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lab study - animals trapped 1984 - 86.

G.p. paeba + G. tytonis - solitary

G. setzeri + G.p. exilis ♀ - semi - tolerant

G.p. exilis ♂ + vallinus - tolerant.

A Comparative Study of Agonistic Behaviour in Hairy-footed Gerbils (Genus *Gerbillurus*)

EDITH R. DEMPSTER & M. R. PERRIN 1989

DEMPSTER, E. R. & PERRIN, M. R. 1989: A comparative study of agonistic behaviour in hairy-footed gerbils (genus *Gerbillurus*). Ethology 83, 43—59.

Abstract

Intraspecific agonistic behaviour was investigated by means of staged encounters in *Gerbillurus paeba paeba, G. p. exilis, G. tytonis, G. setzeri* and *G. vallinus.*

Four groups of behaviour were identified by motivational analysis: i.e. "exploratory and solitary", "aggressive", "submissive", and "sexual" behaviour. Frequencies of acts and levels of interaction differed among species and sexes.

Cluster analysis of behaviour data revealed three clusters which agree partially with the karyology and taxonomy of the genus. *G. p. paeba* and *G. tytonis* were very aggressive and highly active; female *G. p. exilis* and *G. setzeri* less so; while male *G. p. exilis* and *G. vallinus* were least aggressive and active, performing more contact-promoting behaviour than other species. 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*).

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Introduction

The genus *Gerbillurus* (SHORTRIDGE 1942) contains four species, which are all deserticolous and display morphological and ecological similarity (DE GRAAFF 1981; BOYER 1988). The currently-accepted taxonomy is based on morphometric data and general karyology (DE GRAAFF 1981; MEESTER et al. 1986). Three subgenera are recognized and reviewed.

Subgenus *Progerbillurus* (PAVLINOV 1982), includes *G. paeba paeba* (A. SMITH 1836) and four subspecies. This species is widely distributed through the

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arid western areas of southern Africa, its distribution restricted to areas of soft sand where it can construct simple burrows (De Graaff 1981; Meester et al. 1986). *G. paeba exilis* (Shortridge & Carter 1938) occurs as an isolated population in the Alexandria dunefield from the Sundays River mouth to St. George's Strand, eastern Cape Province. Individuals of *G. paeba paeba* from the Namib Desert and *G. paeba exilis* were included in this study.

Subgenus *Paratatera* (Petter 1983) includes only one species, *G. tytonis* (Bauer & Niethammer 1959), which is restricted to the shifting red sand dunes of the Namib Desert (De Graaff 1981; Meester et al. 1986). This species was originally described as a subspecies of *G. vallinus* (Bauer & Niethammer 1959).

The standard karyogram of *G. tytonis*, *G. paeba* and all its subspecies revealed no differences among any of the taxa, with a diploid number of 36 chromosomes and 68 autosomal arms (Schlitter et al. 1984).

Subgenus *Gerbillurus* (Shortridge 1942) contains two species. *G. vallinus* (Thomas 1918) occurs in the northwestern Cape and is restricted to areas of more consolidated soils (Meester et al. 1986; Erasmus, in prep.). *G. setzeri* (Schlitter 1972) inhabits the gravel plains north of the Kuiseb River (Meester et al. 1986). Both species have 60 chromosomes, but *G. vallinus* has 80 autosomal arms and *G. setzeri* 76 (Schlitter et al. 1984).

Comparison of G- and C-banding on chromosomes of *G. paeba* and *G. vallinus* led Qumsiyeh (1986) to suggest that both species arose from a common ancestor which had a diploid number of 44 chromosomes. Including the results of Benazzou et al. (1982) on chromosomal banding in *G. tytonis* led to the conclusion that this species is a sister taxon of *G. paeba* (Qumsiyeh et al. 1987).

Robbins (pers. comm.) derived a phenogram based on electrophoretic analysis of 38 proteins (Fig. 1). In this phenogram, *G. tytonis* and *G. p. exilis* are shown to differ considerably from each other and from *G. paeba*, *G. vallinus*, and *G. setzeri*. Conflicting results may be resolved by additional taxonomic characters; in particular behaviour has not been considered in existing phenograms.

Little information is available on the agonistic behaviour and social structures of *Gerbillurus* species (Stutterheim & Skinner 1973). Agonistic behaviour has been used to elucidate the taxonomy of silky pocket mice, genus *Perognathus* (Martin 1984). The same basic components were present in three species studied,

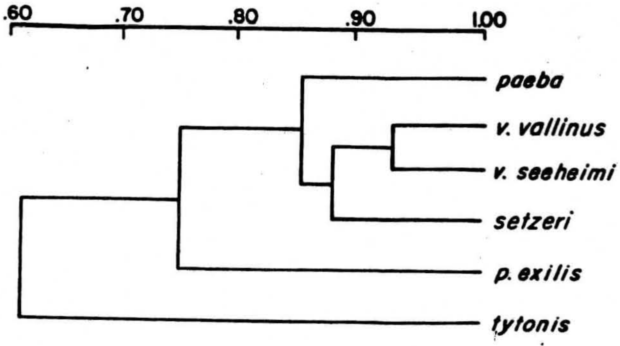


Fig. 1: Phenogram derived from results of protein electrophesis (Robbins, pers. comm.)

but the relative frequencies differed. *Perognathus flavus* and *P. merriami* were considered, on the basis of similarities in agonistic behaviour, to be conspecific (Martin 1984).

In this study, agonistic behaviour was investigated and quantified in 5 taxa of the genus *Gerbillurus.* The patterns of agonistic behaviour were compared and related to the existing taxonomy of the genus, and an attempt was made to elucidate the social structures of the species based on laboratory results.

Methods and Materials

7 *G. paeba* (5 females and 2 males) were trapped near Swakopmund (23°37′ S 14°34′ E) and 12 *G. tytonis* (7 females and 5 males) were trapped in the area south of Gobabeb (23°37′ S 15°01′ E) during Aug. 1984. These were supplemented with labbred *G. paeba* and *G. tytonis.* 12 *G. setzeri* (7 females and 5 males) were trapped near Rössing Uranium Mine (22°31′ S 14°52′ E) in June 1985. 9 *G. paeba exilis* (5 females and 4 males) were trapped in the Alexandria Dunefield (33°41′ S 25°49′ E) in Dec. 1985. 4 *G. vallinus vallinus* (3 males and 1 female) were trapped near Copperton (29°59′ S 22°17′ E), Northern Cape in Aug. 1986.

All gerbils were housed in 60 × 30 × 30 cm glass terraria provided with a layer of sand and a nest box. Food and water were provided ad lib. The light regime was 16L : 8D using light supplied by a 100-W light bulb. The circadian photoperiod was reversed; temperature was maintained at 25 °C.

Agonistic encounters were staged in a terrarium provided with a 3—4 cm layer of sand. The sand was thoroughly mixed between encounters and changed after 10—15 encounters, when the terrarium was also washed out with soap and water to reduce possible pheromonal effects. Lighting was provided by a 40-W red light bulb positioned above the terrarium. 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.

Two animals of the same sex and species were separated by a partition and permitted to investigate the terrarium for five min. Behaviour was recorded during the first 10 min of the encounter using a video camera (JVC Model TK1700EG) and recorder (National Portable VCR NV-180). The animals were weighed after the encounter.

Videotapes were analyzed first by identifying and describing the postures exhibited by the animals during encounters. Twenty-nine acts were described and two-letter codes were used in the transcription of tapes. The VCR used was equipped with "slow forward", "still frame" and "single frame" advance facilities, which permitted a high degree of accuracy in the analysis of very rapid sequences. Duration of acts was not monitored for this analysis, and acts were recorded when an animal changed its behaviour.

Encoded encounters were analyzed by means of a computer programme. The frequency of occurrence of each act and each pair-sequence of acts was calculated for each of the two animals in an encounter. 70 encounters between animals of the same sex and species were analyzed. Owing to the difficulty of trapping *G. vallinus,* only four encounters between males were staged.

Since a high level of variation among individuals occurred, results for frequencies of acts are shown as box-and-whisker plots. Frequencies of acts were compared by the Mann-Whitney U-test in order to identify acts which differed significantly in frequency among species and sexes.

Analysis of sequences was restricted to dyads. Transition frequencies were calculated as follows (Martin 1984):

$P_{jk} = n\,(j, k)/T_j$, where
$n\,(j, k)$ = number of occurrences of jth variable followed by kth variable
T_j = total of jth 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 were omitted from the analysis. This permitted identification of the

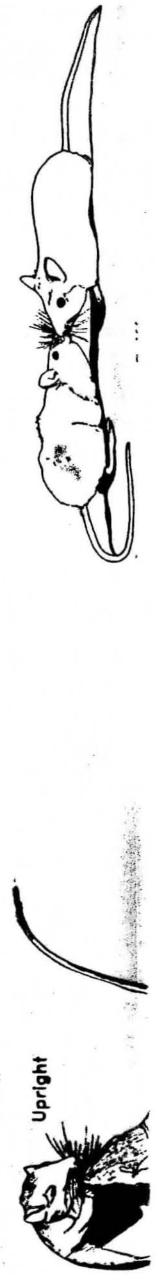
Table 1: List of postures identified in *Gerbillurus* species

Gerbillurus	Equivalent posture in other rodents
AD = Attend	Attend (GRANT & MACKINTOSH 1963)
XX = Kick Back	
DR = Drumming	Drumming, foot-stamping (SWANSON 1974)
AP = Approach	Approach (GRANT & MACKINTOSH 1963)
SN = Sniff facial area	Nose/nose contact (SWANSON 1974)
EX = Explore	Digging + alert (SWANSON 1974)
MA = Move away	Move away (EISENBERG 1967)
SI = Sit	Sitting (EISENBERG 1967)
EA = Eat	Foraging & eating (SWANSON 1974)
GS = Groom self	Grooming (SWANSON 1974)
SB = Sandbathe	Sandbathing (SWANSON 1974)
AL = Attack leap	Attack leap (EISENBERG 1967)
AT = Attack	Attack (SWANSON 1974)
CH = Chase	Chasing (SWANSON 1974)
FI = Locked fight	Locked fight (SWANSON 1974)
UP = Upright	Upright + sparring (SWANSON 1974)
ST = Stop	
TH = Threaten	Threat (GRANT & MACKINTOSH 1963)
EL = Escape leap	Escape leap (EISENBERG 1967)
FL = Flee	Flee (GRANT & MACKINTOSH 1963)
CR = Crouch	Crouch (GRANT & MACKINTOSH 1963)
AE = Approach elongate	Elongate approach (EISENBERG 1967)
SA = Sniff anogenital	Naso-anogenital contact (SWANSON 1974)
MO = Mount	Mounting (SWANSON 1974)
AM = Attempted mount	Attempted mount (EISENBERG 1967)
FO = Follow	Follow (GRANT & MACKINTOSH 1963)
GI = Grooming invitation	Nosing (BARNETT 1975)
GO = Allogrooming	Social grooming (EISENBERG 1967)

most common dyads, which were used to generate kinematic graphs illustrating the most likely sequence of events (MARTIN 1984). Statistical testing of sequence matrices was not attempted since the assumption of stationarity was violated.

Results

Nomenclature used in this study was based on postures described for heteromyid rodents (EISENBERG 1963, 1967) and common laboratory rodents (GRANT & MACKINTOSH 1963). Complete descriptions of postures are to be found in these sources. A list of postures identified in *Gerbillurus* species and equivalent postures for some other rodent species are presented in Table 1. Acts which differ from descriptions given by EISENBERG (1963, 1967), GRANT & MACKINTOSH (1963) and SWANSON (1974) are described below. Diagrams of some postures exhibited by *Gerbillurus* species are included in Fig. 2.



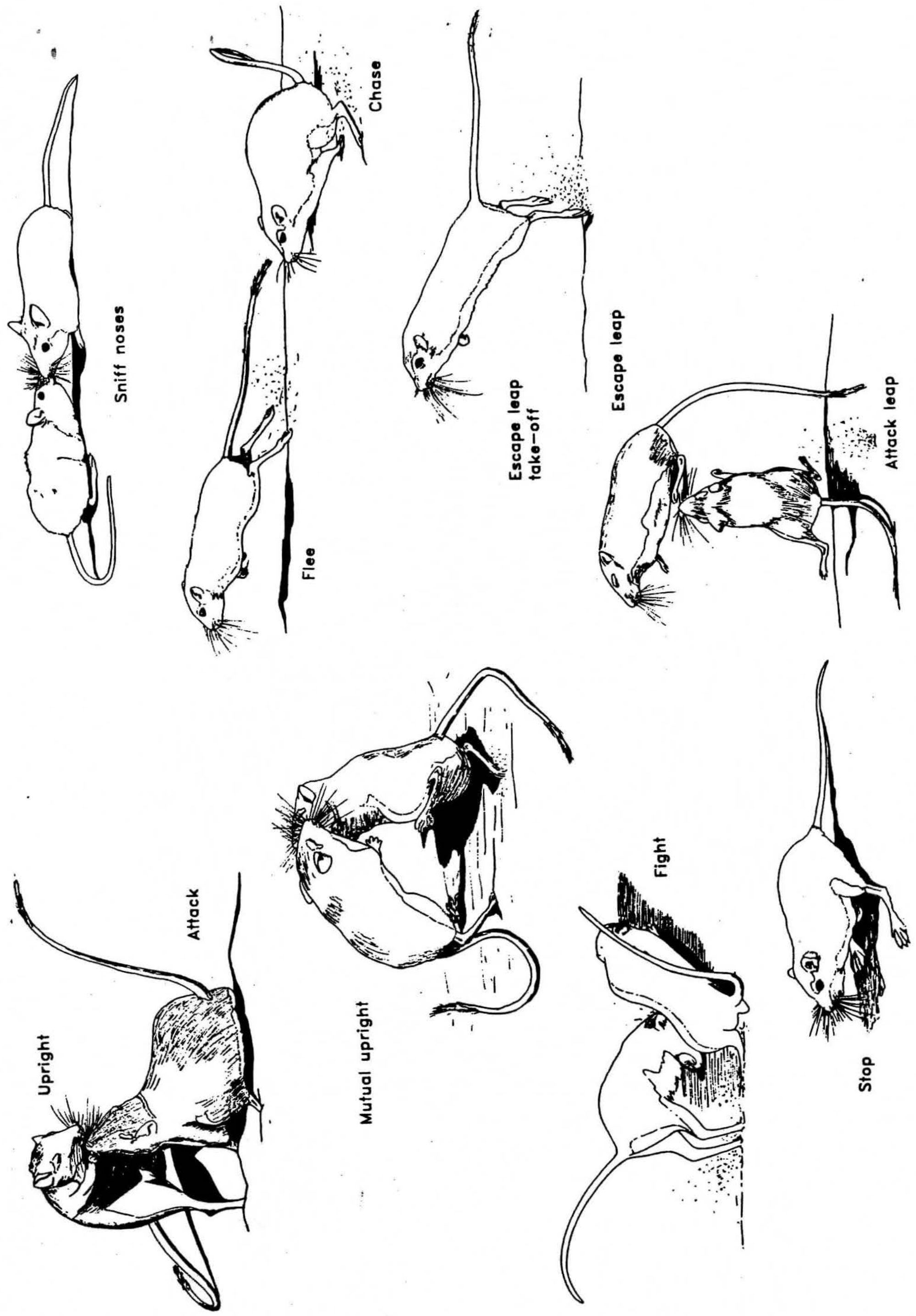
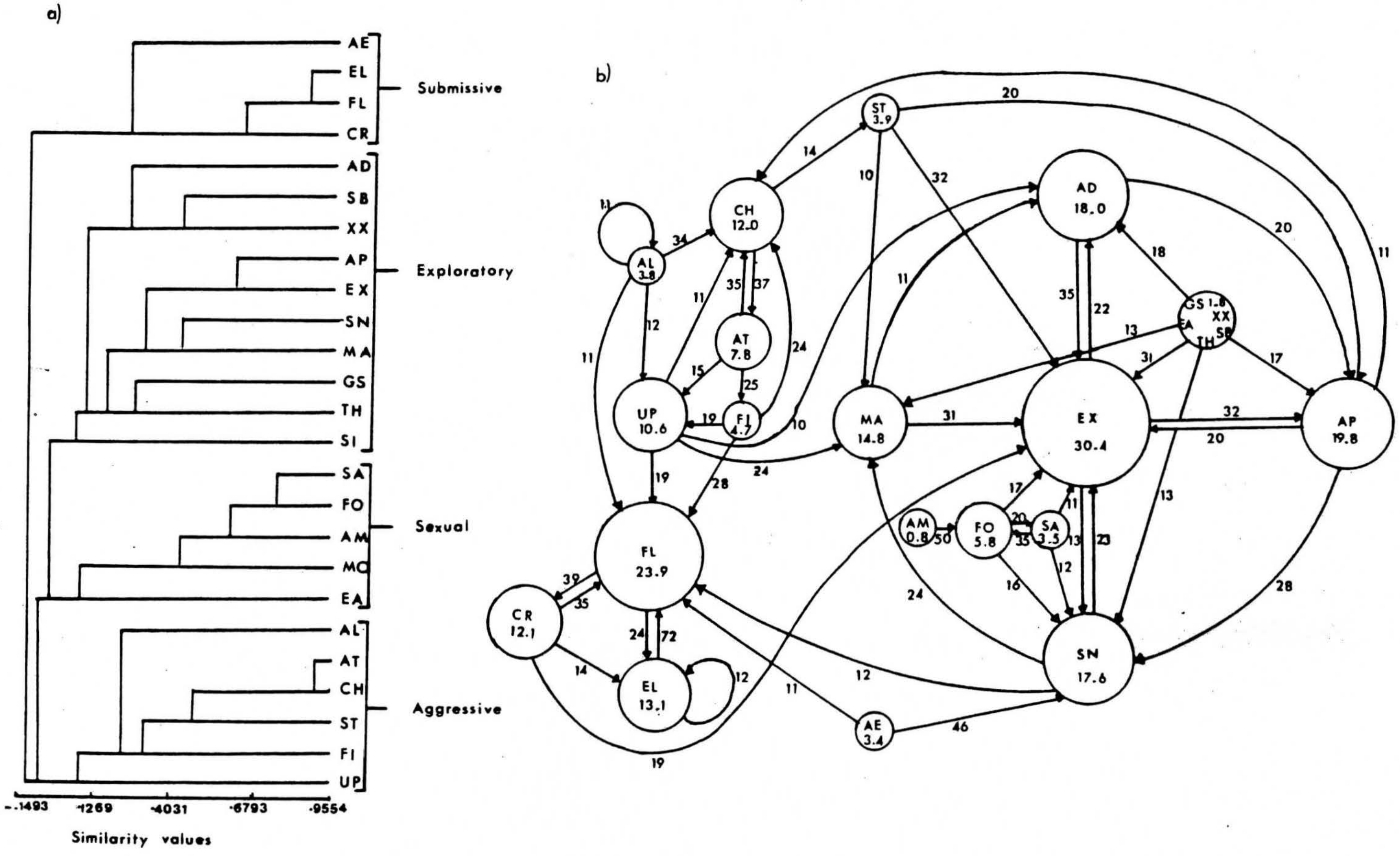


Fig. 2: Postures identified in agonistic encounters


a)
AE
EL
FL
CR
Submissive
AD
SB
XX
AP
EX
SN
MA
GS
TH
SI
Exploratory
SA
FO
AM
MO
EA
Sexual
AL
AT
CH
ST
FI
UP
Aggressive
-.1493
.1269
.4031
.6793
.9554
Similarity values
b)
ST 3.9
CH 12.0
AL 3.8
AT 7.8
UP 10.6
FI 4.7
FL 23.9
CR 12.1
EL 13.1
AD 18.0
MA 14.8
EX 30.4
AP 19.8
SN 17.6
AE 3.4
AM 0.8
FO 5.8
SA 3.5
GS 1.8 XX EA TH SB


c)
AE
FO
AP
EX
Exploratory
d)
22
15

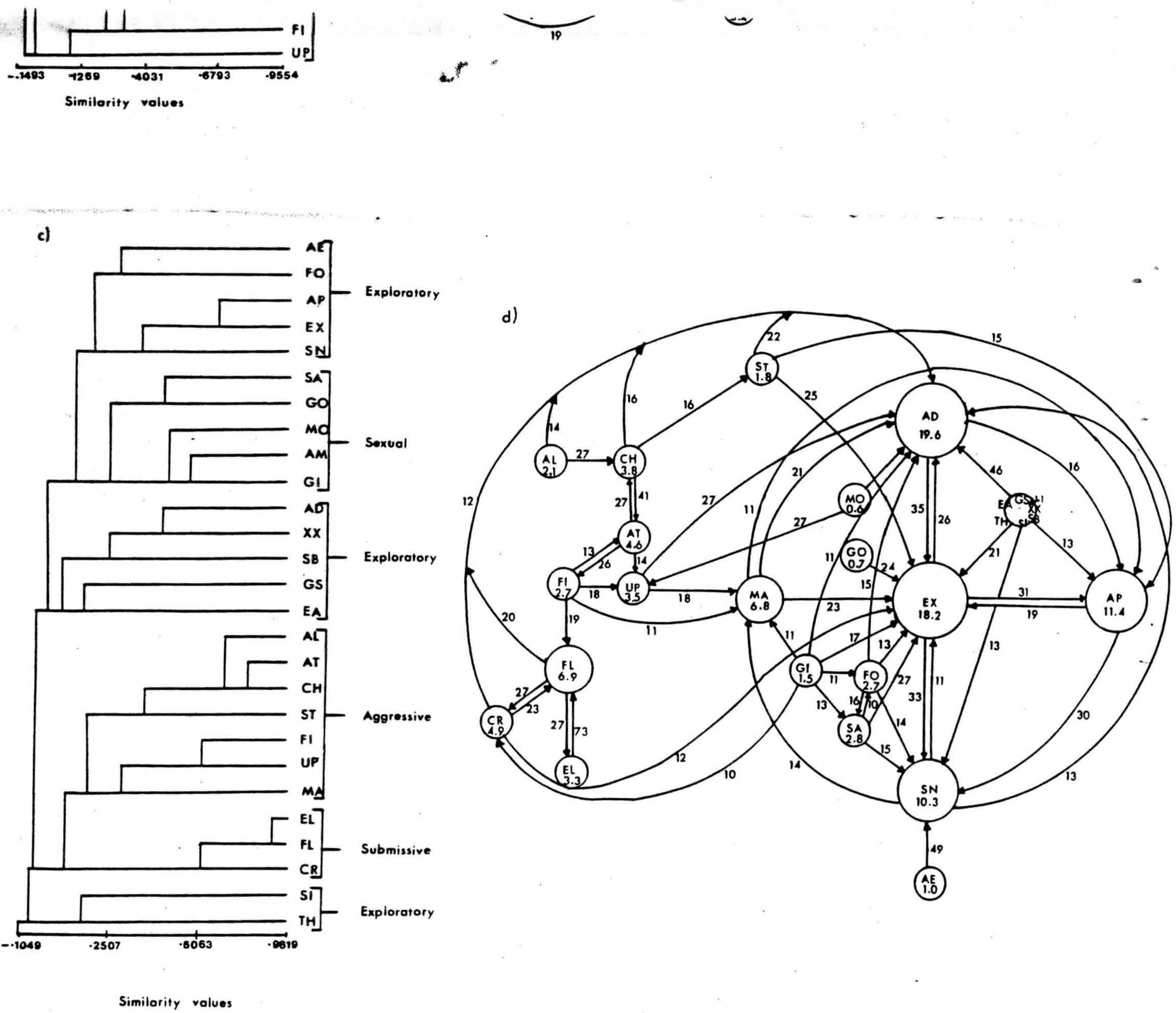


Fig. 3: a) Cluster and b) transition frequency diagrams for *G. tytonis* and *G. p. paeba*; c) cluster and d) transition frequency diagrams for *G. vallinus*, *G. setzeri* and *G. p. exilis*. Numbers in circles: mean frequencies of behaviours, numbers on lines: transition frequencies

Table 2: Levels of interaction (L.I.) in intraspecific same-sex encounters

	L.I.	± SD	n
G. p paeba females	198.8	43.0	20
G. p. paeba males	198.8	56.0	16
G. tytonis females	216.4	64.0	16
G. tytonis males	248.6	84.5	16
G. p. exilis females	129.1	63.5	16
G. p. exilis males	85.8	39.1	16
G. setzeri females	139.8	62.0	16
G. setzeri males	124.0	99.2	16
G. vallinus males	89.6	24.8	8

L.I. for male and female *G. p. paeba* and *G. tytonis* differed significantly from L.I. for male and female *G. p. exilis, G. setzeri,* and *G. vallinus* ($p < 0.02$, Mann-Whitney U-test). All other combinations were not significantly different.

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* do not produce an audible noise, and animals seem to "shiver" their hindquarters rather than "drumming".

SB = Sandbathe: The animal rolls in the sand from the side to dorsum, returning to the same side. A ventral rub is rarely included.

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".

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.

Level of interaction (LI) was computed as the mean number of acts per individual per encounter (PERRIN 1981). Levels of interaction are shown in Table 2. The Mann-Whitney U-test (STATGRAPHICS) was used to compare LI between males and females of the same species; between females, and between males of different species. LI did not differ significantly between males and females of the same species ($p > 0.05$). However, male and female *G. p. paeba* and *G. tytonis* had significantly higher levels of interaction than all other species ($p < 0.05$). Differences among *G. p. exilis, G. setzeri* and *G. vallinus* were not significant ($p > 0.05$).

Weighted pair group cluster analysis based on a correlation matrix (SIGSTAT Programme WPCLUS) was used to determine patterns of covariation of acts. Results were combined into two species-groups in order to facilitate analysis. The groups identified in the comparison of levels of interaction were utilized, i.e. *G. tytonis* and *G. p. paeba* formed one species-group, while *G. setzeri*, *G. p. exilis*, and *G. vallinus* formed a second species-group. The same species-groups were used in analysis of transition frequencies, and motivationally-linked behaviours were identified from both cluster analysis and transition frequency analysis. Results are shown in Fig. 3.

Four groups of behaviour were identified in both analyses. The dominant group consisted of exploratory and solitary behaviours, the most common of which formed a sequence. This began with AD, succeeded by AP, SN, and then MA, which returned to AD or AP. EX was performed between any of these act-sequences. Associated with this high-frequency group of acts were a number of low-frequency acts, including GS, SB, EA, XX, and TH in both species-groups. SI was included in this group in *G. vallinus-G. setzeri-G. p. exilis*, but was of low frequency in *G. tytonis-G. p. paeba*. The low-frequency acts were associated with AD, AP, SN, and EX, but not with MA.

Aggressive behaviour consisted of AT, AL, and CH, followed by ST, which returned to exploratory behaviour. UP and FI were associated with aggressive behaviour in both cluster analyses, but in transition diagrams they linked aggressive and submissive behaviour. The UP posture was succeeded by MA, terminating the aggressive encounter, or by submissive behaviour (*G. tytonis-G. p. paeba*).

Submissive behaviour consisted of EL, FL, and CR, which formed a closely-linked sequence. CR terminated the sequence, which was followed by exploratory behaviour.

Sexual behaviour was of low frequency, but in both species-groups it consisted of SA, FO, MO, and AM. In *G. vallinus-G. setzeri-G. p. exilis*, allogrooming behaviours GI and GO were also associated with sexual behaviour. Sexual behaviour occurred in sequence with SN and EX, but was also succeeded by agonistic behaviour in *G. vallinus-G. setzeri-G. p. exilis*.

The motivational analysis of the behaviour of the two species-groups revealed close similarity in the main groupings of acts. However, a difference was noted in the behaviour AD, which was preceded by 17 behaviours in *G. vallinus-G. setzeri-G. p. exilis*, while only 7 behaviours preceded AD in *G. tytonis-G. p. paeba*.

In order to simplify further analysis, low frequency acts were combined with high-frequency behaviours, based on the results of motivational analysis. Combined behaviours are indicated by 3-letter codes and acts are grouped as follows: Exploratory and solitary behaviour: ATD = AD + XX + DR + SB + GS, APR = AP + AE, SN, EXP = EX + EA + TH + SI, MA. Aggressive behaviour: AGG = AL + AT + CH + ST, UP, FI. Submissive behaviour: SUB = EL + FL + CR. Sexual behaviour: SEX = SA + MO + AM + FO, ALG = GI + GO.

Box-and-whisker plots illustrating the frequencies of acts in encounters are shown in Figs. 4 and 5. Act frequencies which differed significantly between species and sexes are listed in Table 3.

Table 3: Acts which differed significantly among species and sexes ($p < 0.05$, Mann-Whitney U-test)

Species/sexes compared	Acts
Female/male:	
G. p. paeba	FI, SEX, MA
G. tytonis	UP, SEX, ATD, SN, MA
G. setzeri	EXP
G. p. exilis	AGG, FI, ATD, ALG
Female/female:	
G. p. paeba/G. tytonis	FI
G. p. paeba/G. p. exilis	SUB
G. p. paeba/G. setzeri	SUB, ATD
G. tytonis/G. p. exilis	UP, EXP
G. tytonis/G. setzeri	FI, ATD
G. p. exilis/G. setzeri	ATD, EXP
Male/male:	
G. p. paeba/G. tytonis	UP
G. p. paeba/G. p. exilis	ATD, APR, MA, AGG, UP, FI, SEX, ALG
G. p. paeba/G. setzeri	APR, SN, MA, EXP, UP, SEX
G. p. paeba/G. vallinus	APR, SN, EXP, ALG
G. tytonis/G. p. exilis	ATD, APR, MA, EXP, AGG, UP, FI, ALG
G. tytonis/G. setzeri	APR, SN, MA, EXP, AGG, UP, FI
G. tytonis/G. vallinus	APR, SN, MA, EXP, AGG, FI, ALG
G. p. exilis/G. setzeri	ATD, SN, SEX, ALG
G. p. exilis/G. vallinus	UP
G. setzeri/G. vallinus	UP, SEX, ALG

Inter-individual variation was particularly marked in AGG and SUB acts. Contact aggression (UP, FI) was less frequently performed than AGG or SUB in all species except *G. vallinus*, where agonistic behaviour was more frequently expressed as mutual uprights.

Encounters fell roughly into one of two categories, those in which dominance was clearly established, and those in which exploratory-solitary and sexual behaviour predominated. Dominance was clearly evident in agonistic bouts, with dominant animals chasing and attacking submissive animals, which performed escape leaping, fleeing and crouching. The behaviours AGG and SUB were mutually exclusive in agonistic bouts, which accounts in part for the high degree of variability in the frequencies of these two behaviours.

Differences among species were noted in the proportion of encounters which resulted in clearly established dominance: 83 % for *G. p. paeba* (n = 18 encounters), 81 % for *G. tytonis* (n = 16), 44 % for *G. setzeri* (n = 16), 50 % for *G. p. exilis* (n = 16), and 50 % for male *G. vallinus* (n = 4).

Comparison of frequencies between males and females of the same species revealed that male *G. p. paeba* and *G. tytonis* performed significantly more contact aggression (FI, UP) and more exploratory (ATD, MA) and sexual behaviour than females. In *G. setzeri,* males performed significantly less EXP than females. *G. p. exilis* females performed more AGG, FI, and ATD than males, while males allogroomed (ALG) more often than females.

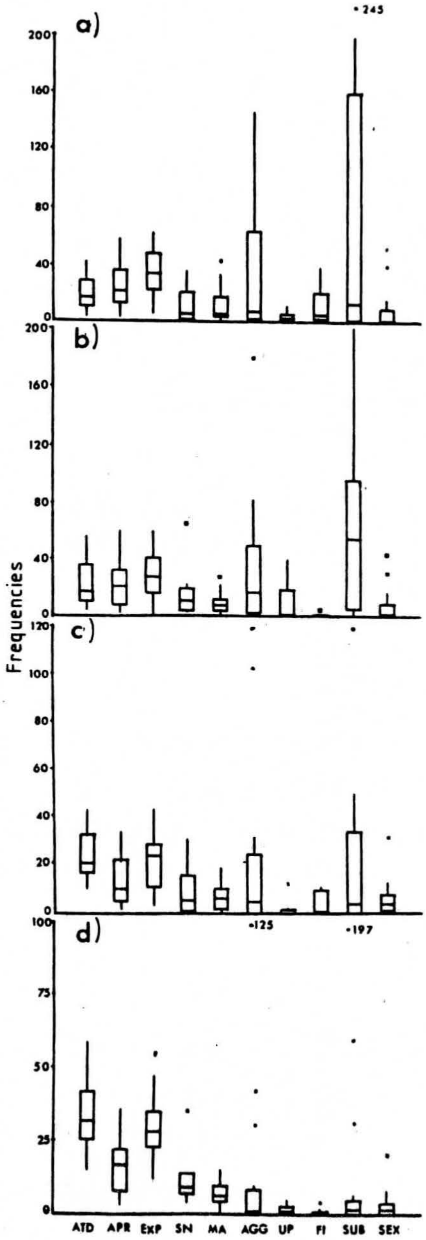


Fig. 4: Behaviour profiles for female *Gerbillurus:* a) *G. tytonis,* b) *G. p. paeba,* c) *G. p. exilis,* d) *G. setzeri* (n = 8 encounters for each species except *G. p. paeba,* where n = 10 encounters)

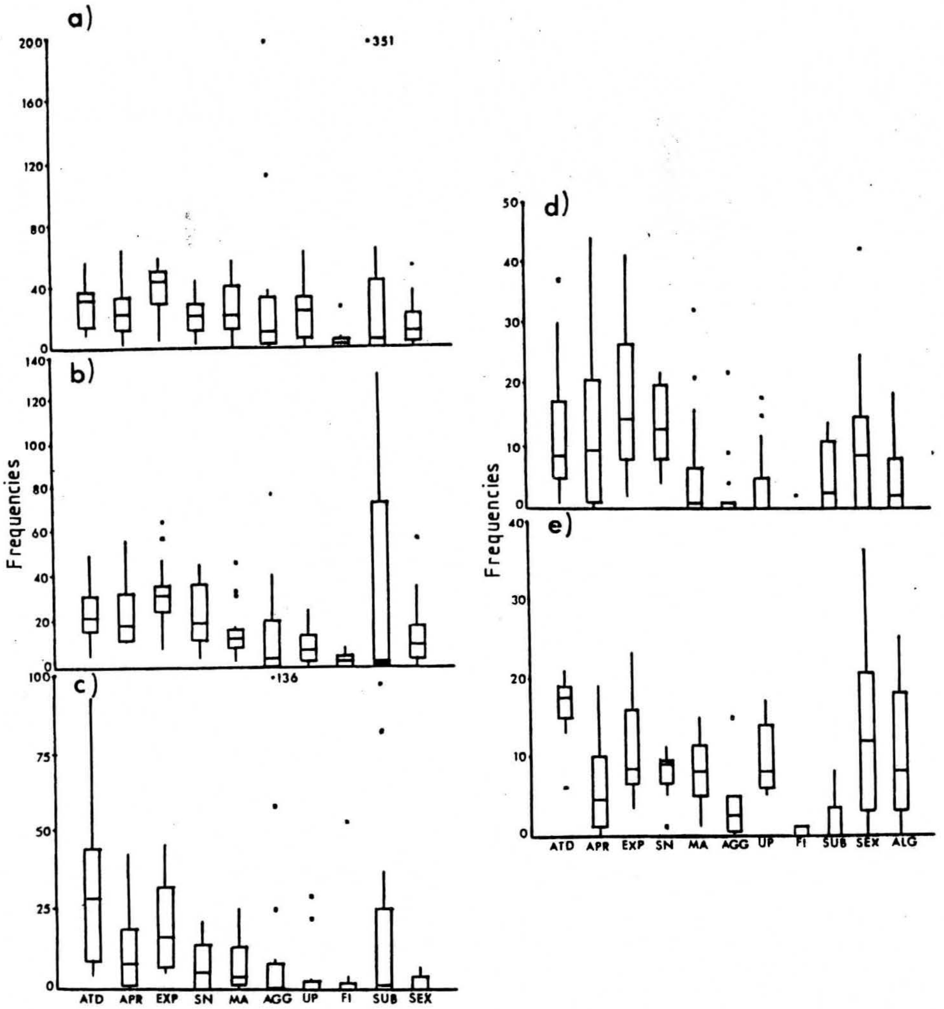


Fig. 5: Behaviour profiles for male *Gerbillurus*: a) *G. tytonis*, b) *G. p. paeba*, c) *G. setzeri*, d) *G. p. exilis*, e) *G. vallinus* (n = 8 encounters for each species except *G. vallinus*, where n = 4 encounters)

Females of different species showed fewer significant interspecies differences than males. *G. p. paeba* and *G. tytonis* females performed agonistic behaviour more frequently than *G. setzeri* and *G. p. exilis* (FI, UP, or SUB), while *G. setzeri* females watched their opponents (ATD) more frequently than other species. *G. p. exilis* explored (EXP) significantly less frequently than *G. setzeri* and *G. tytonis*.

Male *G. p. paeba* and *G. tytonis* differed significantly from other species in a number of behaviours, including more aggressive behaviour (AGG, FI, UP), more exploratory behaviour (APR, EXP, SN, MA) and less allogrooming (ALG). *G. setzeri* males performed less sexual behaviour than other species, and less ALG than *G. p. exilis* and *G. vallinus*. *G. tytonis* males differed significantly

Table 4: Mean mass (g) ± SD of dominant and submissive animals

Species		n	Dominant	Submissive	p
G. p. paeba	males	6	28.5 ± 8.3	30.2 ± 7.5	ns
G. p. paeba	females	10	28.7 ± 4.6	24.5 ± 4.1	ns
G. p. exilis	females	5	28.0 ± 2.7	24.4 ± 2.3	ns
G. tytonis	females	7	30.0 ± 5.2	28.7 ± 4.4	ns
G. tytonis	males	6	28.5 ± 3.7	30.7 ± 6.0	ns
G. setzeri	females	3	49.0 ± 7.5	51.0 ± 7.2	ns
G. setzeri	males	4	36.8 ± 5.4	42.3 ± 7.5	ns
G. vallinus	males	3	40.7 ± 6.1	38.0 ± 6.9	ns

from *G. p. paeba* males in only one behaviour, UP. *G. vallinus* performed more UP than *G. p. exilis* and *G. setzeri*. *G. p. exilis* males watched (ATD) significantly less frequently and sniffed noses (SN) more frequently than *G. setzeri.*

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 4. The means did not differ significantly in any species or sex ($p > 0.05$, t-test).

Finally, mean frequencies and levels of interaction were compared by means of weighted pair group cluster analysis in order to determine levels of similarity within the genus. The resulting dendrogram is shown in Fig. 6.

Male and female *G. p. paeba* and *G. tytonis* and female *G. p. exilis* formed one cluster, while male and female *G. setzeri* formed a second cluster. Male *G. p. exilis* and *G. vallinus* formed a third cluster, which was less closely related to other species.

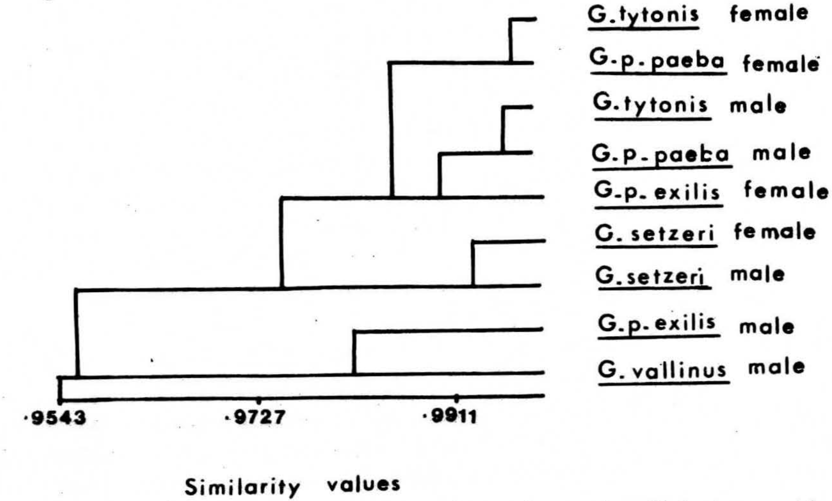


Fig. 6: Phenogram derived from cluster analysis of mean frequencies of behaviours and levels of interaction in encounters

Discussion

Some form of agonistic behaviour was observed in 94 % of encounters involving *Gerbillurus* species. Dominance was clearly established in over 80 % of *G. p. paeba* and *G. tytonis* encounters, and in over 40 % of *G. setzeri*, *G. p. exilis* and *G. vallinus* encounters. Dominance could not be determined in Mongolian gerbils after 10-min encounters (SWANSON 1974), although some agonistic behaviour was displayed in every encounter.

Agonistic behaviour in *Gerbillurus* species was more frequently expressed by chasing, attacking, fleeing, and crouching than by fighting and mutual upright postures. Male *G. p. exilis* and *G. vallinus* were exceptions to this finding, in that aggressive behaviour occurred at a low frequency in both species. In *G. vallinus*, uprights occurred more frequently than chasing and fleeing.

The upright posture has been described for many rodent species, including voles (TURNER & IVERSON 1973), mice, rats, hamsters, and guinea pigs (GRANT & MACKINTOSH 1963), and Mongolian gerbils (SWANSON 1974). It has been described as a mutual testing of dominance tendencies (TURNER & IVERSON 1973). In *Gerbillurus* species, the upright posture frequently terminated a bout of agonistic behaviour, or preceded submissive behaviour. These results support the hypothesis that dominance tendencies are decided in the mutual upright posture.

Sex differences in agonistic behaviour have been observed in several rodent species, with inter-female aggression generally being less intense than inter-male aggression (SWANSON 1974). In both hamsters and Mongolian gerbils, inter-female aggression is just as intense as inter-male aggression, and the same applies in *Gerbillurus* species. Female *G. p. exilis* were significantly more aggressive than males, while male *G. p. paeba* and *G. tytonis* displayed more FI and UP respectively than females.

The grooming invitation posture has been identified as a non-aggressive act in rats, which indicates that the animal performing the act has not attacked nor is about to attack (BARNETT 1975). The incidence of this posture in *Gerbillurus* species was highest in male *G. vallinus* and *G. p. exilis*, both of which exhibited low levels of aggression. These results support BARNETT's (1975) hypothesis that allogrooming is a non-aggressive act.

Results of this study indicate that *Gerbillurus* species differ in levels of interaction and levels of agonistic and contact-promoting behaviour. *G. p. paeba* and *G. tytonis* are most active and most aggressive, followed by female *G. p. exilis* and *G. setzeri*, which are less active and aggressive. Finally, male *G. p. exilis* and male *G. vallinus* are least active and aggressive, and include contact-promoting behaviour in encounters.

EISENBERG (1967) has used the results of neutral encounters 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 behaviour such as allogrooming. Indications from the present study are that *G. p. paeba* and *G. tytonis* are solitary, while male *G. vallinus* and *G. p. exilis* are tolerant. Female *G. p. exilis* and male and female *G. setzeri* are intermediate in solitary-tolerant tendencies.

Burrow structures may provide some information on social structures in the field. *G. setzeri* (Downs & Perrin 1989) and *G. vallinus* have interleading burrow systems and *G. vallinus* is reported to be gregarious (De Graaff 1981). The burrows of *G. paeba* and *G. tytonis* are simple, with one or two entrances. 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. *G. p. exilis* have two types of burrow systems: simple and complex, although no more than two entrances are found (Ascaray 1984). Species which are more tolerant in laboratory encounters have more complicated burrow systems, which may indicate a gregarious social system. However, indirect evidence provided by burrow structures needs to be supported by field observations on social structures.

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. Its conspecific, *G. p. exilis*, differs considerably in agonistic behaviour, this difference being particularly marked in males. The environment of the Alexandria dunefield is less harsh than that of the Namib Desert, while the sandy substrate favoured by *G. paeba* is present in both habitats. *G. p. exilis* are larger than *G. p. paeba*, wild-caught animals having a mass of 32.4 g (n = 181) (Ascaray 1984) and 22.0 g (n = 177) (Boyer 1988) respectively. Thus the reduced agonistic behaviour exhibited by *G. p. exilis* may be ecologically-related.

Evidence from general karyology reveals no differences between *G. p. paeba* and *G. p. exilis* (Schlitter et al. 1984). However, analysis of protein structure (Robbins, pers. comm.) and morphometric data (Meester et al. 1986) indicate considerable divergence of *G. p. exilis* from *G. p. paeba*. Behavioural data support the view that *G. p. exilis* differs considerably from *G. p. paeba*.

G. tytonis is a specialist sand-dune inhabitant which shows close behavioural similarity with *G. p. paeba*. This species inhabits areas of soft sand in the Namib Desert where food and water are scarce (Boyer 1988). The lack of social tolerance suggested by the present study is likely to be related to the harsh environment and competition for scarce resources.

Karyological data indicate a close affinity between *G. p. paeba* and *G. tytonis* (Schlitter et al. 1984; Qumsiyeh et al. 1987). However, protein analysis indicates wide divergence of *G. tytonis* from all other species (Robbins, pers. comm.), while morphometric data place *G. tytonis* closer to *G. setzeri* and *G. vallinus* than to *G. paeba* (Schlitter 1973). Behavioural data support the close relationship of *G. p. paeba* and *G. tytonis*.

G. setzeri and *G. vallinus* exhibit less agonistic behaviour than *G. p. paeba* and *G. tytonis*. These two species inhabit areas of harder gravel or shale, with extremely sparse vegetation in places (Griffin, pers. comm.). Little is known of the ecology of these two species. Possible reasons for the apparent evolution of sociality in these species are predator avoidance, the difficulties of burrow construction in the harder substrate, and improved ability to find food.

G. setzeri and *G. vallinus* are closely associated in karyological, protein, and mormophometric data (SCHLITTER et al. 1984; ROBBINS, pers. comm.; SCHLITTER 1973). However, agonistic behaviour analysis indicates differing levels of sociality between the two species. In the absence of more precise information on the ecology and habits of these two species, reasons for their differing levels of sociality cannot be determined.

Agonistic behaviour is one parameter influencing the spatial arrangements and resource utilization of animals in a particular habitat (DELANY 1974). In extremely arid areas, rodent species may exist at low densities, but evidence indicates that spacing mechanisms are operative (EISENBERG 1975). Although the dispersed food supply may seem to favour solitary existence in deserticolous rodents, a range of social organizations from solitary (*Gerbillus nanus*) to communal (*Tatera indica*) is exhibited (EISENBERG 1967). The present study demonstrates that closely related species may exhibit a range of social structures. Quantitative analysis of agonistic behaviour has revealed patterns of similarity which agree in part with morphometric, karyological, and protein structural data. It is suggested that phylogeny and habitat are both implicated in selection for a social system in *Gerbillurus* species.

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