most readily available (Newton 1979), species which have long breeding seasons that extend into periods when food is less plentiful presumably time their breeding so that the times when most food is needed coincide with the times when food is most plentiful. In the case of the Bearded Vulture, adult birds could be said to be involved in breeding 12 months of the year (Figure 7.29) as young birds become independent of their parents probably only at the start of the next breeding season. Brown (1976b) suggested that the two main times of stress in the breeding cycle of raptors were the pre-laying period when the female needs extra energy to form eggs, and the early nestling period when the male has to obtain food for his mate, nestlings and himself.
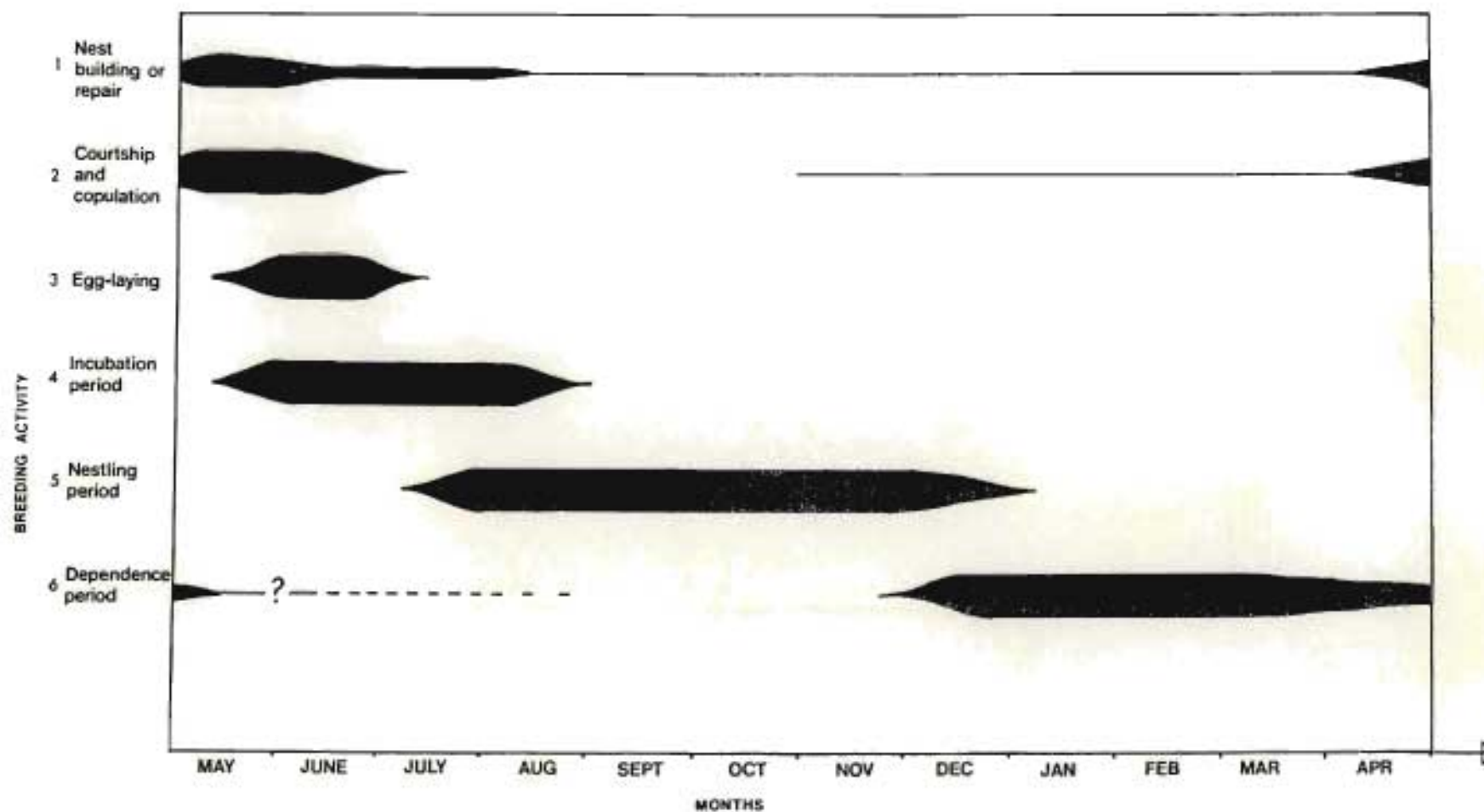
FIGURE 7.29. Timing and duration of breeding events in the Bearded Vulture in southern Africa.

As Bearded Vulture eggs constitute only about 3% of the female's body weight, it is doubtful whether the former is a critical factor (Perrins 1970). In the early nestling period, both male and female birds take turns in foraging, and while the effective foraging time available to the pair is halved, the pressure is no longer on one bird to obtain all the food.

Assuming that Bearded Vultures have synchronized their times of greatest stress with the times when food is most readily available (and looking at breeding success this seems to be the case), then we can turn the question around and ask: what period of the breeding season coincides with the greatest availability of food? Mortality rates of indigenous game for Giant's Castle Game Reserve (animals found dead represent probably less than 20% of all deaths), show a peak from August to October, when food for Bearded Vultures is therefore most abundant (Figure 7.30). This coincides with the end of the incubation period of Bearded Vultures and the first two-thirds of the nestling period. Towards the end of the incubation period (during which time the effective foraging time is cut by 50%) the bird's fat reserves may be running fairly low, a phenomenon which has been documented through the breeding season in the Rüppell's Griffon Vulture Gyps rueppellii (Houston 1976). The foraging potential of the parents remains at 50% until the nestling is at least 60 days old and thereafter it increases only slowly, while at the same time the parents have to provide more and more food. Another consideration is the nature of
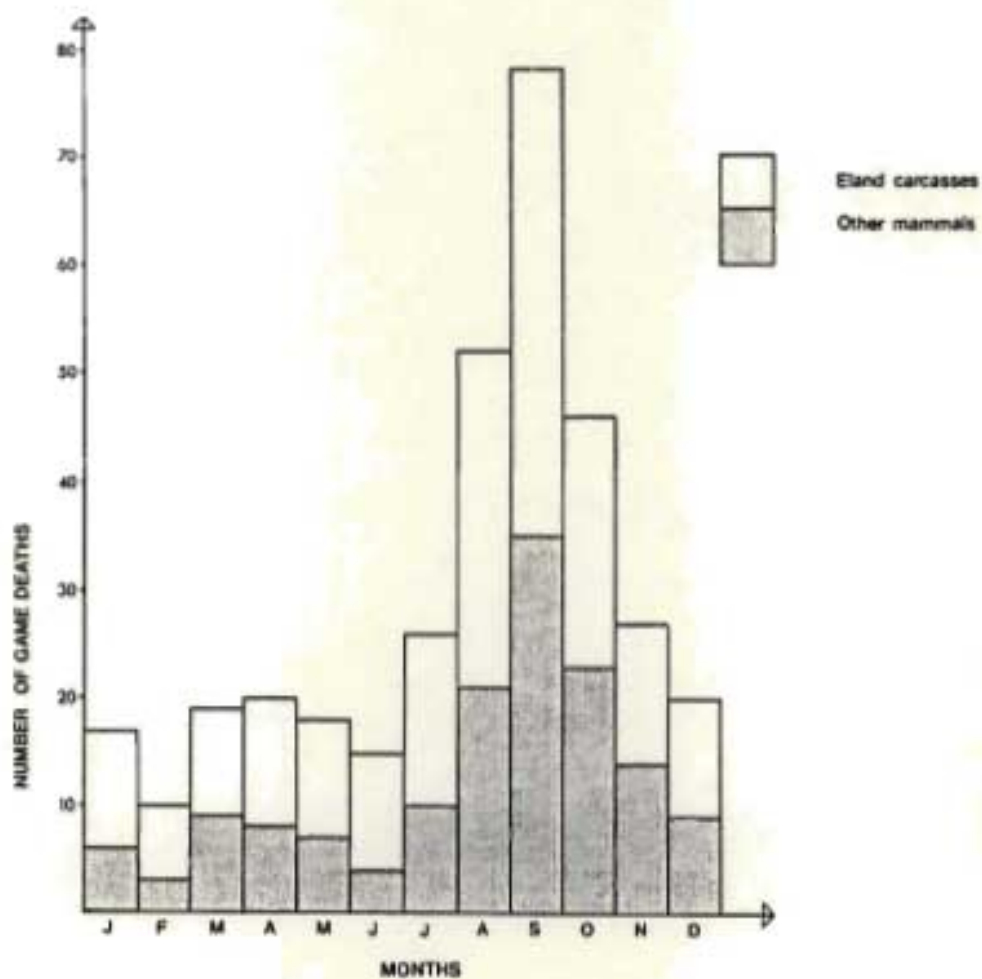
FIGURE 7.30. The number of game carcasses found per month in Giant's Castle Game Reserve from 1976 to 1981.

the food, particularly during the very early nestling period, when more soft tissue than bone is required for the nestling. The period when most food is required from a 50% foraging potential would be between 60 and about 80 days after hatching. Thereafter the nestling is left alone for increasing periods and both parents are free to forage. Thus the period of greatest stress appears to be the first two-thirds of the nestling period.

The Cape Vulture in the Natal Drakensberg breeds slightly earlier than the Bearded Vulture. Birds were seen incubating in mid-May and eggs were confirmed in early June (Brown & Barnes 1984). While the incubation periods of the two vulture species are about the same, the early part of the nestling period, when an adult is always present on the nest, is very much longer (at least 90 days) in Cape Vultures (Mundy 1982). This part of the Cape Vulture's breeding season could be a period of great stress, as the young vulture is consuming a large amount of food yet only one parent can forage at a time. Because the Cape Vulture starts breeding early (about a month before the Bearded Vulture), this time of stress coincides with the period when most food is available.

Mortality of game mammals between August and October, accounting for over 50% of the yearly deaths recorded, is ascribed to the cold dry weather when vegetation quality is poorest (Mentis 1978). Scotcher et al. (1980) found that the crude protein content of the green component of herbage

declined from about 16% in summer to 2% or 3% in winter, and furthermore, the green component declined rapidly from between 50% and 70% of the plant food at the end of April to 20% in July and August. While domestic stock on commercial farms may be nurtured through the winter with additional feeds, more still dies at this time of the year than at other times (e.g. S. De Klerk, J. Botha pers. comm.). In the Lesotho highlands with its primitive pastoral practices, overstocking and extreme weather conditions, the high death rate from August to October must be even more pronounced, although there are no available figures to prove it.

There might also be an increase in the amount of carrion available at other times of the year. Lambing and calving of domestic animals usually takes place in spring and early summer, with a second minor lambing season in autumn. Eland calve in spring. These trends are clearly reflected in the high number of young animals recorded in prey remains from nest sites. Dead newborn mammals are virtually impossible to find in the veld as very little of the carcass remains. These, however, provide some additional food from October to November.

Houston (1976) considered the most critical period for both Whitebacked and Rüppell's Griffon Vultures in Serengeti to be the time at which the young birds leave the nest and become independent of their parents (implying that independence is achieved shortly after first flight). During summer storms, lightning can cause high mortalities mainly

to domestic stock which tend to huddle together, and up to 100 sheep may be killed at a time. These storms are most prevalent from December to February, providing an abundant source of food at a time when adults are still obliged to return to the nesting area with food for their young. Once young Bearded Vultures begin to accompany their parents on foraging trips, the parents no longer need to return to their nest sites with food, and can increase their foraging range and at the same time reduce their energy expenditure at a time when food may be less abundant. Young birds become independent at the start of their parents' next breeding season, i.e. towards the end of June. In July the availability of food starts to increase, this continuing into August and September. Young birds, therefore, become independent at a time of increasing food availability.

7.4.8 Timing of breeding

Although the sample is small, it would appear that Bearded Vultures in the east of their southern African range breed earlier than they do in the west. While food supply may be considered to be the ultimate factor affecting the timing of breeding, day length has been shown to be the proximate factor which brings many birds (including some raptors studied) into condition at the appropriate date (Yapp 1970; Newton 1979). In the case of the southern African Bearded Vulture population, which consists of a single gene pool, daylength is the same across their range, so this alone could not be responsible for the differences

in laying dates observed.

Lack (1954) suggested that through natural selection, birds come to respond to whatever factors provide a reliable indication that breeding will shortly be practicable. A "factor" closely related to the forthcoming availability of carrion would be a drop in temperature. Early frosts cause the early onset of winter, the nutritional value of the vegetation decreases so that the less healthy and the older animals die earlier than they would in areas experiencing late winters. To the west of the Bearded Vultures' range and in the interior of the subcontinent, rainfall is lower and more seasonal than to the east, and colder temperatures with earlier frosts are experienced. The availability of dead animals is therefore likely to occur earlier in the west than in the east. I suggest that Bearded Vultures may be using a combination of proximate factors, namely daylength (as low temperatures and snowfalls can occur in any month of the year in the Drakensberg and Maluti mountains) as well as low temperatures to co-ordinate the timing of their breeding season to synchronise with the time that food is most abundant.

7.4.9 Breeding by subadult birds

In cases in which the sex of raptor species breeding in immature plumage is known, these have usually been females (Newton 1979). It is therefore of interest that the one subadult Bearded Vulture breeding during this study was a male. It may be expected that in species in which the male

hunts and the female incubates (as in most birds of prey) the bird providing the food needs to be more experienced than the bird sitting on the nest and therefore the male would need the extra experience of an adult while the female could be younger.

In species in which incubation and foraging are shared, however, a somewhat less experienced bird (bearing in mind that subadults are about five years old) of either sex could receive assistance from its more experienced mate which may be able to make up any shortfall in the food supplied by the younger bird. It seems likely therefore that, unless some physiological factor prevents the necessary physical state of maturity being reached in either sex, in self-foraging species, either sex should be able to start breeding as subadults, particularly if (or perhaps, provided that) one of the pair is an adult. Whitebacked and Cape Vultures have been recorded breeding in immature plumage (Mundy 1982; Robertson 1984). The sexes of the former were not determined, but of the latter, two of four immatures breeding were females.

7.4.10 Phylogenetic considerations

What light does an intimate knowledge of the breeding biology of the Bearded Vulture throw onto its phylogenetic relationships; is it more closely akin to the eagles or to the vultures? It would seem that very little can be learned. Rather, habitat and food choice are the selection pressures that influence activities and behaviour. Convergence is

clearly apparent in reapose to these two factors as has been documented for the Old World and New World vultures (Newton 1979).

Large, well-lined nests are built in potholes to increase insulation and reduce energy expenditure for thermoregulation and to gain protection from snowfalls. The maintenance of two or more nests may be related to storage of carrion in the nest, or because parasites are particularly persistent in the well-lined and protected nest. In any event, because nests last so long, a number of nests can be maintained at any time with relatively little effort.

Courtship display is well developed because Bearded Vultures have a concealed nest, and this may also account for the relatively high percentage of soaring in the vicinity of the nest, amounting to 7% of the daily activity.

The mortality of the second nestling to hatch is considered an adaptive mechanism that increases reproductive success when food is limiting (Lack 1954). Thus, in many species, e.g. Booted, Golden and African Hawk Eagles, Barn Owl Tyto alba and some seabirds, when food is abundant a high nestling survival rate is achieved, but when food is less abundant, instead of all nestlings competing fiercely, the weaker (and this invariably means the younger) sibling(s) are eliminated, thereby increasing the chances of survival of the remaining young. This is termed facultative brood reduction (Brown & Amadon 1968; Edwards & Collopy 1983; Mikkola 1983; Williams & Cooper 1983). In a number of

species, however, fratricide may be obligate, i.e. the second nestling always dies as in Crowned, Black and Lesser Spotted Eagles and Bearded Vultures (Brown & Amadon 1968; Brown et al. 1977; Meyburg 1974; this study). Brown (1976a) stated that "both Lack (1954) and Wynne-Edwards (1962), arguing from different standpoints, concluded erroneously that it must be a response to food supply". What led Brown to this statement is that, at the time of death of the younger nestling, there is usually an abundance of food on the nest (e.g. Siegfried 1968, Meyburg 1970, 1974; Gargett 1970), and this is also true for the Bearded Vulture.

While studies involving the removal of the second nestling from the nest and replacing it after it is feathered and able to feed itself (e.g. Meyburg 1974; Gargett 1970) show that both nestlings are raised successfully and therefore that parents are capable of obtaining sufficient food for both, I question whether this is in fact testing the ability of parents to provide food over the critical period when only one parent is free to forage or hunt. In the above cases the nestlings were returned to their nests at a stage when neither parent need remain near the nest, and both can be hunting. The earlier period, when one parent only is providing the food is, I suggest, the most critical.

In species which stand a good chance in most years of raising two or more nestlings, a facultative brood-reduction strategy is employed. In other species, the nature of the

food and/or its abundance may mean that parents can less frequently supply sufficient food during the critical period to raise two or more offspring. In such cases it is more economical (and more offspring are produced in the longrun) to reduce their brood as soon as possible. Should two nestlings survive to about 40 days of age and then start to compete fiercely for a limited food resource, the chance of the surviving nestling being seriously injured is much greater than if the younger nestling were killed within the first few days. In addition, the food and energy invested in the younger nestling would have been wasted.

Why then do raptors with obligate fratricide lay two eggs and not reduce their brood at the egg-laying stage (as perhaps have species laying one-egg clutches)? The generally accepted answer to this is that the second egg acts as a reserve in case the first should be damaged or infertile (Brown et al. 1977). Why should some species need this reserve, while others lay a single-egg clutch, e.g. all Old World vultures (except Bearded and Egyptian), the Bateleur, Martial Eagle and the snake eagles. These species have been shown to be no less productive than those laying two eggs (Brown et al. 1977). Perhaps the obligate brood-reducing species with two-egg clutches are as productive as species with one-egg clutches (and not the other way around) only because they do lay two eggs.

I believe that clutch size may be related to the type of nest site used by the species as it affects the chances of damaging an egg. For example, species nesting on cliffs

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where wind currents are unpredictable, and where species have to land directly on their nest or swoop into a small pothole (e.g. Black Eagle, Bearded and Egyptian Vultures) and species nesting in thick forest (e.g. Crowned Eagles) stand a far higher risk of damaging an egg than do species nesting on the tops of trees in savanna or open habitats, especially if these open nests are very large with wide rims (e.g. Martial Eagle, Lappetfaced and Whiteheaded Vultures) or if the birds can land on a cliff ledge or a branch and walk across to their nests (e.g. Cape Vulture and Bateleur (pers. obs.; R. Watson pers. comm.)). This idea needs to be tested, however, by examining eggs within a clutch for damage in species laying one- and two-egg clutches, the latter being from exclusively obligate brood-reducing species.

Self-foraging and shared nesting duties have already been discussed and related to the choice of food. Feeding of the young nestling, not by regurgitation but by tearing pieces of soft tissue from mainly sections of small ungulate limbs and passing these delicately to the young bird may be regarded as rather eagle-like, as most other Old World vultures (except Palmnut and Egyptian) feed their nestlings by regurgitation. Because of the nature of the food collected by Bearded Vultures, adults must tear off small pieces of soft tissue from bones. The bones themselves would be unmanageable for young birds. Some records exist of Bearded Vultures regularly regurgitating food (Ferguson-Lees 1960), but always onto the nest and then feeding small

pieces of this food to the nestling. Why Bearded Vultures in some areas tend to regurgitate more than others may be related to the amount of red meat available.

In the Natal Drakensberg there is a large population of Cape Vultures (at least 1300 (Brown & Piper in press)) which are dominant over Bearded Vultures at carcasses. The Bearded Vultures feed on what is left over, and Cape Vultures, falling into the class of "pulling" feeders (König 1983) are unable to use soft material that requires any dexterity to remove. Thus, most of the soft tissue of the lower sections of the limbs remains, as does muscle attached close to the bone or in less accessible places. Bearded Vultures occurring in areas with a smaller population of griffon vultures may have access to more red meat and therefore carry more food in their crops.

7.4.11 Post-nestling dependent period

Finally, the unusual pattern observed during the dependent period of young birds deserves some comment. During the first four months out of the nest these birds are becoming proficient at flying, carrying food and bone dropping. At the same time, they are exploring the area about their nest site, becoming more and more adventurous. Thus they range over progressively larger areas. Superimposed on this is another movement pattern, much more definite and covering a greater distance. This I interpret as being the young bird accompanying one or both of its parents on a foraging trip.

After four months out of the nest, the young bird's range has increased in size to the extent that the movements alone or with a parent can no longer be distinguished. It would appear that young birds undergo a combination of (a) self instruction, where they gain experience in flight, interactions with other birds, bone dropping, etc., obtaining what food they can for themselves whilst still receiving supplementary feeding from their parents, and (b) parental teaching, where they accompany parents further from the nest, possibly being exposed to greater dangers and new experiences, and being led to sources of food where they have to begin to compete with other birds. Why the young bird accompanies its parents only on some occasions and not on others is not known, but perhaps it does this only when hungry. The start of the next breeding season, when young birds are presumed to become independent also marks the beginning of the period when food becomes more available. The advantage to the future survival of the young vulture of a long dependence period in terms of experience gained is obvious, but even more important may be the survival of the young bird during the relatively lean period of autumn and early winter as far as the food supply is concerned, so that it finally becomes independent when the food supply is increasing.

TABLE 7.1

Some physical parameters of Bearded Vulture nest sites.

Variables	Sandstone cliffs	Basalt cliffs	All cliffs
Number of pairs	4	20	24
Number of nests	12	62	74
Mean no. nests/pair	3,0	3,1	3,1
Nest type: pothole	10	56	66
ledge	0	4	4
pothole/ledge	2	2	4
Overhang or concave cliff above nest: present	11	57	68
absent	1	5	6
Mean distance (range) between alternate nests (m)	52 (2-400)	304 (20-2000)	230 (2-2000)
Mean altitude (range) above sea level (m)	1935 (1850-2134)	2814 (2149-3201)	2578 (1850-3201)
Mean height (range) of nesting cliffs (m)	79 (46-104)	257 (24-732)	212 (24-734)
Mean position of nest on cliff (range) from base (%)	60 (50-87)	76 (21-91)	72 (21-91)

TABLE 7.2.

The periods of direct sunlight (h) on some Bearded Vulture nests and nest entrances, for summer and winter.

Nest site		Mid winter		Mid summer	
		Nest (h)	Nest entrance (h)	Nest (h)	Nest entrance (h)
Gypaetus Point	1	3	7,0	3	8,5
	2	2	6,5	2	8,0
	3	2	5,5	2	7,5
Long Wall south	1	3	9,5	3	11,5
	2	3	9,0	3	10,5
	3	2	8,5	2	10,5
Long Wall north	1	2	4,5	2	6,0
	2	2	5,0	2	7,0
	3	2	5,5	2	7,5
Mt. Durnford	1	1	3,0	1	4,0
	2	2	2,5	2	3,5
	3	3	4,5	3	5,5
Eddystone	1	4	7,0	4	8,5
Roma (8 nests)	1-8	3	9,5	3	11,5
Total	21	55	154,0	55	190,5
Mean		2,6	7,3	2,6	9,1

TABLE 7.3

The distances between Bearded Vulture nests and other birds nesting or roosting nearby.

Species	Same or neighbouring cliff	Nest/ roost	Number of records	Average distance (m)	Minimum distance (m)
Cape Vultures	same	R	11	140	15
	neighbour	R	1	800	800
Black Eagle	same	N	1	120	120
	neighbour	N	4	1025	600
Jackal Buzzard	same	N	2	220	150
Rock Kestrel	same	N	3	90	30
Lanner Falcon	same	N	2	115	9
Peregrine Falcon	same	N	1	80	80
Gymnogene	*same	N	1	120	120
Whitenecked Raven	same	N	4	230	80
	neighbour	N	2	700	400
Bald Ibis	same	N	2	280	200
Black Stork	same	N	1	400	400

* The Gymnogene was nesting in a tree growing out from the base of the cliff directly below a Bearded Vulture's nest.

TABLE 7.4

Clutch size, brood reduction strategies (O = obligate, F = facultative), nesting places and courtship displays of some large African raptors.

Species	Courtship display?	No. eggs	Brood reduction	Nest position
Bearded Vulture	Yes	2 (1)	O	Cliff pothole, access difficult, wind
Palmnut Vulture	Yes	1	–	Mainly Raffia palm, among fronds
Egyptian Vulture	Yes	2 (1-3)	O	Cliff pothole, access difficult, wind
Hooded Vulture	No	1	–	Tree, large fork within canopy
Cape Vulture	No	1	–	Cliff ledge
Whitebacked Vulture	No	1	–	Tree top
Lappetfaced Vulture	No	1	–	Tree top
Whiteheaded Vulture	No	1	–	Tree top
Black Eagle	Yes	2	O	Cliff
Tawny Eagle	Some	2	F	Tree top
Wahlberg's Eagle	Yes	1 (2)	(F)	Tree, fork in/under canopy
Booted Eagle	Yes	2	F	Cliff ledge, base of tree, small nest
African Hawk Eagle	Yes	2 (1)	F	Tree, fork in/under canopy
Ayres Eagle	Yes	1	–	Tree, fork in canopy
Longcrested Eagle	Yes	2 (1)	F	Tree, lateral branch within canopy
Martial Eagle	Some	1	–	Tree, prominent lateral fork
Crowned Eagle	Yes	2	O	Tree, forest, major fork below canopy
Brown Snake Eagle	Some	1	–	Tree top, small nest
Blackbreasted Snake Eagle	Some	1	–	Tree top, small nest
Bateleur	No*	1	–	Tree, major fork below canopy
African Fish Eagle	Yes	2 (1-3)	F	Tree, usually within canopy

* but see text

TABLE 7.5

Breeding success of some large African raptors.

Species	No. pairs studied	No. pairs breeding	No. young per pair	Source
Bearded Vulture	18	18	0,89	This study
Lappetfaced Vulture	65	37	0,37	Namib Desert 1984-86, pers. obs.
Whitebacked Vulture	211	171	0,49	Mundy 1982
Cape Vulture	171	113	0,44	Mundy 1982
Cape Vulture	300	?	0,58	Vernon et al. 1983a
African Fish Eagle	112	71	0,50	Brown & Hopcraft 1973
Black Eagle	652	442	0,50	Gargett 1977
Tawny Eagle	19	16	0,60	Steyn 1973a
Wahlberg's Eagle	33	29	0,40	Tarboton 1977
Wahlberg's Eagle	63	55	0,60	Brown et al. 1977
African Hawk Eagle	23	16	0,60	Brown 1966
Martial Eagle	31	18	0,40	Brown 1966

Chapter 8

BEHAVIOUR, ACTIVITIES AND ENERGETICS

8.1 INTRODUCTION

More is known about the breeding behaviour of raptors than about any other aspect of their lives (Newton 1979). Away from the nest or roost site, it is more difficult to assess how an eagle (or other bird of prey) spends its day (Brown 1976a). As a result, few quantitative data exist on raptor activities away from the nest and that information which does exist is derived mainly from incidental observations. Some exceptions are the studies on the African Fish Eagle Haliaeetus vocifer (Brown 1980), the Bald Eagle H. leucocephalus (Southern 1964; Sherrod et al. 1977; Swenson et al. 1986) and the Osprey Pandion haliaetus (e.g. Stinson 1978; Swenson 1978; Levenson 1979; Boshoff & Palmer 1983). These are all conspicuous species which perch in exposed sites and occur in predictable localities. In addition the activities of the Black Eagle, a more active species but with a fairly small home range, have been intensively studied over a period of nearly two decades (Gargett 1971, 1984) and are well known. The behaviour of Bonelli's Eagle, studied for a much shorter period (Cheylan 1972), is somewhat less well known. Some smaller, more sedentary species with small home ranges have also been the subject of more detailed studies, e.g. the European Sparrowhawk (Newton 1986), and the Peregrine Falcon

(Ratcliffe 1980; Cade 1982). In many species, particular aspects of a bird's activities away from the nest may be well known, such as foraging behaviour in the Gymnogene (Thurow & Black 1981), the Blackshouldered Kite _Elanus caeruleus_ (Mendelsohn 1982) and a number of vulture species (Pennycuick 1972; Houston 1974a); or feeding behaviour in some species of vultures (_e.g._ Kruuk 1967; Houston 1974b; Mundy 1982).

The Bearded Vulture has been the subject of many myths, half-truths and perpetuated fables. The name "Lammergeier" was mistakenly taken to mean lamb-slayer (Bree 1875) and reports of attacks on human adults and children are not uncommon (_e.g._ Bree 1875; Meinertzhagen 1959). Regular activities such as bone-dropping, foraging and interactions with other animals were poorly understood and often contentious.

A detailed knowledge of the activities and behaviour of a species is important in understanding its habitat requirements, the amount of energy expended in performing its various functions and hence its food requirements. Consideration of these factors may help in elucidating reasons for the decline in range of the Bearded Vulture in southern Africa (Boshoff _et al._ 1983), and in the planning of management and reintroduction programmes, such as the current captive breeding and reintroduction project on the European race of the Bearded Vulture in the Alps (Géroudet 1977).

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Hiraldo _et al._ (1979) discuss some of the more important aspects of Bearded Vulture behaviour, and general accounts by Ferguson-Lees (1960), Glutz von Blotzheim _et al._ (1971), Cramp & Simmons (1980), Steyn (1982) and Brown _et al._ (1982) summarize the present state of knowledge of the species.

In this chapter the general behaviour and activities of the Bearded Vulture away from the nest are described and quantified. The data are presented as (a) daily activities (per hour) and (b) yearly activities (per month). Seasonal activities during the non-breeding and different stages of the breeding seasons are compared. Finally, the daily energy budget of Bearded Vultures is calculated from the time-activity budgets for the breeding and non-breeding seasons, using a method that should be applicable to all soaring birds. Foraging and feeding are discussed in Chapter 6, and breeding behaviour in Chapter 7.

8.2 METHODS

Two methods were used to obtain activity patterns and behavioural information. The first is quantitative, involving a form of "instantaneous" opportunistic sampling; the second is descriptive, in which a detailed account was kept of all activities observed.

Brown (1976a) stated that if observers were to record every single sighting of a species, and make notes of what the bird was doing and for how long, they would gain a good idea of how that bird spent its day. As observations on

"target individuals" were not possible, and as I could neither be assured of seeing birds at particular places (apart from nests and artificial feeding sites) nor follow birds, this random method of obtaining information on activities was adopted and all activities for the duration of each sighting were recorded. Two months were spent observing Bearded Vultures, whereafter a field-data form was drawn up. Activities were recorded for all sightings of Bearded Vultures from March 1980 to July 1982 except those at nest sites and at the feeding stations, as I believed that these prolonged observations would bias the random nature of the samples. Observations were made from vehicle, horseback and foot, using 8 x 40 and 16 x 50 binoculars, and were recorded either directly onto the field-data form or into a tape recorder and later transcribed. Observations were made under all but the most severe weather conditions and from all localities visited within the range of the species, but most were made in the Giant's Castle Game Reserve.

The maximum length of time spent on any one observation was restricted to 45 min and no single activity was recorded for a period exceeding 30 min; if a bird was involved in only one activity for a period exceeding 30 min the observation was terminated at that point (although any further activities were recorded descriptively). Although this measure was required in only a few instances, it was adopted in order to reduce bias resulting from observations of birds perched inactive for long periods on cliffs.

An attempt was made to record the following information whenever a Bearded Vulture was sighted: (a) locality, (b) date, (c) weather conditions, (d) time when first sighted, (e) group size, (f) age classes, (g) identification (if marked) and (h) length of time in sight. When more than one Bearded Vulture was seen the time recorded was taken as being per bird, not per group. Results have been treated in relation to time (min) and not numbers of observations. Time-related activity data do not, however, lend themselves readily to statistical analyses. All statistical tests were run, therefore, on the numbers of records of each activity, based on the activity of the bird when first sighted. Data shown in the graphs in this chapter were derived from the time-based figures, as there were only 811 bird sightings but over 73 hours of observations during which birds were in view.

Data were analysed and are expressed per activity (a) as a percentage of all activities recorded, (b) hourly, as a percentage of the daily activity, the day being divided into hourly intervals, from 08h00 to 17h00 (observations from dawn to 08h00 were grouped, as were those from 17h00 to dusk), (c) monthly, as a percentage of the yearly activities and (d) seasonally, for the non-breeding and different stages of the breeding seasons.

The activities of adult and immature birds are compared, but thereafter are treated together.

8.3 RESULTS

8.3.1 The activities

All recognizable activities recorded away from the nest are listed (Table 8.1). They were divided into three basic categories, namely (A) in flight, (B) on cliff face and (C) on ground. In flight was divided into (1) flapping and non-flapping flight, which were recorded concurrently with any other activities being undertaken at the same time, and (2) searching and non-searching flight, which in turn were divided into a number of more specific activities.

Pennycuick (1972) stated that the two main types of activities for which vultures and other large birds use thermal soaring are (i) patrolling in search of food, and (ii) travelling across country. It is often extremely difficult to differentiate between these two activities in Bearded Vultures. For example, an adult bird was seen gliding swiftly along a ridge in the Mokhotlong area of Lesotho carrying the forelimb of a sheep. I assumed that the bird was heading back to its nest and was therefore not searching. However, it turned suddenly and landed on the hillside about 40 m below its line of flight, where, standing on the food acquired earlier, it picked up and swallowed two sheep vertebrae before taking off and proceeding. Similar observations have been made by Houston (1974a) in the Serengeti National Park on griffon vultures, and subsequent observations at a feeding site at Waterberg in South West Africa/Namibia suggest that Cape, Whitebacked and Lappetfaced Vultures may descend to a carcass and fight

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for a place to feed even with a full crop and when only a few cursory pecks are made at the food (pers. obs.). It seems likely that Bearded Vultures are almost always on the lookout for food, and the assumption was therefore made that all flight away from the nest or roost site, which could not be assigned to some other activity, was searching. This nevertheless still represents the absolute minimum amount of searching undertaken by the birds. Birds involved in activities such as thermalling, carrying food, escarpment gliding or even perching on a cliff, might also be searching. These activities can therefore be regarded as forms of lower-intensity foraging. Three different methods of high-intensity searching were identified, and these are discussed under Feeding Ecology in Chapter 6.

Ten predominantly non-searching activities were recognized:

(a) Escarpment-gliding. This refers predominantly to Bearded Vultures using the lift provided by air rising against the escarpment of the High Berg, but also to birds using lift along large cliffs in other areas. Birds use these areas mainly to facilitate swift cross-country travel, gaining considerable altitude above the cliffs, adopting a diving posture and achieving speeds often in excess of 100 km/h. Birds flying close to the ground and using slope lift were not considered to be escarpment-gliding, as they were using the lift to facilitate foraging and not cross-country flying.

(b) Thermalling. This refers to gaining (or the attempt to gain) height by circling in a rising air column.

(c) Recreational soaring. This term is used to describe the Bearded Vulture's apparently aimless gliding and soaring about in the vicinity of the nest or roost site, usually within the activities area.

(d) Courtship display. This is often initially difficult to distinguish from play. A full description of this activity is given in Chapter 7.

(e) Play. This occurs mainly between young birds, or between an adult and young birds. Towards the end of the breeding season adults from adjacent breeding sites sometimes congregate to play.

(f) Attack by Bearded Vulture. This involves the aggressive behaviour of Bearded Vultures towards (i) other Bearded Vultures, and (ii) other species.

(g) Attack on Bearded Vulture. This involves the aggressive behaviour of (i) other Bearded Vultures and (ii) other species towards Bearded Vultures.

(h) Carrying nesting material. This is difficult to see and certainly under-represented. It involves observations of birds carrying either sticks and twigs or nest lining, all of which are usually carried in the feet, though small pieces of wool and hair may be carried in the bill.

(i) Carrying food. Food is always carried in the feet although it may be transferred to the bill for take-off and landing. It is carried in line with the body and

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well tucked up, often covered by the belly and vent feathers and is therefore not easily seen and is probably under-represented.

(j) Bone-dropping. This refers to the deliberate dropping of a bone over a slab of rock or rocky area for the purpose of breaking the bone into consumable sized pieces, and to gain access to the marrow.

Cliff face and on ground activities together constitute all non-flight activities. They are treated together, as many of their subsections are common to both. The activities identified were:

(a) Feeding. This involves the preparation (excluding bone-dropping) and swallowing of food.

(b) Preening. This is taken to include all plumage maintenance and comfort movements.

(c) Inactivity. This refers to periods when no activity is apparent. As many of these observations were made at some distance from the birds, no attempt was made to further categorise "inactive" birds.

(d) Drinking. Bearded Vultures visit water regularly and invariably drink, as opposed to some other vulture species which may visit water for purposes of bathing or thermoregulation. They often wade into the water, thus dampening their breast and belly feathers. Bathing is also quite frequent, and follows drinking. These two activities have been grouped here, as the actual watering site was sometimes out of view.

8.3.2 Total activities

A sample of 811 Bearded Vulture sightings was recorded during which birds were under observation for 73 h 36 min. The average time that a Bearded Vulture was in sight was 5 min 27 s (Table 8.2). Birds on cliffs were in view on average for the longest period (almost 8 min), followed by birds in flight (just over 5 min) and birds on the ground (just under 5 min). Birds in flight were more conspicuous than those perched on cliffs. This bias is partially corrected for by birds in flight being in sight for considerably shorter periods than birds on cliffs.

Table 8.3 lists the activities recorded for Bearded Vultures, the total time recorded for each, the percentage composition of the total activity of each (Figure 8.1) and the percentage of the section or subsection into which each falls. Bearded Vultures spent by far the greatest part of their day in flight (80%), followed by activities on cliffs (16%). Few observations of birds on the ground were made (4%). First-light to last-light radiotelemetry studies (see Chapter 5) showed that Bearded Vultures spent about 78% of their day in flight, which corroborates the figure of 80% obtained by observation.

The proportion of time spent on each of the recognized activities has been analysed for adult birds, for young birds and for those whose ages were not identified (Table 8.4). The activities of birds which were not aged (4% of Bearded Vultures sighted) were markedly different from those of known age. This is to be expected because birds of
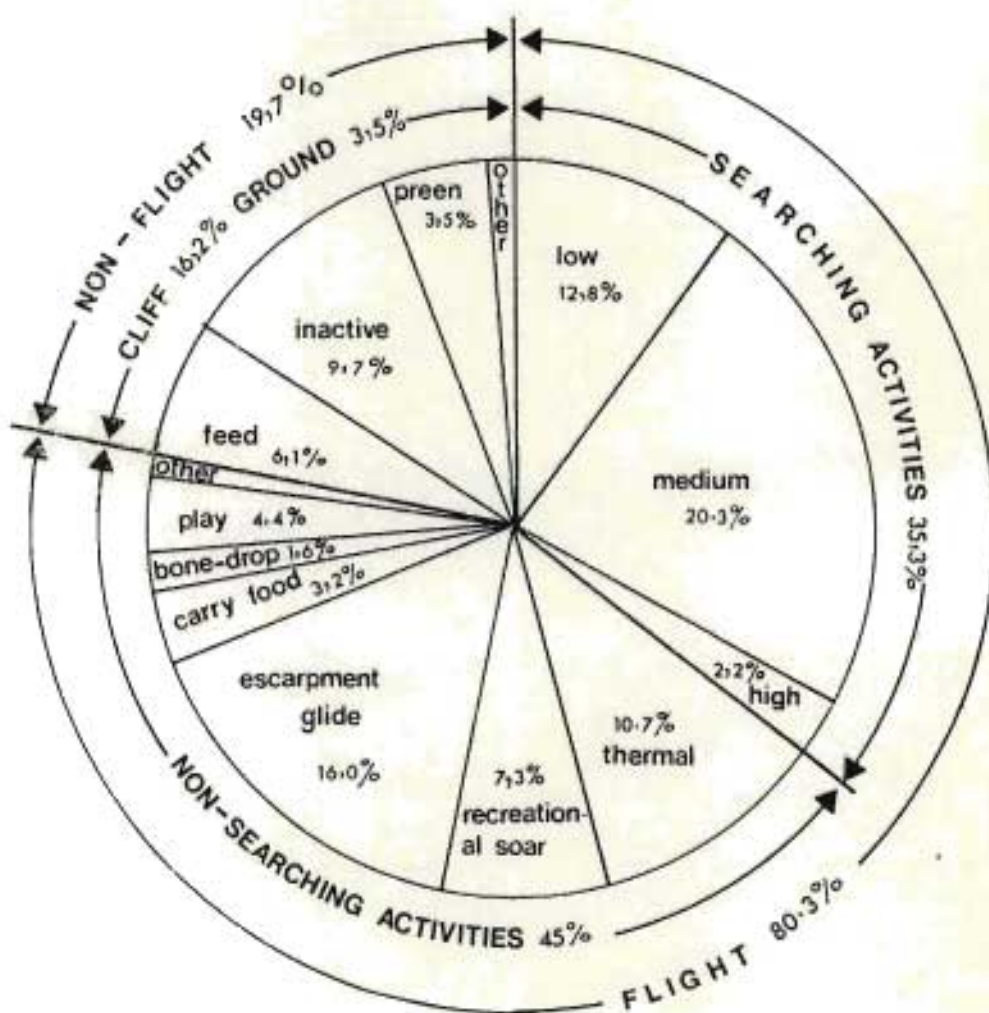
FIGURE 8.1. The diurnal activities of Bearded Vultures away from the nest, for all age classes and throughout the year.

unknown age were always viewed at a considerable distance, and always in flight. Adult and young Bearded Vultures differed significantly in only two activities, namely play and feeding on the ground, both of which were of greater duration for young birds. Although not significant, young birds spent more time searching for food than did adults (37% and 34% respectively). Adults were involved in two breeding-related activities not recorded in young birds, namely courtship display and the carrying of nesting material. Although not significant, adults spent more time interacting aggressively, soaring and resting than did young birds. As the amount of time spent by adult and young birds in the various activities was found to be very similar, the data have been grouped for subsequent analyses.

Flight activities

Bearded Vultures are predominantly gliders. Flapping flight made up only 3% of all recorded flight. At least 44% of flight activity was devoted to foraging. When searching for food was concurrent with some other activity (as to some extent it undoubtedly was, e.g. forms of lower foraging intensity), escarpment gliding and thermalling were the two flight activities most likely to be involved. It is unlikely that any of the other flight activities would be important in this regard. Birds on cliffs also have a good vantage point and could be searching for food, although this has not been taken into account here. The maximum amount of foraging likely to have taken place would account for about 77% of

flight activities, or 62% of all activities. It may be more accurate to say that 44% of flight was devoted to high-intensity foraging and 33% to lower levels of foraging intensity.

Non-searching (including low-intensity foraging) activities made up 56% of flight activities and were composed of 10 different activities (see Table 8.3), the most important of which were escarpment-gliding (19,9 % of total flight), thermalling (13,3%) and recreational soaring (9,1%). The first two are essentially linked to foraging and may occur concurrently with this. The remaining activities each constituted 5% or less of all flight activities.

Non-flight activities

These were made up of activities on cliffs and activities on the ground. For 28% of the time during which birds were viewed on cliffs they were feeding, 21% preening and for the remaining 51%, were resting.

Birds on the ground were most commonly observed feeding (46%), followed by sitting inactive (40%), drinking (11%) and, rarely, preening (4%). For the remainder of this chapter, the same activities for cliff and ground observations have been pooled.

8.3.3 Daily activities

Data on daily activities are shown in Figures 8.2 and 8.3. To put these data into perspective the numbers of hours spent in the field looking for Bearded Vultures, the numbers of birds seen and the length of time that birds were in
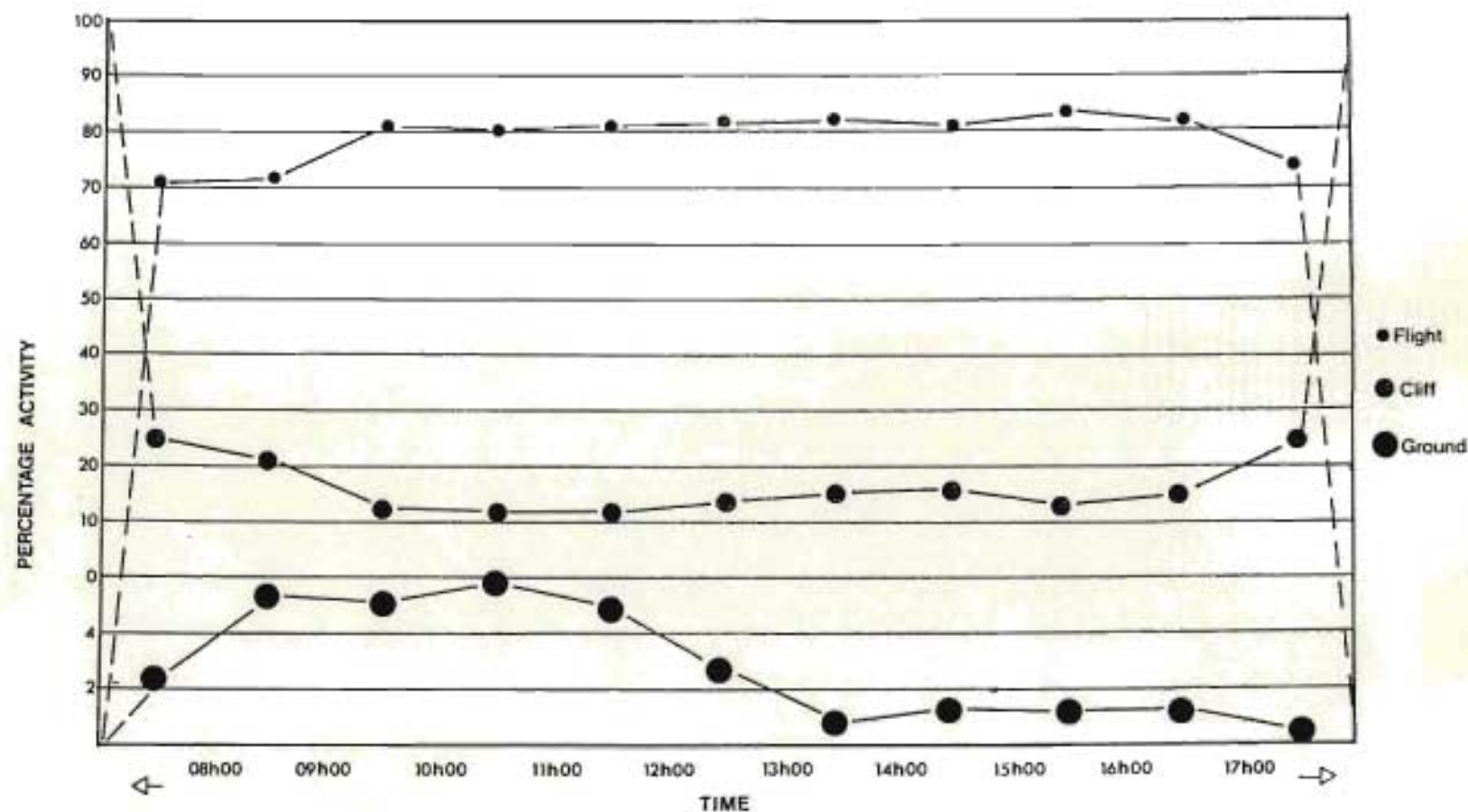
FIGURE 8.2. Daily activity curves of Bearded Vultures _in flight_, _on cliffs_ and _on ground_, as a percentage of the total hourly activities.

a inactivity   d bone-dropping   g playing   j escarpment gliding   m courtship display
b preening   e carrying food   h recreational soaring   k searching
c feeding   f attack on and by   i thermalling   l flapping flight
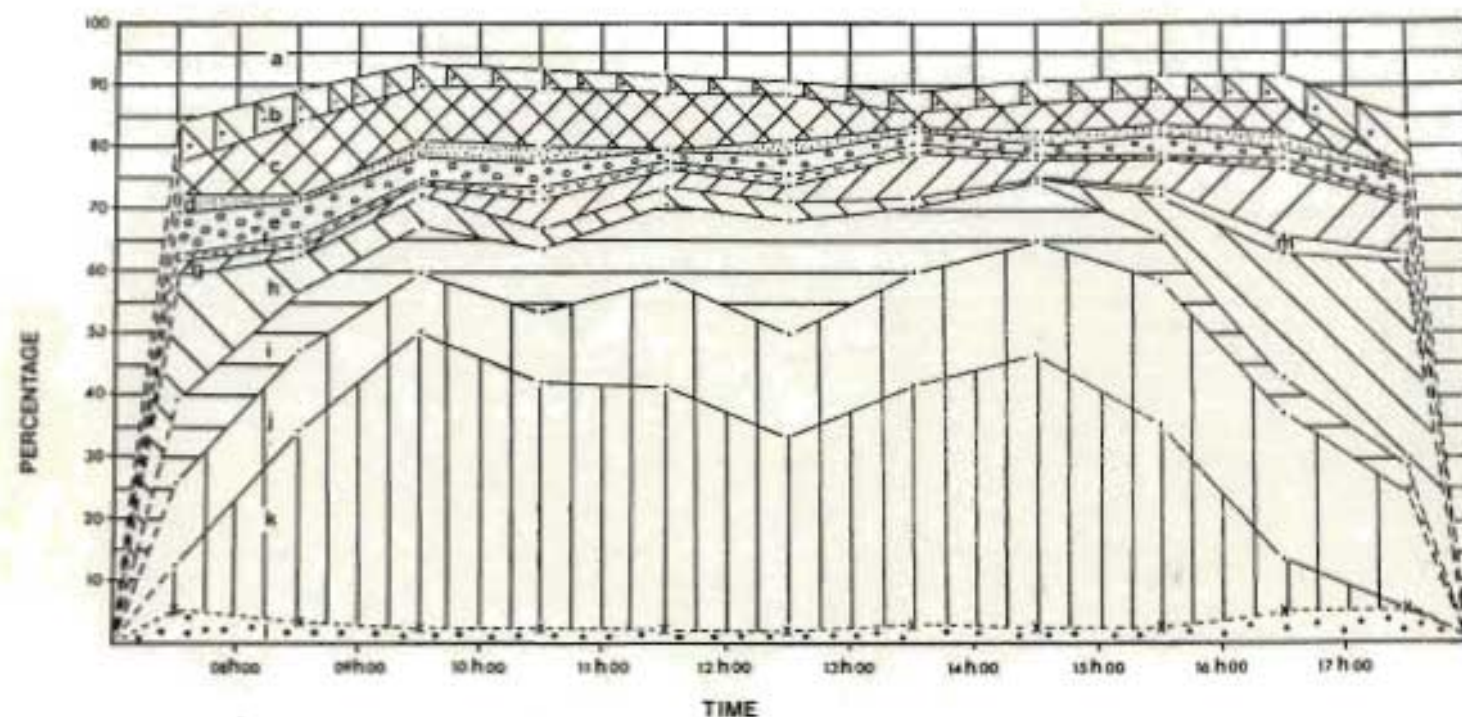
FIGURE 8.3. Daily activities of Bearded Vultures per hour, as a percentage of the total
hourly activities

sight per hourly time interval are shown in Figure 8.4. An accumulative time of 74 h was averaged in the field looking for Bearded Vultures per hourly interval of the day (range 43,5-220 h). The first and last periods of the day received least coverage as access to the most suitable areas required a 2-h horse ride, and only when camping in these areas were data in these time periods obtained. The average numbers of birds seen per hour spent in the field was 0,7 (range 0,6-1,0); more birds were seen in the late afternoons and birds were in sight for longer periods in the early mornings and late afternoons. This was probably because during these periods, Bearded Vultures soared and perched intermittently and were therefore clearly visible, remaining within a relatively small area about their nest or roost site.

The daily activities have not been corrected to sunrise or sunset times as I believed that a spread at both ends of a graph was preferable to one or other side being corrected for and the alternate side being twice as inaccurate. If both sunrise and sunset corrections are made, much detail is lost in the middle of the day, a time when many raptor species may be inactive, but which is important to birds dependent largely or partly on thermals.

Bearded Vultures started flying early, and continued till late each day. Although birds spent their nights on cliffs, little increase in cliff activity was detected in the mornings and evenings (Figure 8.2). This is (a) because birds flew shortly after sunrise and roosted again often after sunset, and (b) because of the survey method in which

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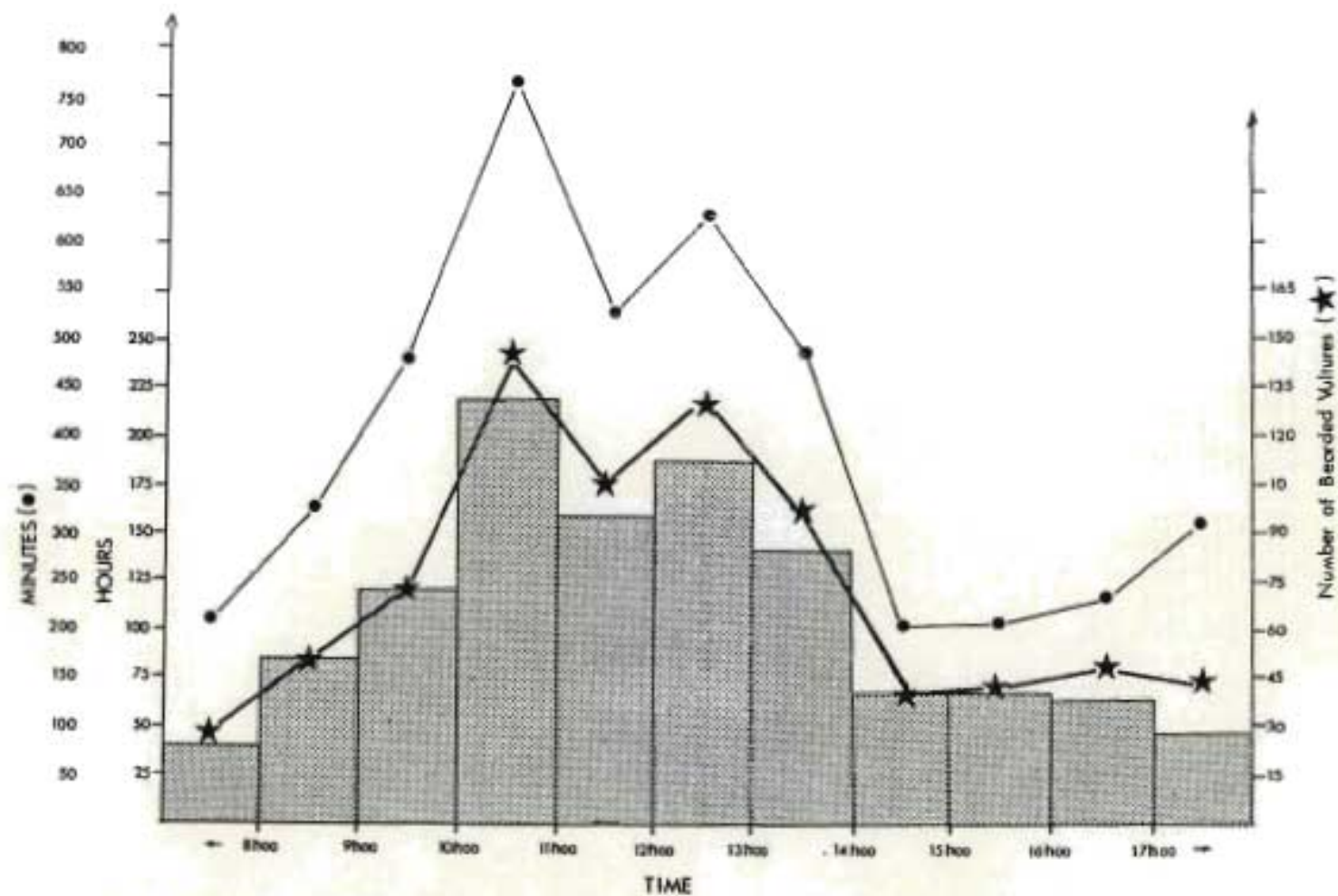
FIGURE 8.4. Number of hours I spent looking for Bearded Vultures, number of birds sighted and number of minutes that birds were in view, per hourly interval of the day.

a horse ride of about 2 h was required to reach the cliff sites from the base camp. Only data obtained when camping below these sites and during nest observations reflect times of first flight (see section 8.3.6 below). Activities on the ground took place mainly during the mornings. Birds seemed reluctant to land later in the day.

Searching was by far the most important daily activity and with the associated foraging activities of thermalling and escarpment gliding, occupied between 60% and 70% of the day (Figure 8.3). A number of different activities showed similar trends; flapping flight, recreational soaring, preening and resting were all of greatest duration in the early mornings and evenings. Foraging (searching) had mid-morning and mid-afternoon peaks. Play and courtship display increased towards evening and escarpment-gliding showed a similar tendency (although the latter might possibly be better attributed to recreational soaring, though difficult to distinguish from it). Most thermalling took place at midday and the carrying of food and feeding mainly in the morning. The remaining activities of bone-dropping and attack on and by Bearded Vultures were fairly consistently observed throughout the day.

In heavily overcast weather and light rain fewer birds were seen than in fine weather (0,38 and 0,27 birds per hour respectively compared to the mean of 0,68). While this could be partly attributed to lower visibility, birds were nevertheless less active on these days; two adult birds observed on overcast days with intermittent light showers

spent 34% and 41% respectively of the days perched inactive and birds caught away from their cliffs in rain invariably settled on a convenient ledge or on the ground and hunched themselves up until the rain stopped. During moderate and heavy rain and snow birds did not fly. During a three-day period of thick low mist and heavy intermittent rain and snow, two radiotagged adult Bearded Vultures remained continuously perched on their cliffs.

Temperature seemed to have little effect on Bearded Vulture activities although slightly more time was spent perching inactive on cold mornings before 08h00 than on warmer mornings (18,4% and 15,1% respectively).

On windy days (winds above about 20 km/h) Bearded Vultures thermalled less (6,3% of all activities compared to the mean of 10,7%) and began foraging earlier. Searching constituted 29% of all activities before 08h00 on windy days compared to the mean of 12,6%.

8.3.4 Yearly activities

The composition of each activity per month is shown in Figure 8.5. Some general trends can be seen from these results, although in some cases, monthly trends emerge more clearly in the next section on seasonal activities.

Searching increased from June through to November, corresponding to the breeding season, while thermalling decreased. Recreational soaring, inactivity and preening showed similar trends, decreasing in the winter months, with some exceptions in July to September due to breeding
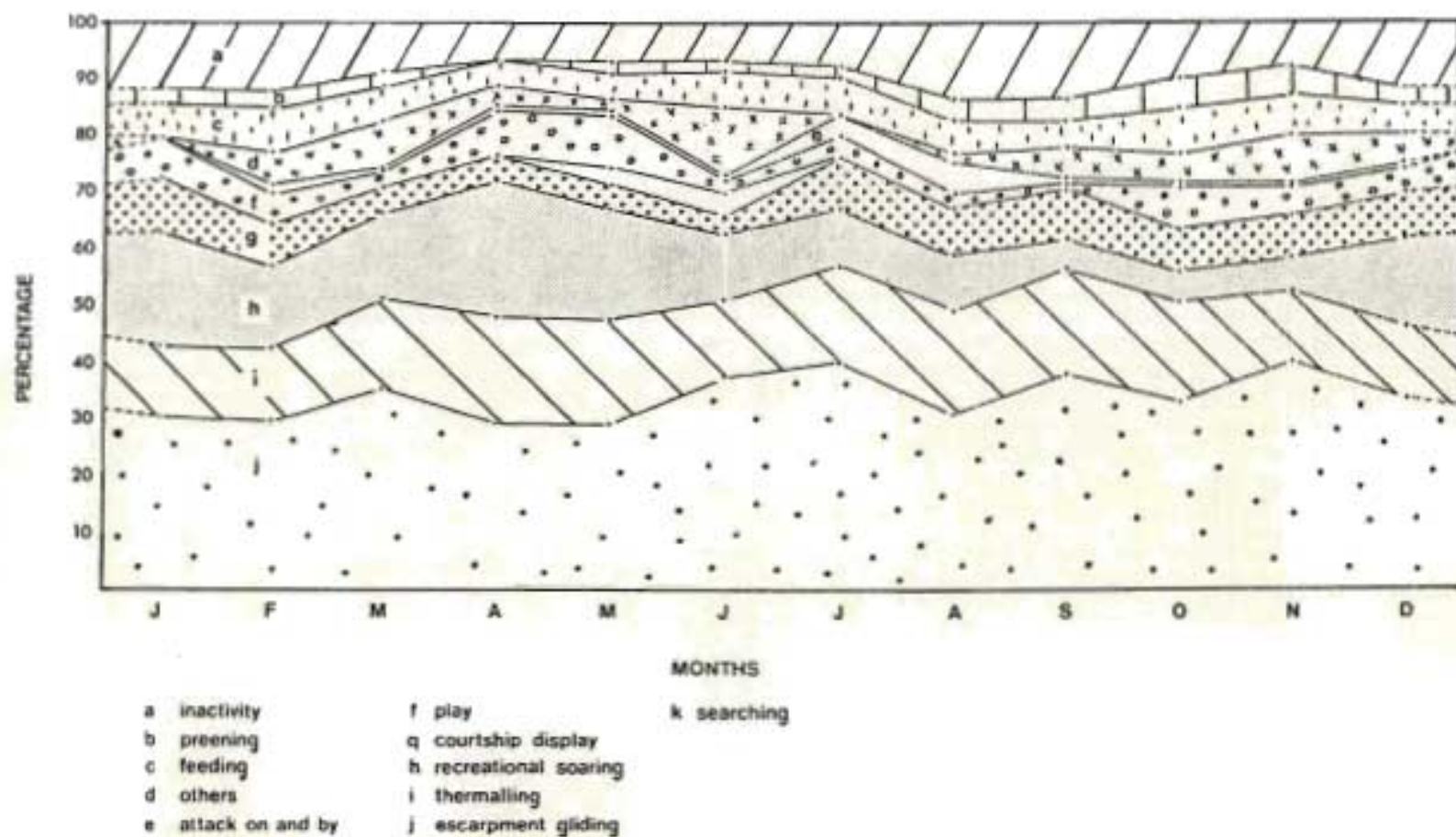
FIGURE 8.5. Yearly activities of Bearded Vultures per month, as a percentage of the total monthly diurnal activities.

activities (discussed later). Play increased during the few months before breeding, decreased sharply during the incubation and close-brooding periods and increased thereafter.

Some activities were restricted to specific times of the year. These include courtship display, (which took place in May and June just before and during the early stages of the breeding season), aggressive behaviour by Bearded Vultures and aggression towards conspecifics. Aggressive interactions might be observed throughout the year but increased from June to September, corresponding to the Bearded Vultures' breeding season and the breeding seasons of other large raptors such as the Black Eagle. A peak of Bearded Vulture aggression (Figure 8.6) occurred in August, corresponding to the hatching of eggs, a time when Bearded Vultures became comparatively intolerant of other large birds near their nests. Away from the nest Bearded Vultures were seen carrying nesting material only in June, corresponding with nest building or repair. This activity could easily be overlooked, however, as the nesting material was carried in the feet and tucked up against the body, often partly obscured by the belly feathers. Observations at nests indicate that nesting material was brought to the nest in varying amounts throughout most of the year. Figures presented for this activity are therefore an underestimate and reflect that this activity was only detected at that time of the year when nest material was most frequently being carried.
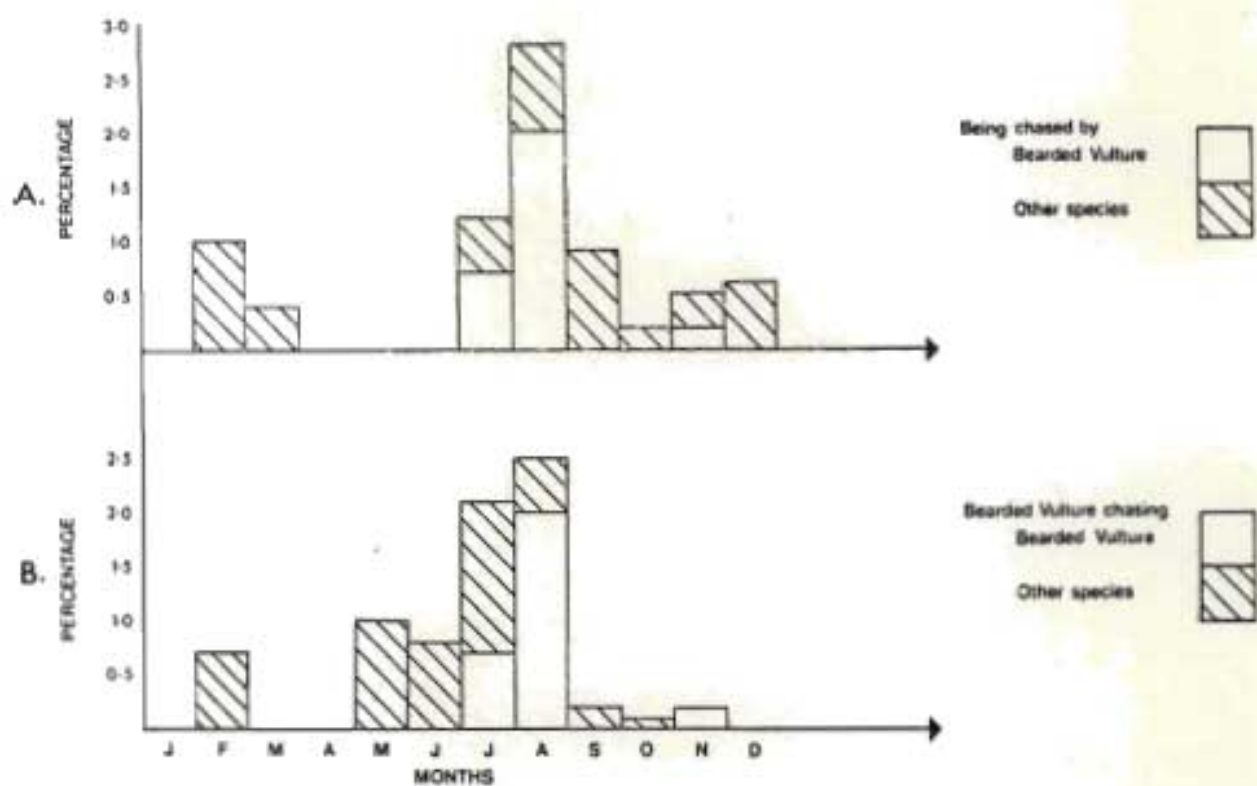
FIGURE 8.6. Attacks on (A) and attacks by (B) Bearded Vultures per month, as a percentage of all diurnal activities.

8.3.5 Seasonal activities

Monthly activities have been grouped for the non-breeding and breeding seasons (January to May and June to December respectively) (Figure 8.7). The breeding season has been divided into three stages, the incubation period (June to August), the close-brooding period (September to October) and the period when the nestling was left unattended (November to December). During the non-breeding season significantly more time was spent thermalling than during the breeding season (Chi-squared test; P<0,001). Play was also more frequently observed. During the breeding season Bearded Vultures spent more time searching for food (37% as opposed to 32%, significant at the 90% confidence limit), soaring, interacting aggressively, carrying food, preening and resting (Table 8.5), although none of these other activities were significantly different from those during the non-breeding season.

During the different stages of the breeding season (i.e. incubation, close-brooding and nestling unattended), the amount of time spent foraging increased as did the number of observations of birds carrying food and birds playing (Table 8.6). Aggressive interactions were recorded mainly during the incubation period, but this is somewhat biased by the fact that most eggs hatched in the last weeks of August, when adult Bearded Vultures are relatively intolerant of other birds near their nests. Other activities showed no real pattern; Bearded Vulture behaviour was generally very consistent throughout the year.
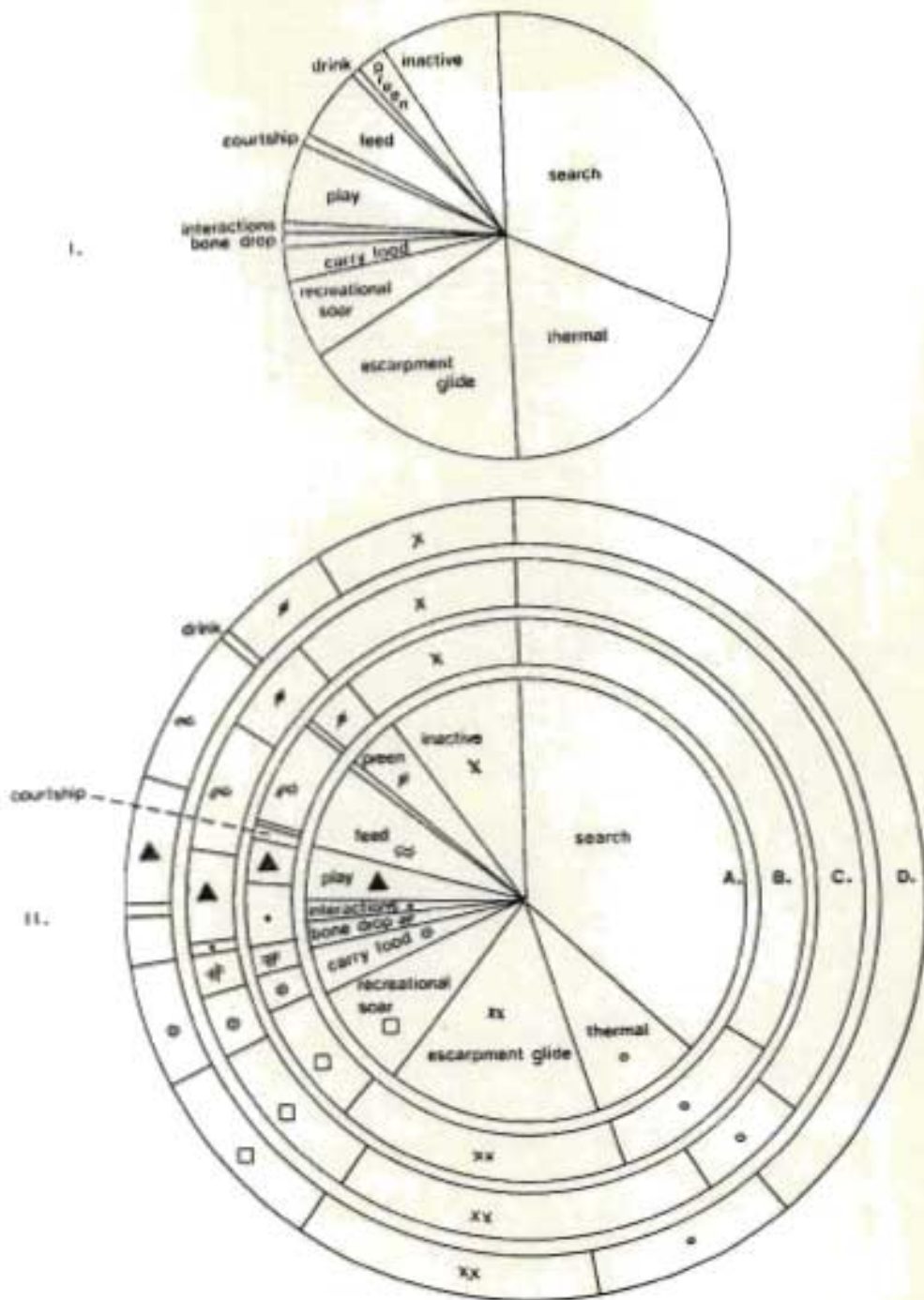
FIGURE 8.7. Seasonal activities as a percentage of all daily activities for I. the non-breeding season and II. the breeding season. The latter is divided into A. the entire breeding season, B. the incubation period, C. the close — brooding period and D. the period when the nestling is unattended.

8.3.6 Daily routine

Bearded Vultures are early risers. Although nests seldom received direct early morning sunlight, roosts usually faced east, and birds nesting in shaded areas usually flew to suitable ledges before sunrise, where they awaited the first rays. The birds invariably presented their backs or sides to the sun. This is consistent with the suggestion (Chapter 4) that the dark back and wings of Bearded Vultures would absorb warmth. The birds could therefore save on metabolic energy on cold, clear mornings. On cold winter mornings birds occasionally spread their wings to the sun but, contrary to the report by Steyn (1982), this was not common practice. During the period before first flight, birds ruffled up their feathers and preened themselves; a typical example of early morning behaviour is given in Figure 8.8.

The time of first flight varied considerably (Figure 8.9). Birds on the High Berg usually began flying 15-30 min after sunrise. These birds started from a position of considerable height, and exploited the prevailing early morning breeze which usually blew eastwards off the high ground. This was particularly pronounced at the heads of valleys and gullies where the air had been funnelled and provided good lift. First flight usually consisted of recreational soaring in the activities area, with more flapping flight than at other times of the day. This is in contrast to the first flight of Cape Vultures. These birds assessed the amount of lift, and if it appeared to be
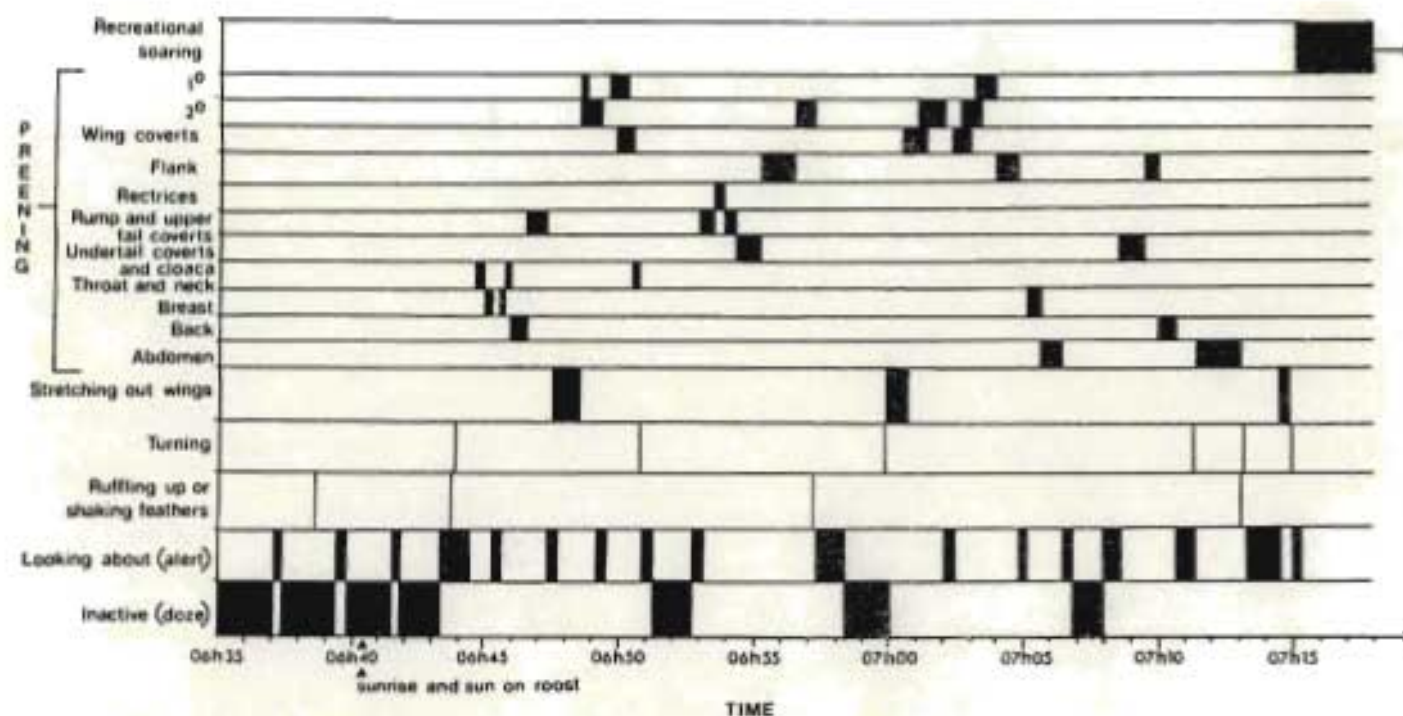
FIGURE 8.8. Typical early morning behaviour of adult Bearded Vultures before foraging. This sequence was of the male Ntabamhlope bird, recorded on 5 July 1982.
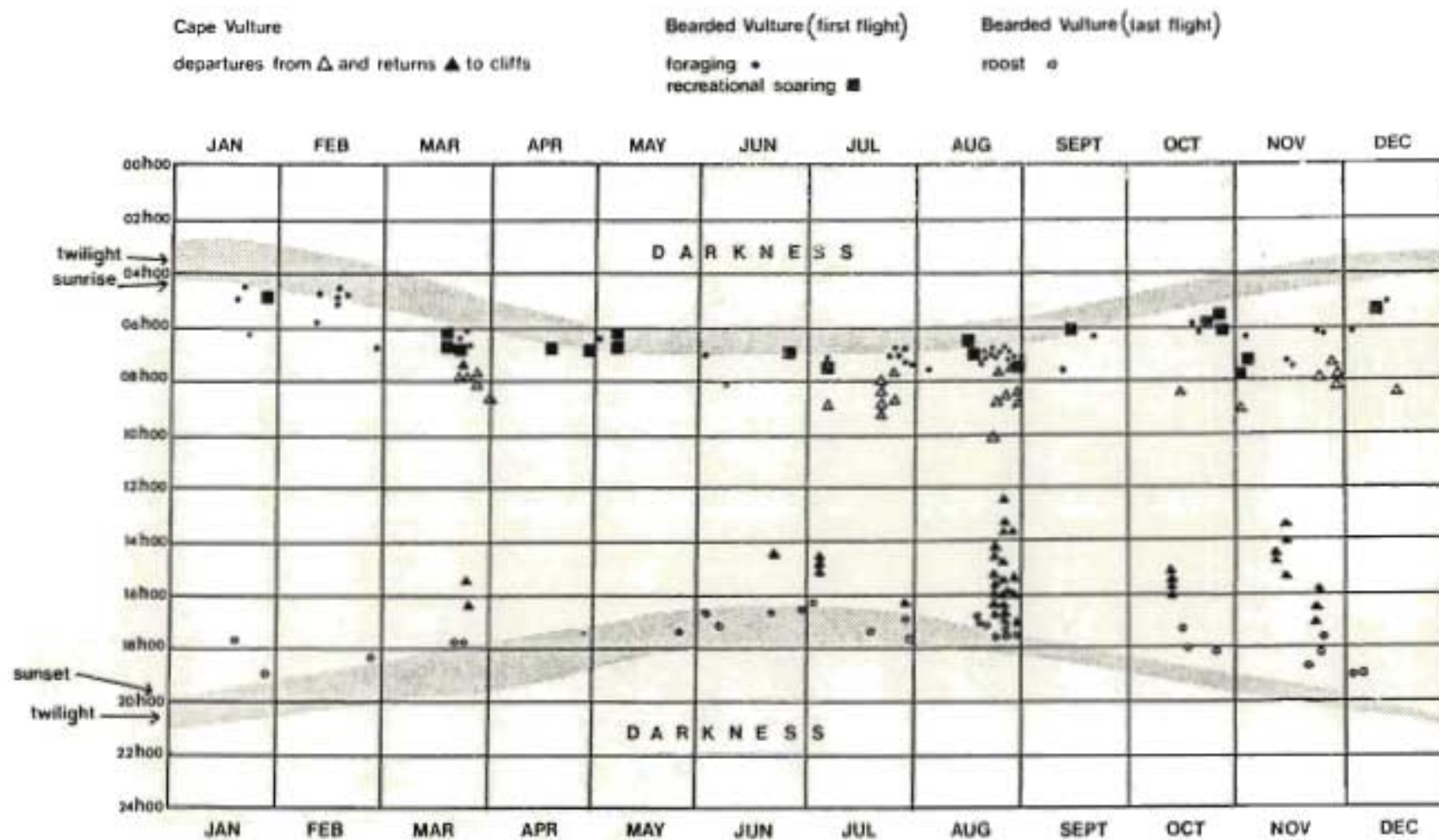
FIGURE 8.9. Times at which Bearded and Cape Vultures in the Natal Drakensberg left their nests and roosts to forage, and times at which they returned, superimposed on the annual day-length pattern.

insufficient, would return to the cliff. Once sufficient lift was obtained, Cape Vultures began foraging immediately. Recreational soaring in Bearded Vultures often continued for an hour or more, often interrupted by the bird returning to the cliffs to perch and preen. However, birds also began foraging very early, and if the whereabouts of a food source was known, they would fly before sunrise.

At the Roma Valley nest site no height advantage was to be had. The morning wind came down off the high ground from the east, while the land sloped down to the west and there were no suitable gullies to force air up. As a result, these birds had to wait for the wind to turn, and consequently began flying considerably later. Although a number of attempts were made, these birds were unable to soar for about the first two hours each day. On one occasion, when the birds were thought to be short of food, the male did depart very early, using flapping flight until out of sight.

At the Ntabamhlope nest site, an inselberg running predominantly north-south, the Bearded Vultures usually flew about 30-60 min after sunrise. The sun warmed the large expanse of east-facing cliff providing a bank of rising air which the birds used to gain a little height before heading west or northwest to the row of ridges about 10 km away, extending out from the Drakensberg where slope lift was encountered. This pair of Bearded Vultures engaged in less morning recreational soaring than did escarpment birds, perhaps in an attempt to keep secret their nesting area,

which was surrounded by a KwaZulu location and commercial farmlands and hence there was a high level of human activity in the vicinity.

While foraging usually began after recreational soaring, it was sometimes the first flying activity of the day. Factors influencing the time of foraging flight included:

(a) topography: (i) a height advantage and (ii) suitable terrain to provide slope lift.

(b) weather: (i) on overcast or misty days birds flew considerably later than on sunny days. When rainfall exceeded a light drizzle, birds did not fly at all. (ii) Bergwinds, which were most frequent during August and September but which might blow irregularly at any time of the year, facilitated early flight and birds were seen many kilometres from their nests before sunrise during these weather conditions.

(c) food: (i) if birds knew of a food source, they might leave their cliff at first light and fly straight to the food. Sometimes birds arrived at the feeding station in the afternoon but did not land (being far more reluctant to land at this time of the day). The following morning, these birds were back at the food, and often already feeding before sunrise, at a distance of 8 km from the nearest nest/roost sites. (ii) If birds had fed the previous afternoon, or had carried food back to their cliff (on two occasions birds were seen roosting overnight on a ledge with a bone clasped in their feet), they were less inclined to forage as early

as other birds, but spent some time in bone-dropping and feeding. (iii) Sometimes birds were thought to be experiencing difficulty in finding sufficient food for themselves and their nestling. This assumption was made when adults were observed returning to the nest after long foraging periods, without food. On many of these occasions, birds departed much earlier than did birds which brought in food regularly.

Other activities that have been recorded in the early morning include drinking (rare), bone-dropping and feeding (particularly when birds had stored food overnight), and play (as part of recreational soaring and particularly by young birds). Young birds often flew over ossuaries in their area each morning before foraging, and fed on any remains that may have been left or overlooked by another bird.

In winter, the interval between first light and first flight, and that between roosting and last light were both shorter than in summer (Figure 8.9). This is probably because of the shorter daylength in winter, of which birds have to make maximum use, particularly as during these months one bird of each pair is in full-time attendance at the nest. In summer, the extra hours of light may enable the birds to spend more time in activities other than foraging. The average recorded time of Bearded Vultures' first flight in winter was at 07h05 (n = 40), while Cape Vultures flew on average 1 h 5 min later at 08h10 (n = 124). The average time of Cape Vultures' first flight in summer was only 4 min

earlier than in winter, at 08h06 (n = 128), while Bearded Vultures were found to fly at 06h40 (n = 35), 25 min earlier than in winter and 1 h 26 min earlier than the Cape Vultures.

Once foraging had been successfully concluded for the day the bird returned to its breeding cliff where it then perched and soared intermittently for the rest of the day. In the non-breeding season birds did not always return to their nesting cliffs, but sometimes roosted on any convenient cliff. Birds were recorded absent from their breeding cliffs for periods of up to five days.

In cases when Bearded Vultures returned to their nesting cliffs before nightfall, they soared about the cliffs usually within the activities area. Birds on the High Berg frequently travelled for 4-5 km from their nest or roost site in both directions along the escarpment, effortlessly gliding along the bank of rising air. Birds from adjacent pairs sometimes came together and young birds were especially quick to join adults and other young birds, resulting in play, with undulating flight and chasing tactics. As many as seven birds were seen chasing and diving on each other at the same time, accompanied by wing striking (making a loud clap) and much flapping flight. After a few minutes the groups would break up, gliding peacefully about each other before returning to their respective cliffs. Most courtship display also took place at this time of the day.

Bone-dropping in the late afternoon seemed to be

usually, although not always, a recreational past-time. The bone was often caught in the air after release and birds were sometimes very slow in following bones to the ground. Birds were also seen to carry the same bone around for a few hours, first dropping it then soaring for half an hour or so with the bone in their talons, then returning to the ossuary to make a single drop, and so on.

By sunset birds had usually returned to their cliffs, where they settled, then departed for a short flight and resettled intermittently, these short flights usually continuing until last light. Birds finally settled for the night either on their nest (usually the female, if that year's offspring was not using it), on an alternate nest (rare) or on an adjacent roosting ledge or pothole. In winter Bearded Vultures settled on average at 17h03 (n = 17), and in summer at 18h13 (n = 13). In contrast, Cape Vultures were far less predictable in their times of returning to their cliffs, and seemed to do so after having fed or bathed after feeding, and irrespective of the time of the day. They roosted soon after arriving at the cliffs, but sometimes departed to soar before settling in for the night. This activity, however, did not seem as common in the Drakensberg as is reported in other areas (e.g. in the Magaliesberg, Transvaal, J. Komen pers. comm.), because on only one of 14 occasions that Cape Vulture colonies were monitored until last light did some birds leave the cliffs to soar, and this was thought to be the result of

disturbance by late incoming birds rather than any intention to soar. The Cape Vultures' average winter roosting time in the Drakensberg was at 15h11 (n = 98), and in summer was at 15h13 (n = 70), 112 and 180 min respectively before Bearded Vultures. Bearded Vultures therefore had a day length of about 10 h in winter and about 11,5 h in summer, while Cape Vultures had about 7 h in both summer and winter.

A number of night observations were made during periods of full moon, but Bearded Vultures were never recorded flying at night. Small movements on the roost ledge were made during the night, but comfort movements and birds moving deeper into a roosting pothole were the only night movements seen. After finally settling in for the night, the birds ruffled up their feathers, preened themselves extensively, then tucked the head into the shoulder or behind a wing, drew their legs up into their body, and slept in this posture. Birds roosting on a nest rested their head on the nest rim.

8.3.7 Energetics

The bioenergetics of raptors have been little studied and hence are poorly known. Current knowledge is based largely on laboratory studies and to a lesser extent on field observations. Any study of energetics should ultimately be concerned with an assessment of the requirements of free-living animals and interpretation of the findings in an ecological context (Sapsford 1984). In recent years particular emphasis has been laid on the

construction of time-energy budgets based on direct observations of time-activity patterns, and the subsequent coupling of various activity states with metabolic coefficients in an effort to assess the contribution of these states to overall costs (e.g. Tarboton 1978; Wakeley 1978; Koplin et al. 1980; Mendelsohn 1982). This approach has been adopted in this study, and detailed daily time-activity patterns have been obtained for each month of the year, as well as for the three main breeding stages i.e. incubation, close-brooding and the period when the nestling is left unattended at the nest.

Limitations of this type of assessment arise mainly from the attachment of coefficients to particular activities. Most of the available coefficients were initially obtained from laboratory studies of passerines, subsequently extrapolated to raptors and other species and often modified to suit the species in question. Such extrapolation, however, may not always be appropriate, especially as regards flight activities. For this reason, in the analysis that follows, I have followed no single model, but have drawn from a number using only those aspects that seem most appropriate. In this way I have attempted to construct a model with coefficients more suited to the lifestyle of large soaring birds.

In addition to the bird's various activities, energy expenditure may vary in response to changing environmental conditions (climate, topography, food availability, etc.).

The results presented here represent the average energy expended during each season or stage, and do not take into account these changing environmental conditions. Actual short-term energy requirements could therefore fluctuate, perhaps quite extensively, about these means. While I have attempted to be as realistic and accurate as possible, in the absence of corroborative laboratory data, the coefficients remain largely intuitive. The results are intended to reflect more importantly the change in daily energy expenditure between seasons and stages rather than the absolute amount of energy expended per se.

8.3.7.1 The non-breeding season

The energy expenditure of non-breeding Bearded Vultures was estimated from the activities recorded during the non-breeding season. The times spent in the respective activities (Table 8.7) were calculated assuming an average 13,5-h daylength period.

The basal metabolic rate (BMR) was determined using methods derived by Aschoff & Pohl (1970) in preference to those of King & Farner (1961) and Lasiewski & Dawson (1967) (explained in Appendix 8.1) because the first mentioned method differentiates between diurnal (BM_d) and nocturnal (BM_n) activities. A slightly higher figure is obtained for the total daily energy expenditure using the Aschoff-Pohl method than the others.

Many workers have tended to clump activities into a few "energy classes", e.g. Koplin et al. (1980) considered three

activity categories only: perched diurnal activity, flying, and nocturnal rest. These equations were designed for non-soaring birds, with large figures being ascribed to the energetics of flight. In this study an attempt was made to derive a figure for each of the various activities recorded for the Bearded Vulture. Where available these have been obtained from other studies (e.g. Tarboton 1978; Wakeley 1978; Mendelsohn 1981), but for some activities no figures are available. In these cases, coefficients have been chosen based on the figures used for activities intuitively judged to be similar in the amount of energy expended.

The energetics of gliding flight were calculated from Pennycuick's (1972) model derived for all gliding birds (Appendix 8.1) and applied by him to the Whitebacked Vulture. Although soaring flight is not free or "effortless" (Pennycuick 1972), neither is it as energy-consuming in species adapted to this mode of locomotion (e.g. vultures, many eagles, storks and pelicans) as some authors believe. To calculate the amount of energy required for soaring, Pennycuick derived an equation for the amount of power required to hold the wing in position, a task thought to be carried out by the deep portion of the pectoralis major muscle (a tonic muscle). Pennycuick (1972) assumed the energy used during soaring to be the sum of the BMR and the energy used by the tonic muscles. However, a raptor in flight does not merely lock its wings and glide, but is involved in constant correction and fine adjustments of

trim. As the bird flies closer to the ground, where the air is more turbulent, the adjustments presumably need to be finer and more frequent. BMR ratings of 1,2 for high, 1,4 for medium and 1,6 for low flight have been added. In addition, Bearded Vultures are searching the ground for food, so presumably an additional factor, similar in magnitude to perch-hunting should be included. A BMR rating of 1,3, somewhat lower than those given by other authors (e.g. BMR x 2,5, Tarboton 1978; BMR x 3,5, Wakeley 1978) was chosen, this being approximately the difference in magnitude between "low activity" and "perch hunting", thereby representing the actual searching component of the energy used. Likewise, birds in thermals are manipulating many muscles which are not taken into consideration by Pennycuick's model, and therefore the energy they use exceeds that calculated by Pennycuick's equation alone. An additional BMR rating of 1,4 was therefore worked into the calculation.

Figures for flapping flight vary from 8-20 times BMR. Pennycuick (1972) estimated that a Whitebacked Vulture flying under power at 44 km/h (in the region of its minimum power speed) would consume 2177 kJ/h, 47 times its BMR of 46 kJ/h! Most authors agree that powered flight is less energy consuming than this; Tarboton (1978) gives a figure of BMR x 17,2 for Blackshouldered Kites (which Mendelsohn (1981) suggests exaggerates the costs of flight), Wakeley (1978) give figures of BMR x 11,5 and BMR x 12,5 for Ferruginous

Hawks *Buteo* *regalis* and Kendeigh *et* *al*. (1977) derive an equation for non-passerines (Appendix 8.1) from which the average energy expenditure is 12,1 times higher than the BMR. For flapping flight in the Bearded Vulture, a figure of BMR x 12 has been adopted.

Figures were derived for the other activities as follows:

(a) preening = BMR x 1,3 (= low activity, Tarboton 1978),

(b) feeding = BMR x 2,5 (Tarboton 1978). It should be noted that while griffon vultures, and to a lesser extent some other vulture species expend considerable energy at food through fighting and competing for a place at the carcass, this does not occur in the Bearded Vulture, so no additional cost factor has been included,

(c) bathing/drinking = BMR x 2,0 (my estimate as no figures are available),

(d) bone dropping = gliding costs + BMR x 2,0 (my estimate),

(e) escarpment gliding and recreational soaring = gliding costs + BMR x 1,2 (equivalent to high flight),

(f) courtship display, play and attacks by and on Bearded Vultures = gliding costs + BMR x 2,4 (my estimates),

(g) carrying both food and nesting material = gliding costs + BMR x 1,4 (my estimate).

A total daily energy budget (DEB) of 2188 kJ was obtained for Bearded Vultures in the non-breeding season using this model. This contrasts markedly with figures calculated using existing models (*i.e*. those of Tarboton (1978), Wakeley (1978) and Koplin *et* *al*. (1980)) which range

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from 3186-10838 kJ. This emphasizes that these existing models cannot be accurately applied to soaring species such as the Bearded Vulture.

Bearded Vultures spent 47% of the 24-hour day (83% of the photoperiod) in flight, expending an estimated 70% of the DEB in this way. High intensity foraging accounted for about 26% of the DEB, while foraging-related activities (e.g. thermalling and escarpment gliding) used a further 21%. It is significant that the mean energy expended on all flying activities was only 1,6 times that of the mean non-flying activities (cf. Blackshouldered Kites where the equivalent figure is between 4,8 and 5,6 times greater for flight than non-flight, from figures presented by Mendelsohn (1981) using the Wakeley (1978) and Koplin et al. (1980) models respectively). Low-expense flying activities such as recreational soaring and escarpment gliding, were usually undertaken in the late afternoon after birds had returned from foraging. The functions of these activities are not immediately obvious, but they use only 1,1 times more energy than the mean daily non-flight activities. It is questionable, therefore, whether it is necessary to justify the time spent in "recreational soaring" by attaching such labels as "territorial display", "nest site advertisement", "pair-bond strengthening" etc. when the amount of energy used is little more than the non-flight activities.

No data are available on foraging success using the different searching methods, but an estimated 52% of the

high-intensity foraging energy went into medium-height searching, 35% into low searching and 12% into the least energy-consuming method of high searching (ignoring the cost of thermalling to the required altitude). It may be expected that the food found is proportional to the energy input of the different searching methods, but because birds change readily from one foraging level to another in response to terrain, weather conditions, activities of other scavengers, known or likely food localities, etc. and because birds are so rarely seen descending to food, foraging success using the different methods would be difficult to quantify.

8.3.7.2 The breeding season

The energy expended by Bearded Vultures was estimated from the activities recorded during the various stages of the breeding season for birds away from the nest. The months of July and August were ascribed to incubation, September and October to close-brooding and November and December to the period when the nestling was left alone on the nest, i.e. when both parents were away foraging. For birds on duty at the nest, activity patterns were obtained from data presented in Chapter 7. For convenience, the stages described above were divided into exactly two-month periods (a fair approximation). During the incubation and close-brooding stages, the parents were assumed to share the nesting duties equally, i.e. each bird was assumed to spend half the photoperiod on the nest. The energetic cost coefficients ascribed to the different activities are the

same as those used for the non-breeding season. Activities unique to the breeding season are:

(a) feeding the nestling, and include food preparation = BMR x 2,5 (the same as for feeding by adults),

(b) standing on the nest and shading the nestling = BMR x 1,2 (a value between "inactive" and "low activity" used by Tarboton (1978),

(c) egg rolling and nest maintenance = BMR x 1,4 (being considered to be somewhat more energy consuming than preening).

The mean DEB of Bearded Vultures during the breeding season was 1905 kJ. This lower figure results from the low energy expenditure during the incubation and close brooding periods of 1707 and 1773 kJ/day respectively, due to long periods of inactivity spent on the nest (Table 8.8). Once the nestling was left alone on the nest and both parents were foraging, the DEB increased to 2233 kJ, slightly greater than that during the non-breeding season.

During the first two stages of the breeding season, more energy was spent in non-flying activities than in flight, while the reverse was true for the remainder of the year. Many of the changes in energy expenditure from one stage to the next are to be expected, e.g. the energy expended in bringing in food increased during the nestling period, the energy expended in defending the nesting area increased at the time the eggs hatch, etc. More subtle differences in energy expenditure may be hidden in the amount of time available for other activities as a result of

nesting duties. If the energy expended on foraging is
calculated for each breeding and non-breeding stage per hour
of available time (i.e. of the photoperiod, after nesting
duties have been subtracted), it can be seen that during the
non-breeding period an average of 42 kJ/h was spent on
foraging. During the incubation period this rose to 44 kJ/h,
during the close-brooding period to 49 kJ/h and when both
parents were free to forage during the period when the
nestling was left unattended in the nest, to 51 kJ/h per
bird. Similarly, if the percentage of energy spent on
foraging is calculated from the total time spent in flight,
then figures of 37%, 40%, 45% and 46% respectively are
obtained. This suggests an increased demand on the adult
Bearded Vultures' time to find the required amount of food.

8.4 DISCUSSION

8.4.1 Activities

Bearded Vultures fly early and roost late. It is
possible for them to be on the wing from first to last
light, although in practice, they seldom appear to need all
this time to find sufficient food. Other avian scavengers
occurring in the same habitat as Bearded Vultures are Cape
Vultures, Whitenecked Ravens and rarely, Yellowbilled Kites
Milvus migrans parasitus. The only mammalian scavenger
found in any numbers is the Blackbacked Jackal. There is no
evidence that Spotted Hyaenas Crocuta crocuta ever occurred
in the area and Brown Hyaenas Hyaena brunnea are rare

vagrants (Smithers 1983).

Houston (1974b) has shown that in the Serengeti, most food is available to griffon vultures shortly after dawn. As most animals die of malnutrition or disease resulting from a weakened condition, they probably die just before dawn. Similarly, in the southern African Drakensberg, the nutritional level of herbage is at its lowest in winter (Scotcher et al. 1980), animals are at their lowest condition towards the end of winter and early spring and, coupled with low temperatures which reach their lowest levels just before dawn, most food would probably be available to diurnal scavengers from first light.

Bearded Vultures flew, on average, just over one hour earlier than Cape Vultures in winter and 1,5 h earlier in summer. While the time of first flight in Cape Vultures was fairly uniform (except when Bergwinds were blowing and they could fly very early), Bearded Vultures could easily, and often did, fly from first light. This means that on average, Bearded Vultures had over an hour to find food before Cape Vultures could be expected to arrive and displace them from a carcass, but if Bearded Vultures began to forage as early as they were able to (i.e. from first light), then they would have as much as 3 h free from competition from Cape Vultures.

Bearded Vultures approached food and began feeding less nervously and more quickly in the early mornings than later in the day and this is reflected in the fact that they were seen carrying food in flight twice as frequently before

09h00 as later in the day. Carcasses found later in the day are likely to be quickly dominated by Cape Vultures, so rather than running the risk of landing and then obtaining little or no food, they may prefer to wait until the Cape Vultures have fed, and then feed safely on what remains. If Bearded Vultures feed from a whole carcass they have to spend considerable time gaining entrance and then tearing off suitable items. Once Cape Vultures have fed on a carcass, however, Bearded Vultures can rapidly disarticulate bones and fly off with sections of limbs or bones to a safe refuge to eat at leisure.

Another species which feeds on carrion and may be considered a competitor of the Bearded Vulture is the Whitenecked Raven. This is also a very early rising bird which probably leads other carrion-feeding species (including the Bearded Vulture) to food. Ravens rarely gather in any numbers except at longterm sources of food, e.g. a feeding station. It is unusual for more than one pair to be seen at a food source in the veld, and they are easily displaced by Bearded Vultures.

Blackbacked Jackals are probably also not serious competitors. On one occasion a jackal and a Bearded Vulture were seen together at a food source. They fed side by side with no interaction between them. Jackals may consume some carrion at night that would otherwise be available to scavenging birds, but this is unlikely to have a great effect on the birds; while some carcasses which were left

exposed overnight showed evidence that jackals had fed, the amounts removed were never great. In a study by Rowe-Rowe (1983) in Giant's Castle Game Reserve only 11% of the jackal's diet was found to be derived from antelopes (i.e. scavenged); a far larger proportion of their diet was found to be small mammals, caught by the jackals themselves. Rowe-Rowe concluded that jackals in the Drakensberg are primarily searchers for small mammals and insects and scavenge only opportunistically.

It can therefore be concluded that, in southern Africa, the Cape Vulture is the Bearded Vulture's only serious competitor for food. Bearded Vultures are unable to dominate Cape Vultures physically, but are able to reduce direct competition to a large degree by (a) flying earlier and getting to food earlier than the Cape Vultures, (b) flying later, and if not actually feeding, then locating possible food sources which can be investigated early the following morning, (c) utilizing what is left over after the Cape Vultures have fed, so that even if displaced from a carcass, a food source remains to be utilized with little or no competition.

Bearded Vultures used thermals to gain altitude mainly from December to May. During the breeding season the home range of Bearded Vultures was considerably smaller than during the non-breeding season, and the amount of high-level searching and cross-country travel was reduced. In addition, good thermalling conditions do not develop to the same extent in winter as in summer, and from July to September

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windy conditions generally prevail (Figure 2.3, p. 20), which tend to favour slope lift.

Although recreational soaring occurred throughout the year as a well-represented activity (between 4-10% of the total daily activity), it decreased from January to June, then increased sharply in July, remaining high for the rest of the year. The decrease after January can be explained by the birds being less tied to their nesting sites once the young vulture had started to fly. During the breeding season recreational soaring may serve to advertise occupancy of a cliff by a pair of (nesting) birds, but once breeding has been completed (after the young bird is able to fly) this may no longer be so necessary and only a little time spent in the area may be sufficient. It is perhaps surprising then that the increase in recreational soaring takes place only in July, while egg-laying occurs about the end of June and nest building starts in May. However, courtship display was observed only in May and June, and if added to recreational soaring (Figure 8.10) as a form of nest-site proclamation (as suggested by Newton 1979), would markedly increase the visual presence of the birds in their nesting areas. While the amount of time spent in courtship and recreational soaring combined in May and June may not be as great as recreational soaring alone from July to January, the quality of the display, i.e. the vigorous activity, undertaken only if breeding is to take place, may be more important than the amount of time per se.
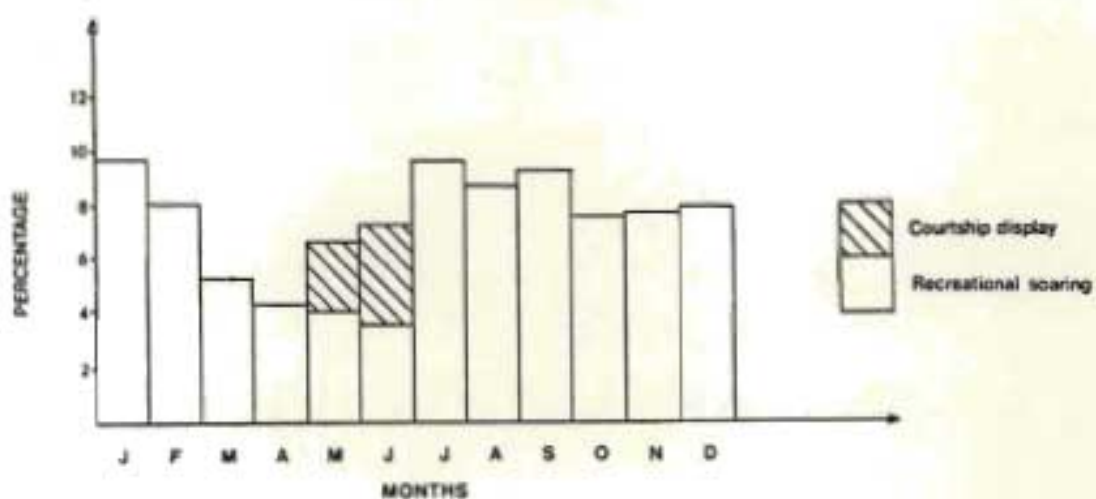
FIGURE 8.10. Recreational soaring and courtship display in Bearded Vultures as a percentage of all diurnal monthly activities.

Play, which took place mainly in the late afternoons, was most frequently observed in the two months before nesting (April and May) and after the nestling could be left unattended. While play between immatures or mixed-age groups of Bearded Vultures was observed about twice as frequently as between adults, adult birds nevertheless spent on average about 25 min per day in play. The usual pattern was for birds to glide out from their nesting area to a point about halfway towards their neighbours' nest area where they would circle until joined by the neighbouring birds. The enjoyment derived from this past-time can be surmised and, in addition, some social functions may be achieved. (a) The presence of a group of "playing" adults is a sign to other Bearded Vultures that the area supports a stable population of birds with nest sites fairly close together. If nests were further than a certain distance apart birds would be unlikely to meet in this way; the Ntabamhlope pair, about 30 km from their nearest neighbours, were never seen to be involved in group play. Play may therefore serve the functions of preventing, or reducing the incidents of competition for nesting areas and contribute to the even spacing of breeding pairs. (b) During the incubation and close-brooding periods of the breeding season one adult of a pair is always in attendance at the nest. The other bird spends more than 60% of its time off the nest in foraging-related activities. During about 50% of this time it is in the company of another adult bird, usually one of its neighbours (see Chapter 6). To achieve such cooperative

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foraging a close relationship is needed between neighbouring birds. Play may therefore be important in maintaining this contact and in strengthening bonds between neighbouring birds so that conflict over food (the most critical resource and one which would be expected to strain any relationship) can be amicably resolved.

The amount of time spent inactive by Bearded Vultures increased in August and September despite the fact that the amount of time being spent on foraging by off-duty birds was increasing. This can be explained by the fact that on-duty birds were more visible, standing at the entrances of nesting potholes shading nestlings (rather than sitting tight on eggs) and progressively moving out of the nest and perching nearby on the cliff. As the nestling grew older so the on-duty bird left the nesting area for longer and longer periods to forage, and this is reflected in the decrease in inactivity in October and November. By mid-December young birds were making their first flights, and they perched inactive for long periods between one short flight and the next. This situation lasted for a few months until the young birds were foraging over a fairly large range (see Chapter 7).

8.4.2 Energetics

The energy requirements of Bearded Vultures given in this study were calculated from time-activity budgets. Craighead & Craighead (1956) have shown that species with body weight ranging from 100-200 g consume about 22% of

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their own weight in food per day, while species of 200-800 g consume about 13% of their own weight. Kendeigh et al. (1977) give equations based on mass and temperature for calculating the daily energy budget of birds:

$$DEB = 1,079 \, W^{0,67} \quad \text{for } 30^{\circ}C$$

$$DEB = 8,059 \, W^{0,50} \quad \text{for } 0^{\circ}C$$

There is no temperature station in the subalpine or alpine belts of the Drakensberg mountains. Extrapolation to 3000 m above sea level from the Cathedral Peak Forestry weather station at 1860 m (where an average decrease of $0,5^{\circ}$ C is experienced with each increase of 100 m in altitude) gives a mean daily temperature of about $7,5^{\circ}C$. Using a mean body weight (W) of 5490 g, a DEB of 2298 kJ is obtained for non-breeding Bearded Vultures. This is within 5% of the value obtained in Table 8.9 using coefficients based on the time-activity budget, and while it lends support to these results, it must be borne in mind that the equations of Kendeigh et al. are based on very few measured DEB values.

Seasonal changes in the estimated daily energy expenditure are more pertinent when compared to the daily food requirements and the food availability for a breeding pair of Bearded Vultures.

During this study it was not possible to determine directly the daily food requirements of the Bearded Vulture. Hiraldo et al. (1979) give figures for the slightly heavier European Bearded Vultures of between 400-500 g per day, and

state that "during the peak demand period, a pair raising a chick must obtain almost 1500 g per day".

The energy requirements of adult Whitebacked Vultures (with an average weight of 5,4 kg, which is only slightly smaller than the southern African Bearded Vulture) was between 1674-2093 kJ/day (Houston 1976). This represents between about 320-400 g of meat. Bearded Vultures probably expend a little more energy per day than do Whitebacked Vultures as they are slightly larger, spend more time in flight and live in a colder environment.

The daily energy expenditure of a pair of Bearded Vultures as calculated from the daily activity-time budget per month is shown in Figure 8.11. An estimate of the daily food requirement for each month of the year per breeding pair is calculated from these figures in the following way.

The Bearded Vulture's diet was estimated to consist of bone (with its associated marrow), muscle and skin in a ratio of 14:5:1, based on this study (see chapter 6) as well as that of Hiraldo et al. (1979), who found that 80% of all food brought to nests in Spain was bone and that 90% of stomach contents examined were bone. Examination of 50 Ethiopian birds showed that all had bones in their stomachs (Cramp & Simmons 1980). It should be remembered, however, that soft material is likely to be digested more quickly and would not be equally represented. As bones obtained by Bearded Vultures usually have some muscle and skin attached, the above ratio would seem to be realistic.

Little information is available on the energy content
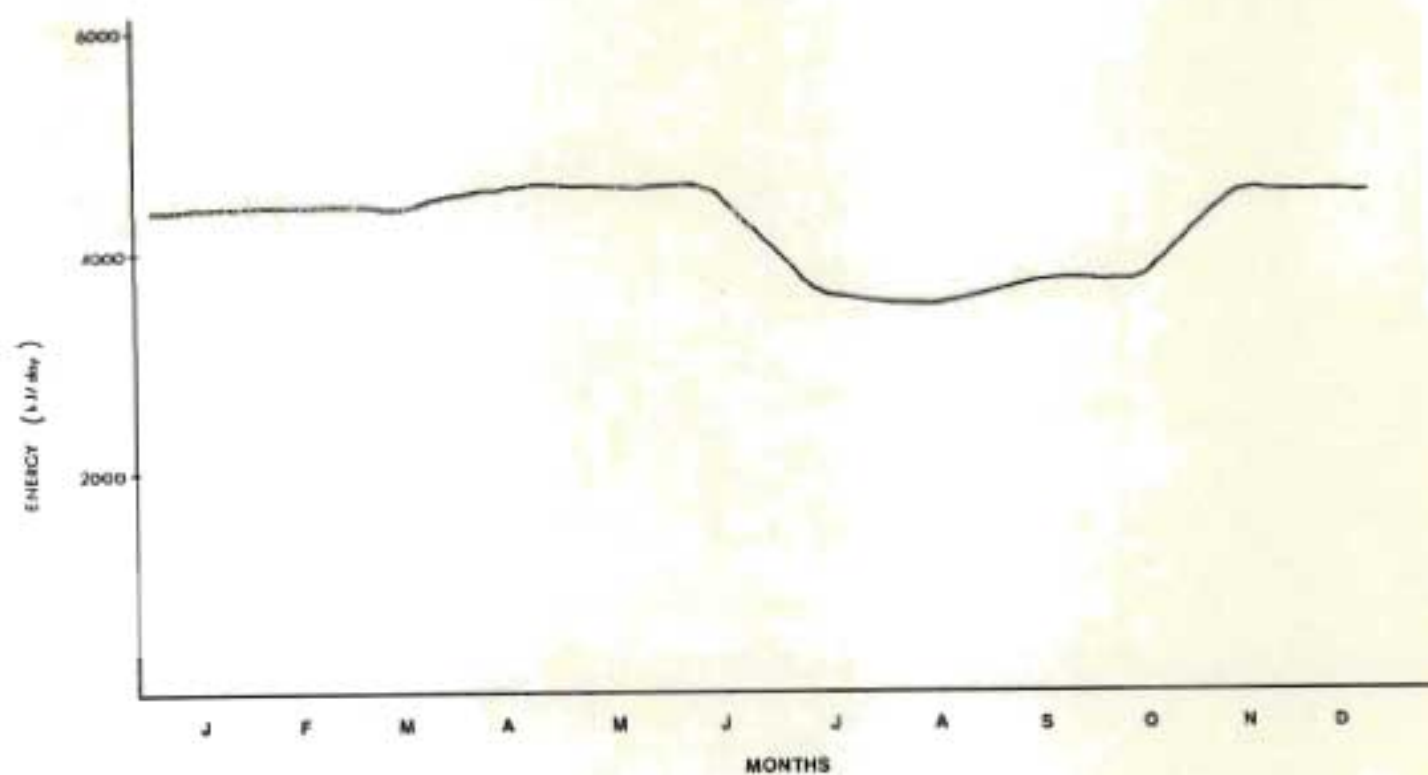
FIGURE 8.11. Average daily energy expended by a pair of breeding Bearded Vultures per month, calculated from the daily activity-time budget as explained in the text.

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of prey components. Variations occur from species to species as well as between different age classes within a species. Values for the energy content of meat are 5,2; 6,1 and 7,0 kJ/g wet weight (Houston 1976; Komen 1984; C.W. Sapsford pers. comm. respectively), while for skin and fur of laboratory mice the figure is about 12,0 kJ/g (C.W. Sapsford pers. comm.). The cleaned but not de-oiled skeleton of a laboratory mouse contained about 16,5 kJ/g dry mass (= about 8,4 kJ/g wet weight), and ash free (i.e. an indication of the energy contained in the marrow) gave about 28,5 kJ/g. As bones get larger so the amount of energy per gram decreases e.g. Vervet Monkey Cercopithecus pygerythrus longbones contain about 8,0 kJ/g and ribs about 5,9 kJ/g while the longbones and ribs of the Red Duiker Cephalophus natalensis contain about 2,5 and 2,9 kJ/g respectively (C.W. Sapsford pers. comm.).

Bearded Vultures generally swallow smaller bones whole, while larger ones are dropped onto rocky sites to crack them open. While it is advantageous to swallow small bones whole thereby saving time on the removal of marrow and adhering soft material, there is an upper limit to the size of bones that a Bearded Vulture can swallow. The energy value of small bones, which contain a relatively low inorganic component, is remarkably high, higher in fact than red meat and compares favourably to liver which contains about 8,8 kJ/g (C.W. Sapsford pers. comm.). While larger bones may also be eaten after being broken into smaller pieces, the number of longbone fragments found at ossuaries attests to the fact

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that once the marrow has been consumed (adhering muscle and skin are usually removed before dropping), the bone fragments are often discarded. Being oily, these bone fragments contain some energy, but the high inorganic content makes them less attractive as an energy source, eaten only when hungry or by young birds. Bearded Vultures scoop out marrow and do not always eat the rest of the bone. They are thus using a very high-energy source of food. An average figure of 6,7 kJ/g wet weight was therefore chosen to represent the energy content of the bone and marrow component of the Bearded Vulture's diet. The average figures adopted for the energy contents of meat and skin were 5,8 and 11,7 kJ/g respectively. From 100 g of food, therefore, a Bearded Vulture would obtain on average about 670 kJ.

The assimilation efficiency of diurnal raptors and owls is generally given in the range of 70-80% (Gessaman 1973; Mosher & Matray 1974; Sapsford & Mendelsohn 1984), although for captive nestling Cape Vultures, Komen (1984) gives a somewhat higher figure of 86,5%. Because of the high inorganic content of the Bearded Vulture's diet, an assimilation figure at the bottom of the accepted range, i.e. 70% was adopted. Thus, for every 100 g of food eaten the actual amount of energy obtained is in the order of 473 kJ. Using these figures, the basic daily food requirement to provide for the average energy expenditure per month for a breeding Bearded Vulture was determined; during the non-breeding season this was calculated to be 464 g of food and

during the breeding season was about 405 g (ranging between about 365 g in the incubation stage to 475 g during the stage when the nestling was left unattended on the nest). These figures are only slightly lower than those given by Hiraldo et al. (1979) for the larger European Bearded Vulture, and similar to the daily food requirement of the similar sized Whitebacked Vulture (Houston 1976).

To determine the overall food requirements of a pair of breeding Bearded Vultures two further aspects have to be taken into account, namely the energy required to produce a clutch of eggs and the amount of food required to feed the nestling until it is independent.

The cost of egg-laying is small, each egg weighing about 3% of the weight of the adult bird. A two-egg clutch represents about 2135 kJ (649 kJ/100g, extrapolated from figures available for domestic chickens as given by Paul & Southgate (1978) and Watt & Merrill (1975)), and at an assimilation efficiency of 70%, requires about 450 g of food.

The food intake of nestling Bearded Vultures from hatching until independence has been extrapolated from figures obtained for the food intake of nestling Whitebacked Vultures (Houston 1976). This extrapolation can be justified on the grounds that the species are of comparable weights, and the lengths of the nestling periods are very similar, i.e. 120-130 days (Maclean 1985). The figures for daily food intake have been increased by about 10%, however, to account for the large bone component in the Bearded Vulture's diet

with its high inorganic content and lower assimilation efficiency compared to the diet of griffon vultures which consists almost entirely of muscle and viscera, as well as the lower ambient temperatures encountered by Bearded Vultures as compared to Whitebacked Vultures. For the first two months after leaving the nest the young vulture obtains all its food from its parents. During the first month it spends most of the day perched inactive, thereafter becoming more and more active. For the purpose of determining the food requirements of a pair of adults and the additional food they need to feed their offspring it was assumed that after the second month out of the nest (i.e. March) they provide decreasing amounts of food to the young bird, which begins to find its own food in increasing amounts, and at the time of independence (i.e. June) parents are providing only 10% of its requirements.

When all these figures of the food requirements are added together, an indication of the daily food requirements of a breeding pair of Bearded Vultures is obtained for each month of the year (Figure 8.12). It is apparent that two periods of particularly high food demand occur, (i) from September to November when the nestling is growing rapidly and the pair need to obtain about 1335 g of food per day during the peak demand period, and (ii) from February to April when the dependent young bird has become active and before it is capable of providing a significant contribution towards its own food requirements. During this period the pair need to obtain about 1270 g of food per day.
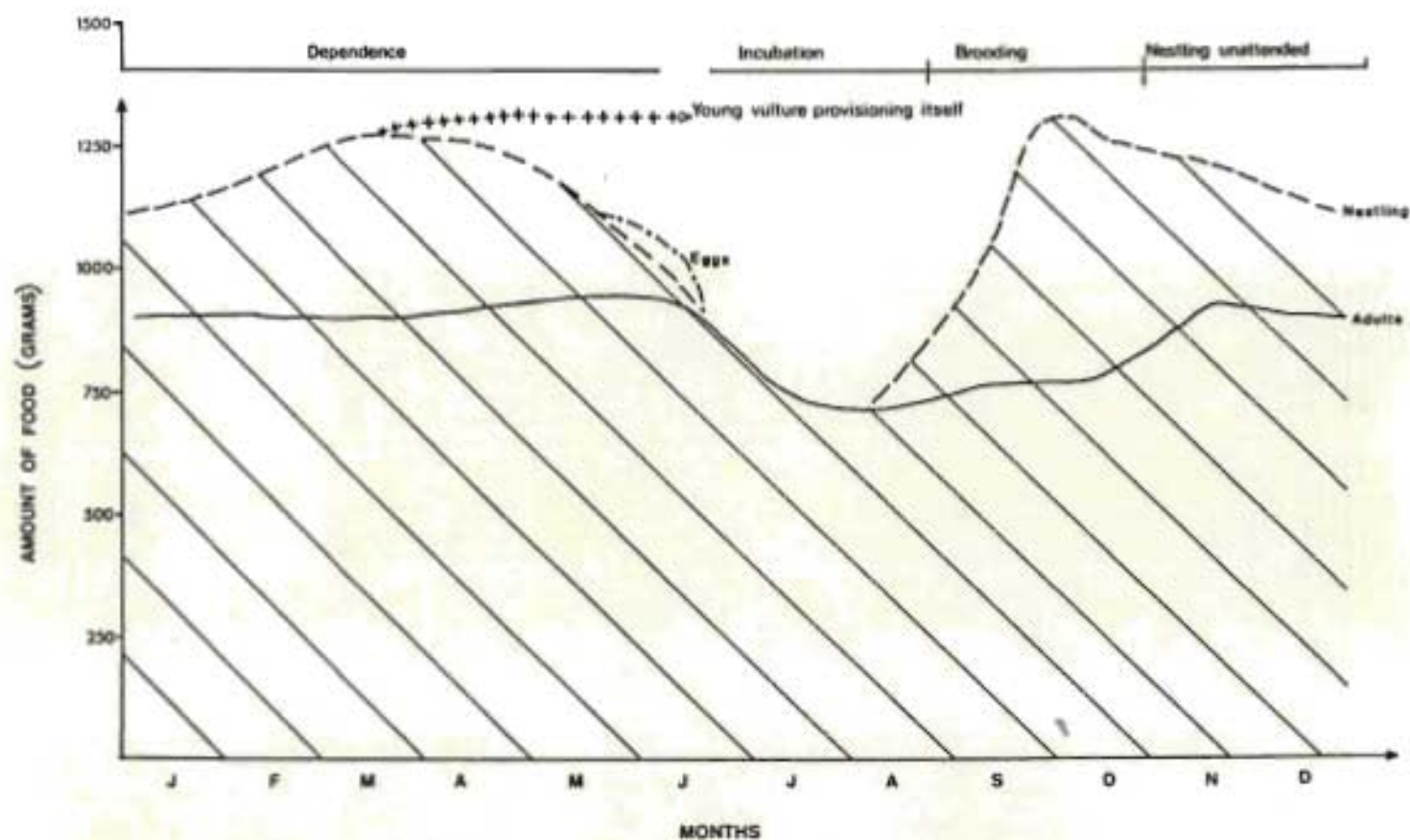
FIIGURE 8.12. Average daily food requirements of a breeding pair of Bearded Vultures for themselves, the laying of a clutch and for their offspring, for each month of the year.

Comparison of food requirements with the monthly food abundance (Figure 8.13) shows that the September to November high demand period coincides closely with the period of greatest food abundance, but the latter slightly precedes the former. The period of food abundance reflects the approximate time of death of the ungulates. Because of their specialised diet of bone, food may be available to Bearded Vultures for a period of weeks or even months after the death of an animal. It would be instructive to investigate the energy content of bones as they age. Bones of a month or more old may be a viable source of food; dried out bones of up to five weeks old were certainly eagerly consumed in preference to fresh bones, but these were not aged in the veld and they were not subjected to the actions of ants and other factors which could strip them of attached flesh and perhaps destroy or denature the marrow. Birds were observed on a number of occasions revisiting the sites of old carcasses and removing bones, some of which had been exposed for between five and six weeks. If these older bones were found to have a reasonable energy content this would mean that the time of food abundance for Bearded Vultures would be considerably extended.

The fact that Bearded Vultures can stockpile food in the nest once the eggs have hatched means that parent birds are able to make optimum use of this period of food abundance by storing food for the time when it is most urgently required. The time of the onset of winter, the severity of the winter and the condition of the veld all
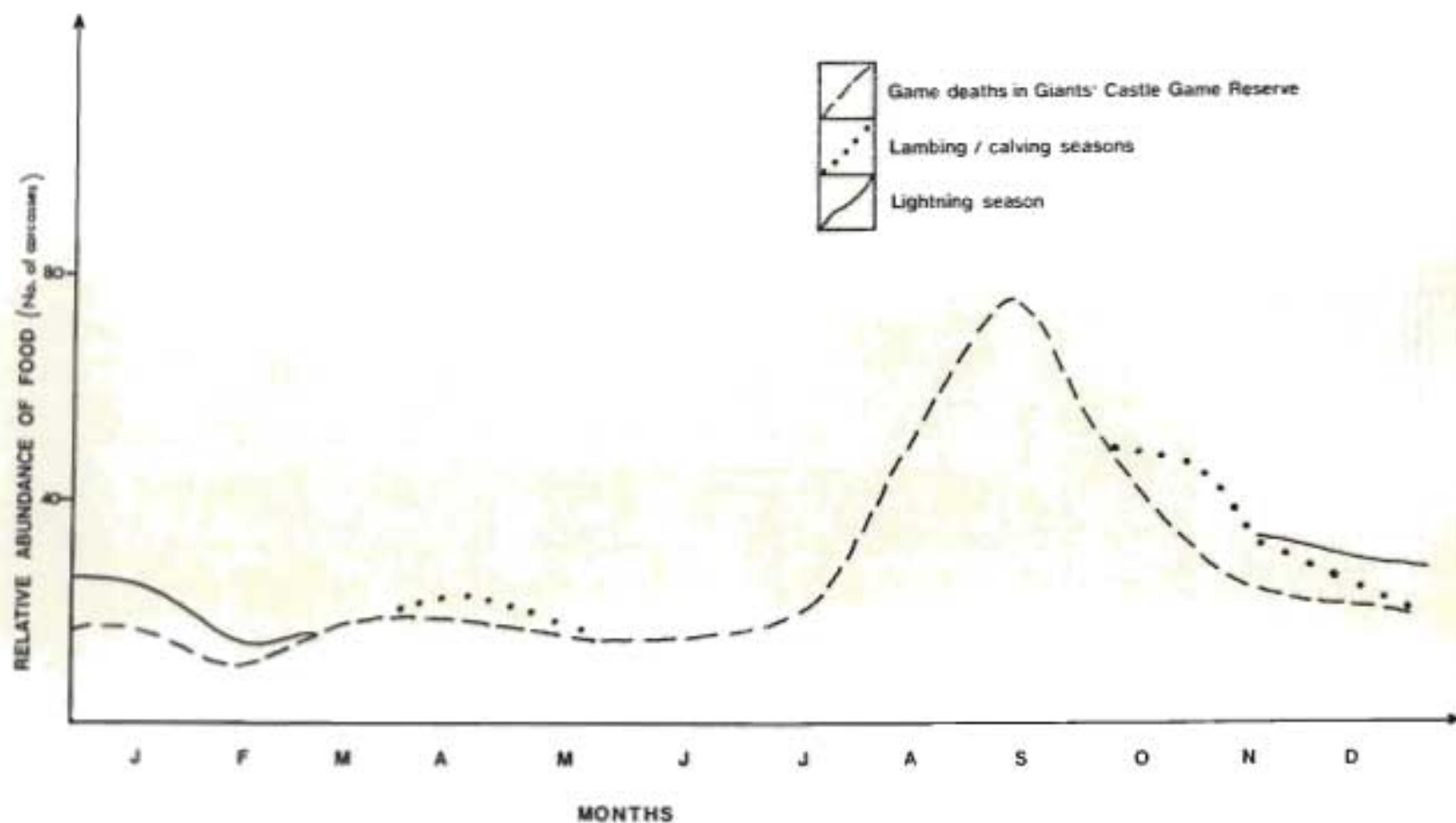
FIGURE 8.13. Relative abundance of carrion in the Natal Drakensberg.

effect the timing and extent of ungulate mortalities. One may therefore expect some variability in the exact timing of the greatest food abundance. By delaying the time of breeding so that the peak demand period occurs slightly later than the period of peak availability, Bearded Vultures ensure that they can make full use of this food supply by (a) storage and (b) protracted use of a food supply which remains viable for perhaps many weeks. If the period of peak demand should precede the period of major food availability (as a result of environmental factors) the nesting success rate that year would be lower because only one parent would be free to forage at a time (and thus restricted to a smaller foraging range) during a high food-requirement stage when little food was available.

Another factor which should be taken into consideration regarding the timing of breeding in relation to the food availability is the type of food required. When the nestling is small it is fed on soft tissue, mainly red meat. This stage of the breeding cycle should therefore coincide closely with the time of highest mortality of the ungulates so that fresh meat is available. If the peak demand and peak abundance periods coincided exactly, the early brooding period would fall at a time when the fresh food supply was low and parent birds might be unable to provide sufficient suitable food for the nestling. By coordinating the time of their requirements of fresh food with the time when this is superabundant, Bearded Vultures also reduce the competition with Cape Vultures for this resource.

During the second period of high daily food requirement (February to April) food is very much less abundant. During this stage, however, parent birds are not under the same constraints as they were during the nestling period. Both parents are free to forage, and the dependent young bird is able to accompany them. This enables the foraging group to cover a considerably larger area in search of food and perhaps forage in areas that were previously outside the range of the birds and where an unexploited food supply might have accumulated (see Chapter 5).

Houston (1976) considered the critical period for Whitebacked and Rüppell's Griffon Vultures to be the time when young birds become independent of their parents, and suggested that the timing of the breeding season is geared to this. In the case of Bearded Vultures, the long dependence period means that young birds become independent shortly before the increase in food abundance. It is possible that the long dependence period has evolved to see the young birds through to the time when food is more abundant. First flight in Cape Vultures takes place from November to December. At the feeding station in the Waterberg Plateau Park, South West Africa/Namibia, young Cape Vultures were first recorded feeding at the provided carcass with other vultures about two months after their first flight (pers. obs.). Mundy (1982) has observed young Cape Vultures up to the age of about three months out of the nest being fed by adults, but not thereafter, while

Robertson (1985) recorded post-fledging dependent periods (for individuals that were known to survive) of 1-7 months. This would indicate that Cape Vultures become independent from January to July, and not consistently at a time when food is most available. In the Natal Drakensberg area, the peak demand period of nesting adults and not the independence of young birds seems to be most important in determining the timing of the breeding season.

Finally, the period of lowest food requirement i.e. the incubation period, is concurrent with the period of lowest food availability. Although the foraging time of the pair is reduced, their energy requirements are low and they have presumably built up a fat reserve. Co-ordinating low energy demand with low food availability may be as important a strategy as the converse.

TABLE 8.1

Bearded Vulture activities recorded away from the nest.

A. IN FLIGHT

    1a. Flapping flight
    1b. Non-flapping flight

    2a. Searching

           (i)   low
           (ii) medium
           (iii) high

    2b. Non-searching

           (i)   escarpment-gliding
           (ii)   thermalling
           (iii) recreational soaring
           (iv)   courtship display
           (v)   play
           (vi)   attack by Bearded Vulture
           (vii) attack on Bearded Vulture
           (viii) carrying nest material
           (ix)   carrying food
           (x)   bone-dropping

B. ON CLIFF FACE

           (i)   feeding
           (ii) preening
           (iii) inactive (resting)

C. ON GROUND

           (i)   feeding
           (ii) drinking
           (iii) preening
           (iv) inactive (resting)

TABLE 8.2

Length of time that Bearded Vultures were recorded in flight, on cliffs and on the ground.

Activity	Number of observations	Time (min)	Average time per observation
A. In flight	688	3547,2	5 min 9 s
B. Cliff face	91	714,8	7 min 51 s
C. On ground	32	154,0	4 min 49 s
Totals	811	4416,0	5 min 27 s

TABLE 8.3

Length of time recorded for each activity identified for Bearde
Vultures, the percentage compositions of the total, section and
subsection respectively.

Activity	Time (min)	Percentage of total	Percentage of section	Percentage subsection
In flight	3547,1	80,3		
Flapping flight	102,6	2,3	2,9	
Non-flapping flight	3444,5	78,0	97,1	
Searching:	1557,3	35,3	43,9	
Low	566,9	12,8		36,4
Medium	894,7	20,3		57,5
High	95,7	2,2		6,1
Non-searching:	1989,8	45,1	56,1	
Escarpment-gliding	705,8	16,0		35,5
Thermalling	471,2	10,7		23,7
Recreational soaring	321,3	7,3		16,1
Courtship display	17,5	0,4		0,9
Play	193,8	4,4		9,7
Attack by B.V.	29,2	0,7		1,5
Attack on B.V.	33,7	0,8		1,7
Carrying nest mat.	3,7	0,1		0,2
Carrying food	141,4	3,2		7,1
Bone-dropping	72,2	1,6		3,6
Non-flight	868,9	19,7		
Cliff face:	714,9	16,2	82,3	
Feeding	198,0	4,5		27,7
Preening	150,0	3,4		21,0
Inactive	366,9	8,3		51,3
On ground:	154,0	3,5	17,7	
Feeding	70,3	1,6		45,6
Drinking	16,9	0,4		11,0
Preening	5,8	0,1		3,8
Inactive	61,0	1,4		39,6

TABLE 8.4.

The time spent by adult, immature and unaged Bearded Vultures in each activity and the percentage contribution of each activity to the total. Differences between adult and immature activities were investigated as described in the text, using the Chi-squared test: * = P < 0,1; ** = P < 0,05.

Activity	Adults		Diff.	Immatures		Unaged		Total
	Time (min)	%		Time (min)	%	Time (min)	%	time (min)
In flight	2319,3	79,3		1037,7	79,8	190,1	100,0	3547,1
Flapping	64,1	2,2		30,9	2,4	7,6	4,0	102,6
Non-flapping	2255,2	77,1		1006,8	77,4	182,5	96,0	3444,5
Searching:	995,0	34,0		485,0	37,3	77,3	40,7	1557,3
Low	360,1	12,3		181,0	13,9	25,8	13,6	566,9
Medium	581,5	19,9		272,3	20,9	40,9	21,5	894,7
High	53,4	1,8		31,7	2,4	10,6	5,6	95,7
Non-searching:	1324,3	45,3		552,7	42,5	112,8	59,3	1989,8
Escrp. gliding	464,1	15,9		189,5	14,6	52,2	27,5	705,8
Thermalling	310,0	10,4		134,6	10,8	26,6	14,0	471,2
Recrt. soaring	220,6	7,5		74,7	5,7	26,0	13,7	321,3
Courtship disp.	17,5	0,6		0,0	0,0	0,0	0,0	17,5
Play	102,0	3,5	**	83,8	6,4	8,0	4,2	193,8
Attack by B.V.	26,2	0,9		3,0	0,2	3,0	0,2	29,2
Attack on B.V.	26,9	0,9		6,8	0,5	0,0	0,0	33,7
Carry nest mat.	3,7	0,1		0,0	0,0	0,0	0,0	3,7
Carry food	107,2	3,7		34,2	2,6	0,0	0,0	141,4
Bone dropping	52,1	1,8		20,1	1,5	0,0	0,0	72,2
Non-flight	605,9	20,7		263,0	20,2	0,0	0,0	686,9
Cliff face:	497,7	17,0		217,2	16,7	0,0	0,0	714,9
Feeding	123,0	4,2	*	75,0	5,8	0,0	0,0	198,0
Preening	109,2	3,7		40,8	3,1	0,0	0,0	150,0
Inactivity	265,5	9,1		101,4	7,8	0,0	0,0	366,9
On ground:	108,2	3,7		45,8	3,5	0,0	0,0	154,0
Feeding	44,3	1,5		26,0	2,0	0,0	0,0	70,3
Drinking	12,7	0,4		4,2	0,3	0,0	0,0	16,9
Preening	5,8	0,2		0,0	0,0	0,0	0,0	5,8
Inactivity	45,4	1,6		15,6	1,2	0,0	0,0	61,0
Totals	2925,2			1300,7		190,1		4416,0

TABLE 8.5

Seasonal activities in Bearded Vultures. Significant differences (Chi-squared test) between the numbers of observations recorded during the breeding and non-breeding seasons are shown: * = P < 0,1; ** = P < 0,001.

Activity	Season					Totals Time (min)
	Non-breeding (Jan-May)		Diff.	Breeding (Jun-Dec)		
	Time (min)	%		Time (min)	%	
Searching	367,4	31,8	*	1189,9	36,9	1557,3
Escrp. gliding	190,2	16,5		515,6	15,8	705,8
Thermalling	209,4	18,1	**	261,8	8,0	471,2
Recrt. soaring	66,9	5,8		254,4	7,8	321,3
Courtship disp.	6,7	0,6		10,8	0,3	17,5
Play	66,8	5,8	*	127,0	3,9	193,8
Attack by B.V.	5,1	0,4		24,1	0,7	29,2
Attack on B.V.	3,2	0,3		30,5	0,9	33,7
Carry nest mat.	0,0	0,0		3,7	0,1	3,7
Carry food	29,8	2,6		111,6	3,4	141,4
Bone-dropping	11,0	1,0		61,2	1,9	72,2
Feeding	63,4	5,5		204,9	6,3	268,3
Preening	25,0	2,2		130,8	4,0	155,8
Drinking	8,1	0,7		8,8	0,3	16,9
Inactivity	102,0	8,8		325,9	10,0	427,9
Totals	1155,0	100,1		3261,0	99,9	4416,0

TABLE 8.6

Percentage of time spent foraging, carrying food and playing during different stages of the breeding season.

Activity	Stage of the breeding season		
	Incubation	Close-brooding	Nestling unattended
Foraging	34	36	39
Carrying food	2	3	5
Play	2	4	5

TABLE 8.7

Activity and energy budgets for Bearded Vultures during the non-breeding season.

Activity	Activity h/24 h	Energy costs	Energy expended (kJ)
A. Non-flight			
Inactive - night	10,5	BM_n	469,7
Inactive - day	1,2	BM_d	66,1
Preening	0,3	BM_d x 1,3	21,3
Feeding	0,7	BM_d x 2,5	96,3
Bathing/drinking	0,1	BM_d x 2,0	10,9
SUBTOTAL	12,8		664,3
B. Flying			
*Flapping	0,3	BM_d x 12	198,0
Foraging - low	1,4	Gliding + BM_d x 1,3 x 1,6	201,3
Foraging - medium	2,3	Gliding + BM_d x 1,3 x 1,4	297,3
Foraging - high	0,6	Gliding + BM_d x 1,3 x 1,2	69,1
Bone-dropping	0,1	Gliding + BM_d x 2,0	13,8
Escarp. gliding	2,2	Gliding + BM_d x 1,2	209,3
Recreat. soaring	0,8	Gliding + BM_d x 1,2	76,2
Thermalling	2,4	Gliding + BM_d x 1,4	254,9
Courtship display	0,1	Gliding + BM_d x 2,4	16,3
Play	0,8	Gliding + BM_d x 2,4	128,9
Attack on/by	0,1	Gliding + BM_d x 2,4	16,3
Carry food/nest mat.	0,4	Gliding + BM_d x 1,4	42,7
SUBTOTAL	11,2		1524,1
GRAND TOTAL - DEB	24,0		2188,4

* Flapping flight was concurrent with other flight activities.

TABLE 8.8

Activities and energy budgets for Bearded Vultures during the incubation period (July & August) and the close-brooding (September & October) and nestling unattended (November and December) stages of the nestling period. (* Flapping flight was concurrent with other flight activities.)

Activity	Energetic cost	Period and stage of the breeding season					
		Incubation period		Close-brooding		Nestling unattended	
		Time (h)	Energy (kJ)	Time (h)	Energy (kJ)	Time (h)	Energy (kJ)
Non-flight							
Inactive: night	BM_n	10,50	469,7	10,50	469,7	10,50	469,7
Inactive: day	BM_d	6,75	371,7	5,65	311,0	1,10	60,7
Preening	$BM_d \times 1,3$	0,45	32,2	0,40	28,5	0,60	43,1
Feeding self	$BM_d \times 2,5$	0,40	55,3	0,55	75,8	0,90	123,9
Feeding nestling	$BM_d \times 2,5$	0,00	0,0	0,50	68,7	0,00	0,0
Bathing/drinking	$BM_d \times 2,0$	0,05	5,4	0,00	0,0	0,10	10,9
Nest shading	$BM_d \times 1,2$	0,30	19,7	1,10	72,8	0,00	0,0
Rolling eggs	$BM_d \times 1,4$	0,20	15,5	0,00	0,0	0,00	0,0
Nest maintenance	$BM_d \times 1,4$	0,10	7,5	0,15	11,7	0,00	0,0
Subtotal		18,75	977,0	18,85	1038,2	13,20	708,3
Flight							
*Flapping	$BM_d \times 12$	0,15	99,2	0,15	99,2	0,30	198,0
Foraging low	Gliding + $BM_d \times 2,08$	0,85	121,8	0,95	136,0	1,90	272,9
Foraging medium	Gliding + $BM_d \times 1,82$	1,25	161,6	1,45	187,5	3,10	401,0
Foraging high	Gliding + $BM_d \times 1,56$	0,10	11,7	0,05	5,4	0,20	23,0
Bone-dropping	Gliding + $BM_d \times 2,0$	0,05	6,7	0,15	20,5	0,30	41,9
Escarpment-gliding	Gliding + $BM_d \times 1,2$	1,25	118,9	1,25	118,9	1,70	161,6
Recreat. soaring	Gliding + $BM_d \times 1,2$	0,60	57,3	0,55	52,3	1,10	105,1
Thermalling	Gliding + $BM_d \times 1,4$	0,65	69,1	0,35	36,8	1,10	117,2
Courtship display	Gliding + $BM_d \times 2,4$	0,00	0,0	0,00	0,0	0,00	0,0
Play	Gliding + $BM_d \times 2,4$	0,15	22,6	0,30	48,6	0,70	113,0
Attack on/by	Gliding + $BM_d \times 2,4$	0,35	56,1	0,05	8,0	0,10	16,3
Carry food/nest mat.	Gliding + $BM_d \times 1,4$	0,05	5,0	0,20	21,3	0,70	74,5
Subtotal		5,30	730,0	5,30	734,5	10,90	1524,5
Total		24,05	1707,0	24,15	1772,7	24,10	2232,8

APPENDIX 8.1

King & Farner (1961) give an equation for basal metabolic rate (kcal/h - to convert kcal to kJ multiply by 4,186) for all birds weighing more than 0,1 kg:

$$\text{Log } M = \log 3,1 + 0,744 \log W \pm 0,074$$

where W is the bird's weight (kg); W = 5,490 kg for Bearded Vultures captured in Giant's Castle Game Reserve. This equation gives a BMR for Bearded Vultures of 46,1 kJ/h.

Lasiewski & Dawson (1967) derive an equation for BMR in non-passerines:

$$\text{Log}_{10} R = 1,894 + 0,723 \log_{10} M$$

where M is the bird's mass (= weight in this case). This equation gives a BMR for Bearded Vultures of 46,8 kJ/h.

Aschoff & Pohl (1970) give two equations for BMR, one for diurnal (BM_d) and one for nocturnal (BM_n) activity:

$$BM_d = 0,5928 W^{0,729}$$

$$BM_n = 0,4616 W^{0,734}$$

giving figures for Bearded Vultures of 55,0 kJ/h and 44,7 kJ/h respectively.

Tarboton (1978) used a BMR intermediate between those given by Aschoff & Pohl (1970):

$$BM_t = 0,5410 W^{0,734}$$

giving a figure of 52,5 kJ/h for Bearded Vultures.

The cost of soaring flight was determined by Pennycuick
(1972), working on Whitebacked Vultures, as the BMR plus the
force exerted by the pectoralis muscles to hold the wings in
a horizontal position. The pectoralis muscles of all soaring
birds consist of a large superficial portion and a smaller
deep portion. This division does not occur in non-soaring
species. The deep portion is probably a specialised tonic
muscle, adapted for holding the wing down with a minimum
expenditure of energy. Pennycuick (1972) derived an equation
for the power (P) consumed by each tonic muscle (in watts):

$$P = \frac{K1F}{t}$$

where K is a dimensionless constant averaging about 0,05;
l is the length of the muscle in metres - in the Whitebacked
Vulture he found this to be about 0,10 m, and I assumed it
to be the same in the Bearded Vulture; F is the force
exerted in Newtons; and t is the intrinsic speed of the
tonic muscle in seconds - taken by Pennycuick (1972) to be
0,5 s and assumed to be the same in the Bearded Vulture.
F can be deduced from the dimensions of the bird. In a
Whitebacked Vulture the moment arm of the deep portion of
the pectoralis about the centre of rotation of the head of
the humerus was found to be about 0,040 m, the figure
adopted for the Bearded Vulture calculation. Each wing has
to support a force of 27 N (half the Bearded Vulture's
weight) at a distance of about 0,6 m from the shoulder joint
(mean wing length of 1,191 m). Therefore the force exerted

by the deep pectoralis muscle is:

$$27 \times \frac{0,6}{0,04} = 405 \text{ N}$$

Therefore, $P = 2^{\left(\frac{0,05 \times 0,1 \times 405}{0,5}\right)} = 8,1 \text{ W}$

To convert watts to kJ/h, multiply by 3,604;

P = 29,2 kJ/h.

The cost of powered flight (flapping) is directly proportional to the weight of the bird, but may differ from species to species depending on different aerodynamic qualities, flapping speed, etc. Kendeigh et al. (1977) give a regression equation:

$$\text{Mh} = 0,3157 \text{ W0,6980} \pm 1,159$$

in which the exponents of weight come close to the predicted values and agree closely with those for BMR on weight, and energy expenditure for powered flight being 12,1 times higher (than BMR).

DISTRIBUTION, STATUS AND POPULATION DYNAMICS

9.1 INTRODUCTION

This chapter investigates three related aspects of the biology of the Bearded Vulture in southern Africa; (a) its distribution, (b) its status and (c) its population dynamics.

The distribution of the Bearded Vulture in southern Africa has been fairly accurately, if somewhat coarsely, mapped by Brown et al. (1982), Steyn (1982) and Maclean (1985). Detailed temporal distributions are presented by Boshoff et al. (1978) and Brooke (1984), but because of lack of data, particularly from Lesotho, the current maps do not reflect the distribution of the species accurately and no attempt has previously been made to map their breeding distribution. Regional distributions are available for the provinces of Natal (Cyrus & Robson 1980) and the Cape (Boshoff et al. 1983), both including records up to the end of 1979. The Transvaal has also been extensively surveyed (Tarboton & Allan 1984) but no recent records were obtained and the species is considered never to have been resident in that province (A.C. Kemp and W. Tarboton in litt.).

The status of the Bearded Vulture in southern Africa has been variously described as "extremely rare", "almost extinct ... less than 20 pairs left", "rare ... almost disappeared with the advance of civilization", etc. (e.g.

Barnes et al. 1962; Anon. 1965; McLachlan & Liversidge 1978). The first reasonable assessment of its status was made by Rudebeck (1956) who pointed out that Bearded Vultures occurred regularly in the high mountains of Lesotho, the Cape Province and Natal. After a 10-day trip in the Lesotho highlands Brown (1977) estimated a population of about 120 pairs with an additional 60 immature birds and Steyn (1982) obtained the same result (i.e. about 300 birds) calculated from road counts carried out by different observers in Lesotho.

No reliable information is available on the population dynamics of the Bearded Vulture; the only attempt at determining its survival rate and longevity in the wild is that of Brown (1977) for the Ethiopian population, and these parameters were extrapolated from the theoretical mortality rates for the Bateleur (Brown & Cade 1972).

9.2 METHODS

The breeding distribution of the Bearded Vulture was determined by locating active nest sites (a) by direct observation, both from the ground and from the air, (b) from reports by Nature Conservation and Forestry staff and other interested people and (c) from a mail questionnaire survey to farmers adjacent to Lesotho in the provinces of Natal, the Cape and the Orange Free State. All nest sites reported by farmers were checked and only those sites for which breeding was confirmed were mapped. Nesting densities for different areas were determined by systematically checking

all suitable cliffs during the early stages of the breeding season, but after all pairs should have started incubating, in late July and August. When searching for nests from an aircraft, a direct view into potholes could be obtained. When viewed from the ground the nest itself was usually out of sight; breeding was confirmed when parent birds were seen relieving each other at the nest. This required that sections of cliffs be watched for up to three days or until a nest site was confirmed.

The "occurrence" distribution (sensu Mundy 1982) was obtained from the same sources as the breeding distribution, and both were plotted on a ¼° (15 min) by ¼° grid. Each locus is termed hereafter a ¼° square.

Road counts of Bearded Vultures were made in Lesotho and the Northeastern Cape Province. Average speeds of travelling were less than 20 km/h. Bird numbers were recorded per distance travelled as well as per time and all birds were aged according to the criteria given in Chapter 3. As the habitat and topography were comparable in all regions within the range of the Bearded Vulture visited, the "visibility" of the birds was considered to be similar throughout.

9.3   RESULTS

9.3.1 Distribution

The post-1980 breeding distribution of the Bearded Vulture in southern Africa (Figure 9.1) covers an area of about 34 000 km^2, although not all the habitat within this
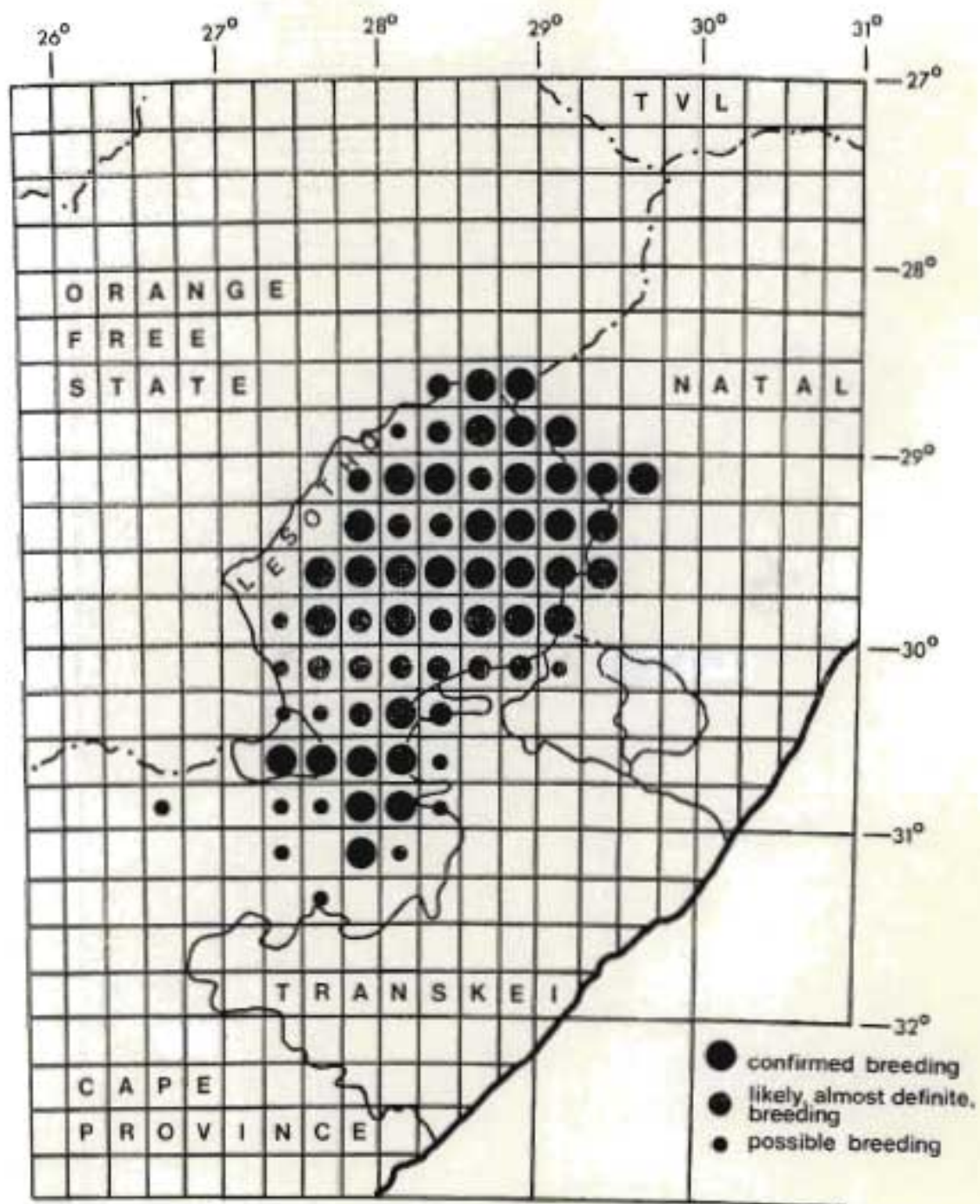
FIGURE 9.1. The post-1980 breeding distribution of the Bearded Vulture in southern Africa, mapped per ½° square.

area is equally suitable. From 1-5 breeding pairs were confirmed from 37 $\frac{1}{4}°$ squares and it is believed to be likely that a further 16 squares contain breeding birds (as judged by their localities and the presence of suitable habitat) but were not visited during the study to confirm this. A number of peripheral squares may support breeding birds but no definite information exists on these areas.

Breeding is confined to highland areas over 1800 m above sea level and most nests were found in the basalt rock formation above 2100 m. Nesting requirements are discussed in Chapter 7. The highlands of Lesotho and adjacent areas provide ample suitable nesting sites, on cliffs along river courses, on mountain peaks or on escarpments. Availability of nest sites was not considered a limiting factor to the size of the Bearded Vulture population in southern Africa (Brown et al. in press).

The post-1980 occurrence distribution of Bearded Vultures in southern Africa was obtained by two different methods: (a) from my observations, augmented by records supplied by reliable colleagues, friends and staff of Forestry and Nature Conservation agencies (Figure 9.2) and (b) from the mailed questionnaire survey which obtained information from 1612 farmers. The distribution of farmers returning questionnaires is shown in Figure 9.3 and is restricted exclusively to the commercial farming areas. An attempt was made to obtain information from Lesotho and the independent homeland of Transkei. Of 48 questionnaires sent to the principals of schools in these areas, one was
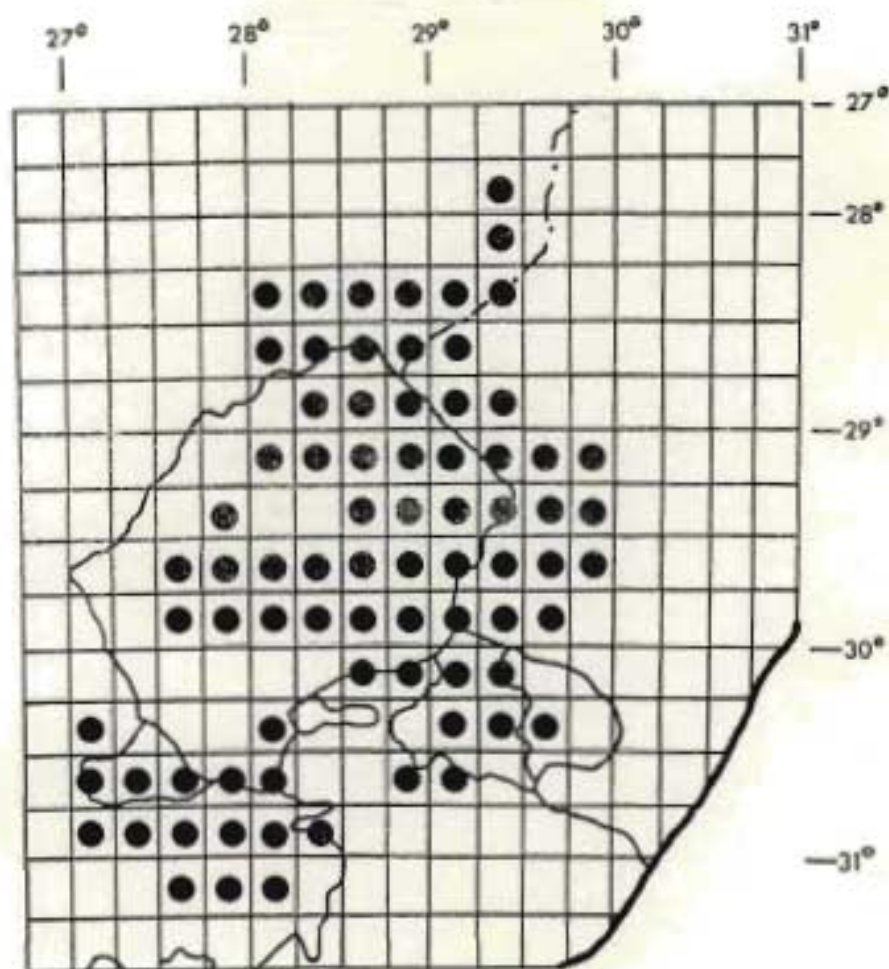
FIGURE 9.2. The post-1980 distribution of the Bearded Vulture
in southern Africa from my sightings augmented by
those of reliable colleagues, friends and staff
of Forestry and Nature Conservation agencies.
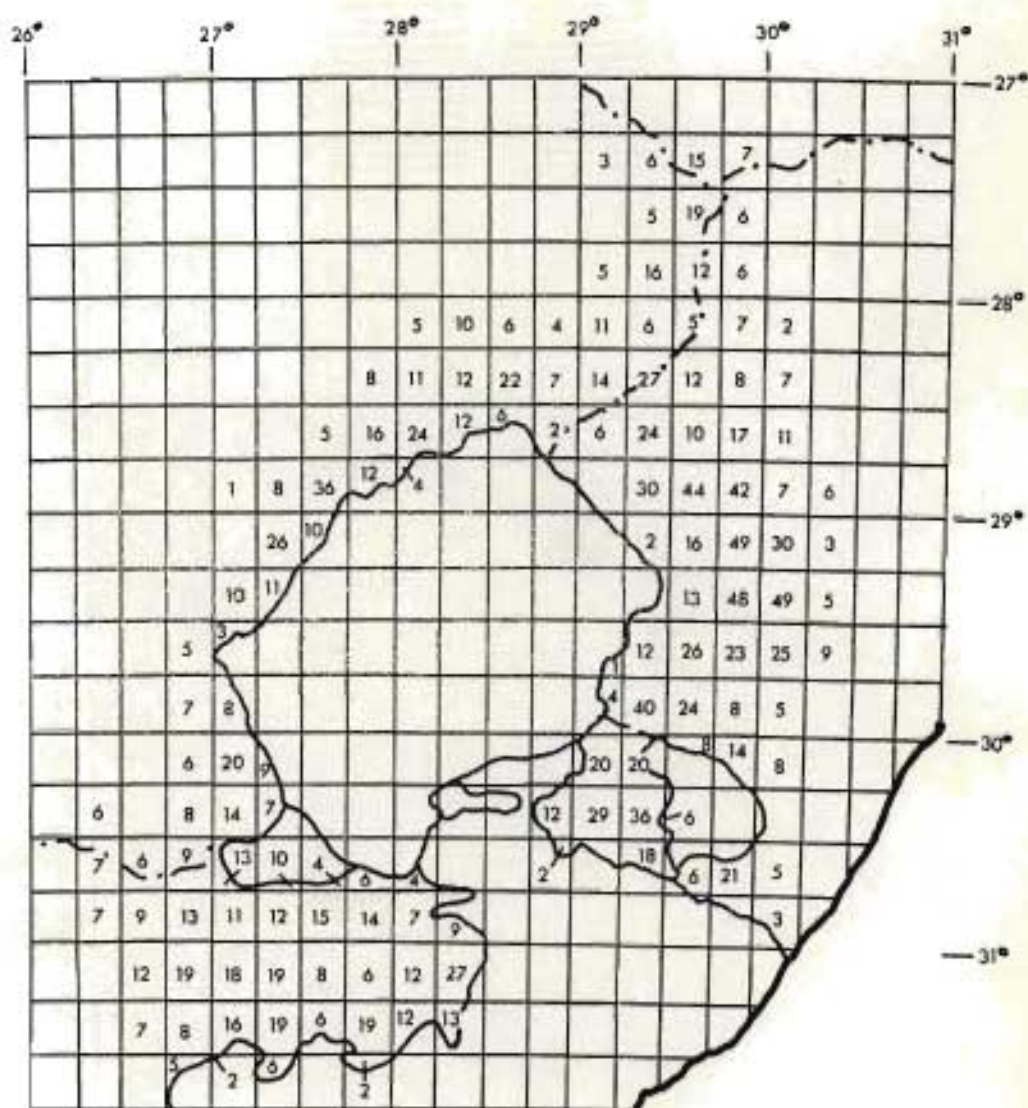
FIGURE 9.3. Number of farmers who returned completed questionnaire forms per $\frac{1}{4}°$ square.

returned. The presence or absence of Bearded Vultures per square was plotted from information provided via the questionnaires (Figure 9.4) and clearly defines the boundary of their range in all areas except the Transkei. In addition, a coarse assessment of their relative abundance on farmlands was obtained (Figure 9.5) based on the percentage frequency with which farmers in a particular $\frac{1}{4}^{o}$ square saw the birds (i.e. daily, weekly, monthly, yearly or never). The frequency of sightings reported in the questionnaires also helped in assessing areas for possible nest sites and identifying areas worth visiting. The frequency of sightings of Bearded Vultures in many of the areas surveyed by the questionnaire was so low (one or two sightings per month and fewer) that, without involving the residents in those areas, no other survey method would have been feasible. It is clear that the farming areas where birds were most frequently seen were along the northern Drakensberg on the Natal/Orange Free State border and along the southern Drakensberg in the Northeastern Cape.

The composite picture of the breeding and occurrence distributions is given in Figure 9.6. The total distribution covers an area almost three times the size of the breeding distribution. The breeding distribution closely coincides with those areas in which Bearded Vultures were seen regularly and at least weekly. Outside the breeding area and in the area of occurrence (i.e. foraging areas only) birds were seen usually monthly or less often. The distribution of sightings is not uniformly spread around the breeding
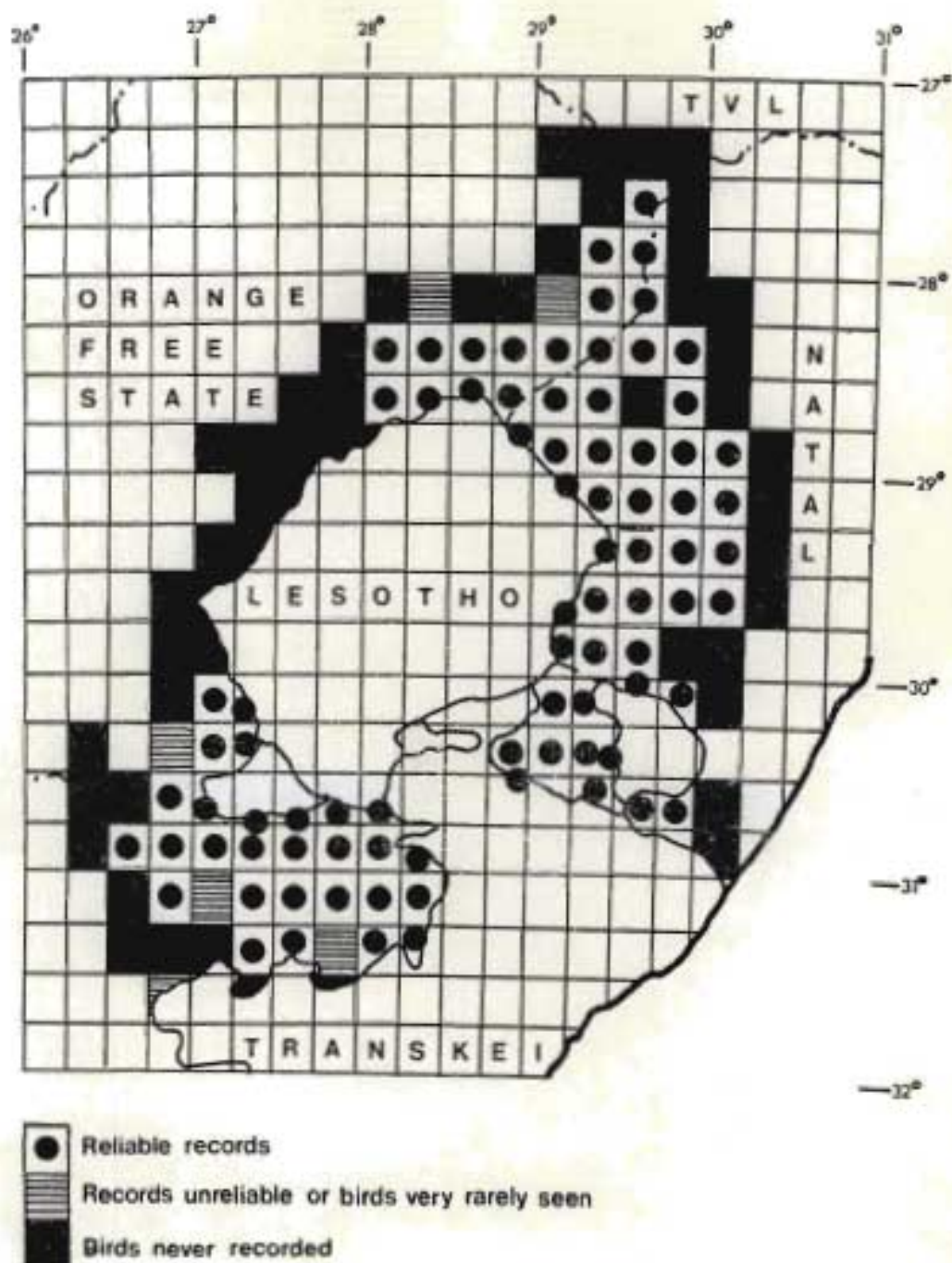
FIGURE 9.4. Post-1980 distribution of Bearded Vultures in areas adjacent to Lesotho, determined from the questionnaire survey to commercial farmers and staff of the Natal Parks Board and Department of Forestry.
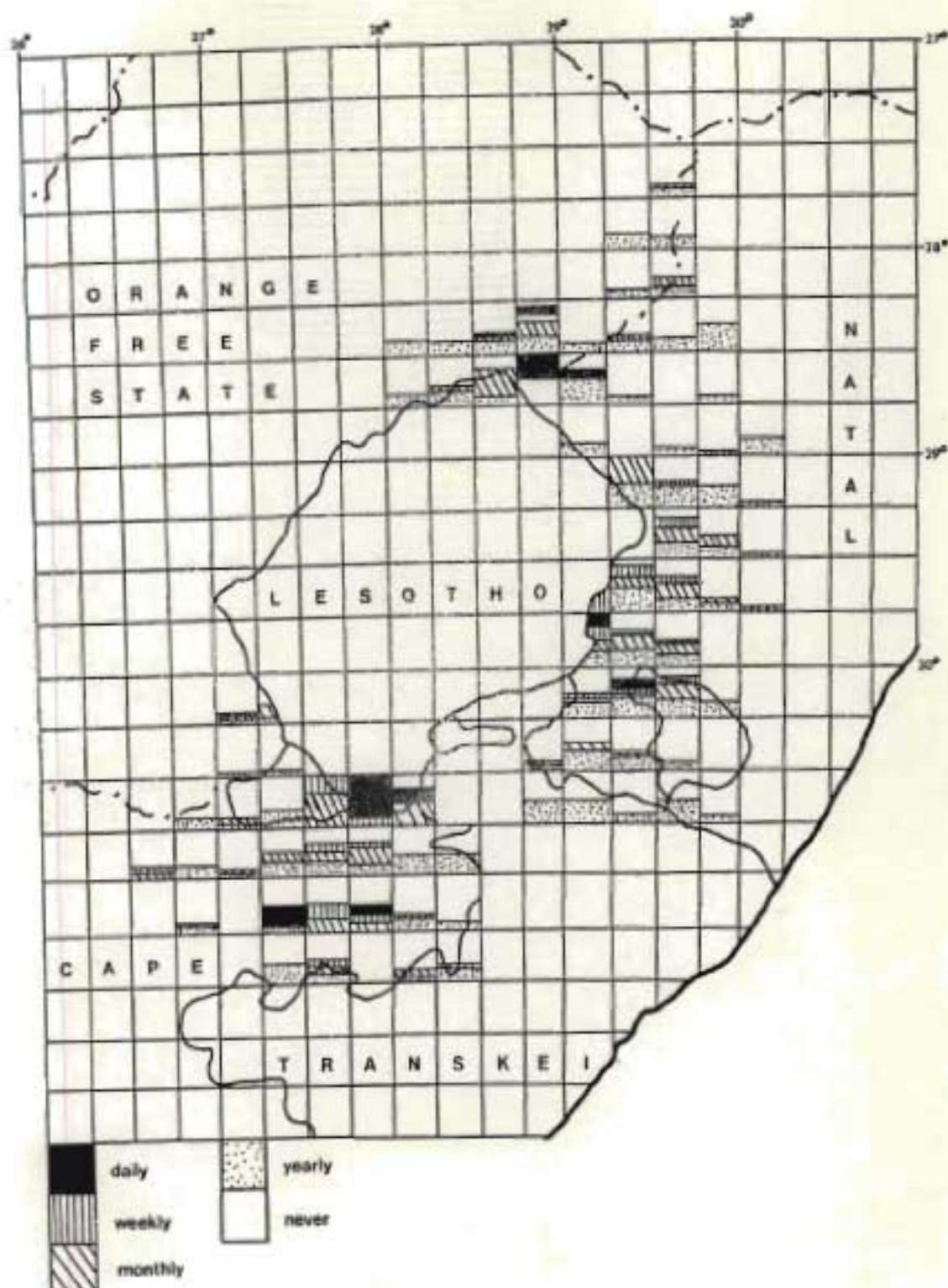
FIGURE 9.5. Frequency of sightings of Bearded Vultures by farmers as a percentage of all sightings per ¼° square.
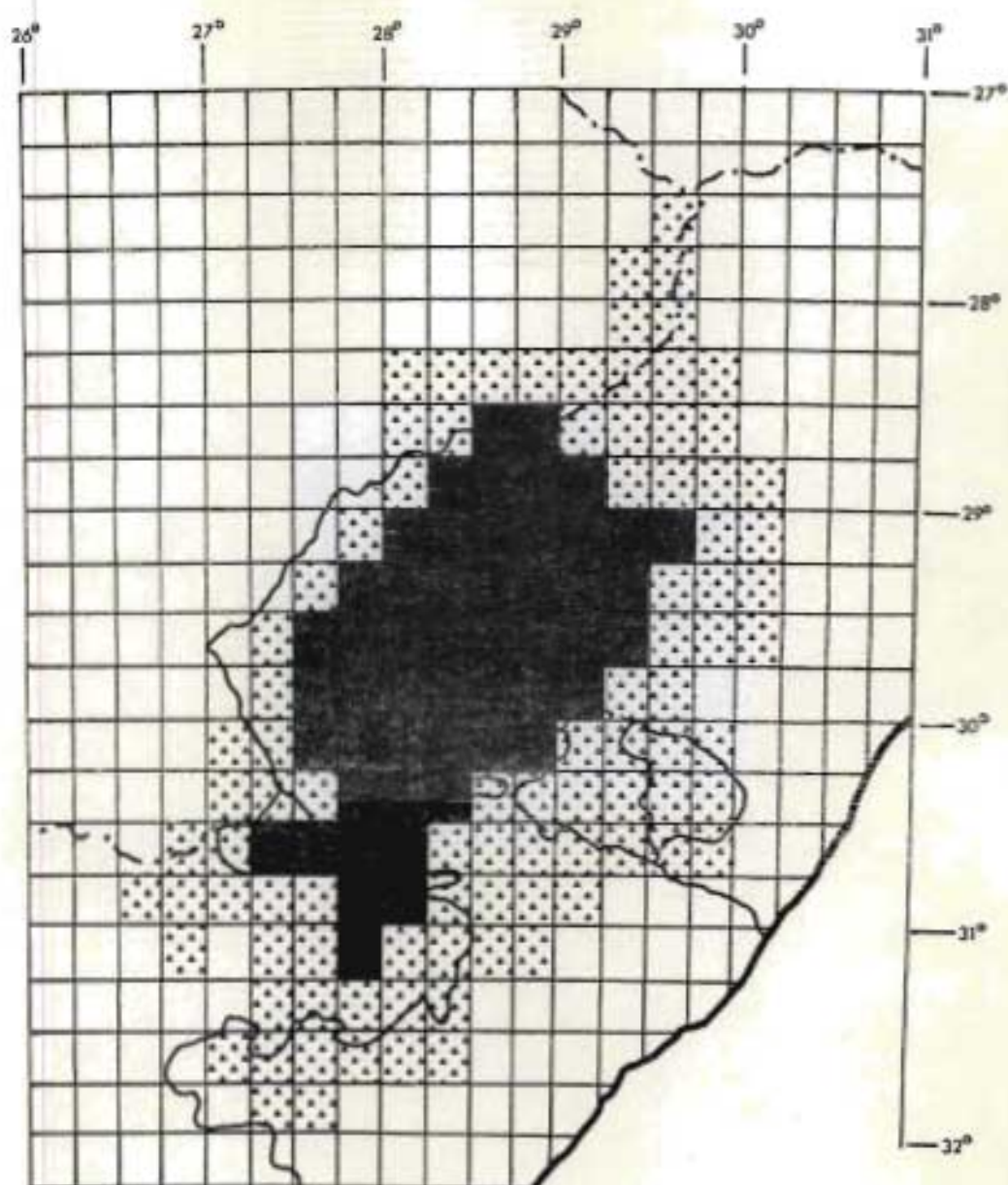
Breeding distribution of the Bearded Vulture, closely corresponding to the area in which the birds can be seen weekly or more often

Occurrence distribution of the Bearded Vulture, closely corresponding to the area in which birds can be seen monthly or less often

FIGURE 9.6. The overall post-1980 breeding and occurrence distributions of the Bearded Vulture in southern Africa.

distribution. On the western side of the species' range along the Lesotho-Orange Free State border the foraging range is much smaller than in other areas. This region is flat with few topographic features to provide the birds with slope lift. To the north, south and southeast of their range the birds move furthest from their nesting areas. These regions are dominated by large mountain ranges, long ridges and escarpments, i.e. in the north the birds follow the Drakensberg escarpment almost to the Transvaal, in the southeast they follow the rugged Drakensberg outliers into the Transkei and in the south they extend into the mountains of the southern Drakensberg, the Witteberge and the Stormberge.

9.3.2 Status

The abundance of Bearded Vultures relative to other resident birds of prey and Whitenecked Ravens is shown for eight regions within the species' range in southern Africa (Figure 9.7). Cape Vultures were most numerous, making up on average 40% (range 25-63%) of total "raptor" (including raven) numbers. Bearded Vultures, Jackal Buzzards and Whitenecked Ravens were recorded as being about equally common (12,4%, 12,9% and 13,4% respectively) followed by Rock Kestrels (7,3%) and Black Eagles (5,4%). Other species constituted less than 3% of all raptors and ravens seen.

Bearded Vultures were comparatively well represented along the Drakensberg escarpment (17,4%), in Giant's Castle Game Reserve (14,5%) and in the Lesotho highlands (12,5%).

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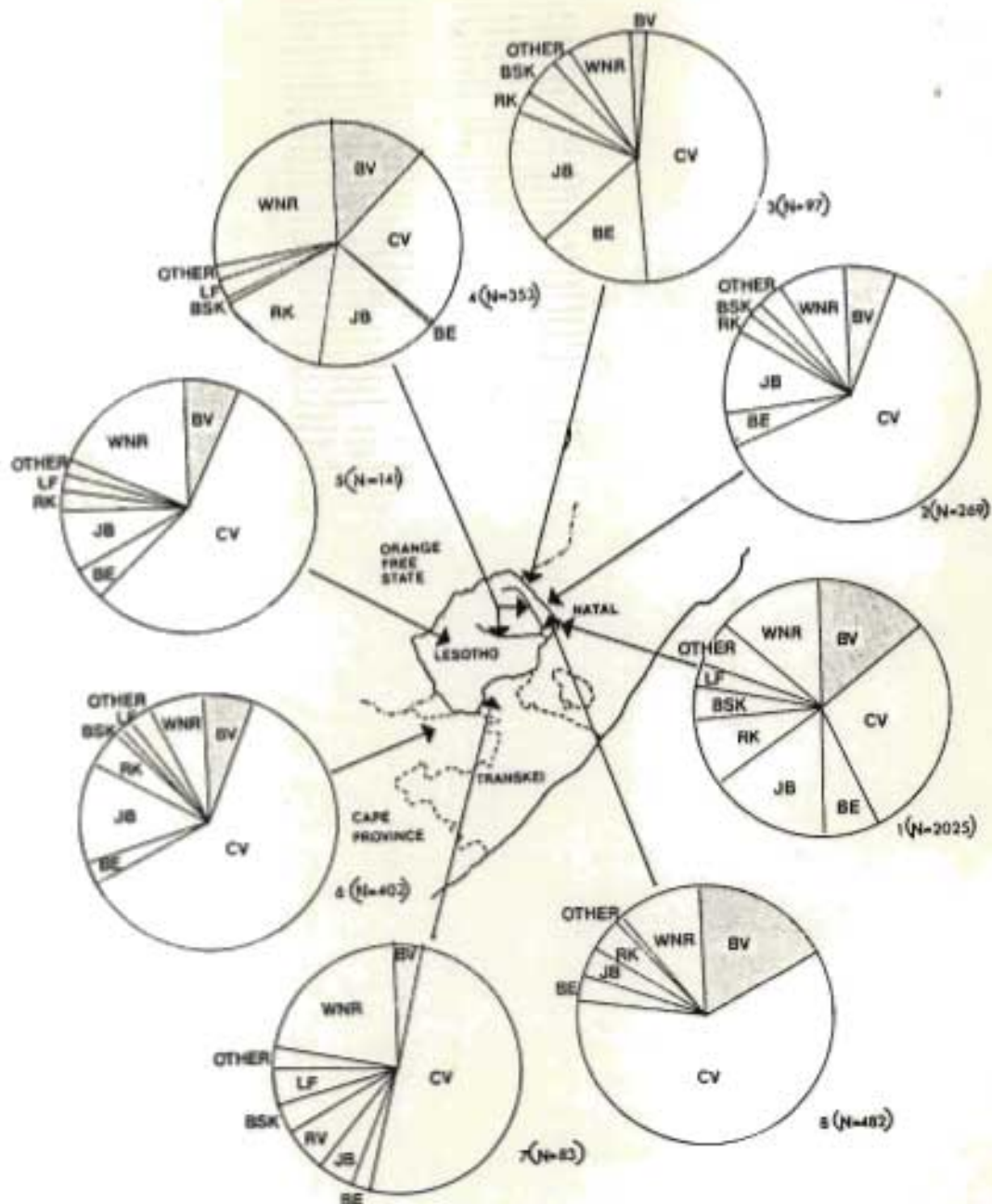
FIGURE 9.7. Relative abundance of non-migrant birds of prey and Whitenecked Ravens in eight regions within the range of Bearded Vultures in southern Africa.

Species abbreviations are as follows: BV = Bearded Vulture, CV = Cape Vulture, BE = Black Eagle, JB = Jackal Buzzard, BSK = Blackshouldered Kite, RK = Rock Kestrel, LF = Lanner Falcon and WNR = Whitenecked Raven. "Other" include Secretary Bird, Martial Eagle, Booted Eagle, Mountain Buzzard, African Goshawk, Redbreasted Sparrowhawk, Black Harrier, Marsh Harrier, Gymnogene and Peregrine Falcon.
Regions are: 1 = Giant's Castle Game Reserve, 2 = Cathedral Peak Forestry Reserve, 3 = Royal Natal National Park, 4 = Road counts in Lesotho highlands, 5 = Roma area, Lesotho, 6 = Northeastern Cape, 7 = Ongeluksnek area, Transkei and 8 = top of Drakensberg escarpment, mainly between Sani Pass and eNjesuthi.

Whitenecked Ravens were most common in Lesotho and the Transkei where subsistence farming is practised. Black Eagles were uncommon in these areas, possibly because the Rock Hyrax, their main food source, is hunted heavily by the local people. While it is possible to extrapolate the numbers of the different raptor species from their percentage compositions, assuming that the population size of one of the species is known, this exercise is of dubious value as there are so many variables, e.g. some species are much more "visible" than others, being larger, foraging at lower altitudes, being on the wing for longer periods, etc.

The population estimate for Bearded Vultures in southern Africa was calculated mainly from nesting densities. Their breeding range was divided into 12 regions (Figure 9.8) based on similarity of habitat, land usage, rainfall, etc. and the population per region was calculated or estimated. In seven regions where nearest neighbours were found with certainty the numbers of active nest sites were determined and nesting densities calculated, either linearly (along the Drakensberg escarpment) or per area (Table 9.1). The number of nests (nearest neighbours) found per region varied from 2-9 (mean = 4,6). Nests were located early in the breeding season but after incubation had begun, from early July to August, and the valid assumption was made that all adults bred each year (see Chapter 7). The only important region from which no information on breeding density was obtained was for the largely inaccessible Maluti highlands, to the west of the Orange River. The Drakensberg

FIGURE 9.8. The 12 regions into which the breeding range of the
Bearded Vulture in southern Africa was divided for
the calculation of the population size.

Regions are as follows: 1 = Natal Drakensberg
escarpment, 2 = Natal Little Berg, 3 = Lesotho
Drakensberg highlands, 4 = Lesotho Maluti highlands,
5 = Maluti escarpment, Qwa Qwa, 6 = Maluti outliers,
Qwa Qwa, 7 = Maluti & outliers, Orange Free State,
8 = Maluti & Drakensberg outliers, Lesotho, 9 =
Drakensberg escarpment, Transkei, 10 = Little Berg,
Transkei, 11 = Drakensberg escarpment, Cape Province,
12 = Northeastern Cape Province.

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and Maluti highlands were separated for population estimates because of the lower rainfall obtained in the Maluti range. An estimation of the population density in the Maluti mountains was obtained from road-count data (Table 9.2). The number of adult Bearded Vultures seen per 10 h and per 100 km was plotted against the mean inter-nest distances for the Drakensberg range of the Lesotho highlands and for the Northeastern Cape (Figure 9.9). The frequency of sightings in the Maluti range can be obtained from the graph, both for time and for distance travelled, giving inter-nest distances of 15,6 km and 15,0 km respectively. The mean figure for the inter-nest distance of 15,3 km was used to calculate the approximate population size in the Maluti highlands.

The total estimate of the adult Bearded Vulture population in southern Africa was 203 pairs (Table 9.3). Of this, about 122 pairs bred in Lesotho, 42 in Natal (37 of these on the Drakensberg escarpment on the Natal side of the Natal-Lesotho border), 17 pairs in the Transkei, 16 in the Northeastern Cape Province, four in QwaQwa and two in the Orange Free State. In addition, using an average adult:young-bird ratio of 1:0,55 (see below) the total southern African population is calculated as being about 406 adult birds and 225 young birds of all age classes, giving an estimated total of 631 birds.
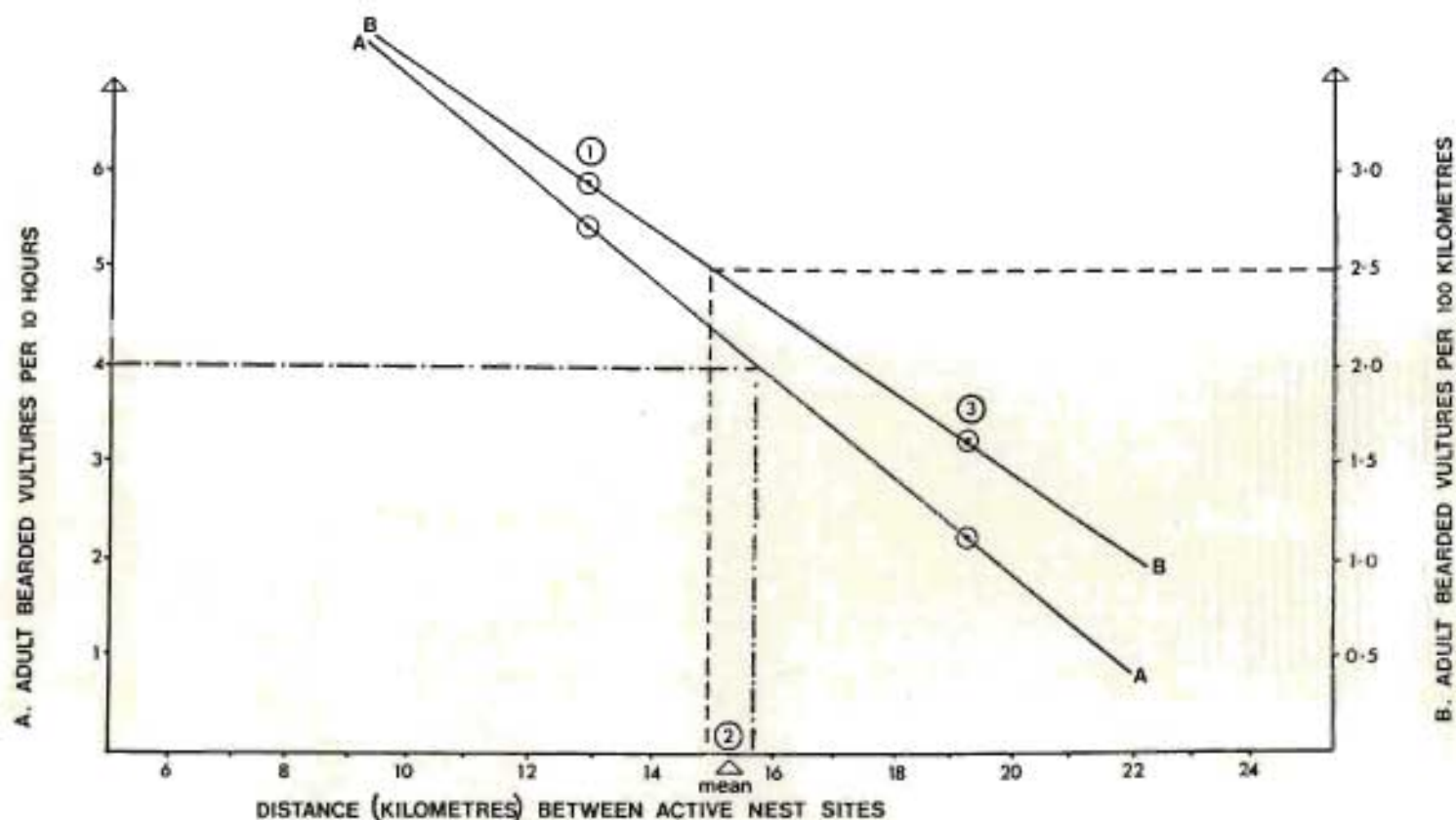
FIGURE 9.9. The relationship between Bearded Vulture nesting density and the frequency with which birds were seen during road counts (a) per 10 hours and (b) per 100 km for 1. the Lesotho highlands, Drakensberg range and 3. the Northeastern Cape Province. From road counts of Bearded Vultures in the Maluti highlands of Lesotho, the nesting density was obtained from the graph (2).

9.3.3 Population Dynamics

Bearded Vultures are K-selected (Pianka 1970) and acquire adult plumage only after five years (Delibes et al. 1984; this study, Chapter 3). In southern Africa adult pairs attempt to breed each year. It would appear that unpaired adult birds are few because a subadult bird was recruited to the breeding population during the course of this study (Chapter 7). Breeding success, calculated from the commencement of nest building or repair to the nestling's first flight averaged 90% (this study, Chapter 9; Hiraldo et al. 1979;). It is assumed that breeding normally starts in the year that adult plumage is first acquired, although it is known that it is physiologically possible for birds to breed earlier. Adult birds are able to survive to well over 40 years of age in captivity (Hiraldo et al. 1979) but no information on longevity under natural conditions is available.

The population structure of the Bearded Vulture in different regions of southern Africa is given in Table 9.4. At very close quarters juvenile and immature birds can be distinguished, but this was possible in less than 10% of young bird sightings, so these two age classes were grouped. Subadult birds could usually be identified quite readily (for criteria see Chapter 3), but subadults just prior to acquiring full adult plumage had very pale heads and could easily be misidentified as adults from a distance. In the Drakensberg escarpment area 73% of the identified Bearded Vultures recorded were adults and 27% were young

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birds of all stages, subadults comprising 2,3% of these. Counts along roadways in Lesotho and in the Northeastern Cape in the Barkly East and Lady Grey areas gave very different population structures. Young birds in these areas were relatively far more numerous, accounting for 42% and 48% of all Bearded Vultures respectively.

Assuming a stable adult population (and as far as a three-year study can give some insight into stability, this has been found to be the case) and assuming that recruitment from the immature population equals the annual adult mortality, then the number of birds in the year class before the assumption of adult plumage (U) should approximate the adult mortality (M). The adult mortality can then be expressed as:

$$M = \frac{U}{2V} \times \frac{100}{1}$$

where V is the number of adult pairs in the population. Equations for the average longevity of adults as adults (Y) are given by Farner (1955) based on the annual survival rate, and Lack (1954) based on the annual mortality. These equations, which give almost identical results are respectively:

$$Y = -\frac{0,4343}{\log_{10} S}$$

$$Y = \frac{2-M}{2M}$$

Using the population figure obtained above of 203 pairs of adult Bearded Vultures in southern Africa and the breeding success rate of 0,9 young/pair/year, the numbers of

young birds, the immature mortality, adult survival and the mean lifespan are calculated using age-class criteria from (a) the Drakensberg Escarpment region and (b) the means for the Lesotho road counts and the Northeastern Cape (Table 9.5).

The numbers of the juvenile plus immature birds and subadult birds calculated from the ratio of adults:young-birds are more than twice as large using the ratio obtained in region (b) as using the ratio found in region (a). This affects the resulting population dynamics characteristics calculated from these figures. Young bird mortality is high, and between 83% and 93% of young birds leaving the nest will die before acquiring subadult plumage. Adult survival, however, is correspondingly high (92-97%). This last set of figures results in very different mean periods for the survival of adult birds as adults. The total mean lifespan expectancy of birds surviving to adulthood is between 18 and 36 years.

9.4 DISCUSSION

9.4.1 Population age structure, mortality and longevity

Population studies on birds usually rely on a marking scheme such as numbered metal leg rings. The returns of these rings, found on dead birds, allow the calculation of the mortality of different age classes and an estimation of longevity. This technique requires a large number of individuals in a population to be marked over a period of years because the percentage of rings returned is very low,

in Cape Vultures averaging about 3% (Piper et al. 1981). In an attempt to increase the rate of data collection from ringed birds a colour-ringing scheme was introduced for use on some vulture species in southern Africa (Ledger 1974). This allowed the identification of individual birds at nest and roost sites, at carcasses, etc. and the ages of these birds could then be determined. While the use of colour rings for the recognition of individual birds was of use in the study of many aspects of vulture biology it did not help in calculating immature mortality or adult survival because the rings used were of poor quality (Mundy 1982) and in some cases lasted for less than two years (per. obs.).

In my study calculations of immature mortality and adult survival are based on the age structure of the Bearded Vulture population, and rely on the ability to identify the pre-adult plumage phase. This method is clearly unsuitable for species such as the Gyps vultures which do not have a distinctive subadult plumage, but has been used successfully in the Bateleur, African Fish Eagle, Golden Eagle and Bald Eagle (Brown & Watson 1964; Brown & Cade 1972; Brown & Hopcraft 1973; Thiollay & Meyer 1978). While Mundy (1982) suggests that colour ringing is a better means of studying population dynamics than plumage characteristics, and in some cases where there is no clear pre-adult plumage this is so, it is not applicable to all species; the lack of success by the Vulture Study Group using this method in long-term studies is clearly shown in the analysis by Piper et al.

(1981) in which adult Cape Vultures were calculated to have a breeding life expectancy of only three years. In addition, in short-term studies of species which cannot be captured or ringed at the nest in large numbers, of species which live in areas where colour-ring sightings are unlikely to be reported and of species with feathered tarsi (all features pertaining to this study) the determination of population-dynamics characteristics using a colour-ringing programme is not feasible.

Both the colour-ringing and the age-structure methods of calculating population-dynamics characteristics are subject to a number of possible biases (Newton 1979), the most important one in the case of the latter method being the need to sample a representative cross-section of the population. There is some evidence that in some raptor species young birds and adults may not be uniformly distributed (e.g. Brown & Hopcraft 1973; Gargett 1975; Brown 1977; Mundy 1982).

In those southern African areas where the adult density of Bearded Vultures is high, the density of young birds is low, and in the areas where the adult density is low, young birds are correspondingly more abundant. During this study the highest breeding density of Bearded Vultures was found to be on the Drakensberg escarpment where the lowest percentage of young birds was recorded (27%). Relatively high percentages (mean = 43%) of young birds were recorded along roadways in the Lesotho highlands and in the Northeastern Cape Province. In Lesotho, because of the

inaccessibility of most of the highland regions to vehicles, the human population is relatively dense along the few roadways with the result that loose village communities have been established along about 34% of the routes travelled. Adult Bearded Vultures tend to avoid human habitation; in these areas the average distance travelled per adult seen was 174 km while in rural areas the distance was 33 km. The converse was true for young birds, with an average distance in villages of 35 km per bird while in rural areas the figure was 86 km per bird.

The Northeastern Cape is on the edge of the present-day breeding range of the Bearded Vulture. The mean inter-nest distance in this area is about three times greater than that on the Drakensberg escarpment. The habitat is highly suitable and it is probable that the food supply is sufficient to support more Bearded Vultures than are in fact occupying the area, a suggestion supported by the relative abundance of Cape Vultures (Figure 9.7). The low adult population of Bearded Vultures probably results from the use of poisons for the control of mammalian predators by small-stock farmers rather than a limited food supply or number of suitable nest sites (see Chapter 10). The population is probably therefore well below the potential carrying capacity of the environment and as such would be an area into which young birds would tend to move.

These examples support the view that young birds tend to move out of areas in which the adult population is high,

and gravitate to areas where the adult density is lower. Young birds are less experienced at finding food than are adults and do not have the intimate knowledge of a home range that adult birds do. In areas where the foraging pressure is high they may not be able to find sufficient food and so move on until they find an area with a less heavily exploited food source.

The population-dynamics figures given in Table 9.5 have been calculated from the figures from (a) the Drakensberg escarpment where the percentage of young birds was relatively low, and (b) the mean of the figures from road counts in the Lesotho highlands and the Northeastern Cape where the percentage of young birds was high. The true proportion of adults to young birds for the entire population is probably between these two sets of figures, but the exact percentages are not known and undoubtedly fluctuate from year to year. Assuming an intermediate figure of 3,3% for the number of subadults in the population, then there would be about 21 subadults and 214 juvenile and immature birds (adult to young bird ratio of 1:0,55), giving a total of about 631 birds in southern Africa. The juvenile and immature mortality rate would be 88,5% and the adult survival rate about 94,8% per year. The average longevity of adults as adults (using Lack's (1954) equation) is 18,7 years and their mean total life is 23,7 years.

Population-dynamics figures, based on plumage characteristics, calculated for other large birds of prey are shown in Table 9.6. In all species the pre-adult age

group comprises about 2-4% of the respective population and the immature mortality (up to the pre-adult stage) is high at 83-95%. Longevity ranges from 20-35 years, which seems reasonable considering that in captivity a Bateleur has lived for at least 55 years (Brown & Amadon 1968). Seabirds show similar trends. For example the Fulmar _Fulmarus_ _glacialis_ has an annual adult survival rate of 97% (Dunnett & Ollason 1978) which gives a mean adult life of 33 years, although there is some evidence that a decline occurs in adult survival with advanced age. The figures obtained for the population dynamics of Bearded Vultures in this study compare well with those for other species.

9.4.2 Breeding success

Bearded Vultures have a high breeding success rate compared to other large raptors (Table 9.7), particularly when considering that no more than one nestling is produced per year. This has a considerable influence on the adult longevity calculation. Assuming that Bearded Vultures produced 0,5 young per year (a fairly average figure for large birds of prey), and using the immature mortality figure of 88,5% given above, there would be 12 subadult birds in the population per year and the annual adult survival rate would be 97%. Adult birds would then need to have a mean total life of 38 years to maintain a stable population which is unlikely because the oldest age achieved in captivity is something over 40 years.

Brown (1977) gives a mean breeding success rate of 0,55

young per pair-year for two pairs of Bearded Vultures in
Ethiopia and one pair in Kenya. These data were obtained
from incidental observations, and in the case of one pair,
only one nest was found. I regard this figure for the
breeding success as highly unlikely because (a) nests are
difficult to find as they are usually out of sight in a
small cave, there is little "whitewash" to mark the site and
birds are wary of giving away the locality. A systematic
search is needed to find nests, not incidental observations
and (b) breeding pairs have two or more nests in all pairs
properly studied (Hiraldo et al. 1979; Cramp & Simmons 1980;
this study). It is probable, therefore, that the nest sites
of some pairs were not located in some years and that the
breeding success is higher than indicated.

Finally, why does the Bearded Vulture have such a high
breeding success rate and such a high immature mortality? Is
the former required to compensate for the latter, and if so,
why do adult birds not rather take off one or more years
from breeding to devote to a more extended period of
parental care (e.g. California Condor Gymnogyps
californianus, Andean Condor Vultur gryphus and some
populations of Crowned and Martial Eagles, Newton 1979;
Brown 1966, 1976b; pers. obs.) and perhaps increase the
survival rate of young birds? It seems very wasteful for 203
pairs of Bearded Vultures to rear 183 nestlings successfully
per year and have 162 young birds die each year. Selection,
after all, operates at the level of recruiting successful

breeding stock to the next generation, not the number of young per se.

Bearded Vultures, like most other large raptors and seabirds, are "K selected" (sensu MacArthur & Wilson 1967) and have all the associated characteristics, e.g. long breeding season, a small number of offspring per breeding attempt and delayed maturity. In Bearded Vultures the young birds of one season become independent only just before the start of the next breeding season; therefore only one breeding attempt per year is possible. While most other vultures and large eagles do not breed every year (Newton 1979), Bearded Vultures do. I have argued (Chapter 7) that Bearded Vultures and other large raptors that rear only one nestling from a two-egg clutch do so because food is limiting at some stage of the nestling period, and to avoid conflict at this stage and at the risk of possible serious injury to both nestlings, sibling aggression takes place when the second egg hatches. This would mean that Bearded Vultures cannot increase their productivity by rearing two young per breeding attempt. They nevertheless produce as many young as possible by being successful in nearly all attempts. This tremendous reproductive effort in conjunction with the high young-bird mortality may suggest that survival is not closely related to population density, but that the more offspring produced the more young are likely to survive to adulthood, even though the percentage might be small.

If the food supply were the factor limiting a stable population, it could be argued that Bearded Vultures would

not have to maintain such a high output because the food supply could support a certain number of young birds per year. It would seem unnecessary and even counterproductive to produce so many in excess of the numbers needed to compensate for adult mortality, because competition for food would further decrease the number of young birds which would survive. While mortality is a prerequisite for the processes of natural selection to operate, the degree of mortality in this case seems excessive.

Large birds are generally considered to have stable populations that remain close to the level that the environment will support. Vacancies in the breeding population, when not affected by man-related mortality, will be few at any given time and selection pressure will favour the production of well-nurtured young by means of deferred maturity. Reasons given for delayed maturity in species such as Bearded Vultures are (a) that young birds do not have sufficient skills in foraging and avoiding dangers and that the body condition necessary to raise young could not be achieved and maintained, and (b) that individuals ultimately produce more offspring by waiting until later in life; early breeding may jeopardize their own chances of survival (Newton 1979).

Bearded Vultures are habitat-specific (an unusual characteristic in scavenging animals) and rarely venture out of their mountainous areas. This habitat usually occupies a relatively small area and is usually separated from other

such habitats by large expanses of other biomes. Bearded Vulture populations are therefore usually small and isolated from one another, e.g. southern Africa, East Africa, northwestern Africa, Yemen, etc. (see distribution in Cramp & Simmons 1980), particularly when compared to other avian scavengers. For example, the southern African vulture with the most limited African distribution is the cliff-nesting Cape Vulture. This species nevertheless occurs over almost the entire subcontinent, avoiding only forested habitats, and young birds can dispense with the need for cliffs until they reach breeding age (Steyn 1982; Mundy 1982). Carrion is a less reliable source of food than is live prey (Newton 1979; see also chapter 6). Historically, before stock-farming ensured a dense, resident population of domestic animals throughout most of the mountainous areas of the world, Bearded Vultures were reliant mainly on game carrion. Game animals are highly mobile and susceptible to adverse weather conditions; animals may have moved out of mountainous areas in times of above average snowfall, low rainfall, large fires, etc.

Because Bearded Vulture populations are often relatively small, isolated and habitat-bound, I suggest that seasonal variations in the food supply in the past may have had a considerable effect on the numbers of these birds. As a result these populations might not have been as stable as those of other large scavenging species which could range over larger areas of different habitats and, if above-average mortality occurred in one area, could rely on rapid

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recruitment from other parts of the species' range. Even in species such as the Cape Vulture, whose population would be "buffered" by its relatively wide distribution, habitat tolerance and ability to cover extremely large distances, increases and decreases in the population size over time have been suggested (Boshoff & Vernon 1980a). Bearded Vulture populations would be even more likely to fluctuate, and to a greater degree than that shown in other vulture species. If this were indeed the case, it would be important for Bearded Vultures to have a high breeding rate and to produce more young birds than species with more stable populations so that population numbers could recover quickly. During the years after a general population decline, the survival of young birds would be likely to be higher than when the population was stable, and the frequency of young birds breeding before acquiring full adult plumage may increase. Such a situation has been reported in other species whose populations had declined to below the environmental carrying capacity, e.g. European Sparrowhawks, Goshawks Accipiter gentilis, Imperial Eagles Aquila heliaca (Newton 1976; McGowan 1975; Valverde 1960). It is possible therefore that Bearded Vultures may maintain a high breeding rate so that they retain the capacity to recover rapidly from population instability. The high rates of immature mortality during stable periods might be the price which has to be paid for this flexibility.

TABLE 9.1

The breeding density of the Bearded Vulture in different regions of southern Africa. Regions: 1 = Natal Drakensberg escarpment between Sani Pass and The Corner in Giant's Castle Game Reserve; 2 = Natal Drakensberg escarpment in Cathedral Peak State Forest; 3 = Maluti escarpment in QwaQwa; 4 = Lesotho highlands (Drakensberg range) near Mokhotlong; 5 = Lesotho, outliers of Thaba Putsoa range east of Roma; 6 = Orange Free State, Maluti outliers in Golden Gate area; 7 = Northeastern Cape Province, Barkly East district.

Region	No. nests	Distance or area (km or km^2)	Density (km^2/pr)	Mean inter-nest distance (km)
1	8	48 km	-	6,0
2	3	21 km	-	7,0
3	2	-	-	8,6
4	9	1250 km	138,9	13,3
5	4	910 km	227,0	17,0
6	2	-	-	9,5
7	4	1160 km	290,0	19,2

TABLE 9.2

The relative abundance of Bearded Vultures in some areas of southern Africa as determined from road counts. Areas: 1 = Lesotho highlands, Drakensberg range, i.e. east of Orange River; 2 = Lesotho highlands, Maluti range, i.e. west of Orange River; 3 = Northeastern Cape Province, mainly Barkly East district.

Area	Sample		No. Bearded Vultures			No. Adults/10 h	No. Adults/100 km
	Time (h)	Distance (km)	Adults	Immatures	Total		
1	33,5	621	18	13	31	5,4	2,9
2	20,0	325	8	5	13	4,0	2,5
3	41,3	552	9	8	17	2,2	1,6

TABLE 9.3

Total estimate of the adult Bearded Vulture population in souther
Africa, calculated for the 12 different regions of the species' range a
shown in Figure 9.8.

Region	Distance or area (km or km²)	Density/pr (km or km²)	Total no. pairs	Known no. of pairs	% pair known
1	233 km	6,3 km	37	19	51
2	-	-	(5)	3	60
3	7501 km²	138,9 km²	54	12	22
4	5144 km²	183,9 km²	28	9	32
5	30 km	8,6 km	3	2	67
6	-	-	(1)	0	0
7	-	-	2	2	100
8	9013 km²	227,0 km²	40	6	15
9	83 km	(6,3 km)	(13)	1	8
10	-	-	(4)	0	0
11	120 km	(15 km)	(8)	1	13
12	*	c.19 km	8	6	75
Totals	-	-	203	61	30

* Not calculated per area because density is not uniform but decrease
rapidly southwards away from Lesotho and Transkei borders. Figures i
brackets indicate estimates where nest densities were not obtained.

TABLE 9.4.

The age classes of Bearded Vultures in different regions of their southern African range. The Drakensberg escarpment region includes data from Giant's Castle Game Reserve, Cathedral Peak State Forestry Reserve, Royal Natal National Park and traverses along the top of the Drakensberg (all within 5 km of the escarpment) between Sani Pass and Bannerman's Pass in Giant's Castle Game Reserve. The Lesotho road counts were made over two routes, making two trips along each route. These were over Sani Pass to Mokhotlong and then west over Menoaneng Pass to Thaba-Tseka and over Blue Mountain Pass to Roma, and from Mokhotlong via Letseng-la-Terae mine and Oxbow to Butha Buthe. Data from the Northeastern Cape were collected mainly in the Barkly East and Lady Grey districts.

Region	Period	Adult		Subadult		Imm. + Juv.		Total No.
		No.	%	No.	%	No.	%	
Drakensberg escarpment	Mar 1980-Nov 1981	280	72,9	9	2,3	95	24,7	384
Lesotho road counts	Jul 1981-Sep 1981	26	57,8	2	4,4	17	37,8	45
Northeastern Cape	Dec 1980-Dec 1981	13	52,0	1	4,0	11	44,0	25

TABLE 9.5.

Some population-dynamics characteristics of the Bearded Vulture in southern Africa calculated from the age class ratios (a) in the Drakensberg escarpment region and (b) the mean figures for the Lesotho road counts and the Northeastern Cape Province, based on a southern African population of 203 pairs and a 90% breeding success rate, giving 183 young Bearded Vultures produced per year.

Population characteristics	Total population estimates based on age ratios from:	
	Drakensberg Escarpment	Lesotho + Northeastern Cape Province
Juv. + Imm.:Ad. ratio	1:2,95	1:1,39
Subad.:Ad. ratio	1:31,11	1:13,00
No. Juv. + Imm. birds	138	292
No. Subadult birds	13	31
Juv. + Imm. mortality (%/yr)	92,9	83,1
Adult survival (%/yr)	96,8	92,4
Mean adult life (years)	30,8	12,7
Age of adulthood (years)	5	5
Mean lifespan (years)	35,8	17,7

TABLE 9.6

Population-dynamics characteristics calculated for some large birds of prey based on age-class plumage characteristics.

Species	Pre-adults in population (%)	Young bird mortality (%/yr)	Adult survival (%/yr)	Longevity (years)	Source
Bearded Vulture	3,3	88,5	94,8	23,7	a
Fish Eagle	4	83,0[1]	94-96	20-28	b & c
Bateleur	2-3	90,8[2]	94-97	23-35	b
Bald Eagle		95	95	19,5	d

1   Calculated from data in Brown & Hopcraft (1973)

2   Calculated from data in Brown & Cade (1972)

Source   a = this study,   b = Brown & Cade (1972),   c = Brown & Hopcraft (1973), d = Sherrod et al. (1977).

TABLE 9.7

Breeding success of some large birds of prey.

Species	Mean no. young per pair-year	Source
Bearded Vulture	0,9 0,9	This study Hiraldo et al. (1979)
Golden Eagle	0,6 0,7	Everett (1971) Murphy (1974)
African Fish Eagle	0,5 0,4	Brown & Hopcraft (1973) Thiollay & Meyer (1978)
Ayres' Eagle	0,7	Brown (1966)
African Hawk Eagle	0,6	Brown (1966)
Bateleur	0,5 0,8	Brown (1955) Brown et al. (1977)
Crowned Eagle	0,4	Brown (1966)
Martial Eagle	0,4	Brown (1966)
Brown Snake Eagle	0,3	Brown (1955)
Tawny Eagle	0,6	Steyn (1973a)
Wahlberg's Eagle	0,6 0,4	Brown (1955) Tarboton (1977)
Black Eagle	0,5	Gargett (1977)
Whitebacked Vulture	0,5	Mundy (1982)
Cape Vulture	0,4	Mundy (1982)
Lappetfaced Vulture	0,4	Mundy (1982)
Whiteheaded Vulture	0,5	Mundy (1982)
Hooded Vulture	0,3	Mundy (1982)

Chapter 10

CONSERVATION AND MANAGEMENT

10.1 INTRODUCTION

Scavenging birds of prey in southern Africa, and in most of the more developed areas of the world, have generally shown a marked decline in both numbers and range in recent years (e.g. Bijleveld 1974; Boshoff & Vernon 1980a, 1980b; Boshoff et al. 1983; Brooke 1984; Cramp & Simmons 1980; Kemp 1978; Mundy 1978; Newton 1979; Tarboton & Allan 1984). The Bearded Vulture is no exception; it is classed as Europe's rarest vulture (Cramp & Simmons 1980), and populations have declined drastically in many other areas (see chapter 1). In southern Africa these birds are now restriced mainly to the highlands of Lesotho and immediate adjacent areas.

In the first South African Red Data Book - Aves (Siegfried et al. 1976) the Bearded Vulture was classed as "rare and threatened", based on an estimate of fewer than 100 individuals surviving in southern Africa. Reasons for the population decline were given as shooting, decrease of carrion, poisoning and disturbance at nests. The revised South African Red Data Book - Birds (Brooke 1984) gives a population of about 120 pairs based on counts made by Brown (1977) and classes the Bearded Vulture as "rare".

The aims of this chapter are (a) to review the decline of the Bearded Vulture in southern Africa, both spatially

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and numerically, (b) to investigate possible reasons for the decline in terms of (i) the availability of food in the different regions in which the species still occurs as well as in regions in which it occurred historically and (ii) mortality resulting from human-related activities, (c) to investigate the attitudes of the farming community to Bearded Vultures on their land and (d) to evaluate the use of artificial feeding sites in the Natal Drakensberg.

Only once the main factors responsible for the decline in the population have been identified can management practices be selected to counter the negative population trends.

10.2 DISTRIBUTION

The past distribution of the Bearded Vulture in southern Africa for different periods has been documented by Boshoff et al. (1978) and Boshoff et al. (1983), and the detailed evidence of the distribution this decade is described in Chapter 9 (Figure 10.1). Evidence for the historic occurrence of Bearded Vultures in the Transvaal is unconvincing (Tarboton & Allan 1984) and the species has probably always been a rare vagrant to that Province.

It is apparent that the main reduction in range of the distribution of Bearded Vultures has taken place in the Cape Province, it being one of seven diurnal raptors to be classed as having experienced a marked range decrease (Boshoff et al. 1983). It is of note that five of the seven species in this category are scavengers.
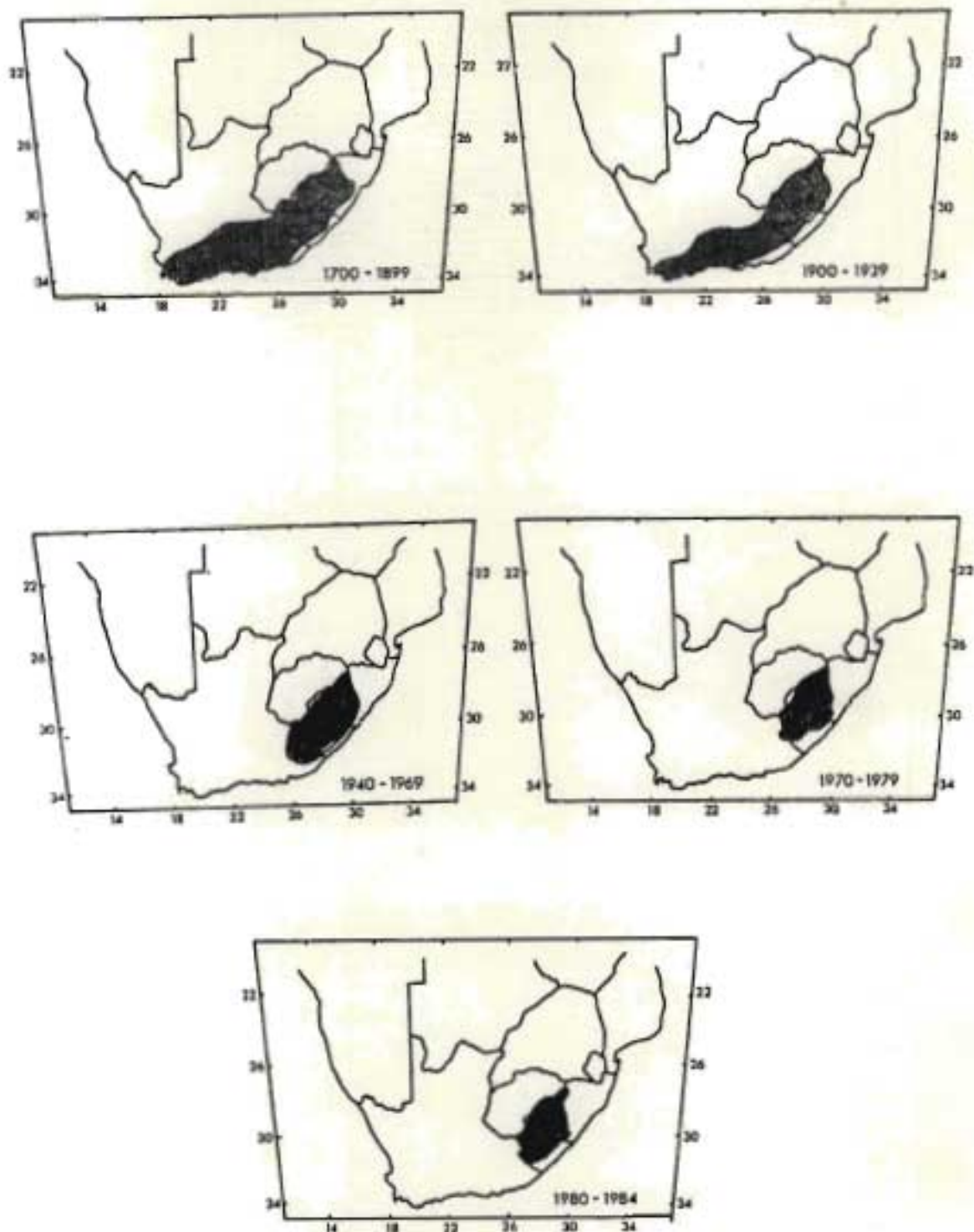
FIGURE 10.1. Past and present distribution of the Bearded Vulture in southern Africa, based on Boshoff _et al_. (1978), Boshoff _et al_. (1983), Brooke (1984) and data presented in Chapter 9.

Reduction in the range of the Bearded Vulture took place from the early part of this century and by 1940 the species no longer occurred regularly in the southern and southwestern Cape mountains. Between this time and 1970 its range contracted still further northeastwards with its elimination from the eastern Cape. The distribution of this species during the 1970s and the early part of this decade has apparently remained constant.

10.3 POPULATION DENSITY

The present breeding population of the Bearded Vulture in southern Africa, consisting of about 203 pairs, covers an estimated area of 34 000 km^2, giving a mean breeding density of 167 km^2 per pair. Its historic breeding range, calculated on the area of suitable mountain habitat in which Bearded Vultures are known to have occurred (topographic 1:500 000 map series, Government Printers), covers an additional 21 000 km^2, most of this being in the Cape Province. Using the above density figure obtained for the present population, the range lost to Bearded Vultures during this century could have supported an additional 125 pairs of birds. The present population represents, therefore, about 62% of the historic southern African population.

While this may look encouraging against the percentage survival of other scavenging raptor populations in southern Africa (e.g. Bateleur, Lappetfaced Vulture, Whiteheaded Vulture), the following should be borne in mind: (a) the initial population was very small, i.e. an estimated 325

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pairs, (b) the species is highly specialized in terms of food choice and habitat requirement, and (c) a large part of the population occurs outside the range of commercial farmlands. If this last factor had not applied and the entire range of the species had coincided with commercial farming areas, the species would probably be extinct in southern Africa today. Newton (1979) has demonstrated in Britain that species which have experienced marked reductions in numbers and range generally had low and localized populations at the start, were often carrion-feeding, and had slow breeding rates. These are all characteristics of the Bearded Vulture.

10.4 POTENTIAL REASONS FOR THE POPULATION DECLINE

Two main factors are considered to influence raptor densities under natural conditions: (a) nest site availability and (b) food supply (Newton 1979).

10.4.1 Nest sites

Even in the most densely populated regions of the Bearded Vulture's southern African range, nest sites were found to be well in excesss of requirements (Brown et al. in press; see Chapter 7) and throughout their range nest sites were considered to be abundant.

10.4.2 Food supply

A decline in the food supply has been suggested as the main cause for the decrease of the Bearded Vulture population, particularly in parts of the Cape Province

(Brown 1977). The section that follows attempts a first approximation at determining the carrying capacity of some areas in the range of the Bearded Vulture in southern Africa. The amount of available carrion was estimated, after which the theoretical population density that the food supply could support was calculated (Table 10.1). The data used, assumptions made and rationale behind the calculations are set out in Appendix 10.1 (Tables 10.2-10.7).

Lesotho had the highest stock losses (annual biomass of 870 kg/km^2) followed in descending order by districts in the Orange Free State, Natal and the northeastern Cape. The Drakensberg conservation areas had the lowest (182 kg/km^2). The amount of carrion actually available to Bearded Vultures was also highest in Lesotho and the calculated mean inter-pair distance for the Bearded Vulture population that could theoretically be supported by the food supply was 9,4 km. The Drakensberg conservation areas had the next best carrying capacity at 9,7 km between pairs, because, despite the biomass of dead animals being low, no carrion was removed for human consumption. These areas were followed, in descending order, by districts in the Orange Free State, Natal and the northeastern Cape, which had estimated food supplies that would support population densities ranging between 10,1 and 11,2 km between pairs.

These calculations were based on exclusive ranges per pair. In practice, ranges overlap (see Chapters 5 and 6) because deaths of mammals are sporadic, temporally and spatially, and result in local superabundances of food that

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cannot be consumed by a single pair. These figures, however, provide some insight by which known densities can be compared with theoretical densities based on food supply, and unexpected trends can be identified. What is immediately apparent is the small difference between the carrying capacities in the different regions. For example, an area of 1000 km^2 in the commercial farming districts of the northeastern Cape, where the food supply was estimated to be the lowest, would theoretically support 10 pairs of Bearded Vultures, while in Lesotho, where food was estimated to be most abundant, 14 pairs could be supported. In general, the actual population densities were lower than the theoretical carrying capacity, but while the two figures were similar for the highlands of Lesotho, they were markedly lower in commercial farming areas, and no birds were found at any distance from Lesotho (see Chapter 9). It would appear that, based on the food supply, quite healthy populations of scavenging birds could be supported in these commercial farming areas, yet this is not the case. Some other population-controlling factor is therefore in play, and this will be investigated in the next section.

One final aspect of the food supply to be investigated is the availability of carrion in districts in which Bearded Vultures occurred historically. Eleven such districts in the southwestern, southern and eastern Cape (Figure 10.2) were evaluated (Table 10.8), based on the same procedure as applied to the other regions (see Appendix 10.1), although
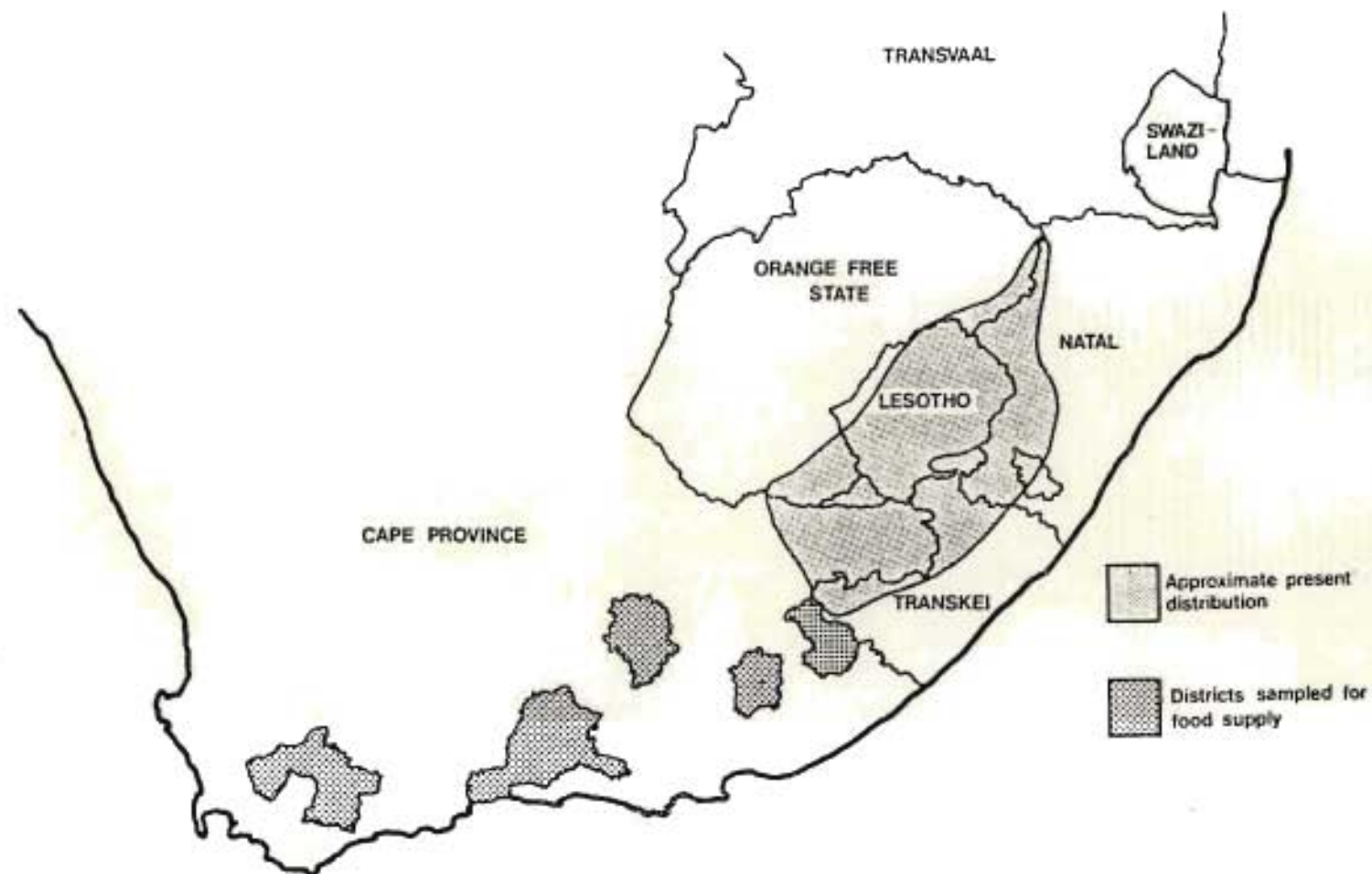
FIGURE 10.2. The 11 districts in the Cape Province, in which Bearded Vultures occurred historically, that were assessed for carrion abundance.

these did not include game mortalities because no data for these regions are available, but in the other commercial farming regions such as Natal, game deaths constituted only about 7% of the carrion by mass.

Carrion available to Bearded Vultures was very scarce in the southwestern Cape where extensive cultivation is practised, but became more abundant towards the east, where mixed farming and stockfarming predominate. The districts of Cathcart and Queenstown in the eastern Cape, where Bearded Vultures have most recently suffered extinction, had comparable amounts of carrion available to that in areas where Bearded Vultures still occur, and these areas could theoretically support a population at a density of about 11-12 km between pairs. These figures give the average amount of carrion for the district, but this will fluctuate from year to year, from farm to farm, between flat and mountainous regions, etc. The cut-off point at which the food supply no longer allows Bearded Vultures to breed successfully, or to survive in that area, is not known. In the southwestern Cape, in districts such as Montagu and Worcester where the land is fragmented into small, intensively managed farms with a high proportion of cultivation and where the available carrion is below 1 kg/km^2, the food supply would presumably be insufficient to support the birds. In the other districts, however, although food was less plentiful than in Lesotho, I would not expect the total extinction of the species as a result of the food supply; stock losses in the mountainous regions are

generally higher than on flatter terrain and, because many
of the mountains fall under the Department of Forestry,
wild ungulates are present. These areas would therefore
provide more carrion than overall figures for the district
would suggest. Although the low food supply in the
southwestern Cape at present is clearly lower than could
support Bearded Vultures, I suggest that in other parts of
southern Africa food supply is not the reason for the range
decline, although it may have reduced the population density
in some regions.

10.4.3 Mortality from human activity

Data on causes of mortality in Bearded Vultures were
obtained from the farming community by means of the postal
questionnaire survey, from published accounts, from the
extensive internal reports of the Natal Parks Board and from
correspondence with colleagues, Wildlife Society members and
other Nature Conservation authorities.

The questionnaire survey reached 4210 commercial
farmers in the provinces of Natal, Orange Free State and the
Cape. The response rate was 38%. Of these, 367 farmers
reported seeing Bearded Vultures on their farms (Table
10.9).

A total of 22 dead birds were reported by farmers, of
which 73% had died of poisons (Table 10.10). Other sources,
since 1960, showed a similar trend (Table 10.11); 25
mortalities were reported of which 40% were confirmed to be
the result of poisoning and 24% were suspected poisoning,

giving a total of 64% ascribed to poisons. The next most important mortality factor was gin traps (24%) while 12% of the birds were shot.

There is a strong bias in this type of sampling. Birds shot or captured in gin traps are there to be positively confirmed. Birds poisoned usually fly away and die where they are very rarely found. Those poisoned birds which are found therefore represent only a fraction of the total. This can be appreciated when considering the number of young birds which die from natural causes (about 88% mortality in young birds) and the number which are found. In three years of intensive fieldwork I found no dead young birds and I am not aware of any such recoveries of young birds dying from natural causes. All but four of the mortalities given above were adult birds.

Poisons are used extensively on commercial farmlands in southern Africa, mainly to kill mammalian predators such as the Blackbacked Jackal, domestic (sometimes feral) dogs and the Caracal (e.g. Berliner 1984; Brown 1985a, 1986; Brown & Piper in press; Ledger 1985, 1986; van Heerden 1985).

Natal farmers were more willing to admit to having used poisons than were farmers in the other two provinces (Table 10.12), probably because the use of poison against predators is legal in Natal, but not in the other two provinces. Farmers not using poisons took the opportunity to point this out and deplore those farmers that did. It is probably reasonable to assume that those farmers who chose not to reply to this section were people who used poisons. If this

is the case, the total figure obtained for the percentage of farmers who poisoned is still probably an underestimation, as the following example illustrates. Before undertaking the questionnaire, a pilot study was run, randomly choosing farmers in the Natal central and southern region, of which 214 responded. As far as possible, personal contact was then established with these farmers to obtain feedback on the phrasing of the questionnaire, and at the same time a "ground truth" survey was conducted once the farmers were confident that their information would not be used for law-enforcement purposes. The only information that needed to be altered significantly was that on the use of poisons. Initially, 18% of farmers admitted to using poisons whereas the final figure obtained was 34%.

The use of poison was strongly correlated with smallstock farming, where 60% of farmers used poison for predator control. On mixed large- and smallstock farms 46% of farmers used poisons while on exclusively cattle farms the figure was 8%. The geographic distribution of poison usage in the central and southern Drakensberg was as follows: on farms within 5 km of conservation areas (5 km being the average home range diameter of a jackal (Rowe-Rowe 1982a)) 60% of farmers used poisons. On farms within 5 km of KwaZulu areas (dog home range?) 41% of farmers used poisons. Away from these areas 21% of farmers poisoned. It is important to note, however, that farms adjacent to these two different forms of landuse are more likely to be in mountainous terrain than farms away from these areas.

Mountainous regions provide more secure habitat for predators and also make stock handling more difficult and hence stock mortalities are generally greater; no movement of jackals from conservation areas onto adjacent farmlands was found by Rowe-Rowe (1982a).

In areas of Natal adjacent to the Drakensberg strychnine was the most commonly used poison (Table 10.13). Most farmers (63%) put the poison into small blocks of meat or the carcass of a small bird (doves were favoured) and distributed these over their farms, while the remainder placed the poison directly into the carcass of a domestic animal, usually one that had recently been killed by a predator (Brown & Piper in press).

The overall use of poison, as confirmed by farmers in both questionnaire surveys, is mapped (Figure 10.3) as the percentage of farmers using poisons per $\frac{1}{4}^\circ$ square. Converted to an easily understood figure, the minimum number of farmers that would set poison baits within each Bearded Vulture's home range of 2400 km^2 on commercial farmlands in Natal is 21, in the Cape is 12 and in the Orange Free State is 8. Bearing in mind that these figures probably underestimate the number of farmers using poisons by half, the devastating impact of poisons and the extinction of the birds on farmlands can be easily understood. In addition, the foraging methods used by Bearded Vultures make them ideally suited to finding all types of poisoned baits, from large carcasses to the smallest blocks of meat; like the Bateleur, they are particularly vulnerable to this form of
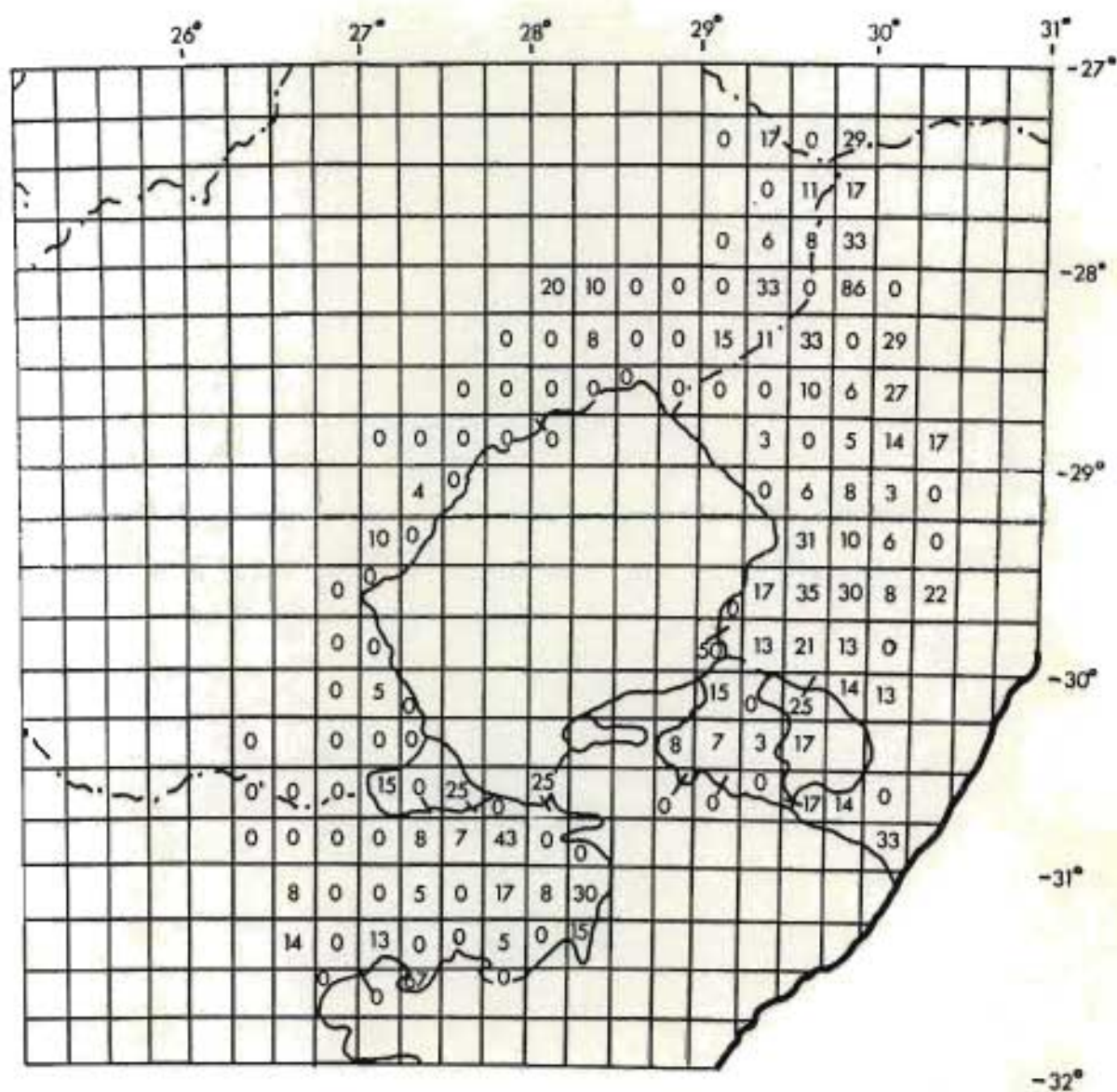
FIGURE 10.3. Percentage of farmers per $\frac{1}{4}^{\circ}$ square who admitted to using poison baits for predator control.

predator control. Feeding trials in Bateleurs have shown that at least 67% of small carrion baits, and all meat blocks, were located by Bateleurs in the Kruger Park, and that, if all scavenging birds were included, an average of 1,2 birds descended to each bait that was in an exposed position (Watson 1986).

It is only in recent years in southern Africa that the effect of poisons on scavenging birds has begun to be recognized, and that the dramatic decline in numbers and ranges of species has been attributed to the use of poisons on farmlands. Information on this aspect has appeared mainly in the form of short publications on opportunistic, incidental findings of poison victims or in general statements in which poisons are listed together with other factors as causing mortality in the species and therefore of conservation concern (e.g. Borello 1985; Brooke 1984; Brown 1985a, 1986; Carlyon 1985; Ledger 1980, 1985; Smit 1984; Tarboton 1986; Vernon et al. 1983b). I consider that the extent of the problem has not been fully realized, and that the injudicious use of poisons by farmers is the overriding cause of mortality leading towards the extinction of the Bearded Vulture in most of the areas in which it formerly occurred, and the same is probably true for the Bateleur, the Whiteheaded Vulture, the Lappetfaced Vulture and the Tawny Eagle in commercial farming areas of southern Africa. Despite the emphasis that has been placed on Cape Vulture research and conservation in southern Africa in recent years (see Brooke 1984), it is worth pointing out that the

colonial scavengers, i.e. the Cape and Whitebacked Vultures, are in a very much more healthy state than are the solitary-nesting scavengers (e.g. Tarboton & Allan 1984). A number of factors may contribute to this, e.g. the solitary species are usually the first to arrive at a carcass, but the most important factor is probably that these birds locate and land to feed on very small scraps of food as well as carcasses, so they are exposed to the small blocks of poisoned meat as well as the poisoned carcasses. This is not the case with the Gyps vultures, which descend only for carcasses.

Poisoning of carcasses is probably on the decline in southern Africa because of adverse publicity and good propaganda given out by the Vulture Study Group and conservation agencies. Little attention has been paid to the use of small poison baits, however, which are in widescale use; in South West Africa/Namibia 76% of smallstock farmers admitted to using poisons to control predators and in one magisterial district 93% of farmers poisoned (Brown 1986), despite the fact that average stock losses due to predators for the area were less than 0,3% per annum (Biggs & Mackay 1986). Small baits were used by over 90% of the farmers (Ledger 1986; C.J.B. unpublished data).

In this section I have attempted to consolidate what little data are available to demonstrate the role played by poisons in the extinction of the Bearded Vulture in many parts of its former range in southern Africa. While more

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detailed research is urgently required on this aspect of farmer-predator-poison-scavenger interaction if acceptable solutions are to be reached for all parties involved. I am confident that poison used for predator control is the single most important cause of mortality in Bearded Vultures and other scavenging species in commercial farming areas of southern Africa.

10.5 FARMERS' ATTITUDES

Boshoff & Vernon (1980b) stated that they had obtained no worthwhile information on Bearded Vultures in the Cape Province from their bird-of-prey questionnaire survey because many reports were based on misidentification. My questionnaire was on a single species which was illustrated at perch, in flight and in both adult and immature plumage. In addition, because information on its biological habits was requested, it was usually fairly easy to detect misidentifications and false information, which made up about 12% of all returns. Most of these misidentifications took place in areas where Bearded Vultures were uncommon or absent.

The greatest degree of confusion (accounting for half the misidentifications) arose from the name "Lammergeyer" or "Lammergeier", being confused with "Lammervanger", an Afrikaans name meaning lamb catcher, which is commonly applied to any large bird accused of killing smallstock. In the mountainous regions of southern Africa it usually refers to the Black Eagle, while in other regions it is applied to

the Crowned and Martial Eagles. This confusion of names is a problem in the Afrikaans farming community (Table 10.14), which comprised 45% of the respondents but which were responsible for 98% of the misidentifications.

The name of the species therefore clearly plays a role in its conservation. "Lammergeyer" and "Lammergeier" should not be used. The English name Bearded Vulture is preferable in this regard as well as being descriptive and the new Afrikaans name, Baardaasvoël (meaning bearded vulture), adopted by Maclean (1985) should be promoted. A similar change in name has been introduced for the original German "Lammergeier" during the recent captive breeding and release programme in the European Alps, where, for the same reasons of inferred predation on smallstock, the name Bartgeier has been adopted (Report of Proceedings 1979).

Farmers who had clearly confused Bearded Vultures with other raptor species were excluded from the questionnaire results. Of those farmers reporting the birds on their farms, 5% considered them harmful in some way to their farming operations. The area with the highest reports of harmful activities was the Cape (11%) and Natal had the lowest (1%). The Natal farmers were found to be generally more conservation-conscious than those in the Cape and Orange Free State and, in addition, the Natal farmers had some years previously all been sent a small brochure about the habits of the Bearded Vulture by the Wildlife Society. This probably also accounted for the Natal farmers being less confused on the identification of the species.

Harmful activities ascribed to the Bearded Vulture were mainly the killing of new-born lambs and goat kids and the general killing of smallstock (Table 10.15). A similar questionnaire sent to some Natal farmers about their attitudes to Cape Vultures indicated that 28% of farmers considered them harmful and a further 12% considered them a nuisance (Brown & Piper in press). Bearded Vultures are, by contrast, viewed much more favourably. Nevertheless, in my experience of the species, I consider even these few allegations to be unlikely. Additional information was therefore solicited from 11 of the farmers who considered the birds to be harmful. None of them had personally witnessed an attack on domestic stock, but two claimed that their shepherds had. Other farmers said that Bearded Vultures "are known to attack lambs/lambing ewes/snow-trapped animals in this district". In Lesotho, where Bearded Vultures were seen walking among herds of lambing sheep and feeding on the afterbirths, the local herders said that they never caused any harm. If stock is in fact lost to predation by Bearded Vultures (which I doubt), it is such a rare occurrence as to not warrant any reprisals from farmers.

10.6 FEEDING STATIONS

The use of artificial feeding sites, often in combination with an observation hide, has been employed in many areas to counteract shortages of carrion, or to provide birds with an uncontaminated source of food (e.g. Newton

1979; Friedman & Mundy 1983; Brown 1985a; Helander 1985; Terrasse 1985). The first feeding site in southern Africa was established in the Giant's Castle Game Reserve in 1966 for the Bearded Vulture (Pringle 1967), and since this date, food has been provided each year during the birds' breeding season (about May to October). The initial aims of this scheme were (a) to supplement the natural food supply when the birds were breeding, (b) to attempt to prevent the birds foraging outside the park on farmlands, thereby reducing the chance of their being shot or poisoned and (c) to provide a means of studying the species.

The original feeding site was closed after about 10 years because of soil erosion caused by vehicles travelling to the hide, and two other sites lower down the mountain were subsequently used. I used the original hide for trapping Bearded Vultures, and the newest hide, completed at the end of 1980, was used by the public to watch the birds. During the study period food was provided at the new hide throughout the year each week. Offal, mainly meaty bones, was obtained from the Estcourt bacon factory, and about six carcasses (cattle and horses) were made available by local farmers per year. Food was put out at the original hide about once per month, using the same source as the new hide, but no carcasses. Information on the age classes of Bearded Vultures was displayed in the hide, and visitors were asked to complete an observation form. I spent a total of 520 h on 92 days over a period of 31 months in the original hide, and

visitors spent 449 h on 105 days over 16 months in the new hide.

No information is available for the time the feeding scheme originally started, neither on the raptor densities in the area nor the extent to which the birds used the food. The particularly high breeding density of Bearded Vultures in the Giant's Castle area (Chapter 9) cannot therefore be positively linked to the artificial feeding, although this would seem likely. This section investigates the current use made of the food provided at the two feeding sites by scavenging birds in the Giant's Castle area and attempts to evaluate the usefulness of this management practice.

The numbers of birds of each species that were attracted to the feeding sites, and the numbers that actually fed, are shown in Figure 10.4. At the original site, Bearded Vultures were the most common species, but less than 30% of them fed. At the new site four species were more common than Bearded Vultures but only the Cape Vulture was markedly so (because of the carcasses). Only 11% of the Bearded Vultures present at the new hide fed. Compared to other species, Bearded Vultures had by far the lowest feeding rate, reflecting their nervousness at landing. There was little change in the frequency of Bearded Vultures feeding over the period examined at the new site (Figure 10.5), but at the original hide the frequency decreased, probably because of the trapping activity. During the first 30 visits a mean of 6,4 different individuals per 10 h was recorded, 36% of which
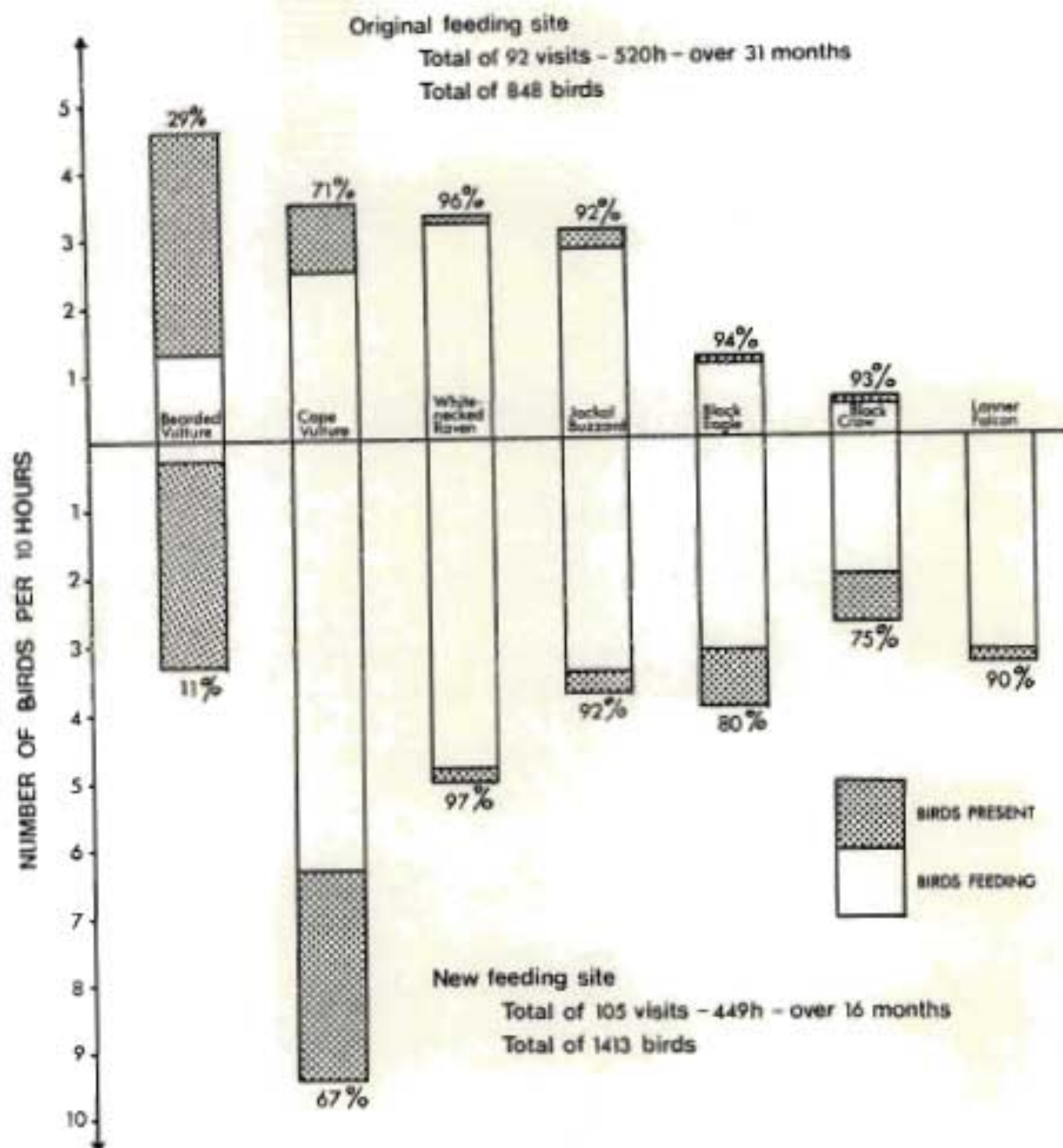
FIGURE 10.4. Numbers of scavenging birds (a) attracted to the feeding sites and (b) feeding, per 10 h of observations. The percentage of the number of birds of each species present that fed are given.
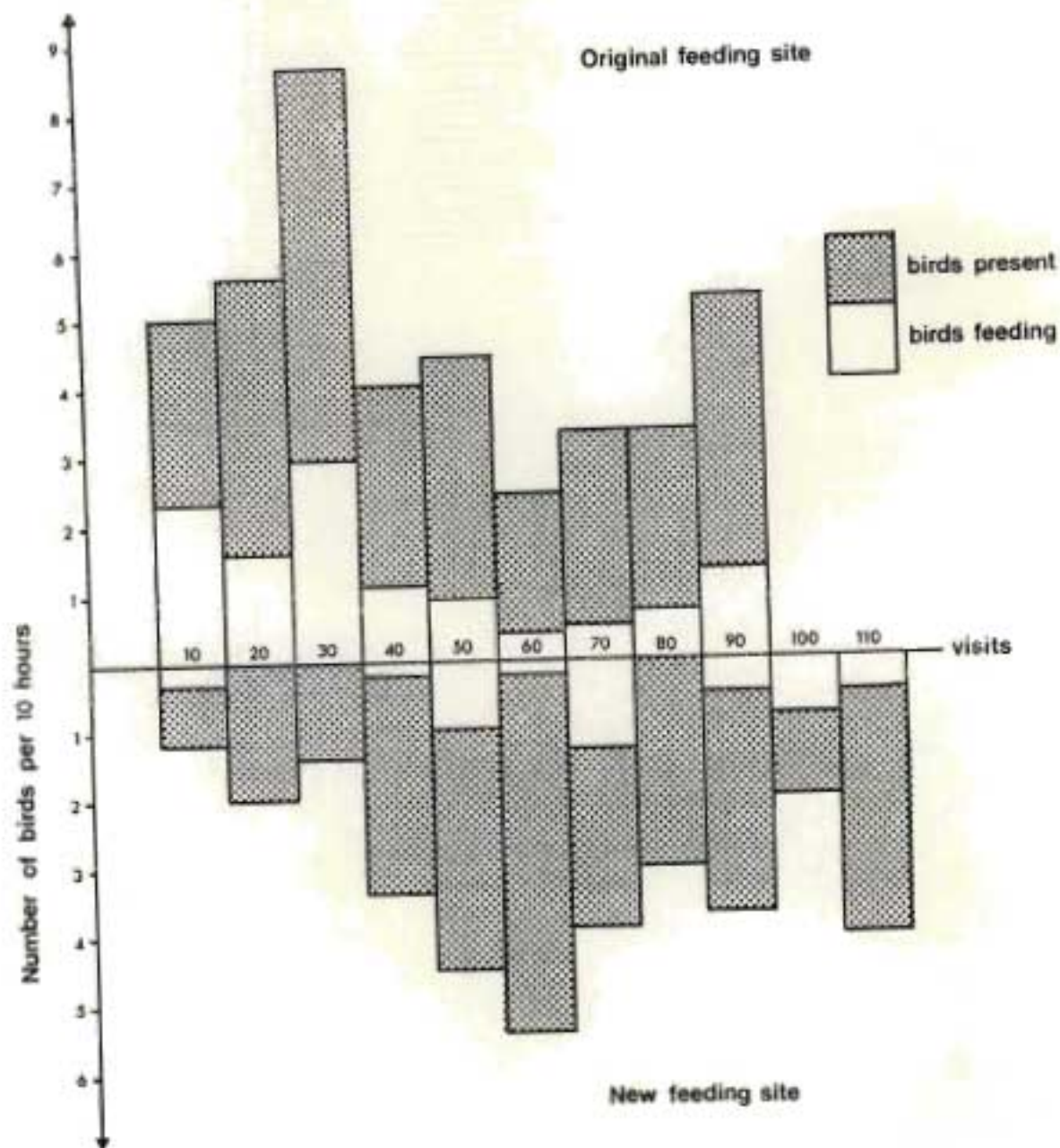
FIGURE 10.5. Number of Bearded Vultures attracted to the
feeding sites and numbers feeding, per every 10
sequential observation periods (visits).

fed, but over the subsequent 62 visits, the mean was 3,7 per 10 h with 21% feeding.

Two factors concerning the location and construction of the new hide and feeding site may be responsible for its low use by Bearded Vultures. Firstly, it is on the lip of a cliff, which is ideal for birds taking off and offers a remarkable view, but opposite the cliff the ground rises up for about 8 m then levels off. This means that the visibility is very restricted on this side, and as soon as Bearded Vultures glide below this level to land, they appear to become aware of the reduced visibility and swoop up. Secondly, the hide has two large sheets of one-way glass, one of which faces the feeding site. The glass is highly reflective and probably a source of alarm to the birds.

Combined data from both feeding sites were used to examine age classes and seasonal trends in the Bearded Vulture's use of the provided food (Figure 10.6). On average, 39% of Bearded Vultures present at these sites were immature, higher than the 27% recorded for the Drakensberg in general (Chapter 9). A seasonal trend was apparent; during the first four months of the year immature birds represented 27% of the population at the feeding sites, this increasing sharply at the start of the breeding season to 43%, when first-year birds become independent. During the last three months of the year the proportion of young birds decreased slightly to 38% (representing possible mortality, improved foraging ability, emigration or a combination). In contrast, adult numbers remained fairly constant throughout
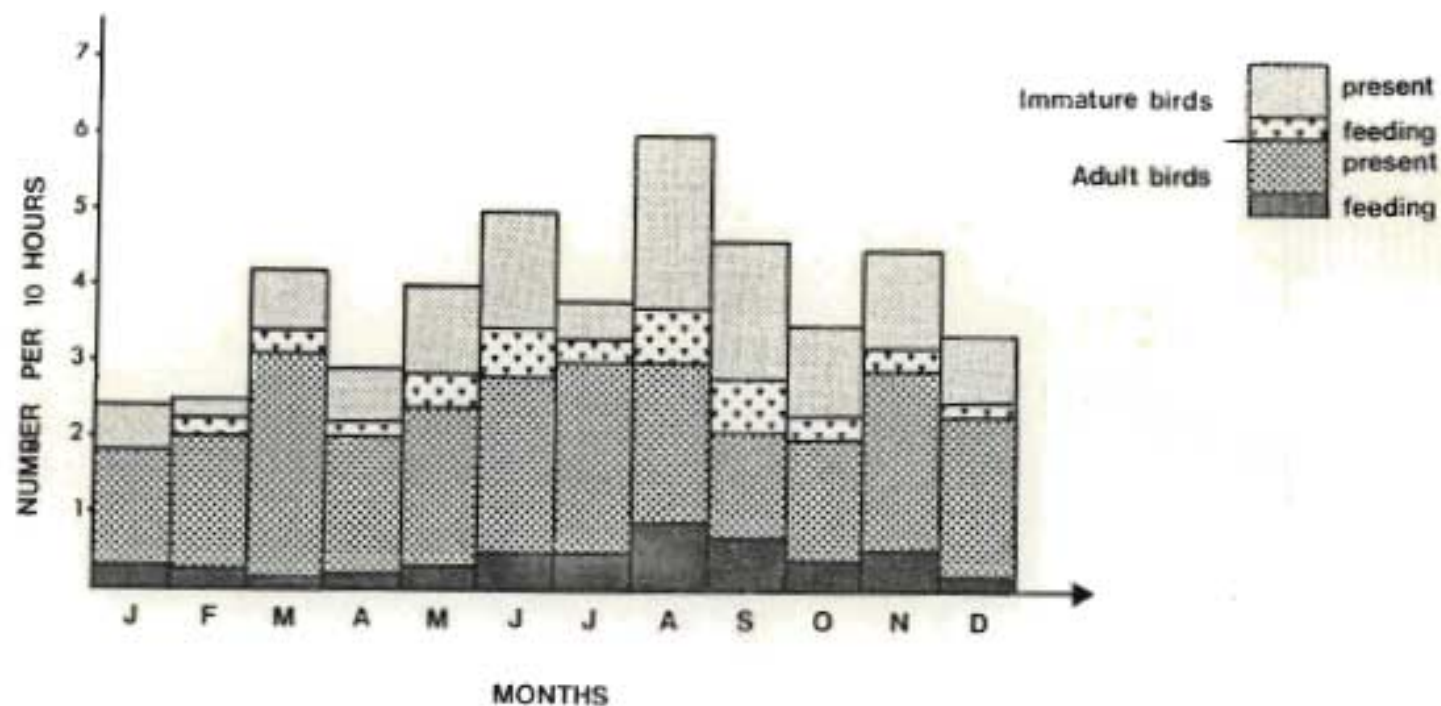
FIGURE 10.6. Numbers of Bearded Vultures attracted to the feeding sites (combined, n = 969 h of observation) and numbers feeding, for adult and immature birds per month.

the year, although more adult birds actually fed during their breeding season, particularly August and September when adults are thought to be under greatest stress to provide food. Immature birds fed more readily at the feeding sites (26% of those present fed) than did adult birds (17%) and this caution displayed by adult birds is reflected in the fewer adult than immature birds captured (8 and 13 respectively).

In conclusion, the feeding sites provided useful locations for capturing Bearded Vultures and for determining the use they make of supplementary food. These sites do not succeed in confining the birds to conservation areas (see Chapter 5) nor is the food provided used by Bearded Vultures in any quantity. I would be surprised if any individual obtained as much as 2% of its annual food requirement from the feeding sites. However, the total amount of food obtained from the feeding sites may not be the important criterion, but rather, that the food is available during those periods when natural food cannot be located. This fact may be particularly important to ensure successful breeding and may account for the relatively dense population in the Giant's Castle area. In addition, the new hide has become very popular with visitors to the park. It has provided people with the opportunity to see Bearded Vultures and six other species feeding and interacting at close quarters. This plays an important educational role and provides the Natal Parks Board with the perfect environment to impart positive orientation programmes on birds of prey. Finally,

other species benefit from the feeding, this being particularly important for the endangered Cape Vulture. The closely related European Griffon Vulture Gyps fulvus has been shown to respond positively to artificial feeding; in the French Pyrénées populations recovered at a rate of 15% per annum (Terrasse 1985).

10.7 MANAGEMENT RECOMMENDATIONS

The Bearded Vulture population in the Lesotho interior is probably secure in the short term, provided poisons for predator control are not introduced. There has been little drastic change to the habitat in this region (apart from overgrazing), Bearded Vulture nest sites are secure from all but the most professional rock climbers (to my knowledge only eight eggs have been collected in southern Africa), no persistent pesticides are used and deliberate persecution is probably low. Genetic variation requirements suggest that the minimum viable population size of any animal should be at least 200 breeding individuals (Soule 1980), and the present Bearded Vulture population is double this size. On the other hand, the southern African population is isolated and covers a geographically small area. Newton (1979) states that the long-term security of any species depends partly on maintaining a wide distribution.

Lesotho is an impoverished country. In 1974-75 exports totalled R10 million while imports amounted to R87 million. The gross national product for Lesotho was calculated by the World Bank in 1972 as at R60 per person per annum,

placing Lesotho in the United Nations list of the world's 25 poorest countries (Ambrose 1976). Any development which can take place to benefit the economy of the country will certainly not be hindered by conservation concerns, and it would be unwise to rely on such a country for the sole conservation of the Bearded Vulture in southern Africa.

Brown (1977) correlated the present distribution of the Bearded Vulture with stock-keeping methods; in areas with primitive pastoral cultures the birds thrive. The correlation made is with the food supply as a result of poor husbandry and high stock mortality. I would not identify the food supply as being the most important factor in the present distribution of Bearded Vultures, but rather the fact that in areas where pastoral practices are unsophisticated and where the rural population is poor, no poisons are used. Further, Bearded Vultures would return to large areas of their former range if poisons were no longer in use. This is supported by the theoretical food supply in many of the commercial farming areas as well as the fact that young birds were recorded on the edge of the species' range in the northeastern Cape in far higher proportions than elsewhere, suggesting a movement into unoccupied areas. In the commercial farming areas that used to support Bearded Vultures, the theoretical food supply would indicate that about 80 pairs could be supported today. This would markedly increase the future prospects for the species in southern Africa.

10.7.1 Conservation areas

As has been demonstrated in Chapter 5, the Drakensberg conservation areas are too small to contain the entire range of a single pair of birds, let alone a viable population. The total protection of at least part of the breeding population and their foraging range is considered essential to ensure the longterm survival of the species. The highest concentration of Bearded Vultures occurs along the Drakensberg escarpment, most of the eastern side of which (with the exception of the Mweni area in KwaZulu and a section of East Griqualand) is already protected in Natal Parks Board and Department of Forestry reserves. The area to the west of the escarpment includes some of the highest land in southern Africa and is not permanently inhabited except for a few isolated villages. This area is also important for the conservation of water; Lesotho, through the shortly-to-be-constructed highlands water scheme, will be exporting water and hydro-generated electricity to the industrial centres in South Africa. It is therefore in the interest of Lesotho to apply strict conservation management to their water catchment areas, and this would also benefit the local flora and fauna. This catchment area, constituting a band of land about 20 km wide along Lesotho's eastern border with Natal, would form an ideal conservation area in conjunction with the present Drakensberg conservation areas and including the Mweni and East Griqualand regions (Figure 10.7). This conservation area could contain at least 65 pairs of Bearded Vultures and support most of the foraging
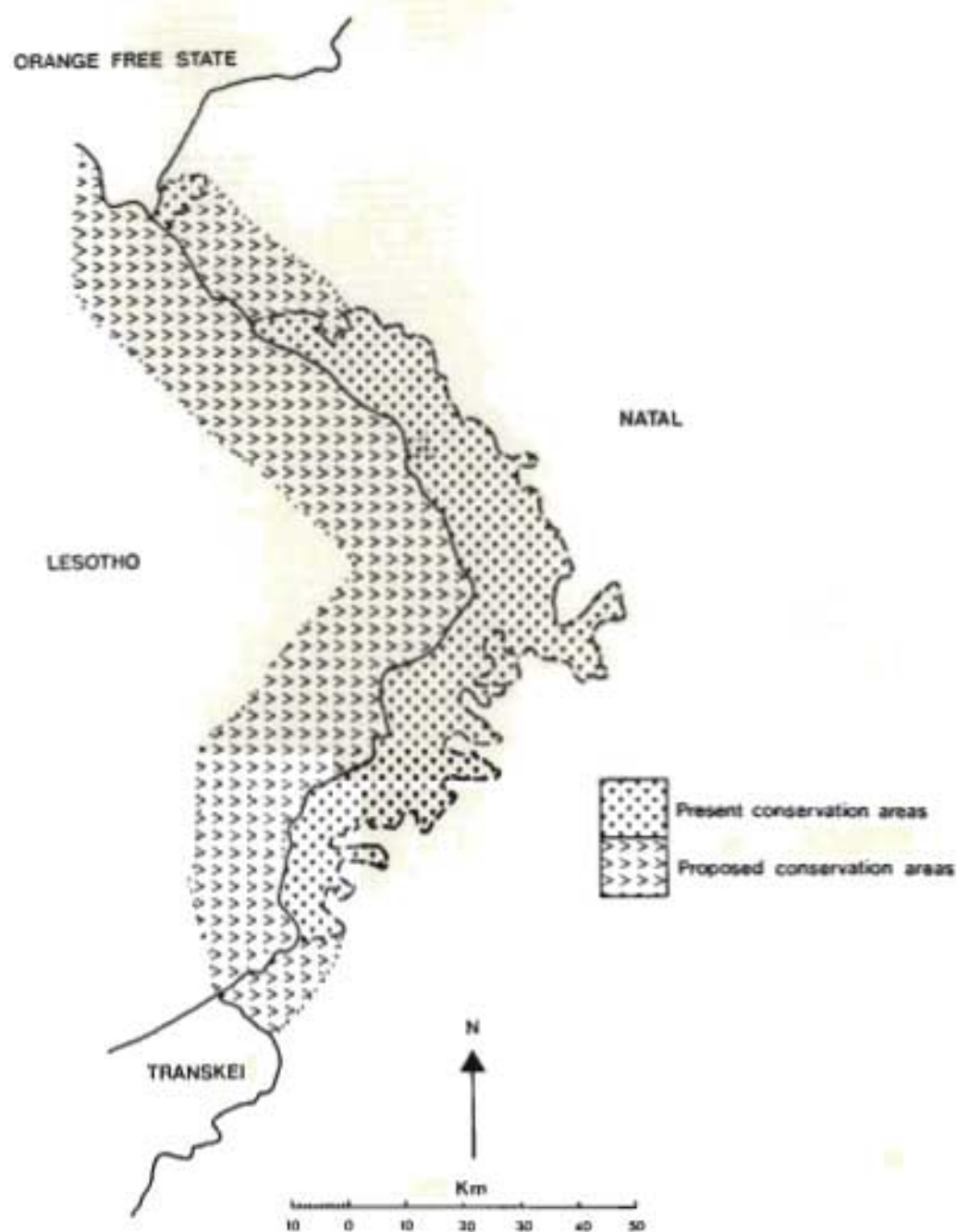
FIGURE 10.7. Present conservation areas in the Natal Drakensberg, and approximate boundaries of proposed new conservation areas in the Lesotho highlands, northern and southern Natal Drakensberg.

ranges of about 40 pairs. In addition, such a conservation area would provide the first real protection for Cape Vulture breeding colonies; 1325 Cape Vultures occur in the High and Little Drakensberg mountain ranges in Natal in 23 breeding colonies and 49 roosts (Brown & Piper in press) and at least another 200 birds occur in the Lesotho area under discussion. Other species listed in the <u>South African Red Data Book - Birds</u> (Brooke 1984) that would benefit from such a conservation area would be the Black Stork, Peregrine Falcon, Mountain Pipit <u>Anthus hoeschi</u> and Yellowbreasted Pipit <u>A.</u> <u>chloris</u>. Finally, the Alpine Vegetation Zone (Killick 1963), which is presently inadequately conserved and managed (Brown & Barnes 1984), would receive protection.

10.7.2 <u>Conservation</u> action

The decline of the Bearded Vulture in southern Africa can be attributed mainly to the methods used by commercial farmers to kill mammalian predators. The entire field of predator control, or more importantly, stock protection, is one which urgently needs investigation in southern Africa to ensure the longterm survival of all scavenging species. At present, some recommendations can be made that would immediately improve the situation.

A. Farmers must be kept regularly up to date with scientifically based information on the animals that occur in their areas. Priority should be given to species that farmers are likely to come into conflict with and species that are likely to be accidentally affected by

farming activities. The lifestyles of these animals should be described, and in particular, any activities of the animals that are of benefit to the farmer should be emphasized. For this purpose I prepared a booklet on the Bearded Vulture based on my research which was published by the Endangered Wildlife Trust (Appendix 10.2, inside back cover). To date about 10 000 copies have been distributed free-of-charge to commercial farmers in areas in which Bearded Vultures are known to occur. The booklets have also been widely distributed in Lesotho.

B. The total banning of the use of all poisons for predator control in all regions of southern Africa should be considered by all conservation agencies, if only to project the official view. It is unlikely, however, that banning of poison will stop its use; poisons have been banned in the Cape Province for a number of years, but there are regular large poisoning incidents reported for Cape Vultures (e.g. Cape Department of Nature and Environmental Conservation press release 20/5/86; Smit 1984; Vernon et al. 1983b). Alternatively, the production of a small pill of poison, such as strychnine, containing a single lethal dose for the animal in question (so that secondary poisoning does not occur), covered in an enteric coat (to contain the smell and taste), being sufficiently costly to deter farmers from scattering them all over their land, and available only after the farmer has attended a predator control course in which the correct use of the pill is explained to prevent the

accidental killing of non-target animals, may be more effective than totally banning all poisons.

C. Gin traps should be totally banned because they are unselective, open to abuse by poachers and ethically unacceptable.

D. The recolonization of areas formerly occupied by Bearded Vultures should be actively promoted by developing community awareness and a conservation pride in the farming districts. This action should be aimed initially at the northeastern Cape Province by the Cape Department of Nature and Environmental Conservation, and in the Natal Little Berg areas by the Natal Parks Board. Incentives could be offered to farming communities that use selective predator-control methods and who have healthy populations of scavenging birds in their districts, and regularly spaced feeding sites could be established where the farmers dumped carcasses and other carrion.

E. The provision of carrion and carcasses at a feeding site in the Giant's Castle Game Reserve should continue on a weekly basis. If logistically possible, this should be done throughout the year, but at least from May to November inclusive. An alternative location should be found for the feeding site, offering good all-round visibility to the birds, and the associated hide should be unobtrusive with a small viewing area of one-way glass. Other conservation areas in the Drakensberg, such

as each Forestry and Natal Parks Board Reserve, should establish feeding sites and record data on the use made of these sites by scavenging species. Finally, these sites should be surrounded by jackal-proof fencing (about 300 x 300 m) to prevent mammals from taking most of the food.

10.7.3 Monitoring the population

The Bearded Vulture population should be monitored on a regular basis.

(a) The fixed-route patrols in the Natal Parks Board areas during which mammal numbers are recorded should be extended to Bearded Vultures, counting and ageing all birds sighted. This would provide long-term information on relative abundances and on the population structure. Other conservation regions in the Drakensberg should do likewise.

(b) To monitor the Lesotho population, road counts along predetermined, popular routes across Lesotho should be co-ordinated by the Vulture Study Group, using reliable observers and recording numbers and ages of Bearded Vultures on standardized data forms. Until such time as sufficient coverage is obtained from private journeys in the area, the Vulture Study Group should organize and subsidize coverage of the area at least every five years. Interested people in Lesotho should be recruited to take part in the road counts.

(c) Finally, the Bearded Vulture breeding population along

the Drakensberg escarpment should be monitored at least every five years. This would best be done from a helicopter, and would entail one flight, starting in the Cape Province south of the Barkly Pass and ending on the western Qwa Qwa-Orange Free State border. The flight, taking one day, should be planned for mid-July. All active Bearded Vulture nest sites should be counted and plotted, and the populations of other large and in some cases endangered species, e.g. Cape Vultures, Black Eagles, Black Storks, should also be monitored.

These monitoring methods are considered to be the most practical means (in terms of manpower, time and costs) of identifying large changes in the Bearded Vulture population. Because of the very rugged terrain, the widely dispersed breeding pairs and the inaccessible nest sites, nothing short of a full-time monitoring programme would provide more accurate information.

TABLE 10.1

Annual total biomass of carrion, carrion available to Bearded Vultures, carrion availability during the season when least food is available and the estimated population density set by the food supply (see Appendix 10.1 for explanation).

Region	Total biomass of carrion (kg/km²)	Biomass available to Bearded Vultures (kg/km²)	Minimum seasonal carrion biomass (kg/km²)	Population density	
				Area/pr (km²)	Inter-pr distance (km)
Cape	400,6	15,1	5,0	97,9	11,2
Natal	476,5	16,4	5,5	90,2	10,7
O.F.S.	525,7	18,5	6,2	79,9	10,1
Conservation areas	182,4	19,9	6,6	74,3	9,7
Lesotho	871,1	21,2	7,1	69,8	9,4

TABLE 10.2

Annual stock losses in commercial farming districts in southern Africa in which Bearded Vultures have been recorded.

Province and district	Animal losses (kg/district/year)						Area (km²)	Biomass (kg/km²)
	Cattle	Sheep	Goats	Horses	Game	Total		
Cape: Barkly East	605150	494410	725	7250	119281	1226816	3582	342,5
Indwe	205800	130795	150	1250	21578	359573	648	554,9
Elliot	469700	408065	1150	4750	64336	948001	1932	490,7
Maclear	665700	378035	1600	7750	80153	1133238	2407	470,8
Lady Grey	302050	148820	2075	1000	43789	497734	1315	378,5
Aliwal North	301000	197260	1400	1750	64069	565479	1924	293,9
Totals	2549400	1757385	7100	23750	393206	4730841	11808	400,6
Natal: Underberg	540750	118300	475	7000	42458	708983	1275	556,1
Impendle	619150	73430	1325	4250	43789	741944	1315	564,2
Mount Currie	1166550	503615	4550	13500	143889	1832104	4321	424,0
Mooi River	60025	111930	950	6500	42890	762520	1288	592,0
Estcourt	1108100	77945	7325	8250	79487	1281107	2387	536,7
Bergville	436750	47215	1000	3750	59474	568189	1786	318,1
Totals	4491550	932435	15625	43250	411987	5894847	12372	476,5
O.F.S.: Harrismith	2122750	782565	3125	39500	254612	3202552	7646	418,9
Bethlehem	2244550	286685	7275	18000	127006	2683516	3814	703,6
Fouriesberg	561400	286685	1400	8250	39361	878546	1182	743,3
Wepener	368550	241115	-	4250	55977	669892	1681	398,5
Zastron	708750	265720	200	4000	59740	1038410	1794	578,8
Totals	6006000	1844220	12000	74000	536696	8472916	16117	525,7

TABLE 10.3

Total stock numbers, annual stock losses and biomass of carrion in Lesotho.

Stock	Stock Numbers	Stock deaths	Total biomass (kg)	Biomass/area (kg/km^2)
Cattle	510000	40800	12852000	424,2
Sheep	1600000	128000	5760000	190,1
Goats	900000	72000	2160000	71,3
Donkeys	100000	8000	2400000	79,2
Horses	115000	9200	3220000	106,3
Totals	3225000	258000	26392000	871,1

TABLE 10.4

Percentage mortality in domestic stock in the districts listed in Table 10.2.

Region	Mortality per species (%)		
	Cattle	Sheep	Goats
Cape	6,5	5,7	10,9
Natal	4,3	5,0	3,8
O.F.S.	5,4	4,4	4,3

TABLE 10.5

Annual mortality of game in the Drakensberg conservation areas.

Species	Numbers	Mortality (kg)	Biomass/area (kg/km^2)
Eland	643	55000	158,5
Grey Rhebuck	386	2412	7,0
Mountain Reedbuck	266	1862	5,4
Oribi	197	697	2,0
Blesbok	89	1223	3,5
Common Reedbuck	60	750	2,2
Red Hartebeest	30	1365	3,9
Total	1671	63309	182,5

TABLE 10.6

Biomass of carrion available to Bearded Vultures (B.V.'s) in different regions per annum.

Region	Mortality/area (kg/km^2)	Biomass left in veld (kg/km^2)	Biomass available to B.V.'s (kg/km^2)
Cape	400,6	130,6	15,1
Natal	476,5	142,5	16,4
O.F.S.	525,7	160,6	18,5
Conservation areas	182,4	182,4	19,9
Lesotho	871,1	174,2	21,2

TABLE 10.7

Biomass of carrion available to Bearded Vultures (B.V.'s) per year in different regions of southern Africa and theoretical population density.

Region	Biomass available to B.V's (kg/km^2)	Population density		Lean-period biomass available to B.V's (kg/km^2)	Population density	
		Area/pr (km^2)	Inter-pair distance (km)		Area/pr (km^2)	Inter-pair distance (km)
Cape	15,1	32,6	6,4	5,0	97,9	11,2
Natal	16,4	30,1	6,2	5,5	90,2	10,7
O.F.S.	18,5	26,6	5,8	6,2	79,9	10,1
Conservation areas	19,9	24,7	5,6	6,6	74,3	9,7
Lesotho	21,2	23,3	5,4	7,1	69,8	9,4

TABLE 10.8

Annual total biomass of carrion from domestic stock deaths, carrion available to Bearded Vultures and the estimated population density set by the food supply in 11 districts in which Bearded Vultures occurred historically.

District	Total carrion biomass (kg/km²)	Biomass available to Bearded Vultures (kg/km²)	Minimum seasonal biomass of carrion (kg/km²)	Population density	
				Area/pr. (km²)	Inter-pair distance (km)
Montagu	51,9	1,9	0,6	770	32,3
Worcester	70,7	2,5	0,8	587	27,3
Swellendam	126,8	4,7	1,6	312	19,9
George	278,1	9,3	3,1	159	14,2
Uniondale	101,7	4,1	1,4	364	21,5
Willowmore	203,6	8,7	2,9	171	14,7
Graaff-Reinet	249,5	10,2	3,4	146	13,6
Adelaide	273,9	10,1	3,4	146	13,6
Bedford	196,0	7,4	2,5	200	16,0
Cathcart	414,2	15,6	5,2	94,5	11,0
Queenstown	377,0	13,4	4,5	110,4	11,9

TABLE 10.9

The farmers' response to the mail questionnaire survey, and the number of farmers reporting Bearded Vultures on their farms.

Province	No. questionnaires reaching farmers	Questionnaires returned		Farmers reporting Bearded Vultures	
		No.	%	No.	%
Natal	1847	789	43	218	28
Cape	908	328	36	90	27
O.F.S.	1455	495	34	59	12
Totals	4210	1612	38	367	23

TABLE 10.10

Causes of mortality in Bearded Vultures as reported by farmers.

Province	Total deaths	Causes of mortality and numbers of Bearded Vultures involved				
		Poisons	Shot	Gin traps	Electrocution	Powerline collisions
Natal	13	10	1	1	0	1
Cape	8	6	1	1	0	0
O.F.S.	1	0	0	0	1	0
Totals	22	16	2	2	1	1
Percent		73	9	9	5	5

TABLE 10.11

Causes of mortality of Bearded Vultures in southern Africa since 1960 from sources other than farmers' reports.

Cause of mortality	No. birds	Region	Source
Confirmed poisoning	1	Natal	P.R. Barnes (Internal NPB report 1969)
	1	Natal	P.R. Barnes (Internal NPB report 1969)
	2	Natal	M.G. Taylor (Internal NPB report 1978)
	2	Natal	R.C. Goetz (Internal NPB report 1978)
	1	Natal	Anon. (1966)
	3	Natal	Symons (1969)
Total	10		
Suspected poisoning	2	Natal	A.E. Root (Internal NPB report 1961)
	2	Natal	P.R. Barnes (Internal NPB report 1969)
	1	Natal	P.R. Barnes (Internal NPB report 1969)
	1	Natal	K. Meiklejohn (Internal NPB report 1969)
Total	6		
Gin trap	2	Cape	A.F. Boshoff (in litt.)
	3	Lesotho	M. van Gelder (Wildlife Society) and the Director, O.F.S. Nature Cons. (in litt.)
	1	Natal	Anon. (1966)
Total	6		
Shooting	1	Natal	Clancey (1963)
	2	Transkei	Anon. (1966)
Total	3		
Grand total	25		

TABLE 10.12

Farmers using poisons for the control of mammalian predators on commercial farmlands adjacent to Lesotho, as indicated by the mail questionnaire survey.

Province	No. questionnaires returned	No. farmers poisoning		Total percent
		Confirmed	Question ignored	
Natal	789	82	22	13,2
Cape	328	26	29	16,8
O.F.S.	495	16	36	10,5
Totals	1612	124	87	13,1

TABLE 10.13

Types of poison used for predator control in commercial farming areas adjacent to Lesotho, as indicated by the mail questionnaire survey.

Poison type	Percentage use
Strychnine	54
Dieldrin	10
"Dip"	7
10-80	3
Toxaphene	3
Not prepared to say	23

TABLE 10.14

Number of farmers of different language groups confusing Bearded Vultures with other birds of prey because of the name "Lammergeyer" or "Lammergeier" being similar to "Lammervanger".

Province	No. questionnaires returned	Farmers confusing Bearded Vultures with other birds of prey		
		No. English	No. Afrikaans	Total %
Natal	789	0	11	1,4
Cape	328	2	37	11,9
O.F.S.	495	0	54	10,9
Totals	1612	2	102	6,5

TABLE 10.15

Harmful activities ascribed to Bearded Vultures by commercial farmers in southern Africa who reported these birds on their farms.

Province	No. farmers reporting Bearded Vultures	Farmers considering Bearded Vultures harmful		No. reports of harmful activities			
		Number	Percent	Kill smallstock	Kill young smallstock	Attack ewes lambing	Attack snow-trapped sheep
Natal	218	3	1,4	1	1	1	-
Cape	90	10	11,1	3	5	1	1
O.F.S.	59	5	8,5	2	3	-	-
Totals	367	18	4,9	6	9	2	1

APPENDIX 10.1

Stock numbers and losses were obtained for 17 commercial farming districts in which Bearded Vultures were recorded during the study period, from Reports on Agricultural and Pastoral Production 1970-71 and 1978-79. The biomass of animals was taken from Meissner et al. (1981) as follows: for cattle, figures for "medium framed" animals were used, adults = 500 kg, young = 200 kg; adult sheep = 50 kg, young = 20 kg; adult goats = 35 kg, young = 15 kg; adult horses = 400 kg, young = 100 kg. It was assumed that 50% of the animals dying were young. No figures for stock losses in horses were given and this was calculated as 2% of the total number of horses per district.

Despite a farm-game questionnaire survey having been undertaken in Natal (Howard & Marchant 1984), no information on game numbers is available, let alone mortality rates. From farms that I have visited in the highland and montane regions adjacent to the Drakensberg, a rough but conservative figure for game biomass is at least 1332 kg/km^2. Assuming a conservative 2,5% mortality per annum, then the biomass of carrion from game would be 33,3 kg/km^2. Because of a lack of data, wherever game animals occur on farmlands, this figure is applied. From these data, the biomass of animals dying on farmlands was calculated (Table 10.2).

In Lesotho, an area of about 30 300 km^2, large numbers of domestic stock occur (Table 10.3) but few game animals

(Ambrose 1976). No figures are available for stock losses in this area, but an approximation can be made by comparing the situation to that in the commercial farming districts already considered (Table 10.4), where mortality ranges between 4% and 11% per annum, but is mainly around 5,5%. Because Lesotho has a generally high altitude, severe climate, overgrazed vegetation, poorly developed animal husbandry and few veterinary facilities, mortality of domestic stock would be considerably higher than on commercial farmlands, and could reasonably expected to be at least 8%. Biomass of Lesotho cattle is taken for "small framed" animals (Meissner et al. 1981), adults = 450 kg, young = 180 kg; adult sheep = 60 kg, young = 30 kg; adult goats = 40 kg, young = 20 kg. Mortality is shared 50:50 between adult and young animals. Donkey and horse masses are 300 kg and 350 kg respectively.

In the Drakensberg conservation areas, although the game-species composition may differ somewhat from area to area, very similar stocking figures (biomass of animals per unit area) have been demonstrated (Rowe-Rowe & Scotcher 1986). The best data available are for the Giant's Castle Game Reserve (Table 10.5) which covers an area of 347 km^2. An adult mortality in game of about 15% was calculated based on (a) stable populations, (b) equal sex ratios, (c) 95% calving success, (d) 60% mortality during the first year, (e) 20% mortality until adult (Eland breed in their fourth year, smaller antelopes in their second to third year). Information is taken from Rowe-Rowe (1982b), Scotcher

(1982), Smithers (1983) and Rowe-Rowe & Scotcher (1986).

These estimations give an idea of the amount of carrion in each area that results from the deaths of the larger animals, but not the amount of carrion that is actually available to Bearded Vultures. The following factors also need to be taken into consideration: (a) competition from more dominant animals such as man, domestic dogs, Cape Vultures and other scavengers, which markedly reduces the amount of carrion available, (b) the fact that not all parts of a carcass can be consumed, and (c) seasonal fluctuations in the food supply, which would dictate that the effective carrying capacity is set during periods when carrion is scarce rather than by a mean annual amount.

The only studies in southern Africa that I am aware of in which the fate of dead animals on farmlands was investigated were those of Jarvis et al. (1974) and Robertson & Boshoff (1986) in the southwestern Cape Province, and my own in South West Africa/Namibia (unpublished data). In the southwestern Cape 22-33% of dead adult sheep were left in the veld by farmers while in South West Africa/Namibia, on 100 farms with an annual mortality of about 600 cattle, 2100 sheep and 550 goats, the proportion of animals of each species left in the veld was 54%, 78% and 61% respectively. In the case of game animals, over 90% of carcasses were left out. On smaller units farmed more intensively and where more farm labour is used, less carrion is left in the veld. Assuming that twice as

many dead animals are used by humans in the commercial farming areas under discussion compared to the situation in South West Africa/Namibia, then 27% of cattle mortalities, 39% of sheep, 31% of goats and 40% of horses and game are left in the veld. In Lesotho the human population was estimated at 1,3 million in 1980 (43 people/km^2) and Jilbert (1982) states that competition for carcasses from herdsmen in Lesotho is increasing with growing human population. For this estimate it is therefore assumed that only 20% of all mortalities are available to avian scavengers in Lesotho. In contrast, in the conservation areas, all mortalities are left in the veld. A certain proportion of the animals die in places inaccessible to Bearded Vultures, particularly the game animals. No data are available, but I assume that this is 5% of all mortalities on farmlands and in Lesotho and 10% in the conservation areas.

Mundy et al. (1983) have shown that for an Impala Aepyceros melampus, 64% of the mass of the animal can be consumed by Gyps vultures. This excludes the skeleton, skin and some other components. Bearded Vultures have little or no competition for the skeletons of animals, and also take some skin and soft tissue in a ratio of about (bone:meat:skin) 14:5:1 (see Chapter 6). Not all bone can be used, however, and the larger the animal that has died the less bone proportionally that can be used. The skeleton makes up about 17% of the mass of an animal (Mundy et al. 1983), and assuming that on average 50% of this can be used (much more in small animals, less in larger animals) and

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that in addition meat and skin are taken in the given ratio and that the remainder of the carcass is eaten by other scavengers, then the food available to Bearded Vultures can be calculated (Table 10.6). This analysis takes no account of other carrion such as hyraxes, baboons, small rodents and birds which contribute over 5% of the overall diet of the Bearded Vulture by numbers (see Chapter 6).

Assuming exclusive ranges and a uniformly distributed supply of food, both temporally and spatially, the theoretical range size needed to support a pair of birds and their offspring can be obtained by calculating the area that would need to be covered to supply 493 kg of food per year, i.e. 1,35 kg of food per day (see Chapter 8). From game deaths in Giant's Castle Game Reserve, monitored as the number of carcasses found per month over six years (1976- 1981), the game deaths in the month with the highest mortality (September) was seven times greater than during the month with the lowest mortality (February). Although Bearded Vultures feed on bones which remain viable as a source of food for long periods and the birds are therefore buffered against short-term fluctuations in food supply, not taking this into consideration, they require about three times as much space to find food during these lean periods. The food supply during these lean periods was therefore taken to calculate the final theoretical range of a pair of Bearded Vultures in each of the areas concerned (Table 10.7).

Chapter 11

SUMMARY

Bearded Vultures have declined markedly in range in southern Africa this century. Before this study their population was generally quoted as between 20 and 120 pairs. They are classed as "rare" in the South African Red Data Book - Birds. Bearded Vultures have been almost eliminated from commercial farming areas, and their distribution is now centred in the Lesotho highlands and along the Drakensberg escarpment. Little information was previously available on the biology of the Bearded Vulture in general and only some anecdotal observations on the southern African population in particular. This research project arose from a need to obtain basic data on the biology and ecology of these birds so that conservation management can be sensibly planned to counter further population declines.

Bearded Vultures were studied from March 1980 to March 1983 throughout their range in southern Africa, but mainly in the Giant's Castle Game Reserve. The area the birds inhabit is mountainous and includes two major ranges, the Drakensberg and the Maluti mountains. The climate is temperate but at high altitudes can be severe. Rain falls mainly in summer and generally decreases from east (2000 mm/year) to west (750 mm/year). During late winter and spring strong winds (Bergwinds) blow from the west and northwest while in summer light winds blow from the east.

Little cultivation has taken place within the Bearded Vulture's range in southern Africa. The natural vegetation consists mainly of grasslands, but at high altitudes (above about 2865 m) low woody heather communities are interspersed with alpine grasses. Domestic stock have mainly or totally replaced the wild ungulates in all areas within the Bearded Vulture's range except in the conservation areas along the Natal Drakensberg. Stocking rates range on average from 9 to 24 cattle per km^2 and 43 to 75 sheep per km^2.

Bearded Vultures have some unusual physical characteristics. They have long wings (wingspan 2,6 m), a high aspect ratio (adults, 8,9:1) and a long tail (47 cm). These features make for good gliding ability, particularly on slope lift, and good manoeuvrability, an essential prerequisite for flying low over rough terrain, accurate bone-dropping and entering small nesting caves, all activities which often takes place in gusty wind conditions. They have a wide gape (70 mm) for the swallowing of large bones and a tufty beard projecting below the lower jaw. The beard probably functions as a tactile organ so that the bird does not insert its head too far into a carcass and thereby risk matting its thickly feathered head with blood.

There was found to be no mensural difference between male and female birds. Young birds were significantly larger than adults in some flight-related characteristics, e.g. outer rectrices and wing area. These gave young birds a lower wing loading and a larger tail area than adults. Young birds have therefore a lower stalling speed and greater

manoeuvrability than adult birds, features thought to be important for birds gaining flying experience.

Adult Bearded Vultures in captivity have pure white feathers on their underparts, whereas in wild birds these regions are a rich rufous colour. The colouring in wild birds is caused by the adhesion of oxides and hydrous oxides of iron. These compounds were found mainly on the outermost layer of feathers and the exposed tips of underlying feathers. They were concentrated mainly in the feather axes and on the barbs and barbules, often forming "blobs" of iron oxide on the ends of barbs and barbules and sometimes binding two or three barbules together. All age classes of Bearded Vultures had iron adhering to their feathers but because the feathers of young birds are darkly pigmented, the rusty colour cannot be seen. The intensity of the rufous colour varied between individuals as well as within individuals over time, mainly following heavy rainfall, when up to 30% of adult birds could become paler than normal. The rufous colour provides adult birds with camouflage against iron-oxide stained cliffs, the coating of iron oxide makes the outer layer of feathers more rigid than those underneath and probably reduces the amount of feather wear that results from contact with the rocks. In addition, the dust from the oxide may act as an ectoparasite control. It is suggested that the iron oxide is acquired passively when the birds come into contact with the chemical on ledges and in caves on cliffs. These areas are often damp, which

facilitates the adhesion of the iron, and this is then spread when the bird preens itself.

Bearded Vultures spend about 77% of the day in foraging-related flight, and can cover up to 430 km per day. During the non-breeding season adult birds were recorded up to 75 km from the nest, and the largest home range was 7468 km^2, although the average was about 4000 km^2. The foraging range was much smaller during the breeding season. During the early nesting period (when a parent was on full-time nest duty) the pair covered about 600 km^2 and during the late nesting period (when the nestling was left unattended) the pair covered about 1300 km^2.

The range of the Bearded Vulture could be divided into four main regions, (a) the territory, up to 500 m about the nest and actively defended against some conspecifics (but not neighbours and immature birds) and Black Eagles, (b) the activities area, about 4,6 km^2 in size and containing the alternate nests, roosts, ossuaries and areas that provide good soaring conditions, (c) the main foraging area, about 300-700 km^2 in size. This is the area in which the birds forage during the early nesting period and in which low and medium-height searching usually takes place and (d) the home range, incorporating the entire area covered by a pair of adult birds.

Data obtained on home ranges from conventional marking-resighting techniques, e.g. leg rings and wing windows, were found to be inadequate, and only once radiotelemetry was introduced could the movements of these birds be reasonably

determined. This casts doubt on the reliability of home range data obtained by conventional methods in other studies, particularly where species are wide-ranging and observers are few.

High-intensity foraging constituted 35% of all diurnal activities of Bearded Vultures away from the nest and an additional 33% was of a lower foraging intensity. Three main foraging methods were identified, (a) low searching, usually 2-4 m above the ground, (b) medium-height searching, usually at 20-70 m above the ground and (c) high searching, usually above 1000 m above the ground. Medium-height searching was most common (58% of all searching) followed by low searching (36%).

Adult Bearded Vultures foraged either singly or in pairs. During the non-breeding season about 55% of adults were in pairs, during the breeding season 44% were paired. During the breeding season off-duty birds from neighbouring nests often paired up to forage together. Young birds foraged with adults, followed Cape Vultures and formed young-bird groups of two or three. During the breeding season, fewer young birds were seen with adults than during the non-breeding season, and the other groupings of young birds were more common.

Bearded Vultures chose bones, particularly if old and dried, in preference to fresh meat or to feeding from a fresh carcass. At carcasses cleaned of most soft material by Cape Vultures, Bearded Vultures disarticulated the bones and

flew off with them. Limb bones were taken first followed by ribs and vertebrae. I estimated that the diet of Bearded Vultures consists of about 70% bone (with the marrow), 25% meat and 5% skin. This diet provides about 15% more energy than does the equivalent weight of red meat. In addition, bones remain viable as a source of food for weeks and perhaps months. From 683 identifiable prey items, domestic stock (mainly sheep) were found to make up at least 75% of their diet. All food is scavenged and I found no evidence to suggest that Bearded Vultures kill prey.

The dropping of bones by Bearded Vultures, to break them into sizes that could be swallowed and to allow access to the marrow, was recorded regularly. Bone-dropping sites (ossuaries) were usually slabs of smooth rock with a mean size of about 2000 m^2 on a gentle slope facing mainly between west-northwest and northeast. The mean number of drops per bone before it broke was 6, but up to 21 were recorded. Although generally non-aggressive, Bearded Vultures were dominant over all birds in the Drakensberg except Cape Vultures and Black Eagles, and adults were dominant over young birds.

Bearded Vultures breed mainly in small caves located high up on large cliffs. Each pair had on average three nests (range 2-8) which were used in rotation. Nests faced mainly between east and south to escape the westerly Bergwinds, but in protected sites this was less important. Courtship flights began in May, were initiated by the male and were less demonstrative than those described for the

European birds. Nest building, allopreening and copulation started at about the same time. All building material was brought by the male; the female brought some of the nest lining and arranged the nesting material.

To the east of the species' range egg-laying took place in mid-June, while to the west it was recorded for the last two weeks of May. This is probably correlated with the timing of ungulate mortalities in the two regions. Most clutches (89%) were of two eggs, the remainder were one-egg clutches. The interval between laying of the eggs was usually 3-5 days. Incubation during the day was evenly shared by the parents but the female incubated at night. The incubation period was 56-57 days. Only one nestling was produced per nest. Little sibling aggression took place, but the older nestling was able to obtain all the food offered by the parents and the younger nestling died usually within two days.

The nestling period was about 124-128 days, but some birds flew earlier. The nestling period was divided into three stages, (a) the early nestling period (first 40 days) during which the nestling was closely brooded, (b) the mid-nestling period (days 40-90) during which the percentage nest attendance steadily decreased and (c) the late nestling period (day 90 to first flight) during which the nestling was visited by the parents only to provide food. Both parents brooded the nestling during the early nestling period, the female bird at night. Food was brought to the

nest only once the first egg had hatched. Thereafter it was stored in the nest cave, sometimes in large amounts. Food was carried in the feet, not regurgitated. Both parents fed the nestling. Both parents left the nesting area for the first time when the nestling was about 58 days old. By the time the nestling was 80 days old the parent birds spent about 50% of the day away from the nest area and the female no longer roosted in the nest at night.

The first flight by young birds was short, and adults brought food to wherever the young bird was. By about the third week out of the nest young birds were flying up to 800 m from the nest and by the first month they spent about 40% of the day in flight and moved up to 3 km from the nest. At 2-3 months out of the nest young Bearded Vultures were regularly covering an area of about 42 km^2, at 3-4 months their range was 78 km^2, and at 4-6 months it was 168 km^2. From about two months out of the nest young birds also accompanied their parents on long foraging trips out of their normal range. Young birds continued to occupy their natal nests at the start of the next breeding season, and adults made no attempt to chase young birds away. Once independent, young birds moved about constantly, settling in an area for a few days to a few months (presumably depending on the food supply) before moving to a new area. The mean distance moved between areas was 31 km (range 22-38 km). Young birds tended to congregate in areas where the density of adult birds was low.

During this study all pairs monitored (40 pair-years)

attempted to breed every year. The breeding succees was 0,89 young/pair/year.

Bearded Vultures spent 80% of the day in flight, 16% perched on cliffs and 4% on the ground. Detailed time-activity patterns were obtained for birds away from the nest during the non-breeding season and during three different periods of the breeding season. Energy budgets were calculated from these activity patterns. For an adult during the non-breeding season, the total daily energy budget (DEB) was calculated to be about 2188 kJ, translating to about 465 g of food per day. During the incubation and close-brooding periods the DEB per adult bird was lower at about 1740 kJ (about 365 g of food per day) because of long inactive periods on the nest, while during the late nestling period, when both parents were foraging, the DEB rose to 2233 kJ (about 475 g of food per day). Taking into account the energy required to lay a two-egg clutch and the amount of food needed to feed a nestling to independence, a breeding pair of Bearded Vultures would need about 493 kg of food per year. It was found that the periods of greatest food requirements of Bearded Vultures coincided closely with the periods of greatest food abundance.

The post-1980 breeding distribution of the Bearded Vulture in southern Africa covers an area of about 34 000 km², and the birds range over an area almost three times larger. The breeding population was estimated as 203 pairs, with 122 pairs in Lesotho, 42 pairs in Natal (37 along the

Drakensberg escarpment), 17 pairs in the Transkei, 16 in the Northeastern Cape, four in QwaQwa and two in the Orange Free State. The ratio of adult to non-adult birds was 1:0,55, giving 225 young birds and a population total of 631 Bearded Vultures in southern Africa. Subadult birds formed about 3,3% of the population. The mortality of young birds was about 88,5% and adult survival was about 94,8% per year. The average longevity of adults as adults was calculated to be 19 years and the mean total life was 24 years.

The decline in the Bearded Vulture population in southern Africa is parallelled by that of all other scavenging raptors. The population at the turn of the century numbered probably about 330 pairs. The present population represents about 62% of the historic one. Compared to other scavenging raptors, e.g. Whiteheaded and Lappetfaced Vultures, Bateleurs and Tawny Eagles, this may seem encouraging, but if this population had occurred on commercial farmlands it would undoubtedly be extinct today.

The amount of food available to Bearded Vultures in different parts of their range was found to be remarkably similar. In Lesotho the mean biomass of carrion actually available to the birds was 21 kg/km^2/year and during the period of the year when food was most scarce, was three times less abundant. This gave a theoretical population density of 14 pairs/1000 km^2, while for the adjacent commercial farmlands the theoretical densities were 10-12 pairs/1000 km^2. In those districts in which Bearded Vultures have become extinct during this century, only in the extreme

southwestern Cape is the food supply insufficient to support a population of Bearded Vultures. In areas further east the districts should support on average between six and 11 pairs per 1000 km^2. In most regions, therefore, the food supply was considered not to be responsible for the decline of the Bearded Vulture population.

Poisons used on farmlands were found to be the main cause of mortality in Bearded Vultures, and this factor is regarded as being responsible for the decline in the population. On average about 34% of farmers set poison baits for mammalian predators. About 63% of farmers used small blocks of meat and the carcasses of small birds and distributed these over their farms. The remainder placed the poison directly into a large-animal carcass. Within the home range of a pair of Bearded Vultures in Natal, an average of 42 farmers would set out poison baits, in the Cape Province about 24 and in the Orange Free State about 16. The methods of foraging used by Bearded Vultures make them particularly vulnerable to finding the farmers' poison baits and birds cannot be expected to survive for long in these areas.

The names "Lammergeier" and "Lammergeyer" were confused with "Lammervanger" by 6,5% of farmers (n = 1612). This was particularly apparent in the Afrikaans communities. The names Bearded Vulture and Baardaasvoël should be promoted to prevent confusion with species of raptors that may prey on some domestic stock. On average 5% of farmers who saw Bearded Vultures on their farms reported some harmful

activity ascribed to the birds, mainly the killing of young smallstock. No farmer had actually ever witnessed such an attack, and herders in Lesotho, where Bearded Vultures are allowed to move undisturbed through flocks of lambing sheep, said that they never caused any damage.

An artificial feeding site has been in operation in the Giant's Castle Game Reserve since 1966. This may account for the high density of Bearded Vultures nesting in the Giant's Castle area, although less than 30% of the Bearded Vultures attracted to the site actally fed (compared to 71-96% in other species). The feeding site does not succeed in keeping birds within the conservation area, but may be important in providing food when natural sources cannot be found. Of particular importance is the educational potential of the feeding site and observation hide.

In conclusion, a number of management recommendations are made. Of particular importance are the control of poisons on farmlands, the establishment of a conservation area in Lesotho so that the entire ranges of some pairs can be protected, the establishment of breeding pairs in areas of former occupation and the continued provision of carrion in Giant's Castle and other reserves and conservation areas. The population should be monitored regularly, at least every five years, by helicopter along the Drakensberg escarpment and by road counts in Lesotho. Adequate protection of the Bearded Vulture's habitat and the successful control of the use of poisons on farmlands would benefit not only these magnificent birds but also many other vulnerable species.

APPENDIX 1

English and scientific names of animals mentioned in this
thesis.

Birds

Fulmar	*Fulmarus glacialis*
White Pelican	*Pelecanus onocrotalus*
Black Stork	*Ciconia nigra*
Marabou Stork	*Leptoptilos crumeniferus*
White Stork	*Ciconia ciconia*
Bald Ibis	*Geronticus calvus*
Secretarybird	*Sagittarius serpentarius*
California Condor	*Gymnogyps californianus*
Andean Condor	*Vultur gryphus*
Osprey	*Pandion haliaetus*
Blackshouldered Kite	*Elanus caeruleus*
Yellowbilled Kite	*Milvus migrans parasitus*
Palmnut Vulture	*Gypohierax angolensis*
African Fish Eagle	*Haliaeetus vocifer*
Bald Eagle	*Haliaeetus leucocephalus*
Egyptian Vulture	*Neophron percnopterus*
Bearded Vulture	*Gypaetus barbatus*
Hooded Vulture	*Necrosyrtes monachus*
Whitebacked Vulture	*Gyps africanus*
Rüppell's Griffon	*Gyps rueppellii*
European Griffon	*Gyps fulvus*
Cape Vulture	*Gyps coprotheres*
Lappetfaced Vulture	*Torgos tracheliotus*
Whiteheaded Vulture	*Trigonoceps occipitalis*
Blackbreasted Snake Eagle	*Circaetus gallicus*
Brown Snake Eagle	*Circaetus cinereus*
Bateleur	*Terathopius ecaudatus*
Gymnogene	*Polyboroides typus*
African Marsh Harrier	*Circus ranivorus*
Black Harrier	*Circus maurus*
Goshawk	*Accipiter gentilis*
African Goshawk	*Accipiter tachiro*
European Sparrowhawk	*Accipiter nisus*
Redbreasted Sparrowhawk	*Accipiter rufiventris*
Ferruginous Hawk	*Buteo regalis*
Mountain Buzzard	*Buteo oreophilus*
Jackal Buzzard	*Buteo rufofuscus*
Augur Buzzard	*Buteo augur*
Lesser Spotted Eagle	*Aquila pomarina*
Tawny Eagle	*Aquila rapax*
Imperial Eagle	*Aquila heliaca*
Wahlberg's Eagle	*Aquila wahlbergi*
Golden Eagle	*Aquila chrysaetos*
Black Eagle	*Aquila verreauxii*

African Hawk Eagle (Bonelli's Eagle)	Hieraaetus fasciatus
Ayres' Eagle	Hieraaetus ayresii
Booted Eagle	Hieraaetus pennatus
Longcrested Eagle	Lophaetus occipitalis
Crowned Eagle	Stephanoaetus coronatus
Martial Eagle	Polemaetus bellicosus
Lanner Falcon	Falco biarmicus
Peregrine Falcon	Falco peregrinus
Rock Kestrel	Falco tinnunculus
Redlegged Partridge	Alectoris rufa
Rock Pigeon	Columba guinea
Wood Pigeon	Columba palumbus
Barn Owl	Tyto alba
Black Swift	Apus barbatus
Pied Crow	Corvus albus
Black Crow	Corvus capensis
Whitenecked Raven	Corvus albicollis
Mountain Pipit	Anthus hoeschi
Yellowbreasted Pipit	Anthus chloris
Zebra Finch	Poephila guttata

Mammals

Chacma Baboon	Papio ursinus
Vervet Monkey	Cercopithecus pygerythrus
Brown Hyaena	Hyaena brunnea
Spotted Hyaena	Crocuta crocuta
Caracal	Felis caracal
Blackbacked Jackal	Canis mesomelas
Genet	Genetta sp.
Rock Hyrax	Procavia capensis
Black Wildebeest	Connochaetes gnou
Red Hartebeest	Alcelaphus buselaphus
Blesbok	Damaliscus dorcas phillipsi
Red Duiker	Cephalophus natalensis
Common Duiker	Sylvicapra grimmia
Klipspringer	Oreotragus oreotragus
Oribi	Ourebia ourebi
Impala	Aepyceros melampus
Grey Rhebok	Pelea capreolus
Eland	Taurotragus oryx
Common Reedbuck	Redunca arundinum
Mountain Reedbuck	Redunca fulvorufula

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A STUDY OF THE BEARDED VULTURE GYPAETUS BARBATUS

IN SOUTHERN AFRICA

by

Christopher Justin Brown

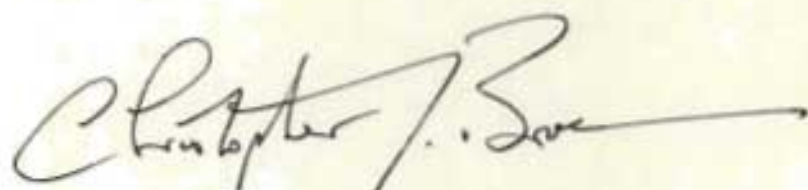Submitted in partial fulfilment of the

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DECLARATION

This thesis, unless specifically indicated to the contrary in the text, is my own original work. It is being submitted for the degree of Doctor of Philosophy in the University of Natal, Pietermaritzburg. It has not been submitted for a degree to any other University.

Christopher Justin Brown

15th day of January, 1988