THE ECOLOGY AND ETHOLOGY OF BALL-ROLLING

DUNG BEETLES (COLEOPTERA : SCARABAEIDAE)

by

GEOFFREY DARRYL TRIBE

Submitted in partial fulfilment of the requirements
for the degree of Master of Science in Agriculture
in the Department of Entomology,
Faculty of Agriculture,
University of Natal

PIETERMARITZBURG.

January, 1976.

THE ECOLOGY AND ETHOLOGY OF BALL-ROLLING DUNG BEETLES
(COLEOPTERA : SCARABAEIDAE)

ACKNOWLEDGMENTS

REFERENCES.

I N T R O D U C T I O N.

This investigation into the ecology and ethology of some ball-rolling dung beetles of southern Africa was carried out as part of a research programme for the Dung Beetle Research Unit, C.S.I.R.O., Division of Entomology, Canberra, A.C.T. based in Pretoria.

The introduction of cattle into Australia in the eighteenth century without their associated dung beetle fauna has created an ecological imbalance as the indigenous Australian dung beetles are mostly incapable of utilising the bovine dung for nesting. Adapted to feeding and breeding on the dry, pellet-like marsupial dung, the indigenous fauna find the moister, less fibrous cow dung unattractive (Bornemissza, 1970; Waterhouse, 1974).

As a result most cow pads dry out and remain unchanged for months before eventually being eroded by weathering or termite attack (Ferrar and Watson, 1970). The significance of this may be seen when one takes into account the thirty million cattle in Australia which drop an average of twelve pads per animal per day, resulting in a loss in grass cover of 5 to 10% an acre per animal per year (Bornemissza, 1960). The zone of tall, rank herbage which develops at the periphery of each dung pad is avoided by cattle and the cumulative effect of the dung pads over a period of time may reduce the effective area of pasture by 20 percent of each acre per year per bovine (Waterhouse, 1974).

These fresh, undisturbed dung pads are the habitat of dung breeding flies which lay their eggs in large batches in the dung. The hatching maggots feed on the dung for six to eight days before they pupate in the soil (Hughes et al, 1972). Thus the native bushfly, _Musca vetustissima,_ and the buffalo fly, _Haematobia exigua_ accidently introduced from Timor Island, are exceedingly abundant in Australia and are serious

blood feeding pests of cattle (Hughes, 1970).

In Africa, where the large herbivores evolved, similar
dung breeding fly species have not become such serious pests
even though they are prolific breeders, because the dung
beetles destroy much of their habitat by burying fresh dung
pads within 48 hours (Bornemissza, 1970).   This results also
in the death of any eggs laid by the flies before the beetles
arrive and those flies which manage to survive from pads
attacked by dung beetles are stunted in size and show a
resultant loss of vigour (Tyndale-Biscoe and Hughes, 1969).

It has been shown experimentally that dung dropped by
a grazing animal is of little nutritional value to plants in
the absence of dung beetles (Bornemissza and Williams, 1970).
Dung beetle activity increases the soil fertility through
the burial of dung, improves the permeability of the soil to
water and increases soil aeration.   Dung beetles have also
been shown to achieve some control of parasitic helminth
worms by reducing the number of infective larvae that reach
the pasture from the dung pad (Waterhouse, 1974).   Another
aspect of fly control is the introduction of predatory Histerid
beetles into Australia.   These beetles feed on maggots in
the dung, but due to the limited searching ability of both
beetles and their larvae they are able to account for only
30-50% of the maggots in a cow pad (Bornemissza, 1967).

Dung beetles carry a number of mites and fungi as well
as endoparasitic nematodes.   Besides these larger, visible
organisms, a beetle may carry serious diseases such as foot
and mouth or rinderpest which could wreak havoc amongst cattle
on a continent thus far isolated from such diseases.   As
explained by Waterhouse (1974), in order to overcome this
possibility dung beetle eggs, surface sterilized, are sent to
Australia instead of the adult beetles.   Further strict
quarantine measures are encountered in Australia where the
eggs are transferred to artificially produced brood-balls.
The transplantation of eggs instead of adults necessitates

the breeding of the selected species in a laboratory.

Selection of candidate beetles for transfer to Australia depends on the biology and ecology of the various species. The amount of dung buried by a beetle, its fecundity, its geographical range and climatic conditions are all taken into account (Bornemissza, 1970).

Furthermore, there are a number of theoretical complications which could arise from the introduction of foreign beetles. The present ecological balance in Australia could be upset by introduced beetles supplanting or displacing the indigenous dung beetle fauna (Bornemissza, pers. comm.) or a predator of an indigenous insect changing from its normal diet to feeding on the introduced beetles. This could result in a species, previously under control by predation, reaching pest status. The recycling of nutrients, if exceptionally successful, could possibly change parts of the Australian landscape by encouraging plant growth, this in turn affecting the ecological balance of the fauna in those areas.

The work from which this thesis is derived concerns the ball-rolling beetle species (excluding the genus Sisyphus) which were set aside initially because of the difficulty experienced in breeding them. Thus the work carried out in the Dung Beetle Research Unit in Pretoria was divided superficially into two sections : one dealing with breeding methods, beetle collecting and the production of eggs for airfreight to Australia; the second with research into the ecology of telecoprid (ball-rolling) species for the selection of suitable species for Australia. Being an applied project, the former section required that over three-quarters of the time and energy be devoted to it. Also due to the relatively short period during which the ball-rolling species appear on the surface, both sections had to be dealt with simultaneously.

Although only five species from four genera have been investigated fairly intensively, in most instances the information obtained applies to the genera as a whole and may

be /....

be used when evaluating other species of these genera as candidates for transfer. For effective control of flies in Australia it will be necessary to introduce as many species as possible from the interacting complex of dung beetle species present in any one geographical area, of which the telecoprids form only a fraction of the total number of species.

The ball-rolling beetles were selected for study because of their abundance and marked efficiency, their unique ball-rolling behaviour which sets them apart from most other dung beetle species, and because they inhabit even extremely low rainfall areas.

This investigation is an attempt to set out as precisely as possible the factors affecting the distribution and abundance of southern African dung-rolling beetles, so that their potential as possible export species may be evaluated and similar habitats in Australia may be pinpointed as release sites. As previous attempts to breed telecoprids in captivity failed, it was also necessary to discover why they are so difficult to breed with the aim of developing methods to overcome this. As virtually no previous work has been done on the factors limiting dung beetle numbers, it is hoped that this investigation will be a significant contribution to the Dung Beetle Programme and form a basis from which to launch further studies of selected aspects.

As there were no controlled environment rooms at the Dung Beetle Research Unit in Pretoria more emphasis was placed on field studies. Field trips, however, were largely limited to the collecting of breeding stock which unfortunately resulted in many important and interesting avenues of investigation being closed to study, as little time was allowed for conducting field research. For the same reason, replication of many field observations e.g. diel flying times, have still to be completed. Furthermore, the lack of technical staff resulted in much valuable time having to be spent on trivial tasks.

Most of the field data were recorded in the Natal and Zululand Game Reserves, mainly Mkuzi Game Reserve.

CHAPTER I.

TAXONOMIC DIFFERENTATION.

The vast majority of species of the subfamily
Scarabaeinae are coprophagous and are morphologically adapted
for feeding on vertebrate excrement in both adult and larval
forms (Halffter and Matthews, 1966). Adult dung beetles
ingest only the liquid or colloidal constituents of the dung
by squeezing portions of moist dung between highly specialised
membranous mandibles and ingesting the expressed juice, whilst
the larvae feed on whole dung particles with the aid of their
chewing mouthparts (Waterhouse, 1974).

The superfamily Scarabaeoidea is characterised by the
larvae being positioned in or near their food source which
has resulted in the larvae of most members of this superfamily
being relatively immobile (Imms, 1973). Adult dung beetles
prepare a ball or dough of dung which is buried in the soil
and in which an egg is laid. On hatching the larva feeds
on the dung with which it is in immediate contact, until
eventually all that remains of the ball is a dried shell
within which the larva pupates.

Dung beetles of the subfamily Scarabaeinae may be
divided into three groups depending on their nesting behaviour
(Halffter and Matthews, 1966; Bornemissza, 1969).

Paracoprids : Construct their nests under or
beside the dung source by excavating
tunnels in which they pack dung.

Endocoprids : Excavate a chamber in the dung pad
itself, forming brood-balls within
this chamber.

Telecoprids : Cut off a portion of dung from the
dung pad, mould it into a ball and
roll it some distance from the dung
source, finally burying it in the
soil.

According to Ferreira (1972), there are some 71 genera of dung beetles of the subfamily Scarabaeinae in Africa, south of the Sahara. The following table gives a rough breakdown of these genera, which is necessary for an understanding of the ball-rolling species :

TABLE 1:   The numerical separation of southern African dung beetles into genera and species according to their nesting behaviour.

Nesting Behaviour	Genera	Species	Majority of Species
Paracoprids	56	1568	Crepuscular
Telecoprids	13	219	Diurnal
Endocoprids	2	6	Diurnal
TOTAL	71	1793	Crepuscular

The estimates in Table 1 are based both on published and unpublished data and because many of the genera are currently under revision, they are subject to alteration, but the main trends will probably remain similar. Both paracoprids and telecoprids have species which are entirely crepuscular or diurnal and there is no distinct dividing line between activity peaks and nesting behaviour.

The largest number of species (914, with 64 varieties) occur in the genus Onthophagus and there are also several monospecific genera e.g. Circellium (Ferreira, 1972).

The most important telecoprid genera in southern Africa have a distribution over a number of Zoogeographical regions, while other genera are entirely Ethiopian in origin (Halffter and Matthews, 1966). The number of species occuring in each genus are recorded in Ferreira (1972) and are listed in Table 2.

TABLE 2: The most important southern Africa telecoprid genera showing the number of species in each genus and the Zoogeographical regions over which each genus occurs.

Genus	No. Species	Zoogeographical Regions
Scarabaeus	72	Ethiopian, Palearctic, Oriental
Kheper	28	Ethiopian, Palearctic, Oriental
Gymnopleurus	59	Palearctic, Ethiopian, Oriental
Sisyphus	25	Ethiopian, Palearctic, Oriental, Mexican and Nicaraguan areas
Anachalcos	8	Ethiopian
Sceliages	6	Ethiopian
Pachysoma	10	Ethiopian
Pachylomera	2	Ethiopian
Neateuchus	2	Ethiopian
Circellium	1	Ethiopian

The genus Kheper is present in Africa and Asia; the African species are much more numerous (Janssens, 1940).

The present study deals mostly with the two genera, Scarabaeus and Kheper, which are very closely related, Kheper sometimes being regarded as a subgenus of Scarabaeus (Halffter and Matthews, 1966) although Balthasar's (1965) division of Scarabaeus into the subgenera Scarabaeus and Scarabaeolus is not recognised by others (Zur Strassen, 1967).

In the following shortened key (after Ferreira, 1972) all three of these genera are recognised, mainly because they form fairly distinct geographical groups within southern Africa (Chapter 2) :

Presence of a single terminal claw on all tarsi ....
genus KHEPER Janssens

Presence /....

Presence of two terminal claws on all tarsi; middle
  · tibiae with a single spur ....
                            subgenus <u>SCARABAEUS</u> Linnaeus
Presence of two terminal claws on all tarsi; middle
      tibiae with two spurs (the second spur as a result
      of the projection of the distal part of the tibia
      itself) ....   subgenus <u>SCARABAEOLUS</u> Balthasar.

Table 3 lists all telecoprid species investigated
although not all species were studied to the same extent.
<u>Kheper nigroaeneus</u> is the species with which this study is
mainly concerned, although fairly comprehensive studies of
<u>K. subaeneus, K. lamarcki, Garreta nitens</u> and <u>Allogymno-
pleurus thalassinus</u> were also made.   Comparisons are made
between these species and the other species listed in Table
3 and a detailed comparative list concerning pheromone
release has been compiled in Chapter 9 (page 131); thus Table
3 was compiled in exactly the same sequence as Table 21.
Chapter 10 is concerned with two specialised genera represented
by the paracoprids <u>Coptorhina klugi</u> and <u>Coptorhina auspicata</u>
and the telecoprids <u>Pachylomera femoralis</u> and <u>Pachylomera
opaca.</u>

Distribution maps were not compiled for all the species
listed, due either to the lack of sufficient recorded
localities of many species or uncertainties in identification.
Many species were studied in captivity, with slow but success-
ful breeding of several species occurring during this period.
A number of paracoprid species are mentioned in various
chapters when their presence is of concern to the investigated
telecoprid species.

The average length of each species is measured from the
central clypeal indentation to the posterior abdomen while the
average width is measured at the widest part of the abdomen.
These are not envisaged as taxonomic characters but merely
the average size of the various species which becomes
important in the following chapter.

                    <u>TABLE 3</u>: /....

TABLE 3:   The average sizes of telecoprid species studied.

Species	Average Length (cm)	Average Width (cm)	Number Examined	Colour
KHEPER:				
K. nigroaeneus (Boheman)	2,62	1,63	47	Bronze
K. bonellii (MacLeay)	2,52	1,59	38	Black
K. subaeneus (Harold)	3,08	1,96	44	Bronze
K. lamarcki (MacLeay)	3,41	2,06	48	Black
K. pustulosus (Gerstaecker)	2,72	1,70	26	Bronze
K. aegyptiorum (Latreille)	2,98	1,86	16	Green
K. aeratus (Gerstaecker)	3,07	1,97	8	Bronze
K. festivus (Harold)	3,00	1,79	12	Bronze
K. paganus (Harold)				Bronze
K. laevistriatus (Fairmaire)	3,28	2,05	3	Black
K. cupreus (Castelnau)	3,01	1,91	15	Bronze
K. prodigiosus (Erichson)	3,65	2,23	17	Black
SCARABAEUS :				
S. goryi (Castelnau)	3,10	2,04	42	Black
S. deludens Zur Strassen	2,63	1,67	29	Black
S. zambesianus Péringuey	2,40	1,62	26	Black
S. satyrus (Boheman)	2,43	1,53	20	Black
S. galenus (Westwood)	2,50	1,52	40	Black
S. westwoodi Harold	2,74	1,64	6	Black
S. rugosus (Hausmann)	2,05	1,38	56	Black
S. savignii MacLeay	2,61	1,67	4	Black
S. suri (Hausmann)	1,92	1,25	37	Black
S. ambiguus (Boheman)	1,78	1,13	52	Black
S. viator Péringuey	1,92	1,23	19	Black

TABLE 3: (continued)

Species	Average Length (cm)	Average Width (cm)	Number Exam- ined	Colour
S. ambulans (Boheman)	1,77	1,22	2	Black
S. natalensis zur Strassen	1,68	1,07	11	Black
S. basuto zur strassen	1,64	1,00	6	Black
S. funebris (Boheman)	1,60	1,00	21	Black
S. bohemani (Harold)	1,17	0,65	44	Black
S. piliventris zur Strassen	1,54	1,15	3	Black
S. alienus Péringuey	1,97	1,20	2	Black
S. catenatus (Gerstaecker)	2,73	1,71	6	Black
S. rusticus (Boheman)	2,06	1,36	4	Black
S. caffer (Boheman)				
S. fritschi Harold	1,85	1,02	2	Black
SCARABAEOLUS :				
S. flavicornis (Boheman)	1,58	0,92	30	Black
S. canaliculatus Fairmaire	1,71	0,97	11	Black
S. damarensis Janssens	1,24	0,68	23	Black
S. intricatus (Fabricius)	1,21	0,67	6	Black
S. inquisitus Péringuey	0,97	0,57	5	Black
S. parvulus (Boheman)	0,83	0,48	50	Black
S. inoportunus Ferreira	1,06	0,60	4	Black
S. clanceyi Ferreira	0,90	0,50	1	Black
S. anderseni Waterhouse				Black
S. ebenus (Klug)				Black
Neateuchus proboscideus (Guérin)	2,92	1,77	11	Black
Drepanopodus costatus (Wiedeman)	1,75	0,94	34	Black
Sceliages hippias Westwood	1,48	1,01	3	Black

TABLE 3: (continued)

Species	Average Length (cm)	Average Width (cm)	Number Examined	Colour
Anachalcos convexus (Boheman)	2,25	1,59	8	Bronze
Garreta nitens (Olivier)	1,50	1,00	32	Green
Garreta unicolor Fahraeus	1,81	1,21	25	Black
Gymnopleurus virens Erichson	0,94	0,63	18	Maroon
Allogymnopleurus thalassinus Klug	1,29	0,85	26	Bronze
Pachylomera femoralis Kirby	3,95	2,39	34	Black
Pachylomera opaca Lansberge	2,86	1,70	32	Black
*Coptorhina klugi Hope	1,17	0,85	2	Black
*Coptorhina auspicata Péringuey	1,76	1,12	5	Black

*Paracoprid species

In the following chapters several paracoprid species
will be mentioned among which the genus Onthophagus features
prominently.   A division was made within this genus by
separating from it the subgenus Proagoderus owing to distinct
differences between the two.   The brightly coloured
Proagoderus species, consisting mainly of shades of blues and
greens, are day flying while the majority of species of the
genus Onthophagus, excluding the subgenus Proagoderus , are
dull brown or black in colour and crepuscular in activity.

Other important paracoprid species which occur in large
numbers in the study areas belong to the genus Phalops which
are usually dull green or blue in colour and diurnal in
activity.

Since dung is voided throughout the year, with relatively small seasonal fluctuations in amount and consistency, it would seem to follow that dung beetles would be in evidence throughout the year in the various areas - but this is not so. At the approach of winter there is a dramatic drop in beetle activity, most species disappearing altogether in winter. This led many early hunters to the conclusion that "the droppings of elephants never attract scarabs or other scavenging beetles; they are almost without scent and resemble turf in composition" (Shortridge, 1934). Dung dropped in winter certainly is not as strong smelling as that voided in the summer season. This is probably due to the rapid growth of plants in summer, the higher temperatures and the green herbage resulting in a corresponding change in the dung composition and odour.

At the start of summer there is an even more dramatic upsurge in beetle activity which follows almost immediately after the first substantial rainfall.

CHAPTER 2.

GEOGRAPHIC DISTRIBUTION.

2.1 TELECOPRID DISTRIBUTION :

The distribution of the Kheper genus in southern Africa is largely limited to a belt stretching from the northern Transkei, through Natal, Mozambique and the eastern and northern Transvaal, Botswana, Rhodesia, the northern South West Africa and into southern Angola (figs. 1 - 6).   An exception to this distribution appears for K. bonellii (fig. 6) where a population occurs today along the south-west Cape coast and they are able to exist because of the unique conditions which are to be found there (Section 2.2.4).

Most species of the subgenus Scarabaeus, especially the larger species (figs. 7 - 10), follow this distribution quite closely but the subgenus Scarabaeolus is confined largely to the drier north western Cape Province and southern South West Africa.   Three typical species of this subgenus, S. flavicornis, S. damarensis and S. parvulus, have their distributions plotted in figures 11, 12 and 13.   However, certain species of Scarabaeus occur outside this belt and are adapted to the climatic conditions to be found in their geographically different areas.   This is seen in the high altitude species S. natalensis (fig. 14) and to a lesser extent in S. ambiguus (fig. 15) and S. bohemani (fig. 16). Garreta nitens (fig. 17) and Allogymnopleurus thalassinus distributions follow quite closely that of the K. lamarcki (fig. 3) but whereas K. lamarcki is most numerous in the higher central areas, the former two species are most abundant in the lowveld region.   The distribution of S. satyrus (fig. 18) to the dry north-west and central Cape is odd for such a large Scarabaeus species and the effect of this distribution on pheromone structures is discussed in Chapter 9.

The only two species of the genus Neateuchus,

N. proboscideus /....

N. proboscideus and N. rixosus, occurring in southern Africa
are limited to the drier areas of the north-western Cape,
Botswana and South West Africa (fig. 19).

The distributions of Pachylomera femoralis (fig. 20) and
Pachylomera opaca (fig. 21) which coincide largely with the
sandy regions of southern Africa are discussed in Chapter 10.

The distribution of the six southern African Kheper
species is determined by a number of interacting climatic
factors as well as the biotic features of the biomes. The
climatic factors may be divided into several components.

2.2. DETERMINING FACTORS :

Although the various climatic factors have been separated
from each other, for the sake of convenience, in reality they
interact to determine the limits of the six Kheper species.
They have been set out below in their order of relative
importance as far as this could possibly be determined.

2.2.1 Temperature :

Temperature directly influences many of the telecoprids'
activities such as flying time (Chapter 4), pheromone release
(Chapter 7) and the seasonal fluctuation in numbers
(Chapter 3).   Hence, temperature is considered to be the
most important factor limiting the distribution of telecoprid
beetles.   There are three aspects of temperature which seem
most important in this respect :-

(i) Effective Temperature:

On plotting all available mean annual temperatures a
very generalised surface temperature distribution is formed
but this cannot be used to deduce the temperature at any
particular point on the map (Climate of South Africa, W.B.28).
This is due to the variation of temperature with altitude.
The alternative of reducing temperatures to mean sea level
is also not applicable to South Africa with its high plateau
(Climate of South Africa, W.B.28).   For these reasons it was
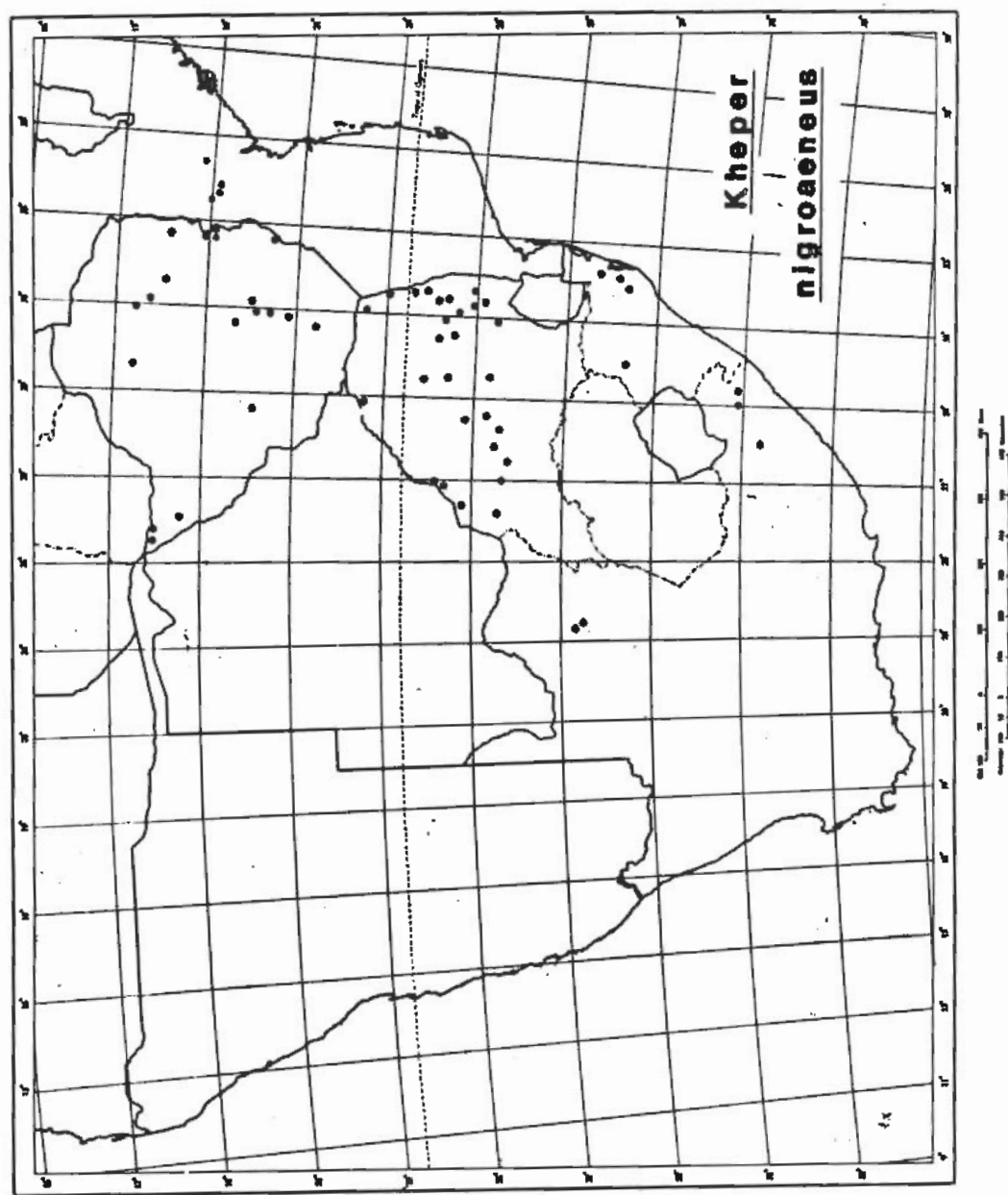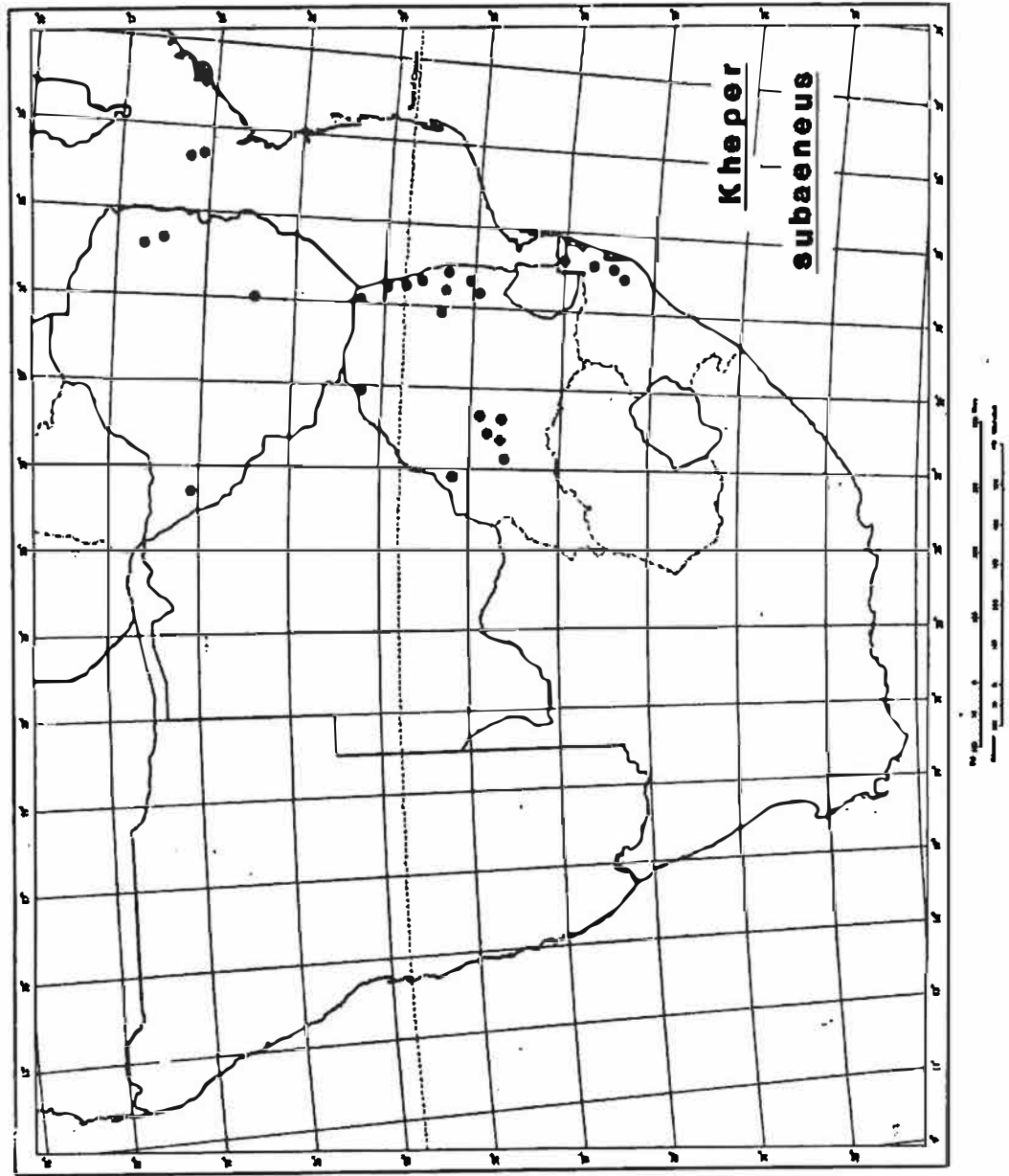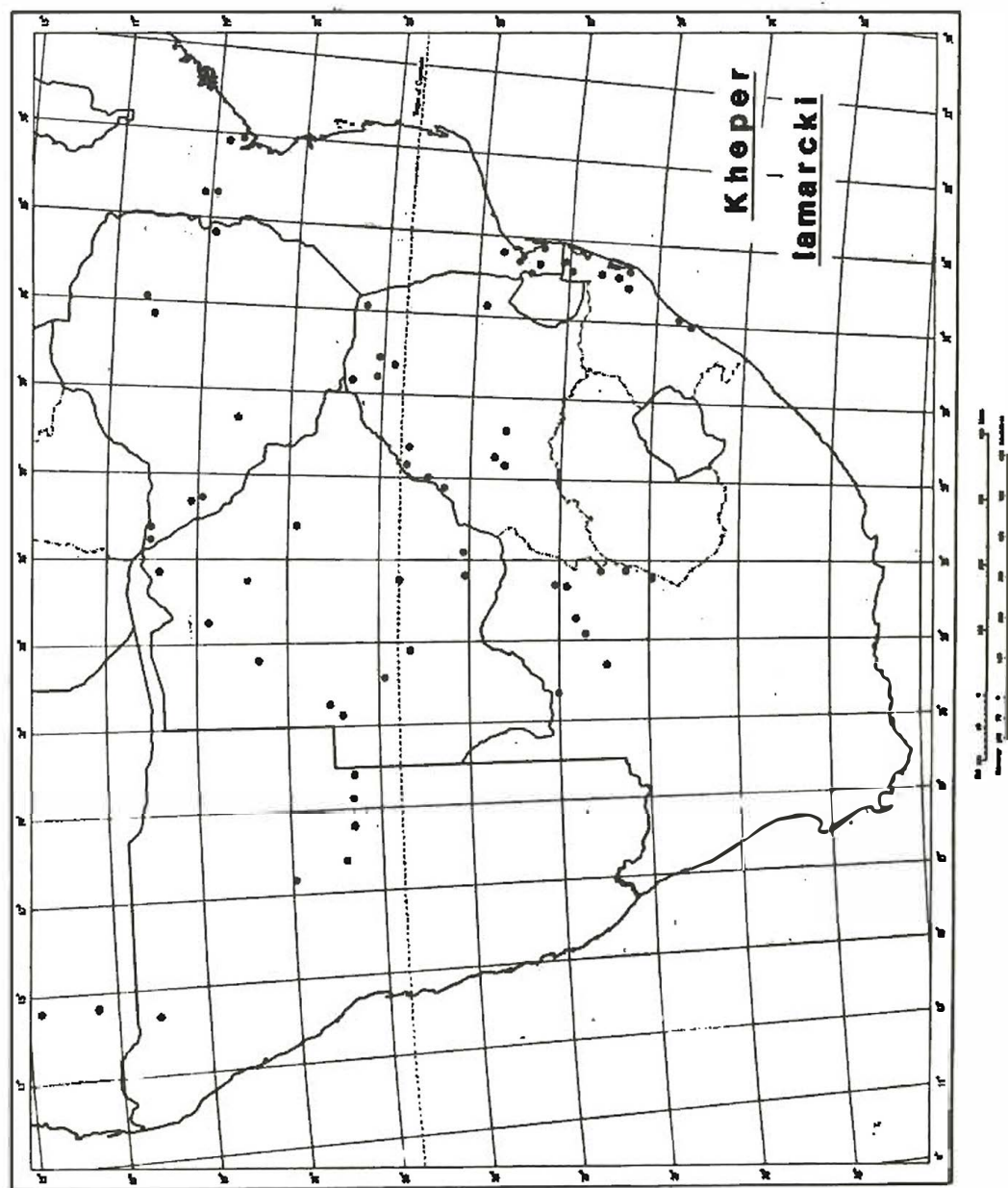
decided /....

FIGURE 1 :
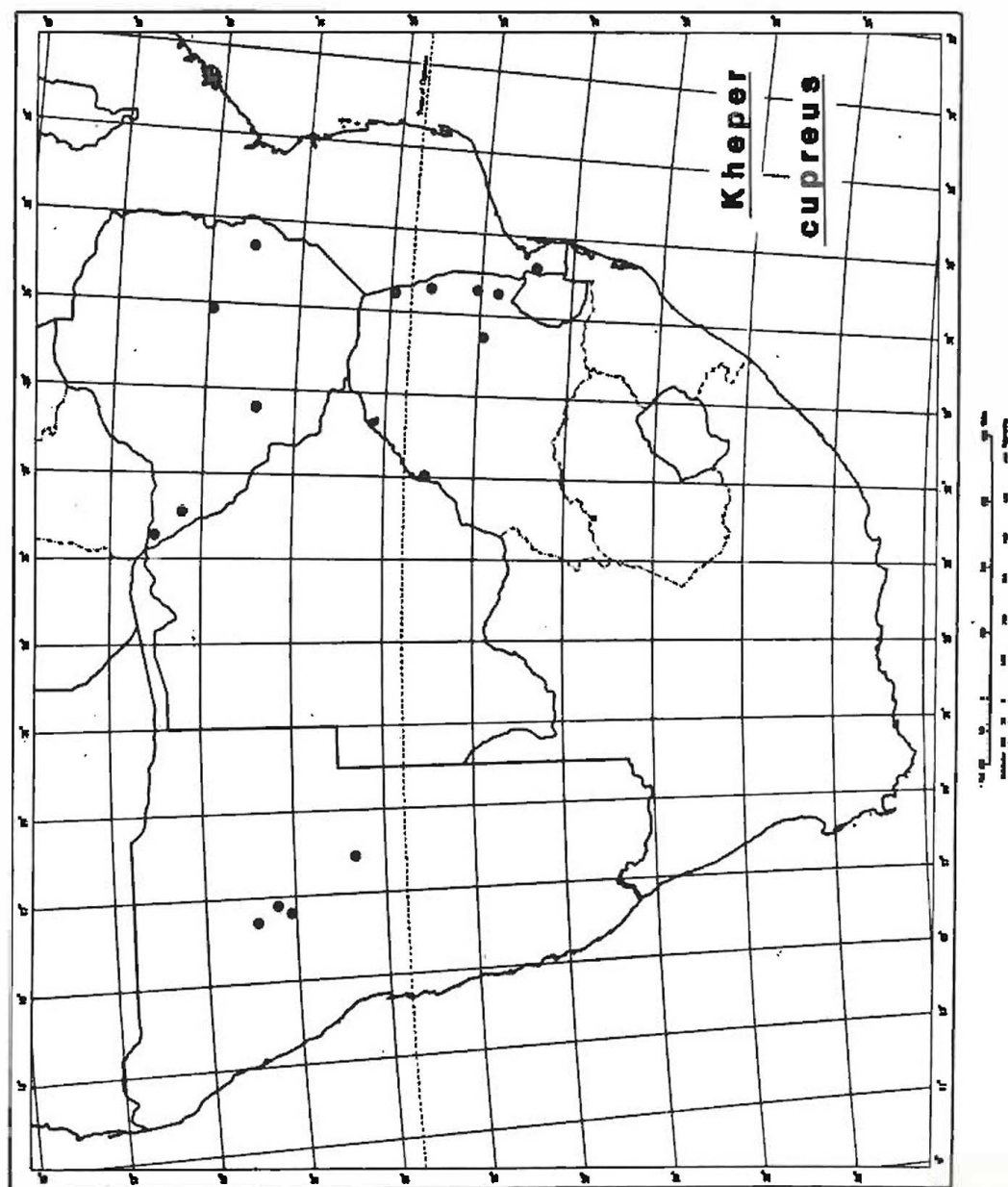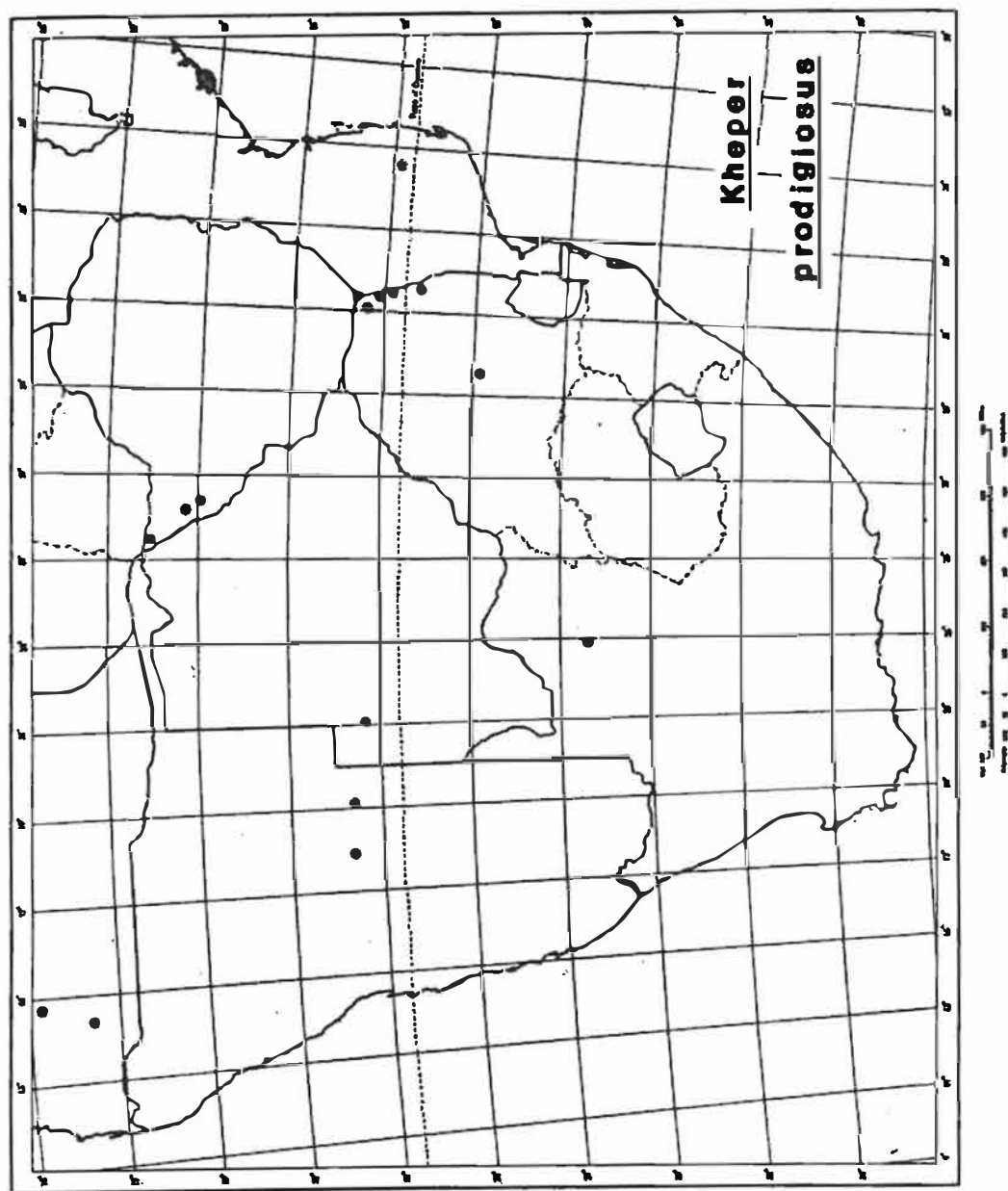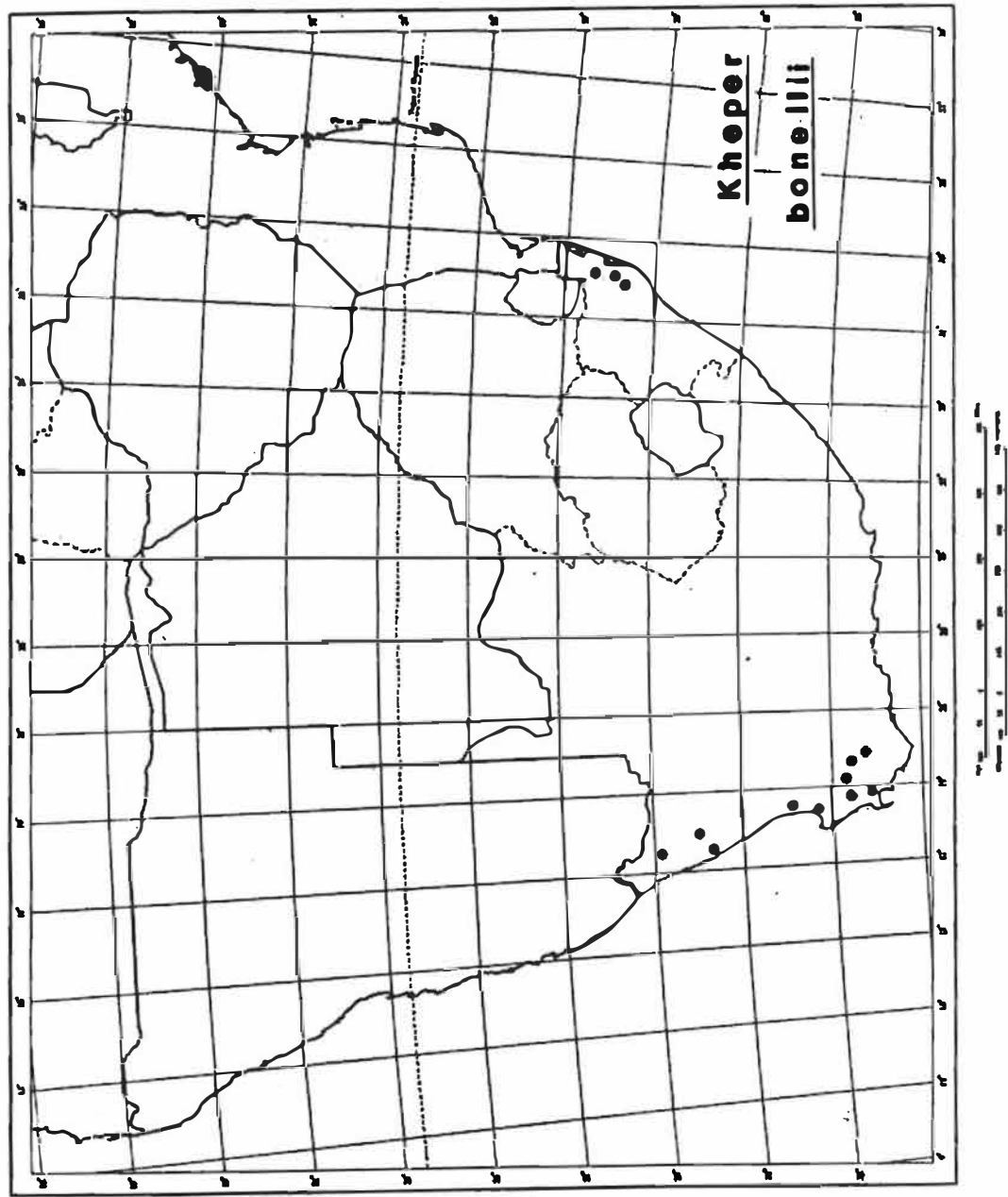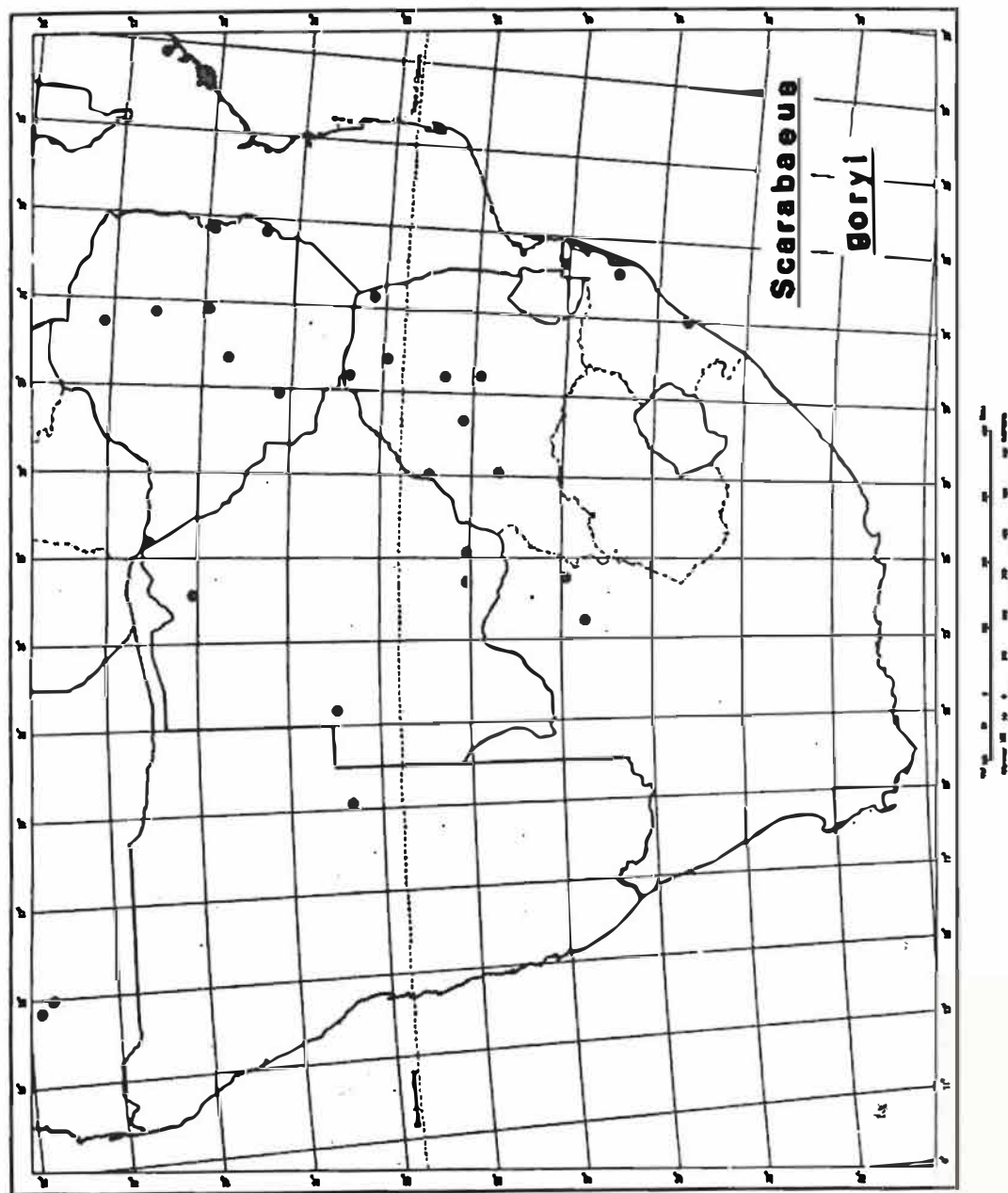
Kheper
—
nigroaeneus

FIGURE 2 :

Kheper
subaeneus

FIGURE 3 :

Kheper
lamarcki

FIGURE 4 :

Kheper
cupreus

FIGURE 5 :

Kheper
prodigiosus

FIGURE 6 :

Kheper
bonellii

FIGURE 7 :

Scarabaeus
goryi

FIGURE 8 :

Scarabaeus deludens

FIGURE 9 :

Scarabaeus
zambesianus

FIGURE 10 :

Scarabaeus

galenus

FIGURE 11 :

Scarabaeolus
flavicornis

FIGURE 12 :

Scarabaeolus
damarensis

FIGURE 13 :

Scarabaeolus
parvulus

FIGURE 14 :

Scarabaeus
natalensis

FIGURE 15 :

Scarabaeus

ambiguus

FIGURE 16 :

Scarabaeus
bohemani

FIGURE 17 :

FIGURE 18 :

Scarabaeus
satyrus

FIGURE 19 :

FIGURE 20 :

Pachylomera
femoralis

FIGURE 21 :

Pachylomera
opaca
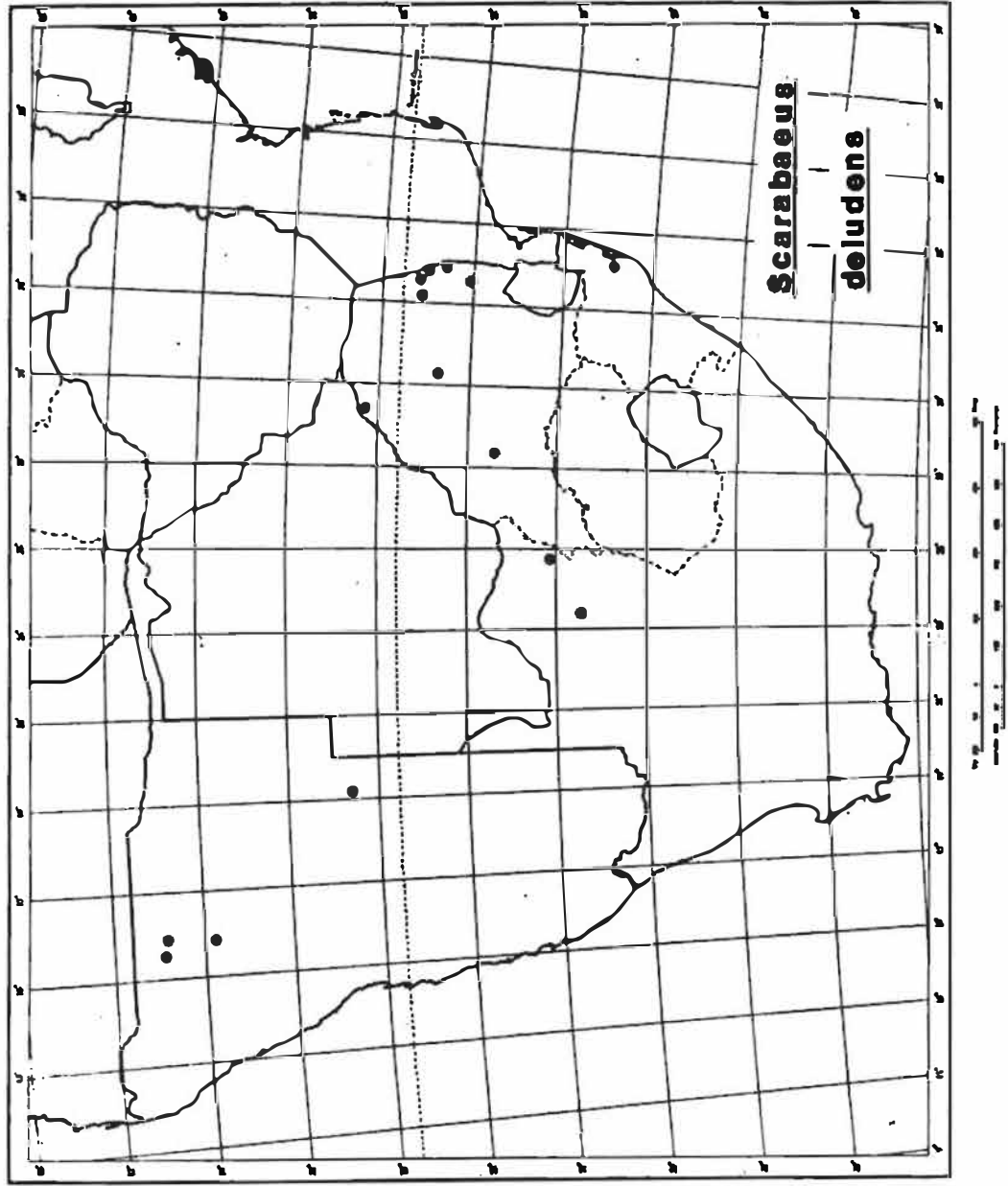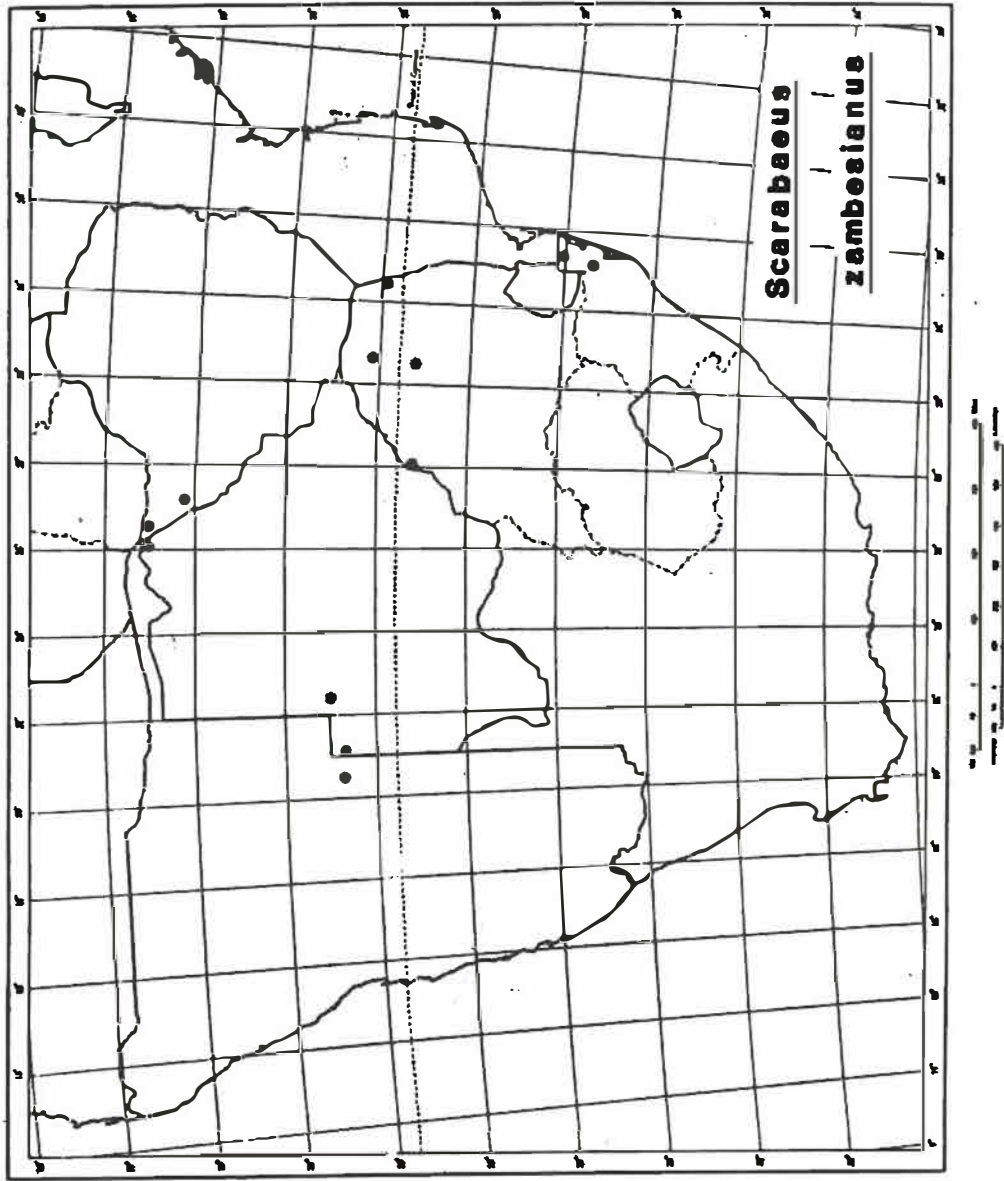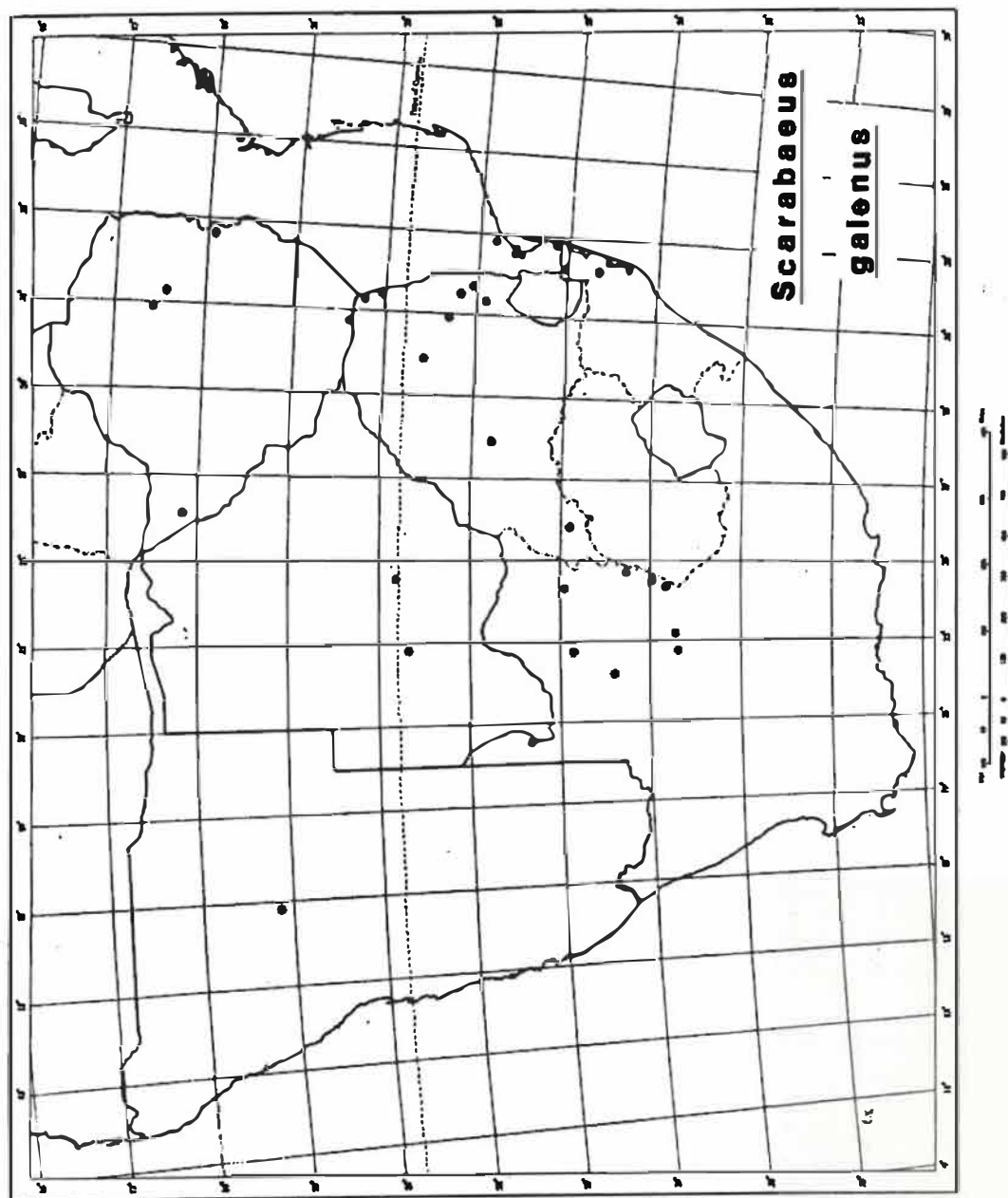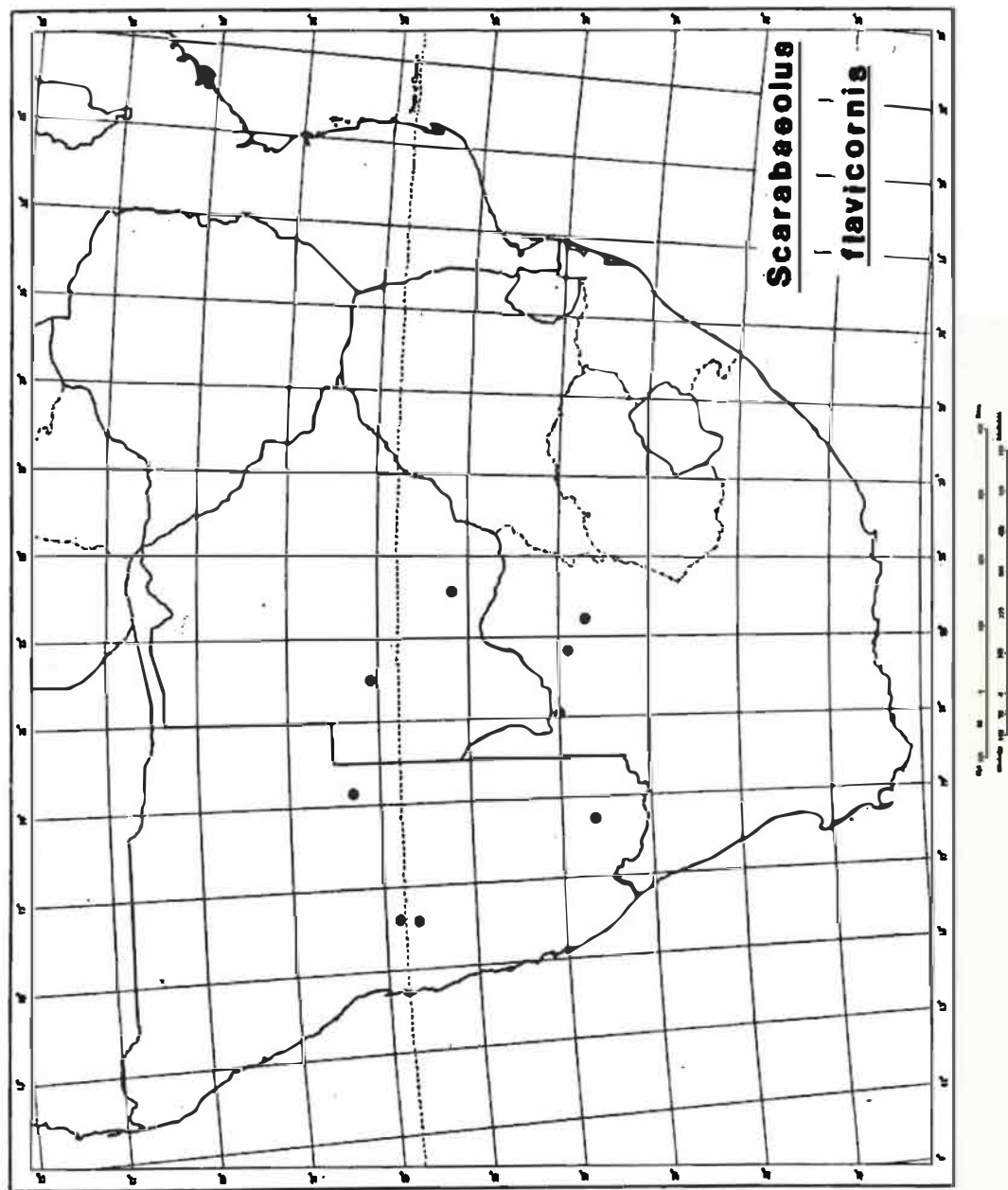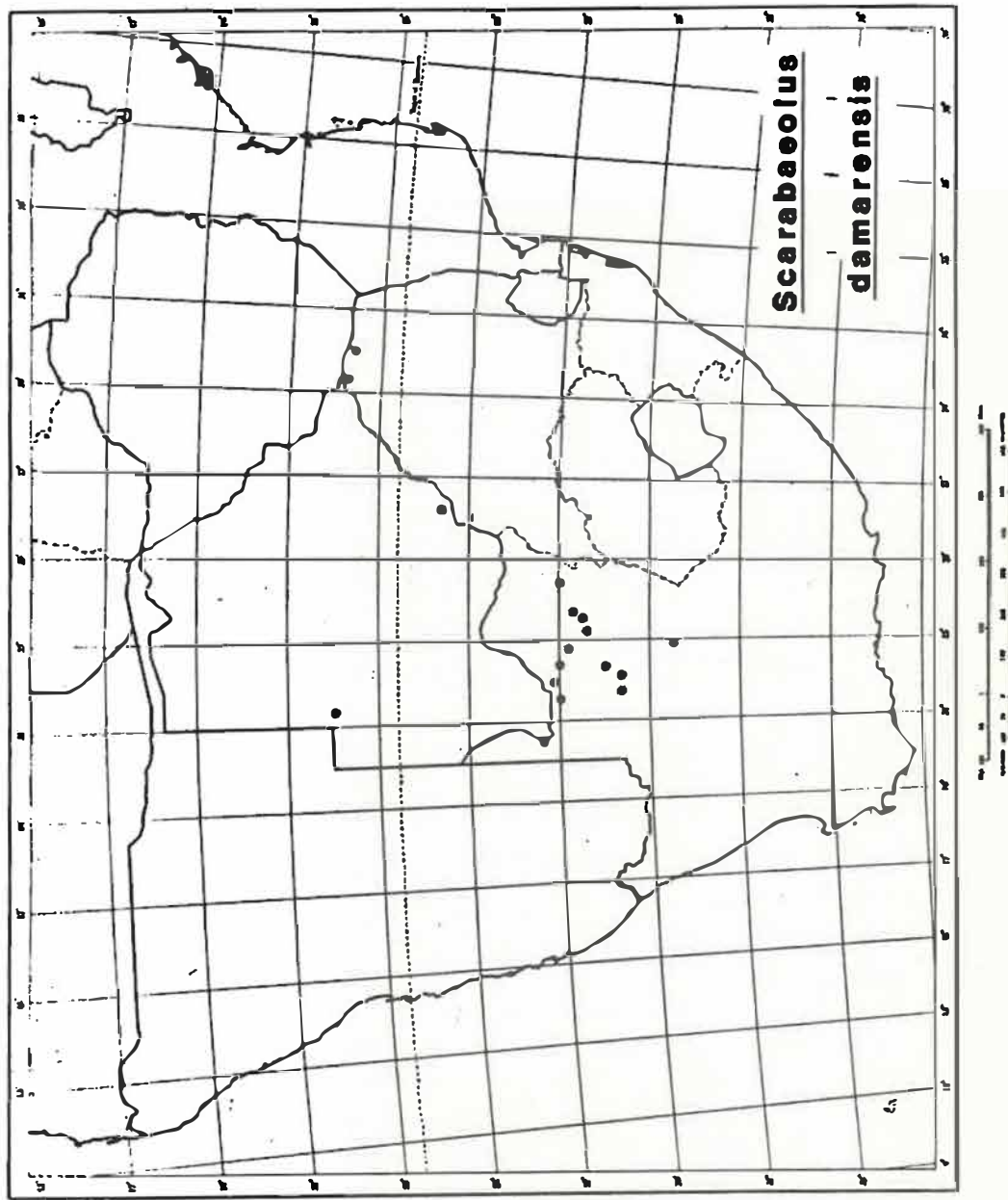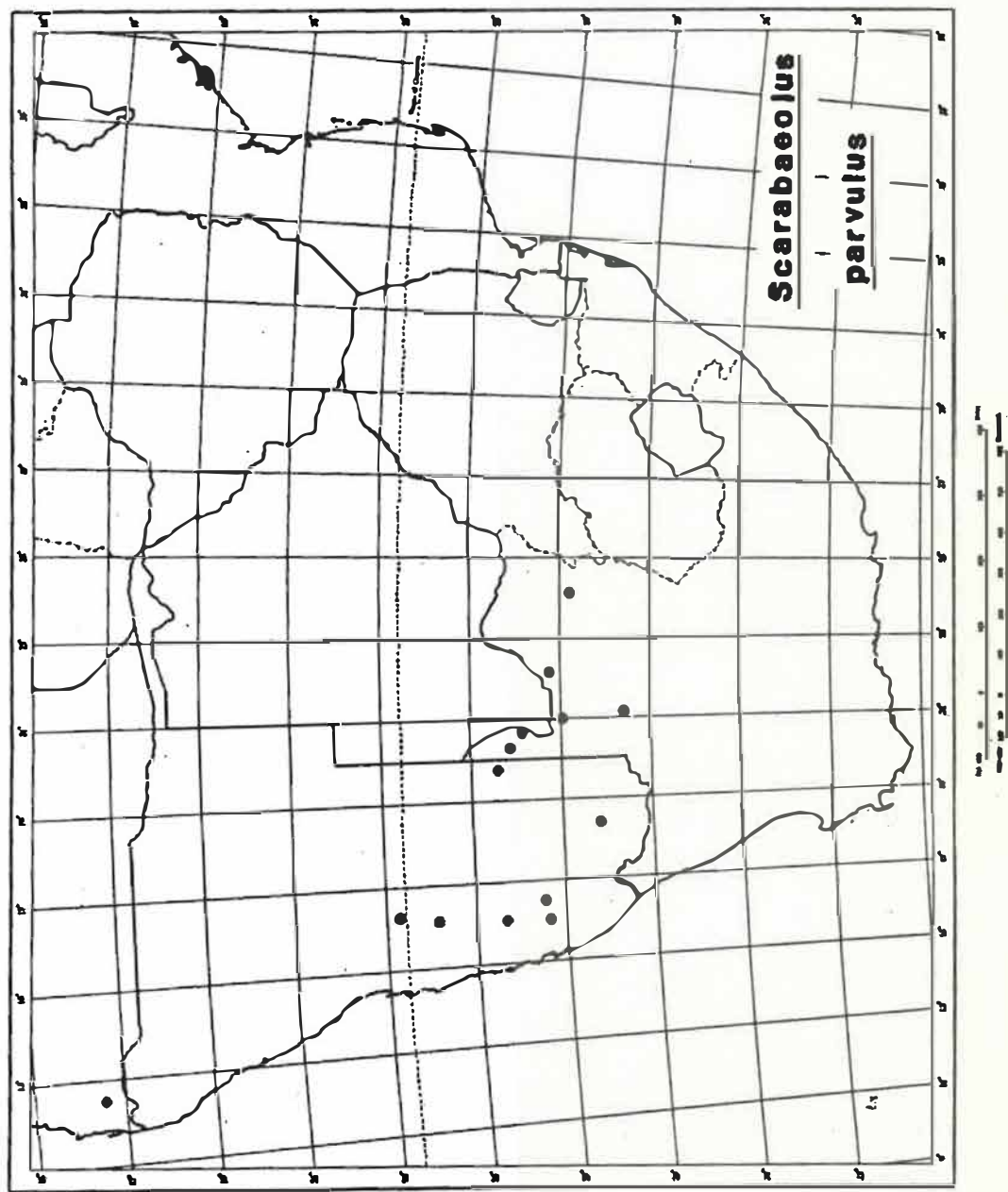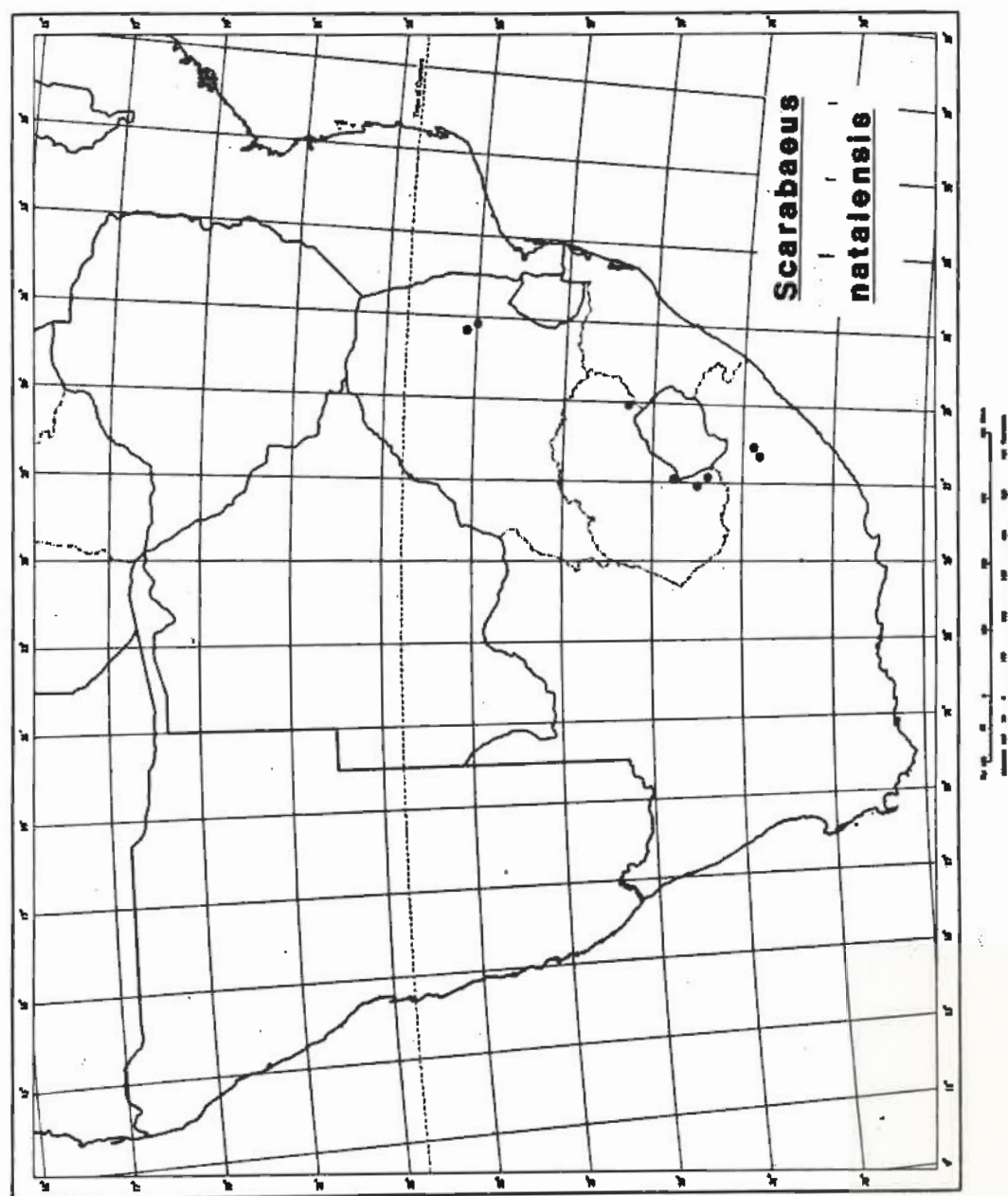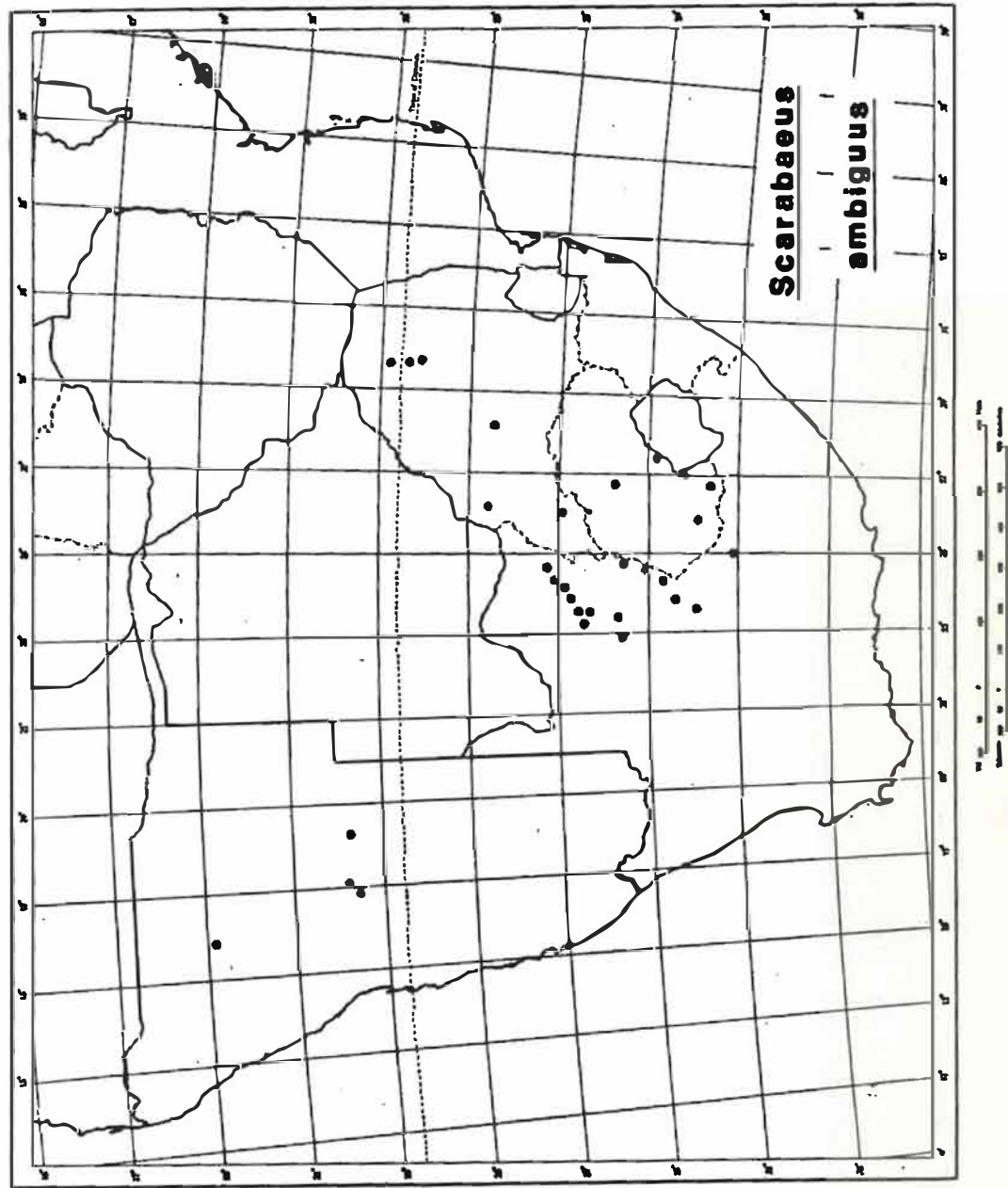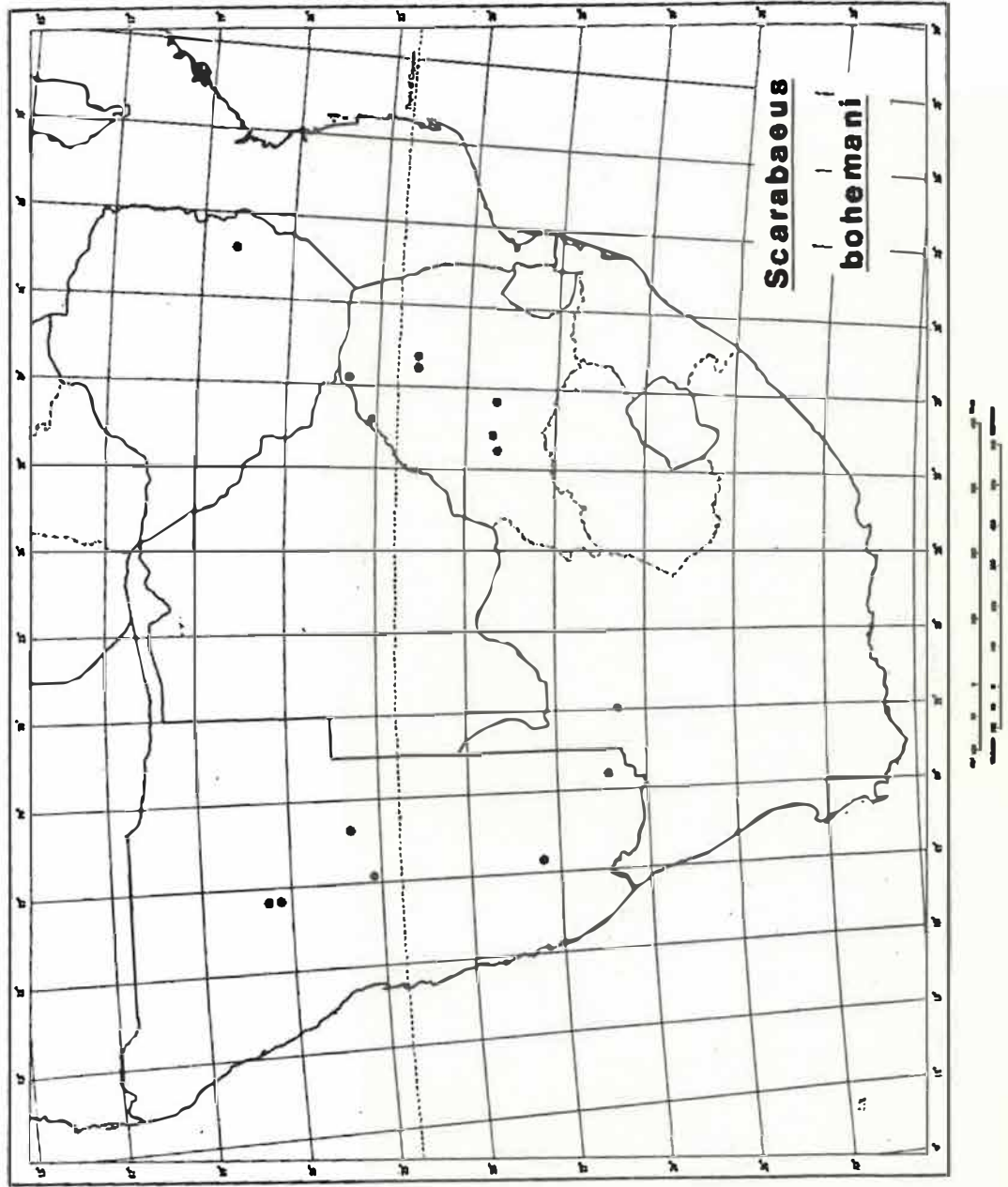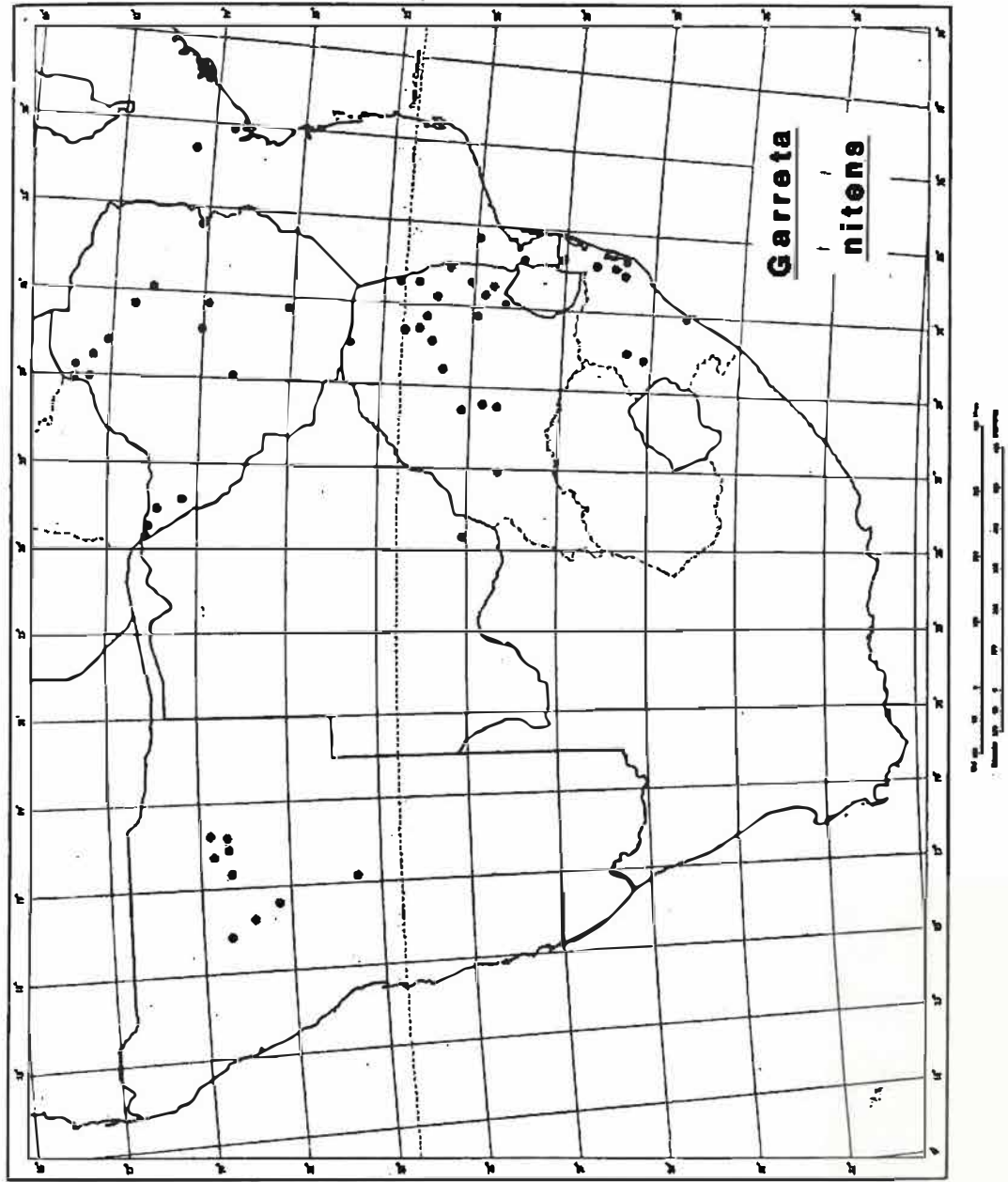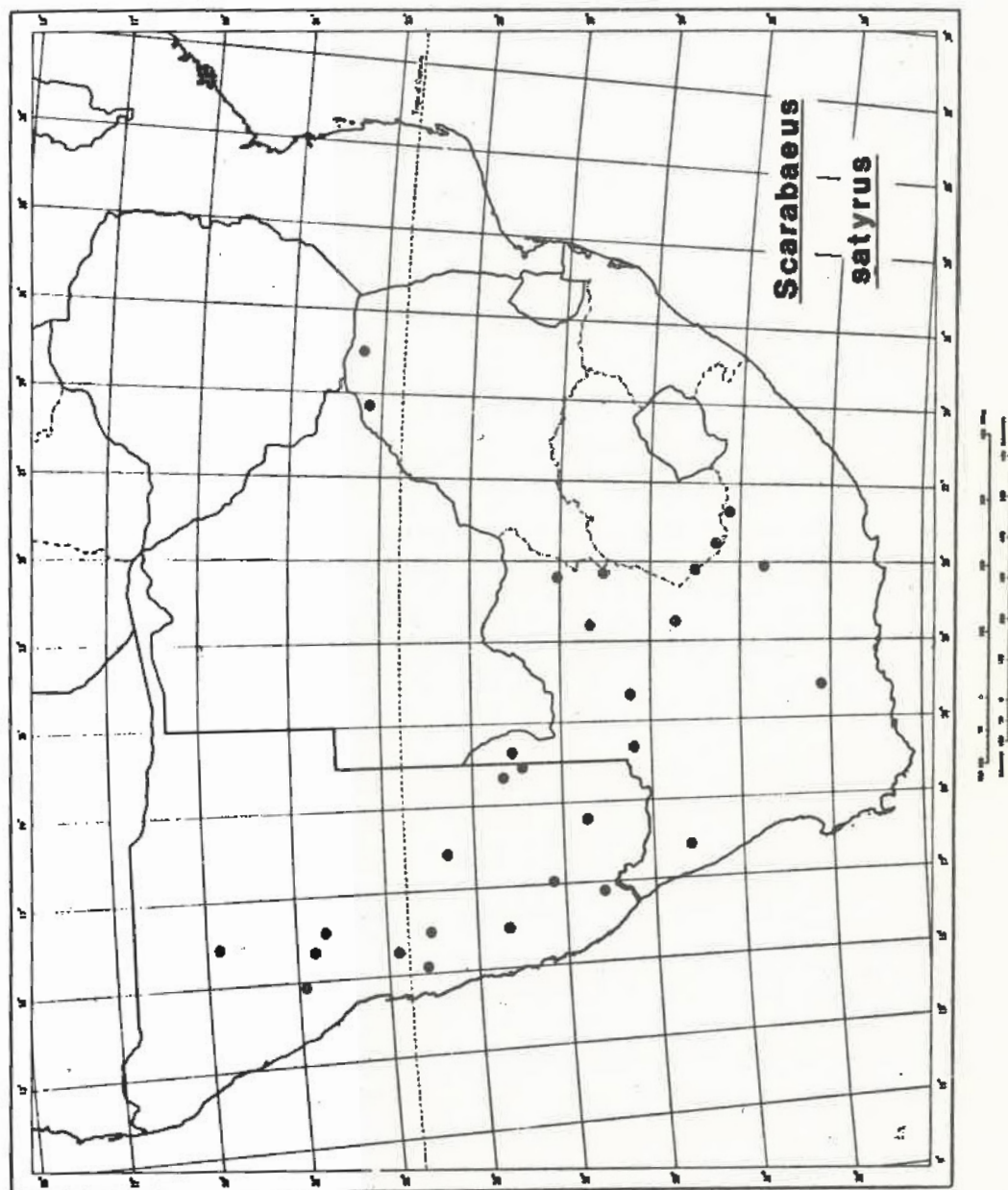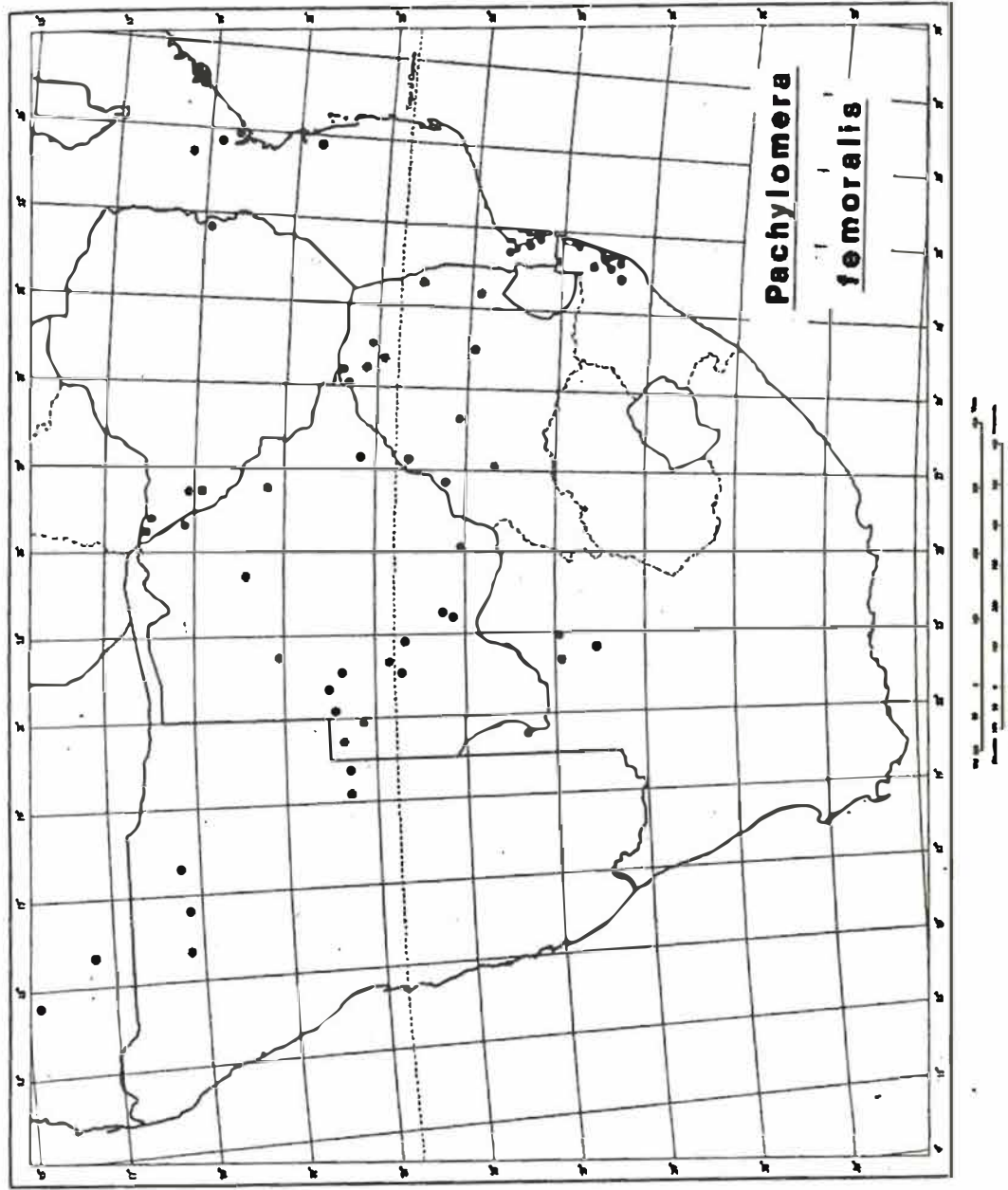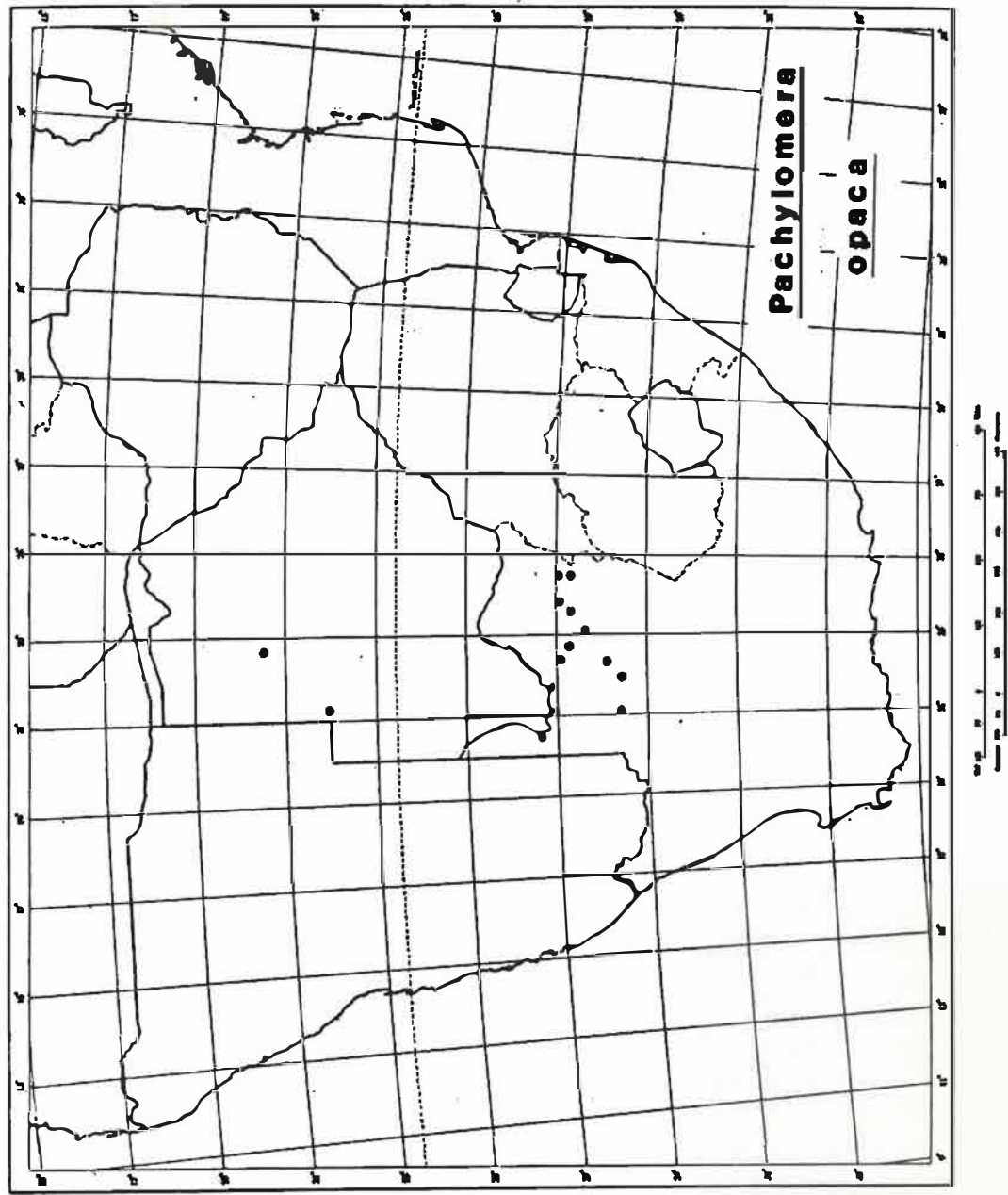
decided to use "effective temperature" (E.T.), in which the
biological importance of the summer months is stressed
(Stuckenberg, 1969).

Effective Temperature is based on the fact that on a
global scale the ebb and flow of life over the seasons are
systematically related to the thermal environment. E.T.
therefore measures warmth by defining a sliding scale specifying
temperatures at the beginning and end of the warm season, and
implicating the duration of that period (Stuckenberg, 1969).
Bailey's (1960) equation may be expressed as :

$$E.T. = \frac{8T + 14AR}{AR + 8} \, {}^{o}C$$

where   T = mean annual temperature and
       AR = the difference between the means of the warmest and
           coldest months.

The effective temperature map for southern Africa by
Stuckenberg (1969) is reproduced in figure 22, but for further
information on this method of expressing temperature the
original paper should be consulted.

According to this map, the $15^{o}C$ effective temperature
isoline is the lower limit of the six Kheper species distri-
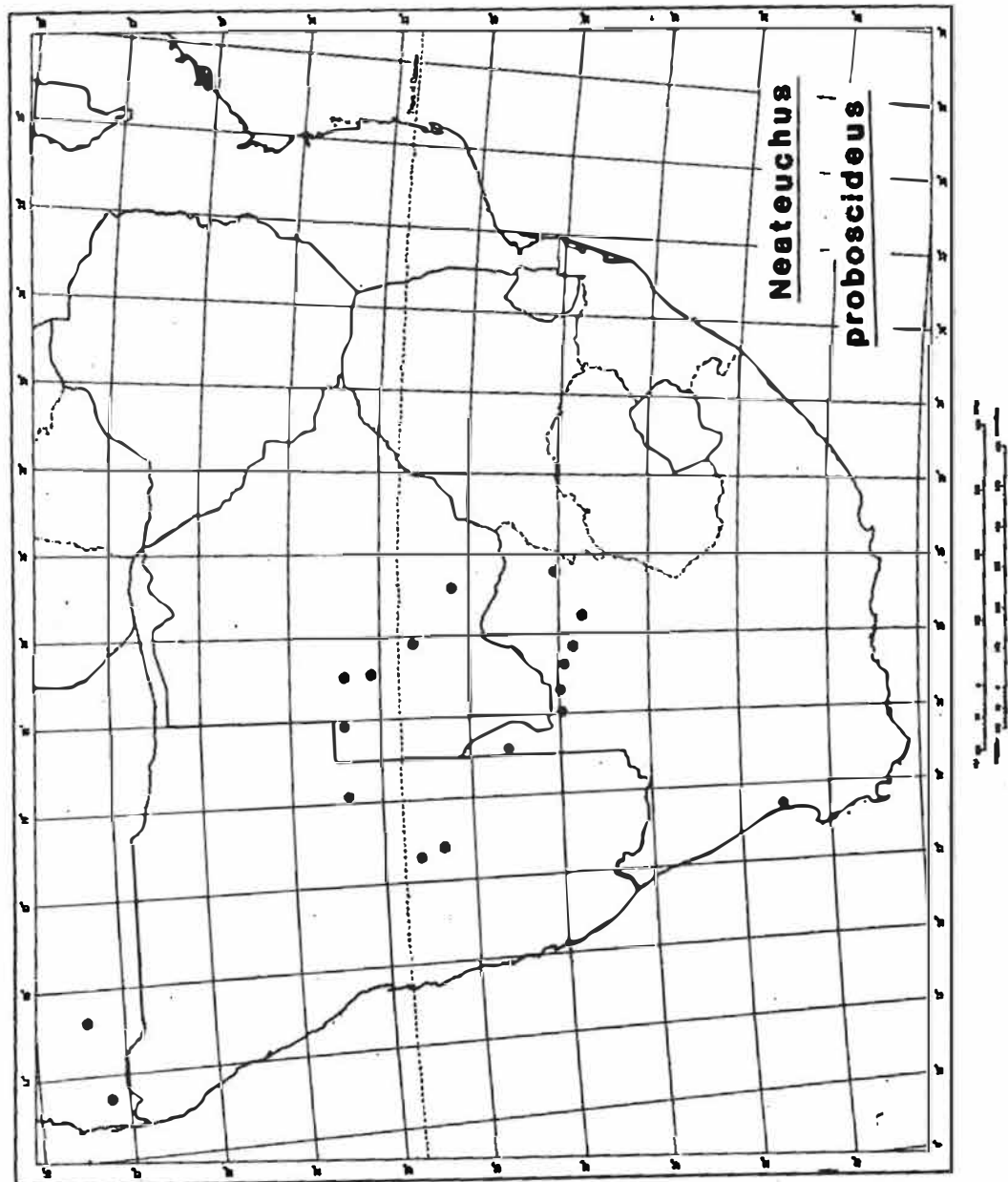bution. As Kheper species have been collected in Mozambique
above the $19^{o}C$ effective temperature isoline, this indicates
that it is only the lower $15^{o}C$ effective temperature isoline
which is the limiting factor on distribution within South
Africa. According to Bailey's (1960) classification in which
the world is divided into ten thermal zones, above $15^{o}C$ E.T.
to $19^{o}C$ E.T. may be described as "warm to very warm", having
more than 214 days of the year in which the mean temperatures
are warmer than the effective temperature.

The $15^{o}C$ E.T. also limits the distribution of most
species of the subgenera Scarabaeus and Scarabaeolus
listed in Chapter 1.   Exceptions occur in Scarabaeus
natalensis, Scarabaeus basuto and Scarabaeus westwoodi,
which occur in the foothills around Lesotho in the Orange Free
State and Eastern Cape at altitudes between 1000 and 2000 metres,
and are therefore coldhardy species found below the $15^{o}C$ E.T.
isoline.

EFFECTIVE
TEMPERATURE
°C

Fig. 2 2
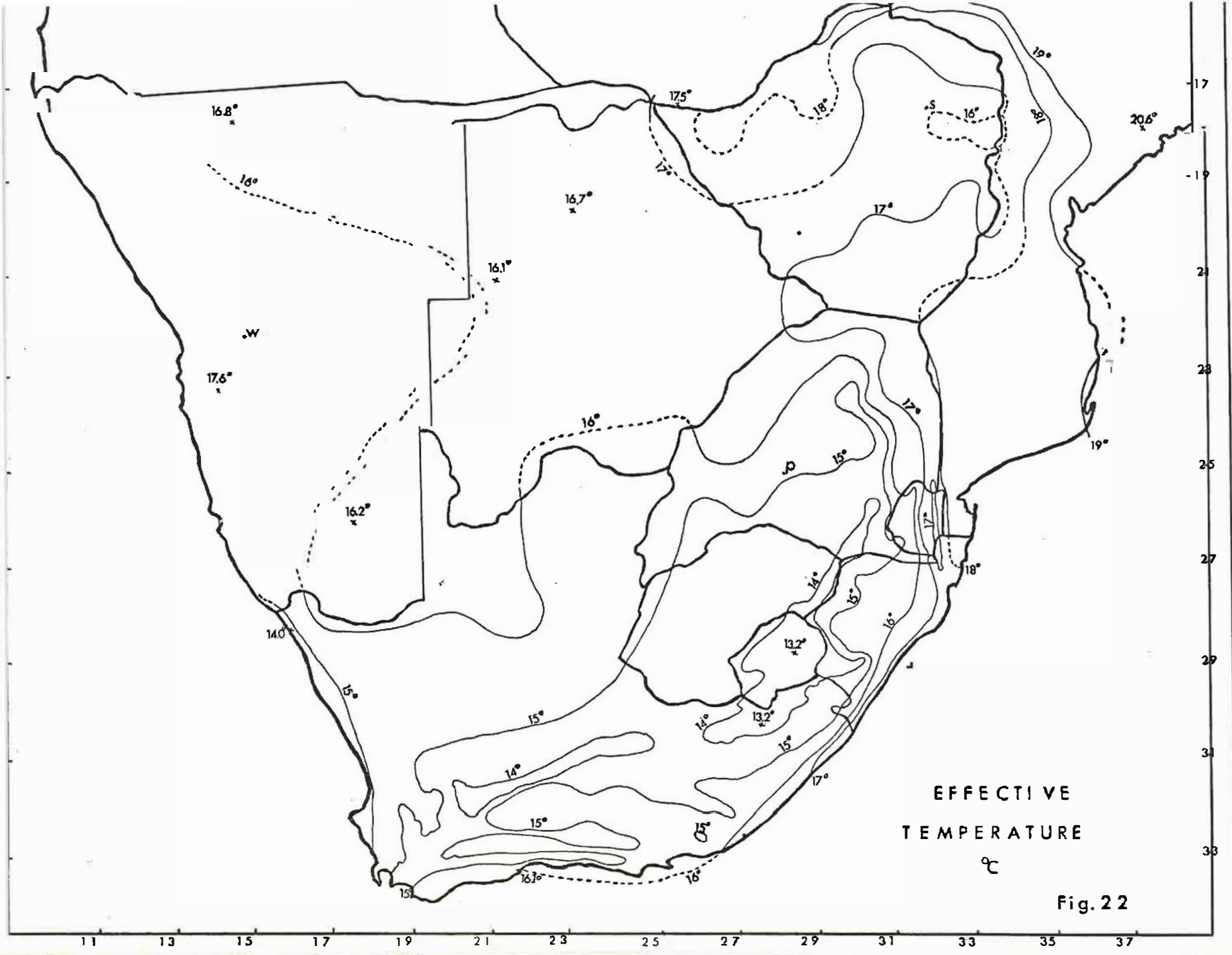
(ii) Number of Days :

By consulting the various Weather Bureau publications further limits may be set on localities which have certain climatic data available. By utilising data from all towns within the six Kheper species distribution and those immediately outside their distribution one is able to further define the temperature limits. Using this method and $\frac{1}{2}$ Maximum and Minimum temperatures at the various stations (Climate of South Africa, WB.19) it becomes apparent that areas with a yearly mean $\frac{1}{2}$ Maximum and Minimum of over $17,2^{\circ}C$ are suitable for the Kheper species, all other factors being favourable. The optimum conditions prevail where the yearly mean $\frac{1}{2}$ Maximum and Minimum is between $19^{\circ}C$ and $23^{\circ}C$. Areas with a yearly mean $\frac{1}{2}$ Maximum and Minimum between $17,2^{\circ}C$ and $18,9^{\circ}C$ may be regarded as marginal areas for the Kheper species. The stations just outside the Kheper distribution have mean $\frac{1}{2}$ Maximum and Minimums of between $15,0^{\circ}C$ and $16,6^{\circ}C$. Where such information is recorded in Australia similar limits may be determined. The Climate of South Africa (WB.19) records the average number of days with maximum temperatures greater than $30^{\circ}C$ and with minimum temperatures greater than $20^{\circ}C$. The six Kheper species occur in areas where the average number of days a year above $30^{\circ}C$ is between 98 and 165 days, all other factors being favourable.

Similarly the number of days a year with minimum temperatures of over $20^{\circ}C$ which are suitable for the Kheper species is between 5,8 days and 82 days. The optimum number of days over Max. $30^{\circ}C$ a year is between 116 and 165 days; minimum temperatures greater than $20^{\circ}C$ - between 52 and 82 days a year.

The Climate of South Africa (WB.19) gives the mean monthly air temperature for a number of stations over the period 1924 to 1950. These data are plotted in figure 23 for four stations within the six Kheper species distribution. Only Otobotini, Zululand, may be considered optimum, the other

three stations are marginal in that although beetles are
caught there, they are caught in limited numbers. Otobotini
has clearly a warmer yearly temperature, which is milder in
winter than that of the other three stations.

(iii) Soil Temperature :

The soil temperature and its effect on brood-balls is
discussed in Chapter 8. Air temperature largely determines
soil temperature although moisture, soil type and the dense-
ness of the vegetation will affect the soil temperature
from locality to locality (Climate of South Africa, WB.28).
There are not enough stations which record soil temperature
to be able to set limits on distribution according to this
factor. The soil temperature may therefore be regarded as
broadly following the isotherms and will not be dealt with
separately.

2.2.2 Rainfall :

Rainfall appears to affect the distribution of
telecoprids, especially the Kheper genus, in two ways.

(i) Annual Rainfall :

According to distribution data, the six southern
African Kheper species are limited by the lower annual rain-
fall limit of 200mm and the upper 1000mm limits as given in
the rainfall maps of Climate of South Africa (WB.22). No
overall optimum annual rainfall can be given for all six
Kheper species, since each species has its specific require-
ments. K. prodigiosus and K. cupreus may be regarded as
occurring at areas of lower annual rainfall than
K. nigroaeneus, K. subaeneus and K. lamarcki (Chapter 9).
Although the effective temperature in the north-western
Cape Province and southern South West Africa is favourable
to the Kheper species, being over 15°C E.T., they are
excluded from this region by insufficient rainfall, directly
as well as indirectly. The telecoprid species which inhabit
this region of below 100mm to 400mm are mainly of the subgenus

Scarabaeolus / .....

Scarabaeolus (figs. 11, 12 and 13) which are very small
beetles, the smallest species being S. parvulus and the
largest S. flavicornis (Table 3, page 10). This may be
compared with the smallest Kheper species, K. bonellii,
and the largest, K. prodigiosus. The reason for the
difference in sizes will become apparent in section 2.3.

(ii) Summer Rainfall :

Not only is the annual rainfall of importance but the
period over which is falls must coincide with temperatures
which are warm enough for beetle activity (fig. 23). Thus
summer rainfall is essential for all Kheper and Scarabaeus
species with the exception of the south-western K. bonellii,
S. rugosus and S.suri populations. Although the effective
temperature is suitable for Kheper and Scarabaeus activity
as far south as Cape Town (fig. 22) the period in which it
falls is unsuitable for the Scarabaeini. The "even" rainfall
area from Port Elizabeth merges into the winter rainfall area
and the temperatures are too low for activity during the
period that rain falls in sufficient amounts. The importance
of rain in releasing aestivating beetles from the hard packed
surface soil is discussed in Chapter 3. During the dry season
when temperatures are favourable for activity the soil has
dried to form a hard crust from which aestivating telecoprids
would not be able to free themselves.

2.2.3 Altitude :

Temperature varies with altitude, and isotherms more or
less follow the contours (Climate of South Africa, WB.28).
At the lower altitudes i.e. the coastal plains and major
river's valleys, the beetle fauna is seen to be extremely
varied and abundant. Pitfall trappings and field trip
data show that the numbers of Kheper beetles drop off sharply
with an increase in altitude, and that they do not occur
above the 1500 metre contour in southern Africa (Table No. 21,
page 138). Species such as K. pustulosus (Kenya) and
K. festivus (Nigeria) were captured at heights between 1600

<div align="right">and /......</div>

RAINFALL AND TEMPERATURE   Fig. 23

Otobotini
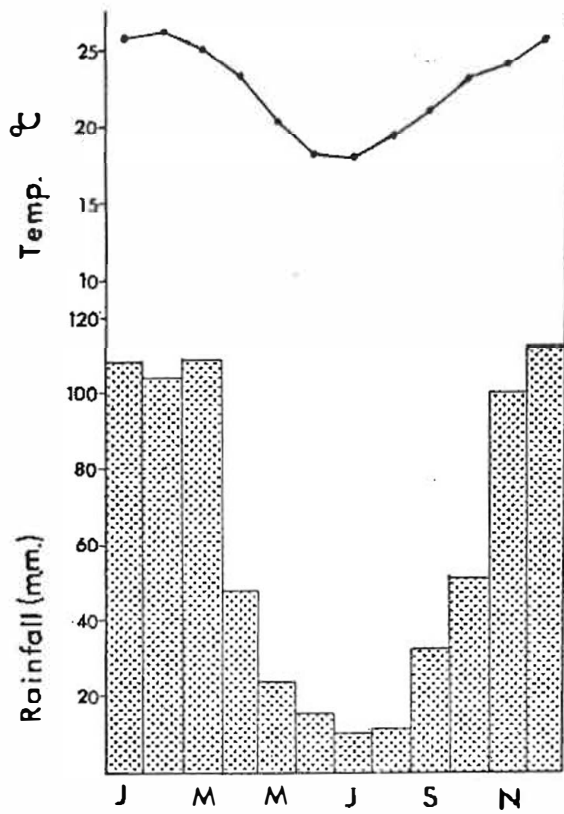
Kuruman
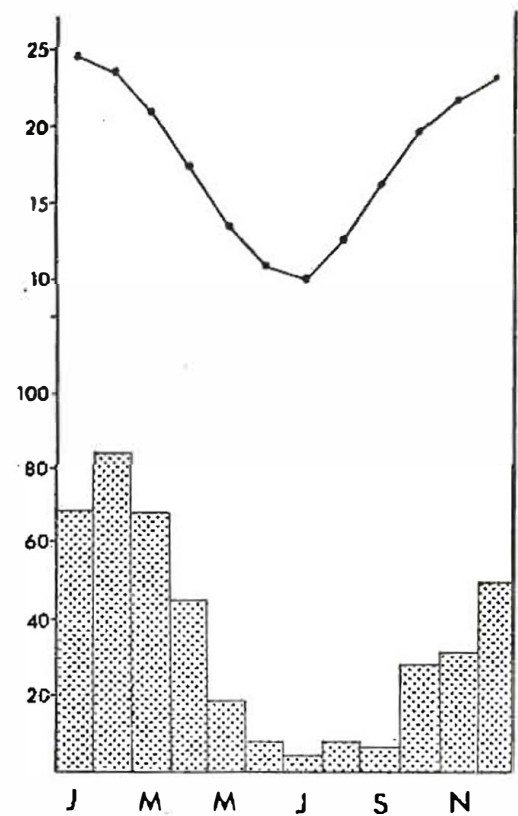
Ghanzi
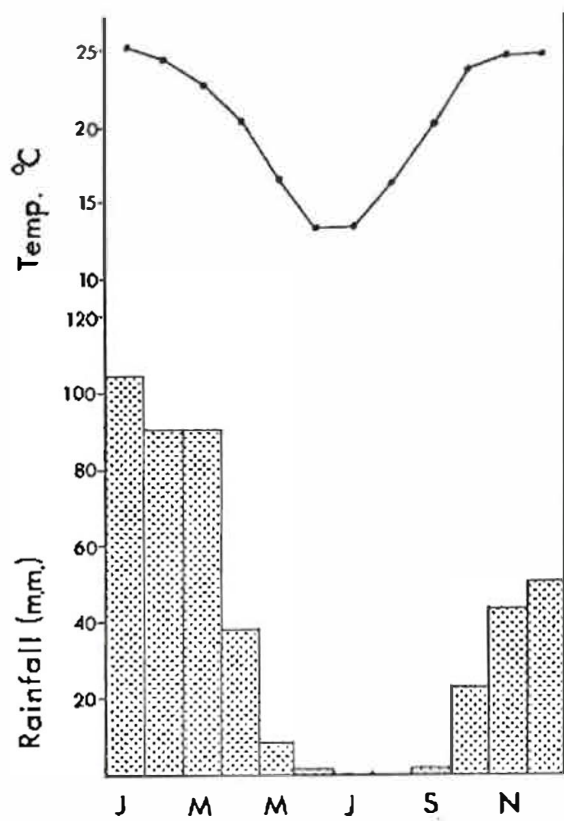
Tsumeb
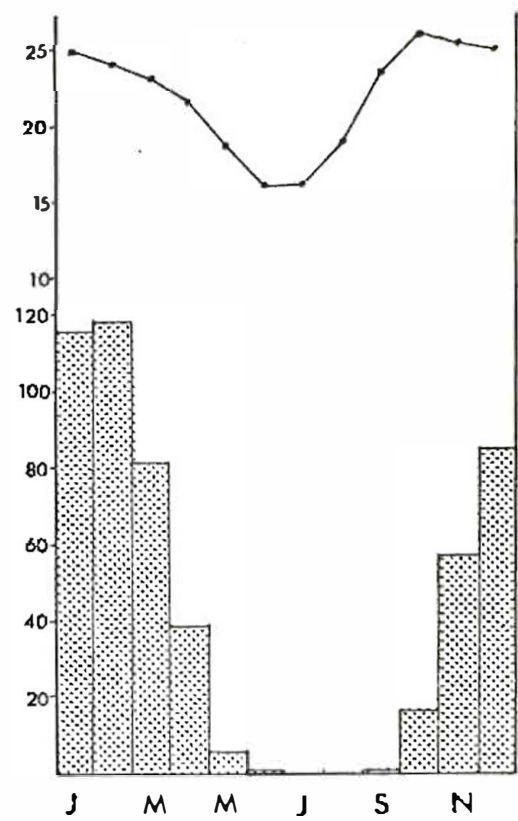
MONTHS

and 1860 metres and 1000 and 2000 metres respectively (A.L.V. Davis, pers. comm.). This may not be compared to southern African conditions, as these tropical species occur at higher latitudes where the warm yearly temperatures are not as drastically affected by altitude.

From the present distribution data of the various telecoprid species, certain species may be seen to occur only at higher or lower altitudes within the 0 - 1500 metre limit. K. bonellii is found only between the 0 and 500 metre contours while K. paganus from Angola between the 500 and 1500 metre contours. The contours consulted occurred in the map with rainfall diagrams (Climate of South Africa, WB.22).

The colour of the beetles in several Kheper species was observed to change with altitude, the higher the altitude the darker and smaller the beetle. Since it becomes progressively cooler with increasing altitude the adaptiveness of this colour change may be associated with the retention of heat from insolation; the higher the altitude the darker the beetle and the greater this retention.

In the case of K. nigroaeneus the colour was recorded with the location at which it was captured, the two divisions being "bronze" (including "bright" and "dull" bronze) and "black" (including black with a green sheen). There seemed to be no correlation with any climatical factors within the colour sub-divisions, so that only the major two colour divisions were plotted (fig. 24). From this it may be seen that the bronze beetles occur in the Eastern Lowveld and Zululand i.e. between 0 and 500 metres while the black beetles occur between 500 and 1500 metres. A t-test of differences in mean size of the two groups was non-significant at the 0,5% level.

The colour of dung-beetles, mostly metallic, is a mechanical characteristic of the cuticle and not due to pigments (Chapman, 1969) and various shades of colours are

present /....

FIGURE 24 :
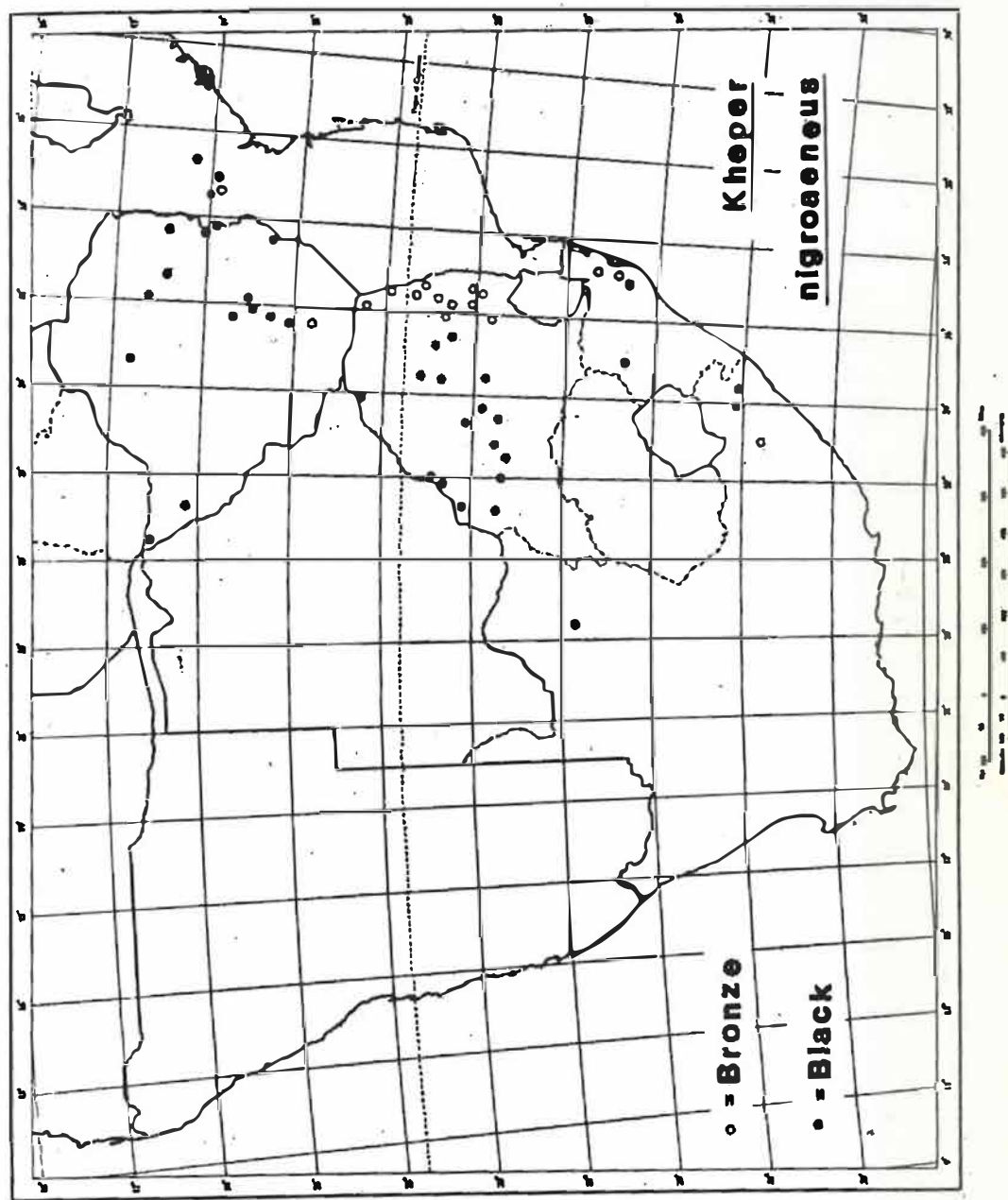
present within certain species.

K. pustulosus, K. aegyptiorum, K. laevistriatus and
K. aeratus are Kenyan species and K. festivus is a Nigerian
species. Since these are all tropical they may occur at
higher altitudes than those Kheper species south of latitude
17°S where an increase in altitude results in temperatures
dropping below those favourable to the beetles. K. paganus
is an Angolan species occurring only as far south as southern
central Angola.

As the range in altitude over the distribution of
S. westwoodi, S. natalensis and S. basuto indicates, these
are cold-hardy, highland fauna and they occur in the
Drakensberg foothills in the Orange Free State and Eastern
Cape. S. ambiguus has a wide distribution from the
Vryburg area into the Northern Transvaal and parts of the
Orange Free State.

2.2.4 Soil Types :

The different soil types of southern Africa affect
the distribution of telecoprids both directly and
indirectly.

The greater part of the telecoprid distribution
occurs in areas which have the soil types located under
the major headings of "Sands" and "Weakly Developed Soils
on Rock" according to the Soil Map of South Africa (1973).

The variation of soil types within an area affects the
distribution of the various species which occur in that
region. Thus in one of the study areas, Scarabaeus galenus
and Scarabaeus zambesianus are found mainly in the sandy
area which juts into Mkuzi Game Reserve, and are mostly
absent from the less sandy areas of the Reserve. The
behaviour of S. galenus differs from that of most
Scarabaeus species, following to a greater extent that of
Pachylomera femoralis (discussed in Chapter 10), which is

also /....

also confined to this sandy area of the Reserve.

Due to the influence of the cold Benguela current off the west coast and the warm Agulhas current off the east coast, there is a difference of 6°C at places on opposite sides of the African continent at the same latitude (Climate of South Africa, W.B.28). Yet the temperature of the west coast regions where K. bonellii occurs, the Velddrif, Leipoldtville and Lamberts Bay areas, is warm enough for Kheper habitation as it is above the 15°C E.T. However, this is a winter rainfall region which normally is detrimental to telecoprids as the rainfall on which they rely in order to emerge from the soil (Chapter 3) occurs during the winter months when temperatures are too low for activity. The reason why K. bonellii is found in this region and is active during the summer months concerns the soil type.

The soil type in which both populations of K. bonellii occur in the South Western Cape and Zululand is littoral and near-littoral sand (Soil Map, 1973). The south west Cape sand may be described as fine sand (according to Loxton, 1962) and is different from the Zululand sand in that as it dries out it does not cement into a hard crust. Thus summer rainfall is not essential in the ecology of the South Western Cape K. bonellii population to release them from the soil. In September 1974 when K. bonellii were active in the South Western Cape, the surface sand was dry to a depth of about 17cm, but beyond this depth the soil was fairly moist as the sand seemed to have retained moisture from the previous rains, the evaporation being less because of the milder temperatures experienced there.

Telecoprids living under sandy conditions have become morphologically adapted to such conditions and the adaptations become more extreme as the aridity increases. They take the form of extremely long hairs on all tibiae, curved hairs on the thorax which aid the removal of sand from the burrows, and paddle-like tibiae, tibial spurs and tarsi. The genera

most /....

most highly adapted to sandy conditions are Pachysoma and Neopachysoma of the Namib desert.

The indirect effect of soil on telecoprid beetles is its effect on the type of vegetation it can support which in turn affects the distribution of the various herbivorous animals.

2.3 INTERRELATIONSHIP WITH LARGE MAMMALS :

Since no species exists in isolation telecoprid ecology can be understood only in context of the association of these beetles with other animals sharing the same habitat. One of the primary factors affecting the distribution and abundance of coprophagous dung beetles (in certain regions) is the availability of dung in their environment (Halffter and Matthews, 1966), especially as they are highly adapted to their coprophagous diet (Waterhouse, 1974). Their large numbers in certain areas thus reflect the copious amounts of dung available in those areas.

The distribution of various telecoprid species in southern Africa in relation to the distribution of large mammals, both past and present, is discussed in section 2.3.1. The large bovine herds of southern Africa are concentrated in the savanna and temperate grasslands to which they are adapted, but within these regions they do not remain in any one area indefinitely. They tend to disperse when food is abundant after rains and surface water is available for drinking (Shortridge, 1934). As the veld dries and surface water becomes scarce, they again tend to move towards areas with permanent water.

The overall distribution of dung beetles is greatly affected by the behaviour and movement of the animals in the biome. Solitary herbivores are mostly exceptions, as herbivores tend to move in aggregations for protection and this results in further clumping of dung in a particular habitat. Clumping of dung may also occur as a result of

territorial behaviour, as in the case of rhinoceroses which defecate on definite middens whenever the group happens to be in a particular area (Roosevelt and Heller, 1914). The rapid fencing and farming of previously open areas in southern Africa in the last century has dramatically affected the distribution of most mammals, as seen in the past and present maps of mammal distribution by du Plessis (1969). For similar reasons the largest game concentrations occur in game reserves and this has also had a striking effect on dung beetle distribution.

An extreme case is <u>Circellium bacchus,</u> a flightless species possessing only vestigial wings which relies on the availability of an abundant dung supply in compensation for its greatly reduced mobility. Today in southern Africa it apparently occurs only in the Addo Elephant Park (near Port Elizabeth) where it feeds largely on elephant, buffalo and zebra dung (I. Temby, pers. comm.). Previously, according to Ferreira (1972), its distribution extended throughout the Cape Province, the Transvaal and Botswana, but except in the Addo Elephant Park the dung in these areas is that of cattle and is widely scattered because the carrying capacity of the veld has been greatly reduced as a result of overgrazing and the encroachment of the Karroo (Acocks, 1953) resulting in fewer animals per hectare. As this species must walk from dung pad to dung pad it is not surprising that it no longer occurs in these areas today. Furthermore, it is an extremely slow breeder, producing a single brood-ball per female per season (Chapter 8), and it is also adapted to fairly sandy areas both of which factors constitute further restrictions.

The animals in reserves are restricted to the geographic regions in which the reserves are situated and although the beetles are fairly well distributed in these restricted areas, habitat differences, however slight they may seem to an observer, nevertheless affect the distribution of the various beetle species within the reserve itself. This is borne out in the pitfall trapping in Mkuzi Game Reserve (Chapter 3). The various species of game occupy particular

niches /....

niches and the beetle fauna associated with them will
naturally occur in the same habitat mainly due to dung pref-
erence (Section 4.2).

The open nature of the grasslands lends itself to the
evolution of telecoprids and Halffter and Matthews (1966)
consider this was due to the fierce competition for dung
with other beetle species. This would conceivably consist
largely of competition from the mainly night-flying para-
coprids. Although the grassland regions have a more
numerous coprophagous population due to the vast amounts
of bovine dung, Halffter and Matthews (1966) consider a
forest region to have a larger number of species due to the
non-availability of such bovine dung, as these species have
adapted to other sources of food and are largely necrophagous.
This change in diet, behaviour and morphology in adapting to
a food source other than dung is considered to have resulted
in a greater diversity of species.

It is most probable that dung beetles and mammals
evolved together (Halffter and Matthews, 1966) so that the
supply of excrement is closely interrelated with other
factors including climate, vegetation, altitude and soil
type to which both types of fauna are subjected in the
same habitat. No one factor, then, can be completely
independent of the others.

2.3.1 Distribution of Mammals :

With coprophagous beetles, food is one more factor
of the biome strictly related to microclimate, edaphic and
vegetational factors and in no way separable from them
(Halffter and Matthews, 1966). The savanna of southern
Africa is characterised by a single short rainy season and
the fauna is adapted to the particular conditions resulting
from this. The gestation period of herbivorous animals
is geared to this short period of plant growth and as a
result young are born usually at the onset of the rainy
season.

The largest mammals, elephant, rhinoceros, buffalo etc., are restricted to those areas of southern Africa which are termed Bushveld by Acocks (1975). The Lowveld Bushveld occurring at altitudes between 150 and 600m above the sea and stretching from the Kruger National Park, through Swaziland and Zululand, is the most favourable habitat for these large mammals. This bushveld occurs mainly on sandy soils (Acocks, 1975) where the rainfall is in the range of 500 - 750mm per annum and falls in summer. The climate is hot, this vegetation occurring above the 15°C effective temperature isoline.

This habitat coincides with that of the Kheper genus. Conceivably these beetles evolved with and adapted to the dung of the larger animals, which their distribution both past and present follows quite closely. This is confirmed by plotting the distribution of the largest mammals from 1652 in southern Africa.

The African elephant distribution was plotted from the writings of hunters, explorers etc. recorded in Shortridge (1934). The plants eaten by elephants and their chemical composition (Dougall and Sheldrick, 1964) relate to the habitat in which they occur. This distribution is most probably incomplete as elephants in South West Africa were occasional migrants moving south in the rainy season (Shortridge, 1934).

Although the previous distribution of the elephant (fig. 25). white rhinoceros (fig. 26) and especially the black rhinoceros (fig. 27) seems considerable, it must be borne in mind that elephants may walk over 100 miles and rhinoceroses over 50 miles from one drinking place or feeding ground to another (Shortridge, 1934). The migrations during the rainy season occur only because there is surface water available and all three species need copious amounts of water. The black rhinoceros drinks twice a day in summer and once a day in winter and as the surface water

evaporates /....

FIGURES 25 - 27

THE GEOGRAPHICAL DISTRIBUTION OF LARGE MAMMALS IN SOUTHERN AFRICA
FROM THE YEAR 1652 ONWARDS.

Figure 25 : The distribution of the African elephant, Loxodonta africana, in
southern Africa (plotted from information acquired in Shortridge, 1934)

Figure 26 : The distribution of the white or square-lipped rhinoceros, Ceratotherium
simum, in southern Africa (after Bigalke, 1963)

Figure 27 : The distribution of the black rhinoceros, Diceros bicornis, in southern
Africa (after du Plessis, 1970)

ANGOLA

RHODESIA

SOUTH-WEST
AFRICA

BOTSWANA

P.E.A.

Tvl.

O.F.S.

Ntl.

CAPE

AFRICAN
ELEPHANT

Fig. 25

ANGOLA

Zambezi R.

SOUTH-WEST
AFRICA

RHODESIA

BOTSWANA

P.E.A.

Limpopo R.

Tvl.

Orange R.

O.F.S.

Ntl.

CAPE

WHITE
RHINOCEROS

Fig. 26

ANGOLA

RHODESIA

SOUTH-WEST
AFRICA

BOTSWANA

P.E.A.

Tvl.

O.F.S.

Ntl.

CAPE

BLACK
RHINOCEROS
(1652)

Fig. 27
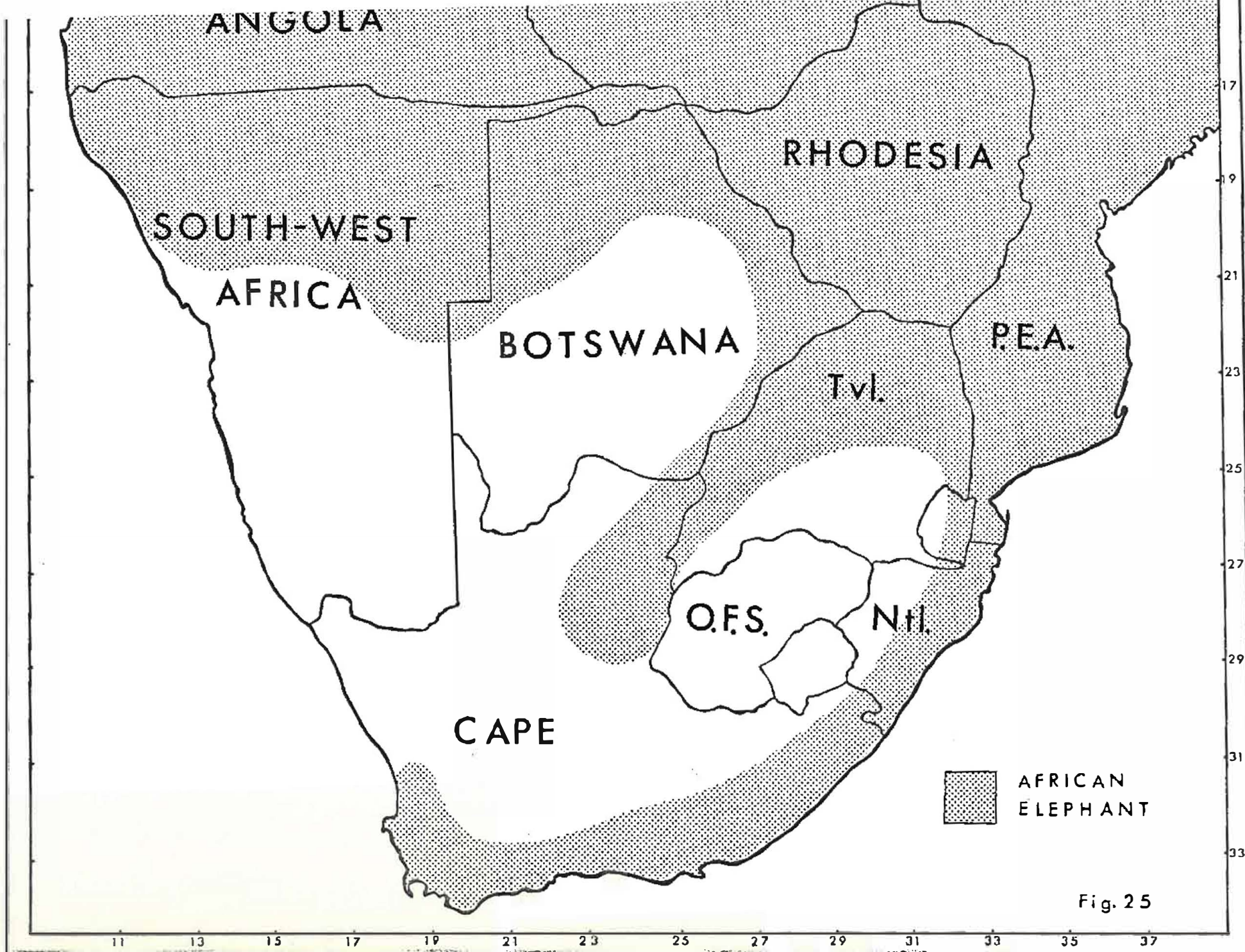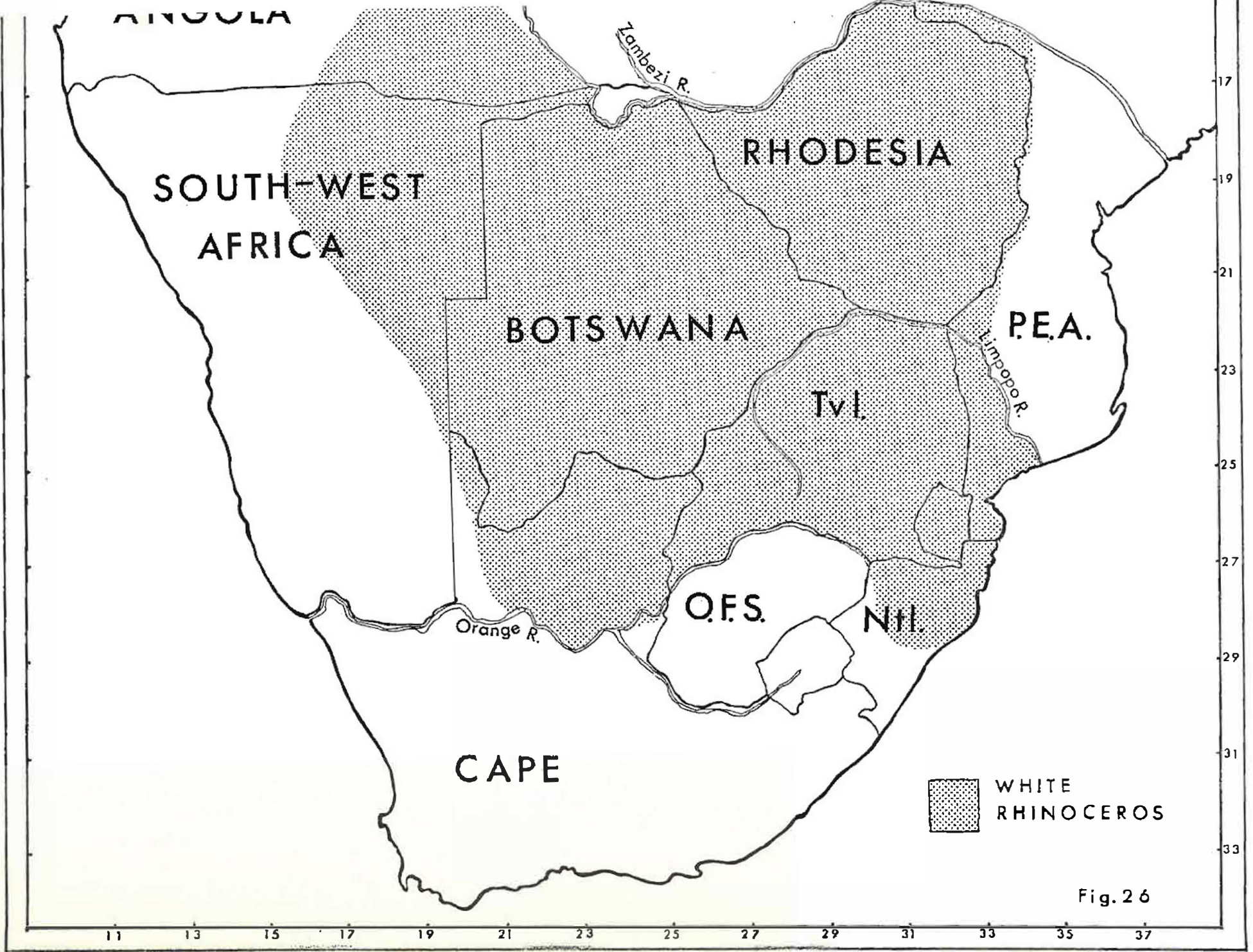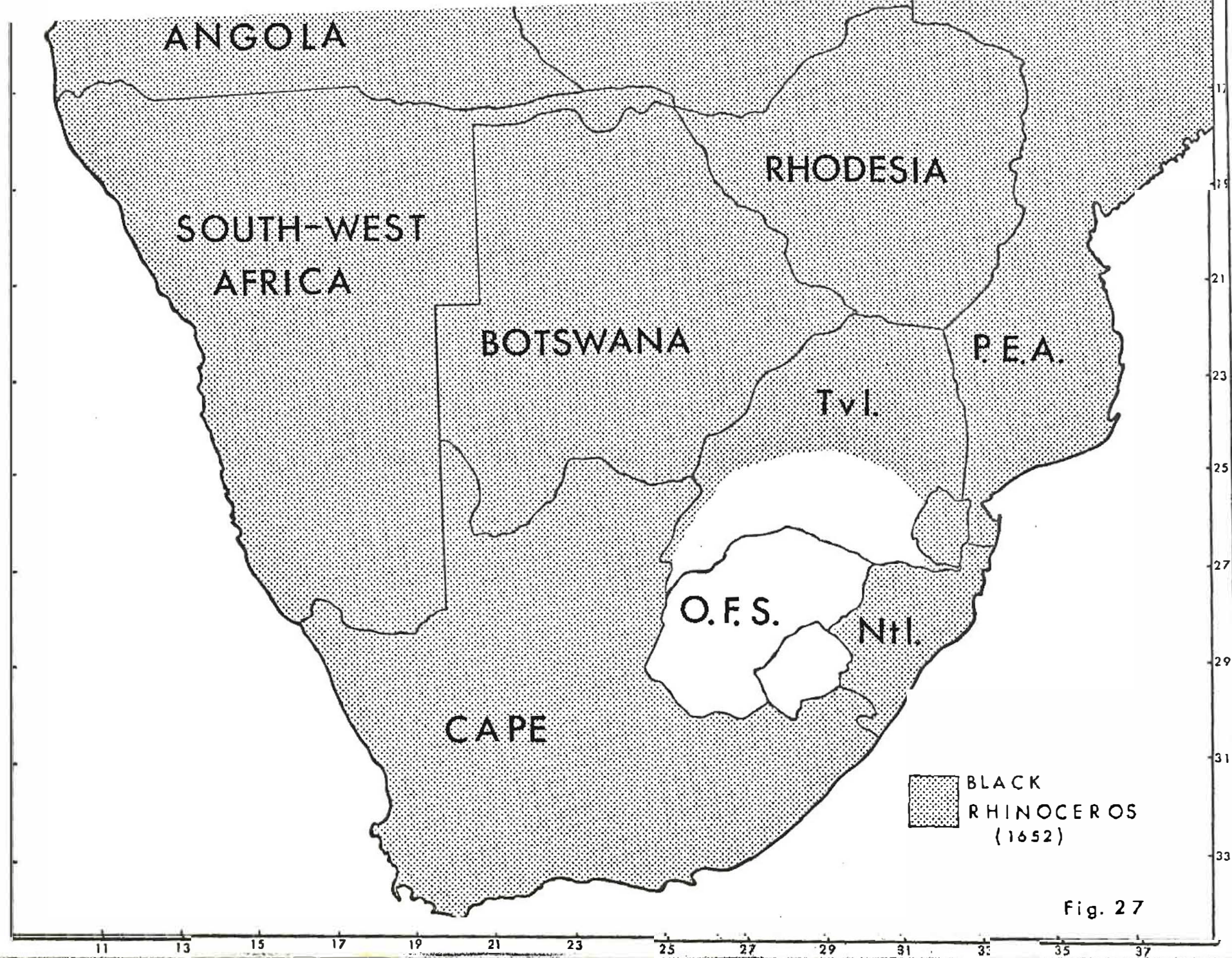
evaporates it becomes restricted to those areas in which there is a permanent supply of surface water, as it cannot dig for subterranean water as elephants do (Shortridge, 1934).

Surface water is important for another reason. The heat regulatory system of rhinoceroses consists of highly vascular subcutaneous tissue which can only be cooled by contact with an external coolant, there being no sweat glands to reduce the temperature by evaporation of a bodily produced liquid (Player and Feely, 1960). Wallowing in mud acts primarily as a method of heat regulation.

The distribution of the black rhinoceros (after du Plessis, 1970) presumably includes these migrations, and they were probably more often recorded when outside their normal habitat as a result of their congregating around the occasional pool of surface water where they were more conspicuous. Various authors, recorded in Shortridge (1934), mention that rivers such as the Vaal and Orange could easily be crossed during the dry season, but when taking into account the reliance on surface water it is unlikely that many animals would cross a river into a drier habitat at this time.

The distribution of the white rhinoceros (after Bigalke, 1963) shows it had a much more restricted habitat than the black rhinoceros, whereas the buffalos' original distribution follows a similar distribution to that plotted for the elephant (fig. 25) and is therefore not reproduced here.

Although the Kheper species occur today over much of the area originally inhabited by these larger mammals (Reference Collection, Dung Beetle Research Unit), within the climatic restrictions placed on them, nowhere do they occur in such numbers as where these animals are present today. The natural carrying capacity of an area containing indigenous animals would be high with a resultant high concentration of dung.

Generally speaking, from data compiled from the reference collection (Dung Beetle Research Unit) and the Transvaal Museum, the Kheper genus may be said to follow the main habitat of the large herbivores, the Scarabaeus subgenus is rather marginal but still within the original range of the large herbivores, and the Scarabaeolus subgenus is mostly outside their range.   The Scarabaeolus subgenus would have originally fed largely on the dryish pellets of the Gemsbok, Springbuck, quagga and the smaller antelope which inhabited the North Western Cape (du Plessis, 1970).

The trend which emerges suggests the availablility of large quantities of dung resulted in the evolution of large telecoprids and that the species became progressively smaller moving across southern Africa from east to west.   The average size of each species was determined by measuring the total beetle length and the width of the abdomen at the widest part of samples of individual beetles.   The results are shown in Table 4.

TABLE 4:   Comparative mean sizes of beetles comprising the Kheper and Scarabaeus genera

Genus or Subgenus	Total length (cm)	Width Abdomen (cm)	Sample Size
Kheper	3,03	1,88	274
Scarabaeus	2,09	1,33	432
Scarabaeolus	1,18	0,67	130

As the dung type cannot be separated from the other factors that make up the habitat the reduced size and other morphological features reflect the nature of the habitat as a

whole /....

whole rather than dung type alone.   Nevertheless, the
abundance of dung appears to be a particularly important
factor in this respect.

The factors limiting the distribution of K. nigroaeneus
are tabulated in Table 5.

TABLE 5:   Summary of the limiting factors of Kheper
nigroaeneus

VARIABLES	OPTIMUM	MARGINAL	RANGE	EXCEPTIONS
Temperature Effective Temp.	> 16°C	> 15°C	16°C-19+°C	

Mean Ann. No. Days :
  > Max. 30°C
  > Min. 20°C
	116 - 165
	52 - 83
		> 78
		> 5,8
			78 - 165
			5,8 - 83	

Mean Ann. $\frac{1}{2}$ Max. & Min.	19°C-23°C	>17,2°C	17,2°-23°C	

Rainfall :
Annual   (mm)
       (inch)
 	
Season
	600-1000
	24 - 40
	
	Summer
		> 200
		> 8
		
		Summer
			200 -1000
			8 - 40
			
			Summer
				(Fine
				  Sand)
				Winter

Altitude : South of Lat. 17°S (m)	150 - 500	500-1500	0 - 1500	2000 + (Tropics)
Soil Type :	Sand	Sandy- Loam	Sand - Sandy Loam	
Vegetation:	Lowveld- Bushveld	Thorn- veld, Mopani veld, Mixed Bushveld	Bushveld	

CHAPTER 3.

SEASONAL ACTIVITY CYCLES.

3.1 PITFALL TRAPS :

To determine the annual fluctuations in beetle numbers of a natural population, baited pitfall traps were set out at intervals at Nsumu Pan in the Mkuzi Game Reserve near a permanent pool of water which ensured continual animal activity in the area. Each trap was set out in a permanent position within the acre which constituted the experimental area and the individual traps were recorded on a map of the area.

The pitfall traps were constructed similarly to those designed by Paschalidis (1974) being larger in size, with the same methods of collection and transportation being adopted. Galvanised iron sheeting (67,5cm x 22,5cm) was bent to form a hollow cylinder, the opposing ends being rivetted together. These iron frames were sunk into excavated pits to form permanent positions in which to place the buckets. White plastic buckets, 63cm in diameter and 20cm in depth, with an overlapping lip were used, the lids covering the buckets were made from green wire gauze (0,15cm x 0,15cm), the ragged edges being turned down and taped with cloth tape to form a firm edge.

Once pulled over the bucket, the lid is held firmly in position and the trap is virtually flush with the surrounding soil surface. The hole through which the beetles enter the trap was made by cutting a cross 5cm x 5cm in the centre of the lid and turning the four triangular pieces to project into the tub. These triangles of gauze serve to retain captured beetles as beetles flying up and just under the

gauze encounter these projections and fall back into the tub.

The traps were baited with a standard amount of 150 gms. of horse dung. Horse dung was selected as bait for the following reasons :-

(a) It was easily accessible in sufficient quantity from the stables near Nsumu Pan.

(b) It is a medium coarse dung which is attractive to most beetle species being neither too coarse nor too sloppy to species showing dung type preference (Table 10, page 77)

(c) It has a strong odour which immediately attracts beetles in the vicinity.

The baited buckets were set out every fortnight for a period of 24 hours by Ranger R. Henwood, by placing them in the circular frames. This fortnightly interval was the shortest period convenient to all concerned. Since the traps were set out at 0600h they were biased in favour of diurnal species as by 1900h the dung in the traps is shredded to such an extent that it is no longer attractive to the incoming crepuscular species. Also the presence of fresh dung in the vicinity of the traps would draw most crepuscular species because of its stronger odour. The traps were set out under sunny conditions whenever possible to standardise conditions, since clouds and rain were previously observed to have an immediate dampening effect on beetle activity. Hence the "fortnight" was sometimes extended as the weather dictated.

After 24 hours exposure the complete contents of the buckets, both beetles and shredded dung, were transferred to correspondingly numbered plastic containers (15,5 x 12,5 x 8,5cm) with tight fitting lids. Aeration was through numerous holes (0,3cm in diameter) punched into the lids and sides of the containers. Many of the smaller Aphodius, Onthophagus and Sisyphus species managed to escape from the air vents so that the traps did not record the total catch, but rather selected species. En route to Pretoria by rail

the /....

the predatory Histerid species accounted for a few _Sisyphus_ and _Phalops_ beetles, but the overall effect of this predation was negligible. Any beetles which died in these containers in hot weather were enumerated without much difficulty.

The information recorded at each trapping interval included the maximum and minimum temperature during the 24 hour period; the date and time set; the cloud cover during trapping; rainfall between trappings; rainfall during the trapping period; and a short note on animal activity in the experimental area.

Eight trapping sites were selected within the experimental area according to sunlight, shade, vegetation cover and altitude differences. Traps one to four were set largely in open ground with the full sun on them; traps five and six were set in the shade of acacia trees at different sites; trap seven was partly shaded and nearer the pan and therefore considerably lower than all the other traps; trap eight was placed in sunlight but in a dense growth of weeds. Because of the seasonal flooding of the nearby riverine forest, no traps could be set out in the dense shade along the river course.

Several methods were used to sex the various species captured in the pitfall traps :

   (a) "Universal method": In the male the last abdominal segment before the operculum is constricted in the centre, whereas in the female it is broad in the centre. Figure 28 shows the differences in _Pachylomera femoralis_ which are distinct. Many species are not as distinct, yet this method is standard for a large number of species of many genera of dung beetles.

   (b) Tibial brushes: In the _Kheper_ genus and in three species of _Scarabaeus_ the males have pheromone dispersal brushes (fig. 85).

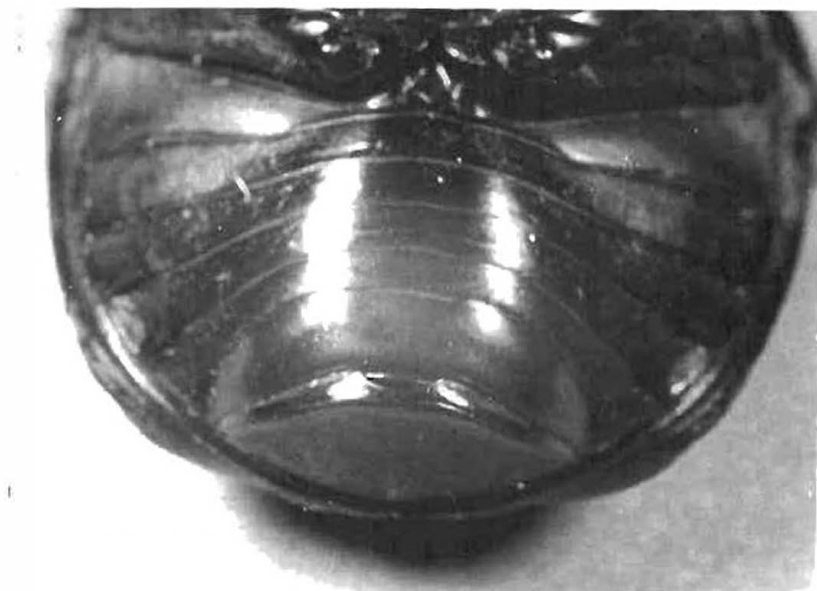   (c) Abdominal bristles: Present only on either two or three of the first abdominal sternites in male

FIGURE 28.

THE "UNIVERSAL" METHOD OF SEXING DUNG BEETLES AS
ILLUSTRATED IN PACHYLOMERA FEMORALIS :

(a) The male mid-line constriction of the sixth
abdominal sternite.

(b) The female mid-line widening of the sixth
abdominal sternite.

Kheper species.   Rudimentary in females
(fig. 71).

(d) Horn: Most male Proagoderus, Copris etc. possess
a clypeal horn which is absent or rudimentary in
the female beetle.

Garreta nitens cannot be sexed by any of the above
methods, although Gymnopleurus species in Korea were sexed by
Paik (1968) by observing a small blunt tooth on the inner
foretibiae present only in the male.   However G. nitens may
be sexed on the basis of distinct behavioural positions taken
up by the beetle pair rolling a brood-ball (Chapter 7).

3.2 CLIMATIC INFLUENCES :

The Nsumu Pan pitfall traps were initially set out in
early September 1974 but it was not until mid-October that the
first beetles were captured (fig. 29).   During the previous
(1973) season beetles had been active during late September.
The difference between the two seasons was that rain fell in
mid-September in 1973 but the first rains of 1974 occurred
only in early October (fig. 30).

In late September 1974, holes were dug in seven
separate localities approximately one kilometer from each
other, in both the Hluhluwe and Mkuzi Games Reserves and the
following was noted.   At all sites the soil was found to
be very hard and extremely dry to a depth of 30cm.   The soil
was so compacted that it seemed impossible that dung beetles
could emerge from it.   Yet at this time there were several
K. subaeneus beetles on the surface rolling food-balls which
they were unable to bury as the soil was too dry and compacted.
During this period the unusual sight was observed of
K. subaeneus beetles rolling food-balls beneath bushes and
half-burying them in ± 3cm of loose surface soil and then
pulling dead leaves and other debris over the still exposed
part of the ball.   No food-balls were actually buried
during the observation period.

These early K. subaeneus beetles presumably aestivated

in /.....

MKUZI PITFALL TRAPS
Fig. 29

Legend:
.... A. thalassinus
——— K. nigroaeneus
– – – Phalops & Proagoderus
········ G. nitens
– ·· – G. virens

Total beetle numbers

Sept.   Oct.   Nov.   Dec.   Jan.   Feb.   Mar.   Apr.   May.

1974   1975
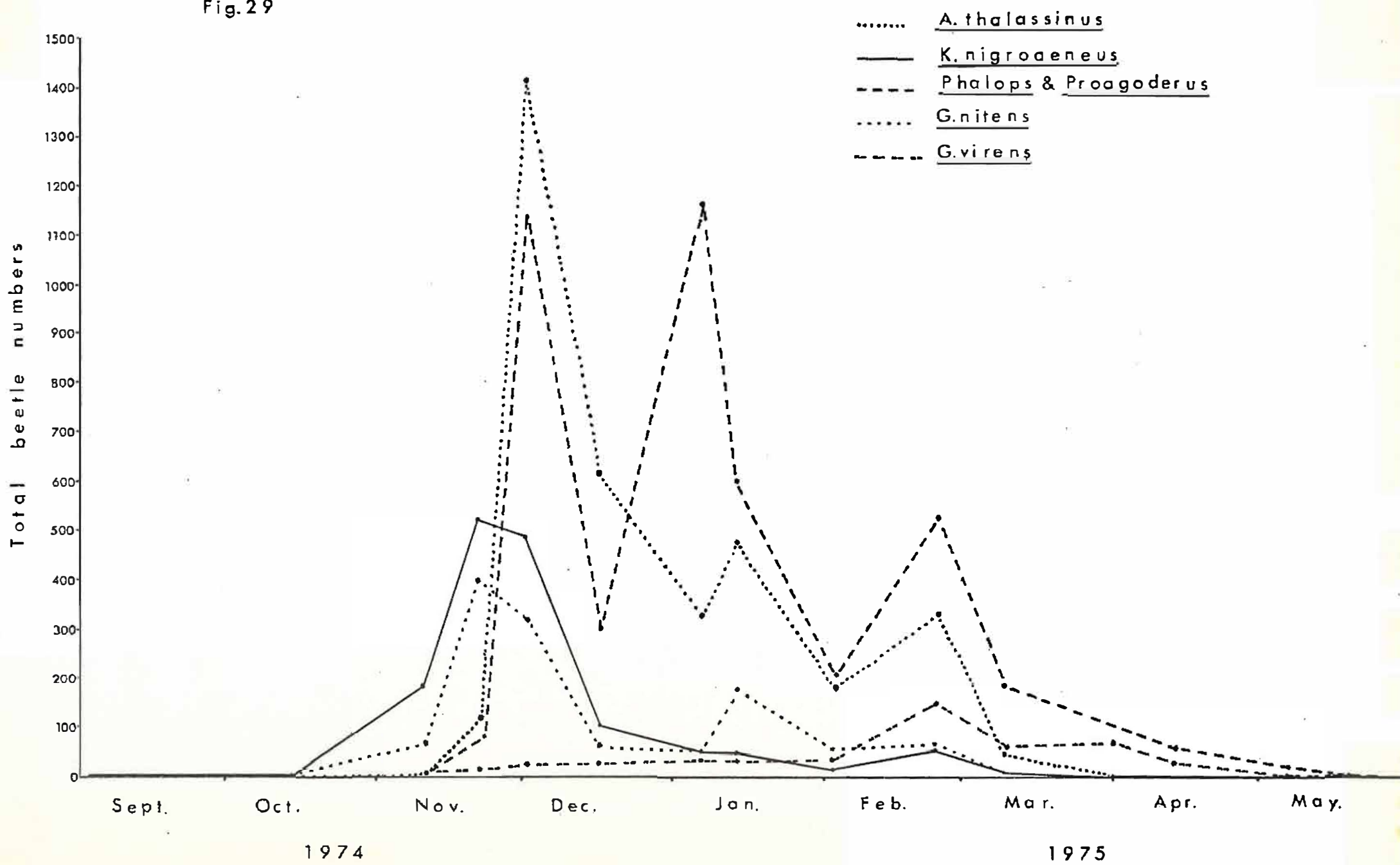
RAINFALL
Mkuzi Game Reserve
Fig. 30

in areas of sandier soil from which they were able to emerge in response to the warmer temperatures. From temperature data recorded with the fortnightly traps it was calculated that the ½ Maximum and Minimum over the period 15th September (1974) to the 24th February (1975) fluctuated slight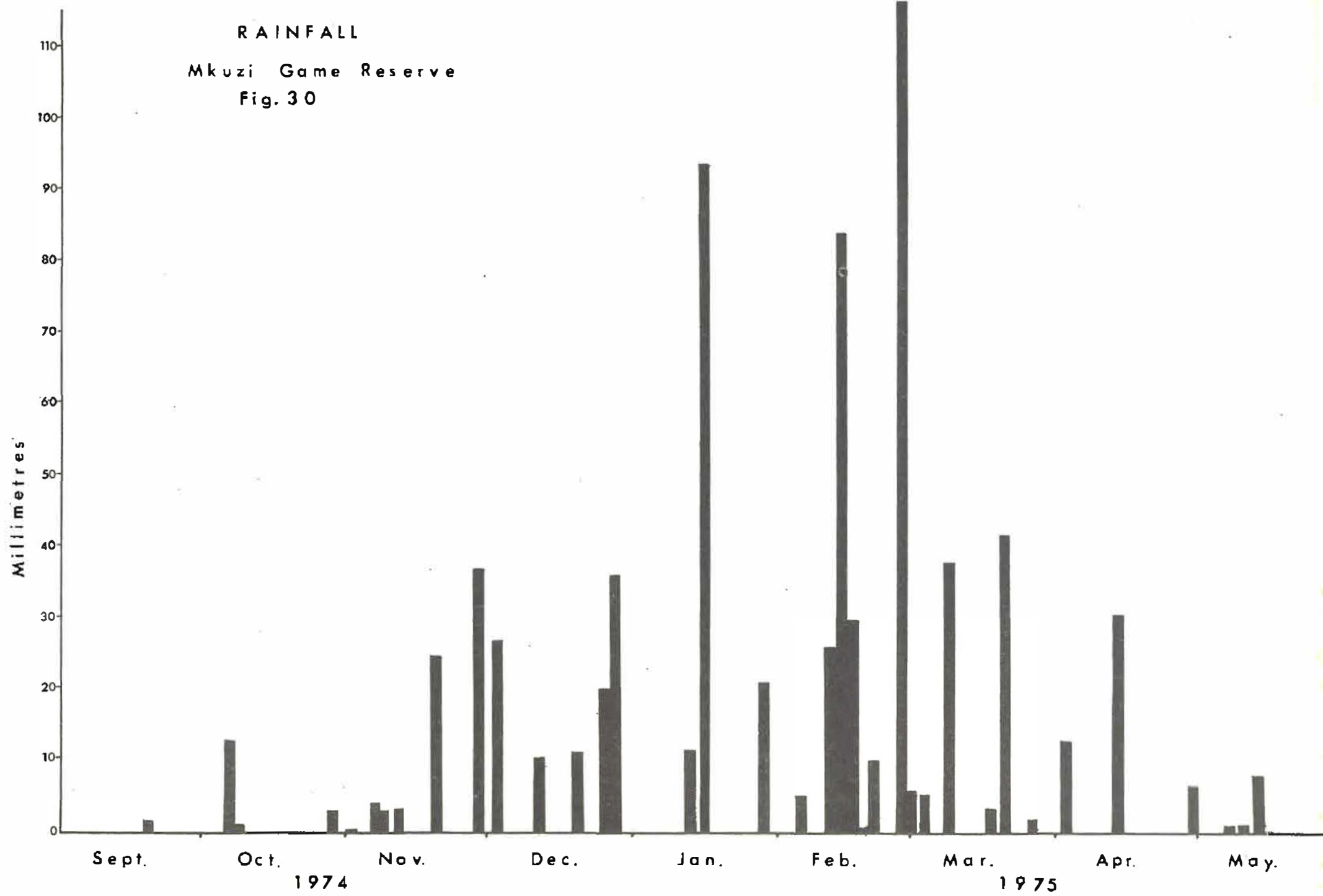ly about 27°C. The highest ½ Maximum and Minimum was recorded on the 15th September, 1974 of 28,5°C, possibly due to the cloudless sky at this time of the year. Temperatures were suitable for emergence from this date, yet beetles only began emerging in mid-October and became abundant only in mid-November (fig.29).

The ½ Maximum and Minimum recorded on the 2nd September, 1974 was 21°C which is presumably too low for beetle activity judging by temperatures later in the season. After the 24th February 1975 the temperature began dropping and the fluctuation in the maximum and minimum temperatures became greater. By April 1975 the temperature drop was rapid, down to the ½ Maximum and Minimum of 20°C on the 12th May at which beetle activity ceased.

The mean daily maximum and minimum temperatures for Otobotini (North of Mkuzi) may be regarded as fairly typical of the region. Figure 31, drawn from data recorded between 1924 - 1950 (Climate of South Africa, W.B.19) has had the critical temperature limits drawn in under which beetle activity ceases. These limits were drawn according to data obtained from the seasonal trappings (fig. 29) and distribution data. The upper critical daily maximum and minimum of 29°C has a corresponding lower limit of 17°C above which telecoprids may be active. Daily maximum and minimum temperatures below these limits result in the aestivation of beetle species during the period in which they prevail.

Frequencies of Otobotini are plotted in figure 32 from data obtained from W.B.19. Based on the beetle activity recorded during the seasonal trappings, further limits may be determined for seasonal activity. The critical number of

days /....

days a month with a daily Maximum $> 30^{o}C$ for activity to occur
is 12, while the critical number of days a month with a daily
Minimum $> 20^{o}C$ for activity to occur is nine.

Sufficient rainfall is needed to bring the beetles to
the surface as long as the temperature is above the critical
limits.   The rapid emergence of beetles after the first
spring rains (usually the cumulative effect of several days
rain) is due to the action of the rain in softening the
compacted soil enabling the beetles to burrow to the surface.
The October 7th and 8th (1974) rains of 14mm were enough to
release K. nigroaeneus from the soil (fig. 30).   The
subsequent rainfalls during the first two weeks of November
(and possibly a higher temperature as A. thalassinus,
P. flavocinctus and P. tersidorsis were shown to be active
diurnally at higher temperatures than K. nigroaeneus) were
sufficient to release the other species from the soil.

Although beetle activity dropped off (fig. 29) as the
amount of rainfall increased (fig. 30) there is no exact
connection between the two, the inverse correlation being of
only little significance in the beetles' level of activity.
Rainfall does affect the beetles activity during and
immediately after each rainfall, both in diurnal activity
and re-emergence, but not to as great an extent.   As seen in
K. nigroaeneus further rainfall after the initial rainfall
has only a small effect on their behaviour, although a much
greater amount of rain had fallen after the initial emergence.
This further indicates that rainfall is necessary only for
releasing the beetles from the soil, playing no decisive role
in the beetles' activity thereafter.

The few unusual cloudbursts over Mkuzi during the winter
months of 1973 did not bring any beetles to the surface
which further indicates that temperature is of prime importance,
rainfall acting only as a releasing agent at a critical time.
Thus no telecoprids have been found in the Winter Rainfall
region of the Cape except where the soil is loosely packed
i.e. fine sand, permitting them to emerge during the dry

summer /.....

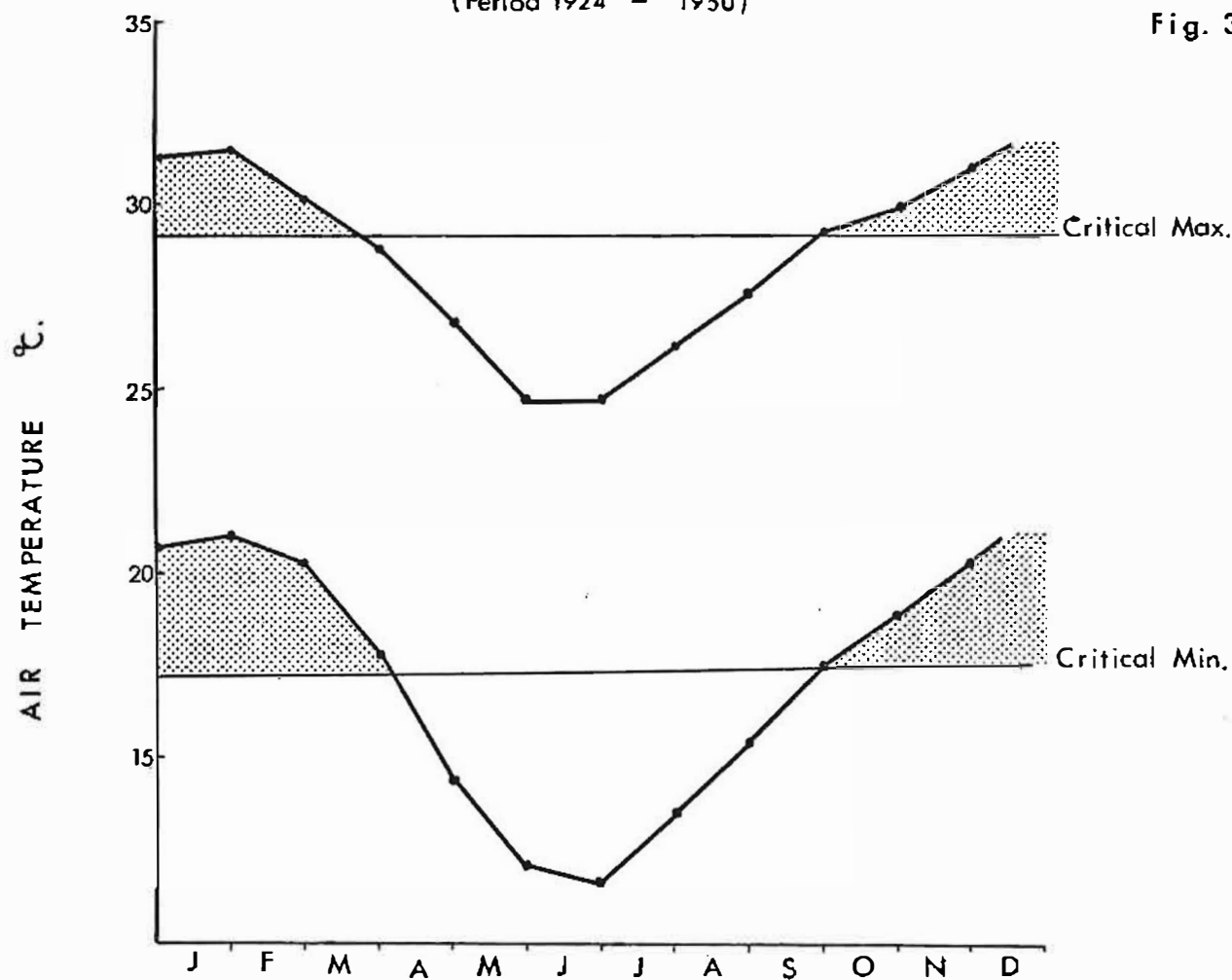OTOBOTINI, (Natal) $\phi = 27°\,25'\,S.$ $\lambda = 32°\,06'\,E.$

MEAN DAILY MAX. AND MIN. TEMPERATURES
(Period 1924 – 1950)

Fig. 31

AIR TEMPERATURE °C.

Critical Max.

Critical Min.

J F M A M J J A S O N D

FREQUENCIES   Fig. 32

NUMBER OF DAYS WITH AV. TEMPS. ABOVE :-

Daily Max. > 30° C.
Daily Min. > 20° C.
Critical Max.
Critical Min.

J F M A M J J A S O N D
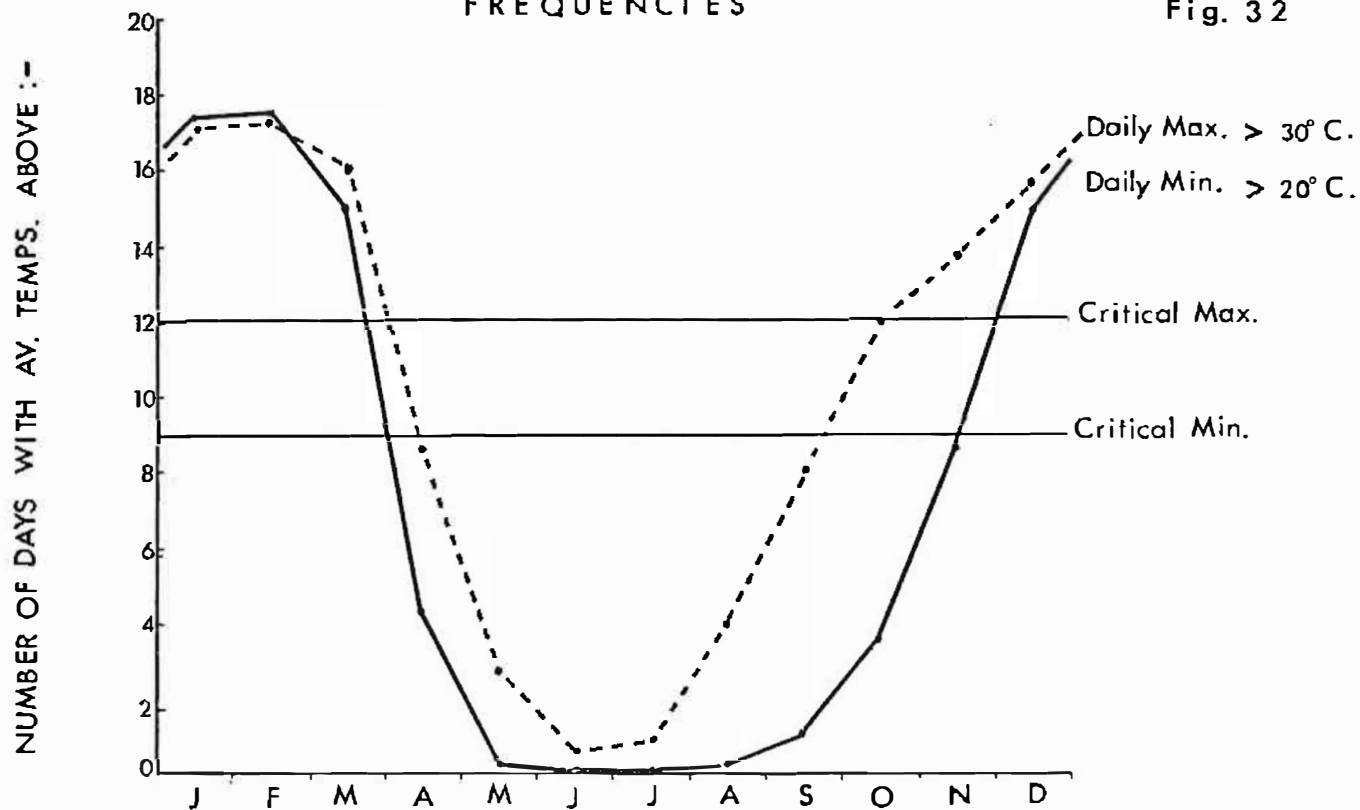
summer months.   Rainfall not only allows the beetles to
emerge but also enables them to bury both food- and brood-
balls, behaviour seen only after the first rains have fallen.
The occasional rainfall is necessary throughout the summer
months to keep the soil workable.

3.2.1 Seasonal Peaks :

In addition to the separable diurnal activity peaks
(Chapter 4), there is a further temporal segregation of
species through differences in seasonal activity.   Figure 33,
showing cumulative percentages of the Nsumu species, gives
a clearer idea of the seasonal distribution of each species
in relation to other sympatric species.   The lateness of
the 1974 rains probably resulted in the concertinaing of the
peaks of a number of species, which would presumably be more
widely spaced as a result of temperature preferences
parallel to the diurnal temperature preferences (Chapter 4).

This is borne out by K. nigroaeneus and G. nitens
preferring cooler diurnal conditions, being the first to
emerge after rain and similarly with G. virens (fig. 34)
which emerges in large numbers only at the end of February.
Since G. virens is active at temperatures below that of
K. nigroaeneus and G. nitens the late rains in October (1974)
perhaps occurred at temperatures too high for it to become
active at that time.   There appear to be two ways it could
adapt to this.   Either by flying earlier in the morning in
the cooler temperatures or by having the peak of activity
later in the season when the overall temperatures are lower.
Although it appears from the gradual increase in numbers
(fig. 34) that the peak is natural, this late emergence does
not leave much time to breed before temperatures become too
low for activity.

K. nigroaeneus reaches its greatest numbers on the
surface almost immediately after the first summer rains
(fig. 35).   This numerical peak begins dropping first
gradually then at an accelerated rate.   As with most dung

MKUZI PITFALL TRAPS

Fig.33

Cumulative percentages

Legend:
- K. nigroaeneus
- G. nitens
- A. thalassinus
- Phalops & Proagoderus
- G. virens

Sept. — Oct. — Nov. — Dec. — Jan. — Feb. — Mar. — Apr. — May

1974   1975
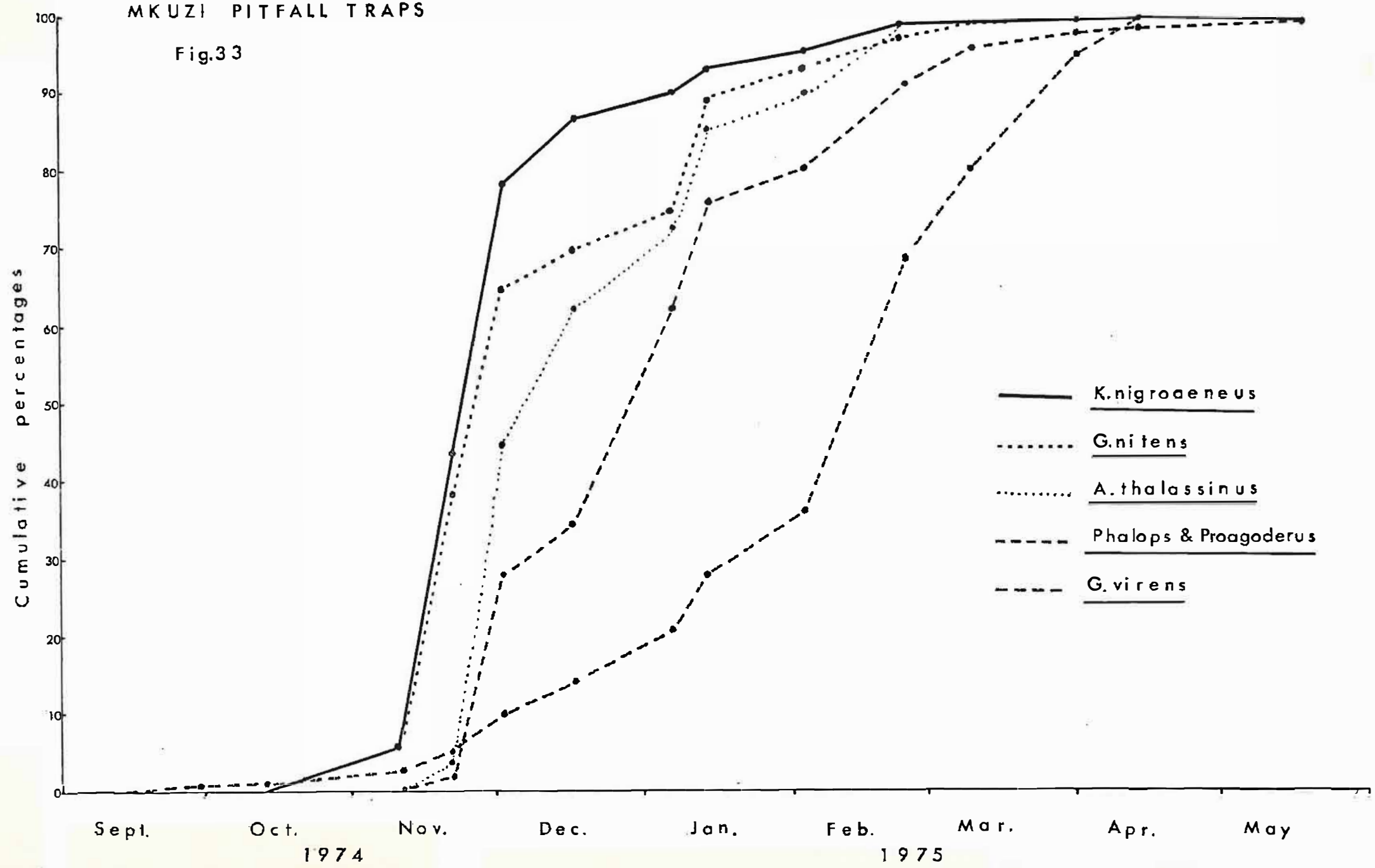
beetles (Halffter and Matthews, 1966), K. nigroaeneus undergo
a maturation feeding period extending over two to three weeks
after emergence. Winter dissections (21.5.75) of
K. nigroaeneus beetles in the laboratory showed that their
guts were almost completely empty and that maturation feeding
is necessary before breeding can commence. During the peak
of activity the behaviour of telecoprids concerns feeding,
either at the pad (G. nitens) or on food-balls rolled away
singly by male or female beetles (Kheper, Scarabaeus).

The accelerated drop in numbers of K. nigroaeneus on
the surface coincides with the onset of the breeding season.
The start of the breeding season is immediately noticeable
by pairs of beetles rolling dung-balls which are buried as
brood-balls. The male K. nigroaeneus returns to the surface
and attracts another mate after an average of four days
(laboratory studies) while the female remains below brooding
for 68 - 84 days. Because of this brood-care fewer females
occur on the surface, with a corresponding drop in the total
number of beetles in evidence.

The minor numerical peak in late February was probably
the result of emerging F_1's although no record was taken of
the proportion which were newly emerged. F_1's are recognised
by the lack of wear on the foretibial teeth, the sharpness of
the tibial spurs and the condition of the tarsi. It is not
possible to separate newly emerged F_1's from the other
generations with any degree of accuracy. From laboratory
studies it was determined that F_1's only feed for the remainder
of the season, breeding starting at the beginning of the
following summer season. Dissections of newly emerged F_1's
showed that they had no food reserves, the gut being completely
empty and fat bodies very sparse. Laboratory studies have
also shown that most K. nigroaeneus beetles live for three
seasons, a few beetles perhaps surviving for a fourth.

A. thalassinus shows a much steeper rise in numbers
(fig. 36) due possibly to the heavy rains of 25mm which fell
in late November (1974), together with the relatively high

$\frac{1}{2}$ Maximum /.....

Gymnopleurus virens

MKUZI PITFALL TRAPS
Fig. 34

Total beetle numbers

150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0

Sept.   Oct.   Nov.   Dec.   Jan.   Feb.   Mar.   Apr.   May.

1974   1975

Kheper nigroaeneus
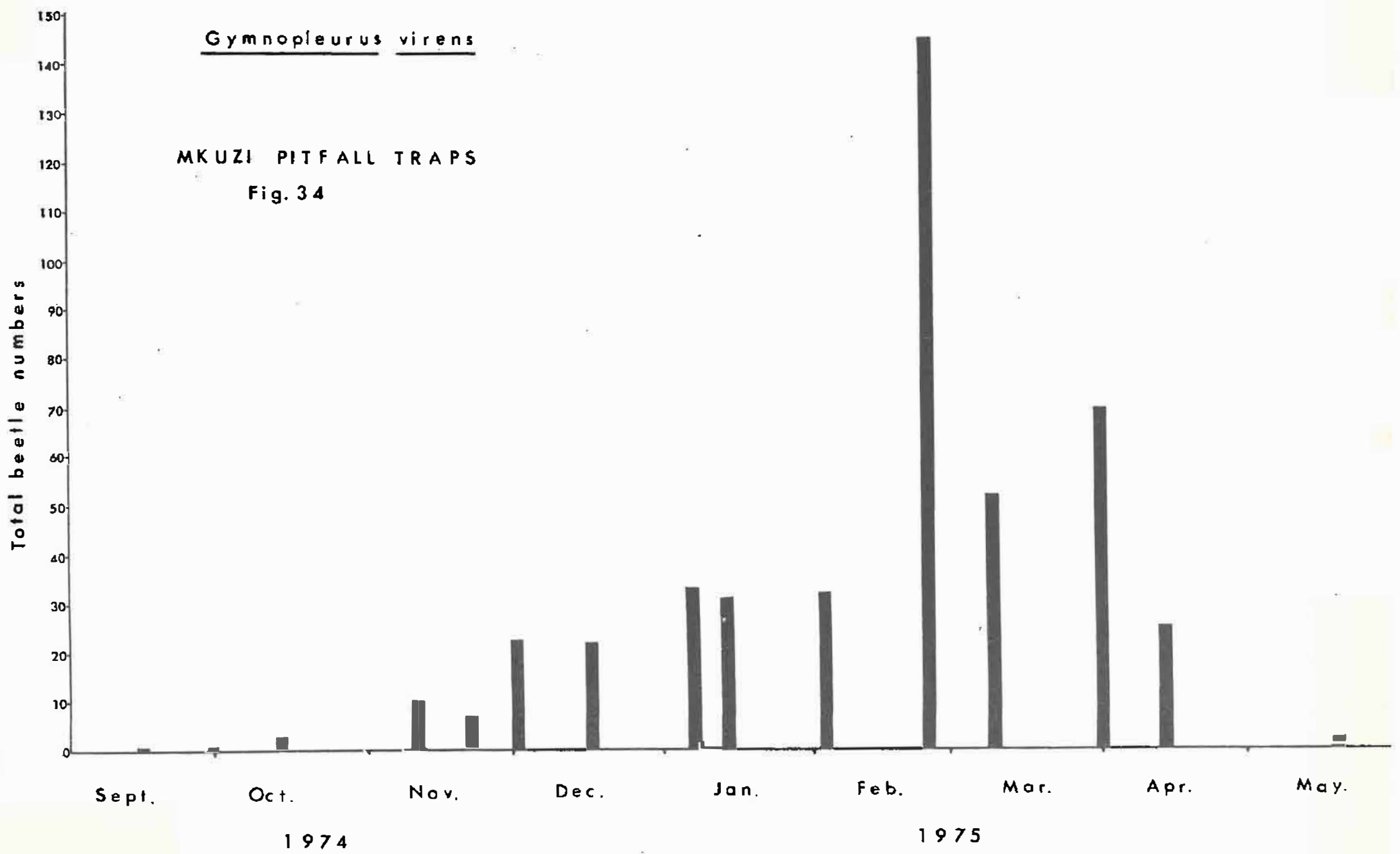
MKUZI PITFALL TRAPS

Fig. 35
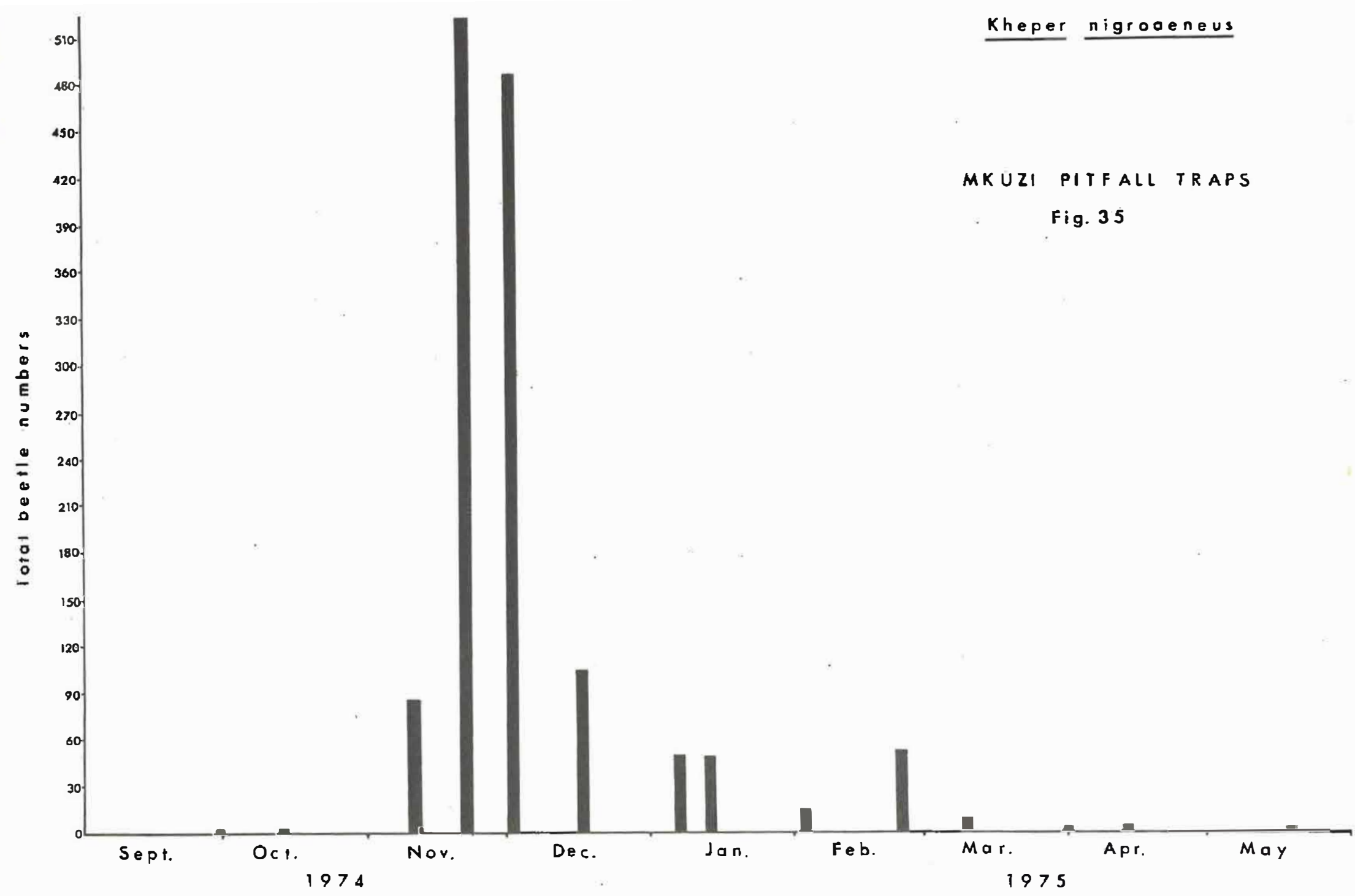
MKUZI PITFALL TRAPS

Fig. 36

Allogymnopleurus thalassinus

Garreta nitens

MKUZI PITFALL TRAPS
Fig. 37
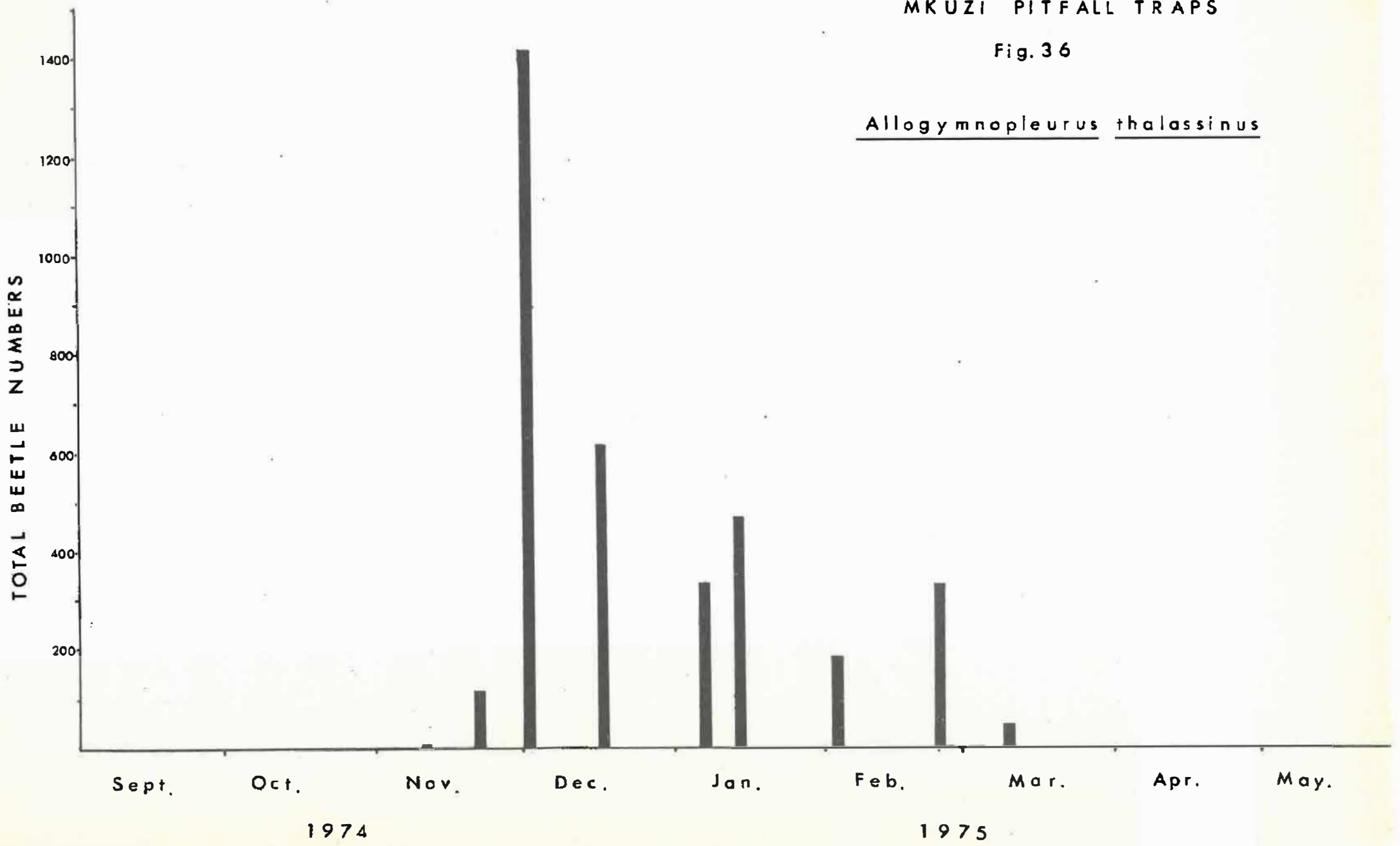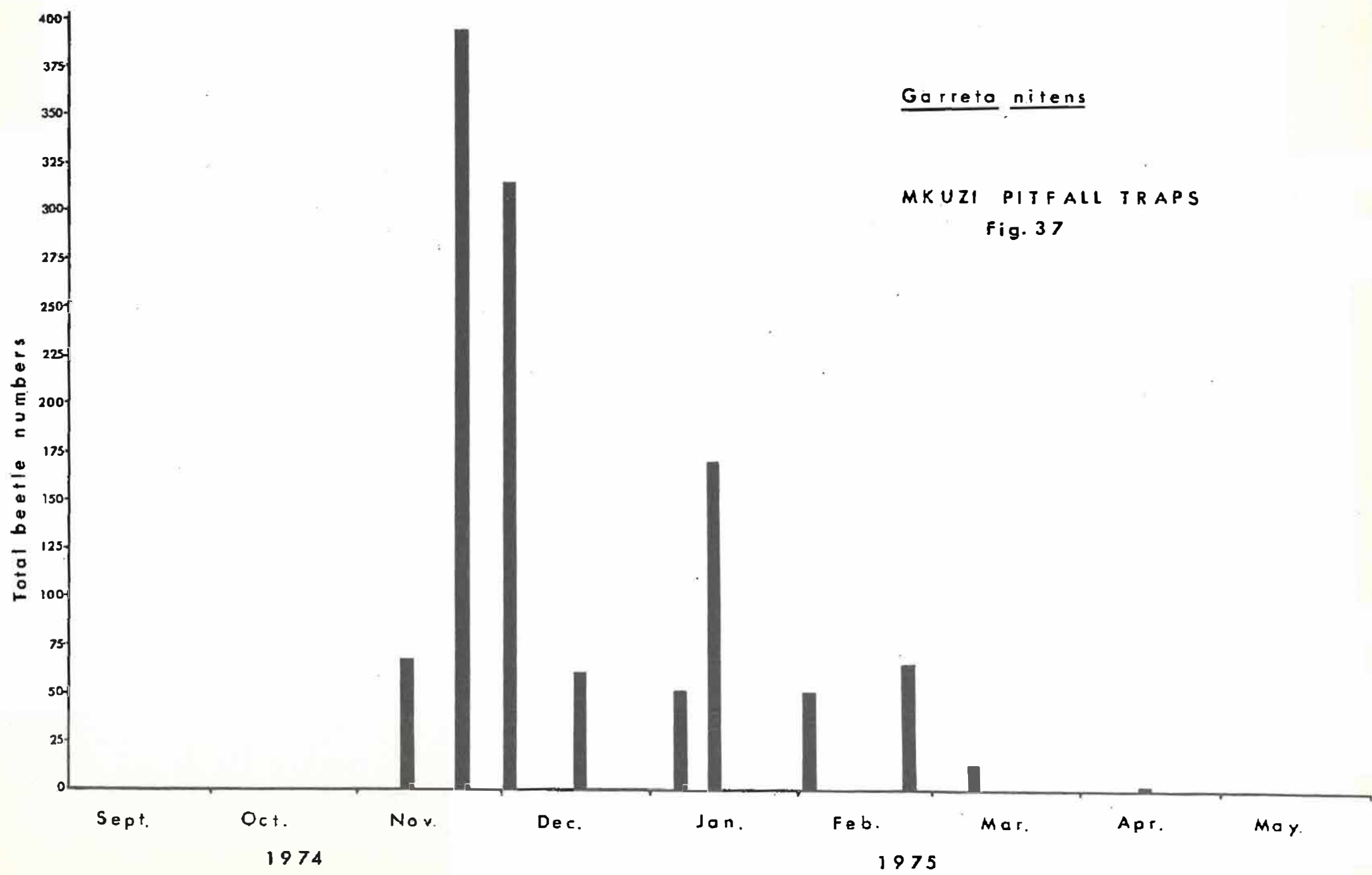
½ Maximum and Minimum temperature of 28°C recorded immediately
before the rainfall and the succeeding warm days.

A drop in A. thalassinus numbers occurs soon after the
initial emergence peak where the maturation feeding period of
one to two weeks was followed by breeding.   The level to
which A. thalassinus drops is not as low as that of
K. nigroaeneus as the former species has no brood care, both
sexes returning to the surface after approximately twelve
days.   The minor peaks in mid-January and late February are
probably again the result of the infusion of newly emerged
F_1's into the parent population.   No data of the proportions
of F_1's to parent generation was recorded.   Laboratory
studies determined that the development of A. thalassinus
from egg to adult emergence takes from 25 to 43 days with an
average of 31 days.

G. nitens takes from 22 to 34 days to emerge as adults
with an average of thirty days.   The effect of moist or dry
soil conditions in the containers in which the brood-balls
were buried did not show any significant effect on the time
taken for the adults to emerge.   G. nitens, which shows no
brood-care behaviour has a second minor peak in mid-January
and an even smaller peak in the late February 1975 (fig. 37)
very similar to that of A. thalassinus.   Newly emerged
laboratory F_1's were not observed to pair off or breed until
the following season, so that the third minor peak is probably
the result of a certain percentage of the parental G. nitens
populations producing second and third generations during the
season.

Figure 38 is a combination of three species, Phalops
flavocinctus, Proagoderus tersidorsis and Proagoderus alcyon,
which were not initially separated from one another because
of taxonomic difficulties further confounded by P. flavocinctus
beetles occurring in many shades of green and blue within the
same locality.   The first of the three species to emerge
was P. flavocinctus, the sharp rise in numbers suggesting an

external /....

THE SEASONAL ACTIVITY PATTERNS OF SYMPATRIC COPROPHAGOUS BEETLE SPECIES AT NSUMU PAN, MKUZI GAME RESERVE, FROM SEPTEMBER 1974 TO AUGUST 1975; NO OR NEGLIGIBLE ACTIVITY BEING RECORDED AFTER MAY 1975.

Figure 38 : Seasonal activity pattern of the combined Onthophagus (Proagoderus) tersidorsis, Onthophagus (Proagoderus) alcyon and Phalops flavocinctus group.

Figure 39 : Seasonal activity patterns of the separated Onthophagus (Proagoderus) tersidorsis, Onthophagus (Proagoderus) alcyon and Phalops flavocinctus species from the dates on which they were recorded separately.

Figure 40 : Seasonal activity pattern of the various Onthophagus species excluding the subgenus Proagoderus. Negligible activity recorded between June and August 1975.

Figure 41 : Seasonal activity patterns of the various Hister species

MKUZI PITFALL TRAPS
Fig. 38

Phalops flavocinctus
Proagoderus tersidorsis
Proagoderus alcyon

Total beetle numbers

Sept.   Oct.   Nov.   Dec   Jan.   Feb.   Mar.   Apr.   May.
        1974   1975

MKUZI PITFALL TRAPS
Fig. 39

Total beetle numbers

Sept.   Oct.   Nov.   Dec.   Jan.   Feb.   Mar.   Apr.   May.

1974   1975

----- Phalops flavocinctus
——— Proagoderus tersidorsis
— — — Proagoderus alcyon
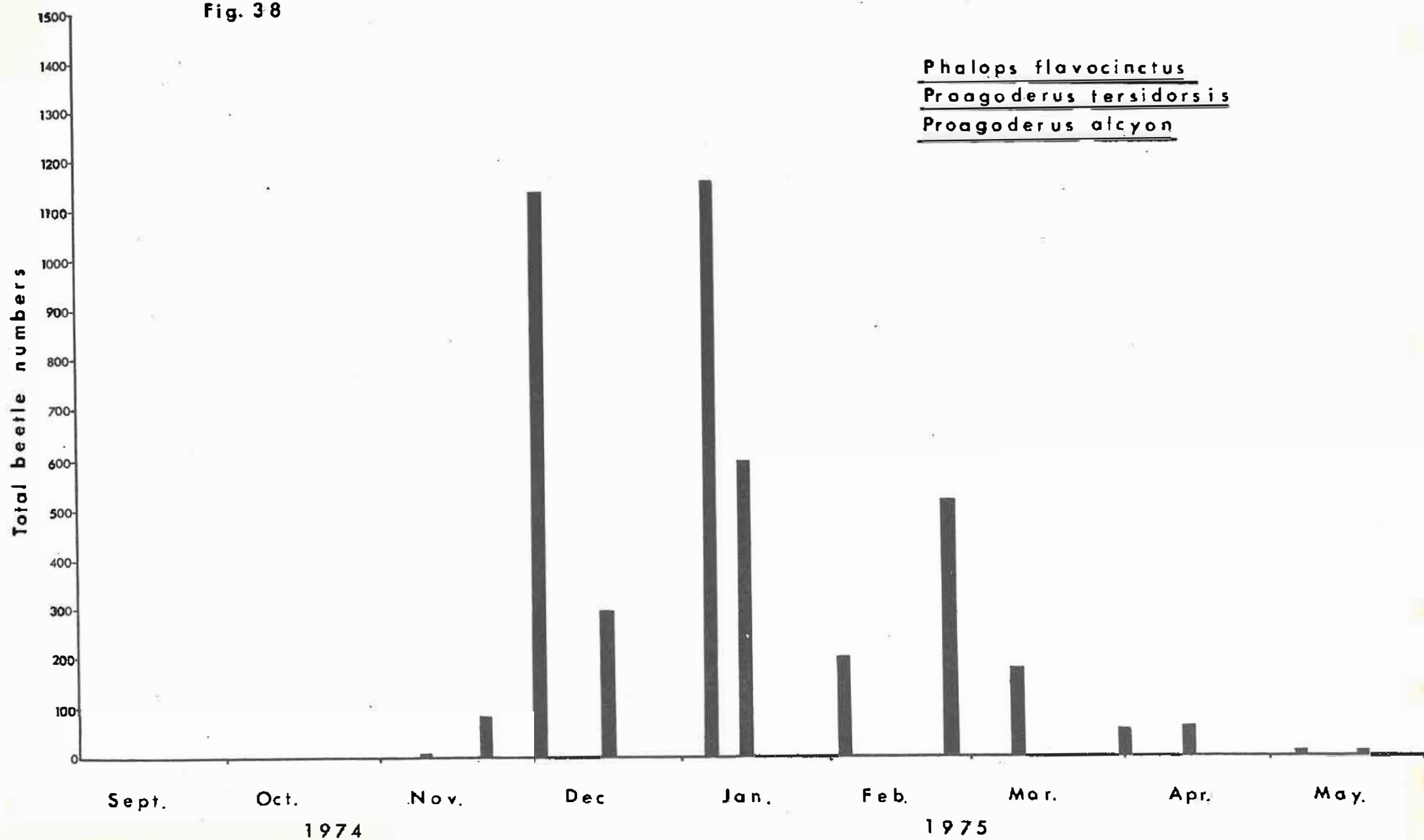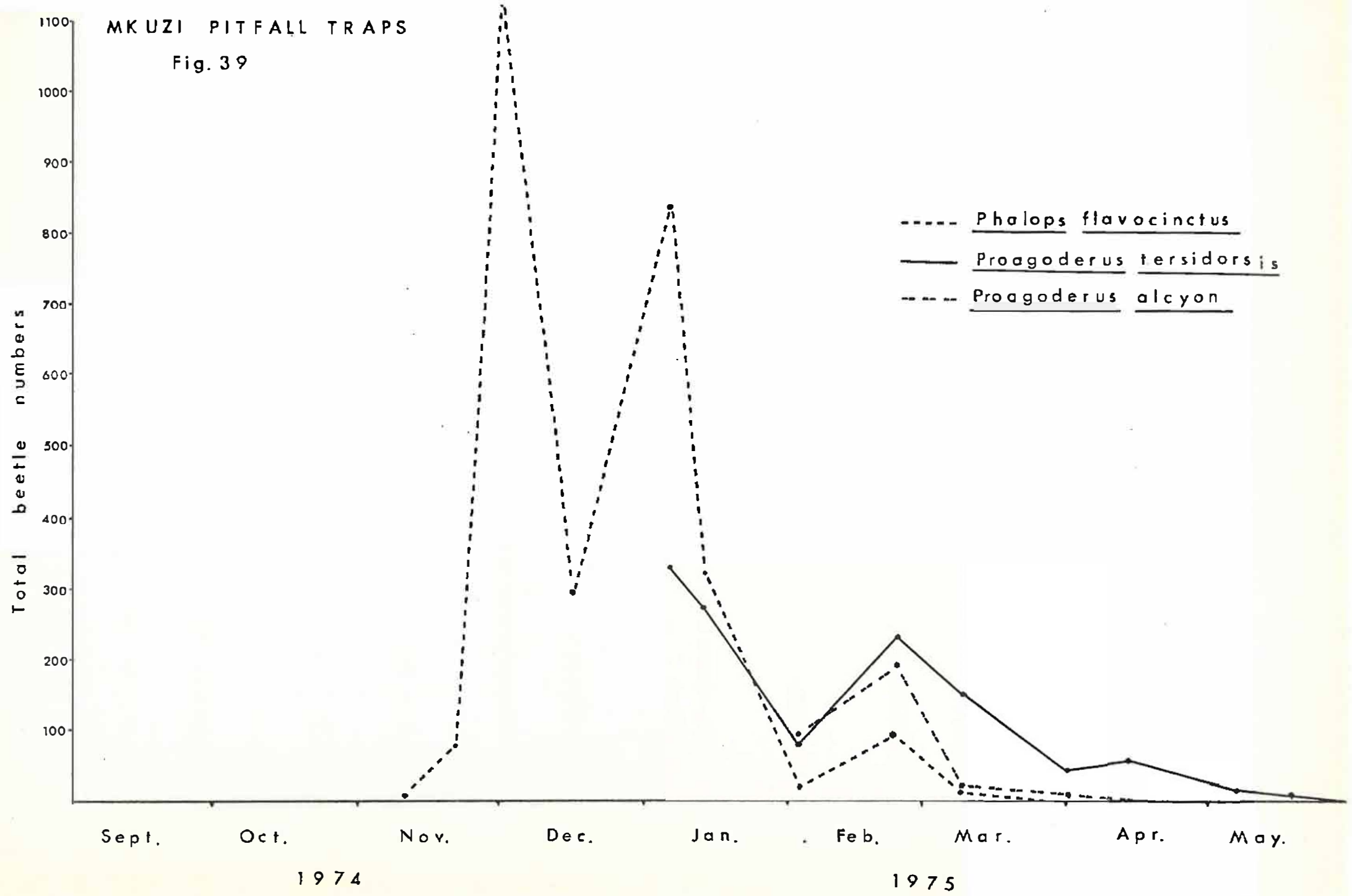
MKUZI PITFALL TRAPS
Fig. 40

Onthophagus spp.

Hister spp.

MKUZI PITFALL TRAPS
Fig. 41

external cue.   P. tersidorsis was recorded separately only
from the 16th December, 1974 and P. alcyon only from the 2nd
February, 1975, the date recorded giving a numerical peak
for P. tersidorsis on the 6th January and for P. alcyon on
the 23rd February, 1975.   However, a total of only 324
beetles of P. tersidorsis was recorded during their peak
(fig. 38) out of a total of 1161 beetles, the majority
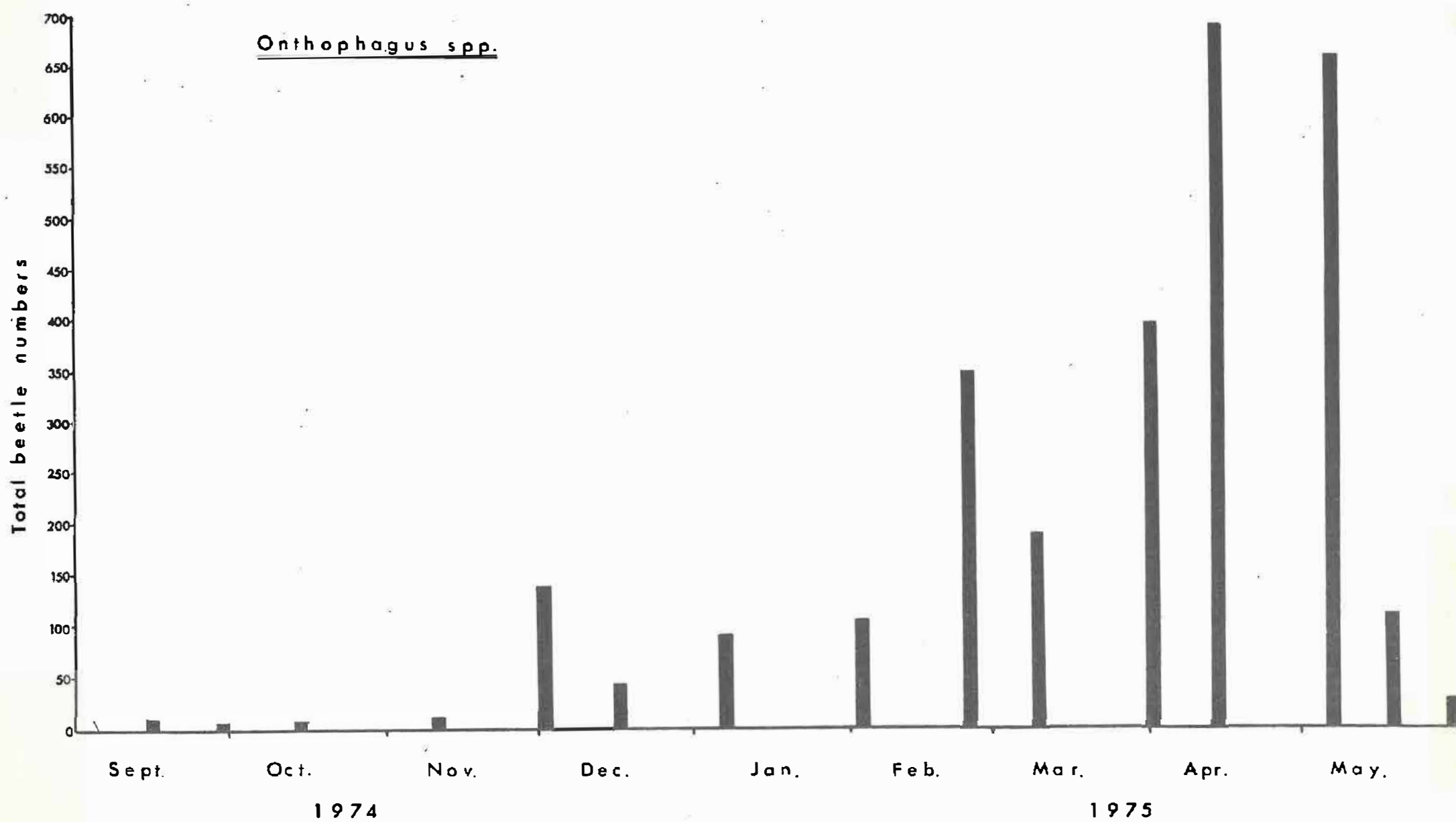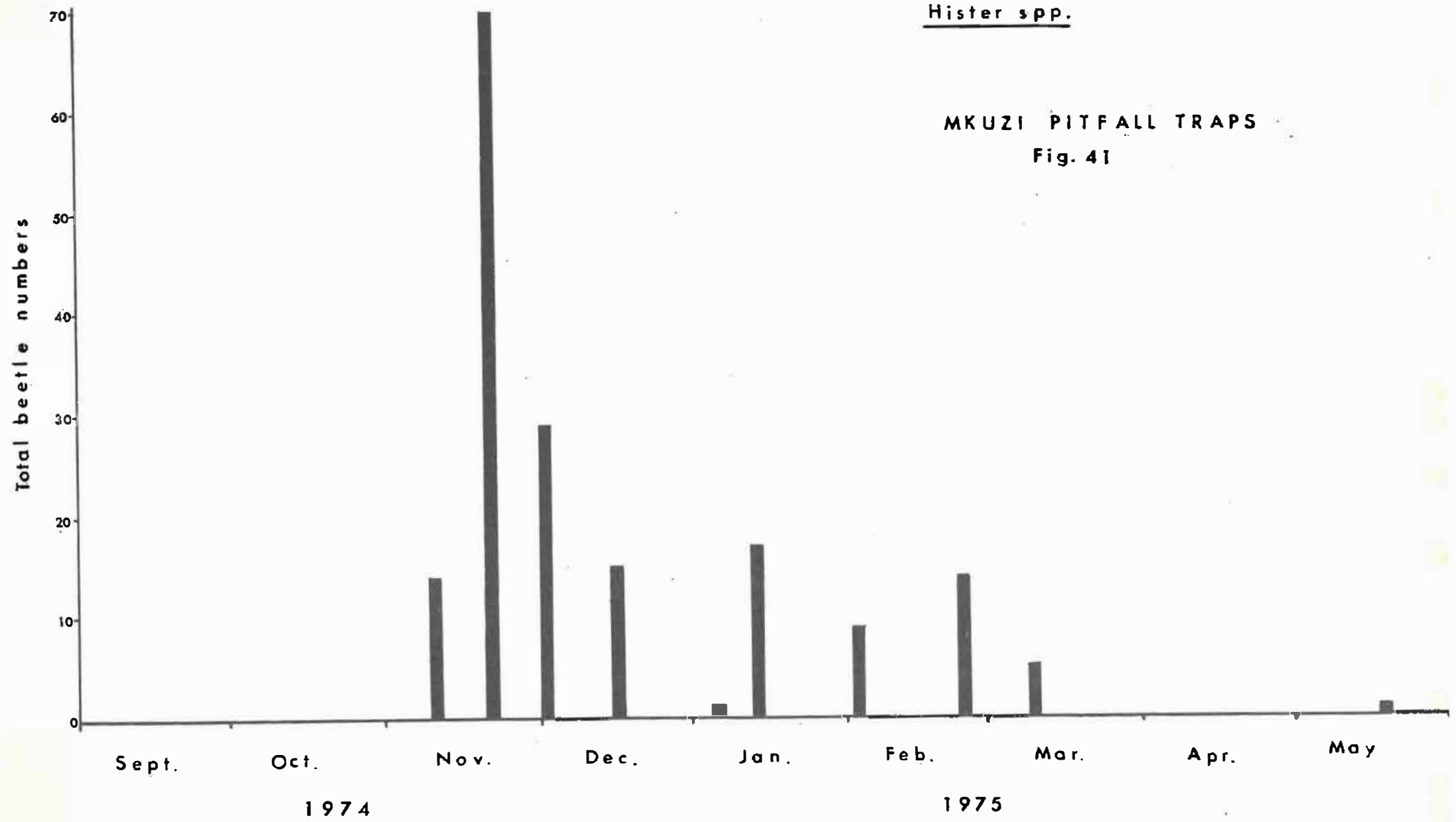presumably being P. flavocinctus.   Similarly only 188
P. alcyon beetles were recorded on the 23rd February out of
a total of 513 beetles (97 of which were P. flavocinctus
and 228 P. tersidorsis (fig. 39).

Since both Gymnopleurus virens and Onthophagus spp.
have their diel activity peaks during the cooler hours of the
day (G. virens at 26°C and Onthophagus spp. at 23°C –
Chapter 4) it is significant that the seasonal peaks of these
two species also occurs in the cooler months, G. virens in
late February (fig. 34) and Onthophagus spp. in mid-April
(fig. 40) which accords with their diel activity.

From figure 29 it becomes apparent that the activity of
the diurnal species, largely telecoprids, becomes reduced as
the season progresses resulting in more dung remaining on
the surface than occurred previously, and this is utilised
by the paracoprid Onthophagus species which are able to
remain active at these lower temperatures.   However, the
numbers of Onthophagus species recorded during the earlier
months were probably not entirely accurate as the bias
caused by the traps being set out at 0600h to the benefit of
the diurnal species may have resulted in fewer Onthophagus
beetles being caught during this period of intense activity.

The predatory Hister species have a seasonal peak of
activity fractionally before the peak activity of their main
prey, the Phalops – Proagoderus species (fig. 41).

3.3 INDIVIDUAL PITFALL TRAPS :

The eight pitfall traps were set out in different
positions as described in 3.1 in order to determine whether

there were differences in the attractiveness of certain locations which would result in more beetles of certain species or more beetles of many species being attracted to them.

The total number of beetles (1 8245) of all species captured in the traps between 2.9.74 and 3.6.75 were tested by means of an F-test to determine whether there were any differences in attraction between the pitfall traps over this period. The results are presented below :

Source of Variation	D.F.	S.S.	M.S.	F.
Between Traps	7	9 8260,66	14 088,67	0 ,55
Within Traps	136	3 49 571 9,50	25 703,8 2	N.S
TOTAL	143	3 593 980,1 6		

S.E. of a single trapping   = 160 ,32
Coefficient of Variance   =   1,27%
S.E. of mean for a single trap   =   37,84

This result shows that the null hypothesis, that there is no significant difference in the number of beetles in the individual traps, may be accepted i.e. no trap site was more attractive than any other. This suggests that the beetle fauna of Nsumu Pan is probably evenly distributed over the whole area and that dung dropped anywhere within the habitat during the summer months would stand an equal chance of being destroyed by the dung beetles.

Observations during the 1973/74 season suggested differences in attraction to dung dropped in places of direct sunlight, shade and rank undergrowth. Based on observed behaviour of a species, group comparisons were made on the positioning of the traps which constitute a classified set.

The seasonal totals of G. virens in the eight traps were

split /....

split into two groups, traps 1 - 4 and 7 in sunlight and traps 5, 6 and 8 in shade or amongst rank undergrowth. The result showed that there was a highly significant difference (p = 0,01) between the numbers of G. virens attracted to the two groups, t(128 D.F.) = 2,83**. This shows that G. virens is attracted to dung dropped in open spaces in direct sunlight. The diurnal activity peak of this species is between 0600 - 0700 hours at a temperature of 26°C and traps in the shade at this time of the morning would record temperatures below this optimum, which are largely shunned by this species.

Although fewer A. thalassinus were attracted to trap No. 8 surrounded by the rank growth of weeds, there was no significant difference between it and the other traps all free from weeds, t(64 D.F.) = 1,61 N.S. However, there is a significant difference when comparing the highest number of beetles captured (Trap 7) and the lowest (Trap 8) :-

Estimate of common variance	= 3311,78
Variance of difference of means	= 735,95
S.E. of the difference	= 27,13
t(16 D.F.)	= 2,28*

Fewer K. nigroaeneus beetles were attracted to trap No. 8 located in dense weeds but there was no significant difference between it and the other traps relatively free from weeds, t(104 D.F.) = 1,23 N.S.

Although a classified set, the trap data were subjected to the overall F-test for the individual species, there being no difference in the attractiveness of the individual traps within one species, all tests being non-significant.

The vegetation which covers Zululand and the Eastern Transvaal is described as Lowveld Bushveld (Acocks, 1975) there being no really dense shade on the plains as the pinnate leaves of the acacia trees allow sunlight to filter through. The most abundant and important species of telecoprids in these regions include K. nigroaeneus, A. thalassinus and G. nitens which are attracted to dung dropped anywhere within this habitat and show no significant attraction to dung

dropped in any special locality.

The only area which does seem to exclude the major telecoprid species is the dense shade along rivers in some places within the bushveld habitat. This riverine forest is rarely visited by the larger herbivores and consequently little or none of their dung is voided there. Cow dung in dense shade near Ndumu Game Reserve was ignored by A. thalassinus which readily attacked pads dropped in the open. Once the pads in the shade were moved from shade, they became equally attractive. Unfortunately, pitfall traps could not be established in the dense shade of the Nsumu Pan riverine forest as this area is subject to seasonal flooding.

3.4 ANNUAL LIFE CYCLE :

Further laboratory studies have shown that there is a cue which causes A. thalassinus and G. nitens to stop breeding in January while conditions are still seemingly suitable for continued breeding. This cue enables the final generation of A. thalassinus and G. nitens to emerge in mid-February and feed before having to burrow into the soil to overwinter.

Pairs of A. thalassinus and G. nitens were set up in individual tubs as part of the breeding programme and the tubs were changed approximately every four days, the number of pairs and brood-balls produced being recorded. This was expressed as the number of brood-balls per pair per day, because the interval between recordings varied to some extent (fig. 42). Brood-ball production dropped off gradually until it became uneconomical to change the numerous tubs (which fluctuated due to the death of individual beetles or pairs) and recover only a few brood-balls, so the programme was halted at this stage. As these tubs were kept in a heated room where temperature fluctuations were minimal the cue to stop breeding could possibly be photoperiod as daylight was not excluded.

It was also determined that naturally or self-paired
A. thalassinus beetles placed in tubs and continually kept
in their pairs, produced on the average more brood-balls than
artificially paired beetles which were simply sexed and placed
in tubs.   However, the difference was not significant between
the two groups.   The physiological state of both sexes must
be complementary for maximum egg production.   This is
achieved to a large extent in the field by having only an
annual summer activity season, the emergence determined for
all by the first sufficient summer rains.

The simplified annual life chart of K. nigroaeneus
(fig. 43) has been drawn from data presented throughout the
thesis.   The importance of temperature and rainfall in the
seasonal life of dung beetles and the fact that these
conditions recur annually within the distribution of the major
telecoprids, overwintering may be due to a temperature and
drought induced aestivation.

The life chart is similar for the Scarabaeus genus
except that it may produce two generations a year due to the
shorter larval period, while K. nigroaeneus is able on the
average to produce only one brood-ball per season (a percent-
age of the population produces two) due to the lengthy brood-
care and to the fact that they are active only for five
months of the year.   Since they live longer than most species
(three seasons) they have the ability to produce three,
possibly four F_1's in a female's lifetime.   Since predation
is low and brood-care is highly developed, the population
remains at a high level.

FIGURE 42

The rate of brood-ball production of <u>Allogymnopleurus thalassinus</u> and <u>Garreta nitens</u> under laboratory conditions between November 1973 and January 1974.

LABORATORY BROOD-BALL PRODUCTION

Fig. 42
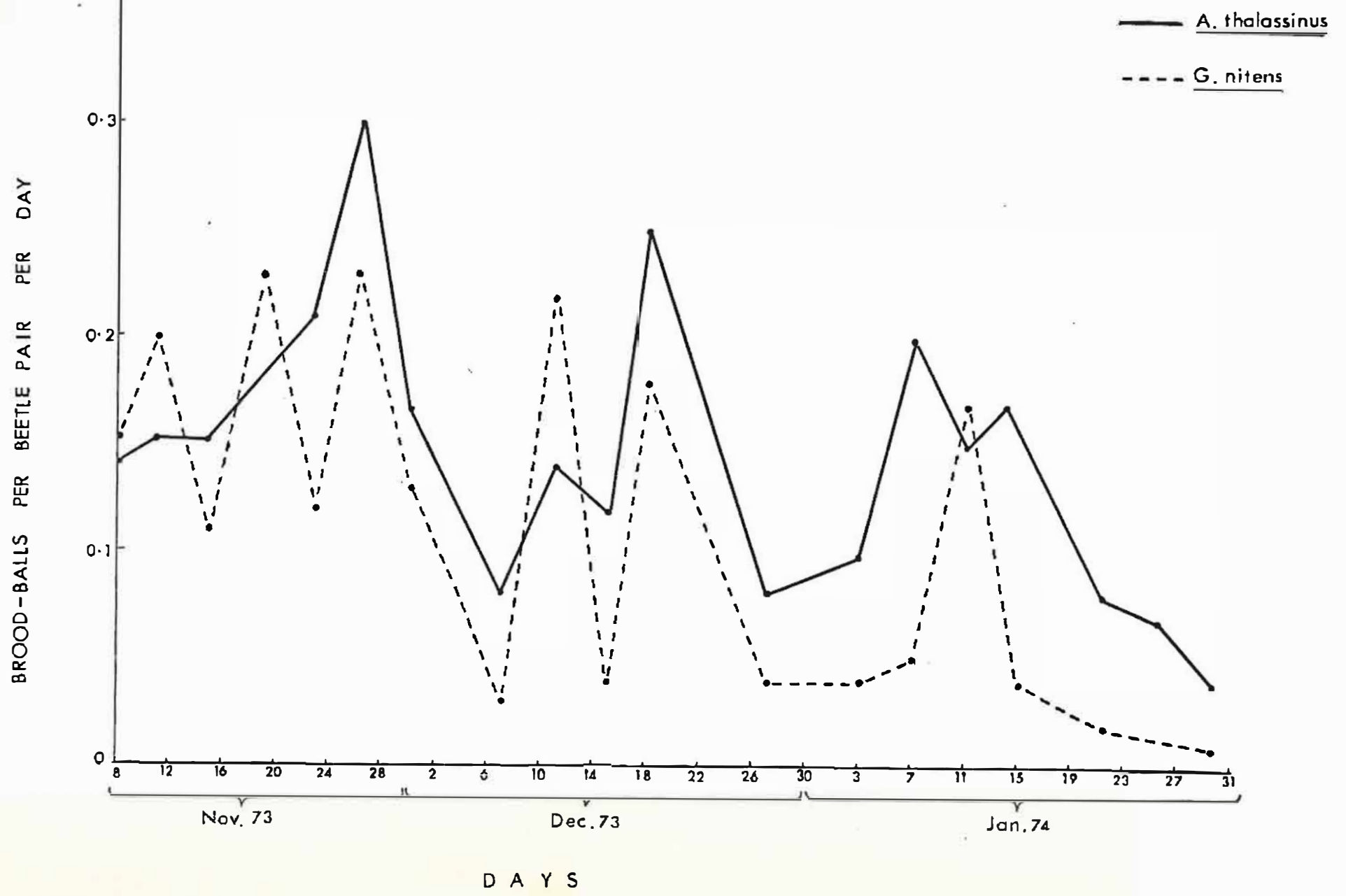
SIMPLIFIED SEASONAL LIFE CHART

Kheper nigroaeneus

Fig. 43

Mean Daily Min. Temp.
Between 17,4 – 21,1 °C.

Mean Daily Min. Temp.
Between 11,6 – 15,3 °C.

RAINFALL

SUMMER

DEC · JAN · NOV · FEB · OCT · MAR · APR · MAY

Breeding
(Brooding ♀'s)

Feeding on Dung-balls

Emergence

Emergence of F₁'s

Feeding at Pad

Burrow into Soil

Aestivation as Adults
(1ˢᵗ, 2ⁿᵈ, 3ʳᵈ generations & F₁'s.)

SEPT. · AUG. · JULY · JUNE

WINTER DROUGHT
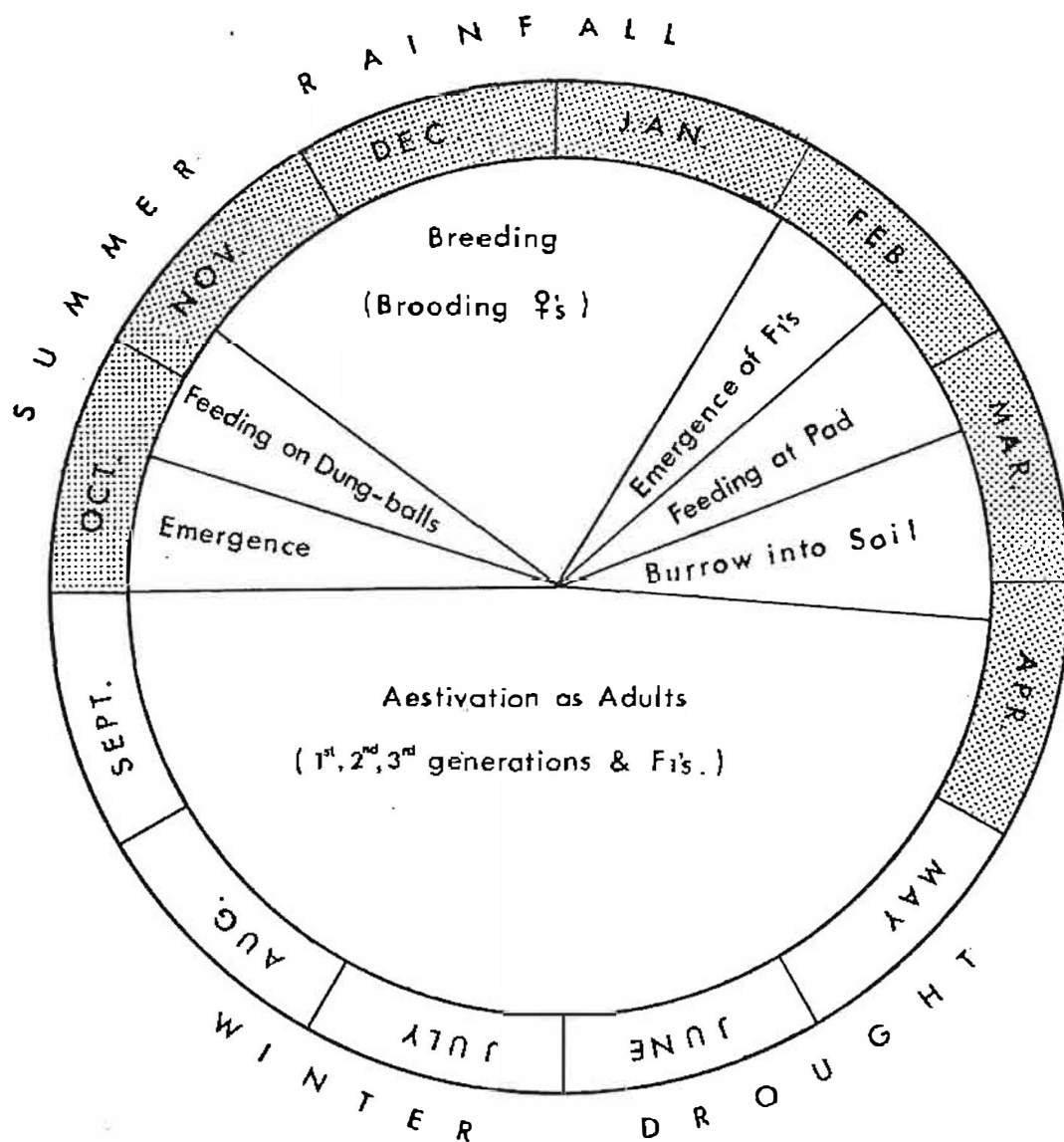
CHAPTER 4.

DIEL ACTIVITY CYCLES.

4.1 HOURLY TRAPPINGS :

During collecting trips in the Natal, Rhodesian and Botswana Game Parks it was noticeable that the different species of day-flying dung beetles successively colonised dung-pads in large numbers with, broadly speaking, one species following another.   This was despite there being representatives of all day-flying species almost throughout the day active at a particular dung source.   A certain species would completely dominate a fresh dung pad for a period of time, followed by another species on the same or more recently dropped dung.

In order to determine the activity periods of various species in a natural environment, baited pitfall traps were set out at Nsumu Pan, Mkuzi Game Reserve.   These pitfall traps were based on those designed by Paschalidis (1974) but enlarged to suit the larger telecoprid species (Chapter 3). The traps were set out on two successive days and changed every hour between 0500h and 1900h.

The dung used to bait the traps was horse dung collected each morning at 0400h from the stables within the Reserve. This dung, relatively beetle free as it is exceptionally freshly dropped in copious amounts at this time of morning, was placed in large plastic buckets which were firmly sealed with a tight fitting lid.   Within an hour, with the lids firmly closed, the few crepuscular beetles (mainly Onthophagus species) which were collected with the dung came to the surface of the dung and were removed.

A hygrometer and thermometer were hung from a large acacia tree at the trapping site at a height of six feet above the ground.   They were at no time in direct sunlight.

The temperature and relative humidity were recorded every hour, simultaneously with the changing of the traps.   The first day (7.12.74) was a typical hot, humid day with hardly a cloud in the sky.   The second day (8.12.74) was a cloudy, overcast day with alternating sunshine and shadow in the morning.   No rain fell on either day.

Five minutes before the end of every hour the replacement traps were baited with a standard amount (150 gms) of horse dung and immediately placed in the sheet-iron frame sunk into the soil as the previous traps were simultaneously removed.   Corresponding traps and buckets were identically numbered.   Data recorded besides temperature and relative humidity were the number of beetles of each species caught in each separate trap every hour, as well as the sex of several of the species.

Each trap was sorted on a tray, the sorted trap material was placed in breadbins with gauze lids which were prepared with soil and fresh dung.   The bins were placed in the shade and covered with a tarpaulin to prevent the dung from attracting presently flying species.

On the 7.12.74 all eight traps were baited and set out at 0500h but four of the traps were suspended at 1200h due to the backlog of unsorted material which was accumulating as a result of the intense activity.   On the second day only four of the traps were set out.   Additional information was gathered by setting out four traps at 1900h and collecting them at 0500h the following morning.

The time of the year in which this trapping was conducted was within the most active period for Kheper nigroaeneus immediately after maturation feeding and at the start of breeding (see fig. 29, page 40).

Results :

From figures 44 and 45 it can be seen that as the temperature rises there is a corresponding drop in the relative

humidity /....

humidity.   The highest temperature recorded in the shade
was just over 35°C between 1200h and 1300h on the 7th
December, 1974.   The following day may be regarded as
atypical as it had a much distorted temperature and relative
humidity pattern (fig. 45) due to the cloudy sky through
which the sun frequently broke.   The relative humidity
never dropped below 50%, the highest R.H. of almost 100%
being recorded at 0500h and the lowest of 58% between 1200h
and 1300h.

The overall result of the two days trapping is presented
in figure 46.   Immediate attention is focused on the vast
difference in numbers of beetles of a few species on the two
successive days.   The beetles from the first day were released
that evening six kilometers from the trapping site and
although this would cause a drop in the population the follow-
ing day, this drop would be slight as most beetles which have
rolled balls the previous day would still be feeding (or
breeding).

Secondly the activity peaks of the various species are
staggered and some peaks are very sharp while others are
flattened.   Also some species occur in very large numbers,
while others occur in relatively small numbers.   This does
not immediately indicate the success of a species in burying
dung as the average size of each species and the amount of
dung it buries must be taken into account.   The frequency
at which dung is buried by each species is also important in
determining its usefulness in recycling nutrients.

For clarity the results presented in figure 46 have
been redrawn individually to show the distinctive features of
each species.   The first day (7.12.75) may be regarded as
a typical day and the following points may be noted :

(i) Allogymnopleurus thalassinus (fig. 47) occurred in the
highest numbers followed by the Phalops flavocinctus,
Proagoderus alcyon and Proagoderus tersidorsis group (fig. 49).

A. thalassinus is a relatively small species compared
with K. nigroaeneus (Table 3).   P. tersidorsis is similar
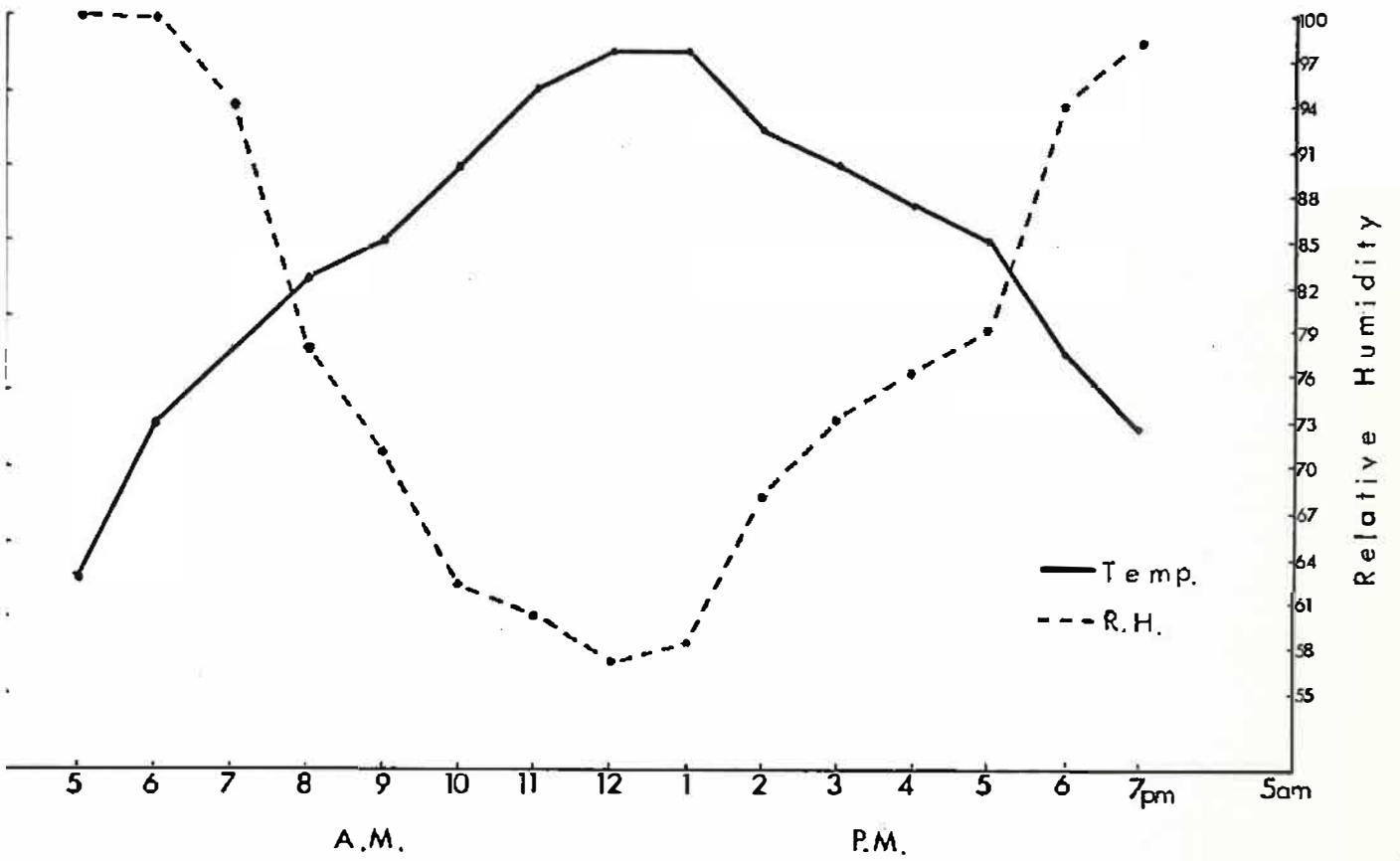
MKUZI GAME RESERVE   Fig. 44
(Nsumu Pan)
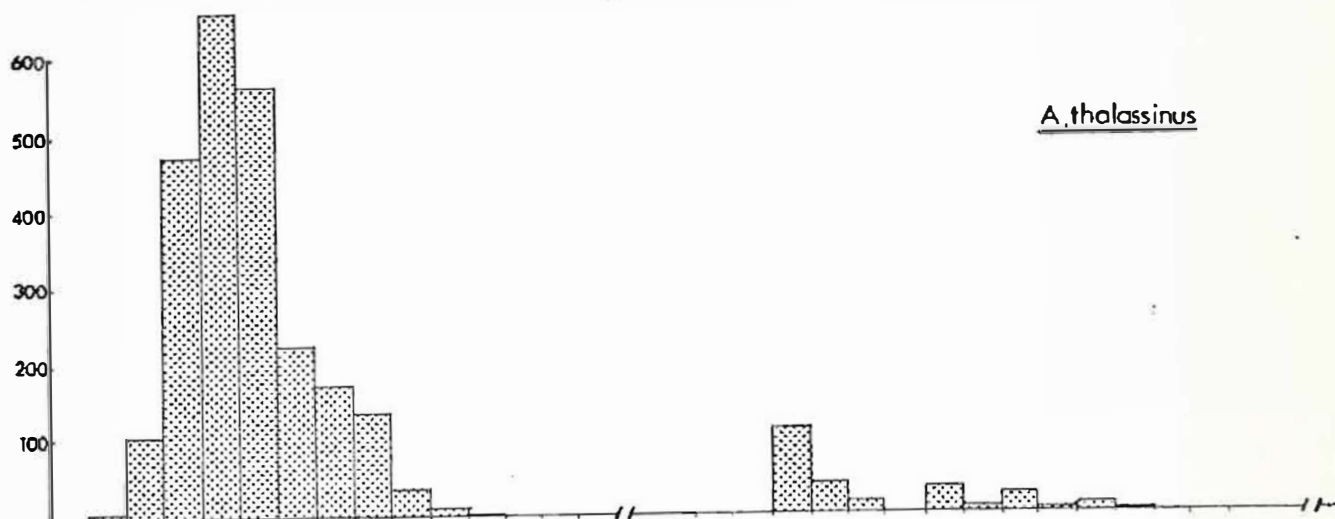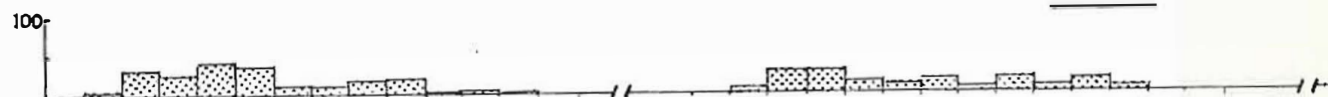
7-12-74
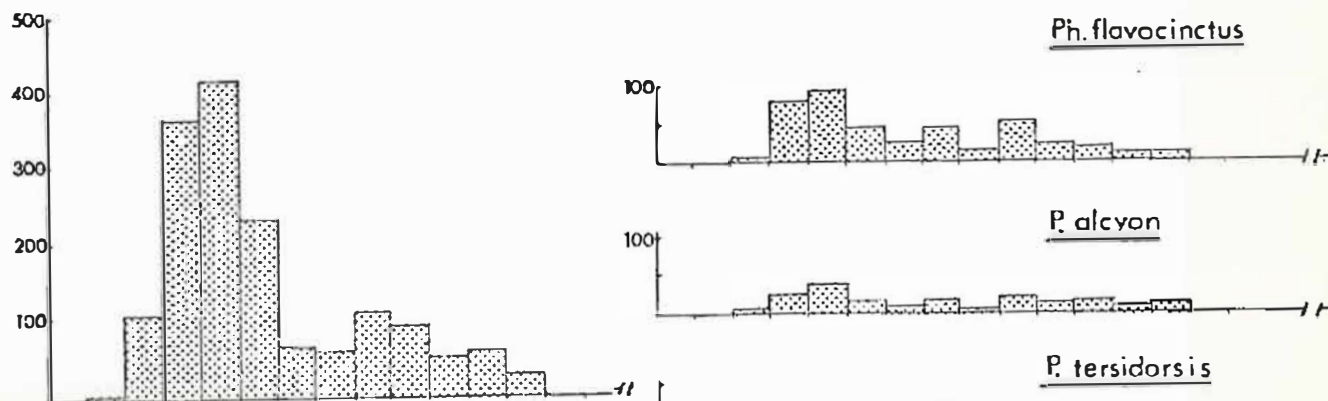
8-12-74   Fig. 45
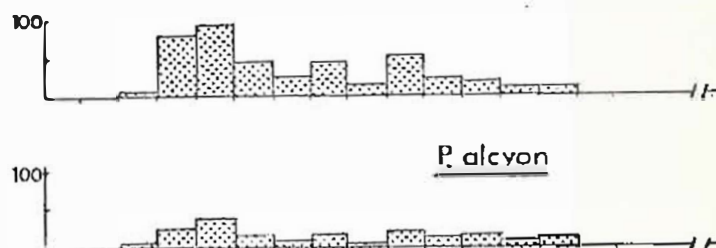
MKUZI HOURLY TRAPPINGS   Fig. 46

HOURS

MKUZI HOURLY TRAPPINGS

7-12-74   Fig. 47

Allogymnopleurus thalassinus

HOURS
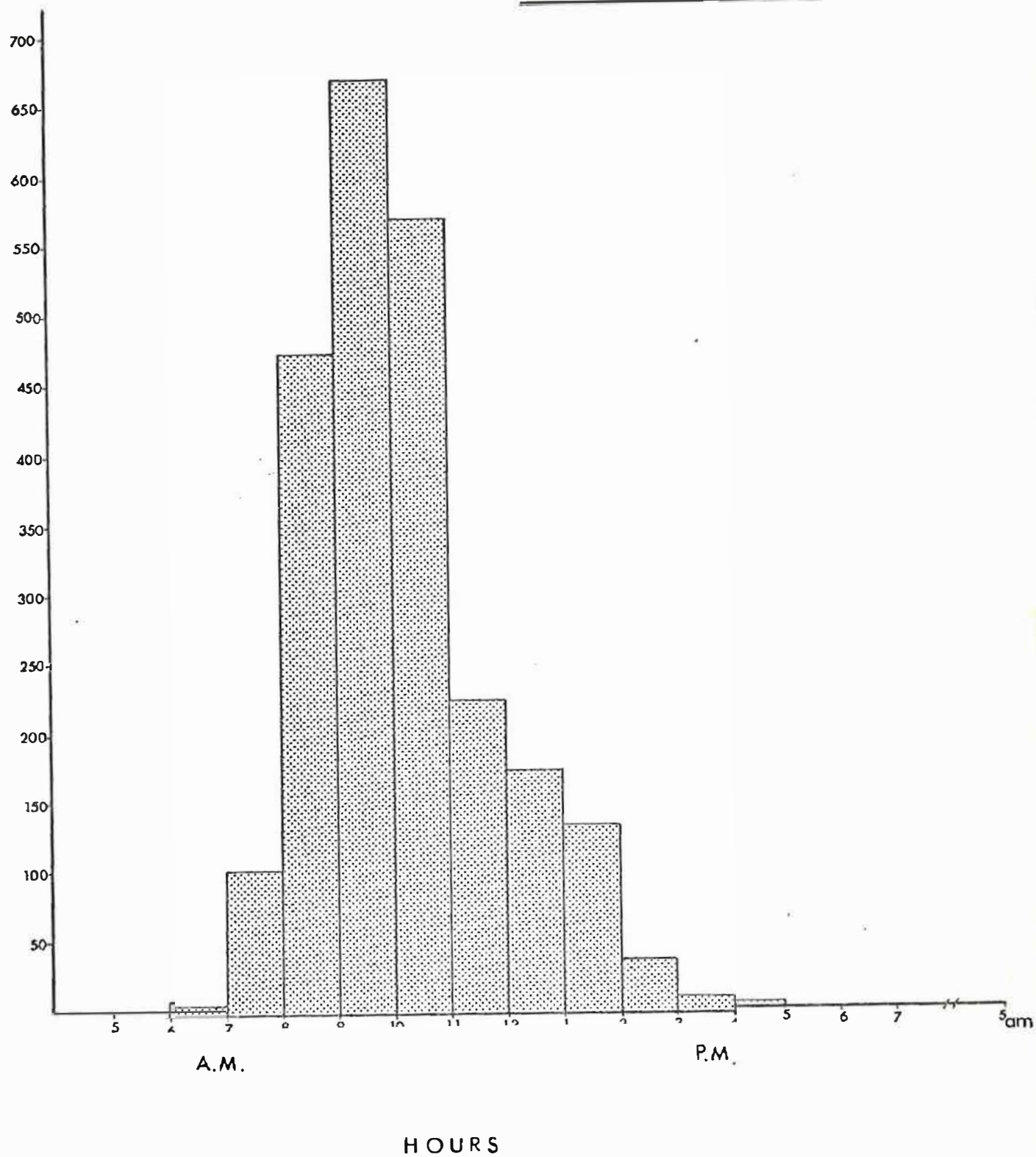
to A. thalassinus in size with P. flavocinctus smaller and
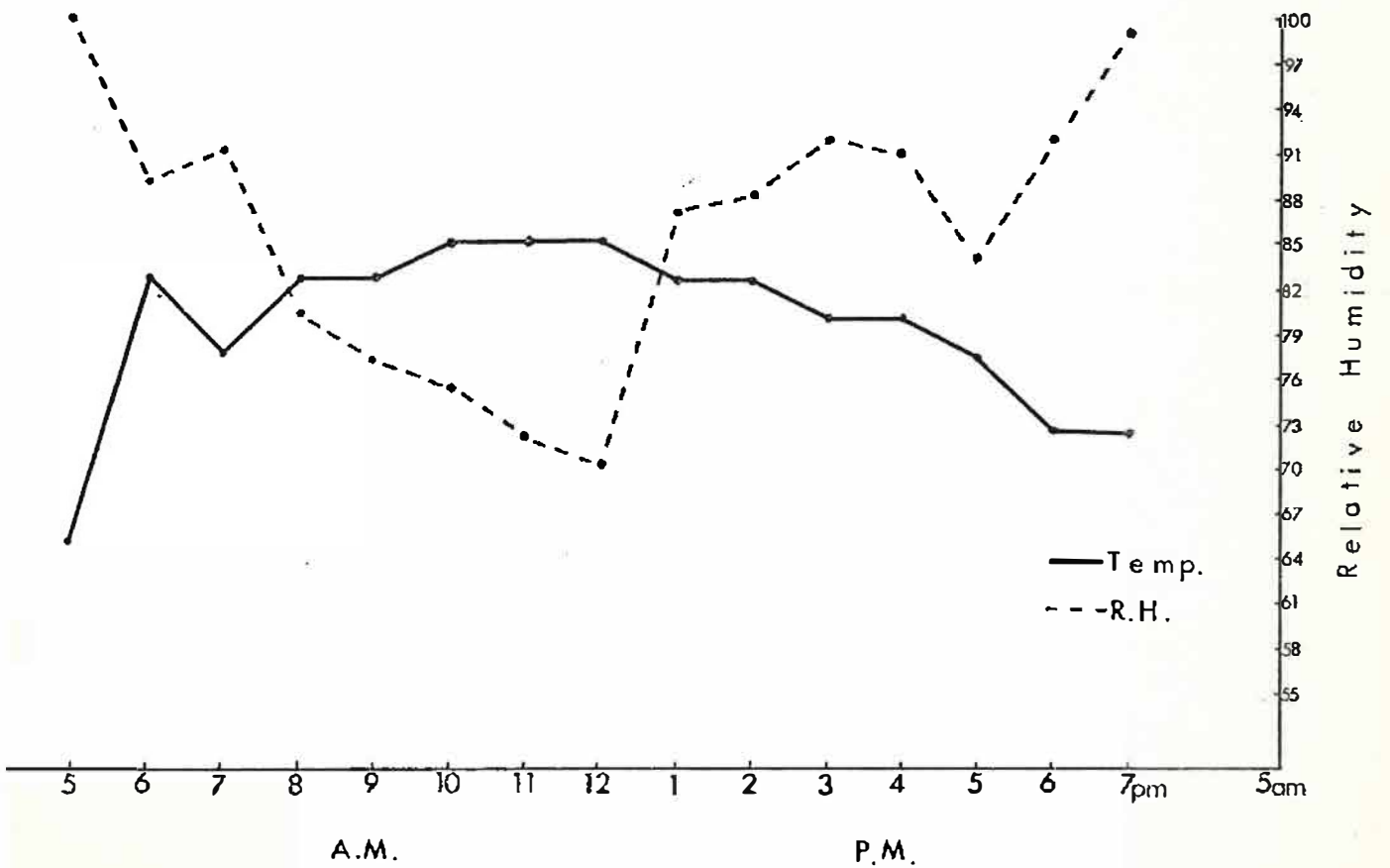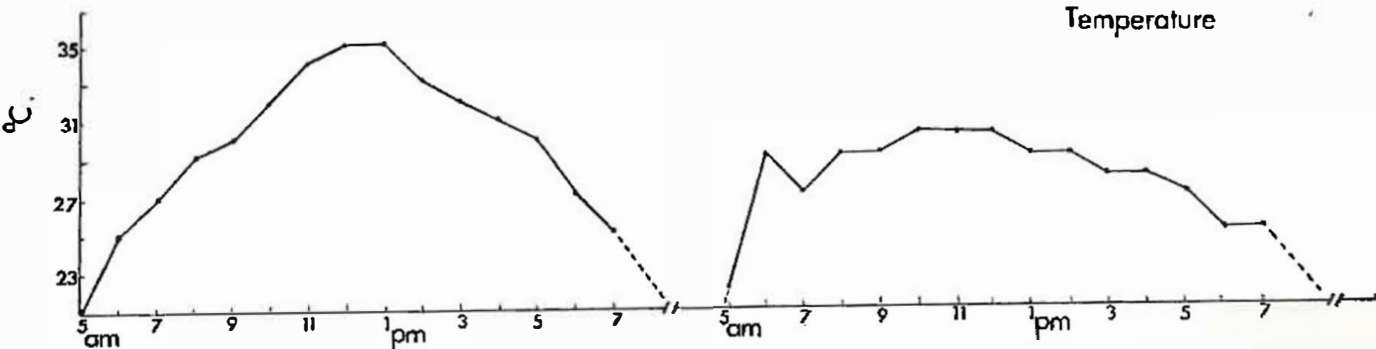P. alcyon smaller still.   Although K. nigroaeneus are fewer
in number they are able to dominate a dung pad because of
their size.

 (ii) The staggered effect of the activity peaks of the
various species is tabulated below :

TABLE 6: Staggered activity peaks of several sympatric
          dung-beetle species of Nsumu Pan.

Species	Activity Peak	Av. Hourly Temp.
Gymnopleurus virens	0600 - 0700h	26°C
Kheper nigroaeneus	0700 - 0800h	28
Hister species	0800 - 0900h	29,5
Allogymnopleurus thalassinus	0900 - 1000h	31
Garreta nitens	0900 - 1000h	31
Phalops flavocinctus*	0900 - 1000h	31
Proagoderus alcyon*	0900 - 1000h	31
Progoderus tersidorsis*	1300 - 1400h	34
Anachalcos convexus	1900 - 2000h	23
Onthophagus spp.	2000 - 2100h	21

*Estimated flying time based on the graphs (figs. 49, 58,
 59 and 60) of the two successive days.

        Unfortunately the backlog of accumulated material on
the first day resulted in the Phalops and Proagoderus species
being lumped together.   These results are represented
graphically for K. nigroaeneus (fig. 48), G. virens (fig. 50),
G. nitens (fig 51) and Hister spp. (fig. 52).

(iii) K. nigroaeneus and G. virens may be considered to have
a minor peak in the afternoon (Table 7).

TABLE 7:   Dual diurnal activity peaks of K. nigroaeneus
            and G. virens.

Species (7.12.75)	Morning Peak		Afternoon Peak		% Population	
	Hours am	% Trapped	Hours pm	% Trapped	0500-1200h	1300-1900h
K. nigroaeneus	7 - 9	35	4 - 6	13	74	26
G. nitens	7 -11	71			77	23
A. thalassinus	8 -11	77			92	8
G. virens	6 - 8	48	3 - 6	22	73	27
Hister spp.	7 -10	79			92	8
P. flavocinctus) P. alcyon) P. tersidorsis)	7 -10	71			77	23

Both species with a minor afternoon peak (figs. 48 and 50) are
characterised by a smaller percentage of their daily number
being recorded at their peak hours.   The fact that only 8%
of the daily population of A. thalassinus and Hister spp.
were present in the afternoon (1300 - 1900h) indicates that
these species have a more precise activity period than the
other species.   Over 73% of the daily population of all
species were captured in the morning (0500 - 1200h).

(iv) The activity peaks of K. nigroaeneus and perhaps
G. virens are related to temperature. Over the fourteen hours
that the trapping was conducted, the highest temperature
recorded was 35°C and the minimum 23°C (see Table 8).

TABLE 8:   Temperature-related diel activity peaks of
           K. nigroaeneus and G. virens.

Species	Activity Peak		Activity Peak	
	hours	Temp. ^{o}C	hours	Temp. ^{o}C
K. nigroaeneus	0700-0800	28	1700-1800	28,5
G. virens	0600-0700	26	1700-1800	28,5

Kheper nigroaeneus
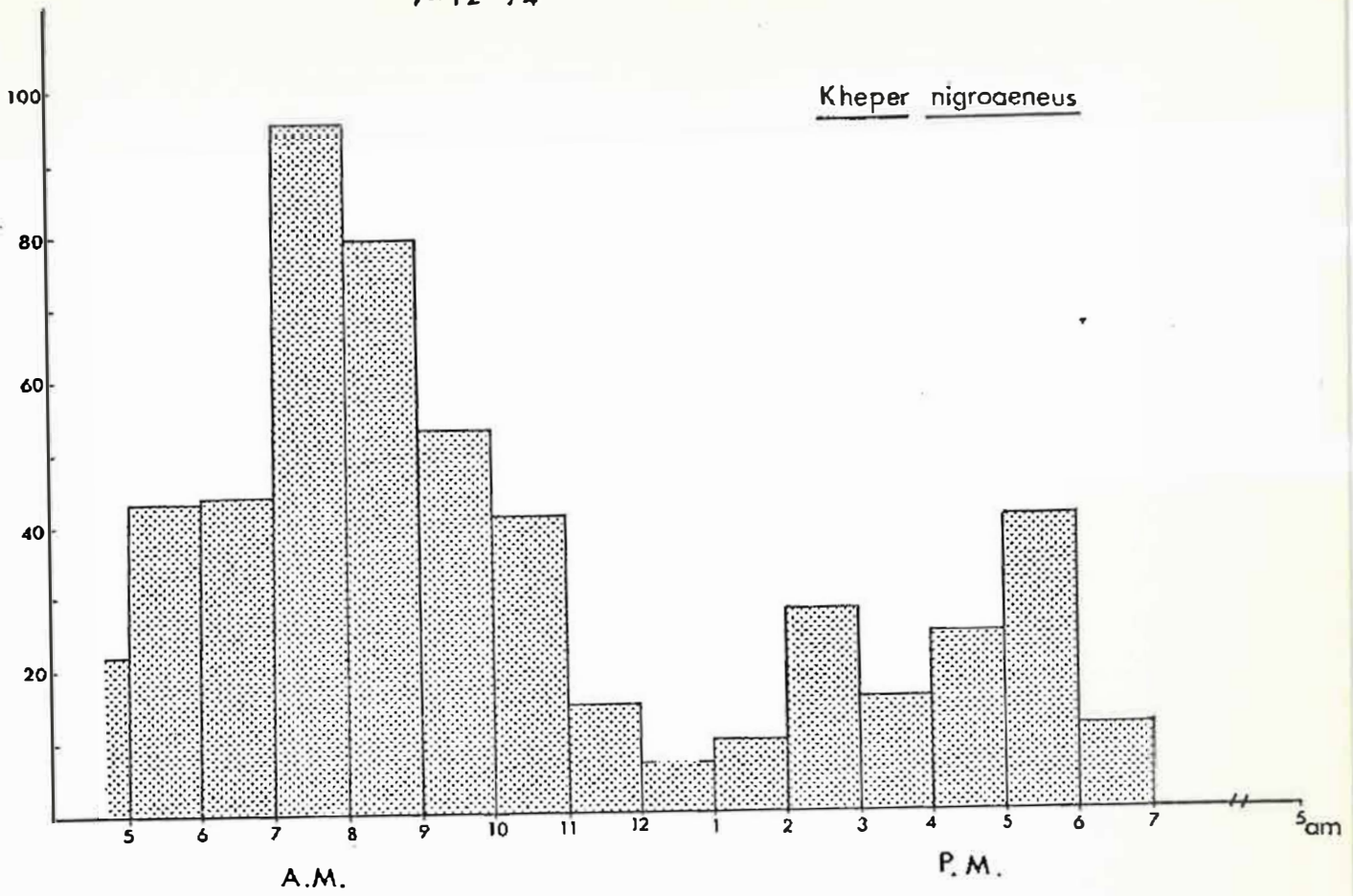
Fig. 4 9

Phalops flavocinctus
Proagoderus alcyon
Proagoderus tersidorsis

TOTAL BEETLE NUMBERS
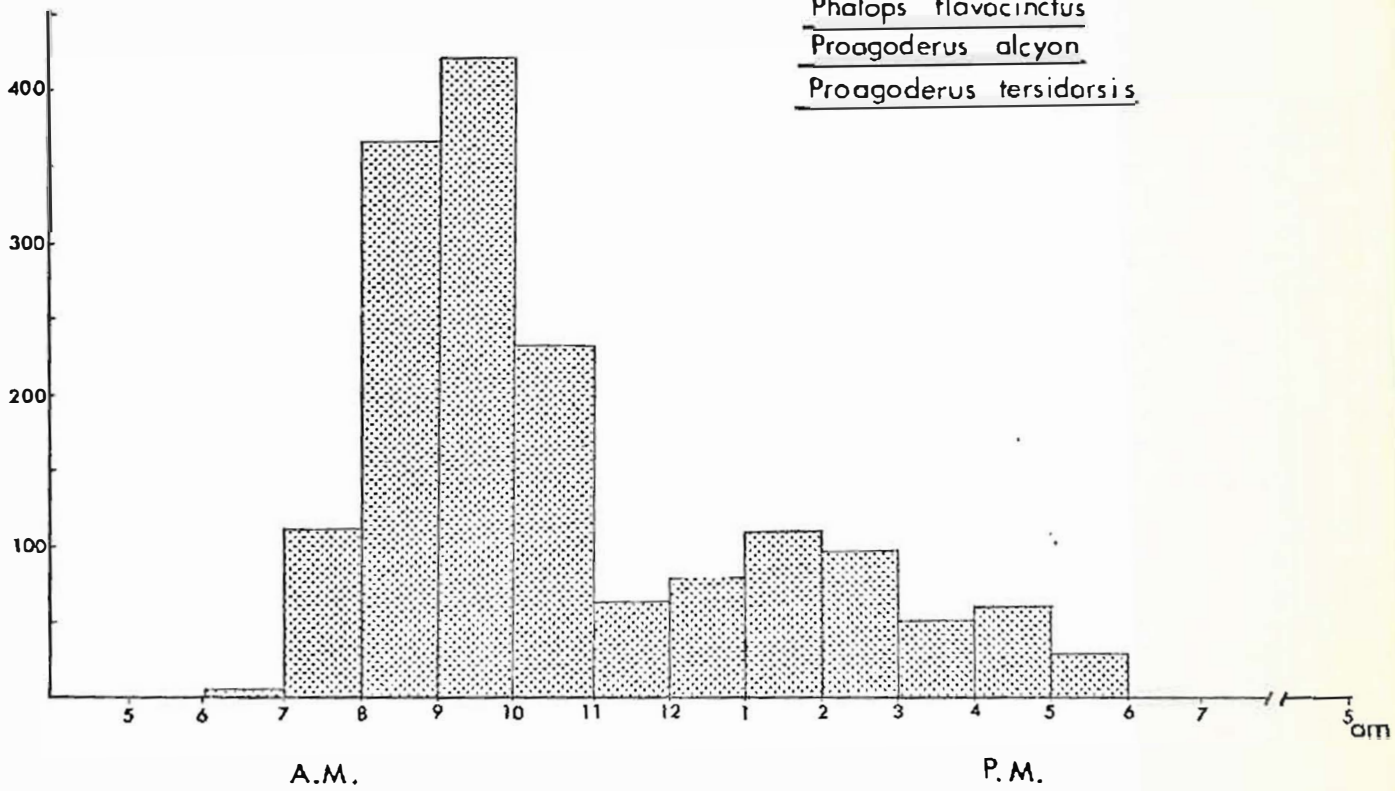
HOURS

MKUZI HOURLY TRAPPINGS
7-12-74

Fig. 5 0

Gymnopleurus virens
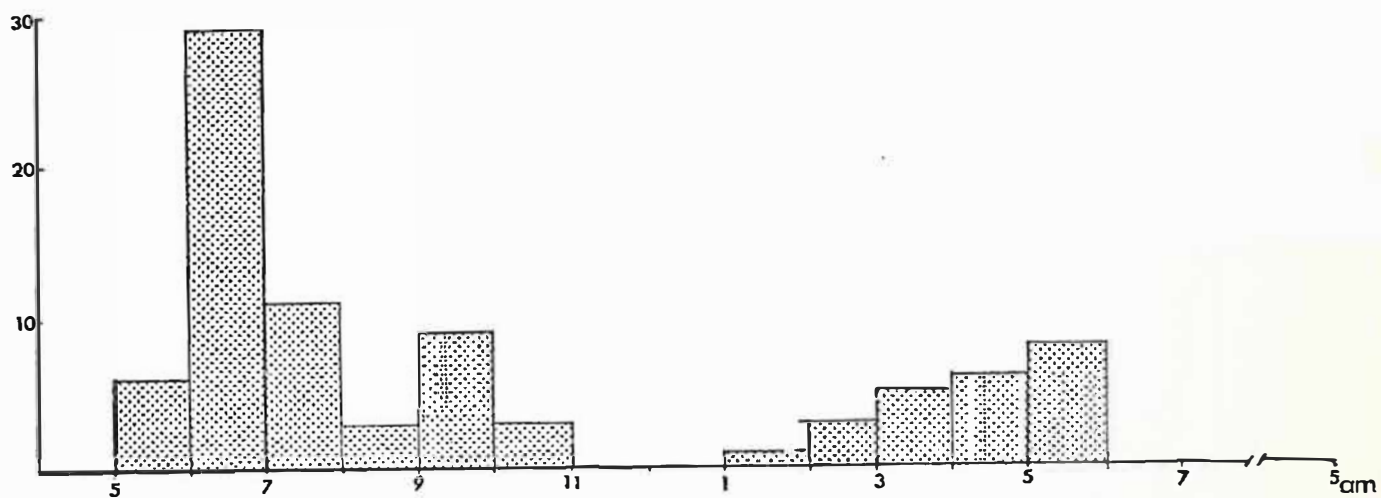
Fig. 51

Garreta nitens

Fig. 5 2

Hister spp.

A.M.

P.M.
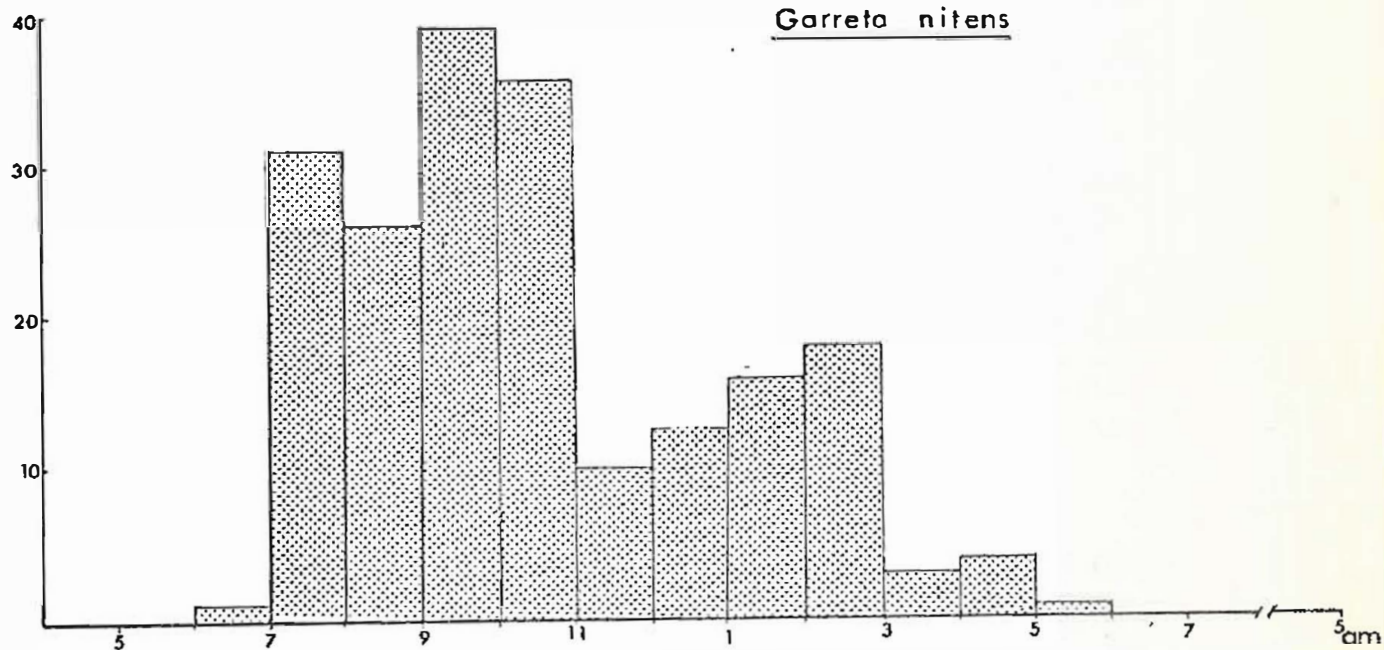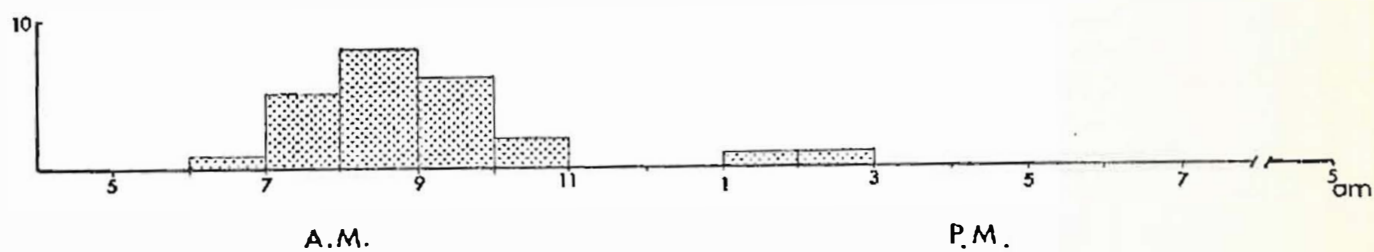
HOURS

The range in temperature presented in figure 44 shows that this peak activity at the same temperature, especially in the case of K. nigroaeneus, is significant. In figure 48 it may be seen that a greater proportion of beetles were present after the major peak between 0700 and 0800h (higher temperature) than before the peak (cooler temperature). This is reversed in the minor peak, more beetles being captured before the minor peak (higher temperature) than after the peak (cooler temperature). This further indicates that it is mainly temperature which controls the activity peaks of K. nigroaeneus.

The results of the second day (8.12.74) indicate that those species that require higher temperatures (Table 9) are more greatly affected by overcast conditions and the resultant drop in temperature.

TABLE 9: Percentage population occurring within the morning activity peaks of various beetle species.

SPECIES (7.12.74)	MORNING ACTIVITY PEAKS		
	Duration in Hours.	% Population	Temp. Range °C
G. nitens	4	71	27 - 32
A. thalassinus	3	77	29 - 32
Hister spp.	3	79	27 - 30
P. flavocinctus) P. alcyon) P. tersidorsis)	3	66	29 - 32
K. nigroaeneus	2	35	27 - 29

Kheper nigroaeneus experiences a dampening effect as regards beetle numbers (fig. 53), but A. thalassinus and the Phalops, Proagoderus group are more greatly affected both in numbers and (in the case of A. thalassinus)in the shift of the activity peak (figs. 54 and 58, 59, 60).

The /....

The species with the lower temperature range (Table 9) such as G. virens is largely unaffected by the cooler conditions and retains its activity peak on both successive days (figs. 50 and 57). The numbers of beetles captured on both days are very similar as well.

The cooling of the soil surface may result in fewer beetles, mainly the thermophilous species, returning to the surface, since the soil temperature indicates the air temperature. This is further indicated as there is a lag between increasing temperature and species returning to the surface. The temperature on the 8th December, 1974 (fig. 45) rose sharply between 0500 and 0800h to 29°C and dropped to 27°C within the next hour. From figure 54, it can be seen that the A. thalassinus peak occurred between 0700 and 0800h at a temperature not in their peak activity range. Table 9 shows that a temperature of 29°C is suitable and as they emerged two hours later, it is possible the delay was caused by the rise in the soil temperature being detected by the beetles.

The great drop in beetle numbers of those species active at higher temperatures may be due to the fact that temperatures on the second day reached a maximum of only 30°C, while presumably a higher temperature is needed before the soil is heated to a depth at which most of the beetles are buried – soil temperature fluctuation is greatest at shallower depths and becomes less the deeper the soil (W.B.28).

On the atypical day, the staggering of the three Phalops and Proagoderus species (figs. 58 - 60) indicates their true flying times.

(v) Included in Table 9 are the number of hours over which the activity peaks may be said to have taken place. Only the hours on either side of the actual peak with numbers approaching that of the actual peak were included so that the "spread" of the major peak may be calculated.

From /....

Figure 53 : The number of Kheper nigroaeneus captured at hourly intervals at Nsumu Pan on the 8th December 1974.

Figure 54 : The number of Allogymnopleurus thalassinus captured at hourly intervals at Nsumu Pan on the 8th December 1974.

Figure 55 : The number of Garreta nitens captured at hourly intervals at Nsumu Pan on the 8th December 1974.

Figure 56 : The number of Sisyphus species captured at hourly intervals at Nsumu Pan on the 8th December 1974.

MKUZI HOURLY TRAPPINGS
8-12-74
Fig. 53

K. nigroaeneus
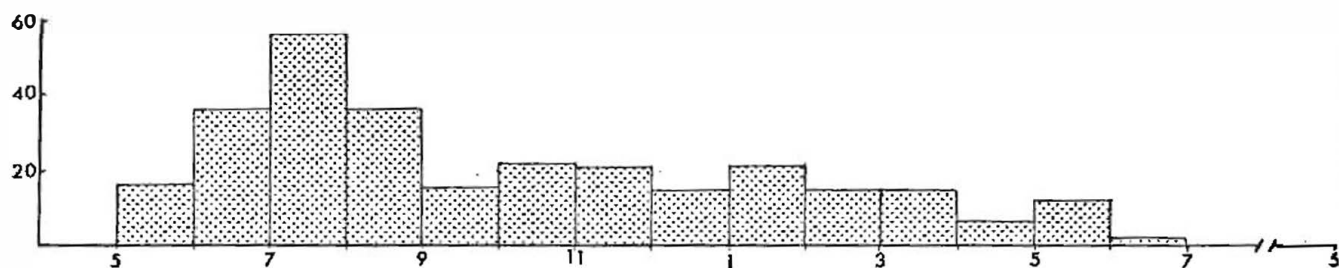
Fig. 54
A. thalassinus
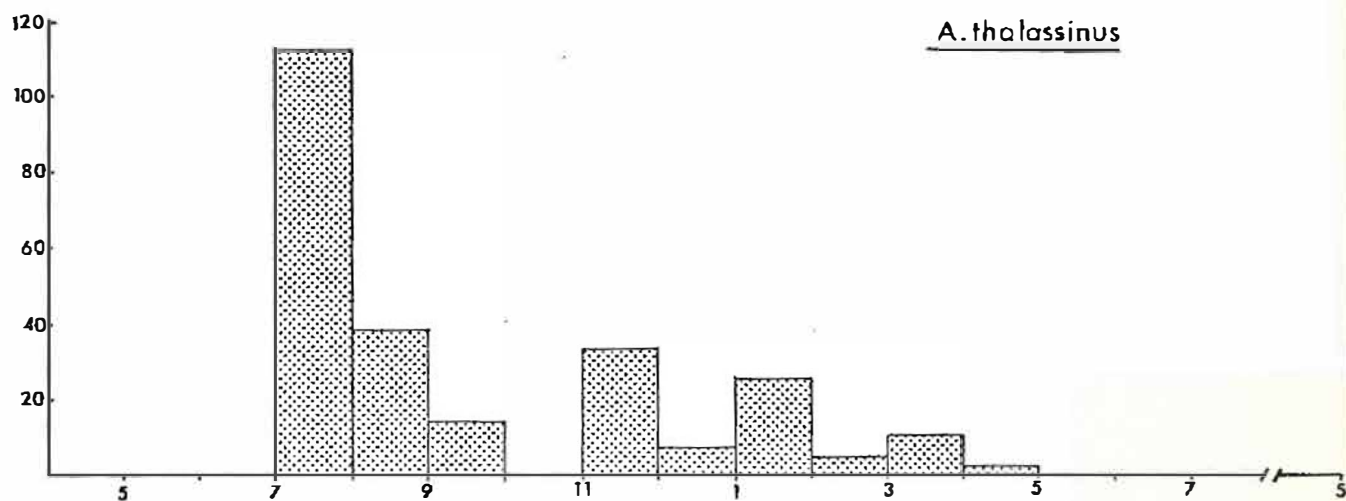
Fig. 55
G. nitens
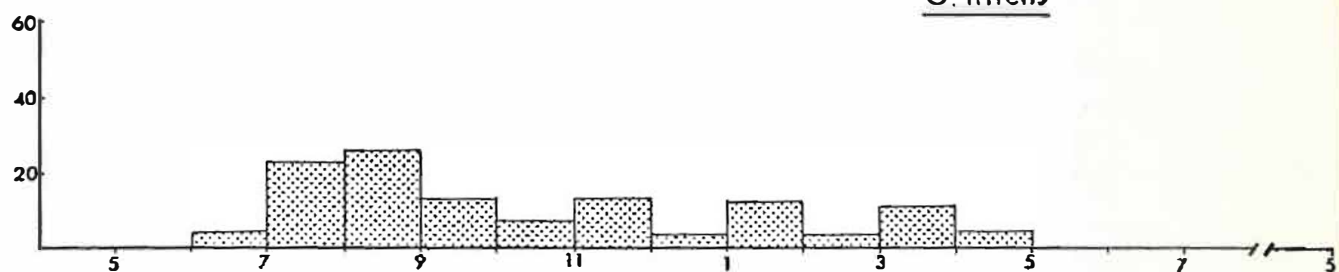
Fig. 56
Sisyphus spp.
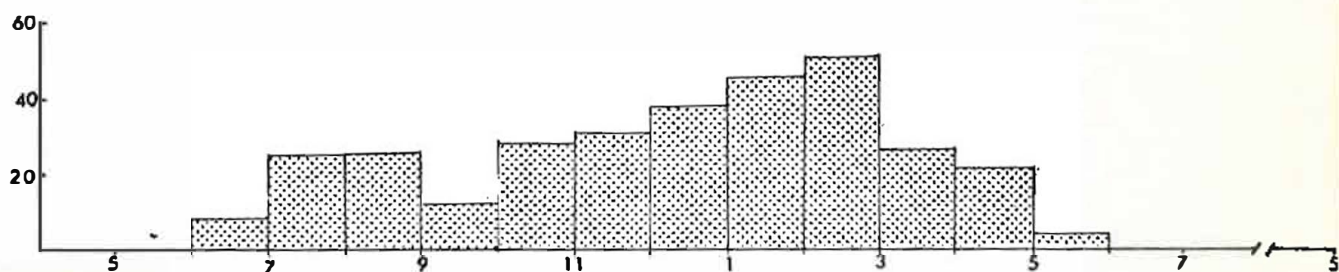
TOTAL BEETLE NUMBERS

A.M.   P.M.

HOURS

Figure 57 : The number of <u>Gymnopleurus virens</u> captured at hourly intervals at Nsumu Pan on the 8th December 1974.

Figure 58 : The number of <u>Onthophagus (Proagoderus) alcyon</u> captured at hourly intervals at Nsumu Pan on the 8th December 1974.

Figure 59 : The number of <u>Phalops flavocinctus</u> captured at hourly intervals at Nsumu Pan on the 8th December 1974.

Figure 60 : The number of <u>Onthophagus (Proagoderus) tersidorsis</u> captured at hourly intervals at Nsumu Pan on the 8th December 1974.

MKUZI HOURLY TRAPPINGS

8-12-74

Fig. 57

G. virens
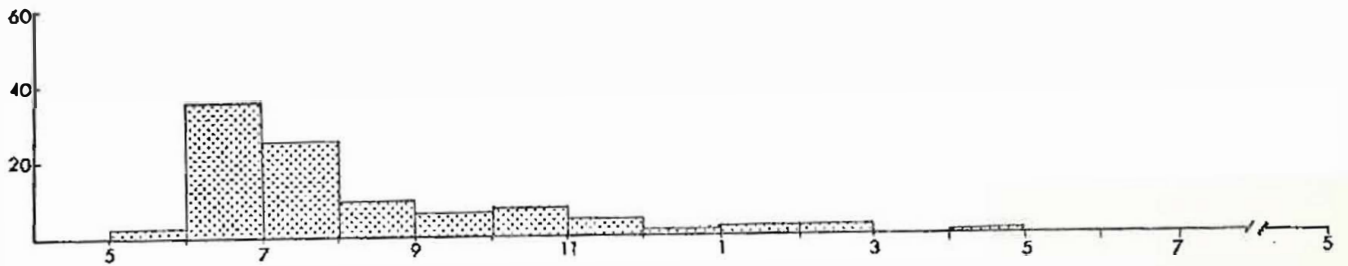
Fig. 58

P. alcyon
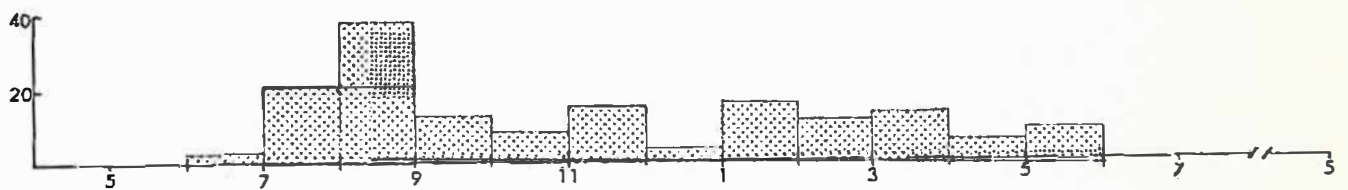
Fig. 59

P. flavocinctus
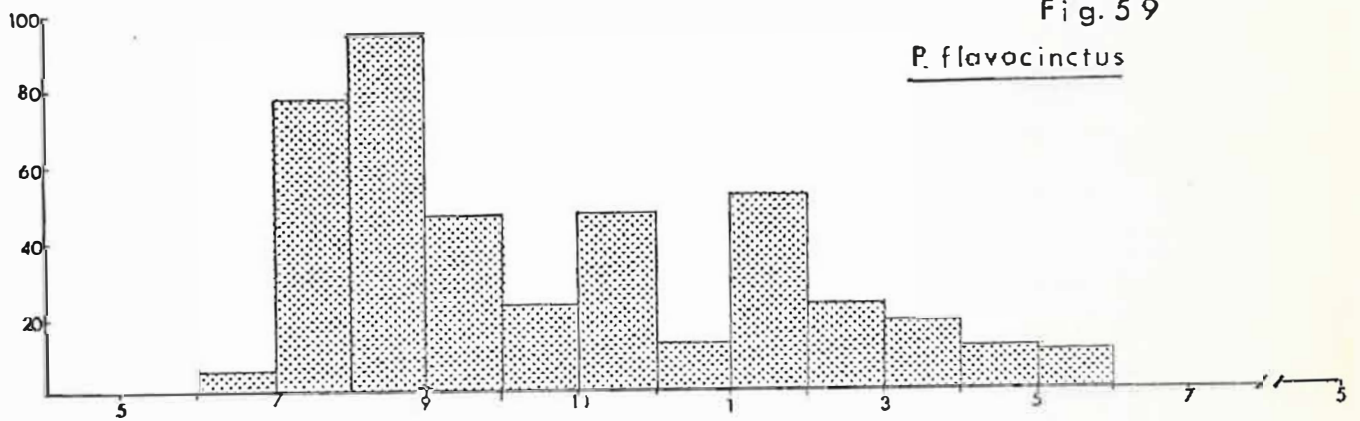
Fig. 60

P. tersidorsis

TOTAL BEETLE NUMBERS

A.M.

P.M.
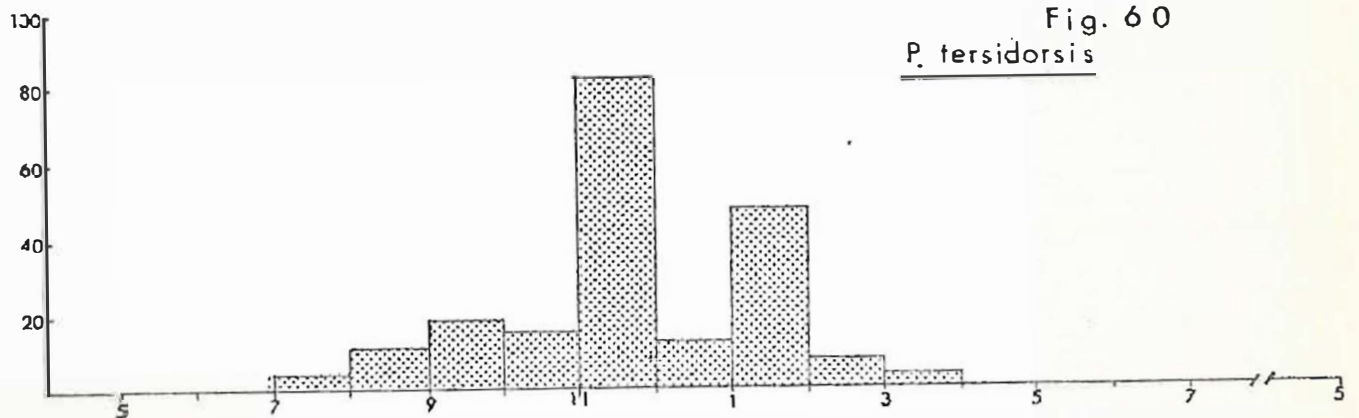
HOURS

From Table 9 and figure 51 it may be seen that G. nitens has a peak extending over four hours with a consequent larger range in optimum temperature for this species.

K. nigroaeneus and G. virens have narrower peaks with more precise temperatures (figs. 48 and 50) under which the majority of beetles are active. A. thalassinus (fig. 47) is most active at a higher temperature than the other species although from the results on the second successive day P. tersidorsis may have the highest temperature tolerance (fig. 60) under which diurnal species in Mkuzi Game Reserve may remain active.

The laboratory data presented in Chapter 5 where the optimum temperature in a painted glasshouse for K. nigroaeneus was between $27^{o}C$ and $29^{o}C$ (fig. 61) correlates fairly closely with the field data obtained in Mkuzi.

(vi) Histerid beetles are predatory in both adult and larval forms on the maggots of coprophilous flies in Java (Bornemissza, 1968). However, the Hister species in Mkuzi Game Reserve (and alsewhere) were observed in the adult stage to be predatory on the smaller day-flying dung beetles, especially Sisyphus, Phalops, Proagoderus and A. thalassinus. The activity peak of the Hister species in Mkuzi is between 0800h and 0900h (fig. 52) with 92% of the daily population (Table 7) flying between the hours 0500h to 1200h.

Histerids drop with great accuracy onto the dung-pad and immediately burrow through it, settling in a position usually at the interface between the pad and the soil. P. flavocinctus, P. tersidorsis and P. alcyon are paracoprids with their combined activity peaks between 0900 and 1000h (fig. 49), also landing with great accuracy on the dung source. They tunnel immediately through to the dung-soil interface to construct their burrows for feeding or breeding. It is here that the majority of these smaller beetles are captured by the histerids lying in wait. The smaller tele-coprids such as A. thalassinus and the Sisyphus species are

captured /....

captured usually during the hottest part of the day when
they shelter from the sun by burrowing into a dung heap
(Section 4.2).

In the laboratory a histerid ate an average of nine
P. tersidorsis a day over a period of three days. The
elytra, thorax and wings were discarded after the inner parts
of the body had been consumed.

It seems very likely that the major food source of
adult histerids are the smaller dung-beetle species during
the summer months. The fierce activity of the coprophagus
fauna in Mkuzi Game Reserve remove most dung within a few
hours, resulting in far fewer flies breeding in the few
pieces of dung which remain untouched. The presence then
of numerous dung beetles, the close correspondence of the
flying time of the histerids to that of the smaller species
of dung beetles (figs. 49 and 52) with the fact that histerids
are absent during the winter months (Chapter 3) when the dung
beetles are also absent, all suggest that adult histerids
prey largely on dung beetles. It is possible that histerid
larvae feed on coprophagus fly maggots but this has never
been observed in the field. Histerids have greatly reduced
eyesight and the possibility exists that they find their
prey in the dung pad by means of a kairomone response.

It may be noted here that the overlapping flying times
of telecoprid and paracoprid beetles is not of great import-
ance from the point of view of competition, as telecoprids
are still able to remove dung from the periphery of the dung
pad while the Proagoderus - Phalops species tunnel immediately
to the soil-dung interface after landing on the pad.

Due to the ecological variation within the Mkuzi Game
Reserve itself, several interesting species were absent from
the hourly trappings conducted at Nsumu Pan. One such
species, trapped at the Rustic Camp, was Scarabaeus
zambesianus which was found to have a flying time between

1830h /.....

1830h and 1915h and also at about 0500h, very few beetles being captured at other times. In the Ndumu Game Reserve S. zambesianus were captured both in the evening and also between 0430h and 0520h and it is a genuine crepuscular or "dawn and dusk" telecoprid species.

In contrast to the majority of other Kheper and Scarabaeus species, S. zambesianus does not first mould pieces of dung into a ball at the dung pad, but immediately after a piece of dung has been detached it is rolled away. This piece of dung may take any shape as a result of the haste in which they remove it from the pad.

This extremely narrow activity peak seems to be a response to the Onthophagus species and other night flying paracoprid species which begin to "rain" on the dung pad after approximately 1900h. The tiny Onthophagus species occur in large numbers which make them extremely important in the ecological web despite their small size.

The only other crepuscular telecoprid recorded in reasonable numbers in Mkuzi is the very primitive Anachalcos convexus, which is an extremely widespread species (Reference Collection, Dung Beetle Research Unit).

Dougall (1964) recorded the times of defecation and the amount of fresh faeces voided by an elephant between 0700h and 1800h. Defecations were found to follow at roughly one hour intervals becoming more frequent after midday, reaching a maximum at about 1800h.

Elephants feed by day and like other herbivores they defecate whilst feeding, the largest amount of dung being voided at the end of the feeding period. As both rhinoceros species feed at night and shelter during the day they probably void most dung during the early hours of the morning. Fresh rhinoceros droppings were found to be relatively abundant just after sunrise in the Natal, Rhodesian and Botswana Game Reserves, with only an occasional fresh dropping being discovered during the rest of the day.

The larger herbivores void most dung at twilight. The majority of beetle species are active during and after twilight periods and it is significant to note that there have not been any strictly nocturnal species recorded in southern Africa to date. Again it is probably due to the effect of temperature on the beetles' activity, the lowest nocturnal temperatures being too low. In a similar manner to diurnal species, crepuscular species have definite peak flying periods (limited data) with the largest number of species flying in the warmer early hours of the evening and with activity diminishing toward midnight. A few beetles of a number of species (mainly Onthophagus) are active again at 0430h, this being a minor activity peak similar to the second peak of K. nigroaeneus and G. virens among day fliers.

Future replication of such trapping periods on typical and atypical days should indicate clearly the effect of temperature on the activity peaks of both diurnal and crepuscular species in different habitats.

4.2 DUNG COARSENESS :

The concentration of herbivorous animals in the grasslands does not lead to severe competition between species for food as most have evolved as specialist feeders. Even when several species graze upon the same plant, they feed at different stages of the plant's growth, on different parts of the same plant and at different heights. They may also be either diurnal or nocturnal in behaviour (Matthews and Carrington, 1970). As a consequence of this co-evolution there is no severe competition for food and the carrying capacity of natural grasslands is extremely high.

The African grasslands contain a great variety of habitats - open grassland grades into wooded savanna and into dense bush with forest along many rivers. Animals show a decided preference for a particular habitat although they may occasionally make excursions into other habitats (Matthews and Carrington, 1970). As a result of this adaptation of

many different kinds of animals to the different food plants, various dung types are produced. This dung varies in texture, consistency, moisture content, microbial content, odour and quantity.

The dung of several animal species is very similar due to the similarity of the food plants consumed. There is thus a close similarity between the dung of the elephant which eats a wide variety of plants, mainly the bark and foliage of trees (Selous, 1908; Dougall and Drysdale, 1964), the black rhinoceros, a browser eating coarse vegetation (Shortridge, 1934) and the white rhinoceros which although a grazer, ingests mostly woody, and therefore not very digestible food (various authors recorded in Shortridge, 1934). The reason why much of the food emerges almost unchanged in the elephant's droppings is because they eat a large volume of food, passing it quickly through the gut so that only the most nutritious parts are digested. In this way they extract adequate nourishment from woody and largely indigestible food (Matthews and Carrington, 1970).

Dung varies mainly in the degree of coarseness. When fresh, elephant faeces have an average moisture content of $80,1 \pm 0,35\%$ with a mean dry weight of $2,1 \pm 0,14$ lb. (Dougall, 1963). As rainfall in the grasslands is often erratic, the moisture content of the dung may vary depending on the season or local conditions. Thus some antelope produce dry pellets due to resorption of water during drought and these may change to moister clumped droppings after rain has fallen.

Table 10 shows some affinities of the various types of dung and a rating of their coarseness.

TABLE 10 : /.....

TABLE 10 : Comparative coarseness ratings of mammal dung.

Species	Coarseness Rating	Dung Characteristics
Black Rhinoceros	+++++	Twigs, bark
Elephant	++++	Twigs, bark, leaves
White Rhinoceros	++++	Woody plant tissue
Zebra	+++	Grass (fine)
Horse	+++	Grass
Cow	++	Grass
Wildebeest	++	Grass
Buffalo	++	Grass, shoots
Impala	++	Pellets
Carnivores	++	Hair, bone chips
Baboon	+	Insect remains, seeds
Monkey	+	Seeds, vegetable matter
Human	+	Vegetable and animal matter

Africa has a wide variety of dung types and although dung beetles are attracted to almost any dung, Halffter and Matthews (1966) noted that in Europe and Central America some species come to only a certain type of excrement, while a large number feed with a low degree of preference.

Although preference seems to depend greatly on the coarseness of the dung, the amount dropped by a particular species as well as its characteristic odour are also important. The largest naturally occurring amount of dung is that of the white rhinoceros that defecates in communal middens. It is important to note that a minor survey of middens in Mkuzi and Hluhluwe Game Reserves showed that the vast majority, 19 out of 21, were completely exposed to the sun.

Animals void their dung either while moving about feeding in their particular habitat or while resting at a different time of the day. Hence various dung types may be found predominantly in shade or in the sun. For example, black wildebeest may drop dung while congregating in the shade

of /....

of a tree at midday and monkey faeces are found in the shade
below the trees they slept in the previous night, while the
impala's pellet-like dung is dropped in clearings and becomes
extremely hard within a few hours.

In the Mkuzi Reserve in summer beetles are attracted
almost exclusively to fresh dung because :

(i) The adult beetles have specialised membranous mouth-
parts to feed on the moist dung which makes older dung
less suitable for feeding.   Older dung forms a hard crust
in many cases;

(ii) The odour of freshly voided dung is stronger than
that of sun baked dung on which a crust forms sealing in
the odour.   Fresh dung is thus more attractive than
older dung;

(iii) Dung more than twenty-four hours old is not available
due to -

    (a) The fierce beetle competition which results in
        most dung being buried within twenty-four hours,
        leaving only freshly voided dung to be found the
        following day,   and

    (b) Termite activity on freshly dropped dung being so
        high that any dung not buried is consumed by termites.

In winter telecoprids are aestivating in the soil
(Chapter 3) so that dung on the surface has no relevance to
them at this time.   It is mostly devoured by termites.

The availability of various types of dung within a
habitat and the fact that avoidance of desiccation consti-
tutes a strong selection pressure explains why dung type
should play a role in the ecology of day-flying telecoprids
in particular.   Although preparations were made for collecting
field data concerning dung preferences of various species,
circumstances prevented this from being done.   However,
the following observations were made and are of importance
to future dung preference trials.

Numerous observations while collecting beetles for

breeding purposes suggest that <u>Kheper</u> species are attracted to any type of dung in the early morning but only to coarser dung as the temperature rises.   In addition under different weather conditions the type of dung to which the <u>Kheper</u> species were attracted also differed.

From sunrise <u>Kheper</u> <u>spp</u>. feed, attract mates and roll balls from most types of dung and show very low preference for particular types.   As the day progresses they show an increasing preference for rhinoceros dung.   By midday only a few may be flying and middens previously covered with beetles seem virtually deserted.   But within the midden are numerous beetles and as temperatures drop in the late afternoon, they again appear on the surface (Section 4.1).

In this way the <u>Kheper</u> species which have not paired off and buried brood-balls escape the effects of the sun at its hottest.   <u>Kheper</u> <u>spp</u>. can only seek refuge from the heat in coarse dung because :-

(i) it occurs in large amounts and retains moisture

(ii) the coarse dung consisting of twigs etc. does not become stuck to the beetle's elytra and legs.   This happens frequently in large laboratory bred beetles which become caked with cow dung, sometimes to the extent that they cannot fly.

Beetles also take refuge in rhinoceros middens on cool days with drizzle, the microclimate being warmer due to the heat generated microbially within the midden.   At the same time, other types of dung in the vicinity are virtually deserted.

<u>A. thalassinus</u> are mostly attracted to smooth dung, slightly later in the morning (0900h to 1000h - Section 4.1) when the temperature has risen to at least 30°C.   Activity is consequently faster than that of the <u>Kheper</u> group, with sexual pairing occurring extremely rapidly as well as the other activities of detaching, rolling and burying the dung.

There /....

There may be a connection between their activity under slightly hotter conditions and their preference for moist, sloppy dung.   It has been observed that such moist dung moistens the soil chamber by condensation, thus creating a favourable microclimate for the beetles.   Under hotter conditions A. thalassinus may also seek temporary refuge in rhinoceros dung.

A. thalassinus is attracted to dung in the sun as seen by the fact that cowpads near Ndumu Game Reserve attracted beetles only if dropped in the sun.   Similar fresh cowpads beneath a heavily leafed tree were unattractive until they were moved into the sun, after which they immediately became attractive.

This preliminary survey of dung preference of diurnal telecoprids in Zululand has indicated factors that should be taken into account in any future investigation.   In order to test dung-type preferences the setting out of standard amounts of each dung type would not be entirely accurate, as this does not take into account the different amounts of each dung type occurring naturally in the veld.   Thus both the quality and the quantity of dung play important roles in the ecology of the various species.   Furthermore, the attraction of certain beetles to dung in the sun or in the shade (such as Sisyphus seminulum and Sisyphus mirabilis - Paschalidis, 1974) would have to be catered for as well as the fact that there are peaks of activity among the different species (Section 4.1) which would affect the time the tests are performed.

CHAPTER 5.

SOIL OR SURFACE DWELLING.

During the summer months telecoprids are observed flying towards and landing beside dung-pads and later emerging from the beetle-covered pad rolling either a food-ball or, if rolling in pairs, a brood-ball which is buried some distance from the dung source. In order to estimate the populations of certain telecoprid species, the following tests were conducted to discover what proportion of each species population was active on the surface over a period of three months.

Beetles of two of the telecoprid species were captured in Mkuzi Game Reserve in late October 1973, as well as Pachylomera femoralis in Botswana. These were transported to Pretoria and set up in cages in a glasshouse. The cages measured 93cm x 190cm in length and consisted of a cement pan 15cm deep filled with soil to the top and covered by wire gauze stretched over a metal framework to a height of 40cm above the surface of the soil in the pan. The soil was a mixture of sand and loam in which several rocks were placed and a number of tufts of grass planted in order to imitate field conditions as closely as possible.

Excess fresh dung was placed in the pans every alternate day while the older dung was removed simultaneously. Once a week the soil was lightly sprinkled with water. To dispel some of the heat which builds up in glasshouses, the glass was painted over on the inside with putty-lime, all windows were opened during the day and fans were used to cool the air under extremely hot conditions. The pans were placed in the glasshouse, as previous tests had shown that the activity of telecoprids was much reduced when placed in a lighted but closed room. The sudden downpours of rain meant that the pans could not be placed in the open as they would become waterlogged.

The /....

The three telecoprid species were placed in three separate cages in the following numbers :

Kheper nigroaeneus   - 120 beetles

Garreta nitens   - 100 beetles

Pachylomera femoralis - 80 beetles

These were taken from natural populations in the field immediately after the first rains (Chapter 3) and the sex ratio was assumed to be natural without causing bias to the results.

Recordings of the following data were taken at various intervals during the day between November 1973 and January 1974: Date, time of day, temperature, relative humidity, number of beetles on the surface, total number of beetles in the pan and date of addition of fresh dung or water to the pan. Dead beetles were recorded on clip-boards hung beside the pans so that the total number of beetles in each pan was known at any time.   The data accumulated were analysed by recording the percentage of beetles of each species on the surface at various temperature levels and intervals during the day.   All recording of data was made from 0800h to 1600h, all three species being day fliers.

From the results summarised in Table 11 it was possible to divide these species into predominantly surface or soil dwellers.

TABLE 11 : The mean and range in the percentage beetle population on the surface in laboratory cages during the period November 1973 to January 1974.

Species	Range in % Population Active on Surface	Range in % Population Below Soil Surface	Mean % of Population Active on Surface
P. femoralis	60 - 85	15 - 40	73
G. nitens	25 - 61	39 - 75	46
K. nigroaeneus	10 - 20	80 - 90	14

P. femoralis may be described as a predominantly surface
dweller, because between 60% and 85% of the population is on
the surface during the hours from 0800h to 1600h (figs. 61
and 62).   The 15% to 40% below the surface were occupied with
activities such as excavating burrows, burying dung and
sheltering.

In contrast with P. femoralis, K. nigroaeneus had only
between 10% and 20% of the population on the surface during
the same hours.   Thus the majority of beetles, between 80%
and 90%, were not on the surface during the daylight hours.
This may be explained largely in terms of the brood-care
exhibited by K. nigroaeneus, where the female beetle remains
below the soil with the brood-balls for 68 to 84 days
(Chapter 8), the sex ratio being 2 females : 1 male (Chapter 6).
Another behavioural trait is that this species only occasion-
ally feeds at the dung pad itself, usually rolling away a
dung-ball which is buried before it is fed on.   Individual
beetles are continually returning to the surface, at various
intervals depending on the sex, breeding state etc., to feed
or find a mate.

P. femoralis feeds fairly often at the dung pad and
is thought by Halffter and Matthews (1966) to have lost the
ability of rolling dung-balls due to the extreme modification
of the forelegs for digging.   However, under laboratory
conditions they have been observed repeatedly rolling dung-
balls in a similar manner to that of the Kheper and
Scarabaeus genera (Section 7.2).   But both P. femoralis and
P. opaca differ from the latter two genera in that in propor-
tion to their sizes, a smaller amount of dung is rolled, and
although morphologically adapted for digging they rarely bury
this dung-ball but instead feed on it at the surface. This
usually occurs beside some obstacle such as a bush or clump
of grass.   As the ball-rolling behaviour has only occasionally
been observed in the field over very short distances, it could
possibly be a result of competition at the dung-pad under
overcrowded laboratory conditions.

Furthermore /......

Furthermore, P. femoralis constructs a burrow near the dung-pad and detaches pieces of dung with which it provisions the burrow, making many journeys to and fro (Section 10.1). This results in further activity at the soil surface for this species.

G. nitens is largely a surface dweller (fig. 61) but has a greater range in the amount of surface activity than is found in the previous two species. Here again there is no brood-care and although food-balls may be rolled away, the larger proportion of this species feeds at the dung source, usually on top of the dung at cooler temperatures and burrowing into it as the temperature rises.

The number of beetles of all three species on the surface varies according to the temperature and relative humidity and also to some extent whenever fresh dung is added or the surface is lightly sprinkled with water. The largest percentage of the population on the surface for all three species is found between the temperatures 27° and $30^{\circ}C$ (c.f. Table 9), which constitutes the optimum temperature, the percentage dropping off as the temperature either rises or declines (fig. 61).

Thus temperature may well play an important role in determining whether a species is soil or surface dwelling; the largest concentration of the soil dwelling K. nigroaeneus being found in the hot, humid Zululand and Eastern Transvaal lowveld where the desiccation potential is higher than the relatively cooler, less humid Botswana where the surface dwelling P. femoralis occurs. Burrowing offers greater protection against variations in temperature and moisture as seen in the small fluctuations at a depth of 30cm when compared to the larger fluctuations above surface (W.B.19). Unfortunately because of the artificial cooling of the glass-house during the hottest part of the day no inferences can be drawn from figure 62.

All three species investigated above were day fliers.

The /.....

Figure 61 : The percentage population of Pachylomera
femoralis, Garreta nitens and Kheper nigroaeneus
confined in large laboratory cages, appearing on
the surface during the period November 1973 to
January 1974 in response to temperature.

Figure 62 : The percentage population of Pachylomera
femoralis and Kheper nigroaeneus confined in
large laboratory cages appearing on the surface
during the period November 1973 to January 1974
at hourly intervals.

SOIL AND SURFACE DWELLING SPECIES
(LABORATORY)

Fig. 61

P. femoralis

G. nitens

K. nigroaeneus

TEMPERATURE °C.

Fig. 62

P. femoralis

K. nigroaeneus

A.M.　　　　　P.M.
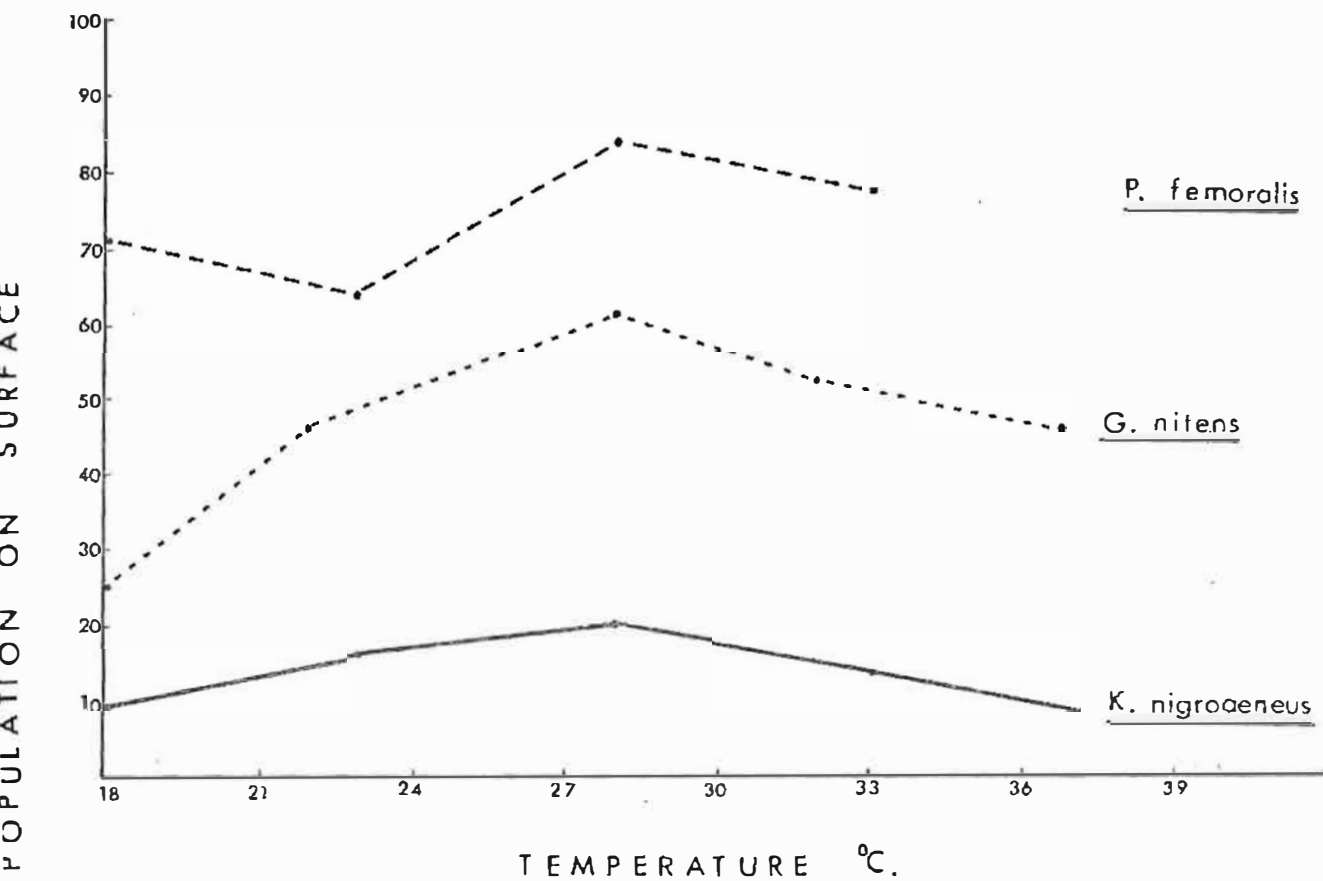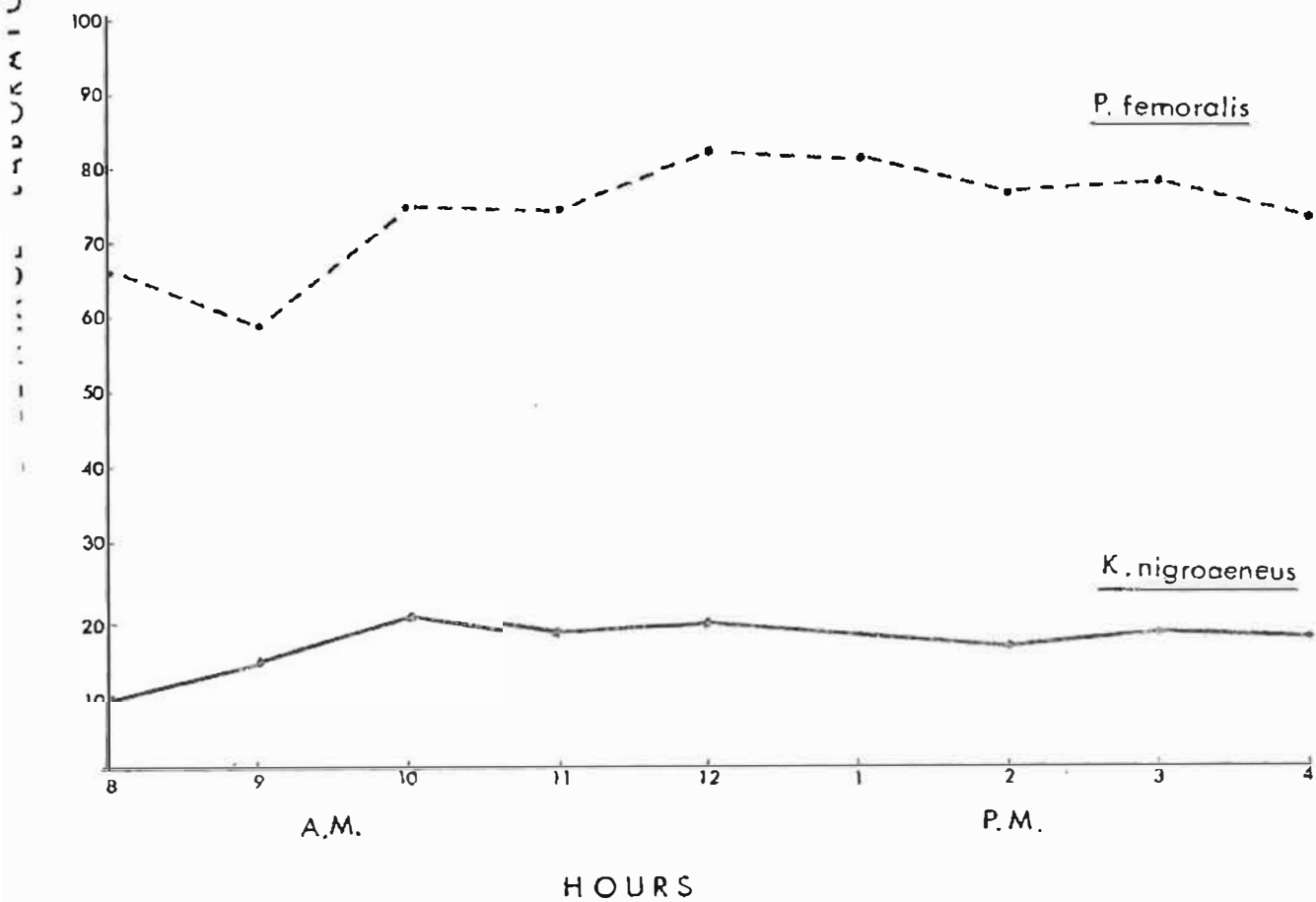
HOURS

The distinctly crepuscular species are all below surface during the daylight hours, either buried in the soil or under a dung-pad (Chapter 4).

There are strong indications that crepuscular species may also be divided into predominantly soil or surface dwellers. However, in contrast to the diurnal species which shelter in the soil because of extreme heat, the crepuscular species may similarly burrow into the soil for warmth. Since temperature largely determines activity (Chapter 4.1) and as the soil temperature is warmer than the air temperature during the coldest part of the night (The Climate of South Africa, W.B.19) burrowing into the soil probably occurs as temperatures become too low for activity.

The behaviour of all Kheper species thus far investigated in southern Africa (Chapter 1) closely follows that of K. nigroaeneus which is also very similar to that of Scarabaeus. Similarly the Garreta, Gymnopleurus and Allogymnopleurus genera are similar in behaviour to G. nitens. Consequently sampling methods and estimations of populations in an area must take into account this important behavioural grouping of species into predominantly soil or surface dwellers.

CHAPTER 6.

PRE-BREEDING BEHAVIOUR.

6.1 EMERGENCE AND MATURATION FEEDING :

The F_1 K. nigroaeneus beetles emerging in January and
February have, on dissection, shown that they have no food in
their gut and virtually no fat reserves.   For the remainder
of the season their main activity is concerned only with
feeding and no laboratory bred F_1's have been observed to
attract mates during this period.   From February to April
the F_1's burrow into the soil together with the adult
generations where they aestivate until the following spring
when they re-emerge in response to increased temperature and
sufficient rainfall, together with beetles of other genera-
tions (fig. 29).

This emergence is followed by an intensive maturation
period during which no K. nigroaeneus beetles are seen
rolling dung-balls in pairs.   Dissections of freshly emerged
beetles have shown that the female ovaries, as well as the
male pheromone glands are still immature.   Also the gut in
nearly all cases is empty.   This maturation feeding is common
to most Scarabaeidae and numerous cases have been recorded
in Halffter and Matthews (1966).   During this phase aggression
is very evident in both sexes as they fight for possession of
dung.

After approximately three weeks the maturation feeding
phase is replaced by the breeding phase in which many beetles
are observed rolling dung-balls in pairs.

6.2 SEX RATIOS :

6.2.1 Seasonal sex ratio fluctuations :

The overall sex ratio of all K. nigroaeneus recorded
from the Mkuzi pitfall traps was 538 males and 846 females or

one /.....

one male to 1,57 females (fig. 63). However because of brood-care where the female beetles remains below the surface with the brood-ball while the male returns to the surface after four days (Chapter 8) the above sex ratio is biased in favour of males. At the peak of their seasonal activity after emergence from the soil and before breeding began (21.11.74), the sex ratio was 174 males and 349 females or one male to two females. An equal number of males would result in numerous males on the surface in January while most females are brooding below the surface. The aggressiveness of the males (Chapter 7) would result in confusion if the sex ratio were equal.

A. thalassinus does not show brood-care, both partners returning to the surface after several days. Thus the overall sex ratio for the 1974/75 season of 1677 males and 1833 females or approximately one male to one female may be regarded as reasonably accurate (fig. 64). At their peak of activity on emergence (1.12.74) the ratio of 796 males and 623 females or 0,78 males to one female was recorded.

The sex ratio of K. nigroaeneus naturally does not remain constant due to brood-care. By eliminating the uneven sex ratio by plotting percentages of the sexes, it was determined that the percentage female population progressively dropped off to nil in early February (1975) with a correspon- ding gradual increase in the male percentage as more females were mated and remained below with their brood-balls (fig. 65). The percentage evened out again as the F_1's emerged and more females were relieved of their brooding in February and March.

The same sex ratio fluctuations have been recorded in a number of instances during field collecting trips. Thus all 72 Scarabaeus ambiguus beetles captured at Vryburg in February 1973 were found to be males. It is also common experience to find that when collecting K. lamarcki beetles in mid-season in Mkuzi and Botswana the greater proportion

are /....

are males.

The sex ratio of A. thalassinus fluctuates slightly, there being initially a higher male percentage but later a higher female percentage (fig. 66).   As no brood-care is involved the percentages remain fluctuating within narrower limits.

The sex ratio of P. tersidorsis was recorded only from the 6th January, 1975 onwards with 290 males to 883 females or one male to three females.   Presumably the female of this paracoprid species constructs the brood burrow and/or moulds the brood-dung while the male returns to the surface.

6.2.2 Diel Sex Ratio :

The sex ratio of the total day's trapping of K. nigroaeneus on the typical first day (7.12.74) during the hourly trapping (Section 4.1) was found to be 179 males to 326 females, or roughly one male to two females.   As the trapping period coincided with the seasonal activity peak (fig. 35) and the start of the breeding season, this may be regarded as being close to the true sex ratio for K. nigroaeneus in the field.

By constructing histograms of the numbers of K. nigroaeneus of both sexes captured at the hourly intervals (fig. 67) it may be seen that a greater number of males are present at the earlier hours than females.   By combining the data from all eight traps the greater proportion of males arriving first at the dung pad is even more clearly observed (fig. 68).   The females arrive in greater numbers only after 0700h when the male beetles flying in have become progress- ively fewer in number.

The same pattern was present on the atypical day (8.12.74) when a greater proportion of the male population arrived at the dung source before the majority of females began flying (fig. 69).   The difference in the flying peaks of the sexes of K. nigroaeneus may be as a result of the

males /......

Fig. 63

Kheper nigroaeneus

- - - - Female
——— Male

Fig. 64

Allogymnopleurus thalassinus

——— Male
- - - - Female

Beetle numbers

800
750
700
650
600
550
500
450
400
350
300
250
200
150
100
50

Sept.　Oct.　Nov.　Dec.　Jan.　Feb.　Mar.　Apr.　May.

1974　　　　　　　　　　1975
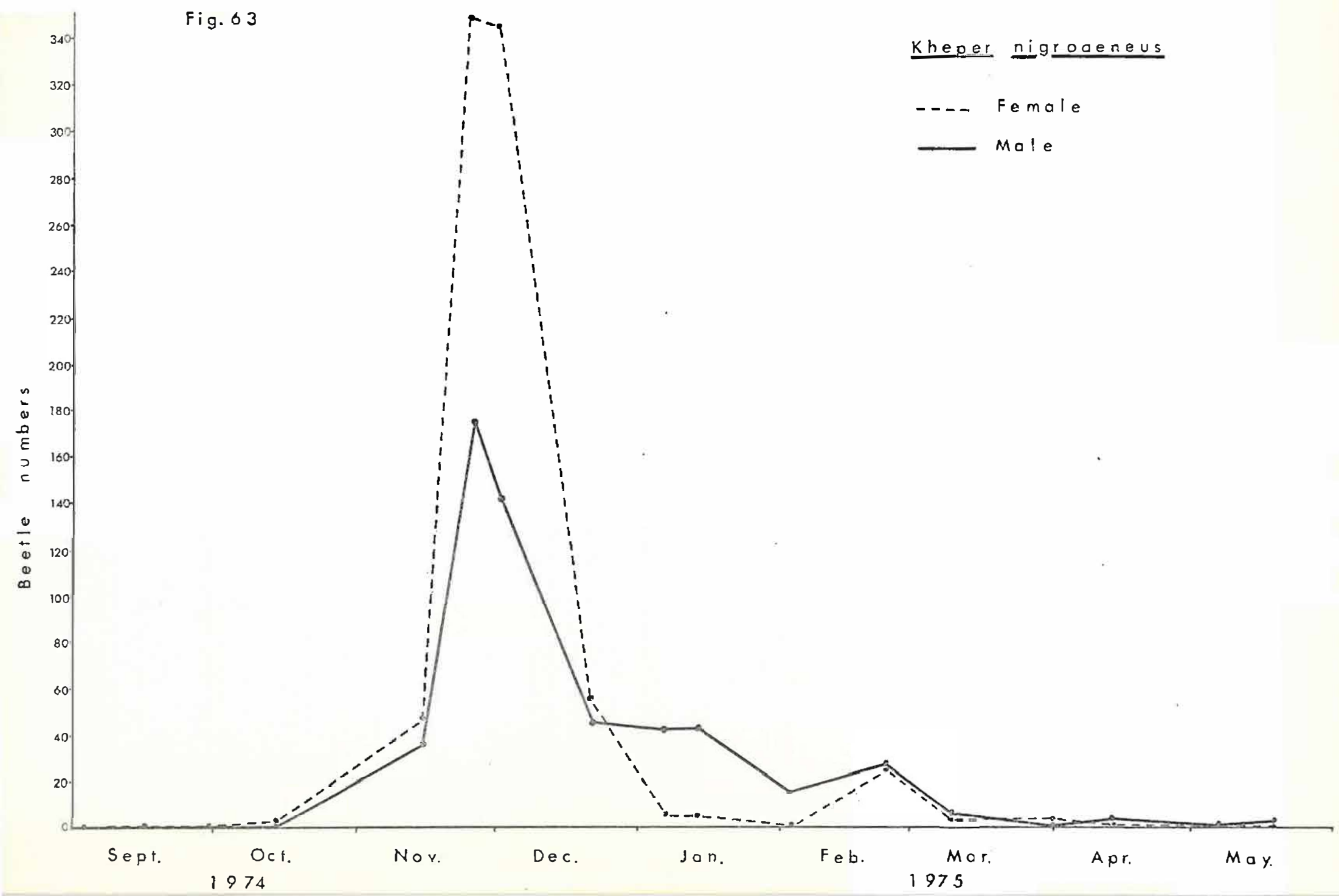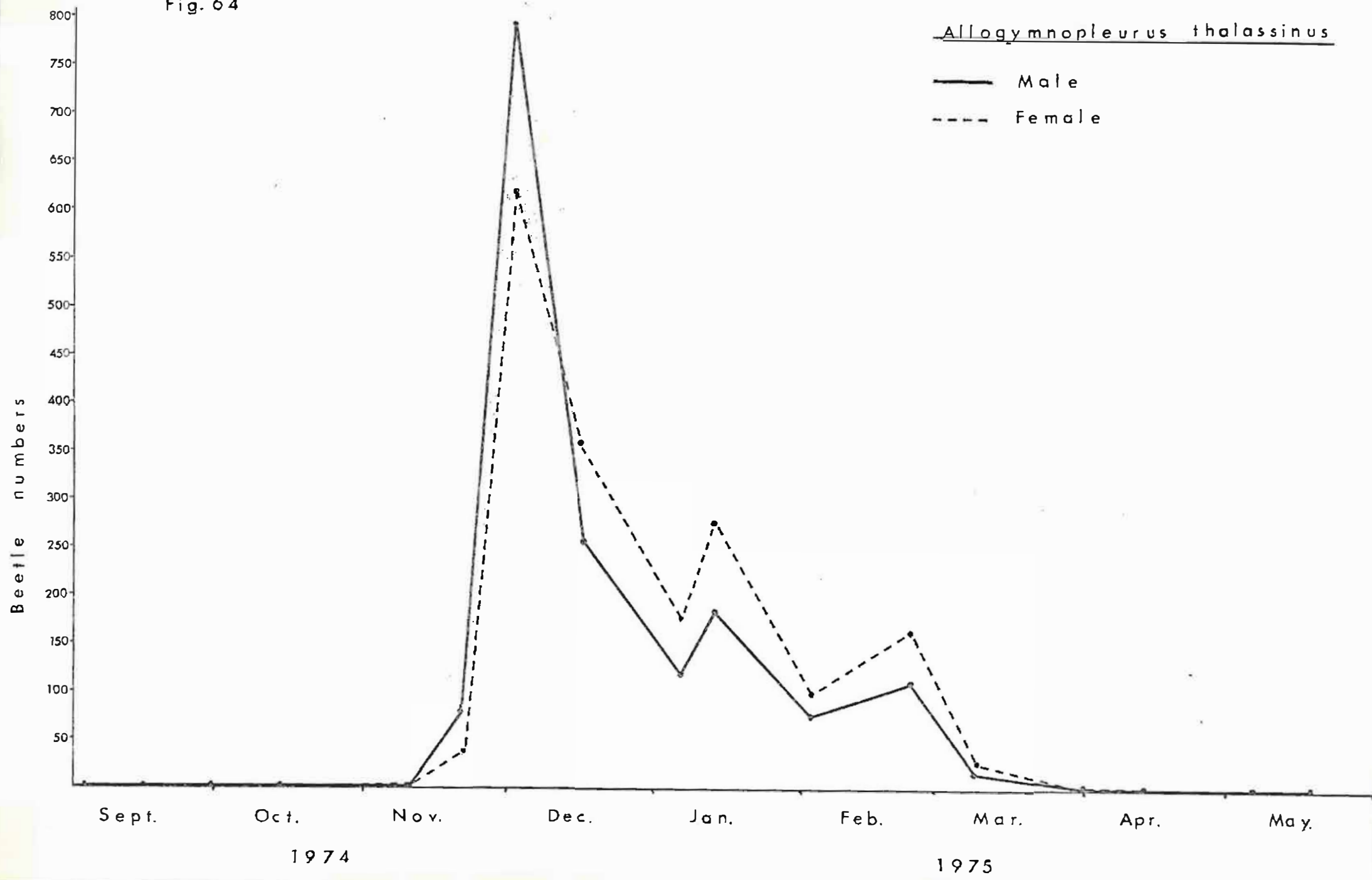
THE SEASONAL SEX RATIOS OF TWO SPECIES EXPRESSED AS PERCENTAGES OF THE TOTAL NUMBER OF
BEETLES OF EACH SPECIES CAPTURED DURING EACH TRAPPING PERIOD AT NSUMU PAN, MKUZI GAME
RESERVE.   For accuracy, only the months from September 1974 to February 1975 are
represented.

Figure 65 : Seasonal sex ratio of Kheper nigroaeneus expressed as percentages of
            each captured total.

Figure 66 : Seasonal sex ratio of Allogymnopleurus thalassinus expressed as
            percentages of each captured total.

Fig. 63

Kheper nigrogeneus
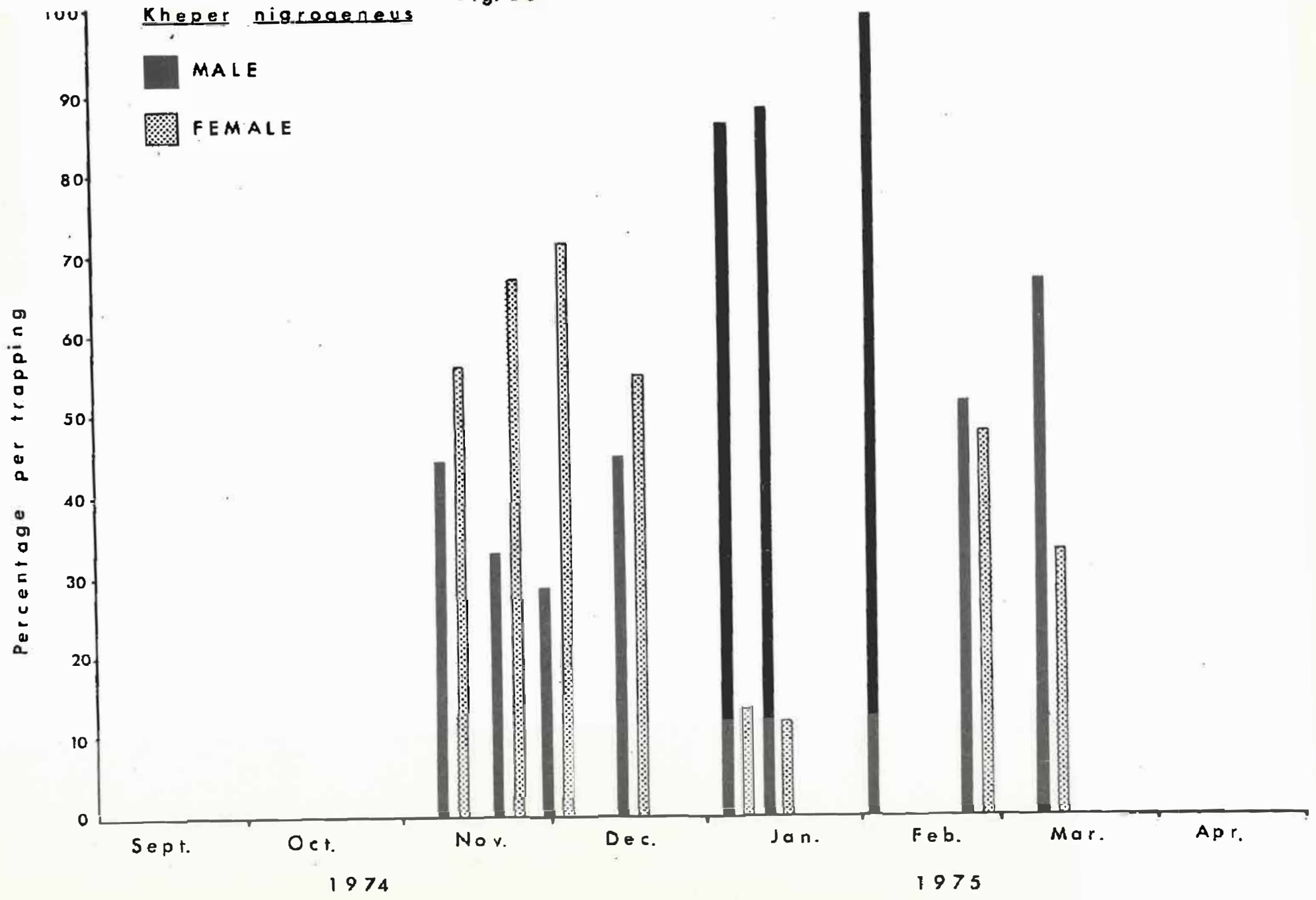
Fig. 66
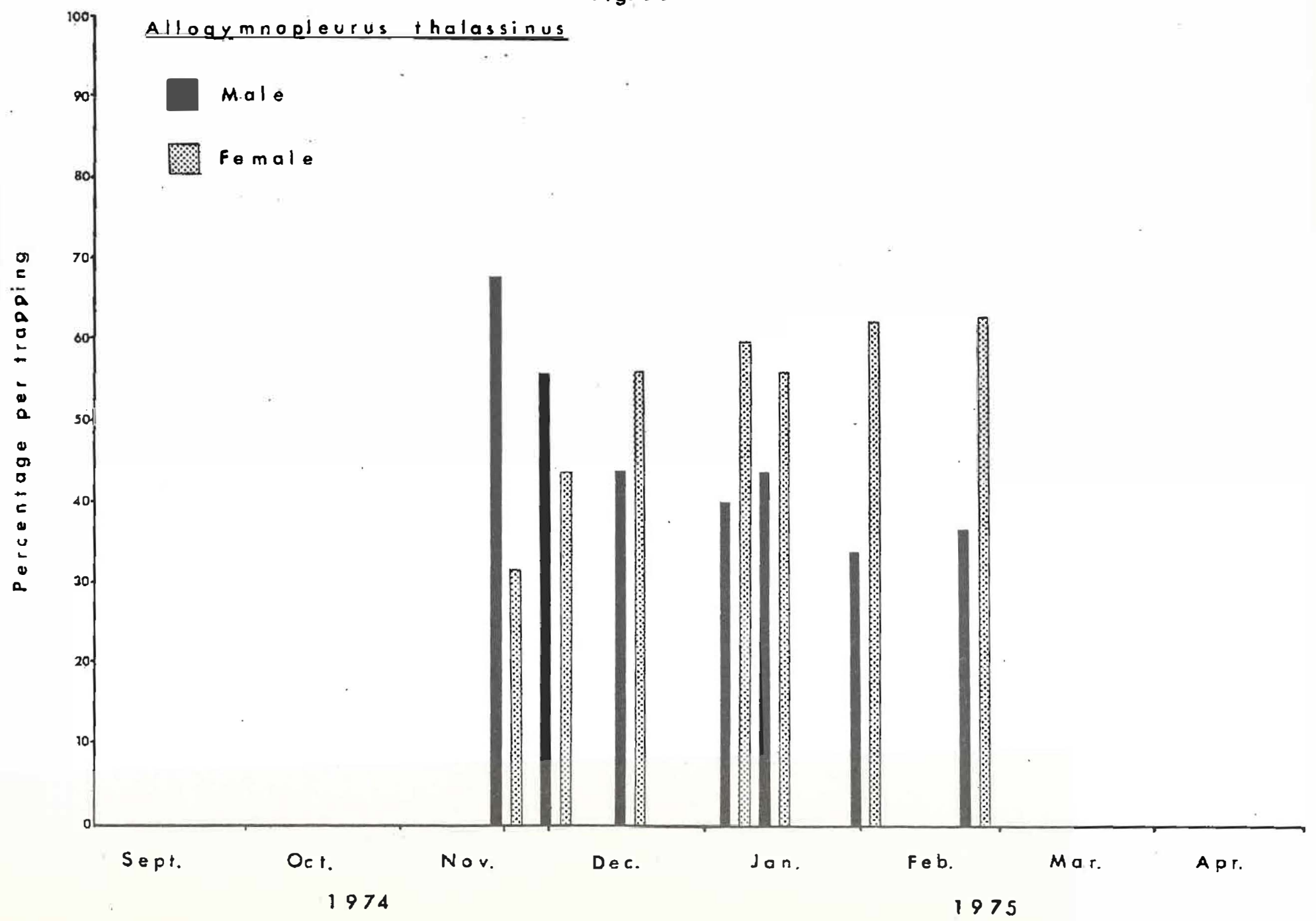
males being more active at slightly cooler temperatures than the females.

The significance of this becomes apparent when the males are known to produce a sex pheromone and then only if they are in possession of some dung (Section 7.1). By arriving at the dung pad in the early morning before the females they are able to ensure that they have some dung and may begin releasing pheromone to attract the females as they arrive. As this trapping was conducted after the maturation feeding and at the start of the breeding season it is possible that those males which arrive first at the dung pad are physiologically mature and ready for mating while those arriving later are still concerned with feeding. Similarly the first arrivals among the females could be in a mature breeding state unlike later arrivals. Unfortunately only two days could be spent collecting these data and no dissections to determine the state of gonadal development were performed.

FIGURES 67 - 69

THE DIEL SEX RATIOS OF KHEPER NIGROAENEUS CAPTURED AT NSUMU
PAN, MKUZI GAME RESERVE, ON TWO SUCCESSIVE DAYS IN DECEMBER
1974.

Figure 67 : The diel sex ratios of Kheper nigroaeneus
            recorded from four pitfall traps on the
            7th December 1974.

Figure 68 : The combined sex ratios of Kheper nigroaeneus
            recorded from all eight pitfall traps between
            0500h and 1200h on the 7th December 1974.

Figure 69 : The diel sex ratios of Kheper nigroaeneus
            recorded from four pitfall traps on the
            8th December 1974.

MKUZI HOURLY TRAPPINGS

Kheper nigroaeneus

■ MALE

▦ FEMALE

7-12-74   Fig. 67

Traps 1,3,5,7.

7-12-74   Fig. 68

Traps 1 - 8.
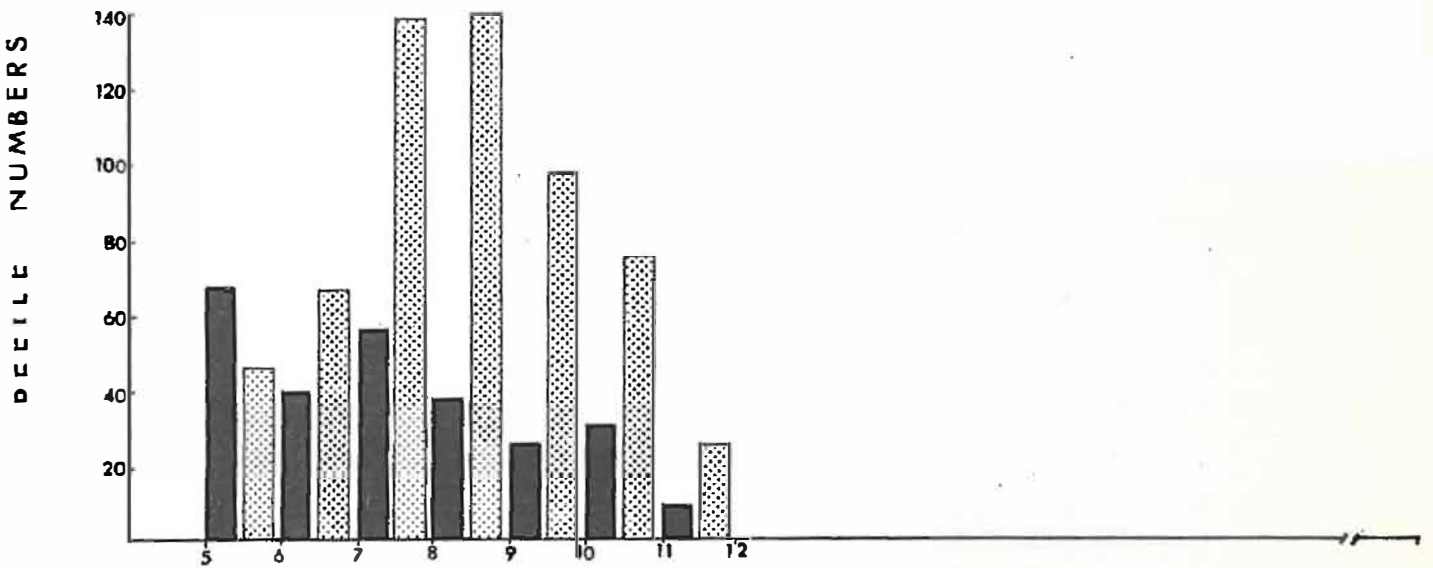
8-12-74   Fig. 69

Traps 1,3,5,7.
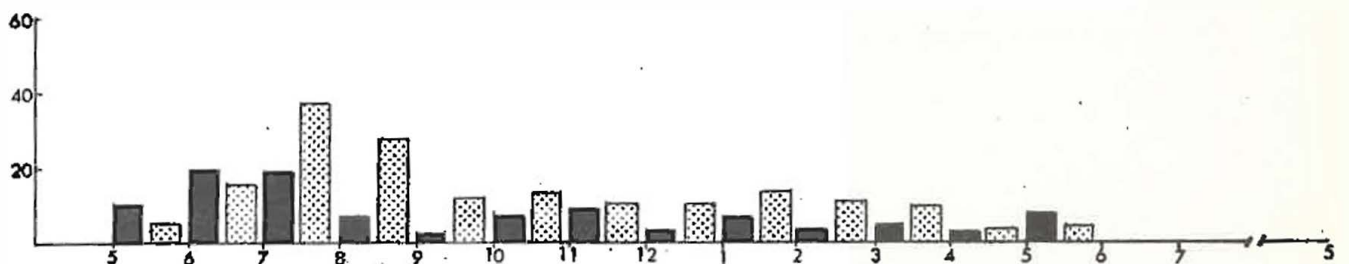
A.M.   P.M.

CHAPTER 7.

BREEDING BEHAVIOUR.

7.1 PHEROMONE RELEASE :

Attractant pheromones in Coleoptera are generally
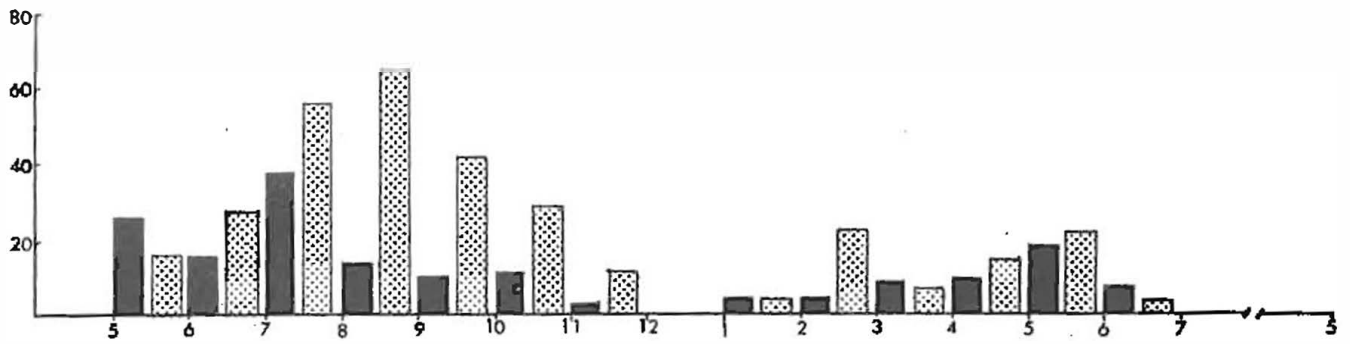sex pheromones or aggregating pheromones, the release of sex
pheromones usually occurring irrespective of habitat whenever
the releasing individual is ready to mate, while aggregation
pheromones are usually released by either or both sexes when
a suitable breeding habitat is located (Jacobson, 1972).
According to Jacobson (1972) Coleopteran pheromones are
produced mainly by the female of a species and only two
cases of males luring females have been recorded.

No scent disseminating structures have been described
for Coleopteran species, most pheromones, especially aggre-
gation pheromones such as those of the Scolytidae, being
excreted on the frass (Borden, 1974) while the sex pheromones
of the boll-weevil Anthonomus grandis is simply released by
the male in the plant in which it is established (Cross and
Mitchell, 1966). The best known of the many pheromone
dissemination structures in insects are probably the "brush
organs" of Lepidoptera (Percy and Weatherston, 1974). The
range in structure and positioning of these is great, as
they are highly specialised and adapted to the individual
requirements of each species (McColl, 1969).

The production and dissemination of pheromones by
dung beetles has not previously been recorded, although
aggregation at particular dung pads while others in the
vicinity are ignored has been observed in several species
(Halffter and Matthews, 1966; Paschalidis, 1974). Paik
(1968) in Korea, used the "small polished patch" found only
in males of Scarabaeus affinis on each side of the first
abdominal sternites as a character for separating the sexes
although this was not recognised as a pheromone release
site.

After /....

After three weeks of maturation feeding, K. nigroaeneus beetles arrive singly at fresh rhinoceros dung in their hundreds and minutes later emerge as pairs from this mass of beetles, rolling brood-balls. During the period from arrival at the dung source to emergence as pairs rolling a brood-ball, a single beetle has had to distinguish between the sexes, to determine the state of maturity of the opposite sex and to engage the co-operation of the selected partner in moulding and rolling a brood-ball. This is achieved by pheromonal and behavioural means.

7.1.1 Disseminating Structures :

The pheromone produced by the male Kheper nigroaeneus is visible as a white, flocculent substance emerging from a depression on either side of the first abdominal sternite. The depressions (fig. 70) consist of several hundred tiny openings, resembling a sieve (fig. 71), which are supplied from a large gland complex immediately underlying the depressions. The gland complex consists of an interwoven mass of unicellular glands (fig. 72).

Male abdominal sternites two, three and four also have numerous tiny pores supplied by smaller separate gland complexes, one complex to each sternite. These pores are widely distributed and not concentrated into definite depressions as found in the first sternite.

Similar sparsely distributed pores are also present in female K. nigroaeneus beetles on the first five abdominal sternites and although fairly concentrated on either side of the sternites, they do not form definite depressions as in the male (fig. 73). These pores are of two types: small direct openings to the exterior and, interspersed amongst these, small depressions, slightly larger than the direct openings (fig. 74) and each containing numerous minute pores (fig. 75). The glands supplying these pores are grouped immediately interiorly to the five abdominal sternites and are much smaller than those of the male. There are narrow inter-

segmental /....

FIGURES 70 - 72

MORPHOLOGY OF MALE KHEPER PHEROMONE STRUCTURES.

Figure 70 : Left half of the abdomen of a male Kheper
lamarcki showing the depression filled with
numerous pheromone pores and two rows of
bristles   x 17

Figure 71 : Scanning electron micrograph of part of the
depression of a male Kheper lamarcki showing
pores and a row of bristles.   x 125

Figure 72 : Unicellular glands of a male Kheper lamarcki
concentrated immediately behind the abdominal
depression   x 20

Figure 70

Figure 71
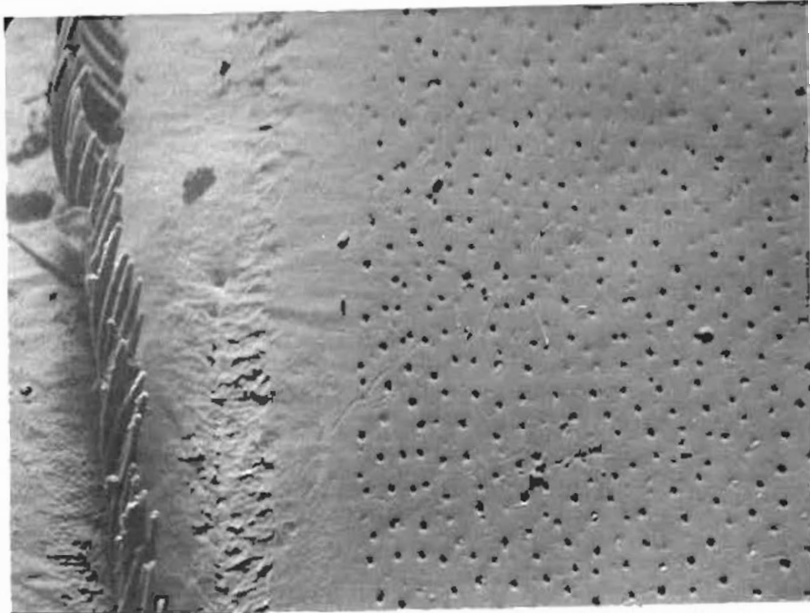
Figure 72
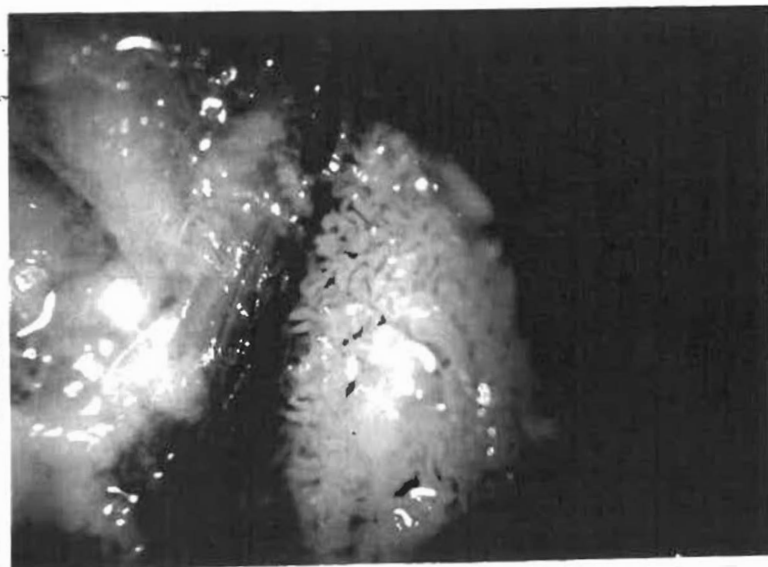
FIGURES 73 - 75

MORPHOLOGY OF FEMALE <u>KHEPER</u> STRUCTURES SIMILAR TO THE
PHEROMONE STRUCTURES PRESENT IN MALES, AS SEEN FROM
SCANNING ELECTRON MICROGRAPHS.

Figure 73 : Female <u>Kheper nigroaeneus</u> pores distributed
over the first and second abdominal sternites

x 17

Figure 74 : The two pore types found on female <u>Kheper</u>
<u>nigroaeneus</u> abdominal sternites.   The small
(lighter) depressions are interspersed
among the single opening pores   x   162

Figure 75 : A single enlarged depression of a female
<u>Kheper nigroaeneus</u> showing twenty-four
tiny openings present within this depression.

x 650

Figure 73
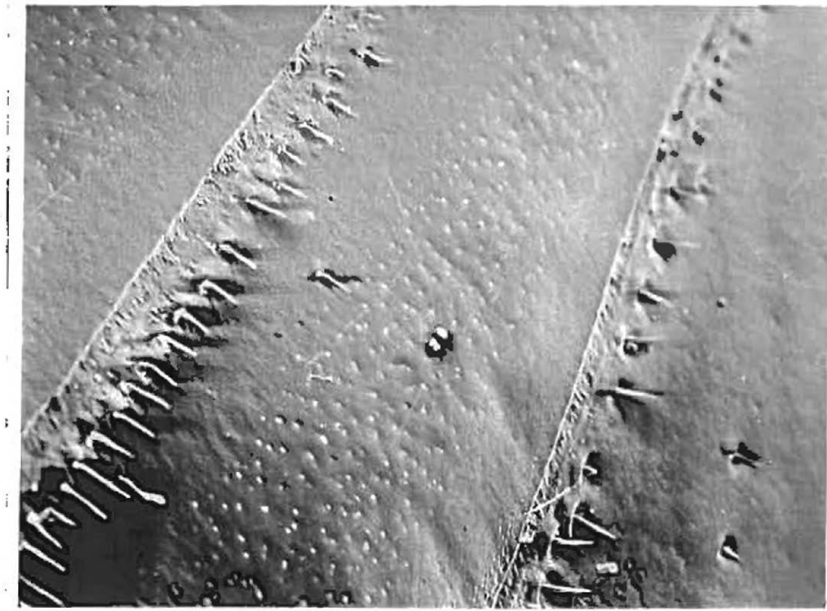
Figure 74
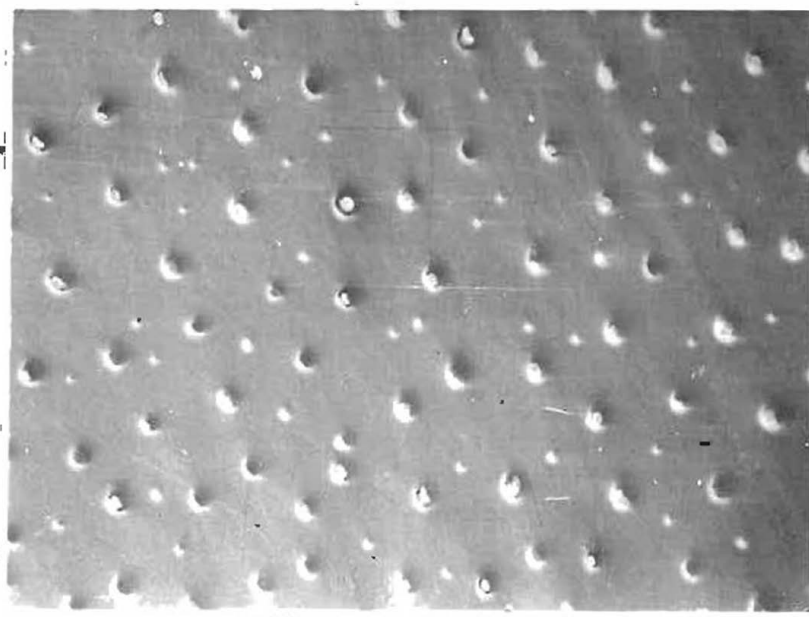
Figure 75
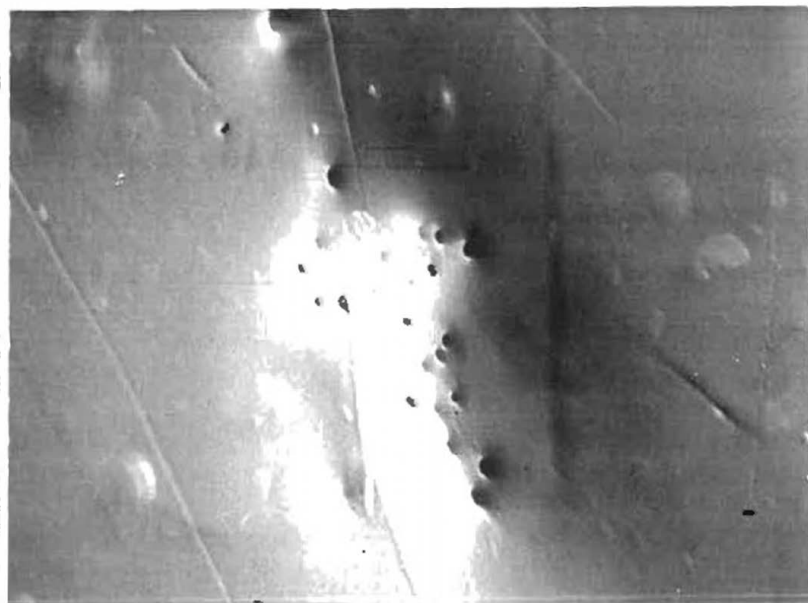
segmental spaces separating the five groups of glands from
one another.

Both sexes have numerous hairs along the dorsal length
of the tibiae of the hind legs.   In addition the male beetle
has a dense concentration of hairs, about midway along the
tibiae, which form definite brushes.   Such brushes are
absent in the female although a number of females - 73 out
of 114 -   have been found with an indistinct concentration
of hairs on the tibiae.

Along part of the anterior sections of the second,
third and fourth male abdominal sternites immediately
posterior to the depressions, are found single rows of semi-
rigid bristles which are anteriorly curved towards the
depression (fig. 71).   These rows of bristles become pro-
gressively smaller from the second to the fourth sternite and
also diminish in size from the sides of the sternites towards
the mid-line.   The strongly anteriorly curved bristles
nearer the extremities of the sternites become gradually more
straightened towards the centre.   These rows of bristles
are not continuous across the segments but are localised
posterior to the depressions.   Females have similar bristles,
but these are spaced widely apart and are straighter and
smaller than those of the males.

7.1.2 Release Stance :

A mature male K. nigroaeneus arriving at a fresh dung
pad will tend to occupy as high a position as possible on the
pad.   Several such males may be found on one pad, territorial
behaviour determining the position taken up by each individual
male.   Orientated with head upwind and the front two pairs
of legs on the dung surface, the male raises his hind legs
and lowers his head into the dung, resulting in his body
being at an angle of roughly 45° to the dung surface (fig. 76).

FIGURES 76 - 78

THE RELEASE STANCE ADOPTED BY THE KHEPER MALE SHOWING THE PHEROMONE CARRIER EMERGING FROM THE BEETLE DURING THIS DISPLAY.

Figure 76 :   Pheromone release stance adopted by the male Kheper subaeneus showing tibial brushes covered with pheromone carrier   x 2

Figure 77 :   Scanning electron micrograph of paraffin carrier impregnated with pheromone emerging from pores in the depression of a male Kheper nigroaeneus   x 500

Figure 78 :   Pheromone carrier emerging from the incapacitated side of a male Kheper lamarcki which has had a leg removed by surgery.   x 2

Figure 76

Figure 77
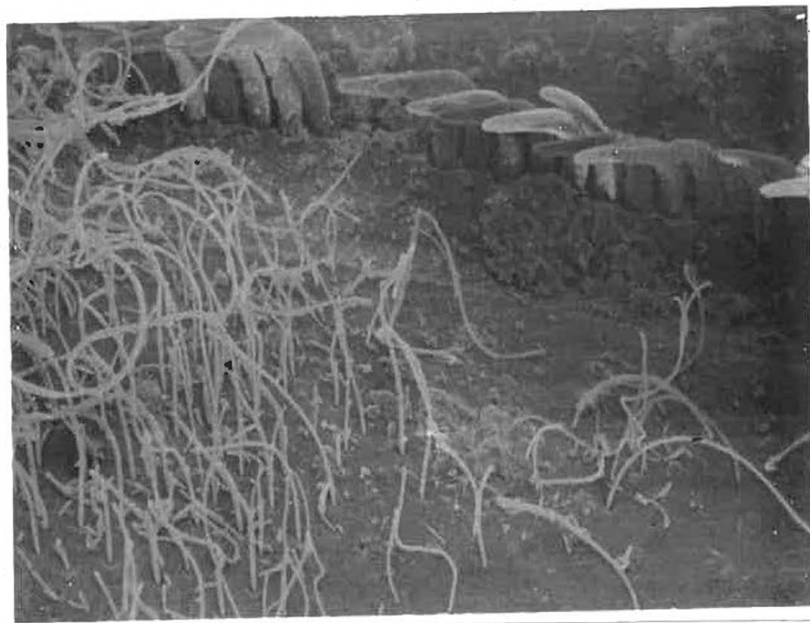
Figure 78
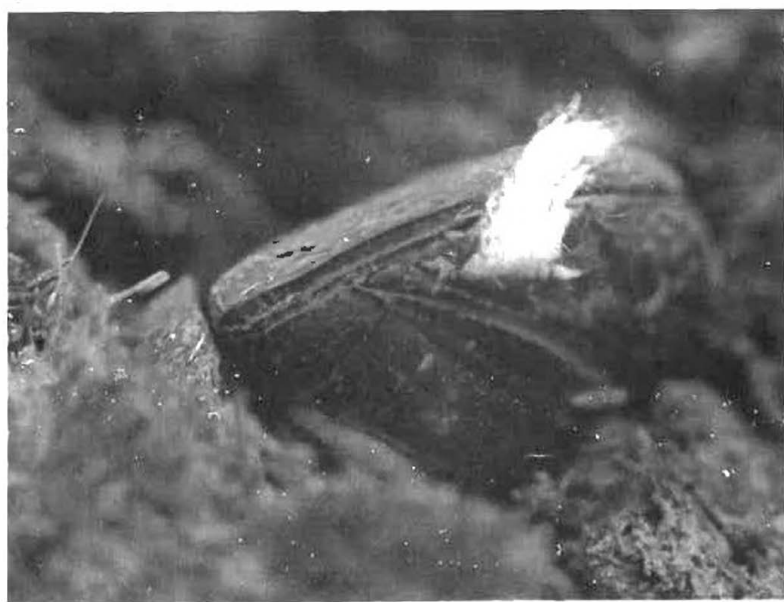
During pheromone release the hind legs are retracted
simultaneously inwards towards the sides of the body and are
then simultaneously extended. This movement results in the
tibial brushes brushing the attractant, which is emerging
from the depression, (fig. 77) against the rows of curved
abdominal bristles, causing puffs of attractant to rise into
the air from both sides of the insect. After a short time,
approximately 20 to 30 seconds, the legs are again withdrawn
inwards against the sides of the body and again rapidly
extended. The various telecoprid species have specific
rhythms of brushing behaviour, some having two or more
brushing strokes over the depression in quick succession
before the legs are properly extended. Garreta nitens which
assumes the release stance but has no pheromone brushes draws
the legs alternatively over the abdomen before extending them
in the air, while a criss-crossing of the extended tibiae
in Scarabaeus is specific to that genus. No comparable
release stance has been observed in any female beetles.

The attractant is released only if dung is present,
which may be in the form of (i) a dung pad, (ii) a dung
ball, or (iii) at the entrance to a burrow in which dung has
previously been buried by the male. In the field the most
common place for pheromone release is at a fresh dung pad
immediately after the male arrives. No male beetle has yet
been observed releasing pheromone at the entrance to a burrow
in the field. A female will only pair off with a male in
possession of some dung.

On landing on or close to the dung pad the female
climbs to the top where she encounters the male. When the
male perceives the female through her movement, he will
return to a horizontal position and challenge the female by
raising his head and forelegs from the dung surface and
advancing towards her. Her response is a submissive one in
which her forelegs are kept on the surface and her head is
lowered. If a second male arrives and is challenged by the

male /......

male releasing the attractant he will respond by raising his forelegs and head and combat will follow.

After the initial challenge, a brief touching of antennae between male and female occurs and the female becomes fully accepted by the male.   The pair then set about preparing a brood-ball, the greater part of the work, especially the cutting of the dung by using the forelegs and clypeus, is performed by the male, the female helping by compacting the dung into a ball using her foretibiae.

Under laboratory conditions, if a female does not arrive after the male has been releasing pheromone for approximately twenty minutes, the male will cut and mould a dung-ball.   The ball is then usually rolled to the foot of the pad and the male again begins releasing attractant while perched on the highest portion of the ball.   If no female arrives, the male rolls the dung-ball a short distance from the pad where he buries it.   The male then returns to the surface and releases attractant at the entrance to the burrow.

The arrival of a female at this stage results in a challenge from the male.   If accepted by the male, the female enters the burrow immediately followed by the male which attempts to copulate.   Under laboratory conditions, a female is attracted to a male releasing attractant at the burrow entrance.   Possibly the odour of the dung acts additively or synergistically with the pheromone.

In a laboratory cage 2 x 1m containing 50 males and 50 females of K. nigroaeneus, males were found releasing attractant more frequently at the burrow entrance.   The probable explanation of this behaviour is the fact that the female exhibits brood-care for up to 84 days while the male returns to the surface a few days after the brood-ball is buried (Chapter 8).   Since the laboratory population occurred in a 1 : 1 ratio instead of the field ratio of 1 male to 2 females, this resulted in a shortage of females on the

surface /....

surface and the resultant release of pheromone by males at
the burrow entrance.   Laboratory data recording the number
of males releasing pheromone in this cage from November 1973
to January 1974 revealed that on the average only 4% of the
male population was releasing pheromone on any one day.

The male beetle rolls the ball from the dung-pad and
the female clings to it by digging into it the spurs at the
apex of the tibiae.   The male interrupts the rolling every
now and again, and appears to test the ground with his fore-
legs and clypeus for a suitable spot, which is both moist and
soft, in which to bury the ball.   When such a spot is found
he begins to bury the ball by loosening the soil next to the
dung-ball.   He then pushes the dung-ball onto this spot
and returns to his digging beneath the ball.   The ball
slowly sinks into the soil as the male digs beneath it.   The
female takes up a position on the top of the ball and rapidly
pats the ball with her forelegs.   This is the only time that
the female seems to become as active as the male.   As the
ball sinks lower into the soil, she endeavours to clear the
sand from the top of the ball.   Copulation takes place below
the soil surface perhaps in response to the release of an
aphrodisiac pheromone by the female who now seems to take
control of the brood-ball.

K. nigroaeneus males produce a large amount of pheromone
when attracting a mate.   After the amputation of a hind leg
the pheromone emerges from the incapacitated side in a con-
tinuous ribbon up to 1,5cm long and 1 x 0,08mm in width in
a period of 45 minutes and may easily be collected (fig. 78).
By manipulating the legs of males caught releasing pheromone,
one is able to continue the process for a while.   The
movement of the hind legs may help in the extrusion of the
attractant.   However, it is impossible to induce a male to
release attractant by simply manipulating his legs as various
external cues are necessary, including fresh dung and
temperatures in the vicinity of 29°C.

The emerging substance is white in colour and actually

consists /....

consists of a paraffin carrier impregnated with the volatile
pheromone (R. Crewe, pers. comm.) and the paraffin tubules
appear to be hollow and formed in layers (fig. 79). The
puffs of carrier and pheromone which are dispersed rhythmically
into the air at short intervals by the brushing process are
presumed to assist in guiding the female to the male. Wright
(1962) maintains that an insect entering a pheromone cloud
is inhibited from turning as long as the interval between
the pulses tends to decrease, thus the attracting insect
could actively assist the guiding process by emitting the
scent in a series of short puffs. The only other insect
known to secrete paraffin hydrocarbon tubules is the late
instar larva of the butterfly Epipyrops anomala and this is
thought to be a form of excretion resulting from the ingestion
of large amounts of lipids (Marshall et al, 1974).

Since the diel activity peak in the field is between
approximately 0700h and 0800h for K. nigroaeneus this is the
period in which pheromone release would occur most readily.
The predation of male K. nigroaeneus would also probably be
proportionally greater than that of females, as the male is
the active partner and, being more often on the surface, is
more vulnerable to predation especially by a number of bird
species.

The angle of elevation of the body when releasing
pheromone may differ greatly from species to species. As
recorded previously, K. nigroaeneus takes up a position of
approximately 45° to the surface while for Pachylomera opaca
the angle is approximately 33° from the horizontal. S. galenus
takes up the release stance at an angle just off vertical at
the burrow entrance, while S. ambiguus straddles the burrow
at right angles to the soil surface.

7.1.3 Territorial Behaviour ;

Territorial behaviour may be defined as the active
defence of a certain area by an animal, the defended area
sometimes moving with the individual (Klopfer and Hailman,
1967).

All /....

Figure 79 : Scanning electron micrograph of a single
paraffin carrier tubule from a single pore
of a male Kheper nigroaeneus depression
showing its hollow structure   x   6500
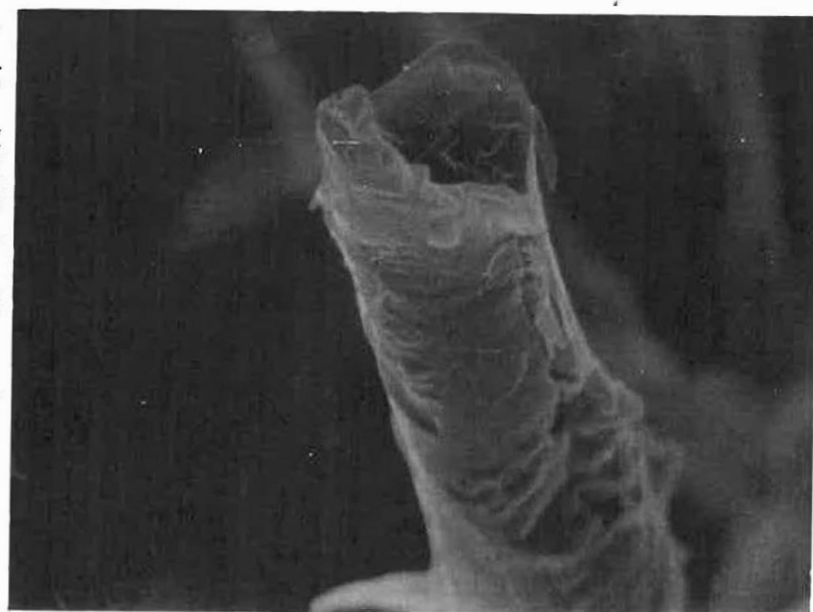
Figure 81 : The different positions assumed by a Kheper
subaeneus pair when rolling a brood-ball
- the male pushing the ball with the hindlegs
while the female clings tightly to the dung-ball.
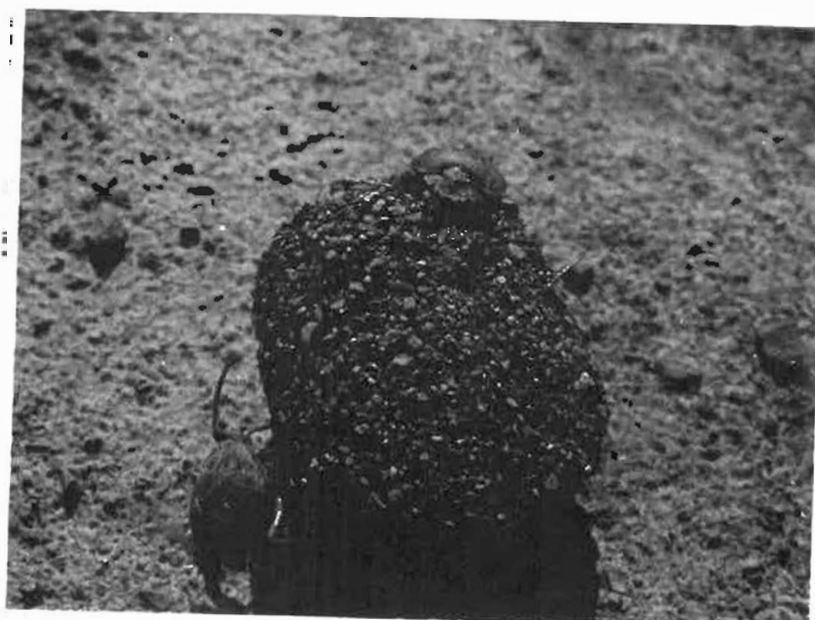
All telecoprid species investigated have been observed displaying territorial behaviour. The territory defended is always dung although a certain area around the dung may also be defended depending on the burrowing behaviour of the particular species. Since dung is a perishable commodity and must be fresh, the beetles are constantly claiming and defending new territories.

While undergoing maturation feeding, both sexes of K. nigroaeneus will fight off any beetle which attempts to "hijack" its food ball, irrespective of sex. Although it is not so noticeable during the breeding months, if a beetle returns to the surface to feed it will fight off any beetle even of the opposite sex.

During the breeding season a male K. nigroaeneus will assume as high a position on the dung-pad as possible and will attack any male beetle within a radius of approximately six centimetres around him. During this time he will release pheromone, returning to the horizontal position to challenge any beetle entering this area. If the intruder responds by lifting his forelegs and head in an identical challenging manner, he is recognised as a male and combat follows .

The beetle with the highest position on the dung-pad (or dung-ball) is almost certain to win the combat. The trespassing or attacking male is flipped off the dung by the defender with a hard thrust upwards and outwards with his foretibiae. As long as the defending male retains this elevation he may withstand numerous attempts to dislodge him from either a dung-pad or ball.

The combat centring around a dung-ball is fierce and here the sharp tibial spurs, especially those of the hindlegs, are of utmost importance to the defending beetle. As the territory is a moving one the beetle must become attached to it in some way. The immediate behaviour of a beetle which is attacked while rolling a ball is to dig these long sharp tibial spurs into the ball. Thus while defending a dung-ball

the /...

the male is able to hold firm on top of it and is difficult
to dislodge from this position. Besides defence, these spurs
are used when a brood-ball begins tumbling down an incline –
the beetle simply digging them into the ball and rolling with
the ball. Consequently a male rolling a dung-ball is usually
only dislodged if a second male climbs onto the ball from the
opposite side to that of the actively rolling beetle, and
having gained this elevation is able to dispossess the owner
of the ball.

If a second male arrives at the burrow entrance down
which dung has been buried and where a male is releasing
pheromone, a lengthy struggle results which has been observed
to last as long as 36 minutes and may result in injury to
the combatants. The immediate territory defended is the
burrow entrance and not a dung-ball where one beetle may
gain elevation at the expense of the second.

A raised finger or any other object moved within a
few centimetres of a male K. nigroaeneus is challenged and
attacked indicating that it is mainly the attitude and
movement which elicits this response.

A mature male K. nigroaeneus with a dung-ball will
fight off any other male but will accept a female.
Frequently in the laboratory a male K. nigroaeneus may be
observed rolling a ball onto which three females are clinging.
All three are individually challenged and accepted by the
male. When the ball is stationary, either at an obstacle
or at the burial site, the female which is the most active
begins remoulding the ball. She will touch the other females
with her antennae and on discovering them will challenge
them in a manner similar to that of the male. When the
other female responds by the submissive lowering of her head
and foretibiae she is thrown from the brood-ball by the
challenging female. Usually the females take a relatively
long time to discover one another because of their sub-
missive behaviour and the necessity for clinging to the
rolling ball (see Section 7.2). Initially a female seems to

detect /....

detect another female on the brood-ball by her passivity in contrast to a male which would be extremely active once the ball stopped.

A male beetle takes no part in combat between females. Whatever position a female finds herself in once the ball becomes stationary, she will move to the top of the brood-ball. In this way one female is bound to discover another. Even when a male succeeds in hijacking a brood-ball together with a clinging female, he does not expel her, but may challenge her.

The following observations were made of K. nigroaeneus beetles in the field. Brood-balls were interchanged between different pairs of beetles and were almost immediately accepted by the pairs. The male beetles would climb to the top of the ball (a behaviour performed when an obstacle is encountered), then take up the rolling position and roll the ball and female away. The interchanging of a enormous brood-ball with a small one (approximately half the size) resulted in no obvious change in behaviour, both balls being accepted by the different pairs. A similar interchanging of males only or females only does not result in any change in behaviour as the new partner is immediately accepted by the other.

7.1.4 Mating :

Kheper nigroaeneus beetles generally mate below the soil surface. No mating at the dung pad or elsewhere on the surface was ever observed in the field and was observed only infrequently in laboratory populations. This was especially noticeable in very overcrowded conditions when trasnferring beetles from one place to another in small containers. K. lamarcki and K. subaeneus were also never observed to mate on the surface in the field.

Species which have been observed to mate on the surface in both the field and especially the laboratory

include Scarabaeus rugosus, Scarabaeus bohemani and Pachylomera
femoralis. These species are found in the drier central
and western regions of southern Africa unlike the three
Kheper species, which occur in the hot humid areas of the
east. S. rugosus which is found in relatively large numbers
in the Hondeklipbaai, Velddrif area is active under the
cooler conditions which prevail there and mating on the
surface is frequently observed. Hence, it appears that
whether a species mates above or below the surface is related
to the desiccating properties of the atmosphere in the habitat
in which they occur.

Several telecoprid species have been observed to
"stroke" one another whilst copulating. The male draws his
foretibiae alternately up and down the length of the female's
elytra whilst the female of a species may draw alternate
hind-legs across the aedeagus of the male. Under laboratory
conditions the following species have been observed on
numerous occasions to stroke one another during copulation.

TABLE 13 : Comparative stroking behaviour of several
species during mating.

Species	Male strokes Female Elytra	Female Strokes Male Aedeagus
K. nigroaeneus	+	
K. subaeneus	+	
K. lamarcki	+	
S. rugosus	+	
S. ambiguus	+	
S. bohemani	+	
S. satyrus	+	
S. galenus	+	
Sc. flavicornis	+	
Sc. damarensis	+	
G. nitens	+	+
G. unicolor	+	+

Only the two Garreta species have females stroking the aedeagus on the basis of present observations.   The female beetle strokes the aedeagus with the hindmost pair of legs alternately extending one whilst drawing the other back across the aedeagus.

Sperm release mechanisms of most Kheper, Scarabaeus and Garreta species are similar to that of P. femoralis which is described in more detail.   The P. femoralis aedeagus has two pairs of hooks, one pair at the distal part of the aedeagus and the other proximally (fig. 80).   By pressing against the lower pair of hooks on a recently killed P. femoralis male the two chitonized flanges, joined by a membranous area, pull towards one another and effectively close the aedeagus opening.   On releasing the pressure on the lower hooks and applying it to the upper hooks the flanges open and the membranous area is stretched.

Observations on how this mechanism works during mating have shown that on the initiation of copulation the distal pair of hooks are the first to catch on the indented apex of the female operculum.   Once the male is secure on the back of the female, the aedeagus is moved further into the cloaca until the proximal pair of hooks catch on the indented apex of the operculum.   With pressure applied on these hooks the flanges open and the sperm is released in the form of a ball, due probably to the further constriction of the aedeagus at the area of the hooks.   The aedeagus is then withdrawn.

7.2 CO-OPERATIVE BALL ROLLING :

Co-operative ball-rolling between two beetles of opposite sex occurs only if both partners are sexually mature, the dung-ball becoming the future brood-ball.   There are three basic positions adopted by telecoprids in southern Africa when co-operatively rolling brood-balls.

(i) Male rolls the dung-ball on which the female clings:

The male is the active partner that attracts the female, detaches and moulds the dung-ball, rolls it from the dung

Pachylomera femoralis

Fig. 80

AEDEAGUS (x11)

proximal hooks

distal hooks
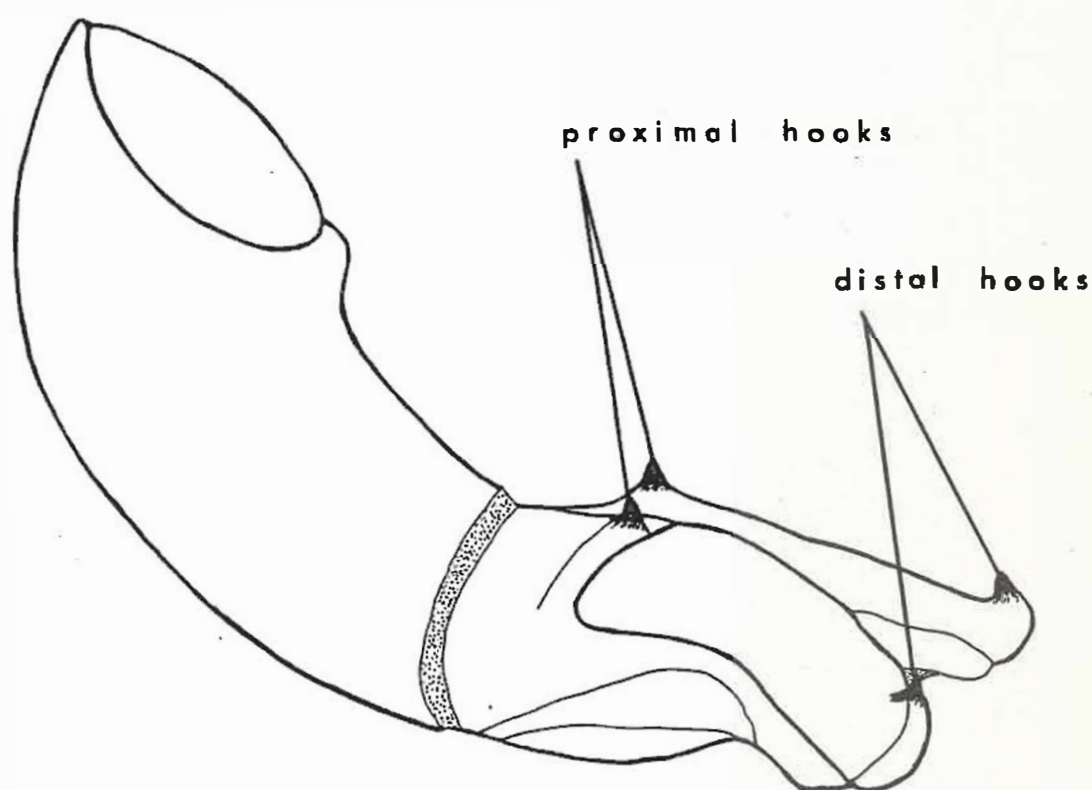
source and buries it. The female may co-operate in moulding
the dung-ball but the moment the male begins rolling it she
takes up a position on the ball and flattens herself, making
an indentation in the dung-ball with her body. The female
digs the tibial spurs into the dung and remains in this
position while the ball is being rolled. The brood-balls
of this group are usually extremely large (fig. 81, page 104).
This ball-rolling behaviour has been observed in all southern
African Kheper species, Circellium bacchus and a number of
Scarabaeus species.

A related behaviour to the above is found in the
Canthon genus of America where Halffter and Matthews (1966)
record that the male beetle is in the rolling position while
the female balances on the top of the ball, as on a treadmill,
as it is being rolled.

(ii) Male rolls the dung-ball, while the female follows :

The male is the active partner in attracting the
female at the dung-pad and in detaching and moulding the
brood-ball, although he may be assisted by the female. This
behaviour has been observed in only a single species of
telecoprid in southern Africa - Scarabaeus bohemani. Once
the dung-ball has been detached from the pad, the female is
thrown from the ball by the male and she follows the male as
he rolls the ball, keeping a distance of approximately 4cm
behind him at all times. If the male slows or stops to
negotiate an obstacle, the female still remains 4cm from him.
This manner of rolling is extremely fast and the dung-ball is
relatively very small, almost the same size as the beetle.
It may be that the normal tendency of the female to follow
the rolling male, instead of pulling or climbing on the ball
may have something to do with this small size of the ball
(Halffter and Matthews, 1966).

In contrast to Europe, the largest herbivores occur in
Africa and it is not surprising that the larger Kheper and
Scarabaeus species have adopted a more elaborate method of
co-operative ball rolling in response to the copious amounts
of /....

of dung.   Besides being considerably smaller than the average
Scarabaeus (Table 3), S. bohemani is also dorsoventrally
flattened and extremely light in weight.

This behaviour is common in Palearctic Scarabaeus
species which have been shown by various authors to have
a preference for human excrement (Halffter and Matthews,
1966).   S. bohemani shows a similar preference for human
excrement and was first recorded from Mamelodi Township,
Pretoria.   Fifty-six beetles were captured on two human
droppings while five cow-pads nearby were deserted.   Under
laboratory conditions S. bohemani will feed on cow and
horse dung but the dung-balls are always much smaller than
those made with human excrement.

The female follows the male both visually and by means
of the odour trail left by the strong smelling human excrement.
A female has been observed to follow an odour trail for a
distance of 24cm before flying back to the dung source.
S. bohemani is the only Scarabaeus species which shows a
definite high degree of preference for human excrement in
southern Africa and is the only species with this type of
behaviour.

(iii) "Pushing" and "pulling" behaviour :

Halffter and Matthews (1966) describe the behaviour
for (mainly Paelarctic) species of Gymnopleurus co-operating
in pairs as "pushing" in the head-down rolling position and
"pulling" in the head-up position.   This behaviour has been
observed for many southern African species of Gymnopleurus,
Allogymnopleurus and Garreta genera.   Whereas only the
female is the active partner in the Gymnopleurus species
investigated by Halffter and Matthews (1966), either sex may
be the dominant partner in southern African species depending
on the species.

(a) Male pushes, female pulls :

This behaviour present in Allogymnopleurus
thalassinus where both sexes mould the ball but the male rolls

the ball with his hindlegs while the female stations
herself ahead of the ball which she pulls along with her
forelegs.

(b) <u>Female pushes, male pulls</u> :

Recorded in <u>Garreta nitens</u> and <u>Garreta unicolor</u>
where the female rolls the dung-ball although the male is
still aggressive especially in the defence of the ball.

CHAPTER 8.

BROODING BEHAVIOUR.

8.1 NAKED OR SOIL COATED BROOD-BALLS :

After the burial of the brood-ball further moulding takes place until the dung-ball is almost spherical in shape. This is done by either removing all adhering foreign particles (which accumulate on the fresh dung as it is rolled) or by pressing these particles, usually sand, into the outer layer of dung to form a soil shell. Parental care was previously reported to occur only in the genera Copris and Synapsis. In coprine beetles which do not brood the larvae, the brood-balls are as a rule coated with a clay shell (Halffter and Matthews, 1966).

Among the telecoprid species of southern Africa which were studied (Chapter 1) it was found that brood-care was associated with naked brood-balls and soil coated brood-balls with non-brooding behaviour. Moreover, naked or soil coated brood-balls (and hence brooding and non-brooding) seem to be distinctive of the various genera.

The genus Kheper and sub-genus Scarabaeus can now be reported also to practise brood-care and all species of these genera thus far studied in southern Africa show this behaviour. The behaviour of the sub-genus Scarabaeolus in this respect is still unknown. The genera Garreta, Gymnopleurus and Allogymnopleurus coat their brood-balls with a mixture of sand and dung and both sexes desert the buried ball once this soil shell is completed. Although this outer coating is only up to 2mm in thickness, it dries to form a hard outer shell which keeps the inner dung mass fairly moist. As the whole brood-ball slowly dries the inner dung mass pulls away from the rigid soil shell.

Halffter /....

Halffter and Matthews (1966) consider the function of the soil shell to be the protection of the larva under dry or other adverse conditions.

8.2 THE BROOD-BALL :

The pair of beetles which have detached a portion of dung from the dung pad, mould it into a rough ball and immediately roll it away. Usually the easiest path with the least number of obstacles is followed and finally the ball is buried in the soil once a suitable site has been found.

There seems to be no uniform depth at which a species buries its brood-balls as this is largely determined by the soil type and the soil moisture content from place to place, soil moisture varying according to the rainfall (Climate of South Africa, W.B.28). K. nigroaeneus may bury its brood-ball under half an inch of soil if the soil is compacted through dryness or a little over 32cm if the soil is moist and fairly sandy. The usual depth of brood-ball burial in the laboratory for Garreta nitens and Allogymnopleurus thalassinus is between 10cm and 20cm, while that of K. lamarcki and K. subaeneus in the field under moist sandy conditions is about 32cm. From the above species and various other species observed on occasions (both paracoprid and telecoprid), the general trend seems to indicate that the depth at which a species buries its brood-ball under suitable conditions increased with an increase in the size of the species. However, there are exceptions viz. Pachylomera femoralis, the behaviour of which is discussed in Chapter 10.

The following points concerning soil temperatures in South Africa appear in the Climate of South Africa (W.B.28);

(i) Diurnal variation ceases to occur at about 60cm below the soil surface.

(ii) The diurnal variation is much greater under bare soil than under grass cover, this being affected

by /....

by the denseness of the vegetation.

(iii) Soil temperature is on average about 4°C lower under
a thick grass cover than under bare soil, the
difference being greater in summer and smaller
in winter.

(iv) Below a depth of about 15cm the soil is warmer in
the evening than during the day as a result of a
lag in the penetration of heat through the soil.

At a depth of 1cm there are considerable fluctuations
in soil temperature – the absolute maximum of $58,7^{o}$C and
the absolute minimum of $0,9^{o}$C recorded between 1958 and
1961 at Roodeplaat, near Pretoria (W.B.28). At 5 and 10cm
the earth temperature may be considered to read a maximum
at 1400 hours S.A.S.T. and a minimum at about 0600 hours in
summer and 0800 hours in winter.

At a depth of 15 to 20cm the maximum soil temperature
occurs at about 1700 or 1800 hours. With increasing depth
the daily fluctuations decrease progressively and become
negligible between 60cm and 120cm, although they are still
affected by annual variations. The large fluctuations in
soil temperature at 1cm are a result of alternate clear and
cloudy periods with rain.

The lowest soil temperatures are confined to the
eastern high plateau and these temperatures increase west-
wards and northwards with the highest mean soil temperatures
(at all depths) in the northern Transvaal Lowveld. With
increasing depth the amplitude decreases and the maximum and
minimum are progressively delayed. The amplitude of the
annual variation in natural undisturbed soil is of the order
of 1°C at a depth of 9,15 to 10,52 metres. As one proceeds
eastwards and northwards across South Africa, the annual
soil temperature variation decreases probably due to moisture
content (and soil type) which is presumably higher in the
east due to the greater rainfall (W.B.28).

An example of the mean soil temperatures under grass

cover recorded at Skukuza in 1970 may be used as an indicator
of the soil temperatures experienced by K. nigroaeneus,
G. nitens and A. thalassinus which occur in this area (Report
on Meteorological Data of the Year 1970, 1972).

TABLE 14 :   Soil temperatures recorded at Skukuza (1970).

	Beetles Active			Beetles in Aestivation						Beetles Active		
	Jan.	Feb.	Mar.	Apr.	May	June	Jul.	Aug.	Sept	Oct.	Nov.	Dec.
20 cm												
800h	32,8	30,6	29,7	27,7	22,9	19,7	18,0	22,1	25,5	25,6	28,5	28,4
1400h	34,5	32,6	31,4	28,7	23,8	20,4	19,3	23,6	27,0	28,2	31,6	30,7
2000h	36,9	34,1	33,2	31,4	25,7	22,3	21,7	25,3	27,7	30,2	32,9	31,7
30 cm												
800h	32,8	30,9	30,0	27,9	23,2	19,9	18,5	22,3	25,7	26,1	28,7	26,2
1400h	33,6	31,9	30,8	28,6	24,0	20,5	19,3	23,5	26,7	27,5	30,7	27,3
2000h	35,3	32,6	31,7	30,4	25,0	21,7	20,7	24,3	26,9	29,7	32,4	31,6
60 cm												
800h	32,0	31,4	30,9	29,3	25,6	22,9	21,1	23,4	26,1	27,1	29,4	29,9
1400h	32,0	31,4	30,9	29,3	25,5	22,8	21,1	23,4	26,0	27,0	29,2	29,8
2000h	32,1	31,5	30,8	29,2	25,5	22,7	21,0	23,4	26,0	27,0	29,2	29,8

From the above table it may be seen that the month in
which the highest soil temperature occurred at all three depths
was January and the lowest occurred in July.   Further, at 60cm
the average monthly soil temperature for January was the
lowest of the three depths, yet at 60cm in July the soil
temperature was slightly higher than the average recorded for
20cm and 30cm.

These temperatures show that species which bury brood-
balls at shallow depths will experience greater daily
fluctuations in temperature than those at the deeper levels.
Generally speaking, the beetle species that bury their brood-
balls at the greater depths are the larger ones, they practise

brood-care /......

brood-care and the brood-balls are naked. On the other hand, those species that bury their brood-balls shallowly are smaller, have soil shells around their brood-balls and do not practise brood-care. Hence it appears that one of the functions of the soil shell around the brood-ball of the latter species is to combat the greater fluctuation in temperature which occurs at shallower depths.

An exception is the very large paracoprid species, Heliocopris andersoni which buries clay-coated brood-balls at relatively shallow depths ($\pm$ 35cm) for so large a beetle. The clay covering is possibly necessary in this species which overwinters as a larva or pupa and therefore endures much lower temperatures at this critical stage than brooding telecoprids which aestivate only as adults, all F_1's having emerged before the onset of winter. The low temperatures during the winter would largely inactivate any beetle attempting to exercise brood care, and present information indicates that brooding occurs only in species which complete their breeding during the summer months.

Hence clay covered brood-balls are restricted to species with shallowly buried brood-balls, and species which over-winter as larvae or pupae.

Since the soil is cooler during the day and hotter during the evening this would provide an ideal habitat for soil-dwelling beetle species. They are able to escape excess heat by burrowing into the relatively cool soil during the day and the soil temperatures are warmer during the coldest part of the night.

The gradually increasing soil temperatures from July (some 2° - 3°C average per month) could be detected by beetles buried in the soil and only rainfall would then be necessary to bring the beetles to the surface.

Telecoprids of the genera Kheper and Scarabaeus are mainly excluded from the highveld plateau (Chapter 2) due to the low winter temperatures, the soil temperature perhaps

affecting /....

affecting to a larger extent those species which may be termed soil-dwelling.

Since the Kheper genus in southern Africa overwinters as adults a constant warm soil temperature would ensure that all beetles were fully developed and ready to emerge soon after the first substantial rainfall.

The Kheper brood-ball is enclosed by a chamber hollowed out in the soil which creates a suitable microclimate where possibly the drying dung keeps the chamber moist through condensation. The thick clay coating of Heliocopris andersoni brood-balls removed from similar chambers to that of Kheper, cracks into pieces when placed even in a cool room out of the sun. By continually moistening the clay this cracking may be prevented. The entrance to the Kheper chamber is always automatically blocked off as these beetles dig a perpendicular hole under the dung-ball which gradually sinks from sight, the soil falling on top of the brood-ball thus blocking off the chamber.

The brood-balls of southern African telecoprids of the genera Kheper and Scarabaeus are characterised by a conical projection similar to that of Phanaeus vindex recorded by Matthews in Mexico (in Halffter and Matthews, 1966). The projection is formed by the female beetle as a result of preparing a depression in the topmost portion of the brood-ball and the drawing up of the sides surrounding this depression to which a large amount of soil is added, virtually isolating the egg from the dung mass. Once the egg is laid in this cavity the sides are brought together to form the projection enclosing the egg.

G. nitens and A. thalassinus have no marked projection but the brood-ball is slightly oval in shape. The egg is laid in a cavity which is formed within the dung mass, the sides of the cavity being brought together to seal the chamber. The resultant slight bump seems to function largely as an air vent in these species (fig. 82).

Figure 82 : Diagrammatic section through K. nigroaeneus and G. nitens brood-balls.
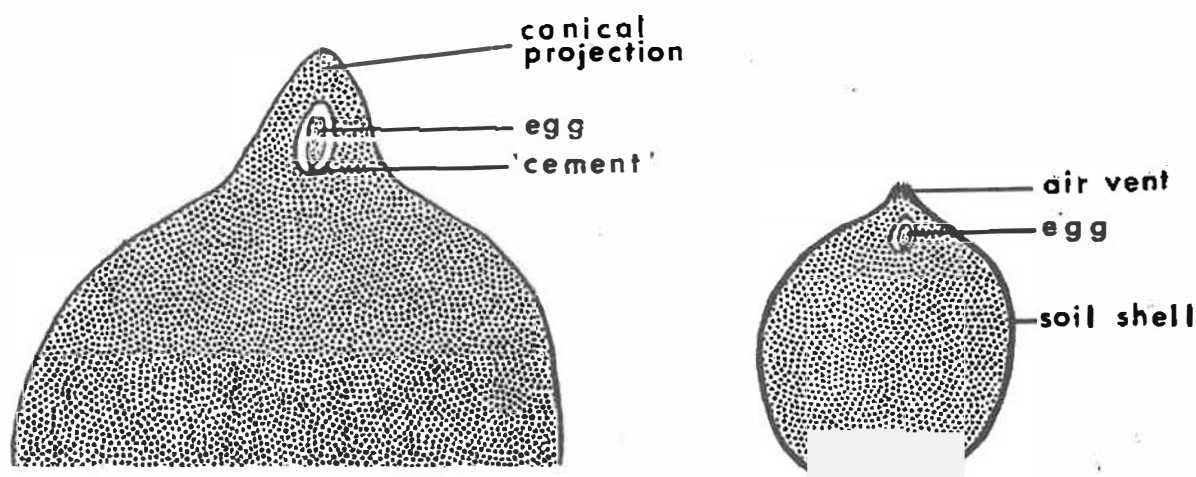
K. nigroaeneus   G. nitens

On removing the projection of K. nigroaeneus, one removes the egg as well, but not so in G. nitens. Most paracoprid species form "sausages" of dung with several eggs and no projection is found in these species or in the five southern African endocoprid species.

A single egg is laid in each brood-ball, the yellowish, elongate egg usually remaining perpendicular to the floor of the egg chamber to which it is cemented by the female. Thus the egg touches the egg chamber at only one spot, and then with the smallest surface area of the egg.

8.3 BROOD-CARE :

Once the brood-ball is buried, mating takes place below the soil surface, the male re-emerging on the surface on the average after four days (in the laboratory). Only then does

the /.....

the female begin to construct the egg chamber which she coats
with a dark liquid which may be either oral or anal in origin
as the female has never been observed in the actual process
of coating the chamber.   Halffter and Matthews (1966)
consider this liquid in Copris species to perhaps have anti-
biotic properties.   If this should prove to be so, this may
have replaced coating the egg-chamber with clay (thus
separating the egg from the dung mass) in a number of fairly
primitive species recorded by Halffter and Matthews (1966).

Only the female remains below with the brood-ball
(Table 15).   She continues feeding while brooding by feeding
in a circular manner around the brood-ball, at a much reduced
rate.   Frass is sometimes found in the brood chamber which
may have resulted from the female feeding on dung which was
detached from the ball during the remoulding process before
the egg was laid.   On numerous occasions the female
K. nigroaeneus was removed from her brood chamber in the
laboratory pans with particles of dung in her mouthparts.
In other cases, yellowish "squeezed" portions of dung on the
otherwise dark-brown brood-ball is an indication that feeding
has taken place.

The female coats the brood-ball on the outside with
her own faecal material as she moves slowly around it while
feeding.   After a number of weeks the female thus seems to
eat her own faeces along with dung particles during the
lengthy period she remains brooding.   At room temperatures
the period taken from egg to adult without a female in
attendance was from 68 - 84 days (n = 23).

The Kheper and Scarabaeus larvae store their faecal
material in the hump formed by the dilation of a number of
abdominal segments and except for mending any tear in the
shell of the brood-ball, this faecal material is only released
prior to the prepupal stage.   The entire stored waste
products are voided and used by the larva to coat the inside
of the chamber.   This dries to form a hard, black pupal cell.

At /....

At about this stage the brooding female has fed on the
surface of the brood-ball to the extent that the outside of
the brood-ball is also coated with a layer of similar black
faecal material. As this layer dries and hardens, the
pupa becomes doubly protected by the inner and outer faecal
shells.

Halffter and Matthews (1966) consider that brooding
behaviour may be functional in the removing of moulds as
only when the brooding parent was removed did mould growth
form. The microclimate in the brood chamber of
K. nigroaeneus is ideal for mould growth yet on every
brood-ball uncovered in the laboratory, no sign of mould
was found. If the female faecal material contains anti-
biotics, the coating of the brood-ball by the female would
account for the absence of such moulds. On removing the
female from the brood-ball a light mould would form on
K. nigroaeneus brood-balls in the laboratory, after a few
weeks. Fresh dung placed touching twenty K. nigroaeneus
brood-balls in a plastic container became covered with
fruiting bodies of various moulds within three days, yet
only a few such bodies became established on a few of
the brood-balls, and then only after a period of three
weeks.

From Table 15 it may be seen that the female remains
brooding right up to the time of the emergence of the
F_1 adult. As breeding begins tapering off in February
and stops altogether in April, a female could conceivably
overwinter with the F_1 still in the brood-ball and emerge
simultaneously with it the following Spring. From the
results in Table 17 it would appear that this occurs only
rarely, if at all.

TABLE 15 : /....

TABLE 15 : Brood care by the K. nigroaeneus female only, occurring throughout the development stages from egg to adult.

Date Pans examined	Total No. Brood-Balls	Females in Atten-dance	Males in Atten-dance	Stage			
				Egg	Larva	Pupa	Adult
23.12.74	15	15	0	3	11	1	
7. 1.75	12	12	0	10	2		
9. 1.75	31	31	0	19	12		
22. 1.75	19*	18	0	12	7		
20. 2.75	18	18	0	3	15		
20. 3.75	41[+]	39[++]	0	6	29	5	1

* one rotten egg

+ one dead larva

[++] One female dead and the brood-ball very delapidated by the action mainly of enchytraeids, but larva still alive.

The conical projection of the K. nigroaeneus brood-ball is found to be absent soon after the early larval stage has been reached. Only the egg stage still possesses the projection (Table 16). The larva on hatching immediately begins feeding downwards into the dung mass and is able to close off any opening into the chamber by cementing it over with faecal material. This also occurs in a large number of species recorded in Halffter and Matthews (1966).

TABLE 16 : /....

TABLE 16 : The presence or absence of conical projections of K. nigroaeneus brood-balls according to the developmental stages.

Date Pans Examined	Total No. Brood-balls	Protuberance Present		Protuberance Absent	
		No.	Stages	No.	Stages
23.12.74	15	4	Egg (3) Early larval(1)	11	Late larval (10) Pupa (1)
7. 1.75	12	12	Egg (10) Early larval(2)	0	
9. 1.75	31	19	Egg (19)	12	Late larval(12)
22. 1.75	19	12	Egg (12)	7	Larval (7)
20. 2.75	18	3	Egg (3)	15	Larval (15)
20. 3.75	41	9	Egg (6) Early larval(3)	32	Larval (26) Prepupal (5) Adult (1)
TOTAL	136	59	Egg (53) Early larval(6)	77	Larval (70) Pupal (6) Adult (1)

All fifty-five brood-balls removed from K. nigroaeneus females during the egg stage retained the projection until F_1 emergence occurred and thus the female removes the projection and not the larva. A brood-ball with the projection removed resembles a food-ball except it is black in colour from the female faeces which are pressed into the dung-ball by the female.

The behaviour of removing the projection may have arisen for the following reasons :

(i) After a certain interval (indications are that this is approximately fifteen days) the egg hatches and the larva moves into the dung mass by excavating a chamber as it feeds. Thus any egg which does not hatch could be immediately

detected /....

detected when the female removes the projection. This would
enable the female to return to the surface to find another
mate instead of brooding for 84 days on a sterile egg.
Evidence is provided by the fact that two brood-balls out of
a total of 136 were found with a decaying egg and a dead
late larva. Both these brood-balls were deserted by the
female. It is not known whether desertion by the female is
the cause or effect of larval death in this case. Isolated
brood-balls in situ which have been deserted by females
should stand a good chance of survival if they are faecal
coated brood-balls of the late instar larvae. The brooding
female probably responds to stimuli from a live larva which
moves around continually while scraping the dung from the
chamber's walls and a lack of such movement from a dead larva
may result in desertion. Alternatively, chemical stimuli
may be involved, either pheromones from live larvae or amines
and amides from dead ones. Table 17 has been separated from
the previous table as the greater mortality is a result of
winter conditions.

TABLE 17 : Larval K. nigroaeneus mortality.

Date Pans examined:	Total No. Brood-balls:	Females in Atten-dance:	No. Brood-balls with live Occu-pants:	No. Brood-balls with dead occu-pants :	
				No.	Stage
20. 3.75	41	39	39	1	Larval (1)
20. 5.75	19	3	3	16	Larval (16)
21. 5.75	6	2	2	4	Egg (1) Larval (3)

Here too, it is not known whether the larvae died as a
result of desertion by the brooding females. Under the

unnaturally /.....

unnaturally cold soil conditions experienced in the laboratory, the soil being only 15cm deep in the container and therefore subject to greater extremes of temperature, it is more likely that the larvae succumbed before the brood-balls were deserted. The high proportion of deaths in May compared to previous months supports this assumption.

(ii) In most instances the F_1 adult emerges from its pupal cell at a spot which would have been just below the conical projection, had it not been removed. On opening many faecal shells and measuring the thickness of the walls it was found that the thinnest part of the shell (average 0,26cm compared with 1,0cm) and therefore the site of emergence, was below the area of the removed projection. Various K. nigroaeneus brood-balls were placed horizontally, vertically and at a number of different angles and still the adult emerged from this thin part of the brood-ball. Emergence occurred at the base of the projection of those fifty-five brood-balls removed in the egg stage and placed in plastic containers.

(iii) By removing the projection the female may more easily rotate the ball during feeding. The fact that the ball is rotated during the circular feeding is seen from the numerous positions in which the projection site may be found when a brood-chamber is excavated.

8.4 FECUNDITY :

The Scarabaeinae are characterised by the extreme reduction of the reproductive organs to a single ovariole on the left side (Halffter and Matthews, 1966). Willimzik (1930) points out that the degree of ovarian reduction is directly related to the degree of brood-care, Copris having the greatest reduction associated with the lowest fecundity among continental species.

A similar reduction in the Kheper genus of southern Africa also occurs. The removal of Copris elephenor brood ovoids at regular intervals (weekly) results in this species

continuing to produce further eggs. Yet the removal of the
brood-ball from either K. lamarcki, K. subaeneus or
K. nigroaeneus does not result in a second brood-ball being
produced until a number of weeks have passed, and depending
on the time of the season no further brood-balls may be made.
This results in an even slower breeding rate in Kheper
species (Table 18).

TABLE 18 :   The relatively small number of brood-balls
produced by the large laboratory population
of K. nigroaeneus.

Date Pans examined:	Number Beetles			Number Brood-balls Produced:
	Male	Female	Total	
23.12.74	71	84	155	15
7. 1.75	65	83	148	12
9. 1.75	46	93	139	31
22. 1.75	61	89	150	18
20. 2.75	58	89	147	18
20. 3.75	30	85	115	41
20. 5.75	49	68	117	19
21. 5.75	50	78	128	6
22. 5.75	25	75	100	0

The reduction of the ovary to a single ovariole may
be seen from the diagram (fig. 83) of K. nigroaeneus. This
female had previously laid an egg as indicated by the presence
of the corpus luteum. From the number of females dissected
at various times of the 1974/75 season, the maturation of
immature oocytes takes a fairly long time, there being
usually no subsequent oocytes being visibly differentiated
as in the case of many other species e.g. Onthophagus gazella
(fig. 84). On emerging from aestivation, the female's gut
is completely empty, and collapsed. There follows a feeding

period /....

period of between two and three weeks before breeding begins.
On removing a brood-ball from a brooding female she must once
again undergo maturation feeding before a second egg can be
laid - usually from three to five weeks. Similarly newly
emerged F_1's have no stored food reserves and usually spend
the remainder of that season feeding, beginning to breed for
the first time only in the following summer (Section 6.1).

By comparison, the subgenus Scarabaeus has been found
to have a less drastic ovarian reduction than that of Kheper.
S. ambiguus is able to produce brood-balls at a greater rate
than Kheper as the time from egg to adult is much reduced,
being roughly between 35 and 45 days, with the maturing
oocytes being slightly more visible as bulges in the ovariole.
Yet their single ovariole together with the brood-care shown
by the subgenus Scarabaeus results in their also being slow
breeding beetles. The Scarabaeus species occur largely in
the marginal areas of Kheper distribution (Chapter 2) and
thus face greater extremes in climate. This may have resulted
in a slightly higher fecundity potential in this subgenus.

G. nitens and A. thalassinus have several oocytes
differentiating simultaneously, one behind the other in
different stages of maturity. Yet this is still much
reduced when compared to the ovariole of certain southern
African Onitis species. This enables removal of a brood-
ball from these two species every four days, with, on the
average, only half the number of pairs producing brood-balls
i.e. one brood-ball per pair every eight days. As it takes
from six to eight days for the egg to hatch, changing the
breeding tubs every four days results in all brood-balls
containing only the egg stage.

From this it would seem that the greater fecundity of
G. nitens and A. thalassinus among the telecoprids, together
with the fact that they produce soil coated brood-balls,
indicates a greater larval mortality in these two species
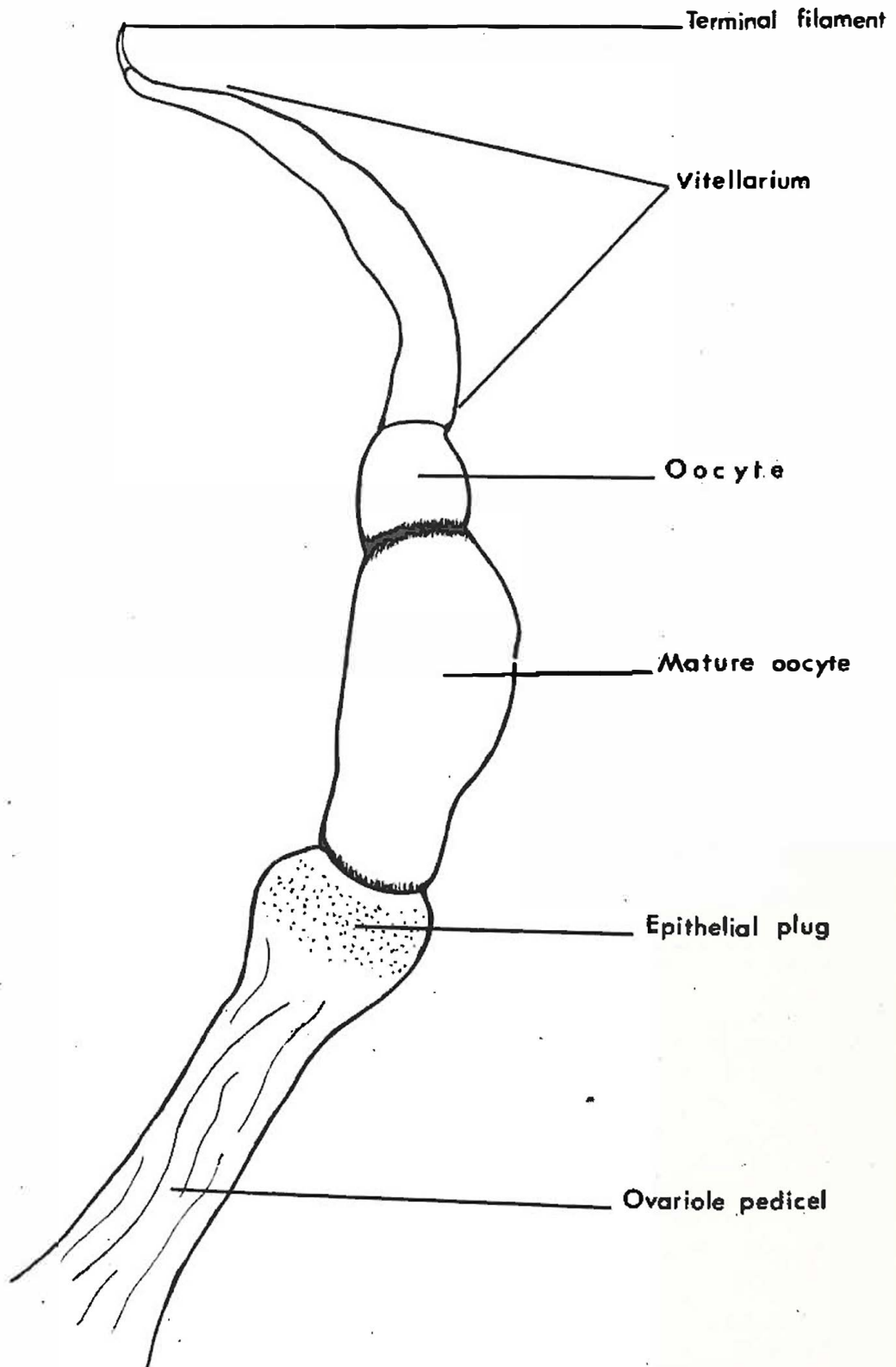than in K. nigroaeneus which has a high natural survival
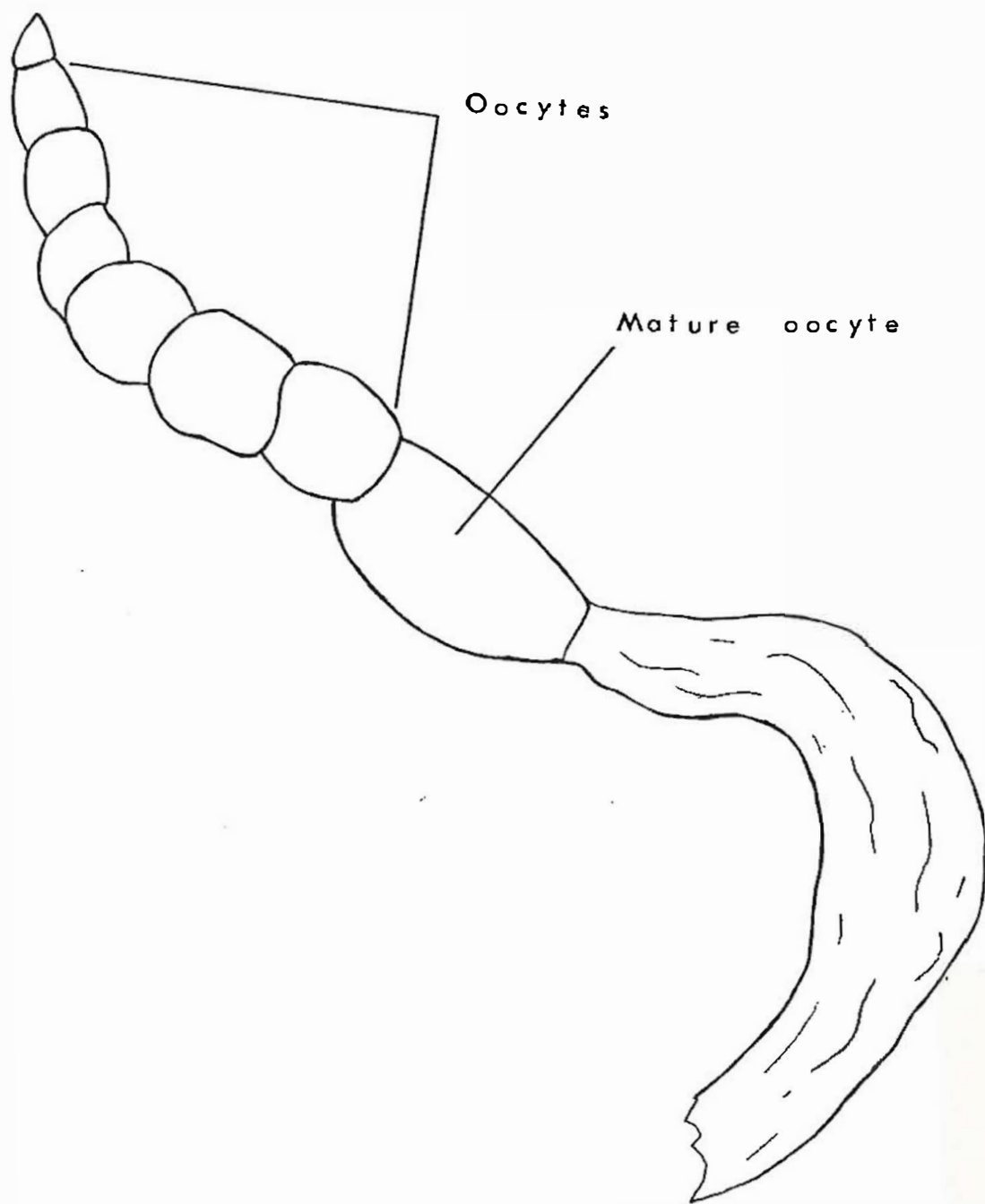
rate /....

OVARIOLE   (x 11)

Fig. 83

Kheper nigroaeneus

(10 - 3 - 75)

Terminal filament

Vitellarium

Oocyte

Mature oocyte

Epithelial plug

Ovariole pedicel

Onthophagus gazella   Fig. 84

OVARIOLE ×13·2

Oocytes

Mature oocyte

rate (Table 15).

Field observations indicate that telecoprid species
are eaten by a wide range of birds and animals.   Both gut
contents and faecal material have been found to contain
their remains.   In most cases this predation seems to be
fairly low.   However, predation of K. subaeneus in Umfolozi
Game Reserve by groups of pied crows accounts for a relatively
large portion of the population, judging from the beetle
remains scattered over rhinoceros middens.   The beetles
appear to be taken from the surface only and the abdomens
and foretibiae are eaten while the head and thorax, with
only stumps of the forefemurs remaining, are discarded.

CHAPTER 9.

THE CREPUSCULAR HABIT.

9.1 CHARACTERISTICS OF THE CREPUSCULAR HABIT :

Initial surveys conducted in Natal, Rhodesia and
Botswana resulted in only diurnal telecoprids being captured
and the large majority of telecoprids, if not all, were
regarded as day flying.   Subsequent more intensive surveys
resulted in the discovery of several night flying telecoprid
species, from which it was possible to predict the flying
times of those species in museum collections that had not yet
been taken by members of the Research Unit.   The characters
used were shown to be accurate in determining whether a
species was crepuscular or diurnal as more unrecorded species
were captured and more information became available.   Much of
the field data that established the crepuscular habit of
various species in which it has been predicted was recorded
by A.L.V. Davis and I.D. Temby (personal communications).

Crepuscular telecoprids may be distinguished from
diurnal telecoprids by means of various characteristics,
some or all of which they possess.   These characteristics
are arranged below in order of importance and although no
single characteristic, with the possible exception of the
first two, is sufficient on its own, any combination of
characteristics will readily determine whether a beetle is
crepuscular in habit or not.   Some of these characteristics
may also be extended to encompass paracoprid species.

(i) The eyes, both dorsal and ventral to the gena, of
night fliers are larger and protrude more than those of
diurnal species.   The eyes appear to have become larger at
the expense of the gena.   Although dung beetles may be
regarded as living in a world of mainly olfactory and tactile
stimuli (Halffter and Matthews, 1966) presumably the larger
eyes of crepuscular telecoprids are able to absorb more

diffuse /....

diffuse light at night and so function more efficiently. As
in day fliers, many of which immediately fly off if a large
shadow passes over them, it is probable that the perception
of movement is necessary in crepuscular species both in
escaping from nocturnal predators and in responding to a
prospective mate (Chapter 7).

 (ii) On death, the eyes of many night flying species turn
milky, usually with minute black spots scattered through
them.   This may be caused by a different visual arrangement
that compensates for the lower light intensity in which they
function.

(iii) Only crepuscular or extremely early diurnal species
of telecoprid males possess pheromone disseminating tibial
brushes.   The length of the brush in relation to the tibial
length indicates whether a species is crepuscular or not.
The greater the ratio the more definitely it determines the
species as crepuscular.   A percentage brush to tibial ratio
over 50% indicates that the species is crepuscular in the
Kheper genus.   In the Scarabaeus genus, all species with
tibial brushes are crepuscular although not all crepuscular
species have tibial brushes (Section 9.2).

 (iv) Nearly all crepuscular telecoprids in southern Africa
captured by members of the Dung Beetle Research Unit are
shiny black in colour.   Telecoprid species found between
500 and 1500m (south of latitude 17°S) in all instances
recorded, are black or nearly so in colour, although there is
sometimes a range in colour in a single species from a metallic
bronze colour to black with a progressive increase in altitude.
However, this black is usually dull, similar to those
Scarabaeus species found along the western coast of the Cape
Province and South West Africa.   The dull black in these
species, and species such as Pachylomera femoralis of Botswana,
is almost certainly associated with heat absorption from
insolation.   The activity period of these species is in the
morning along coastal or inland regions where temperatures

are much cooler than those on the eastern coast, and the absorption of heat prior to activity becomes necessary.

Crepuscular species fly at a time when temperatures are lower and as black absorbs all wavelengths of light (Chapman, 1969) a black beetle would absorb heat more readily, its metabolism would be increased and this would enable it to be active at temperatures too low for diurnal species. If all wavelengths are reflected equally, the reflecting surface appears white (Chapman, 1969). For example, Tenebrionid species found in the Namib desert are white in colour (Transvaal Museum Collection). On the other hand, many diurnal species of dung beetles, both telecoprid and paracoprid, especially of the genera Phalops, Kheper, Garreta, Gymnopleurus and Onthophagus (Proagoderus) are of bright metallic colours.

(v) The hairs on all parts of a crepuscular beetle, especially the tibial brushes, are red in colour or have a reddish tinge. Diurnal species have black hairs on all parts of the beetle where hairs are found.

(vi) The largest telecoprids are crepuscular in both the Kheper and Scarabaeus genera, and most night fliers are large. Size is mainly connected with habitat (Chapter 2) and the largeness of crepuscular telecoprids generally may be the result of reduced competition with other telecoprid species.

(vii) A few species of crepuscular telecoprids have what may be described as a very small vestigial horn on the clypeus. This has been found to occur in both sexes of Scarabaeus zambesianus, Neateuchus proboscideus and N. rixosus. Its function is unknown.

9.2 SIGNIFICANCE OF PHEROMONE BRUSHES :

The pheromone dissemination brushes on the tibiae of the hindlegs of the six Kheper species occurring in southern Africa vary in size and in the denseness of the hairs of which they are formed. It was further noted that the size

and /....

and thickness of the brushes seemed to increase with increasing crepuscular activity of each species. This impression was tested by measuring the brush length of individual beetles of each species and expressing this as a percentage of the total tibial length. The results are given in Table 19 together with the accurate or estimated peak activity period for each species. These estimates are derived from data collected in the field from light and pitfall traps.

TABLE 19: Average percentage brush to tibia ratio of the six southern African Kheper species

Species	Mean Brush length as % of tibial length:	Range		n	Diel Activity Peak:
		Min %	Max %		
K. nigroaeneus	25,40	19,83	32,67	41	0700-0800h
K. bonellii	34,23	26,36	44,92	18	0600-0800h
K. subaeneus	39,25	34,72	50,39	24	0600-0800h
K. lamarcki	50,61	39,86	62,99	54	0400-0500h*
K. cupreus	51,43	43,33	58,97	8	1900-2000h*
K. prodigiosus	65,68	54,88	79,09	15	2000-2200h*

*Precise data not available.

The data indicate that the proportional length of the pheromone brushes does indeed increase with increasing crepuscular activity of the species.

A further observation is related to this. The concentration of tibial hairs into brushes is related to a corresponding concentration of pores into a depression. Thus the larger brushes found in the more nocturnal species is indicative of a correspondingly greater number of pheromone pores with a corresponding increase in the number and size of the glands supplying them. Generally speaking, the

overall /....

overall size of a species increases with increasing nocturnal activity but the area covered by the depression is nevertheless proportionally larger in the more nocturnal species. The thickness of the tibial brushes also increased with increasing crepuscular activity (fig. 85, a - j).

The two regional populations of K. bonellii in southern Africa show slight differences in the average size of the tibial brushes. The late flying Velddrif population (because of the cooler Western Cape coastal conditions) appears to have, on the average, slightly smaller pheromone brushes than the earlier flying Zululand population, although the difference is not statistically significant.

The diurnal G. nitens with a diel activity peak between 0900h - 1000h and the diurnal Coptorhina klugi have no pheromone brushes or hairs.

Air temperature decreased with increasing crepuscular into nocturnal conditions, with a corresponding increase in the relative humidity. Thus the evolution of larger brushes in nocturnal species may have been affected by decreasing evening temperatures and the increasing relative humidity.

At lower temperatures it is possible that the pheromone volatiles are less odoriferous and that as a consequence a larger amount is released and more widely disseminated by the larger brushes of crepuscular beetles.

From Table 3 it may be seen that of those species which are not black in colour, only two, K. cupreus and A. convexus, are crepuscular. If colour is a consequence of the habitat, it may be taken as an indication of the climatic factors of that habitat. Hence, using colour as a criterion within the distribution range of K. nigroaeneus, the average percentage brush length was recorded and correlated with habitat differences. The results are given in Table 20.
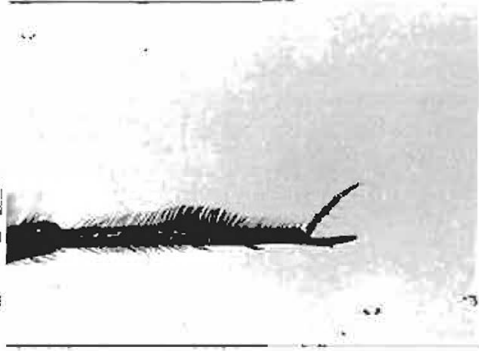
TABLE 20 : /......

FIGURE 85.

COMPARISON OF MALE TIBIAL PHEROMONE DISSEMINATING
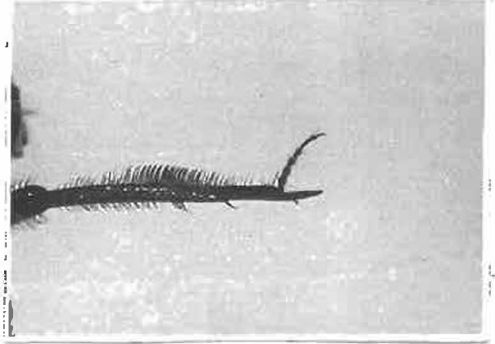BRUSHES OF TEN DUNG BEETLE SPECIES.   x   2

    (a) *Kheper nigroaeneus*

    (b) *Kheper bonellii*

    (c) *Kheper subaeneus*

    (d) *Kheper lamarcki*

    (e) *Kheper cupreus*

    (f) *Kheper prodigiosus*

    (g) *Scarabaeus goryi*

    (h) *Scarabaeus deludens*

    (i) *Scarabaeus zambesianus*

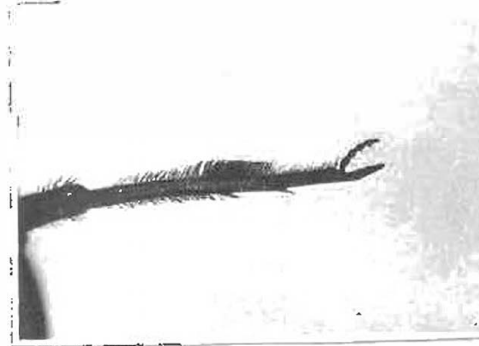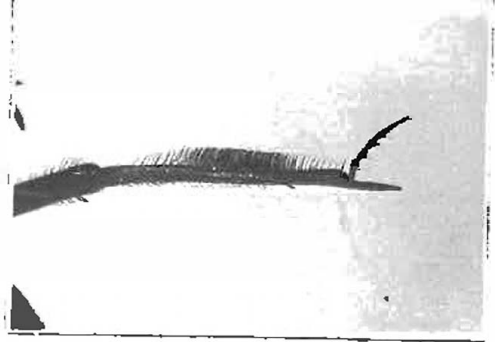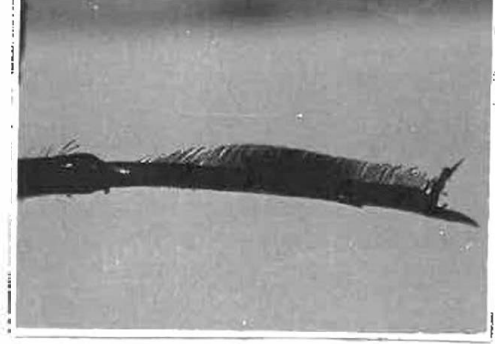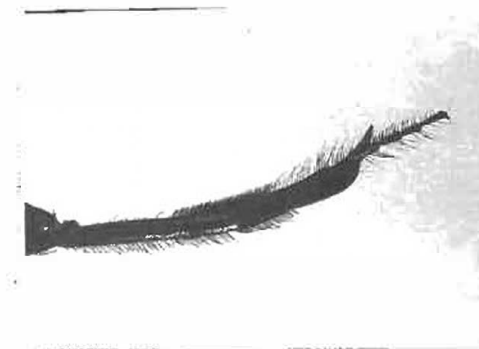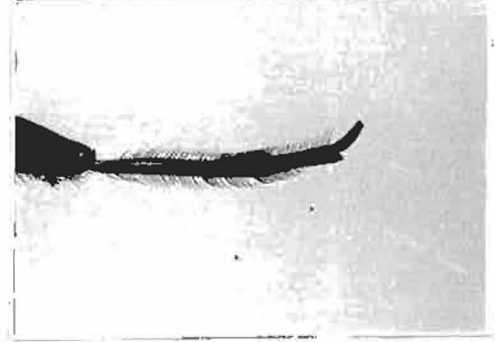   (j) *Scarabaeus ambiguus*

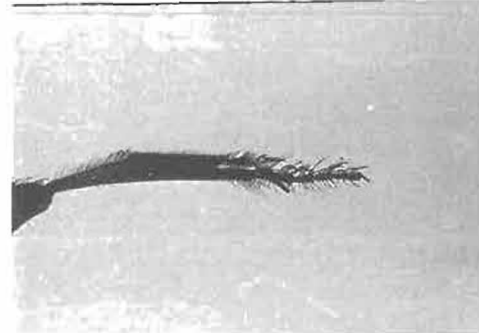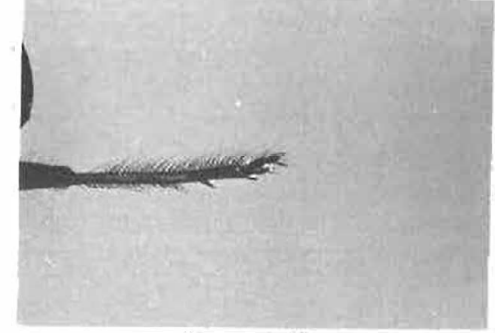# FIGURE 85.

a

b

c

d

e

f

g

h

i

j

TABLE 20 : Proportional brush length of K. nigroaeneus beetles within their distribution range using colour variations as an indication of habitat variation.

Colour	n	Ave. Brush %	Altitude
Black	10	23,22	) 500 - 1500 m
Black/bronze	10	24,64	)
Bronze (bright)	7	26,27	)
Green/black	7	26,75	) 0 - 500 m
Bronze (dull)	7	27,37	)

Thus, with increasing altitude there is a decrease in proportional brush length within the K. nigroaeneus distribution range. A possible interpretation is the following. As the black K. nigroaeneus occur in marginal regions of the species distribution and also in the marginal regions of the large herbivores distribution, the inter-specific competition there is less fierce and dung location becomes more important than finding a mate amongst thousands of beetles which occur at middens in the optimum region of 0 - 500m. Hence the slight reduction in the proportional brush length which is, however, not statistically significant.

9.3 EVOLUTIONARY SPECULATION :

In an attempt to determine why, of all listed species in the Kheper genus, only certain of the Scarabaeus subgenus and no Scarabaeolus or other telecoprid species have brushes in the male for the dissemination of pheromone, Table 21 was compiled. Field data, Dung Beetle Research Unit reference collection and personal communications from A.L.V. Davis on the diel activity and altitude range of certain species were used in the construction of the table.

TABLE 21 : /....

TABLE 21 : Comparative table of pheromone release in telecoprids.

+ = Present   O = Absent

Species	Diel Activity Peak	Male Tibial Brushes	Depressions with Pores	Abdominal Bristle Rows	"Headstand" Release Stance	Annual Rainfall Range (mm)	Altitude Range (m)	Pheromone Carrier Visible
K. nigroaeneus	Diurnal	+	+	3	+	400 -1000	0 - 1500	+
K. bonellii	Diurnal	+	+	3	+	100 -1000	0 - 500	+
K. subaeneus	Diurnal	+	+	3	+	500 -1000	0 - 1500	+
K. lamarcki	Diurnal	+	+	2	+	300 -1000	0 - 1500	+
K. pustulosus	Diurnal	+	+	3		500 - 800	1600-1900	
K. aegyptiorum	Diurnal	+	+	3	+	500 -1000	250 - 1400	+
K. aeratus	Diurnal	+	+	2	+	200 - 500	200 - 500	+
K. festivus	Diurnal	+	+	3		800 -1000	1000-2000	
K. paganus	Diurnal	+	+			800 -1000	500 -1500	
K. laevistriatus	Crepuscular	+	+	3		200 - 800	250 -1100	
K. cupreus	Crepuscular	+	+	3		400 - 800	0 - 1500	
K. prodigiosus	Crepuscular	+	+	2	+	300 - 800	0 - 1500	+
S. goryi	Crepuscular	+	+	0	+	300 -1000	0 - 1500	+
S. deludens	Crepuscular	+	+	0		300 - 800	0 - 1500	

Species	Diel Activity Peak	Male Tibial Brushes	Depressions with Pores	Abdominal Bristle Rows	"Headstand Release Stance	Annual Rainfall Range (mm)	Altitude Range (m)	Pheromone Carrier Visible
S. zambesianus	Crepuscular	+	O	O	+	300 - 800	0 - 1500	O
S. satyrus	Crepuscular	O	O	O	+	*100 - 500	250-1500	O[e]
S. galenus	Diurnal	O	O	O	+	400 - 800	0 - 1500	O
S. westwoodi	Diurnal	O	O	O		500 - 800	1000-2000	
S. rugosus	Diurnal	O	O	O	+	*100 - 300	0 - 500	O
S. savignii	Diurnal	O	O	O		400 - 600	0 - 500	
S. suri	Diurnal	O	O	O		100 - 400	0 - 500	
S. ambiguus	Diurnal	O	O	O	+	300 - 800	1000-2000	O
S. viator	Diurnal	O	O	O		200 - 400	0 - 1500	
S. ambulans	Diurnal	O	O	O		300 - 800	0 - 1500	
S. natalensis	Diurnal	O	O	O		600 -1000	1500-2000	
S. basuto	Diurnal	O	O	O		500 - 800	1000-2000	
S. funebris	Diurnal	O	O	O	+	300 - 800	0 - 1500	O
S. bohemani	Diurnal	O	O	O	+	200 - 800	500-1500	O
S. piliventris	Diurnal	O	O	O		200 - 400	500-1000	
S. alienus	Diurnal	O	O	O		*100 - 200	500-1000	
S. catenatus	Diurnal	O	O	O		200 - 600	400-1500	
S. rusticus	Diurnal	O	O	O		600 - 800	1000-1500	
S. caffer	Diurnal	O	O	O		600 - 800	1000-1500	
S. fritschi	Diurnal	O	O	O		*100 - 200	500-1000	
Sc. flavicornis	Crepuscular	O	O	O	+	*100 - 400	500-1500	O

Species	Diel Activity Peak	Male Tibial Brushes	Depress-ions with Pores	Abdom-inal Bristle Rows	"Head-stand" Release Stance	Annual Rainfall Range (mm)	Altitude Range (m)	Phero-mone Carrier Visible
Sc. canaliculatus	Diurnal	0	0	0		200 - 400	0 - 500	
Sc. damarensis	Diurnal	0	0	0	+	100 - 400	500-1500	0
Sc. intricatus	Diurnal	0	0	0		200 - 300	0 - 1000	
Sc. inquisitus	Diurnal	0	0	0		400 - 600	500-1500	
Sc. parvulus	Diurnal	0	0	0		*100 - 300	500-1000	
Sc. inoportunus	Diurnal	0	0	0		200 - 400	500-1000	
Sc. clanceyi	Diurnal	0	0	0		400 - 600	0 - 1000	
Sc. anderseni	Diurnal	0	0	0		300 - 400	1000-1500	
Sc. ebenus	Diurnal	0	0	0		400 - 600	0 - 1000	
N. proboscideus	Crepus-cular	0	0	0		200 - 500	0 - 1000	
D. costatus	Diurnal	0	0	0		*100 - 400	500-1500	
Scel. hippias	Diurnal	0	0	0	+	600 - 700	1000-1500	0^e
A. convexus	Crepus-cular	0	0	0	+	400 -1000	0 - 1500	0^e
S. impressipennis	Diurnal	0	0	0	+	500 -1000	500-1500	0
G. nitens	Diurnal	0	0	0	+	400 -1000	0 - 1500	+
A. thalassinus	Diurnal	0	0	0		400 -1000	0 - 1500	0
P. femoralis	Diurnal	0	0	0	+	300 -1000	0 - 1500	0^e
P. opaca	Diurnal	0	0	0	+	200 - 400	500-1500	0
^Copt. klugi	Diurnal	0	0	0	+	600 - 800	1000-1500	+
^Copt. auspicata	Diurnal	0	0	0	+	600 - 800	1000-1500	+

* = below 100mm   ^ = paracoprids   e = visible under S.E.M.

It may immediately be seen that all male beetles of those species with pheromone brushes are crepuscular in behaviour or nearly so. The diurnal Kheper species are active so early in the morning that they may almost be termed twilight species of a twilight genus. Due to the temperature linked activity peaks of dung beetles, the diurnal Kheper species may be considered to be secondarily diurnal in activity. The most elaborate pheromone dissemination structures are found only in the crepuscular and twilight species.

However, there are four crepuscular telecoprid species, Scarabaeus satyrus, Scarabaeus (Scarabaeolus) flavicornis, Neateuchus proboscideus and Anachalcos convexus, that have no tibial brushes or depressions with numerous pores. Of these A. convexus stands out as belonging to a separate group of beetles. It is an extremely primitive species resembling tenebrionids in shape. The other three species differ from the twilight group in that they occur in the drier central Cape, southern South West Africa and the north-western Cape — a distribution similar to most of the remaining Scarabaeus and Scarabaeolus species — whereas all species with tibial brushes are found in the wetter eastern regions of southern Africa or the tropics. The apparently wide range in annual rainfall in the range of K. bonellii is due both to the widely separated populations (fig. 6) and the special soil conditions prevailing in the low annual rainfall in the South Western Cape. K. bonellii is essentially a high rainfall species typically found in the Zululand region.

The data of Table 19 showed that the pheromone brushes of crepuscular telecoprids become progressively larger the later the flying time. As visual perception must play only a limited part in nocturnal species, olfaction will be of greater importance in locating a mate which may account for the elaborate pheromone disseminating organs in these species. The selection pressures which led to the formation of such dispersal mechanisms could possibly include :

(i) Competition: /....

(i) <u>Competition</u>: According to field collections, pitfall
trappings and the reference collections of the Dung Beetle
Research Unit and the Transvaal Museum, the greatest numbers
of species and beetles occur in the hot, humid lowveld areas
of southern Africa.   The activity period of most species
is confined to the hours on either side of twilight with a
resultant fierce inter- and intraspecific competition between
beetles.   The need to attract and recognise the opposite
sex in telecoprids in the shortest possible time becomes of
extreme importance in securing dung for a brood-ball.   The
fewer number of beetles and species in the arid, higher
altitudes does not result in such intense competition and
different flying times of species in these regions would be
enough to prevent direct competition.   It is possible that
pheromones could serve as recognition signals which would
constitute good isolating mechanisms especially where inter-
specific competition is great, but the odour released by
sympatric <u>Kheper</u> species is remarkably similar, being virtually
identical to an observer.

(ii) <u>Distribution of Dung</u>: The largest herbivores are found
to be most prevalent in the hot, humid lowveld regions,
migrating into marginal areas as conditions permit. Droppings
in these drier areas are consequently more widely distributed
and usually in the form of pellets in the semi-desert regions.
The location of dung would then be of primary importance and
once at the pad, only short-range sex pheromones would be
necessary with the resultant reduced selection pressure for
elaborate dissemination mechanisms.

(iii) <u>Windless Conditions</u> : The hot, humid, relatively wind-
less conditions which prevail in the lowveld regions, the
main distribution area of those species with tibial brushes,
may have been an inportant factor which contributed to the
formation of disseminating mechanisms.   There would be an
advantage under these conditions in actively discharging
attractant into the air.   Birch (1974) states that the
mechanisms for disseminating the scent material in the

Noctuidae /....

Noctuidae is achieved with considerable force, a factor apparently common to brush-organs wherever they are located.

The conclusion reached is that the elaborate brush mechanism for pheromone dissemination evolved in telecoprid species confined to hot, humid, low altitude regions and which were active during the twilight hours or, perhaps previously, were totally nocturnal.

Although the brush-organs of the Noctuidae are not comparable anatomically or even strictly functionally to the brush mechanism of Kheper species, they are relevant to this discussion. The male moth brush organs are located on the abdomen and may be retracted into abdominal folds after mating, the pheromone particles adhering to the brushes acting solely as an aphrodisiac once the female has been encountered. They were regarded by Birch (1974) as the most elaborate brushes to be found amongst the Lepidoptera and it is significant that the Noctuidae is a predominantly nocturnal family. Similarly, many sphingid species, which also possess complex male abdominal brush-organs, are also crepuscular or nocturnal (Birch, 1969). Other nocturnal Lepidopteran families which possess brush-organs include the Geometridae and the Archiidae while hair-pencils are common in the diurnal Satyridae family and the Danainae (Birch, 1974). Brower (1963) suggests that in general a complex male scent apparatus was likely to develop in those species or groups where visual signals are reduced or are confusing, since they help to overcome the potential difficulty of visual recognition between species. This applies to nocturnal species, especially those which are subject to maximum competition.

Halffter and Matthews (1966) propose that since the Scarabaeidae are closely associated with the soil in both adult and larval forms, their ancestors encountered their food in the soil and this was followed by an intermediary saprophagus stage before becoming coprophagus. Since the

majority /....

majority of southern African dung beetles are crepuscular,
it is probable that the whole group was originally night
flying until further adaptations overcame the threat of
desiccation.   Because of the behaviour of telecoprid species,
which results in their being active on top of the dung pad
instead of in or under the pad as in the case of endocoprids
and paracoprids, there would have been considerable pressure
on them to evolve elaborate pheromone dissemination structures,
especially the crepuscular species subjected to intense
competition.

The pheromone release stance is recorded in many
genera and further observations should reveal how widespread
this behaviour is among telecoprids.   The pheromone carrier
is visible in many Kheper species, occasionally visible in
Garreta nitens and present in Coptorhina klugi and Coptorhina
auspicata.   The biochemical pathway in the formation of the
paraffin carrier from the food may possibly be similar for
both the coprophagus species and the mycetophagous Coptorhina
species.   The pheromones released by K. nigroaeneus,
K. subaeneus, K. bonellii and K. lamarcki have a remarkably
similar odour which is similar to the chemical skatole
(R. Crewe, personal communication).   In the laboratory a
beetle releasing pheromone can be immediately located as the
pheromone is odoriferous to man.

There seems to be no known reason why the number of
rows of abdominal bristles in the various Kheper species
should be either two or three in number.   The crepuscular
Scarabaeus species have rows of hairs on the abdominal
sternites which are not comparable to bristles and are common
to many paracoprid species.

Although the different Kheper species' tibial brushes
vary in size and denseness, the greatest differences
occurring amongst sympatric species due to different flying
times (figs. 85 a - f), those of the three Scarabaeus species
differ widely from Kheper and from one another.   Male

Scarabaeus goryi (fig. 85, g) have their pheromone brushes situated on the inner lateral part of the hind-tibiae and are dense and also short and bristly.   Male Scarabaeus deludens brushes are also located on the inner lateral part of the hind-tibiae but are not as dense as those of S. goryi and are also much longer (fig. 85, h).

Male Scarabaeus zambesianus have most distinctive brushes covering almost the whole length of the tibiae and are located on the outer lateral parts of the hind-tibiae. The brushes are extremely dense and also very short - in the form of a "crew cut" (fig. 85 i).   S. zambesianus is the only crepuscular species which possesses brushes but no depression.   Although the pheromone pores are not concentrated into a depression, they are highly concentrated in the first abdominal sternite (fig. 86) and may represent a stage before further concentration into a depression or may perhaps indicate a secondary espacement of the pores.

Kheper tibial brushes are curved to different degrees towards the outside of the tibiae.   This is shown clearly in the late flying K. prodigiosus (fig. 85, f) and functions to disseminate the pheromone more forcefully into the air. The brushes are curved in the opposite direction to the abdominal bristles, the result being that the emerging pheromone is brushed from the depressions in an almost interlocking action against the bristles.   This causes the pheromone "dust" to be forced higher into the air on either side of the beetle.

Garreta nitens and the Coptorhina species have hairless tibiae, flattened on the inner surface in Coptorhina into a scoop.   Hairs similar to those of Scarabaeus ambiguus (fig. 85, j) are found on the legs of all other Scarabaeus examined.

Scanning electron micrographs were taken of several other species of dung beetles other than the Kheper species and the important characteristics of each species are

recorded /....

FIGURES 86 - 88.

DIFFERING ABDOMINAL PHEROMONE STRUCTURES OF THREE MALE
TELECOPRID SPECIES.

Figure 86 : Scanning electron micrograph of the
fairly concentrated pheromone pores
on the first abdominal sternite of
a male Scarabaeus zambesianus   x 25

Figure 87 : Scanning electron micrograph of the
"furrow" present on the first abdominal
sternite of a male Scarabaeus satyrus

x 25

Figure 88 : Scanning electron micrograph of pheromone
carrier emerging from a single abdominal
pore of a male Pachylomera femoralis

x 250

Figure 86

Figure 87
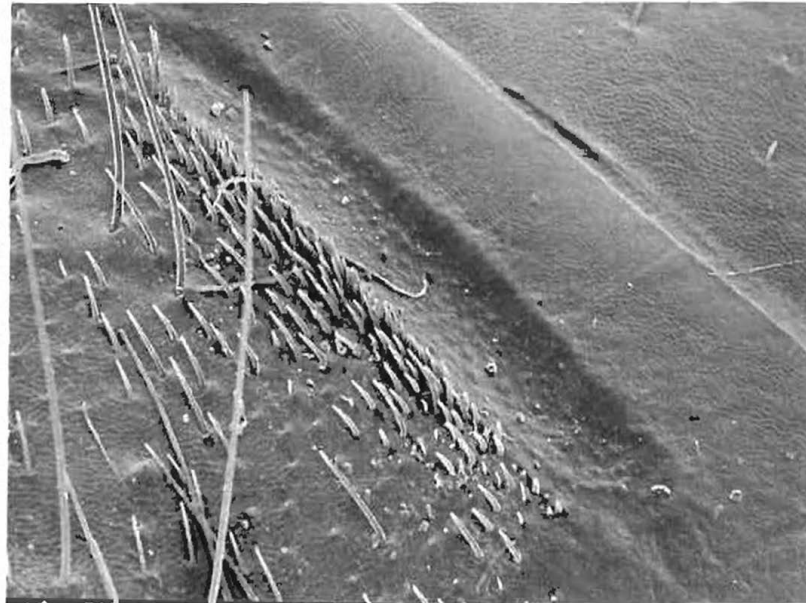
Figure 88
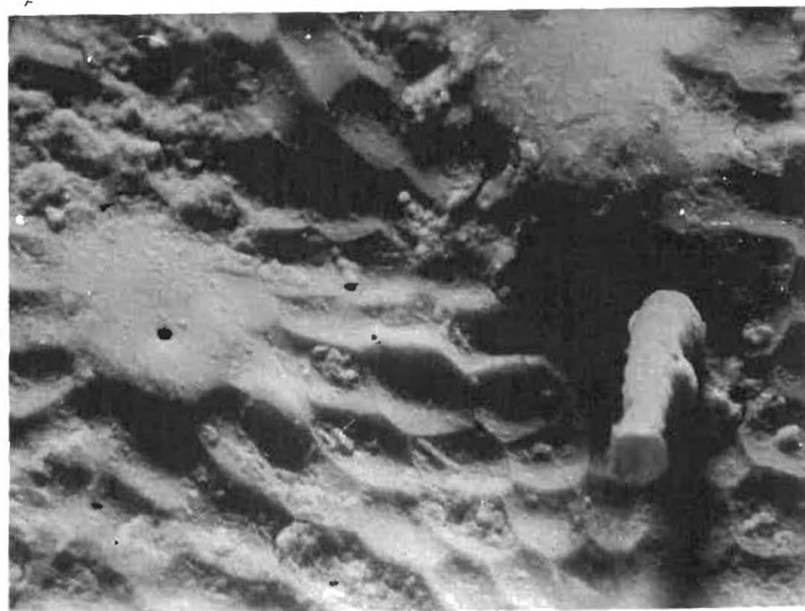
recorded below.

TELECOPRIDS :

S. satyrus ♂ : Two furrow shaped depressions on the first abdominal sternite containing pores (fig. 87) which are widely spaced apart and not similar to those of the Kheper genus.

S. rugosus ♂ : ⎫ Numerous widely spaced pores over
S. bohemani ♂ : ⎭ the first four abdominal sternites.

A. convexus ♂ : Slightly elevated pores, even more widely spaced apart.

P. femoralis ♂ : ⎫ Pores widely spaced apart, similar
P. femoralis ♀ : ⎭ in all respects for both sexes, the paraffin carrier visible under the S.E.M. (fig. 88).

PARACOPRIDS :

Heliocopris andersoni ♂ : Very widely spaced pores.

ENDOCOPRIDS :

Oniticellus pictus ♂ : Very widely spaced pores.

It is possible that sex pheromones are produced widely in many or all species of dung beetles, the degree of elaboration of the apparatus depending on the behaviour and habitat of the species. Dung possibly plays an important synergic role with the pheromone in telecoprids, but is probably the primary attraction for paracoprids and endocoprids in which short range sex pheromones are probably released within the dung pad. Hence the most primitive pheromone structures — isolated pores — occur in these groups.

CHAPTER 10.

SPECIALISED GROUPS.

10.1 PACHYLOMERA :

Both species of the exclusively Ethiopian Pachylomera genus occur in southern Africa, but do not overlap in distribution. P. femoralis inhabits wetter areas (600mm - 1250mm isohyets), occurring from St. Lucia (Natal), through the Northern Transvaal and into north-eastern Botswana. P. opaca is smaller than P. femoralis and inhabits the drier N.W. Cape (around Vanzylsrus and Twee Rivieren) and southern South West Africa.

Both Pachylomera species are strongly modified morphologically for digging, possessing enormous forelegs with shortened, weakly developed hindlegs. Their distribution coincides with the Kalahari sandveld (Soil Map, 1973) and it is not surprising that these modifications have taken place. Similarly in Natal P. femoralis is found only in the sandveld of the coastal plain. Although P. femoralis has been able to adapt to conditions of high rainfall along the Natal coastal plain, from numbers captured during field-trips and pitfall traps in Mkuzi Game Reserve, this region is marginal. They occur most abundantly within the 400 - 500mm isohyets in Botswana and the Northern Transvaal. P. opaca has a narrower distribution range dependent on the 100 - 400mm isohyets which encompass a much smaller region.

Although the 15° E.T. and summer rainfall are limiting factors of the Pachylomera genus, the soil type - sand - plays a far more important role in limiting this genus than it does for other telecoprid species.

P. femoralis is attracted to most types of dung and readily attacks cow-dung which is most prevalent in the region they inhabit in Botswana. P. femoralis and P. opaca

have /....

have only occasionally been observed to roll dung-balls in
the field but do so often in the laboratory, P. opaca rolling
with astonishing speed.   In the field, feeding normally
occurs at the dung pad and it is possible that in the laboratory
ball-rolling may be the result of competition due to over-
crowding.   The balls are relatively small for such large
beetles and they are not buried, but consumed under cover of
tufts of grass or other sheltered places.   The highly
developed prothorax and forelegs of the Pachylomera led
Halffter and Matthews (1966) to question whether this genus
had lost the ability to roll dung balls.

The typical behaviour of Pachylomera in the field is
to construct an unbranched tunnel within 30cm of the dung
pad by digging with the foretibiae and clypeus and then
turning around in the burrow and pushing out the loosened
soil, using the broad prothorax as a shovel.   The tunnel is
long, approximately 120cm, and slopes gently downwards to a
maximum depth of approximately 20cm depending on the hardness
of the soil.   The loose excavated soil is used to build a
ramp which leads to the dung pad.   The entrance to the
burrow is not circular, opening vertically into the soil as
in most telecoprid species, but is semi-circular and sloping
at an angle into the soil.   Two other telecoprid species,
Scarabaeus galenus and Scarabaeus rugosus, also construct
semi-circular entrances near the dung source and also are
restricted to sandy areas, S. galenus has a wide distribution
similar to that of P. femoralis while S. rugosus is restricted
to the western Cape coastal region from Hondeklipbaai south-
wards.   Both these species are adapted to sandy conditions
having curved hairs on the perimeter of the prothorax, which
aid the removal of soil from the burrow, and hairy legs
adapted to running on sand.

The Pachylomera burrows are provisioned with dung by
the beetle making several trips to and from the dung pad.
Pieces of dung are detached using the clypeus and foretibiae
by means of an action similar to that of a dog digging - the

pieces of dung being passed between the legs.   The pieces
are then either butted with the head or rolled to the burrow
entrance and pushed inside with the head.   P. femoralis is
very aggressive, defending both a large section of the dung
pad and the ramp against any intruder.   This species is well
endowed with sharp spines on the inner surfaces of the tibiae
and femora.   An opponent is held between the tibiae and
femora and the spines are pressed with considerable force
against it.   Once released the victim immediately flees,
no instance having been observed in which the combat proceeded
beyond this stage.

Once the end of the burrow has been provisioned with
dung the beetle returns to the entrance and takes up a
pheromone release stance, the body having an angle of
approximately 33° to the soil surface.   Both male and
female beetles have been observed to assume this stance.
Although they do not possess definite brushes the hind-
tibiae are covered by three rows of dense hair, largely an
adaptation to sandy conditions.   The hindlegs are extended
and withdrawn as in other telecoprid species but the intervals
between brushing movements are extremely long (2 - 3 minutes)
and the movements are slow.

Since both sexes have an almost identical distribution
of widely separated pores on the abdominal sternites under
the S.E.M., they would seem to have an equal chance of
attracting the opposite sex.   No beetles have been observed
to pair off at the dung pad and the construction of the
burrow is completed by a single beetle.   The pheromone
produced by the beetles is likely to be only a short range
sex pheromone due to the sparse distribution of pores and
primary attraction would be to the dung pad, the beetles of
both sexes constructing their burrows within 30cm of the pad.
These observations suggest that both sexes can attract each
other and that each sex produces a different pheromone.
Beetles arriving later at the dung pad after beetles have
provisioned their burrows would be attracted by the opposite

sex.

10.2 COPTORHINA :

Mycetophagus breeding in the Australian dung beetle
Onthophagus dunningi has been described by Bornemissza (1971)
although this species had been previously captured on faeces.
Although a number of Onthophagus species in southern Africa
have been recorded on both mushrooms and dung, the two species
of Coptorhina, C. auspicata and C. klugi, have only been
captured on mushrooms and are morphologically adapted to a
mycetophagous habit.   When presented with both mushrooms
and dung in the laboratory, only mushrooms are attractive to
them and are consumed.   The same morphological adaptations in
all Coptorhina species in museums throughout South Africa
indicate that mycetophagy is universal in this genus.

These two Coptorhina species have been recorded only
infrequently so that their distribution cannot be plotted
with accuracy.   Those specimens captured have all been in
areas above the 600mm isohyet.   A high rainfall would be
necessary for the growth of mushrooms and the distribution
of Coptorhina is bound to be within rainfall areas that are
suitable for mycelium growth.   The soil type where these
beetles occur has been mostly grey sandy-loam, in vleis or
under trees.

C. auspicata and C. klugi are diurnal paracoprid
species which may be brought to the surface in the laboratory
by moistening the soil in the pan.   Moisture is also respon-
sible for the immediate appearance of the fruiting bodies of
mushrooms and toadstools on the surface, rainfall probably
acting as the cue to which both plant and beetles respond.
Temperature is important in the seasonal behaviour of the
species as they overwinter between March and October in the
soil and return to the surface after the first summer rainfall.
Coupled with temperature, mushrooms only form fruiting bodies
during the summer rainfall season and any beetles returning to
the surface during winter would not be able to feed.

C. auspicata and C. klugi have been captured on three
species of mushroom identified by Dr. van der Westhuisen
(Herbarium, Plant Protection Research Institute) as :

the giant "puff-ball" Calvatia lepidophora, the smaller white
puff-ball Lycoperdon hyemale and the parasol mushroom Lepiota
zeyheri. They do accept other mushrooms under laboratory
conditions. The puff-ball species are only attacked in the
immature stage before the spores have been fully formed.
Coptorhina beetles land near the toadstool and construct a
burrow beside the stalk of the fruiting body. This burrow
is then extended upwards into the body of the toadstool and
pieces are dragged into the burrow. After much activity the
toadstool may consist of an outer shell only, being hollowed
out within, or it may be totally consumed. The size of the
mushroom seems to determine the number of beetles which feed
on it, the giant C. lepidophora may support up to seven
beetles while the small L. hyemale has never yet been found
with more than a single beetle feeding on it.

The behaviour in relation to a parasol mushroom is
slightly different. The burrow is excavated beside the
stalk, but the beetle does not burrow within it as does
O. dunningi (Bornemissza, 1971). Instead it climbs the
stalk and detaches pieces of the gills. These pieces fall
to the ground and are individually collected by the beetle
by holding them with the forelegs and walking backwards into
the burrow.

The southern Africa Coptorhina species are characterised
by bidentate clypei of various modifications depending on the
species. Portions of the gills are detached in the follow-
ing manner. The bidentate clypeus (fig. 89, a) is pressed
against the vertical edge of a gill and the forelegs are
brought forward and pull the lower part of the gill down-
wards, resulting in a tear beside the clypeus. The clypeus
is pushed further into this tear and the forelegs again pull
downwards widening the tear. This is repeated until a
piece of mushroom is detached, the head and prothorax of the

beetle /....

beetle acting as a wedge.

The nesting burrow is dug to a depth of approximately 12cm and ends in a bulbous cul-de-sac in which the mushroom pieces are stored. These pieces are kneaded into a black coloured brood-ball which is covered with clay, the top half consisting almost entirely of soil (fig. 89, b). The soil averages 1cm in thickness in the lower half of the brood-ball, the upper portion, consisting only of soil, contains the egg. On construction, a depression is made in the brood-ball and is then completely coated with soil, the egg being laid in this depression and covered with a large soil cap. The egg hatches and the larva feeds downwards into the mushroom dough and creates a chamber inside the clay shell. Both adults desert the brood-ball and the soil shell prevents attack by soil organisms, mostly mites. The severity of attack on a naked ball was determined by removing part of the clay shell and reburying the ball.

Food-balls are prepared and buried in the same way and are usually also kneaded into a dough before being fed upon. If disturbed while cutting pieces of mushroom, the beetle immediately drops to the ground, folds in its legs and excretes a foul smelling substance. The only important competitors for the same food source are the numerous mycetophagous flies. The following species were identified through Dr. Stuckenberg, Natal Museum :

Platypeza rhodensiensis and Plesioclythia basilewskyi

The beetles ignore mushrooms infested with maggots and successfully utilise only those mushrooms not attacked by maggots or in which the fly eggs have not yet hatched.

The activity of the flies is also determined by rainfall. In the laboratory the maggots of P. rhodensiensis leave the mushroom where they have been feeding and burrow into the soil. After an interval of approximately ten days the adults will emerge within hours of water being added to the soil, the number of days taken for emergence depending on

FIGURE 89.

(a) A digrammatic representation of the bidentate
     clypeus of Coptorhina auspicata adapted to
     feeding on mushrooms   x 11,2

(b) Transverse section through the brood-ball
     of Coptorhina klugi   x 1,5

when water is added.

The two _Coptorhina_ species possess a sex pheromone which is released by males only at the food-source. Whereas other dung beetles must be in possession of dung before pheromone is released, _Coptorhina_ must be in possession of mushroom. Only two positions may be assumed by male beetles — at the fruiting body or at the entrance to the burrow in which pieces of mushroom have been buried. The males possess no brushes but have flattened inner surfaces of the hind tibiae which act as scoops to disseminate the visibly emerging pheromone and carrier while in the standard pheromone release stance.

Many so-called "dung beetles" have been observed feeding on various kinds of substances including pawpaws (_P. femoralis_ — R. Henwood, pers. comm.) and dead millipedes (_Onthophagus_ spp) but previously no southern African species was known to feed exclusively on a substance other than dung. Thus as the mycetophagous _Coptorhina_ genus is entirely Ethiopian in origin (Halffter and Matthews, 1966) and occur within grassland areas where copious amounts of dung have always been supposed to predominate, this specialisation is likely to have arisen at an early stage of their evolution while the _Pachylomera_ adaptations are only secondarily acquired.

CHAPTER 11.

TELECOPRID POTENTIAL IN FLY CONTROL.

In the ecological habitat of Nsumu Pan it has been shown that the activity of the diurnal dung-beetle species is such that all variations within that habitat in which dung may be dropped is within the range of activity of the beetles (Section 3.3). The diurnal coprophagous fauna of this ecological web consists mainly of telecoprid species among which direct competition is largely prevented in various ways although a great deal of overlapping e.g. in flying times, does occur.

Telecoprids are found almost throughout southern Africa and are adapted to the vastly different regions in which they are present. They may be roughly divided into three groups determined largely by annual rainfall :

Wet (501 - 1000mm)	Kheper, Garreta, Gymnopleurus, Allogymnopleurus, some Scarabaeus
Medium (30. - 500mm)	Scarabaeus, Neateuchus, Pachylomera femoralis
Dry (50 - 300mm)	Scarabaeus (Scarabaeolus), Pachylomera opaca, Drepanopodus.

Since Australian bush flies have been reported to breed in dung throughout the above rainfall range (Hughes et al., 1972), the potential importance of the telecoprid group in controlling them is evident.

Although the greatest importance of telecoprids would be in buffalo fly and bush fly control, they also contribute to the recycling of dung. When feeding below the surface on a food ball a large amount of frass remains below when the beetle returns to the surface. Similarly on weighing the dried shells of Kheper nigroaeneus brood-balls once the F_1's

have /....

have emerged, an average of 21 gms was found to remain in the soil.

To achieve success in controlling flies in Australia the major species from any particular habitat in Africa would have to be introduced into a similar habitat in Australia and telecoprids would form only a fraction of the introduced species.   However, this would be a very important fraction due to the similarities in habitats and behaviour of tele-coprids and the flies.   The following points pertain largely to the southern African Kheper species :

(i) Fresh Dung :

Both bushflies and telecoprids are attracted to fresh dung.   Freshly dropped dung is particularly attractive to gravid bushflies as an oviposition site;   once the dung has formed even a thin dry crust it becomes less attractive unless cracks or crevices expose moist dung (Hughes et al., 1972).   The bushfly larvae eat the liquid and soft-solid parts of the dung (Greenham, 1970) which makes it necessary that the dung must be fairly fresh.   Thus telecoprids which are all attracted to fresh dung will compete directly with the bushflies for exactly the same resource.

(ii) Diurnal Activity :

Although adult bushflies emerge from the soil where they have pupated between midnight and dawn (Greenham, 1970) they are active only during daylight hours (Hughes et al., 1972).   Most telecoprids are day fliers enabling them to destroy pads before the flies oviposit or to destroy pads immediately after the flies have oviposited in them.

(iii) Bushfly Oviposition Time :

Observations in the field by Hughes et al. (1972) suggest that fewer gravid flies are caught in the afternoon. Although they suggest that this situation might be expected if plenty of oviposition sites were available in the morning, the flies may have a definite diel activity peak

similar to that of various telecoprid species. The relatively cooler morning temperatures and the availability of much fresh dung in the early morning resulted in over 70% of the telecoprid species' diurnal populations being captured between 0500h and 1200h. The largest number of gravid female bushflies were recorded between 0900h and 1000h (Hughes et al., 1972).

(iv) Optimum Temperature :

Temperature influences bushflies at all developmental stages but larval development is particularly affected. Optimum temperatures of between $21^{o}C$ and $27^{o}C$ are found between the two threshold extremes of $12^{o}C$ and $46^{o}C$ at which death occurs (Hughes et al., 1972). The optimum temperature for Zululand telecoprids is between $26^{o}C$ and $30^{o}C$, temperature controlling seasonal activity and many other behavioural traits.

(v) Humidity :

Humidity is extremely important for bushflies especially in the egg and larval stages; relative humidities of less than 100% slow the rate of development (Greenham, 1970). The moisture content of a dung pad is dependent to a great degree on the humidity of the habitat, and could possibly determine the number of fly generations per year. The most humid regions of southern Africa are the eastern lowveld regions - the "home" of the Kheper species. The relation between rainfall and bushfly abundance was found to be clear (Hughes and Nicholas, 1974).

(vi) Seasonal Changes in Dung :

Greenham (1972) related the favourability of dung as a larval food to the state of maturity of the pasture from which it was derived and found that as pastures passed through maturity to senescence, so the survival of bushfly larvae declined. Thus the bushfly population would reach its peak condition soon after the first rainfalls at the same time that telecoprids would be at their activity peaks.

(vii) Bushfly /....

(vii) Bushfly Oviposition Sites :

Bushfly eggs are normally laid in crevices in the dung
of animals or at the interface between the dung and soil
(Hughes et al., 1972). These areas are attractive to both
bushflies and telecoprids as they are often the only moist
parts of a dung pad over which a thin dry crust has formed.
Thus the area in which flies lay their eggs are, for the
same reason, the sites at which the telecoprids (especially
the Gymnopleurus species) feed and which most of them use
as the starting point in the formation of dung balls. The
bushfly eggs would be either eaten or exposed to desiccation
and predators in much the same way as dung-breeding flies in
southern Africa.

(viii) Dung-pad Size :

Greenham (1970) discovered that the larger the dung pad
the greater the survival rate of bushfly larvae and he con-
sidered that the high surface-to-volume ratio of small pads
increased the rate of drying, which caused decreased survival.
Bushfly larvae may prematurely vacate a drying dung-pad
resulting in stunted adults emerging from the pupae in the
soil (Hughes et al., 1972). Telecoprid behaviour of rolling
pieces of dung away from the dung pad helps in reducing the
dung-pad and causing it to dry out faster. The large
telecoprid species are especially attracted to large herbivore
droppings, Kheper nigroaeneus rolling dung-balls ten or more
times larger than themselves.

(ix) Shade :

Both adult bushflies (Hughes et al., 1972) and most
telecoprid species, especially the diurnal species, avoid
deep shade and are observed in the field covering dung pads
in the sun while mostly ignoring pads in deep shade a few
metres away. Thus the preference for pads dropped in
clearings is the same for both telecoprids and bushflies.

A biological indicator of areas suitable for Kheper

colonisation is the presence of Jacaranda trees (Bignoniaceae) which have been introduced into both southern Africa and Australia from Brazil (Menninger, 1962). This indicator covers the complete range of the Kheper distribution, marginal areas usually being indicated by complete leaf-fall during winter. Besides Jacaranda trees (found in northern New South Wales and Queensland - I.D. Temby, pers. comm.), the sausage tree, Kigelia pinnata (Bignoniaceae) of Africa has been introduced into Australia (Menninger, 1962) and is a more precise indicator of the optimum conditions for Kheper.

The potential of telecoprids in bushfly control far exceeds that of both paracoprids and endocoprids but they can only achieve a high level of control if the latter groups are also introduced. However, the climatic factors on which the telecoprids are very dependent, will finally decide the true value of these species under Australian conditions. The areas of highest cattle concentration in Australia must also be the areas of similar optimum climatic conditions for the telecoprids. The distribution of sandy soil in Australia may prove to be the final factor of vital importance to the success of the telecoprids.

ACKNOWLEDGMENTS.

REFERENCES.

ACOCKS, J.P.H. 1975. Veld Types of South Africa.
Bot. Surv. S. Afr. Mem. Govnt. Printer,
Pretoria.

BAILEY, H.P. 1960. A method of determining the warmth and
temperateness of climate.
GEOGR. ANNLR., 42 : 1-16. Cited in
Stuckenberg, 1969.

BALTHASAR, V. 1965. Eine neue Untergattung und neue Arten
der Familie Scarabaeidae (Col.)
ACTA ENT. BOHEMOSL., 62(1) : 14-23

BIGALKE, R. 1963. The extermination of the Square-lipped
or White Rhinoceros (Ceratotherium simum simum
(Burch.)) in Transvaal and its reintroduction.
A Historical and Critical Review.
Fauna Flora, Pretoria, 14, 5-14

BIRCH, M.C. 1969. Scent organs in male Lepidoptera
D. Phil. thesis (University of Oxford)
Cited in Birch, 1974.

BIRCH, M.C. 1974. Aphrodisiac pheromones in insects.
In Pheromones. edt. M. Birch, 115-134
Amsterdam: North Holland.

BORNEMISSZA, G.F. 1960. Could dung eating insects improve
our pastures?
J. Aust. Inst. agric. Sci. 26(1), 54-56

BORNEMISSZA, G.F. 1968. Studies on the Histerid beetle
Pachylister chinensis in Fiji, and its
possible value in the control of Buffalo
fly in Australia.
Aust. J. Zool. 16, 673 - 688

BORNEMISSZA, G.F. 1969. A new type of brood care observed
in the dung beetle Oniticellus cinctus
(Scarabaeidae) Pedobiologia 9, 223-225

Pheromone Release by Dung Beetles (Coleoptera: Scarabaeidae)

Of the various exocrine secretions produced by Coleoptera, the most extensively studied have been defence secretions.[1] pheromones such as the aggregation pheromones of the Scolytidae,[2] and sex pheromones of a number of families.[3,4] The sex pheromones were found to be produced by males in two cases[4] and females in a third.[3] Studies of sex pheromones in the Scarabaeidae have been restricted to a demonstration of their production by females of the Japanese beetle.[3] I wish to record the previously unreported discovery of a sex pheromone, produced by male dung beetles of the genus *Kheper*.

The dissemination of pheromones by insects is accomplished in a variety of ways, ranging from the well-known 'brush organs' of Lepidoptera,[5] the setae of cockroaches,[5] to scent disseminated on particles as in the butterfly *Danaus*.[6,7] These dissemination mechanisms are highly specialised and are adaptive. In the case of the male *Kheper nigroaeneus* the pheromone is produced as a white, flocculent substance emerging from a depression on either side of the first abdominal ternite. The depressions (Fig. 1) consist of several hundred minute openings, resembling a sieve (Fig. 2), which are supplied from a large gland complex immediately underlying the depressions. The gland complex consists of an interwoven mass of single-celled glands.

Both sexes have numerous long hairs along the dorsal length of the tibiae of the hind legs and in the male these are concentrated centrally to form definite brushes. In the female such a concentration is, at best, indistinct.

Along part of the anterior sections of the second, third and fourth male abdominal sternites immediately posterior to the depressions, are found single rows of semi-rigid bristles which are anteriorly curved towards the depression (Fig. 2). The bristles are not continuous across the segments but are localised posterior to the depressions.

The dispersal apparatus functions in the following manner. The hind legs are retracted simultaneously inwards towards the sides of the body and are then simultaneously extended. This movement results in the tibial brushes brushing the pheromone, which is emerging from the pores in the depression (Fig. 3), against the rows of curved abdominal bristles causing puffs of pheromone 'dust' to rise into the air from both sides of the beetle. After a short interval, of 20 to 30 seconds, the legs are again withdrawn inwards against the sides of the body and again rapidly extended. The various ball-rolling species have specific rhythmic patterns of brushing behaviour and certain features such as criss-crossing of the extended tibia in *Scarabaeus*.

Male *K. nigroaeneus* beetles generally arrive first at the fresh dung pad and, orientated with heads towards the wind, they take up the pheromone release stance with their bodies at an angle of roughly 45° to the dung surface, with hind-legs outstretched (Fig. 4). No comparable release stance has been observed in any female beetles.
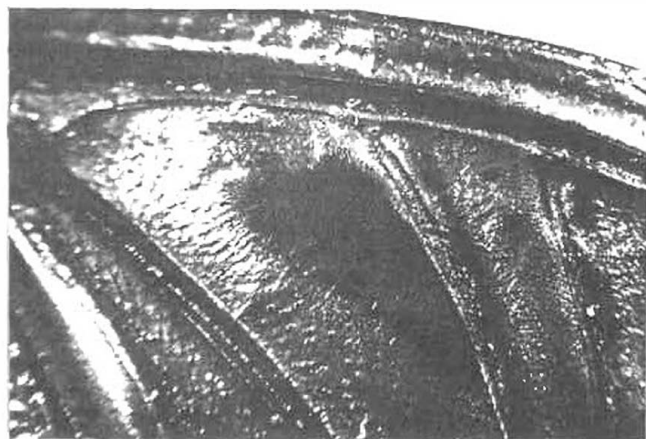

Fig. 1 Left half of the abdomen of a male *Kheper lamarcki* showing the depression filled with numerous pheromone pores and two rows of bristles.   x 9
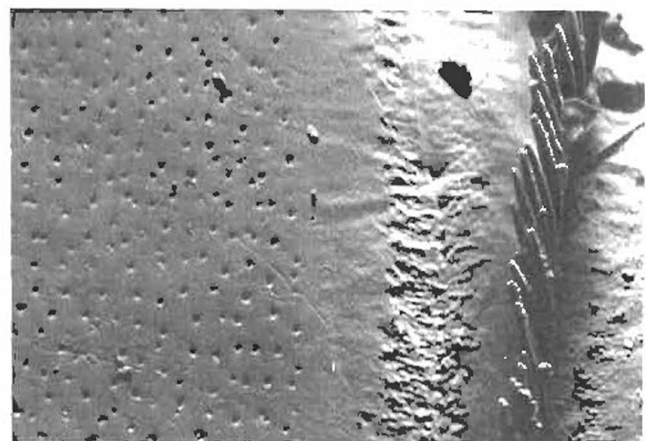

Fig. 3 Scanning electron micrograph of paraffin carrier impregnated with pheromone emerging from pores in the depression of a male *Kheper nigroaeneus*.   x 20

Fig. 2 Scanning electron micrograph of part of the depression of a male *Kheper lamarcki* showing pores and a row of bristles.   x 100

Fig. 4 Pheromone release stance adopted by the male *Kheper nigroaeneus* showing tibial brushes covered with pheromone carrier.   x 1.6

Through amputation of a hind leg, the pheromone will emerge from the incapacitated side in a continuous ribbon up to 1.5 cm long and 1 x 0.08 mm in cross-section within a period of 45 minutes and may easily be collected. By manipulating the legs of male *K. nigroaeneus* caught releasing pheromone, the process may be continued for some time. The movement of the hind legs thus appears to assist in the extrusion of the pheromone. However, it is impossible to induce a male to release pheromone by simply manipulating his legs as various external stimuli are necessary, including fresh dung and a temperature in the vicinity of 29°C.

Pheromone pores are also present on the first five abdominal sternites in *K. nigroaeneus* females and, although sparsely distributed, are concentrated on either side of the sternites but do not form definite depressions as in the male. The rows of abdominal bristles in the females are more widely spaced and are straighter and smaller than in the males.

The production of the pheromone and the behaviour associated with its release by *K. nigroaeneus*, show a number of similarities to those of other insect species. The release stance is similar to the "head-stand" adopted by carabid beetles about to discharge their defensive secretions,[1] which is in turn mimicked by glandless beetles to their advantage.[8] As with the host tree in the aggregation of the Scolytidae,[2] dung probably acts as a synergist with the *Kheper* pheromone in a similar manner. The volatile component in *K. nigroaeneus* pheromone is dispersed on a paraffin carrier (R. Crewe, personal communication), functionally comparable to the protein carrier of the butterfly *Danaus*.[6,7] Other than *Kheper*, the only other insect known to secrete paraffin hydrocarbon tubules is the late instar larva of the butterfly *Epipyrops anomala* and this is thought to be a form of excretion resulting from the ingestion of large amounts of lipids.[9]

The behaviour released by the secretion of *Kheper* is being studied in conjunction with an analysis of its chemical composition by Dr R. M. Crewe, University of Natal, Pietermaritzburg.

I wish to thank Dr Crewe for his help and the Natal Parks Board for permission to study and collect beetles in their Reserves.

G. D. TRIBE

Plant Protection Research Institute,
Private Bag X134, Pretoria, 0001.
(Attached to the Dung Beetle Research Unit,
CSIRO Division of Entomology,
Canberra, A.C.T., Australia.)

[1] Eisner, T. (1970). Chemical defence against predation in Arthropods. In *Chemical Ecology*, edit. E. Sondheimer and J. S. Simeone, Chap. 8, pp. 157–217. Academic Press. New York.

[2] Borden, J. H. (1974). Aggregation pheromones in the Scolytidae. In *Pheromones*, edit. M. Birch, Chap. 8, pp. 135–160. North-Holland, Amsterdam.

[3] Ladd, T. L. (1970). Sex attraction in the Japanese beetle. *J. econ. Ent.*, 63, 905–908.

[4] Jacobson, M. (1972). *Insect Sex Attractants*. Academic Press, New York.

[5] Percy, J. E. and Weatherston, J. (1974). Gland structure and pheromone production in insects. In *Pheromones*, edit. M. Birch, Chap. 2, pp. 11–34. North-Holland, Amsterdam.

[6] Pliske, T. E. and Eisner, T. (1969). Sex pheromone of the Queen butterfly; Biology. *Science, N.Y.*, 164, 1170–1172.

[7] Meinwald, J., Meinwald, Y. C. and Mazzocchi, P. H. (1969). Sex pheromone of the Queen butterfly; Chemistry. *Science, N.Y.*, 153, 1174–1175.

[8] Raske, A. G. (1967). Morphological and behavioural mimicry among beetles of the genus *Moneilema* (Coleoptera, Cerambycidae). *Pan-Pacif. Ent.*, 43, 239–244.

[9] Marshall, A. T., Lewis, C. T. and Parry, B. (1974). Paraffin tubules secreted by the cuticle of an insect *Epipyrops anomala* (Epipyropidae, Lepidoptera). *J. Ultrastruct. Res.*, 47, 41–60.