



Effects of early experience on subsequent parental behaviour and reproductive success in oldfield mice, *Peromyscus polionotus*

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Studies of a variety of taxa have almost universally shown an increase in survivorship between the first cohort of young reared by a female (or both parents) and subsequent litters. Here, we examine the effect of early experience with sibling pups during the subadult period on later maternal behaviour and reproductive success in oldfield mice. 'Experienced' females remained with their mothers through the rearing of a litter of siblings. 'Inexperienced' females were removed from their parents at 20 days of age and had no prior exposure to pups before they reproduced. Twenty-four experienced females and 24 inexperienced females (each a full sibling of an experienced female) were paired with noninbred, inexperienced males through the birth and rearing of three litters. Litter survival improved significantly with experience and increasing parity. Pairs with experienced females showed improved nest-building behaviour and averaged significantly more surviving pups than did pairs with inexperienced females. Inexperienced mates of experienced females showed improved nest building, as well, consistent with the results of previous studies showing that paternal care tends to match that of mates. Maternal body weight did not appear to influence reproductive performance. These findings support the contention that individuals may accrue significant fitness benefits by delaying their own reproduction and gaining experience.

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The performance of adequate parental behaviour has obvious implications for successful reproduction. This may be particularly significant in animals that produce altricial young. Prior experience rearing offspring may lead to improved parental behaviour in such species. In most iteroparous animals for example, litter viability tends to be greater in later litters than in first litters (Wang & Novak 1994; Lacy et al. 1996; Margulis 1998a), presumably due at least in part to prior experience with previous litters. Female laboratory rats with experience have been found to show increased maternal behaviour when exposed to alien pups (Stern & Rogers 1988) compared with females with no prior exposure to pups. Female rats with no prior experience with young show

appropriate parental behaviours, including pup retrieval and nest building, less often than rats that have given birth and cared for young previously (Fleming & Luebke 1981). Similarly, the duration of previous maternal experience strongly affects the latency of house mice and rats to respond to young (Cohen & Bridges 1981; Koch & Ehret 1989). The relationship between experience and reproductive performance is not fully resolved however, and interestingly, a number of studies using altricial species have found no such relationship between parity and litter survival. Grotta (1973) found no effect of either parity or experience on maternal behaviour in rats. König & Markl (1987) and Hartung & Dewsbury (1979) reported similar findings in *Mus* and *Peromyscus*, and Paul & Kuester (1996) found a similar lack of effect in Barbary macaques, *Macaca sylvanus*.

Increased survivorship and/or improved parental care between the first cohort of young reared and subsequent cohorts has been found in numerous mammalian species

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(rats: Cohen & Bridges 1981; tamarins: Tardif et al. 1984; gerbils: Salo & French 1989; vervet monkeys: Fairbanks 1990). The seminal work by Harlow for example (Harlow & Harlow 1962) in rhesus macaques, *Macaca mulatta*, definitively showed that abnormal social experience early in life can lead to impairments in sexual and parental behaviour later in life. More recently, studies of animals in zoos have shown that experience leads to improved maternal behaviour in a variety of species (e.g. primates, carnivores and rodents: Baker et al. 1996), and absence of such experience may lead to reproductive impairment (Hawaiian crows, *Corvus hawaiiensis*: Harvey et al. 2002). This has also been demonstrated in domestic cats, *Felis catus* (Mellen 1992), as a model for captive management of small felids.

Juveniles may remain with their parents beyond sexual maturity and delay their own reproduction (primates: French 1997; canids: Moehlman & Hofer 1997; meerkats: Clutton-Brock et al. 2001). In some cases, female puberty may be delayed or reproductive suppression induced by contact with the mother, thereby enabling a maturing female to remain in the family group (golden lion tamarin, *Leontopithecus rosalia*: French et al. 1989; California mouse, *P. californicus*: Gubernick & Nordby 1992). Adult golden lion tamarins that have infant-carrying experience as juveniles are more successful at rearing their own offspring than are animals without comparable experience (Hoage 1978). Similar patterns have been found in other callitrichid species (Tardif et al. 1984; Goldizen 1987). These studies suggest that in some cases, a young, nulliparous female may gain significant fitness benefits from remaining with her mother through the rearing of another litter. Such a female might potentially benefit from gaining experience and increase her chances of rearing a successful first litter of her own. In this context, delayed dispersal may represent a response to the benefits that may be accrued by remaining in the natal group (such as an increased chance of inheriting a breeding territory, fitness gains through helping rear siblings, and survival advantages of living in a group). Alternatively, delayed dispersal may be a consequence of reproductive constraints, in that shortages of breeding territories or partners, or a reduced chance of successfully breeding without experience or assistance may influence whether or not offspring disperse (Emlen 1994).

Maternal care has an obvious and strong effect on offspring survival. Selection experiments with laboratory mice have found a heritable component to maternal care, driven largely by greater litter survival in lines selected for a high 'maternal care index', independent of initial litter size (Cheng et al. 2002).

Taken together, these findings suggest that there may be a significant fitness benefit to remaining in the natal group while siblings are being reared from birth to weaning. In the present study, we examined the effect of exposure to sibling neonates during the subadult period on subsequent parental behaviour and reproductive success in the oldfield mouse. *Peromyscus polionotus* is a monogamous rodent that displays biparental care (Foltz 1979, 1981; Margulis 1996). Unlike the related California mouse, in which males engage in all aspects of parental

care at levels comparable to that of females (Gubernick & Nelson 1989; Gubernick et al. 1993), *P. polionotus* paternal behaviour is more modest, and does not appear to have a significant effect on litter survival in the controlled laboratory environment (Margulis 1996, 1998b). Males do however engage in parental care (nest building and huddling with pups) and evidence from the field points to the mated pair remaining together through the birth and rearing of multiple litters (Foltz 1979, 1981).

Age of first oestrus in oldfield mice has been reported to be as early as 30 days of age, with age of first conception as early as 35 days of age (Millar 1989). Females undergo a postpartum oestrus and gestation is approximately 23–24 days (Smith 1966; Millar 1989). In the wild, oldfield mice have a relatively short tenure as territory-holding, breeding adults (probably not more than 2–3 months) (Smith 1966; Rave & Holler 1992; J. Layne, unpublished data). Only limited details on age of dispersal and maturity are available for *P. polionotus*. However, in an extensive field study on *P. polionotus*, Foltz (1981) found evidence of multiple litters present in nests. In some cases, a female might be pregnant, lactating, and have older offspring present simultaneously. Given these life-history parameters, and the finding of presumed consecutive litters in nests in the wild, it is likely that pups often remain with their parents beyond the age of sexual maturity and during at least part of the rearing of a litter of siblings. Furthermore, it is unlikely that a breeding pair will produce more than two or three litters in their lifetime. For a species with such limited breeding potential, actions that increase the survival probability of litters, particularly first litters, are likely to be advantageous.

Here we describe the results of a study in which we evaluated the relationship between prior experience with pups and litter survival in oldfield mice. We tested three predictions of the hypothesis that prior experience with a sibling litter enhances reproductive success. First, pairs in which females had prior pup experience should enjoy greater pup survival than pairs with inexperienced females. Second, experienced females should show enhanced parental care compared with inexperienced females. Third, inexperienced mates of experienced females should show enhanced paternal care compared with those of inexperienced females. Differences between experienced and inexperienced pairs should also decline with increasing parity, as naïve females gain experience with their own pups.

METHODS

Subjects and Study Site

We conducted the study at the Brookfield Zoo Mouse Colony, Brookfield, Illinois, U.S.A. The colony has been the site of intensive genetic and demographic research by Lacy and coworkers (Brewer et al. 1990; Lacy et al. 1996; Lacy & Ballou 1998), and more recently, behavioural research (Margulis 1997, 1998a, b; Margulis & Altmann 1997; Ryan & Altmann 2001; Ryan et al. 2003) on several subspecies of *P. polionotus*. Here, we used the subspecies

P. polionotus rhoadsi. All subjects in the present study were noninbred (inbreeding coefficients of 0.1 or less; Lacy et al. 1996), and were 10th to 15th generation descendants of 52 animals wild-caught in 1990 and 1991 near the town of Lake Placid, Highlands County, Florida, U.S.A. Although some loss of genetic variability is inevitable in a closed population, maintenance of detailed pedigrees ensured that some noninbred individuals were continuously available.

The limited field data on *P. polionotus* indicate that typically, both parents are present during pup rearing, but this is not always the case; Foltz (1981) found that 50.5% of burrows did indeed contain an adult male and female, but 13.4% of excavated burrows contained an adult female and young. The remaining burrows contained single individuals, subadults or in some cases two or more adults of the same sex. Laboratory studies (Margulis 1996, 1998b) have shown that maternal behaviour has a much greater effect on litter survival than does paternal behaviour (Margulis 1998b).

Establishing Experimental Stocks

To maintain stocks and generate experimental subjects, pairs were housed in standard polycarbonate mouse cages, and received mouse chow and water ad libitum. They were maintained on a 12:12 h light:dark cycle. All subjects were at least 60 days of age when paired. Parental stocks were maintained by weaning pups (removing them from their parents) at 20 days of age, at which time the breeding pair was separated. Because females undergo a postpartum oestrus, the next litter was generally born within 1 week of weaning of the prior litter. The female then reared the second litter without her mate. Given the limited life history information available for *P. polionotus*, the impact of removing the mate was not likely to have a substantial impact on litter survival in the controlled laboratory environment. In any case, the breeding paradigm used here produced animals that had never previously been exposed to pups until they themselves reproduced.

To generate subjects for our experienced and inexperienced experimental groups, when the pups reached 20 days of age, we removed the father, but instead of removing all pups at this time, we left at least two pups (a female and a sibling of either sex) with their mother through the birth and weaning of the next litter. These animals were removed from their mother at the weaning of the subsequent litter. They were approximately 45 days old at this time. Animals were then housed in same-sex groups until the start of the experiment. These females became the 'experienced' females in the present study. Those pups that were not left with their mother were removed at 20 days of age, and housed in same-sex groups until eventual pairing. These animals became the 'inexperienced' females, indicating that they had no prior exposure to younger pups before producing their first litter.

Twenty-four experienced females and 24 inexperienced females (each a full sibling of an experienced female) were

paired with noninbred, inexperienced males. All subjects were at least 60 days old at the time of pairing (mean age \pm SE: females: 68.3 ± 1.6 days; males: 77.2 ± 1.97 days). Pairs in which the female remained with her parents through the rearing of a subsequent litter are hereafter referred to as 'experienced' pairs; pairs in which the nulliparous female had no prior experience are referred to as 'inexperienced' pairs. To generate a meaningful and species-typical number of litters per pair ($N = 3$), experimental pairs were separated at the weaning of the second litter. Females went on to rear their third litters on their own. Although this design resulted in third litters being reared in a somewhat atypical manner, this manipulation was necessary to prevent further conceptions.

We did not weigh subjects at the time of pairing. Thus, we could not evaluate directly whether maternal body weight might confound the results. To assess whether an effect of differential body weight might have influenced results (e.g. experienced females might be larger, and larger mothers might have greater reproductive success as a result), we used another data set in which maternal body weight, litter size and litter survival were measured for 66 litters across 35 females maintained under the same conditions as those in the present study. This other study was designed to test effects of inbreeding and nutritional stress on growth and reproductive success (J. Lacy, unpublished data). For the comparison of maternal body weight and reproductive success, only noninbred females receiving a standard diet were analysed.

Behavioural Observations

At all times throughout data collection, the observer was not aware of the experimental status of subjects (experienced or inexperienced). Cages were checked for the presence of litters each morning. Upon discovery of a litter, we recorded initial litter size and conducted a 20-min focal observation (Altmann 1974) of the parents and neonates. The observer stood approximately 1 m from the cage and, using a palmtop computer, recorded parental activity, the time that each parent spent in contact with pups and the number of times each parent nuzzled or carried pups (Table 1). After 10 min, we then added cotton nesting material to the food hopper and collected an additional 10 min of nest-building data. All pairs built nests by the end of the first day, although not all pairs did so during the observation period. We recorded the total time spent nest building as well as the latency to begin nest building. Our experience working with the mice in our colony has shown that providing mice with nesting material prior to the birth of the litter may lead to decreases in pup survival, because the cotton may become stuck to the wet pups, and the parents, in the process of grooming the cotton off, may injure or kill the pups (R. C. Lacy, unpublished data). Previous observations throughout the 20-day period of parental care have shown that maternal behaviour during the immediate postpartum period is representative of behaviour throughout the full period, and is as strong a predictor of litter survival as is

Table 1. Behaviours recorded during postpartum observations

Behaviour	Definition
Active	Subject locomotes about cage, consumes food, or self-grooms
Inactive	Subject sits, immobile, eyes open or closed
Contact	Subject huddles over pups or lies in cotton bedding with pups
Nest building	Subject uses teeth and paws to bring nesting material into the cage from food hopper, or manipulates nesting material already in cage
Cannibalize	Subject consumes pup
Carry pup	Subject transports pup in mouth
Nuzzle	Subject licks or places its muzzle in contact with mate or pup

behaviour throughout the full period (Margulis 1996, 1998b).

Analyses

We used logistic regression (Hosmer & Lemeshow 1989; SAS Institute 1999) to evaluate the effect of prior experience on litter survival, and the influence of maternal body weight on litter survival, as has been used in prior studies of effects on litter survival in this species (Lacy et al. 1996). Because mortality is negligible after the first 10 days (Margulis 1996), young were counted as 'surviving' if they survived to weaning, at 20 days of age. The fate of pups in a litter was not independent. Rather, litters tended to survive or die completely when litters were not inbred (Margulis 1997). Therefore, in those few cases in which some but not all pups in a litter survived, we measured litter survival dichotomously, with litters categorized as surviving if more than half the pups in the litter survived, and as not surviving if half or fewer pups survived (Lacy et al. 1996). In the present study, females could gain prior experience in two ways. First, they could be part of the experimental group (experience as a juvenile). Second, they could gain experience via increasing parity (both experimental and control groups).

We measured litter size at birth and at weaning for pairs with experienced versus inexperienced females and assessed differences using Student's *t* tests on log-transformed data (Sokal & Rohlf 1981). We used Pearson correlation coefficients to determine whether there was a relationship between litter size and litter survival. We used survival analysis (Kalbfleisch & Prentice 1980; SAS Institute 1999) to analyse the time elapsed until onset of nest-building behaviour for experienced and inexperienced females and their mates. Not all subjects began nest building during the observation period. Unlike most statistical techniques, survival analysis allows such incomplete information to be included as 'censored' data, and not omitted as missing data. We used a Wilcoxon two-sample test, with normal approximation for $N > 10$ (SAS Institute 1999) to assess behavioural differences between both males and females in pairs with experienced females

and inexperienced females. Behavioural data for first and later litters were analysed separately.

RESULTS

Among the experimental pairings of this study, the probability of litter survival was substantially greater for experienced pairs than inexperienced pairs (survival probability = 0.96 for experienced pairs, 0.76 for inexperienced pairs). When experience, parity, and their interaction were included in the logistic regression model, no significant effect was found (Wald $\chi^2_5 = 2.29$, $P = 0.808$). However, when the interaction was removed from the model, both experience and parity significantly improved survival (experience: $\chi^2_1 = 5.33$, $P = 0.021$; parity: $\chi^2_2 = 6.51$, $P = 0.038$). When the effect of parity was broken down by litter, first litters had significantly lower survival than later litters ($\chi^2_1 = 6.47$, $P = 0.011$), but second and third litters did not differ significantly ($\chi^2_1 = 0.12$, $P = 0.729$). Although there was not a significant interaction between the effects of experience and parity on litter survival ($\chi^2_2 = 0.004$, $P = 0.998$), the difference in survival narrowed for the third litters, by which time survival was 100% for experienced pairs and approaching that for inexperienced pairs (Fig. 1). There was no significant difference in litter size at birth for experienced and inexperienced females (inexperienced females: 4.82 ± 0.15 pups; experienced females: 5.23 ± 0.16 pups; two-sample *t* test: $t_{115} = 1.95$, $P = 0.073$), and there was no correlation between litter size at birth and litter survival (Pearson correlation: $r_{117} = 0.13$, $P = 0.06$).

The litter sizes and litter survival rates of the inexperienced dams were very similar to what has been reported previously for mice from this stock (Lacy et al. 1996). In the earlier study (which used only inexperienced dams), the mean number of pups born in litters 1 and 2 were 3.93 and 4.84, respectively, when adjusted for an inbreeding coefficient of 0. Mean survival was 0.66 and 0.89 for first and second litters, respectively. Using data collected in a related study (R. C. Lacy, unpublished data), maternal

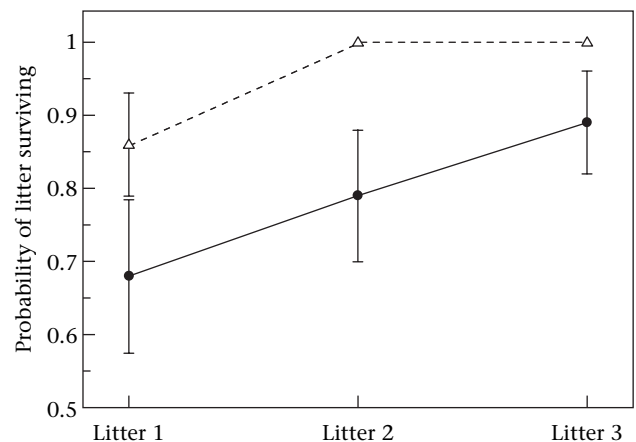


Figure 1. Probability of litter survival for pairs with experienced (Δ) and inexperienced (●) females. The absence of error bars for second and third litters of experienced pairs is due to 100% litter survival.

body weight had no significant effect on litter survival (logistic regression: Wald $\chi^2_1 = 0.126$, $P = 0.73$).

Latency to begin nest building was significantly shorter for experienced females and their mates for later litters, but not for first litters (survival analysis: females' later litters: Wald $\chi^2_1 = 4.69$, $P = 0.03$; females' first litters: $\chi^2_1 = 0.43$, $P = 0.51$; Fig. 2; males' later litters: $\chi^2 = 4.53$, $P = 0.03$; males' first litters: $\chi^2 = 2.11$, $P = 0.146$; Fig. 3). Experienced females spent significantly more time nest building during the 10-min observation period than did inexperienced females for first litters (Wilcoxon two-sample test: $Z = 2.09$, $N = 38$, $P = 0.037$) and subsequent litters ($Z = 1.97$, $N = 71$, $P = 0.049$). For males, the difference was significant only for first litters ($Z = 2.03$, $N = 38$, $P = 0.042$). We found no significant differences for males or females in the amount of time spent in contact with pups, locomoting, or carrying pups based on experience, for either first or later litters. Experienced females nuzzled pups significantly more frequently than did inexperienced females for second litters ($Z = 2.26$, $N = 40$, $P = 0.0237$).

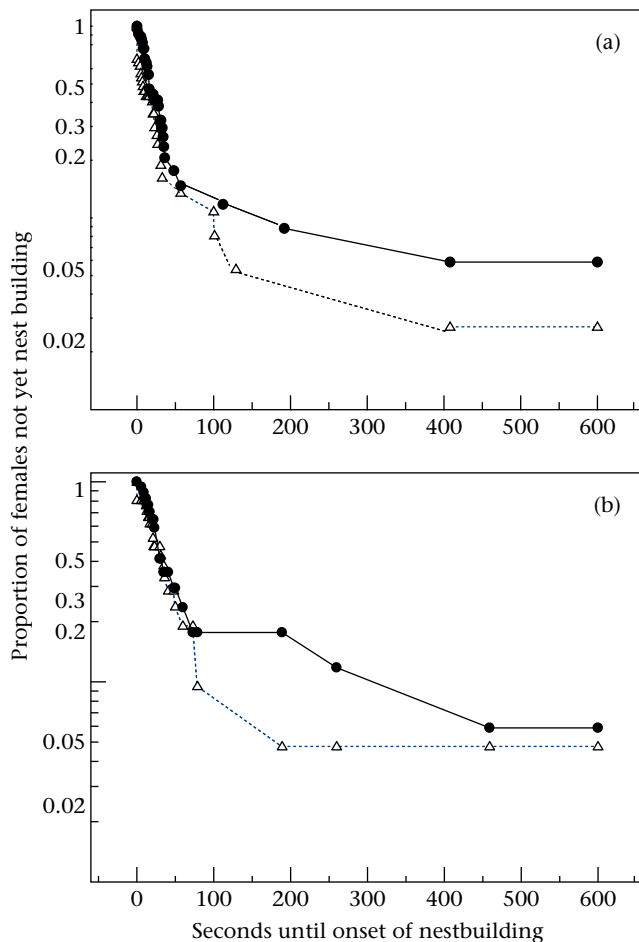


Figure 2. Proportion of females not yet beginning to build nests at the end of the 10-min observation period for pairs with experienced (Δ) and inexperienced (\bullet) females: (a) excluding first litters (Wilcoxon $\chi^2_1 = 4.69$, $P < 0.03$); (b) first litters only (Wilcoxon $\chi^2_1 = 0.43$, $P < 0.54$).

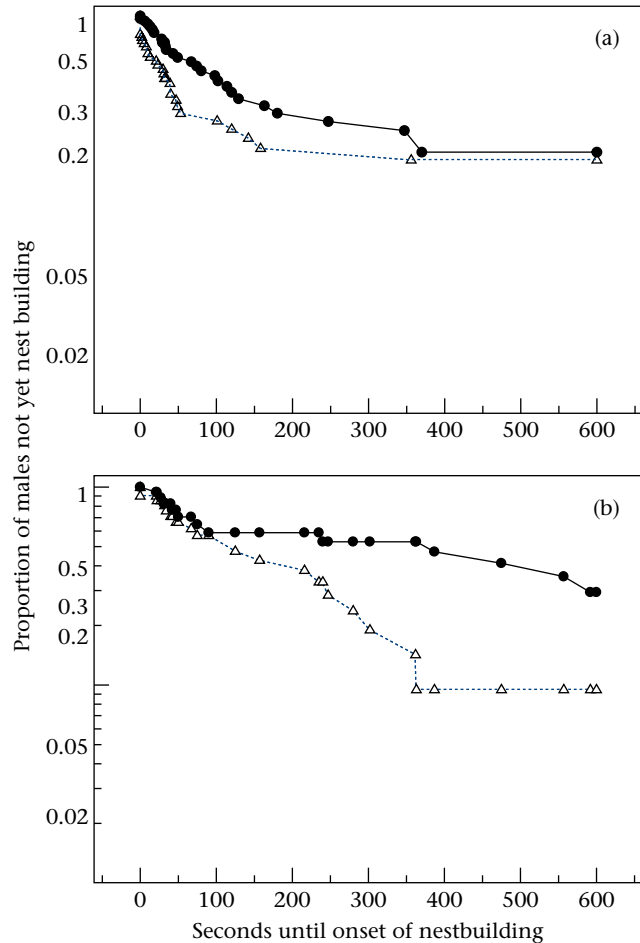


Figure 3. Proportion of males not yet beginning to build nests at the end of the 10-min observation period for males with experienced (Δ) and inexperienced (\bullet) mates: (a) excluding first litters (Wilcoxon $\chi^2_1 = 4.53$, $P < 0.03$); (b) first litters only (Wilcoxon $\chi^2_1 = 2.11$, $P < 0.15$).

DISCUSSION

There must be compelling reasons for young, sexually mature females to remain in the nest and forego immediate reproduction. Several censuses on wild populations of *P. polionotus* have found that immature females remain in their natal nests beyond sexual maturity (Foltz 1979, 1981). Advantages of philopatry and constraints on dispersal must both be considered with respect to whether or not offspring should disperse (Emlen 1994). For *P. polionotus*, possible reasons for delayed dispersal and reproduction may include a shortage of suitable nest sites, increasing inclusive fitness via kin selection, and gaining experience by helping to rear sibling offspring. While all three of these explanations may be involved, the present results most directly support the third possibility. Our findings suggest that young females who remain with their mothers through the rearing of a sibling litter gain direct fitness benefits through their increased chances of successfully rearing their own pups. Some evidence from laboratory rats suggests that older siblings may be interacting directly with younger siblings, but the nature of

that interaction is not clear. Gilbert et al. (1983) observed first litters of rats attending younger siblings in the nest, and occasionally licking or handling the neonates. Interestingly, survival of second litters was relatively low, although the authors found no direct evidence of interference or aggression by older siblings towards younger siblings. They suggest that perhaps competition for milk might be involved, although they did not quantify weight gain. Woodside et al. (1981) however, found that in laboratory rats, the presence of a litter of older siblings did not lead to declines in weight gain in younger siblings.

We were not able to evaluate the possible indirect fitness consequences of helping among *P. polionotus*, because virtually all interactions with pups occur inside the nest (Margulis 1996). It is possible that juveniles may interact with younger siblings and provide allomaternal care, and thus gain both direct and indirect fitness benefits. Alternatively, juvenile females may become sensitized to the presence of pups or primed for maternal behaviour, as has been shown in laboratory rats (Stern & Rogers 1988), thereby enhancing their own future reproductive success without any inclusive fitness benefits. In either case, the expected outcome is enhanced litter survival following such prebreeding exposure, as has been reported, for example, in gerbils (Salo & French 1989), meerkats (Clutton-Brock et al. 2001), New World primates (Snowdon 1996), and cooperatively breeding birds (Stacy & Koenig 1990).

Because experienced females in the present study remained with their mothers until approximately 45 days of age, and therefore might have continued to nurse, they may have started to breed with more body fat than inexperienced females. Litter size and nonpregnant body weight both increase with parity (Margulis 1996, unpublished data), suggesting a possible relationship between body weight and litter size. Although we did not weigh females at pairing, other studies in our laboratory found no effect of maternal body weight on litter survival. Thus, assuming that this was also the case in the present study, our results suggest that it was experience with pups prior to reproduction, and not greater body mass due to the potential extended duration of nursing that influenced litter survival.

In many mammals, primiparous females are less successful at rearing litters, both in terms of birth weight and total number of surviving offspring (Ingram 1978; Wang & Novak 1994; Baker et al. 1996). This may not always be the case however; Hartung & Dewsbury (1979) found no effect of parity on parental behaviour in two species of *Peromyscus*. In a study on house mice (König & Markl 1987), parity was again not found to influence parental behaviour, although the relationship between parity and litter size combined with the short breeding life span of *Mus* may partially explain this finding. In the present study, however, survival of the first litters of experienced females approximated the survivorship values of second litters reared by inexperienced females and was significantly greater than the survivorship of first litters for inexperienced females. This suggests that experience before reproduction can negate the common 'first litter' effect. A female who remains with her parents through the

rearing of a litter of siblings may be delaying her own reproduction, but gains the benefits of having experienced one litter, without the energetic and physiological costs she would have incurred had her first litter experience been with her own pups. In addition, a delay of breeding until about 45 days of age (the age at weaning of younger siblings) would amount to a delay of no more than about 10 days over the minimum possible age of breeding for *P. polionotus* (Millar 1989).

One of the mechanisms underlying this significant survivorship difference in *P. polionotus* between experienced and inexperienced females may be some aspect of nest building (Margulis 1998b). Experienced pairs spent significantly more time nest building during the observation period than did inexperienced pairs. Large, well-built nests are an important component of fitness in mice, as demonstrated by Bult & Lynch (1997) in their experiments on house mice. Nests are vital to achieve adequate temperature regulation for the pups; they affect both survival of pups and the body weight of pups at weaning. The capacity for temperature regulation without shivering is crucial to the survival of both the closely related *Peromyscus maniculatus* (Moffatt et al. 1993) and *Mus musculus* (Lacy et al. 1978), as well as domestic rabbits, *Oryctolagus cuniculus* (Canali et al. 1991). Adequate nests are essential to maintaining body temperature in pups before they are fully able to thermoregulate on their own. Our results show that being in the presence of their parents during the care and nest building for a sibling litter increased the capacity of female mice to build nests. This or other aspects of maternal care then presumably influenced the survivorship of their own litters.

Males paired with experienced females showed behavioural changes similar to those observed in their mates. None of the males in this study had prior experience with pups, so the significant change observed in the amount of nest building they performed can be attributed to social facilitation. This supports earlier findings on paternal behaviour in *P. polionotus* (Margulis 1996, 1998b).

We cannot evaluate the extent to which these findings may apply to animals in the wild. Clearly, the laboratory environment presents little of the environmental variability that might influence litter survival in natural populations. Although the absence of the sire during the rearing of litters is probably not typical, it does occur with some frequency. In free-living *P. polionotus* (Foltz 1981) prior studies have shown that litter survival increases with parity and does not decline in the absence of the sire (Margulis 1998b). Furthermore, previous analyses on the effects of both maternal and paternal care on litter survival have shown that male care has little additional impact on litter survival in the controlled laboratory environment. Studies on wild-caught or first-generation, captive-born animals would enhance the generalizability of these findings. However, given the ecology of *P. polionotus*, delayed dispersal from the natal nest burrow would appear to offer some clear benefits. For a short-lived rodent with a limited number of opportunities to breed, increased survival of offspring in the first few litters may substantially affect lifetime reproductive success.

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References

- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, **49**, 227–267.
- Baker, A. J., Baker, A. M. & Thompson, K. V. 1996. Parental care in captive mammals. In: *Wild Mammals in Captivity* (Ed. by D. G. Kleiman, M. E. Allen, K. V. Thompson & S. Lumpkin), pp. 497–512. Chicago: University of Chicago Press.
- Brewer, B. A., Lacy, R. C., Foster, M. L. & Alaks, G. 1990. Inbreeding depression in insular and central populations of *Peromyscus* mice. *Journal of Heredity*, **8**, 257–266.
- Bult, A. & Lynch, C. B. 1997. Nesting and fitness: lifetime reproductive success in house mice bidirectionally selected for thermoregulatory nest-building behavior. *Behavioral Genetics*, **27**, 231–240.
- Canali, E., Ferrante, V., Todeschini, R., Verga, M. & Carenzi, C. 1991. Rabbit nest construction and its relationship with litter development. *Applied Animal Behaviour Science*, **31**, 259–266.
- Cheng, C. F., Johnson, R. K. & Nielsen, M. K. 2002. Selection for maternal behavior in mice: direct and correlated responses. *Applied Animal Behaviour Science*, **79**, 311–323.
- Clutton-Brock, T. H., Russell, A. F., Sharpe, L. L., Brotherton, P. N. M., Mcllraith, G. M., White, S. & Cameron, E. Z. 2001. Effects of helpers on juvenile development and survival in meerkats. *Science*, **293**, 2446–2449.
- Cohen, J. & Bridges, R. S. 1981. Retention of maternal behavior in nulliparous and primiparous rats: effects of duration of previous maternal experience. *Journal of Comparative and Physiological Psychology*, **95**, 450–459.
- Emlen, S. T. 1994. Benefits, constraints and the evolution of the family. *Trends in Ecology and Evolution*, **9**, 282–285.
- Fairbanks, L. A. 1990. Reciprocal benefits of allomothering for female vervet monkeys. *Animal Behaviour*, **40**, 553–562.
- Fleming, A. S. & Luebke, C. 1981. Timidity prevents the virgin female rat from being a good mother: emotionality differences between nulliparous and parturient females. *Physiology & Behavior*, **27**, 863–868.
- Foltz, D. W. 1979. Genetics and mating system of the oldfield mouse (*Peromyscus polionotus*). Ph.D. thesis, University of Michigan.
- Foltz, D. W. 1981. Genetic evidence for long-term monogamy in a small rodent, *Peromyscus polionotus*. *American Naturalist*, **117**, 665–675.
- French, J. A. 1997. Proximate regulation of singular breeding in callitrichid primates. In: *Cooperative Breeding in Mammals* (Ed. by N. G. Solomon & J. A. French), pp. 34–75. Cambridge: Cambridge University Press.
- French, J. A., Inglett, B. J. & Dethlefs, T. M. 1989. The reproductive status of non-breeding group members in captive golden lion tamarin social groups. *American Journal of Primatology*, **18**, 73–86.
- Gilbert, A. N., Burgoon, D. A., Sullivan, K. A. & Adler, N. T. 1983. Mother–weanling interactions in Norway rats in the presence of a successive litter produced by postpartum mating. *Physiology & Behavior*, **30**, 267–271.
- Grota, L. J. 1973. Effects of litter size, age of young, and parity on foster mother behaviour in *Rattus norvegicus*. *Animal Behaviour*, **21**, 78–82.
- Goldizen, A. W. 1987. Tamarins and marmosets: communal care of offspring. In: *Primate Societies* (Ed. by B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker), pp. 34–43. Chicago: University of Chicago Press, Chicago.
- Gubernick, D. J. & Nelson, R. J. 1989. Prolactin and paternal behavior in the biparental California mouse, *Peromyscus californicus*. *Hormones and Behavior*, **23**, 203–210.
- Gubernick, D. J. & Nordby, J. C. 1992. Parental influences on female puberty in the monogamous California mouse, *Peromyscus californicus*. *Animal Behaviour*, **44**, 259–267.
- Gubernick, D. J., Wright, S. L. & Brown, R. E. 1993. The significance of father's presence for offspring survival in the monogamous California mouse, *Peromyscus californicus*. *Animal Behaviour*, **46**, 539–546.
- Harlow, H. F. & Harlow, M. K. 1962. Social deprivation in monkeys. *Scientific American*, **207**, 136–146.
- Hartung, T. G. & Dewsbury, D. A. 1979. Paternal behavior in six species of murid rodents. *Behavioral and Neural Biology*, **26**, 466–478.
- Harvey, N. C., Farabaugh, S. M. & Druker, B. B. 2002. Effects of early rearing experience on adult behavior and nesting in captive Hawaiian crows (*Corvus hawaiiensis*). *Zoo Biology*, **21**, 59–75.
- Hoage, J. 1978. Parental care in *Leontopithecus rosalia rosalia*: sex and age differences in carrying behavior and the role of prior experience. In: *The Biology and Conservation of the Callitrichidae* (Ed. by D. G. Kleiman), pp. 293–305. Washington, D.C.: Smithsonian Institution Press.
- Hosmer, D. W., Jr & Lemeshow, S. 1989. Applied Logistic Regression, New York: J. Wiley.
- Ingram, J. C. 1978. Parent–infant interactions in the common marmoset (*Callithrix jacchus*). In: *The Biology and Conservation of the Callitrichidae* (Ed. by D. G. Kleiman), pp. 289–291. Washington, D.C.: Smithsonian Institution Press.
- Kalbfleisch, J. D. & Prentice, R. L. 1980. The Statistical Analysis of Failure Time Data, New York: J. Wiley.
- Koch, M. & Ehret, G. 1989. Estradiol and parental experience, but not prolactin are necessary for ultrasound recognition and pup-retrieving in the mouse. *Physiology & Behavior*, **45**, 771–776.
- König, B. & Markl, H. 1987. Maternal care in house mice, I: the weaning strategy as a means for parental manipulation of offspring quality. *Behavioral Ecology and Sociobiology*, **20**, 1–9.
- Lacy, R. C. & Ballou, J. D. 1998. Effectiveness of selection in reducing the genetic load in populations of *Peromyscus polionotus* during generations of inbreeding. *Evolution*, **52**, 900–909.
- Lacy, R. C., Lynch, C. B. & Lynch, G. R. 1978. Developmental and adult acclimation effects of ambient temperature regulation of mice selected for high and low levels of nest building. *Journal of Comparative Physiology B*, **123**, 185–192.
- Lacy, R. C., Alaks, G. & Walsh, A. 1996. Hierarchical analysis of inbreeding depression in *Peromyscus polionotus*. *Evolution*, **50**, 2187–2200.
- Margulis, S. W. 1996. The effects of inbreeding on parental behavior and reproductive success in two subspecies of the oldfield mouse, *Peromyscus polionotus*. Ph.D. thesis, The University of Chicago.
- Margulis, S. W. 1997. Inbreeding-based bias in parental responsiveness to litters of oldfield mice. *Behavioral Ecology and Sociobiology*, **41**, 177–184.

- Margulis, S. W.** 1998a. Differential effects of inbreeding at juvenile and adult life-history stages in *Peromyscus polionotus*. *Journal of Mammalogy*, **79**, 326–336.
- Margulis, S. W.** 1998b. Relationships among parental inbreeding, parental behavior and offspring viability in oldfield mice. *Animal Behaviour*, **55**, 427–438.
- Margulis, S. W. & Altmann, J.** 1997. Behavioral risk factors in the reproduction of inbred and outbred oldfield mice. *Animal Behaviour*, **54**, 397–408.
- Mellen, J. D.** 1992. Effects of early rearing experience on subsequent adult sexual behavior using domestic cats (*Felis catus*) as a model for exotic small felids. *Zoo Biology*, **11**, 17–32.
- Millar, J. S.** 1989. Reproduction and development. In: *Advances in the Study of Peromyscus (Rodentia)* (Ed. by G. L. Kirkland & J. N. Layne), pp. 169–232. Lubbock: Texas Tech University Press.
- Moehlman, P. D. & Hofer, H.** 1997. Cooperative breeding, reproductive suppression, and body mass in canids. In: *Cooperative Breeding in Mammals* (Ed. by N. G. Solomon & J. A. French), pp. 76–128. Cambridge: Cambridge University Press.
- Moffatt, C. A., Devries, A. C. & Nelson, R. J.** 1993. Winter adaptations of male deer mice (*Peromyscus maniculatus*) and prairie voles (*Microtus ochrogaster*) that vary in reproductive responsiveness to photoperiod. *Journal of Biological Rhythms*, **8**, 221–232.
- Paul, A. & Kuester, J.** 1996. Infant handling by female Barbary macaques (*Macaca sylvanus*) at Affenberg Salem: testing functional and evolutionary hypotheses. *Behavioral Ecology and Sociobiology*, **39**, 133–145.
- Rave, E. H. & Holler, N. R.** 1992. Population dynamics of beach mice (*Peromyscus polionotus ammobates*) in southern Alabama. *Journal of Mammalogy*, **73**, 347–355.
- Ryan, K. K. & Altmann, J.** 2001. Selection for male choice based primarily on mate compatibility in the oldfield mouse, *Peromyscus polionotus rhoadsi*. *Behavioral Ecology and Sociobiology*, **50**, 436–440.
- Ryan, K. K., Lacy, R. C. & Margulis, S. W.** 2003. Impacts of inbreeding on components of reproductive success. In: *Reproduction Science and Integrated Conservation* (Ed. by W. V. Holt, A. R. Pickard, J. C. Rodger & J. C. Wildt), pp. 82–95. Cambridge: Cambridge University Press.
- Salo, A. L. & French, J. A.** 1989. Early experience, reproductive success, and development of parental behaviour in Mongolian gerbils. *Animal Behaviour*, **38**, 693–702.
- SAS Institute** 1999. *SAS/STAT User's Guide. Version 8*. Cary, North Carolina: SAS Institute.
- Smith, M. H.** 1966. The evolutionary significance of certain behavioral, physiological, and morphological adaptations of the old-field mouse, *Peromyscus polionotus*. Ph.D. thesis, University of Florida.
- Snowdon, C. T.** 1996. Infant care in cooperatively breeding species. In: *Parental Care: Evolution, Mechanisms, and Adaptive Significance* (Ed. by J. S. Rosenblatt & C. T. Snowdon), pp. 643–689. New York: Academic Press.
- Sokal, R. R. & Rohlf, F. J.** 1981. *Biometry*. 2nd edn. San Francisco: W. H. Freeman.
- Stacy, P. B. & Koenig, W. D.** 1990. *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behaviour*, New York: Cambridge University Press.
- Stern, J. M. & Rogers, L.** 1988. Experience with younger siblings facilitates maternal responsiveness in pubertal Norway rats. *Developmental Psychobiology*, **21**, 575–589.
- Tardif, S. D., Richter, C. B. & Carson, R. L.** 1984. Effects of sibling rearing experience on future reproductive success in two species of Callitrichidae. *American Journal of Primatology*, **6**, 377–380.
- Wang, Z. & Novak, M. A.** 1994. Alloparental care and the influence of father presence on juvenile prairie voles, *Microtus ochrogaster*. *Animal Behaviour*, **47**, 281–288.
- Woodside, B. R., Wilson, P. C. & Leon, M.** 1981. Resource partitioning during reproduction in the Norway rat. *Science*, **211**, 76–77.