



# An experimental examination of the consequences of communal versus solitary breeding on maternal condition and the early postnatal growth and survival of degu, *Octodon degus*, pups

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Individuals of numerous rodent species engage in group living, in which they share an area of activity, a nest (or den), and interact more frequently with group members than with individuals from other such groups. Members of social groups may engage in communal breeding when they rear their young together in a common nest. We conducted an experimental study under laboratory conditions to explore the costs and benefits linked to early postnatal investment in offspring by female degus. In particular, we examined the quality and quantity of offspring produced by females rearing their litters in the presence of a second lactating (related or unrelated) female ('communally breeding') with offspring produced by lactating females in the presence of a nonbreeding (related or unrelated) female ('singularly breeding'), and the offspring of solitary females. The physical condition of mothers (mass lost through lactation) was also examined. We studied 70 female degus and their litters, and 13 additional nonbreeding females, under constant conditions of adult density, nest availability, restricted food availability and breeding experience of subjects. The number of pups, the mass of pups, and the physical condition of mothers breeding communally did not differ from those of singularly and solitarily breeding females. Similar results were obtained when kinship of breeding females was considered. When reproductive performance of individuals within communally breeding groups was examined, we found that costs and benefits were not shared equally. Weanlings of litters born in the presence of a previous litter were smaller and less numerous than weanlings of litters born when no other young were present. Taken together, our results show that female degus derive no apparent reproductive benefits from early postnatal rearing of their offspring. Moreover, a proportion of females seem to pay a net cost.

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Numerous rodent species live in groups in which individuals share an area of activity, and interact more frequently with group members than with individuals from other such groups. When group members also share a nest during breeding and rear their young together, they are regarded as communal breeders (Lewis & Pusey 1997; Solomon & Getz 1997; Hayes 2000). The most frequently cited benefits of communal breeding include protection of

young from infanticide or predation, improved thermo-regulation of young, improved offspring growth, improved immunocompetence of young, reduction of maternal energy costs and adoption of orphaned young (Riedman 1982; Lee 1989; Lewis & Pusey 1997; Roulin & Heeb 1999; Hayes 2000). Costs, however, may include increased offspring competition, suppressed reproduction, increased parasite transmission, or mothers diverting resources to unrelated offspring (Hayes 2000; McGuire et al. 2002). Thus, an examination of the short-term consequences associated with communal breeding represents a first step towards understanding the current adaptive value of this behaviour.

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Compared with studies on reproductively skewed birds and mammals (Brown 1987; Solomon & French 1997; Koenig & Dickinson 2004), studies examining the reproductive consequences in species where most individuals breed are rather scant, but more importantly, they are equivocal in supporting benefits to communal breeders. The number of weaned offspring (a measure of direct fitness) declines with the size of nesting associations in black-tailed prairie dogs, *Cynomys ludovicinus* (Hoogland 1981, 1995) and in social tuco-tucos, *Ctenomys sociabilis* (Lacey 2004), and daughters of communally breeding female voles, *Microtus arvalis*, are less likely to attain breeding age than are daughters of solitarily breeding females (Boyce & Boyce 1988). In contrast, the per capita number of offspring weaned by solitarily and communally breeding females does not differ in dormice, *Glis glis* (Pilastro et al. 1996), white-footed mice, deer mice, *Peromyscus* spp. (Wolff 1994) and wood mice, *Apodemus sylvaticus* (Gerlach & Bartmann 2002). In prairie voles, *Microtus ochrogaster*, and yellow-bellied marmots, *Marmota flaviventris*, direct fitness of individuals in small communally breeding groups tends to be higher than that of solitarily nesting individuals (Armitage & Schwartz 2000; McGuire et al. 2002; Hayes & Solomon 2004). However, direct fitness declines in larger communal groups (with three or more individuals) of these species (Armitage & Schwartz 2000; McGuire et al. 2002; Solomon 2003). In contrast, female house mice, *Mus domesticus*, that communally breed wean larger and heavier litters compared with solitary females (Sayler & Salmon 1971; König 1994; Manning et al. 1995). Collectively then, both the magnitude and nature of direct fitness benefits accrued by communal breeders vary across species. More intriguingly, direct fitness benefits to communal breeders are not evident in some cases.

Performance of communally breeding groups seems, to some extent, to be linked to kinship. Kin selection theory states that individuals derive indirect fitness benefits through cooperating more with conspecifics that are genetically related (Hamilton 1964). Thus, communally breeding individuals should perform overtly better when group members include close kin. Some support for this expectation comes from the behaviour of bank voles, *Clethrionomys glareolus*, where neighbouring females that are related produce more recruits than neighbouring females that are unrelated (Mappes et al. 1995). In the house mouse, sisters behave less aggressively, establish communal litters more often, breed more and wean more offspring than nonsisters (König 1994; Dobson et al. 2000; Rusu & Krackow 2004). In partial agreement with kin selection expectations, the number of pups weaned among communally breeding mother–daughter pairs of wood mice is greater than that of solitary females, but not so when communal groups consist of sisters (Gerlach & Bartmann 2002), suggesting that indirect benefits may not always contribute to inclusive fitness differences between solitarily and communally breeding rodents.

When consequences of communal breeding in rodents are examined within groups, costs and benefits may differ between group members. Thus, female pairs of the communally breeding wood mouse establish dominance

relationships, and the reproductive success of the subordinate nestmate is lower than that of the dominant nestmate (Gerlach & Bartmann 2002). Similarly, reproductive success among female house mice is highly skewed in favour of dominant females (Rusu & Krackow 2004). In contrast to wood mice and house mice, costs and benefits of communal breeding are shared more equally among nestmates in prairie voles (Hayes & Solomon 2004), supporting the idea of a species gradient from despotic to more egalitarian communal groups (i.e. Sherman et al. 1995).

Collectively then, studies of species where breeding seems egalitarian are needed to examine the consequences of communal breeding. We studied short-term consequences linked to early postnatal investment in offspring by female degu, a caviomorph rodent that meets these requirements. Postnatal investment in offspring is especially costly to small rodents because energy demands during lactation are at their highest (Thompson 1992). More importantly, future fecundity of lactating rodents may be lower than that of nonlactating individuals (Huber et al. 1999), because lactating females lose mass and energy reserves during lactation (Wauters & Dhondt 1989). With regard to offspring, small offspring have lower survival and become small adults that mate less successfully (Solomon 1994; Neuhaus 2000). Therefore, selection might be expected to favour female rodents that breed communally as a strategy to invest more efficiently in pups at a reduced cost to their own physical condition and future reproduction.

Several features make degus an outstanding model to examine the functional basis of communal breeding. Degus are social rodents where a variable number of females (1–4) and one or two males share an underground burrow system and a foraging area (Fulk 1976; Ebensperger et al. 2004). Typically, degus breed once per year (Ebensperger & Hurtado 2005), and most adults do not survive after their second year of age (Meserve et al. 1993, 1995), suggesting that success during the first breeding event has an important effect on lifetime fitness. Similar to other rodents, lactation represents the highest energy cost to breeding females (Veloso 1997; Veloso & Bozinovic 2000), and degu pups are more dependent on maternal milk to complete their postnatal development than are other precocial rodents (Veloso & Kenagy 2005): degu pups do not eat solid food before 6 days of age (Reynolds & Wright 1979; L. A. Ebensperger, personal observations). Communal nesting by lactating females under seminatural and natural conditions has been well demonstrated (Ebensperger et al. 2002, 2004), implying that degus are communal breeders. This suggestion has been confirmed in captivity, where females readily rear their litters together even if nesting places are not limited (Ebensperger et al. 2002). Ongoing field observations support the notion that most individuals breed within communal groups (L. Hayes, A. Chesh & L. Ebensperger, unpublished data), implying that breeding is egalitarian. On the other hand, communal groups may be composed of either close (first degree) kin or totally unrelated females (Ebensperger et al. 2004), suggesting that lactating females attend to communal litters with related and

unrelated young. Taken together, these life history, demographic and social behaviour features provide an appropriate scenario for female degus to benefit from communally rearing their pups.

The objective of this study was to experimentally examine the joint influence of communal breeding and kinship on both the early postnatal growth and survival of pups to weaning age and the physical condition of lactating females. To do so, we compared the mass change of dams and the mass attained by their pups when they were allowed to rear offspring solitarily (i.e. solitarily breeding) or in the presence of either a full sister or an unrelated breeding female (i.e. communally breeding). We further considered a third experimental condition in which a lactating female was allowed to rear her offspring in the presence of either a full sister or an unrelated, nonbreeding female (i.e. singularly breeding). This additional social condition allowed us to quantify the potential effects of alloparenting by degus that occasionally may not breed.

## METHODS

### Study Subjects, Animal Housing and Pairing

The study subjects were 1-year-old female descendents from pregnant females caught during July–August 2002 at Lampa (33°17'S, 70°53'W), near Santiago. Upon weaning (ca. 30 days of age), degu subjects were kept in same-sex sibling pairs in clear polycarbonate rat cages (45 × 23 × 21 cm) with a bedding of hardwood chips, and water and food (rabbit commercial pellet) provided ad libitum. Animals were kept in a ventilated room exposed to natural photoperiod and ambient temperature (yearly minimum = 13.4 ± 0.2°C; yearly maximum = 24.9 ± 0.2°C). When 3 months of age, female siblings were marked with an eartag and transferred to a cage with either a full sister (related) or an unrelated female. Pairs of related and unrelated females were then allowed to mate with a same-age, unrelated male when 8 months of age. Males remained with the females for 60 days, at which time pregnant females were easy to recognize. The annual rate of females becoming pregnant in our colony ranged from 49 to 75%.

Approximately 7–10 days before the expected delivery of pups, pregnant females were transferred to clear acrylic aquaria (experimental cages) and housed in a different (i.e. experimental) room. Cages of solitary females measured 61.5 × 31.5 × 40.5 cm and each contained one nestbox made of clear glass (18 × 29 × 15 cm) in the rear section of the aquarium. Cages of singularly and communally breeding females measured 61.5 × 62.0 × 40.5 cm and each contained two nestboxes (18 × 29 × 15 cm), placed side by side, in the rear section of the aquarium. These cage dimensions were chosen to keep adult density constant through the experiments. Cage size (and the resulting space per animal) may influence food intake and metabolic expenditure in captive rodents (Steyermark & Mueller 2002). While in these cages, degu subjects were supplied with a 1–2-cm layer of saw dust as bedding

material, and water ad libitum. Food, however, was restricted in such a way that females were fed daily with rabbit commercial pellet representing 80% of the empirically determined energy requirements for adult lactating and nonlactating females (Veloso 1997). Benefits of communal breeding may be realized only under limiting ecological conditions (Magrath 2001; Hayes & Solomon 2004), so exposure to easily accessible and unlimited food may offset potential costs of lactation (e.g. milk sharing; Hayes 2000), given the positive effects of food availability on offspring production and female condition in rodents (Koskela et al. 1998; Liang & Zhang 2006). Thus, our restricted food regime provided our experimental subjects with an energetically challenging environment without causing mortality of mothers and pups (Perrigo 1987; Hayes & Solomon 2004).

Owing to limitations in the number of experimental aquaria and of overall space to house the aquaria, we conducted our experiments during a 3-year period. However, every year we assigned animal subjects so that all experimental treatments were equally represented. Our degu colony was maintained so that animals never bred with close kin, and the animals' annual breeding event was timed to match the breeding schedule of wild populations (Ebensperger & Hurtado 2005). Thus, lactating females were always observed in October–November. Maximum and minimum temperatures of the experimental room during this time averaged 24.1 ± 0.2°C and 18.2 ± 0.2°C, respectively.

The nesting condition to which females were assigned (solitary, singular, communal breeding) depended on the number of females that became pregnant previously. When two females became pregnant, they were assigned to either the communally or the solitarily (unrelated pairs only) breeding-female condition. When only one female of the pair became pregnant, she was assigned to either the singularly or the solitarily breeding-female condition. It could be argued that this design introduced a bias against increased weight gain or survival of pups from singularly breeding groups if nonbreeding females did not breed because they were in poor physical condition. This seems unlikely, however; pups of singularly breeding females tended to attain a larger size and survive better than pups of other communally breeding dams (see Results). Note also that pairs of related and unrelated females were equally familiar with each other, a realistic condition for degus.

### Data Collection

Once born, pups were individually marked with a single toe clip. Litter size may influence subsequent offspring quantity and quality in rodents (Mendl 1988; Koskela 1998; Koskela et al. 1999; Neuhaus 2000), so we standardized all litters to six pups at this time (i.e. the mean litter size for degus, Veloso 1997). Of the 70 litters examined, we reduced litters by either one pup ( $N = 19$ ), two pups ( $N = 9$ ), or three pups ( $N = 5$ ), and increased litters by either one pup ( $N = 13$ ) or two pups ( $N = 1$ ). The sex of pups removed or added was chosen randomly. The remaining 23 litters had six pups and remained unchanged.

There was no indication that the distribution of our litter adjustment across treatments deviated from random (log-likelihood ratio test:  $G_{\text{adj},4} = 2.69$ ,  $P = 0.612$ ). We cross-fostered removed pups to genetically related recipient mothers with pups of similar age, although lactating degus do not discriminate against unrelated offspring, even in the presence of own offspring (Ebensperger et al. 2006). All cross-fostered pups were readily adopted by lactating females in our breeding colony. We weighed mothers and pups to 0.05 g at birth (day 1) and then every other day until day 31, always during morning hours. We used these data to compare the mass attained by pups through lactation. In the case of dams, we calculated the percentage of body mass lost through lactation as an estimate of body condition. Body mass is a predictor of body condition in rodents (King & Allainé 2002). At day 31, we further tallied surviving pups to record survivorship of weanlings.

## Data Analysis

We examined the potential effects of breeding condition ('nesting condition') on pup growth and survival with the general linear model (GLM) of Statistica 6.0 (StatSoft Inc., Tulsa, Oklahoma, U.S.A.). We ran the GLM procedure with nesting condition (solitary, singular, communal) as a fixed main factor. The mean mass of pups on days 1, 7, 15, 21, 27 and 31 was entered in the analyses as a repeated measure, random factor (i.e. 'day of lactation'). For pup survival, we examined the percentage of young surviving to day 31 (i.e. weaning time). For both analyses, we entered both the mean mass of mothers through the 30-day lactation period and the mothers' original litter size (hereafter 'litter size') on the day of pup delivery as covariates, because maternal body size may affect subsequent pup growth in rodents (Solomon 1994) and because mothers may be hormonally primed to rear the number of pups that they had in utero (Mendl 1988). Data on mean mother's mass (g) and litter size (number of pups) were  $\log_{10}(x + 1)$ -transformed to fit the assumptions of normal distribution (Kolmogorov–Smirnov test:  $P > 0.20$ ) and homogeneity of variances (Levene's test:  $P > 0.20$ ). In the case of pup survival, data were arcsine-square-root transformed. We examined the influence of nesting condition on mothers' mass loss throughout lactation using the GLM procedure, with nesting condition entered as a main fixed factor and litter size entered as a covariate.

To determine whether female relatedness interacts with nesting condition to influence pup growth and survival, we used data from singularly and communally breeding subjects. We ran the GLM procedure with breeding condition (singular versus communal breeding) and female relatedness (sisters versus unrelated females) as fixed main factors. As before, the mean mass of pups on days 1, 7, 15, 21, 27 and 31 was entered as a repeated measure, random factor; mass of mothers through lactation and litter size were entered as covariates. We also examined the potential joint effect of female relatedness and breeding condition on mothers' mass loss during lactation with the

GLM procedure, with female relatedness and nesting condition entered as main fixed factors and litter size entered as a covariate.

To examine whether the order in which litters were born within communal groups affected pup mass and survival, we used data from communally breeding subjects. We ran the GLM procedure with delivery order (first born versus second born) as a main fixed factor. We entered the mean mass attained by the pups on days 1, 7, 15, 21, 27 and 31 as a repeated measure, random factor, and the mean mass of mothers during lactation, the time elapsed between delivery of litters and litter size as covariates. The influence of delivery order on mothers' mass loss during lactation was examined with delivery order entered as a main fixed factor, and litter size entered as a covariate. Data on delivery time difference (in days) were  $\log_{10}(x + 1)$ -transformed to fit the assumptions of normal distribution and homogeneity of variances.

All statistical tests were two tailed. We followed Nakagawa & Foster (2004) in reporting the size of statistical effects and  $P$  values, instead of reporting post hoc (retrospective) power analysis. We report  $\eta^2$  values (i.e. instead of partial eta-squared) as estimates of size effects. Eta-squared values represent the percentage of variance accounted for by a variable (Levine & Hullett 2002). Data are presented as  $\bar{X} \pm \text{SE}$ .

## RESULTS

Seventy breeding female degus and their litters served as subjects (26 in 2003, 23 in 2004, 21 in 2005). Thirteen additional nonbreeding females were used to establish the singularly breeding condition. Mean litter size before pup adjustment ( $6.5 \pm 0.1$  pups) did not differ across nesting conditions ( $F_{2,54} = 1.39$ ,  $P = 0.2569$ ). The maximum extent of pregnancy, as estimated from the time of male introduction to the time of pup delivery, averaged  $101 \pm 1$  days. Dams weighed  $210.4 \pm 3.0$  g on day 1 of lactation, and lost  $10.1 \pm 1.4\%$  of their mass when observations ended on day 31. During experiments, pup mass averaged  $13.5 \pm 0.2$  g on day 1 and  $33.6 \pm 1.5$  g near weaning age on day 31. Overall, of the six pups present in each litter on day 1,  $5.2 \pm 0.2$  pups survived to day 31.

### Influence of Nesting Condition

The data set used to examine the effect of nesting condition on early postnatal investment in offspring included 31 female subjects breeding singularly, 13 females breeding singularly (in the presence of a nonbreeding female) and 13 females breeding communally (in the presence of a second breeding female). Communally breeding females always placed their young together in one nest. The GLM procedure revealed a statistically significant interaction between mothers' mass and day of lactation ( $F_{5,260} = 3.86$ ,  $P = 0.0021$ ,  $\eta^2 = 0.05$ ), where heavier mothers produced larger pups through day 27 ( $P < 0.05$ ), but less so after day 31 ( $t_{55} = 1.95$ ,  $P = 0.0570$ ). Litter size did not influence pup mass during lactation ( $F_{1,52} = 0.03$ ,  $P = 0.8611$ ,  $\eta^2 < 0.01$ ).

When considered separately, nesting condition also did not influence pup mass during lactation ( $F_{1,52} = 2.72$ ,  $P = 0.0755$ ,  $\eta^2 = 0.08$ ), but nesting condition significantly interacted with day of lactation ( $F_{5,260} = 5.58$ ,  $P < 0.0001$ ,  $\eta^2 = 0.16$ ; Fig. 1). However, the post hoc analysis showed no significant differences in pup mass between conditions for any day of lactation examined (unequal sample Tukey HSD test:  $P > 0.05$ ). Thus, the statistically significant interaction between mothers' mass and day of lactation was not influenced by nesting condition or pup age.

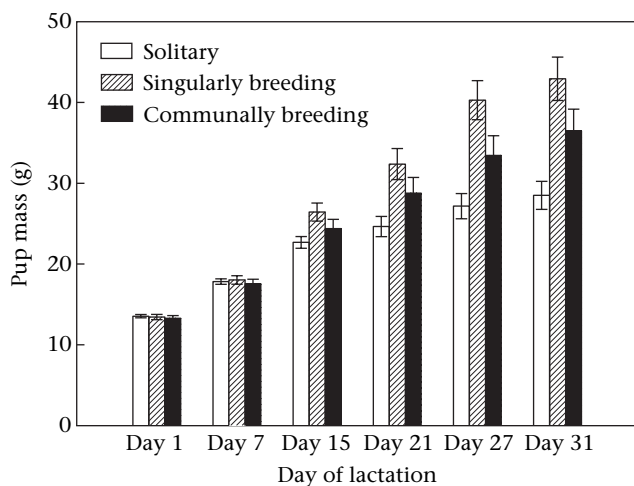
Nesting condition did not influence the number of pups surviving to day 31 ( $F_{2,52} = 2.18$ ,  $P = 0.1233$ ,  $\eta^2 = 0.07$ ; Fig. 2a). None of the covariates, namely litter size ( $F_{1,52} = 0.07$ ,  $P = 0.7891$ ,  $\eta^2 < 0.01$ ) and mean mass of mothers through lactation ( $F_{1,52} = 1.89$ ,  $P = 0.1753$ ,  $\eta^2 = 0.03$ ), affected pup survival.

All but three experimental degu mothers lost mass when observations ended. However, nesting condition did not influence mothers' mass loss from day 1 through to day 31 ( $F_{2,51} = 2.50$ ,  $P = 0.0920$ ,  $\eta^2 = 0.63$ ; Fig. 2b). Loss of mothers' mass was similarly unaffected by litter size ( $F_{1,52} = 0.08$ ,  $P = 0.7737$ ,  $\eta^2 = 0.01$ ) or mass of mothers on day 1 ( $F_{1,52} = 2.85$ ,  $P = 0.0975$ ,  $\eta^2 = 0.36$ ).

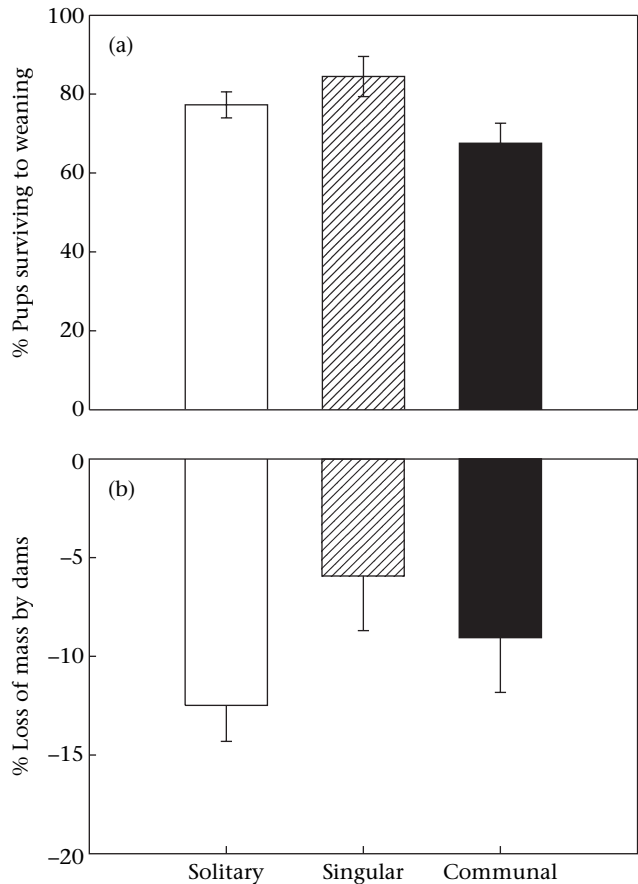
To summarize, nesting condition of female breeders had no effect on the growth and survival of pups. Likewise, nesting condition did not influence the physical condition of breeding females. Pup growth was affected only by the weight of their mothers, where heavier mothers produced heavier offspring.

### Influence of Female Relatedness

The data set used to examine the potential interaction between nesting condition and genetic relatedness among female subjects consisted of 13 singularly breeding and 13 communally breeding females. Six of the 13 singularly breeding females reared pups in the presence of a non-breeding sister and seven reared pups in the presence of an unrelated, nonbreeding female. In the case of



**Figure 1.** Mean  $\pm$  SE mass (g) of pups produced by solitary females and mothers of singularly and communally breeding groups during lactation.

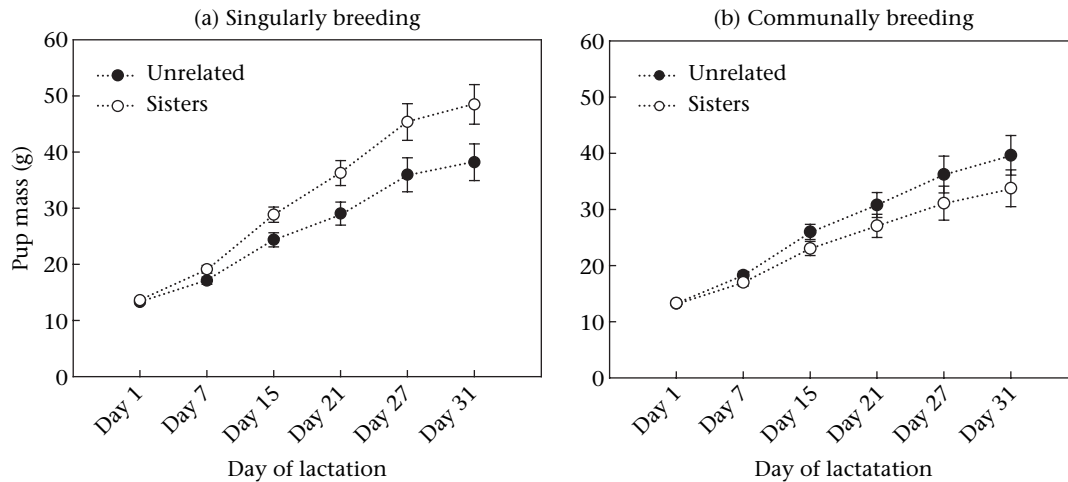


**Figure 2.** (a) Mean  $\pm$  SE percentage of pups surviving to day 31 of lactation (i.e. weaning age). (b) Mean  $\pm$  SE percentage body mass loss experienced by solitary females and mothers of singularly and communally breeding groups.

communally breeding degus, six focal females reared pups in the presence of a breeding sister and seven reared pups in the presence of an unrelated, breeding female.

Relatedness of breeding females did not influence pup mass during lactation ( $F_{1,20} = 0.46$ ,  $P = 0.5052$ ,  $\eta^2 = 0.01$ ), where mass of pups reared by females housed with a sister ( $28.1 \pm 1.2$  g) was similar to that of pups reared by females housed with an unrelated female ( $26.8 \pm 1.2$  g). A significant three-factor interaction involving female relatedness, nesting condition and day of lactation ( $F_{5,100} = 3.07$ ,  $P = 0.0127$ ,  $\eta^2 = 0.11$ ) indicated that pups of singularly breeding sisters were significantly larger than those of communally breeding sisters on days 27 and 31, but not on other days during lactation (Fig. 3). The influence of mother's mass through lactation on pup mass remained statistically significant, where larger females produced larger offspring ( $F_{1,20} = 4.67$ ,  $P = 0.0043$ ,  $\eta^2 = 0.15$ ). The effect of litter size was not statistically significant ( $F_{1,20} = 0.17$ ,  $P = 0.6819$ ,  $\eta^2 < 0.01$ ).

Relatedness of females did not influence the number of pups surviving to weaning age ( $F_{1,20} = 2.07$ ,  $P = 0.1657$ ,  $\eta^2 = 0.07$ ), meaning that the number of pups weaned by females housed with sisters ( $90.5 \pm 4.3\%$ ) and nonsisters ( $82.5 \pm 4.3\%$ ) was similar. None of the covariates, namely litter size ( $F_{1,20} = 1.68$ ,  $P = 0.2100$ ,  $\eta^2 = 0.06$ ) and mean



**Figure 3.** Mean  $\pm$  SE mass (g) of pups produced by mothers breeding in the presence of a nonbreeding sister or an unrelated female (a: singularly breeding) and in the presence of a breeding sister or an unrelated breeding female (b: communally breeding).

mass of mothers through lactation ( $F_{1,20} = 0.68$ ,  $P = 0.4188$ ,  $\eta^2 = 0.02$ ), influenced pup survival.

Loss of mass by mothers was similarly unaffected by female relatedness ( $F_{1,21} = 1.22$ ,  $P = 0.1637$ ,  $\eta^2 = 0.05$ ), implying that mass loss of sisters ( $10.1 \pm 3.0\%$ ) was similar to that of nonsisters ( $5.3 \pm 3.0\%$ ) from day 1 through to day 31. Mother's mass loss was not influenced by litter size ( $F_{1,20} = 0.01$ ,  $P = 0.9349$ ,  $\eta^2 < 0.01$ ).

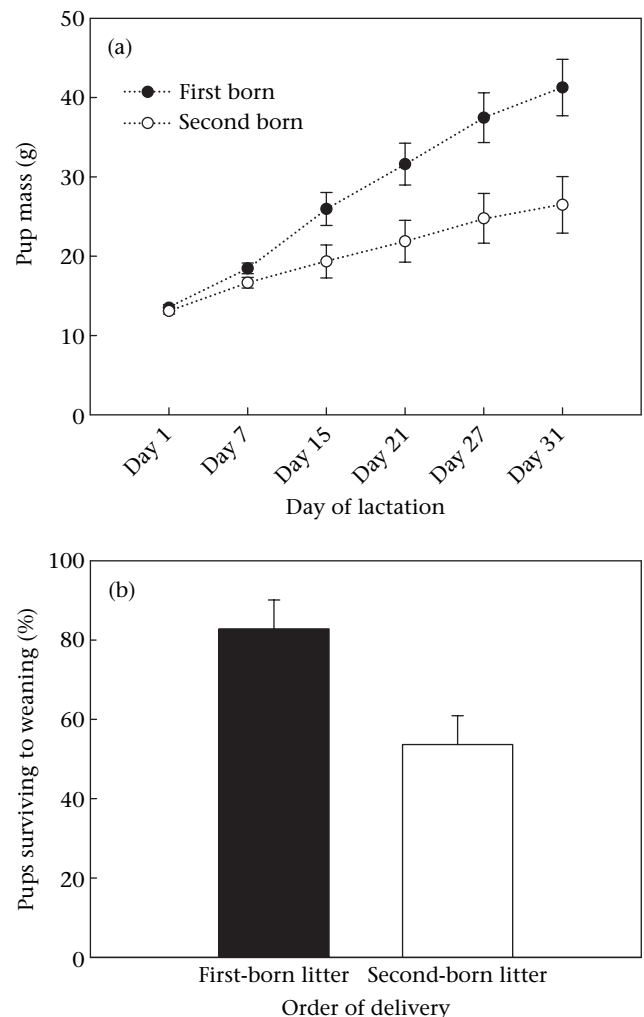
In short, pups reared by sisters and nonsisters showed similar growth and survival. In the case of mothers, the physical condition of lactating females nesting with a sister was not different from that of lactating females nesting with an unrelated female.

### Order of Pup Delivery

We used the 13 communally breeding degu pairs to examine whether breeding success of females varies with the order in which pups are born in communal litters. The mean time difference between delivery of both litters was  $6.5 \pm 1.1$  days (range 2–14 days).

We found a statistically significant effect of litters' delivery order on pup mass during lactation ( $F_{1,21} = 5.82$ ,  $P = 0.0251$ ,  $\eta^2 = 0.21$ ). The mean pup mass of first-born litters ( $28.0 \pm 1.9$  g) was 37% larger than that of second-born pups ( $20.4 \pm 1.9$  g). Although these differences tended to be greater near weaning age, because pup delivery interacted with day of lactation ( $F_{5,105} = 4.77$ ,  $P = 0.0006$ ,  $\eta^2 = 0.17$ ; Fig. 4a), post hoc analyses revealed no significant effect of delivery order within any day of lactation (unequal sample Tukey HSD test:  $P > 0.05$ ). Neither mother's mean mass through lactation ( $F_{1,21} = 0.02$ ,  $P = 0.8968$ ,  $\eta^2 < 0.01$ ), litter size ( $F_{1,21} = 0.59$ ,  $P = 0.4526$ ,  $\eta^2 = 0.02$ ), time elapsed between delivery of litters ( $F_{1,21} = 0.41$ ,  $P = 0.5290$ ,  $\eta^2 = 0.01$ ), nor any factor interaction was statistically significant ( $P > 0.67$ ).

Delivery order did influence the number of pups surviving to weaning age ( $F_{1,21} = 5.82$ ,  $P = 0.0251$ ,  $\eta^2 = 0.21$ ), meaning that females that produced litters



**Figure 4.** (a) Mean  $\pm$  SE mass of pups and (b) mean  $\pm$  SE percentage of pups surviving to day 31 of lactation that were produced by communally breeding females whose litters were born first or in the presence of a previous litter.

earlier than other females in their group weaned more pups ( $82.8 \pm 7.3\%$ ) than females that gave birth in the presence of a previous litter ( $53.6 \pm 7.3\%$ ; Fig. 4b). None of the covariates, namely litter size ( $F_{1,21} = 0.79$ ,  $P = 0.3852$ ,  $\eta^2 = 0.03$ ), time elapsed between litter delivery ( $F_{1,21} = 0.44$ ,  $P = 0.5162$ ,  $\eta^2 = 0.02$ ) and mean mass of mothers through lactation ( $F_{1,21} = 0.04$ ,  $P = 0.8411$ ,  $\eta^2 < 0.01$ ), influenced pup survival.

Loss of mass by mothers through lactation was unaffected by the order of litter delivery ( $F_{1,20} = 2.17$ ,  $P = 0.1560$ ,  $\eta^2 = 0.09$ ). Thus, mass loss of dams who delivered their pups earlier ( $5.5 \pm 2.5\%$ ) was similar to that of females that delivered their pups later ( $10.0 \pm 2.7\%$ ). Mothers' mass loss was unaffected by litter size ( $F_{1,20} = 2.11$ ,  $P = 0.1623$ ,  $\eta^2 = 0.09$ ) and by the time elapsed between delivery of litters ( $F_{1,20} = 0.11$ ,  $P = 0.7485$ ,  $\eta^2 < 0.01$ ).

Thus, pups of communal nests that were born earlier grew and survived better than pups that were born later.

## DISCUSSION

### Fitness Consequences to Communally Breeding Degus

Our results add to previous findings showing that communally breeding rodents do not attain short-term fitness benefits compared with solitarily breeding individuals (Wolff 1994; Pilastro et al. 1996; Gerlach & Bartmann 2002), but depart from some others that report such benefits (Manning et al. 1995; Hayes & Solomon 2004). When early parental investment was examined across all three social conditions, neither offspring quantity (number of pups weaned) nor quality (size of pups weaned) differed significantly between communally and solitarily breeding female degus. Similarly, communally breeding females did not attain a better physical condition than solitarily breeding females at the end of lactation.

Intriguingly, our findings did not vary with kinship of adults. Indirect benefits of communal breeding, where sisters cooperate to wean more and better-quality offspring as compared with nonsisters, were not detected in degus. Again, the physical condition of sisters was not different from that of unrelated females. These results depart from those of house mice, where females prefer to nest communally with close kin (Manning et al. 1992; Dobson et al. 2000), and where sisters behave less aggressively, establish communal litters more often, breed more, and wean more offspring than do nonsisters (König 1994; Dobson et al. 2000; Rusu & Krackow 2004). In contrast, our findings agree more with those reported for wood mice, where the numbers of pups weaned by communally nesting sisters and nonsisters are similar (Gerlach & Bartmann 2002). However, mother–daughter dyads of wood mice show higher reproductive success than do sister dyads. While we did not assess mother–daughter dyads, these associations may be less likely to occur in degus. Contrary to wood mice, degus typically breed once per year and most adults do not survive after their second year of age (Meserve et al. 1993, 1995; Ebensberger &

Hurtado 2005), suggesting that opportunities for the overlap of generations within communally breeding groups are limited.

When reproductive benefits to individuals within communally breeding groups were examined, we found that short-term costs and benefits of communal breeding are not shared equally among nestmates: females breeding later pay a greater cost in terms of weaning fewer and (probably) lower-quality offspring. Differential costs and benefits to communally breeding house and wood mouse females seem linked to the establishment of dominance relationships (Gerlach & Bartmann 2002; Rusu & Krackow 2004). In the case of degu females, mechanisms that might explain the seemingly high cost paid by younger litters may include increased pup competition over milk, differential attendance of pups by mothers, or enhanced dominance and aggression by early breeding dams (the examination of these alternatives will be reported elsewhere).

Nonbreeders may contribute to pup survival by decreasing episodes of passive cooling of pups or by enhancing grooming stimulation to the pups, both of which may enhance the growth of breeders' offspring (Dudley 1974; Bertino 1982; Hill 1983; Newkirk et al. 1998). Female degus that were lactating in the presence of a nonbreeding female did not produce significantly larger pups or end lactation in better physical condition than communally breeding or solitarily breeding females. Thus, contributions of nonbreeding degu females are predicted to have small, if any, effects on the short-term reproductive performance of breeders, a situation that characterizes some rodent species with alloparents (French 1994), but not others (Solomon 1991).

Collectively then, our results showing no apparent short-term benefits of communal breeding in degus further contribute to the available evidence on communally breeding rodents. We note, however, that further studies are needed to examine other potential benefits that female degus may accrue from rearing their litters communally (e.g. improved immunocompetence of young, or adoption of orphaned young). One additional benefit, namely protection of young from infanticide, does not apply to degus because nonparental infanticide is uncommon (Ebensberger 2001a).

### Adaptiveness of Communal Breeding: Short-term and Long-term Benefits

Examining the adaptive value of communal breeding requires that overall (long-term) fitness benefits accrued by communal breeders be greater than those of solitarily breeding individuals. Clearly, approaches that focus on short-term benefits of communal breeding (e.g. early growth and survival of litters) may underestimate benefits that are expressed later. For instance, postweaning survival of offspring may be higher at communal dens and this benefit may outweigh any costs in terms of loss of condition or lower pup body weight (e.g. Taber & Macdonald 1992; Hatchwell et al. 2004).

Regarding long-term consequences of communal breeding in rodents, evidence from three species (*Ctenomys sociabilis*, *Cynomys ludovicianus*, *Microtus arvalis*) suggests a net cost in terms of direct fitness to individuals breeding communally (Hoogland 1981, 1995; Boyce & Boyce 1988; Lacey 2004). Studies on two other species (*Peromyscus leucopus*, *Peromyscus maniculatus*) found neither net costs nor benefits in terms of per capita number of offspring produced (Wolff 1994). In *Microtus ochrogaster* and *Marmota flaviventris*, females in small groups (2–3 individuals) attain direct fitness benefits, but not so when in larger breeding groups (Armitage & Schwartz 2000; McGuire et al. 2002). In house mice, communally nesting females wean more total offspring (but not offspring of higher quality) than do solitarily nesting females (Manning et al. 1995).

Given that females of most plurally breeding species studied so far attain few reproductive benefits from breeding communally, why do female rodents nest together and rear their offspring communally? Three explanations seem pertinent. First, other, not yet examined benefits to communally breeding rodents exist (Hayes 2000). Second, nest site availability represents a constraint where individuals are forced to share a limited number of appropriate nest sites and burrows (Powell & Fried 1992; Ebensperger 2001b; Solomon 2003). Alternatively, communal breeding represents a nonadaptive by-product of communal nesting, where individuals benefit from communal nesting through decreased costs of thermoregulation, decreased costs of nest construction, or increased opportunities to mate (West & Dublin 1984; Ferkin & Seamon 1987; Ebensperger & Bozinovic 2000). Assignment of species to a particular hypothesis is difficult at present because the potential benefits and constraints have not been examined simultaneously for any species (Ebensperger 2001b).

Why do degus rear their litters communally? The answer must await further studies that examine long-term fitness benefits of communal breeding (i.e. including postweaning benefits). In addition, examinations of benefits linked to communal nesting are guaranteed. Captive degus have been shown to reduce their energetic expenditure by huddling with conspecifics (Canals et al. 1989), coordinate their digging activities and move more soil per capita than do solitary diggers (Ebensperger & Bozinovic 2000).

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