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A COMPARATIVE STUDY OF AGONISTIC BEHAVIOUR IN HAIRY-FOOTED
GERBILS OF THE GENUS *GERBILLURUS* (Shortridge, 1942)

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PREFACE

The experimental work described in this thesis was carried out in the Department of Zoology, University of Natal, Pietermaritzburg, from July, 1984 to December, 1986, under the supervision of Professor M.R. Perrin.

These studies represent original work by the author and have not been submitted in any form to another University. Where use was made of the work of others it has been duly acknowledged in the text.

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ABSTRACT

Agonistic behaviour was investigated by means of staged encounters in three species and two subspecies of deserticolous rodents of the genus *Gerbillurus*. Individuals of the species *G.paeba paeba*, *G.paeba exilis*, *G.tytonis*, *G.setzeri*, and *G.vallinus* were used in intraspecific and interspecific encounters. Intraspecific territoriality was tested in animals of the same sex of the species *G.p.paeba*, *G.tytonis*, and *G.setzeri*.

Analysis of agonistic behaviour permitted identification of four groups of behaviours in most classes of intraspecific encounters. These were "exploratory and solitary", "aggressive", "submissive", and "sexual" behaviours. Males of four species were less aggressive than females in same-sex encounters, and were dominated by females in different-sex encounters; the reverse was observed in *G.setzeri*. Male *G.tytonis* and *G.setzeri* were more tolerant of conspecifics in the territoriality apparatus than females were.

In *G.tytonis-G.p.paeba* encounters a hierarchy emerged: female *G.tytonis* were most aggressive, followed by female *G.p.paeba*, male *G.tytonis*, and finally male *G.p.paeba*. In areas of syntopy, *G.tytonis* may displace *G.p.paeba* through aggressive interactions. A reduction in the level of aggression was exhibited in *G.p.paeba-G.setzeri* and *G.tytonis-G.setzeri* interactions. This result may reflect

the phylogenetic divergence and selection of a different habitat by *G.setzeri*. *G.vallinus* dominated *G.p.paeba*, a result which may have been influenced by past experience and body size, since these two species are syntopic and *G.vallinus* is larger than *G.p.paeba*.

Cluster analysis of behaviour profiles of different species and sexes revealed two groups, which agree partially with the karyology of the genus. *G.p.paeba* and *G.tytonis* formed one cluster, while *G.setzeri* and female *G.p.exilis* formed a second group. Male *G.p.exilis* and *G.vallinus* were less closely related to both groups. It is suggested that several stages in the process of speciation are represented in species of this genus. A range of social types is exhibited from solitary (*G.p.paeba* and *G.tytonis*) through semi-tolerant (*G.setzeri* and female *G.p.exilis*) to tolerant (male *G.p.exilis* and *G.vallinus*). Habitat has a strong influence on social type.

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CHAPTER 1. AIMS AND OBJECTIVES

The term "agonistic behaviour" refers to any combative behaviour involving a struggle or contest among individuals of the same species (King, 1973). Agonistic behaviour has been listed as one of the parameters determining the spatial arrangements and resource utilization by animals in a particular habitat (Delany, 1974). This study examines agonistic behaviour in four species of deserticolous rodents of the genus *Gerbillurus*. The purpose of the study was threefold:

- 1) To investigate the nature of agonistic behaviour in the four species.
- 2) To compare the agonistic behaviour between species and to relate this to the phylogeny of the species.
- 3) To investigate patterns of dominance and submission in interspecific encounters between species which are sympatric.

1.1 INTERFERENCE COMPETITION

Interference competition has been defined as competition which occurs when the organisms seeking a resource harm one another in the process, even if the resource is not in short supply (Birch, 1957). Such competition may be interspecific or intraspecific (Krebs, 1985). Krebs (1985) has proposed that competitive ability in organisms has evolved by animals becoming more efficient resource users or by developing interference mechanisms that keep

competing species from using scarce resources. A result of the evolution of interference between species is that it will often affect members of the same species as well (Krebs, 1985).

In contrast to Krebs' conceptualisation, Branch (1985) has suggested that interspecific competition may have arisen as a result of intraspecific competition or predation, which later proved adaptive against interspecific competitors.

Aggressive behaviour in animals has been superimposed on competition for resources in many situations. An idealized evolutionary gradient of competition in relation to population density has been proposed (Krebs, 1985):

Low density - colonization and growth
↓
High density - resource competition
↓
High density - interference mechanisms prevent
resource competition

Branch (1985) has proposed that the nature and outcome of interspecific competition is dependent on species characteristics (i.e. mobile or sessile), the limiting resource and the mode of competition. Mobile species compete more often for food than for space, and this competition is more frequently expressed in the form of exploitation than interference. Exploitation involves dominant individuals attaining and using most of a resource, whereas interference involves one individual interfering with another in such a way as to deny it access to a

resource. The outcome of exploitation is coexistence, with one species becoming dominant, while the outcome of interference is competitive exclusion. This is supported by evidence from competing species of marine invertebrates in sympatry compared with conspecifics in allopatry.

Competitive interaction for space seems likely to be a general phenomenon among rodent species, and it has been shown that there is considerable overlap in diets in at least three pairs of inferred competitors in North America (Grant, 1972). Aggression between sympatric species utilizing similar resources has been investigated in a number of rodent species (Grant, 1972; Cranford & Derting, 1983).

In instances where field evidence indicates that one species might be competitively superior to the other, it is also generally the dominant one in laboratory encounters (Grant, 1972). The validity of extrapolation of results from laboratory encounters to the natural environment has been queried (Banks & Fox, 1968); however "natural" experiments investigating agonistic behaviour in rodents would be extremely burdensome to conduct. Where two or more species coexist it seems unlikely that they would have developed a system of complete behavioural avoidance, particularly where resources are limited. Although it is unlikely that the intensity of interaction observed in laboratory-based studies would ever occur in nature, it is

nevertheless felt that laboratory results can be used cautiously as indicators of what happens in the natural situation (Banks & Fox, 1968).

The components of intraspecific aggression are usually the same in form as those used in predator-prey or interspecific interactions (King, 1973; Grant, 1972). Huntingford (1976) has provided evidence of motivational links between aggressive behaviour expressed towards conspecifics, predators, and potential prey. However, the function of intraspecific aggression is different. Winners in an agonistic encounter may gain social status, access to resources, freedom of movement and reproductive success, while losers are more likely to be killed, injured or chased away and may be reproductively repressed (King, 1973). Frequent agonistic encounters may result in physiologically stressed individuals which readily succumb to shortages of necessary resources, are exposed to predation and severe weather, or fail to mature and reproduce (King, 1973). Agonistic behaviour often increases with population density, with the result that selection favours animals possessing those attributes which render them more successful in agonistic encounters (Grant, 1972). Consequently, genetic factors become involved in the control of behaviour (Krebs, 1970). Some ecological factors influenced by agonistic behaviour are reproduction, dispersion, dispersal and the gene pool (King, 1973).

1.2 EVOLUTION

Interspecific competition may influence the evolution of a species in four ways:

- a) the species becomes extinct or rare
- b) the niche width becomes reduced or shifted
- c) improved competitive ability is selected for
- d) the likelihood and nature of speciation is influenced.

(Branch, 1985; Grant, 1972)

Branch (1985) has proposed a "competitive elimination hypothesis" which considers the role of competition, amongst other selective agents, in shaping the nature of a species at its inception. Species-specific characters could be fixed in the genetic component of a newly-arising species; niche breadth is restricted by the presence of competitors and genotypes which overlap substantially with existing species are eliminated. Areas where congeners coexist are generally areas of increasing specialization of species. An implication of the competitive elimination hypothesis is that in any group of coexisting related species, the first species to evolve should be a generalist, while subsequent species should be increasingly specialized.

Recent views on the nature of speciation suggest that it is most likely in small, isolated populations, occurs relatively rapidly, and involves the fixation of certain characters followed by periods of stasis. Branch's (1985)

hypothesis coincides with these ideas as well as considering the possibility that species-specific characteristics, such as specialization, may be promoted by competition.

Diamond (1986) has identified seven stages in the process of speciation and has provided evidence from the montane avifauna of New Guinea to support these evolutionary stages. Briefly, these stages are:

1. A single subspecies which does not vary geographically is found throughout the habitat.
2. A chain of subspecies differentiates, varying through the geographical area occupied by the species.
3. Local extinctions result in distributional gaps between populations of different subspecies.
4. The degree of difference between geographically isolated subspecies increases until the populations are reproductively isolated and can be considered allospecies.
5. The sister species expand their distribution until they overlap in the area representing the limits of their distribution, but areas of allopatry of both species still exist.
6. One species expands its distribution until it completely over-runs the sister species, but it still retains an area of allopatry.
7. The remaining taxon expands its distribution until the two species are completely sympatric throughout the habitat.

Diamond (1986) has provided evidence that in the montane

avifauna of New Guinea, ecological segregation evolved more frequently in sympatry than in allopatry, i.e. at stage 5 in the speciation process. However, if at stage 2 or 3, the isolated subspecies inhabit areas which differ markedly, then ecological segregation may occur earlier. Further, Diamond (1986) found support for the hypothesis that sympatric competing species tend to evolve in such a way as to reduce competition between them, and that the further speciation has progressed through steps 1 to 7, the more fixed the niche requirements are. However, Diamond (1986) suggests that this outcome is dependent on whether niche differences tend to evolve in sympatry rather than in allopatry. If niche differences evolve in allopatry, the "ghost of competition past" hypothesis may not apply.

1.3 SUBJECT SPECIES

The hairy-footed gerbils, genus *Gerbillurus* (Shontridge, 1942) are deserticolous rodents endemic to Southern Africa (De Graaff, 1981). They have large eyes and tympanic bullae; hindlimbs are well developed, and associated with their saltatorial mode of locomotion. The tail is longer than the head-body length and bears a tassel of long hairs at the tip (De Graaff, 1981). Four species are recognized: *Gerbillurus paeba*, *G. tytonis*, *G. vallinus*, and *G. setzeri* (Meester et al., 1986). Details of the taxonomy and distribution of the species comprising this genus are given in Chapter 2 of this thesis.

Boyer (pers. comm.)* has found extensive overlap in the diets of *Gerbillurus paeba paeba* and *G.tytonis* in the eastern region of the Namib dunefield, where the two species are sympatric and syntopic. Partial spatial separation in habitat selection may occur at certain seasons, since *G.paeba* were more frequently trapped on the dune trough and slope, and *G.tytonis* on the dune crest. *G.p.paeba* and *G.setzeri* have both been trapped at Rössing, South West Africa, (Downs & Perrin, pers.comm.*); while *G.setzeri* is reported to cross the Kuiseb River at times and enter the sand dunes, which are normally occupied by *G.tytonis* (De Graaff, 1981). All three species have been trapped at Gobabeb (De Graaff, 1981). *G.vallinus vallinus* and *G.p.paeba* are sympatric and syntopic in the northern Cape province (Erasmus #, pers. comm.), although *G.p.paeba* was more frequently trapped in areas of softer sand, while *G.vallinus* was more abundant on the harder gravel plains. An isolated population, *G.paeba exilis*, has been found in the Alexandria dunefield, eastern Cape Province (De Graaff, 1981).

No information has been published on dietary preferences, habitat selection or activity in these co-existing species.

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Competition for food and water is likely to be high in arid areas where these resources are severely restricted. However, competition for space (suitable nest-sites) and mates may also occur.

Species of the *Gerbillurus* genus provide an excellent opportunity for examining interference competition in three groups of sympatric species, and for comparing the behaviour of individuals of allopatric populations of one species. Comparison of agonistic behaviour in intraspecific encounters may elucidate the phylogeny of the group, while also providing information on the social structure and dispersion of animals in the natural environment. This formed the basis of this thesis, which was part of a larger study on the evolution of ecological segregation in the species of the genus *Gerbillurus*. Boyer (pers. comm.) has investigated the ecology of *G.tytonis* and *G.p.paeba* in the Namib Desert, while Ascaray (1984) examined the ecology of *G.p.exilis* in the Alexandria dunefield. Downs (pers. comm.) is studying eco-physiology in species of the genus *Gerbillurus*. Perrin (pers. comm.) has investigated water turnover rates in *G.tytonis* in the field and will examine gastric morphology in species of this genus.

1.4 TERRITORIALITY

Territoriality results from the behaviour of animals maintaining an exclusive area by aggressive or ritualized

means (Huntingford, 1984). Territory defence may be passive, e.g. by scent marking, vocalisations or the production of toxins, or active, by means of agonistic interactions. The benefits resulting from territoriality may include an improved food supply, mate acquisition, young-rearing and/or predator avoidance (Huntingford, 1984). In extremely arid areas, where the carrying capacity of the environment is typically low, rodent species may exist at low densities, and evidence indicates that spacing mechanisms may be operative (Eisenberg, 1975). These spacing mechanisms may operate at the intraspecific level, but interspecific spacing may also be important in areas of syntopy. Among the heteromyid rodents, most of the species investigated appeared to be intolerant of conspecifics in the same burrow system, although home ranges may be shared (Eisenberg, 1975). Territorial defense appeared to be restricted to the burrow and a limited area around the burrow, ensuring defense of the seed cache.

Marked aggressive behaviour is generally shown by normally solitary species when artificially confined. Eisenberg (1967) has reported that the testing of social tolerance in captivity will often correlate with distribution patterns found in the field. Although solitary burrow occupancy is characteristic of heteromyid rodents, other arid-adapted rodents show a range of social organisations. Within the

subfamily Gerbillinae, *Gerbillus nanus* is relatively solitary while *Tatera indica* has a communal social structure based on the extended family group (Eisenberg, 1967). Thus despite the dispersed food supplies, which may be conducive to the development of a solitary social system, other factors may be involved in selection for a certain social system. Predator avoidance, food caching, burrow construction, reproductive behaviour and parental care may all influence the spacing system selected for in a species (Eisenberg, 1967).

Although some information is available on the area and dispersion of home ranges of *G.paeba exilis* (Ascaray, 1984), *G.paeba paeba* and *G.tytonis* (Boyer, pers. comm.), nothing is known of the social systems or territorial behaviour of the species within the *Gerbillurus* genus. In this study, a preliminary investigation was made into space utilization by groups of four animals of the same sex and species; space utilization was investigated in *G.paeba paeba*, *G.tytonis* and *G.setzeri*.

CHAPTER 2. LITERATURE SURVEY

2.1 HISTORY OF THE TAXONOMY OF THE GENUS GERBILLURUS

The pigmy gerbils were first placed in the genus *Gerbillus* by Desmarest in 1804. *Gerbillus swalius*, later re-named *Gerbillurus paeba* was found extensively in South-West Africa (Shortridge, 1934). Shortridge (1934) also reported that *Gerbillus calidus* had a wide range in Botswana, and that *Gerbillus paeba* was found in the western part of the Cape Province. The eastern record of the genus appeared to be in the Soutpansberg, and the species found there was named *Gerbillus coombesi*. *Gerbillus vallinus* was first described by Thomas in 1918 (Shortridge, 1934). It was described as being similar in size to *G. paeba*, but with an unusually large area of the hindfoot soles naked, and with very large auditory bullae. It was trapped in Namaqualand (northern Cape), where it was recorded as the only plentiful gerbil in the area.

Shortridge (1942) subsequently proposed the new subgenus *Gerbillurus* in order to separate the Southern African pigmy gerbils from the North African members of the genus *Gerbillus*. The division was based on the shape and position of the tympanic bullae, the presence of a white patch behind the short ears, the presence of a tufted tail, and the hairy soles of the hindfeet of *Gerbillurus* (De Graaff, 1981). Davis (1975), however, is not convinced that the Southern African pigmy gerbils should be separated from the North

African genus, nor that *G.paeba* and *G.vallinus* belong in the same subgenus or genus. There is agreement that the previously-recognised species *Gerbillus swalius*, *Gerbillus calidus* and *G.coombsi* are members of a single species, now named *Gerbillurus paeba*, and Meester et al. (1986) are of the opinion that *Gerbillurus* is a valid genus. Pavlinov (1982) has placed *Gerbillurus paeba* in the subgenus *Progerbillurus* and has retained the subgenus *Gerbillurus* for *Gerbillurus vallinus*.

Gerbillurus tytonis was first described by Bauer and Niethammer (1959) from skulls recovered from the pellets of the barn owl, *Tyto alba*. It was originally described as a subspecies of *Gerbillus vallinus*, but later raised to species rank by Schlitter (1972) and Davis (1975). Petter (1983) has placed *G.tytonis* in the subgenus *Paratatera*, a decision which has provisionally been accepted by Meester et al. (1986). *Gerbillurus setzeri* was first described by Schlitter (1972), and has been placed in the subgenus *Gerbillurus* by Meester et al. (1986). *G.vallinus* is regarded as a rare species and is listed in the South African Red Data Book (Meester, 1976)

2.2 CURRENT TAXONOMIC STATUS AND DISTRIBUTION OF THE SPECIES BELONGING TO THE GENUS GERBILLURUS. (Meester et al., 1986)

SUBGENUS PROGERBILLURUS Pavlinov, 1982

Gerbillurus paeba paeba (A.Smith, 1836). Found throughout the

drier western areas of southern Africa.

Gerbillurus paeba coombsi (Roberts, 1929). Isolated population found in the Soutpansberg, northern Transvaal.

Gerbillurus paeba exilis (Shortridge & Carter, 1938). Isolated population from the sand dunes along the coast from the Sundays River mouth to St. George's Strand, eastern Cape.

Gerbillurus paeba infernus (Lundholm, 1955). Isolated population from the northern Namib, South West Africa.

Gerbillurus sp. aff. paeba. A darker grey form found on the Cape Flats, and believed to be a new species (De Graaff, 1981).

SUBGENUS PARATATERA (Petter, 1983)

Gerbillurus tytonis (Bauer & Niethammer, 1959). Found only on the shifting red sand dunes of the Namib Desert, south of the Kuiseb River, South West Africa.

SUBGENUS GERBILLURUS (Shortridge, 1942)

Gerbillurus vallinus vallinus (Thomas, 1918). Found in the northwestern Cape from Kenhardt in the east to the lower Orange River. Erasmus (pers. comm.) reports that their distribution extends south of the Orange River to Brandvlei in the west and Prieska to the east, and that they are common in parts of their range.

Gerbillurus vallinus seeheimi (Lundholm, 1955). From the Kuiseb river (Gobabeb area) to the Karas Mountains, South West Africa. Griffin⁺ (pers. comm.) disagrees that
⁺ Mr. M. Griffin, S.W.A. Nature Conservation, P/Bag 13186, Windhoek.

G.vallinus occurs as far north as the Kuiseb River, and this record may be for *G.setzeri*.

Gerbillurus setzeri (Schlitter, 1972). Found on the gravel plains north of the Kuiseb River. Since this species was only recognized in 1972, earlier records of *G.vallinus* may in fact be *G.setzeri*.

Karyotypes of the four species recognized by Davis (1975), the four subspecies of *G.paeba* and the unnamed species from the Cape Flats have been prepared by Schlitter, Rautenbach and Coetzee (1984). *G.paeba* and *G.tytonis* both have a diploid number of 36 (confirmed by Capanna*, pers. comm.) with 68 autosomal arms; and the two species were indistinguishable on the basis of the standard karyotype. Specimens of all four subspecies of *G.paeba* and the unnamed species from the Cape Flats were found to be karyotypically similar. Consequently, it was suggested that the unnamed species should be recognized as a subspecies of *G.paeba* and named *G.paeba mulleri*. It was further suggested that *G.tytonis* should not be placed in a separate subgenus from *G.paeba*, although there are morphological differences in the skulls of the two species.

G.vallinus and *G.setzeri* both have a diploid number of 60 with *G.vallinus* having 80 autosomal arms while *G.setzeri* has 78 autosomal arms. Capanna (pers. comm.) has confirmed the

* Prof. E. Capanna, Dipartimento di Biologia Animale, Università di Roma.

chromosome number for *G.vallinus*. It is suggested that these two species form a closely related species group, although not as closely related as *G.paeba* and *G.tytonis*.

Qumsiyeh (1986) has examined G- and C-banding on chromosomes of *G.paeba* and *G.vallinus*, and has confirmed the chromosome numbers for these two species. On the basis of comparison of chromosome structure, Qumsiyeh (1986) has suggested that *G.paeba* and *G.vallinus* arose from a common ancestor that had a diploid number of 44 chromosomes.

Karyotyping and chromosome structure have elucidated some aspects of the taxonomic and phylogenetic affinities of the genus; comparative behavioural studies may assist in unravelling the evolution of this taxon.

2.3 GENERAL BIOLOGY OF THE STUDY SPECIES.

With the possible exception of taxonomy, studies of the species belonging to the genus *Gerbillurus* are poorly represented in the literature, with only a few papers on *G.paeba* and little or no information on the other three species.

All members of the genus dig burrows (De Graaff, 1981) and are thought to be nocturnal. The nocturnal habit of *G.paeba* in the laboratory has been confirmed (Perrin, 1981a).

Tunnel systems of *G.paeba paeba* have been excavated in the

Nossob River bed (De Graaff & Nel, 1965) and in the area south of Gobabeb (Holm & Scholtz, 1980; Downs & Perrin, pers. comm.). Firm sand was selected, and burrows were frequently constructed under the roots of narra plants (*Acanthosicyos horrida*). No nests were found, but a few narra seeds and plant fragments were found. *G.p.exilis* burrows excavated in the Alexandria dunefield were constructed among the roots of *Gazania* plants and contained large grass nests and stored food (Ascaray, 1984; Dempster, unpubl. obs.). Burrows excavated by Laycock (1975) in a dune valley south of the Kuiseb river and 10km west of Gobabeb were reported to belong to *G.p.paeba*. Since *G.p.paeba* is seldom trapped in this area, it is more likely that these burrows were constructed by *G.tytonis* (Perrin, pers. comm.). These burrows and several excavated by Downs and Perrin (pers. comm.) contained some stored food, but no nest.

Burrow entrances of *G.setzeri* were less than 1m apart, and 3 - 8 entrances were found in one mound. Tunnels were interleading, but contained no nest material or stored food (Downs & Perrin, pers. comm.). Burrows of *G.vallinus* in the Northern Cape are also reported to be interleading (De Graaff, 1981).

Aspects of the ecology of *G.p.paeba* in the southern Kalahari have been reported by Nel and Rautenbach (1975), and Nel (1978; 1983). It was the most commonly trapped rodent in

all habitats studied and was subject to wide population fluctuations. *G.p.paeba* coexisted with a number of rodents, including *Rhabdomys pumilio* in the riverbed habitat, and *Desmodillus auricularis*, *Tatera brantsii* and *Mus minutoides* on the low dune habitat. Considerable overlap in activity and food selection existed among *T.brantsii*, *D.auricularis* and *G.p.paeba* (Nel, 1978). The diet consisted of equal quantities of "white" (seeds, roots and stems) and "green" plant material and also insects in summer. In winter, more "white" than "green" plant material was taken.

G.p.exilis was the only rodent species resident in the dune slacks in the Alexandria dunefield (Ascaray, 1984). Population numbers fluctuated markedly, with highest numbers occurring in late summer following spring and summer breeding. The diet consisted chiefly of seeds, particularly of *Arctotheca populifolia*, and arthropods in summer.

With regard to predation, *Gerbillurus* spp. have been found to constitute the major portion of the diet of two Namib Desert owl species, *Tyto alba* and *Bubo africanus* (Tilson & Le Roux, 1983; Skinner et al., 1980; Nel, 1969; Stuart, 1975)

Microhabitat preference and reproductive rate relative to water availability has been investigated in *G.p.paeba*, *R.pumilio* and *D.auricularis* at two study sites on the

eastern border of the Namib Desert (Christian, 1979a, 1980). The provision of additional water resulted in extension of the breeding season of *G.p.paeba* and *R.pumilio*, but not *D.auricularis*. Water turnover rates of *G.p.paeba* and *R.pumilio* were lower than that of *D.auricularis*, hence Christian (1979b) has suggested that the latter species has better water-conserving abilities than the former two species.

The dependence of *G.p.paeba* on an exogenous supply of water in the diet has been reported (Louw, 1972; Withers, Louw & Henschel, 1980), while Buffenstein (1985) found that *G.p.paeba* was able to survive indefinitely on a diet of millet without access to free water. The presence of crystalline allantoin in the urine of *G.p.paeba*, *G.tytonis* and *G.setzeri* resulted in a considerable saving of water (Buffenstein, Campbell & Jarvis, 1985).

G.p.paeba had a high daily energy expenditure (D.E.E.) (Withers, Louw & Henschel, 1980), but this declined when the animals' diet had a high fibre content with ad lib. water (Buffenstein, 1985). The high D.E.E. was thought to be due to the high level of activity exhibited by the animals in captivity (Withers, Louw & Henschel, 1980).

The nocturnal activity cycle and burrow occupancy of *G.p.paeba* has been related to its ability to survive the extreme heat and low atmospheric humidity in its environment

(Louw, 1972). *G.p.paeba* was unable to survive temperatures above 38°C (Buffenstein, 1985) and did not control its body temperature precisely over a range of ambient temperatures (Nel & Rautenbach, 1977). Evaporative cooling mechanisms such as salivation and panting were evoked at high ambient temperatures (Buffenstein, 1984). The distribution of *G.p.paeba* may be limited by its dependence on burrows to enable it to avoid the extremes of temperature and humidity experienced in arid areas (Buffenstein, 1984). In the light of the dependence of these animals on burrows, competition for space is likely to be a major factor in determining the distribution of individuals in their habitat.

The breeding of captive gerbils has been described for *G.p.exilis* (Ascaray, 1984), *G.p.coombsi* (Hallett & Keogh, 1971), *G.p.paeba* (Stutterheim & Skinner, 1973; Dempster & Perrin, in prep.) and *G.tytonis* (Dempster & Perrin, in prep.). Young are altricial and develop slowly in each species, with *G.tytonis* having the slowest rate of growth and development. *G.p.exilis* young are reported to nipple-cling (Ascaray, 1984), while *G.p.paeba*, *G.p.coombsi* and *G.tytonis* do not. Litters of *G.p.exilis* varied in size between 1 and 6, with a mean of 3.7 (n = 14); *G.p.paeba* had litters of 2 - 6 young (mean 4.6; n = 7) and *G.tytonis* had litters of 2 - 6 young (mean 4.7; n = 7).

The general behaviour of *G.p.coombsi* (Hallett & Keogh, 1971) and *G.p.paeba* (Stutterheim & Skinner, 1973) has been

described. Animals of both subspecies were very active during the dark phase of their light cycle, and spent much of their time digging in the sand. Grooming, nest-building, and food-hoarding were reported in both subspecies. Hamer (1985) investigated sandbathing and grooming in *G.p.paeba* and *G.tytonis*, and reported that both species performed the same actions in sandbathing and grooming, but the frequencies of acts differed between the two species.

CHAPTER 3. METHODS AND MATERIALS

3.1 TRAPPING AND MAINTENANCE

Seven *G.paeba* (5 females and 2 males) and twelve *G.tytonis* (7 females and 5 males) were trapped in the area south of Gobabeb (23°37'S 15°01'E) during August 1984. Twelve *G.setzeri* (7 females and 5 males) were trapped near Rössing Uranium Mine (22°31'S 14°52'E) in June 1985. Nine *G.paeba exilis* (5 females and 4 males) were trapped in the Alexandria Dunefield (33°41'S 25°49'E) in December 1985. One *G.vallinus seeheimi* male was trapped near Keetmanshoop (26°36'S 18°08'E) in June 1986, and four *G.vallinus vallinus* (3 males and 1 female) were trapped near Copperton (29°59'S 22°17'E), Northern Cape in August, 1986. Six *G.paeba* were also trapped in the same area on this excursion and returned to the laboratory.

All gerbils were toe-clipped on arrival at the Animal House at the Department of Zoology, University of Natal, Pietermaritzburg, and housed in aquarium tanks (60 x 30 x 30cm) provided with a layer of sand and a plastic bottle as a nest box. Food was provided ad libitum and consisted of a mixture of sunflower seed, wild bird seed, rolled oats and "Pronutro", supplemented with carrots, fresh greens, mealworms and alate termites. Water was provided ad libitum. The light regime was 16L:8D using light supplied by a 100W light bulb. The circadian photoperiod was reversed; temperature was maintained at 25°C.

3.2 AGONISTIC ENCOUNTERS

Agonistic encounters were staged in a 60 x 30 x 30cm aquarium tank provided with a 3 - 4cm layer of sand. This sand was thoroughly mixed between encounters and changed after 10 - 15 encounters, when the tank was also washed out with soap and water. A partition was used to separate the opponents initially and they were permitted to investigate the tank for a few minutes before the partition was removed. Lighting was provided by a 40W red light bulb positioned above the tank. All encounters were staged during the dark phase of the light cycle when the animals were most active. Individual animals were not used repeatedly over a short period of time.

After removal of the partition, the first 10 minutes of the encounter were recorded using a video camera (JVC Model TK1700EG) and recorder (National Portable VCR NV-180). The animals were weighed after the encounter and the condition of the genitalia was noted. Males were recorded as having scrotal testes if the testes were clearly descended and the epididymes were visible. Testes were recorded as abdominal if they were not visible and could not be pushed down into the scrotum. A third category, "testes intermediate" was used for animals which had testes visible in the scrotum, but where the epididymes were not visible. Females were recorded as having perforate or imperforate vaginae. Dominance was subjectively assigned to the animal which

clearly chased and attacked more frequently than its opponent; encounters in which no overtly aggressive behaviour occurred were recorded as "draws".

Videotapes were analysed first by identifying and describing the postures and acts exhibited by the animals during encounters. Thirty-two behavioural acts and postures were described and where possible sketches were made of the postures (Appendix 1). Two acts, "urinate" and "mark", were later eliminated from the list since it was found that they could not be reliably identified from the videotapes. "Roll over" occurred less than ten times in any species, and this behaviour was also eliminated from the analysis. Two-letter codes were derived for each behaviour, and were used in the transcription of tapes, which was done by hand. Each animal's number and the code were recorded for each behaviour exhibited in an encounter. The VCR used was equipped with "slow forward", "still frame" and "single frame" advance facilities, and this permitted a high degree of precision in the analysis of very rapid sequences. Duration of acts was not taken into account for this analysis, and acts were recorded when an animal changed its behaviour. In order to determine the accuracy of identification of the various acts and postures, five randomly-selected encounters were re-analysed several weeks after the first analysis.

Encoded encounters were entered on a HP150 microcomputer

using a BASIC programme written for this purpose (Appendix 2). Each encounter was stored on a disc in the coded form, whereafter various forms of statistical analysis were applied. The frequency of occurrence of each behaviour for each of the two animals in an encounter was calculated and printed. Comparison of frequencies of occurrence of acts by means of chi-square contingency table analysis was performed to test the null hypothesis that different species do not differ in the frequencies of performance of behavioural acts in agonistic encounters. The frequency of occurrence of all possible sequences of two actions for each individual in an encounter was calculated and printed as a 30 x 30 matrix.

In addition to analysing individual encounters, the programme also created accumulative files to store the results of a number of encounters of a certain class. A "class" of encounters refers to a group of encounters involving the same combination of species and sexes. For example, the results for frequencies of occurrence of acts for female *G.p.paeba* versus female *G.p.paeba* encounters were stored in one accumulative file, while the results for female *G.tytonis* vs *G.tytonis* were stored in another accumulative file. Similarly, the results for sequences of acts were stored in separate accumulative files for any class of encounter.

The following classes of encounters were staged and analysed:

Intraspecific encounters. (Eight encounters of each class were staged, unless stated otherwise.)

Male versus male: *G.p.paeba*

G.p.exilis

G.tytonis

G.setzeri

G.v.vallinus (4 encounters)

Female versus female: *G.p.paeba* (10 encounters)

G.p.exilis

G.tytonis

G.setzeri

Male versus female: *G.p.paeba*

G.p.exilis

G.tytonis

G.setzeri

G.vallinus (3 encounters)

Interspecific encounters. (Five encounters of each class)

G.paeba paeba female versus *G.tytonis* female

G.paeba paeba female versus *G.tytonis* male

G.paeba paeba female versus *G.setzeri* female

G.paeba paeba female versus *G.setzeri* male

G.paeba paeba female versus *G.paeba exilis* female

G.paeba paeba female versus *G.paeba exilis* male

G.paeba paeba male versus *G.tytonis* male

G.paeba paeba male versus *G.tytonis* female

G.paeba paeba male versus *G.setzeri* male

G.paeba paeba male versus *G.setzeri* female

G.paeba paeba male versus *G.paeba exilis* male
G.paeba paeba male versus *G.paeba exilis* female
G.tytonis female versus *G.setzeri* female
G.tytonis female versus *G.setzeri* male
G.tytonis male versus *G.setzeri* male
G.tytonis male versus *G.setzeri* female
G.v.vallinus female versus *G.p.paeba* (N.Cape) female (1 encounter)
G.v.vallinus female versus *G.p.paeba* (N.Cape) male (1 encounter)
G.v.vallinus male versus *G.p.paeba* (N.Cape) male (3 encounters)
G.v.vallinus male versus *G.p.paeba* (N.Cape) female (3 encounters)

A total of 105 intraspecific and 88 interspecific encounters were analysed.

When all the encounters in a certain class had been completed, the results from accumulative files were printed. Total frequencies of each act were printed, mean frequency per fight and relative frequency of occurrence of each act were calculated and printed. Relative frequency was calculated as described by Martin (1984), i.e.

$p = n(k)/N$ = relative frequency of events for kth variable

where N = total number of events for all variables

n = observed number of events

k = variable

$n(k)$ = observed frequency of kth variable

These frequencies were converted to percentages for ease of manipulation.

Analysis of sequences was restricted to dyads, or using Markov chain terminology, first order chains (Lehner, 1979). A first order chain is defined as "the probability of occurrence of a particular behaviour is dependent on only the immediately preceding behaviour" (Lehner, 1979).

The occurrence of each dyad was calculated as follows (Martin, 1984):

$$P_{jk} = n(j,k)/T_j$$

where $n(j,k)$ = number of occurrences of j th variable followed by k th variable

T_j = total of j th row

P_{jk} = probability of occurrence of dyad j,k

Probabilities were converted to percentages, and those less than 10% were omitted. Dyads which occurred less than 10 times (5 times in *G.vallinus* males) were omitted from the analysis. This permitted identification of the most common dyads, which were used to generate kinematic graphs illustrating the most likely sequence of events (Martin, 1984).

3.3 TERRITORIALITY

Territorial behaviour was observed in an observation chamber constructed for this purpose as shown in Appendix 3. One animal was placed in each section of the box with the partitions in place. After one week, each animal was

marked on the ears with water-soluble fluorescent paint (Kryolan Day Glow face painting cream) and the partitions were removed. On the following seven to twelve days, the animals were observed under an ultraviolet light and their movements were recorded on a tape recorder. Observations were of the "focal animal type" (Lehner, 1979), with the movements of each animal being recorded separately and continuously for five minutes. In order to record the movements, the chamber was divided into five areas: the centre box, and boxes A, B, C, and D which included the tunnels leading to these boxes.

A Basic programme was written to calculate the total time spent in each box during the five-minute observation period and the number of visits to each box. Two repeats of each of the following sets of animals were observed: female *G.paeba paeba*; male *G.paeba paeba*; female *G.tytonis*; male *G.tytonis*; female *G.setzeri*; and one set of male *G.setzeri*. Due to insufficient numbers of animals, *G.paeba exilis* and *G.vallinus* were not observed in this apparatus.

CHAPTER 4 RESULTS

4.1 INTRASPECIFIC ENCOUNTERS

Wild-caught animals of all species were used in intraspecific encounters, in addition lab-bred animals of *G.p.paeba* and *G.tytonis* were used. The numbers of individuals of each species used in these encounters are shown in Table 1.

TABLE 1: NUMBERS OF INDIVIDUALS OF EACH SPECIES USED IN ENCOUNTERS.

SPECIES	NO. OF MALES	NO. OF FEMALES
<i>G.p.paeba</i>	7	11
<i>G.p.exilis</i>	4	5
<i>G.tytonis</i>	9	10
<i>G.setzeri</i>	5	7
<i>G.vallinus</i>	3	1
<i>G.p.paeba</i> (N.Cape)	3	3

Descriptions of the behavioural acts and postures identified in agonistic encounters are given below. Diagrams of some postures are included in Appendix 1.

CODES AND BEHAVIOURS IDENTIFIED IN AGONISTIC ENCOUNTERS

AD = Attend: The animal is immobile, watching the opponent. The body of the animal attending is rounded or slightly elongated; the ears are pricked and tail prostrate. This behaviour may be performed between bouts of "exploring", "grooming", or "sandbathing".

XX = Kick back: The animal crouches on the sand and kicks the sand back with its hindfeet. A tense posture with attention focussed on the opponent is usually associated with this behaviour.

DR = Drumming: An animal drums by striking the substrate with the hindfeet alternately, producing a pattering noise. *G.setzeri* differs from the other species in that drumming does not produce an audible noise, and the animal seems to "shiver" its hindquarters rather than "drumming".

AP = Approach: The animal approaches its opponent by means of quadrupedal saltations; the body is rounded, ears are pricked, and tail is prostrate.

SN = Sniff head region: Opponents stretch towards each other and sniff noses. They may also turn their heads slightly and sniff each other's cheeks and under each other's chins.

EX = Explore: The animal moves around the test arena sniffing the sand and digging in various places.

MA = Move away: One animal moves away from the opponent after a contact. The body is rounded and the animal moves by quadrupedal saltation or walking.

SI = Sit: An animal sits immobile, the body is rounded and the animal is not watching its opponent as in "attend".

EA = Eat.

GS = Groom self: The animal grooms and scratches itself.

Grooming bouts involving scratching only were included in the total number of grooming acts.

SB = Sandbathe: The animal rolls in the sand and flicks its body.

AL = Attack leap: One animal leaps at the opponent and appears to kick at it with the hindfeet.

AT = Attack: One animal lunges at the other from the side or from the rear. It is difficult to determine whether biting is involved, but no wounds have been observed in staged encounters.

CH = Chase: One animal chases the other using quadrupedal saltation. The tail is held low on the substrate, although sometimes if the chase is very vigorous, the tail may undulate; ears are pricked.

FI = Fight: The animals roll over together. Normally, fights are of very brief duration, and it is impossible to see whether biting is involved.

UP = Upright: Animals rear up on their hindlegs and push at each other with their forepaws. Noses are pressed together, but mouths seem to be closed. In some encounters, one animal adopts a more upright posture than the opponent. Pawbeating at each others' paws is also seen at times.

ST = Stop: The animal which has been chasing stops and remains immobile. The body has a rounded form, ears are pricked, and the tail is prostrate.

TH = Threaten: One animal turns quickly and aggressively

towards the opponent. Physical contact between the animals does not occur in "threaten".

EL = Escape leap: One animal leaps away from the other, sometimes backwards or over the top of the pursuing animal.

FL = Flee: One animal runs away, using quadrupedal saltation. The tail is held high and undulates as the animal "flees". Ears are pricked.

CR = Crouch: The animal flattens itself dorsoventrally on the sand, often in a corner of the tank. The tail is directed posteriorly and head is held down on the sand. The ears are pricked, but the animal is immobile, watching the other animal.

VO = Vocalize: A very high-pitched metallic "rattling" noise is sometimes heard during an encounter. It is a repetitive sound made with the mouth closed, and has only been recorded in encounters involving *G. tytonis*.

AE = Approach elongate: The animal's body is elongated and flattened dorsoventrally. Ears are pricked and tail extended posteriorly. The animal moves by means of a quadrupedal walk, and approaches cautiously.

SA = Sniff anogenital region: One animal approaches and sniffs the anogenital region of the opponent. Mutual anogenital sniffing results in circling.

MO = Mount: One animal approaches from the rear and mounts the opponent.

AM = Attempted mount: An animal approaches the opponent from the side or the rear and places a paw on the back of the opponent.

FO = Follow: This behaviour is distinguished from "chase" because it is slower and involves one animal hopping or walking behind the other.

GI = Grooming invitation: An animal lies down in front of the opponent and exposes its neck and belly fur; the eyes are sometimes closed. In *G.vallinus*, one animal approaches the other and crouches with its nose adjacent to or under the other animal.

UR = Urinate: The animal lifts its tail while in a sitting position, remains motionless and deposits a drop of urine on the sand.

MK = Mark: The animal presses its perineal region on the sand and drags itself forward slightly.

RO = Roll over: An animal which has been mounted may roll over onto its back and push the other animal away with its forepaws.

The last three behaviours were eliminated from the analysis.

NOTE: In all graphs and tables, behaviours are listed in the order given above. Codes used throughout the text, figures, tables and graphs correspond with the behaviours described above.

4.2 REPEAT ANALYSES

Five encounters which were re-analysed several weeks after the first analysis were compared to assess the reliability of identification of behaviours. Chi-square contingency table analysis (SIGSTAT programme CHISQ) was used to test the hypothesis that the proportions of the various behaviours did not differ in the original analyses and the repeat analyses. Although there were differences between the originals and repeats, this difference was not significant ($p > 0.5$). Results are shown in Table 2.

TABLE 2: RESULTS OF ORIGINAL AND REPEAT ANALYSES. (N = 10 individuals)

	ORIGINAL	REPEAT		ORIGINAL	REPEAT
AD	210	233	UP	86	76
XX	13	18	ST	62	47
DR	18	21	TH	5	10
AP	162	164	EL	109	114
SN	117	98	FL	181	194
EX	265	275	CR	78	76
MA	185	186	VO	0	0
SI	5	0	AE	35	38
EA	12	11	SA	71	66
GS	24	28	MO	5	4
SB	19	18	AM	5	7
AL	27	25	FO	91	101
AT	59	56	GI	1	0
CH	86	88	GO	0	0
FI	12	15			

4.3 LEVEL OF INTERACTION

Level of interaction was computed as the mean number of acts per individual per encounter (Perrin, 1981b). All acts were included since it was decided that acts such as "sandbathe" and "groom", although not overtly aggressive, may nevertheless transmit information between opponents.

Levels of interaction were compared using the t-test (SIGSTAT programme TTEST); results are shown in Table 3 and levels of interaction in Table 4.

4.4 BEHAVIOUR PROFILES

A "behaviour profile" refers to the histogram derived from the relative frequencies of behaviours seen in encounters of a certain class. Total frequencies of behaviours in intraspecific, same-sex encounters were compared by chi-squared contingency table analysis (SIGSTAT programme CHISQ). Comparisons were made between males and females of the same species, between females of different species, and between males of different species. All total frequency profiles were significantly different from one another ($p < 0.001$). Behaviour profiles for intraspecific same-sex encounters are shown in Figures 1 to 9 and Tables 4 and 5.

Examination of Figures 1 to 9 reveal that certain behaviours occurred more frequently than others, and that the overall shape of the profile was consistent when different species and sexes were compared. Clearly, Figs. 1 and 2 show that female *G.p.paeba* performed relatively less AD than *G.p.exilis* and both species exhibited similar levels of AP, SN, EX, and MA. DR did not occur in either species, and XX, SI, EA, GS, and SB occurred at low frequencies in both species. The proportion of AL was higher than that of AT in female *G.p.paeba*; this was reversed in *G.p.exilis*.

TABLE 3: RESULTS OF T-TEST FOR COMPARISON OF LEVELS OF INTERACTION
IN INTRASPECIFIC SAME-SEX ENCOUNTERS. (Degrees of freedom
are shown in parentheses.)

FEMALES				MALES			
	<u>G.p.p.</u>	<u>G.t.</u>	<u>G.s.</u>	<u>G.p.e.</u>	<u>G.p.p.</u>	<u>G.t.</u>	<u>G.s.</u>
<i>G.p.exilis</i> ♀♀	3.9*** (34)	3.9*** (30)	0.5n.s. (30)	2.3* (30)			
<i>G.p.paeba</i> ♀♀		1.0n.s. (34)	3.4** (34)		0.0n.s. (34)		
<i>G.tytonis</i> ♀♀			3.4** (30)			1.2n.s. (30)	
<i>G.setzeri</i> ♀♀							0.5n.s. (30)
<i>G.p.exilis</i> ♂♂					6.6*** (30)	7.0*** (30)	1.4n.s. (30)
<i>G.p.paeba</i> ♂♂						2.0n.s. (30)	2.6* (30)
<i>G.tytonis</i> ♂♂							3.8*** (30)
<i>G.v.vallinus</i> ♂♂				0.3n.s. (22)	5.2*** (22)	5.2*** (22)	1.0n.s. (22)

* = $0.05 > p > 0.01$

** = $0.01 > p > 0.001$

*** = $p < 0.001$

n.s. = not significant

In all tables and graphs, the following abbreviations are
used:

G.p.p. = *G.p.paeba*

G.p.e. = *G.p.exilis*

G.t. = *G.tytonis*

G.s. = *G.setzeri*

G.v. = *G.vallinus*.

TABLE 4: MEAN FREQUENCIES OF BEHAVIOURS IN INTRASPECIFIC SAME-SEX ENCOUNTERS. (MEAN PER INDIVIDUAL PER ENCOUNTER)

	FEMALES				MALES				
	<u>G.p.p</u>	<u>G.t.</u>	<u>G.p.e</u>	<u>G.s.</u>	<u>G.p.p</u>	<u>G.t.</u>	<u>G.p.e</u>	<u>G.s.</u>	<u>G.v.</u>
AD	18.3	14.6	19.2	27.9	16.4	22.8	10.2	23.1	15.3
XX	1.0	0.1	1.8	0.7	1.0	0.1	0.3	5.9	0.0
DR	0.0	0.0	0.0	1.0	0.0	0.0	0.0	1.1	0.0
AP	19.0	19.8	12.1	14.6	18.7	21.9	11.2	11.2	5.6
SN	16.3	10.9	9.4	12.3	23.1	20.8	13.3	7.4	7.8
EX	27.2	29.8	18.0	28.9	30.1	36.6	13.6	17.9	7.3
MA	8.9	11.4	6.3	7.1	16.2	24.7	5.8	7.2	8.1
SI	0.2	0.9	0.6	0.8	1.0	0.1	2.8	1.3	2.6
EA	0.4	1.9	1.8	0.6	1.4	2.3	0.4	0.2	0.0
GS	2.3	3.1	1.6	1.6	3.5	4.4	1.1	1.6	1.0
SB	1.7	0.9	0.5	3.2	3.1	1.4	0.2	0.9	0.0
AL	7.2	2.8	1.3	3.6	2.9	1.8	1.1	3.3	0.0
AT	5.3	9.9	6.7	4.7	4.1	12.4	0.6	6.9	2.8
CH	11.6	15.1	8.1	4.9	7.7	12.4	0.4	3.9	0.0
FI	0.8	11.0	3.8	0.8	3.0	5.3	0.3	7.1	0.5
UP	8.3	3.7	1.9	1.7	9.1	21.8	3.6	3.7	9.8
ST	3.4	5.3	5.1	0.9	1.8	4.1	0.4	0.9	1.1
TH	0.3	1.0	0.2	0.0	0.6	0.9	0.4	0.1	1.1
EL	12.9	17.3	5.0	6.5	4.8	13.2	0.1	3.3	0.0
FL	26.7	30.5	11.9	8.4	17.6	19.8	0.4	10.5	0.0
CR	16.9	15.8	7.1	4.4	12.6	4.8	4.6	4.8	1.9
VD	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
AE	4.1	1.4	0.9	1.9	5.6	2.1	0.9	0.6	0.1
SA	1.6	2.2	1.9	1.2	5.3	5.3	6.4	0.3	5.8
MO	0.4	0.0	0.6	0.2	2.1	0.1	0.7	0.3	2.4
AM	0.3	0.4	0.0	0.4	1.1	1.5	0.1	0.0	0.8
FO	4.3	5.7	3.4	1.8	5.6	8.3	3.4	1.3	4.5
GI	0.0	0.0	0.0	0.1	0.0	0.0	1.7	0.0	9.9
GO	0.0	0.1	0.0	0.3	0.1	0.0	2.8	0.0	0.3
TOTAL	198.8	216.4	129.1	139.8	198.8	248.6	85.8	124.0	89.6
±SD	43.0	64.0	63.5	62.0	56.0	84.5	39.1	99.2	24.8
N	20	16	16	16	16	16	16	16	8

90 of Table 4

TABLE 5: RELATIVE FREQUENCIES OF BEHAVIOURS IN INTRASPECIFIC SAME-SEX ENCOUNTERS.

	FEMALES				MALES				
	<u>G.p.p</u>	<u>G.t.</u>	<u>G.p.e</u>	<u>G.s.</u>	<u>G.p.p</u>	<u>G.t.</u>	<u>G.p.e</u>	<u>G.s.</u>	<u>G.v.</u>
AD	9.2	6.8	14.9	20.0	8.3	9.2	11.9	18.6	17.1
XX	0.5	0.1	1.4	0.5	0.5	0.0	0.4	4.7	0.0
DR	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.5	0.0
AP	9.6	9.1	9.3	10.5	9.4	8.8	12.3	9.0	6.3
SN	8.2	5.0	7.3	8.8	11.6	8.3	15.5	5.9	8.7
EX	13.7	13.7	13.9	20.7	15.2	14.7	15.8	14.5	8.1
MA	4.5	5.3	4.8	5.1	8.1	9.9	6.7	5.8	9.1
SI	0.1	0.4	0.4	0.6	0.5	0.0	3.2	1.1	2.9
EA	0.2	0.9	1.4	0.4	0.7	0.9	0.4	0.2	0.0
GS	1.1	1.4	1.2	1.1	1.8	1.8	1.3	1.3	1.1
SB	0.9	0.4	0.4	2.3	1.5	0.6	0.2	0.7	0.0
AL	3.6	1.3	1.0	2.5	1.5	0.7	1.2	2.7	0.0
AT	2.6	4.6	5.2	3.4	2.0	5.0	0.7	5.5	3.1
CH	5.8	7.0	6.3	3.5	3.9	5.0	0.4	3.1	0.0
FI	0.4	5.1	2.9	0.5	1.5	2.1	0.3	5.7	0.6
UP	4.1	1.7	1.5	1.2	4.6	8.8	4.2	3.0	10.9
ST	1.7	2.5	4.0	0.7	0.9	1.7	0.4	0.7	1.3
TH	0.1	0.5	0.1	0.0	0.3	0.4	0.5	0.1	1.3
EL	6.5	8.0	3.9	4.6	2.4	5.3	0.1	2.7	0.0
FL	13.4	14.1	9.3	6.0	5.8	7.9	0.4	8.5	0.0
CR	8.5	7.3	5.5	3.2	6.3	1.9	5.3	3.9	2.1
VO	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
AE	2.1	0.7	0.7	1.3	2.8	0.8	1.1	0.5	0.7
SA	1.5	1.0	1.5	0.8	2.6	2.1	7.5	0.2	6.4
MO	0.2	0.0	0.4	0.1	1.1	0.1	0.8	0.2	2.7
AM	0.2	0.2	0.0	0.3	0.6	0.6	0.1	0.0	0.8
FO	2.2	2.6	2.6	1.3	2.8	3.3	3.9	1.0	5.0
GI	0.0	0.0	0.0	0.1	0.0	0.0	2.0	0.0	11.1
GO	0.0	0.0	0.0	0.2	0.1	0.0	3.3	0.0	0.6
N	20	16	16	16	16	16	16	16	8

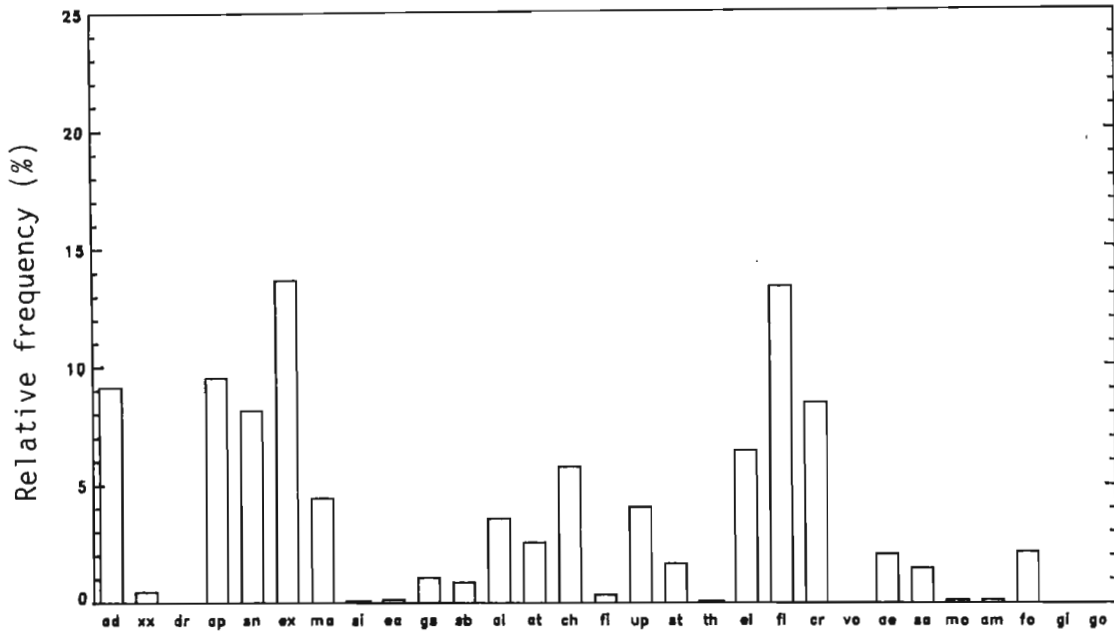


Fig. 1. Behaviour profile for female *G.p. paeba* (n = 20)

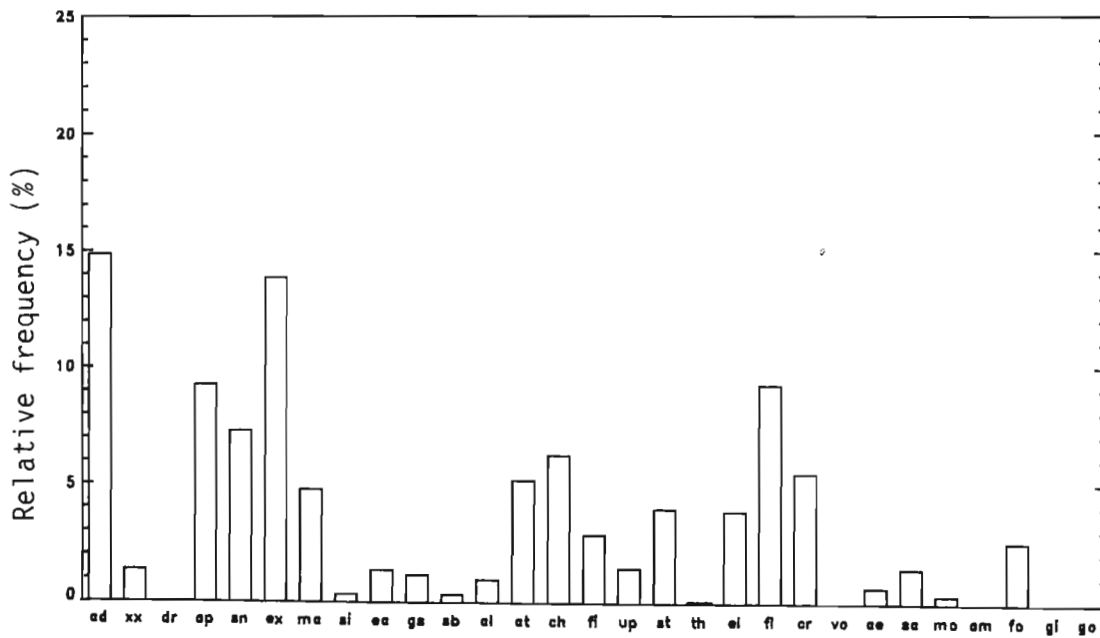


Fig. 2. Behaviour profile for female *G.p. exilis* (n = 16)

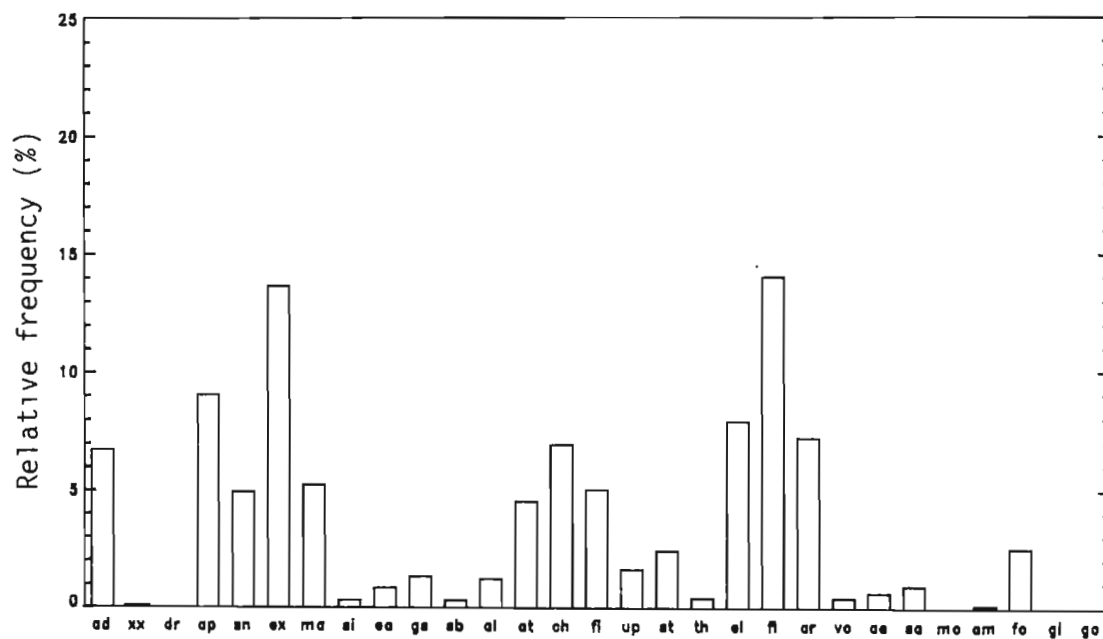


Fig. 3. Behaviour profile for female *G. tytonis* (n = 16)

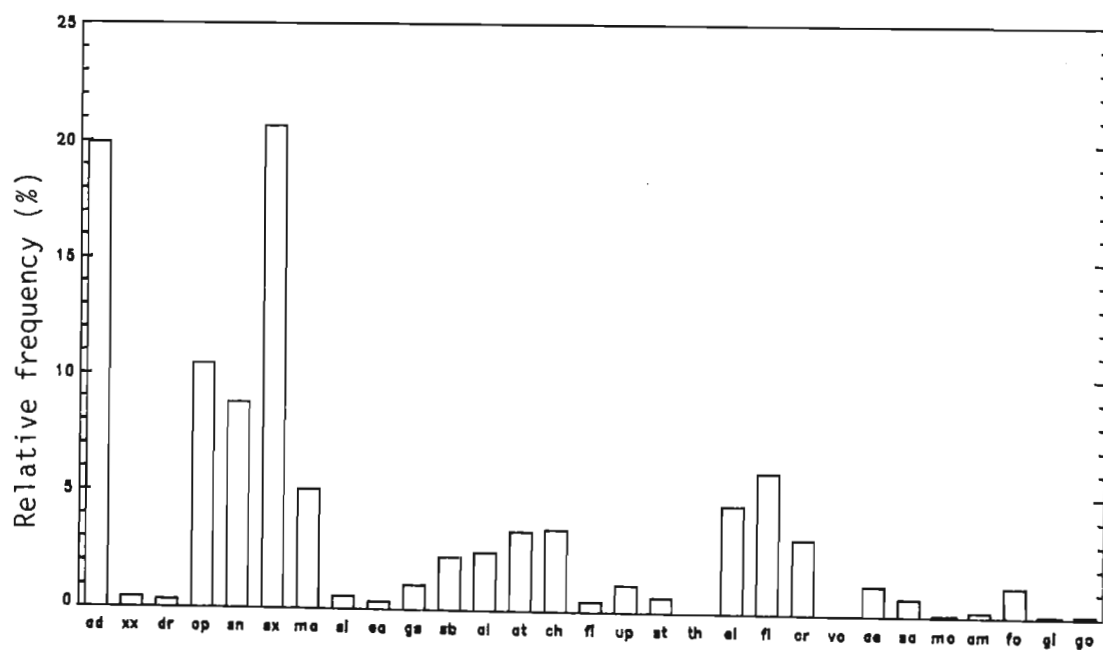


Fig. 4. Behaviour profile for female *G. setzeri* (n = 16)

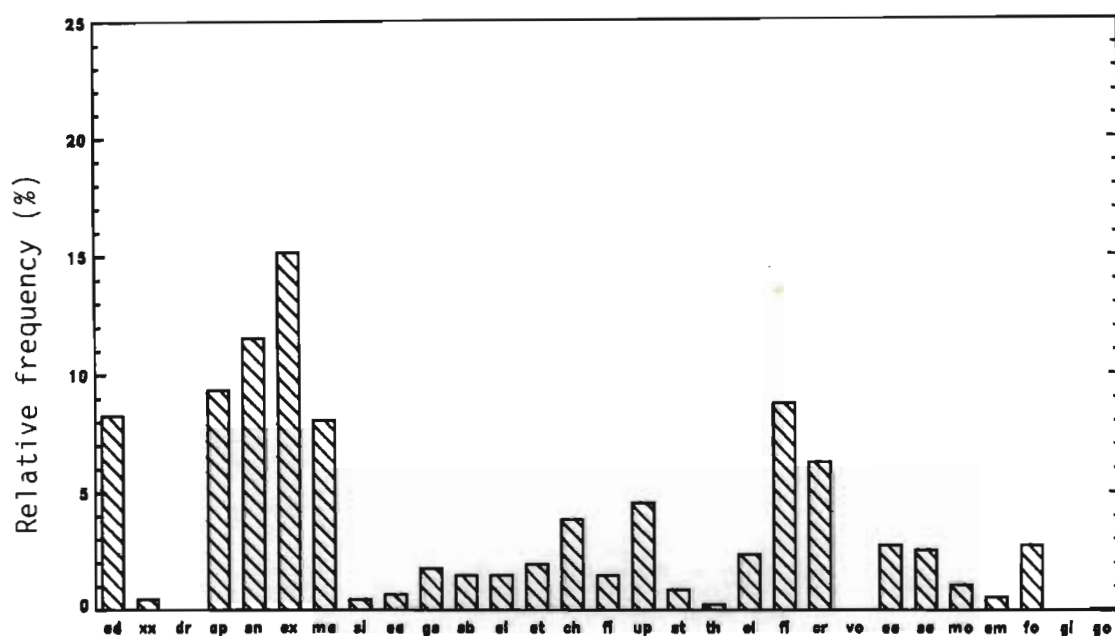


Fig. 5. Behaviour profile for male *G. p. paeba* (n = 16)

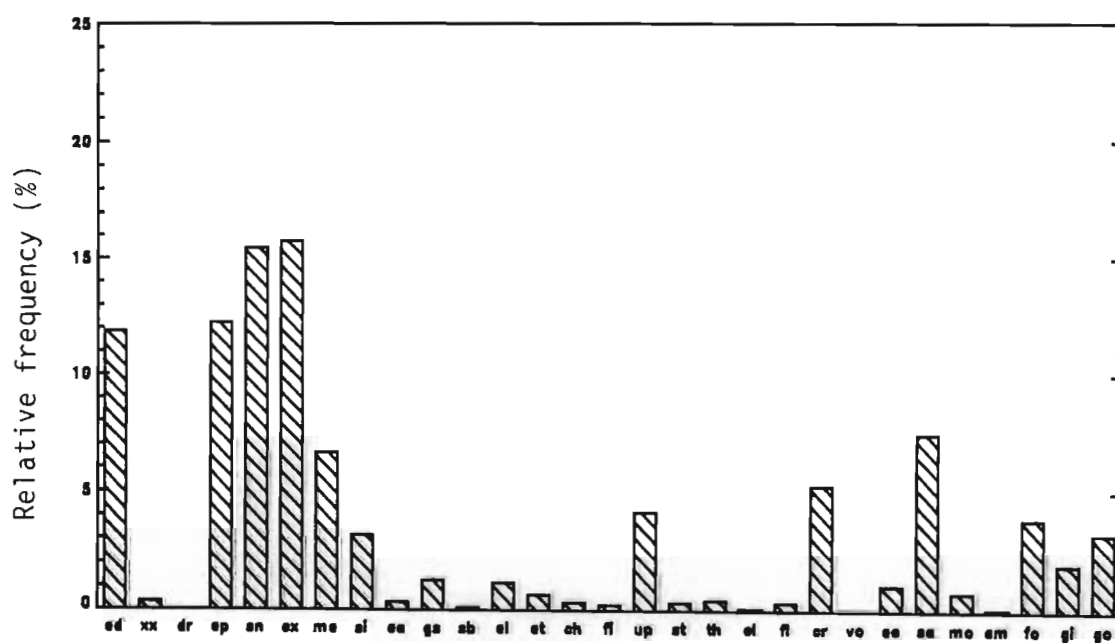


Fig. 6. Behaviour profile for male *G.p. exilis* (n = 8)

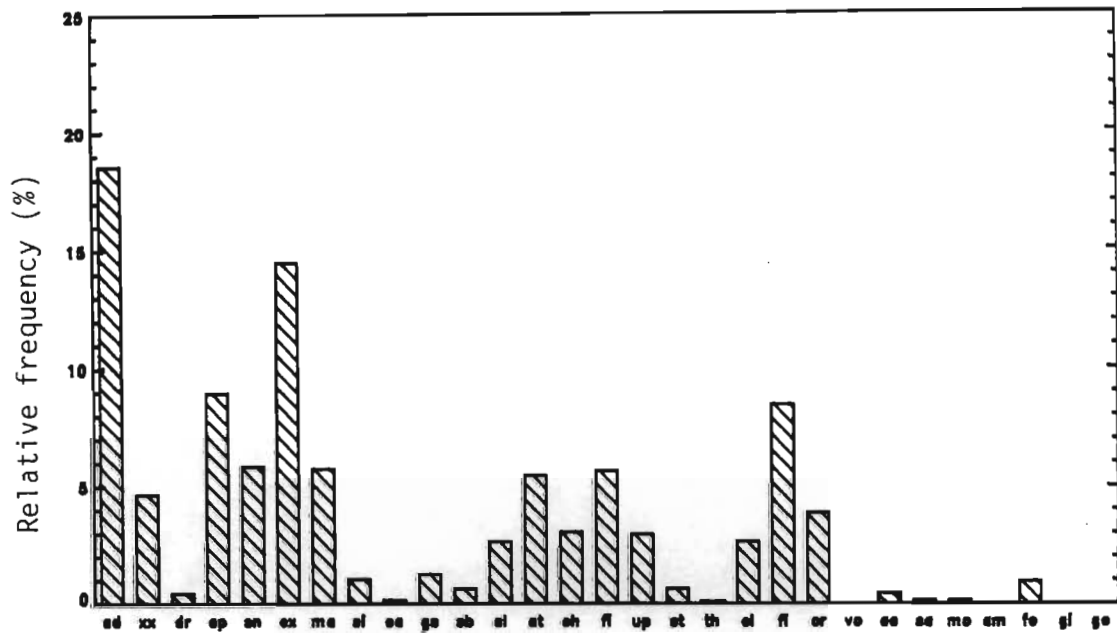


Fig. 7. Behaviour profile for male *G. setzeri* (n = 16)

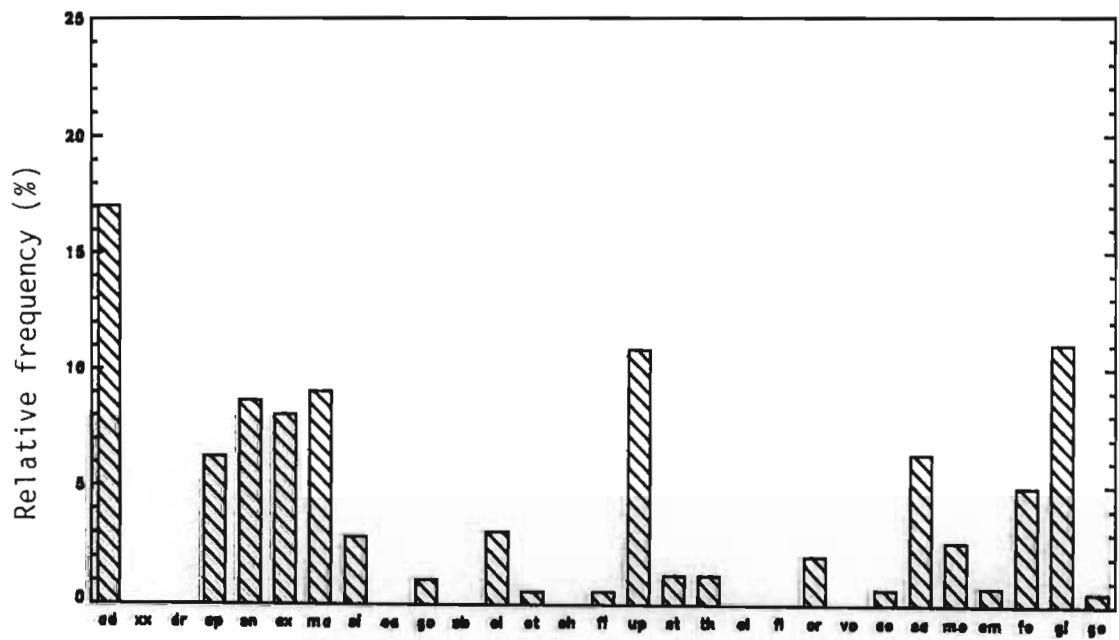


Fig. 8. Behaviour profile for male *G. vallinus* (n = 8)

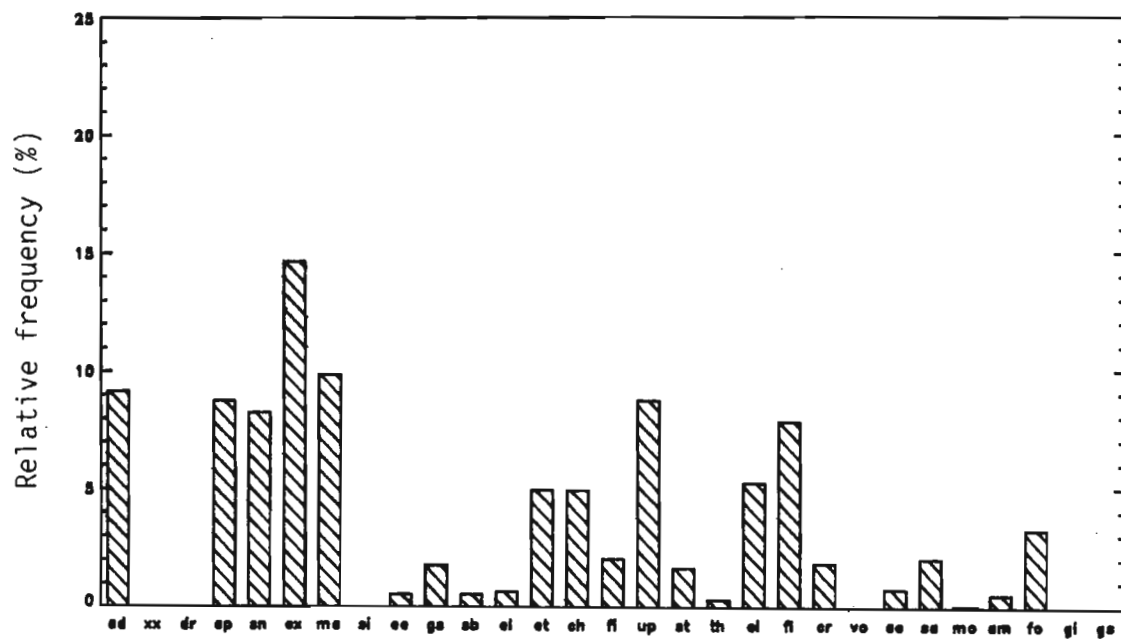


Fig. 9. Behaviour profile for male *G. tytonis* (n = 16)

Similarly, FI occurred relatively less frequently than UP in *G.p.paeba*, while the reverse was true in *G.p.exilis*. CH and ST occurred at a similar relative frequency in both species, while TH was seldom identified. EL, FL, and CR occurred relatively more frequently in female *G.p.paeba* than in female *G.p.exilis*: VO was absent in both species. The proportions of AE, SA, MO, AM, and FO were similar in both species, and GI and GO were absent.

Comparison of female with male profiles of animals of the same species reveals that males of three species (*G.p.paeba*, *G.p.exilis*, and *G.tytonis*) performed relatively less of the behaviours associated with overt aggression and submission (i.e. behaviours AL - CR) and relatively more of the non-aggressive behaviours (AD - SB and AE - GO). This trend was reversed in *G.setzeri*. Behaviours EL, FL, and CH were absent in male *G.vallinus* and occurred infrequently in male *G.p.exilis*, while GI and GO, which were absent in all female profiles and in male *G.p.paeba*, *G.tytonis* and *G.setzeri*, occurred more frequently in male *G.p.exilis* and *G.vallinus*. Comparisons of behaviour profiles between species and sexes are commented on in more detail in the discussion.

4.5 MOTIVATIONAL ANALYSIS

Weighted pair group cluster analysis (SIGSTAT Programme WPCLUS) was used to determine patterns of covariation of behaviours in each sex and species. Frequencies of

occurrence of behaviours in the individual encounters constituting a class of encounters were clustered. Behaviours which occurred less than 10 times (5 times in *G.vallinus*) in all intraspecific same-sex encounters were not included in the cluster analysis. Transition frequencies were illustrated as flow diagrams representing the most common sequences of acts performed intra-individually. Diagrams derived from the cluster analysis and transition frequencies are shown in Figs. 10 - 27; transition frequency matrices are included in Appendix 3.

Figures 10 and 11 are discussed to illustrate the value of the techniques of cluster analysis and transition frequency analysis in order to establish which behaviours are motivationally linked. Figures 12 to 27 are included in Appendix 3.

The first group of behaviours identified by cluster analysis consisted of MA, EA, FO, SN, and SA. In the transition diagram, four of these behaviours were linked in a sequence, while EA was a low-frequency behaviour which was followed by EX. SN was followed more frequently by EX than by other behaviours, therefore it is regarded as a linking behaviour between two groups of behaviour. This will be referred to as the "sexual" group of behaviours.

The second group identified in the cluster diagram includes VO, CR, FL, and EL. These are "submissive" behaviours, which are linked in a sequence as seen in Fig. 11. VO was

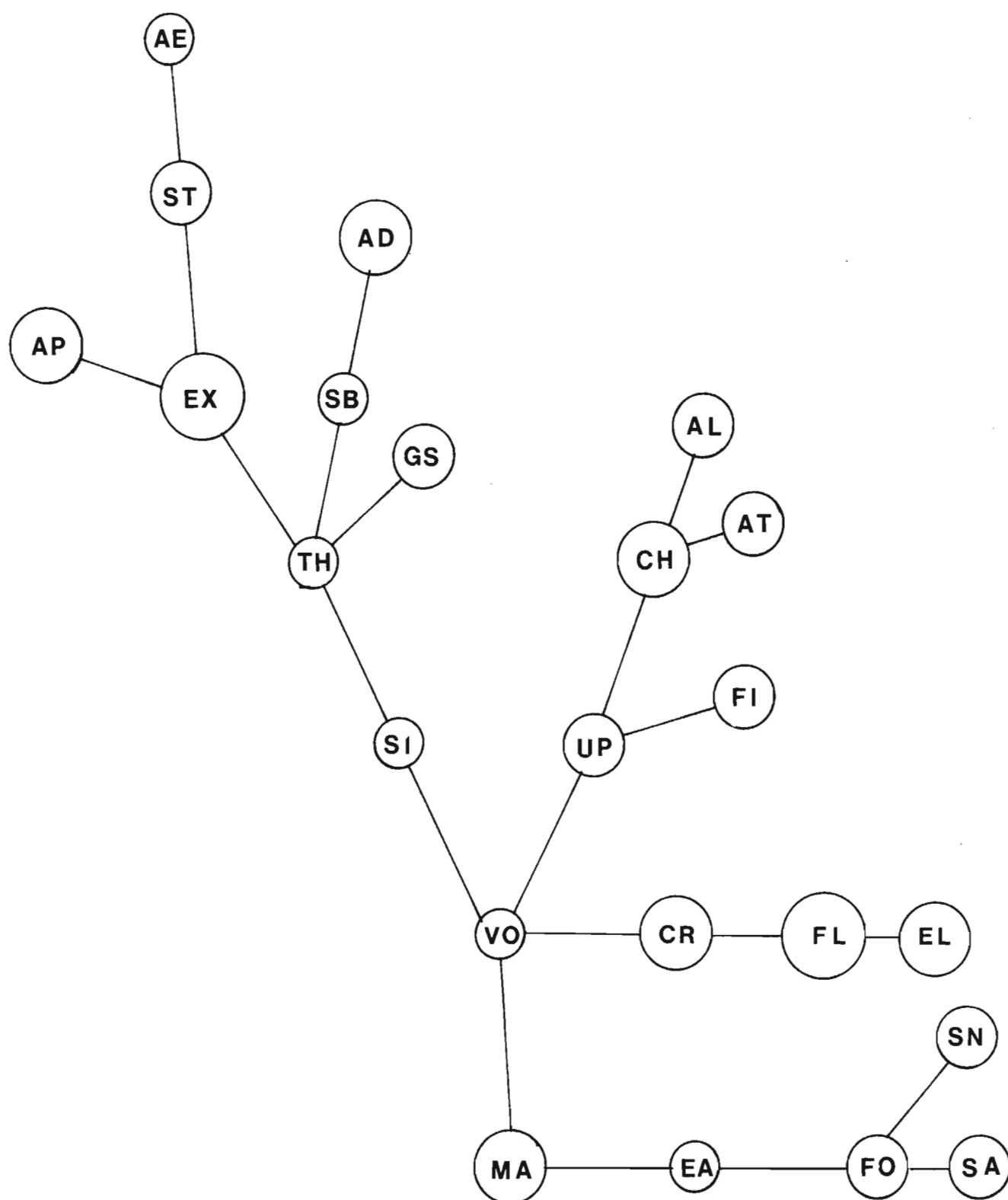


Fig. 10. Cluster diagram for female *G. tytonis* ($n = 16$)
 In all cluster diagrams, diameters of circles are proportional to relative frequencies of behaviours. Line lengths are proportional to similarities determined by weighted pair group cluster analysis.

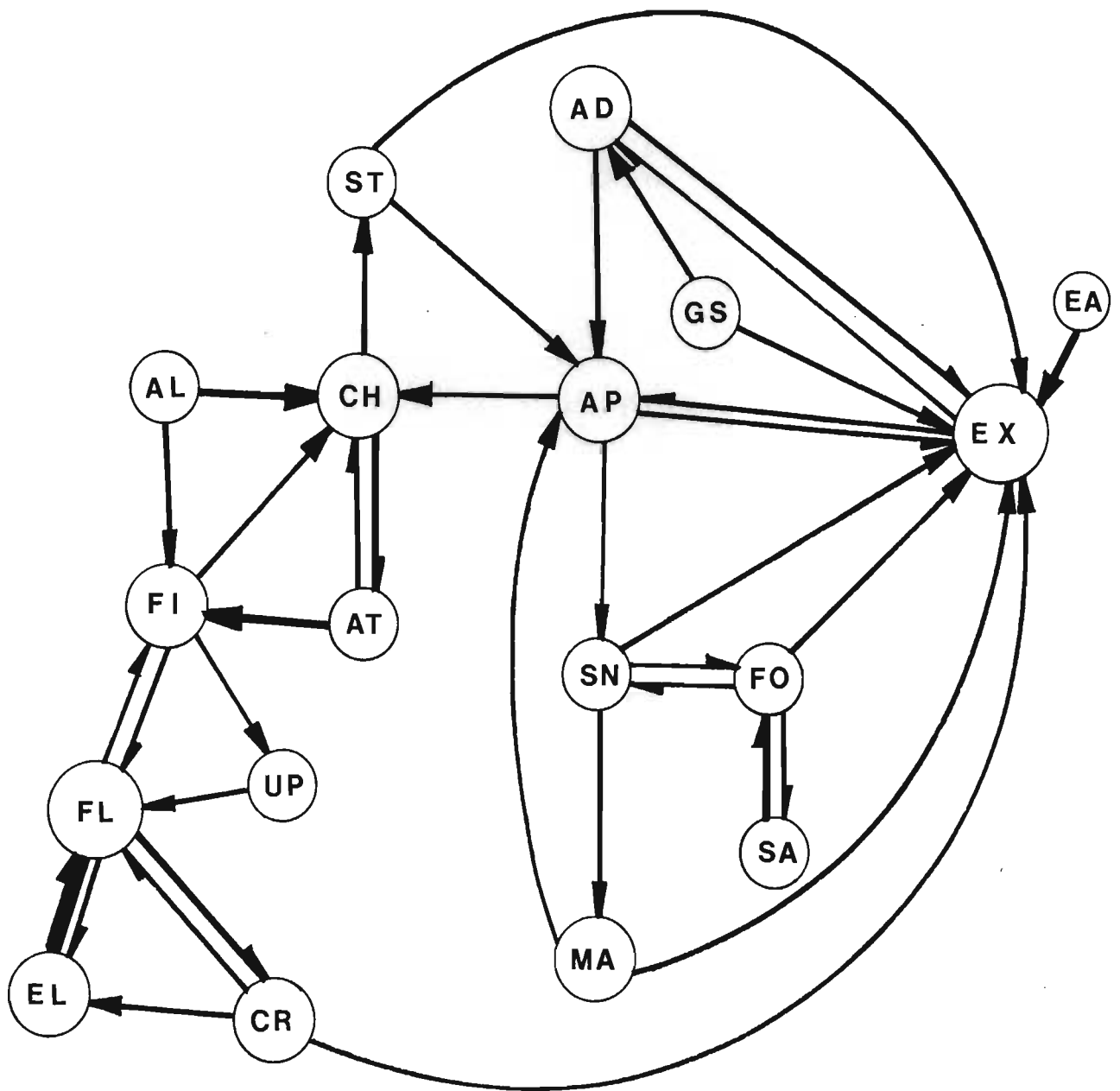


Fig. 11. Transition frequencies for female *G. tytonis* ($n = 16$)
 In all transition diagrams diameters of circles are proportional to
 relative frequencies of behaviours. Line widths are proportional
 to transition frequencies.

a low-frequency behaviour which occurred only in female *G. tytonis*. In other species and sexes, EL-FL-CR was the most common group of submissive behaviours.

Aggressive behaviours formed the third group identified by cluster analysis, and included UP, FI, CH, AT, and AL. In the transition analysis, these behaviours occurred in a sequence, with FI and UP forming linking behaviours between the aggressive and submissive groups. The behaviour ST, which succeeded the aggressive behaviours in the transition diagrams, was associated with AE and EX in the cluster analysis.

The fourth group of behaviours is referred to as "exploratory and solitary" behaviour. Three behaviours formed the most common members of this group: AD, AP, and EX but behaviours such as GS, SB, XX and SI also belong to this group. The transition diagram illustrates that EX was preceded by a variety of behaviours of all groups, and that it formed a linking behaviour between these groups of behaviour.

It should be noted that links between the exploratory and aggressive-submissive behaviours were weak, i.e. encounters tended to involve either predominantly aggressive-submissive behaviour or predominantly exploratory-sexual behaviour. The following groups of behaviours were identified in seven out of nine cluster and transition diagrams, with some interspecific variation in the behaviours forming a group:

1. Exploratory and solitary behaviours: AD, XX, DR, AP, SN, EX, MA, SI, EA, GS, SB.
2. Aggressive behaviours: AL, AT, CH, FI, UP, ST, TH
3. Submissive behaviours: EL, FL, CR, VO
4. Sexual behaviours: AE, SA, MO, AM, FO, GI, GO

Throughout this thesis, the grouping of behaviours as given above is adhered to.

In order to determine whether any of the solitary or exploratory behaviours were displacement activities, it was necessary to compare their frequency of occurrence in "conflict" encounters with an expected frequency based on their frequency of occurrence in "low-conflict" encounters. Information was available from a series of encounters conducted after animals had been caged together for approximately three weeks. These encounters were characterized by a lower level of interaction and a marked reduction in aggressive and submissive behaviours.

Expected frequencies of occurrence of non-aggressive and non-submissive behaviours were generated according to the following formula:

$$EF(i) = F(i) \times \frac{T_c - (T(A + S))_c}{T_{Lc} - (T(A + S))_{Lc}}$$

where $EF(i)$ = expected frequency of behaviour i

$F(i)$ = actual frequency of i in low-conflict encounters

T_c = Total no. of behaviours in high-conflict encounters

$T(A + S)_H$ = Total no. of aggressive and submissive behaviours in high-conflict encounters

T_{Lo} = Total no. of behaviours in low-conflict encounters

$T(A + S)_{Lo}$ = Total no. of aggressive and submissive behaviours in low-conflict encounters

Expected frequencies were compared with actual frequencies by means of χ^2 goodness-of-fit tests applied to individual behaviours. Results are shown in Table 6; in males and females behaviours AD, SB, and AE occurred significantly more frequently than expected, while SN, SI, and GS occurred less frequently than expected. Females performed AP more frequently than expected, while this difference was not significant in males. Males performed significantly more MD, AM, FO and less GO than expected.

4.6 DOMINANT/ SUBMISSIVE RELATIONSHIPS

Intraspecific same-sex encounters in which one animal clearly dominated the other were compared in order to identify those behaviours in which the proportion relative to the total number of acts differed significantly in dominant and submissive animals. Figures 28 - 35 illustrate the relative frequencies of all behaviours in summed encounters resulting in clear dominance. Male *G.p.exilis* were excluded from this analysis since dominance was not established in any of their encounters.

It is clear from Figs. 28 - 35 that dominant animals of all

TABLE 6 : EXPECTED¹ AND ACTUAL FREQUENCIES OF EXPLORATORY AND
SEXUAL BEHAVIOURS IN MALE AND FEMALE G.P.PAEBA.

	MALES		FEMALES	
	EXPECTED	ACTUAL	EXPECTED	ACTUAL
AD	100	263***	90	365***
XX	0	16	0	19
DR	0	0	0	0
AP	327	299n.s.	225	380***
SN	456	369***	469	326***
EX	467	482n.s.	514	543n.s.
MA	270	259n.s.	180	177n.s.
SI	154	16***	225	4***
EA	15	23n.s.	0	8
GS	100	56***	144	45***
SB	30	49***	9	34***
AE	36	89***	36	82***
SA	95	84n.s.	36	31n.s.
MO	21	34**	27	8***
AM	5	18***	0	6
FO	56	89***	72	86n.s.
GI	0	0	18	0
GO	11	2**	36	0

1 EXPECTED FREQUENCY BASED ON ENCOUNTERS BETWEEN
"FAMILIAR " ANIMALS (N=6 FOR FEMALES; N=12 FOR MALES)

** = $0.01 > p > 0.001$

*** = $0.001 > p$

n.s. = not significant

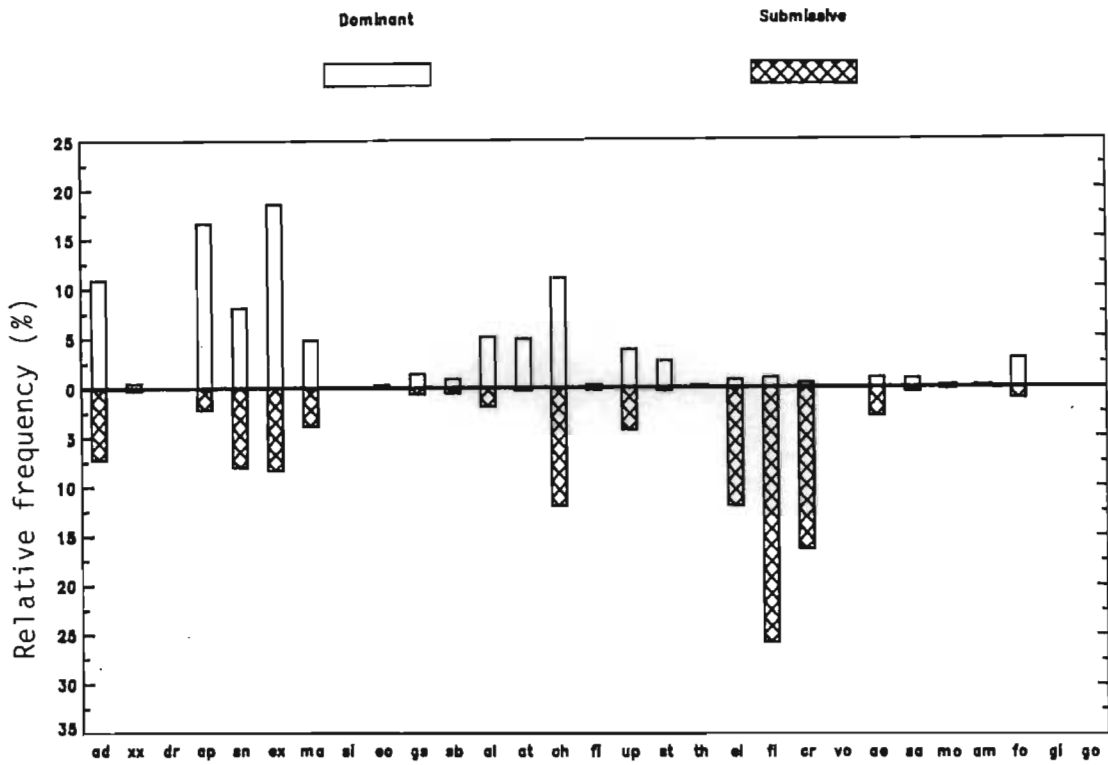


Fig. 28. Behaviour profiles for dominant and submissive female *G.p. paeba* (n = 10 encounters)

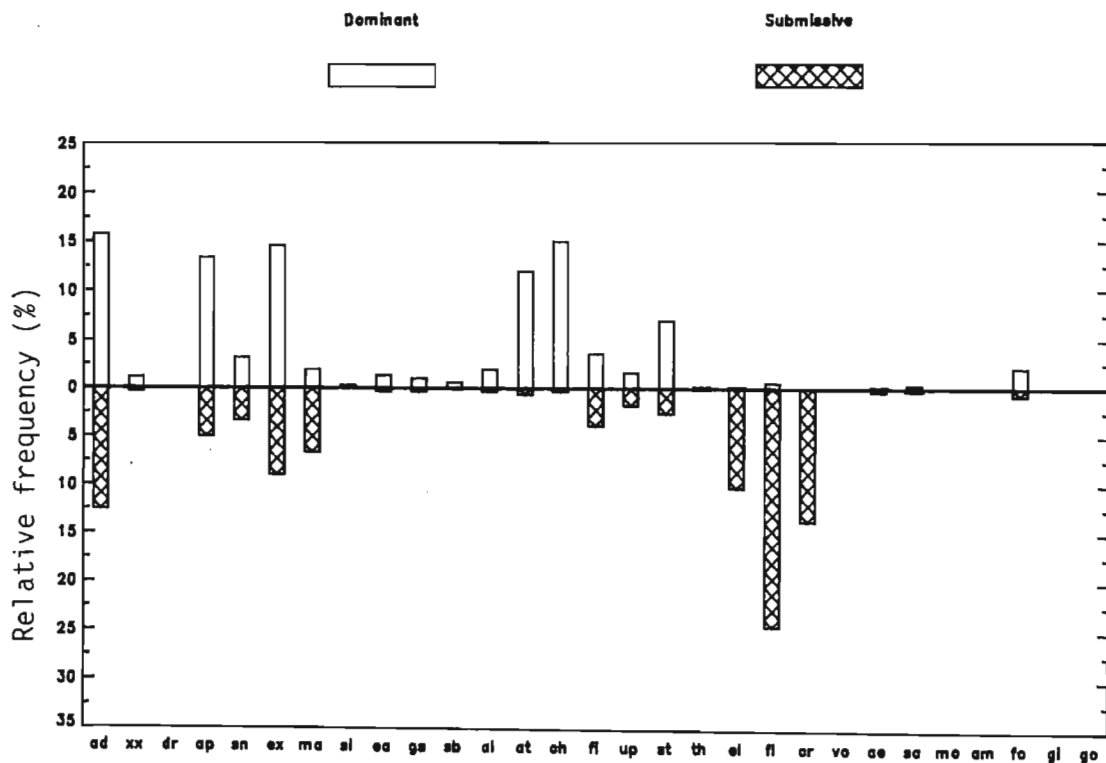


Fig. 29. Behaviour profiles for dominant and submissive female *G.p. exilis* (n = 6 encounters)

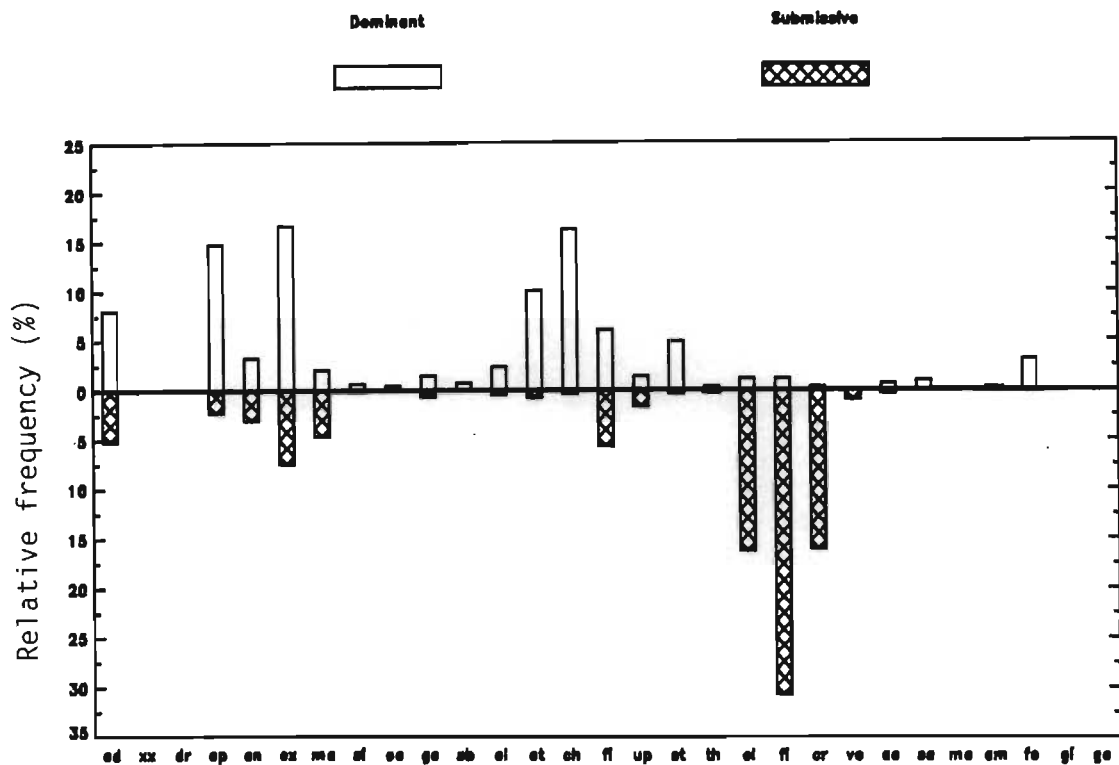


Fig. 30. Behaviour profiles for dominant and submissive female *G. tytonis* (n = 6 encounters)

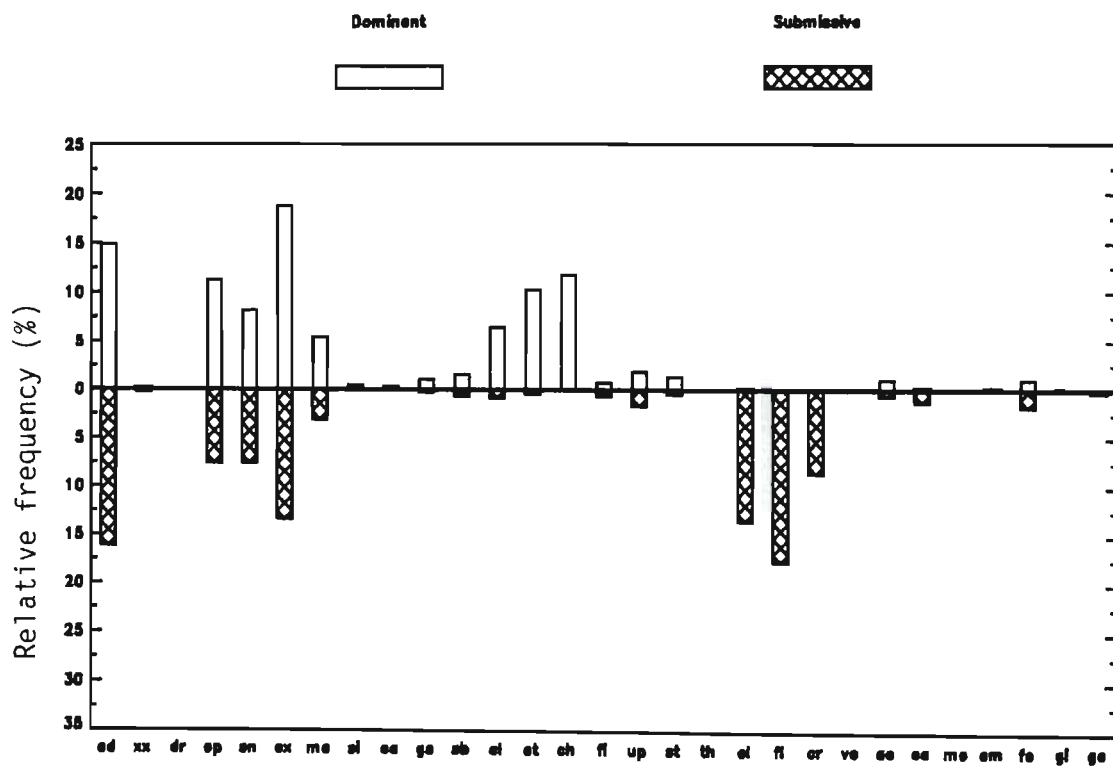


Fig. 31. Behaviour profiles for dominant and submissive female *G. setzeri* (n = 5 encounters)

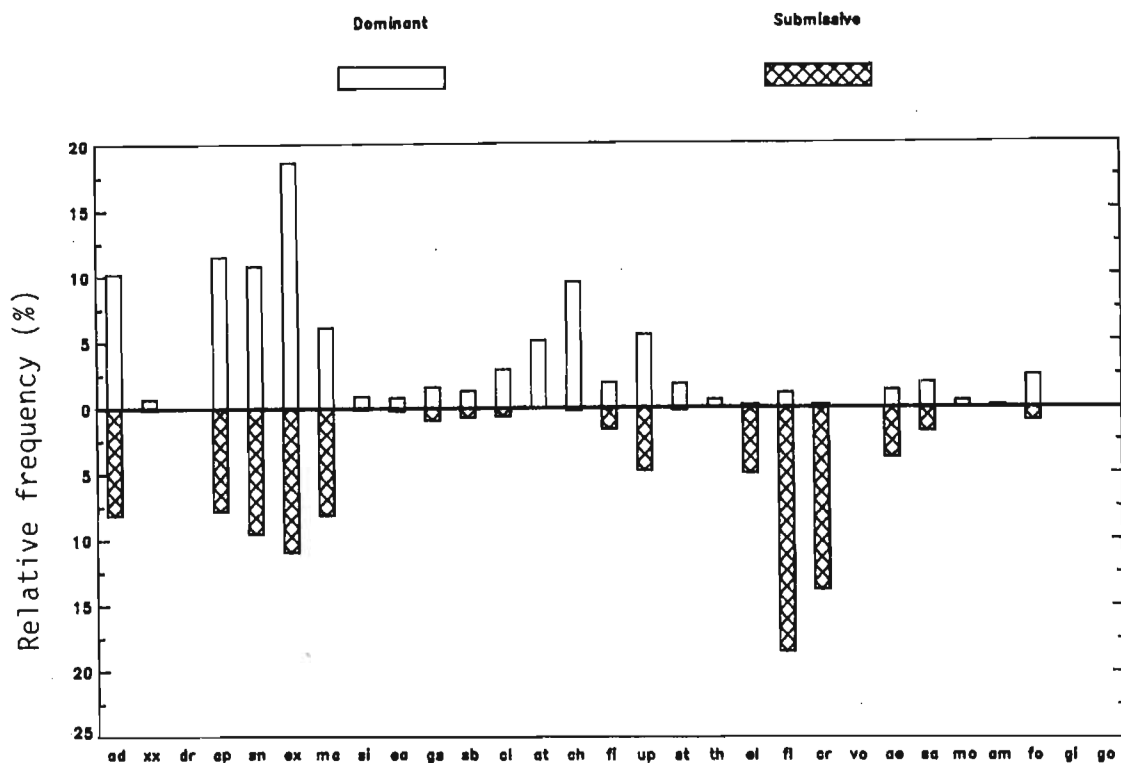


Fig. 32. Behaviour profiles for dominant and submissive male *G.p. paeba* (n = 16 encounters)

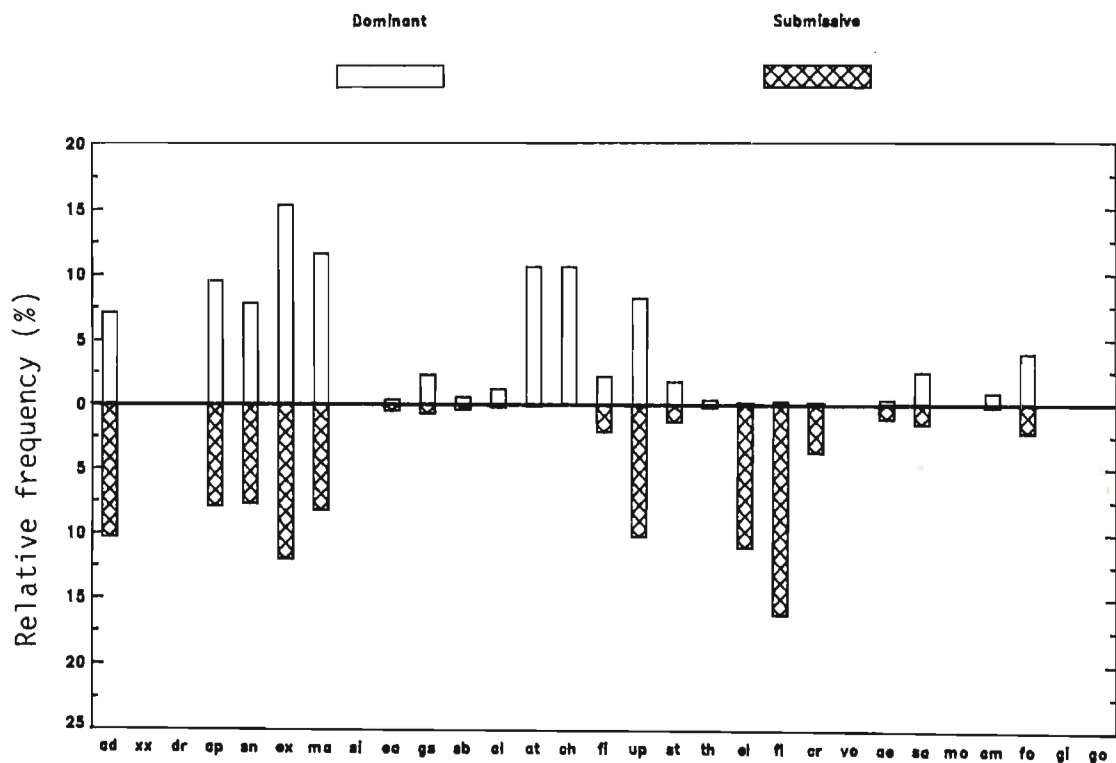


Fig. 33. Behaviour profiles for dominant and submissive male *G. tytonis* (n = 6 encounters)

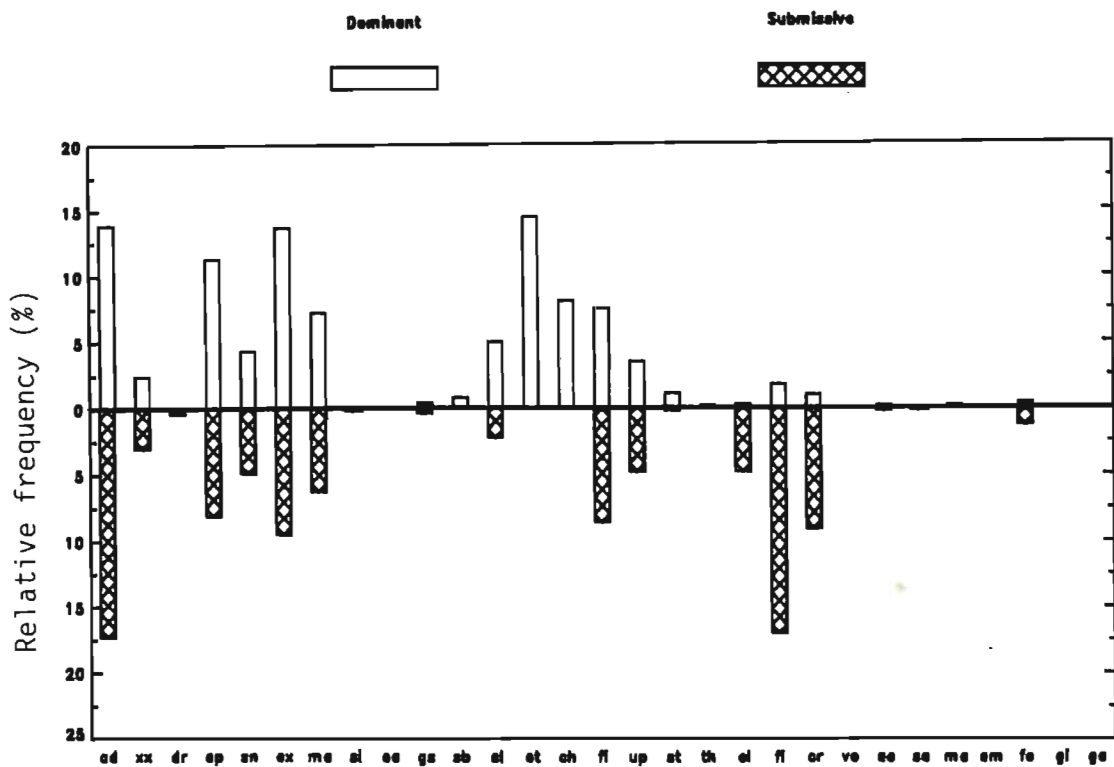


Fig. 34. Behaviour profiles for dominant and submissive male *G. setzeri* (n = 3 encounters)

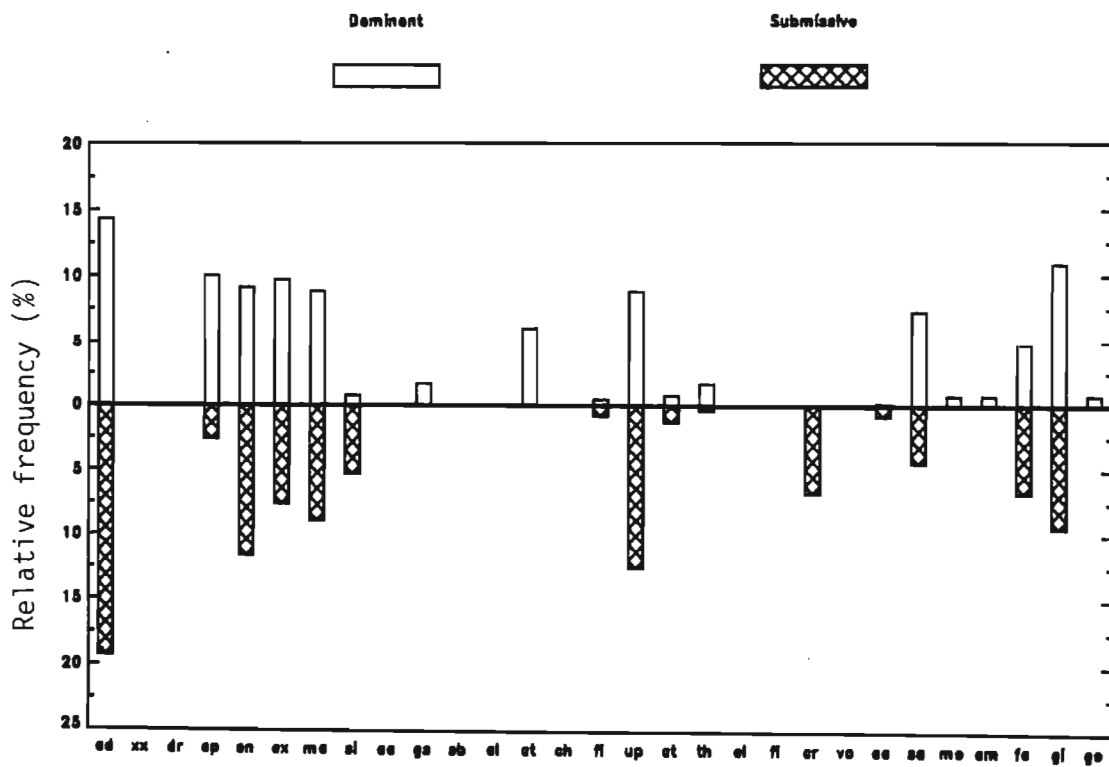


Fig. 35. Behaviour profiles for dominant and submissive male *G. vallinus* (n = 3 encounters)

species and sexes performed a greater variety of behaviours than did submissive animals. Submissive behaviours formed a large proportion of the behaviour of submissive animals, while aggressive behaviours were seldom performed by submissive animals. Conversely, dominant animals seldom performed submissive behaviours. Some exploratory and solitary behaviours were more frequently performed by dominant than by submissive animals, these differences being less marked in male *G.vallinus*.

Chi-square 2 X 2 contingency table analysis was used to test the null hypothesis that dominant and submissive animals did not differ in the frequency of occurrence of behaviours other than overtly aggressive behaviours. Behaviours which occurred less than five times were excluded from this analysis. Two behaviours, AP and EX occurred significantly more frequently in dominant animals in seven out of eight sets of results. Clearly, the aggressive behaviours AL, AT and CH and submissive behaviours EL, FL and CR were almost completely mutually exclusive.

A scoring system was applied to the results of all intraspecific different-sex and interspecific encounters in order to determine the dominance/submissive relationships between different species and sexes. Dominance/submissive scores were calculated by summing the following total frequencies:

(AT, AL and CH) x 2,

(AF and EX) \times 1

(EL, FL and CR) \times -2.

Relative frequencies of behaviours in intraspecific, different-sex encounters are shown in Figures 36 - 40 and Table 7. Interspecific encounters are shown in Figures 41 - 58 and Tables 8 - 15 (Appendix 3); dominance/submissive relationships are shown in Table 16.

In intraspecific, different-sex encounters it is clear that the dominant/submissive trends are not as clear as in Figs. 28 - 35. Both males and females performed a variety of behaviours, but in three species, females performed more aggressive behaviours and less submissive behaviours than males. The reverse was true in *G.setzeri* male-female encounters, and very little aggressive or submissive behaviour was performed by male and female *G.vallinus*. Male *G.p.paeba* and *G.p.exilis* performed more sexual behaviour than females did, but sexual behaviours formed a consistently low proportion of all behaviours in male-female encounters.

In interspecific encounters between *G.tytonis* and *G.paeba*, both males and females displayed a large proportion of exploratory and solitary behaviours, and also a considerable proportion of aggressive and submissive behaviours. Animals which behaved submissively, e.g. male *G.tytonis* in Fig. 44, were more restricted in the range of behaviours performed than their opponents. Figures 41 and 42

TABLE 16 : DOMINANCE/SUBMISSIVE RELATIONSHIPS IN INTRASPECIFIC
DIFFERENT-SEX AND INTERSPECIFIC ENCOUNTERS.

	G.t.♀	G.p.p.♀	G.s.♀	G.s.♂	G.p.p.♂	G.t.♂
<i>G.tytonis</i> ♀ vs		672	176	220	818	1100
<i>G.p.paeba</i> ♀ vs	-902		512	353	321	668
<i>G.setzeri</i> ♀ vs	-410	-665		-194	319	-418
<i>G.setzeri</i> ♂ vs	-219	-519	173		-693	-851
<i>G.p.paeba</i> ♂ vs	-794	-559	1	358		-54
<i>G.tytonis</i> ♂ vs	-1533	-1134	340	287	362	

(5 encounters of each type were staged)

	G.p.p.♀	G.p.e.♀	G.p.p.♂	G.p.e.♂
<i>G.p.paeba</i> ♀ vs		100	321	464
<i>G.p.exilis</i> ♀ vs	99		240	840
<i>G.p.paeba</i> ♂ vs	-559	-180		246
<i>G.p.exilis</i> ♂ vs	-303	-361	22	

(5 encounters of each type were staged)

	G.v.v.♀	G.v.v.♂	G.p.p.♀	G.p.p.♂
<i>G.v.vallinus</i> ♀ vs		49	60	69
<i>G.v.vallinus</i> ♂ vs	19		138	194
<i>G.p.paeba</i> ¹ ♀ vs	-17	-120		
<i>G.p.paeba</i> ¹ ♂ vs	26	-123		

(3 encounters of each type were staged: 1 encounter of

G.v.vallinus ♀ vs *G.p.paeba* ♂ and *G.p.paeba* ♀)

*G.p.paeba*¹ = *G.p.paeba* from Northern Cape

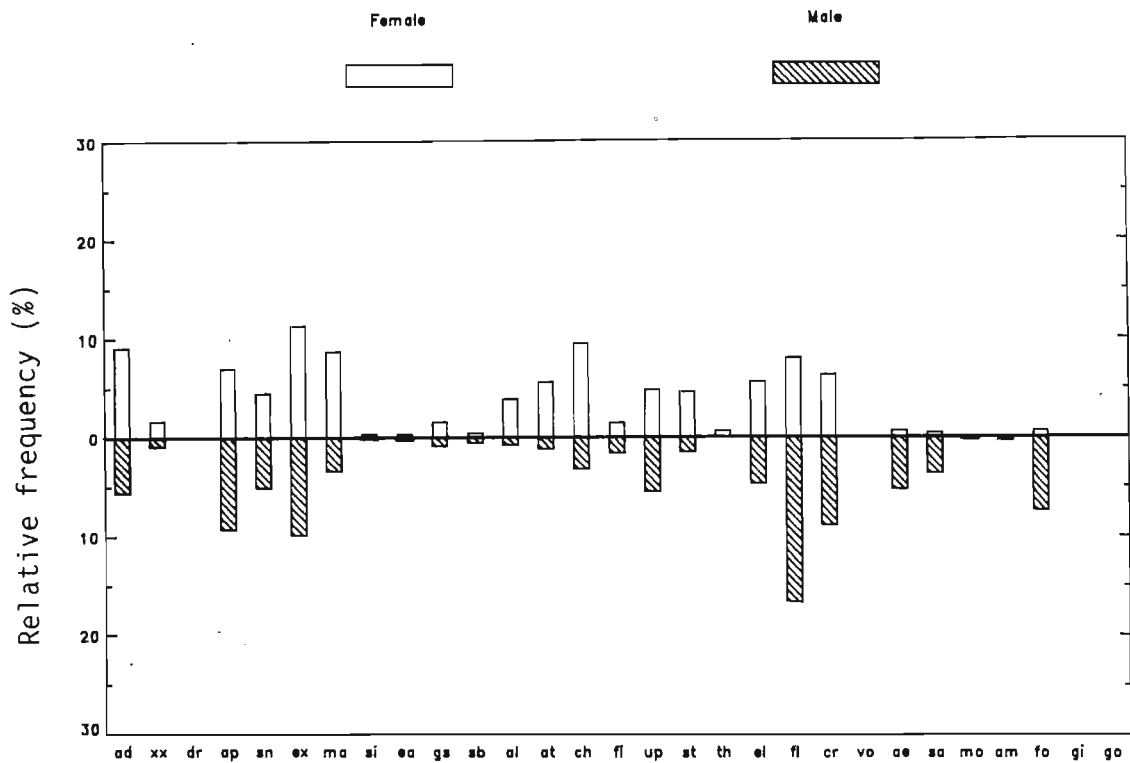


Fig. 36. Behaviour profiles for male versus female *G.p. paeba* encounters (n = 8 encounters)

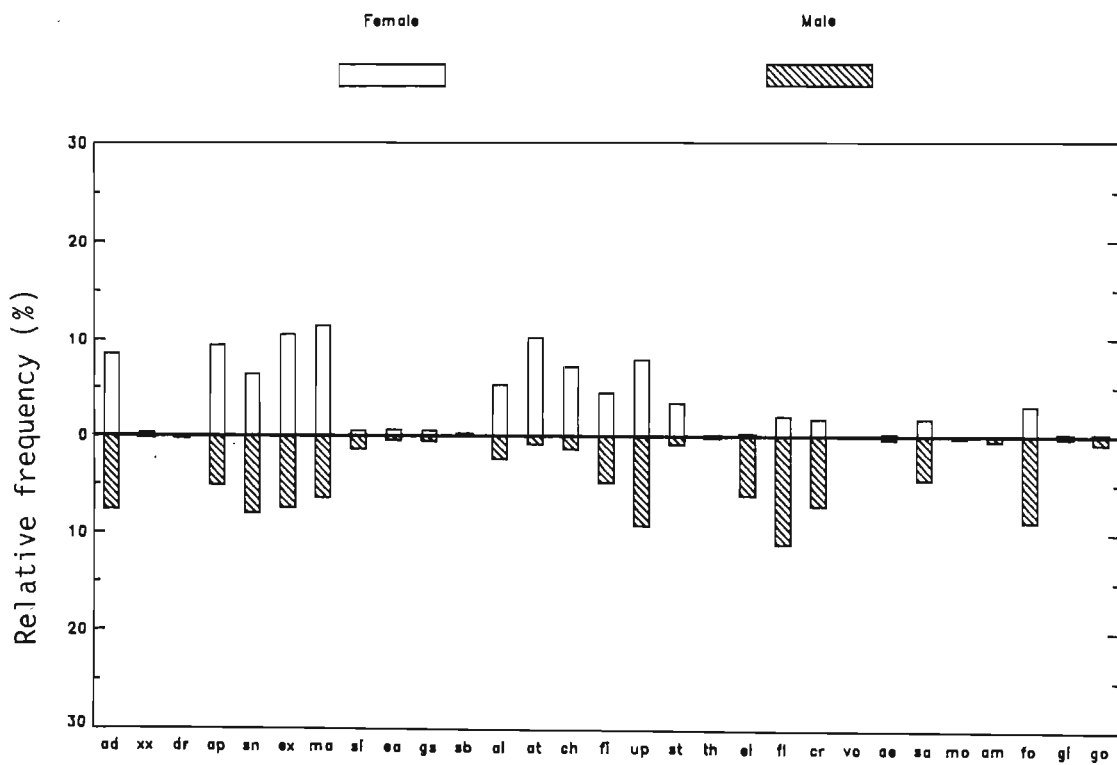


Fig. 37. Behaviour profiles for male versus female *G.p. exilis* encounters (n = 8 encounters)

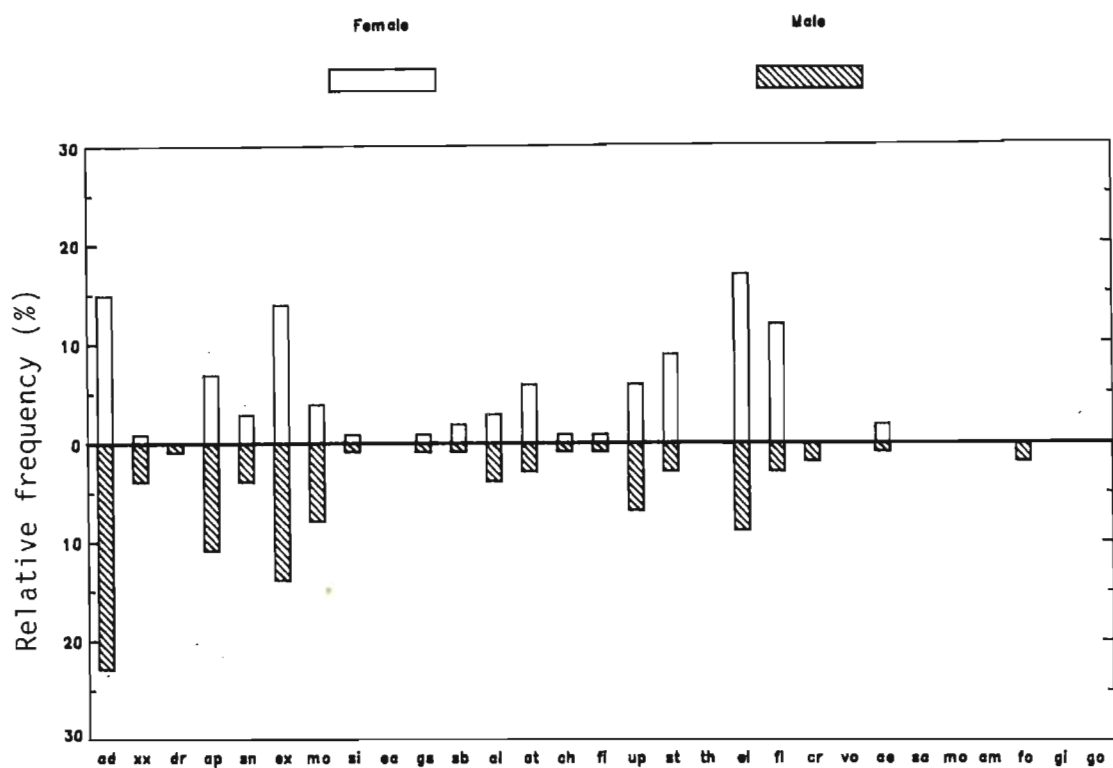


Fig. 38. Behaviour profiles for male versus female *G. setzeri* encounters (n = 8 encounters)

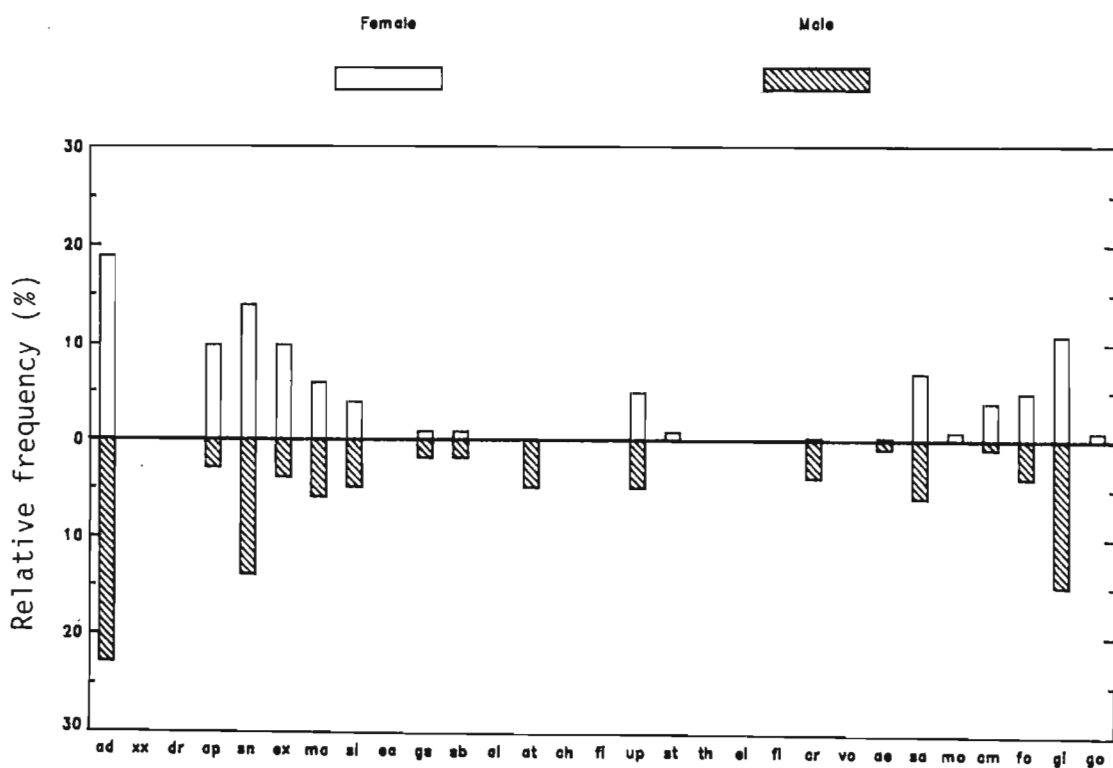


Fig. 39. Behaviour profiles for male versus female *G. vallinus* encounters (n = 3 encounters)

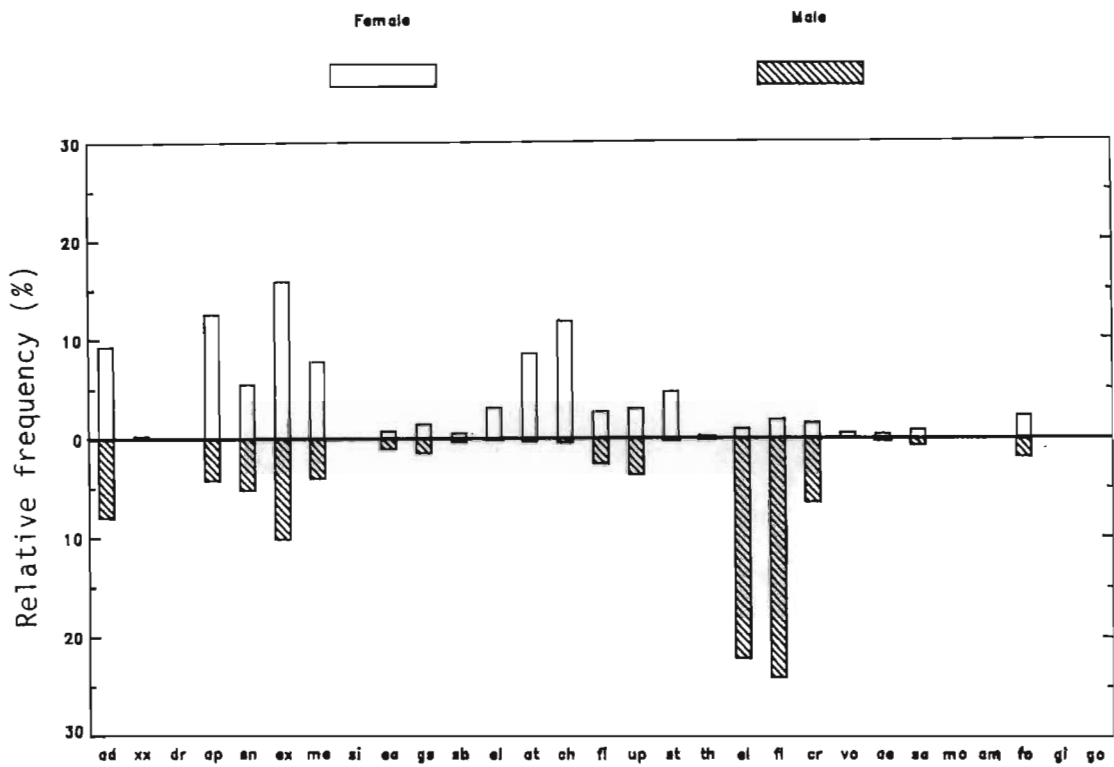


Fig. 40. Behaviour profiles for male versus female *G. tytonis* encounters (n = 8 encounters)

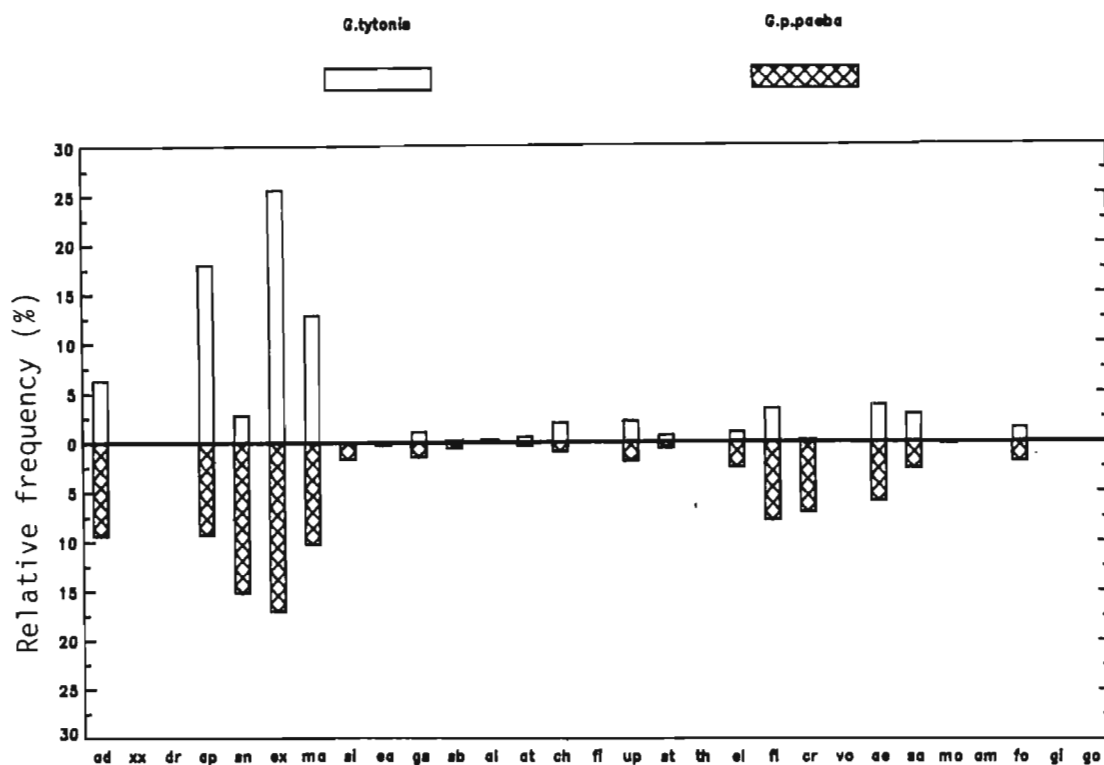


Fig. 41. Behaviour profiles for male *G. tytonis* versus male *G.p. paeba* encounters (n = 6 encounters)

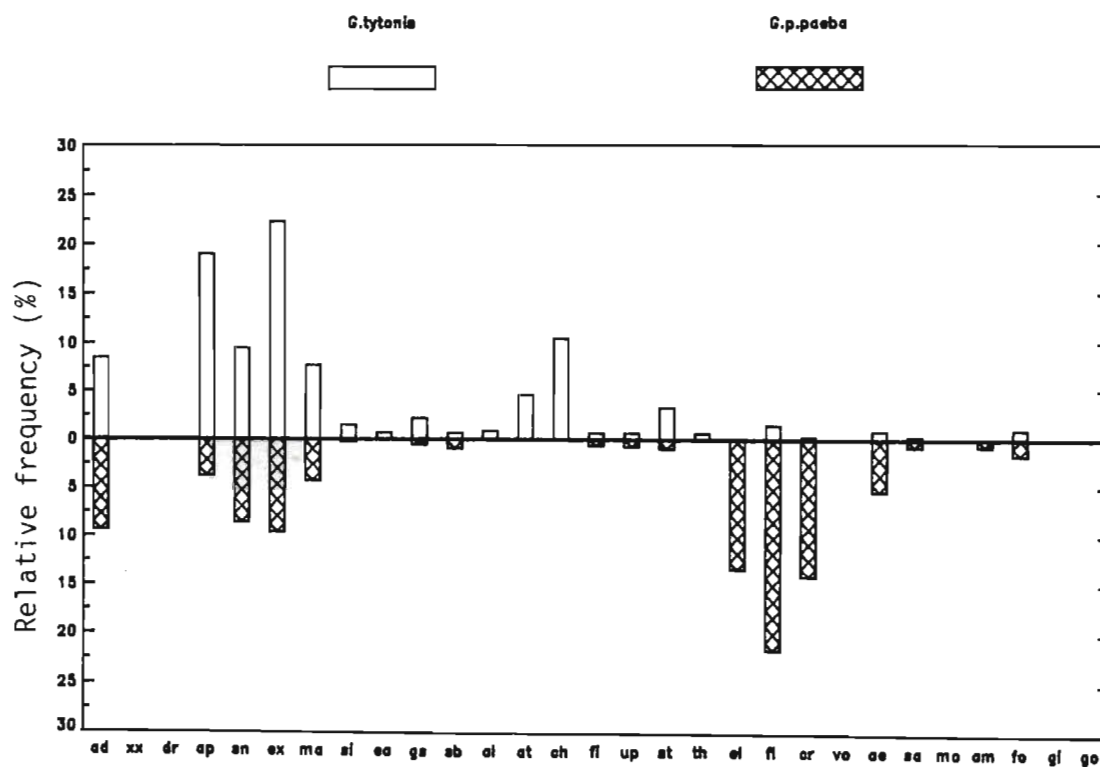


Fig. 42. Behaviour profiles for female *G. tytonis* versus female *G.p. paeba* encounters (n = 5 encounters)

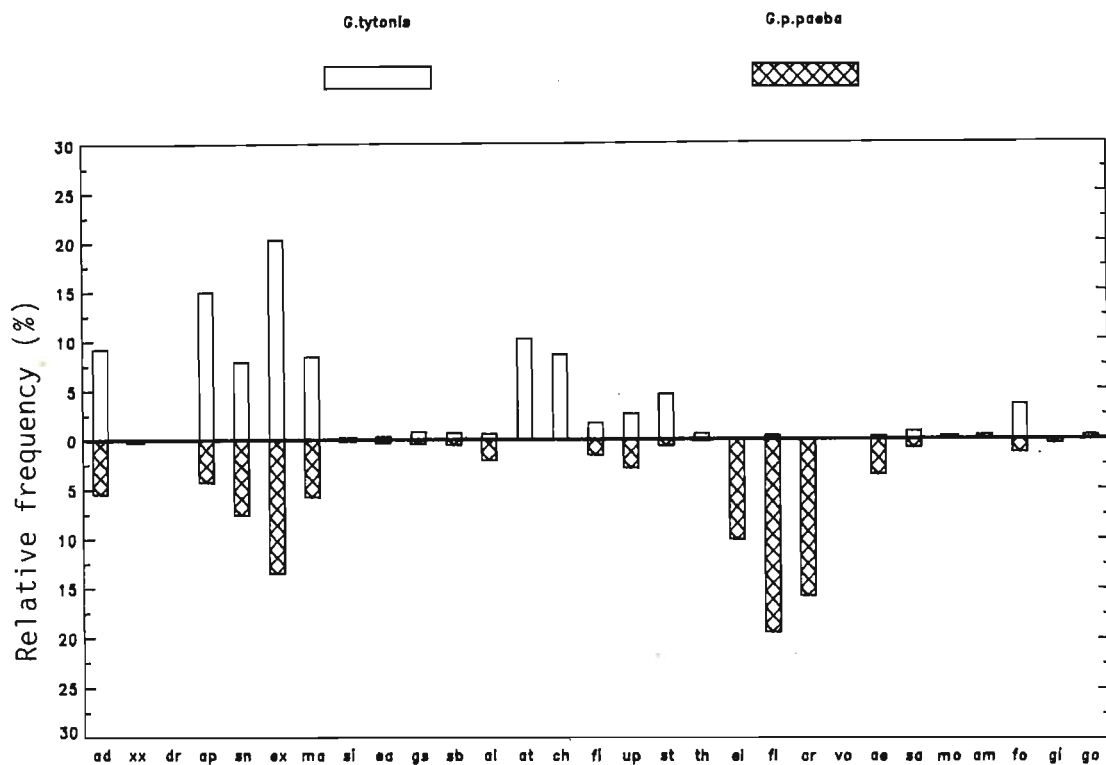


Fig. 43. Behaviour profiles for female *G. tytonis* versus male *G.p. paeba* encounters (n = 5 encounters)

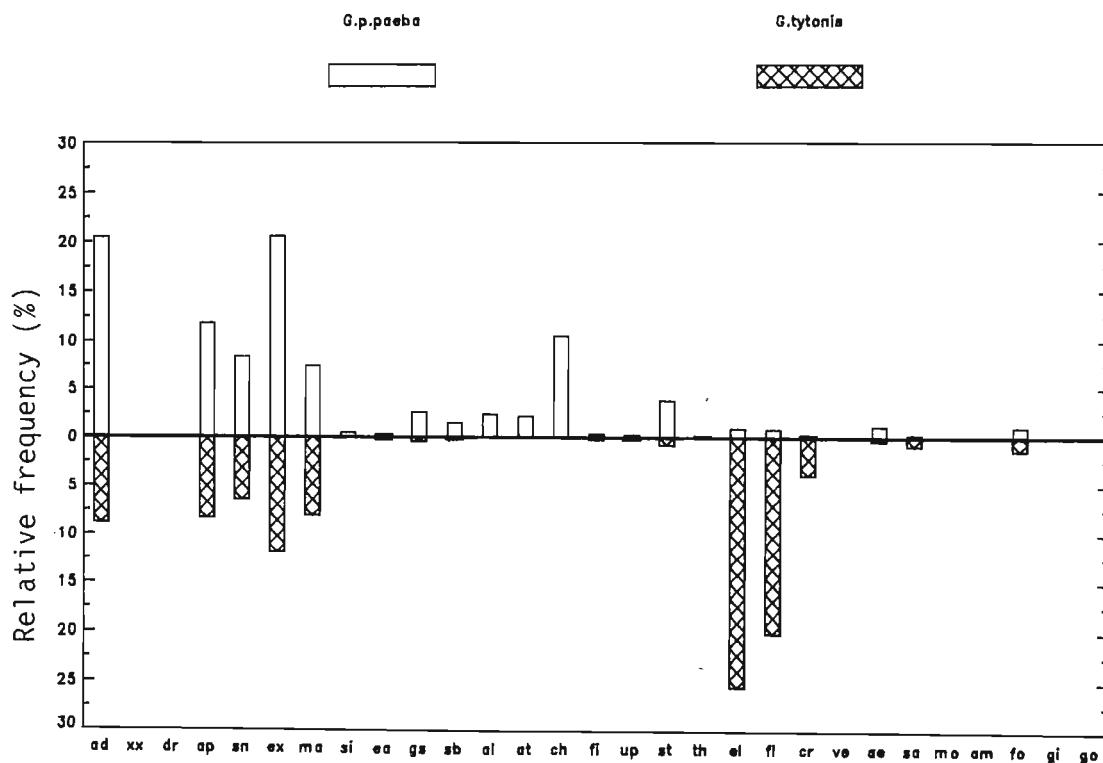


Fig. 44. Behaviour profiles for female *G.p. paeba* versus male *G. tytonis* encounters (n = 6 encounters)

illustrate the fact that males of these two species were less aggressive towards each other than females were, and this is also observed in Figs. 43 and 44, which indicate that females of both species dominated males of both species.

In *G.p.paeba* - *G.setzeri* encounters (Figs. 45 - 48), exploratory and solitary behaviours predominated, with little aggressive behaviour being displayed in all classes of encounter. Male and female *G.setzeri* behaved submissively, despite the low level of aggressive behaviour displayed by their opponents. Female *G.setzeri* performed some aggressive behaviour towards male *G.p.paeba*, which accordingly performed some submissive behaviour. Sexual behaviours formed a low proportion of all behaviours, but were exhibited more frequently by male and female *G.p.paeba* than *G.setzeri*.

Figures 49 - 52 illustrate encounters between *G.tytonis* and *G.setzeri*. These encounters were characterised by a high frequency of exploratory behaviours, little aggression, and submissive behaviour performed by both species. Male and female *G.setzeri* performed more submissive behaviour than their opponents. Sexual behaviours were seldom performed, and more frequently by *G.tytonis* than *G.setzeri*.

Encounters between male *G.vallinus* and male and female *G.p.paeba* (N.Cape) indicate that exploratory behaviours constituted the group of behaviours performed most

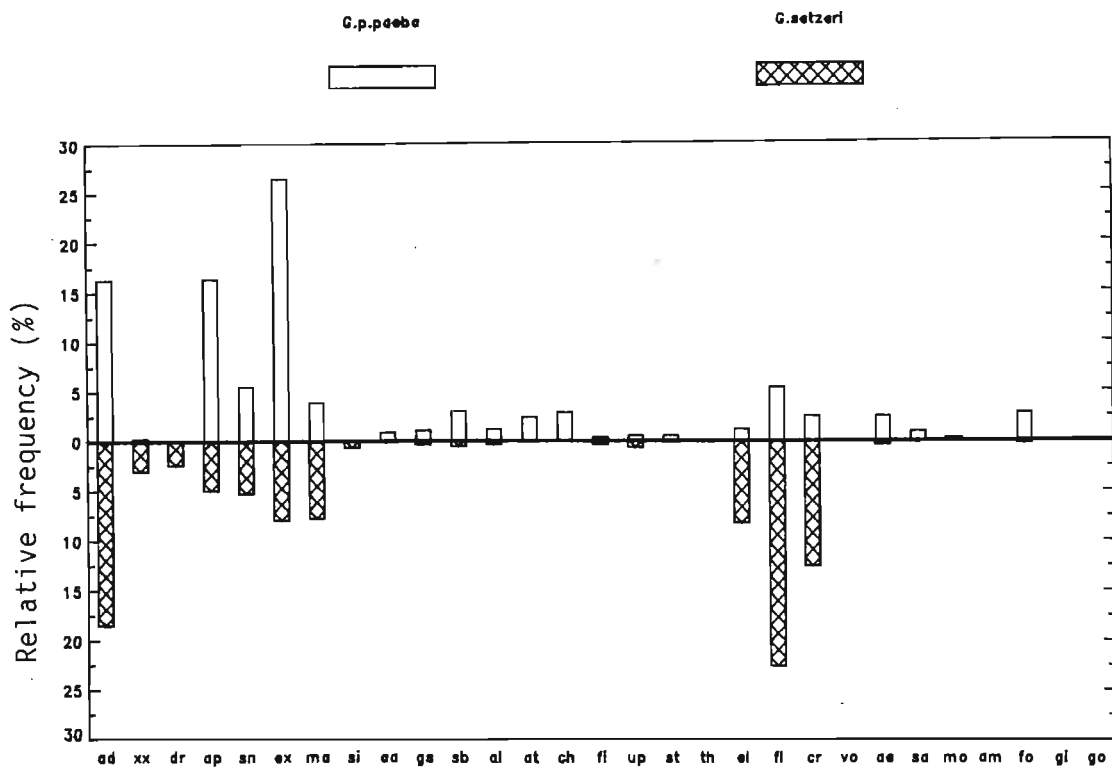


Fig. 45. Behaviour profiles for male *G.p. paeba* versus male *G. setzeri* encounters (n = 5 encounters)

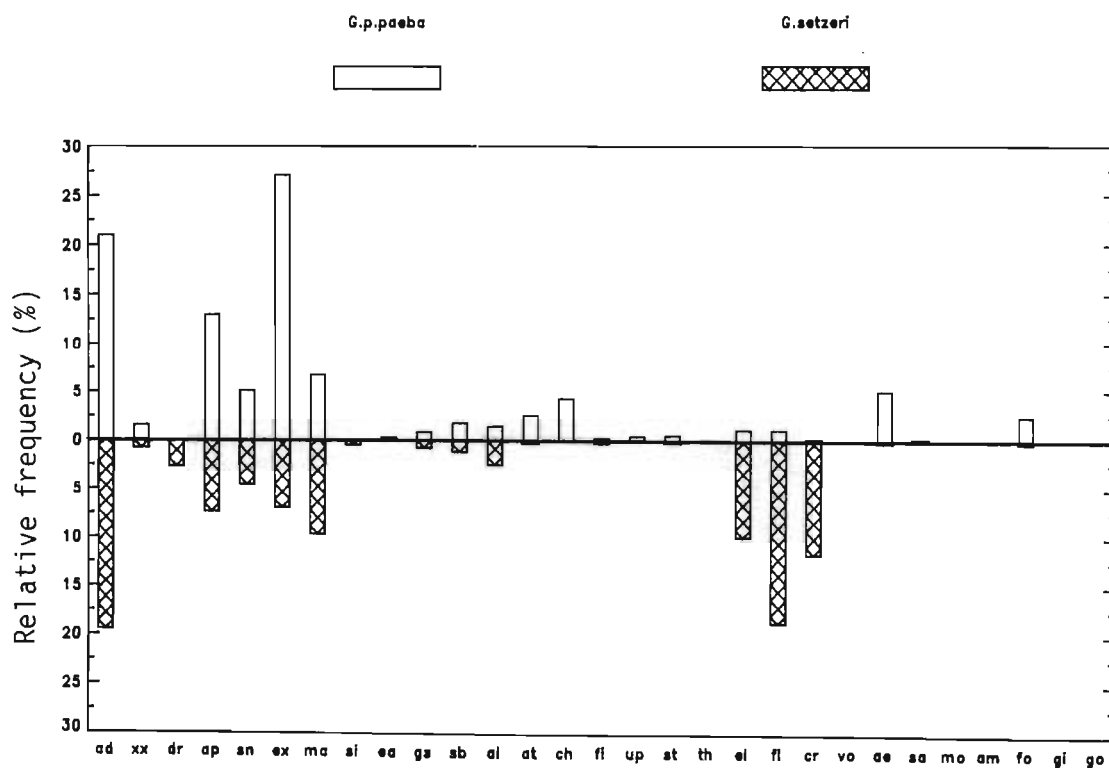


Fig. 46. Behaviour profiles for female *G.p. paeba* versus female *G. setzeri* encounters (n = 5 encounters)

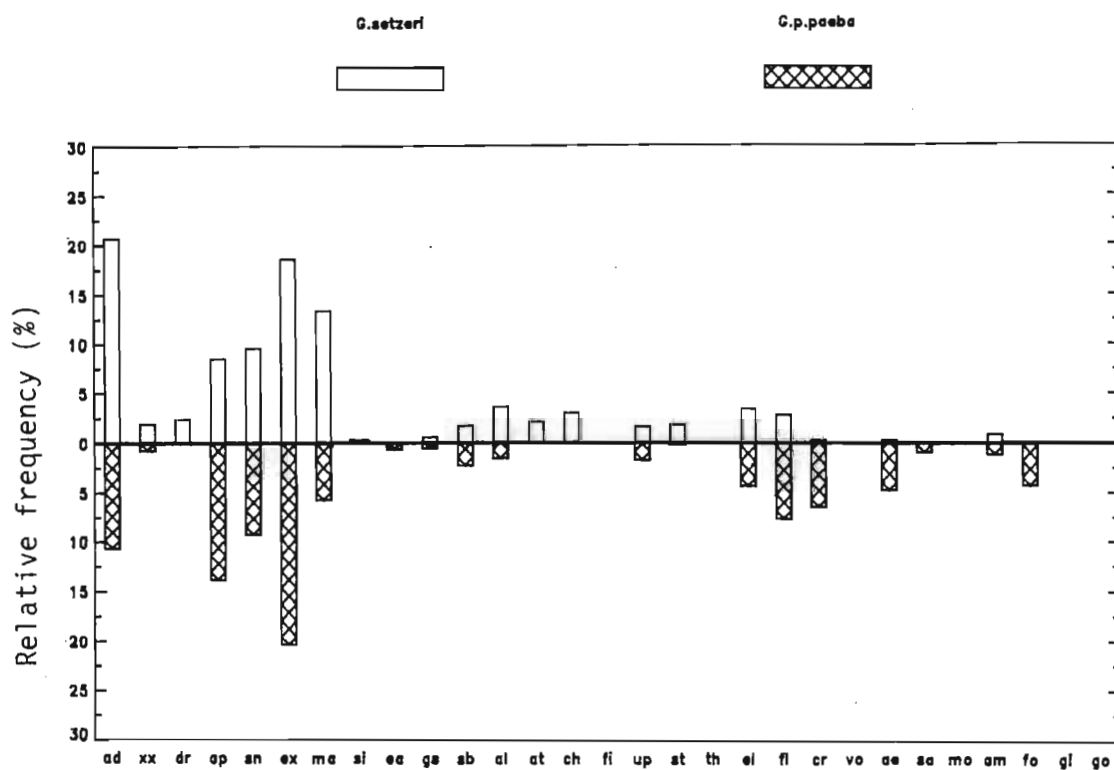


Fig. 47. Behaviour profiles for female *G. setzeri* versus male *G.p. paeba* encounters (n = 5 encounters)

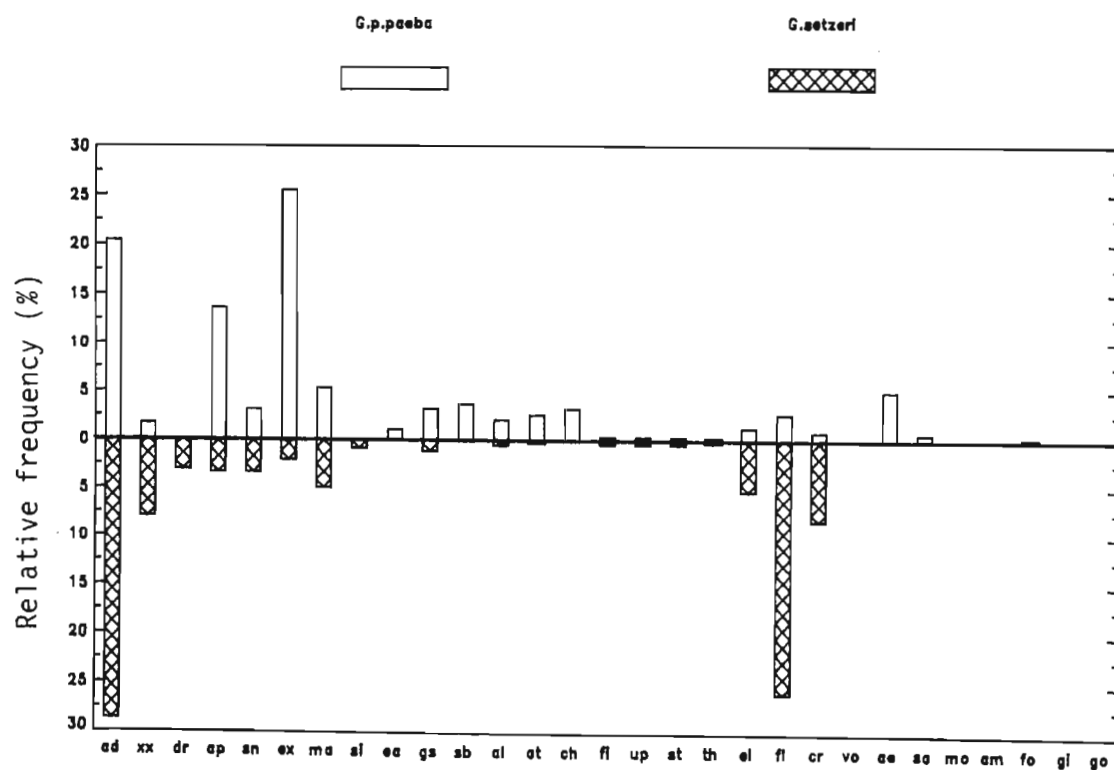


Fig. 48. Behaviour profiles for female *G.p. paeba* versus male *G. setzeri* encounters (n = 5 encounters)

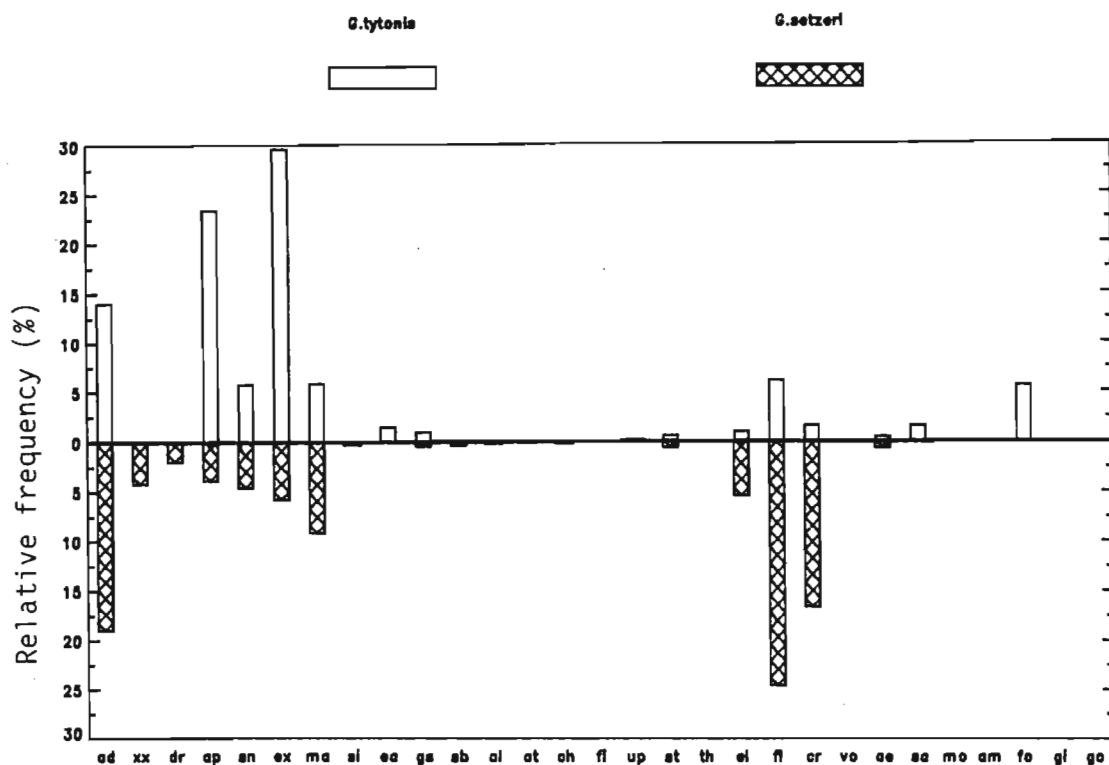


Fig. 49. Behaviour profiles for male *G. tytonis* versus male *G. setzeri* encounters (n = 5 encounters)

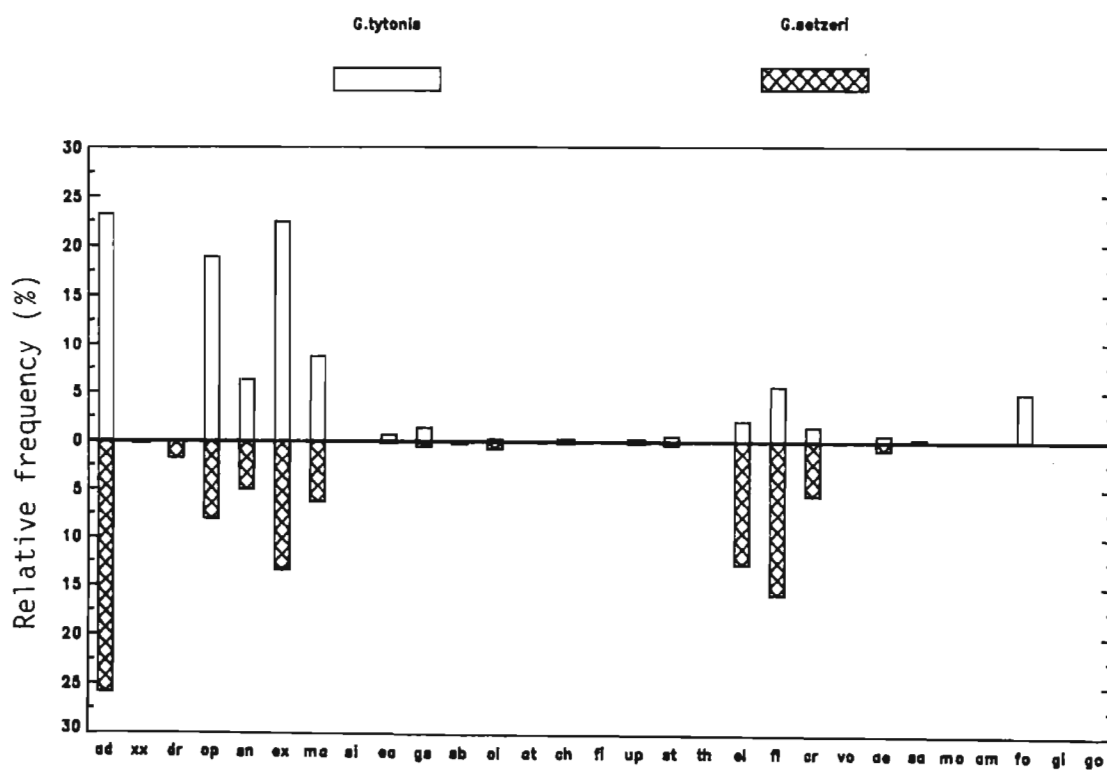


Fig. 50. Behaviour profiles for female *G. tytonis* versus female *G. setzeri* encounters (n = 5 encounters)

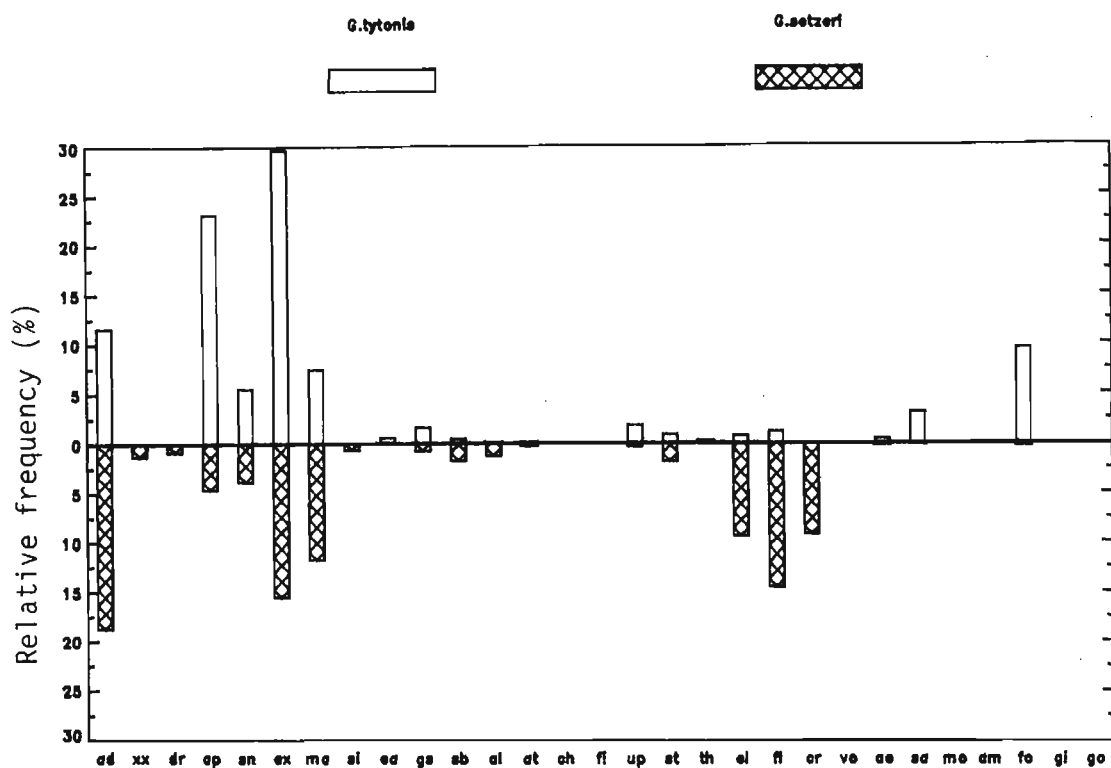


Fig. 51. Behaviour profiles for male *G. tytonis* versus female *G. setzeri* encounters (n = 5 encounters)

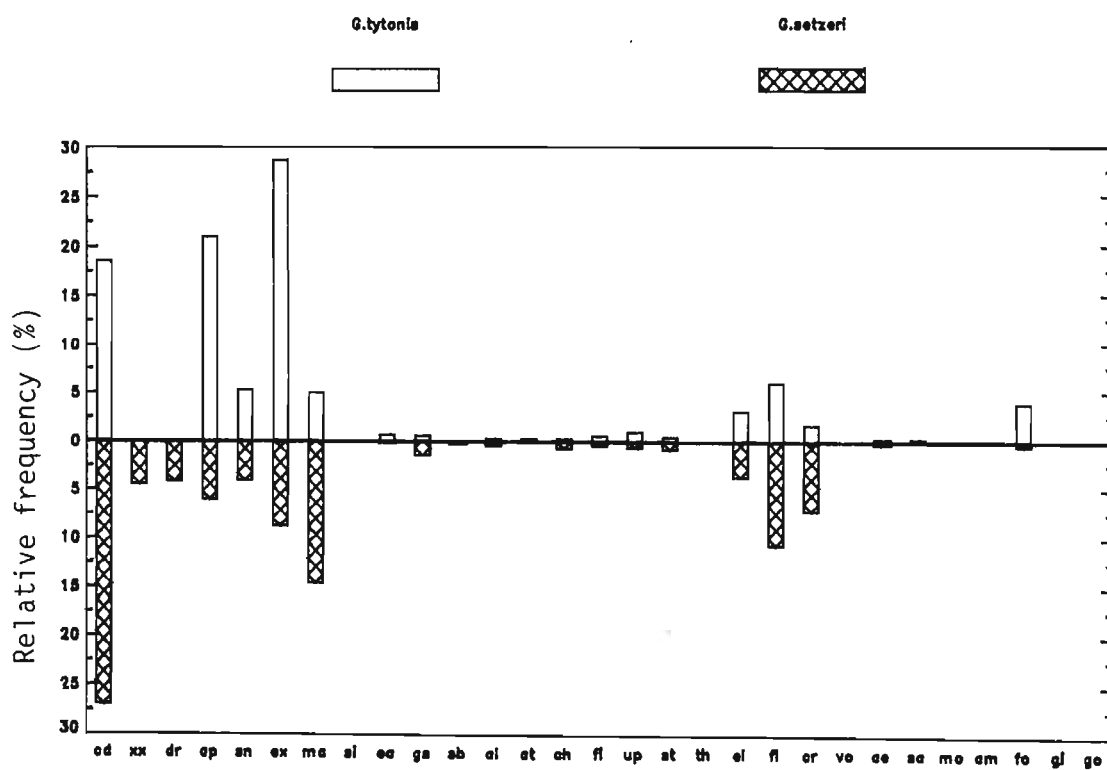


Fig. 52. Behaviour profiles for female *G. tytonis* versus male *G. setzeri* encounters (n = 5 encounters)

frequently (Figs. 53 & 54). Male *G.vallinus* performed more aggressive behaviour than *G.p.paeba* and no submissive behaviour, while the converse was true for *G.p.paeba*. Sexual behaviours, including GI, which occurred frequently in intraspecific *G.vallinus* encounters, were seldom seen in interspecific encounters.

Figures 55 - 58 illustrate encounters between *G.p.paeba* and *G.p.exilis*, and indicate that a wide variety of behaviours was performed by both species and sexes, although exploratory and solitary behaviours predominated. Aggressive and submissive behaviour was reduced in same-sex encounters, but occurred at a higher frequency in different-sex encounters. Sexual behaviour was displayed more frequently by males than by females.

Dominance/submissive relationships are discussed in Chapter 5.

4.7 DOMINANCE AND BODY SIZE

In order to test the null hypothesis that dominants and subordinates did not differ in body mass, mean mass of dominant animals was compared with mean mass of subordinates in intraspecific encounters. Results are shown in Table 17. The means did not differ significantly in any species or sex ($p > 0.05$, t-test).

4.8 PHYLOGENY

Behaviour profiles from intraspecific, same-sex encounters

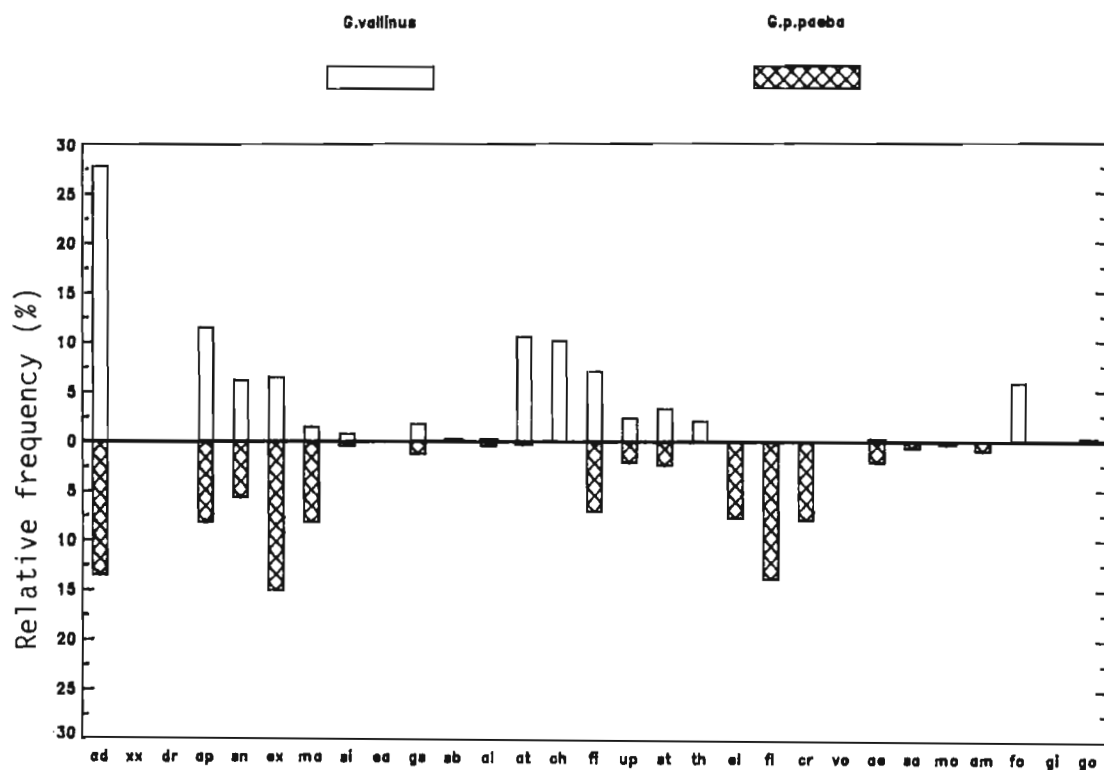


Fig. 53. Behaviour profiles for male *G. vallinus* versus male *G.p. paeba* (N. Cape) encounters (n = 3 encounters)

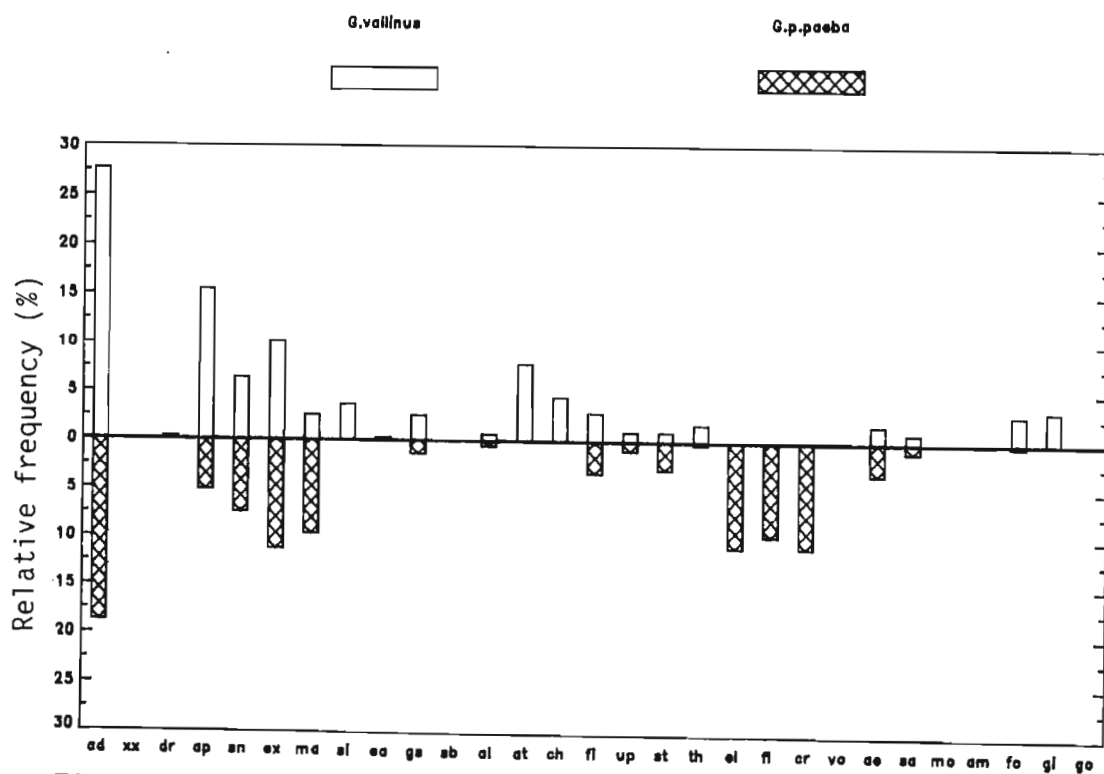


Fig. 54. Behaviour profiles for male *G. vallinus* versus female *G.p. paeba* (N. Cape) (n = 3 encounters)

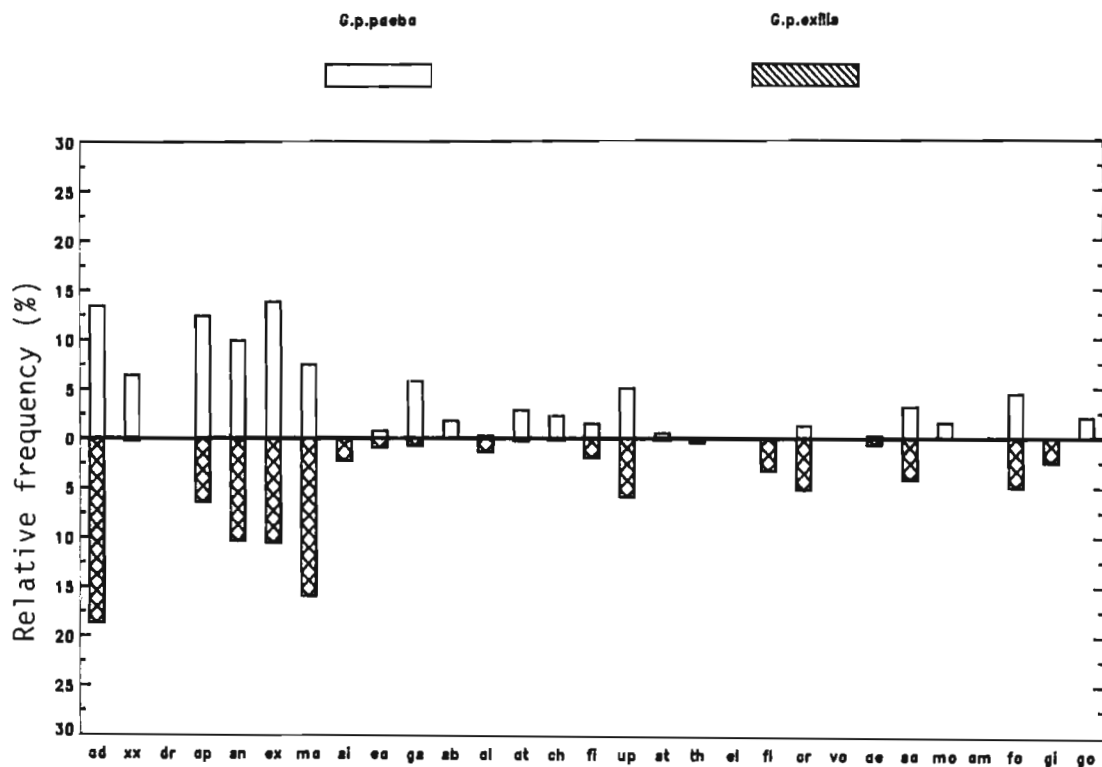


Fig. 55. Behaviour profiles for female *G.p. exilis* versus male *G.p. paeba* encounters (n = 5 encounters)

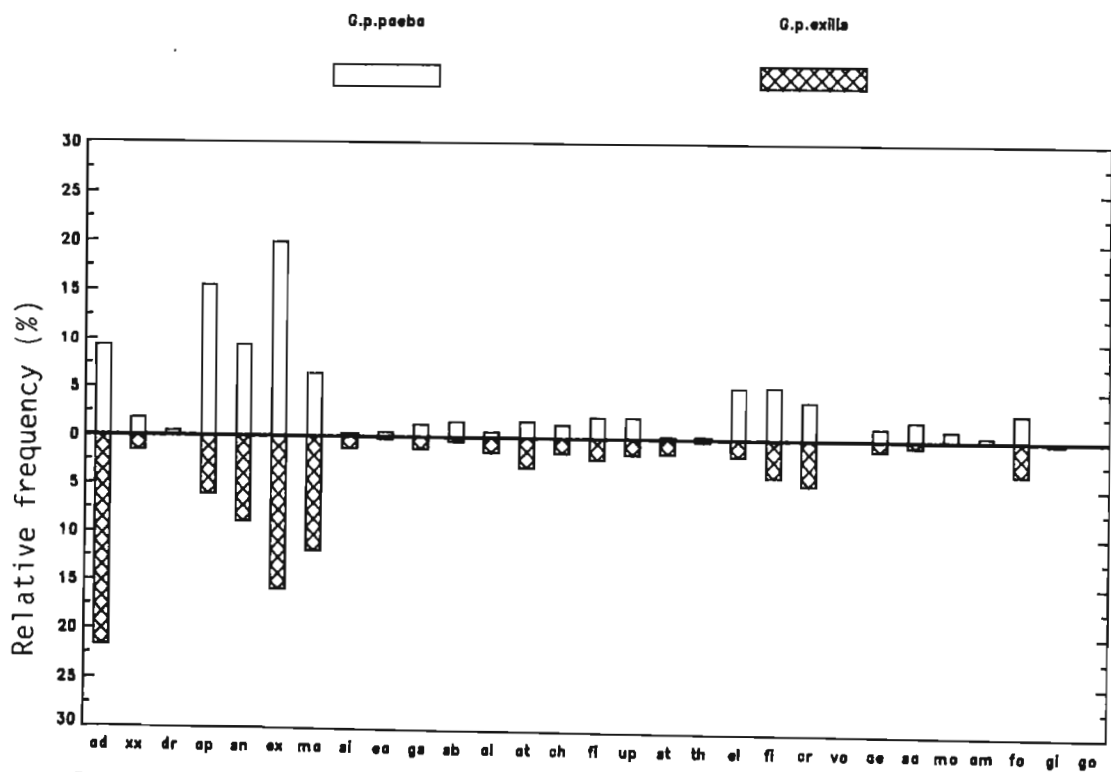


Fig. 56. Behaviour profiles for female *G.p. paeba* versus female *G.p. exilis* encounters (n = 5 encounters)

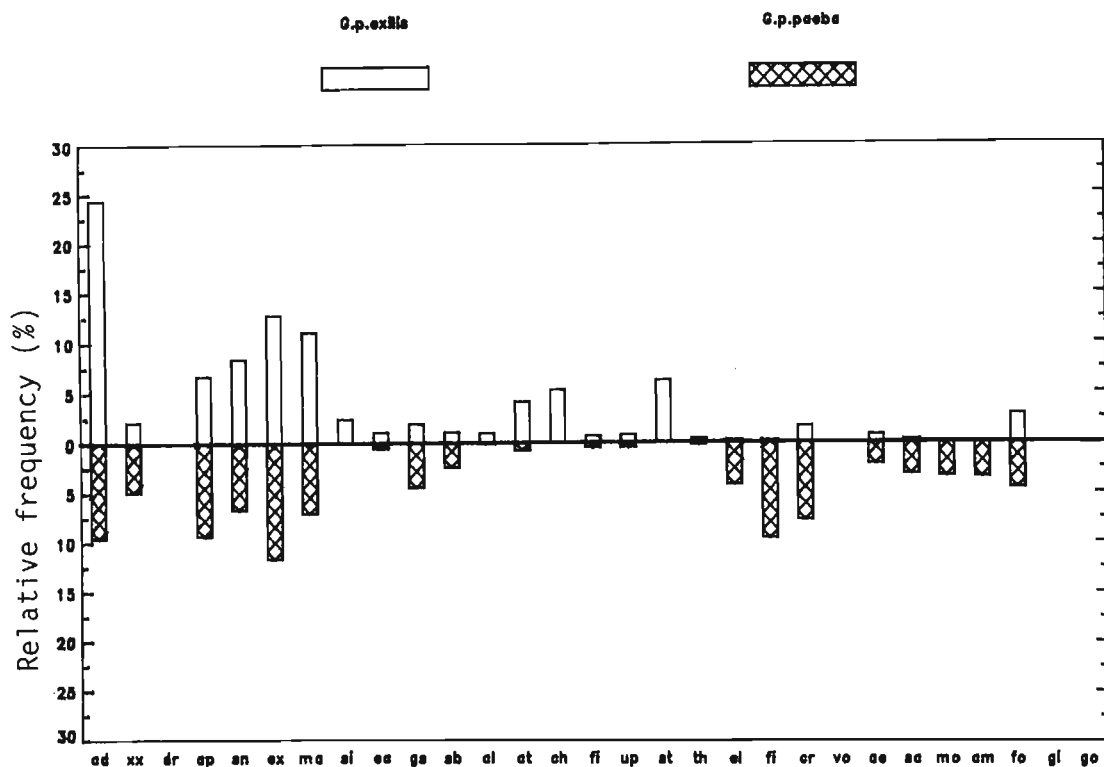


Fig. 57. Behaviour profiles for female *G.p. exilis* versus male *G.p. paebs* encounters (n = 5 encounters)

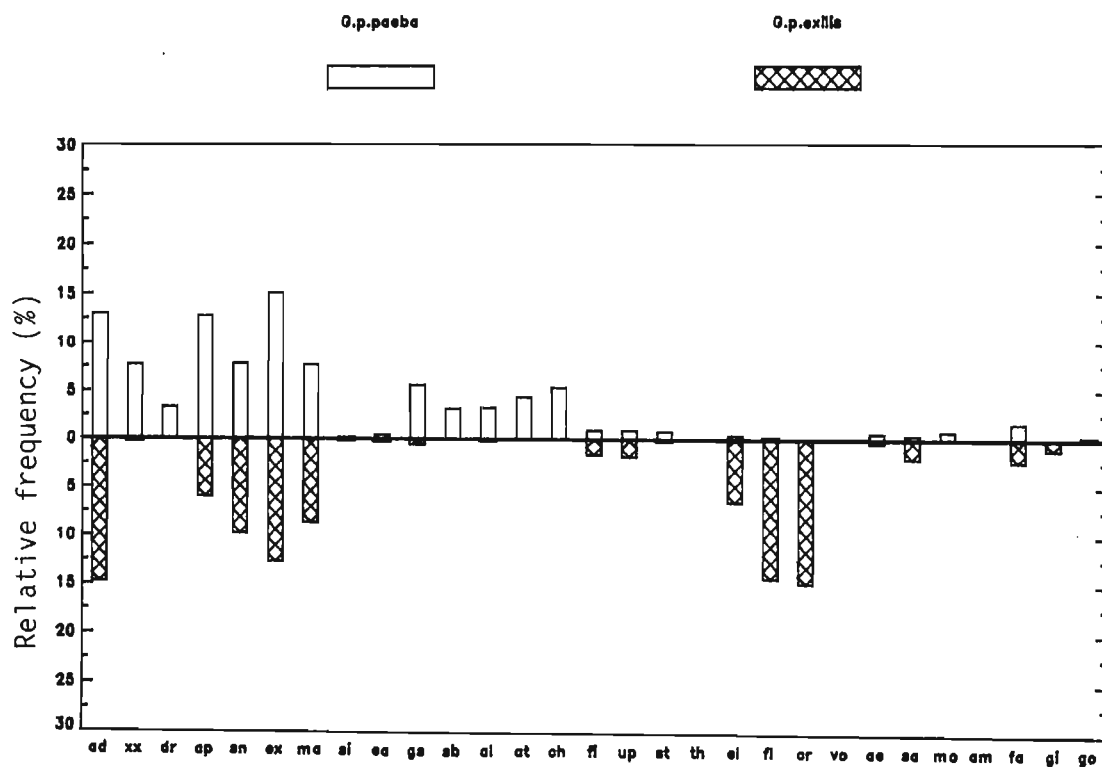


Fig. 58. Behaviour profiles for female *G.p. paebs* versus male *G.p. exilis* encounters (n = 5 encounters)

TABLE 17: MEAN MASS OF DOMINANT AND SUBMISSIVE
ANIMALS IN INTRASPECIFIC ENCOUNTERS

(Mass is given in grams.)

SPECIES	N	MEAN \pm SD		p
		DOMINANT	SUBMISSIVE	
<i>G.p.paeba</i> ♂	6	28.5 \pm 8.3	30.2 \pm 7.5	n.s.
<i>G.p.paeba</i> ♀	10	28.7 \pm 4.6	24.5 \pm 4.1	n.s.
<i>G.p.exilis</i> ♂	5	28.0 \pm 2.7	24.4 \pm 2.3	n.s.
<i>G.tytonis</i> ♀	7	30.0 \pm 5.2	28.7 \pm 4.4	n.s.
<i>G.tytonis</i> ♂	6	28.5 \pm 3.7	30.7 \pm 6.0	n.s.
<i>G.setzeri</i> ♀	3	49.0 \pm 7.5	51.0 \pm 7.2	n.s.
<i>G.setzeri</i> ♂	4	36.8 \pm 5.4	42.3 \pm 7.5	n.s.
<i>G.vallinus</i> ♂	3	40.7 \pm 6.1	38.0 \pm 6.9	n.s.

were compared by means of weighted pair group cluster analysis in order to determine levels of similarity within the group. The resulting dendrogram is shown in Figure 59. Male and female *G.p.paeba* and *G.tytonis* formed one cluster, while male and female *G.setzeri* and female *G.p.exilis* formed a second group. Male *G.p.exilis* and *G.vallinus* differed considerably from either of these two groups. The significance of this clustering is discussed in Chapter 5.

4.9 TERRITORIALITY

Time spent in each area of the apparatus by each individual is shown in Table 18 and Figs. 60 - 70 (Appendix 3). The chi-squared goodness-of-fit test was applied to the data to test the null hypothesis that all animals spent equal amounts of time in each section of the apparatus; for all individuals of all species the null hypothesis was rejected. The second null hypothesis to be tested was that each animal's movements were restricted to its original area and the common central area. Chi-squared analysis revealed that for 40 of the 48 animals, this hypothesis was rejected; results are shown in Table 19 (Appendix 3).

Although animals did not maintain their originally-occupied areas, they did not move randomly through the apparatus. It was therefore decided to investigate the amount of overlap in time spent in various areas of the apparatus by different individuals. In order to calculate the overlap, time spent in each area by every individual was compared for

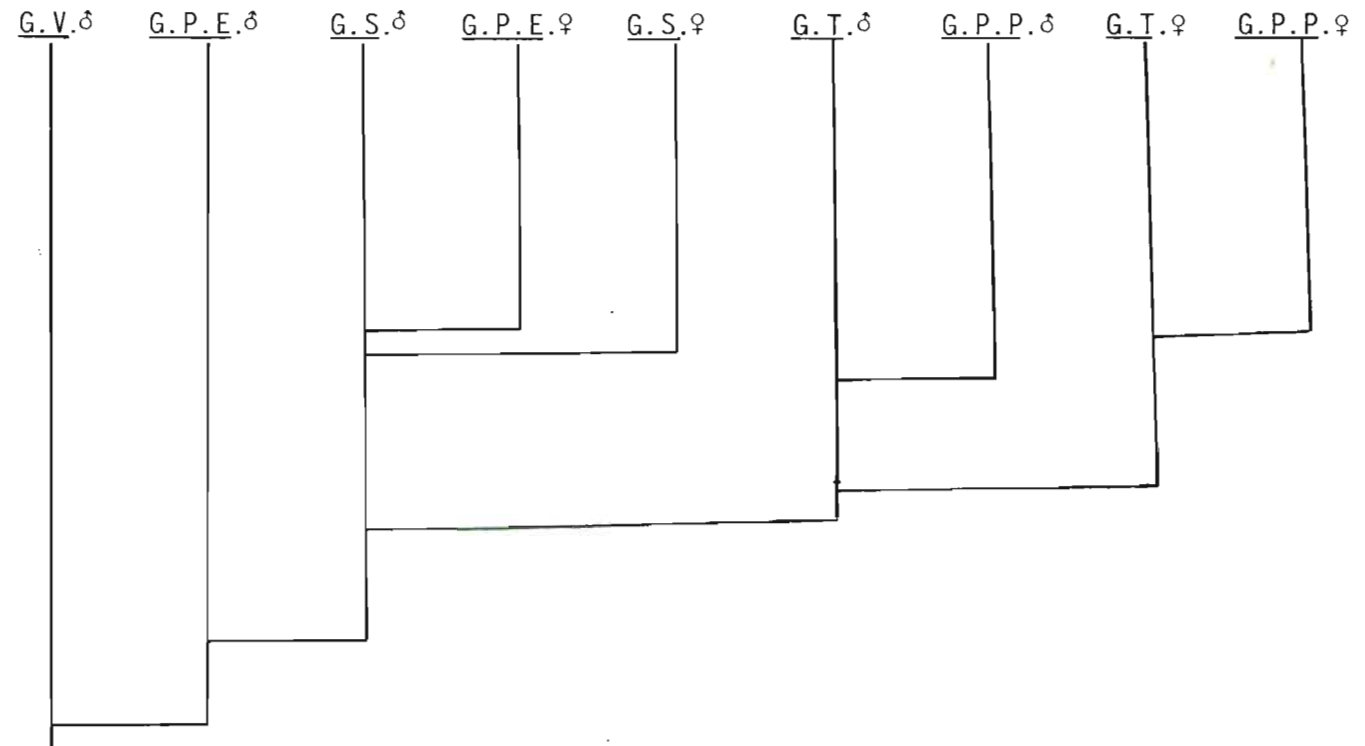


Fig. 59. Dendrogram derived from cluster analysis of relative frequencies of behaviours in agonistic encounters.

each observation period. Where two or more individuals utilized the same areas, the lowest figure was taken to represent the overlap. Overlap was analysed for all possible combinations of two, three and four individuals. Overlaps on separate observations were then summed, and the mean overlap for two and three individuals was computed. This was expressed as a percentage of the total observation time to facilitate comparisons.

Replicates of the same sex and species were compared using the t-test for significant differences between two means (Lehner, 1979). Differences were not significant, with the exception of the two replicates for *G.p.paeba* females. All other sets of data were pooled for replicates of the same sex and species. Differences in the means for different sexes and species were tested using the t-test; results are given in Tables 20 and 21.

Female *G.setzeri* and *G.tytonis* overlapped for significantly less time than males of these two species. Male *G.p.paeba* shared areas significantly less frequently than *G.tytonis*, which overlapped significantly less frequently than male *G.setzeri*. Since the two replicates of female *G.p.paeba* differed significantly, they were not included in this analysis.

TABLE 20: MEAN OVERLAP IN AREA UTILISATION BETWEEN TWO, THREE OR FOUR INDIVIDUALS IN THE TERRITORIALITY APPARATUS. (Overlap is expressed as a percentage of the total observation time \pm S.D.

SPECIES	SEX	OVERLAP IN AREAS OCCUPIED						TOTAL TIME
		2 ANIMALS	N	3 ANIMALS	N	4 ANIMALS	N	
<i>G. tytonis</i>	♀♀	21.7 \pm 22.9	12	5.3 \pm 7.0	8	0.8 \pm 1.1	2	2400
<i>G. tytonis</i>	♂♂	50.1 \pm 20.3	12	33.2 \pm 16.9	8	22.9 \pm 9.6	2	2550
<i>G.p. paeba</i>	♀♀	36.0 \pm 17.3	6	15.0 \pm 12.4	4	3.6	1	3600
<i>G.p. paeba</i>	♀♀	5.7 \pm 2.8**	4	0.6	1			1725
<i>G.p. paeba</i>	♂♂	17.4 \pm 19.3	12	3.0 \pm 4.1	8	0.5 \pm 0.7	2	2362
<i>G. setzeri</i>	♀♀	26.1 \pm 31.3	12	8.2 \pm 9.2	8	3.6 \pm 5.0	2	2400
<i>G. setzeri</i>	♂♂	68.4 \pm 11.0	6	59.5 \pm 7.5	4	54.8	1	2100

** = differences in mean overlap in the two sets of female *G.p. paeba* is significant ($0.01 > p > 0.001$, two-tailed t-test, 8 d.f.).

TABLE 21: RESULTS OF T-TEST FOR COMPARISON OF MEAN OVERLAP BETWEEN SEXES AND SPECIES.

SPECIES OR SEXES COMPARED	OVERLAP BETWEEN 2 INDIVIDUALS		OVERLAP BETWEEN 3 INDIVIDUALS	
	T-STATISTIC	D.F.	T-STATISTIC	D.F.
<i>G.setzeri</i> ♂♂ & ♀♀	3.1805**	16	11.1517***	10
<i>G.tytonis</i> ♂♂ & ♀♀	4.0605***	22	4.9037***	14
<i>G.p.paeba</i> ♂♂ & <i>G.tytonis</i> ♂♂	4.0605***	22	4.9037***	14
<i>G.p.paeba</i> ♂♂ & <i>G.setzeri</i> ♂♂	5.9691***	16	17.2398***	10
<i>G.setzeri</i> ♂♂ & <i>G.tytonis</i> ♂♂	2.2689*	22	2.9224*	10
<i>G.setzeri</i> ♀♀ & <i>G.tytonis</i> ♀♀	0.3892n.s.	22	0.7095n.s.	14

n.s.= not significant

* = $0.05 > p > 0.01$

** = $0.01 > p > 0.001$

*** = $p < 0.001$

CHAPTER 5. DISCUSSION

5.1 ANALYSIS OF BEHAVIOUR

5.1.1. EXPLORATORY BEHAVIOURS

The most common sequence of behaviours was AD (attend) --> AP (approach) --> SN (sniff noses) --> MA (move away), each of these behaviours branching to EX (explore), which emerged as a linking behaviour between bouts of aggressive and submissive behaviour in all species except male *G.vallinus*. The alternative behaviour was sit (SI), which was most frequently observed in male *G.p.exilis*, *G.setzeri* and *G.vallinus*. These groups also had the lowest level of activity. GS (self-groom), SB (sandbathe), XX (kick-back) and EA (eat) were followed by AD or EX in those species where they were represented. SB occurred most frequently in *G.setzeri* females, XX was performed most frequently by *G.setzeri* males and *G.p.exilis* females.

Comparison of actual frequencies with expected frequencies in *G.p.paeba* revealed that AE (approach elongate) and AD in both sexes and AP in females occurred significantly more frequently in the conflict situations than expected. EX occurred more frequently than was expected, but this difference was not significant.

5.1.1.1 AUDITORY COMMUNICATION

Since all four species of *Gerbillurus* possess enlarged tympanic bullae, auditory communication may be expected to play a role in social contacts. Vocalizations were heard

only in *G.tytonis*; ultrasonic communications were not recorded in this study. Tooth-chattering, as described for *Rattus rattus*, *Rattus norvegicus* (Barnett, 1975) and for several heteromyid rodents (Eisenberg, 1963a) was not heard in species of the *Gerbillurus* genus.

Drumming has been recorded in several species of heteromyid rodents (Eisenberg, 1963a) and may function in territorial defense and advertisement in bannertail kangaroo rats, *Dipodomys spectabilis* (Randall, 1984). Eisenberg (1963a) described foot-drumming as occurring by the repeated striking of one hindfoot against the substrate. In species of the *Gerbillurus* genus, two distinct types of foot-drumming were observed, although these rarely occurred in agonistic encounters. *G.p.paeba*, *G.p.exilis* and *G.tytonis* performed foot-drumming by striking the substrate with the hindfeet alternately in short "rolls", while *G.setzeri* were seen to "shiver" the hindquarters without producing an audible sound. *G.setzeri* was the only species to drum in agonistic encounters, and did so more frequently in interspecific than in intraspecific encounters.

5.1.1.2 VISUAL COMMUNICATION

The initial orientation of animals towards each other indicated that vision was important in the identification of an opponent. Animals spent a large proportion of their total behaviour watching each other, this being particularly marked in *G.p.exilis* and *G.setzeri*.

Submissive animals seldom stopped watching their opponents, since during the crouch posture, the animal's eyes were constantly directed towards the opponent.

5.1.1.3 OLFACTORY COMMUNICATION

Olfaction has been found to contribute significantly to the co-ordination of the social behaviour of rodents (Eisenberg, 1963a; Barnett, 1975). The deposition of chemical substances which exert an influence on another animal's behaviour is achieved by perineal dragging, sandbathing and urination in heteromyid rodents (Eisenberg, 1963a). Rats leave odour trails when they run regularly over a light surface (Barnett, 1975), and Mongolian gerbils (*Meriones unguiculatus*) have been found to mark objects by skimming them with a midventral sebaceous scent gland (Thiessen, 1968; Roper & Polioudakis, 1977). Bank voles (*Clethrionomys glareolus*) leave urine trails in novel areas, which other voles react to (Johnson, 1975).

The deposition of chemical marking substances on a substrate as unstable as the sand dunes would seem to serve little purpose in communicating information to other individuals. "Marking" by means of a perineal rub was identified in *Gerbillurus* species, but did not occur in staged encounters. Similarly urination was identified, but eliminated from the repertoire of behaviours exhibited in encounters because it was impossible to adequately identify this act from the videotapes.

Sandbathing occurred in all *Gerbillurus* species, and more frequently than expected in same-sex *G.p.paeba* encounters. Eisenberg (1963b) has suggested that sandbathing originated from a combination of stretching and perineal dragging, which in the primitive condition served to mark the nest or burrow. The presence of a communal sandbathing spot has been recorded for *Dipodomys ingens* (Eisenberg, 1963a), and locus specificity of sandbathing in heteromyid rodents has been observed (Eisenberg, 1967). Sandbathing may be regarded as serving a marking as well as a pelage-dressing function. The indications from the present study are that sandbathing may function as a means of chemical communication, however specific sandbathing loci have not been identified in the field for *G.tytonis* and *G.p.paeba* (Boyer, pers.comm.). The incidence of sandbathing was highest for *G.setzeri* females and *G.p.paeba* males, while lowest mean number of sandbathing acts was recorded for *G.p.exilis* males and females and *G.vallinus* males. These trends were noted in intraspecific different-sex encounters, however sandbathing occurred at a much higher frequency in male *G.vallinus* in these encounters.

It has been suggested that the presence of oil on the pelage reduces evaporative water loss, but excess oil needs to be removed by sandbathing (Borchelt et al., 1976). *G.p.exilis* inhabits areas where water is available (Ascaray, 1984) and it was noted, although not quantified, that the

pelage did not become as oily as that of the other species. *G.p.paeba* and *G.tytonis* always selected fine, dusty sand for sandbathing in preference to any other substrate (Hamer, 1985). These observations indicate the need for further investigation into the role of sandbathing as a marking behaviour in the *Gerbillurus* species.

Naso-nasal contacts occurred frequently and succeeded exploratory or approach behaviour. Males made naso-nasal contact with other males more frequently than with females, except in *G.setzeri*, where females made naso-nasal contacts with females more frequently than with males. *G.vallinus* performed more SN in different-sex than in same-sex encounters. Sniffing of the facial area seems to be important in the identification of an opponent, however it occurred significantly less frequently than expected in same-sex encounters between "unfamiliar" male and female *G.p.paeba* ($p < 0.001$).

5.1.1.4 DISPLACEMENT ACTIVITIES

Self-grooming (GS) was exhibited by all species, and has been listed as a displacement activity in four species of laboratory rodents, where it is described as an abbreviated face wash (Grant & Mackintosh, 1963). Although grooming was seen in staged encounters in *Gerbillurus* species, this occurred less frequently than expected in *G.p.paeba* and is not considered to be a displacement activity in this species.

Displacement digging has been described in guinea-pigs (Grant & Mackintosh, 1963), and digging and kick-back has been described in connection with courtship behaviour in *Perognathus* spp., *Microdipodops* spp. and *Dipodomys* spp. (Eisenberg, 1963a). Eisenberg (1967) has classed this as a displacement activity in these genera. Kicking back (XX) in species of the genus *Gerbillurus* was performed most often while an animal watched its opponent, and occurred most frequently in male *G.setzeri*. It may be regarded as a displacement activity in this genus.

Displacement eating has been described as an abbreviated form of the normal activity in laboratory rodents (Grant & Mackintosh, 1963). Eating was rarely observed in staged encounters between members of the genus *Gerbillurus*, and the difference between observed and expected frequencies was not significant in male *G.p.paeba*.

5.1.2. AGGRESSIVE BEHAVIOUR

Attacking was achieved by means of an attack leap (AL) or an attack (AT), and no clear differences were evident in the behaviour profiles. AT occurred more frequently than AL in most groups, exceptions being female *G.p.paeba* and male *G.p.exilis*.

In transition frequency diagrams, it is clear that AT - AL - CH (chase) were closely linked and terminated in CH or ST (stop), both of which returned to exploratory behaviours. CH occurred more frequently in females than in males.

"Attack" as defined in this study appears to be similar to "rushing" described by Eisenberg (1963a), in which an animal approaches the opponent and strikes at it with the forepaws and body. The part of the body to which an attack was directed was usually the flank, but in animals which were caged together, bites were found on the tail and rump. The result of an attack was that the opponent fled and was chased by the attacker, which then attempted to bite the retreating animal. If the retreating animal was caught, a fight ensued, as described by Eisenberg (1963a). Fights were usually followed by further chasing. The attack leap seen in the gerbils was similar to that described by Eisenberg (1963a) and the "attack" described by Barnett (1975). A bout of aggressive behaviour terminated in "stop" (ST), after which exploratory activities were resumed.

FI (fight) and UP (upright) were included in the aggressive group of behaviours in 6 cluster diagrams, while in male *G.setzeri*, UP - FI was linked with CR. In male *G.p.exilis* and *G.vallinus*, UP was associated with AD. UP occurred more frequently in males than in females, and was most frequent in male *G.vallinus* where it was of longer duration than in the other species. It is clear from transition frequency diagrams that UP and FI are linking behaviours between the aggressive and submissive groups of behaviours. The aggressive group of behaviours was absent in male

G.p.exilis and represented only by UP and AT in male *G.vallinus*.

The upright posture has been described for a large number of rodent species (Grant & Mackintosh, 1963; Eisenberg, 1963a; Barnett, 1975). In certain species, e.g. *Mus musculus* there is a distinction between an upright offensive posture, and an upright defensive posture (Scott, 1970). Turner and Iverson (1973) described a "mutual upright" in voles and suggested that this posture appeared to be a mutual testing of dominance tendencies. Eisenberg (1963a) has stated that the angle of the body to the substrate enables the distinction between two functionally different uprights: the more vertical the animal's body is, the less likely it is to attack. Conversely, an angle of about 30° to the substrate indicates that an animal is likely to attack.

Scott (1970) has reported that the upright posture in rats may be interpreted in three ways:

- a) both rats are behaving defensively;
- b) both rats are behaving offensively;
- c) one rat is behaving defensively while the other is attacking.

In this study, no distinction was made between the offensive and defensive upright posture. The upright posture in *Gerbillurus* species was more closely associated with aggressive behaviours in cluster analysis, but

occupied an intermediate position between aggressive and submissive behaviours in transition diagrams. The upright posture was succeeded by "move away" (MA) or "attend" (AD) more frequently than any other behaviour in most species and sexes. It was preceded by other aggressive behaviours more frequently than by submissive behaviours, thus it would seem, in this genus, to be an offensive act, after which the interaction terminated. This supports Turner and Iverson's (1973) suggestion that information relating to dominance tendencies is exchanged in the upright posture.

Results from the testing of territoriality indicates that males of three species were more tolerant of conspecifics than females were. Males performed more uprights in staged encounters than females did. *G.vallinus*, which are reported to be gregarious (De Graaff, 1981), had a high incidence of upright postures, and these were of longer duration than the upright of any other species. The correlation of the frequency of occurrence of upright postures with the social structure of rodents merits further investigation.

"Threat" is an important component of aggressive behaviours in the rat (Barnett, 1975) and in mice, guinea-pigs and hamsters (Grant & Mackintosh, 1963). The descriptions of these postures as given by these two authors would seem to indicate that the behaviour referred to is not the same in both studies. In the rat, it is described as a "dance"

with the flank presented to the opponent, back arched and legs fully extended. No such act was seen in the gerbils, where the behaviour identified as "threat" appeared to be an intention movement of attacking, as described for the hamster (Grant & Mackintosh, 1963). This behaviour occurred infrequently in gerbils.

5.1.3. SUBMISSIVE BEHAVIOURS

Escape leap (EL) and flee (FL) were closely associated and occurred more frequently in females than in males, with the exception of FL in *G.setzeri*, where the reverse was observed. These behaviours were not exhibited in male *G.vallinus*, while only CR (crouch) was observed in *G.p.exilis*. Submissive behaviours terminated in CR, which then returned to the investigatory group of behaviours.

A submissive posture in which one animal lies flat on its back after a fight has been described in *R.rattus* and *R.norvegicus* (Barnett, 1975); several heteromyid rodents, where it is referred to as "defeat" (Eisenberg, 1963a); and in rats and hamsters (Grant & Mackintosh, 1963). This posture was not observed in this study. "Retreat", defined as a directed movement away from the opponent (Grant & Mackintosh, 1963), was seen in two contexts in this study and was termed "move away". In a sexual context, an animal moved away from a "following" animal, and in exploratory behaviour, an animal moved away after approaching, chasing or sniffing noses with an opponent.

A high intensity form of "move away" is "flee" (FL), which appears to be similar in form in all rodents (Grant & Mackintosh, 1963; Eisenberg, 1963a). However, included in the submissive behaviours and closely linked with "flee" is the escape leap, a wild erratic jumping performed while being chased, as described for heteromyid rodents (Eisenberg, 1963a).

The "crouch" (CR) posture described for mice, rats and guinea-pigs (Grant & Mackintosh, 1963) approximates the crouch seen in gerbils. Eisenberg (1963a) describes a "withdrawal" posture in which the body is rounded, eyes are half-closed and ears folded. The most striking feature of the crouch posture in gerbils was the flattening of the body against the substrate and the complete immobility of the animal while eyes and ears remained directed towards the opponent. The white parts of the body were concealed. After a period of crouching, an animal resumed a more rounded posture and watched the opponent, or it began cautious exploration of the test arena.

5.1.4. SEXUAL BEHAVIOURS

Behaviours included in this group were follow (FO), sniff anogenital region (SA), mount (MO) and attempted mount (AM). These were linked with SN and terminated in MA or EX. Male *G.setzeri* did not display sexual behaviours, while these were identified in the cluster diagram for female *G.setzeri*, but did not form a clear sequence in the

transition diagrams. Approach elongate (AE) was associated with this group of behaviours in five cluster diagrams, and preceded SN in these five transition diagrams. The sexual group of behaviours included contact-promoting behaviours GI and GO in male *G.p.exilis* and male *G.vallinus*.

Sexual behaviours MO, AM, and FO occurred significantly more frequently than expected in male *G.p.paeba*, while MO occurred significantly less frequently than expected in female *G.p.paeba*.

Eisenberg (1963a) has distinguished between "following," "driving" and "chasing" in heteromyid rodents, regarding these as a single behavioural continuum. "Follow" (FO) was seen in two contexts in this study: an animal sniffed the ano-genital region of the opponent and followed when it moved away, or follow occurred as a slow form of "chase". "Follow" was closely associated with sniffing of the anogenital region, sniffing of the nose, and it frequently terminated in exploratory behaviour. In different-sex encounters, males performed this behaviour more frequently than females, except in *G.vallinus*.

"Attempted mount" (AM) and "mount" (MO) were performed by males and females, but lordosis was not seen and copulation did not occur in staged encounters. The performance of "male" sexual behaviours such as mounting has been recorded in female *Dipodomys panamintinus* during oestrus (Eisenberg,

1963a). It was recorded in females of all the *Gerbillurus* species.

Comparison of sexual behaviours between same-sex and different-sex encounters revealed that male *G.p.paeba* and *G.p.exilis* performed significantly more "following" in different-sex encounters (chi-square 2 x 2 contingency table, $p < 0.05$). Male *G.p.exilis* exhibited significantly more SA and AM, while male *G.p.paeba* performed significantly more MO. In other species, differences were not significant ($p > 0.05$).

Since the oestrus cycle was not considered in this study, and encounters were staged at different times of the year, it is not known whether these results were influenced by the female's oestrus condition. Changes in sexual behaviour in relation to the oestrus cycle have been described in the mongolian gerbil, *Meriones unguiculatus* (Burley, 1980); some heteromyid rodents (Eisenberg, 1967) and hamsters (Payne & Swanson, 1970). Although the condition of the external genitalia was noted at the time of the encounter in this study, this is not a reliable indicator of the stage of the oestrus cycle in some rodents (Measroch, 1953). Attempts were made to obtain vaginal smears from female *Gerbillurus* species, but these failed to reveal a clear cycle. *G.setzeri* and *G.vallinus* failed to breed in the laboratory, and certain individuals of the other three species also failed to reproduce. Random selection of

females and random distribution of tests throughout the year may have diminished the influence of the oestrus cycle on the results.

The contact-promoting behaviours, "groom invitation" (GI) and "allogroom" (GO), occurred rarely in all species except male *G.vallinus* and *G.p.exilis*. "Grooming invitation" has been described as "submissive posture" in *R.norvegicus* (Barnett, 1975), in which an animal lies down on one side with the eyes closed or narrowed. This is often performed on the approach of another rat. In gerbils, the degree of rotation of the body varied, sometimes only the head was turned laterally, while at other times the whole body was rotated. Barnett (1975) regards this as a non-aggressive act which indicates that the animal performing the submissive act has not nor is about to attack the opponent.

The form of GI was different in *G.vallinus* and more closely approximated "nosing" (Barnett, 1975). "Crawling under", as described for *R.norvegicus* and *R.rattus* was not observed in *Gerbillurus* species. Grant & Mackintosh (1963) described "crawling under" as associated with sexual motivation, and occurring most commonly in laboratory mice. The close association of this behaviour with FO in *G.p.exilis* and with FO and SA in male *G.vallinus* indicates that it is associated with sexual behaviours in these species. GI occurred more frequently in dominant than in submissive male *G.vallinus*.

The response to GI in male *G.p.exilis* was for the opponent to groom the animal performing the GI. GO was rarely observed in *G.vallinus*, indicating that the behaviour named GI performs a different function in this species. Allo-grooming has been described in rats (Barnett, 1975), some heteromyid rodents (Eisenberg, 1967) and as a component of aggressive behaviour in rats, mice, hamsters and guinea-pigs (Grant & Mackintosh, 1963). The aggressive groom was seen rarely in *G.p.exilis*, and was not distinguished from allogrooming in the quantification of encounters. The animal performing the allogrooming also mounted the opponent frequently and then returned to exploratory behaviour. Eisenberg (1967) has suggested that grooming is important as a behavioural mechanism to ensure contact and familiarity without fighting.

The absence of GI and GO in encounters involving other species is not an indication of the absence of these behaviours in the repertoire of these species. In encounters recorded between "familiar" male and female *G.p.paeba*, these behaviours occurred significantly more frequently than in encounters between "strangers". These behaviours were recorded in the ethogram for all species, but were inhibited in encounters between "strangers".

5.2 TERRITORIALITY

Overlap in areas visited was significantly higher in males than in females of *G.setzeri* and *G.tytonis*. Male *G.setzeri*

overlapped significantly more than male *G.tytonis*, which had a higher level of overlap than male *G.p.paeba*. Female *G.setzeri* and *G.tytonis* had similar levels of overlap. Since the two sets of data for female *G.p.paeba* differed significantly, no comparisons were made between this group and any other group. Thus it would seem that males of *G.setzeri* and *G.tytonis* are more socially tolerant than females of these species, and that male *G.p.paeba* are less tolerant of conspecifics than male *G.tytonis* or male *G.setzeri*.

Animals of both sexes and three species did not defend or remain in the areas in which they spent the first week of the test. However, they did not move randomly through all areas of the apparatus, thus it would appear that they were occupying a "home" area, but this was not always the area originally occupied by the animal.

5.3 COMPARISON BETWEEN SPECIES

Two groups of species were identified on the basis of significant differences in levels of interaction. Male and female *G.p.paeba* and *G.tytonis* were significantly more active than male and female *G.p.exilis* and *G.setzeri* and male *G.vallinus*. Within these two groups, levels of interaction did not differ significantly, with the exception of *G.p.exilis* males, which were significantly less active than females.

Eisenberg (1967) has used the results of neutral encounters and encounters in a territorial box to separate study animals into "solitary" or "tolerant" species. Solitary animals avoid close contact or engage in agonistic behaviour, while tolerant species perform more contact-promoting behaviours such as allo-grooming. Indications from the present study are that male *G.vallinus* are tolerant, while male and female *G.p.paeba* and *G.tytonis* are solitary. Male and female *G.setzeri* were intermediate in solitary-tolerant tendencies. The behaviour of *G.p.exilis* appears to be sexually dimorphic, with females being solitary while males are tolerant. A range of social types is thus exhibited by species of this genus.

The advantages of living in groups include, inter alia, improved protection against predation and enhanced ability to find food (Krebs & Davies, 1981). Costs associated with group living include increased conspicuousness, social stress and competition for food. Eisenberg (1967) has correlated the essentially solitary existence of heteromyid rodents with the fact that the genera *Dipodomys* and *Microdipodops* cache food, a characteristic which is facilitated by the presence of large, fur-lined cheek pouches. All species of the genus *Gerbillurus* have been observed to hoard seeds in the laboratory, and food caches have been found in the burrows of *G.tytonis*, *G.p.paeba* and *G.p.exilis* in the field. The highly aggressive nature of *G.tytonis* and *G.p.paeba* may be related to their habit of

caching their food; however, *G.p.exilis*, which is more tolerant, also caches food. Eisenberg (1967) notes that a solitary existence is not always a concomitant of caching.

The possession of different social systems by species of the same genus has been described in *Peromyscus crinitus* and *P.eremicus*, both of which are equally arid-adapted (Eisenberg, 1967). The adoption of different social systems in conspecifics depending on external factors such as population density and food availability has been described for many species (Krebs & Davies, 1981; Lott, 1984). What is selected is a "social predisposition", and this can be modified according to various factors (Lott, 1984). The selective advantage of apparently differing social systems in congenetics of the genus *Gerbillurus* will remain obscure until more information on energy needs, food collection and recruitment rates is available. Some of this information should be provided by Downs' study of the ecophysiology of *Gerbillurus* species, and Boyer's study of the ecology of *G.p.paeba* and *G.tytonis*.

5.4 MALE-FEMALE DOMINANCE

Agonistic, territorial-type behaviour is common in rodents and was exhibited by eleven out of twelve species of Rhodesian rodents kept in captivity (Choate, 1972). In this study, female gerbils of three species displayed more aggression and less social tolerance than males of their own species, while one species, *G.setzeri*, produced

conflicting results: males were more tolerant than females in the territoriality apparatus, but dominated females in intraspecific different-sex encounters. Female *G.p.paeba*, *G.tytonis* and *G.p.exilis* are thought to be solitary and competitively superior to males of these species, while male and female *G.setzeri* and *G.vallinus* are gregarious.

Support for this hypothesis from the field is limited. Christian (1980) reported that female *G.p.paeba* were more frequently trapped in areas with dense cover than areas with sparse cover where males were trapped. Competition for suitable nest-sites and areas providing better protection from aerial predators may result in females occupying more favourable areas.

G.p.exilis in the Alexandria dunefield had large home ranges which overlapped considerably in males and less so in females (Ascaray, 1984). Adult males moved significantly greater distances than females in the breeding season (Ascaray, 1984). Adult females were found to be nesting with their subadult young (Dempster, unpubl. obs.) and adult males shared a burrow system (Wingate*, pers. comm.).

G.setzeri (Downs & Perrin, pers. comm.) and *G.vallinus* (De Graaff, 1981) have been reported to have interleading burrow systems; *G.vallinus* is reported to be gregarious (De

* Mr. L.R. Wingate, Kaffrarian Museum, P.O.Box 1434, King William's Town.

Graaff, 1981). Nel (1975) has described the social structure of *G.p.paeba* in the Kalahari Desert as "social, solitary clustered", with individuals living in close proximity to others and with a fair degree of social tolerance and interaction. This classification was based on deductions made from trapping results, laboratory observations and comparison with findings in adjacent areas.

Evidence for sexual dimorphism of social structure in rodents is provided in the literature for a range of species and habitats. Females of the solitary heteromyid, *D.panamintinus*, performed more submissive behaviour than males (Eisenberg, 1963a). However Ågren (1979) reported that female gerbils of the species *Meriones libycus* were territorial while males had overlapping ranges of movement, and exhibited a dominance hierarchy. Females were more aggressive than males in agonistic encounters in the field. *Psammomys obesus*, the leaf-eating Saharan gerbil, had a territorial system with females occupying the best food-sites. Males selected sites relative to the females' positions (Daly & Daly, 1974). Male striped field-mice (*Rhabdomys pumilio*) exhibited a dominance hierarchy among males, with a single dominant male which behaved territorially, and several subordinate males (Johnson, 1980; Brooks, 1974). Breeding females were territorial, although there was seasonal fluctuation in territoriality.

Ferrin (1981b) has suggested that the function of aggressive behaviour may differ in males and females: males behave aggressively to ensure mate acquisition, dispersal and interspecific segregation. Female territorial behaviour may increase inclusive fitness by maximizing reproductive success. In the arid environment, females may be competitively superior to males in order to ensure access to sufficient food to supply the energy required for successful reproduction. In gregarious species, a communal food cache may reduce the intra-colony competition for food and intraspecific aggression is accordingly reduced.

5.5 DOMINANCE/SUBMISSIVE RELATIONSHIPS AND INTERFERENCE COMPETITION.

Results from interspecific encounters generally confirm the results of intraspecific encounters. Species which were most aggressive in intraspecific encounters dominated species which were less aggressive in intraspecific encounters. Two groups of interspecific encounters between species which have been reported to coexist will be discussed separately, since the purpose of this section was to investigate dominance-submissive relationships in species which may be competing for certain resources.

1. *G.p.paeba* - *G.tytonis* - *G.setzeri* (South West Africa)

G.tytonis females dominated other sexes and species.

The greatest difference between dominant and submissive animals was exhibited in *G.tytonis* male-female encounters.

It is notable that male and female *G.setzeri* behaved submissively in encounters with male and female *G.p.paeba* and *G.tytonis*, despite the lack of overtly aggressive behaviour. However, *G.p.paeba* and *G.tytonis* exhibited more exploratory and approaching behaviour than *G.setzeri*. Exploratory behaviour was found to be directly related to aggressiveness in *Microtus agrestis* (Perrin, 1971), and occurred significantly more frequently in dominant than in subordinate individuals of the *Gerbillurus* species ($p < 0.05$, chi-squared contingency table analysis).

Interactions between *G.p.paeba* and *G.tytonis* were more active than those involving *G.setzeri*. "Drumming" (DR) occurred more frequently in *G.setzeri* males and females in interspecific encounters than in intraspecific encounters. The function of drumming in this context is not known.

The linear dominance hierarchy suggested by interspecific encounters involving these three species is:

1. *G.tytonis* females
2. *G.p.paeba* females
3. *G.tytonis* males
4. *G.p.paeba* males
5. *G.setzeri* females
6. *G.setzeri* males

2. *G.vallinus* - *G.p.paeba* (N.Cape)

G.v.vallinus males and females dominated *G.p.paeba* (N.Cape)

males and females. The grooming invitation posture (GI) exhibited in *G.vallinus* intraspecific encounters was infrequently performed in interspecific encounters. It was also noted that olfactory investigation (SN and SA) occurred less frequently in interspecific encounters.

The implications of these results are that ecological segregation of the species studied may be partly achieved by aggressive interactions. Such separation due to interference competition has been recorded in several groups of coexisting rodent competitors. In coastal southern California, *Microtus californicus*, *Reithrodontomys megalotis* and *Mus musculus* coexist (Blaustein, 1980). The diets of these three species overlap considerably, but competition for nest sites is considered to be more likely than competition for food. In staged laboratory encounters, *Microtus californicus* dominated the other two species. These results were supported by the observation that when *Microtus californicus* became extinct on a certain patch, *R.megalotis* and *Mus musculus* successfully colonised the area.

A correlation has been found between levels of aggression in staged encounters and coexistence of meadow voles (*Microtus pennsylvanicus*) and red-backed voles (*Clethrionomys gapperi*) in spruce forest (Turner, Perrin & Iverson, 1975). Aggression was low in winter, when the two species coexisted, but increased aggression was demonstrated at the

onset of the breeding season, when *M.pennsylvanicus* left the forest. It was suggested that seasonal fluctuations in reproduction-related aggression were responsible for the coexistence or separation of these two species.

Wolff, Freeberg and Dueser (1983) have investigated interspecific territoriality in two sympatric species of *Peromyscus*. The two species studied were morphologically and ecologically similar. Behavioural trials were conducted in the home range of one of the animals, and it was found that dominance was site-specific and not species-specific. Defense was strongest in the centre of an animal's home range and decreased towards the periphery. This implies that the animals were territorial. Competitive coexistence in these two closely related, physically similar species was thought to be mediated through interspecific territoriality.

It has been suggested that interspecific aggression between *Perognathus parvus* and *Peromyscus maniculatus* may result in a narrowing of the niche breadth in the subordinate species in areas of sympatry (Ambrose & Meehan, 1977). *Perognathus parvus* was found to be dominant in 11 out of 12 staged laboratory encounters. Dietary overlap between the two species is reduced in areas of sympatry, mainly due to a shift in the diet of the subordinate species from mainly seeds to few seeds. *Perognathus parvus* is reported to be a specialist granivore, while *Peromyscus maniculatus* is a

generalist. This is in agreement with the findings of Blaustein and Risser (1976) that the specialist species *Dipodomys ordii* and *D.panamintinus* dominated the generalist species *D.merriami* in Nevada.

Rose and Spevak (1978) found no evidence to support the hypothesis that competitive interference resulted in the invasion of collared lemmings (*Synaptomys cooperi*) of an area previously occupied by prairie voles (*Microtus ochrogaster*). However, collared lemmings (*Dicrostonyx groenlandicus*) were reported to be more aggressive than meadow voles (*Microtus pennsylvanicus*) near Churchill, Manitoba (Banks & Fox, 1968). Experience seemed to have influenced the outcome of encounters, since animals from areas of sympatry were more aggressive towards each other than animals from areas of allopatry. This result was also noticed in areas of contact between *Perognathus flavescens* and *P.merriami* (Martin, 1984). Martin (1984) has suggested that *P.flavescens* is a specialized species and that it has an included niche within the broader niche of the generalist, *P.merriami*. It is more aggressive than *P.merriami* and occupies the more favourable habitat.

To date, no information has been published on the realized niches of the species of the *Gerbillurus* genus. *G.p.paeba* is reported to be a "generalist", with a wider habitat-niche breadth than *Rhabdomys pumilio* and *Tatera brantsii* in the southern Kalahari (Nel, 1978). *G.p.paeba* was

dominated by *G.tytonis* in encounters observed in this study, thus *G.tytonis*, which is more restricted in its distribution than *G.p.paeba*, may represent the specialist species. Support for the hypothesis that *G.tytonis* is a specialist species must come from field studies of the habitat and food requirements of this species.

The interactions between *G.p.paeba* and *G.setzeri* and between *G.tytonis* and *G.setzeri* were characterized by mutual avoidance rather than aggressive interaction. Evidence from karyology (Schlitter et al., 1984) and distribution (Boyer, pers.comm.; Griffin, pers.comm.) indicates that *G.setzeri* may have a different phylogeny from the other two species and that the three species are rarely syntopic. Behavioural differences resulting from differing phylogenies and habitats have resulted in a reduction in interaction between the species. It is suggested that interference competition may not play a significant role in areas of contact between *G.setzeri* and *G.tytonis* or *G.paeba*.

G.vallinus males performed more aggressive behaviour towards *G.p.paeba* than towards conspecifics of either sex. It is suggested that *G.vallinus* displaces *G.p.paeba* in areas of syntopy by means of interference competition. The higher incidence of nasonasal and nasoanal contact in intraspecific encounters implies that olfactory communication is important in the identification and subsequent behaviour in these two species. Since the animals used in this study were all

trapped within an area of approximately one hectare, past experience may have influenced these results. Due to the small sample size, these results are tentative.

5.6 BODY SIZE AND DOMINANCE

Grant (1972) reports that in intraspecific encounters between rodents, the larger animal nearly always becomes dominant. Support for this hypothesis is provided by Payne and Swanson (1970), who identified body weight as the major factor influencing the outcome of encounters between hamsters of the same and different sexes.

In this study, mean body mass of dominant and submissive animals did not differ significantly in intraspecific same-sex encounters ($p > 0.05$, two-tailed t-test). The outcome of an encounter between members of the *Gerbillurus* genus was not dependent on body size.

Grant (1972) has further stated that in interspecific encounters between rodents, absolute body size becomes less important, but size relative to the maximum for that species is important. Interspecific encounters between three sympatric species of kangaroo rats revealed that the largest species (*Dipodomys panamintinus*) was dominant while the smallest species (*D. merriami*) was the least dominant (Blaustein & Risser, 1976). It is suggested that interspecific aggression is one mechanism whereby ecological separation is maintained in these species.

Individuals of the *Gerbillurus* species used in this study were generally larger than the mean mass quoted from field studies (*G.p.paeba*: $33.9\text{g} \pm 10.2$, $n = 19$; *G.p.exilis*: $30.7\text{g} \pm 5.6$, $n = 9$; *G.tytonis*: $29.9\text{g} \pm 4.9$, $n = 16$; *G.setzeri*: $44.7\text{g} \pm 10.6$, $n = 14$; *G.vallinus*: $40.9\text{g} \pm 8.9$, $n = 5$; *G.p.paeba* (N.Cape): $27.6\text{g} \pm 4.9$, $n = 6$). The assumption is made that all individuals were near the maximum body size for the species. However, dominance did not correlate with body size in *Gerbillurus* species. *G.setzeri*, the largest species, was dominated by the smaller *G.tytonis* and *G.p.paeba*. Body size may have been the deciding factor in encounters between the larger *G.vallinus* and *G.p.paeba*. Grant's (1972) statement is only partially supported by these data.

5.7 PHYLOGENY

From the dendrogram derived from cluster analysis of behaviour profiles (Fig. 59), it is clear that the species and sexes separate into two groups. These two groups were also identified in the analysis of levels of interaction. *G.p.paeba* females are most similar to *G.tytonis* females, and the males of these two species are also similar. *G.p.paeba* and *G.tytonis* are considered to form one group. *G.p.exilis* females and *G.setzeri* females are most similar to *G.setzeri* males, while *G.p.exilis* and *G.vallinus* males are the most divergent.

The grouping of *G.p.paeba*-*G.tytonis* in one group and

G.setzeri-*G.vallinus* in another group is in agreement with the karyology of the group (Schlitter et al, 1984). However, *G.p.paeba* and *G.p.exilis*, which are identical karyologically, differ substantially in agonistic behaviour. These differences were consistent in levels of interaction and in comparison of behaviour profiles. In interspecific interactions, female *G.p.paeba* and *G.p.exilis* shared the same index of dominance, but male *G.p.exilis* were dominated by female and male *G.p.paeba*, a result which was expected from the results of intraspecific encounters.

G.p.exilis exists as an isolated population, the limits of whose distribution are not precisely known. The habitat of this subspecies in the Alexandria dunefield is markedly different from the habitat of *G.p.paeba* in the Namib Desert. The mean mass of *G.p.exilis* (32.4g, n = 181; Ascaray, 1984) is greater than that of *G.p.paeba* ($22.2g \pm 4.0$, n = 177; Boyer, pers.comm.) in the Namib, but skull morphology is identical (Schlitter et al., 1984).

On the basis of results obtained in this study, it is suggested that *G.p.paeba* exhibits a range of social types from solitary to social. Evidence indicates that although *G.p.paeba* from the Namib Desert is highly aggressive in initial contacts, animals which have been caged together become tolerant and engage in contact-promoting behaviours. *G.p.exilis* from the Alexandria dunefield exhibit less

aggressive behaviour, with males exhibiting tolerant and contact-promoting behaviour even in encounters between "strangers".

Analysis of agonistic behaviour has been used to elucidate the taxonomy of silky pocket mice, genus *Perognathus* (Martin, 1984). Martin (1984) found, in agreement with Eisenberg (1967) that the same basic components were present in three species studied, but the relative frequencies differed. *Perognathus flavus* and *P. merriami* were considered, on the basis of similarities in agonistic behaviour, to be conspecific. However these two species exhibited more similarities when individuals were from parapatric populations than from allopatric populations. Conversely, *P. merriami* and *P. flavescens* revealed greater differences when individuals were from parapatric than from allopatric populations. Martin's (1984) study illustrates the fact that different populations of a single species may exhibit divergent behaviour patterns, but if these differences are insufficient to ensure premating isolation, the populations are still regarded as conspecific (Martin, 1984). Evidence for intraspecific variation in social systems according to environment, experience and other unknown factors has been reviewed by Lott (1984).

Mayr (1970) has stated that a shift into a new niche or adaptive zone is almost without exception initiated by a change in behaviour. Structural adaptations are

secondarily acquired: this is illustrated by the existence of sibling species which differ little in morphological features.

The results obtained in this study, considered in conjunction with evidence from the karyology, ecology, and distribution of the subspecies, indicate that stage 2 or 3 in the process of speciation (Diamond, 1986) has been reached, i.e. *G.paeba* is represented in Southern Africa by a number of subspecies which differ in food selection (Ascaray, 1984; Boyer, pers. comm.; Nel, 1978) and agonistic behaviour. *G.p.paeba* and *G.p.exilis* differ morphologically in size and pelage colour. Further evidence from heterosexual encounters should indicate whether pre-mating isolating mechanisms will prevent successful reproduction between *G.p.paeba* and *G.p.exilis*.

The evidence from comparison of behaviour profiles confirms the close relationship of *G.p.paeba* and *G.tytonis*. No evidence is provided for the separation of *G.tytonis* in a separate subgenus, as suggested by Petter (1983). These two species may represent stage 5 in Diamond's (1986) stages of speciation, i.e. the sister species have evolved in isolation and their distribution has expanded until they overlap in an area representing the limits of their distribution. Morphologically, the species differ in the size of the tympanic bullae and in length of the hindfeet, but diets are similar (Boyer, pers. comm.). The close

behavioural similarities in these two species may reflect the similarities in their habitats.

An alternative explanation could be proposed in terms of Branch's (1985) competitive elimination hypothesis: the two species evolved in sympatry, with *G.tytonis* being the specialist sand-dune species, thus reducing competition by means of a niche shift in habitat selection. In areas of syntopy, *G.tytonis* is competitively superior to *G.p.paeba* and may be expected to displace it.

G.setzeri differs behaviourally from *G.tytonis* and *G.p.paeba* in many respects, including a decreased level of interaction and increased social tolerance, particularly amongst males. The placing of *G.setzeri* in a separate subgenus (Meester et al., 1986) is supported by these data. The preliminary investigations into the agonistic behaviour of *G.vallinus* indicate that it is widely divergent in the behaviour profile, although *G.setzeri* and *G.vallinus* seem to share the characteristic of being socially more tolerant than *G.p.paeba* or *G.tytonis*. The individuals of *G.setzeri* and *G.vallinus* used in these encounters were from widely separated populations, and distribution maps indicate no overlap in the distribution of the two species (De Graaff, 1981; Griffin, pers.comm.). *G.setzeri* is restricted to the gravel plains north of the Kuiseb River, while *G.vallinus* occurs on the consolidated soils further south (De Graaff, 1981).

The evolution of sociality in these two species may be related inter alia to the difficulty of burrowing in the hard substrate and limited availability of suitable nest-sites. *G.setzeri* and *G.vallinus* may represent stage 4 of Diamond's (1986) stages in speciation and ecological segregation. The species are geographically isolated and are recognized as reproductively isolated species. However their distribution has not expanded so the two species are not sympatric. Diamond (1986) has recognized that expansion of sister species until they are sympatric need not occur. In the case of *G.vallinus* and *G.setzeri* it is suggested that morphological, karyological and behavioural changes have occurred in allopatry. Further investigation into the ecology of these two species is required to elucidate the level of ecological segregation between them.

G.vallinus and *G.p.paeba*, which are known to be syntopic in the northern Cape (Erasmus, pers.comm.), may have reached stage 5 or 6 in Diamond's (1986) stages of speciation, i.e. the two species have evolved in areas of allopatry and have subsequently expanded their distribution so that they now overlap in some areas, while *G.p.paeba* still occupies areas of allopatry. Insufficient detailed information on distribution is available to support or refute this hypothesis, and the diets and activity patterns of these two species in areas of sympatry remain unknown.

Huntingford (1984) has stated that comparative studies of behaviour can assist in unravelling the evolutionary history of the behaviour. Reconstructing the course of evolution of a particular behaviour is most successful if accurate phylogenies of the animals concerned are available. In the genus *Gerbillurus*, sufficient detailed information is not available, and therefore the data provided can only suggest possible phylogenetic sequences which may bear only partial resemblance to the actual evolutionary events.

The karyological and behavioural differences between the *G.p.paeba-G.tytonis* group and the *G.setzeri-G.vallinus* group indicate that the two groups diverged early in their evolutionary history (Qumsiyeh, 1986). In order to determine the ancestral behaviour type in a group of species, the behaviour pattern which is most widely distributed among the members is determined (Huntingford, 1984). In the species of the *Gerbillurus* genus, "solitary" and "tolerant" species are equally represented. Solitary existence in rodents is regarded as a phylogenetically ancient trait (Eisenberg, 1967), and is thus regarded as the ancestral behaviour type in the genus *Gerbillurus*.

On the basis of its widespread distribution and "generalist" diet, *G.p.paeba* is considered to be most similar to the ancestral type in the *G.paeba-G.tytonis* taxon. *G.tytonis* evolved as a specialist sand-dune inhabitant, which has become highly aggressive and less socially tolerant. The

population of *G.paeba* which became isolated in a comparatively favourable habitat in the Alexandria dunefield has become less aggressive, while *G.paeba* in less favourable habitats remained solitary.

Socially tolerant behaviour is a characteristic of *G.setzeri* and *G.vallinus*, and it has already been suggested that this may be related to the nature of the substrate. The social systems of these two species warrant further investigation in order to elucidate the apparently differing levels of sociability exhibited by them.

No explanation is offered for the apparent convergence in agonistic behaviour between female *G.p.exilis* and male and female *G.setzeri*. Eisenberg (1967) has found that social tendencies in rodents are species-specific, with a range of social forms exhibited in some higher taxa, e.g. at generic or sub-family level. Convergence in social structure, agonistic behaviour, sandbathing, habitat, general ecology, size, and reproduction has been demonstrated in *Gerbillus nanus* (subfamily Gerbillinae) and three species of the family Heteromyidae, viz. *Perognathus parvus*, *P.inornatus* and *P.longimembris*. The similarity observed between female *G.p.exilis* and *G.setzeri* may be a consequence of the reduction in aggression and hence a higher relative frequency of exploratory behaviours.

CHAPTER 7. CONCLUSION

Agonistic behaviour was found to be similar in form in all four species, differences being noted in the relative frequencies of performance of the different acts and postures identified in encounters, and in the intensity of interactions. Male *G.p.exilis* and *G.vallinus* were exceptions in that their behaviour profiles reflected a marked reduction in aggressive and submissive behaviour and an increase in sexual behaviour.

Two sex and species groups were identified on the basis of intensity of interaction: male and female *G.p.paeba* and *G.tytonis* were significantly more active than male and female *G.p.exilis*, *G.setzeri*, and male *G.vallinus*. *G.p.paeba* and *G.tytonis* were also linked in cluster analysis of behaviour profiles, while female *G.p.exilis* and male and female *G.setzeri* were closely linked in the dendrogram. Male *G.p.exilis* and *G.vallinus* were less closely linked to other species.

The testing of territoriality revealed that male *G.p.paeba* were least tolerant of conspecifics, followed by male *G.tytonis* and *G.setzeri*, which were most tolerant. Results for female *G.p.paeba* were inconsistent; female *G.tytonis* were less tolerant than *G.setzeri*, but this difference was not significant.

It is suggested that a range of social types is exhibited by

species of the genus *Gerbillurus*, from *G.p.paeba* and *G.tytonis*, which are thought to be solitary, through female *G.p.exilis* and *G.setzeri*, semi-tolerant; and male *G.p.exilis* and *G.vallinus*, tolerant. This is supported by observations on burrow structures, which are interleading in *G.setzeri* and *G.vallinus* and single in *G.p.paeba* and *G.tytonis*. Simple and complex burrows are constructed by *G.p.exilis*. The separation of *G.p.paeba* and *G.tytonis* from *G.setzeri* and *G.vallinus* reflects the karyology of the species: however, *G.p.exilis* is karyologically identical to *G.p.paeba*, but converges with *G.setzeri* and *G.vallinus* in relative frequencies of occurrence of agonistic behaviours. It is suggested that habitat may influence the social structure of the species: *G.p.paeba* and *G.tytonis* inhabit areas of soft sand where burrow construction is facilitated. Due to competition for the limited food resources, the species are solitary, which is considered to be the ancestral social type in this genus. Two mechanisms have been proposed which may account for the evolution of these two species.

- 1) *G.tytonis* evolved in sympatry with *G.p.paeba* as a sand-dune specialist which later evolved elongated hindfeet and enlarged tympanic bullae. As a specialist species, it is more aggressive than the generalist *G.p.paeba*
- 2) *G.tytonis* evolved as an isolated population in the sand-dunes which later diverged morphologically and expanded its distribution to overlap with that of *G.p.paeba*.

Habitat differences are thought to account for the change in behaviour in *G.p.exilis*. The comparatively abundant availability of water and food in the Alexandria dunefield, together with the availability of nest-sites, has resulted in a reduction in aggression and a trend towards increased sociability. The two subspecies are thought to represent an early stage in the process of speciation since they are allopatric, but reproductive isolation has not been demonstrated.

The evolution of sociality in *G.setzeri* and *G.vallinus* is thought to be a result of their shift into the gravel plains, where sites suitable for burrow construction are limited. The trend towards sociality is more pronounced in *G.vallinus* than in *G.setzeri*. These two species may represent an intermediate stage in speciation, since they are allopatric with no overlap in their distribution. Reproductive isolation has not been demonstrated, but they differ karyologically in the number of autosomal arms.

Intraspecific different-sex encounters revealed that females of four species dominated males, the exception being *G.setzeri*, where the reverse was observed. Female *G.setzeri* and *G.tytonis* were less tolerant of conspecifics than males of these species in the territoriality apparatus. It is suggested that interference competition may influence the dispersion of *G.p.paeba* and *G.tytonis* in areas of syntopy, since encounters were characterized by a high

level of interaction. Females of both species dominated males of both species, while in interspecific same-sex encounters, *G.tytonis* was dominant. Females may gain access to better nest-sites and food supplies than males through their aggressive superiority.

G.setzeri-*G.p.paeba* and *G.setzeri*-*G.tytonis* encounters revealed a lower level of aggression and mutual avoidance respectively. It is suggested that this reflects a lack of previous experience, since these species are rarely syntopic. *G.setzeri* differs substantially behaviourally, morphologically and karyologically and it inhabits an area of hard consolidated gravel. Interference competition may not influence the dispersion of these species in areas of sympatry.

G.vallinus dominated *G.p.paeba* in encounters between individuals trapped in the same area. Body size may have influenced the outcome of these encounters, since *G.vallinus* were larger than *G.p.paeba*. Interference competition may contribute to the ecological segregation of these two species.

The interpretation of results obtained in this study will be facilitated when more information on the ecology, distribution and ecophysiology is available. It is anticipated that this information for some species will shortly be forthcoming.

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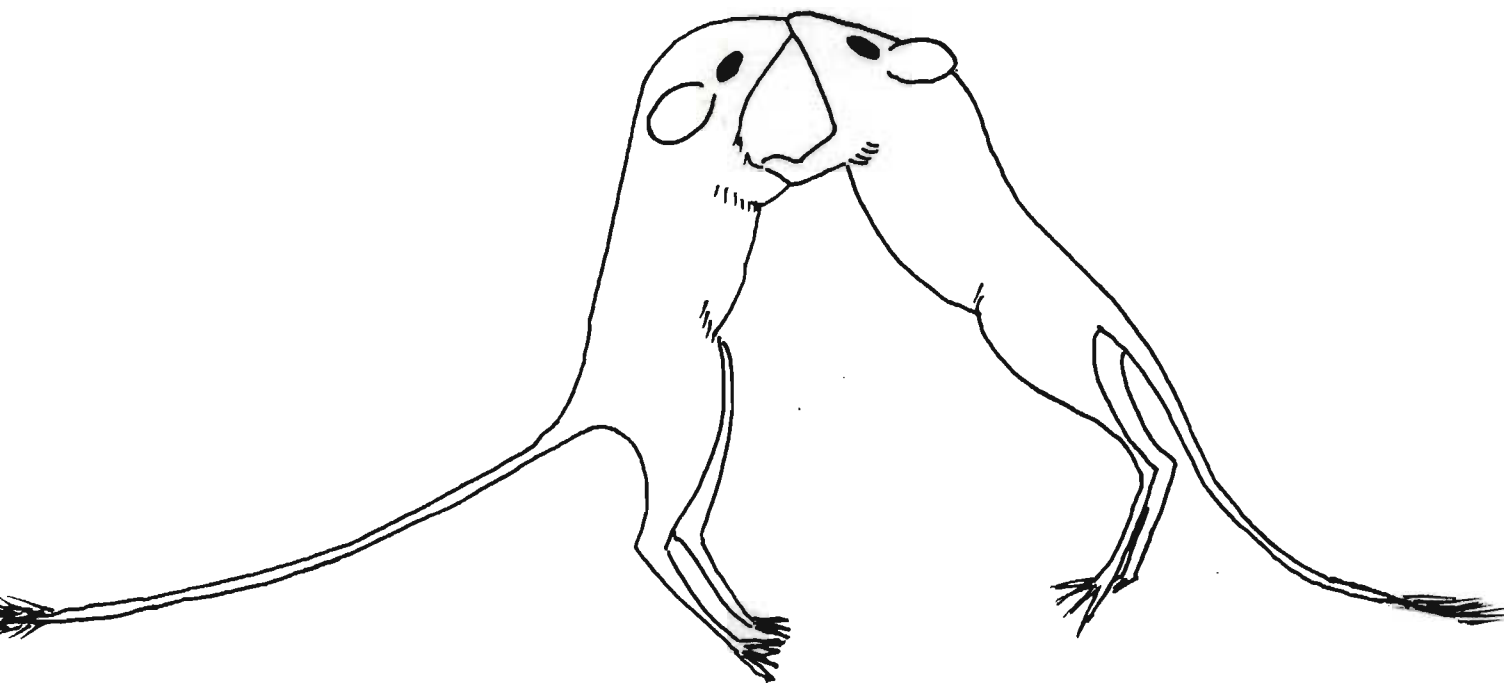
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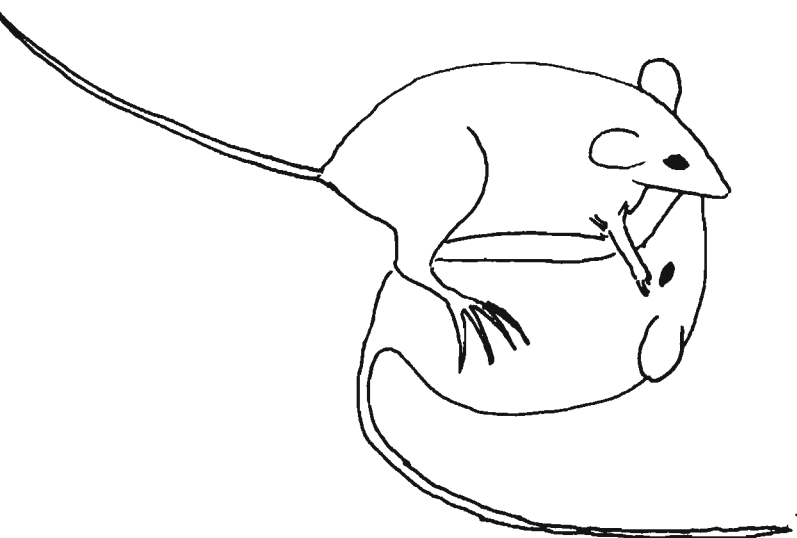
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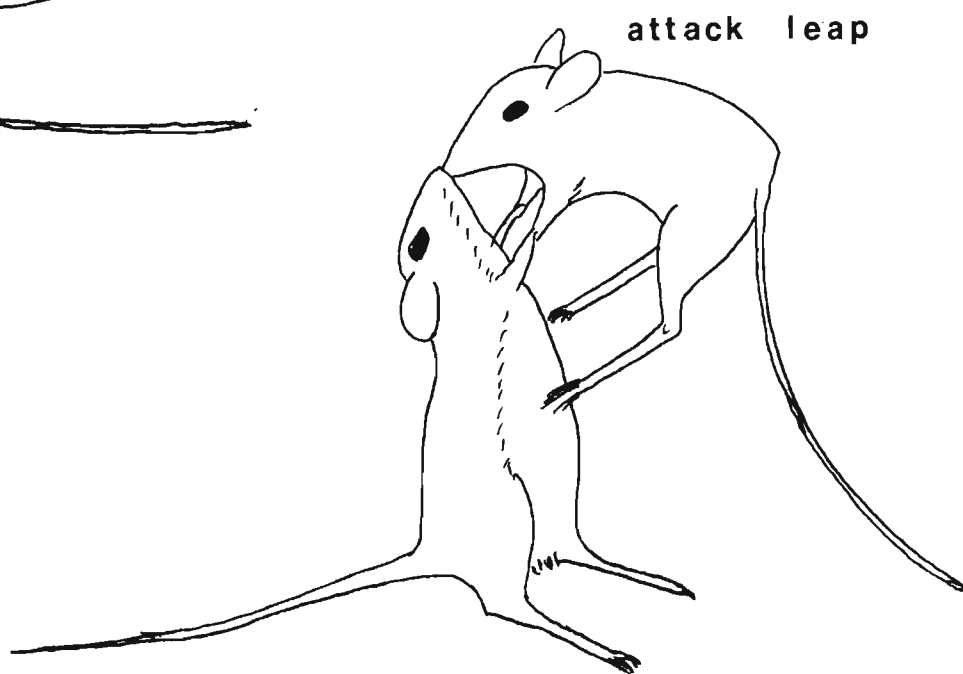
APPENDIX 1: Diagrams of acts and postures identified in
agonistic encounters.



upright

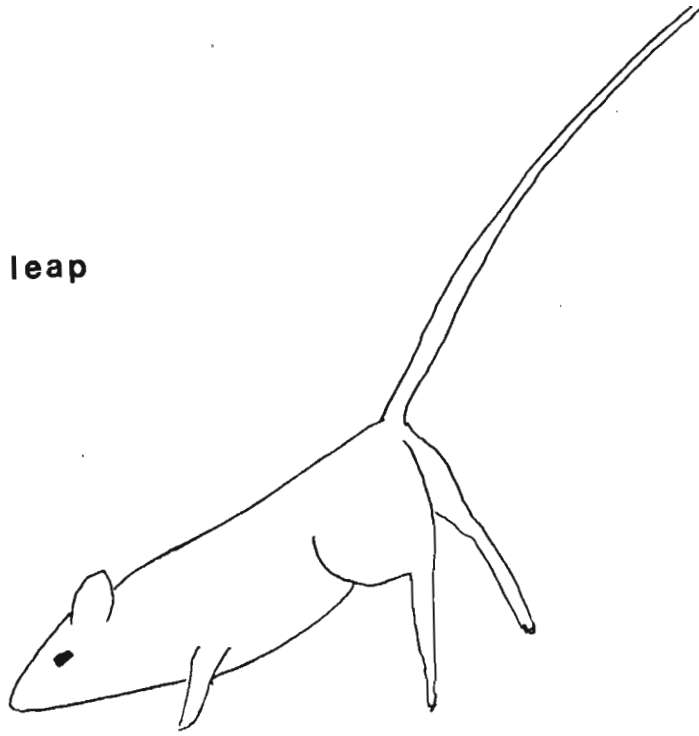


fight

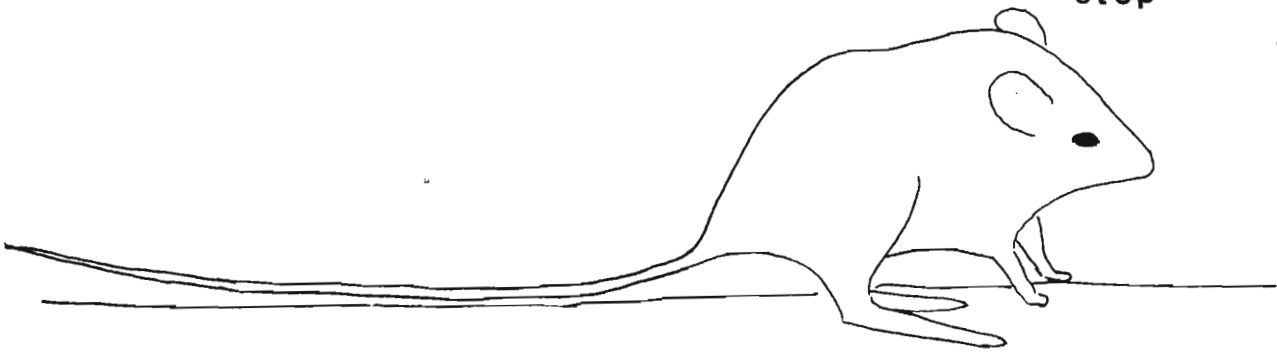


attack leap

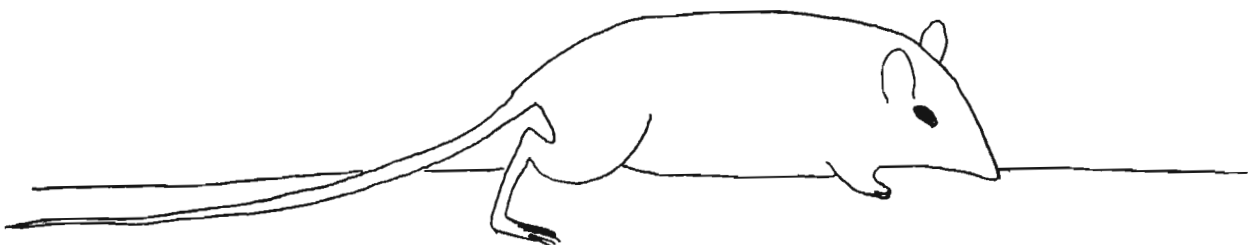
escape leap



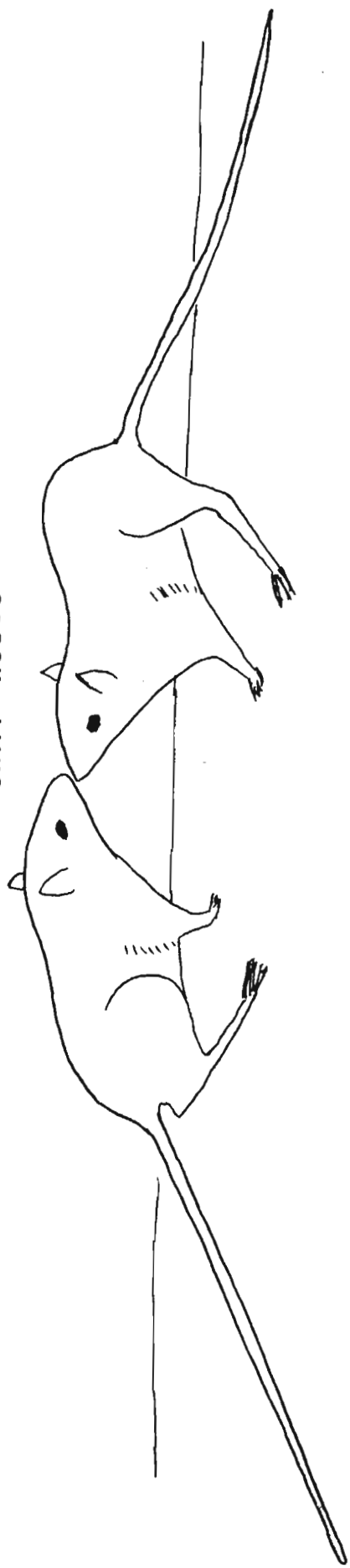
stop



crouch



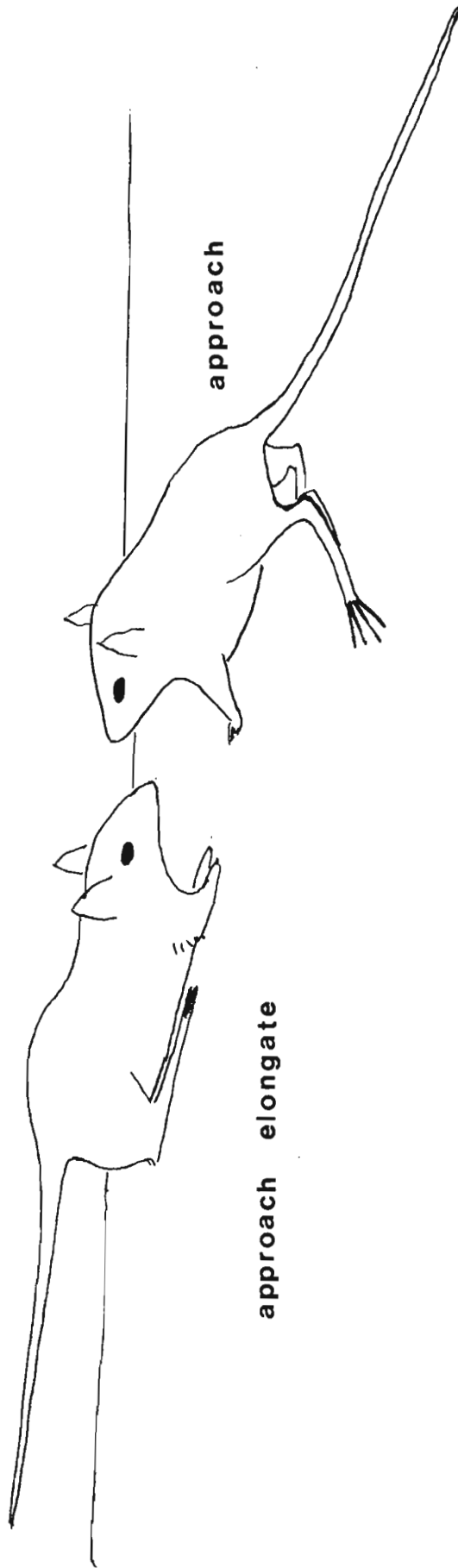
sniff noses



sniff anogenital region

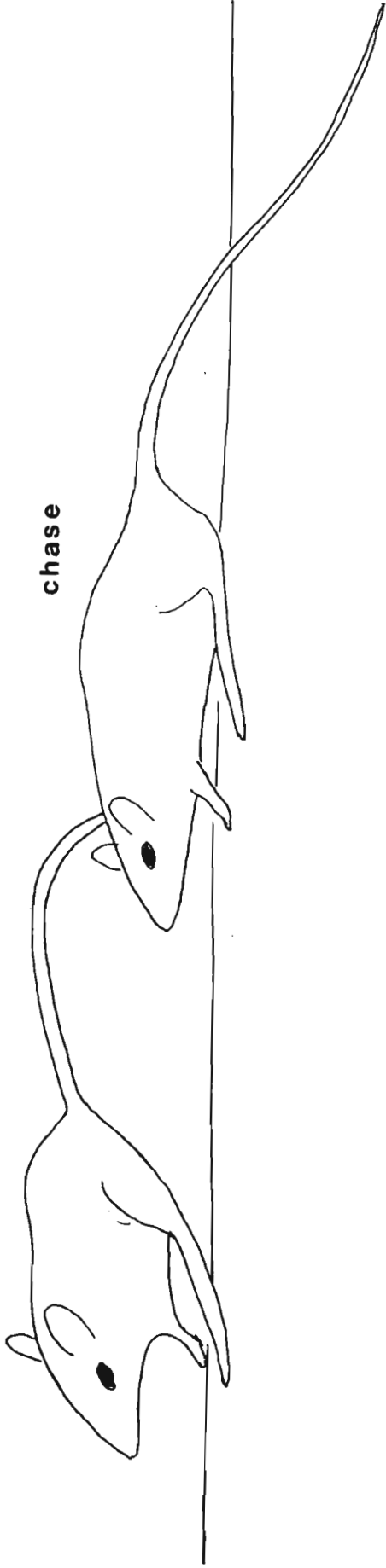


approach



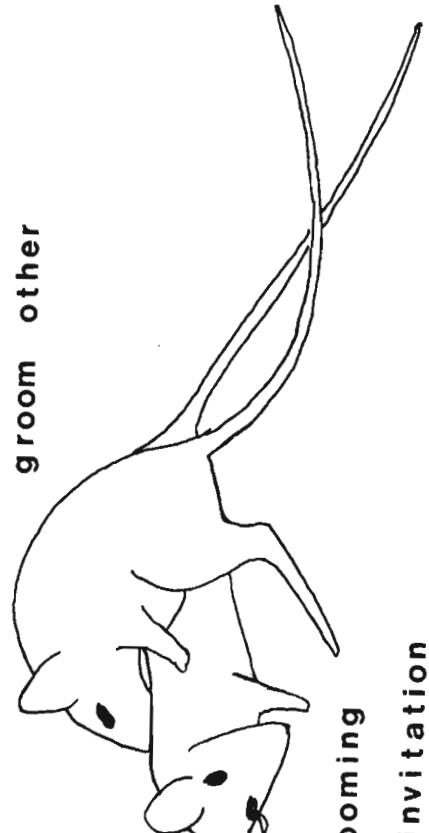
approach elongate

flee



chase

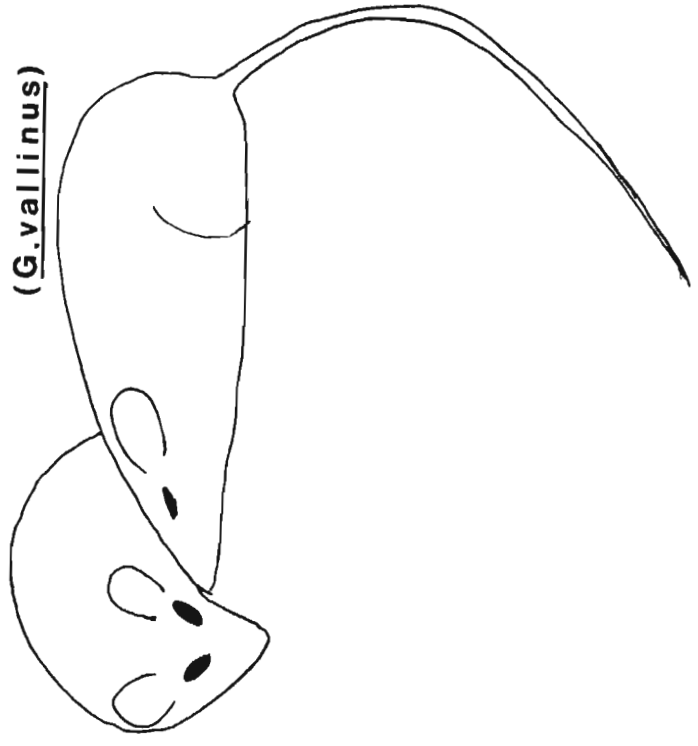
groom other

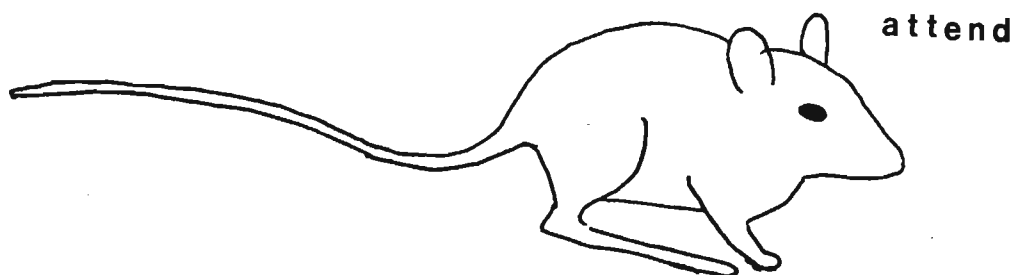
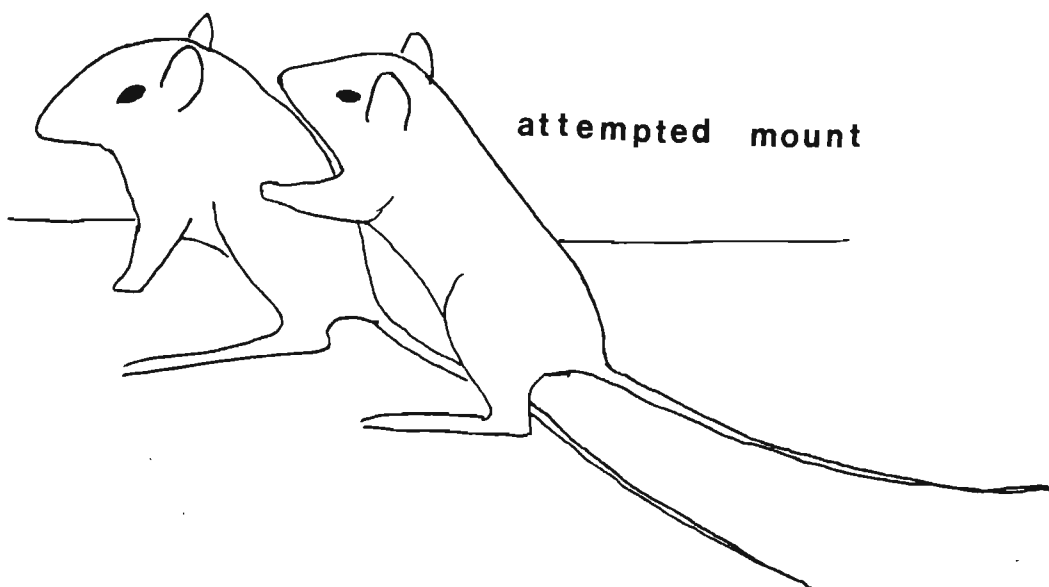


grooming

invitation

grooming invitation
(G.vallinus)





APPENDIX 2: Programmes

```

10 REM program for entering information and calculating frequencies and
20 REM sequences of acts
25 DIM R$(5),C$(32),FREQ(32),AKS$(32),G(32),TF$(10),DES$(100)
26 DIM TS$(10),NB$(3),L$(150),A(33,33),B(33,33),DSEQ$(100)
27 DIM T(33),CP(33,33),S(33),EF(33,33),SP$(3),FR$(10)
30 R$="efsqp"
35 ESC$=CHR$(27):FF$=CHR$(12)
40 DEF FNHOME$ =ESC$+"H"+ESC$+"J"
41 DEF FNBOLDON$=ESC$+"(s10hu6B"
42 DEF FNBOLDOFF$=ESC$+"(s10huB
43 DEF FNULON$=ESC$+"&d3D"
44 DEF FNULOFF$=ESC$+"&d @"
50 PRINT FNHOME$
60 PRINT "e(nter data)"
70 PRINT "f(requency calculation)"
90 PRINT "s(equences calculation)"
130 PRINT "q(uit program)"
135 PRINT "p(rint a file)"
140 PRINT "selection?";
150 INPUT A$
160 FOR I=1 TO 5
170 IF A$=MID$(R$,I,1) THEN GOTO 210
180 NEXT I
190 PRINT "invalid selection"
200 GOTO 50
210 ON I GOSUB 500, 3000,4230,230,5590
220 GOTO 50
230 PRINT "bye from data processing program"
240 STOP
500 REM subroutine for entering data
510 PRINT
530 PRINT "enter date (yy/mm/dd)",
540 INPUT D$
550 PRINT "date entered is ";D$;" Is this correct?(y/n)",
560 INPUT ANS$
570 IF ANS$="y" GOTO 580 ELSE 530
580 PRINT "enter name of encounter",
590 INPUT F$
600 PRINT "name entered is ";F$;" Is this correct?(y/n)",
610 INPUT ANS$
620 IF ANS$="y" GOTO 630 ELSE 580
630 PRINT "Enter first animal's number",
640 INPUT N1
650 PRINT "enter second animal's number",
660 INPUT N2
670 PRINT "first animal's number is ";N1;" Is this correct?(y/n)"
680 INPUT ANS$
690 IF ANS$="y" GOTO 700 ELSE 630
700 PRINT "second animal's number is ";N2;" Is this correct?(y/n)"
710 INPUT ANS$
720 IF ANS$="y" GOTO 730 ELSE 650
730 PRINT "which animal is the dominant?",
740 INPUT N3
750 PRINT "Dominant animal is ";N3;" Is this correct?(y/n)",

```

```

760 INPUT ANS$
770 IF ANS$="y" GOTO 780 ELSE 730
780 PRINT "What sex is animal ";N1; "(m/f)",
790 INPUT S1$
800 PRINT "What sex is animal ";N2; "(m/f)",
810 INPUT S2$
820 PRINT "Animal ";N1; " is ";S1$; " and animal ";N2; " is "; S2$;
830 PRINT " Is this correct?(y/n)";
840 INPUT ANS$
850 IF ANS$="y" THEN 855 ELSE 780
855 RESTORE 2730
860 FOR I=1 TO 32
870 READ C$(I)
880 NEXT I
890 PRINT "What will this filename be?",
900 INPUT N$
910 PRINT "filename entered is ";N$; " Is this correct?(y/n)"
920 INPUT ANS$
930 IF ANS$="y" GOTO 940 ELSE 890
940 OPEN "O",#1,N$
950 PRINT #1,D$;",";F$;",";N1;N2;S1$;",";S2$;",";N3;
960 GOSUB 1500
970 GOSUB 2500
980 W$=INKEY$
990 IF LEN(W$)=0 THEN 980
1000 PRINT W$
1010 IF W$<>"/" THEN 1040
1015 PRINT SUM," ",K$," ",W$
1020 PRINT#1,SUM;",";K$;",";W$;",";
1030 GOTO 960
1040 IF W$="$" THEN 1070
1050 PRINT "mistake! Re-enter data",
1060 GOTO 960
1070 PRINT#1,SUM;",";K$;",";W$
1080 CLOSE #1
1090 PRINT "bye from this subroutine"
1100 RETURN
1500 REM subroutine to get number
1510 PRINT "Enter number";
1520 SUM=0
1530 W$ = INKEY$
1540 IF LEN(W$)=0 THEN 1530
1550 PRINT W$;
1560 IF W$<"0" OR W$>"9" THEN 1590
1570 SUM = SUM*10 +VAL(W$)
1580 GOTO 1530
1590 IF SUM = N1 OR SUM = N2 THEN 1620
1600 PRINT: PRINT "error"
1610 GOTO 1500
1620 PRINT
1630 RETURN
2500 REM subroutine to get code
2510 PRINT "Enter code";
2520 K$=" "

```

```

2530 FOR I=1 TO 2
2540 W$=INKEY$:IF LEN(W$)=0 THEN 2540
2550 PRINT W$;
2560 MID$(K$,I,1) = W$
2570 NEXT I
2580 FOR I=1 TO 32
2590 IF C$(I)=K$ THEN 2630
2600 NEXT I
2610 PRINT "Mistake! Re-enter code"
2620 GOTO 2500
2630 PRINT
2640 RETURN
2650 ON ERROR GOTO 2660
2660 CONT$="Y"
2670 IF ERR<>53 THEN 2710
2680 PRINT "File not found"
2690 CONT$="N"
2700 RESUME NEXT
2710 PRINT "Error number is ";ERR
2720 STOP
2730 DATA ae,ad,ap,sn,sa,al,at,fi,up,ch,el,fl,cr,st,ex,gs,ea,sb,dr,ma,mo
2740 DATA ur,mk,am,ro,si,gi,fo,th,go,vo,xx
3000 REM subroutine for calculating frequency of behaviours
3015 RESTORE 2730
3017 FOR I=1 TO 32
3018 READ AKS$(I)
3019 NEXT I
3020 PRINT "Which file do you wish to open?",
3030 INPUT N$
3040 FOR I=1 TO 32
3045 FREQ(I)=0
3047 NEXT I
3050 OPEN "I",#1,N$
3070 INPUT#1,D$,F$,N1,N2,S1$,S2$,N3
3075 IF EOF(1) GOTO 3190
3080 PRINT FNHOME$
3090 PRINT "Filename is ";N$
3100 PRINT
3110 PRINT "Date is ";D$
3120 PRINT
3130 PRINT "Encounter is ";F$
3140 PRINT "Animals used were ";S1$;N1;" and ";S2$;N2;" Dominant is ";N3
3150 PRINT
3160 PRINT "Is this the correct file?(y/n)";
3170 INPUT ANS$
3180 IF ANS$="y" GOTO 3210
3190 CLOSE #1
3200 RETURN
3210 PRINT "Select an animal number ";N1;" or ";N2;" or 999 (end subroutine)"
3220 INPUT M2
3225 IF M2=999 GOTO 3230 ELSE 3240
3230 CLOSE #1:RETURN
3240 WHILE NOT EOF(1)

```

```

3250 INPUT#1,M1,C1$,S$
3260 IF M1<>M2 GOTO 3310
3270 FOR I=1 TO 32
3280 IF AKS$(I)=C1$ THEN 3300
3290 NEXT I
3300 FREQ(I)=FREQ(I)+1
3310 WEND
3315 CLOSE #1
3320 PRINT "Do you wish to print these results?(y/n)";:INPUT ANS$
3325 IF ANS$<>"y" GOTO 3440 ELSE 3330
3330 LPRINT FF$:LPRINT FNULON$;;LPRINT " Animal number ";M2," Date ";D$
3340 LPRINT
3350 LPRINT " Type of observation ";F$
3360 LPRINT
3370 LPRINT " Animals are ";S1$;N1;" and ";S2$;N2;
3375 LPRINT ".Dominant animal is ";N3
3380 LPRINT FNULOFF$
3390 LPRINT " ACTION","FREQUENCY"
3400 FOR I=1 TO 32
3410 IF FREQ(I) = 0 GOTO 3430
3420 LPRINT " ";AKS$(I),FREQ(I)
3430 NEXT I
3440 PRINT "Do you wish to update the total frequencies file?y/n)"
3445 INPUT ANS$
3450 IF ANS$="y" GOTO 3455 ELSE 3460
3455 CLOSE #1:GOTO 3830
3460 CLOSE #1:RETURN
3470 RETURN
3830 REM subroutine to calculate total frequencies
3840 PRINT "Do you wish to initialize a file?(y/n)";
3850 INPUT ANS$
3860 IF ANS$="y" GOTO 3870 ELSE 3880
3870 GOSUB 4100
3880 PRINT "Which file do you wish to update?"
3890 INPUT TF$
3900 OPEN "I",1,TF$
3910 INPUT #1,N,DES$
3920 PRINT "File description is: ";DES$;". Is this correct?(y/n)"
3925 INPUT ANS$
3930 IF ANS$<>"y" GOTO 3940 ELSE 3950
3940 CLOSE #1:GOTO 3440
3950 FOR I=1 TO 32
3960 INPUT #1,G(I)
3970 IF EOF(1) THEN 3990
3980 NEXT I
3990 CLOSE #1
4000 FOR I=1 TO 32
4010 G(I)=G(I)+FREQ(I)
4020 NEXT I
4030 N=N+1
4040 OPEN "O",1,TF$
4050 PRINT #1,N;DES$;",";
4060 FOR I=1 TO 32
4070 PRINT #1,G(I)
4080 NEXT I
4090 CLOSE #1:RETURN

```



```

4100 REM FILE INITIALIZATION SUBROUTINE
4110 PRINT "What name do you wish to give this file?"
4120 INPUT TF$
4130 PRINT "Enter file description":INPUT DES$
4140 N=0
4150 OPEN "0",#1,TF$
4160 PRINT #1,N;DES$,",";
4170   FOR I=1 TO 32
4180   PRINT #1,0
4190   NEXT I
4200 CLOSE #1
4210 PRINT TF$;" file initialized"
4220 RETURN
4230 REM subroutine for calculating pair-sequences
4240 RESTORE 2730
4250 FOR I=1 TO 32
4260   READ AKS$(I)
4270   NEXT I
4280 RESTORE 2730
4290 FOR J=1 TO 32
4300   READ AKS$(J)
4310   NEXT J
4320 FOR I=1 TO 32
4330   FOR J=1 TO 32
4340     A(I,J)=0
4350   NEXT J
4360 NEXT I
4370 I=0:J=0
4380 PRINT "Which file do you wish to open? ";;INPUT N$
4390 OPEN "I",1,N$
4400 INPUT #1,D$,F$,N1,N2,S1$,S2$,N3
4410 IF EOF(1) GOTO 4420
4420 PRINT FNHOME$
4430 PRINT "Filename is ";N$
4440 PRINT:PRINT "Date is ";D$
4450 PRINT:PRINT "Encounter is ";F$
4460 PRINT:PRINT "Animals used were ";S1$;N1;" and ";S2$;N2;
4465 PRINT ". Dominant is ";N3
4470 PRINT:PRINT "Is this the correct file?(y/n)";
4480 INPUT ANS$
4490 IF ANS$<>"y" GOTO 4500 ELSE 4510
4500 CLOSE #1:GOTO 4230
4510 PRINT:PRINT "Select an animal number ";N1;" or ";N2;
4515 PRINT " or 999(end subroutine)";
4520 INPUT M2
4530 IF M2=999 THEN CLOSE #1:RETURN
4540 N4=999
4550 WHILE NOT EOF(1) AND N4<>M2
4560   INPUT #1,N4,C1$,S$
4570 WEND
4580 OLD$=C1$
4590 WHILE NOT EOF(1)
4600   N4=999
4610   WHILE NOT EOF(1) AND N4<>M2
4620     INPUT #1,N4,C1$,S$

```

```

4630 WEND
4640 IF N4=M2 THEN 4650 ELSE 4750
4650 CODE$=C1$
4660 FOR I=1 TO 32
4670 IF AKS$(I) =OLD$ THEN 4690
4680 NEXT I
4690 FOR J=1 TO 32
4700 IF AKS$(J)=CODE$ THEN 4720
4710 NEXT J
4720 A(I,J)=A(I,J)+1
4730 OLD$=CODE$
4740 WEND
4750 PRINT "Do you wish to print these results?(y/n)":INPUT ANS$
4760 IF ANS$<>"y" GOTO 5120 ELSE 4770
4770 LPRINT FF$
4780 LPRINT FNULON$
4790 LPRINT " Animal number: ";M2;"Date: ";D$
4800 LPRINT
4810 LPRINT
4820 LPRINT " Type of observation: ";F$
4830 LPRINT
4840 LPRINT " Animals are ";S1$;N1;" and ";S2$;N2;
4845 LPRINT ". Dominant animal is ";N3
4850 LPRINT FNULOFF$
4860 LPRINT " ";
4870 FOR J= 1 TO 16
4880 LPRINT " ";AKS$(J);
4890 NEXT J
4900 LPRINT
4910 FOR I=1 TO 32
4920 LPRINT " "; AKS$(I);
4930 FOR J=1 TO 16
4940 IF A(I,J)=0 GOTO 4960
4950 LPRINT USING "####";A(I,J);:GOTO 4970
4960 LPRINT " .";
4970 NEXT J
4980 LPRINT:NEXT I
4990 LPRINT FF$:LPRINT " ";
5000 FOR J=17 TO 32
5010 LPRINT " ";AKS$(J);
5020 NEXT J
5030 LPRINT
5040 FOR I=1 TO 32
5050 LPRINT " ";AKS$(I);
5060 FOR J=17 TO 32
5070 IF A(I,J)=0 GOTO 5090
5080 LPRINT USING "####";A(I,J);:GOTO 5100
5090 LPRINT " .";
5100 NEXT J
5110 LPRINT: NEXT I
5120 CLOSE #1
5130 PRINT FNHOME$
5140 PRINT "Do you wish to update a file?(y/n)":INPUT ANS$
5150 IF ANS$<>"y" GOTO 5580

```

```

5160 PRINT "Enter filename ";;INPUT TS$
5170 PRINT "Is this a new file?(y/n)";: INPUT ANS$
5180 IF ANS$<>"y" GOTO 5320
5190 REM SUBROUTINE FOR INITIALIZING A FILE
5200 PRINT "Enter file description ";;INPUT DSEQ$
5210 N=0
5220 OPEN "O",1,TS$
5230 PRINT #1,N;DSEQ$;",";
5240   FOR I=1 TO 32
5250     FOR J=1 TO 32
5260       B(I,J)=0
5270       PRINT #1,B(I,J)
5280     NEXT J
5290   NEXT I
5300 CLOSE #1
5310 PRINT TS$;" file initialized"
5320 REM SUBROUTINE FOR UPDATING AN ACCUMULATED SEQUENCES FILE
5330 OPEN "I",1,TS$
5340 INPUT #1,N,DSEQ$
5350 PRINT FNHOME$
5360 PRINT "File description is: ";DSEQ$;
5370 PRINT " Is this the correct file?(y/n)";:INPUT ANS$
5380 IF ANS$<>"y" GOTO 5140
5390   FOR I=1 TO 32
5400     FOR J= 1 TO 32
5410       INPUT #1,B(I,J)
5420     NEXT J
5430   NEXT I
5440 CLOSE #1
5450   FOR I=1 TO 32
5460     FOR J=1 TO 32
5470       B(I,J)=B(I,J) + A(I,J)
5480     NEXT J
5490   NEXT I
5500 N=N+1
5510 OPEN "O",1,TS$
5520 PRINT #1,N;DSEQ$;",";
5530   FOR I=1 TO 32
5540     FOR J=1 TO 32
5550       PRINT #1,B(I,J)
5560     NEXT J
5570   NEXT I
5580 CLOSE #1:RETURN
5590 REM SUBROUTINE TO PRINT AGGREGATES AND AVERAGES
5600 RESTORE 2730
5610 FOR I=1 TO 32
5620 READ AKS$(I)
5630 NEXT I
5640 PRINT "Do you wish to print a frequency file?(y/n)":INPUT ANS$
5650 IF ANS$<>"y" GOTO 5930 ELSE 5660
5660 PRINT "Which frequency file do you wish to print?":INPUT TF$
5670 OPEN "I",1,TF$
5680 INPUT #1,N,DES$

```

```

5690 PRINT FNHOME$
5700 PRINT "File description is: ";DES$;". Is this correct?(y/n)"
5710 INPUT ANS$
5720 IF ANS$<>"y" GOTO 5730 ELSE 5740
5730 CLOSE #1:GOTO 5590
5740 FOR I = 1 TO 32
5750   INPUT #1,G(I)
5760   IF EOF(1) THEN 5780
5770   NEXT I
5780 CLOSE #1
5790 LPRINT FF$
5800 LPRINT FNULON$;:LPRINT "Filename: ";TF$
5810 LPRINT
5820 LPRINT "Number of animals tested: ";N
5830 LPRINT:LPRINT "Description of file: ";DES$:LPRINT FNULOFF$
5840 LPRINT "      ACTION","FREQUENCY","AVERAGE","REL. FREQ.(%)"
5850 TOT = 0
5860 FOR I=1 TO 32
5870   TOT=TOT + G(I)
5880 NEXT I
5890 FOR I=1 TO 32
5900   LPRINT "      ";AKS$(I),G(I),CINT(G(I)/N),CINT(G(I)/TOT*100)
5910 NEXT I
5920 RETURN
5930 PRINT"Do you wish to print a sequences file?(y/n)":INPUT ANS$
5940 IF ANS$<>"y" GOTO 7180 ELSE 5950
5950 RESTORE 2730
5960   FOR I=1 TO 32
5970     READ AKS$(I)
5980   NEXT I
5990 PRINT "Which sequence file do you wish to print?":INPUT TS$
6000 PRINT FNHOME$
6010 OPEN "I",1,TS$
6020 INPUT #1,N,DSEQ$
6030 PRINT "File description is: ";DSEQ$;" Is this correct?(y/n)"
6040 INPUT ANS$
6050 IF ANS$<>"y" GOTO 6060 ELSE 6070
6060 CLOSE #1:GOTO 5930
6070   FOR I=1 TO 32
6080     FOR J=1 TO 32
6090       INPUT #1,B(I,J)
6100       IF EOF(1) GOTO 6130
6110     NEXT J
6120   NEXT I
6130 CLOSE #1
6140 LPRINT FF$
6150 LPRINT FNULON$;
6160 LPRINT "Filename is: ";TS$
6170 LPRINT
6180 LPRINT "File description is: ";DSEQ$
6190 LPRINT:LPRINT "Number of animals tested: ";N
6200 LPRINT FNULOFF$
6210 LPRINT "      ";

```

```

6220 FOR I=1 TO 32:T(I)=0:NEXT I
6230 FOR I=1 TO 32
6240   FOR J=1 TO 32
6250     T(I)=T(I)+B(I,J)
6260   NEXT J
6270 NEXT I
6280 FOR J=1 TO 32:S(J)=0:NEXT J
6290 FOR J=1 TO 32
6300   FOR I=1 TO 32
6310     S(J)=S(J)+B(I,J)
6320   NEXT I
6330 NEXT J
6340 TOT=0
6350 FOR I=1 TO 32
6360   TOT=TOT+T(I)
6370 NEXT I
6372 FOR I=1 TO 32
6374   FOR J=1 TO 32
6375     EF(I,J)=0:CP(I,J)=0
6376   NEXT J
6378 NEXT I
6380 FOR I=1 TO 32
6390   FOR J=1 TO 32
6400     EF(I,J)=T(I)*S(J)/TOT
6410     IF B(I,J)<10 GOTO 6430
6420     CP(I,J)= B(I,J)/T(I)*100
6430   NEXT J
6440 NEXT I
6450 FOR J=1 TO 16
6460   LPRINT " ";AKS$(J);
6470 NEXT J
6480 LPRINT
6490 FOR I=1 TO 32
6500   LPRINT " ";AKS$(I);
6510   FOR J=1 TO 16
6520     IF B(I,J)=0 GOTO 6540
6530     LPRINT USING "####";B(I,J);:GOTO 6550
6540     LPRINT " .";
6550   NEXT J
6560 LPRINT
6570 NEXT I:LPRINT " SUM";
6580 FOR J=1 TO 16
6590   LPRINT USING "####";S(J);
6600 NEXT J
6610 LPRINT FF$
6620 LPRINT " ";
6630 FOR J=17 TO 32
6640   LPRINT " ";AKS$(J);
6650 NEXT J
6660 LPRINT " SUM":LPRINT
6670 FOR I=1 TO 32
6680   LPRINT " ";AKS$(I);
6690   FOR J=17 TO 32

```

```

6700     IF B(I,J)=0 GOTO 6720
6710     LPRINT USING "####";B(I,J);:GOTO 6730
6720     LPRINT "    .";
6730     NEXT J
6740     LPRINT USING"#####";T(I):NEXT I
6750     LPRINT " SUM";
6760     FOR J=17 TO 32
6770     LPRINT USING "####";S(J);
6780     NEXT J
6790     LPRINT USING "#####";TOT
6800     LPRINT FF$
6810     CLOSE #1
6820     PRINT FNHOME$
6830     PRINT "Do you wish to print conditional probabilities?(y/n)";
6835     INPUT ANS$
6840     IF ANS$="y" GOTO 6850 ELSE 7190
6850     LPRINT FNULON$;
6860     LPRINT "Conditional probabilities of ";DSEQ$
6870     LPRINT:LPRINT "Number of animals tested: ";N
6880     LPRINT FNULOFF$
6890     LPRINT "    ";
6900     FOR J=1 TO 16
6910     LPRINT "    ";AKS$(J);
6920     NEXT J
6930     LPRINT
6940     FOR I=1 TO 32
6950     LPRINT "    ";AKS$(I);
6960     FOR J = 1 TO 16
6970     IF CP(I,J)<10 GOTO 6990
6980     LPRINT USING "####";CP(I,J);:GOTO 7000
6990     LPRINT "    .";
7000     NEXT J
7010     LPRINT:NEXT I
7020     LPRINT FF$
7030     LPRINT "    ";
7040     FOR J=17 TO 32
7050     LPRINT "    ";AKS$(J);
7060     NEXT J
7070     LPRINT
7080     FOR I=1 TO 32
7090     LPRINT "    ";AKS$(I);
7100     FOR J=17 TO 32
7110     IF CP(I,J)<10 GOTO 7130
7120     LPRINT USING "####";CP(I,J);:GOTO 7140
7130     LPRINT "    .";
7140     NEXT J
7150     LPRINT
7160     NEXT I
7170     LPRINT FF$
7180     PRINT FNHOME$
7700     RETURN

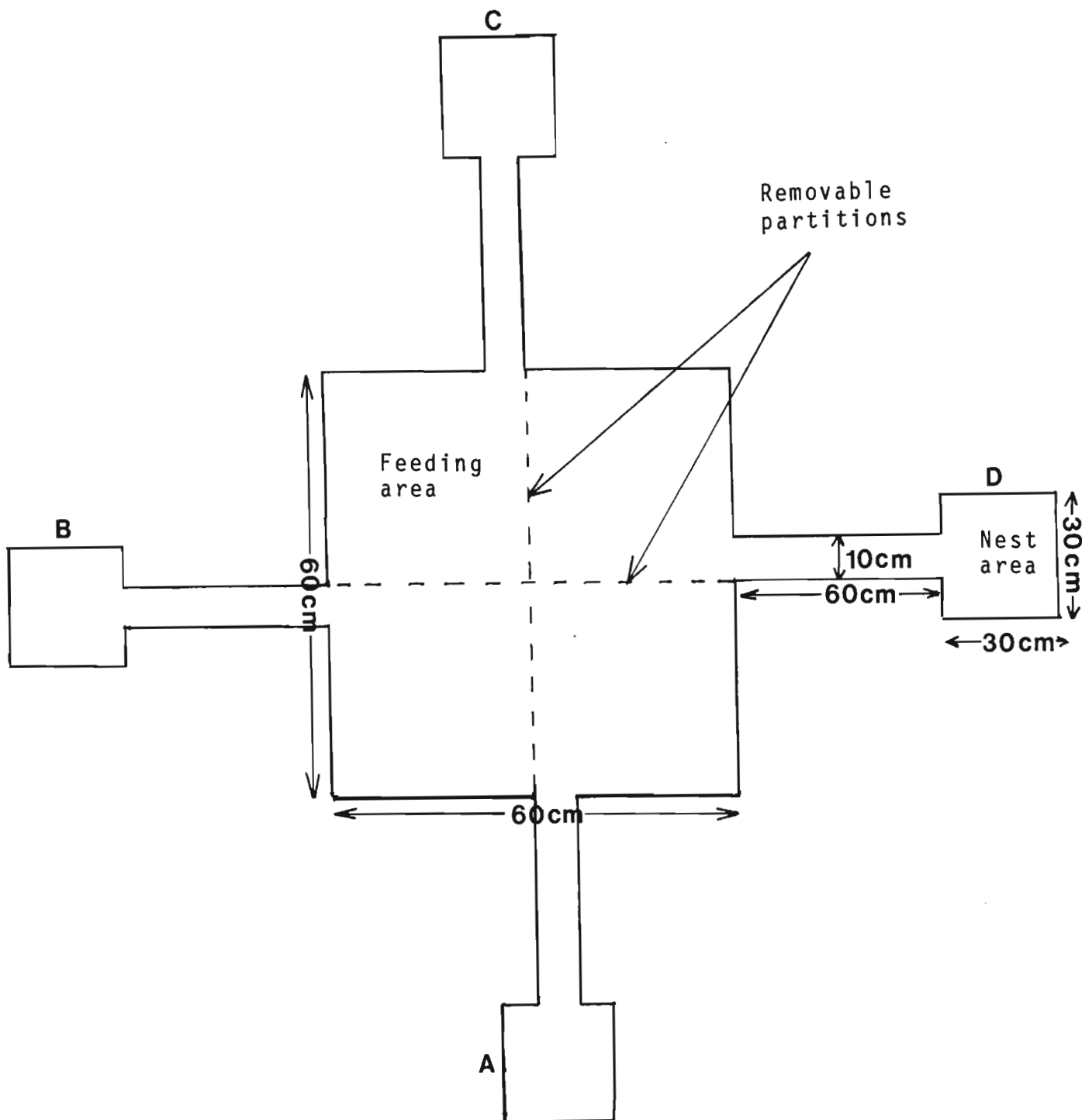
```

```

10 REM program for storing information on territoriality
20 DIM BOX$(4),T(4),F(4)
30 PRINT "enter animal's number"
40 INPUT A
50 PRINT "enter date"
60 INPUT D$
70 PRINT "enter original boxes occupied by this animal"
80 INPUT O$
90 FOR I=1 TO 4
100 READ BOX$(I)
110 NEXT I
120 PRINT "press box code when animal enters a box"
130 INPUT BOK$
135 IF BOK$="e" THEN 340
140 TIME$="00:00:00"
150 PRINT "press Z when animal leaves box or E if end of session"
160 INPUT Z$
170 TYD$=TIME$
180 FOR I=1 TO 4
190 IF BOX$(I)=BOK$ THEN 240
200 NEXT I
210 PRINT "rewind and start again"
220 GOTO 120
240 LPRINT BOK$,TYD$
250 D1$=MID$(TYD$,4,1)
260 D2$=MID$(TYD$,5,1)
270 D3$=MID$(TYD$,7,1)
280 D4$=MID$(TYD$,8,1)
290 S=VAL(D1$)*600+VAL(D2$)*60+VAL(D3$)*10+VAL(D4$)
300 T(I)=T(I)+S
310 F(I)=F(I)+1
320 IF Z$="e" THEN 340
330 GOTO 120
340 LPRINT
350 LPRINT "animal number: ";A,"date: ";D$
360 LPRINT
370 LPRINT "boxes originally occupied by this animal: ";O$
380 LPRINT
390 LPRINT "box","frequency","time(seconds)"
400 FOR I=1 TO 4
410 LPRINT BOX$(I),F(I),T(I)
420 NEXT I
430 DATA a,b,c,d
440 END

```

APPENDIX 3: Tables and Figures



APPARATUS FOR TESTING TERRITORIALITY

Apparatus is made of aluminium, with sides 10cm high. A perspex lid is fitted over the feeding area and tunnels. nest areas are covered with gauze lids.

Pair sequences of behaviours in intraspecific, same-sex encounters. "Preceding" acts are listed on rows; "following" acts on columns. "Conditional probabilities" = transition frequencies (See Chapter 3 for calculation of transition frequencies). Number of animals tested = number of encounters X 2. Some individuals were used more than once in any class of encounters.

File description is: TOTAL SEQUENCES FOR MALE G.P.PAEB

	ae	ad	ap	sn	sa	al	at	fi	up	ch	el	fl	cr	st	ex	gs
ae	.	1	.	45	3	.	.	.	2	4	4	10	1	.	8	2
ad	13	4	58	22	.	4	2	.	1	3	3	20	3	.	96	3
ap	2	17	8	107	19	2	3	.	6	19	2	10	2	.	54	3
sn	.	11	7	7	26	3	5	.	15	13	6	44	7	.	79	7
sa	.	1	2	13	2	.	.	.	5	.	2	2	.	.	7	2
al	.	2	.	.	.	5	2	3	9	15	.	5	.	2	2	.
at	.	1	.	.	.	4	2	19	9	22	.	.	.	2	2	.
fi	.	4	.	.	.	4	2	.	16	8	2	8	.	3	.	.
up	.	7	1	8	3	5	3	3	1	26	1	40	4	1	7	.
ch	.	11	3	1	.	8	42	1	18	2	.	.	.	14	21	.
el	.	2	1	3	3	.	10	50	4	.	.	.
fl	5	18	6	1	.	5	.	17	27	.	33	2	146	2	14	2
cr	22	6	22	13	.	.	.	1	3	.	7	66	1	.	50	4
st	.	1	5	5	1	1	1	.	.	10	.
ex	36	108	119	59	1	5	3	.	5	7	5	15	15	.	7	19
gs	4	6	6	8	1	.	.	.	1	.	.	4	.	.	10	.
ea	.	2	4	4	1	.	.	1	.	.	4	.
sb	2	4	11	1	3	.	18	1
dr	3	38	39	33	1	1	.	1	13	2	1	2	15	1	61	8
ma	.	.	1	8	1	.	.	.	2	1	5	1
mo
ur
mk
am	.	1	.	2	3	.	.	.	1	1
ro	.	.	.	3	1	1	.
si	.	1	2	4	1	.	.	3	.
gi
fo	.	3	1	24	23	.	1	.	7	1	9	.
th	.	2	.	1	1	.	.	.	1	2	1
go	1	.
vo
xx	1	6	1	1	4	2
SUM	88	257	297	369	84	47	65	48	146	123	76	281	201	28	475	56

[illegible]

Conditional probabilities of TOTAL SEQUENCES FOR MALE G.P.PAIBA

Number of animals tested: 16

[illegible][illegible]

[illegible]

Number of animals tested: 20

[illegible]

File description is: TOTAL SEQUENCES FOR MALE G.TYTONIS

	ae	ad	ap	sn	sa	al	at	fi	up	ch	el	fl	cr	st	ex	gs
ae	.	1	1	7	6	.	1	.	4	1	2	4	.	.	1	.
ad	9	3	63	33	2	1	9	2	22	16	5	20	8	.	123	5
ap	1	14	2	113	23	3	9	.	31	34	4	4	2	2	50	.
sn	.	20	6	2	12	.	7	1	16	6	4	26	2	1	84	6
sa	1	2	1	10	4	.	1	.	3	4	.	.	.	1	7	.
al	1	2	1	.	.	2	1	1	7	7	.	3	.	.	1	.
at	.	6	1	.	.	6	20	39	54	53	.	.	.	2	5	.
fi	.	3	.	3	.	.	4	.	27	18	7	19	.	1	.	.
up	.	55	4	9	2	7	12	.	23	27	3	57	10	5	19	1
ch	.	33	4	1	1	2	99	2	22	1	.	1	.	16	7	1
el	.	2	1	1	.	.	.	3	6	2	59	127	3	1	2	.
fl	3	27	6	2	1	3	1	31	58	1	104	7	40	10	17	2
cr	4	3	5	4	1	.	8	23	1	.	16	4
st	.	3	14	5	.	.	1	.	1	2	3	6	1	.	17	1
ex	6	126	165	90	3	1	5	.	22	2	5	6	3	3	6	36
gs	2	10	11	8	.	.	4	.	3	1	22	.
ea	.	4	7	5	1	.	1	10	4
sb	.	2	4	2	.	.	1	.	1	.	.	1	.	.	8	1
dr
ma	4	31	49	19	2	3	10	5	31	13	7	10	6	22	150	7
mo	1	1
ur
mk
am	.	.	1	3	2	.	.	.	2
ro	1	.	.	1
si
gi
fo	2	13	3	14	25	.	9	.	11	9	.	1	.	2	26	2
th	.	.	1	1	.	.	3	.	2	5	.
go
vo
xx
SUM	33	360	350	332	84	28	198	84	348	198	211	316	76	66	576	71

[illegible]

F

•

Number of animals tested: 16

[illegible]

[illegible]

Number of animals tested: 8

[illegible][illegible]

File description is: Total sequences for male G.paeba exilis fights.

Number of animals tested: 16

	ae	ad	ap	sn	sa	al	at	fi	up	ch	el	fl	cr	st	ex	gs
ae	.	1	.	11
ad	4	5	13	38	5	4	1	.	15	2	1	2	15	.	20	3
ap	.	2	1	54	32	2	2	.	6	.	.	.	1	.	31	.
sn	.	35	1	4	32	.	1	.	8	.	.	1	19	2	56	1
sa	.	5	.	22	1	.	.	.	3	.	.	.	1	.	30	3
al	.	1	1	1	9	1	.	1
at	.	.	1	.	.	.	1	2	3	1
fi	.	1	1	.	1
up	.	16	2	8	1	4	.	.	2	1	1	1	1	1	.	.
ch	.	1	1	.	1	1	1	.
el	1	.	.	.	1	.	.	.
fl	.	3	.	.	.	1	.	1	1	.	.	.
cr	2	14	2	15	2	4	.	5	.
st	.	1	1	1	1	.
ex	2	23	96	39	6	4	.	2	7
gs	.	4	2	4	2	5	1
ea	.	.	2	2	.
sb	.	.	1	.	2
dr
ma	1	8	26	2	2	3	1	.	4	1	29	1
mo
ur
mk
am
ro
si	1	14	1	5	7	2	.	.	1	.	.	.	2	.	5	.
gi	.	3	18	.	.	.
fo	.	8	.	11	11	1	1	.	4	.	.	.	7	.	5	.
th	.	3
go	.	4	1	2	4	2	10	4
vo
xx	.	4
SUM	10	156	150	216	107	17	9	4	57	6	2	6	74	7	202	20

[illegible]

[illegible]

Number of animals tested: 16

[illegible]

Number of animals tested: 16

	ae	ad	ap	sn	sa	al	at	fi	up	ch	el	fl	cr	st	ex	gs
ae	.	.	.	3	.	.	1	1	.	.	1	1	.	.	1	.
ad	3	2	75	16	.	3	4	1	2	3	2	42	8	.	86	13
ap	.	16	2	45	.	8	19	.	3	5	5	14	.	.	35	.
sn	.	11	.	.	1	1	6	1	.	3	1	7	3	1	55	.
sa	2	.
al	.	2	.	.	.	1	9	8	5	15	1	8	.	.	1	.
at	.	5	.	.	.	8	8	46	10	22	.	1	.	2	4	.
fi	.	6	1	.	.	10	25	6	19	5	2	8	17	1	.	.
up	.	3	.	2	.	1	7	11	2	7	.	9	5	1	2	.
ch	.	14	.	.	.	3	22	1	2	5	8	.
el	.	5	2	1	.	1	39	1	.	2	.
fl	1	57	4	.	.	8	.	15	2	.	31	2	23	1	8	1
cr	1	5	2	2	.	4	.	12	9	.	3	11	3	.	10	2
st	.	2	2	1	.	.	.	5	1
ex	5	109	66	38	2	2	7	.	1	.	4	11	2	2	1	3
gs	.	11	2	2	1	.	3	.
ea	.	1	.	1	1	.
sb	.	5	1	.	1	.	.	1	.	.	3	1
dr	.	6	1	.	.	.	1
ma	.	29	6	3	.	4	.	12	1	.	2	9	10	.	34	.
mo	.	1
ur
mk
am
ro
si	.	3	1	4	10	2
gi
fo	.	5	1	1	1	.	1	.	1	2	.	.	.	1	5	.
th	.	1
go
vo
xx	.	61	14	1	3	3	.	6	1
SUM	10	360	178	118	4	53	110	114	59	62	53	168	76	14	282	25

[illegible]

Number of animals tested: 16

[illegible][illegible]

[illegible]

Conditional probabilities of TOTAL SEQUENCES FOR F G.SETZERI

Number of animals tested: 16

[illegible][illegible]

Cluster diagrams and transition diagrams for intraspecific, same-sex encounters. Diameters of circles are drawn proportional to relative frequencies of behaviours; line lengths in cluster diagrams are proportional to similarities determined by weighted pair group cluster analysis; line widths in transition diagrams are drawn proportional to transition frequencies.

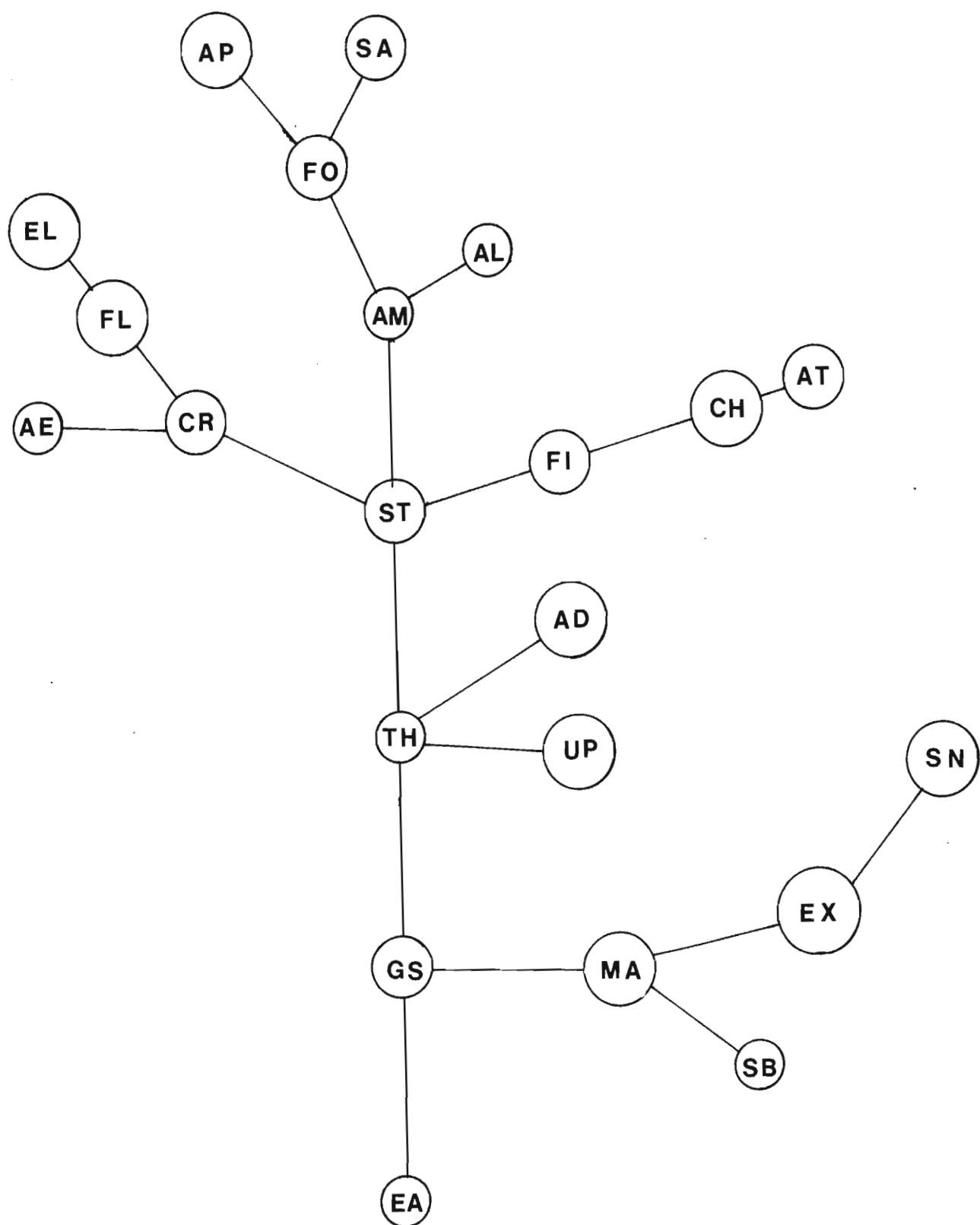


Fig. 12 Cluster diagram for male *G. tytonis* ($n = 6$)

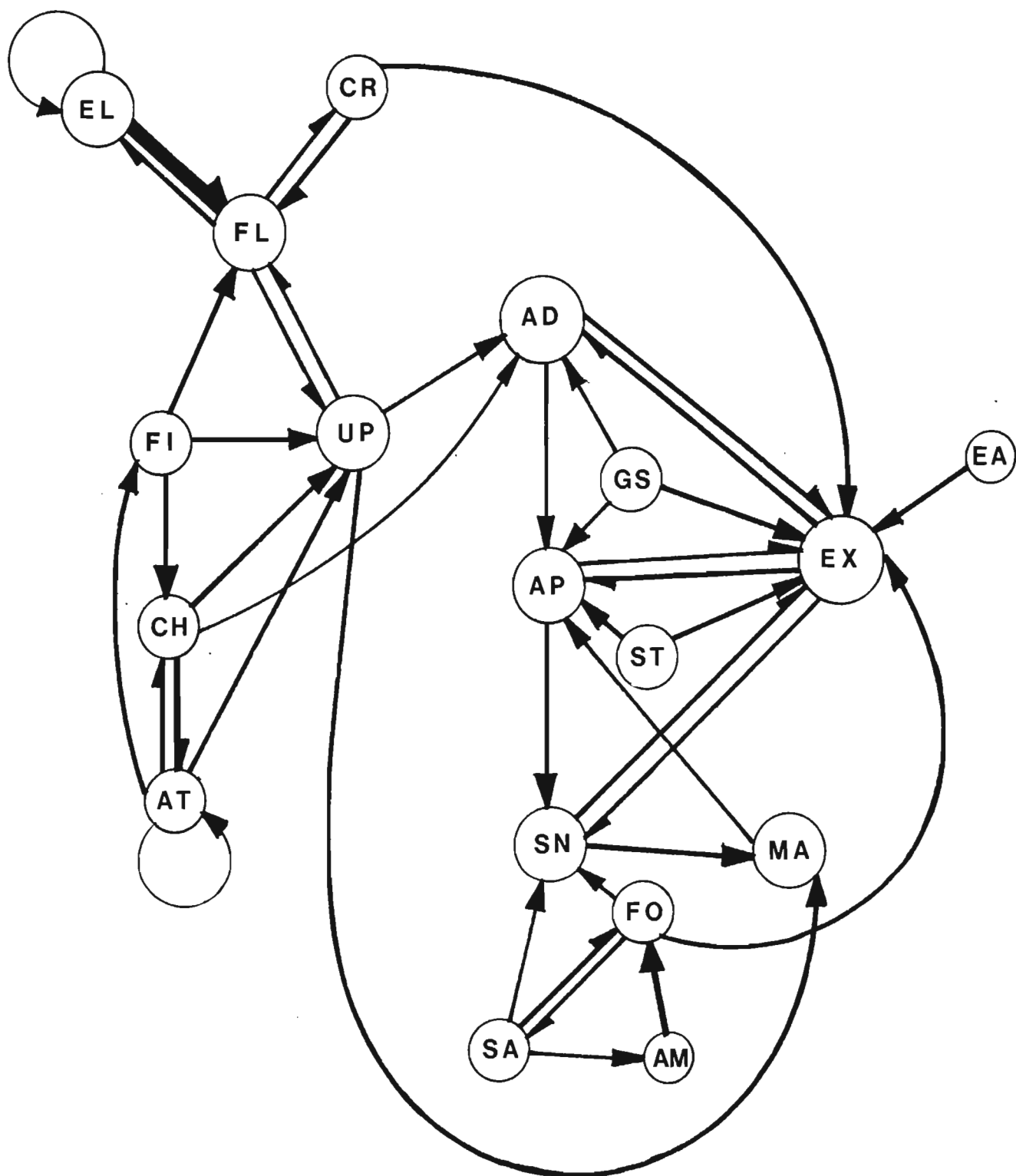


Fig. 13. Transition frequencies for male *G. tytonis* (n = 16)

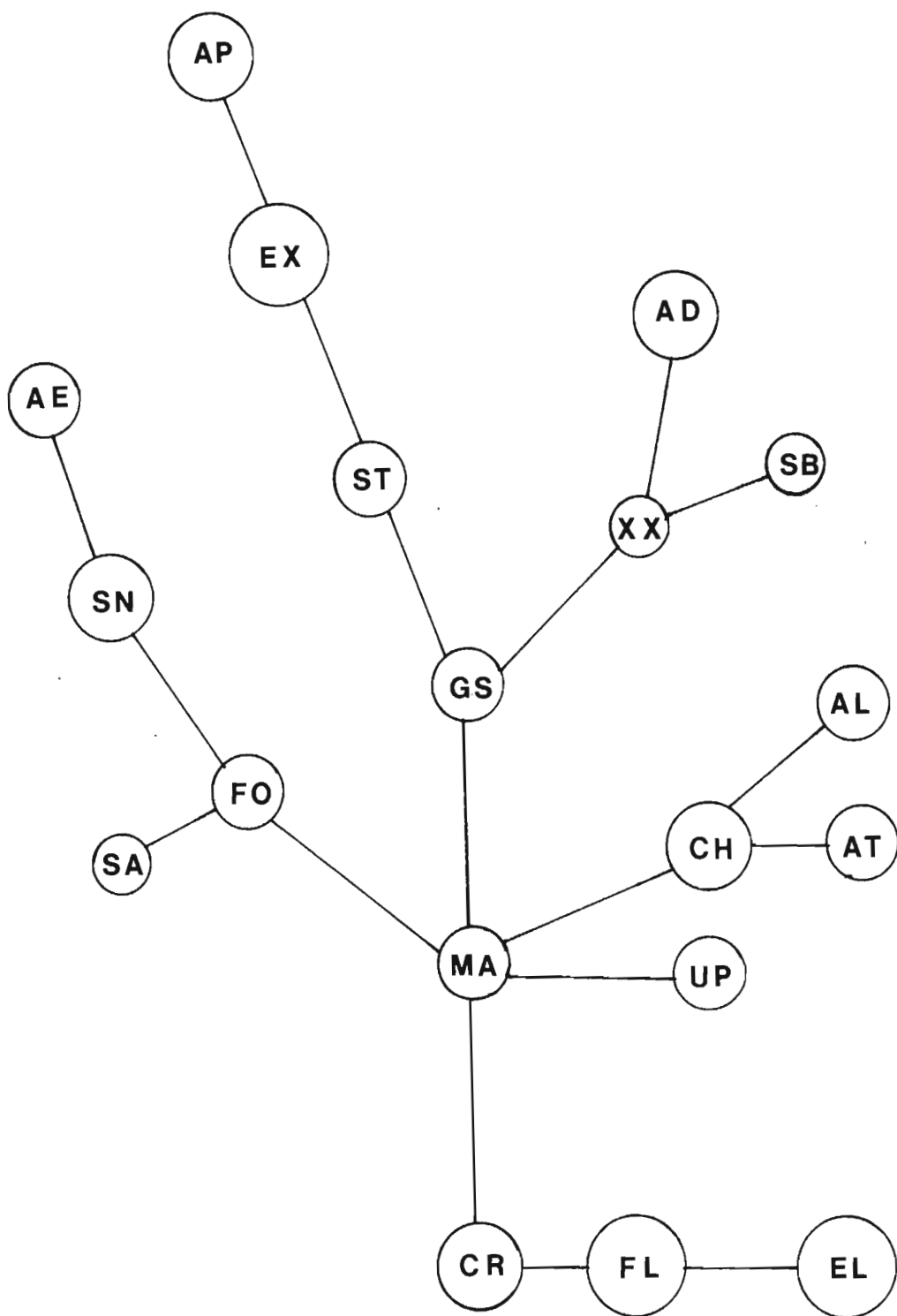


Fig. 14. Cluster diagram for female *G. p. paeba* (n = 20)

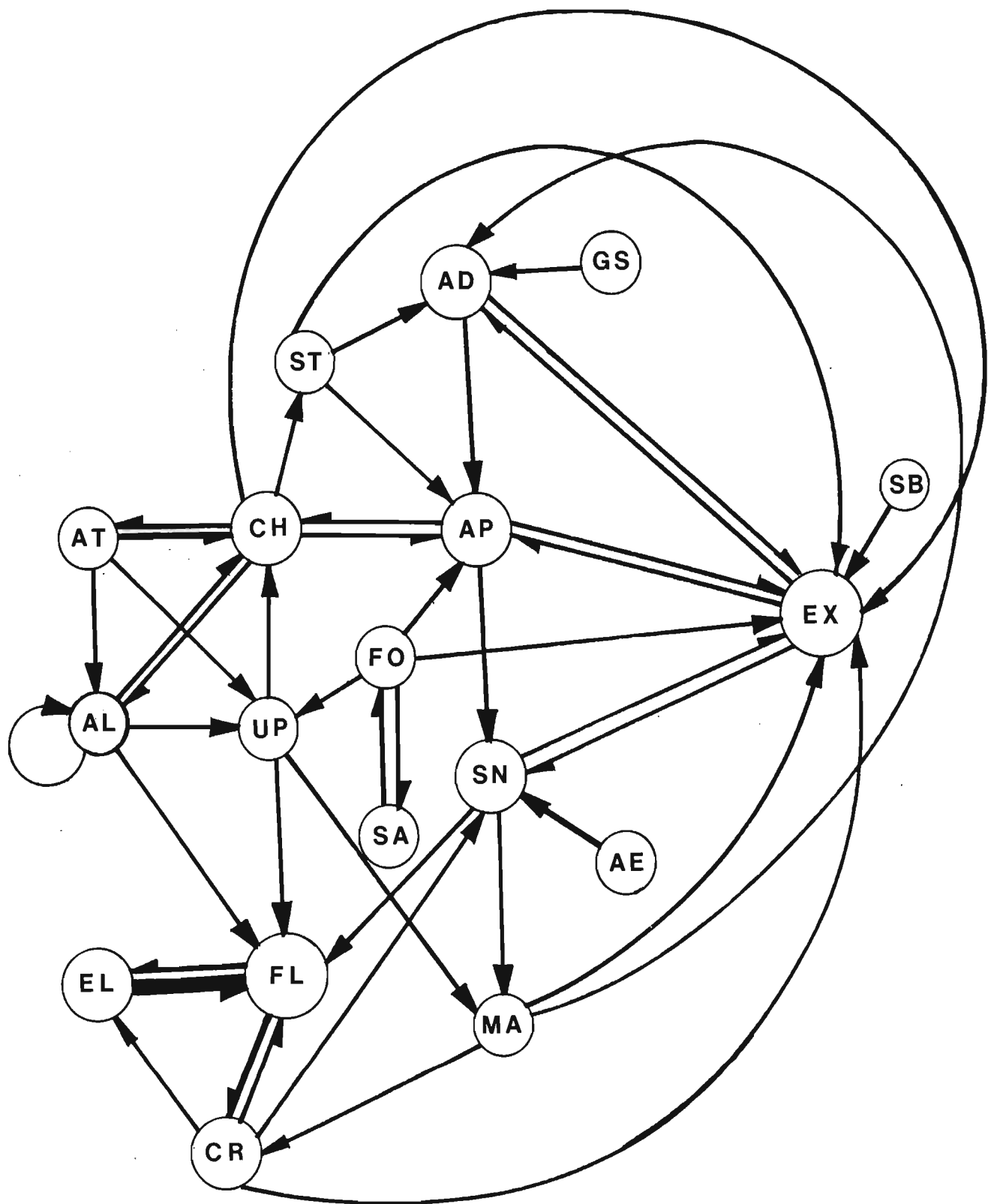


Fig. 15. Transition frequencies for female *G.p. paeba* ($n = 20$)

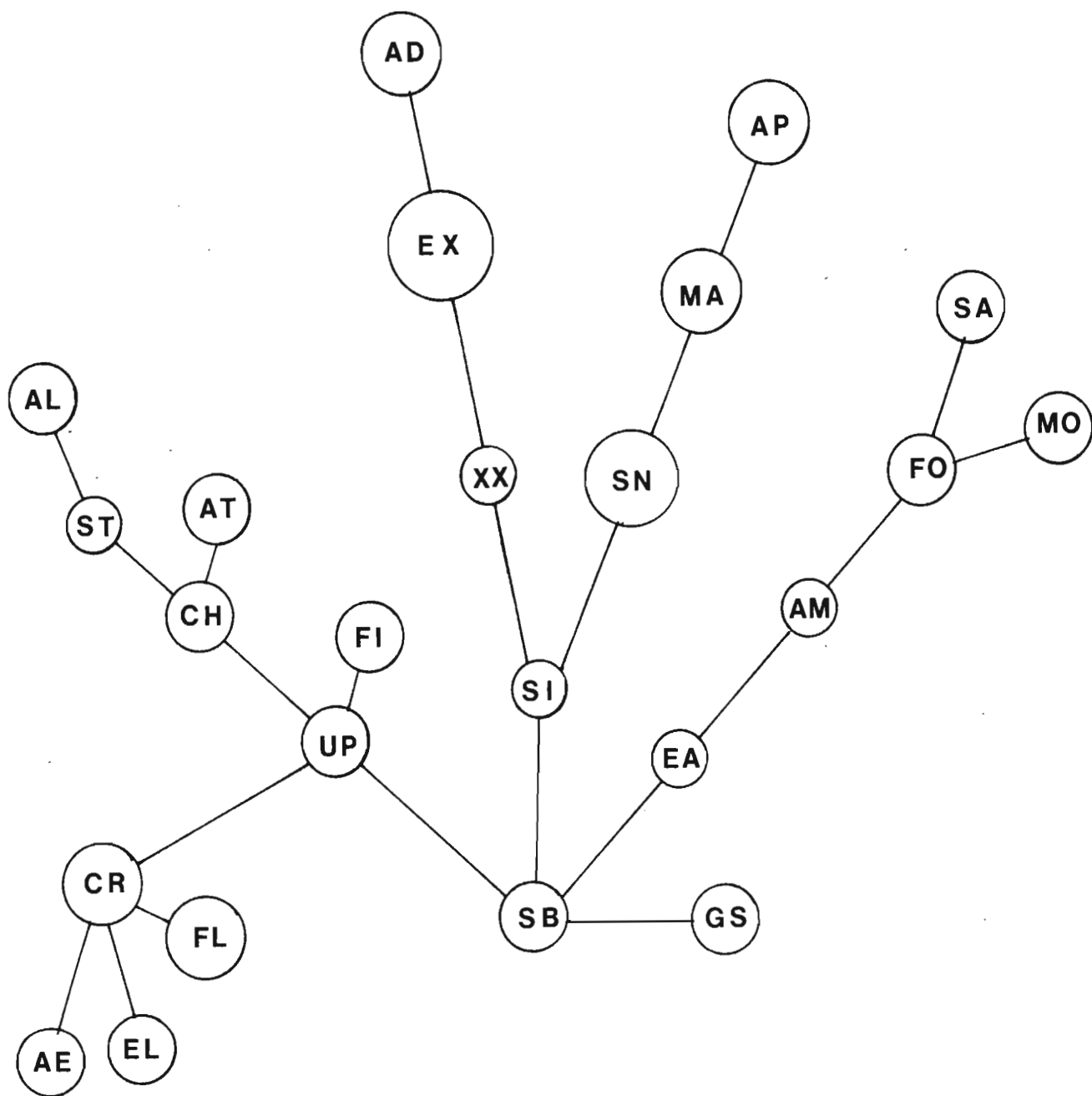


Fig. 16. Cluster analysis for male *G.p. paeba* ($n = 16$)

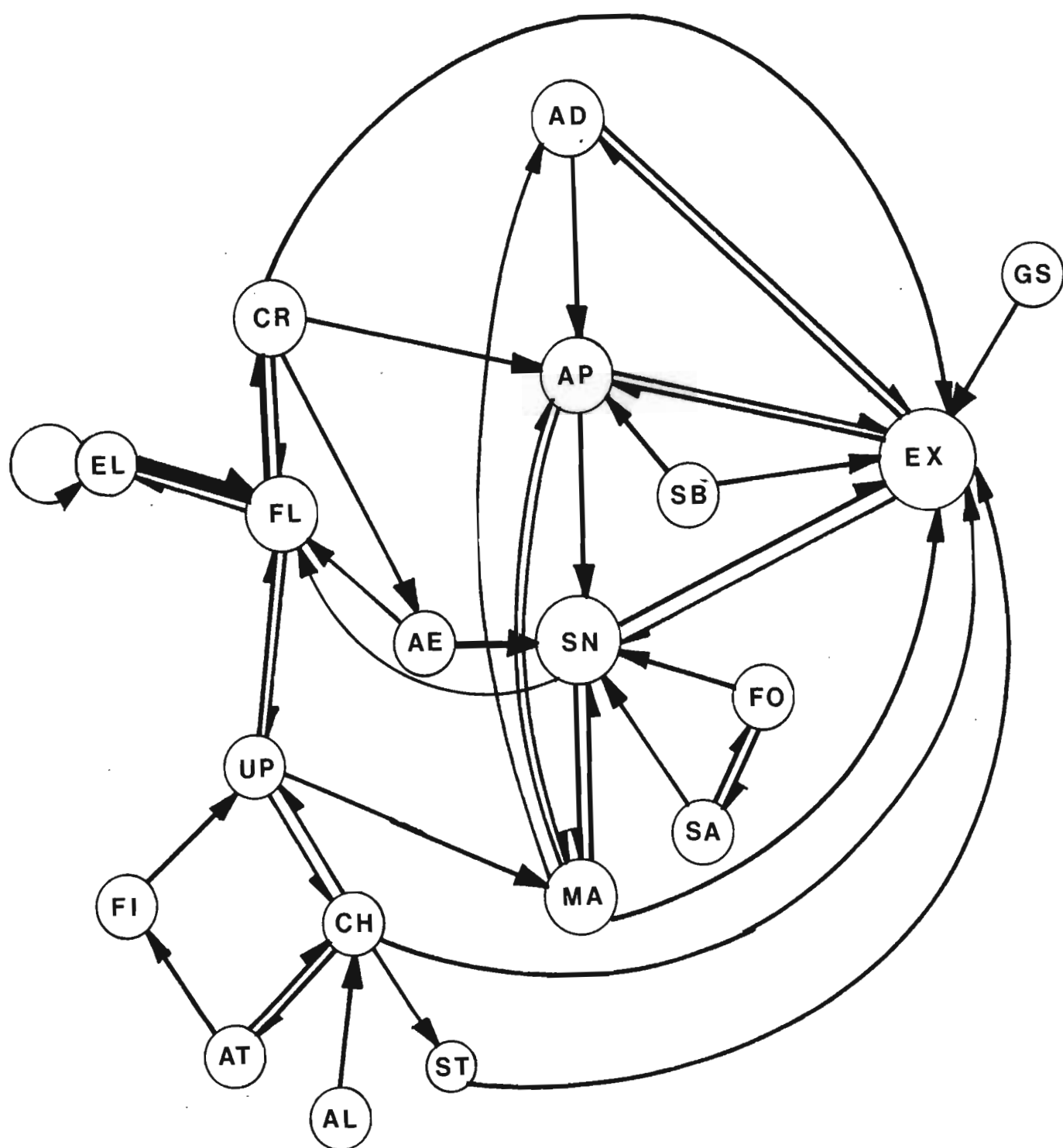


Fig. 17. Transition frequencies for male *G.p. paeba* (n = 16)

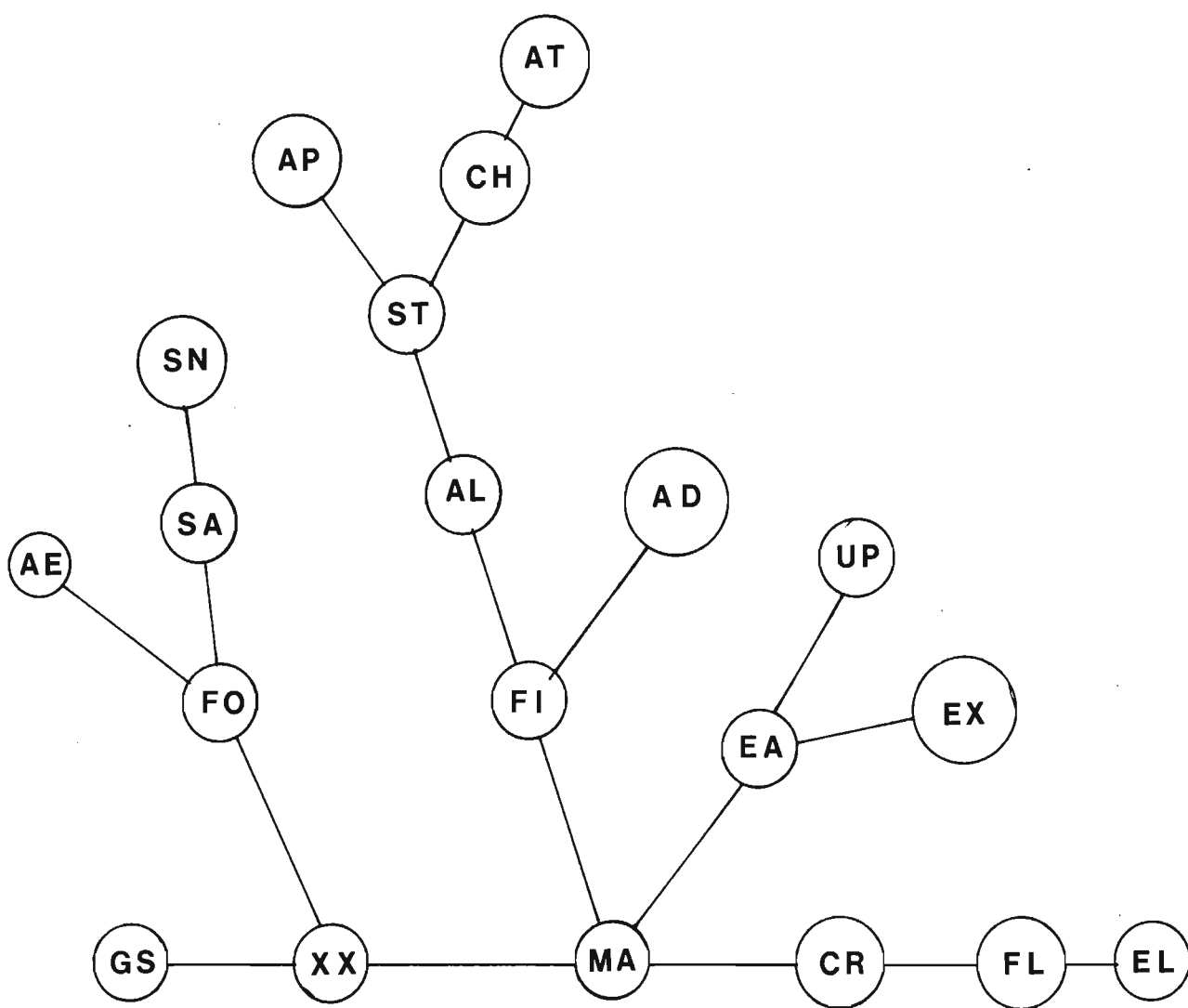


Fig. 18. Cluster diagram for female *G.p. exilis* ($n = 16$)

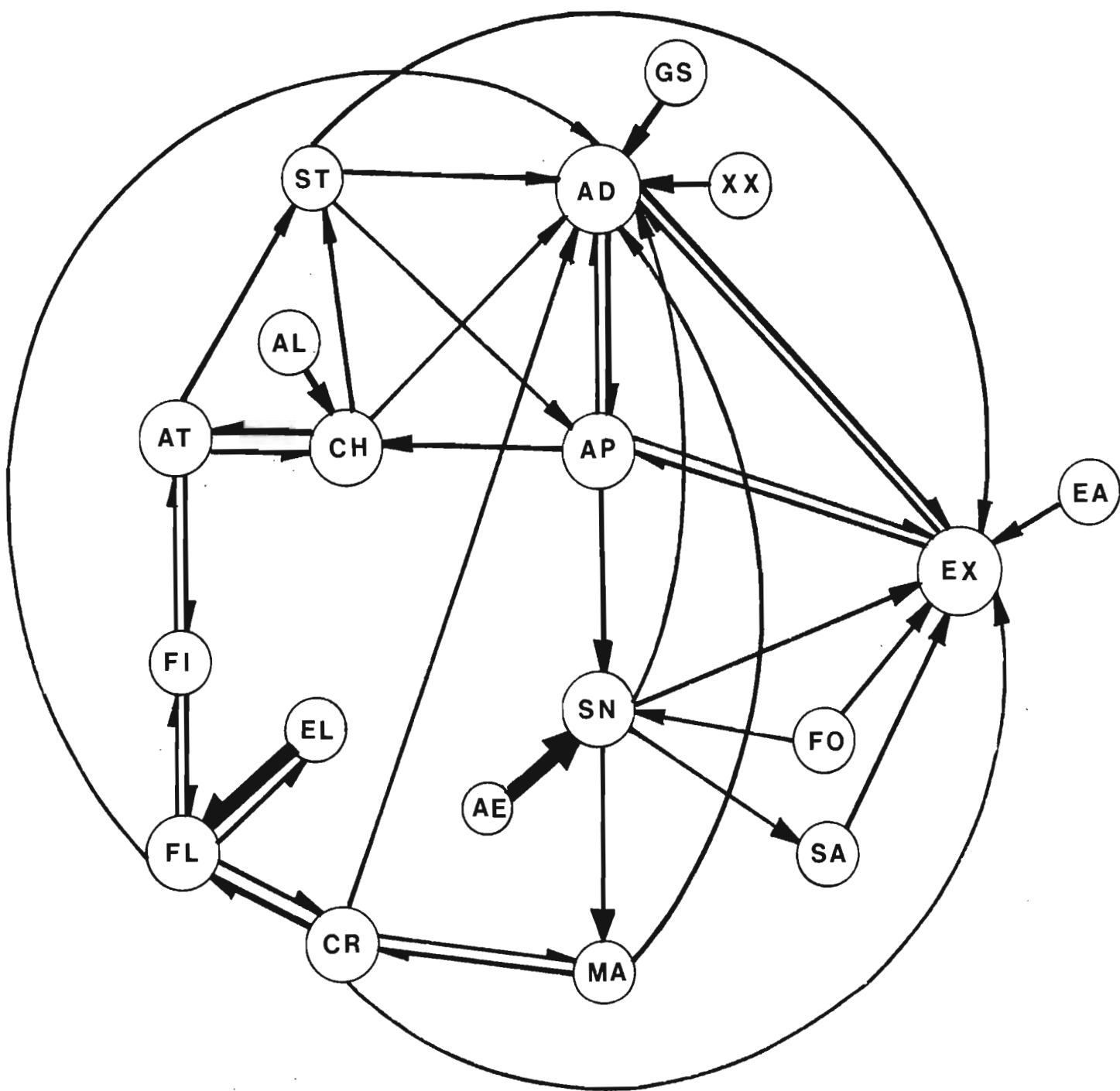


Fig. 19. Transition frequencies for female *G.p.exilis* (n = 16)

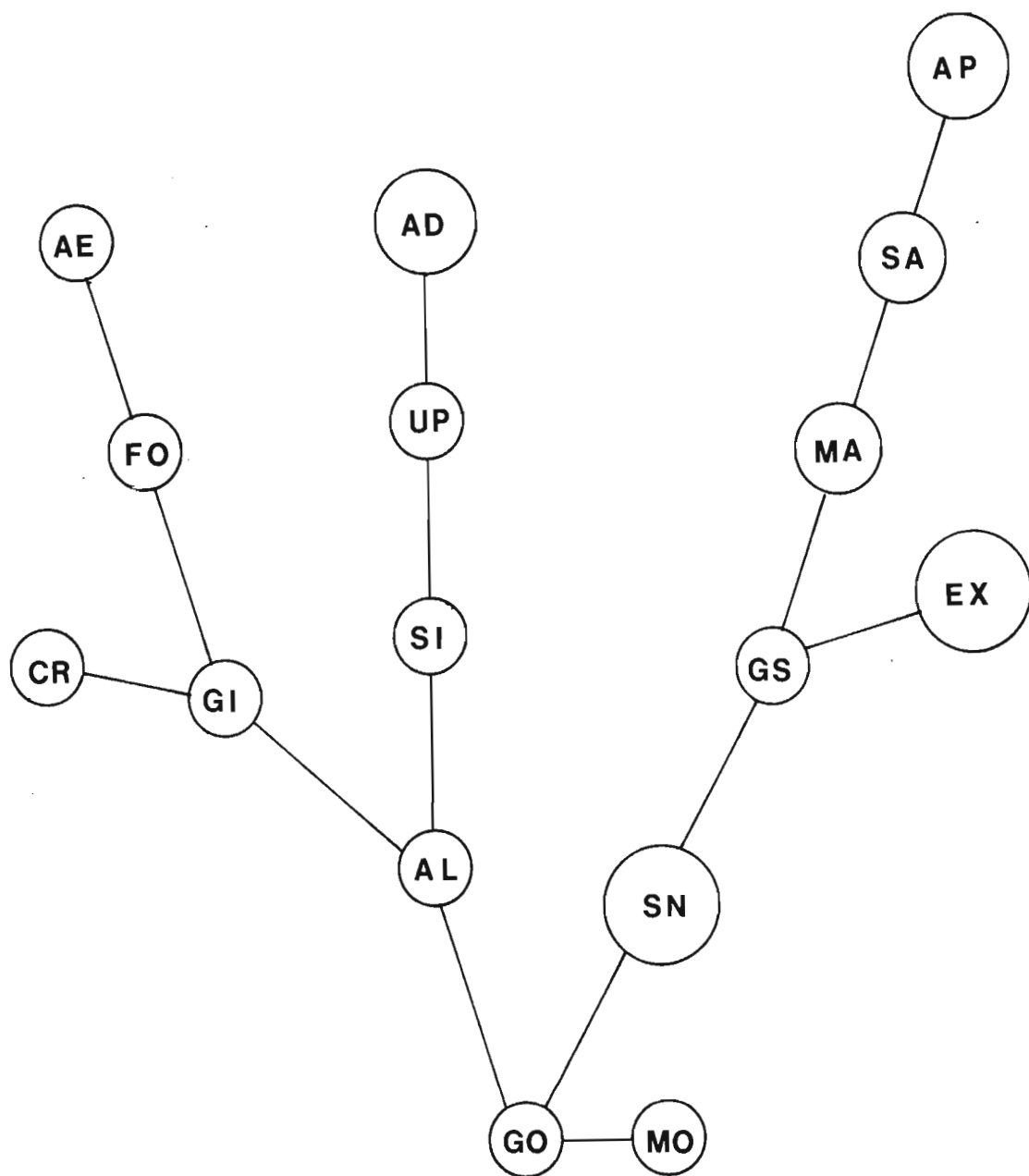


Fig. 20. Cluster diagram for male *G. p. exilis* (n = 16)

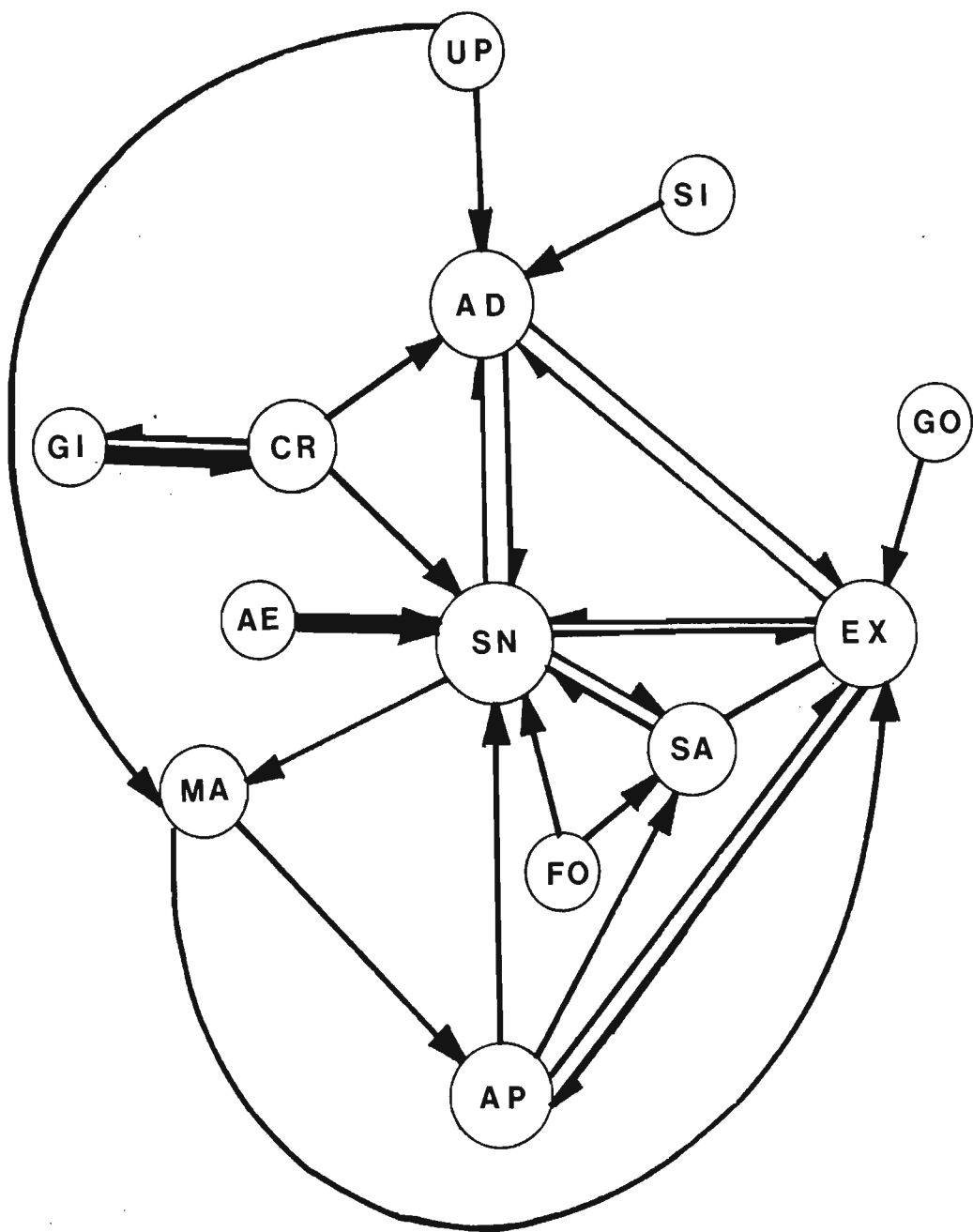


Fig. 21. Transition frequencies for male *G.p. exilis* (n = 16)

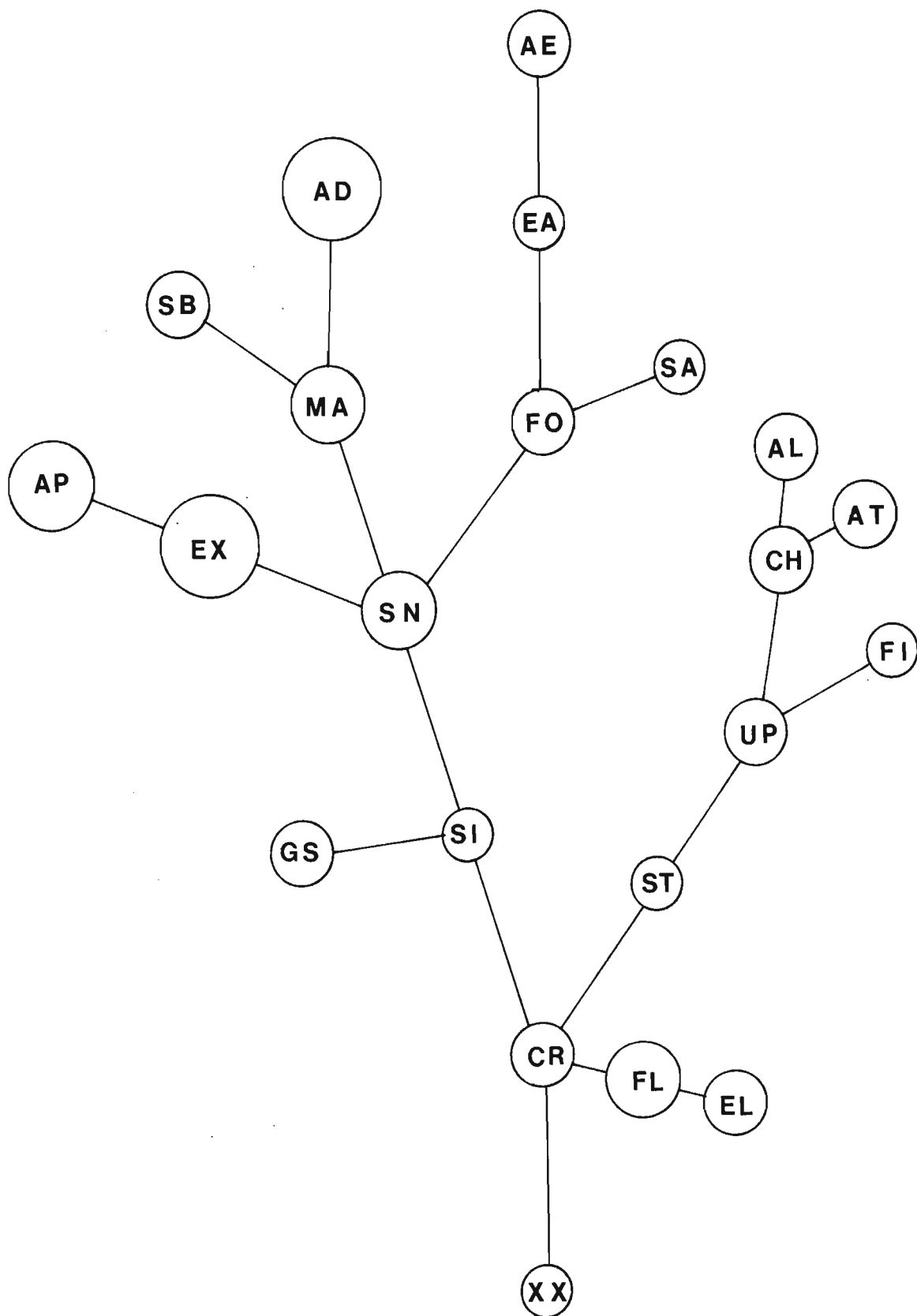


Fig. 22. Cluster diagram for female *G. setzeri* (n = 16)

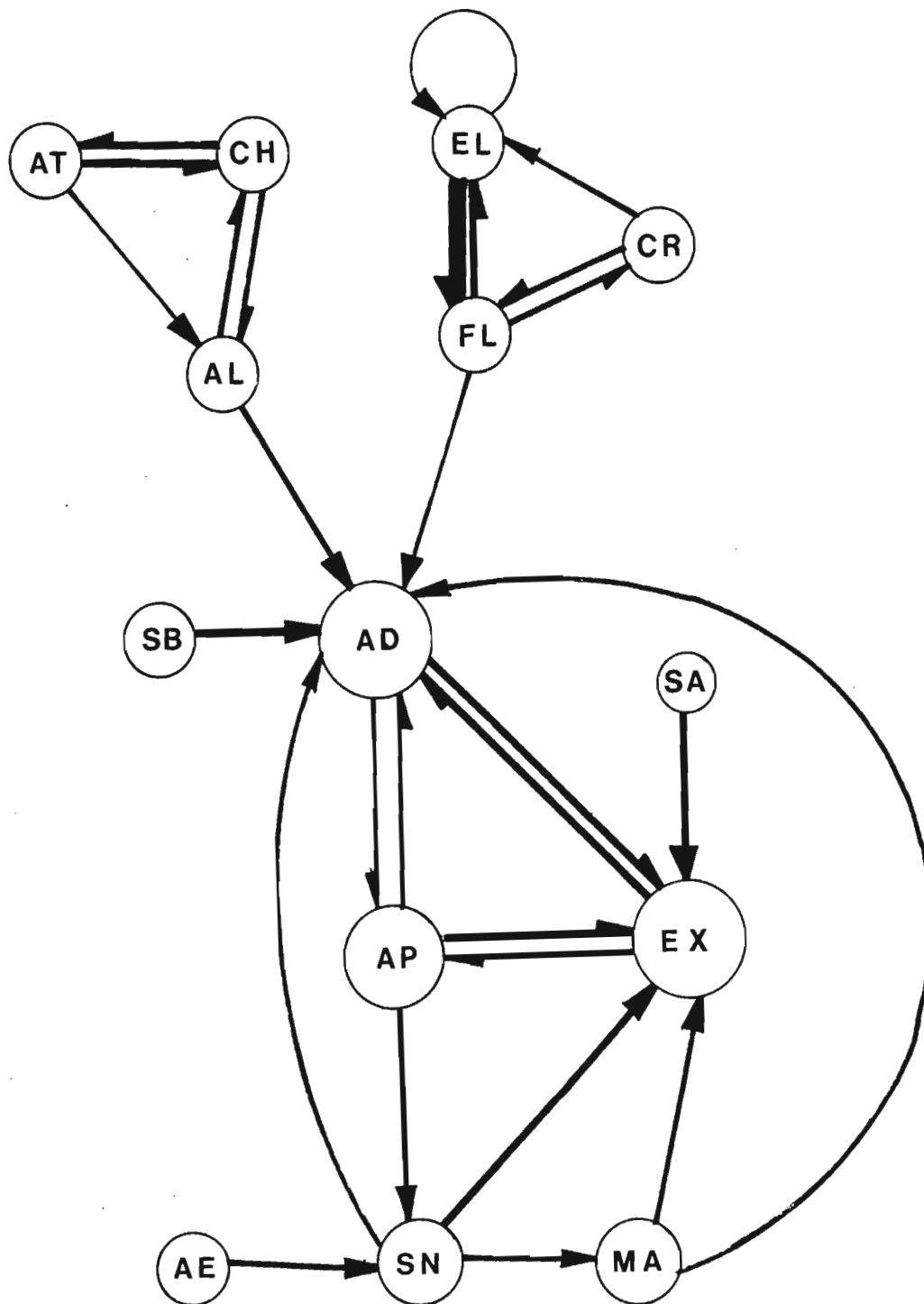


Fig. 23. Transition frequencies for female *G. setzeri* (n = 16)

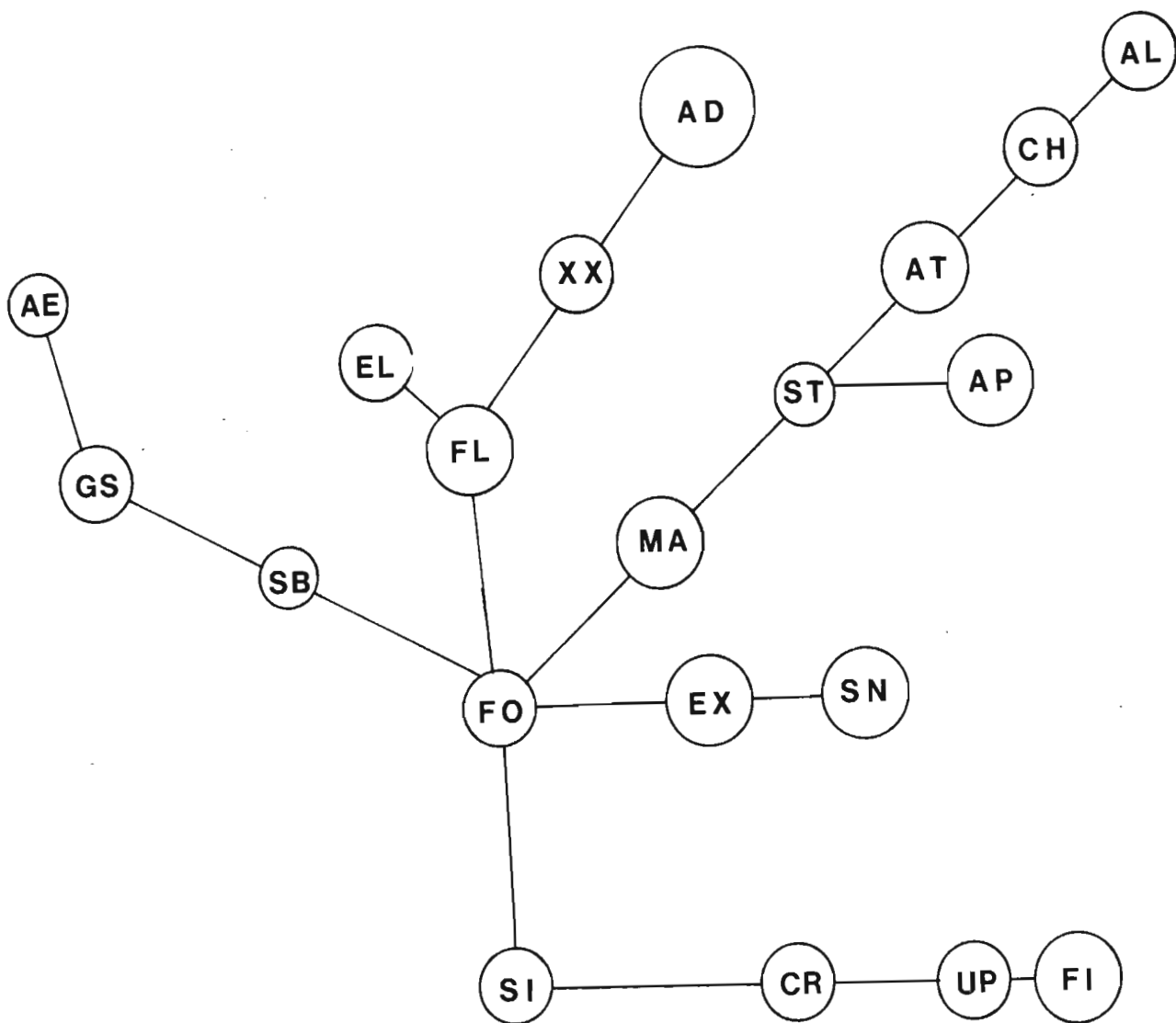


Fig. 24. Cluster diagram for male *G. setzeri* (n = 16)

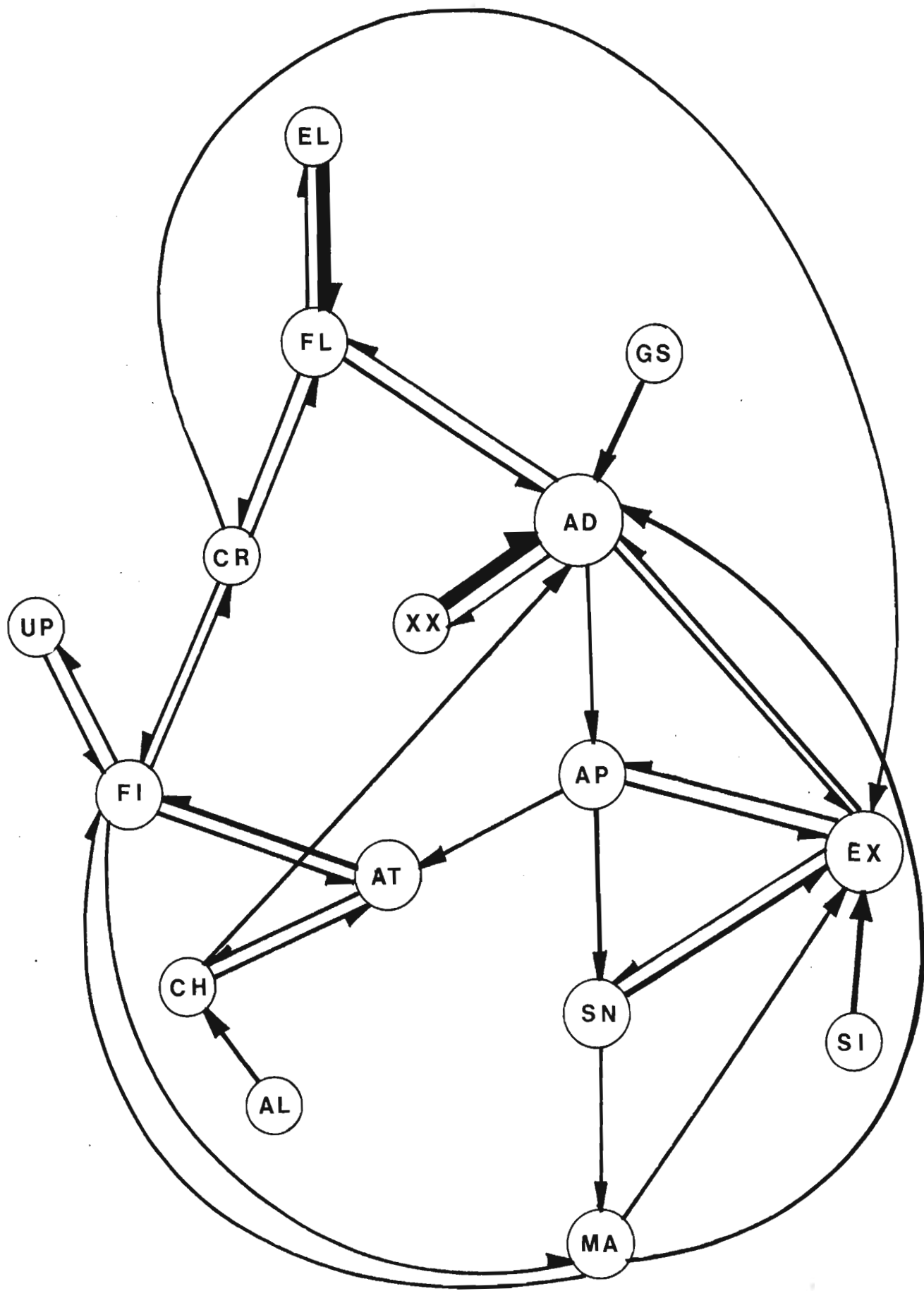


Fig. 25. Transition frequencies for male *G. setzeri* (n = 16)

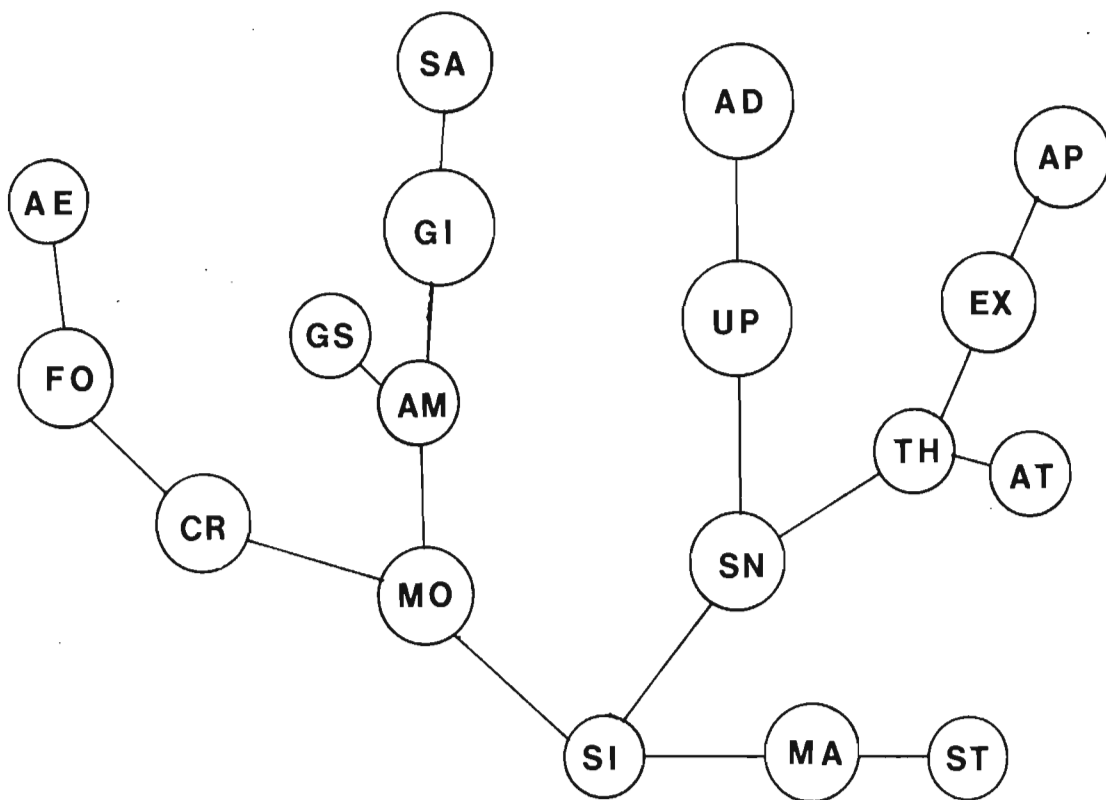


Fig. 26. Cluster diagram for male *G. vallinus* ($n = 8$)

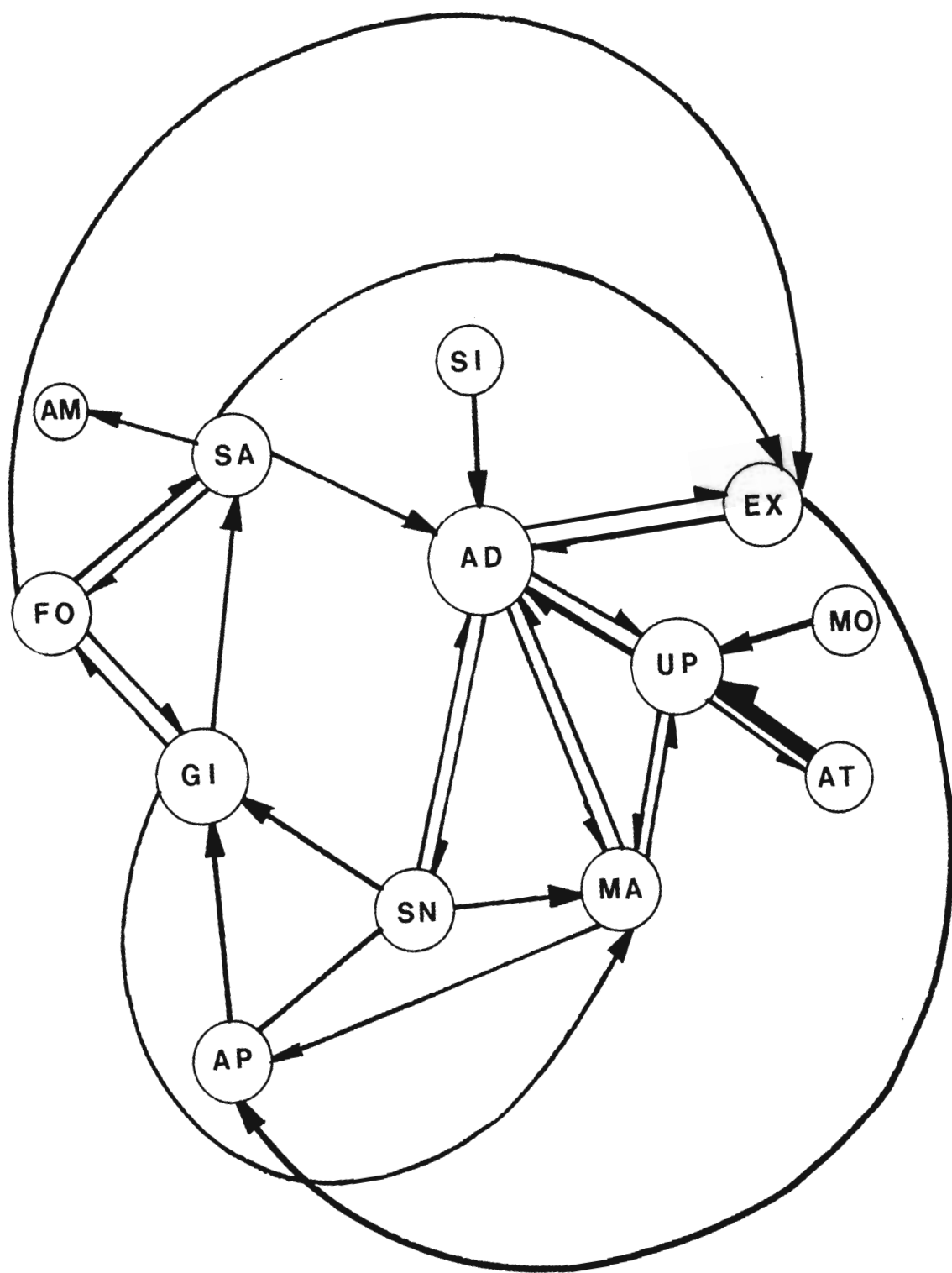


Fig. 27. Transition frequencies for male *G. vallinus* (n = 8)

Relative frequencies of behaviours in intraspecific, same-sex encounters resulting in one animal dominating the other; in intraspecific different-sex encounters; and in interspecific encounters.

TABLE 8 : RELATIVE FREQUENCIES OF BEHAVIOURS FOR MALE G.P.PAEB IN
ENCOUNTERS WITH OTHER SEXES AND SPECIES.

	<u>G.p.p.</u> <u>♂ dom</u>	<u>G.p.p.</u> <u>♂ sub</u>	<u>G.p.p.</u> <u>♀</u>	<u>G.t.</u> <u>♂</u>	<u>G.t.</u> <u>♀</u>	<u>G.s.</u> <u>♂</u>	<u>G.s.</u> <u>♀</u>	<u>G.p.e.</u> <u>♂</u>	<u>G.p.e.</u> <u>♀</u>
AD	10.3	8.2	5.7	9.5	5.6	16.4	10.8	13.5	9.7
XX	0.8	0.1	1.0	0.0	0.3	0.4	0.9	6.5	5.0
DR	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
AP	11.6	7.9	9.4	9.4	4.4	16.5	14.0	12.5	9.5
SN	10.9	9.6	5.2	15.3	7.7	5.6	9.4	10.0	6.8
EX	18.7	11.0	10.0	17.2	13.6	26.6	20.5	13.9	11.8
MA	6.2	8.2	3.5	10.4	5.9	4.0	5.9	7.6	7.2
SI	1.0	0.1	0.2	1.8	0.2	0.0	0.0	0.1	0.0
EA	0.9	0.3	0.3	0.4	0.5	1.0	0.8	0.9	0.7
GS	1.7	1.0	1.0	1.6	0.6	1.2	0.7	5.9	4.6
SB	1.4	0.8	0.8	0.7	0.7	3.1	2.4	1.9	2.6
AL	3.0	0.7	0.9	0.0	2.2	1.3	1.7	0.4	0.1
AT	5.2	0.0	1.3	0.5	0.0	2.5	0.0	3.0	0.9
CH	9.6	0.3	3.4	1.1	0.0	3.0	0.0	2.4	0.0
FI	2.0	1.7	1.7	0.0	1.7	0.5	0.0	1.6	0.6
UP	5.6	4.9	5.6	2.1	3.0	0.7	1.9	5.2	0.6
ST	1.9	0.3	1.6	0.8	0.8	0.7	0.2	0.7	0.0
TH	0.7	0.0	0.0	0.0	0.2	0.1	0.0	0.1	0.4
EL	0.2	5.1	4.8	2.7	10.2	1.3	4.5	0.0	4.4
FL	1.2	18.6	16.8	8.0	19.5	5.5	7.8	0.0	9.8
CR	0.2	13.9	9.0	7.2	15.9	2.6	6.6	1.4	7.9
VO	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
AE	1.4	3.9	5.4	6.1	3.7	2.6	4.9	0.4	2.3
SA	2.0	1.9	3.8	2.8	1.0	1.1	1.1	3.3	3.3
MO	0.6	0.0	0.3	0.2	0.0	0.3	0.0	1.7	3.5
AM	0.3	0.0	0.5	0.1	0.0	0.0	1.3	0.1	3.6
FO	2.5	1.1	7.5	2.1	1.5	2.9	4.4	4.6	4.7
GI	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0
GO	0.0	0.0	0.0	0.0	0.0	0.1	0.0	2.2	0.1
N	6	6	8	5	5	5	5	5	5

TABLE 9 : RELATIVE FREQUENCIES OF BEHAVIOURS FOR FEMALE G.P.PAEB I
ENCOUNTERS WITH OTHER SEXES AND SPECIES.

	<u>G.p.p.</u> ♀ dom	<u>G.p.p.</u> ♀ sub	<u>G.p.p.</u> ♂	<u>G.t.</u> ♀	<u>G.t.</u> ♂	<u>G.s.</u> ♀	<u>G.s.</u> ♂	<u>G.p.e.</u> ♀	<u>G.p.e.</u> ♂
AD	11.0	7.3	9.3	9.5	20.6	21.1	20.5	9.4	13.1
XX	0.5	0.4	1.8	0.0	0.0	1.7	1.8	1.9	7.8
DR	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	3.4
AP	16.7	2.3	7.1	3.9	11.9	13.1	13.7	15.6	12.9
SN	8.1	8.2	4.6	8.7	8.4	5.2	3.2	9.5	7.9
EX	18.7	8.5	11.4	9.7	20.7	27.2	25.6	20.0	15.2
MA	4.9	4.0	8.8	4.4	7.5	6.8	5.4	6.6	7.8
SI	0.0	0.1	0.5	0.4	0.6	0.0	0.0	0.3	0.2
EA	0.3	0.0	0.5	0.0	0.3	0.4	1.2	0.6	0.6
GS	1.5	0.8	1.7	0.7	2.7	1.0	3.3	1.4	5.7
SB	1.0	0.7	0.6	1.1	1.6	1.9	3.8	1.7	3.3
AL	5.1	2.0	4.0	0.0	2.5	1.6	2.2	0.7	3.4
AT	4.9	0.3	5.7	0.0	2.3	2.7	2.7	1.8	4.5
CH	11.1	0.5	9.6	0.0	10.7	4.4	3.3	1.5	5.5
FI	0.4	0.4	1.6	0.8	0.5	0.4	0.5	2.3	1.1
UP	3.9	4.4	4.9	0.9	0.4	0.6	0.5	2.3	1.1
ST	2.8	0.5	4.7	1.1	3.9	0.7	0.5	0.4	1.0
TH	0.2	0.0	0.8	0.0	0.2	0.1	0.3	0.3	0.0
EL	0.9	12.1	5.7	13.5	1.1	1.3	1.4	5.4	0.6
FL	1.1	25.9	8.1	21.7	1.0	1.3	2.8	5.5	0.3
CR	0.5	16.5	6.4	14.2	0.3	0.2	1.0	4.0	0.0
VO	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
AE	1.1	3.0	0.8	5.5	1.3	5.2	5.1	1.4	0.8
SA	1.0	0.6	0.6	0.9	0.4	0.2	0.8	2.1	0.6
MO	0.2	0.2	0.0	0.0	0.0	0.0	0.0	1.2	1.0
AM	0.2	0.1	0.0	0.9	0.0	0.0	0.0	0.6	0.0
FO	3.0	1.3	0.8	1.8	1.2	2.6	0.3	2.9	1.8
GI	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
GO	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3
N	10	10	8	5	6	5	5	5	5

TABLE 10: RELATIVE FREQUENCIES OF BEHAVIOURS FOR MALE G.TYTONIS
IN ENCOUNTERS WITH OTHER SPECIES AND SEXES.

	G.t. ♂ dom	G.t. ♂ sub	G.t. ♀	G.p.p. ♂	G.p.p. ♀	G.s. ♂	G.s. ♀
AD	7.2	10.4	8.1	6.4	9.0	14.1	11.7
XX	0.0	0.0	0.0	0.0	0.0	0.0	0.0
DR	0.0	0.0	0.0	0.0	0.0	0.0	0.0
AP	9.6	8.0	4.3	18.1	8.5	23.5	23.2
SN	7.9	7.8	5.3	2.9	6.6	5.9	5.6
EX	15.4	12.1	10.3	25.7	12.0	29.7	29.8
MA	11.7	8.3	4.1	13.0	8.2	6.0	7.5
SI	0.0	0.0	0.0	0.0	0.0	0.0	0.0
EA	0.5	0.6	1.2	0.1	0.3	1.6	0.7
GS	2.4	0.8	1.6	1.2	0.6	1.1	1.7
SB	0.7	0.5	0.5	0.2	0.3	0.0	0.6
AL	1.3	0.3	0.2	0.3	0.0	0.0	0.1
AT	10.7	0.1	0.5	0.7	0.0	0.0	0.1
CH	10.7	0.0	0.6	2.1	0.0	0.0	0.0
FI	2.3	2.2	2.7	0.0	0.4	0.0	0.0
UP	8.3	10.3	3.8	2.2	0.3	0.2	1.9
ST	1.9	1.4	0.3	0.8	0.9	0.7	1.0
TH	0.5	0.3	0.2	0.0	0.0	0.0	0.3
EL	0.2	11.1	22.3	1.1	25.6	1.1	0.9
FL	0.4	16.3	24.2	3.4	20.2	6.2	1.3
CR	0.2	3.8	6.6	0.2	4.0	1.7	0.0
VD	0.0	0.0	0.0	0.0	0.0	0.0	0.0
AE	0.5	1.2	0.3	3.8	0.5	0.6	0.6
SA	2.6	1.6	0.9	2.9	1.0	1.7	3.2
MO	0.1	0.0	0.0	0.0	0.0	0.0	0.0
AM	1.0	0.3	0.0	0.0	0.0	0.1	0.1
FO	4.0	2.3	2.0	1.5	1.5	5.7	9.6
GI	0.0	0.0	0.0	0.0	0.0	0.0	0.0
GO	0.0	0.0	0.0	0.1	0.0	0.0	0.0
N	7	7	8	5	6	5	5

TABLE 11: RELATIVE FREQUENCIES OF BEHAVIOURS FOR FEMALE G.TYTONIS

IN ENCOUNTERS WITH OTHER SPECIES AND SEXES.

	<u>G.t.</u> ♀ dom	<u>G.t.</u> ♀ sub	<u>G.t.</u> ♂	<u>G.p.p.</u> ♀	<u>G.p.p.</u> ♂	<u>G.s.</u> ♀	<u>G.s.</u> ♂
AD	8.2	5.3	9.4	8.5	9.3	23.3	18.7
XX	0.0	0.1	0.4	0.0	0.0	0.1	0.0
DR	0.0	0.0	0.0	0.0	0.0	0.0	0.0
AP	14.9	2.4	12.8	19.1	15.1	19.0	21.1
SN	3.4	3.2	5.6	9.6	8.0	6.4	5.4
EX	16.8	7.6	16.0	22.4	20.4	22.5	28.8
MA	2.2	4.8	8.0	7.8	8.5	8.8	5.1
SI	0.8	0.1	0.1	1.6	0.2	0.0	0.0
EA	0.6	0.0	0.9	0.8	0.4	0.8	0.8
GS	1.6	0.8	1.6	2.3	0.9	1.5	0.7
SB	0.9	0.0	0.7	0.8	0.8	0.1	0.0
AL	2.5	0.6	3.2	1.0	0.7	0.4	0.4
AT	10.2	0.9	8.7	4.7	10.3	0.0	0.4
CH	16.4	0.5	12.0	10.6	8.7	0.3	0.4
FI	6.2	5.8	2.8	0.8	1.8	0.0	0.7
UP	1.5	1.8	3.1	0.8	2.7	0.3	1.1
ST	5.0	0.5	4.8	3.4	4.7	0.7	0.6
TH	0.5	0.3	0.2	0.8	0.7	0.1	0.0
EL	1.3	16.4	1.1	0.1	0.0	2.2	3.2
FL	1.3	30.8	2.0	1.6	0.5	5.7	6.1
CR	0.5	16.2	1.7	0.4	0.0	1.6	1.8
VO	0.0	1.1	0.7	0.0	0.0	0.0	0.0
AE	0.8	0.5	0.6	1.0	0.4	0.8	0.3
SA	1.1	0.0	1.0	0.4	0.9	0.4	0.4
MO	0.0	0.0	0.0	0.1	0.3	0.0	0.0
AM	0.3	0.0	0.1	0.0	0.5	0.0	0.1
FO	3.2	0.1	2.4	1.1	3.6	5.0	4.0
GI	0.0	0.0	0.0	0.0	0.0	0.0	0.0
GO	0.0	0.0	0.0	0.0	0.5	0.0	0.0
N	6	6	8	5	5	5	5

TABLE 12: RELATIVE FREQUENCIES OF BEHAVIOURS FOR MALE G.SETZERI
IN ENCOUNTERS WITH OTHER SPECIES AND SEXES.

	<u>G.s.</u> ♂ dom	<u>G.s.</u> ♂ sub	<u>G.s.</u> ♀	<u>G.p.p.</u> ♂	<u>G.p.p.</u> ♀	<u>G.t.</u> ♂	<u>G.t.</u> ♀
AD	14.0	17.4	27.3	18.6	28.8	19.1	27.1
XX	2.5	3.1	3.8	3.1	8.1	4.3	4.6
DR	0.0	0.5	1.4	2.5	3.2	2.1	4.3
AP	11.4	8.2	9.4	5.1	3.5	4.0	6.2
SN	4.4	5.0	3.1	5.4	3.5	4.7	4.2
EX	13.8	9.6	13.9	8.1	2.2	5.9	8.9
MA	7.3	6.4	7.7	7.9	5.1	9.3	14.7
SI	0.0	0.2	1.1	0.8	1.0	0.3	0.0
EA	0.1	0.0	0.4	0.1	0.0	0.0	0.2
GS	0.5	0.5	0.9	0.5	1.3	0.6	1.6
SB	0.9	0.0	1.1	0.7	0.1	0.5	0.3
AL	5.1	2.3	2.9	0.5	0.7	0.2	0.6
AT	14.6	0.0	2.0	0.1	0.3	0.0	0.1
CH	8.2	0.0	4.8	0.0	0.1	0.2	0.9
FI	7.6	8.7	0.9	0.5	0.6	0.0	0.6
UP	3.6	4.9	1.0	0.8	0.6	0.0	0.8
ST	1.2	0.3	1.2	0.1	0.6	0.8	1.0
TH	0.3	0.0	0.5	0.1	0.3	0.0	0.0
EL	0.4	4.9	2.4	8.4	5.4	5.6	3.8
FL	1.9	17.1	8.8	22.7	26.1	24.7	10.8
CR	1.1	9.2	3.1	12.7	8.5	16.8	7.3
VD	0.0	0.0	0.0	0.0	0.0	0.0	0.0
AE	0.3	0.3	0.7	0.5	0.1	0.8	0.3
SA	0.0	0.2	0.2	0.1	0.0	0.0	0.0
MD	0.3	0.0	0.0	0.0	0.0	0.0	0.0
AM	0.0	0.0	0.0	0.0	0.0	0.0	0.0
FD	0.5	1.4	1.6	0.4	0.0	0.0	0.6
GI	0.0	0.0	0.0	0.0	0.0	0.0	0.0
GO	0.0	0.0	0.0	0.0	0.0	0.0	0.0
N	3	3	8	5	5	5	5

TABLE 13: RELATIVE FREQUENCIES OF BEHAVIOURS FOR FEMALE G.SETZERI
IN ENCOUNTERS WITH OTHER SPECIES AND SEXES.

	<u>G.s.</u> ♀ dom	<u>G.s.</u> ♀ sub	<u>G.s.</u> ♂	<u>G.p.p.</u> ♀	<u>G.p.p.</u> ♂	<u>G.t.</u> ♀	<u>G.t.</u> ♂
AD	15.0	16.3	19.2	19.6	20.8	26.0	18.9
XX	0.2	0.4	0.6	0.9	2.0	0.2	1.4
DR	0.0	0.0	0.2	2.8	2.5	1.9	1.0
AP	11.4	7.7	9.1	7.5	8.6	8.2	4.8
SN	8.3	7.7	2.9	4.7	9.7	5.1	4.0
EX	18.9	13.5	13.8	7.1	18.7	13.5	15.7
MA	5.6	3.2	4.4	9.8	13.5	6.4	11.9
SI	0.6	0.1	0.6	0.6	0.3	0.0	0.8
EA	0.5	0.0	0.2	0.0	0.0	0.2	0.0
GS	1.2	0.4	0.8	0.9	0.7	0.7	0.9
SB	1.7	0.8	2.1	1.3	1.8	0.4	1.9
AL	6.6	1.0	2.5	2.6	3.7	0.9	1.4
AT	10.4	0.6	4.5	0.3	2.2	0.0	0.3
CH	11.9	0.0	4.9	0.0	3.1	0.2	0.0
FI	0.9	0.8	0.8	0.4	0.0	0.0	0.0
UP	2.0	1.8	0.8	0.0	1.7	0.2	0.5
ST	1.5	0.6	0.2	0.2	1.9	0.5	2.0
TH	0.0	0.0	0.0	0.0	0.0	0.0	0.0
EL	0.2	13.6	7.4	10.0	3.5	12.8	9.6
FL	0.0	17.8	13.9	18.8	2.9	15.9	14.7
CR	0.0	8.7	9.2	11.8	0.4	5.7	9.4
VO	0.0	0.0	0.0	0.0	0.0	0.0	0.0
AE	1.2	0.8	1.7	0.2	0.6	1.0	0.2
SA	0.3	1.4	0.0	0.0	0.4	0.1	0.1
MO	0.2	0.1	0.0	0.0	0.0	0.0	0.0
AM	0.3	0.1	0.0	0.0	0.0	0.0	0.0
FO	1.2	1.9	0.2	0.4	1.0	0.0	0.3
GI	0.2	0.1	0.0	0.0	0.0	0.0	0.0
GO	0.2	0.3	0.0	0.0	0.0	0.0	0.0
N	4	4	8	5	5	5	5

TABLE 14: RELATIVE FREQUENCIES OF BEHAVIOURS FOR G.VALLINUS
AND G.P.PAEBI IN ENCOUNTERS WITH OTHER SPECIES AND
SEXES.

	<u>G.v.v.</u> <u>♂ dom</u>	<u>G.v.v.</u> vs <u>G.v.v.</u> <u>♂ sub</u>	<u>G.v.v.</u> vs <u>G.v.v.</u> ♀	<u>G.p.p.</u> <u>♂</u>	<u>G.p.p.</u> <u>♀</u>	<u>G.p.p.</u> ♂ vs <u>G.v.v.</u> <u>♂</u>	<u>G.p.p.</u> ♀ vs <u>G.v.v.</u> ♀
AD	14.4	19.4	22.6	27.9	27.8	13.6	18.9
XX	0.0	0.0	0.0	0.0	0.0	0.0	0.0
DR	0.0	0.0	0.0	0.0	0.4	0.0	0.0
AP	10.1	2.7	2.7	11.6	15.6	8.3	5.3
SN	9.2	11.7	14.2	6.3	6.5	5.8	7.6
EX	9.8	7.7	4.0	6.6	10.3	15.2	11.4
MA	8.9	9.0	5.8	1.6	2.7	8.3	9.8
SI	0.9	5.4	4.9	0.9	3.8	0.6	0.0
EA	0.0	0.0	0.0	0.0	0.4	0.0	0.0
GS	1.8	0.0	2.2	1.9	2.7	1.4	1.5
SB	0.0	0.0	2.2	0.3	0.0	0.0	0.0
AL	0.0	0.0	0.0	0.3	0.8	0.6	0.7
AT	6.1	0.0	4.9	10.7	8.0	0.3	0.0
CH	0.0	0.0	0.0	10.3	4.6	0.0	0.0
UP	8.9	12.6	4.9	7.2	3.0	7.2	3.4
FI	0.6	0.9	0.0	2.5	1.1	2.2	1.1
ST	0.9	1.4	0.0	3.4	1.1	2.5	3.0
TH	1.8	0.5	0.4	2.2	1.9	0.0	0.4
EL	0.0	0.0	0.0	0.0	0.0	7.8	11.0
FL	0.0	0.0	0.0	0.0	0.0	13.9	9.8
CR	0.0	6.8	4.0	0.0	0.0	8.0	11.0
VD	0.0	0.0	0.0	0.0	0.0	0.0	0.0
AE	0.3	0.9	1.3	0.3	1.9	2.2	3.4
SA	7.4	4.5	5.8	0.0	1.1	0.8	1.1
MO	0.9	0.0	0.0	0.0	0.0	0.3	0.0
AM	0.9	0.0	0.9	0.0	0.0	1.1	0.0
FD	4.9	6.8	4.0	6.0	3.0	0.0	0.4
GI	11.0	9.5	14.6	0.0	3.4	0.0	0.0
GO	0.9	0.0	0.0	0.0	0.0	0.0	0.0
N	3	3	3	3	3	3	3

TABLE 15: RELATIVE FREQUENCIES OF BEHAVIOURS FOR MALE AND FEMALE G.P.EXILIS IN ENCOUNTERS WITH OTHER SEXES AND SPECIES.

	<u>G.P.EXILIS</u> MALES VS.			<u>G.P.EXILIS</u> FEMALES VS.				
	<u>G.p.e.</u> ♀	<u>G.p.p.</u> ♂	<u>G.p.p.</u> ♀	<u>G.p.e.</u> ♀ dom	<u>G.p.e.</u> ♀ sub	<u>G.p.e.</u> ♂	<u>G.p.p.</u> ♀	<u>G.p.p.</u> ♂
AD	7.7	18.8	14.9	15.9	12.7	8.6	21.8	24.5
XX	0.2	0.4	0.3	1.2	0.5	0.5	1.7	2.2
DR	0.4	0.0	0.0	0.1	0.0	0.0	0.0	0.0
AP	5.2	6.6	6.1	13.5	5.2	9.5	6.2	6.8
SN	8.1	10.5	9.9	3.2	3.5	6.5	9.0	8.5
EX	7.5	10.7	12.8	14.7	9.1	10.8	16.0	12.9
MA	6.5	16.1	8.8	2.0	6.8	11.6	12.0	11.2
SI	1.5	2.4	0.2	0.4	0.0	0.8	1.4	2.5
EA	0.6	1.1	0.3	1.4	0.5	0.8	0.4	1.2
GS	0.7	0.9	0.7	1.1	0.5	0.7	1.4	2.0
SB	0.0	0.0	0.0	0.7	0.1	0.3	0.6	1.2
AL	2.5	1.5	0.2	2.0	0.5	5.4	1.7	1.1
AT	1.0	0.4	0.0	12.1	0.8	10.3	3.2	4.2
CH	1.5	0.2	0.0	15.1	0.5	7.3	1.7	5.4
FI	4.9	2.1	1.7	3.6	4.0	4.6	2.3	0.8
UP	9.3	6.0	1.9	1.7	1.9	8.0	1.8	0.9
ST	1.0	0.2	0.2	7.1	2.7	3.5	1.7	6.3
TH	0.2	0.6	0.0	0.2	0.1	0.2	0.4	0.5
EL	6.2	0.0	6.6	0.2	10.4	0.3	1.9	0.2
FL	11.2	3.4	14.4	0.7	24.6	2.2	4.0	0.2
CR	7.3	5.3	14.9	0.0	13.8	1.9	4.8	1.7
VD	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
AE	0.5	0.8	0.5	0.2	0.5	0.4	1.2	0.9
SA	4.6	4.3	2.1	0.5	0.3	1.9	0.8	0.3
MD	0.4	0.0	0.0	0.0	0.0	0.0	0.1	0.2
AM	0.7	0.0	0.0	0.0	0.0	0.1	0.1	0.0
FD	8.9	5.1	2.4	2.1	0.9	3.2	3.6	2.9
GI	0.4	2.6	1.2	0.0	0.0	0.3	0.3	0.0
GD	1.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0
N	8	5	5	5	5	8	5	5

Results of observations in territoriality apparatus.

TABLE 18: TIME SPENT IN EACH AREA OF THE TERRITORIALITY APPARATUS. TOTAL TIME IS GIVEN IN SECONDS: THE ACTUAL TIME SPENT IN EACH AREA IS EXPRESSED AS A PERCENTAGE OF THE TOTAL OBSERVATION TIME.

SPECIES & SEX	NO. OF ANIMAL	TOTAL TIME	BOXES				
			A	B	C	D	CENTRE
<i>G. tytonis</i>	42	2100	5	10	30	9	46
females	47	2100	22	8	26	5	33
I	10	2100	5	8	26	30	31
	5	2100	0	100	0	0	0
	10	2700	1	6	74	16	2
	11	2700	100	0	0	0	0
II	7	2700	0	1	57	37	6
	40	2700	23	64	0	0	13
<i>G.p. paeba</i>	31	2100	0	2	0	86	13
females	52	2100	59	17	2	1	17
I	27	600	0	100	0	0	0
	32	2100	2	21	72	0	5
	15	3600	13	8	19	44	11
II	18	3600	30	13	21	1	35
	23	3600	20	7	4	33	35
	21	3600	16	3	7	64	11
<i>G. setzeri</i>	12	2700	12	60	27	0	1
females	8	2700	24	16	44	12	5
	9	2700	28	21	28	2	21
	10	2700	12	61	25	0	1
	9	2100	9	6	0	86	0
	8	2100	85	0	0	0	15
	11	2100	14	86	0	0	0
	12	2100	0	86	14	0	0
<i>G. tytonis</i>	39	3000	26	26	16	5	2
males	41	3000	30	0	31	39	0
I	38	3000	35	10	21	22	11
	12	3000	48	4	12	31	5
	37	2100	4	8	17	48	24
II	41	2100	7	11	10	32	40
	12	2100	0	28	40	20	11
	6	2100	20	26	35	1	19
<i>G.p. paeba</i>	19	3000	0	0	100	0	0
males	17	3000	14	33	3	27	23
I	28	3000	13	4	3	29	52
	30	3000	18	35	3	25	18
	28	1800	0	0	81	1	18
II	29	1800	0	80	0	0	20
	34	1500	16	21	12	30	18
	48	1800	0	0	76	1	20
<i>G. setzeri</i>	7	2100	87	0	1	0	12
males	1	2100	86	14	0	0	0
	3	2100	79	1	14	0	5
	6	2100	50	0	7	29	14

I = first experiment

II = replicate

TABLE 19: RESULTS OF CHI-SQUARE TEST FOR THE NULL HYPOTHESIS THAT EACH ANIMAL OCCUPIES ONLY ITS ORIGINAL AREA AND COMMON CENTRAL AREA.

SPECIES & SEX	NO. OF ANIMAL	ACTUAL TIME	EXPECTED TIME	χ^2
<i>G. tytonis</i> females	42	1592***	2100	122.65
I	47	1149***	2100	430.21
	10	1288***	2100	313.59
	5	2100	2100	0
II	40	2079	2700	142.60
	11	2700	2700	0
	7	1150***	2700	889.24
	10	2048***	2700	157.20
<i>G.p. paeba</i> females	31	2083	2100	0.13
I	52	1588***	2100	124.59
	27	600	600	0
	32	1621***	2100	109.03
II	15	679***	3600	2369.26
	18	2013***	3600	699.16
	23	2004***	3600	707.12
	21	2700***	3600	224.75
<i>G. setzeri</i> females	9	121***	2100	1864.03
I	8	2089	2100	0.05
	11	0***	2100	2100
	12	0***	2100	2100
II	9	623***	2700	1596.98
	8	567***	2700	1684.28
	10	687***	2700	1500.06
	12	358***	2700	2030.60
<i>G. tytonis</i> males	39	836***	3000	1560.24
I	41	931***	3000	1426.23
	38	990***	3000	1346.03
	12	1594***	3000	658.48
II	37	585***	2100	1092.24
	41	1518***	2100	161.02
	12	1070***	2100	504.70
	6	942***	2100	638.00
<i>G.p. paeba</i> males	28	1770	1800	0.48
I	29	1800	1800	0
	34	551***	1500	599.77
	48	365***	1800	1143.22
II	19	0***	3000	3000
	17	1104***	3000	1197.64
	28	1622***	3000	632.50
	30	1308***	3000	953.72
<i>G. setzeri</i> males	7	2082	2100	0.15
	1	0***	2100	2100
	3	106***	2100	1892.40
	6	303***	2100	1536.86

*** = $p < 0.001$; I = first experiment; II = replicate

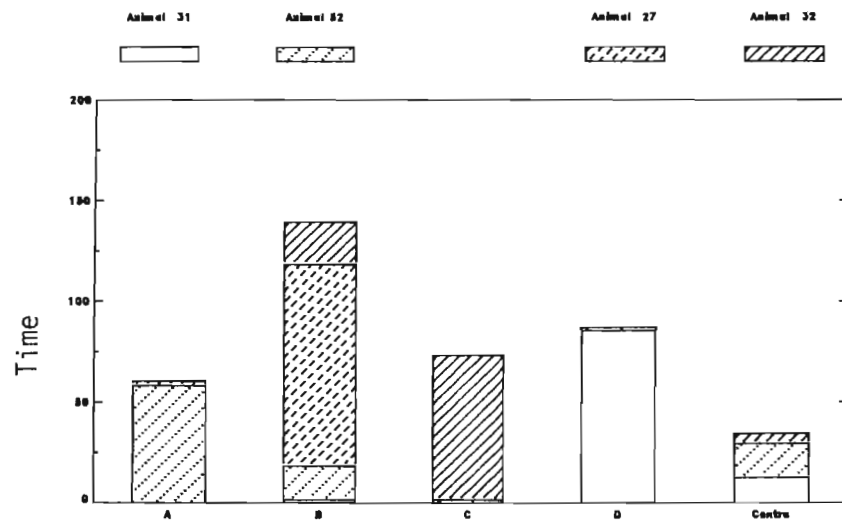


Fig. 60. Female *G.p. paeba I*

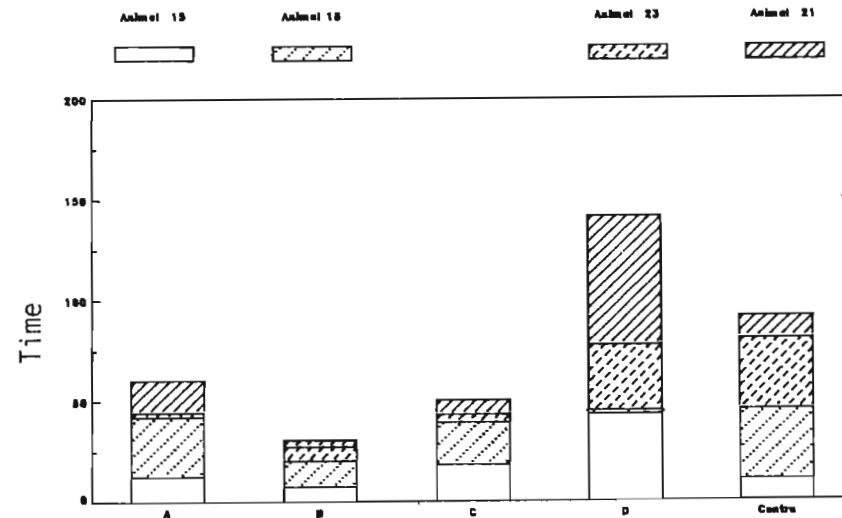


Fig. 61. Female *G.p. paeba II*

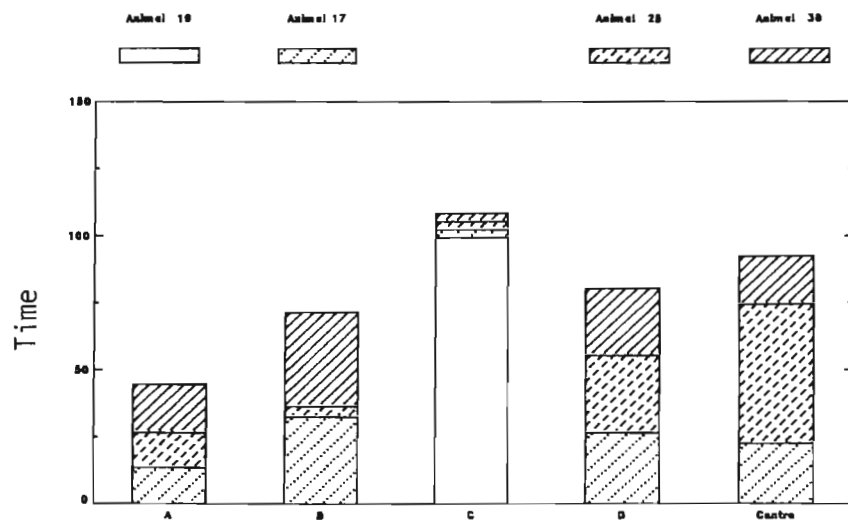


Fig. 62. Male *G.p. paeba I*

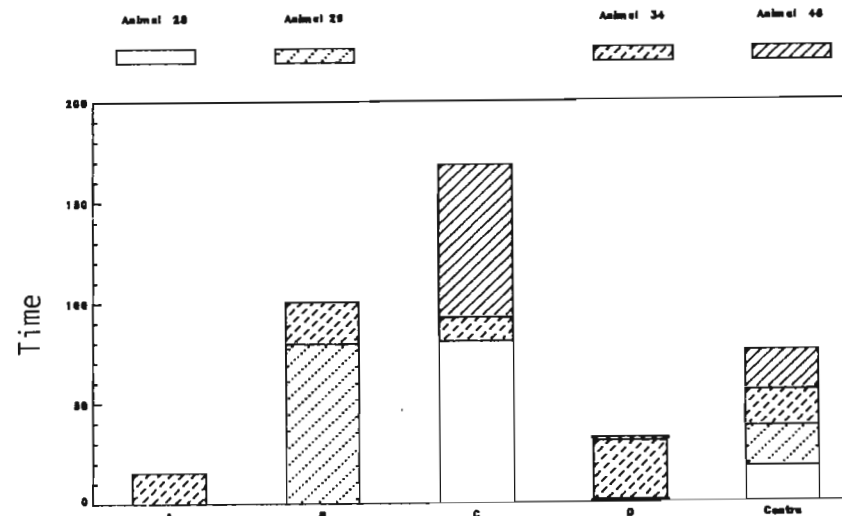


Fig. 63. Male *G.p. paeba II*

NOTE: Figures 60-70 illustrate time spent in each area of the territoriality apparatus. Time is represented as a percentage of the total observation time.

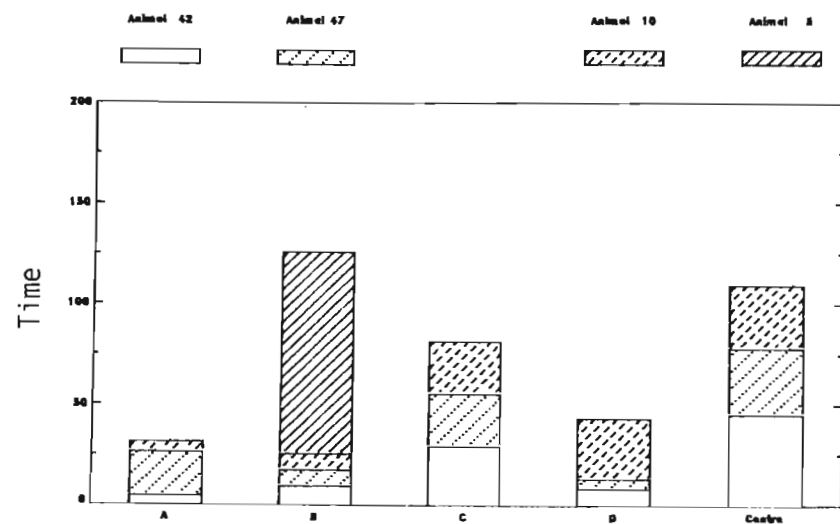


Fig. 64. Female *G. tytonis* I

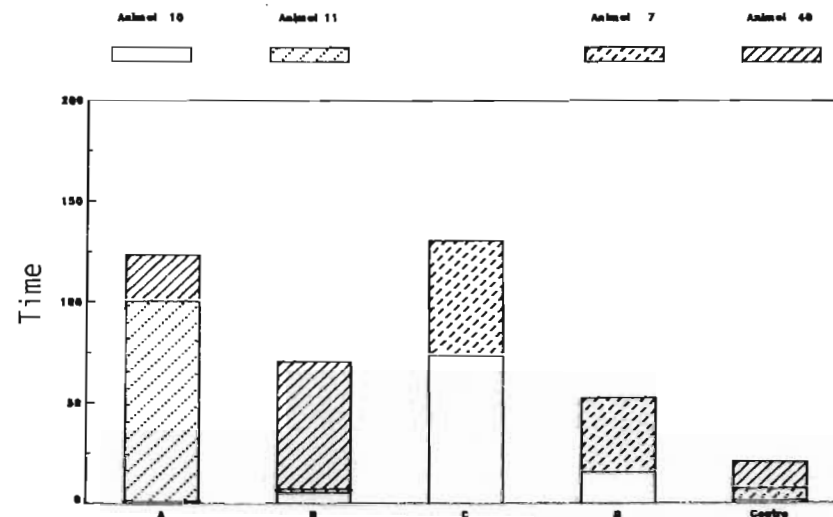


Fig. 65. Female *G. tytonis* II

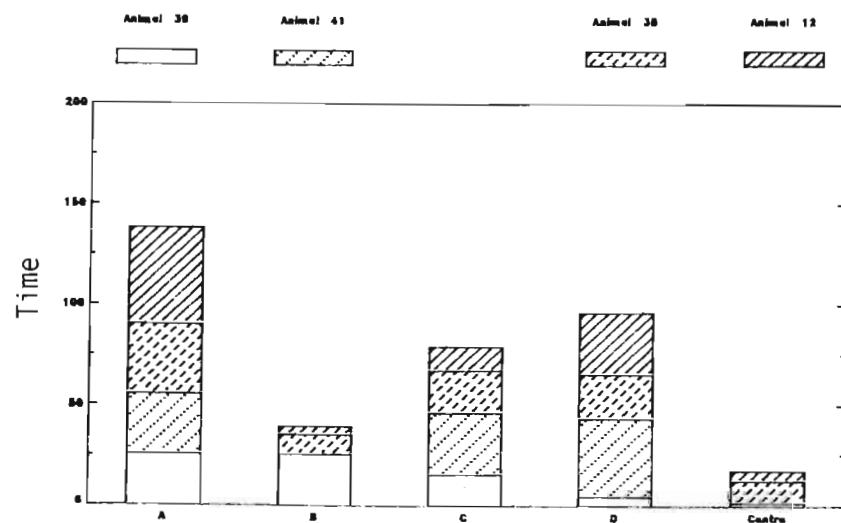


Fig. 66. Male *G. tytonis* I

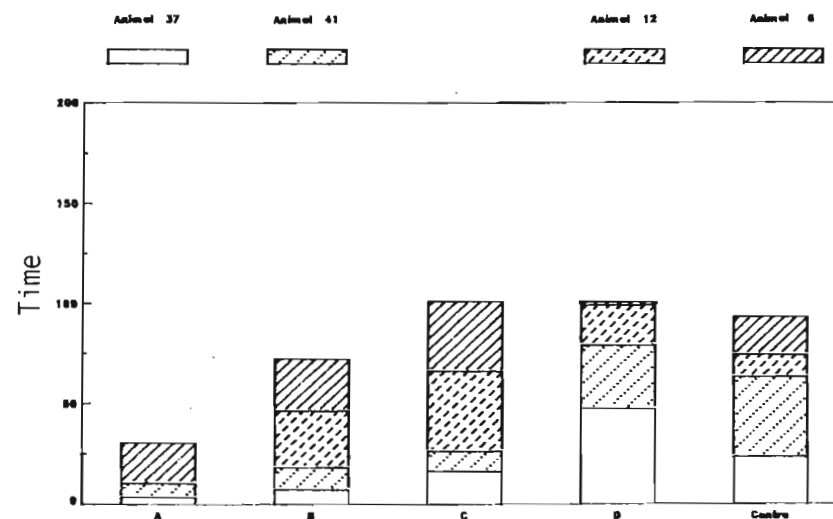


Fig. 67. Male *G. tytonis* II

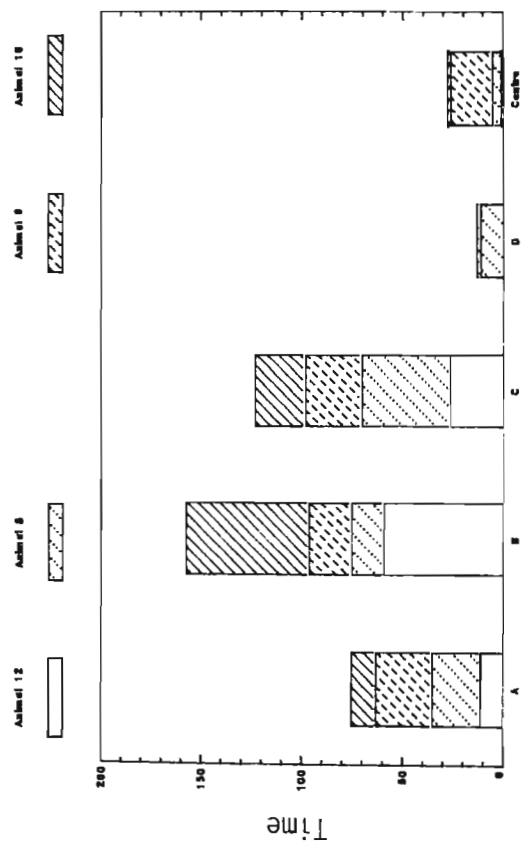


Fig. 68. Female *G. setzeri* I

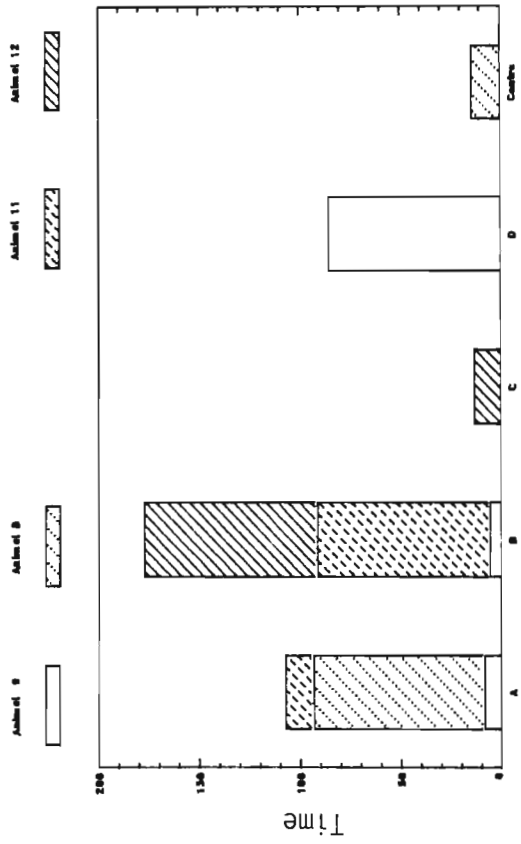


Fig. 69. Female *G. setzeri* II

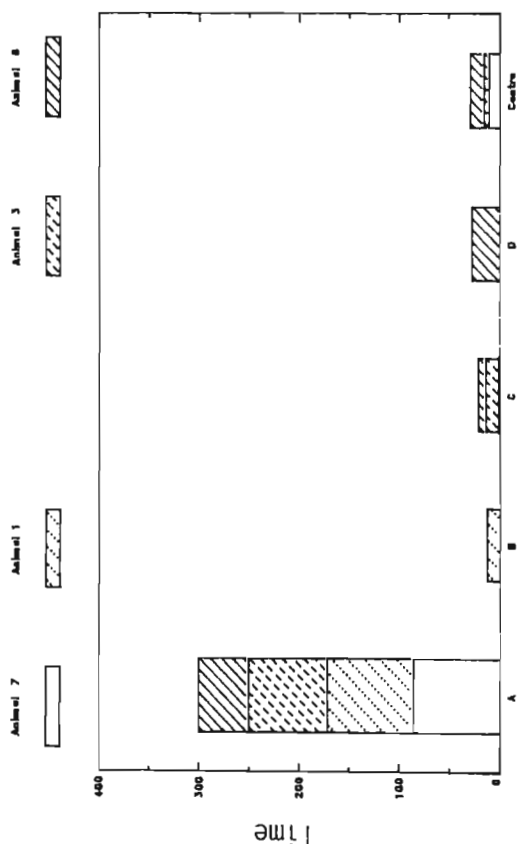


Fig. 70. Male *G. setzeri*

APPENDIX 4: Maternal behaviour and neonatal development in
three species of Namib Desert rodents (paper
in prep.).

CAPTIONS FOR FIGURES

- Figure 1 Growth in mass of G. paeba (—; n = 21), G. tytonis (.....; n = 16) and P. collinus (— · —; n = 19).
- Figure 2 Growth in head-body length of G. paeba (—; n = 6), G. tytonis (.....; n = 11) and P. collinus (— · —; n = 11).
- Figure 3 Growth in tail length of G. paeba (—; n = 6), G. tytonis (.....; n = 11) and P. collinus (— · —; n = 11).
- Figure 4 Growth in hindfoot length of G. paeba (—; n = 6), G. tytonis (.....; n = 11) and P. collinus (— · —; n = 11).
- Figure 5 Relative birth mass versus adult mass for seven Cricetid rodents.
- Figure 6 Relative growth rate in mass versus adult mass for seven Cricetid rodents. See text for calculation of growth rates.
- Figure 7 G. paeba 13-day-old pup.
- Figure 8 G. tytonis 20-day-old young.
- Figure 9 P. collinus female with nipple-clinging young.
- Figure 10 "Mouth-licking" in P. collinus.
- Figure 11 G. tytonis female brooding young.

MATERNAL BEHAVIOUR AND NEONATAL DEVELOPMENT

IN THREE SPECIES OF NAMIB DESERT RODENTS

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ABSTRACT

Gerbillurus paeba paeba, *G.tytonis* and *Petromyscus collinus* inhabit arid areas of southern Africa. Seven litters of each of the *Gerbillurus* species and eight litters of *P.collinus* were bred in the laboratory; aspects of maternal behaviour and development of neonates are reported in this paper. Maternal behaviour involves brooding the young, grooming them and ingesting faeces and urine. *P. collinus* mothers defend their young, whereas *G. paeba* and *G. tytonis* do not.

P.collinus has a smaller litter size and the young are more precocial at birth than young of *G. paeba* or *G. tytonis*. Growth rates relative to adult size are slowest in *G.tytonis* for all physical parameters measured. *P.collinus* has the highest relative growth rate in head-body and hindfoot length, while *G.paeba* increases most rapidly in mass and tail length. Rate of physical and behavioural development is highest in *P. collinus*, intermediate in *G. paeba* and lowest in *G. tytonis*. Young of *P. collinus* nipple-cling from birth, but those of *G. paeba* and *G. tytonis* do not. In comparison with other members of the subfamily Gerbillinae, *G. paeba paeba* and *G. tytonis* are more precocial at birth than *Tatera leucogaster*, *T. brantsii* or

Desmodillus auricularis, and the last three species have lower relative rates of growth in all physical parameters measured.

G. paeba exilis differs from *G. paeba paeba* in having young which nipple-cling, smaller litter size, and relatively longer tail and hindfoot measurements at birth.

G. paeba and *G. tytonis* are r-selected in terms of reproductive strategies, indicating that they perceive the desert environment as being unfavourable. *P. collinus* is considered to be more arid-zone adapted than the *Gerbillurus* species, as reflected in its more K-selected reproductive strategem. Nipple-clinging is associated with surface-nesting animals which are more exposed to predation than burrowing animals.

SAMEVATTING

Gerbillurus paeba paeba, *G. tytonis* en *Petromyscus collinus* bewoon droë streke van suider Afrika. Sewe werpsels elk van die *Gerbillurus* spesies en agt werpsels van *P. collinus* is in die laboratorium geteel; aspekte van moederlike gedrag en ontwikkeling van pasgeborenes word in hierdie artikel berig. Moederlike gedrag behels broei van kleintjies, hulle versorging en opname van faeces en urine. *P. collinus* wyfies verdedig hulle kleintjies, in teenstelling met die van *G. paeba* en *G. tytonis*.

P. collinus het 'n kleiner werpsel en die kleintjies is meer jonkselstandig by geboorte as die kleintjies van *G. paeba* of *G. tytonis*. Groeitempo relatief tot volwasse grootte is stadigste in *G. tytonis* vir alle fisiese parameters gemeet. *P. collinus* het die hoogste relatiewe groeitempo in kop-liggaam en

agtervoet lengte, terwyl *G.paeba* die vinnigste in massa en stert lengte toeneem. Die tempo van fisiese- en gedragsontwikkeling is die hoogste in *P.collinus*, intermediër in *G.paeba*, en die laagste in *G.tytonis*. Kleintjies van *P.collinus* klou aan 'n tepel vanaf geboorte, maar nie die van *G.paeba* en *G.tytonis* nie. In teenstelling met ander lede van die subfamilie Gerbillinae, is *G.paeba paeba* en *G.tytonis* meer jonkselstandig by geboorte as *Tatera leucogaster*, *T.brantsii* of *Desmodillus auricularis*, en laasgenoemde drie spesies het laer relatiewe groeitempo's in alle fisiese parameters gemeet. *G.paeba exilis* verskil van *G.paeba paeba* daarin dat hulle kleintjies het wat tepel-klou, 'n kleiner werpsel, en relatief langer agtervoet en stert afmetings by geboorte het.

G.paeba en *G.tytonis* is r-selektief in terme van reprodusktiewe strategieë, wat aandui dat hulle die woestyn omgewing as ongunstig waarneem. *P.collinus* word beskou as beter aangepas by droë streke as die *Gerbillurus* spesies, soos gesien kan word aan hulle meer K-selektiewe voortplantingstrategie. Tepel-klou word geassosieër met diere in bo-grondse neste wat meer aan predasie blootgestel is as grawende diere.

INTRODUCTION

Lack of water, scarcity of food and extremes of temperature are a few of the adverse environmental conditions experienced by desert animals. These unfavourable conditions must be overcome before breeding, with its associated additional physiological stress on the female, can be successfully achieved. Young must be protected from the hostile environment and from predators until they are able to survive independently. A knowledge of the seasonality of breeding and numbers of young per litter can be gained from trapping animals at regular intervals in the field. This information can be supplemented with studies on the maternal behaviour and development of the young, a subject which in rodents, is best studied in the laboratory. A comparison of the reproductive strategies adopted by different species in similar environments can reveal significant differences, which may be related to the phylogeny of the species, and/or to the demography of the populations from which they have come. The plasticity of reproductive strategies within a species, genus or subfamily can be elucidated by comparing these strategies in separate populations of one species, between species, or between genera.

In this study, the maternal behaviour and neonatal development of three species of rodents which inhabit the Namib Desert are described and compared with information of other species belonging to several genera within the family Cricetidae, and with similar information on an isolated population of one of the species.

Gerbillurus paeba paeba, the pigmy hairy-footed gerbil, is known to occur throughout the arid and semi-arid areas of Southern Africa (De Graaff, 1981). It is generally not found in the central or western parts of the Namib dunefield, where *G.tytonis* is common (Boyer, pers.comm.*). An isolated population, *G.p.exilis* occurs in the Alexandria dunefield north of Port Elizabeth. The ecology of this subspecies and its neonatal development has been described by Ascaray (1984). *G.p.paeba* has been kept in the laboratory, and its general behaviour and breeding has been described (Stutterheim & Skinner, 1973). Hallett and Keogh (1971) were unsuccessful in breeding *G.p.coombsi* in the laboratory, while Els (1984) examined the histology of the reproductive tract of *G.paeba*. This species exhibits large fluctuations in population density in the Southern Kalahari and inhabits a wide range of habitats (Nel & Rautenbach, 1975). In the Namib Desert, Christian (1979) found that *G.paeba* was a seasonal breeder, and that provision of extra drinking water extended the breeding season beyond that of a control group.

G. tytonis, the dune hairy-footed gerbil, has only been found on the shifting red sand dunes south of the Kuiseb River (Boyer, pers. comm.; De Graaff, 1981). Both *G.paeba* and *G.tytonis* are bipedal saltatorial rodents, but *G.tytonis* has longer hindfeet and toes than *G.paeba*. This species has not previously been kept in the laboratory, and is poorly represented in the literature.

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The pigmy rock mouse, *Petromyscus collinus*, inhabits areas where rocks and boulders predominate throughout the South West arid zone (De Graaff, 1981). Withers (1983) reported that *P. collinus* is a seasonal breeder, and suggested that only one litter consisting of two to three young is produced per year. *P. collinus* can survive on a diet of air-dried seeds and has a low water turnover rate (Withers, Louw and Henschel, 1980).

METHODS AND MATERIALS

Specimens of the hairy-footed gerbils, *G. paeba paeba* and *G. tytonis* were trapped south of Gobabeb in the Namib Desert in August, 1984, while the *P. collinus* were trapped near Wereldsend in Damaraland on the same excursion. All rodents captured were intended for use in comparative behavioural and physiological studies. When breeding commenced in December, 1984, records were kept of the development of the young and maternal behaviour, which is reported here.

Gerbils were initially housed in pairs in laboratory cages, but no breeding took place. Later, several pairs were maintained in glass aquaria (60 x 30 x 30cm) provided with sand and a nesting box (plastic bottle); in two tanks an artificial tunnel was created to provide a more natural environment and to permit viewing of the young (Eisenberg, 1963). Rock mice were housed in laboratory cages/aquaria provided with sand and a nest box. Grass or cotton waste was provided as nest material.

Gerbils and mice were fed on a mixture of sunflower seeds, wild bird seed, oats and "Pronutro*". This diet was supplemented

* Commercial balanced diet

with carrots, apples, grass and insects: water was provided ad libitum. The animals were maintained at 25°C in reversed daylight, the cycle being 16h L:8h D.

Females were removed from males when a pregnancy was obvious. Young were weighed at intervals of 1 to 6 days on a Mettler balance, accurate to 0.1g. In some litters, the standard body measurements of head and body length, tail length and hindfoot length were also made by using a ruler accurate to 1.0mm. A problem was experienced in the derivation of growth curves, since individual litters were not measured at the same ages, nor were records kept for individual pups. To overcome this problem, the measurements of individual pups within a litter were summed for each day on which they were measured. Graphs were then drawn for the sum of the measurements within each litter. Measurements summed for all litters were divided by the total number of pups to obtain an average value. This method was used to calculate growth curves for mass, head-body length, tail length and hindfoot length.

Growth rate was calculated using the method described by Case (1978) for the relatively linear phase of growth from about 10% of adult body mass to approximately 50% of adult body mass. Similarly, growth rates for head-body length and hindfoot length were calculated for growth from 40% to 70% adult body length, and for tail length from 16% to 50% of adult body length, such that

$$G = \frac{M_e - M_b}{A_e - A_b}$$

where G = growth rate (g/day or mm/day)

Me = measurement (g or mm) at end of growth period

Mb = measurement (g or mm) at beginning of growth period

Ae = Age (days) at end of growth period

Ab = Age (days) at beginning of growth period

Growth rate was scaled to adult body size by dividing the growth rate by the average adult measurement.

Physical development was assessed on the days of weighing. Developmental criteria used in assessing the level of physical development were as follows: ear pinnae free or attached; toes fused or separated; hair proliferation, i.e. a dark pigmentation was taken to represent the beginning of hair proliferation; eyes closed or open (Meester & Hallett, 1970).

Maternal behaviour and behaviour of the young was observed daily without disturbing the young, and when young were removed for weighing. Behaviour was recorded on videotape using a camera (JVC model TK1700EG) adapted for use at low light intensities. Tapes were transcribed later, greater accuracy being ensured by playing rapid action sequences at a slower speed (National Portable VCR NV-180). The results presented were gained from many hours of observations of several individuals.

RESULTS

Newly-paired gerbils generally behaved aggressively towards each other, with a great deal of chasing and fighting being observed. In 22 pairs of *G. pacha*, 12 were separated because the male had been wounded by the female, and in three further pairs, the male was killed by the female. Eight pregnancies

resulted from pairings of *G. paeba*. In 21 pairings of *G. tytonis*, one male was killed by a female, and six pairs were separated because males were wounded by females. Seven pairings resulted in pregnancies. In one *P. collinus* pair a female was removed when it was noticed that she had wounds on her tail and rump.

Table 1 gives details of litters born between December 1984 and February 1986. Mating was never observed, so the gestation period could not be determined. The shortest interval between pairing and the birth of young was 27 days for *G. paeba* and 24 days for *G. tytonis*. Since males were removed before the birth of young and they were not replaced until the young were weaned, the minimum interval between litters could not be determined. The shortest interval between litters was 65 days for *G. paeba*, 64 days for *G. tytonis* and 45 days for *P. collinus*. In the case of *P. collinus*, a female was mated by one of her own young and was found to be nesting with her previous litter and the new litter. A *P. collinus* female who was left with her mate continuously had an interval of 87 days between litters.

MATERNAL BEHAVIOUR

NEST-BUILDING

Mothers of each species did not seem to make any special preparations for the birth of the young. All animals, whether pregnant or not, made a nest when supplied with grass or cotton waste. The grass was cut into short lengths and carried into the

TABLE 1: LITTERS BORN DURING THE PERIOD DECEMBER 1984 TO FEBRUARY 1986

SPECIES	NUMBER OF FEMALE	LITTER NUMBER	DATE OF BIRTH	NO. OF YOUNG	NO. OF SURVIVORS
<u>G.paeba</u>	16	1	17/12/84	2	1
	18	2	12/01/85	5	5
	20	3	31/01/85	4	4
	16	4	21/02/85	5	5
	27	5	09/06/85	6	6
	52	6	09/10/85	4	0
	27	7	01/11/85	6	6
			Average:	4.6	
<u>G.tytonis</u>	11	1	24/01/85	4	0
	5	2	19/02/85	5	5
	5	3	27/05/85	5	5
	5	4	31/07/85	6	2
	40	5	03/02/86	5	0
	5	6	05/02/86	4	4
	47	7	11/02/86	2	1
			Average:	4.4	
<u>P.collinus</u>	1	1	28/02/85	2	2
	1	2	04/06/85	3	3
	2	3	28/07/85	2	2
	1	4	26/08/85	3	3
	1	5	01/10/85	3	3
	3	6	16/10/85	3	3
	1	7	11/12/85	3	0
	3	8	11/01/86	3	3
			Average:	2.8	

nest, where it was shredded and shaped into a cup, the animal using forepaws and nose to shape the nest. *P.collinus* made smaller nests of grass than the gerbils, but if given cotton wool they shaped this into a round cup-shaped nest. On three occasions, pregnant female *G. paeba* were found to have taken food into the nest. This was not seen in *G.tytonis* or *P.collinus*.

PARTURITION

Birth was observed on one occasion. A female *G.tytonis* was seen to be sitting in the nest bottle, eating a placenta, which she held in her forepaws. Three newborn young were visible in the nest. The female adopted a quadrupedal posture while her abdomen contracted strongly, after which she groomed her genital region and rested with her head on the ground. After four such contractions, the female sat up and began to groom the new-born pup and her own genital region. The placenta was consumed after the pup had been groomed. The female then groomed herself vigorously, after which she curled over the young and slept for about two hours, waking frequently and grooming herself and the young.

POSTNATAL BEHAVIOUR

Female gerbils were usually found in the nest, crouching over the young. In the brooding position, the young were under the female, while she had her hindfeet widely spaced and forepaws stretched over the young. This behaviour continued until the pups were 28-30 days old. When she left the nest, the female sometimes covered the young with grass and sand, and blocked the

entrance to the nest with sand. Some female *G. tytonis* and *G. paeba* displayed "agitated" behaviour for the first day or two after parturition, and moved the young several times. Mothers did not defend the young, but immediately left the nest if disturbed.

Nipple-clinging was not observed in *G. tytonis*, but frequently female *G. paeba*, when disturbed, rushed out of the nest with one or more young attached to the teats. The young released the teats or were detached by the mother and carried back to the nest. Female gerbils mouth-carried their young, gripping them in the middle of the abdomen. As they became more mobile, the mother retrieved them by grasping them by the base of the tail, pulling them towards herself, and then carrying them back to the nest. The retrieval response waned when the young were 17-23 days old.

Female gerbils groomed their young frequently, holding them in the forepaws and licking and nibbling each pup. Licking the anogenital region seemed to stimulate urination and defaecation, and the mother ingested faeces and urine. Grooming continued as long as the young remained with the mother, mutual grooming becoming common between littermates and also between pups and mother. Females often reconstructed their nests while the young were present and this resulted in young being displaced from the nest along with nest material. The female then turned and retrieved the young and the nest material.

P. collinus young were firmly attached to the nipples immediately following birth and could only be detached with difficulty. With one exception, the mothers remained in the nest

when disturbed, and one mother defended her young by tooth-chattering and adopting a threatening posture when disturbed. The females were seldom seen to leave the nest, and hence it is not known whether they forage with the young attached to the teats. One female detached her young by grasping them in the middle of the abdomen and pulling them from the teats. All mothers mouth-carried their young if they were detached, and also retrieved older young which left the nest. The retrieval response waned after 21 days.

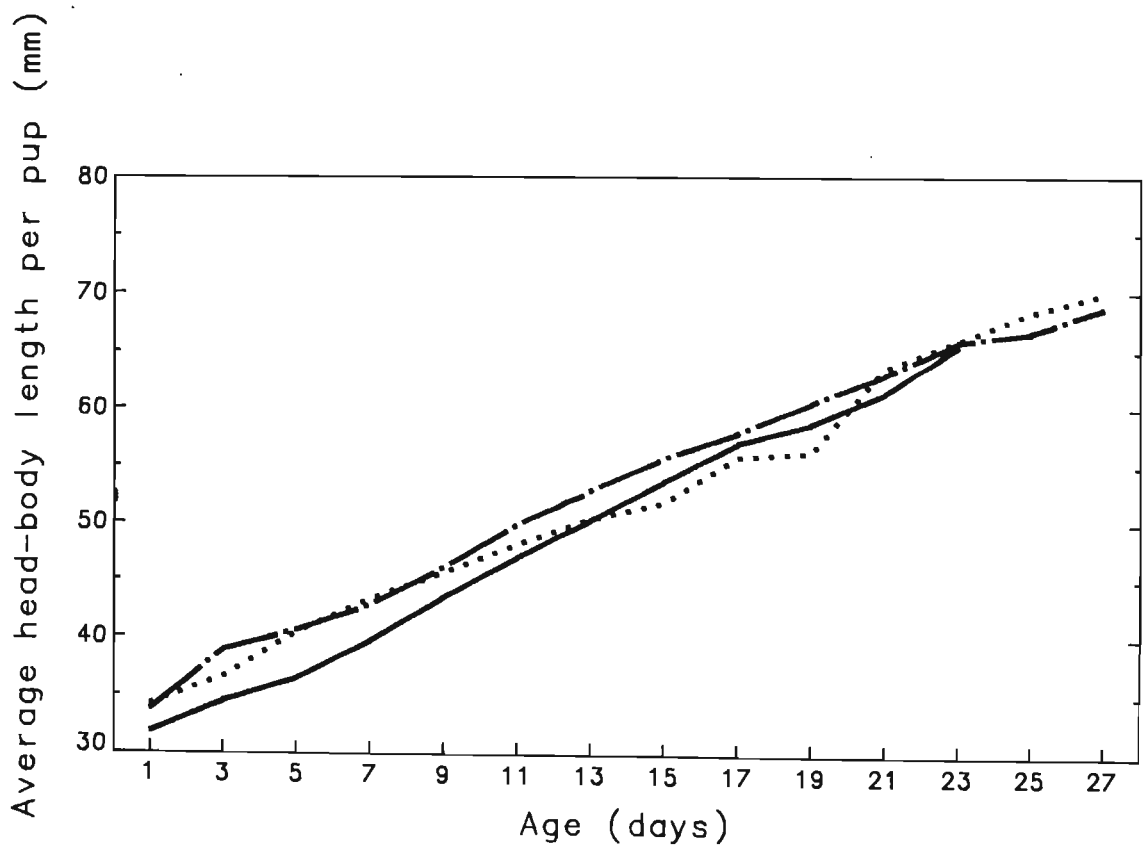
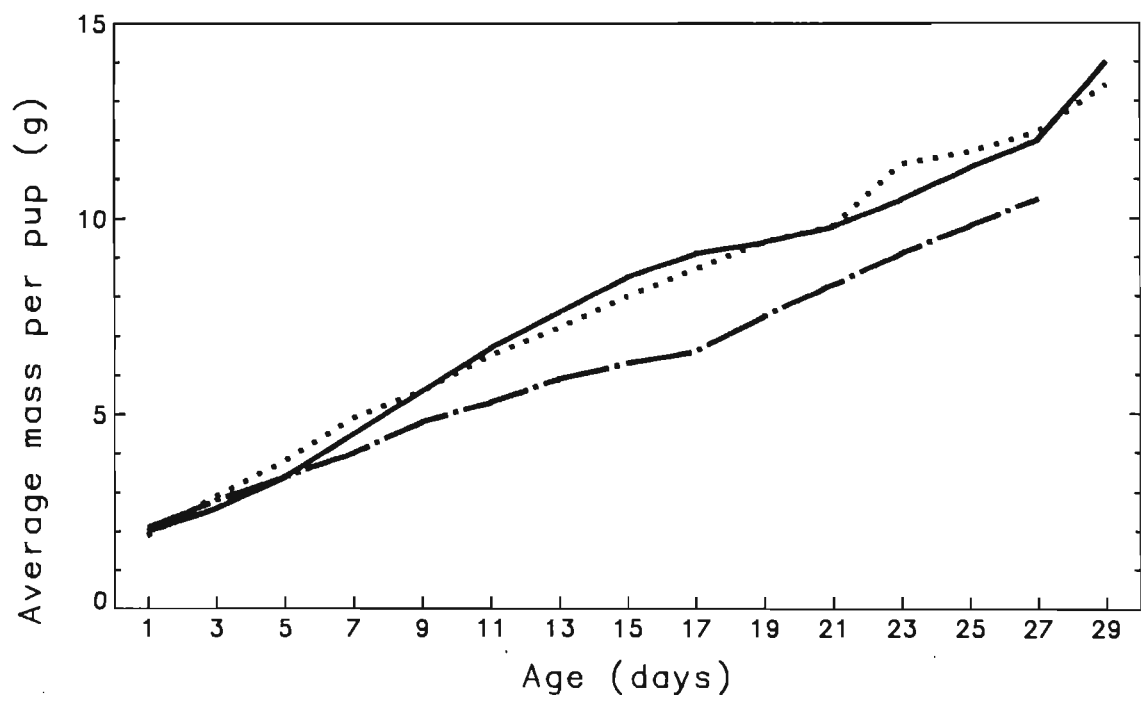
Grooming was rarely seen in *P. collinus*, most observations having been made when the young were returned to the nest after weighing. The mother licked and nibbled the young and cleaned the anogenital region while the young were attached to the teats.

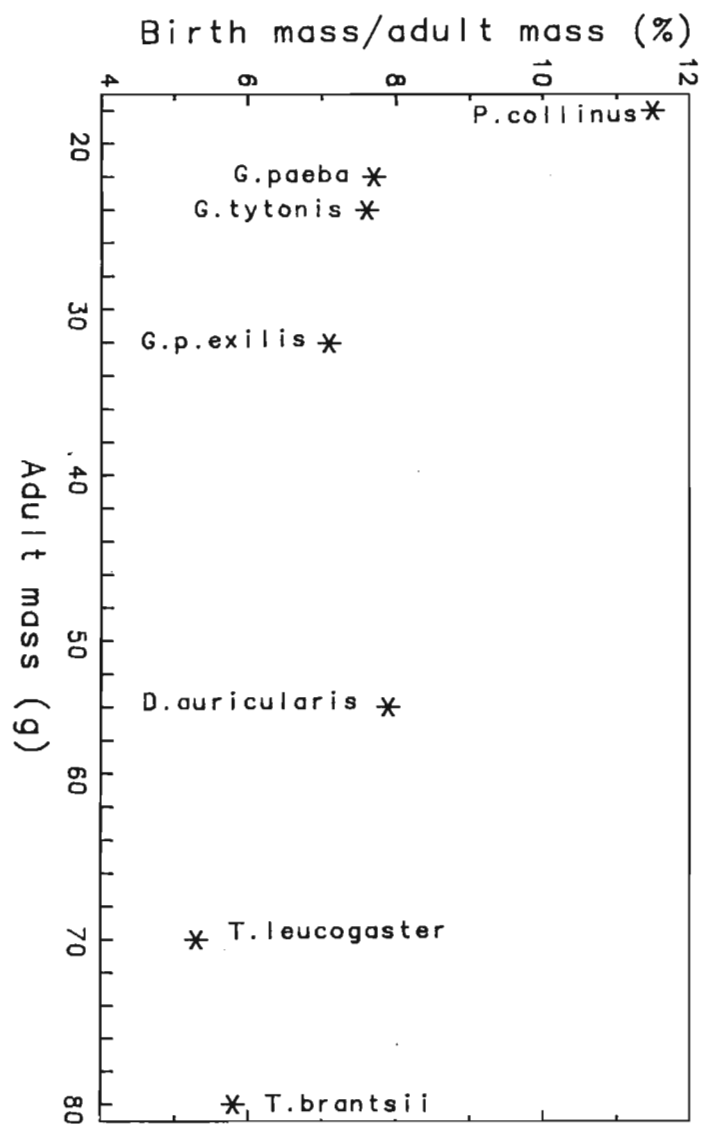
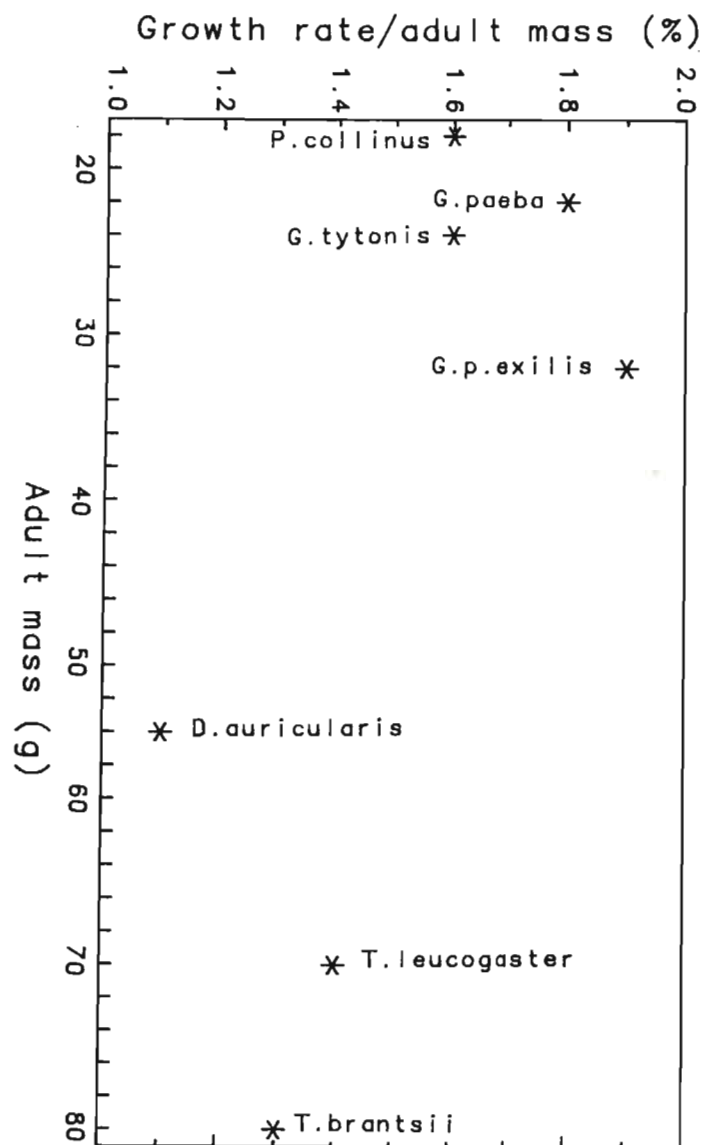
Male *P. collinus* who were left with the female after the birth of the young nested with the female and the litter, but were not seen to groom or retrieve young. Females did not show aggression towards males.

DEVELOPMENT OF THE YOUNG

GROWTH

Figures 1 to 4 show the growth in mass and body dimensions of the three species from day 1 to day 29. In figure 5, birth mass/adult mass is plotted against adult mass, and in figure 6, growth rate/adult mass is regressed against adult mass. Sizes of young at birth relative to adult body size are given in Table 2A and B. *G. paeba* and *G. tytonis* adult body mass, tail length and hindfoot length were taken from information supplied





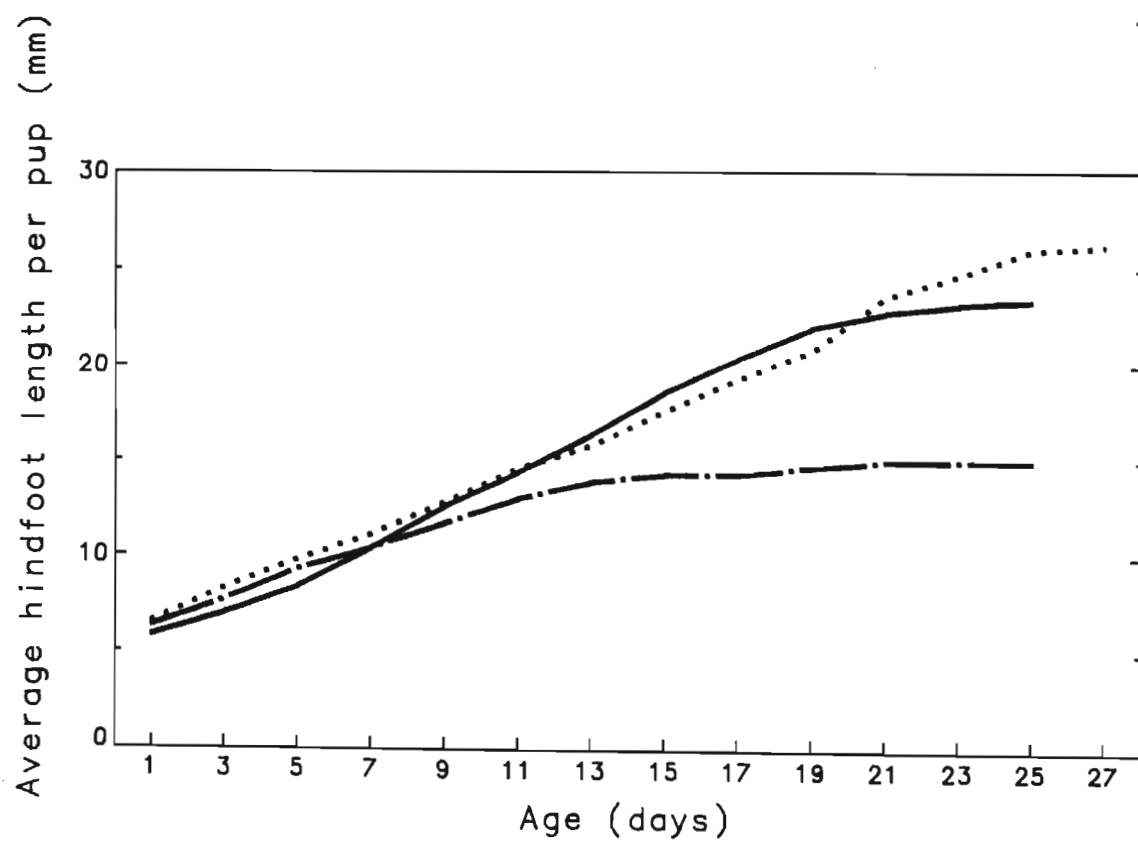
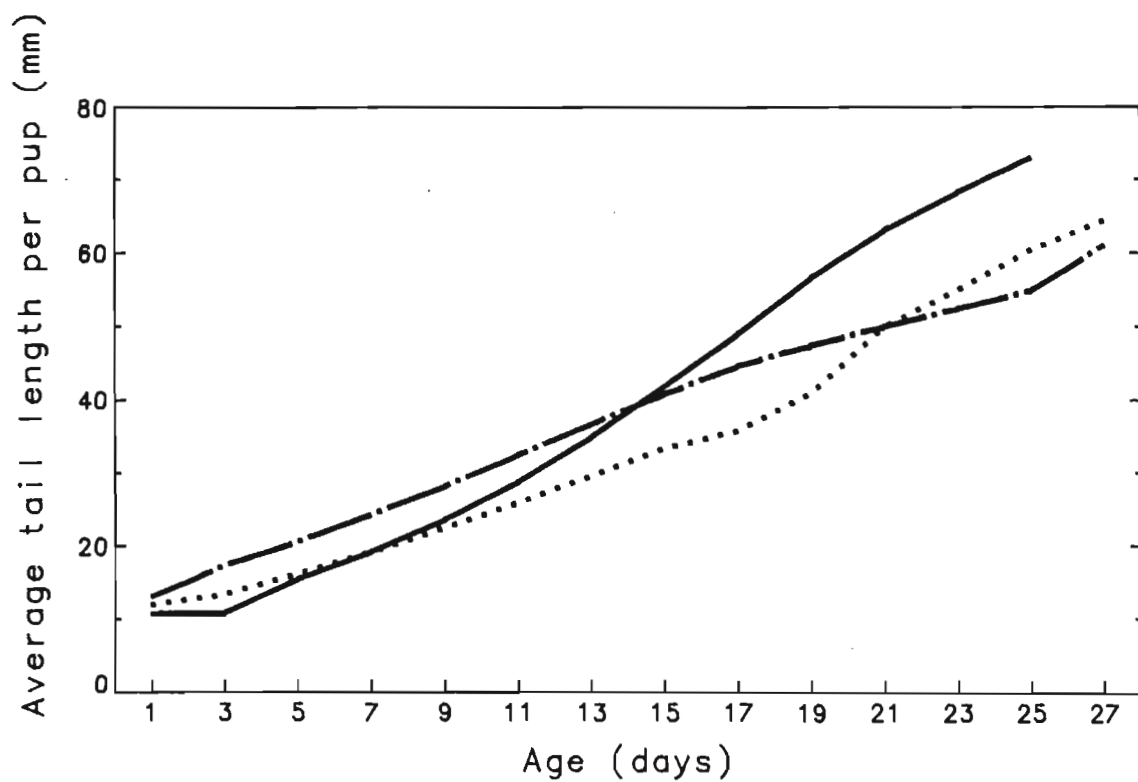


TABLE 2A: INDIVIDUAL MASS AND LITTER MASS AT BIRTH COMPARED WITH ADULT MEASUREMENTS.

SPECIES	MASS			SIZE	LITTER	
	\bar{x} BIRTH (g)	\bar{x} ADULT (g)	BIRTH ADULT %		MASS (g)	LITTER ADULT %
<u>P. collinus</u> ⁸	2.1 (5)	18.2 (10)	11.5	2.8 (7)	5.9	31.3
<u>G.p. paeba</u> ⁸	1.7(10)	22.0 ⁷ (177)	7.7	4.6 (7)	7.8	35.5
<u>G.p. exilis</u> ¹	2.3(21)	32.4(181)	7.1	3.7(11)	8.5	26.0
<u>G. tytonis</u> ⁸	1.9(22)	25.0 ⁷ (168)	7.6	4.4 (7)	8.4	33.4
<u>T. brantsii</u> ²	4.7(53)	80.0 ⁶ (130)	5.8	3.0(21)	13.8	17.2
<u>T. leucogaster</u> ²	3.7(50)	70.0 ⁶ (696)	5.3	3.2(18)	12.0	17.1
<u>D. auricularis</u> ³	1.8 (5)	55.0 ⁵ (18)	3.3	2.0 (5)	3.7	6.6
<u>D. auricularis</u> ⁴	4.4(19)	55.0 ⁵ (18)	7.9	3.3(15)	14.3	25.5

1 = Ascaray (1984); 2 = Scott (1979); 3 = Nel & Stutterheim (1973); 4 = Keogh (1973); 5 = De Graaff (1981); 6 = Smithers (1983); 7 = Boyer (pers. comm.); 8 = present study.

Unless otherwise indicated, adult sizes quoted are those given by the original author. T. brantsii and T. leucogaster adult mass quoted by Scott (1979) was much higher than that quoted by any other author (125.9g and 103.4g respectively). Consequently, in this table adult mass for these species is quoted from Smithers (1983) for a large sample size. Figures in parentheses indicate sample size.

TABLE 2B: INDIVIDUAL HEAD-BODY, TAIL AND HINDFOOT LENGTHS AT BIRTH COMPARED WITH ADULT MEASUREMENTS.

SPECIES	HEAD-BODY LENGTH			TAIL LENGTH			HINDFOOT LENGTH		
	\bar{x} BIRTH (mm)	\bar{x} ADULT (mm)	BIRTH ADULT %	\bar{x} BIRTH (mm)	\bar{x} ADULT (mm)	BIRTH ADULT %	\bar{x} BIRTH (mm)	\bar{x} ADULT (mm)	BIRTH ADULT %
<u>P. collinus</u> ⁸	33.7 (3)	80.8(13)	41.7	13.0 (3)	82.2 (9)	15.8	6.3 (3)	15.3(13)	41.2
<u>G.p. paeba</u> ⁸	31.8(10)	95.4(12)	33.3	10.7(10)	108.0 ⁷ (170)	9.9	5.8(10)	28.1 ⁷ (178)	20.6
<u>G.p. exilis</u> ¹	29.6(21)	94.0	31.5	13.3(21)	117.0	11.4	7.7(21)	28.1	27.4
<u>G. tytonis</u> ⁸	34.2(16)	96.4 (9)	35.5	12.0 ⁷ (16)	125.0 ⁷ (168)	9.6	6.5 ⁷ (16)	32.8 ⁷ (168)	19.8
<u>T. brantsii</u> ²	46.1(53)	163.5	28.2	16.2(53)	154.3	10.5	8.4(53)	34.4	24.4
<u>T. leucogaster</u> ²	42.4(50)	157.0	27.0	13.3(50)	143.0	9.3	8.1(50)	31.8	25.5
<u>D. auricularis</u> ³	28.2 (5)	112.0 ⁵ (48)	25.3	9.5 (5)	88.0 ⁵ (48)	10.8	6.4(5)	24.5 ⁵ (48)	26.1

See Table 2A for references.

by Boyer (pers. comm.) on a large sample ($n = 250$) of wild-caught animals from the area south to south-east of Gobabeb. Tail length and hindfoot length were very similar for wild-caught and laboratory animals, but head-body length differed considerably. It was decided to use adult head-body length from laboratory animals, despite the smaller sample size, since the discrepancy between laboratory and wild animals may have been due to observer technique. The adult body measurements of *P. collinus* were taken from laboratory animals ($n = 16$). Growth rates were calculated for other members of the subfamily Gerbillinae for which data were available from the literature; these results are shown in Table 3.

PHYSICAL DEVELOPMENT

Physical development of *G. paeba*, *G. tytonis* and *P. collinus* is summarized in Table 4. At birth, neonates of all three species were hairless and red in colour. Vibrissae were present on the nose. The skin of young gerbils was translucent and the abdominal organs could be seen through the skin. In three litters of pigmy rock mice, a dark purplish pigmentation was visible on the dorsum at birth, but in another three litters this pigmentation did not appear until 2-4 days after birth. The appearance of the darker pigmentation was taken to represent the beginning of hair proliferation which began at 8-10 days in *G. paeba* young, and at 10-13 days in *G. tytonis*. Fur was visible on the dorsum first, with white fur appearing on the ventrum some 4-6 days later in the gerbils. White fur was noticed on *P. collinus* young at 9 days. The fur spread gradually to the

TABLE 3: GROWTH RATES OF SEVEN CRICETID RODENTS

SPECIES	MASS			HEAD-BODY LENGTH			TAIL LENGTH			HINDFOOT LENGTH		
	Growth phase (%adult)	Growth rate (g/day)	Growth rate Adult mass (%)	Growth phase (%adult)	Growth rate (mm/day)	Growth rate Adult size (%)	Growth phase (%adult)	Growth rate (mm/day)	Growth rate Adult size (%)	Growth phase (%adult)	Growth rate (mm/day)	Growth rate Adult size (%)
<i>P. collinus</i> ⁴	12-50	0.3(19)	1.6	40-70	1.5(14)	1.9	16-50	2.0(14)	2.4	40-80	0.7(14)	4.6
<i>G.p. paeba</i> ⁴	12-50	0.4(21)	1.8	40-70	1.7 (6)	1.8	16-50	3.0 (6)	2.8	40-80	1.0 (6)	3.6
<i>G.p. exilis</i> ¹	7-50	0.6(21)	1.9	30-67	1.4(21)	1.5						
<i>G. tytonis</i> ⁴	12-50	0.4(16)	1.6	40-70	1.4(11)	1.5	16-50	2.3(11)	1.8	40-80	0.9(11)	2.7
<i>T. brantsii</i> ²	12-50	1.0(53)	1.3	40-70	1.8(53)	1.1	16-50	2.3(53)	1.5	40-80	0.8(53)	2.3
<i>T. leucogaster</i> ²	12-50	1.0(50)	1.4	40-70	1.9(50)	1.2	16-50	2.4(50)	1.7	40-80	0.8(50)	2.5
<i>D. auricularis</i> ³	3.3-52	0.6 (5)	1.1									

1 = Ascaray (1984); 2 = Scott (1979) 3 = Nel & Stutterheim (1973); 4 = present study.

Figures in parentheses indicate sample size.

TABLE 4: PHYSICAL DEVELOPMENT OF SELECTED RODENTS
(Ages are given in days)

SPECIES	EAR PINNAE FREE	TOES SEPARATE	HAIR APPEARS	EYES OPEN	LOWER INCIS- ORS APPEAR
<u>P.collinus</u> ¹	0-3	2-4	0-4	12-14	
<u>G.p.paeba</u> ¹	3-6	3-5	8-10	14-18	
<u>G.p.exilis</u> ²	6	7	7	17	12
<u>G.tytonis</u> ¹	6-7	6-8	10-13	22-24	
<u>D.auricul-</u> <u>aris</u>	4-5 ³ 3-4 ⁴	6 ³ 3-4 ⁴	4 ³ 4 ⁴	21-23 ³ 4 ⁴	14 ³ 8-10 ⁴
<u>T.brantsii</u> ⁵	4-5	4-6	3-5	16-19	4-6
<u>T.leucogaster</u> ⁵	3-5	3-5	2-5	15-17	7-9
<u>Liomys pictus</u> ⁶		0	9-10	18-21	1-3
<u>Perognathus</u> ⁶ <u>californicus</u>		0	9	14-16	9
<u>Dipodomys</u> ⁶ <u>nitratoides</u>		0	6	10-11	4-7
<u>Notomys</u> ⁷ <u>alexis</u>	1		0	16-20 ⁷ 18-23 ⁸	6-10
<u>Jaculus</u> ⁹ <u>jaculus</u>	1		12	38	27
<u>Acomys</u> ¹⁰ <u>dimidiatus</u>	0	0	0	0	0
<u>Gerbillus</u> ¹⁰ <u>dasyurus</u>	16-18	4-6	4-5	22-25	10-12
<u>Zelotomys</u> ¹¹ <u>woosnami</u>	2	4	2	16-17	10-12

1 = Present study; 2 = Ascaray (1984); 3 = Nel & Stutterheim (1973);
4 = Keogh (1974); 5 = Scott (1979); 6 = Eisenberg (1963);
7 = Breed (1981); 8 = Crichton (1974); 9 = Happold (1970);
10 = Al-Khalili & Delany (1986); 11 = Birkenstock & Nel (1977)

first litter, this female must have been mated by one of her own offspring. Assuming the gestation period is 21 days, the young males must have been capable of reproducing at 24 days. *G.paeba* males were seen to have scrotal testes as early as 35 days (2 litters), while *G. tytonis* males had scrotal testes at 56 days (2 litters). A female *G. tytonis* had a perforate vagina at 63 days, while a female *G.paeba* was perforate at 42 days. Another female *G. paeba* gave birth to young when she was 120 days old, but the litter did not survive.

BEHAVIOURAL DEVELOPMENT

Behavioural development is summarized in Table 5; two behaviours each exhibited by only one species were not included.

G.paeba young exhibited a "startle reaction" from 12-15 days of age. When the nest was disturbed, pups rushed out and scattered across the sand before crouching flat on the surface.

In the first *P.collinus* litter, a pup was seen to approach its mother, and push its nose against her mouth. The pup then appeared to lick the mother's mouth (Figure 10). When one pup moved away, the other took up its position and repeated the same behaviour. The mother made no attempt to escape from the young. This behaviour was seen when the young were 26, 28, 31 and 48 days old and lasted for 1-2 hours. Food and water were available at the time; however at times water bottles became blocked and this behaviour may represent an interesting adaptation to the arid environment.

TABLE 5: BEHAVIOURAL DEVELOPMENT IN P.COLLINUS, G.PAEBE AND G.TYTONIS.

SPECIES	AGE (DAYS)	BEHAVIOURAL DEVELOPMENT
<u>LOCOMOTION</u>		
<u>P.collinus</u> <u>G.paeba</u> <u>G.tytonis</u>	birth	Crawling with head and belly down on substrate and legs splayed laterally, tendency to roll over. Forepaws move alternately, hindlegs simultaneously. <u>P.collinus</u> young remain stationary while rotating their heads laterally.
<u>P.collinus</u> <u>G.paeba</u> <u>G.tytonis</u>	3 - 4 6 8	Lift head while crawling, less rolling over.
<u>P.collinus</u> <u>G.paeba</u> <u>G.tytonis</u>	5 - 7 8 16	Lift bellies while crawling, forelegs under body, hindlegs splayed laterally, but moving alternately. Gerbils walk with hindfeet plantigrade initially, later digitigrade.
<u>P.collinus</u> <u>G.paeba</u> <u>G.tytonis</u>	13 - 14 17 21	Rapid quadrupedal running, climbing, sand-digging and jumping. Bipedal saltation and quadrupedal walking, sand-digging and jumping.
<u>FEEDING</u>		
<u>P.collinus</u> <u>G.paeba</u> <u>G.tytonis</u>	Birth-14	<u>P.collinus</u> nipple-cling, <u>G.paeba</u> and <u>G.tytonis</u> are suckled while lying on their backs under the female; frequent teat-changes.
<u>P.collinus</u> <u>G.paeba</u> <u>G.tytonis</u>	15 - 30	Gradual change to solid food. Young <u>P.collinus</u> continue to suck although some were artificially weaned at 33 days.
<u>GROOMING</u>		
<u>P.collinus</u> <u>G.paeba</u> <u>G.tytonis</u>	7 - 10	Scratch body and head with hindfoot. Sit and use forepaws to groom noses.
<u>P.collinus</u> <u>G.paeba</u> <u>G.tytonis</u>	11 - 26	Groom cheeks and ears using forepaws. Turn laterally and groom flank. Nibble toenails after scratching. Groom belly fur. Turn laterally and groom tail, holding this in forepaws and grooming from base to tip.
<u>P.collinus</u> <u>G.paeba</u> <u>G.tytonis</u>	19 24 - 26	Sandbathing - rolling in sand from side to dorsum.
<u>SOCIAL BEHAVIOUR</u>		
<u>G.paeba</u> <u>G.tytonis</u>	birth	Young huddle together when left in nest.
<u>G.paeba</u> <u>G.tytonis</u>	18 35	Social interactions involving mounting between cage-mates, aggressive interactions and allo-grooming. Aggressive interactions initially involve "sparring", i.e. pups beat at each other with their forepaws while in an upright position. Later, chasing and leaping were seen. Locked fighting was seldom seen, but wounds on tails and rumps necessitated the eventual separation of cage-mates.
<u>P.collinus</u>		No allo-grooming, mounting or aggressive behaviour.

VOCALIZATIONS

P. collinus new-born young squeaked loudly when disturbed and also produced a "clicking" noise rhythmically. Young gerbils made four sounds: "squeaking" was often heard when the female entered or re-arranged the nest; a low-pitched "grunt" was heard as the young rested or climbed over each other in a pile; "clicking" was heard as for *P. collinus*; and a high-pitched metallic "tick" sound which was produced rhythmically and was associated with contractions of the abdomen. These sounds gradually became less frequently heard, until at 35 days, both gerbils and rock mice were only "squeaking". Adult *G. paeba* have not been heard to vocalize, while adult *G. tytonis* occasionally produce a high-pitched "rattling" sound. Adult *P. collinus* squeak loudly when disturbed.

DISCUSSION

GESTATION PERIOD

The estimated gestation periods of 27 days for *G. paeba* and 24 days for *G. tytonis* approximate gestation periods quoted in the literature. Stutterheim and Skinner (1973) reported an interval of 26 days from an observed mating until the birth of a litter of *G. paeba*, Hallett and Keogh (1971) noted a gestation period of 23 days for one litter of *G. paeba coombsi*, and Ascaray (1984) reported 21 days as the shortest interval between pairing and parturition in *G. paeba exilis*. Thus gestation in these gerbils is short, a factor which is usually associated with animals living in unstable environments. Intervals between litters were short in all three species. This differs from

Withers' (1983) suggestion that *P.collinus* breed only once a year in the wild.

MATERNAL BEHAVIOUR

Nest-building and storage of food in burrows has been reported for *G. paeba exilis* in the Alexandria dunefield (Ascaray, 1984) and for *G.paeba paeba* in the Namib Desert (Boyer, pers.comm.). In the laboratory, all individuals of *G. paeba paeba* and *G. tytonis* established caches of food in their cages by burying food in one area. *P.collinus* were not seen to bury food in a particular cache, but rather to "scatter-hoard" seeds by pushing their noses into the sand and leaving seeds in several different places in the cage. The hoarding of seeds in burrows has been recorded for *Desmodillus auricularis* (Keogh, 1973), *Liomys pictus* (Eisenberg, 1963) and in several *Peromyscus* spp. (Eisenberg, 1968). The caching of seeds in burrows may be important in providing a source of food for lactating females.

The behaviour of female gerbils after the birth of the young is similar to that described by Eisenberg (1963) for several heteromyid rodents, and for *Peromyscus* spp. (Eisenberg, 1968). The brooding posture, grooming of the young, ingestion of urine and faeces was similar in the three species described in this paper. *P.collinus* differed from the gerbils in that the young clung to the teats from birth.

NEONATAL DEVELOPMENT

Measurements referred to in this section are all relative to adult body sizes, unless otherwise indicated. From the results, it is clear that *P.collinus* at birth are more advanced than either *G.paeba* or *G.tytonis* in all physical parameters measured, but there was little difference between the two *Gerbillurus* species. Behavioural development followed the same sequence in the three species, although *G.tytonis* developed more slowly than the other two species. Cephalocaudal progression was evident in the development of locomotion and grooming.

Within the subfamily Gerbillinae, comparable data are available for *D. auricularis* (Nel & Stutterheim, 1973; Keogh, 1974), *Tatera brantsii* (Scott, 1979; Meester & Hallett, 1970), *T. leucogaster* (Scott, 1979) and *G. paeba exilis* (Ascaray, 1984). In all parameters measured, *P.collinus* is closer to adult body size at birth than any of the Gerbillinae. Within the Gerbillinae, the three *Gerbillurus* species were the most precocial in respect of mass and head-body length, while tail and hindfoot lengths were similar within the group. *G.tytonis*, which has the longest hindfeet relative to the head-body length as an adult, starts life with the shortest relative hindfoot length.

Stearns (1983) and Blueweiss et al. (1978) have shown that size has a strong impact on patterns of covariation in life-history traits for a large number of mammal species. In this study, a negative correlation was found between relative size at birth and adult body size. Absolute growth rates in rodents have been found to increase with increase in adult body mass

(Case, 1978), a finding which is supported by these data. However, when growth rates are scaled to adult body sizes, the reverse trend is observed, with the smaller rodents (*P.collinus* and the *Gerbillurus* spp.) growing faster than the larger gerbils (*Tatera* spp. and *D.auricularis*).

REPRODUCTIVE STRATEGIES

Neal (1986) has found a positive correlation between long gestation, small litter size and precocial development in several African rodents. It has been suggested that r-selected species inhabit unstable or unfavourable habitats, and will be expected to have a short gestation period with relatively large litters of altricial young. K-selected species live in predictable or stable environments, breed continually, have long gestation periods and small litters of precocial young. *G.p.paeba*, *G.tytonis* and *G.p.exilis* fit the r-selected strategem in all four respects, i.e. short gestation period, large litter size, altricial young and seasonal breeding. *P.collinus* and *D.auricularis* appear to be more K-selected although neither species has precocial young.

Neal (1986) suggests that species with good water-conserving abilities perceive the desert as being more stable than species with poorer water-conserving ability. *P.collinus* is able to survive on a diet of air-dried seed and has a low water turnover rate (Withers, Louw & Henschel, 1980). *D.auricularis* has been found to breed aseasonally in the Namib Desert, and the provision of extra drinking water did not extend the breeding of this species as it did in the case of *G.p.paeba* (Christian,

1979a). *D.auricularis* had lower water requirements than *G.p.paeba* (Christian, 1979b). Thus *P.collinus* and *D.auricularis* may be better arid-zone adapted (i.e. more water-independent) than *G.p.paeba*, which may result in a tendency towards K-selection.

Neal (1986) has found that some small rodents may have large precocial young and a small litter, so litter mass is mainly an inverse function of adult body mass. Tuomi (1980) has suggested that some small mammals have a small litter size because of their relatively high birth weight. In this study, the two *Tatera* species, which have the largest body mass have a smaller litter mass than *Gerbillurus* species. Thus Neal's hypothesis is supported by these data. Litter size and litter mass relative to adult mass of species in this study demonstrate the converse trend and support allometric scaling effects (Western & Ssemakula, 1982).

Eisenberg and Isaac (1963) have suggested that a reduced litter size is an adaptation to the arid environment since it reduces temporally the physiological strain on the lactating female. Evidence from this and other studies indicate that a small litter size is not a general characteristic of arid-adapted rodents. *P.collinus* has a small litter size relative to those of *G.paeba* and *G.tytonis*; in North America *Dipodomys* species have smaller litters than *Perognathus* species (Eisenberg, 1963); in Saudi Arabia, *Acomys dimidiatus* has a long gestation period with a small litter, while *Gerbillus dasyurus* has a short gestation and large litter (Al-Khalili & Delany, 1986).

PRECOCIAL/ALTRICIAL DEVELOPMENT

The classification "altricial" or "precocial" has been subjectively applied to many mammalian and avian young. However no definitive criteria have been established for this classification. In the group of rodents discussed in this paper, *P. collinus* would be the most precocial, while the *Gerbillurus* spp. would be more precocial than either *Tatera* or *Desmodillus*. This classification is based on the level of development at birth, and is further supported by the ages at which certain physical milestones are achieved.

G. tytonis achieved physical milestones at the slowest rate of all the Gerbillinae. This slower rate of development may be related to its bipedal locomotion, as has been suggested for bipedal *Dipodomys* spp., which have a longer gestation period than quadrupedal heteromyid rodents (Eisenberg & Isaac, 1963). Other bipedal rodents having slow rates of development include *Jaculus jaculus*, the Sudanese jerboa, a litter of which were unable to use their hindlegs at 38 days (Happold, 1970). Australian hopping mice (*Notomys* spp.) are furred at birth, but their eyes do not open until approximately three weeks of age (Crichton, 1974). *Gerbillus dasyurus* achieves physical milestones at approximately the same rate as *G. tytonis* (Al-Khalili & Delany, 1986), while *Acomys dimidiatus*, a quadrupedal rodent, develops precocially..

NIPPLE-CLINGING

Nipple-clinging has been described for a number of rodent species, although its function has not been clearly established, nor has it been clearly defined. In this study, young were said to nipple-cling if they did not spontaneously detach themselves from the teats until weaning. It has been suggested that nipple-clinging enables the mother to remove her whole litter from danger, or that it provides the young with a continuous milk supply (Meester & Hallett, 1970; Crichton, 1974).

Nipple-clinging seems to have evolved independently in different families, and even within different subspecies of a species. It is reported that *G.paeba exilis* nipple-cling (Ascaray, 1984), although only from the age of 7 days, while *G. paeba paeba* do not; *T. brantsii* are "partial" nipple-clingers while *T. leucogaster* do not nipple-cling (Scott, 1979); *Praomys (Mastomys) natalensis* are not nipple-clingers (Baker & Meester, 1977) while *P. tullbergi* are (Happold, 1978).

Information relating nipple-clinging to litter size and nesting habits for a number of Southern African rodents is presented in Table 6. Six species reported to nipple-cling have an average of 3.0 young per litter, while nine species which do not nipple-cling have an average of 5.2 young per litter. If nipple-clinging enables the young to obtain a continuous milk supply, then nipple clingers may be expected to have a higher growth rate than non-nipple-clingers. *P.collinus* does not have a significantly higher growth rate than any of the gerbilline species, hence its growth rate must be dependent on factors other

TABLE 6: LITTER SIZE AND NESTING HABITS OF SOME SOUTHERN AFRICAN RODENTS

	SPECIES	LITTER SIZE	NESTING HABITS ¹
NIPPLE-CLINGERS	<u>Petromyscus collinus</u>	2.8 ¹¹	Unknown
	<u>Mystromys albicaudatus</u>	2.5 ²	Burrow
	<u>Aethomys chrysophilus</u>	3.1 ³	Nest in rock crevices and under stones,
	<u>A.namaquensis</u>	4.0 ⁴	also burrow at times.
	<u>Thallomys paedulus</u>	2.7 ⁴	Nest in hollow tree trunks.
	<u>Thamnomys dolichurus</u>	2.7 ⁵	
"PARTIAL" NIPPLE- CLINGERS	<u>Tatera brantsii</u>	3.0 ²	Burrow
	<u>Gerbillurus paeba exilis</u>	3.7 ⁶	Burrow
NON-NIPPLE-CLINGERS	<u>G.paeba paeba</u>	4.6 ¹¹	Burrow
	<u>G.tytonis</u>	4.4 ¹¹	Burrow
	<u>Lemniscomys griselda</u>	4.2 ²	Grass nests on the surface of the ground
	<u>Saccostomus campestris</u>	6.3 ²	Burrow
	<u>Praomys natalensis</u>	11.3 ⁷	Burrow
	<u>Tatera leucoqaster</u>	3.2 ²	Burrow
	<u>Desmodillus auricularis</u>	2.0 ⁸	Burrow
	<u>Zelotomys woosnami</u>	4.7 ⁹	Burrow
	<u>Rhabdomys pumilio</u>	6.5 ¹⁰	Burrow

1 = De Graaff (1981); 2 = Scott (1979); 3 = Brooks (1972);
 4 = Meester & Hallett (1970); 5 = Panagis & Nel (1981); 6 = Ascaray
 (1984); 7 = Baker & Meester (1977); 8 = Nel & Stutterheim
 (1973); 9 = Birkenstock & Nel (1977); 10 = Brooks (1974);
 11 = Present study

than a continuous supply of milk.

If nipple-clinging is related to the removal of young from danger, then it would be expected to be more common in animals which occupy "dangerous" habitats, i.e. where predation is high or where shelter is scarce. Burrows provide a protected environment for the development of young, hence fewer animals which rear their young in burrows would be expected to nipple-cling. Three species which rear their young in burrows are nipple-clingers or "partial" nipple-clingers, while four species which bear their young on the surface have young which nipple-cling. Amongst non-nipple-clingers, one species is a surface-breeding animal, while eight rear their young in burrows. Thus nipple-clinging may be an adaptation of surface-breeding animals which are more exposed than young which are reared in a burrow.

CONCLUSION

P. collinus (subfamily Petromyscinae), the smallest rodent included in this study, is easily distinguished from the subfamily Gerbillinae on the basis of its larger size relative to adult size at birth, more rapid rates of physical and behavioural development and nipple-clinging young. Members of the subfamily Gerbillinae share a similar level of development at birth, but the larger species (*Tatera* spp. and *D. auricularis*) have higher rates of increase in mass. *G. tytonis* differs markedly in the slower rate of physical development, which may possibly be related to the evolution of longer hindfeet. Behavioural development follows the same course in all species, but *P. collinus* young and adults are notably less active than

Gerbillurus spp. The two subspecies of *G. paeba* differ in respect of nipple-clinging, level of development at birth, and growth rates.

In relation to adaptation to the environment, *P. collinus* and *D. auricularis* appear to be more arid-adapted than *G. paeba* or *G. tytonis*, and this is reflected in reproductive strategies which are generally associated with K-selected animals. *G. paeba* and *G. tytonis* exhibit several characteristics of r-selected animals, as do *T. leucogaster* and *T. brantsii*.

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