NA-9163.

9235

59

Ethology 83, 326—334 (1989)

ISSN 0179-1613

G. p - paeba
p. exilis
tytonis.
setzeri
vallinus

1984 - 86,
lab study

Department of Zoology and Entomology, University of Natal, Pietermaritzburg

Male-Female Interactions in Hairy-footed Gerbils (Genus *Gerbillurus*)

EDITH R. DEMPSTER & M. R. PERRIN 1989

DEMPSTER, E. R. & PERRIN, M. R. 1989: Male-female interactions in hairy-footed gerbils (genus *Gerbillurus*). Ethology 83, 326—334.

Abstract

Staged 10-min encounters between male and female gerbils of the same species were characterized by high levels of exploratory and solitary behaviour, variable levels of agonistic behaviour, and little contact-promoting behaviour. Female *Gerbillurus paeba paeba*, *G. p. exilis* and *G. tytonis* dominated males of these species, while male and female *G. setzeri* and *G. vallinus* were equally aggressive.

Results of this study indicate that *G. p. paeba*, *G. p. exilis* and *G. tytonis* are aggressively solitary and that females behave aggressively towards unfamiliar males, while *G. setzeri* and *G. vallinus* are more tolerant. This is in partial agreement with findings for other gerbil species.

Corresponding author: E. R. DEMPSTER, Department of Zoology and Entomology, University of Natal, Pietermaritzburg 3200, South Africa.

Introduction

Hairy-footed gerbils (genus *Gerbillurus*) are nocturnally active, burrow-dwelling rodents of the arid areas of southern Africa. Four species, including two subspecies of one species, were investigated in this study. *G. paeba paeba* inhabits areas of soft sand throughout the arid western half of southern Africa; *G. p. exilis* exists as an isolated population in a coastal dunefield in the Eastern Cape province, South Africa. *G. tytonis* is restricted to the sand-dunes of the Namib Desert. *G. setzeri* is found on the gravel plains of the Namib Desert north of the Kuiseb River, while *G. vallinus* inhabits areas of shaley soil in the north-western Cape province and southern parts of Namibia (SMITHERS 1983).

Little information is available on the social structures of these species. Gerbilline rodents are reported to be basically solitary, females occupy relatively small home ranges which do not overlap extensively, while males occupy large, overlapping home ranges. Generally, adult gerbils occupy separate burrows and exhibit low tolerance of conspecifics (DALY & DALY 1974, 1975; ÅGREN 1979). In

U.S. Copyright Clearance Center Code Statement: 0179-1613/89/8304-0326$02.50/0

the Saharan gerbil, *Meriones libycus*, only females were observed to attack conspecifics (ÅGREN 1979), and female *M. crassus* dominated males in laboratory encounters (DALY & DALY 1975).

Female Mongolian gerbils (*M. unguiculatus*) were just as aggressive in same-sex encounters as males (SWANSON 1974). Females behaved aggressively with strange males, even when in oestrus (ÅGREN 1984), and females were more aggressive towards males than to other females (SWANSON 1974). Familiarity between males and females is essential to ensure breeding in this species (SWANSON 1974).

Intraspecific same-sex encounters in *Gerbillurus* species indicated differing levels of social tolerance among species. *G. p. paeba* and *G. tytonis* were most aggressive, female *G. p. exilis* and *G. setzeri* less so, and male *G. p. exilis* and male *G. vallinus* performed little agonistic behaviour. The last two species included contact-promoting behaviour in encounters between unfamiliar animals (DEMPSTER 1986). Burrow structures were simple in highly aggressive species (*G. p. paeba* and *G. tytonis*), and more complex in *G. setzeri* and *G. vallinus* (DOWNS & PERRIN 1989). Both simple and complex burrows were found in the habitat of *G. p. exilis* (ASCARAY 1984).

In the present study, the behaviour of males and females in intraspecific male-female encounters was observed. It was anticipated that the behaviour of different species would reflect the social structures inferred from same-sex encounters.

Methods and Materials

7 *G. p. 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 lab-bred *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 individually 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 16 L : 8 D using light supplied by a 100-W light bulb. The circadian photoperiod was reversed; temperature was maintained at 25 °C.

A male and female of the same species were introduced into a neutral arena (60 × 30 × 30 cm glass terrarium) and permitted to investigate the arena for 5 min while separated by a partition. The first 10 min of interaction were videorecorded after removal of the partition. The oestrous stage was not considered in this study, and all males had scrotal testes.

Videotapes were transcribed using 2-letter codes for each of 29 acts and postures which had been identified in same-sex encounters. Subsequently, low-frequency acts were combined with co-occurring high-frequency acts to give a final list of 11 behaviours.

8 encounters for each species were staged, except for *G. vallinus*, where the small number of animals trapped permitted only 3 encounters. Individual animals were not used repeatedly over a short period of time.

Frequencies of acts were calculated by means of a computer programme, which also calculated frequencies of all possible pair-sequences of acts. Since sample sizes for each species were small, results of pair-sequence analysis were pooled for males of all species and for females of all species.

Conditional probability of each dyad was calculated as

$$P_{ij} = n(i, j)/T_i$$

where $n(i, j)$ = frequency of dyad i−j
T_i = total frequency of act i
P_{ij} = probability of occurrence of dyad i−j

Dyads occurring less than 10 times and those with conditional probabilities less than 10 % were omitted from the analysis.

Results

Kinematic graphs constructed from the results of sequence analysis are shown in Fig. 1. Behaviours and equivalent codes are listed in Table 1.

Table 1: List of behavioural acts and codes, and proportion of total number of encounters in which > 5 acts (> 1 act for ALG) were exhibited

Original acts	Combined acts	Proportion of encounters Males n = 35	 Females n = 35
AD = attend DR = drum with hindfeet XX = kick sand back with hindfeet GS = self-grooming SB = sandbathe	ATD	83 %	97 %
AE = elongate approach AP = approach	APR	69 %	80 %
SN = sniff noses	SN	60 %	60 %
EX = explore EA = eat SI = sit TH = threaten	EXP	89 %	97 %
MA = move away	MA	63 %	66 %
SA = sniff anogenital region FO = follow AM = attempted mount MO = mount	SEX	54 %	37 %
GI = groom invitation GO = allogroom	ALG	23 %	20 %
AT = attack AL = attack leap CH = chase ST = stop	AGG	31 %	63 %
FI = fight	FI	26 %	26 %
UP = upright	UP	46 %	40 %
EL = escape leap FL = flee CR = crouch	SUB	57 %	34 %

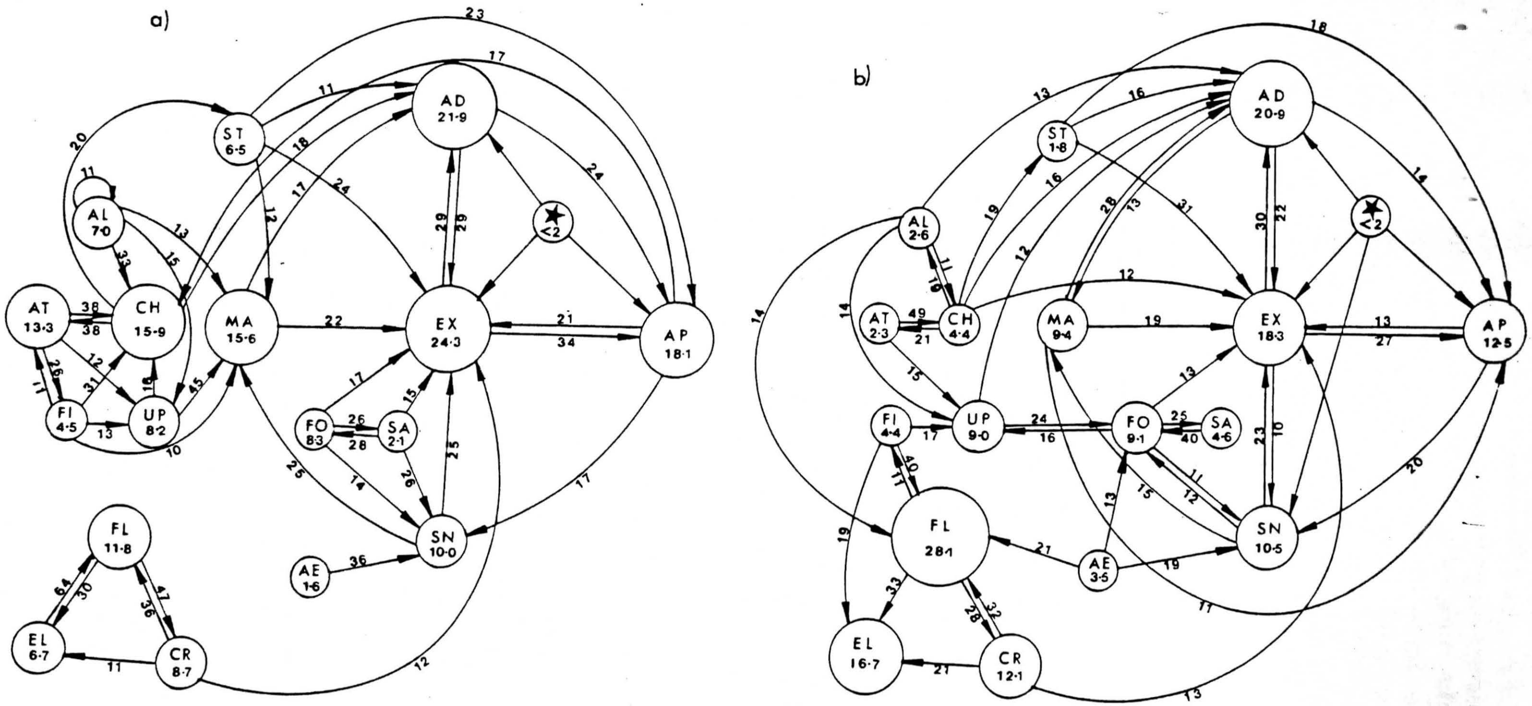

Fig. 1: Kinematic graphs indicating the most common sequences of acts for a) females and b) males in male-female encounters. Numbers in circles: mean frequencies, numbers on lines: conditional probabilities. * = SI, TH, SB, EA, GS, XX, DR

Males and females followed similar sequences of behaviour. Non-agonistic behaviour formed a sequence which included naso-nasal sniffing, and several low-frequency behaviours such as self-grooming, sandbathing and eating. Sexual behaviour was represented by SA and FO, which occurred in sequence with SN and EX. In males, AE was associated with sexual behaviour, and UP occurred in sequence with FO.

Aggressive behaviour (AT, AL, CH, ST) was initiated by AP in females, but not in males. Male aggressive and submissive (EL, FL, CR) behaviour was linked by UP and FI, but these two groups of behaviour were not linked in females. FI in females occurred in sequence with aggressive behaviour, while in males FI was associated with submissive behaviour.

Statistical analysis of sequences was not attempted since the assumption of stationarity was violated.

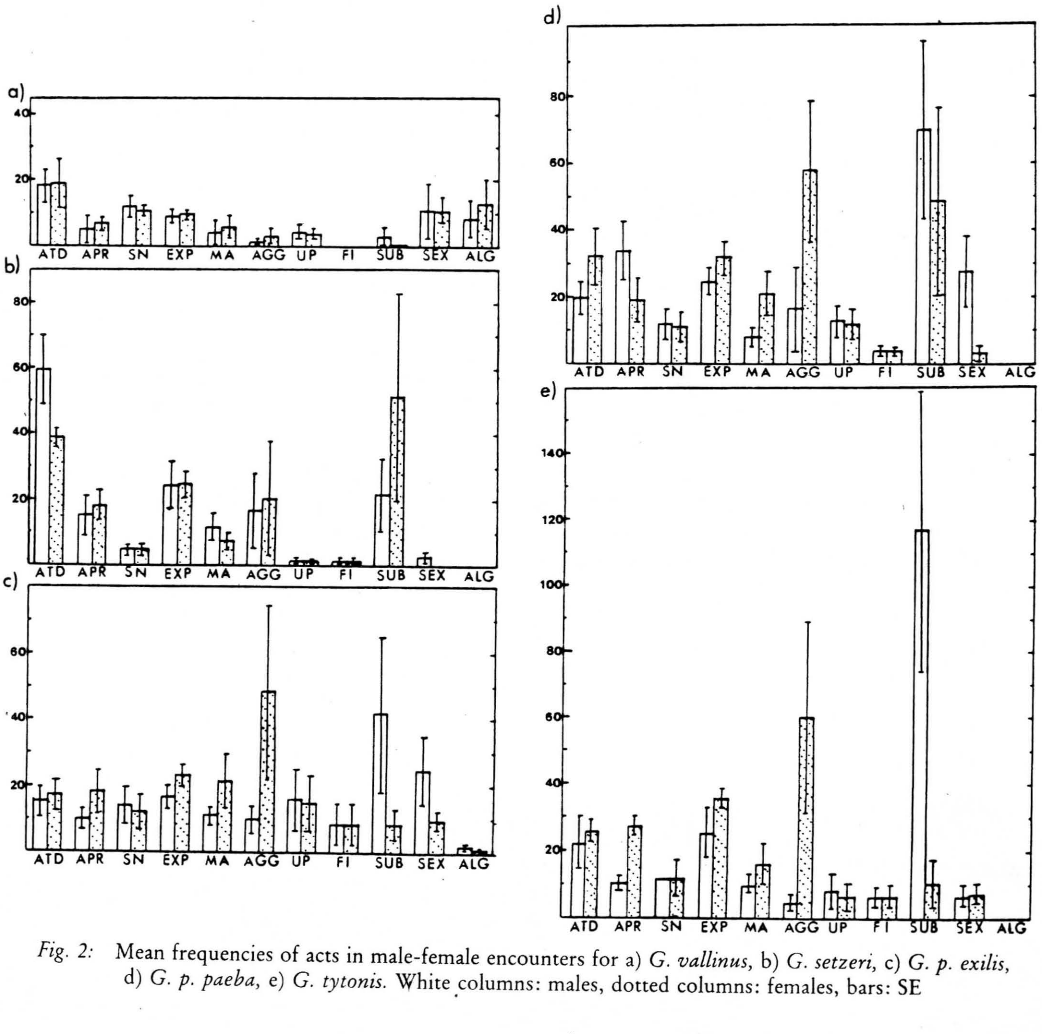

Fig. 2: Mean frequencies of acts in male-female encounters for a) *G. vallinus,* b) *G. setzeri,* c) *G. p. exilis,* d) *G. p. paeba,* e) *G. tytonis.* White columns: males, dotted columns: females, bars: SE

Mean frequencies of behaviours are illustrated in Fig. 2. Frequencies of behaviours were compared between males and females (excluding *G. vallinus*) by means of the Wilcoxon sign-ranked test; differences were not significant for any behaviour except SEX in *G. p. paeba*. In four species (*G. p. paeba, G. p. exilis, G. tytonis* and *G. setzeri*), the mean frequency of aggressive behaviour was higher for females than for males. Male *G. p. paeba, G. p. exilis* and *G. tytonis* were more submissive than females of these species. These differences were not significant for individual species, but combined results for *G. p. paeba, G. p. exilis* and *G. tytonis* revealed that females were significantly more aggressive and males more submissive ($p < 0.05$, Wilcoxon sign-ranked test). Combined results for *G. setzeri* and *G. vallinus* were not significantly different.

Pair-wise comparisons among species (excluding *G. vallinus*) were conducted in order to identify behaviours which differed significantly among species. Significant differences are listed in Table 2.

Table 2: Behaviours which differed significantly in frequency among species ($p < 0.05$, Mann-Whitney U-test)

Species compared	Behaviours Females	 Males
G. p. paeba & *G. p. exilis*	SEX ($e^2 > p^1$)	APR ($p > e$)
G. p. paeba & *G. tytonis*	—	APR ($p > t^3$)
G. p. paeba & *G. setzeri*	SEX ($p > s^4$)	ATD ($s > p$) UP, SEX ($p > s$)
G. tytonis & *G. p. exilis*	EXP ($t > e$)	—
G. tytonis & *G. setzeri*	ATD ($s > t$) SEX ($t > s$)	ATD ($s > t$)
G. setzeri & *G. p. exilis*	SEX ($e > s$)	ATD ($s > e$) SEX ($e > s$)

p^1 = *G. p. paeba*
e^2 = *G. p. exilis*
t^3 = *G. tytonis*
s^4 = *G. setzeri*

Female *G. p. exilis* displayed significantly more sexual behaviour than *G. p. paeba*, female *G. tytonis* and *G. p. exilis* also performed significantly more sexual behaviour than *G. setzeri*. Among males, *G. p. paeba* and *G. p. exilis* showed more sexual behaviour than *G. setzeri*.

Agonistic behaviour in the form of mutual uprights was significantly more frequent in male *G. p. paeba* than male *G. setzeri*. A high level of individual variation in aggressive (AGG) and submissive (SUB) behaviour in all species is indicated by large SE. Allogrooming was performed only by *G. p. exilis* and *G. vallinus*.

Exploratory behaviour (EXP) occurred significantly more frequently in female *G. tytonis* than female *G. p. exilis*. Male and female *G. setzeri* watched (ATD) each other more frequently than other species, and male *G. p. paeba* approached (APR) females more frequently than male *G. tytonis* and *G. p. exilis*.

Discussion

The behaviour of *Gerbillurus* species in male-female encounters closely resembled that in same-sex encounters (DEMPSTER & PERRIN 1989). This is in contrast to Mongolian gerbils, in which females displayed increased levels of aggression in male-female encounters, and males displayed more footstomping and sexual behaviour (SWANSON 1974).

Fewer significant inter-sex and interspecific differences were noted in male-female encounters than in same-sex encounters (DEMPSTER & PERRIN 1989). This could be due to the smaller sample size in male-female encounters. However trends observed in same-sex encounters were also evident in the present study. *G. setzeri* watched (ATD) more frequently than other species; male *G. p. paeba* performed more uprights than *G. setzeri* and *G. p. exilis*, and agonistic behaviour in *G. vallinus* occurred in the form of uprights rather than chasing, attacking and fleeing. *G. p. exilis* and *G. vallinus* were observed to allogroom in same-sex encounters, and were the only two species to allogroom in male-female encounters.

Female *G. p. paeba*, *G. p. exilis* and *G. tytonis* were aggressively superior to males of these species, while male and female *G. setzeri* and *G. vallinus* were equally aggressive.

Female hamsters were aggressively dominant over males, except for a short period at oestrus, when aggressive behaviour was suppressed by sexual behaviour (PAYNE & SWANSON 1970). It is suggested that the female's unreceptive state is communicated to the male by her aggressive behaviour rather than by olfactory stimuli (PAYNE & SWANSON 1970).

The present results, together with those for same-sex pairings, indicate that three *Gerbillurus* taxa, namely *G. p. paeba*, *G. p. exilis* and *G. tytonis* are aggressively solitary, and females dominate males. This is in agreement with findings for other gerbil species, except some *Tatera* and *Taterillus* species, which are communal (DALY & DALY 1975). *G. setzeri* are less aggressive than other species, but lack the contact-promoting behaviour of *G. vallinus*. These two species may possess a more tolerant social system, with *G. vallinus* being more social than *G. setzeri*.

The present study shows closer behavioural similarity between *G. p. paeba* and *G. p. exilis* than was evidenced in same-sex encounters (DEMPSTER & PERRIN 1989). Allogrooming, which is performed by *G. p. exilis* and not by *G. p. paeba*, inhibits aggression (BARNETT 1975), and may indicate a difference in social tolerance between the two subspecies.

Chromosomal (SCHLITTER et al. 1984) and ecological (BOYER 1988) similarities between *G. p. paeba* and *G. tytonis* ($2n = 36$) may be reflected in similarities in their agonistic behaviour. These two species exhibited high levels of aggression in intraspecific and interspecific encounters (DEMPSTER & PERRIN 1989; DEMPSTER 1986), providing strong evidence for the solitary nature of these species.

The aggressive superiority of female *G. p. paeba* and *G. tytonis* may be related to the necessity for territorial defence of scarce food resources in the extremely arid environment of *G. p. paeba* and *G. tytonis*. Female territoriality maximizes reproductive success by limiting resource utilization in a defended area (PERRIN 1981). Food caching, which is characteristic of all *Gerbillurus* species (ASCARAY 1984; DEMPSTER & PERRIN, unpubl. obs.), may increase the aggressiveness of females as they defend food resources which supply additional energy required for pregnancy and lactation. The environment of *G. p. exilis* is less arid than that of *G. p. paeba* (ASCARAY 1984), thus reduced competition for food may result in greater social tolerance in this subspecies.

G. setzeri and *G. vallinus* both have a diploid number of 60 chromosomes (SCHLITTER et al. 1984), but little is known of their ecology. Both species inhabit gravel plains where food and shelter are extremely scarce in areas (DOWNS & PERRIN, pers. obs.). Burrow structures (DOWNS & PERRIN 1989) and studies of agonistic behaviour are indicative of a more tolerant social structure, with no evidence of male or female dominance. Male-female aggression was more intense in *G. setzeri* than *G. vallinus*, and allogrooming was not performed in observed encounters. Thus *G. vallinus* may be more colonial than *G. setzeri*. This evidence is supported by studies of intraspecific same-sex and interspecific encounters (DEMPSTER & PERRIN 1989; DEMPSTER 1986).

The role of aggression in maintaining reproductive isolation in closely-related species has been investigated in four chromosomal species of mole-rats (NEVO et al. 1986). Hairy-footed gerbils, like Mongolian gerbils (SWANSON 1974) and hamsters (PAYNE & SWANSON 1970) were generally intolerant of conspecifics in male-female encounters. No copulations were observed in 35 encounters between unfamiliar animals. Aggressive behaviour, as in hamsters (PAYNE & SWANSON 1970) may inhibit sexual behaviour in hairy-footed gerbils. The conditions for female receptivity and successful copulation are unknown at present, and the behavioural mechanisms operating in the recognition of conspecific mates are currently being investigated.

Acknowledgements

We are grateful to Mr. R. DEMPSTER for assistance with programming. This study was supported by a C.S.I.R. Bursary for M.Sc. study (DEMPSTER), and research funding from the C.S.I.R. and University of Natal Research Fund (PERRIN).

Literature Cited

ÅGREN, G. 1979: Field observations of social behaviour in a Saharan gerbil: *Meriones libycus*. Mammalia **43**, 135—146.

— — 1984: Pair formation in the Mongolian gerbil. Anim. Behav. **32**, 528—535.

ASCARAY, C. M. 1984: An ecological study of the hairy-footed gerbil, *Gerbillurus paeba* in an eastern Cape dunefield. Unpubl. M.Sc. Thesis, Univ. of Port Elizabeth, Port Elizabeth.

BARNETT, S. A. 1975: The Rat: A Study in Behaviour. Revised ed. Univ. of Chicago Press, Chicago.

BOYER, D. 1988: Effects of rodents on plant recruitment production in the dune area of the Namib desert. Unpubl. M.Sc. Thesis, Univ. of Natal, Pietermaritzburg.

DALY, M. & DALY, S. 1974: Spatial distribution of a leaf-eating Saharan gerbil (*Psammomys obesus*) in relation to its food. Mammalia **38**, 591—603.

— — 1975: Socio-ecology of Saharan gerbils, especially *Meriones libycus*. Mammalia **39**, 289—311.

DEMPSTER, E. R. 1986: A comparative study of agonistic behaviour in hairy-footed gerbils of the genus *Gerbillurus* Shortridge 1942. Unpubl. M.Sc. Thesis, Univ. of Natal, Pietermaritzburg.

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

DOWNS, C. T. & PERRIN, M. R. 1989: An investigation of the macro- and micro-environments of four *Gerbillurus* species. Cimbebasia, in press.

NEVO, E., HETH, G. & BEILES, A. 1986: Aggression patterns in adaptation and speciation of subterranean mole rats. J. Genet. **65**, 65—78.

PAYNE, A. P. & SWANSON, H. H. 1970: Agonistic behaviour between pairs of hamsters of the same and opposite sex in a neutral observation area. Behaviour **36**, 259—269.

PERRIN, M. R. 1981: Seasonal changes in agonistic behaviour of *Clethrionomys gapperi* in southeastern Manitoba and its possible relation to population regulation. Am. Midl. Nat. **106**, 102—110.

SCHLITTER, D. A., RAUTENBACH, I. L. & COETZEE, C. G. 1984: Karyotypes of southern African gerbils, genus *Gerbillurus* Shortridge, 1942 (Rodentia: Cricetidae). Ann. Carnegie Mus. **53**, 549—557.

SMITHERS, R. N. 1983: Mammals of the Southern African Subregion. Univ. of Pretoria, Pretoria.

SWANSON, H. H. 1974: Sex differences in behaviour of the Mongolian gerbil (*Meriones unguiculatus*) in encounters between pairs of the same or opposite sex. Anim. Behav. **22**, 638—644.

Received: June 13, 1989

Accepted: September 11, 1989 (W. Wickler)