When to live alone and when to live in groups : ecological determinants of sociality in the African striped mouse (*Rhabdomys pumilio*, Sparrman, 1784)

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ABSTRACT. One aim in animal behaviour is to explain why and when animals live in groups. The main approach has been to compare closely related gregarious and solitary species. Here, I discuss data of a medium sized, diurnal muroid rodent, the striped mouse, which demonstrates a high level of intraspecific variability of its social system. In the arid Succulent Karoo, the social structure of the striped mouse is best described as a territorial group living solitary forager with communal breeding and helpers at the nest. Groups can consist of up to 30 adult mice, i.e. four breeding females, one breeding male and their adult offspring. In contrast, the striped mouse is solitary in the mesic grasslands of South Africa, with females inhabiting intrasexually exclusive territories and male territories overlapping those of several females. Association between the sexes is limited to mating, and offspring leave their mother's territory as juveniles. Home ranges in the grasslands are much larger than in the Succulent Karoo. I suggest that the main ecological reasons for these differences in social organization are food abundance, the availability of suitable nesting sites, and the possibility of sun-basking. Whether these ecological differences acted as selection pressures in the past that caused genetic differences and finally speciation (as proposed by a recent study), or whether these ecological differences lead to behavioural differences via an ontogenetic pathway, remains a topic for further research.

KEY WORDS : social flexibility, *Rhabdomys*, striped mouse, ecological determinants of sociality.

INTRODUCTION

The striped mouse (*Rhabdomys pumilio*) is a medium sized (adult body weight 30-70g) muroid rodent, which is active mainly during mornings and afternoons (KRUG, 2002; SCHRADIN & PILLAY, 2004). It is widely distributed in southern Africa, inhabiting many different habitats, such as grasslands, marshes, forests, semi-deserts and deserts (KINGDON, 1974). The social organization of the striped mouse differs dramatically in correlation with the habitat it occupies. In moist grasslands, both sexes have territories that overlap with territories of several individuals of the opposite but not the same sex (BROOKS, 1974; CHOATE, 1972; PERRIN, 1980a; SCHRADIN & PILLAY, SUBM-B; WILLAN, 1982; WILLAN & MEESTER, 1989; WIRMINGHAUS & PERRIN, 1993), females raise their young alone, and associations between males and females are only for mating (BROOKS, 1974; WILLAN, 1982). In sum, the striped mouse in the grasslands is a solitary species (SCHRADIN & PILLAY, SUBM-B). In contrast, studies conducted in xeric habitats indicate that the striped mouse is a social species here, e.g. in the Kalahari (NEL, 1975; own observ.). A detailed study revealed that the striped mouse is social in the Namib desert, with groups consisting of one breeding female, her offspring that sometimes remain within the maternal territory even after reaching adulthood, and sometimes one adult breeding male that is permanently associated with one female and her offspring, (KRUG, 2002). This is similar to the situation in the Succulent Karoo, a desert in the north west of South Africa, where groups are even larger and more complex (SCHRADIN & PILLAY, 2004). In the Succulent Karoo, groups normally consist of one breeding male, up to four breeding females and their non-reproducing adult offspring of both sexes which remain in their natal territory (SCHRADIN & PILLAY, 2004). Males are permanently associated with groups of breeding females and participate in parental care (SCHRADIN & PILLAY, 2003). However, whereas mice of one group sleep in the same nest, have the same group territory and interact highly amicably with one another, they forage alone (SCHRADIN, SUBM) and react highly aggressive towards mice from other groups (SCHRADIN, 2004; SCHRADIN & PILLAY, 2004). These differences in social organization between striped mice from the xeric areas and the moist grasslands lead to the question of whether there is only one single species, *R. pumilio* (WILSON & REEDER, 1993). In fact, there appears outbreeding depression between different populations, which also show assortative mate choice decisions in captivity, i.e. females prefer males of their own population (PILLAY, 2000a; PILLAY, 2000b). An allozyme study of 23 different populations revealed significant differences between populations, with genetic distance being correlated with geographical distance (MAHIDA et al., 1999). Whereas this study suggested the existence of different subspecies, no evidence for different species was found. However, recent studies using mitochondrial DNA proposes the existence of two different species, with *R. pumilio* representing the social species living in the xeric deserts and semi-deserts, and *R. dilectus* representing the closely related solitary sister species living in the mesic grasslands (RAMBAU & ROBINSON, 2003). These two branches have separated less than three millions years ago and further studies will have to test whether the new species *R. dilectus* will be recognized (RAMBAU & ROBINSON, 2003).

To what extent can genetic differences between social and solitary striped mouse populations explain the observed social differences? An answer to this question is not apparent, but males from the solitary populations in the grasslands show highly-developed paternal care in captivity (SCHRADIN & PILLAY, 2003), for which no evidence exists from the field (SCHRADIN & PILLAY, submb; WILLAN, 1982). Also, there is no difference in paternal response in captivity between males from the Succulent Karoo, where the striped mouse is highly social, and the grasslands (SCHRADIN & PILLAY, 2003). In this paper I discuss how ecological differences between the Succulent Karoo and the grasslands can explain the extreme differences in social organization between striped mice from the two localities. Whether these ecological differences lead to genetic or to ontogenetic differences causing population typical social structures remains hereby unknown.

The Ecological Model

Basic ecological differences

The main difference between the two habitats is the pattern of rainfall. The grasslands in the eastern part of South Africa are a mesic habitat, obtaining more than 1000 mm of rainfall per annum, which occurs mainly during summer (ACOCKS, 1988). In contrast, the Succulent Karoo is an arid habitat, situated in a winter rainfall region, and receives only 50-400 mm rain per annum (ACOCKS, 1988; COWLING et al., 1999) and 160 mm at my field site. Differences in rainfall pattern lead to dramatic difference in plant cover. In grasslands, the entire area is covered by a sea of grasses and herbs, whereas shrubs are the dominant growth form in the Succulent Karoo, with in between open areas inhabited by succulents and in spring wildflowers (COWLING et al., 1999). The Succulent Karoo is rich in endemic plant species (COWLING et al., 1999) and regarded as one of 20 global biodiversity hotspots (MYERS et al., 2000). In the following sections, the ecological consequences of these differences in rainfall and by this vegetation are discussed. The ecological model for the Succulent Karoo is shown in Fig. 1a, for the grasslands in Fig. 1b. Different critical points are marked within the figures, and their importance is outlined below in a chronically order for both habitats.

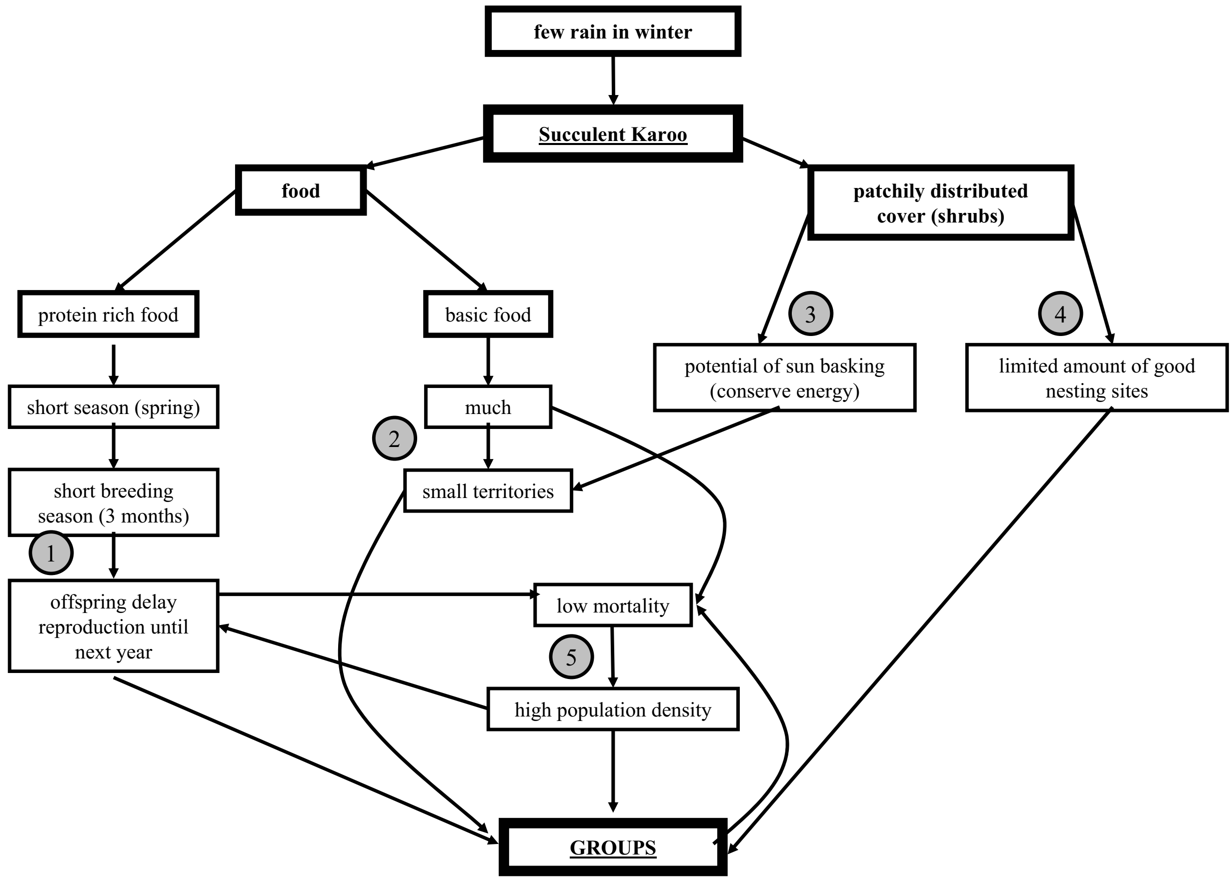
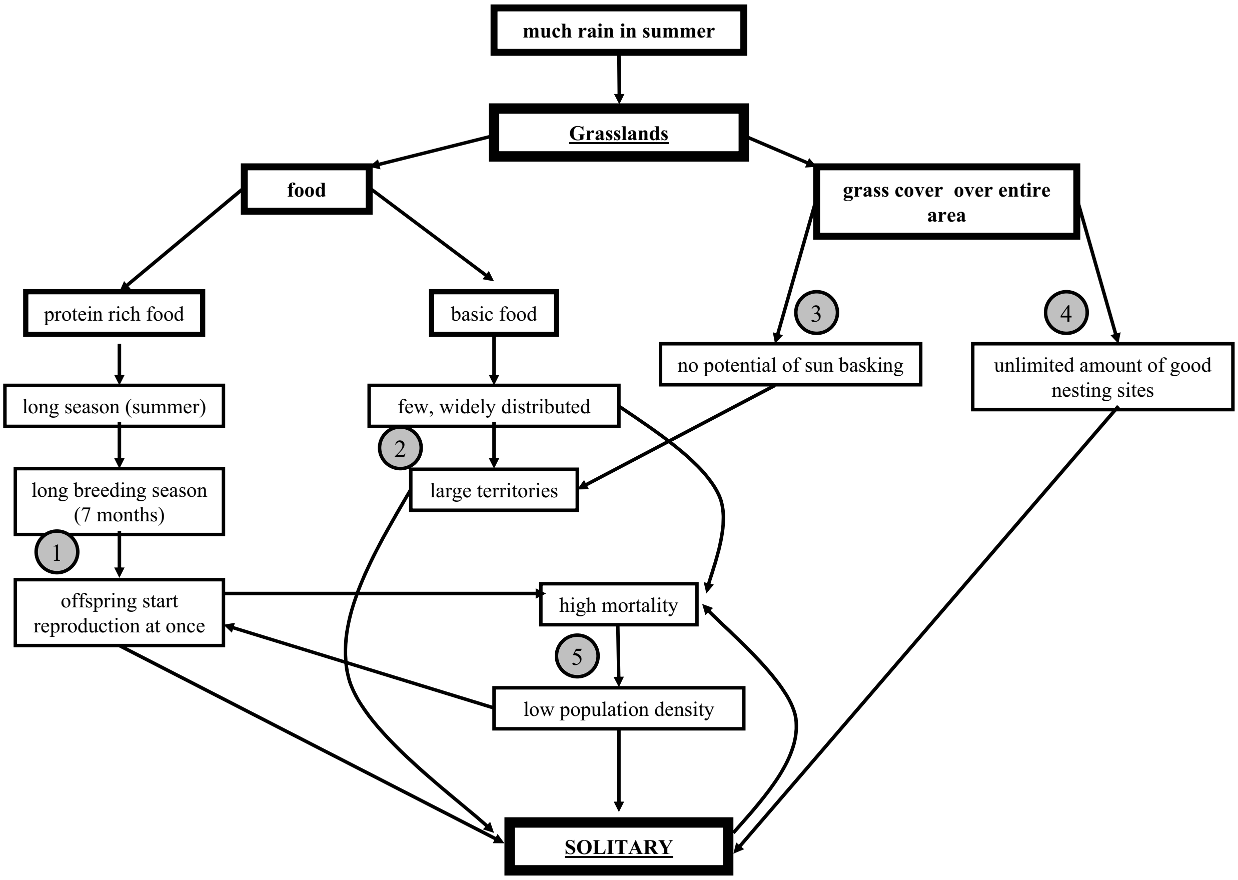


Fig. 1. – A model proposed for the connections between rainfall, protein content of food, food abundance and cover availability, and the social structure of the striped mouse in (a) the Succulent Karoo, and (b) the grasslands of southern Africa. For detailed descriptions see text.



Succulent Karoo (Fig. 1a)

1) Food abundance is high in spring after the winter rains. Wildflowers are particularly important food resources during spring (unpubl. data), and together with other newly-emerged plant material and insects are important protein sources. Since protein is essential for the onset and maintenance of reproduction (PERRIN, 1980a), breeding occurs during spring and lasts for three months (SCHRADIN & PILLAY, SUBM-A). Striped mice reach sexual maturity at two months of age (BROOKS, 1982), such that the first pups born during a particular breeding season could reproduce during the season of their birth. However, this would be at the end of the breeding season, with already declining food abundance, and offspring survival may be compromised then. Also, investing energy into reproduction would reduce the survival probability of young parents, since energy could alternatively be invested in somatic development or stored as fat to buffer the effects of poor food supply during summer. (SCHRADIN & PILLAY, SUBM-A). This could explain why adult offspring stay at home and invest in personal survival until the next breeding season rather than into reproduction during the season of their birth.

2) Whereas protein rich food occurs primarily during spring, overall food abundance is high throughout the year. The dominant plant species, such as *Zygophyllum retrofractum* shrubs and several succulents are available year round and provide a stable food supply. Nevertheless, the mice show considerable loss in body weight during the hot, dry summer (SCHRADIN & PILLAY, SUBM-A). Plant growth starts again in autumn when the rain falls again (COWLING et al., 1999), and food availability improves and reaches a peak in spring. It appears that striped mice in the Succulent Karoo do not need large territories and can share their territories including resources with up to 30 other group members (SCHRADIN & PILLAY, 2004), without experiencing severe competition for food.

3) The patchily distributed plant cover makes it possible for mice to sun bask. In the morning and afternoon, the mice of one group sit together in front of their nest, which is typically situated in a large *Zygophyllum* bush, and warm themselves up in the sun (SCHRADIN & PILLAY, 2004). The time when the sun starts shining on their nest has a significant effect on the initiation of activity (unpubl. data; KRUG, 2002). Sun basking might work as a method of energy saving and as thus leads to reduced demand of food intake, reduced foraging activity and as thus small territory size.

4) Striped mice preferably nest inside dense and thorny *Zygophyllum* shrubs (SCHRADIN & PILLAY, 2004). However, the number of bushes of this species that are big enough for a striped mouse group is limited, and there is strong competition between striped mice and syntopic bush karoo rats (*Otomys unisulcatus*) for access to these

nesting sites (SCHRADIN, SUBM). As bush karoo rats weigh more than double that of striped mice, they typically win all encounters. The limited number of nesting sites might also promote staying at home at a good nesting site instead of leaving the natal nest and nesting alone at a suboptimal place.

5) Individuals that are present in early summer after the breeding season have a chance of 30% to survive until the next breeding season (SCHRADIN & PILLAY, SUBM-A). This survival probability is very high compared to that of grasslands, where it is less than 3% (BROOKS, 1982). It can be explained by the investment of energy into survival instead of reproduction (1), the overall good food supply (2), and benefits of group living. As striped mice in the Succulent Karoo forage alone, but share one nest, benefits of group living must be related to nest sharing : 1. Communal infant care (SCHRADIN & PILLAY, 2004) including paternal care (SCHRADIN & PILLAY, 2003); 2. Thermoregulatory benefits through huddling during the night (ANDREWS & BELKNAP, 1986; CONTRERAS, 1984; temperatures can drop below zero in winter and spring and are even in summer typically below 15 degrees C and thus clearly below the thermal neutral point which might be around 30 degrees, CANALS et al., 1998); 3. Increased vigilance during the night towards potential predators approaching the nest (which is built aboveground using hay). Support for points 2 and 3 is available through unpublished results of videotaping inside two natural nests, in which mice were sleeping closely huddled together, and quickly left the nest during the middle of the night after a disturbance. In conclusion, the high survival probability leads to a high population density of over 50 mice/ha at the start and 200 mice/ha after the breeding season (SCHRADIN & PILLAY, SUBM-A). The resulting habitat saturation might then force offspring to stay at home, as no vacant territories are available for emigration.

Grasslands (Fig. 1b)

1) The main protein-rich food sources in the grasslands are grass seeds and insects. These food sources are available throughout the entire spring and summer, and the breeding season stretches over this period of six to seven months (BROOKS, 1974; PERRIN, 1980a; PERRIN et al., 2001). Thus, mice born at the beginning of the breeding season can potentially reproduce in the season of their birth for several months. In the grasslands, mice do not stay at home, but emigrate as juveniles and breeding occurs in young individuals weighing less than 30g (WILLAN, 1982); this does not occurs in the Succulent Karoo (SCHRADIN & PILLAY, SUBM-B).

2) Whereas the green grasslands give the impression of high food abundance, this may not be the case. In contrast to other syntopic rodents like vlei rats (*Otomys irroratus*), the striped mouse does not feed on grass (PERRIN, 1980b). Its main food comprises seeds, berries and herbs (CURTIS & PERRIN, 1979; PERRIN, 1980b). These food sources are patchily distributed and scarce. The low abundance of food sources may explain why striped mice have 6 times (females) or even 10 times (males) larger home ranges in the grasslands than in the Succulent Karoo (SCHRADIN & PILLAY, SUBM-B). This difference is even greater when one takes into account that home ranges are exclusive in the grasslands, i.e. overlap only to a small extent with other individuals, but overlap with 5 to 30 other group members in the Succulent Karoo (SCHRADIN & PILLAY, SUBM-B). The low food abundance in the grasslands would make it more costly to live in groups, as sharing the territory with other mice that use the same food resources would force territories to become even bigger, thereby increasing the energetic costs of traveling.

3) In the grasslands, the vegetation covers the entire area. Thus, here it is impossible for mice to come out of the cover and perform sun basking to reduce energetic demands by passive warming up. Instead, mice have to increase their body temperature by metabolic heat, for which they have to find more food, and thus need larger territories to fulfill this need.

4) Nest sites in the grasslands are abundant, particularly in areas of dense grass (own observ.).

5) Survival probability of juveniles in the grasslands is only about two months and annual survival probability is only 2.3% (BROOKS, 1974). Low food abundance (PERRIN, 1980b) and low ambient temperatures during winter probably lead to high mortality. Cold weather is a critical factor, as mice are solitary and thus do not benefit from the advantage of huddling in a group. Early dispersal of juveniles is probably another important factor influencing survival probability, as dispersal into unknown habitat is likely to reduce survival probability. Furthermore, young adults do not invest in survival (accumulating resources such as fat to survive the winter), but immediately invest into reproduction. In the grasslands, mice of both sexes start reproducing with a body weight below 30g, whereas in the Succulent Karoo offspring of both sexes remain at home without reproducing, reaching body weights above 40g before reproducing (SCHRADIN & PILLAY, SUBM-B). The low population density, which results from the low survival probability, means that territories are vacant into which offspring can immigrate when reaching adulthood.

DISCUSSION

The model described here is no more than a plausible explanation for the observed patterns of sociality in free-living striped mice. However, it shows associations between abiotic variables (level and season of rainfall), the biotic environment (plant cover, food availability and protein content of food) and social organization in one species (*Rhabdomys pumilio*). Other factors than the ones described in the model might also have effects. One such factor could be predation pressure, which is very difficult to estimate.

A model is only good if it can do two things : First it has to describe the phenomena observed in nature. Above I outlined how the model describes the patterns observed in the Succulent Karoo and the grasslands. One test would be to determine if it also can describe patterns observed in the Namib (described by KRUG, 2002). The main social difference between striped mice in the Succulent Karoo and the Namib is that groups are smaller in the Namib and no cooperative breeding occurs. This is in accordance with the ecological difference that availability of protein rich food is lower (1 in Fig. 1a), but more constant over time (2 in Fig. 1a), such that a clear breeding season is absent (1 in Fig. 1a; KRUG, 2002). As in the Succulent Karoo, good possibility for basking exists (3 in Fig. 1a) and does occur (KRUG, 2002), good nesting sites are extremely limited (4 in Fig. 1a), and the habitat is saturated in the Namib with sometimes extremely high population densities (5 in Fig. 1a), which can explain group living as a result of the lack of emigration possibilities (KRUG, 2002). Thus, it seems that the model is also suitable for the Namib, although the unique environmental parameters for this habitat would have to be included.

The second prerequisite for the usefulness of a model is that it makes predictions that can be tested. Below I state the predictions made by the model for both habitats, again referring to the important aspects pointed out in Fig. 1. Hereby it is not expected that a single factor will "cause" group living or a solitary lifestyle, but that it is the combination of factors and predictions that are important, as illustrated in Fig. 1.

Predictions in Succulent Karoo

1. Offspring born at the end of the breeding season have a lower survival probability. Heavier mice (i.e. greater body fat) of the same age group have a higher survival probability.

2. Territory size should increase during seasons with poor food supply. In areas with a lower food supply, smaller groups are expected.

3. The body temperature of mice increases significantly when basking (to be measured by implants) and energy expenditure is lower during periods of good sun basking opportunities (summer compared to winter; to be measured by doubled labeled water).

4. Removal of bush karoo rats should lead to striped mice occupying their abandoned nest sites.

5. Low population density leads to a more solitary lifestyle. Removal of groups should lead to adult offspring of other groups leaving their group and taking over these vacant territories.

Many of these predictions might be testable in future. The Succulent Karoo is known to have a low, but highly predictable rainfall pattern (COWLING et al., 1999) and as such predictable food abundance for the striped mouse. However, the Succulent Karoo is currently (2003) experiencing the severest drought since many years. Thus, while my model indicates high survival probability and high population density in the Succulent Karoo, these are unlikely in 2003. This dramatic drought will thus offer the opportunity to study the effects of a reduced population density on the social organization of the striped mouse. It will be possible to test which individuals survived (prediction 1), and it will be interesting to see if there are changes to the social structure (i.e. are the mice solitary, prediction 2 and 5). At the same time, bush karoo rats became nearly locally extinct at my field site, making it possible to test prediction 4.

Predictions in grasslands

1. Mice born at the end of the breeding season should stay longer in their natal territory.

2. Experimental increase of food availability should lead to larger population density (shown by PERRIN & JOHNSON, 1999), smaller home ranges, increased survival probability, and eventually to habitat saturation and finally to a higher level of sociality.

3. Striped mice in warmer grassland habitats (e.g. in the area of Pretoria) should have smaller home ranges than mice in colder grassland habitats (e.g. high in the Drakensberg) because of a lower energy need due to the higher ambient temperature.

4. Providing super-optimal nesting sites should lead to increased sociality. The obvious option for this would be to present nest boxes, but pilot studies with artificial nest boxes were not successful (unpubl. data).

5. Increased survival probability by providing food in the field should lead to a higher degree of sociality, as pointed out in point 3.

CONCLUSIONS

The striped mouse is a convenient model for studying the environmental determinants of sociality. Hereby, it is not of crucial importance, whether the striped mouse is one or two closely related sister species (see Introduction). In this paper, the intention was to point out the ecological differences that explain differences in sociality. Whether these ecological differences acted as selection pressures in the past that caused genetic differences and finally speciation, or if these ecological differences lead to behavioural differences via an ontogenetic pathway, remains a topic for further highly interesting and important research. Further studies should experimentally test the predictions outlined in this paper to test the model described.

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REFERENCES

ACOCKS, J.P.H. (1988). *Veld Types of South Africa*, 3rd edition. Botanical Research Institute, Pretoria.

ANDREWS, R.V. & R.W. BELKNAP (1986). Bioenergetic benefits of huddling by deer mice (*Peromyscus maniculatus*). *Comp. Biochem. Physiol.,* 85 : 775-775.

BROOKS, P.M. (1974). *The Ecology of the Four-Striped Field Mouse,* Rhabdomys pumilio *(Sparrman, 1984), with particular Reference to a Population on the Van Riebbeeck Nature Reserve, Pretoria*. PhD thesis, University of Pretoria, South Africa.

BROOKS, P.M. (1982). Aspects of the reproduction, growth and development of the four-striped mouse, *Rhabdomys pumilio* (Sparrman, 1784). *Mammalia,* 46 : 53-64.

CANALS, M., M. ROSEMANN, F.F. NOVOA & F. BOZINOVIC (1998). Modulating factors of the energetic effectiveness of huddling in small mammals. *Acta Theriologica,* 43 : 337-348.

CHOATE, T.S. (1972). Behavioural studies on some Rhodesian rodents. *Zoologica Africana,* 7 : 103-118.

CONTRERAS, L.C. 1984. Bioenergetics of huddling : test of a psycho-physiological hypothesis. *J. Mamm.*, 65 : 256-262.

COWLING, R.M., K.J. ESLER & P.W. RUNDEL (1999). Namaqualand, South Africa - an overview of a unique winter-rainfall desert ecosystem. *Plant Ecology,* 142 : 3-21.

CURTIS, B.A. & M.R. PERRIN (1979). Food preferences of the vlei rat (*Otomys irroratus*) and the four-striped mouse (*Rhabdomys pumilio*). *S. Afr. J. Zool.,* 14 : 224-229.

KINGDON, J. (1974). *East African Mammals*. Academic Press, London.

KRUG, C.B. (2002). *The behavioural ecology of Rhabdomys pumilio in the Namib Desert.* PhD thesis, Rheinische Friedrich-Wilhelms-Universität Bonn, Germany.

MAHIDA, H., G.K. CAMPBELL & P.J. TAYLOR (1999). Genetic variation in *Rhabdomys pumilio* (Sparrman, 1784) : an allozyme study. *S. Afr. J. Zool.,* 34 : 91-101.

MYERS, N., R.A. MITTERMEIER, C.G. MITTERMEIER, G.A.B.D. FONSECA & J. KENT (2000). Biodiversity hotspots for conservation priorities. *Nature,* 403 : 853-858.

NEL, J.A.J. (1975). Aspects of the social ethology of some Kalahari Rodents. *Z. Tierpsychol.,* 37 : 322-331.

PERRIN, M.R. (1980a). The breeding strategies of two co-existing rodents, *Rhabdomys pumilio* (Sparrman, 1784) and *Otomys irroratus* (Brants, 1827). *Acta Oecol.,* 1 : 383-410.

PERRIN, M.R. (1980b). The feeding habits of two co-existing rodents, *Rhabdomys pumilio* (Sparrman, 1784) and *Otomys irroratus* (Brants, 1827), in relation to rainfall and reproduction. *Acta Oecol.,* 1 : 71-89.

PERRIN, M.R., C. ERCOLI & E.R. DEMPSTER (2001). The role of agonistic behaviour in the population of two syntopic African grassland rodents, the striped mouse *Rhabdomys pumilio* (Sparrman, 1784) and the multimammate mouse *Mastomys natalensis* (A. Smith, 1834) (Mammalia Rodentia). *Trop. Zool.,* 14 : 7-29.

PERRIN, M.R. & S.J. JOHNSON (1999). The effect of supplemental food and cover availability on a population of the striped mouse. *S. Afr. J. Wildl. Res.,* 29 : 15-18.

PILLAY, N. (2000a). Female mate preference and reproductive isolation in populations of the striped mouse *Rhabdomys pumilio*. *Behaviour,* 137 : 1431-1441.

PILLAY, N. (2000b). Reproductive isolation in three populations of the striped mouse *Rhabdomys pumilio* (Rodentia, Muridae) : interpopulation breeding studies. *Mammalia,* 64 : 461-470.

RAMBAU, R.V. & T.J. ROBINSON (2003). Molecular genetics of *Rhabdomys pumilio* subspecies boundaries : mtDNA phylogeography and karyotypic analysis by fluorescence *in situa* hybridization (FISH). *Molec. Phyl. Evol.,* 28 : 564-575.

SCHRADIN, C. (2004). Territorial defense in a group living solitary forager : who, where against whom? *Behav. Ecol. Sociobiol.,* 55 (5) : 439-446.

SCHRADIN, C. (SUBM). Whole day follows of the striped mouse.

SCHRADIN, C. & N. PILLAY (2003). Paternal care in the social and diurnal striped mouse (*Rhabdomys pumilio*) : laboratory and field evidence. *J. Comp. Psychol.,* 117 : 317-324.

SCHRADIN, C. & N. PILLAY (2004). The striped mouse (*Rhabdomys pumilio*) from the succulent karoo of South Africa : A territorial group living solitary forager with communal breeding and helpers at the nest. *J. Comp. Psychol.,* 118 (1) : 37-47.

SCHRADIN, C. & N. PILLAY (SUBM-A). Demography of the striped mouse (*Rhabdomys pumilio*) in the Succulent Karoo : an unique population in an extreme environment.

SCHRADIN, C. & N. PILLAY (SUBM-B). Extreme social flexibility in the South African striped mouse : when to live in groups and when to be alone?

WILLAN, B.R. (1982). S*ocial ecology of* Otomys irroratus, Rhabdomys pumilio *and* Mastomys natalensis. PhD thesis, University of Natal.

WILLAN, K. & J. MEESTER (1989). Life-history styles of southern African *Mastomys natalensis*, *Otomys irroratus* and *Rhabdomys pumilio* (Mammalia, Rodentia). In : M.N. BRUTON (ed), *Alternative Life-History Styles of Animals,* Kluwer Academic Publishers, Dordrecht, pp. 421-439.

WILSON, D.E. & D.M. REEDER (1993). *Mammal Species of the World. A Taxonomic and Geographic Reference*, 2nd edition. Smithsonian Institution Press, Wahingtons D.C.

WIRMINGHAUS, J.O. & M.R. PERRIN (1993). Seasonal-changes in density, demography and body-composition of small mammals in a Southern temperate forest. *Journal of Zoology,* 229 : 303-318.

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