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ORIGINAL ARTICLE

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Sociality reduces individual direct fitness in a communally breeding rodent, the colonial tuco-tuco (*Ctenomys sociabilis*)

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Abstract In many social vertebrates, remaining in the natal group leads to at least short-term reductions in the direct fitness of philopatric animals. Among communally breeding rodents, the direct fitness costs of philopatry appear to increase as the frequency of successful natal dispersal decreases, suggesting a functional link between constraints on natal dispersal and the reproductive consequences of sociality. To explore this relationship empirically, I documented patterns of direct fitness among female colonial tuco-tucos (*Ctenomys sociabilis*), which are group-living subterranean rodents from southwestern Argentina. Demographic data suggest that successful natal dispersal is rare in this species, leading to the prediction that natal philopatry in *C. sociabilis* is associated with significant reductions in individual direct fitness. Using data obtained during 1996–2001, I compared the direct fitness of females that dispersed from their natal group and bred alone as yearlings to that of females that lived and bred in their natal group as yearlings. Philopatric yearlings reared significantly fewer young to weaning than did disperser (lone) yearlings. Although neither survival to a second breeding season nor the estimated lifetime number of pups reared to weaning differed between dispersal strategies, the annual direct fitness of group-living females was 23–40% less than expected, suggesting that philopatric animals experienced a substantial direct fitness cost by remaining in their natal group. These data yield important insights into the adaptive bases for group living in *C. sociabilis* and suggest that constraints on natal dispersal are an important factor favoring group living in this species.

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Introduction

Sociality (i.e., group living; Alexander 1974) is expected to occur when the fitness benefits of remaining in the natal group exceed those of dispersing and breeding elsewhere in the habitat (Koenig et al. 1992; Emlen 1995; Mumme 1997). In many vertebrate species, however, remaining in the natal group leads to at least short-term reductions in the direct fitness of philopatric animals (Stacey and Koenig 1990; Mumme 1997; Solomon and French 1997). Although indirect fitness benefits may help to compensate for these costs, ecological constraints on dispersal are thought to be the primary selective factors favoring natal philopatry in numerous vertebrates (Emlen 1982, 1991; Brown 1987; Koenig et al. 1992; Lacey and Sherman 1997). Specifically, ecological factors may decrease the probability of successful natal dispersal to the point that philopatry is favored despite the associated direct fitness costs (Emlen 1991). Reproductive skew theory predicts that, as the difficulty of successful natal dis-persal increases, individuals should be willing to accept greater decreases in direct fitness to remain in their natal group (Vehrencamp 1983; Keller and Reeve 1994; Clutton-Brock 1998). As a result, the magnitude of the direct fitness costs incurred by group-living individuals may reflect the intensity of the environmental pressures favoring natal philopatry and, hence, the formation of social groups.

Studies of the fitness consequences of sociality have tended to focus on high-skew, highly cooperative societies in which reproduction is restricted to only a few individuals per group and non-breeders help to rear the offspring of reproductive group mates (e.g., Woolfenden 1975; Rabenold 1984; Creel and Waser 1994; Clutton-Brock et al. 2001). Analyses of the reproductive consequences of group living in these species, however, may be confounded by the effects of alloparental care. Although natal philopatry and alloparental care co-occur in many species, they are distinct phenomena (Brown 1987; Emlen 1991; Lacey and Sherman 1997), suggesting that to understand fully the adaptive bases for the former, it must be separated from the latter. As a result, low-skew (i.e., plural breeding; Brown 1987) societies that are characterized by minimal intra-group cooperation may provide more tractable systems for testing hypotheses regarding the fitness consequences of natal philopatry and group living.

Due to their considerable behavioral and ecological diversity, communally breeding rodents offer numerous opportunities to explore the adaptive bases for philopatry and group living (Solomon and Getz 1997; Hayes 2000; Solomon 2003). More than a dozen species of rodents have been identified as communal breeders (Hayes 2000), meaning that most, or all, females in a group produce offspring. The reproductive consequences of group living in these animals are generally poorly known, but available data suggest marked interspecific variation in the direct fitness consequences of communal breeding. For example, in some species, the number of offspring reared to weaning does not differ between lone and group-living animals (e.g., *Peromyscus maniculatus* and *P. leucopus*, Wolff 1994; *Glis glis*, Marin and Pilastro 1994; Pilastro et al. 1994; *Marmota flaviventris*, Van Vuren and Armitage 1994), while in at least one species, the black-tailed prairie dog (*Cynomys ludovicianus*), the number of offspring reared declines significantly with group size (Hoogland 1995). Compared to black-tailed prairie dogs, natal philopatry tends to be less common and less enduring in those communally breeding species in which the number of offspring produced does not differ with group size (Armitage 1991; Marin and Pilastro 1994; Wolff 1994; Hoogland 1995), suggesting a causal relationship between the prevalence of natal philopatry, the direct fitness consequences of sociality, and the severity of constraints on natal dispersal.

To explore this apparent relationship empirically, I characterized the reproductive consequences of group living in the colonial tuco-tuco (*Ctenomys sociabilis*), a communally breeding species of subterranean rodent from southern Argentina. Burrow systems of colonial tuco-tucos are occupied by one to six adult females and, in some cases, a single adult male (Lacey et al. 1997; Lacey and Wieczorek 2004). Trapping records, mark-recapture data, and radiotelemetry studies of free-living *C. sociabilis* (Lacey et al. 1997) as well as observations of captive animals (Lacey, unpublished data) indicate that, within a group, all females reproduce and rear their young in a single, shared nest. Group members are not known to engage in specialized, cooperative interactions (e.g., alloparental care by non-breeders) and all adult burrow mates participate in shared activities such as tunnel excavation, nest construction, nest attendance, and predator detection (Lacey, unpublished data). Natal dispersal appears to be limited to a single, several-month period at the end of a female's juvenile summer; females do not disperse as adults and, hence, individuals remain members of the same social group throughout adulthood (Lacey and Wieczorek 2004). Long-term demographic studies of individually marked animals indicate that few female *C. sociabilis* succeed in dispersing from their natal group and establishing themselves as breeders elsewhere in the habitat (Lacey and Wieczorek 2004).

Based on these observations, I predict that, in *C. sociabilis,* the direct fitness of group-living females is less than that of females who live and breed alone. Specifically, the apparent restriction of female dispersal to a single, several-month period during an individual's lifetime, the relative permanence of social groupings, and the low rate of successful natal dispersal suggest that opportunities to live and breed outside of the natal burrow system are limited. As a result, individuals may be willing to accept a decrease in direct fitness in order to remain in their natal group. To test the prediction that group living is associated with reduced female direct fitness, I compare patterns of annual and lifetime reproductive success for lone versus group-living female *C. sociabilis*. These analyses provide critical information regarding the adaptive consequences of group living in this species. At the same time, comparisons between colonial tuco-tucos and other communally breeding societies of rodents yield new insights into relationships among direct fitness, dispersal constraints, and the diversity of vertebrate social systems.

Methods

Study site and natural history of the study population

The study population of *C. sociabilis* was located on Estancia Rincón Grande, Provincia Neuquén, Argentina (40°57′S, 71°03′W). The study site consisted of a ca. 20-ha area of open meadow dominated by seasonal grasses and sedges and containing several species of woody shrubs; a detailed description of the site is provided by Lacey and Wieczorek (2003). Behavioral and ecological studies of this population began in 1992; an intensive mark-recapture program aimed at characterizing the demography of this population commenced in 1996. Initially, field efforts focused on animals resident in a ca. 6-ha portion of the western edge of the site. In 1999, I expanded the area under study to ca. 10 ha, which encompassed all tuco-tuco burrows within a 1-km radius of the original 6-ha study area. This larger, 10-ha area was occupied by 15–25 social groups per year, with a mean (±1 SD) density of 4.0 (±2.7) adults per hectare (*n*=7 years).

C. sociabilis is almost exclusively subterranean; individuals emerge from their burrows only briefly to crop vegetation and, while at the surface, the animals rarely venture more than half a body length from an open burrow entrance. Members of the study population were captured when they emerged to forage. The animals were caught using hand-held nooses that had been placed around active burrow entrances (Lacey et al. 1997). Upon first capture, each animal was individually marked by injecting a magnetically coded bead (IMI-1000 Implantable Transponders, BioMedic Data Systems, Seaford, DE) beneath the skin at the nape of neck. Implanted beads were read using a hand-held scanner (DAS4004 Pocket Scanner, BioMedic Data Systems, Seaford, DE). The locations of all captures were recorded to the nearest meter using a geo-referenced grid established on the site in 1996.

Demographic monitoring

The demography of the study population is described in detail by Lacey and Wieczorek (2004). In brief, while some females disperse from their natal burrow system at the end of their juvenile season, others are philopatric and remain in their natal burrow as adults. All females are reproductive as yearlings. Philopatric yearlings typically share their natal burrow with one or more closely related females (e.g., mother, siblings). In contrast, females that disperse from their natal burrow live and breed alone (i.e., without other females) as yearlings, although these animals may share their burrow system with philopatric daughters in subsequent years.

To determine the dispersal histories of individuals in the study population, adults on the study site were captured each year in early to mid October, during the period when females were giving birth. Each individual caught was fitted with a $\leq$7-g radio collar (SM1-Mouse transmitter, AVM Instruments, Colfax, CA). Radiotelemetry was used to confirm social group composition; individuals that exhibited extensive spatial overlap ($\geq$66%) and that shared the same nest site were considered members of the same social group (Lacey et al. 1997). Adults were recaptured and juveniles were captured for the first time during November–December, as soon as young of the year first began foraging for themselves. The procedures used to ensure that all residents of a burrow system were captured are described by Lacey et al. (1997).

Quantifying female fitness

Female *C. sociabilis* produce a single litter of young per year. Within a group, all females typically become pregnant, give birth, and nurse young, as indicated by patterns of weight change as well as the presence of enlarged, milk-producing teats and, in cases of female mortality, the presence of fetuses or recent placental scars (Lacey et al. 1997). By capturing all residents of a burrow system when juveniles first began foraging on surface-growing vegetation (see above), I was able to determine the number of pups reared to weaning by each social group.

Female kin groups represent the core social and reproductive unit in the study population and variation in group size is primarily due to variation in the number of females that share a burrow system (Lacey et al. 1997; Lacey and Wieczorek 2004). As a result, analyses of the reproductive consequences of sociality focused on female direct fitness. For lone females and females in male–female pairs, annual direct fitness equaled the number of pups reared to weaning. Due to low levels of microsatellite variability among members of the study population (Lacey 2001), I was unable to determine the maternity of pups reared in burrow systems containing more than one adult female. Consequently, for multi-female groups, I divided the total number of pups weaned by the number of adult females in the group to yield a per capita estimate of annual female direct fitness. Per capita estimates of direct fitness reflect the mean number of pups weaned by female group mates and, hence, these data provide an appropriate measure for assessing the average effect of group living on the annual direct fitness of females. Estimates of lifetime direct fitness were generated by summing actual or per capita measures of annual direct fitness for females captured each year throughout their lifetime.

Quantifying female survival

Adult females do not disperse between breeding seasons and immigration of females into the study population is rare (<2% after the study site was expanded in 1999; Lacey and Wieczorek 2004) suggesting that emigration is also uncommon. As a result, I attributed the disappearance of adult females from one year to the next to mortality. Thus, annual survival was calculated as the proportion of adult females captured during a given breeding season that were still present in the following breeding season. Similarly, post-weaning juvenile survival was calculated as the proportion of pups captured in 1 year that were recaptured on the study site as adults in the following year. Because emigration is more common among males and because <50% of burrow systems contained an adult male during the portion of the year when data were collected (Lacey and Wieczorek 2004), I restricted analyses of post-weaning survival to data from juvenile females.

Data analysis

In some rodent species, litter size varies with maternal age (Sherman and Morton 1984; Keller 1985; Hoogland 1995; Malizia and Busch 1997). Female *C. sociabilis* that live alone (i.e., without other females) are typically yearlings that dispersed from their natal burrow system at the end of their juvenile season; in contrast, multi-female groups may contain up to four generations of breeding females (Lacey and Wieczorek 2004). The majority of known-age, group-living females (65.1±26.7%, *n*=65 females in 31 groups), however, were yearlings, suggesting that age-related differences in fecundity and survival were unlikely to have substantially altered the results of this study. Nevertheless, to minimize the potential effects of age differences among females, I restricted two-sample comparisons of the fitness and survival of lone versus group-living females to data from yearling animals.

Each lone female represents a unique series of dispersal, survival, and reproductive events and, hence, data from lone animals were clearly independent. In contrast, data from philopatric yearlings resident in the same social group during the same year were not independent. Consequently, the per capita number of pups reared to weaning by a group containing a philopatric yearling was used only once in analyses of female direct fitness, even if that group contained multiple yearlings. No two females for which data on lifetime reproductive success were available shared the same social history and thus data from these females were treated as independent. For analyses of annual survival, both the overall proportion of group-living yearlings that survived to a second breeding season and the per-group proportion of yearlings that survived to a second season were compared to survival rates for lone yearling females.

Parametric statistics were used for all analyses unless the distribution of data points indicated that non-parametric procedures were required. Analyses of covariance were performed using JMP 5.0 (SAS Institute 2002). G tests were completed using Statview 5.0.1 (SAS Institute 1998). With the exception of power analyses, all other statistical procedures were performed using Statistica 6.0 (StatSoft 2002). Power analyses were completed using G*Power (Erdfelder et al. 1996). Standard power analysis algorithms were not available for some of the non-parametric tests employed and, in general, the power of these tests is lower than that of parametric procedures (Siegel and Castellan 1988). Consequently, for primary conclusions based on non-significant non-parametric analyses, the associated data are presented as quantile plots (Sokal and Rohlf 1995) to allow direct, visual assessment of differences between lone and group-living females.

Results

Annual direct fitness of lone versus group-living females

Analyses of covariance revealed that, when data for lone females and multi-female groups were combined, the presence of an adult male had no significant effect on either the total number of pups reared to weaning (t_{40}=–0.66, *P*=0.50) or the per capita number of pups reared to weaning (t_{41}=–0.11, *P*=0.90) and thus I focused exclusively on the number of adult females per burrow system for the subsequent analyses of reproductive success. The total number of pups reared to weaning in-

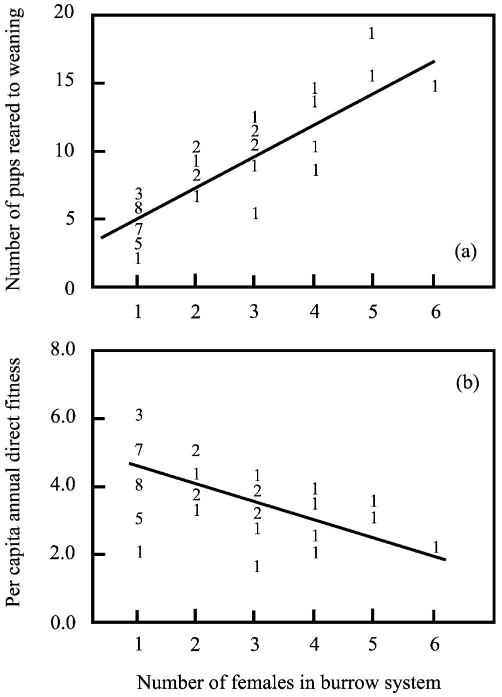

Fig. 1a, b Annual direct fitness of female *Ctenomys sociabilis* as a function of the number of adult females resident in a burrow system. In **a**, the total number of pups reared to weaning is indicated for 44 burrow systems from which all animals were captured at the time when juveniles first became active above ground. In **b**, the per capita number of pups reared to weaning is presented for the same 44 burrow systems. In both panels, the *numbers* shown represent the number of overlapping data points (i.e., same *x* and *y* values)

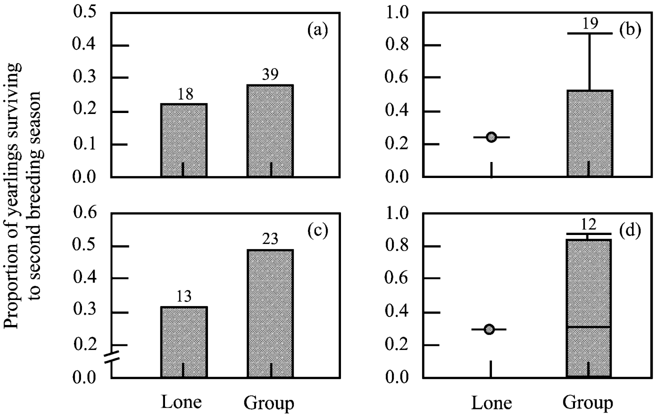

Fig. 2a–d Survival of yearling female *C. sociabilis* to a second breeding season. In **a**, the overall proportions of lone and group-living yearlings that survived to a second season are shown; data are from 1996–2001. Because survival by multiple yearlings in the same social group may not have been independent, a quantile plot of the per-burrow-system proportion of yearlings that survived during 1996–2001 is shown in **b**; data for lone females represent the same overall proportion of survivors depicted in **a**. In **c**, the overall proportion of lone and group-living females is shown, with data from the 1998 drought excluded. In **d**, a quantile plot of the per-burrow system proportion of yearlings that survived during this period (1998 excluded) is presented; data for lone females represent the same overall proportion of survivors depicted in **c**. For **a** and **c**, the *number shown above each bar* represents the number of females for which survival was monitored; for **b** and **d**, the *number above the quantile plot* represents the number of burrow systems for which survival of group-living yearlings was monitored

creased as a function of the number of adult females in a burrow system (r^2=0.792, $F_{1,42}$=164.42, P<0.001; Fig. 1a). In contrast, per capita direct fitness for females decreased as a function of the increasing number of adults in a burrow system (r^2=–0.247, $F_{1,42}$=15.12, P<0.001; Fig. 1b). When only data from yearlings were considered, the mean number of pups reared to weaning by lone females (4.3±1.2, n=19) was significantly greater than the mean per capita number of pups reared to weaning by group-living females (3.4±0.9, n=13) (t_{30}=3.21, two-tailed P=0.003).

As a post-hoc effort to explore the causality of the relationship between group size and per capita direct fitness (Creel and Waser 1994), I regressed the between-year change in per capita number of pups reared to weaning against the between-year change in group size (number of adult females) for each burrow system monitored during two successive field seasons (i.e., Granger causation; Johnston 1991). This analysis revealed a significant negative relationship (r^2=–0.376, $F_{1,10}$=6.03, P=0.03) between these variables, indicating that an increase in group size from one year to the next was associated with a concomitant decrease in per capita female direct fitness. Across all groups, the mean annual change in group size was not significantly different from zero (–0.2±1.8 individuals, n=20 groups, t_{19}=0.00, two-tailed P=1.00) and group size did not consistently increase or decrease across consecutive years (paired t_{19}=0.13, two-tailed P=0.90), as expected for a temporally stable population.

The observed decrease in per capita direct fitness for group-living females was not due to incomplete captures of larger groups. Repeated trapping of four multi-female groups at several-week intervals during 1996 failed to reveal any unmarked juveniles, indicating that all animals in these burrow systems had been captured at the time that juveniles first began foraging for themselves. Further, no unmarked females were captured in these burrows during the 1997 breeding season, providing no evidence that juveniles had evaded capture during the previous summer. Thus, although the total number of pups reared to weaning increased with group size, per capita annual direct fitness was greatest for lone females.

Survival of lone versus group-living yearlings

Survival of yearling females to a second breeding season was not significantly associated with having lived with a male (G=0.64, n=25, P=0.42) and, hence, males were not considered in the following analyses of annual female survival. The proportion of yearling females that survived from one breeding season to the next was greater for group-living animals than for lone individuals (Fig. 2a), although the association between living in a group and increased survival to a second breeding season was not significant (G=0.23, n=57, P=0.63; $1-\beta$=0.99). Because survival by multiple philopatric yearlings in the same social group may not represent independent events, I also examined survival of group-living yearlings on a per-burrow-system basis; the per-burrow-system proportion of group-living yearlings that survived to the next breeding season was not significantly different from the proportion of lone yearlings that survived to a second breeding season (Wilcoxon T=91.0, n=19, P=0.87; Fig. 2b).

The breeding season in 1998 was characterized by an extreme drought, which greatly affected survival by members of the study population, with the result that only four adult females were resident on the original, 6-ha study area in the spring of 1999. When data from 1998–1999 were excluded from analyses, neither the association between group living and yearling survival nor the difference in per-burrow-system survival by lone and group-living yearlings were statistically significant (G=1.01, n=36, P=0.31; $1-\beta$=0.54; Fig. 2c) (Wilcoxon T=33.0, n=12, P=0.64; Fig. 2d). Thus, despite apparently higher rates of survival for group-living animals, survival to a second breeding season did not differ between lone and group-living yearling females.

Only 7 (12.3%) of the 57 known yearling females monitored during this study survived to a third breeding season. All of these females reproduced as 3 year olds. Six (85.7%) of these seven females had been philopatric as yearlings. Although the small number of 3-year-old females detected precluded statistical analysis of the association between dispersal history and survival to a third breeding season, these data suggest that philopatric individuals are more likely than dispersers to survive to rear a third litter of young.

Lifetime direct fitness of dispersing versus philopatric females

As indicated above, females that dispersed from their natal group and bred alone as yearlings reared a significantly greater number of pups to weaning than did females that bred in their natal group as yearlings. Of the four lone yearlings that survived to the next breeding season (data from 1998 excluded), three (75%) shared their burrow system with at least one adult daughter after their yearling season. These data suggest that the primary difference in social setting between dispersing and philopatric females occurred during their yearling season.

Because adult males had no effect on the annual direct fitness of females, I did not partition data according to the presence of an adult male when quantifying the lifetime direct fitness for females. When data from all years were considered, the estimated mean lifetime number of pups reared to weaning did not differ between females that lived alone versus those that lived in groups during their yearling season (Mann-Whitney U=86.5, n=12,18, P=0.36; Fig. 3a). Similarly, there was no significant difference between the estimated mean lifetime number of pups reared to weaning when data from animals that died during 1998–1999 were excluded (Mann-Whitney U=23.5, n=7,7, P=0.90; Fig. 3b). These analyses suggest that despite the greater annual direct fitness of lone yearlings, the lifetime number of young reared to weaning did not differ as a result of a female's dispersal history.

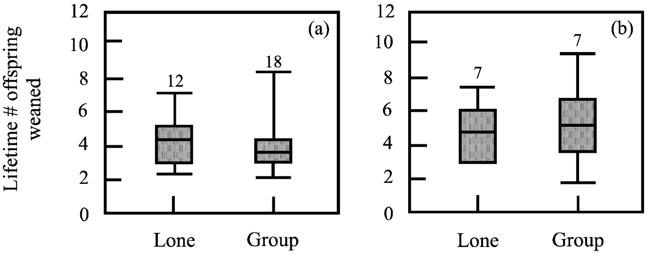

Fig. 3a, b Quantile plots of the estimated lifetime number of offspring weaned by female *C. sociabilis* that lived alone as yearlings versus those that lived in their natal group as yearlings. Data for all years (1996–2001) are shown in **a**. In **b**, data from females that died during the 1998 drought are excluded. In both panels, the *number above each quantile plot* represents the number of females for which lifetime reproductive success was determined

Production of yearling daughters by lone versus group-living females

Because groups of *C. sociabilis* form due to natal philopatry by females and because dispersal by juvenile females leads to the formation of new social units (Lacey and Wieczorek 2004), I also examined the number of yearling (reproductive) daughters produced by lone versus group-living females. The sex ratio of pups reared in multi-female groups (1.13 female:1 male; n=160 pups) was more female-biased than the sex ratio of pups reared by lone females (0.93 female:1 male; n=85 pups). Although neither sex ratio differed significantly from unity (lone: χ^2_1=0.11, P=0.74; group: χ^2_1=0.63, P=0.43), the more female-biased ratio for groups may help to explain why the mean number of daughters weaned per year by lone and group-living females did not differ (all years: Mann-Whitney U=124.0, n=22,14, P=0.34; 1998 excluded: Mann-Whitney U=66.5, n=17,9, P=0.93; Fig. 4a, b) despite the greater annual direct fitness of lone females (Fig. 1). The proportion of female pups reared to weaning that survived until their yearling season was greater for lone than for group-living females (Fig. 5a); this association between mother's social setting (lone versus group-living) and juvenile female survival was significant (data from 1998–1999 excluded; G=4.33, n=126, P=0.04). The failure to produce any surviving yearling daughters, however, was also significantly associated with the number of adult females in a burrow system (lone: 9 of 17=0.53; group: 1 of 9=0.11; G=4.21, n=25, P=0.04; Fig. 5b). Although all females in this sample were reproductive, a larger proportion of lone individuals reared no daughters, with the result that the mean per capita number of yearling daughters produced did not differ between lone and

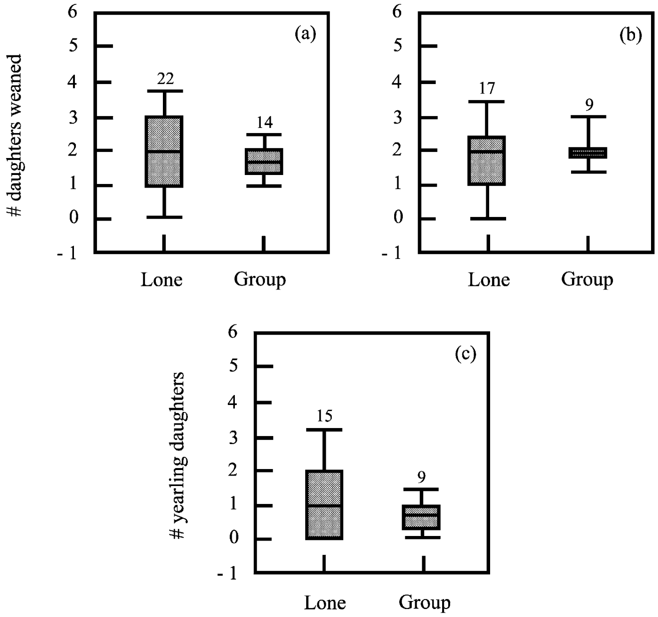

Fig. 4a–c Quantile plots of the number of daughters produced by lone versus group-living yearling female *C. sociabilis*. In **a**, the number of daughters reared to weaning is shown for yearling females resident in the study population during 1996–2001. In **b**, data from yearling females resident on the study site during the 1998 drought have been excluded. In **c**, the number of daughters that survived to yearling status is shown; data from the 1998 drought are excluded. In all panels, the *number above each quantile plot* represents the number of females for which the production of daughters was monitored

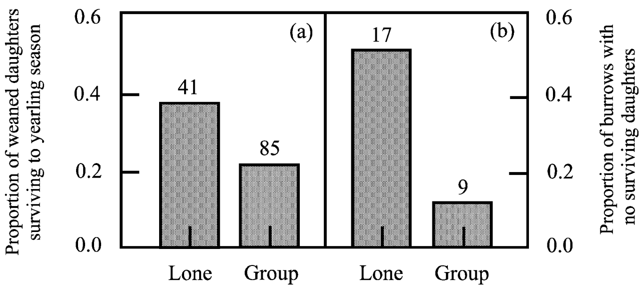

Fig. 5a, b Survival by weaned daughters of lone and group-living female *C. sociabilis*. In **a**, the proportion of female pups reared to weaning that survived to yearling status is shown. In **b**, the proportion of burrow systems that failed to produce any yearling daughters is shown. In **a**, the *number above each bar* represents the number of females for which offspring survival was monitored. In **b**, these values represent the number of burrow systems monitored

group-living females (Mann-Whitney U=67.5, n=15,9, P=1.00; Fig. 4c). Thus, although overall survival to yearling status was greater for the daughters of lone females, the higher failure rate (zero daughters reared) for lone females resulted in similar annual per capita numbers of yearling daughters for lone and group-living females.

Discussion

Direct fitness consequences of group living

The data presented here indicate that, on an annual basis, female colonial tuco-tucos incur a direct fitness cost by living and breeding in groups. As predicted, per capita annual direct fitness for lone females was greater than that for group-living females. Among yearling females, the number of pups reared to weaning was directly linked to dispersal history; lone females were typically yearling animals that had dispersed from their natal burrow (Lacey and Wieczorek 2004) and, hence, natal dispersal was associated with greater annual direct fitness among yearlings. This difference in direct fitness, however, did not appear to persist over the lifetimes of individual females. Although survival to a second breeding season did not differ significantly between lone and group-living yearlings, the greater probability of survival for philopatric animals appeared to offset the increased direct fitness for yearlings that had dispersed from their natal group, such that the estimated lifetime number of pups produced by females did not differ with dispersal history. Similarly, the per capita number of yearling daughters produced per year did not differ between lone and group-living females. Although survival to the yearling season was greater for the daughters of lone females, a greater proportion of lone females failed to produce any daughters, resulting in similar mean per capita numbers of yearling daughters reared per year by lone and group-living females.

The apparent absence of significant differences in the estimated lifetime number of pups reared to weaning and the number of yearling daughters produced per year suggests that direct fitness is similar for dispersing and philopatric female *C. sociabilis*. This statement, however, is somewhat misleading, as it masks the substantial decrease in direct fitness experienced by group-living females. On an annual basis, both the per capita number of pups weaned and the per capita number of yearling daughters produced by group-living females were considerably less than expected given values for the same measures of direct fitness for lone females. Compared to lone females, the per capita number of pups reared to weaning was, on average, 23% lower for group-living animals, which represents a loss of ca. one pup per female per year. The per capita number of daughters that survived to yearling status was, on average, 40% (ca. 0.4 daughters per year) lower for group-living females. Assuming that lone and group-living females do not differ with regard to fecundity, these data suggest that group-living animals generate fewer offspring than they are capable of producing, indicating that group living is associated with a marked reduction in the direct fitness of females.

Decreased direct fitness, competition, and reproductive skew

Negative relationships between group size and direct fitness are generally attributed to competition among conspecifics that live and breed together (Alexander 1974; Armitage and Schwartz 2000; Woodroffe and Macdonald 2000). This competition may be manifest in a number of ways, including greater density-dependent mortality of young (May and Anderson 1979; Brown and Brown 1996), infanticide within social groups (Vehrencamp 1977; Mumme et al. 1983; Hoogland 1985, 1995), and reproductive skew among adult group mates (Vehrencamp 1983; Keller and Reeve 1994; Clutton-Brock 1998). At present, it is not known what aspects of competition contribute to decreased direct fitness among group-living female *C. sociabilis*. Anecdotal observations indicate that respiratory and eye infections are more common among juveniles reared in multi-female burrow systems (Lacey, unpublished data), although the impact of these conditions on pup survival is unknown. Similarly, it is not known if adult female *C. sociabilis* commit infanticide; although adult females behave amicably toward pups in all contexts that can be monitored, the subterranean lifestyle of these animals prevents detailed observations of adult–infant interactions. To date, low levels of genetic variation within social groups (Lacey 2001) have precluded the assignment of individual young to specific females and, thus, it has not been possible to determine the degree of reproductive skew within groups of *C. sociabilis*. Future studies of these animals will address the effects of competition on reproductive success by exploring the mechanisms underlying decreased annual direct fitness among group-living females.

Adaptive bases for sociality in colonial tuco-tucos

Given that natal philopatry is associated with a significant reduction in direct fitness, why do some female *C. sociabilis* remain in their natal group? Philopatry may occur because ecological or other factors make successful dispersal so unlikely that the average fitness benefits of remaining in the natal group exceed those of dispersing, despite the reduction in direct fitness observed for philopatric females (Emlen 1991; Koenig et al. 1992). Dispersal is thought to be particularly difficult for subterranean rodents, since individuals adapted to life in underground burrows must often travel above-ground for considerable distances in order to reach new areas of habitat (Braude 2000; Busch et al. 2000). Overall, less than 30% of females weaned in the study population were recaptured as yearlings; combined with low rates of immigration, these data suggest that post-weaning mortality is high among juvenile females (Lacey and Wieczorek 2004). The analyses of direct fitness reported here included only females that survived to breed as yearlings. As a result, these data do not consider the proportion of dispersing versus philopatric females that failed to survive to their yearling season. Including non-survivors in calculations of lifetime direct fitness may substantially alter the average fitness returns for dispersing versus philopatric females, especially if rates of mortality differ markedly between dispersal options. If non-survivors are included in these analyses, I expect that the average lifetime direct fitness of dispersing females will be less than that of philopatric females, suggesting that natal philopatry occurs because remaining in the natal group and producing some offspring yields greater average fitness returns than dispersing and, most likely, failing to reproduce at all.

Implications for studies of vertebrate sociality

For some communally breeding rodents, the number of offspring reared to weaning does not appear to be affected by the number of adults that live together (e.g., Pilastro et al. 1994; Van Vuren and Armitage 1994; Wolff 1994). In these species, membership in the natal group may be relatively brief, with females sometimes switching from living in a group to living alone (or vice versa) between successive rounds of reproduction (Downhower and Armitage 1971; Armitage 1991; Marin and Pilastro 1994; Wolff 1994). In contrast, colonial tuco-tucos and black-tailed prairie dogs (*Cynomys ludovicianus*: Hoogland 1995) exhibit a negative relationship between group size and the number of young reared to weaning. Females in these species often remain in their natal group for life (Hoogland 1995; Lacey and Wieczorek 2004), suggesting that direct fitness costs to sociality are associated with reduced frequencies of natal dispersal. The number of offspring reared to weaning represents only one component of direct fitness (Clutton-Brock 1988) and, thus, additional data are needed to determine the full extent to which patterns of reproductive success vary with dispersal opportunities. Nevertheless, comparisons of communally breeding rodents suggest that the direct fitness consequences of group living are related to the frequency of dispersal from the natal group, providing a potentially important connection between fitness, philopatry, and the severity of constraints on natal dispersal.

In most vertebrates, the costs of natal dispersal are difficult to quantify due to the logistical challenges of following individuals after they leave the natal area (Koenig et al. 1996). Constraints on natal dispersal play a significant role in conceptual treatments of philopatry and group living (Emlen 1982, 1991; Brown 1987; Koenig et al. 1992) yet, for most social vertebrates, the severity of these constraints has not been quantified. If the relationship between natal dispersal and direct fitness suggested above is correct, then data on the direct fitness costs of group living may provide a convenient estimator of the extent to which dispersal is constrained. As the severity of these constraints increases, the proportion of individuals that successfully disperse and breed alone should decrease, eventually reaching the point at which successful dispersal is so rare that societies are considered “obligate” cooperative breeders (Courchamp et al. 1999). Because reproductive competition (e.g., skew) and cooperation among group mates should also increase as natal dispersal becomes more difficult (Sherman et al. 1995; Lacey and Sherman 1997), knowledge of the direct fitness consequences of group living may provide a functional link between the environmental pressures favoring philopatry and the degree of social elaboration that is likely to occur within different vertebrate societies.

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References

Alexander RD (1974) The evolution of social behavior. Annu Rev Ecol Syst 5:325–383

Armitage KB (1991) Social and population dynamics of yellow-bellied marmots: results from long-term research. Annu Rev Ecol Syst 22:379–407

Armitage KB, Schwartz OA (2000) Social enhancement of fitness in yellow-bellied marmots. Proc Natl Acad Sci USA 97:12149–12152

Braude SH (2000) Dispersal and new colony formation in wild naked mole-rats: evidence against inbreeding as the mating system. Behav Ecol 11:7–12

Brown CR, Brown MB (1996) Coloniality in the cliff swallow: the effect of group size on social behavior. University of Chicago Press, Chicago

Brown JL (1987) Helping and communal breeding in birds. Princeton University Press, Princeton

Busch C, Antinuchi CD, del Valle JC, Kittlein MJ, Malizia AI, Vassallo AI, Zenuto RR (2000) Population ecology of subterranean rodents. In: Lacey EA, Patton JL, Cameron GN (eds) Life underground: the biology of subterranean rodents. University of Chicago Press, Chicago, pp 182–226

Clutton-Brock TH (ed) (1988) Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago

Clutton-Brock TH (1998) Reproductive skew, concessions, and limited control. Trends Ecol Evol 13:288–292

Clutton-Brock TH, Russell AF, Sharpe LL, Brotherton PNM, McIlrath GM, White S, Cameron EZ (2001) Effects of helpers on juvenile development and survival in meerkats. Science 293:2446–2449

Courchamp F, Grenfell B, Clutton-Brock T (1999) Population dynamics of obligate cooperative breeders. Proc R Soc Lond B 266:557–563

Creel SR, Waser PM (1994) Inclusive fitness and reproductive strategies in dwarf mongooses. Behav Ecol 5:339–348

Downhower JF, Armitage KB (1971) The yellow-bellied marmot and the evolution of polygamy. Am Nat 105:355–370

Emlen ST (1982) The evolution of helping. I. An ecological constraints model. Am Nat 119:29–39

Emlen ST (1991) Evolution of cooperative breeding in birds and mammals. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach, 3rd edn. Blackwell, Oxford, pp 301–337

Emlen ST (1995) An evolutionary theory of the family. Proc Natl Acad Sci USA 92:8092–8099

Erdfelder E, Faul F, Buchner A (1996) GPOWER: a general power analysis program. Behav Res Methods Instrum Comput 28:1–11

Hayes LD (2000) To nest communally or not to nest communally: a review of rodent communal nesting and nursing. Anim Behav 59:1–12

Hoogland JL (1985) Infanticide in prairie dogs: lactating females kill offspring of close kin. Science 230:1037–1040

Hoogland JL (1995) The black-tailed prairie dog: social life of a burrowing mammal. University of Chicago Press, Chicago

Johnston J (1991) Econometric methods. McGraw-Hill, New York

Keller B (1985) Reproductive patterns. In: Tamarin RH (ed) Biology of New World *Microtus*. Spec Publ 8 American Society of Mammalogists, pp 725–768

Keller L, Reeve HK (1994) Partitioning of reproduction in animal societies. Trends Ecol Evol 9:98–102.

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

Koenig WD, Van Vuren D, Hooge PN (1996) Detectability, philopatry, and the distribution of dispersal distances in vertebrates. Trends Ecol Evol 11:514–517

Lacey EA (2001) Microsatellite variation in solitary and social tuco-tucos: molecular properties and population dynamics. Heredity 86:628–637

Lacey EA, Sherman PW (1997) Cooperative breeding in naked mole-rats: implications for vertebrate and invertebrate sociality. In: Solomon NG, French JA (eds) Cooperative breeding in mammals. Cambridge University Press, Cambridge,pp 267–301

Lacey EA, Wieczorek JR (2003) The ecology of sociality in rodents: a ctenomyid perspective. J Mammal 84:1198–1211

Lacey EA, Wieczorek JR (2004) Kinship in colonial tuco-tucos: evidence from group composition and population structure. Behav Ecol (in press)

Lacey EA, Braude SH, Wieczorek JR (1997) Burrow sharing by colonial tuco-tucos (*Ctenomys sociabilis*). J Mammal 78:556–562

Malizia A, Busch C (1997) Breeding biology of the fossorial rodent *Ctenomys talarum* (Rodentia: Octodontidae). J Zool 242:463–471

Marin G, Pilastro A (1994) Communally breeding doormice, *Glis glis*, are close kin. Anim Behav 47:1485–1487

May RM, Anderson RM (1979) Population biology of infectious diseases. Part 2. Nature 280:455–461

Mumme RL (1997) A bird's eye view of mammalian cooperative breeding. In: Solomon NG, French JA (eds) Cooperative breeding in mammals. Cambridge University Press, Cambridge, pp 364–388

Mumme RL, Koenig WD, Pitelka FA (1983) Reproductive competition in the communal acorn woodpecker: sisters destroy each other's eggs. Nature 306:583–584

Pilastro A, Gomiero T, Marin G (1994) Factors affecting body mass of young fat dormice (*Glis glis*) at weaning and by hibernation. J Zool (Lond) 234:13–23

Rabenold KN (1984) Cooperative enhancement of reproductive success in tropical wren societies. Ecology 65:871–885

SAS Institute (1998) Statview 5.0.1. SAS Institute, Cary NC

SAS Institute (2002) JMP 5.0. SAS Institute, Cary NC

Sherman PW, Morton ML (1984) Demography of Belding's ground squirrels. Ecology 65:1617–1628

Sherman PW, Lacey EA, Reeve HK, Keller L (1995) The eusociality continuum. Behav Ecol 6:102–108

Siegel S, Castellan NJ (1988) Nonparametric statistics for the behavioral sciences, 2nd edn. McGraw-Hill, New York

Sokal RR, Rohlf FJ (1995) Biometry, 3rd edn. WH Freeman, New York

Solomon NG (2003) A reexamination of factors that influence natal philopatry in rodents. J Mammal 84:1182–1197

Solomon NG, French JA (1997) The study of mammalian cooperative breeding. In: Solomon NG, French JA (eds) Cooperative breeding in mammals. Cambridge University Press, Cambridge, pp 1–10

Solomon NG, Getz LL (1997) Examination of alternative hypotheses for cooperative breeding in rodents. In: Solomon NG, French JA (eds) Cooperative breeding in mammals. Cambridge University Press, Cambridge, pp 199–230

Stacey PB, Koenig WD (1990) Introduction. In: Stacey PB, Koenig WD (eds) Cooperative breeding in birds: long-term studies of ecology and behavior. Cambridge University Press, Cambridge, pp ix-xviii

StatSoft (2002) Statistica 6.0. StatSoft,Tulsa, OK

Van Vuren D, Armitage KB (1994) Reproductive success of colonial and non-colonial female yellow-bellied marmots (*Marmota flaviventris*). J Mammal 75:950–955

Vehrencamp SL (1977) Relative fecundity and parental effort in communally nesting anis, *Crotophaga sucirostris*. Science 197: 403–405

Vehrencamp SL (1983) A model for the evolution of despotic versus egalitarian societies. Anim Behav 31:667–682

Wolff JO (1994) Reproductive success of solitarily and communally nesting white-footed mice and deer mice. Behav Ecol 5:206–209

Woodroffe R, Macdonald DW (2000) Helpers provide no detectable benefits in the European badger (*Meles meles*). J Zool (Lond) 250:113–119

Woolfenden GE (1975) Florida scrub jay helpers at the nest. Auk 92:1–15