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Abstract

When males of a species follow different reproductive strategies in different habitats, one might expect the strategy adopted to maximize fitness payoffs under particular ecological conditions. Striped mice (Rhabdomys pumilio) males in the moist grasslands of South Africa follow a roaming mating strategy, visiting several receptive females, and do not participate in parental care. In contrast, males in the arid succulent karoo are permanent members of social groups and help care for young. We predicted that paternal care leads to fitness benefits in striped mice from the succulent karoo but not from the grasslands. Experiments were conducted simultaneously in both locations under captive seminatural conditions to study offspring growth and survival to weaning in two experimental groups: father absent and father present. In the succulent karoo, offspring development was faster when the father was present, but the father's absence did not affect offspring growth in the grasslands. The significantly lower night temperatures in the succulent karoo compared to the grasslands negatively influenced offspring development during the first 3 days after birth, which in turn influenced offspring development until weaning. Exposure to low temperatures is energetically costly to free-living mice, as indicated by a greater loss of body weight during cold spring nights than warmer summer nights. We suggest that paternal care, particularly huddling of pups, improves offspring development in the succulent karoo, whereas the presence or absence of the father does not appear to directly influence offspring growth in the grasslands.
The influence of the father on offspring development in the striped mouse

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When males of a species follow different reproductive strategies in different habitats, one might expect the strategy adopted to maximize fitness payoffs under particular ecological conditions. Striped mice (Rhabdomys pumilio) males in the moist grasslands of South Africa follow a roaming mating strategy, visiting several receptive females, and do not participate in parental care. In contrast, males in the arid succulent karoo are permanent members of social groups and help care for young. We predicted that paternal care leads to fitness benefits in striped mice from the succulent karoo but not from the grasslands. Experiments were conducted simultaneously in both locations under captive seminatural conditions to study offspring growth and survival to weaning in two experimental groups: father absent and father present. In the succulent karoo, offspring development was faster when the father was present, but the father’s absence did not affect offspring growth in the grasslands. The significantly lower night temperatures in the succulent karoo compared to the grasslands negatively influenced offspring development during the first 3 days after birth, which in turn influenced offspring development until weaning. Exposure to low temperatures is energetically costly to free-living mice, as indicated by a greater loss of body weight during cold spring nights than warmer summer nights. We suggest that paternal care, particularly huddling of pups, improves offspring development in the succulent karoo, whereas the presence or absence of the father does not appear to directly influence offspring growth in the grasslands. [Behav Ecol 16:450-455 (2005)]

Social flexibility, that is, intraspecific variation in social systems, is widely distributed among vertebrates (Lott, 1984). Differences in ecological conditions may well underpin these differences in social organization (Lott, 1991). In the pied kingfisher (Ceryle rudis), unrelated males associate with breeding pairs as helpers in habitats with poor or difficult foraging conditions, whereas only related males remain as helpers in habitats with a good food supply (Reyer, 1980, 1984). In the golden jackal (Canis aureus), groups of up to 20 individuals form in populations living in habitats with high food abundance, whereas monogamous pairs form in areas of low food abundance (Macdonald, 1979).

Studies of social flexibility have considered mainly bird models, in which both ultimate and proximate explanations for social flexibility have been investigated (e.g., Davies et al., 1996; Parish and Coulson, 1998; Smith, 1995; Wingfield et al., 1990, 2000). Although social flexibility is also common in mammals (Lott, 1991), the reasons underlying such flexibility are seldom known and, if known, are poorly understood (McGuire and Getz, 1995). For example, prairie voles (Microtus ochrogaster) can be monogamous, solitary promiscuous, or polygynous depending on the area in which they occur (Roberts et al., 1998) or even within the same population (McGuire and Getz, 1998), but the reasons for these variations in mating systems are not understood (McGuire and Getz, 1995).

One mammal that offers a good opportunity for studying the ecological reasons for population differences in social organization is the African striped mouse (Rhabdomys pumilio). The striped mouse is a small (40 g), diurnal murid rodent that occurs throughout southern Africa and parts of East Africa, inhabiting a wide range of habitats including moist grasslands and arid deserts (Kingdon, 1974). Whereas the striped mouse is solitary in grasslands (Brooks, 1974; Perrin, 1980; Schradin and Pillay, 2005b; Willan and Meester, 1989), it forms social groups in desert habitats (Schradin and Pillay, 2004). In the succulent karoo, a desert habitat, males are permanently associated with social groups containing several communally breeding females and share their territory with these females (Schradin and Pillay, 2004). Males also interact amicably with juveniles, retrieve pups (Schradin and Pillay, 2003), and participate in infant care inside the nest (unpublished data). In contrast, striped mice males in grasslands are solitary and do not associate with juveniles. Instead, males follow a roaming mating strategy, utilizing large home ranges that overlap with the home ranges of several females; males visit females only for mating (Schradin and Pillay, 2005b; Willan, 1982; Willan and Meester, 1989). In captivity, however, striped mice males from both the semimoist highveld grasslands and the arid succulent karoo of South Africa display well-developed paternal care (Schradin and Pillay, 2003).

Evolutionary theory predicts that paternal care should occur only if it improves the father’s fitness (Trivers, 1972). Whether or not paternal care leads to an increase in fitness might depend on ecological conditions. It has been predicted, but never shown, that rodent males may exhibit flexibility in their social behavior, providing paternal care only under ecological conditions where this behavior improves fitness (Dewsbury, 1985). Accordingly, we predicted that paternal care leads to a higher fitness benefit for striped mice fathers in the arid succulent karoo than for fathers in the semimoist highveld grasslands. The likely ecological explanation for these differences in benefits was expected to be a difference in minimum night temperature. As night temperatures are lower in the succulent karoo than in the highveld grasslands, huddling of the pups by the father might yield a significantly higher energetic benefit for offspring in the colder succulent karoo than in warmer grasslands.

Paternal care in rodents enhances offspring development when animals are kept under conditions simulating the cold

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night temperatures experienced in nature (Cantoni and Brown, 1997; Gubernick et al., 1995) but not when animals are kept under ideal laboratory conditions with optimal ambient temperatures (Gerling and Yahr, 1979; Gubernick et al., 1995). In this study, we investigated whether the presence or absence of the father influenced the preweaning growth and survival of litters in the succulent karoo and in the highveld grasslands. Experiments were conducted simultaneously in both locations under captive seminatural conditions in which mice experienced natural variation in ambient temperatures.

MATERIALS AND METHODS

Animals

Only wild-caught adult individuals were used for breeding. Mice were trapped using metal live traps (26 × 9 × 9 cm) baited with a mixture of bran flakes, sea salt, and salad oil. Traps were checked at least every 2 h. No trap deaths occurred.

Housing conditions

Animals were kept in 40 H-210 cages. Coarse wood shavings were provided as bedding and tissue paper as nesting material. Ecolab mouse cubes and water were provided ad libitum. Five grams of sunflower seeds was provided daily.

Animals were kept under natural weather conditions at two localities. In the succulent karoo, cages were kept at the research station in Goegap Nature Reserve, adjacent to our field site; Goegap Nature Reserve (Rösch, 2001) is located in the Northern Cape Province of South Africa where we have been conducting field studies since 2001 (Schradin and Pillay, 2003, 2004). Cages were placed on a verandah, which was protected from the sun. In the highveld grassland, cages were placed on a protected verandah on the grounds of the Agricultural Research Council in Pretoria, Gauteng Province, South Africa. Average annual rainfall is 160 and 740 mm at Goegap Nature Reserve and Pretoria, respectively.

Procedure

At the beginning of September 2002, one of us (C.S.) established 20 pairs of wild-caught Rhabdomys in the succulent karoo (Goegap), while the other (N.P.) established 32 pairs during September 2002 and September 2003 in the highveld grassland (Pretoria). Breeding pairs comprised randomly selected males and females that were trapped 250 m (grasslands) or 5 km (succulent karoo) apart and were unlikely to be related, which might otherwise have negatively influenced breeding success (Pillay, 2002). All 32 pairs in the grasslands produced litters, and 18 of the 20 pairs reproduced in the succulent karoo.

Pairs were randomly assigned to one of two experimental groups: (1) Father absent—the father was removed 1 week before expected parturition and the mother raised the offspring alone and (2) Father present—the father was present at parturition and the litter was raised by the pair. In the succulent karoo, 11 mothers raised their offspring alone and 7 (weaning) and growth rate (g/day) of litters was calculated from birth to day 3 and from day 3 to weaning. The first period (days 0–3) was selected because the ontogeny of striped mice is most sensitive to external temperatures during this time (i.e., pups are hairless and thus more vulnerable to heat loss; Brooks, 1982). Litters rather than individuals were considered because offspring in a litter are not statistically independent (Boonstra and Hochachka, 1997). At weaning, the number of surviving pups per litter was recorded.

Field data

We collected data on weight loss overnight of free-living striped mice in the succulent karoo to obtain a surrogate measure of energy expenditure during the night. Mice were trapped and weighed during our field studies in Goegap in 2002 (Schradin and Pillay, 2004). Nest locations were determined from radio tracking at night (Schradin and Pillay, 2005b), and traps were placed directly outside these nests. This allowed us to trap mice immediately after they emerged from their nest in the morning or before they entered their nest for the night. Mice entered traps repeatedly, that is, they were “trap-happy,” and it was therefore possible to record body weight for the same individuals during the afternoon before they entered their nest (afternoon day 1), the following morning immediately after they emerged from their nest (morning day 2), and again in the afternoon of the same day (afternoon day 2) before they entered their nest at night. These data were used to determine body mass loss overnight, as well as weight gain the next day. Because changes in female body weight are influenced by many factors such as lactation, only males were used for these analyses. Comparisons were made between seasons using the data collected in September (spring) and November (summer).

Statistics

Offspring survival data were analyzed using the generalized linear model analysis (GLZ) with a multinomial error structure and link function, in which we tested whether the number of pups in a litter that died (response variable) was influenced by two fixed effects variables (locality and treatment) and two fixed effects covariates (average minimum temperature from days 0 to 16 and litter mass at birth). Offspring development during days 0–3 and days 3–16 were analyzed using the general linear model (GLM) analysis, in which we tested whether growth rate (g/day) of a litter (response variable) was influenced by two fixed effects variables (locality and treatment) and three fixed effects covariates (average minimum temperature during sampling—days 0–3 or days 3–16, litter size prior to adjustment to five pups, and litter size on day 3 or day 16). To account for carryover effects, we also included growth rate during days 0–3 as a fixed effect covariate in the analysis of growth during days 3–16. Changes in the weight of free-living males were analyzed using the GLM analysis, with multiple dependent variables, with weight
loss overnight and weight gain during the day as the response variables and season (spring and summer) as the fixed effects variable. The Tukey’s honest significant difference post hoc test was used to reveal differences within and between fixed effects. Data are presented as mean ± SEM.

RESULTS
In the grassland locality, data were collected in both 2002 and 2003. Statistical analyses revealed no significant differences between years (\(F_{1,25} = 0.38, p = .543\)), treatments (\(F_{1,25} = 0.04, p = .843\)), or year × treatment (\(F_{1,25} = 0.03, p = .864\)). In addition, there were no significant associations between growth rate and minimum night temperature (\(F_{1,25} = 0.10, p = .754\)), litter size before adjustment (\(F_{1,25} = 0.29, p = .595\)), and litter size on day 16 (\(F_{1,25} = 0.52, p = .478\)). Therefore, data for the 2 years were pooled for analysis.

Offspring survival was high. In the grasslands, a single pup died in four father-present and two father-absent litters. In the succulent karoo, all offspring survived to weaning in the father-present treatment, but all offspring died in two father-absent litters. There were no other mortalities. Offspring mortality was not statistically different between localities (\(W = 0.90, df = 1, p = .399\); Wald Statistic GLZ analysis), treatments (\(W = 0.00, df = 1, p = .999\)), and the interaction between these variables (\(W = 0.01, df = 1, p = .926\)). The power of this test was \(\beta = 0.71\). To detect significant differences, the difference in pup survival between the father-absent and father-present treatments, regardless of population, would have needed to be at least 7% greater than the observed values, and the difference between the father-absent treatment in the succulent karoo and the remaining three treatments would have needed to be at least 7.5% greater. Neither minimum night temperature (\(W = 1.95, df = 1, p = .163\)) nor litter mass at birth (\(W = 3.27, df = 1, p = .072\)) was significantly associated with offspring mortality.

During days 0–3, litters from the grasslands had faster growth rates than litters from the succulent karoo (\(F_{1,43} = 9.06, p = .004\)), and litters raised by both parents grew significantly faster than litters raised by the mother only (\(F_{1,43} = 21.37, p < .001\)). The statistical interaction between locality and treatment was also significant (\(F_{1,43} = 14.66, p < .001\)). Post hoc tests revealed that litters in the father-absent treatment in the succulent karoo had the slowest growth rates compared with litters from other locality × treatment combinations and that there were no differences in growth rates between treatments in the grassland locality (Figure 1a). There was also no significant association between growth rate and original litter size (\(F_{1,43} = 0.01, p = .904\)) or litter size on day 3 (\(F_{1,43} = 1.66, p = .204\)). However, there was a significant association between growth rate and mean minimum night temperature (\(F_{1,43} = 4.12, p = .048\)) mainly because of the poor growth rate of father-absent litters in the succulent karoo (least squares mean values).

For days 3–16, growth rates were faster in litters from the grasslands than those from the succulent karoo (\(F_{1,42} = 5.06, p = .029\)) and faster in litters in the father-present rather than the father-absent treatment (\(F_{1,42} = 4.56, p = .039\)). The statistical interaction between locality and treatment was also significant (\(F_{1,42} = 7.96, p = .007\)). Post hoc tests again revealed that litters in the father-absent treatment in the succulent karoo had the slowest growth rates compared with litters from all other locality × treatment combinations and that there were no differences in growth rates between treatments in the grassland locality (Figure 1b). Growth rates during days 3–16 were significantly related to growth between days 0 and 3 (\(F_{1,42} = 4.27, p = .045\)). There was no significant association between growth rate and any of the covariates, original litter size (\(F_{1,42} = 2.14, p = .151\)), mean minimum night temperature (\(F_{1,42} = 0.12, p = .727\)), and litter size on day 16 (\(F_{1,42} = 1.27, p = .267\)).

The mean minimum night temperatures were significantly higher in the grasslands (13.2°C ± 0.5°C) than in the succulent karoo (10.8°C ± 0.4°C; \(t_{48} = 3.52, p < .001\); t test) for the duration of our study.

Field data
Minimum night temperatures from the succulent karoo were significantly lower in September (13.8°C ± 0.8°C) than in November (16.7°C ± 0.7°C; \(t_{48} = 2.85, p < .01\)). Comparison of male body weight over 2 days (i.e., afternoon day 1, morning day 2, and afternoon day 2) revealed significant weight fluctuations (\(F_{1,20} = 4.29, p = .03\); GLM analysis; Figure 2). Overnight weight loss was greater in spring (September) than in summer (November, \(p = .02\); post hoc tests). Males also gained more weight between the morning and afternoon of day 2 in spring compared to summer (\(p = .01\)).

DISCUSSION
The presence or absence of the father had no significant effect on pup survival in either the succulent karoo or highveld grassland striped mouse populations. This was possibly due to low statistical power of our analysis, and a larger sample size might have detected differences in survival. As predicted, however, litters in the succulent karoo grew faster when the father was present, whereas the presence or absence of the father did not influence offspring development in the grasslands. The ecological determinant underlying offspring development, particularly during the first 3 days of life, appears to be a difference in ambient temperature between the succulent karoo and the grassland localities. Because nights are warmer in the grasslands, there is little need for a second caregiver to provide thermoregulatory benefits for the pups. In fact, the growth rate of offspring in the father-absent treatment in the warmer grasslands was greater than the growth rate of offspring raised by both parents in the colder succulent karoo. Therefore, climatic differences between the grasslands and the succulent karoo may partially explain the regional differences in male reproductive strategies in striped mice populations.

Litters grew faster when the father was present than when the father was absent, particularly in the succulent karoo. We suggest that by huddling (Schradin and Pillay, 2003), male
stripped mice in the succulent karoo reduce heat and energy loss by the pups, as also occurs in *Peromyscus californicus* (Gubernick et al., 1993). We found an effect of ambient temperature on offspring development only in the succulent karoo and for only days 0–3 but not for days 3–16. This is potentially a result of the increased vulnerability to cold stress by young pups because they are smaller, have no fur, and lack the ability to fully regulate their body temperature. Under ideal captive conditions, as in our experiments, in which the mother or both parents were permanently present and food was available ad libitum, older pups may have been buffered from exposure to lower temperatures. Nevertheless, growth during early development in the striped mouse influenced later growth (i.e., there were carryover effects), and poor growth rates during infancy can have pronounced effects into adulthood in mammals, influencing both survival and reproductive success (Lummaa and Clutton-Brock, 2002). This demonstrates the importance of a second caregiver during cold nights.

We found that free-living male mice in the succulent karoo lost body weight overnight, which we used as a surrogate measure of energy expenditure. The loss of body weight was greater during cold spring nights than during warmer summer nights, despite food availability being higher in spring than in summer (Schradin, in press). Thus, striped mice expended less energy during summer than spring nights, either because of the warmer ambient temperature or because the larger social groups that formed during the summer breeding season provided secondary thermoregulatory benefits (Schradin and Pillay, 2004). Our data do not allow us to differentiate between these two hypotheses, but both factors may be important.

The presence of the father did not influence offspring development in the grasslands. Nonetheless, males from this population provide paternal care in captivity (Schradin and Pillay, 2003). It is possible that paternal care is a plesiomorphic characteristic that was inherited from the striped mouse ancestor, which apparently inhabited arid areas (Rambau and Robinson, 2005). Alternatively, paternal care may represent a mating strategy (Rohwer et al., 1999), if males providing paternal care have priority of access to females when they become receptive again during postpartum estrus.

During our experiments, nights in the grasslands were significantly warmer (by $3^\circ$C on average) than in the succulent karoo. Under natural conditions, this difference in temperature during the mating season would be even more pronounced because the breeding season in the grasslands only starts in September/October, a month later than in the succulent karoo, and lasts several months longer, extending throughout the entire warm summer (Brooks, 1974; Perrin, 1980). In contrast, breeding in the succulent karoo begins in August, at the end of winter, when night temperatures can be below freezing, and finishes in December, at the start of summer (Schradin and Pillay, 2005a). These population differences in the timing of the breeding season are related to seasonal differences in rainfall and hence the timing of the appearance of protein-rich young plants and insects (Nel, 2003; Perrin, 1980; Taylor and Green, 1976). The succulent karoo receives winter rain, whereas the grasslands receive summer rain (Schradin, in press).

Striped mice females are single breeders in the grasslands (Perrin, 1980; Schradin and Pillay, 2005a; Willan and Meester, 1983) whereas females in the succulent karoo breed communally (Schradin and Pillay, 2004; definitions available in Hayes, 2000). Reasons for females breeding alone in grasslands appear to be relatively low food abundance and low survival rate of striped mice, leading to low population density (Schradin, in press). Consequently, males in the grasslands follow a roaming mating strategy in search of receptive females. In contrast, mice living in the succulent karoo experience a stable food supply all year round and have a high probability of survival, which in turn leads to a high population density, habitat saturation, forced philopatry, and communal breeding (Schradin, in press). Therefore, males can ensure access to several females by defending one group of communally breeding females and becoming a permanent member of this social unit. Enhanced pup development would then be simply another fitness benefit of this reproductive strategy because the male is already present in the nest and can provide paternal care at a presumably low cost.

It is unclear if the father’s role in providing infant care in the succulent karoo is important under natural conditions because two to four females raise their litters communally and might therefore be able to meet the thermoregulatory requirements of pups without needing paternal assistance. However, the male adds numerically to an existing group of females, which may provide appropriate thermal conditions for young pups. Using a combination of geometric analyses and published data for 13 small mammal species (10 genera), Canals et al. (1989, 1998) postulate that the optimal group size for huddling in small rodents is approximately four to five individuals, which coincidentally is the number of adults, including the male, in most free-living striped mouse groups at our succulent karoo study site (Schradin and Pillay, 2004). Experimental data from captive and field studies in the succulent karoo showed that striped mice in larger huddling groups spend comparatively less energy at low ambient temperatures (Scantlebury and Schradin, unpublished data). A further way in which the father could contribute to the thermoregulatory requirements of young pups is by huddling them when females are absent from the nest, as occurs during the day (Schradin, submitted); spring daytime temperatures may be as low as $10^\circ$C–$15^\circ$C in the succulent karoo.

Although we found significant associations between overnight temperatures and the effects of the father’s presence on offspring development during days 0–3 in striped mice in the succulent karoo, we cannot rule out other reasons for population differences in male reproductive strategies. Differences in food abundance, mortality, and population density

![Figure 2](image-url)

Changes in body mass overnight and the next day of adult male striped mice in spring (black bars, $N = 8$) and summer (clear bars, $N = 15$) in the succulent karoo.
are known to influence sociality in striped mice (Schradin and Pillay, unpublished; see also Schradin, in press; Schradin and Pillay, 2005b). These factors may explain the differences in mating system and distribution of males but are unlikely to explain why males perform paternal care in the succulent karoo or why paternal care should be beneficial to pups in the succulent karoo and not in the grasslands. Because experiments were conducted in only one location per habitat type, differences in pup growth between the grassland and succulent karoo populations could have been due to other unknown factors. Nonetheless, the difference in the paternal effect on offspring growth between habitats is interesting and appears to be related to differences in social behavior of males.

Although potential confounding influences cannot be fully ruled out, our data indicate that paternal care in the succulent karoo leads to fitness benefits to the male, as indicated by faster offspring growth and, presumably, better later survival and reproductive success. Thus, we suggest that the most parsimonious explanation of our results is that low nighttime temperatures, typical of the succulent karoo, select for huddling of offspring by the male and one or more females. In the warmer grasslands, the mother alone appears able to provide for the thermoregulatory requirements of young pups.

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