

Kinship in colonial tuco-tucos: evidence from group composition and population structure

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Kinship plays a significant role in shaping the social and genetic structures of many vertebrate populations. Evidence of kinship, however, may be substantially influenced by the spatial and temporal scales over which co-ancestry is monitored. For example, while data on social group composition may yield little indication of relatedness among reproductive partners, data on the demographic structure of a population may reveal considerable shared ancestry among mates. We explored relationships among social group composition, individual movements, and population-level patterns of kinship using data from a 7-year field study of the colonial tuco-tuco (*Ctenomys sociabilis*), a group-living subterranean rodent that is endemic to southwestern Argentina. Our analyses indicate that social groups are composed of 1–4 generations of closely related females and a single, immigrant male, suggesting that reproductive partners are not related to one another. Monitoring individual movements, however, revealed that (1) most male dispersal occurs within the local population and (2) most new social groups are founded by females born in the study population, indicating that individuals reared in different burrow systems may share considerable co-ancestry. Simulation analyses revealed that up to 67% of reproductive partnerships consist of animals that share co-ancestry within the last 5–7 generations. Thus, while analyses of social group composition provide little evidence of kinship among reproductive partners, population-level analyses of dispersal and group formation suggest that co-ancestry among mates is common. These findings have important implications for interpreting social interactions and genetic structure in this species. *Key words:* *Ctenomys*, dispersal, kinship, philopatry, sociality, tuco-tucos. [*Behav Ecol* 15:988–996 (2004)]

Kinship plays a significant role in shaping social and reproductive interactions in vertebrates. For example, kinship is thought to underlie the evolution of apparently altruistic interactions in which individuals accrue indirect fitness benefits by enhancing the reproductive success of relatives (Hamilton, 1964; Michod, 1982; West-Eberhard, 1975; but see Clutton-Brock, 2002). Kinship may also influence patterns of individual movement and mate choice (Le Galliard et al., 2003; Petrie et al., 1999; Ryan and Lacy, 2003). In particular, sex-biased natal dispersal is often interpreted as a mechanism for inbreeding avoidance because it results in the spatial segregation of closely related (e.g., sibling) males and females (Bengtsen, 1978; Gundersen and Andreassen, 1998; Kerth et al., 2002a; Packer, 1985; Pusey, 1987).

Through its effects on social, reproductive, and dispersal behavior, kinship is expected to influence the genetic structure of a population. The stronger the tendency for close kin to aggregate and to remain reproductively isolated, the greater the genetic substructure (i.e., spatial segregation of alleles that are identical by descent) that should be evident within a population (Dobson, 1998; Sugg et al., 1996). Thus, the genetic structure of a population is expected to reflect its kin structure, particularly in highly social species in which spatial relationships are often strongly delineated by patterns of kinship (Dobson et al., 1998; Faulkes et al., 1997; Pope, 1998; Richardson et al., 2002; Spong et al., 2002). As a result, knowledge of a population's kin structure not only provides an essential framework for interpreting social interactions among individuals, but it also yields critical, predictive insights into patterns of genetic variation among conspecifics.

Interpretations of kin structure may be substantially influenced by the spatial and temporal scales over which co-ancestry is monitored. For example, while data collected over relatively small scales (e.g., annual changes in social group composition) may provide evidence of inbreeding avoidance via sex-biased natal dispersal (Dobson et al., 1998; Getz and Carter, 1998; Kerth et al., 2002b; McNutt, 1996; Zahavi, 1990), data obtained from larger spatial and temporal samples (e.g., all members of the study population monitored across multiple generations) may indicate considerable shared ancestry among reproductive partners (Gibbs and Grant, 1989; Hoogland, 1995; Van Noordwijk and Scharloo, 1981). Although numerous behavioral studies have documented kinship within social groups, fewer have examined patterns of kinship at the population level (but see Baglione et al., 2003; Creel and Creel, 2002; Spong and Creel, 2004). Both perspectives are important and both are required to understand relationships between individual-level patterns of behavior and population-level patterns of genetic variation.

Studies of colonial tuco-tucos (*Ctenomys sociabilis*) provide an ideal opportunity to explore the behavioral and genetic correlates of kinship across multiple spatial and temporal scales. These small, subterranean rodents are endemic to Neuquén Province, Argentina, where they occur in patches of wet meadow known as “mallines” (Lacey and Wieczorek, 2003; Pearson and Christie, 1985). Unlike other members of the genus *Ctenomys* studied to date, the colonial tuco-tuco is social; burrow systems of this species are routinely inhabited by multiple adult females and, in some cases, a single adult male, all of whom share a single, communal nest (Lacey et al., 1997). Studies of other group-living subterranean rodents indicate that kinship plays an important role in shaping social interactions among conspecifics (Bennett and Faulkes, 2000; Reeve, 1992; Reeve and Sherman, 1991). This finding, combined with extensive literature on the population genetics of some subterranean species (Patton and Smith, 1990;

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Steinberg and Patton, 2000), suggests that colonial tuco-tucos are particularly appropriate subjects for studies aimed at characterizing interactions between kinship, social behavior, and genetic structure.

Based on field observations of burrow occupancy and nest sharing (Lacey et al., 1997), we predict that the primary social unit in *C. sociabilis* consists of a group of closely related females and a single, apparently unrelated adult male. The formation of female kin groups is common among mammals (Dunbar, 1986; Michener, 1983; Packer, 1986; Rubenstein, 1986), lending credence to the hypothesis that, in *C. sociabilis*, female burrow mates are close kin. At the population level, however, both sexes may be related to each other within the span of a relatively limited number of generations. Habitats occupied by *C. sociabilis* are patchily distributed (Lacey and Wiczorek, 2003; Lacey EA, personal observation), suggesting that migration between populations is difficult. As a result, most dispersal is expected to occur within the local population, leading to an increased probability that reproductive partners will be descended from a recent common ancestor.

To test these predictions, we use dispersal records and spatial relationships among individuals to infer patterns of kinship within a free-living population of *C. sociabilis*. Specifically, we combine field data on dispersal and social group composition with simulation analyses of individual movements to characterize kinship among social and reproductive partners. These analyses provide the first characterization of the demography of *C. sociabilis*; as a result, they represent the first detailed investigation of kinship in a non-bathyergid species of social, subterranean rodent, as well as one of the first quantitative field studies of dispersal and kin structure in ctenomyid rodents. The resulting data are essential to understanding the social system of *C. sociabilis* and yield important insights into the effects of spatio-temporal scale on interpretations of kinship, social behavior, and genetic structure in natural populations of vertebrates.

METHODS

Study site and study animals

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 ~20 ha area of open meadow dominated by seasonal grasses and sedges; a detailed description of the site is provided by Lacey and Wiczorek (2003). An intensive mark-recapture program was initiated in 1996 to characterize the demography of this population. From 1996–1999, demographic monitoring focused on animals resident in a ~6 ha area on the western edge of the site. In 1999, the area under study was expanded to ~10 ha to include all burrow systems located with a 1-km radius of the original 6-ha site. This larger site was occupied by 13–25 social groups per year, with a mean (± 1 SD) density of 4.0 ± 2.7 adults per ha ($n = 7$ years).

C. sociabilis is almost exclusively subterranean. Individuals emerge from their burrows only briefly to forage 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 by placing a soft elastic noose around the perimeter of an active burrow entrance (Lacey et al., 1997). When an animal emerged to forage, the noose was pulled tight, preventing the animal from retreating back into its burrow. Captured animals were immediately retrieved and transferred to cloth handling bags. Upon first capture, all animals were individually and permanently marked by injecting a magnetically coded bead (IMI-1000 Implantable Transponders, BioMedic Data Systems, Inc.) beneath the skin

at the nape of the neck. Implanted beads were read using a hand-held scanner (DAS 4004 Pocket Scanner, BioMedic Data Systems, Inc.). The locations of all captures were recorded to the nearest meter using a geo-referenced grid established on the study site in 1996.

A total of 683 individuals representing 105 social units were captured 1062 times during this study. During 1996–1998, all animals in 23 social units were captured. Following the expansion of the study site at the start of the 1999 field season, all animals in 51 social units were captured. All adults (but not all juveniles) were captured in an additional 13 social units; for these social units, we used the significant linear relationship between number of adult females per burrow system and number of pups reared to weaning (Lacey, in press) to estimate the number of juveniles that evaded capture. For the remaining 18 social units (neither all adults nor all juveniles captured), we used daily field notes to assess the probable number of uncaught animals. Patterns of activity for adults and juveniles differ markedly and, in many cases, uncaught individuals were observed foraging, allowing us to ascertain the age, sex (for adults), and approximate number of the individual(s) remaining in a burrow system. Based on these data, we estimate that 14 adults and 104 juveniles remained uncaught during 1996–2002. This represents 14.7% of the estimated total number of animals ($n = 801$) present on the site during these years.

Demographic monitoring

To characterize the kin structure of *C. sociabilis*, we monitored spatial relationships among and patterns of dispersal by members of our study population. During 1996–2000, adults in the study population were captured between early and mid October, shortly after females gave birth to their single litter of young per year. Each animal was fitted with a ≤ 7 g radio collar (SM-1 Mouse transmitter, AVM Instruments, Inc.), after which the locations of collared adults were monitored several times per day as described by Lacey et al. (1997). Individuals that exhibited extensive spatial overlap ($\geq 66\%$ of area of activity; Lacey et al., 1997) and that shared the same nest site were identified as members of the same social group. Adults were recaptured and juveniles were captured for the first time during November–December, as soon as young of the year began foraging above ground (age: 4–5 weeks). Radio collars were removed from adults at the time of recapture. The procedures used to ensure that all residents in a burrow system were caught are described in Lacey et al. (1997).

During 2001–2002, temporal constraints on fieldwork limited trapping to the period when young of the year first became active above ground (November–December). In these years, adults were typically caught only once per field season, at the time when juveniles were first captured and marked. Due to the limited opportunity to recapture adults, use of radio collars was restricted to only a single individual per burrow system. Telemetry data from 1996–2000 indicated that (1) each adult used all portions of the burrow system in which it was resident and (2) the spatial distributions of individuals from different burrow systems never overlapped. Consequently, during 2001–2002, telemetric monitoring of a single adult was used to determine the spatial limits of each burrow system, after which the capture localities of individuals were used to assign social group membership.

Because juveniles were caught before weaning was complete, we were able to determine the natal burrow system for each pup captured on the study site. Individuals that were later recaptured as adults (after the start of their first breeding season, age: ~9 months) were determined to have dispersed if the burrow system occupied at the time of recapture did not

overlap spatially with the natal burrow system. Conversely, individuals were considered philopatric if the burrow system occupied as an adult overlapped at least partially with the natal burrow system. For animals captured as adults during two or more field seasons, dispersal between field seasons was said to have occurred if the burrow systems occupied in consecutive years did not overlap spatially with one another. Because burrow systems are spatially discrete entities that (1) are often separated by tens to hundreds of meters and (2) tend to have roughly the same boundaries across multiple years, the criterion of spatial overlap provided an unambiguous means of determining patterns of movement by members of the study population.

Data analysis

The number of adults per burrow system varied from 1–6 (Lacey et al., 1997; Figure 1). Hence, we use the term “social unit” to describe the set of animals—adults and juveniles—that were resident in a single burrow system during a given field season. To date, low levels of microsatellite variability among members of the study population (Lacey, 2001) have precluded genetic analyses of paternity and, hence, kin relationships among individuals were monitored primarily via maternal ancestry. We defined a matriline as all social units whose female members were linearly descended from the same ancestral social unit. For statistical analyses, parametric tests were used unless the distribution of data points indicated that nonparametric procedures were required. Associations between sex and demographic parameters were examined using Fisher’s Exact test. Statistical analyses were performed using Statistica 5.1. Means are reported ± 1 SD.

Simulation analyses

To determine how observed patterns of dispersal and social group composition influence kin structure at the population level, we simulated the effects of individual movement and social unit survival on population-level patterns of co-ancestry, with emphasis on the degree of kinship among reproductive partners. For these analyses, we assumed that the male resident in a burrow system was the sire of the pups reared in that system in that year. We also assumed that dispersal within the study population was random with respect to the location of an individual’s natal burrow system and, hence, models of individual movements were not spatially explicit. Simulation analyses were performed as follows.

Effects of matriline dynamics on kinship among social units

We used observed patterns of matriline formation and extinction to assess the typical degree of relatedness among social units in the study population. To begin, we assumed no relatedness among the 18 social units (observed mean number of social units per year) in our simulated population. For each generation (year), we randomly selected a subset of six of these 18 burrow systems (mean annual rate of social unit extinction) that would be unoccupied at the start of the spring breeding season. We then assigned five dispersing females (mean number of marked dispersers per year) to these unoccupied (destination) burrows. The natal (source) social unit for each dispersing female was determined randomly by assigning that individual to one of the 17 other (i.e., non-destination) burrow systems occupied during the previous breeding season. By definition, a dispersing animal could not move to its natal social unit and, hence, the number of source burrows for each disperser was one less than the total number of occupied burrow systems in the population. Because natal dispersal typically occurred prior to

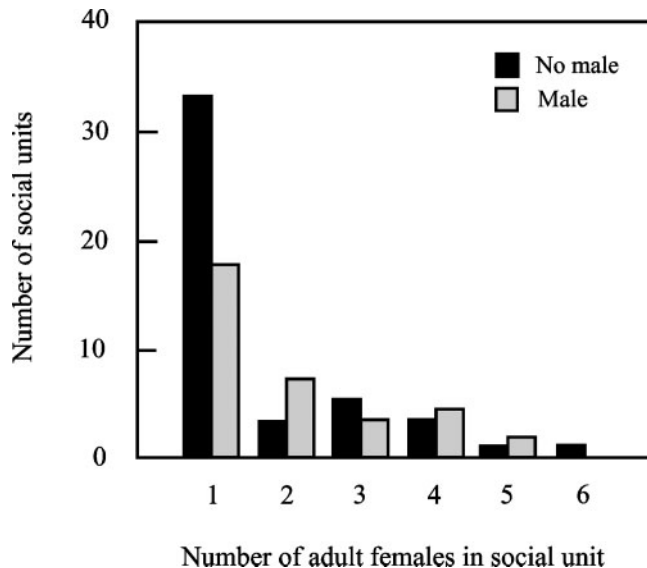


Figure 1

Histogram of the number of adult females per social unit. Data are from 87 social units captured during 1996–2002. All adults in each social unit were captured during the period between the birth and weaning of young. The number of social units of each size that contained an adult male is indicated.

the overwinter extinction of social units, the social units present during the previous breeding season were used as the sources for dispersers. A kinship link between the source and the destination of each dispersing female was recorded; this link was generation-specific, allowing us to identify the most recent connection between burrow systems. Finally, an immigrant female (no kinship to other members of the simulated population) was assigned to the sixth empty burrow system; this represents the observed annual rate of female immigration and associated introduction of new matriline to the study population.

Initially, this series of steps was repeated 1000 times. This analysis indicated that, at most, 14 years were required for the number of matriline in the simulated population to reach a temporally stable value. The simulation was then run for 1014 years; data from the last 1000 years were used to calculate (1) the mean number of matriline present on the study site during each breeding season and (2) the mean minimum number of generations separating different social units belonging to the same matriline.

Effects of male dispersal on kinship among reproductive partners

Dispersal by males represents the primary mechanism by which genetic material is exchanged among social units and matriline. To examine the effects of male dispersal on kinship within the study population, we incorporated patterns of male dispersal and survival into the simulation of matriline dynamics described above. At the start of each generation (year), five males (mean number of marked dispersers per year) were randomly assigned to social units in the study population. The natal (source) social unit for each dispersing male was determined using the same procedure outlined above for females. A generation-specific kinship link was recorded between the source and destination of each male. Males in the study population typically breed for only a single season (see Results). As a result, all burrow systems not receiving an intra-population disperser were assigned an immigrant male having no genetic relationship to members of

Table 1
Sex-specific rates of immigration in colonial tuco-tucos from 1996–2002

Sex	All years		1999–2002	
	Males	Females	Males	Females
No. of immigrants	23	56	10	3
Total no. of adults captured	53	361	26	192
% Immigrants	43.4	15.5	38.5	1.6

Individuals that were first captured as unmarked adults were classified as immigrants. After expansion of the study site in 1999, all active burrow systems on the 10-ha study site were monitored; for this reason, data from 1999–2002 are presented separately.

the study population; because some instances of intra-population dispersal may have gone undetected due to male mortality prior to capture, this procedure should be conservative with respect to estimates of kinship among male and female burrow mates. For all social units, the male's heritage was compared to that of the female(s) in the destination social unit. The most recent kinship link between these animals was identified and the number of generations since the occurrence of the common ancestor (if any) was calculated. The heritage of the male was then combined with that of the female(s) and, for all social units that did not go extinct prior to the next breeding season (see female simulation above), this combined legacy was carried into the next generation.

Preliminary analyses revealed that reproductive partners were separated by a maximum of ~30 generations, and, hence, the simulation was run for 1030 years to insure that all instances of co-ancestry among reproductive partners were detected; only data from the last 1000 generations were used to estimate relatedness between reproductive partners. Initially, the simulation was run using the parameters specified above, which reflect observed rates of intra-population dispersal by males. Not all social units still contained a male during the portion of the year when animals were captured; as a result, this analysis likely underestimates the actual frequency of intra-population dispersal by males and the degree of co-ancestry among reproductive partners. Consequently, we used the sum of the observed number of dispersers and the estimated number of "missing" males that had been intra-population dispersers to determine the total number of males dispersing within the population each year (T). This value was calculated using the following formula:

$$T = D + M \left(\frac{D}{D + I} \right)$$

where D = the observed mean number of males per year that disperse within the population, I = the observed mean number of males per year that immigrate into the study population, and M = the mean number of social units per year lacking an adult male during the portion of the year when data were collected. We then ran the simulation a second time using T as the number of within-population dispersers that were randomly assigned to social units at the start of each breeding season.

RESULTS

Composition of social units

All adults were captured in 82.9% of the social units ($n = 105$) monitored during this study. More than half (59.8%) of these

social units contained a single adult female (Figure 1); the remaining social units each contained 2–6 adult females, with a mean of 3.0 ± 1.2 females per burrow system. The mean number of generations of females present within a multi-female social unit was 2.0 ± 1.0 (range = 1–4, $n = 19$ groups for which generational relationships were known for all females). Less than half (43.7%) of the social units for which all adults were captured also contained an adult male (Figure 1). The number of adult males in single- versus multi-female social units was not significantly different from expected given the proportion of each type of social unit in the study population ($\chi^2 = 2.41$, $df = 1$, $p > .10$), although there was a marginally significant association between multi-female groups and the presence of an adult male (Fisher's Exact test, two-tailed $p = .048$).

Females in burrow systems that lacked an adult male typically (>93%) reared pups to weaning and, thus, these animals must have had contact with one or more males earlier in the breeding season in order to become pregnant. On only three occasions was an adult male found living alone in a burrow system, indicating that the absence of adult males from many social units was not associated with the presence of numerous "bachelor" (i.e., lone) males elsewhere in the study population. Assuming that rates of migration to and from the study population were comparable, these data suggest that the large number of social units lacking an adult male was not a result of post-mating migration within or emigration from the study population. Instead, it seems most likely that the small number of adult males captured during the period between the birth and weaning of young reflects high levels of mortality among males.

Demographic isolation of the study population: immigration and emigration

Apparent rates of immigration into the study population were markedly higher for males than for females (Table 1). This association between sex and number of unmarked animals was significant when data from all years were examined, as well as when only data from 1999–2002 were considered (Fisher's Exact tests, all two-tailed $p < .0001$). Assuming that the subset of reproductive males that disappeared (i.e., emigrated or died prior to capture; see above) was not biased toward unmarked immigrants, these figures should represent maximum rates of immigration for both sexes given that some of the unmarked adults captured on the study site may have been individuals that were born there but that evaded capture as juveniles.

Juvenile movement: natal dispersal and natal philopatry

For males, only 7.4% of the 324 animals first captured as juveniles were recaptured as yearlings; for females, this figure was 24.5% ($n = 314$ animals captured as juveniles). Although the large number of individuals that were not recaptured after their juvenile season probably reflects dispersal as well as mortality, comparing the percentage of young that disappeared before their yearling season (males: 92.6%; females: 75.5%) to the percentage of apparent immigrants to the study population (males: 43.4%; females: 15.5%; Table 1) suggests that more than 50% of juveniles died before the start of their yearling season.

For those marked juveniles that were recaptured as yearlings, the pattern of natal dispersal differed markedly between the sexes. While essentially all males that were recaptured as yearlings had dispersed from their natal burrow system, approximately two-thirds of recaptured females were still resident in their natal burrow as reproductive yearlings

Table 2
Sex-specific patterns of natal dispersal in colonial tuco-tucos during 1996–2002

	Number (%) of animals recaptured as adults	
	Philopatric	Dispersed
Males	1 (4.5)	21 (95.5)
Females	59 (69.4)	26 (30.6)

All individuals in the study population that were captured as juveniles and later recaptured as adults are included. As adults, philopatric animals were still resident in the area encompassed by their natal burrow system. In contrast, as adults, dispersing animals were resident in areas not encompassed by their natal burrow system. For animals captured as adults during more than one field season, only data from the first adult season are included.

(Table 2). This association between sex and natal philopatry was significant (Fisher's Exact test, two-tailed $p < .0001$). The sole philopatric male reported was resident in a group of five females (including three females with which the male had been reared) that had formed due to the fusion of two adjacent but previously distinct social units. This was the only such fusion event detected during this study; because the male's place of residence prior to fusion of these groups was not known, he was reported as still resident in his natal social unit.

In contrast, adult females routinely shared burrow systems with animals with which they had been reared. Approximately two-thirds (67.8%) of philopatric yearling females ($n = 59$) shared their natal burrow system with at least one other yearling female that had been born in the same system and 35.6% of these animals shared a burrow system with at least one female who had been a breeding adult in that system during the previous year. Migration of females to existing social units was never detected during this study; all cases of female recruitment to existing social units ($n = 59$) resulted from natal philopatry.

Female natal dispersal and the formation of new social units

The majority (84.6%) of the females that dispersed from their natal area as juveniles (Table 2) were found living alone as reproductive yearlings. Exceptions ($n = 4$) occurred when (1) two females from the same natal burrow were found living together in a different burrow system as yearlings and (2) two females from different natal burrows were found sharing a third burrow system as yearlings. In all other cases, the burrow systems that disperser females occupied as yearlings had either been unoccupied during the previous year ($n = 17$) or had been occupied by members of a different social unit ($n = 5$), none of which were still present at that location at the time that the disperser female was captured.

A year after a dispersal event was detected, 41.7% of the burrow systems to which females had dispersed ($n = 24$) contained either the dispersed female(s), her daughters, or both, indicating that female natal dispersal (followed, in many cases, by natal philopatry by daughters) was the mechanism by which new social units were formed. The remaining 58.3% of burrow systems to which females had dispersed were either unoccupied during the following year ($n = 12$) or were occupied by a newly dispersed female from a different social unit ($n = 2$). Of the 35 new social units established during the course of this study, 74.3% were founded by marked yearling females that were known to have dispersed within the study population. The remaining new social units were also

founded by females that must have dispersed, given that those burrow systems had not been occupied during the previous breeding season; these females were unmarked and, thus, their age and natal burrow system were not known.

Adult movement: annual dispersal

Only four of the 24 juvenile males recaptured as yearlings were present on the study site during a second adult season. As two-year-olds, each of these males was resident in a different burrow system from the one that he had occupied as either a juvenile or a yearling. Although the sample size is small, these data suggest that adult males disperse between breeding seasons. In contrast, none of the 20 yearling females that were recaptured as two year olds had changed burrow systems between seasons. Furthermore, of 21 females first caught as adults and that were captured during two or more seasons, none had relocated to a new burrow system between years. Collectively, these data indicate that adult females do not disperse between breeding seasons. The association between sex and adult dispersal was significant (Fisher's Exact test, two-tailed $p < .0001$).

Data from social units that were captured during two or more consecutive years support the assertion that adult males relocate between breeding seasons; none of the 30 social units that contained an adult male in one year contained the same adult male during the following year. In all four instances in which a social unit contained an adult male during two consecutive years, a different male was resident in that unit during each breeding season. Thus, while adult females remain in the same burrow system from year to year, it appears that adult males disperse between years such that they are not resident in the same burrow system for more than one breeding season.

Combined with data on juvenile dispersal by members of the study population, these findings indicate that female *C. sociabilis* disperse, at most, only once during their lifetime, during the period between weaning and their first breeding season. Because adult females do not disperse between breeding seasons, a philopatric female spends her entire lifetime in her natal burrow while a female that leaves her natal area spends the remainder of her lifetime in the burrow system to which she dispersed at the end of her juvenile season. In contrast, because males appear to relocate between each breeding season, the number of times that an individual disperses is determined by the number of breeding seasons that he survives.

Intra-population dispersal: co-ancestry among social units

Between 1999 and 2002, 26.7% of the social units monitored ($n = 60$) contained an adult male that had been born in the study population. Plotting patterns of movement for these males revealed that individuals routinely dispersed across the study site within a single year (Figure 2), providing no evidence that the study population was spatially structured with regard to the distribution of adult males that had been born on the site. Tracing individual movements across multiple breeding seasons revealed 17 direct paternal links between pairs of burrow systems and, in seven cases, direct paternal connections among three or more social units. Thus, for males, the combination of limited immigration (Table 1), annual dispersal (Table 2), and regular movement of individuals between burrow systems (Figure 2) suggests that, over the course of multiple years, numerous social units in the study population are likely to share paternal ancestry.

During the same period, 86.7% of new social units ($n = 15$) were founded by females that had been born in the study

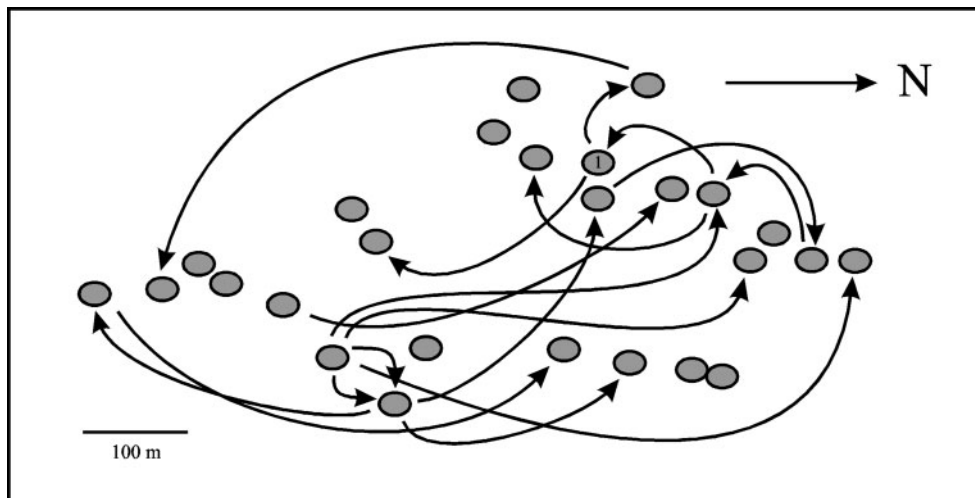


Figure 2

Map of 17 male dispersal events recorded during 1999–2002. Shaded ovals denote the locations of burrow systems occupied during this period; numbers within these ovals indicate the number of philopatric males detected in each social unit. Each arrow denotes a dispersal event; the direction of movement is from the tail to the head of the arrow.

population. Plotting the movements of females (Figure 3) revealed that, although individual females crossed much of the study site within the course of a single year, dispersal distances tended to be shorter than those for males (females: 114.9 ± 80.0 m, $n = 13$; males: 211.0 ± 107.1 m, $n = 17$); this difference was significant ($t = 2.68$, $df = 27$, two-tailed $p = .012$). Nearly two-thirds (61.5%) of the females for which dispersal was documented moved to an adjacent, unoccupied burrow system (Figure 3), compared to only 17.6% of males that dispersed to adjacent burrow systems (Figure 2); this association between sex and the tendency to disperse to an adjacent burrow system was significant (Fisher's Exact test, two-tailed $p = .023$). Because females did not immigrate into existing social units, female dispersal did not lead to the exchange of genetic material across matriline. Nevertheless, limited immigration (Table 1) and the tendency for new social units to be formed from within the study population (Figure 3) suggest that shared maternal ancestry among social units is common.

Simulation analyses: co-ancestry among reproductive partners

Simulation analyses based on data regarding female dispersal and social unit persistence revealed that a mean of 7.2 ± 1.4

different matriline were represented in the study population each year. Given a mean of 18.0 ± 5.5 social units per year (1996–2002), this suggests that, during a given breeding season, each matriline consisted on average of 2.5 social units. These data are in accord with our field observations, which documented 1–4 social units per year for known matriline. For social units belonging to the same matriline and present during the same breeding season, simulation analyses revealed a mean of 4.3 ± 2.3 generations since divergence from a common ancestral social unit. Based on these data and the observed frequency of intra-population dispersal by males, we estimated that the probability that a male will disperse into a social unit from his own matriline is 0.09. Assuming that a male mates with the female(s) in any social unit to which he immigrates (i.e., assuming no subsequent mate choice that may lead to rejection of a male), this suggests that $\sim 10\%$ of reproductive partnerships consist of animals that share maternal ancestry within the last five generations.

For simulations that included male dispersal, the proportion of reproductive partners with shared co-ancestry was greater than that indicated by simulations of female movements alone (Table 3). At the same time, including male movements increased the mean number of generations separating those reproductive partners for which co-ancestry was detected (Table 3); this increase was due to the inclusion of partners

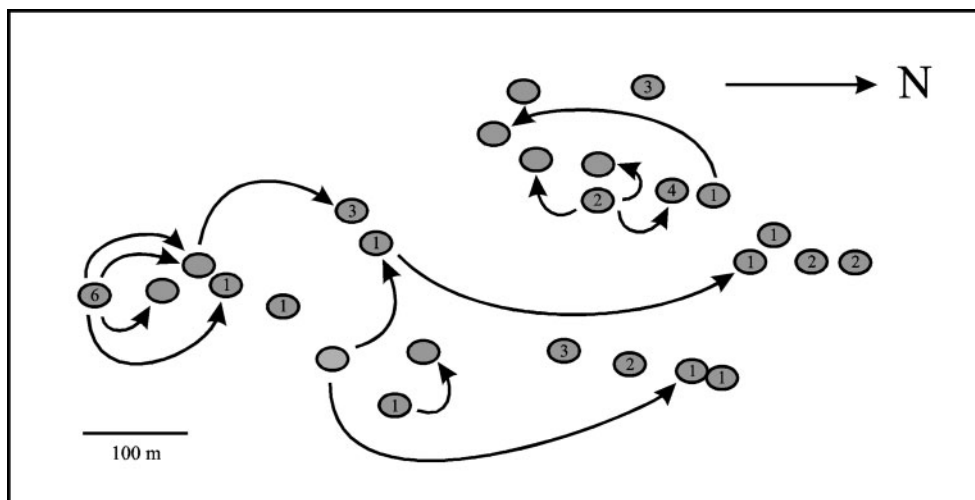


Figure 3

Map of 13 female dispersal events recorded during 1999–2002. Shaded ovals denote the locations of burrow systems occupied during this period. Numbers within these ovals indicate the number of philopatric females detected in each social unit; because more than one female may have remained in her natal burrow system during the same year, the number shown for a given burrow system may exceed the number of years during which data were collected. Each arrow denotes a dispersal event that resulted in the formation of a new social unit; the direction of movement is from the tail to the head of the arrow.

that were more distantly related than the 4.3 generations separating males and females from the same matriline. As the proportion of marked males in the population increased, both the frequency and degree of relatedness among mates increased (Table 3), suggesting that population-level patterns of dispersal by both sexes contribute to co-ancestry among group mates, including reproductive partners.

DISCUSSION

Our data indicate significant sex-based differences in dispersal in *C. sociabilis*. While males in the study population typically dispersed from their natal burrow prior to their yearling season, nearly two-thirds of females that survived to their yearling season were still resident in their natal burrow system as reproductive adults. Males appeared to disperse after every breeding season; in contrast, females that dispersed did so only once, at the end of their juvenile season. Monitoring of marked individuals confirmed that burrow sharing by female *C. sociabilis* arises due to natal philopatry. Thus, social groups consisted of close female kin that had been reared in the same burrow system plus, in some cases, a single adult male that had immigrated into the group.

These analyses indicate that social groups of *C. sociabilis* are strongly kin-structured. Patterns of individual movements, however, suggest that this spatial structuring of kinship may not be apparent at larger spatial and temporal scales. Specifically, intra-population dispersal by females and males should, over time, lead to increased levels of co-ancestry among members of the study population, including reproductive partners. The results of simulation analyses confirm this prediction, indicating that up to 67% of reproductive partners share co-ancestry within the last 4–7 generations. Indeed, the number of generations separating some reproductive partners was no greater than the number of generations separating members of some social groups.

Implications for social behavior

Among social vertebrates, participation in both cooperative and competitive interactions often reflects the degree of relatedness between individuals (Hamilton, 1964; West et al., 2002). Indirect fitness benefits increase as a function of the relatedness between the participants in a social interaction (Hamilton, 1964) and, hence, kin-selected forms of cooperation should be most prevalent among closely related individuals. *C. sociabilis* engage in several potentially cooperative activities, including alarm calling at predators, excavating shared burrows, and, at least in captivity, allonursing young. Because social groups of *C. sociabilis* are composed primarily of female kin, females may accrue indirect as well as direct fitness benefits from their interactions with burrow mates. In contrast, because adult males are typically more distantly related to the females with which they live (≥ 4 –7 generations since shared co-ancestry), potential indirect fitness benefits to males are expected to be considerably smaller. As a result, cooperation and other kin-selected activities should occur primarily among females of this species.

Implications for inbreeding

Sex-biased natal dispersal is frequently interpreted as a mechanism for inbreeding avoidance because it typically leads to the spatial segregation of opposite-sex kin (Bengtsen, 1978; Packer, 1985; Pusey, 1987). Among mammals, natal dispersal is generally male-biased, with philopatry being more common among females (Dobson, 1982; Greenwood, 1980). Our data on natal dispersal are consistent with this pattern, suggesting

Table 3

Estimated co-ancestry among reproductive partners in *C. sociabilis*

Analysis	Proportion of reproductive partners with co-ancestry	Mean number of generations since co-ancestry
Females only ^a	0.10	4.3 ± 2.3
Both sexes (5 male dispersers/year)	0.24	7.2 ± 3.0
Both sexes (13 male dispersers/year)	0.67	5.7 ± 1.4

^a Proportion of reproductive partners with co-ancestry determined statistically. Observed mean number of female generations per social unit = 2.0 ± 1.0 (range = 1–4; $n = 19$ social units).

Data are from simulation analyses of individual movements and survival based on observed patterns of natal dispersal and matriline persistence. Initially, the simulation was run using demographic data from females only. Data for males were then incorporated into the analysis and the simulation was repeated using the observed ($n = 5$) and the estimated total ($n = 13$) number of males that dispersed within the study population each year. All simulations were run for 1000 generations. Means are shown ± 1 SD.

that reproduction by individuals reared in the same burrow system is effectively absent in *C. sociabilis*. Our simulation analyses, however, suggest that up to two-thirds of reproductive partners may share co-ancestry within a relatively limited number of generations. Thus, while reproduction by close kin (i.e., animals reared in the same burrow system) appears to be rare in *C. sociabilis*, co-ancestry among reproductive partners is relatively common and, in some cases, approaches the degree of relatedness evident among females in the same social unit.

The simultaneous occurrence of apparent inbreeding avoidance at the level of the social unit but sometimes pronounced co-ancestry at the level of the population raises intriguing questions regarding the nature of inbreeding and the role of kin recognition in mediating reproductive and social relationships. Assuming that natal dispersal by male *C. sociabilis* represents a form of inbreeding avoidance (Pusey, 1987; Pusey and Wolf, 1996), these data imply that while selection has acted to minimize reproduction by immediate kin (i.e., animals reared together), it has not produced mechanisms for preventing reproduction by more distant relatives, including members of the same matriline reared in different social units. Patterns of kin recognition in this species are expected to have evolved accordingly, leading us to predict that while animals reared in the same social group will be recognized as kin, this distinction will not extend to members of other social units regardless of the actual degree of genetic relatedness between individuals.

Implications for population genetic structure

In general, studies of group-living mammals support the prediction that genetic structure is strongly associated with social structure. For example, data from black-tailed prairie dogs (Dobson et al., 1998), lions (Spong et al., 2002), howler monkeys (Pope, 1998), and Australian rabbits (Richardson et al., 2002) indicate that, within populations, social groups are genetically differentiated from one another. In each of these species, social groups are composed of closely related adult females and one to a few immigrant adult males. This group structure closely parallels that reported here for *C. sociabilis*, suggesting that genetic differentiation among social units should be evident within our study population.

While the formation of kin groups is expected to increase genetic structure within a population, a high rate of inter-group migration should decrease differentiation among social units in much the same way that gene flow among populations serves to reduce the diversifying effects of drift and local selection (Pope, 1998). The tendency for new groups to be formed from within the study population should also serve to reduce variation among social units by reducing the probability of “founder effects” in which groups are established by animals (e.g., immigrants to the population) with distinctive genotypes. Both of these attributes are characteristic of our study population of *C. sociabilis*, suggesting that population-level processes may play a significant role in shaping the genetic structure of these animals.

Preliminary surveys of microsatellite variation have revealed low levels of allelic variation and heterozygosity among members of the study population (Lacey, 2001). These data are consistent with the hypothesis that population-level processes such as inter-group migration and within-population group formation have a strong homogenizing effect on genetic variation in our study animals. At the same time, low levels of microsatellite diversity may reflect population history; analyses of microsatellite allele structure suggest that the study population may have experienced one or more bottlenecks that also served to reduce within-population levels of variation (Lacey, 2001). Determining the extent to which these different forces have shaped the genetic structure of the study population is challenging, and a detailed knowledge of kin structure and relatedness is required to determine how current demographic processes influence genetic variation. As evidenced by our studies of *C. sociabilis*, the spatial and temporal scales over which demographic patterns are monitored can substantially influence interpretations of kin structure and, hence, the understanding of both social behavior and population genetic structure.

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REFERENCES

- Baglione V, Canestrari D, Marcos JM, Ekman J, 2003. Kin selection in cooperative alliances of carrion crows. *Science* 300:1947–1949.
- Bengtsston BO, 1978. Avoiding inbreeding: at what cost? *J Theor Biol* 73:439–444.
- Bennett NC, Faulkes CG, 2000. African mole-rats: ecology and eusociality. Cambridge: Cambridge University Press.
- Clutton-Brock TH, 2002. Breeding together: kin selection and mutualism in cooperative vertebrates. *Science* 296:69–72.
- Creel S, Creel NM, 2002. The African wild dog. Princeton, NJ: Princeton University Press.
- Dobson FS, 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Anim Behav* 30:1183–1192.
- Dobson FS, 1998. Social structure and gene dynamics in mammals. *J Mammal* 79:667–670.
- Dobson FS, Chesser RK, Hoogland JL, Sugg DW, Foltz DW, 1998. Breeding groups and gene dynamics in a socially structured population of prairie dogs. *J Mammal* 79:671–680.
- Dunbar RIM, 1986. The social ecology of gelada baboons. In: Ecological aspects of social evolution (Rubenstein DI, Wrangham RW, eds). Princeton, NJ: Princeton University Press; 332–351.
- Faulkes CG, Abbott DH, O'Brien HP, Lau L, Roy MR, Wayne RK, Bruford MW, 1997. Micro- and macrogeographic genetic structure of colonies of naked mole-rats, *Heterocephalus glaber*. *Mol Ecol* 6: 615–628.
- Getz LL, Carter CS, 1998. Inbreeding avoidance in the prairie vole, *Microtus ochrogaster*. *Ethol Ecol Evol* 10:115–127.
- Gibbs HL, Grant PR, 1989. Inbreeding in Darwin's medium ground finches (*Geospiza fortis*). *Evolution* 43:1273–1284.
- Greenwood PJ, 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim Behav* 28:1140–1162.
- Gundersen G, Andreassen HP, 1998. Causes and consequences of natal dispersal in root voles, *Microtus oeconomus*. *Anim Behav* 56: 1355–1366.
- Hamilton WD, 1964. The genetical evolution of social behavior I and II. *J Theor Biol* 7:1–52.
- Hoogland JL, 1995. The black-tailed prairie dog: social life of a burrowing mammal. Chicago, IL: University of Chicago Press.
- Kerth G, Mayr F, Petit E, 2002a. Extreme sex-biased dispersal in the communally breeding, non-migratory Bechstein's bat (*Myotis bechsteinii*). *Mol Ecol* 11:1491–1498.
- Kerth G, Safi K, König B, 2002b. Mean colony relatedness is a poor predictor of colony structure and female philopatry in the communally breeding Bechstein's bat (*Myotis bechsteinii*). *Behav Ecol Sociobiol* 52:203–210.
- Lacey EA, 2001. Microsatellite variation in solitary and social tuco-tucos: molecular properties and population dynamics. *Heredity* 86: 628–637.
- Lacey EA, in press. Sociality reduces individual direct fitness in a communally breeding rodent, the colonial tuco-tuco (*Ctenomys sociabilis*). *Behav Ecol Sociobiol*.
- Lacey EA, Braude SH, Wiczorek JR, 1997. Burrow sharing by colonial tuco-tucos (*Ctenomys sociabilis*). *J Mammal* 78:556–562.
- Lacey EA, Wiczorek JR, 2003. The ecology of sociality in rodents: a ctenomyid perspective. *J Mammal* 84:1198–1211.
- Le Galliard J-F, Ferriere R, Clobert J, 2003. Mother-offspring interactions affect natal dispersal in a lizard. *Proc R Soc Lond Ser B* 270:1163–1169.
- McNutt JW, 1996. Sex-biased dispersal in African wild dogs, *Lycan pictus*. *Anim Behav* 52:1067–1077.
- Michener GR, 1983. Kin identification, matriarchies, and the evolution of sociality in ground-dwelling sciurids. In: Advances in the study of mammalian behavior (Eisenberg JF, Kleiman DG, eds). Special publication 7 of the American Society of Mammalogists. Lawrence, KS: Allen Press; 528–572.
- Michod RE, 1982. The theory of kin selection. *Ann Rev Ecol Syst* 13: 23–55.
- Packer C, 1985. Dispersal and inbreeding avoidance. *Anim Behav* 33: 676–678.
- Packer C, 1986. The ecology of sociality in felids. In: Ecological aspects of social evolution (Rubenstein DI, Wrangham RW, eds). Princeton, NJ: Princeton University Press; 429–451.
- Patton JL, Smith MF, 1990. The evolutionary dynamics of the pocket gopher, *Thomomys bottae*, with emphasis on California populations. University of California Publications in Zoology 123:1–161.
- Pearson OP, Christie MI, 1985. Los tuco-tucos (genero *Ctenomys*) de los parques nacionales Lanin y Nahuel Huapi, Argentina. *Hist Nat* 5:337–344.
- Petrie M, Krupa A, Burke T, 1999. Peacocks lek with relatives even in the absence of social and environmental cues. *Nature* 401:155–157.
- Pope TR, 1998. Effects of demographic change on group kin structure and gene dynamics of populations of red howling monkeys. *J Mammal* 79:692–712.
- Pusey AE, 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends Ecol Evol* 2:295–299.
- Pusey AE, Wolf M, 1996. Inbreeding avoidance in animals. *Trends Ecol Evol* 11:201–206.
- Reeve HK, 1992. Queen activation of lazy workers in colonies of the eusocial naked mole-rat. *Nature* 358:147–149.
- Reeve HK, Sherman PW, 1991. Intracolony aggression and nepotism by the breeding female naked mole-rat. In: The biology of the naked mole-rat (Sherman PW, Jarvis JUM, Alexander RD, eds). Princeton, NJ: Princeton University Press; 337–357.

- Richardson BJ, Hayes RA, Wheeler SH, Yardin MR, 2002. Social structures, genetic structures and dispersal strategies in Australian rabbit (*Oryctolagus cuniculus*) populations. *Behav Ecol Sociobiol* 51:113–121.
- Rubenstein DI, 1986. Ecology of sociality in horses and zebras. In: *ecological aspects of social evolution* (Rubenstein DI, Wrangham RW, eds). Princeton, NJ: Princeton University Press; 282–302.
- Ryan KK, Lacy RC, 2003. Monogamous male mice bias behaviour toward females according to very small differences in kinship. *Anim Behav* 65:379–384.
- Spong G, Creel S, 2004. Effects of kinship on territorial conflicts among groups of lions, *Panthera leo*. *Behav Ecol Sociobiol* 55: 325–331.
- Spong G, Stone J, Creel S, Bjorklund M, 2002. Genetic structure of lions (*Panthera leo* L.) in the Selous Game Reserve: implications for the evolution of sociality. *J Evol Biol* 15:945–953.
- Steinberg EK, Patton JL, 2000. Genetic structure and the geography of speciation in subterranean rodents: opportunities and constraints for evolutionary diversification. In: *Life underground: the biology of subterranean rodents* (Lacey EA, Patton JL, Cameron GN, eds). Chicago, IL: University of Chicago Press; 301–331.
- Sugg DW, Chesser RK, Dobson FS, Hoogland JL, 1996. Population genetics meets behavioral ecology. *Trends Ecol Evol* 11:338–342.
- Van Noordwijk AJ, Scharloo W, 1981. Inbreeding in an island population of the great tit. *Evolution* 35:674–688.
- West SA, Pen I, Griffin AS, 2002. Cooperation and competition between relatives. *Science* 296:72–75.
- West-Eberhard MJ, 1975. The evolution of social behavior by kin selection. *Quart Rev Biol* 50:1–33.
- Zahavi A, 1990. Arabian babblers: the quest for social status in a cooperative breeder. In: *Cooperative breeding in birds: long-term studies of ecology and behavior* (Stacey PB, Koenig, WD, eds). Cambridge: Cambridge University Press; 103–130.