Alloparents in the Mongolian gerbil: impact on long-term reproductive performance of breeders and opportunities for independent reproduction

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The presence of alloparents in cooperatively breeding groups may enhance the reproductive performance of the breeding pair but tests of this hypothesis in mammalian cooperative breeders have typically examined short periods in the reproductive life span of breeders. The present experiment was designed to evaluate the long-term effects of the presence of alloparents on reproductive performance under laboratory conditions in Mongolian gerbils (*Meriones unguiculatus*), and to evaluate the possibility that alloparents may attempt independent reproduction during their tenure as alloparents. Pairs were established with either 0 or 4 alloparents and breeding performance was monitored over a 13.5-month period. The presence of alloparents did not enhance reproductive rates in breeding pairs, and neither enhanced nor delayed developmental rates in offspring. Variation in litter size, offspring survival, pup growth, and interbirth interval did not vary significantly as a function of the breeding females' reproductive tenure. Seven of 49 female alloparents of breeding age in family groups produced offspring. Alloparent breeding was associated with long interbirth intervals in the breeding adult female. Neonatal survival in litters born to alloparents was higher in litters that were temporally synchronized with litters produced by the older breeding female than in asynchronously produced litters. Under the conditions in this experiment, then, few indirect benefits accrue to helpers as a consequence of their alloparental effort, and immediate (the opportunity for independent reproductive attempts) and delayed (parental skills acquisition) direct benefits may account for helping behavior in this species. *Key words:* alloparental care, cooperative breeding, helping behavior, life history, lifetime fitness, *Meriones unguiculatus*, parental behavior. *[Behav Ecol 5:273–279 (1994)]*

Cooperative breeding systems in avian and mammalian taxa can be differentiated according to the number of adults per group that simultaneously engage in reproductive activity. Species in which several adults of either sex are likely to breed (e.g., acorn woodpecker, *Melanerpes formicivorus*: Koenig and Mumme, 1987) are described as "multiple" breeders, and species in which only one individual of each sex is likely to breed at any given time (e.g., Florida scrub jay, *Aphelocoma c. coerulescens*: Woolfenden and Fitzpatrick, 1984; dwarf mongoose, *Helogale parvula*: Rood, 1980) are described as "singular" breeders. Studies on the origin and maintenance of singular cooperative breeding systems (Brown, 1987; Emlen, 1991) have traditionally concentrated on three central questions: (1) Why do some individuals show delayed dispersal? (2) Why is breeding delayed in the alloparents? and (3) Why do alloparents express caregiving behavior to offspring that are not their own? The first two questions are typically addressed with reference to resource constraints on dispersal and independent reproduction, and/or benefits that may be associated with philopatry (Koenig et al., 1992).

Empirical tests of the latter question (Why help?) have usually involved comparing the impact of helping experiences for the individual engaging in alloparental care (future direct benefits) and the fitness consequences for the breeders who are themselves (or whose offspring are) the recipients of alloparental care (indirect benefits; Brown, 1987). These proposed benefits of alloparental care for an individual are contrasted with potential costs associated with alloparental care, among them reduced lifetime reproductive success during the period of residence as a subordinate (and, in singular breeding species, as a nonbreeder) while delivering alloparental care to others' offspring. There are other alternative (but not necessarily mutually exclusive) accounts of the origin and maintenance of alloparental care in cooperatively breeding species (see, for example, Emlen, 1991, and Jamieson, 1989).

Recently, attention has been directed toward the possibility that alloparents may increase immediate direct fitness by attempting independent reproduction. Breeding attempts by alloparents ("failures" of reproductive suppression) in taxa which typically show singular breeding have been reported in a number of species of mammals (dwarf mongooses, *Helogale parvula*: Creel and Waser, 1991; Rood, 1980; cotton-top tamarins, *Saguinus oedipus*: Price and McGrew, 1991; common marmosets, *Callithrix jacchus*: Rothe and Koenig, 1991; golden lion tamarins, *Leontopithecus rosalia*: Dietz and Baker, 1993; African wild dogs, *Lycaon pictus*: Malcolm and Marten, 1982). This phenomenon represents a potentially important alternative route to enhanced inclusive fitness among subordinates residing in cooperatively breeding social groups.

The contrast between the fitness costs and benefits of alloparental care is clearly founded in life history theory (e.g., Partridge and Harvey, 1988). This perspective suggests that while moment-to-moment reproductive performance may vary across

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different life stages, organisms should maximize reproductive performance over their entire lifetime. Long-term studies in avian cooperative breeders reveal that the presence of helpers can have beneficial effects on the reproductive success of the breeders that receive aid, and that alloparents may receive considerable direct fitness enhancement as a consequence of alloparental activity (Stacey and Koenig, 1990). In contrast to the research in avian cooperative breeding species, our knowledge of the fitness consequences of alloparental behavior in mammals is less complete, and data on the lifetime consequences of alloparental behavior are available for only a few species. The presence of alloparents is associated with enhanced reproductive performance of breeders in two species of jackal (*Canis mesomelas* and *C. aureus*: Moehlman, 1979, 1987), the dwarf mongoose (Rood, 1990), and in at least two species of tamarins (*Saguinus fuscicollis*, Goldizen, 1987; *S. mystax*; Garber et al., 1984). There have been several experimental tests in captivity of the contribution of alloparents to the reproductive performance of cooperatively-breeding rodents. Solomon (1991) reported that prairie vole (*Microtus orchrogaster*) pups raised in the presence of alloparents had faster rates of development than pups reared in pairs with breeders only. In addition, breeding females tended to have shorter interbirth intervals when alloparents were present, especially if they had large litters. Female pine voles (*M. pinetorum*) who reared pups in the presence of three alloparents had shorter interbirth intervals than females rearing offspring in social groups with two or fewer alloparents (Powell and Fried, 1992). Wang and Novak (1992) recently demonstrated that the presence of juvenile alloparents and adult males led to reduced parental effort by the breeding female in captive groups of the communally breeding prairie vole but not in the promiscuously breeding meadow vole (*M. pennsylvanicus*). The impact of alloparents on reproductive performance was not evaluated. Two studies have examined the short-term consequences of the presence of juvenile alloparents in the Mongolian gerbil (*Meriones unguiculatus*). Ostermeyer and Elwood (1984) compared parental behavior and weight gain in pups raised in the presence of a breeding adult male and female with either zero or two older siblings who served as alloparents. The presence of juveniles had only minimal effects on parental effort by the adults and was associated with a slower rate of weight gain by pups, relative to those reared in the absence of juveniles. French JA and Dethlefs TM (in preparation) compared parental effort by adults, parental effort by alloparents, pup growth and development, and reproductive performance by the breeding pair in groups which contained zero, two, or five juvenile alloparents. While the presence of helpers reduced the breeders' effort in certain parental behaviors (e.g., nest building) and supplemented their efforts for others (e.g., nest attendance, pup grooming), the presence of helpers had no significant consequences on either the reproductive performance of the breeding pair or on the survivorship of neonates to weaning at 21 days of age.

Thus, for both gerbil and voles in captive settings, the presence of alloparents can significantly reduce parental effort by breeders, but their presence has only small effects on pup growth and little impact on the reproductive performance of the breeding pair. However, no study with cooperatively breeding rodents has systematically evaluated the impact of the presence of alloparents on the lifetime reproductive performance of a breeding pair. It is possible that enhanced weight gain in pups and reduced parental effort by breeders could accumulate over the reproductive tenure of a breeding pair and could produce greater lifetime reproductive performance than pairs without access to alloparents. In addition, long-term observations are necessary to evaluate the possibility that alloparents may enhance immediate direct fitness by engaging in reproductive activity during their tenure as subordinates in the social group. In this experiment, I compared the reproductive and developmental consequences of the presence versus absence of alloparents during the reproductive lifetime of breeding pairs of gerbils. I also systematically monitored the incidence of independent breeding efforts by female alloparents in their natal family groups, evaluated factors associated with these efforts, and monitored the success of alloparents in rearing their offspring.

METHODS

Eighteen breeding pairs of Mongolian gerbils served as subjects in this long-term breeding performance experiment. I created pairs from the offspring of stock animals maintained in the University of Nebraska at Omaha gerbil breeding program. The original source breeders for the colony were from outbred lines acquired from Tumblebrook Farms (West Brookfield, MA, USA). All animals who served as subjects had been reared in intact family groups, had been exposed to at least one litter of younger siblings while in their family groups, and had been housed in same-sex peer groups for approximately 20–30 days prior to pairing. Males and females were 60–80 days old at the time of pairing. All breeding pairs were run as one cohort (i.e., all pairs were constituted at the same time). Two breeding pairs failed to produce more than two litters of offspring, and so were not included in the study.

Breeding males and females, juvenile alloparents, and dependent offspring were housed as family groups in transparent plastic cages (45 × 25 × 20 cm) with wire lids. Pelleted rodent chow, water, and sunflower seeds were provided freely at all times. A 14 h : 10 h light : dark cycle was in effect, with light onset at 2000 h. Temperature in the gerbil breeding facility was maintained at 23° ± 2°C. Ground corncobs, newspaper, and paper towels were provided to the gerbils for nest construction and bedding material. Breeders and alloparents both participated extensively in the construction and maintenance of elaborate nests.

At the birth of the first litter, I assigned pairs randomly to one of two treatment conditions: Helpers Present (HP, $n = 9$) and Helpers Absent (HA, $n = 7$). For pairs in the HA condition, all pups born in the first litter were removed 21 days after birth. For pairs in the HP condition, litters were reduced to four individuals (two males and two females in most cases) 21 days postpartum. The weanling gerbils served as alloparental helpers. The juveniles remained in their natal family group

Table 1

Reproductive, developmental, and postnatal treatment of gerbil pups reared in the presence and absence of juvenile alloparents

Measure	Experimental condition: Helpers present (n = 9)	Helpers absent (n = 7)	t[a]	p[a]
Reproductive measures				
Number of litters	9.56 ± 0.38[b]	9.14 ± 0.80	0.47	n.s.
Litter size	5.71 ± 0.24	5.73 ± 0.21	0.05	n.s.
Total number of pups	54.89 ± 3.75	53.14 ± 5.78	0.25	n.s.
Interbirth interval (days)	40.28 ± 1.51	38.56 ± 1.19	0.89	n.s.
Neonatal/Postnatal weights				
Pup weight (g), day 0	3.11 ± 0.05	3.31 ± 0.06	2.59	.02
Litter weight (g), day 0	17.76 ± 0.69	18.99 ± 0.80	1.16	n.s.
Cumulative litter weight (g), day 0	170.85 ± 11.85	175.89 ± 19.90	0.22	n.s.
Pup weight (g), day 21	14.23 ± 0.45	14.96 ± 0.36	1.27	n.s.
Litter weight (g), day 21	72.61 ± 3.82	77.09 ± 5.62	0.66	n.s.
Cumulative litter weight (g), day 21	698.18 ± 56.25	720.60 ± 89.56	0.21	n.s.
Pup mortality/injury[c]				
Number of pups injured	1.44 ± 0.58	2.00 ± 0.65	0.64	n.s.
Number of pups killed/missing	5.89 ± 0.98	4.57 ± 1.29	0.81	n.s.

[a] Independent samples t statistic (df = 14) and associated p value.

[b] Values indicate mean ± SEM; each breeding pair represented by a single value in the analysis.

[c] Cumulative incidence of injury and mortality for each pair over the course of the study.

throughout the time during which three additional litters were produced by the breeding pair. After residence in the group for three successive litters, the older alloparents were removed, and four animals from the current weanling litter were selected to serve as alloparents for the next three litters in the manner described above. This timing of alloparental replacement is consistent with available information on the duration of philopatry and the dynamics of dispersal in wild Mongolian gerbils (Ågren et al., 1989; Naumov and Lobachev, 1975). Data collection continued for 13.5 months after pairing, at which point breeders were 16.5–17 months old. Mean age of last parturition in gerbils is 15.4 months (Norris and Adams, 1982) and 90% of females cease reproduction with no visible signs of subsequent implantation by 16 months of age (Marston and Chang, 1965).

Cages were checked seven days per week early in the morning and new litters, pup mortality or disappearance, and injuries sustained by pups were recorded. On the day of birth, individual neonates were identified by a unique toe clip and weighed to the nearest 0.1 g. Pups were also weighed 7, 14, and 21 days after birth. From the breeding colony records, I evaluated three general aspects of reproductive performance. Rates of offspring production were calculated using: (1) number of litters produced during the 13.5-month study; (2) total number of pups produced; (3) mean litter size; and (4) interbirth interval (IBI, in days). Energetic investment in offspring by females was evaluated by mean pup weight and mean litter weight on days 0 and 21 postpartum; and total litter weights on days 0 and 21 summed over the study. Pup survivorship was evaluated using the total number of pups that died prior to day 21 and the total number of pups that were injured prior to day 21. I evaluated treatment effects in two ways. First, long-term differences between pairs with and without alloparents were evaluated by comparing breeding performance across the experiment with independent samples t tests. Second, the possibility that the effects of alloparents might vary with age or experience of the breeding pair was evaluated for a number of measures by regression analysis. When daughters in HP family groups produced litters, pups were treated identically to pups born to adult females (i.e., toe clipped for identification, weighed, checked for injuries).

RESULTS

Over the 13.5 months of the study, breeding pairs produced an average of slightly more than nine litters, with mean litter sizes of 5.7 pups at birth. No significant differences between groups with and without helpers were noted for any reproductive parameter (Table 1). Mean pup weight on the day of birth was significantly (p = .02) heavier in HA groups than in HP groups. Mean pup weights at day 21, mean litter weights at day 0 and day 21, and cumulative litter weights on day 0 and day 21 did not differ significantly between helper conditions. Neither pup injuries nor pup mortality differed as a function of the presence or absence of helpers. Table 2 presents the results of a regression analysis which evaluated differences in reproductive performance across female breeding experience (parturitions) for the HP and HA groups. Female reproductive experience accounted for a low proportion of variance in reproductive performance for both HP and HA groups (r^2s < .07). The slope of the regression lines differed from 0 only for offspring survival to 21 days of age in the HP group, and the relationship was a negative one (i.e., offspring survival tended to be lower in later litters). However, this relationship accounted for only 6% of the variance in offspring survival.

Table 2

Regression analysis of changes in reproductive performance as a function of reproductive experience in Mongolian gerbil pairs in the presence and absence of alloparental helpers

Dependent measure	Helpers present (n = 9)				Helpers absent (n = 7)			
	r^2 [a]	Slope[b]	t[c]	p[c]	r^2	Slope	t	p
Litter size (day 0)	<0.01	−0.03	−0.31	n.s.	<0.01	−0.03	0.37	n.s.
Litter size (day 20)	0.02	−0.14	−1.49	n.s.	<0.01	−0.03	−0.35	n.s.
Percent offspring survival	0.06	−0.03	−2.20	.03	0.01	−0.01	−0.70	n.s.
Pup weight (g), day 0	0.05	−0.02	1.98	n.s.	<0.01	−0.01	−0.16	n.s.
Pup weight (g), day 20	0.04	−0.25	1.89	n.s.	0.03	−0.15	−1.44	n.s.
IBI (days)	0.01	−0.35	−0.66	n.s.	<0.01	−0.62	−1.10	n.s.

[a] Proportion of variance accounted for by relationship between dependent measure and female reproductive experience (number of parturitions).

[b] Slope of regression relationship between dependent measure and female reproductive experience.

[c] t statistic (and associated p value) testing departure of slope from value of 0.

Breeding by subordinate female alloparents

Seven female alloparents (of 49 female alloparents of breeding age in nine HP groups) produced offspring during the course of the experiment. Age at parturition for these alloparents was 123.5 ± 9.81 days (mean ± SEM, throughout). Overall, female alloparents were very similar to adult females in HP groups with respect to reproductive performance. While litter size for alloparents (6.43 ± 0.80 pups; n = 7) tended to be larger than litters born to adult females (5.37 ± 0.24 pups; n = 9) these differences were not significant ($t(14) = 0.85$, n.s.). Mean pup weight at birth for offspring born to alloparents (3.12 ± 0.24 g) did not differ from offspring produced by adult females (3.11 ± 0.05 g; $t(14) = 0.04$, n.s), nor was total litter weight on the day of birth different between the two classes of females (alloparents: 19.59 ± 2.32 g; adult females: 17.76 ± 0.69 g, $t(14) = 0.76$, n.s.). Excluding the two reproductively active alloparents who suffered 100% pup mortality prior to weaning, mean weight of pups on day 21 was significantly less for alloparents (11.75 ± 1.03 g) than for adult females (14.23 ± 0.45 g; $t(12) = 2.48$, $p < .05$). However, because alloparents tended to have larger litters, total litter weight on day 21 did not differ between alloparents (69.24 ± 19.70 g) and adult females (72.61 ± 3.82 g; $t(12) = 0.17$, n.s.). Pup mortality was higher for female alloparents than for adult females (alloparents = 41.2% ± 19.1%, adult females = 10.4% ± 1.4%). While mean differences in pup mortality were not significant ($t(14) = 1.44$, n.s.), variance in pup mortality differed greatly between adult females and breeding alloparents. An association between pup mortality and the temporal synchrony of the daughters' parturition with that of their mothers accounted for a sizable proportion of the variance in pup mortality for daughters. Alloparental females who delivered their litters immediately after their mothers delivered litters tended to have lower pup mortality than those daughters whose litters were born 2 weeks or more after the mother's delivery (r = .72, p = .06, n = 7; see Figure 1).

I evaluated the possibility that a reproductive anomaly in the breeding adult female may have contributed to the onset of reproduction in subordinate alloparents in the following way. The mean interbirth interval for adult females was calculated for all intervals except that interval during which the alloparents conceived their litters. This value was compared (with a correlated-samples t test) to the IBI for the same breeding adult females during the interval in which their daughters conceived offspring. The occurrence of reproduction by alloparents was associated with an atypically long IBI in breeding adult females. The IBI for breeding adult females during the interval in which their daughters conceived litters that were carried through parturition (58.33 ± 7.65 days) was significantly longer than the mean IBI for all other intervals in which daughters were reproductively quiescent (36.91 ± 0.53 days; $t(5) = 2.78$, p = .039).

While no systematic behavioral observations were made of groups with two reproductively active females, records were maintained ad libitum on the identity of pups that were nursing with both the breeding adult female and the reproductively active daughter, especially for those pairs in which parturition was temporally synchronous (and hence a high proportion of the daughter's pups survived). Two nests were typically established, one by the older and one by the younger female. Pups were more or less evenly distributed between the two nests. During one of the seven instances of multiple female breeding, a single large nest was constructed and all pups, both those belonging to the mother and the daughter, were located in this communal nest.

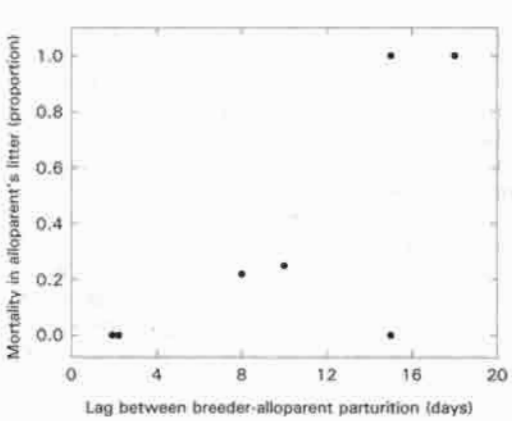

Figure 1
Relationship between time lag in days between delivery of litter by dominant breeding females and the subsequent parturition of reproductively active female alloparents, and the proportion of offspring surviving in the litters of the alloparents.

DISCUSSION

Mongolian gerbils live in age-structured stable social groups (i.e., families) in both wild and semi-free ranging conditions and adult males and older juveniles attend the nest throughout the year (Ågren, 1984; Ågren et al., 1989; Naumov and Lobachev, 1975). Social group demography has important influences on reproductive success: breeding attempts by females in the absence of the adult male are less successful than those in which both the adult male and female attend the nest, even under ideal laboratory conditions (Gerling and Yahr, 1979). In addition, pups develop more slowly in the absence of the breeding male than in his presence, again under laboratory conditions (Elwood and Broom, 1978). The observations described in this article suggest that unlike the importance of the presence of the breeding male, the presence of alloparents has little overall impact on the lifetime reproductive performance of breeding females or on rates of pup development in Mongolian gerbils. Pairs with alloparents in the social group throughout their breeding lifetime had litter sizes, rates of pup production, mean and cumulative litter weights, and rates of pup injury and mortality that were similar to pairs without alloparents. The observations also revealed that female alloparents were capable of producing offspring, and did so on seven occasions. In each case the production of offspring in the daughter was associated with a long interbirth interval in the breeding adult female. Survivorship of the daughter's litter was associated with the degree of synchrony with the adult female: the sooner the daughter produced offspring with respect to the mother, the more likely it was that the daughter's offspring would survive.

The data presented here argue against a central role for indirect fitness in accounting for alloparental care and cooperative breeding in the Mongolian gerbil. However, the ideal laboratory conditions in which the animals were housed (e.g., constant warm temperature, ad libitum access to food) may have mitigated against demonstrating any beneficial effects of the presence of alloparents. Two points, though, lend support to the conclusion that indirect benefits of alloparental care may be of minor importance in this species. First, a recent study simulated an ecological condition (cold stress) under which the presence of alloparents could have been expected to enhance reproductive outcomes in the breeding pair. Pup survival and weight gain in gerbil groups housed at 6°C was poorer than in groups housed at 23°C, but the presence of alloparents with breeding pairs in the cold environment did not enhance either survivorship or weight gain of pups relative to pairs without alloparents (Lai, 1991). Second, several studies in other species of cooperatively breeding rodents have demonstrated enhanced reproductive performance under conditions of ad libitum access to food and water and only slight temperature stress (Powell and Fried, 1992; Solomon, 1991). It is certainly possible that under certain combinations of both food and thermal constraints, the presence of alloparents could significantly enhance the reproductive performance of breeders. For instance, alloparents could serve an important role as nest attendants or as foragers during periods of increased foraging demand that require long absences from the natal burrow at times when temperatures are low. Experiments simulating these conditions are currently underway in our laboratory.

In most species of cooperatively breeding mammals, reproduction is typically limited to a single dominant female (Emlen, 1991). Mongolian gerbils show this pattern in captive settings (Payman and Swanson, 1980; Swanson and Lockley, 1978), in seminatural enclosures (Ågren, 1984), and in free-ranging populations in the wild (Ågren et al., 1989). Recent interest in the dynamics of cooperative breeding systems in mammals has focused on exceptions to singular breeding in these species. A central question has been the following: under what conditions do subordinates attempt reproduction, and are these attempts consistent with predictions from life history profiles? Creel and Waser (1991) have recently shown that the distribution of breeding attempts by subordinate female dwarf mongooses is consistent with predictions derived from estimates of expected indirect fitness for alloparents in the absence of direct reproductive attempts. Older female alloparents who tend to be unrelated to the dominant breeding pair have the least indirect fitness gains in return for alloparental care, and they are the most likely to attempt independent reproduction (Creel and Waser, 1991). Recent DNA-fingerprinting analysis of paternity in dwarf mongoose social groups suggests that subordinate male alloparents, too, engage in successful reproductive attempts. Within mongoose litters there is evidence of multiple paternity *and* maternity (Keane B, Waser PM, Minchella DDJ, Elliott LF, and Creel SR, personal communication). Breeding attempts by subordinate male and, especially, female callitrichid primates (marmosets and tamarins) in both field (e.g., Dietz and Baker, 1993) and captive settings (Price and McGrew, 1991; Rothe and Koenig, 1991) are also more common than previously suspected. The data presented here on the Mongolian gerbil, along with other examples of multiple breeding females in social groups from both captive (Payman and Swanson, 1980) and field studies (Naumov and Lobachev, 1975) indicate that the gerbil may be a useful species for evaluating factors that lead to breeding attempts by subordinate alloparents.

What conditions lead to the failure or removal of reproductive inhibition in subordinate female gerbils? Previous work has demonstrated that two contexts are associated with reproductive activation of subordinate females (usually daughters) in gerbil social groups: removal of the breeding adult female, and regular removal of pups produced by the adult female (Payman and Swanson, 1980). These observations suggest that subordinates initiate reproductive efforts in the event that the dominant breeding female disappears or experiences reproductive failure. The data reported here further suggest that subordinate females may be sensitive not only to the presence or absence of the dominant breeding female or her pups, but also to subtle changes in the reproductive status of the breeding adult female. Female alloparents engaged in reproductive activity when the breeding adult female showed an atypically long interbirth interval that occurred in an otherwise regular cycle of conceptions and parturitions. Future studies would do

well to examine changes in behavioral interactions between female breeders and alloparents, and changes in olfactory cues produced by the female breeder in association with spontaneous or experimentally induced delays in breeding on the part of the adult female.

In the event that juvenile or subadult alloparents engaged in reproductive attempts, success by the alloparent in rearing offspring was related to the degree of birth synchrony with the adult female in the social group. Pup mortality was lowest in cases where the two litters in the group were produced in close temporal synchrony and highest where the two litters were produced asynchronously. This finding has been documented in diverse mammalian species (e.g., lions, *Panthera leo*: Packer and Pusey, 1983; Norway rats, *Rattus norvegicus*: Mennella et al., 1990). Several mechanisms have been proposed for the enhanced survival of offspring in synchronously produced litters (or, conversely, the higher mortality in asynchronously produced litters) and could apply to the results reported here on Mongolian gerbils. First, interlitter competition in asynchronous litters, particularly in the form of milk stealing or nipple monopolization by the offspring in the older litter, may reduce the survivorship of the offspring in the younger litter (Bertram, 1975; Mennella et al., 1990; Packer and Pusey, 1983). Milk stealing by older siblings has been implicated in lower weaning weights in two cooperatively breeding rodents: Mongolian gerbils (Ostermeyer and Elwood, 1984) and pine voles (Powell and Fried, 1992). In the present study, pup weight at 21 days postpartum (but not on the day of birth) was significantly lighter for pups born to alloparents compared to pups born to adult females, and competition for milk from offspring of the older litter may have contributed to the weight differential. In other cooperatively breeding mammals, subordinate females are less capable than adult female breeders in the provisioning of nutrition for their offspring (e.g., reduced lactation and provisioning of pups born to subordinate females in wild dogs, *Lycaon pictus*; Frame et al., 1979; Malcolm and Marten, 1982). Thus, asynchronous breeding by subordinate alloparents may accentuate this initial deficit. Second, considerable advantages may accrue to litters that are produced synchronously. Potential benefits of synchronous birth include reduced thermal and energetic demands on multiple mothers, communal nursing, and joint defense of young (Boinski, 1987; Mennella et al., 1990; Packer et al., 1992; Saylor and Salmon, 1969). The enhanced survivorship and greater weight at 21 days of age in gerbil pups born to alloparents who delivered their litters in close temporal association with the adult female in the social group may be a consequence of one or more of these advantages of birth synchrony. Communal nursing and joint nesting were both observed during the course of these observations, lending credence to this interpretation.

In summary, the observations reported here are consistent with the notion that indirect fitness for alloparents plays a minor role in accounting for the expression of alloparental care in the Mongolian gerbil. Under the conditions of housing described herein, alloparents reduce parental effort (French and Dethlefs, unpublished) but have little effect on either short-term or long-term reproductive performance of the breeding pair. Our previous demonstration of future direct benefits of alloparental experience (Salo and French, 1989) combined with our documentation of reproductive efforts by both male (French and Dethlefs, unpublished) and female (this study) subordinate alloparents provides alternative mechanisms for the maintenance of alloparental care and communal breeding in the gerbil.

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REFERENCES

Ågren G, 1984. Pair formation in the Mongolian gerbil. Anim Behav 32:528–535.

Ågren G, Zhou Q, Zhong W, 1989. Ecology and social behaviour of Mongolian gerbils, *Meriones unguiculatus* at Xilinhot, Inner Mongolia, China. Anim Behav 37: 11–27.

Bertram BCR, 1975. Social factors influencing reproduction in wild lions. J Zool (London) 177:463–482.

Boinski S, 1987. Birth synchrony in squirrel monkeys (*Saimiri oerstedi*): a strategy to reduce neonatal predation. Behav Ecol Sociobiol 21:393–400.

Brown JL, 1987. Helping and communal breeding in birds. Princeton, New Jersey: Princeton University Press.

Creel SR, Waser PM, 1991. Failures of reproductive suppression in dwarf mongooses (*Helogale parvula*): accident or adaptation? Behav Ecol 2:7–15.

Dietz JM, Baker AJ, 1993. Polygyny and female reproductive success in golden lion tamarins (*Leontopithecus rosalia*). Anim Behav 46:1067–1078.

Elwood RW, Broom DM, 1978. The influence of the litter size and parental behaviour on the development of Mongolian gerbil pups. Anim Behav 26:438–454.

Emlen ST, 1991. Evolution of cooperative breeding in birds and mammals. In: Behavioural ecology: an evolutionary approach (Krebs JR, Davies NB, eds). London: Blackwell Scientific; 301–335.

Frame LH, Malcolm JR, Frame GW, Lawick H, 1979. Social organization of African wild dogs (*Lycaon pictus*) on the Serengeti plains, Tanzania 1967–1978. Z Tierpsychol 50:225–249.

Garber PA, Moya L, Malaga C, 1984. A preliminary field study of the moustached tamarin monkey (*Saguinus mystax*) in northeastern Peru: questions concerned with the evolution of a communal breeding system. Folia Primatol 42:17–32.

Gerling S, Yahr P, 1979. Effect of the male parent on pup survival in Mongolian gerbils (*Meriones unguiculatus*). Anim Behav 27:310–311.

Goldizen AW, 1987. Facultative polyandry and the role of infant carrying in wild saddle-back tamarins (*Saguinus fuscicollis*). Behav Ecol Sociobiol 20:99–109.

Jamieson I, 1989. Behavioral heterochrony and the evolution of birds' helping at the nest: an unselected consequence of communal breeding? Am Nat 133:394–406.

Koenig WD, Mumme RL, 1987. Population ecology of the cooperatively breeding acorn woodpecker. Princeton, New Jersey: Princeton University Press.

Koenig WD, Pitelka FA, Carmen WJ, Mumme RL, Stanback MT, 1992. The evolution of delayed dispersal in cooperative breeders. Q Rev Biol 67:111–150.

Lai Q, 1991. The influence of temperature and presence of helpers on reproductive performance and parental behavior in Mongolian gerbils (*Meriones unguiculatus*) (MA thesis). Omaha, Nebraska: University of Nebraska at Omaha.

Malcolm JR, Marten K, 1982. Natural selection and the communal rearing of pups in African wild dogs (*Lycaon pictus*). Behav Ecol Sociobiol 10:1–13.

Marston JH, Chang MC, 1965. The breeding management and reproductive physiology of the Mongolian gerbil *Meriones unguiculatus*. Lab Anim Care 15:34–48.

Mennella JA, Blumberg MS, McClintock MK, Moltz H, 1990. Inter-litter competition and communal nursing among Norway rats: advantages of birth synchrony. Behav Ecol Sociobiol 27:183–190.

Moehlman PD, 1979. Jackal helpers and pup survival. Nature 277:382–383.

Moehlman PD, 1987. Social organization in jackals. Amer Sci 75:366–375.

Naumov NP, Lobachev VS, 1975. Ecology of desert rodents of the U.S.S.R. (jerboas and gerbils). In: Rodents in desert environments (Prakash I, Ghosh PK, eds). The Hague: D. W. Junk; 465–598.

Norris ML, Adams CE, 1982. Lifetime reproductive performance of Mongolian gerbils (*Meriones unguiculatus*) with 1 or 2 ovaries. Lab Anim 16:146–150.

Ostermeyer MC, Elwood RW, 1984. Helpers(?) at the nest in the Mongolian gerbil *Meriones unguiculatus*. Behaviour 91:61–77.

Packer C, Lewis S, Pusey A, 1992. A comparative analysis of non-offspring nursing. Anim Behav 43:265–282.

Packer C, Pusey AE, 1983. Adaptations of female lions to infanticide by incoming males. Am Nat 121:716–728.

Partridge L, Harvey PH, 1988. The ecological context of life history evolution. Science 241:1449–1455.

Payman B, Swanson H, 1980. Social influence on sexual maturation and breeding in the female Mongolian gerbil *Meriones unguiculatus*. Anim Behav 28:528–535.

Powell RA, Fried JJ, 1992. Helping by juvenile pine voles (*Microtus pinetorum*), growth and survival of younger siblings, and the evolution of pine vole sociality. Behav Ecol 3:325–333.

Price EC, McGrew WC, 1991. Departures from monogamy: survey and synthesis from colonies of cotton-top tamarins. Folia Primatol 57:16–27.

Rood JP, 1980. Mating relationship and breeding suppression in the dwarf mongoose. Anim Behav 28:143–150.

Rood JP, 1990. Group size, survival, reproduction, and routes to breeding in dwarf mongooses. Anim Behav 39:566–572.

Rothe H, Koenig A, 1991. Variability of social organization in captive common marmosets (*Callithrix jacchus*). Folia Primatol 57:28–33.

Salo AL, French JA, 1989. Early experience, reproductive success, and the development of parental behaviour in Mongolian gerbils. Anim Behav 38:693–702.

Saylor A, Salmon M, 1969. Communal nursing in mice: influence of multiple mothers on the growth of the young. Science 164:1309–1310.

Solomon NG, 1991. Current indirect fitness benefits associated with philopatry in juvenile prairie voles. Behav Ecol Sociobiol 29:277–282.

Stacey PB, Koenig WD (eds), 1990. Cooperative breeding in birds: long-term studies of ecology and behavior. New York: Cambridge University Press.

Swanson HH, Lockley MR, 1978. Population growth and social structure of confined colonies of Mongolian gerbils: scent gland size and marking behaviour as indices of social status. Aggress Behav 4:57–89.

Wang Z, Novak MA, 1992. Influence of the social environment on parental behavior and pup development of meadow voles (*Microtus pennsylvanicus*) and prairie voles (*M. orchrogaster*). J Comp Psychol 106:163–171.

Woolfenden GE, Fizpatrick JW, 1984. The Florida scrub jay: demography of a cooperative-breeding bird. Princeton, New Jersey: Princeton University Press.