Z. Säugetierkunde 55 (1990) 392–398

ISSN 0044-3468

Interspecific aggression in sympatric *Gerbillurus* species

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Receipt of Mr. 27.08. 1989

Abstract

Studied interspecific aggression in four *Gerbillurus* species, which are closely related and ecologically similar. Areas of sympatry between *G. paeba* and *G. tytonis*, *G. paeba* and *G. setzeri*, *G. tytonis* and *G. setzeri*, and *G. paeba* and *G. vallinus* have been identified. Interspecific agonistic behaviour was investigated by means of staged encounters between sympatric species in order to ascertain whether interference competition may influence ecological segregation.

Results showed that the ecological "specialists" *G. tytonis* and *G. vallinus* dominated the ecological "generalist" *G. paeba*, while *G. setzeri* avoided contact with *G. paeba* or *G. tytonis*. Interference competition through agonistic behaviour may result in ecological segregation of sympatric *Gerbillurus* species.

Introduction

Two or more closely-related and/or ecologically similar species of organisms coexisting in a particular habitat are likely to affect one another. If these species suffer as a result of the association, competition is said to occur, which may take the form of resource competition or interference competition (Krebs 1985).

Competitive ability evolves by animals becoming more efficient resource users, and/or by the evolution of interference mechanisms that prevent competing species from using scant resources (Krebs 1985). Thus, aggressive behaviour has evolved in many animals and forms part of resource competition in some situations.

Interference competition through agonistic behaviour has been implicated in several taxa of coexisting, ecologically-similar rodent species (Blaustein 1980; Grant 1972; Cranford and Derting 1983). Clear evidence for the dominance of one species in laboratory encounters is provided in most cases (Blaustein and Risser 1976; Ambrose and Meehan 1977; Banks and Fox 1968). Staged laboratory encounters have been criticized because of their artificial nature (Banks and Fox 1968), but nevertheless provide results which are usually consistent with field observations (Grant 1972).

Four species of the genus *Gerbillurus* inhabit the arid areas of Southern Africa and have similar diets (Boyer 1988; Erasmus in litt.). Several areas of sympatry have been identified: *G. paeba* and *G. tytonis* coexist along the eastern border of the Namib dunefield and along the Kuiseb River, Namibia; *G. setzeri* is reported to cross the Kuiseb River and enter the dunefield, which is normally occupied by *G. tytonis*, at times of high population density (de Graaff 1981); *G. setzeri* and *G. paeba* have been trapped together on the gravel plains near Rössing Uranium Mine; *G. vallinus* and *G. paeba* coexist in the northern Cape province (Erasmus, in litt.). All four species are nocturnally active and diurnally fossorial.

The ecology of *G. tytonis* in two areas of allopatry and in one area of syntopy with *G. paeba*, has been studied (Boyer 1988). Considerable dietary overlap between these two species occurs, but partial spatial separation may occur at certain seasons, since *G. paeba* prefer the dune trough and slope, and *G. tytonis* the dune crest. *G. paeba* and *G. tytonis* were found to be highly aggressive, *G. setzeri* less so, and *G. vallinus* least aggressive in

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intraspecific agonistic encounters (DEMPSTER and PERRIN 1989). In this study, interference competition by aggressive interaction was investigated in all species combinations known to be sympatric. It was predicted that interspecific encounters would reflect the levels of agonistic behaviour observed in intraspecific encounters. Dominant species in laboratory encounters would be expected to displace subordinate species in the field.

Materials and methods

Seven *G. paeba* (5 females, 2 males) were trapped near Swakopmund (23° 37′ S, 14° 34′ E) and 12 *G. tytonis* (7 females, 5 males) were trapped in the area south of Gobabeb (23° 37′ S, 15° 01′ E) during August 1984. Twelve *G. setzeri* (7 females, 5 males) were trapped near Rössing Uranium Mine (22° 31′ S, 14° 52′ E) in June 1985. Four *G. vallinus* (3 males, 1 female) and six *G. paeba* were trapped near Copperton (29° 59′ S, 22° 17′ E), Northern Cape in August 1986.

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 tank 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 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.

A partition was used to separate the two opponents initially and to permit investigation of the tank for 5 min before the partition was removed. Ten-min encounters were videorecorded using a video camera (JVC Model TK1700EG) and recorder (National Portable VCR NV-180). The animals were weighed after the encounter. Twenty encounters including all possible sex combinations were staged in *G. paeba-G. tytonis, G. paeba-G. setzeri,* and *G. tytonis-G. setzeri* combinations. The small numbers of animals trapped permitted only 9 encounters in the *G. vallinus-G. paeba* combination.

Agonistic behaviour in intraspecific same-sex encounters consisted of attacking (AT), attack leaping (AL), chasing (CH), fighting (FI), uprights (UP), stop/freeze (ST), escape leaping (EL), fleeing (FL), and crouching (CR). The aggressive acts AT, AL, and CH and the submissive acts EL, FL, and CR were mutually exclusive, i.e., dominance was established at the beginning of an encounter. In addition, approaching (AP) and exploring

Table 1. **Mean dominance – submissive scores in interspecific encounters**
n = 5 encounters for each combination, except where indicated in parentheses

Subject	Opponent *G. t.* ♀	*G. t.* ♂	*G. s.* ♀	*G. s.* ♂	*G. p.* ♀	*G. p.* ♂	*G. v.* ♀	*G. v.* ♂
G. tytonis ♀			25.5	32.6	63.7	66.0		
G. tytonis ♂			51.4	44.4	−68.5	35.3		
G. setzeri ♀	−30.3	−21.8			−46.1	31.8		
G. setzeri ♂	−25.7	−74.1			−54.4	−57.0		
G. paeba ♀	−76.9	65.4	53.9	46.2			26.0 (1)	−32.9 (3)
G. paeba ♂	−61.2	10.0	2.3	44.7			−17.0 (1)	−23.1 (4)
G. vallinus ♀					69.0 (1)	60.0 (1)		
G. vallinus ♂					35.3 (3)	47.7 (4)		

(EX) were significantly more frequently performed by dominant than by submissive animals ($p < 0.05$, chi-squared contingency table analysis).

A scoring system was applied to the results of all interspecific encounters in order to determine the dominance/submissive relationships. Scores were calculated for each individual in each encounter by summing the following frequencies:

Offensive behaviour: (AT, AL and CH) × 2
Exploratory behaviour: (AP and EX) × 1
Submissive behaviour: (EL, FL and CR) × −2

A mean score for each species in each class of encounters was calculated. Dominance/submissive scores were compared by means of Wilcoxon's T-test.

Results

Mean frequencies (± S.E.) of agonistic behaviours are shown in Figures 1 to 4, and dominance scores in Table 1.

Encounters between *G. tytonis* and *G. paeba* (Fig. 1) involved a high level of interaction and aggression. Males were less aggressive towards each other than females were, and females of both species dominated males of both species. Differences between dominance indices for all *G.paeba-G. tytonis* encounters were not significant, however if female *G. paeba*-male *G. tytonis* encounters were excluded, *G. tytonis* was significantly dominant over *G. paeba* ($p < 0.005$).

In *G. paeba-G. setzeri* encounters (Fig. 2), little aggressive behaviour was displayed in all classes of encounter. Male and female *G. setzeri* behaved submissively, despite the low

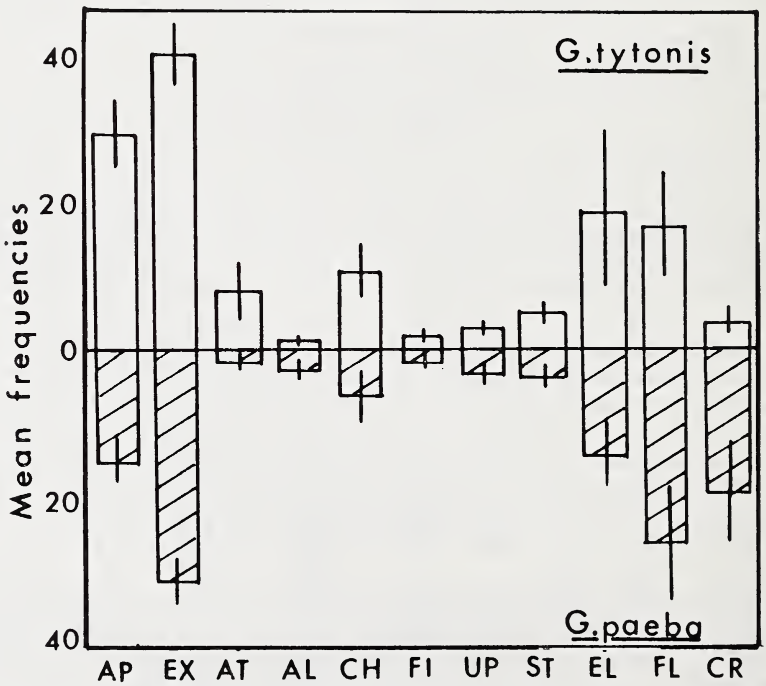

Fig. 1. Mean frequencies (± S.E.) of agonistic behaviours in *G. tytonis-G. paeba* encounters (n = 20)

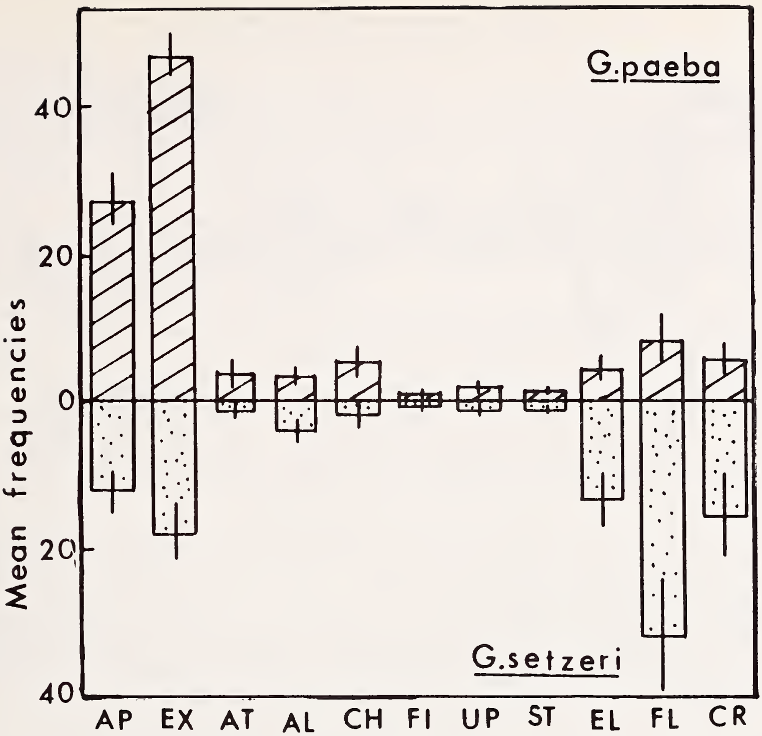

Fig. 2. Mean frequencies (± S.E.) of agonistic behaviours in *G. paeba-G. setzeri* encounters (n = 20)

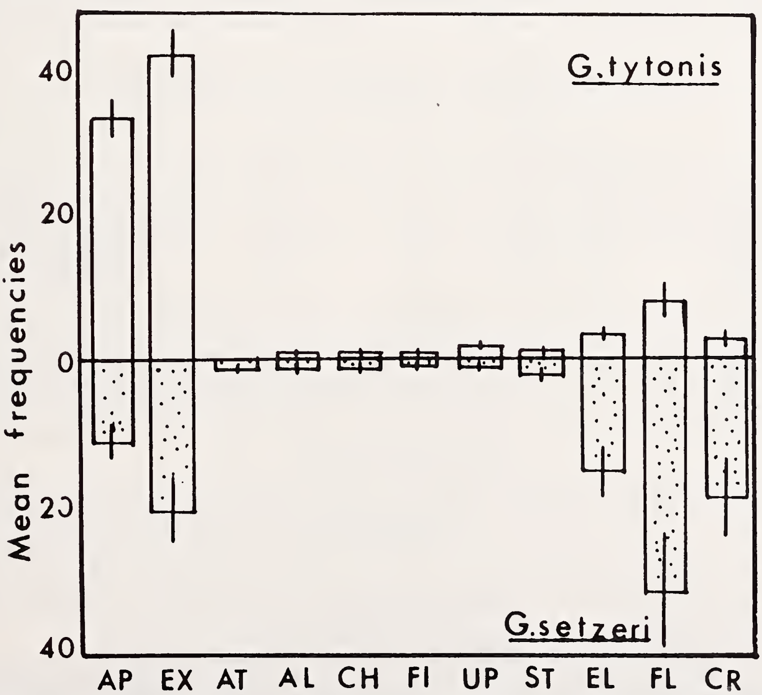

Fig. 3. Mean frequencies (±S.E.) of agonistic behaviours in *G. tytonis–G. setzeri* encounters (n = 20)

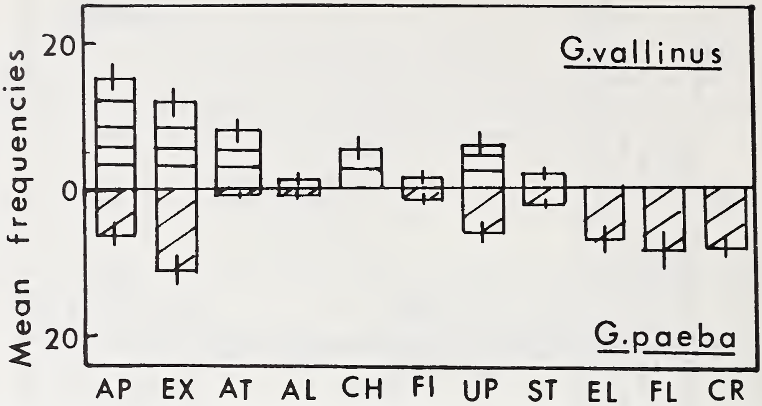

Fig. 4. Mean frequencies (± S.E.) of agonistic behaviours in *G. vallinus*-*G. paeba* encounters (n = 9)

level of aggressive behaviour displayed by their opponents. Most aggression was observed in female *G. setzeri*-male *G. paeba* encounters. Differences in dominance indices were significant for all encounters ($p < 0.01$).

Encounters between *G. tytonis* and *G. setzeri* (Fig. 3) were characterised by little aggression, and submissive behaviour performed by both species. Male and female *G. setzeri* performed more submissive behaviour than their opponents. *G. tytonis* was significantly dominant over *G. setzeri* in all encounters ($p < 0.001$).

In nine encounters between *G. vallinus* and *G. paeba* (N. Cape) (Fig. 4), *G. vallinus* performed more aggressive behaviour than *G. paeba* and no submissive behaviour, while the converse was true for *G. paeba*. Dominance indices did not differ significantly ($p > 0.1$).

Table 2. **Mean mass (g) of laboratory and wild-caught gerbils**

Species	Laboratory mean ± S.D.	n	Wild-caught	n
G. paeba	33.9 ± 10.2	19	22.0	177 (Boyer 1988)
G. tytonis	29.9 ± 4.9	16	25.0	168 (Boyer 1988)
G. setzeri	44.7 ± 10.6	14	37.6	31 (this study)
G. vallinus	40.9 ± 8.9	5	31.5	17 (this study)

Since dominance may be influenced by body size, the mean mass of laboratory and wild-caught individuals is shown in Table 2. Individual animals used in this study were generally larger than the mean mass quoted from field studies. *G. setzeri* was the heaviest species, followed by *G. vallinus*, while *G. tytonis* and *G. paeba* were the lightest species.

Discussion

The linear dominance hierarchy suggested by interspecific encounters involving *G. paeba, G. tytonis* and *G. setzeri* is: 1. *G. tytonis* females; 2. *G. paeba* females; 3. *G. tytonis* males; 4. *G. paeba* males; 5. *G. setzeri* females; 6. *G. setzeri* males.

This hierarchy reflects the results of intraspecific agonistic encounters, in which *G. paeba and G. tytonis* were identified as more aggressive than *G. setzeri* (Dempster and Perrin 1989).

Male and female *G. vallinus* dominated male and female *G. paeba* (N. Cape), however, differences were not statistically significant. This contradicts the results of intraspecific agonistic encounters, which identified *G. vallinus* as less aggressive than *G. paeba* from the Namib desert (DEMPSTER and PERRIN 1989).

Body size has been implicated in the dominance patterns of sympatric species of kangaroo rats (BLAUSTEIN and RISSER 1976; FRYE 1983). GRANT (1972) has stated that in interspecific encounters between rodents, absolute body size is less important than size relative to the maximum for that species.

The assumption is made that all individuals used in this study were near the maximum body size for the species. However, dominance did not always correlate with body size. *G. setzeri,* the largest species, was dominated by the smaller *G. tytonis* and *G. paeba.* Body size may have influenced the outcome of encounters between the larger *G. vallinus* and *G. paeba.* GRANT's (1972) statement is only partially supported by these data.

Ecological "specialist" species generally dominate ecological "generalist" species (BLAUSTEIN and RISSER 1976; AMBROSE and MEEHAN 1977; MARTIN 1984), however, experience may influence the outcome of encounters. Animals from areas of sympatry are more aggressive towards each other than are animals from areas of allopatry (BANKS and FOX 1968; MARTIN 1984).

To date, little information has been published on the realized niches of the species of the genus *Gerbillurus. G. 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). PAVLINOV (1982) regards *G. paeba* as the most primitive of the *Gerbillurus* species, and the other three species as "specialists". *G. paeba* was dominated by the "specialists" *G. tytonis* and *G. vallinus*, supporting the hypothesis of dominance of "specialist" species.

Interactions between *G. paeba* and *G. setzeri* and between *G. tytonis* and *G. setzeri* were characterized by mutual avoidance rather than aggressive interaction. However, the "specialist" *G. setzeri* was dominated by the "generalist" *G. paeba*, and by the "specialist" *G. tytonis.* Behavioural differences resulting from differing habitats may have resulted in a reduction in interaction between the species. It is suggested that interference competition may result in the displacement of *G. setzeri* in areas of sympatry, but that mutual avoidance is more likely to occur than aggressive interaction.

Past experience may have influenced the results of encounters between *G. vallinus* and *G. paeba*, since the animals used in this study were all trapped within an area of approximately one hectare. It is suggested that the "specialist" species *G. vallinus* displaces the "generalist" species *G. paeba* in areas of syntopy. Due to the small sample size, these results are tentative.

The present study provides laboratory evidence of interspecific aggression in four *Gerbillurus species*, with clear patterns of dominance emerging in most species combinations. Field evidence is now required in order to assess more fully the role of interference competition in the ecological segregation of these species.

Acknowledgements

This study was supported by a C.S.I.R. bursary for M. Sc. study (E.R.D.), research funding from the C.S.I.R. and University of Natal Research Fund (M.R.P.). We wish to thank the Directorate of Nature Conservation, Namibia, for their cooperation.

Zusammenfassung

Zwischenartliche Aggression unter sympatrischen Gerbillurus-Arten

Die vier Arten der Gattung *Gerbillurus* sind nah verwandt und ökologisch ähnlich. Sympatrische Vorkommen sind gefunden worden bei *G. paeba* und *G. tytonis, G. paeba* and *G. setzeri, G. tytonis* und *G. setzeri* und *G. paeba* und *G. vallinus.* Meist sind die Arten aber allopatrisch. In Begegnungs-

versuchen in Gefangenschaft wurde geprüft, ob die Dominanzbeziehungen bei Auseinandersetzungen zwischen den Arten ihre ökologische Trennung im Freiland erklären können.

Die Versuche ergaben, daß die ökologischen Spezialisten *G. tytonis* und *G. vallinus* dem Generalisten *G. paeba* überlegen waren. *G. setzeri* wich *G. paeba* und *G. tytonis* aus. Danach könnte agonistisches Verhalten die Separation der Arten in sympatrischen Vorkommen mit bedingen.

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