Rymer, Tasmin L., and Pillay, Neville (2011) *The influence of the early rearing environment on the development of paternal care in African striped mice.* Ethology, 117 (4). pp. 284-293.

http://dx.doi.org/ 10.1111/j.1439-0310.2011.01873.x

The influence of the early rearing environment on the development of paternal care in African striped mice

Development of paternal care. T. L. Rymer & N. Pillay

TASMIN L. RYMER & NEVILLE PILLAY

School of Animal, Plant and Environmental Sciences, University of the Witwatersrand,
Private Bag 3, Wits 2050, South Africa

N. Pillay; Neville.Pillay@wits.ac.za (corresponding author)

---

* This is the Accepted Version of a paper published in the journal Ethology:
Rymer, T. L. & Pillay, N. 2011. The influence of the early rearing environment on the development of paternal care in African striped mice. *Ethology*, **117**, 284–293.
Note: First author is now at James Cook University: email Tasmin.Rymer@jcu.edu.au.

Abstract

In some biparental mammals, paternal care is important for offspring development and survival. We investigated the influence of the early post-natal environment on the development of paternal care in the naturally paternal desert-dwelling African striped mouse (*Rhabdomys pumilio*). Our aim was to establish whether the expression of paternal care in adult sons is influenced by their experience of paternal care. Offspring were raised in one of three conditions: both parents raised young; mothers raised young alone; and mothers raised young alone but were separated from the father with a barrier. The paternal care behaviour of sons was investigated when they were adults. Contrary to expectations, adult sons raised by the mother alone displayed greater levels of huddling behaviour of their own pups compared to sons raised by both parents. This response appears to be influenced by the early mother–son relationship, because mothers raising pups alone compensated for the absence of fathers by increasing the time spent with pups compared to mothers raising pups with fathers. The mechanisms underpinning the development of paternal care are not apparent in our study. Nonetheless, the development of paternal care is condition-dependent in male striped mice, indicating that the potential for greater levels of care occurs in the absence of the father and concomitant compensation of maternal care during early development.

Keywords: Behavioural development, early rearing environment, paternal care, *Rhabdomys pumilio*

---

* This is the Accepted Version of a paper published in the journal Ethology:
Rymer, T. L. & Pillay, N. 2011. The influence of the early rearing environment on the development of paternal care in African striped mice. *Ethology*, **117**, 284–293.
Note: First author is now at James Cook University: email Tasmin.Rymer@jcu.edu.au.

Introduction

Paternal care is rare in mammals, occurring in 5–10% of species (Wright 2006). In these species, fathers may play a crucial role in offspring development (behavioural and cognitive) and survival (Gubernick & Teferi 2000; McCarty & Southwick 1977; Outscharoff et al. 2006; Wright 2006). In addition, the existence of this behaviour in some mammals suggests that it has been favoured by selection and is transmitted between generations (Gomendio et al. 2008). A number of studies have shown the importance of the early mother–daughter relationship in shaping the development of maternal care (e.g. Curley et al. 2008; Francis et al. 1999; Kikusui et al. 2005); yet, it is curious that few studies have investigated the role fathers play in the development and expression of paternal care in their sons.

Behaviour has both genetic and non-genetic components, and behavioural expression is a product of gene–environment interactions (Goodenough et al. 2001). Many studies have only reported either one or the other components; for example, Bester-Meredith & Marler (2003) demonstrated a non-genetic basis for paternal care in California mice (*Peromyscus californicus*): male pups that were retrieved less often showed lower levels of retrieval behaviour themselves as adults. In contrast, Freeman-Gallant & Rothstein (1999) found that feeding rates (a measure of paternal investment) of savannah sparrow (*Passerculus sandwichensis*) fathers and their sons closely corresponded, indicating genetic determination. Clearly, more studies are needed to determine the relative importance of non-genetic and genetic factors on the development of parental care within a species. This study investigates the importance of the early rearing environment on the development of parental care in the biparental African striped mouse (*Rhabdomys pumilio*).

The striped mouse offers a unique opportunity to investigate the influence of the father on the development and expression of paternal care, as striped mice from the succulent karoo of South Africa show high levels of direct paternal care both in nature and in captivity, displaying all the behaviours shown by females (including huddling, licking and grooming and retrieving pups), apart from lactation (Schradin & Pillay 2003), in equal measure (huddling, licking and time spent in the nest; Schradin & Pillay 2003; Schubert et al. 2009). In addition, males typically show a nearly threefold increase in the time spent in the nest when pups are present (Schradin & Pillay 2003) and offspring development in this population is faster when fathers are present (Schradin & Pillay 2005). Under conditions of high population density, striped mice in the succulent karoo live in groups of 3–4 adult females and one adult breeding male (Schradin & Pillay 2004). Offspring are typically philopatric for a number of months because of the limited availability of suitable nesting sites (Schradin et al. 2010) and the benefits of group living, such as reduced energy expenditure afforded by group huddling (Scantlebury et al. 2006).

In species with paternal care, it is not apparent whether a male must experience direct care from its father to display appropriate levels of paternal care to its own offspring. Therefore, the aim of our study was to establish the extent to which paternal care in striped mice is influenced by the early experience of paternal care. To test this, we studied paternal care in striped mice in captivity, using males raised under three treatments: (1) by both parents; (2) by the mother only; or (3) by the mother physically separated from the father. We predicted that if paternal care was significantly influenced by the early experience of paternal care received, sons raised by their mothers only would show lower levels of paternal care than sons raised by both parents. Alternatively, if paternal care was merely a response to the presence of young, independent of an individual’s previous experience of paternal care, neither the presence nor the absence of fathers would influence the level of paternal care displayed by their sons.

Methods

Subjects

Striped mice were F1–F4 generation individuals derived from Goegap Nature Reserve (succulent karoo, Northern Cape Province, South Africa; 29.41.56 S, 18.1.60 E) housed under partially controlled environmental conditions (14 L:10 D cycle, lights on at 0500 hours; 20–24┐ C; 30–60% relative humidity).

A total of 22 breeding pairs were established and housed in glass tanks (46 x 30 x 32 cm). The floor of the tanks was covered with a layer of wood shavings for bedding. A plastic nest box (13 x 9 x 10 cm) was provided. Nesting material comprised a handful of dry grass provided weekly and approximately 5 g of paper towel provided twice weekly. One cardboard roll/paper cup was provided weekly per mouse for behavioural enrichment. Subjects had access to water *ad libitum* and were fed approximately 5 g of mixed seed (sprinkled throughout the cage to stimulate foraging behaviour) and 10 g of fresh fruit/vegetables daily per mouse.

Experimental design

The intention was to obtain three consecutive litters per breeding pair and randomly assign each litter to one of three different treatments. Nine pairs produced the required three litters, three pairs each produced two litters and three pairs each produced one litter only. Data from an additional seven pairs (two pairs produced two litters each and five pairs produced one litter each) were distributed among all treatments to achieve the required sample size.

We used single breeding pairs, rather than communally nesting groups, to remove the effects of female–female aggression (Schubert et al. 2009) and to reduce the likelihood of infanticide (Schradin et al. 2010). Experiments involved two phases. In Phase 1 (denoted below as Ph1), breeding pairs were subjected to three treatments in random sequence. (1) Mother + father (M + F) – both parents raised the young together until weaning (21 d of age). Because striped mice show a post-partum oestrus, mothers were normally pregnant during the rearing of their litter. (2) Mother alone (M – F) – the father was removed from the mother a few days prior to parturition and housed in a holding cage (42 x 26 x 14 cm) in a separate room. Thus, males had no contact with the female and young post-partum. (3) Mother + father separated (M/F) – the father was removed from the mother a few days prior to parturition by inserting a wire mesh barrier (30 x 32 cm, 1 x 1 cm squares) into the tank and placing the female and male on opposite sides. The father had visual, olfactory and auditory contact with the female and young post-partum, but no physical contact. This treatment was designed to test whether the close proximity of the father, but without physical contact, influenced the parental care behaviour of mothers and the subsequent expression of parental care in the offspring. At weaning, offspring (all treatments) were housed in same-sex sibling pairs in holding cages under the conditions described above until sexual maturity (approximately 90 d of age).

In Phase 2 (Ph2), one male (son = S) from each litter per treatment was randomly selected and paired with an unrelated mate (obtained from biparental pairs in our breeding colony) of approximately the same age, resulting in three treatments: SM + F, SM – F, SM/F (son from M + F, M – F and M/F, respectively). Pairs were housed as described for M + F.

Parental care

For Ph1 pairs, the maternal care displayed by mothers (all treatments) and the paternal care displayed by fathers (M + F treatment only) was video recorded for 15 min every second day, starting on Day 1 (Day 0 = day of birth) until Day 11 (i.e. for 6 d), following the protocol of Schradin & Pillay (2003) and Schubert et al. (2009). These data were used to assess the contribution of parental care of the mother only or both parents to the development of paternal care in sons. Recordings were made until Day 11 as young striped mice start eating solid food at this time (Pillay 2000) and parental care decreases after this time. Recordings were made between 0700 and 1100, coinciding with peak striped mouse activity, and no observers were present in the room. Using continuous sampling, we scored the behaviour of test subjects and summed the time spent in maternal (mothers) and paternal (fathers) care for the 6 d of taping. Parental care was scored using the following behaviours (after Schradin & Pillay 2003): time spent in close proximity (<2 cm) of pups (designated near); huddling; grooming (includes sniffing) pups; and retrieving pups. We could not distinguish between nursing and huddling pups for maternal care, so the data were grouped and collectively classified as huddling (as described by Schubert et al. 2009). The incidence of retrieval behaviour was very rare and did not vary among the treatments, and therefore, the results are not included here.

For Ph2 pairs, the paternal care displayed by males (SM + F, SM – F, SM/F) from all three treatments was recorded as described for Ph1.

Offspring growth

We recorded the growth rate of male and female pups in litters produced in both phases. For this, the masses of all males and all females in a litter were recorded to the nearest 0.1 g every day after birth for the first 7 d and every 3 d thereafter until day 21. Growth rates were calculated using the formula: (LN mass day 21 – LN mass day 1)/20 d.

Statistics

Statistica 7.1 (Statsoft Inc, http://www.statsoft.com) was used in all analyses. All parental care data met the assumptions of normality (Shapiro–Wilk's test) and homogeneity of variances (Levene's test). All tests were two-tailed, and the model-level significance was determined at $\alpha = 0.05$.

The data set for the three behaviours (near, huddling, grooming) for maternal (mothers) and paternal (fathers and sons) care over the 6 d of video-recording was first analysed with the variance components analysis using the Restricted Maximum Likelihood method to assess the effects of the following random factors on the behavioural variables: litter order (i.e. the first to third litter produced by a pair, accounting for previous breeding experience and reproductive condition of the females) and breeding pair identity (i.e. not all Ph1 pairs produced three litters and we used one or two litters each from additional breeding pairs to achieve the required sample size). In all cases, both random factors were not significant predictors of parental care ($p > 0.05$), indicating that parental care did not change with maternal parity. Therefore, they were not considered in further analyses. The data set was then analysed using a General Linear Model (GLM) with repeated measures, multivariate design, in which treatment was the categorical predictor, the behaviours were the dependent variables, 6 d (time) of recording were the repeated measures variables (to assess changes in behaviours over time), and litter size was the covariate. Fisher's HSD *post hoc* tests were used to identify specific differences in the main effects (treatment, time). For the interaction (treatment x time), orthogonal polynomial decomposition for linear and quadratic components was used to assess whether the changes in behaviour over time were random.

We compared the parental care displayed by mothers (Ph1) and sons (Ph2) using linear regressions. Growth rate data were arcsine transformed and analysed initially using variance components, which showed that litter order and breeding pair identity were not significant predictors of growth rates ($p > 0.05$). We then analysed the growth rates of offspring in each phase separately using a GLM, with a repeated measures design, in which treatment was the categorical predictor, male and female growth rates in a litter were the repeated measures variable, and litter size and sex ratio (M:F) were covariates.

Results

Maternal Care (care provided by mothers only in Ph1)

Treatment, time (6 d of recording) and treatment x time were all significant predictors of maternal care (Table 1). *Post hoc* tests revealed that mothers raising their young together with fathers (M + F) spent more time near their pups than mothers raising young alone (M/F, M – F; Fig. 1). In contrast, in the absence of their partners, mothers spent more time huddling (M – F) and grooming (M – F, M/ F) pups (Fig. 1). Time spent near pups was greatest on days 9 and 11 (i.e. last post-natal period). Huddling was greatest shortly after birth (days 1 and 3) compared to days 9 and 11. Grooming was greater on days 3, 5 and 7 compared to other days (Fig. 1, Table 1). For the treatment x time interaction, polynomial components were not significant for the time spent near (linear: $t = 1.27$, p = 0.210), huddling (linear: $t = 0.33$, p = 0.739; quadratic: $t = 1.83$, p = 0.072) and grooming (linear: $t = 1.42$, p = 0.162; quadratic: $t = 0.51$, p = 0.614) pups. However, there was a significant quadratic component for the time spent near pups ($t = 3.36$, p = 0.001), which fluctuated over time in the M – F treatment. Therefore, the general pattern in the relationship between treatment and time is random.

Total Parental Care (care provided by both parents in Ph1)

We compared total parental care provided by both parents (M + F) with mothers raising young alone (M – F and M/F). Treatment and treatment x time were significant predictors of parental care (Table 1). Parents in the M + F treatment spent more time near their pups compared to mothers raising young alone, but the levels of huddling and grooming for all treatments were similar (Fig. 2). For the treatment x time interaction, polynomial components were not significant for time spent near (linear: $t = 0.06$, p = 0.950; quadratic: $t = 0.24$, p = 0.811), huddling (quadratic: $t = 1.01$, p = 0.318) and grooming (linear: $t = -0.50$, p = 0.622; quadratic: $t = -0.88$, p = 0.382) pups. However, there was a significant linear component for the time spent huddling pups ($t = -3.67$, p = 0.001), which decreased over time in the M + F treatment. The general pattern between treatment and time is random.

Both parents (M + F) spent the greatest amount of time near pups on day 11 (Fig. 2), and M/F mothers spent the least time near pups on day 3 (Fig. 1); all other treatment/time combinations grouped together. Mothers alone (M – F, M/F) huddled their pups most on days 1 and 3. Pairs (M + F) showed lower levels of huddling than mothers raising young alone (M – F, M ⁄ F) on all days, but the least amount was shown by M/F mothers on day 11 (Fig. 1). Grooming did not show clear treatment x time distinctions, but was lowest in M – F mothers on day 1 and greatest in M + F (both parents) on day 11 (Fig. 2). Time and litter size did not influence parental care (Table 1).

Paternal Care (care provided by sons only in Ph2)

Treatment was the only significant predictor of paternal care displayed by sons (i.e. Ph2 pairs; Table 1). *Post hoc* tests revealed that males in the SM – F treatment showed the greatest level of huddling pups, but there was no difference in the level of time spent near pups and grooming pups among the treatments: SM – F, SM + F, SM/F (Fig. 3). A linear regression of parental care for all days combined revealed that there was a significant and strongly positive relationship for the time spent huddling pups between the mothers (Ph1) and their sons (Ph2; $R^2 = 0.56$; $F_{1,96} = 123.98$, p < 0.001; Fig. 4), but there was no relationship for time spent near ($R^2 = 0.18$; $F_{1,96} = 2.91$, p = 0.091) and grooming ($R^2 = 0.01$;

$F_{1,96} = 0.01$, p = 0.921) pups. Time, treatment x time, and litter size did not influence paternal care.

Offspring Growth (Ph1 and Ph2)

The growth rates of male and female offspring in each of the two phases are presented in Table 2. In both phases, treatment was not a significant predictor of growth rate, indicating that the absence or presence of the father (Phase 1) and the rearing history of sons (Phase 2) did not influence the growth of offspring. In addition, males and females in a litter had similar growth rates, indicating similar investment in both sexes by parents. Litter size and sex ratio were also not significant predictors of growth (Table 2).

Discussion

Male striped mice raised in the absence of their fathers (SM – F) spent more time huddling their pups compared to males raised by mothers physically separated from fathers (SM/F). Furthermore, males raised by both parents (SM + F) showed the lowest levels of huddling, suggesting that the level of paternal care provided by sons is influenced by the absence of prior experience of paternal care. Our results are surprising in the light of empirical evidence from at least two other rodent studies that show that early social interactions with fathers may influence the development of paternal care in their offspring (McGuire 1988; Bester-Meredith & Marler 2003). In contrast, our study suggests that, in striped mice, the role of the father in the development of paternal care in the sons is not as clear as originally anticipated. In addition, although fathers are beneficial for development of striped mice under natural weather conditions (Schradin & Pillay 2005), we found no influence of paternal care on offspring growth in either Phase 1 or Phase 2, possibly because optimal conditions in captivity minimize the energetic constraints usually associated with parental care (Brown 1993).

In the absence of their mates, Ph1 females increased their time spent huddling and grooming young by 1½ times. Provision of care by mothers raising young alone was thus similar to the total care provided by both mothers and fathers in the M + F treatment, indicating that females show compensation of care (defined here as an increase in maternal investment by the mother in an effort to overcome a loss of investment by her mate; adapted from Osorno & Székely 2004). Compensation of maternal care in the absence of a mate is common in the bird literature (e.g. magnificent frigatebirds (*Fregata magnificens*); Osorno & Székely 2004) and occurs in some mammals (e.g. rock cavies (*Kerodon rupestris*); Tasse 1986; female coyotes (*Canis latrans*); Sacks & Neale 2001). The expression of paternal care, in particular huddling behaviour, in striped mouse sons (Ph2) was subsequently influenced by this compensation of maternal care. We found no difference in growth rate between the sexes in litters (Ph1), suggesting that there is no differential allocation of maternal care between sons and daughters. Male offspring were thus not receiving obvious physical benefits from their mothers, at least in terms of increased growth, which does not explain why they showed increased paternal care later as adults (Ph2).

Decreased maternal care (huddling and grooming) when her mate is present may be the result of reduced maternal workload (McGuire 1997). However, the motivation to mate by both parents during post-partum oestrus could also disrupt maternal care (McGuire 1997). If so, we would have expected maternal care to be lowest when females were physically separated from their mates by a barrier than when females were raising young alone or with their mates, because separated females would spend more time attempting to access their mates through the barrier. This was not the case, however, as these separated females showed higher levels of huddling than females raising young with a mate. Although we cannot conclusively rule out sexual motivation as a causal factor for decreased maternal care (because separated females did show lower levels of grooming of pups than females raising young alone), it is more likely that females decrease maternal care when their mates are present because the males reduce maternal workload by helping raise the young (Schradin 2006; Schradin & Pillay 2005).

The mechanism underlying the development of paternal care, specifically the influence of the mother on the son's behaviour, is not apparent in our study. Nonetheless, we propose four possible explanations. (1) Some behavioural phenotypes can be non-genomically transmitted through the germline by epigenetic mechanisms (Curley & Mashoodh 2010), although this was not explicitly tested here. (2) Raising pups alone could increase stress hormone levels for Ph1 mothers, leading to increased interest in their young, as seen in rhesus macaques (*Macaca mulatta*, Maestripieri 2005). In addition, because corticosterone can be transferred to offspring via milk (Yeh 1984), this could have affected the paternal care behaviour displayed by striped mouse sons, as seen in female macaques (Maestripieri 2005). (3) Both mothers and fathers are known to influence the neuronal development of offspring (Liu et al. 2000; Outscharoff et al. 2006). For example, female Long-Evans hooded rats that receive high levels of maternal care (licking, grooming and arched-back nursing) show increased formation of hippocampal synapses (Liu et al. 2000) and also display greater levels of maternal care to their own young (Francis et al. 1999). (4) Many rodent mothers are reliable demonstrators for young (Lupfer et al. 2003) and we have previously shown that young striped mice are more likely to learn about novel food from their mothers than their fathers, possibly because mothers provide multiple channels (e.g. olfactory cues on the breath and gustatory cues in milk) for information transfer (Rymer et al. 2008). Similarly, because striped mouse mothers raising sons alone (M – F, M/F) had a closer association with them during the pre-weaning phase, females may also be reliable demonstrators of parental care for their sons. Clearly, untangling the proximate factors influencing the development of paternal care in striped mice requires rigorous examination in future.

A female striped mouse, which increases maternal investment in the absence of the male, produces sons that display greater levels of care for her descendants (i.e. grand-offspring) or her next litter (i.e. helpers at the nest; Schradin & Pillay 2004). This maternal effect is condition dependent, however, requiring a specific set of conditions for (1) its occurrence (females breeding alone) and (2) it to be advantageous (male mating strategy). For the occurrence (1), during periods of low population density, striped mouse females prefer raising offspring alone because of the costs associated with reproductive competition (e.g. increased female–female aggression, Schubert et al. 2009; infanticide, Schradin et al. 2010), but under conditions of high population density, they are often forced to nest in groups because of the limited availability of nesting sites (Schradin & Pillay 2004; Schradin et al. 2010). Group-living female striped mice gain a number of benefits associated with alloparenting (Schubert et al. 2009), such as reduced thermoregulatory costs (Scantlebury et al. 2006) and improved offspring growth (Schradin & Pillay 2005). For the advantages (2), adult male striped mice can adopt one of three mating strategies: territorial breeding males with paternal care, helpers at the nest or roaming breeding males that show no paternal care (Schradin 2008). If males adopt the roaming breeding strategy, which occurs under low population density (Schradin 2008), their potential to show care may never be realized. However, when population density increases, males may become territorial breeders or helpers at the nest, and both display alloparental care (Schradin 2008).

While the predictions about the development and expression of paternal care from fathers to sons were not supported in our study, our data reveal some unique insights into parental care in striped mice. First, there is a direct association between huddling and grooming by mothers and the expression of paternal behaviour of their sons. Although only huddling behaviour was correlated between mothers and sons, we cannot rule out the influence of the combined effect of various maternal care behaviours on the expression of paternal care in sons. Second, for female striped mice, the benefits of communal nesting may outweigh the delayed benefits of improved paternal care displayed by sons raised by their mothers alone. In the absence of the male and helpers, however, increased maternal compensation may reflect a contingency strategy that allows females to trade-off between current and future investment in their offspring. As compensation by mothers could result from natural variations in family structure and social rearing conditions within a species (Ahern & Young 2009), we propose a compensation hypothesis for biparental female rodents that favour solitary nesting, but are ecologically constrained to nesting in groups, such as in striped mice (Schradin et al. 2010). Finally, the development of paternal care may be condition dependent in male striped mice and illustrates a flexibility that has also been observed in male mating strategy in this species in response to prevailing environmental conditions (Schradin et al. 2009).

Acknowledgments

This study complied with the current laws and regulations in South Africa. Animal ethics clearance no. 2005/51/2A, University of the Witwatersrand. We are grateful to Megan Jones, Sneha Joshi and Melanie Schubert for providing technical assistance and to Carsten Schradin for comments on an earlier version of the manuscript. Funding was provided by the National Research Foundation (grant number: 2069110; DOL Scarce Skills scholarship) and the University of the Witwatersrand.

References

Ahern, T. H. & Young, L. J. 2009: The impact of early life family structure on adult social attachment, alloparental behavior, and the neuropeptides systems regulating affiliative behaviors in the monogamous prairie vole (*Microtus ochrogaster*). Front. Behav. Neurosci. **3**, 1–19.

Bester-Meredith, J. K. & Marler, C. A. 2003: Vasopressin and the transmission of paternal behavior across generations in mated, cross-fostered *Peromyscus* mice. Behav. Neurosci. **117**, 455–463.

Brown, R. E. 1993: Hormonal and experiential factors influencing parental behaviour in male rodents: an integrative approach. Behav. Processes **30**, 1–28.

Curley, J. P. & Mashoodh, R. 2010: Parent-of-origin and trans-generational germline influences on behavioral development: the interacting roles of mothers, fathers, and grandparents. Dev. Psychobiol. **52**, 312–330.

Curley, J. P., Champagne, F. A., Bateson, P. & Keverne, E. B. 2008: Transgenerational effects of impaired maternal care on behaviour of offspring and grandoffspring. Anim. Behav. **75**, 1551–1561.

Francis, D., Diorio, J., Liu, D. & Meaney, M. J. 1999: Nongenomic transmission across generations of maternal behavior and stress response in the rat. Science **286**, 1155–1158.

Freeman-Gallant, C. R. & Rothstein, M. D. 1999: Apparent heritability of parental care in Savannah sparrows. Auk **116**, 1132–1136.

Gomendio, M., García-González, F., Reguera, P. & Rivero, A. 2008: Male egg carrying in *Phyllomorpha laciniata* is favoured by natural not sexual selection. Anim. Behav. **75**, 763–770.

Goodenough, J., McGuire, B. & Wallace, R. A. 2001: Perspectives on Animal Behaviour, 2nd edn. Wiley, Toronto, Canada.

Gubernick, D. J. & Teferi, T. 2000: Adaptive significance of male parental care in a monogamous mammal. Proc. R. Soc. Lond. B **267**, 147–150.

Kikusui, T., Isaka, Y. & Mori, Y. 2005: Early weaning deprives mouse pups of maternal care and decreases their maternal behavior in adulthood. Behav. Brain Res. **162**, 200–206.

Liu, D., Diorio, J., Day, J. C., Francis, D. D. & Meaney, M. J. 2000: Maternal care, hippocampal synaptogenesis and cognitive development in rats. Nat. Neurosci. **3**, 799–806.

Lupfer, G., Frieman, J. & Coonfield, D. 2003: Social transmission of flavour preferences in two species of hamsters (*Mesocricetus auratus* and *Phodopus campbelli*). J. Comp. Psychol. **117**, 449–455.

Maestripieri, D. 2005: Effects of early experience on female behavioural and reproductive development in rhesus macaques. Proc. Roy. Soc. Lond. B **272**, 1243–1248.

McCarty, R. & Southwick, C. H. 1977: Paternal care and the development of behavior in the southern grasshopper mouse, *Onychomys torridus*. Behav. Biol. **19**, 476–490.

McGuire, B. 1988: Effects of cross-fostering on parental behavior of meadow voles (*Microtus pennsylvanicus*). J. Mammal. **69**, 332–341.

McGuire, B. 1997: Influence of father and pregnancy on maternal care in red-backed voles. J. Mammal. **78**, 839–849.

Osorno, J. L. & Székely, T. 2004: Sexual conflict and parental care in magnificent frigatebirds: full compensation by deserted females. Anim. Behav. **68**, 337–342.

Outscharoff, W., Jr., Helmeke, C. & Braun, K. 2006: Lack of paternal care affects synaptic development in the anterior cingulated cortex. Brain Res. **1116**, 58–63.

Pillay, N. 2000: Fostering in the African striped mouse: implications for kin recognition and dominance. Acta Theriol. **45**, 193–200.

Rymer, T., Schradin, C. & Pillay, N. 2008: Social transmission of information about novel food in two populations of the African striped mouse, *Rhabdomys pumilio*. Anim. Behav. **76**, 1297–1304.

Sacks, B. N. & Neale, J. C. C. 2001: Does paternal care of pups benefit breeding female coyotes? Southwest. Nat. **46**, 121–126.

Scantlebury, M., Bennett, N. C., Speakman, J. R., Pillay, N. & Schradin, C. 2006: Huddling in groups leads to daily energy savings in free-living African four-striped grass mice, *Rhabdomys pumilio*. Funct. Ecol. **20**, 166–173.

Schradin, C. 2006: Whole-day follows of striped mice (*Rhabdomys pumilio*), a diurnal murid rodent. J. Ethol. **24**, 37–43.

Schradin, C. 2008: Differences in prolactin levels between three alternative male reproductive tactics in striped mice (*Rhabdomys pumilio*). Proc. R. Soc. Lond. B. **275**, 1047–1052.

Schradin, C. & Pillay, N. 2003: Paternal care in the social and diurnal striped mouse (*Rhabdomys pumilio*): Laboratory and field evidence. J. Comp. Psychol. **117**, 317–324.

Schradin, C. & Pillay, N. 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**, 37–47.

Schradin, C. & Pillay, N. 2005: The influence of the father on offspring development in the striped mouse. Behav. Ecol. **16**, 450–455.

Schradin, C., Scantlebury, M., Pillay, N. & König, B. 2009: Testosterone levels in dominant sociable males are lower than in solitary roamers: Physiological differences between three male reproductive tactics in a sociably flexible mammal. Am. Nat. **173**, 376–388.

Schradin, C., Köenig, B. & Pillay, N. 2010: Reproductive competition favours solitary living while ecological constraints impose group-living in African striped mice. J. Anim. Ecol. **79**, 515–521.

Schubert, M., Pillay, N. & Schradin, C. 2009: Parental and alloparental care in a polygynous mammal. J. Mammal. **90**, 724–731.

Tasse, J. 1986: Maternal and paternal care in the rock cavy, *Kerodon rupestris*, a South American hystricomorph rodent. Zoo Biol. **5**, 27–43.

Wright, H. W. Y. 2006: Paternal den attendance is the best predictor of offspring survival in the socially monogamous bat-eared fox. Anim. Behav. **71**, 503–510.

Yeh, K. Y. 1984: Corticosterone concentration in the serum and milk of lactating rats: parallel changes after induced stress. Endocrinology **115**, 1364–1370.

Table 1 Predictors (Treatment, time, treatment x time, litter size) of parental care displayed by female (mothers) and male (sons) striped mice

Predictors	Statistics	Post hoc comparisons
Maternal care (Phase 1)		
Treatment	**$F_{6, 114} = 9.02, p < 0.001$**	Near: M + F > M – F > M/F Huddling: M – F > M/F > M + F Grooming: M – F = M/F, M – F > M + F
Time	**$F_{15, 45} = 10.65, p < 0.001$**	Near: (D11, D9) > (D1, D3, D5, D7) Huddling: (D1, D3) > (D5, D7) > (D9, 11) Grooming: (D5, D3, D7), (D7, D9, D1, D11)
Treatment x Time	**$F_{30, 90} = 6.06, p < 0.001$**	See text.
Litter size	$F_{3, 57} = 0.29, p = 0.831$	
Total parental care (Phase 1)		
Treatment	**$F_{6, 114} = 15.76, p < 0.001$**	Near: M + F > M/F = M – F Huddling: M + F = M/F = M – F Grooming: M + F = M/F = M – F
Time	$F_{15, 45} = 1.63, p = 0.104$	
Treatment x Time	**$F_{30, 90} = 1.85, p = 0.014$**	See text
Litter size	$F_{3, 57} = 0.72, p = 0.546$	
Paternal care (Phase 2)		
Treatment	**$F_{6, 86} = 2.65, p = 0.021$**	Near: SM + F = SM/F = SM – F Huddling: SM – F > SM + F = SM/F Grooming: SM + F = SM/F = SM – F
Time	$F_{15, 31} = 1.66, p = 0.114$	
Treatment x Time	$F_{30, 62} = 0.70, p = 0.859$	
Litter size	$F_{3, 43} = 1.77, p = 0.166$	

Statistics = General Linear Model with a repeated measures design. *Post hoc* comparisons are provided for significant predictors (indicated in bold) for the main effects: homogeneous (non-significant) subsets are given in parentheses. M + F = mothers and fathers raised young together, M/F = mothers separated from fathers by a metal barrier and raised young alone, M – F = mothers raised young alone; D = day.

Table 2. Mean (± SE) growth rates for male and female offspring during the first 21 d after birth for treatments in two phases

Phase/ Treatment	**Male growth rate**	**Female growth rate**	**Statistics**
Phase 1			
M + F	0.085 (0.004)	0.087 (0.003)	Treatment: $F_{2, 25} = 0.19$, p = 0.828
M/F	0.076 (0.007)	0.077 (0.006)	Male vs female: $F_{1, 25} = 0.99$, p = 0.330
M – F	0.085 (0.002)	0.083 (0.002)	Litter size: $F_{1, 25} = 0.89$, p = 0.356
			Sex ratio: $F_{1, 25} = 0.03$, p = 0.866
Phase 2			
SM + F	0.079 (0.003)	0.077 (0.003)	Treatment: $F_{2, 21} = 0.55$, p = 0584
SM/F	0.077 (0.002)	0.078 (0.002)	Male vs female: $F_{1, 21} = 0.06$, p = 0.831
SM – F	0.082 (0.003)	0.081 (0.002)	Litter size: $F_{1, 21} = 3.27$, p = 0.085
			Sex ratio: $F_{1, 21} = 0.05$, p = 0.831

Statistics, General Linear Model with a repeated measures design, indicate that none of the predictors were significant. M + F = mothers and fathers raised young together, M/F = mothers separated from fathers by a metal barrier and raised young alone, M – F = mothers raised young alone, SM + F = sons from M + F treatment, SM/F = sons from M/F treatment, SM – F = sons from M – F treatment.

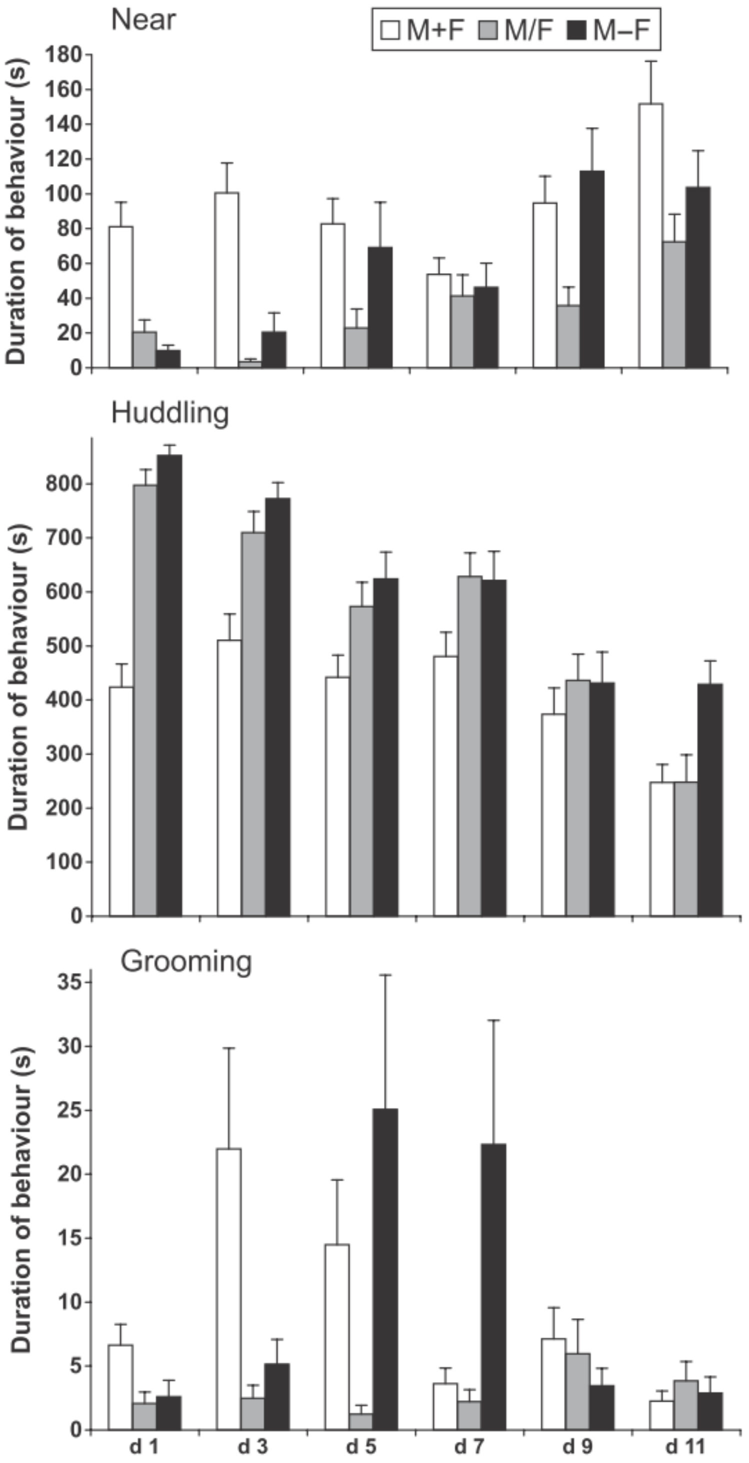

Fig. 1: Maternal care during Phase 1. Mean ± SE time (seconds) spent on three parental care behaviours by female striped mice for 6 taping days (Day 1–Day 11). Results of the statistical analyses are presented in Table 1. M + F = mothers and fathers raised young together, M/F = mothers separated from fathers by a metal barrier and raised young alone, M – F = mothers raised young alone.

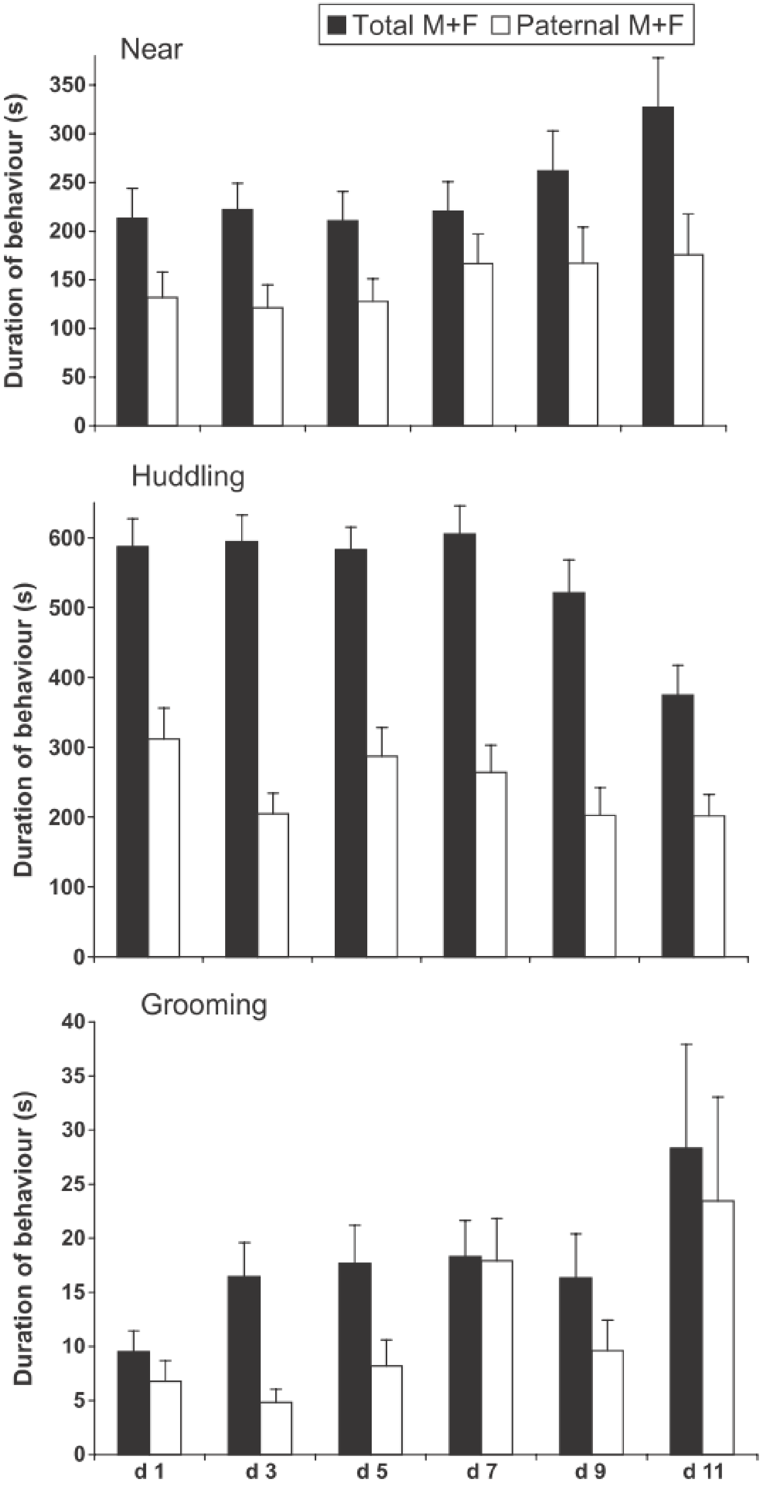

Fig. 2: Paternal care and total parental care during Phase 1. Mean ± SE time (seconds) spent on three parental care behaviours by male striped mice and both parents combined (Total M + F, Phase 1) for 6 taping days (Day 1–Day 11). Results of the statistical analyses are presented in Table 1. M + F = mothers and fathers raised young together.

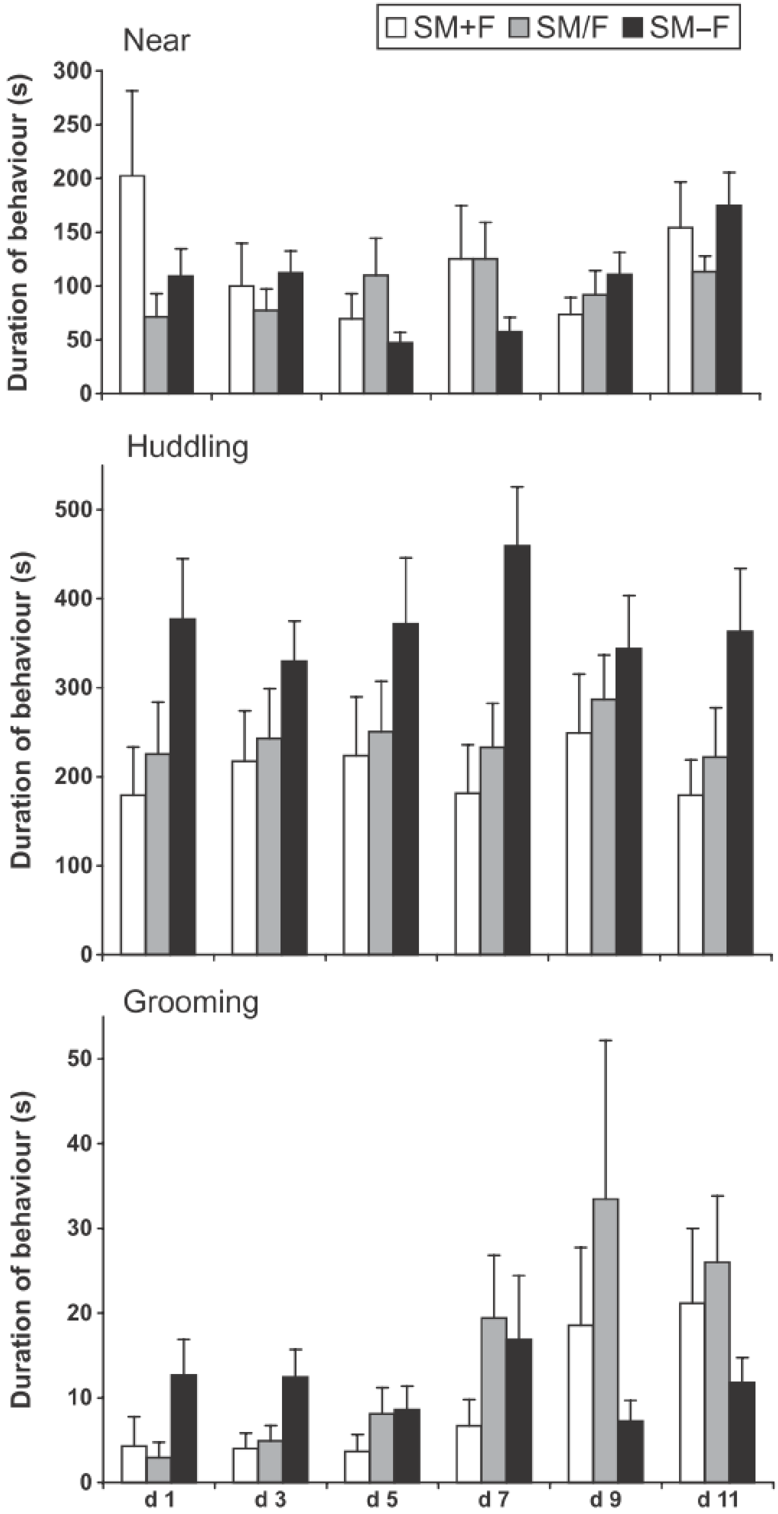

Fig. 3: Paternal care during Phase 2. Mean ± SE time (seconds) spent on three parental care behaviours by male (adult sons) striped mice for 6 taping days (Day 1–Day 11). Results for the statistical analyses are presented in Table 1. SM + F = sons from M + F treatment, SM/F = sons from M/F treatment, SM – F = sons from M – F treatment.

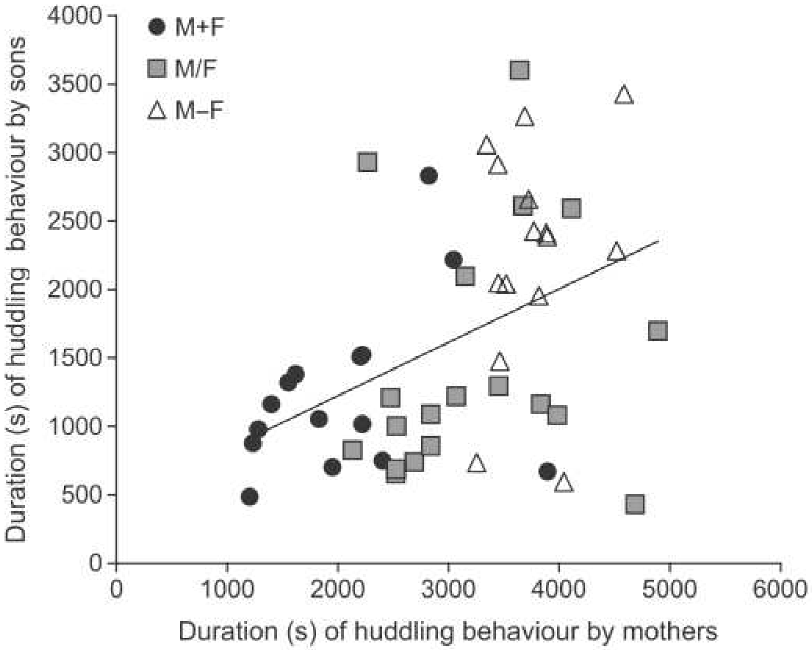

Fig. 4: The relationship in huddling behaviour between mothers (Phase 1) and their sons (Phase 2). Huddling behaviour is the sum of the 6 days of sampling. Breeding conditions indicated as: M + F = mothers and fathers raised young together, M/F = mothers separated from fathers by a metal barrier and raised young alone, M – F = mothers raised young alone. The formula for the regression line: $y = 443.21 + 0.39x$.