PARENTAL AND ALLOPARENTAL CARE IN A POLYGYNOUS MAMMAL

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We studied maternal, paternal, and alloparental care in striped mice (*Rhabdomys pumilio*), which nest and breed communally in the succulent karoo, South Africa. A total of 18 triads, each consisting of 2 adult female littermates and an unfamiliar adult male, were set up under natural weather conditions. We expected that relationships within captive triads that breed communally would be egalitarian, and that all individuals would participate in the rearing of offspring, but we assumed that the degree of caregiving behavior would vary between mothers, fathers, and alloparents, because individuals obtain different fitness benefits. Social interactions in the triads were predominantly amicable and in the majority of triads, both females produced litters in a communal nest. All 3 adults in a triad participated in care of the offspring, with mothers spending 43%, fathers 26%, and alloparents 24% of observations in caregiving activities. Our results indicate that sisters can form stable cooperative relationships, but members of a communal nest allocate their caregiving to individual offspring according to potential trade-offs between direct and indirect fitness benefits. Large amounts of paternal care can occur in a polygynous species, which contrasts with the common belief that paternal care is a characteristic of monogamy.

Key words: alloparental care, communal breeding, maternal care, paternal care, polygyny, *Rhabdomys pumilio*, South Africa, striped mouse

Sexual conflict results in variance in the reproductive investment by each sex, which is determined by a trade-off between fitness gains through current offspring versus reduction of future survival and fecundity as a consequence of current investment (Trivers 1972). Although mammalian mothers are typically constrained by lactation to rearing the offspring, breeding males can consider the trade-off between investment in their young and the time spent seeking additional mating opportunities (Trivers 1972). Nonetheless, paternal care does occur and is common in monogamous species of mammals (Kleiman and Malcolm 1981), where it probably evolved to enhance survival of the young (Woodroffe and Vincent 1994), thereby enhancing the fitness of paternal males. In contrast, polygynous males invest more in mating effort than do monogamous males, leading to lower levels of paternal care (McGuire and Novak 1984, 1986;

Oliveras and Novak 1986; Patris and Baudoin 2000). Thus, polygynous males may compensate for any effects of their lowered care by increasing their mating success with 1 or more additional females. Polygynous males also may allocate their contribution unequally among females (Smith et al. 1994) or provide less paternal care as certainty of paternity decreases (Adrian et al. 2005). Paternal activities may be shown as a courtship strategy (cotton-top tamarins [*Saguinus oedipus*—Price 1990]) or may be correlated with group size, with males providing less care in large groups, where helpers are available (common marmosets [*Callithrix jacchus*—Rothe et al. 1993]).

In addition to parents, other group members might help in rearing offspring that are not their own (alloparents—Riedman 1982). Helping occurs in a variety of vertebrates (fishes [Taborsky and Limberger 1981], birds [Cockburn 1998; Hatchwell 1999], and mammals [Packer et al. 1992; Riedman 1982]), and is found in social groups, where a single pair monopolizes reproduction (singular breeders) or where reproduction is shared among several individuals (plural breeders—Hayes 2000). Numerous studies have mentioned a beneficial influence of helpers on the breeding performance of mothers and on growth and survival of offspring (Hayes and

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Solomon 2004, 2006; Mitani and Watts 1997; Price 1992b; Ross and MacLarnon 2000; Xi et al. 2008; but see Wolff 1994). However, helping also entails costs, such as a decrease in foraging time, which may result in reduced future reproductive success (Heinsohn and Legge 1999; Hodge 2007; Price 1992a). Thus, the decision to help depends on the trade-off between costs and benefits, as well as the contributions made by other group members (Trivers 1972).

Several mechanisms have been proposed for alloparental care. Helping might be an unselected by-product of the presence of young (Jamieson 1991) or function to gain social prestige within groups (Zahavi 1974, 1995). Alloparental care also may strengthen social relationships among group members (Gaston 1978), or may be favored by kin selection (Hamilton 1964). Thus, helping might have evolved by several mechanisms increasing either indirect or direct fitness of the helpers.

But how much help should an alloparent provide? Helpers often differ in the amount of care they are willing to provide. In some species, alloparents contribute more (meerkats [*Suricata suricatta*—Clutton-Brock et al. 2004] and naked mole-rats [*Heterocephalus glaber*—Lacey and Sherman 1991]) or as much (Goeldi's monkey [*Callimico goeldii*—Schradin and Anzenberger 2001]) care as parents, whereas in other species parents invest more than helpers (banded mongoose [*Mungos mungo*—Gilchrist and Russell 2007; Hodge 2007]). Because helping incurs costs, it is traded off against a helper's own reproduction. Thus, if alloparents are likely to breed themselves, they are less willing to provide high levels of costly care for offspring that are not their own (Gilchrist and Russell 2007; Hodge 2007).

We studied maternal, paternal, and alloparental behavior in the striped mouse (*Rhabdomys pumilio*), a small muroid rodent that is widely distributed throughout southern Africa (Kingdon 1974). In the succulent karoo, a desert habitat, striped mice live in stable social groups of up to 30 group members of both sexes (Schradin and Pillay 2004). Social groups are extended family groups consisting of 1–4 communally breeding females, 1 breeding male, and their offspring (Schradin and Pillay 2004). Juveniles and young adults of both sexes delay dispersal and remain as nonreproductive ''helpers at the nest'' (Schradin and Pillay 2004). At the start of the next breeding season, males disperse and achieve breeding status by immigrating into groups of communally nesting females, whereas females stay at their natal nest and become breeders themselves. Within social groups, the breeding females reproduce synchronously (Schubert 2005) and rear their offspring together in 1 communal nest (Schradin and Pillay 2004). The litter size of individual females is about 5 pups, with a sex ratio at birth of close to 1:1, which also characterizes adult populations (Brooks 1974). Females have a postpartum estrus (Choate 1972) and a gestation period of 23 days (Brooks 1974), and females in the desert population produce 2 or 3 litters per breeding season (Schradin and Pillay 2005a).

We do not know the extent to which females in communal groups of striped mice display alloparental care. Breeding

males are permanently associated with females and their offspring and display paternal care in the field (Schradin and Pillay 2003). In captivity, males kept in monogamous pairs show the same pattern of parental care as females and to the same extent, with the exception of nursing (Schradin and Pillay 2003). Males huddle, lick, and retrieve pups and increase the time spent in the nest 3-fold when pups are present (Schradin and Pillay 2003).

Here, we present data from behavioral observations of captive polygynous groups, consisting of 2 adult female littermates and 1 unrelated adult male. The 1st objective of this study was to describe the social relationships among group members. We tested the prediction that relationships in communal groups that successfully raise offspring are predominately amicable, because communal breeding is mainly expected to occur in egalitarian societies (Gerlach and Bartmann 2002). A 2nd objective was to document maternal, paternal, and alloparental behavior. We expected that mothers would be the main care providers for their own pups, because of the direct fitness benefits. Aunts also were expected to provide alloparental care, but at lower levels than mothers, because fitness benefits are lower when rearing their sister's pups than when rearing their own. Furthermore, we predicted that fathers would display paternal behavior, but at lower levels than reported under monogamous conditions (i.e., less than mothers—Schradin and Pillay 2003), because reduced paternal care might be compensated for by alloparental care provided by aunts.

MATERIALS AND METHODS

Study site, housing, and sample collection.—This study was conducted at the research station in the Goegap Nature Reserve (29°37′S, 17°59′E), South Africa, which is situated in the natural habitat of the study species. The study took place from September 2004 to March 2005. Test subjects were housed on the veranda of the research station and therefore were exposed to the natural light–dark cycle and temperatures. Test subjects were protected from wind, rain, and direct sunshine by shade cloth. The lowest recorded temperature was 2°C and the maximum temperature was 38.5°C during the study.

We established a total of 18 triads consisting of 2 sisters (littermates, $n = 36$) and 1 unfamiliar male ($n = 18$). Individuals were born in captivity (3rd generation from a founder generation trapped in the Goegap Nature Reserve in 2002). The mean age at pairing was 159 days $\pm$ 88 *SD* for females and 128 days $\pm$ 111 *SD* for males. All study animals were sexually naïve. Before pairing, study subjects were housed in their family groups, which consisted of the parents and other littermates. On the day of pairing, 2 randomly selected female siblings were removed simultaneously and placed in a neutral glass tank for about 20 min. The same procedure was used for each male. Thereafter, all 3 individuals were released into glass tanks (see below) simultaneously to avoid territoriality. Subsequently, the social interactions of the

TABLE 1.—Description of the parental and alloparental behaviors in the striped mouse (*Rhabdomys pumilio*). Data for huddling include nursing by females because it was not possible to ascertain whether or not pups attached to nipples suckled during behavioral observations. Some behaviors recorded were not mutually exclusive. For example, an individual could have made body contact and groomed (or huddled) another individual at the same time. In such situations, we only recorded grooming (or huddling) behavior, as body contact is a precondition for grooming (or huddling).

Behavior	Definition
Sitting in body contact	Test subject was in very close proximity with a pup.
Huddling	Test subject was crouching over pups.
Grooming	Test subject wiped, licked, and nibbled the pups' fur with forepaws and tongue.
Retrieving	Test subject carried the pup in its mouth to the nest.
Nest building	Test subject carried tissue paper or hay into the nest, or rearranged nesting material within the nest.
Spending time in nest	Test subject associated with the pups in nest. Being in nest with the offspring included several different behaviors such as sitting in body contact, huddling, nursing, and grooming. Because nesting material sometimes obscured the view of test subject and pups, we grouped all mentioned behaviors into spending time in nest.

triad were observed for 15 min through direct observation by an observer situated about 2 m in front of the glass tank. Because animals were habituated to human presence, the use of a blind was not necessary. No aggression was observed in any triad at the start of experiments.

Each triad was housed in 2 glass tanks (49.0 × 33.5 × 40.0 cm), which were connected with a polyvinyl chloride tube (110 cm length, 4 cm diameter), thereby providing females with a choice of whether to share 1 nest and rear their offspring communally or to nest singly (i.e., each female in a separate nest). Each glass tank contained a polyvinyl chloride nest box (13 × 10 × 10.5 cm). Additionally, small branches and different kinds of cardboard, such as empty toilet paper rolls, were provided for environmental enrichment. Glass tanks were provided with a 2.5-cm-thick bedding of hay; data collection was not hampered by tank enrichment and hay. All tanks were cleaned weekly. Water was provided ad libitum. Each mouse received 4 g of seed mix (Marltons Pets and Products, Durban, South Africa; seeds from Agricol, Brackenfell, South Africa) in the morning and a piece of fruit or lettuce 6 times per week at midday. In the evenings, 3 pieces of tissue paper were supplied for nest building and each individual received 15 sunflower seeds. Food was allocated during the day to prevent obesity and to mimic natural foraging behavior (Schradin 2005a). We followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007) for the capture, handling, and care of mammals.

To determine pregnancy status, all females were weighed twice per week. Triads were separated if both females did not produce offspring within 3 months. Because the 3-month period is theoretically longer than 3 gestation periods and represents the duration of the natural breeding season (Schradin and Pillay 2005c), females had sufficient time to reproduce. Triads that reproduced were separated after approximately 4 months, which represents the duration of the natural breeding season (Schradin and Pillay 2005c) plus an additional month to provide extra time for the test subjects to become accustomed to the experimental setup. Glass tanks were checked daily for neonates. At parturition, the female that had lost >10 g of body mass was regarded as the mother (Nel 2003). Litter size and body mass of pups was determined

on the day of birth (day 0) and the last day of weaning (day 16—Brooks 1982). Pups were removed from the nest with a glove to prevent the transfer of human scent. To differentiate between the pups of the 2 females, 1 group of pups was marked on the back and on the tail with gentian violet, a purple nontoxic dye. The 2nd group of pups and all adults of the triad were sham marked with dried gentian violet. Therefore, all individuals in the communal group had the same smell, whereas only 1 litter was marked with color (Pillay 2000). Because the color faded quickly, the dorsal fur of 1 litter was clipped on day 3 and again on day 10. By using this procedure, marked pups could be easily detected in the communal nest and distinguished between the pups of the other female, which were unmarked.

Social interactions within triads.—Female striped mice were individually marked with black hair dye (Inecto Rapid, Pinetown, South Africa) for individual identification (Schradin and Pillay 2004). Observations were done in the first 2 weeks after pairing, at least 1.5 weeks before pups were born. Because striped mice tend to be most active during early morning hours and in the late afternoon (Schradin 2005a), each triad was observed 3 times in the morning (0630–0930 h) and 3 times in the afternoon (1700–1900 h) for 15 min. All positive social interactions (allogrooming or sitting in body contact) between adults were recorded using continuous recording (Martin and Bateson 1993). No aggressive interactions were observed at the beginning of tests.

Parental and alloparental care in communal groups.—Each litter was observed on 16 occasions from day 0 to day 16. Observations lasted 15 min per session, with a 15-s interscan interval (Martin and Bateson 1993). The parental behaviors recorded for the 3 adults in a triad were collected simultaneously during behavioral observations (Table 1). As part of colony management, all adults were euthanized (overdosed with sodium pentobarbital) at the end of experiments. Young striped mice produced during the study were housed with their littermates and used in other experiments.

Retrieval experiment.—During the first 2 days after birth, a single retrieval test was performed. Newborn pups were removed from the natal nest and placed in the unused nest box in the 2nd tank of each triad (see above). During the

experiment, all adults remained in the tank and were tested simultaneously for pup retrieval, which is defined as the retrieving of pups to the natal nest. Observations were performed until all pups were retrieved (approximately 5 min).

Data and statistical analyses.—Observations of social relationships among individuals of the triad were available for all 18 triads. However, of the original 18 triads, sufficient data from only 8 triads were available for the analyses of parental and alloparental care. Triads were excluded when only 1 female had pups ($n = 3$) or no female reproduced ($n = 3$; because we did not look for implantation scars, we cannot be sure whether any of these females became pregnant and then aborted). Furthermore, in 1 nest both females died shortly after parturition and in another 2 triads pups were found dead or eaten. In 1 communal nest both females always gave birth synchronously (time interval of 1 day), and we could not obtain reliable alloparental data. Because the retrieval experiment was conducted during the 1st or 2nd day after parturition, data from the synchronously breeding triad, from the triad where both females died, and from the 2 triads where pups were found dead also were available for retrieval data.

All caregiving behaviors were calculated as percentages of the total number of scans. Paternal care was calculated from the amount of parental care shown by the male for the pups of both females. For each female, we calculated the amount of care shown for its own pups (maternal care) and for pups of her sister (alloparental care). Data for maternal care were collected only when a female was a mother and not an aunt at the same time. Similarly, data of alloparental care were only collected from females that were not mothers at the same time. Thus, we knew whether the pups a female was huddling were her own or her sister's offspring.

We did not adjust litter sizes in the experiment, but we correlated the amount of caregiving behavior (independently for mothers, aunts, and fathers) with the number of pups to examine whether there was an influence of litter size on parental care.

Comparison of social interactions.—To avoid pseudoreplication, for each triad, we calculated the mean of the social interactions between the sisters and between both sisters and the male, and compared within- and between-sex social interactions using a Wilcoxon matched-pairs test.

Comparison between maternal, paternal, and alloparental care.—For each triad, we calculated the mean of both maternal and alloparental care for both females to avoid pseudoreplication. For males, we summed care for both litters when comparing with caregiving behavior of females. Comparisons were done using a Friedman test followed post hoc with Wilcoxon matched-pairs tests with Bonferroni adjustment.

Comparison between maternal and alloparental care.—To test whether females show more maternal than alloparental care, we compared maternal and alloparental care of the same females that were both mother and alloparent at another time ($n = 10$ females), using Wilcoxon matched-pairs tests.

Comparison of paternal care for offspring of both females.—For each male, we determined the amount of care shown for the pups born to the female that gave birth 1st and pups born to the 2nd female. Paternal care was compared using a Wilcoxon matched-pairs test.

Because the sample size was small and the data set violated the assumptions of normality despite efforts to transform the data, we used nonparametric analyses. All data are reported as median and interquartile ranges (1st and 3rd). All statistical tests were performed using the software SPSS (version 13.0; SPSS Inc., Chicago, Illinois).

RESULTS

Social interactions and reproduction.—The level of positive social interactions between sisters (median: 6.0 min/h, 1st and 3rd quartile: 4.3 min/h, 9.2 min/h) was not significantly different from those between females and the male in the triads (5.2 min/h, 4.0 min/h, 6.3 min/h; Wilcoxon matched-pairs test: $n = 18$, $Z = -1.285$, $P = 0.199$). Aggressive behavior was not observed in any of the 18 triads during the first 2 weeks after pairing. However, 3 triads had to be separated several weeks later because of damaging fights between females (in 2 triads in which only 1 female reproduced and in 1 triad where none of the females produced offspring). Relationships were amicable within all the other triads during the entire study period.

Of the 18 triads, both females bred in 12 triads. Pups were always born and raised together in the communal nest. The mean litter size for individual females was 5.3 pups $\pm$ 1.8 *SD*. When 1 female gave birth, the other female gave birth on average 6.5 days later (range: 0–17 days). The interlitter interval for individual females was 28 days (range: 23–46 days). The survival of young to weaning did not differ between the female giving birth 1st and the female giving birth 2nd (91.7.7% [75.7%, 100.0%] versus 91.7% [45.0%, 100.0%], $n = 11$, $Z = -1.120$, $P = 0.263$).

Comparison between maternal, paternal, and alloparental care.—In general, all individuals showed caregiving behavior, but the amount of total care provided (all behaviors combined) differed significantly (Friedman test: $\chi^2 = 6.250$, *d.f.* = 2, $P = 0.044$), with mothers engaging more in parental activities than aunts (post hoc: $P = 0.016$; Fig. 1); and also than fathers, but only with a statistical tendency ($P = 0.069$, Fig. 1). When comparing the amount of the different behavior patterns within triads, there was no significant difference in any caregiving behavior between mothers, aunts, and fathers (Table 2). Caregiving behavior did not correlate with the number of pups present in the nest for mothers (Spearman rank correlation: $r_s = 0.348$, $P = 0.359$), aunts ($r_s = 0.488$, $P = 0.220$), or fathers ($r_s = 0.017$, $P = 0.966$). Fathers showed paternal care toward litters of both females, and the amount did not differ significantly ($Z = -1.690$, $P = 0.091$). Males were observed providing paternal care to the litter of the female that gave birth 1st in 28.5% (25.2%, 40.8%) of observations, and to the litter of the female that gave birth 2nd in 25.2% (14.4%, 30.3%) of the observations.

Individual female mice showed significantly more maternal care toward their own pups than alloparental care toward the
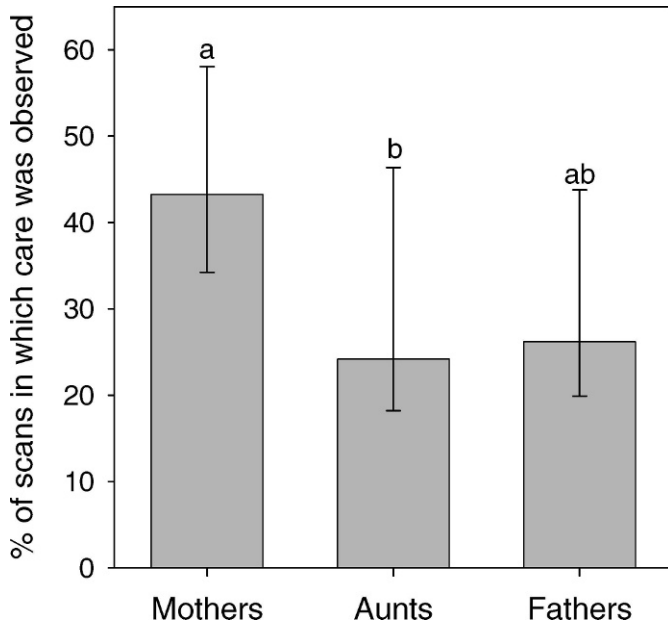
FIG. 1.—Overall caregiving behavior provided by mothers, aunts, and fathers ($n = 8$). Data are reported as percentages of total scans and are shown as median (25th and 75th percentile). A mean value per nest was calculated for each female. For males the mean amount of care for litters of both females was calculated. Different letters indicate significant differences ($P < 0.05$); see text for statistics.

pups of their sisters ($n = 10$, $Z = -2.497$, $P = 0.013$). Overall, females were observed caring for their sister's pups in 30.0% (25.3%, 36.4%) of the observations compared to 49.9% (36.3%, 53.1%) of the observations caring for their own pups, with mothers demonstrating higher levels of huddling, grooming, and retrieving pups. The level of nest-building behavior, spending time in nest, and sitting in contact with pups did not differ between mothers and aunts (Table 3).

Retrieval experiment.—Females retrieved pups back to the nest more than did males (Fisher's exact test: $P = 0.007$). Four of 12 males and 20 of 24 females retrieved pups. There was a trend for females to retrieve more pups to the nest when they were mothers compared to when they were aunts ($n = 14$, $Z = -1.884$, $P = 0.060$).

DISCUSSION

In the present study, we documented social interactions and maternal, paternal, and alloparental care in triads of striped mice, each composed of 2 sisters and 1 unrelated male. In the majority of triads, interactions among group members were amicable and both females reproduced. All individuals of the triads made contributions to rearing offspring, but mothers provided significantly more care than did aunts, whereas aunts and fathers provided similar levels of care.

Social interactions and reproductive output.—In the majority of triads (15 of 18), relationships between sisters were amicable during the entire study period. Amicability is known to be important for the formation of cooperative breeding alliances between females (Charnov and Finerty 1980; Rusu and Krackow 2004). Moreover, kinship facilitates associations among females (Manning et al. 1995), improving the occurrence of communal nesting and breeding (Hayes 2000; Rödel et al. 2008b; Rusu and Krackow 2004). In our study, in most (12 of 15) triads, both females produced offspring and there were no differences in offspring survival probabilities, indicating a low reproductive skew. In general, egalitarian relationships are more often established between same-aged and related individuals (Rusu et al. 2004). In the Mongolian gerbil (*Meriones unguiculatus*), older females dominate younger ones by inhibiting their reproductive development (Clark and Bennet 2001) and in wild house mice (*Mus musculus*), breeding alliances between females are strongly influenced by age (Rusu et al. 2004). In our study, females were littermates and were familiar with each other from birth. Thus, close genetic relatedness, familiarity, and same age might favor communal breeding with low reproductive skew in striped mice, but more detailed studies are needed.

Maternal, paternal, and alloparental care.—All individuals of the triads exhibited caregiving behavior. Helping might present a temporal coordination of caregiving activities; for example, 1 individual takes care of the pups while the others are absent foraging (Wynne-Edwards 1995). Thus, by leaving pups alone less often, offspring might experience thermoregulatory benefits and increased survival (Wynne-Edwards

TABLE 2.—Comparison of paternal care with maternal and alloparental care of striped mice (*Rhabdomys pumilio*). Interquartile ranges for 6 caregiving behaviors are reported. Data are presented as percentages of total scans. To avoid pseudoreplication, we calculated mean values for maternal and alloparental behavior of both females of the triad per nest. Statistics are Friedman test, power (β), and effect size values.

Behaviors	Maternal care	Paternal care	Alloparental care	Statistical comparison
Huddling/nursing	7.9 (7.6, 13.02)	2.1 (0.2, 3.8)	1.9 (1.1, 3.4)	$\chi^2 = 5.097$, $d.f. = 2$, $P = 0.078$, $\beta = 0.52$, effect size = 0.33
Groom	1.2 (0.7, 1.5)	0.8 (0.5, 1.2)	0.5 (0.2, 0.8)	$\chi^2 = 1.750$, $d.f. = 2$, $P = 0.417$, $\beta = 0.04$, effect size = 0.33
Retrieve pups	0.5 (0.3, 0.7)	0.0 (0.0, 0.2)	0.2 (0.1, 0.5)	$\chi^2 = 3.308$, $d.f. = 2$, $P = 0.191$, $\beta = 0.05$, effect size = 0.26
Time in nest with pups	28.6 (17.5, 33.2)	15.6 (10.1, 32.6)	23.8 (15.2, 29.8)	$\chi^2 = 4.750$, $d.f. = 2$, $P = 0.093$, $\beta = 0.68$, effect size = 0.32
Nest building	0.3 (0.2, 0.7)	0.1 (0.0, 0.3)	0.7 (0.0, 1.0)	$\chi^2 = 1.355$, $d.f. = 2$, $P = 0.508$, $\beta = 0.11$, effect size = 0.17
Sitting in contact with pups	2.7 (2.2, 6.3)	4.2 (3.1, 6.4)	2.5 (1.8, 4.6)	$\chi^2 = 1.750$, $d.f. = 2$, $P = 0.417$, $\beta = 0.09$, effect size = 0.19

TABLE 3.—Comparison of the caregiving behaviors performed by female striped mice (*Rhabdomys pumilio*) for their own and for their sister's pups. Interquartile ranges for 6 caregiving behaviors are shown as percentages of total scans. Statistics are Wilcoxon matched-pairs rank sign test; significant comparisons are indicated in bold.

Behaviors	Own pups	Sister's pups	Statistics[a]
Huddling/nursing	11.4 (5.0, 17.3)	1.8 (1.4, 4.2)	−2.701, **P = 0.007**
Groom/lick	1.3 (0.6, 2.0)	0.4 (0.1, 1.0)	−2.091, **P = 0.037**
Retrieve pups	0.8 (0.3, 1.5)	0.1 (0.0, 0.2)	−2.666, **P = 0.008**
Time in nest with pups	28.6 (20.3, 37.9)	24.4 (14.9, 26.8)	−1.784, P = 0.074, β = 0.41, effect size = 0.55
Nest building	0.1 (0.1, 0.8)	0.1 (0.0, 0.8)	−0.296, P = 0.767, β = 0.06, effect size = 0.07
Sitting in contact with pups	2.6 (1.6, 3.8)	2.2 (1.4, 4.0)	−0.357, P = 0.721, β = 0.07, effect size = 0.02

[a] Power (β) and effect size values are provided for nonsignificant (P > 0.05) probabilities.

1995). Although all triad members displayed care toward the offspring, mothers were the main care providers, showing caregiving activities in 43% of the observations. In a previous study by Schradin and Pillay (2003) conducted under similar housing conditions, but in a laboratory, mothers spent 63% of their time in the nest with the pups. Thus, communally nesting female striped mice may be able to reduce their maternal investment with the presence of alloparents as in other species (Price 1992b; Ross and MacLarnon 2000; Schradin and Anzenberger 2001; Xi et al. 2008), but so far no direct comparison is available.

Aunts showed alloparental care in 24% of observations, and there was no significant difference between maternal and alloparental care in nest-building behavior, spending time in the nest, and sitting in body contact with the offspring. However, aunts showed behaviors that are associated with higher energetic costs, such as huddling and nursing, grooming, and retrieving of their sister's pups, significantly less often. Lactation, in particular, is highly energetically demanding (Rogowitz 1996) and may impact the female's future reproductive (Koivula et al. 2003) and lactational performance (Rödel et al. 2008a). Thus, our results indicate that aunts consider potential trade-offs between their contributions to closely related offspring and their own reproduction.

Males provided paternal care toward the offspring of both females. Because females share a communal nest, males have the opportunity to care for all pups in the nest. Furthermore, because polygynous males in our study did not have to engage with male competitors and had exclusive access to both females, paternity was certain. This might be different from the situation in the field, where members of a communal nest forage alone during the day (Schradin and Pillay 2004). Because communally breeding females reproduce synchronously, uncertainty about paternity may increase as the number of communally breeding females per nest increases because males might be unable to successfully guard several females at the same time (Rusu and Krackow 2004).

In a previous study of monogamously paired male striped mice, fathers exhibited the same behavioral repertoire as mothers (with the exception of nursing) and to the same extent (Schradin and Pillay 2003). In our study, males spent on average 26% of the observations engaged in parental behavior compared to 43% for mothers. The difference was not significant, but the statistical power of the tests was low because of our small sample sizes. Males are expected to reduce their paternal investment when alloparents provide infant care or when fitness benefits from alternative activities outweigh benefits gained by rearing current offspring (Whittingham and Dunn 1998). Although polygynous fathers tended to show less care than mothers, they provided similar levels of caregiving behavior as aunts (24%). Although polygynous males might have lowered their parental effort per litter in comparison to monogamous males, overall paternal effort may have been similar or higher because polygynous males provided care for the offspring of both females.

In monogamously paired striped mice, the presence of the father improves offspring development by reducing heat and energy loss experienced by pups (Schradin and Pillay 2005b). Aunts alone may not fulfill this role entirely and additional care might still be of advantage for pup development. To understand the evolution of high levels of paternal care, it is important to know the costs and benefits associated with this behavior. The main costs are believed to be a decrease of time available for mate searching and territory defense (Schradin 2007). In our experimental setup, males had no alternative to pup care apart from investing in social relationships with the 2 females. Thus, high levels of paternal care in the polygynous striped mice in our study might be explained by low costs and direct benefits of paternal care.

Our results indicate that sisters can form stable cooperative relationships. All 3 individuals in a triad participated in the rearing of offspring, but mothers were the main caregivers, with aunts and fathers providing similar but smaller amounts of care. The difference between maternal and alloparental care may be due to differential fitness costs and benefits associated with providing care for their own offspring versus offspring of their sister. Nonetheless, where alloparents are related to the young they assist in rearing, alloparental care enhances the inclusive fitness of helpers (Hamilton 1964), and might serve other roles, such as the formation of social bonds (Libhaber and Eilam 2004; Lonstein and De Vries 2001; Reinhold 2002). Females may gain benefits from breeding communally by obtaining thermoregulatory benefits (Scantlebury et al. 2006), or increasing opportunities to mate (Ebensperger et al. 2006), or both. In addition, communal nesting may be favored under challenging natural conditions such as habitat saturation (Hayes 2000), which is thought to be the main reason for communal breeding in striped mice (Schradin 2005b). The most important result of our study is that extensive amounts of paternal care can occur in a polygynous species,

which contrasts with the common belief that paternal care is a characteristic of monogamy (Dewsbury 1981; Kleiman 1981).

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