

Levels of social behaviors and genetic structure in a population of round-tailed ground squirrels (*Xerospermophilus tereticaudus*)

Karen E. Munroe · John L. Koprowski

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Abstract Ground-dwelling sciurids exhibit a continuum of sociality and several models predict levels of sociality within this taxon. Models of ground squirrel sociality predict round-tailed ground squirrels (*Xerospermophilus tereticaudus*) to be solitary; however, previous behavioral studies suggest round-tailed ground squirrels have a matrilineal social structure. To resolve this discrepancy, we combined behavioral observations with genetic analyses of population structure. We assessed levels of agonistic and amicable behaviors combined with fine-scale population genetic structure of round-tailed ground squirrels in a multi-year study in AZ. Only 45 agonistic and 40 amicable interactions were observed between adults in over 137 h of observations. Overall rates of agonistic or amicable interactions between adults were low ($\leq 0.69/h$), with no relationship between relatedness of individuals and rates of either amicable or agonistic interactions. Interactions between juvenile littermates were predominantly amicable. Population substructure was not evident with Bayesian analyses, global or pairwise F_{ST} values; average relatedness among females was not different from males. However, in 2006, the year after a population reduction through targeted animal elimination, a population bottleneck was detected within at least five of seven loci. Contrary to previous behavioral studies, this population of round-tailed ground squirrels, although aggregated spatially, did not exhibit high levels of social behavior nor

subpopulation genetic structure. Analyses of the genetic relationships and sociality along a continuum, particularly within aggregates of individuals, may lead to insights into the origin and maintenance of social behaviors by elucidating the mechanisms by which aggregates with intermediate social levels are formed and maintained.

Keywords Arizona · Bottleneck · Microsatellites · Sociality · Sciuridae

Introduction

Solitary individuals and integrated groups of often highly related individuals represent two ends of a sociality spectrum (Lott 1984). Solitary individuals should either avoid conspecifics or behave neutrally or agonistically in interactions with conspecifics; whereas individuals living in groups should exhibit social behaviors that define and maintain relationships within the group (Lott 1984) to maintain group structure (Slobodchikoff and Shields 1988). Intermediate levels of grouping (i.e., aggregates of individuals) occur in many species, yet are poorly understood, particularly the presence and function of social behaviors and the levels of genetic relatedness among individuals (Lott 1991). Thus, the combined analysis of social behaviors and population genetic substructure is essential to understand the evolution of social behaviors and the origin of group formation.

Three levels of hypotheses have been proposed to explain the origin of group formation: phylogenetic constraint, ecological (i.e., environmental) selection, and genetic (i.e., kin selection, Slobodchikoff and Shields 1988). Each hypothesis suggests a different proximate mechanism of group formation, but many of the ultimate benefits of social behaviors remain the same. The ecological selection hypothesis articulates that environmental constraints restrict individuals to coexist as aggregates as the cost of living solitarily is high (i.e., spatially

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K. E. Munroe (✉) · J. L. Koprowski
Wildlife Conservation and Management, School of Natural
Resources and the Environment, 325 Biological Sciences East,
The University of Arizona, Tucson, AZ 85721, USA
e-mail: kmunroe@bw.edu

Present Address:

K. E. Munroe
Department of Biology and Geology, Baldwin Wallace University,
275 Eastland Rd, Berea, OH 44017, USA

and temporally heterogeneous resources and harsh climate: Griffin and West 2002; West et al. 2002; Blundell et al. 2004; Matocq and Lacey 2004; Hare and Murie 2007; Túnez et al. 2009; predator avoidance: Connor 1995; Mesterton-Gibbons and Dugatkin 1992). Genetic hypotheses predict that benefits of inclusive fitness create and maintain kin group formation (Hamilton 1964; Alexander 1974; Armitage 1981; Koprowski 1996). In mammals, female philopatry and male-biased dispersal produce and maintain clusters of related individuals that overlap in space and time (Greenwood 1980; Armitage 1981, 1999) and ultimately a population structure with subpopulations of related females (Clutton-Brock and Lukas 2012; Dobson et al. 1998; Sugg et al. 1996). Behaviors costly to solitary individuals could be maintained within groups of highly related individuals (Hamilton 1964; Alexander 1974; Sherman 1981) by reducing costs of intraspecific competition (Bradbury and Vehrencamp 1976; Wrangham and Rubenstein 1986) and parasite and disease transmission (Lott 1991) while increasing benefits of inclusive fitness of genetically related group members (i.e., kin selection, Hamilton 1964; Armitage 1981; Trivers 1985; Emlen 1994, 1995). Determining whether genetic or ecological selection is likely to have influenced the apparent aggregation of individuals can be resolved by examining genetic relatedness among individuals. In general, genetic selection results in fine-scale genetic structure and groups of highly related individuals (i.e., kin clusters), whereas ecological selection results in spatial aggregation without genetic structure within the population.

Ground-dwelling sciurids exhibit a continuum of sociality including several species with highly social behaviors and population genetic substructure (e.g., Olympic marmots, *Marmota olympus*: Barash 1973; Gunnison's prairie dogs, *Cynomys gunnisoni*: Hoogland 1995) and species of isolated solitary individuals (Franklin's ground squirrels, *Poliocitellus franklini*: Iverson and Turner 1972; Murie 1973; woodchucks, *Marmota monax*: Maher 2009). Several models have been proposed to describe the levels of sociality in ground squirrels (Armitage 1981; Michener 1983, 1984; Blumstein and Armitage 1998).

The general model predicts sociality in large-bodied ground squirrels (>600 g, Armitage 1981) when juvenile and adult activity periods overlap >70 % (Michener 1984) wherever adequate resources are located. This pattern suggests social behaviors evolved to minimize aggressive and competitive interactions due to the timing and sequence of the annual activity cycle (Michener 1984), to improve care of young (Armitage 1981), increase efficient defense of resources (Slobodchikoff 1984), and decrease predation risk (Blumstein and Armitage 1998). Understanding the genetic structure of ground-dwelling sciurid populations combined with the levels of social behavior, particularly species classified as of intermediate sociality, should yield insights into the evolution of group formation within this taxon.

Round-tailed ground squirrels (*Xerospermophilus tereticaudus*) are small (~125 g) ground squirrels that inhabit desert areas of the southwestern USA including southeastern California, southern Nevada, and western AZ, as well as northeastern Baja California, and northwestern Sonora, Mexico (Hall 1981). Individuals are typically active from late January to August at which time they enter an inactive phase or shallow torpor (Dunford 1975; KM and JK, unpublished data). Males emerge first from burrows in late January, mating begins in early March (Ernest and Mares 1987), males enter torpor and young are born in late April to late June with lactation extending through June (Neal 1965; KM and JK, unpublished data). Juvenile dispersal of 29–45 % of young occurs during June and July (Dunford 1977a). Models of ground squirrel sociality predict round-tailed ground squirrels to be solitary or form aggregates in favorable habitat based on small body size, relatively long period of activity, and short period of adult-juvenile overlap (Armitage 1981). However, previous behavioral observational studies suggest round-tailed ground squirrels may have a greater social organization with a matrilineal population structure resulting in clusters of related females (Drabek 1973; Dunford 1977b), with high levels of social behavior, which would position round-tailed ground squirrels as a unique outlier in ground-dwelling sciurid sociality models. Population densities in these studies ranged from 5.3/ha (Drabek 1973) to 40/ha (Dunford 1977a). Home range size estimated by the minimum-area method was 0.30 ha with overlap among adults with no differences found between males and females (Drabek 1973). However, little is known about the degree of relatedness within or between clusters of females within a population. Furthermore, the extent to which social interactions within this species are kin-biased are currently unclear.

In this study, we combined field behavioral observations with genetic analyses to investigate the spatial genetic structure of two clusters of round-tailed ground squirrels and compare this with observed social behaviors. The ground squirrel sociality models predict round-tailed ground squirrels to have low levels of social behaviors and neighboring females to have a low genetic relatedness. Whereas the previous behavioral studies predict that round-tailed ground squirrels should have high levels of social behavior and neighboring females will have a high level of genetic relatedness. To test these predictions, we combined field data on observed rates of social behaviors analyses with fine-scale genetic population structure.

Methods

We studied round-tailed ground squirrels at Casa Grande Ruins National Monument in Coolidge, Pinal County, AZ from January 2004 to June 2007. Creosote bush (*Larrea tridentata*)

dominated the landscape and was relatively evenly dispersed with occasional barrel (*Opuntia* sp.), saguaro (*Cereus giganteus*), and planted ornamental cacti with trees around the visitors' center and picnic area. Due to a large population size and potential damage to known and unexcavated archeological ruins, a population reduction through shooting and poisoning within the Monument occurred during summer 2005, authorized by the National Park Service and performed by the Department of Agriculture's Animal and Plant Health Inspection Service (APHIS). This reduction of the population provided an opportunity to monitor how population structure and social behaviors would change.

After an initial trapping year where we attempted to trap all individuals within the Monument, we established two 2500-m² study plots with a 2500-m² buffer area border at two random locations within the Monument. We used Sherman live traps (H.B. Sherman Traps, Inc, Tallahassee, Florida) baited with sunflower seeds and/or peanut butter to trap adult squirrels at burrows during the day. Squirrels were immobilized with a cloth handling cone (Koprowski 2002) and all individuals were released at the point of capture.

We determined sex and age class (juvenile < 6 mon, sub-adult 6–12 mon, adult > 12 mon) of squirrels upon initial capture after hibernation. We marked individuals with a unique freeze-mark (Rood and Nellis 1980; Koprowski 1996) and hair dye (Clairol Balsam Lasting Color, True Black #618, Procter & Gamble, Cincinnati, Ohio) for permanent and immediate identification in the field. We used surgical scissors to collect a 4-mm² tissue sample from the tail tip upon initial capture for genetic analysis. We stored tissue samples in 1-mL DMSO buffer solution at –20 °C upon exit from the field.

Behavioral observations and analysis

We observed round-tailed ground squirrels in the two 2500-m² study plots during periods of daily activity from 0600 to 1800 hours. We used binoculars to observe behaviors from a blind at a distance of 40 m. Scan samples at 10 min intervals recorded any individuals present and focal animal observations were taken for 9 min to determine individual behavior and interaction rates (Altmann 1974). Focal animals were chosen at random, and marked individuals were never sampled more than twice a day separated by < 1 h, but typically > 3 h. Focal animal samples occurred over the course of the day, between trap checks in 2 h blocks. Quantified behaviors included frequency and classification (amicable or agonistic) of any physical contact with other individuals.

Amicable interactions included oral-oral and oral-nasal nuzzles, an olfactory “greeting” (Armitage 1962). Agonistic interactions included chasing and lateral display, where two animals were side by side with their bodies and tails held low to the ground and their bodies were curved outward, and these typically ended in a chase (i.e., “ready-alert”; Armitage 1962).

Because animals did not always remain in view for the entire 9 min focal animal sample, we converted interactions to rates when appropriate. We combined all the previously described interactions to create composite variables of amicable and agonistic behaviors and rates. To avoid pseudoreplication due to the dyadic interactions, each interaction was only counted once.

DNA extraction and genotyping

We used standard phenol-chloroform methods (Sambrook and Russell 2001) with proteinase K, and a Tris-based cell lysis buffer to extract genomic DNA. We amplified seven polymorphic microsatellite DNA loci from other closely related species of ground squirrel (IGS-1, B-109, B-126, GS-12, GS-14, GS-25, GS-26; May et al. 1997; Stevens et al. 1997; Garner et al. 2005) with GoTaq polymerase (Promega Corp, Madison, WI) including a fluorescently labeled forward primer (6-FAM or HEX, IDT DNA Technologies, IL, USA) and an unlabelled reverse primer. We conducted PCR amplifications in 25- μ l volumes containing 50 ng genomic DNA, 1 μ M each of fluorescently and non-fluorescently labeled primer, 0.2 mM of dNTP's, 1.5 mM of MgCl₂, 5 ng BSA, 1 \times clear flexibuffer, 1 U of GoTaq polymerase and 8.8 μ l of PCR water. The thermal profile consisted of a denaturation cycle at 94 °C (4 min); 35 cycles of 94 °C (30 s) denaturation, 51 °C (30 s) annealing, a 72 °C (30 s) elongation; and a final extension at 72 °C (5 min). We visualized PCR products on a 2 % agarose gel to detect positive PCR. We performed post-PCR mixing of products known to be different allele size categories before visualization on an ABI 3130 (Applied Biosystems, Foster City, CA). Genotypes were visualized with GENOTYPER software (v 3.7, Applied Biosystems, Foster City, CA). We scored chromatogram data twice with two different observers to reduce scoring errors. We excluded individuals typed at fewer than five loci.

Data analysis

We used GENEPOP 4.0 (Rousset 2008) to assess characteristics of microsatellites, and test Hardy-Weinberg equilibrium, null allele frequency, and Polymorphic Information Content (PIC), which refers to the value of a marker for detecting polymorphism within a population that depends on number of detectable alleles and distribution of their frequency. We also calculated allele frequencies, allele number, observed H_o and expected H_e heterozygosities, and genotypic linkage disequilibria (Rousset 2008). We used four approaches to investigate how genetic variation was distributed within the population. All input file preparations were made using CONVERT version 1.31 (Glaubitz 2004).

We used Bayesian assignment techniques to test for population structure using the program STRUCTURE

(version 2.3.2.1, Pritchard et al. 2000; Falush et al. 2003). This method identifies genetically distinct clusters (K) of genetically similar individuals from multilocus genotypes without prior knowledge of genetic relatedness incorporating the likelihood of the data for different values of K . Given the typical mammalian philopatric structure, the previous studies on round-tailed ground squirrels (Drabek 1973; Dunford 1977b) and the increased amount of time females are active throughout the year, we limited analyses of population genetic structuring to adult females. We did not include juvenile offspring in our models because genetically distinct clusters tend to be overestimated when large groups of highly related individuals are included in the sample (Anderson and Dunham 2008). We ran STRUCTURE with and without the “admixture model” option with 10 repetitions of 1,000,000 iterations following a burn-in period of 500,000 iterations. We assessed data from each year individually since only two females remained on the study plot between years. We used HARVESTER to graph outputs from STRUCTURE. To determine the most likely number of clusters, we used the method presented by Pritchard and Wen (2002), the value of K that maximizes the estimated model averaged log-likelihood, $\log(P(X|K))$. Recently, this method has been shown to perform as well as or better than the method presented by Evanno et al. (2005) and Waples and Gaggiotti (2006).

We estimated population differentiation between study plots and among years in ARLEQUIN version 3.1 (Excoffier et al. 2005). We calculated pairwise F_{ST} values using methods outlined in Weir and Cockerham (1984). A Bonferroni correction for multiple tests was used to determine significance of F_{ST} values among sampling locations and years (Zar 1999). An analysis of molecular variance (AMOVA) was also calculated. We used estimates of Wright’s (1931) F statistics, F_{IS} (genetic structure within localities), and F_{ST} (among localities), to further investigate population differentiation by examining the degree of genetic differentiation between our study plots and generated corresponding 95 % confidence intervals with FSTAT 2.9.3 (Goudet 1995). F statistics describe the amount of inbreeding-like effects within subpopulations F_{IS} , among subpopulations F_{ST} , and within the entire population F_{IT} . The fixation index, or differentiation coefficient of populations (F_{ST}), is used to evaluate the differentiation of subpopulations. An F_{ST} value less than 0.05 denotes low differentiation between subpopulations, 0.05 to 0.14 denotes a medium differentiation between subpopulations, while an F_{ST} value of more than 0.15 means high differentiation between subpopulations (Wright 1978; Hartl and Clark 1997).

F_{IS} and F_{IT} are inbreeding coefficients that give the probability of two identical alleles at a locus being derived by descent from a common ancestor within the subpopulation (F_{IS}) or from a common ancestor in the total population (F_{IT}). Positive values of F_{IS} and F_{IT} occur when there is increased

homozygosity in a population including inbreeding and mating system effects (Wright 1965; Nei 1977).

We used RE-RAT (Relatedness Estimation and Rarefaction Analysis Tool; Schwacke et al. 2005) to calculate average relatedness for each group using the Queller and Goodnight (1989) relatedness estimator (R) based on Hamilton’s coefficient of relatedness, r . We calculated standard errors by performing a 10,000 jackknife re-sampling procedure across all loci. Over all 4 years, we calculated the overall relatedness for all males and females in the Monument and separately for each of the 3 years in the smaller study plots.

To test for the indication of a genetic bottleneck due to the target population reduction, we used the program BOTTLENECK version 1.2.02 (Cornuet and Luikart 1996; Piry et al. 1999) applying two mutation models: the stepwise-mutation model (SMM), and two-phase model (TPM) of microsatellite mutation. The TPM combines the stepwise and infinite allele mutation models (Cornuet and Luikart 1996). We ran the TPM analysis with the default setting of 70 % stepwise-mutation model and 30 % variation from the infinite allele model (IAM). A total of 10,000 iterations were performed in each case. These models test whether observed gene diversity is higher than expected for mutation-drift equilibrium from the number of observed alleles in each locus. We performed two-tailed Wilcoxon sign-rank tests for heterozygote deficiency, indicative of a recent population bottleneck.

We used an analysis of variance (ANOVA) to test for difference in overall rates of amicable and agonistic interactions and linear regression to determine if rates of amicable or agonistic behavior were related to the genetic relatedness between pairs of adults and average relatedness within a litter of juveniles. We performed all analyses using JMP-IN (SAS Institute Inc. 2003). Means are reported \pm SE.

Results

We captured and genotyped 351 unique round-tailed ground squirrels (98 adult females, 114 adult males, 51 juvenile females, 88 juvenile males) from February 2004 to May 2007. Density of animals was greater than any previously reported study (40/ha, Drabek 1973) and ranged from 5 to 18 resident adult females per 2500-m² plot. Of the 40 adult females resident in the two 2500-m² study plots over the 3 years (2005: $n=18$; 2006: $n=12$; 2007: $n=10$), only two females were present in the same plot in consecutive years; one female showed natal philopatry (2006) by settling and reproducing in the plot where she was born and one female immigrated into a plot, did not disperse after breeding, and did not produce a litter in the subsequent year. Round-tailed ground squirrels were aggregated on the study plots (5–18 females/2500-m² plots) but dispersal and turnover rates do not support the formation of matrilineal kin clusters.

Social behavior

Agonistic interactions included chasing and lateral displays; amicable interactions included oral-oral and oral-nasal nuzzles: Only 45 agonistic and 40 amicable interactions were observed between adults in more than 137 h of behavioral observations with one instance of burrow sharing. The overall ratio of total agonistic to amicable interactions was 1.13:1. The overall rates of social behavior in adults were low ($\leq 0.69/h$) and did not differ between years. No differences between rates of agonistic or amicable behavior between male-male, female-female, or male-female adult interactions (ANOVA, $F_{6,79}=1.45$, $P=0.21$) were observed (Table 1, Fig. 1). Total agonistic ($y=0.006x+0.053$, $t_{44}=-0.22$, $P=0.83$; Fig. 1a) and amicable interactions ($y=0.059x+0.006x$, $t_{39}=-0.02$, $P=0.99$; Fig. 1b), nor individual male-male, male-female, female-female pairs were explained by level of relatedness for adult interactions.

For juveniles, we observed seven litters and a total of seven agonistic and 34 amicable interactions for a ratio of 0.21:1 agonistic to amicable interactions. The agonistic interactions were observed in a single litter of seven offspring during 2004. The level of amicable interactions was not explained by the average relatedness of the litter ($y=1.79x+0.28$, $t_6=1.32$, $P=0.24$). No above-ground interactions between offspring of different litters, mothers and their offspring, or mothers and other juveniles were observed.

Population substructure

We detected 68 alleles at seven microsatellite loci with 4–18 alleles per locus. All loci ($n=7$) had a low (<0.039) frequency of null alleles and the absence of deviations from Hardy-Weinberg equilibrium or patterns of linkage suggest that chosen loci were suitable for use in this study (for details see Table 2 in Munroe and Koprowski 2011). Average relatedness of females within a plot did not differ from males ($z=0.011$, $P>0.99$) or between plots within a year (2005: $z=-0.012$, $n=$

Table 1 Rates of agonistic and amicable interactions of round-tailed ground squirrels (*X. tereticaudus*) at the Casa Grande Ruins National Monument, Pinal Co., AZ (2004–2007) for male-male, female-female, male-female dyads by adults and juveniles. Sample size indicated in parentheses

| | Agonistic | Amicable |
|--------------------------|-----------|----------|
| Male-Male (adult) | 0.04 (7) | 0.05 (7) |
| Male-Male (juvenile) | 0.03 (4) | 0.02 (3) |
| Female-Female (adult) | 0.04 (6) | 0.07 (7) |
| Female-Female (juvenile) | 0.02 (5) | 0.05 (3) |
| Male-female (adult) | 0.06 (7) | 0.06 (6) |
| Male-female (juvenile) | 0 | 0.01 (2) |

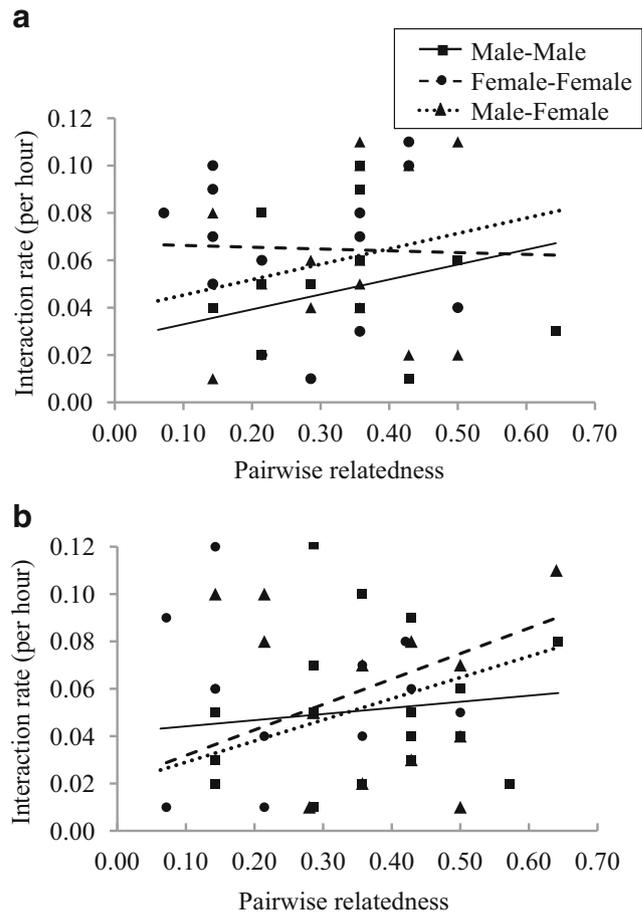


Fig. 1 Regression of pairwise relatedness of participants on rates of agonistic (a) and amicable interactions (b) of adult round-tailed ground squirrels (*X. tereticaudus*) at the Casa Grande Ruins National Monument, Pinal Co., AZ (2004–2007). Squares represent male-male interactions, circles represent female-female interactions, and triangles represent male-female interactions

18, $P>0.99$; 2006: $z=-0.028$, $n=12$, $P>0.98$; 2007: $z=0.003$, $n=10$, $P>0.99$; Fig. 2). No population structuring was evident in this population, and the most likely number of clusters was one ($K=1$; Fig. 3). Global F_{ST} values for each year and across years were less than 0.05 (Table 2). However, global F_{IS} among female residents was different from zero (Bonferroni corrected $P=0.001$, Table 2). Pairwise F_{ST} values did not show subpopulation structure between plots or among years (Table 2). Most genetic variation (84 %) in the population was due to differences within and among individuals (16 %) and <0.8 % was explained between groups indicated by the AMOVA (Table 3).

Bottleneck

In 2006, the year after population reduction, we detected evidence of a genetic bottleneck. In the two-phase model (TPM), where 70 % of mutations are stepwise, a heterozygosity deficiency was only detected in five of seven loci (Wilcoxon sign-rank, $P=0.08$); however, the stepwise-

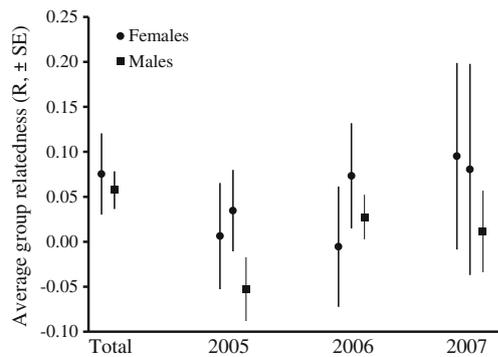


Fig. 2 Estimates of mean relatedness (R) and standard error through standard jackknife procedure (10,000) as calculated by the program RE-RAT for all female round-tailed ground squirrels (*X. tereticaudus*) in the population at the Casa Grande National Ruins Monument, Pinal Co., AZ over all 4 years (2004–2007), all males in the population over all 4 years, and subpopulation comparison for females in each of two plots for 2005–2007

mutation model (SMM) detected a heterozygosity deficiency in six of seven loci (Wilcoxon sign-rank, $P=0.02$). No deficiency in heterozygotes was detected by the TPM (2005: $P=0.47$; 2007: $P=1.0$) nor the SMM (2005, $P=0.81$; 2007, $P=0.58$) in the year prior to (2005) or after (2007) the population reduction. Furthermore, detection of this change in heterozygosity suggests that the genetic power is sufficient to detect population substructure if present.

Discussion

The population of round-tailed ground squirrels that we studied, although aggregated spatially, was not social thus supporting predictions of ground squirrel sociality models in conflict with previous studies (Drabek 1973; Dunford 1977a).

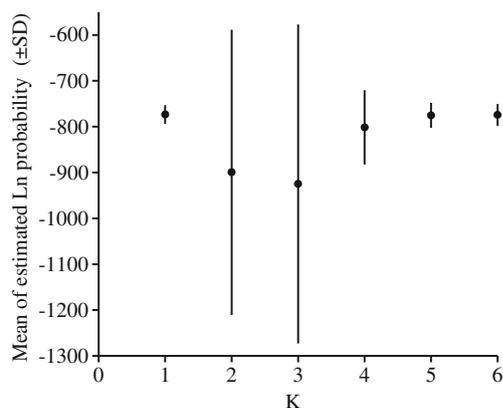


Fig. 3 Mean of estimated Ln probability (\pm SD) by the potential number of populations of round-tailed ground squirrels (*X. tereticaudus*) at the Casa Grande National Ruins Monument, Pinal Co., AZ (2005–2007) from the program STRUCTURE, the value of K that maximizes the estimated model averaged log-likelihood, $\log(P(X|K))$ indicates the number of clusters (Pritchard and Wen 2002)

Table 2 F statistics (F_{ST} , F_{IT} , F_{IS}) calculated from the program FSTAT measure the genetic differentiation for female round-tailed ground squirrels (*Xerospermophilus tereticaudus*) at the Casa Grande Ruins National Monument, Pinal Co., Arizona, per year (2005–2007) and total over all years \pm SE

| Year | F_{ST} | F_{IT} | F_{IS} |
|-------|--------------------|-------------------|-------------------|
| 2005 | 0.021 \pm 0.016 | 0.281 \pm 0.086 | 0.266 \pm 0.090 |
| 2006 | -0.015 \pm 0.024 | 0.239 \pm 0.110 | 0.252 \pm 0.116 |
| 2007 | 0.033 \pm 0.033 | 0.190 \pm 0.148 | 0.159 \pm 0.133 |
| Total | -0.010 \pm 0.008 | 0.215 \pm 0.103 | 0.223 \pm 0.103 |

We would expect individuals living solitarily to be either neutral, avoidant or agonistic to each other and individuals living in groups should exhibit behaviors that maintain relationships within the group. Within our population of adult round-tailed ground squirrels, few social behaviors occur above ground but tolerance of individuals in the aggregate was common. Overall rates of interactions between adults above ground were low and similar to other sciurid species, which range from 0.43 to 5.00/h (Morton 1975; Streubel 1975; Zegers 1981; Betts 1976; Leger et al. 1983; Loughry 1993).

Observation of social behaviors does not always imply a high degree of genetic relatedness among participants. Recently, evidence for the ecological selection hypothesis of group formation (Griffin and West 2002; West et al. 2002; Blundell et al. 2004; Matocq and Lacey 2004; Hare and Murie 2007; Túnez et al. 2009) suggests models based on mutualism, reciprocal altruism and ecological advantages (i.e., access to a limited resource or predator avoidance, Connor 1995; Mesterton-Gibbons and Dugatkin 1992) can favor and maintain social behaviors. Rates of vigilance in Columbian ground squirrels (*Urocitellus columbianus*) did not differ between kin groups or groups of unrelated members (Fairbanks and Dobson 2010). Social behaviors and tolerance of neighbors may occur despite a group having a low relatedness (Trivers 1971; Wrangham 1982), which may imply a high benefit-to-cost ratio for these associations and behaviors. Social behaviors of ground squirrels may be directed toward maximizing direct fitness instead of indirect fitness (Hamilton 1964; Armitage 1988) and therefore kin selection would not be necessary to explain the frequency of social behaviors.

Furthermore, occurrence of the population reduction and genetic bottleneck in our population of round-tailed ground squirrels did not change the genetic structure of the population nor alter rates of social behavior further supporting the overall low level of sociality within the population. A reduction in population size can modify population structure and rates of behavior (Meffert and Bryant 1991; Svobodová et al. 2011). An increase in population size may lead to an increase in agonistic interactions (Butler 1980) and a reduction in population size may lead to decreased agonistic and increased

Table 3 Pairwise F_{ST} values of round-tailed ground squirrels (*X. tereticaudus*) at the Casa Grande Ruins National Monument, Pinal Co., AZ from the program ARLEQUIN for each study plot per year. P values from jackknifing procedure (10,000) are reported in parentheses

| | Plot 1, 2007 | Plot 2, 2007 | Plot 1, 2006 | Plot 2, 2006 | Plot 1, 2005 | Plot 2, 2005 |
|--------------|---------------|--------------|--------------|---------------|--------------|--------------|
| Site 1, 2007 | 0 | | | | | |
| Site 2, 2007 | -0.024 (0.59) | 0 | | | | |
| Site 1, 2006 | 0.079 (0.14) | 0.010 (0.66) | 0 | | | |
| Site 2, 2006 | 0.034 (0.22) | 0.044 (0.10) | 0.042 (0.37) | 0 | | |
| Site 1, 2005 | -0.041 (0.99) | 0.013 (0.75) | 0.041 (0.57) | -0.004 (0.94) | 0 | |
| Site 2, 2005 | 0.016 (0.43) | 0.006 (0.52) | 0.025 (0.56) | 0.050 (0.20) | 0.018 (0.64) | 0 |

amicable behavior due to a reduction in the number of possible roles (Blumstein and Armitage 1998).

The majority of interactions between juvenile littermates were amicable (83 %) with agonistic interactions only observed in a single litter. The percentage of those interactions that were amicable is similar to other sciurid species, which range from nearly 100 to 30 % (Rayor and Armitage 1991). Neither amicable nor agonistic above-ground interactions between mother and offspring were observed. Social tolerance by adults towards young other than their own offspring is a necessary step in the evolution of sociality (Lott 1984); non-related adult and juvenile individuals did not interact.

Contrary to previous studies (Drabek 1973; Dunford 1977b), but similar to the predictions of the models of ground squirrel sociality (Armitage 1981; Michener 1983, 1984; Blumstein and Armitage 1998), female aggregates in our population of round-tailed ground squirrels were not highly related to each other and did not show subpopulation genetic structuring. Field observations showed a 97 % annual turnover rate for adult females and over 95 % of female natal dispersal from the study plots. Mean coefficient of relatedness for females on the plot were neither different overall, between plots for all 3 years, nor compared to relatedness among males. Bayesian analysis, global F_{ST} values for each year, and all pairwise F_{ST} values between study plots and years further support the lack of population substructure. Global F_{IS} values differed from zero, suggesting probable inbreeding; however, this may be due to the high degree of promiscuity and non-random mate choice (Weir and Cockerham 1984; Cockerham and Weir 1987; Chesser 1991) in this population (Munroe and Koprowski 2011) and confounded with the effects of a recent bottleneck due to target population reduction. Overall, these results suggest a lack of genetic structure within this population, but not panmixia.

Female kin associations occur among several species of ground-dwelling squirrels (Barash 1973, 1974; Slade and Balph 1974; Owings et al. 1977; Michener 1979; Festa-Bianchet 1981; Sherman 1981; McLean 1982; Harris and Murie 1984; Vestal and McCarley 1984; Hoogland 1995; van Staaden et al. 1996; Maher 2009). However, other ecological and environmental factors likely influence sociality in ground-dwelling sciurids, including predation, the distribution

and availability of resources in space and time (i.e., food, burrows) and harsh environments (Emlen and Oring 1977; Ebersperger 2001; Armitage 2007; Hare and Murie 2007).

Spatial distribution and general abundance of food resources do appear to have been instrumental in the evolution of ground squirrel sociality. In Gunnison's prairie dogs, social groups form in environments with patchy resource abundance (Slobodchikoff 1984; Travis and Slobodchikoff 1993; Travis et al. 1995). In black-tailed prairie dogs, although nepotism has been noted, amicable and aggressive interactions also varied between seasons rather than with degree of relatedness (Hoogland 1986). Within our study area, food resources, including creosote bushes, were evenly distributed (Woodell et al. 1969) but varied temporally through extreme environmental conditions with high daily temperatures and extended droughts (Munroe and Koprowski, in review).

Furthermore, predators on the site were common and included gopher snakes (*Pituophis melanoleucus*), Mohave rattlesnakes (*Crotalus scutulatus*), western diamondback rattlesnakes (*Crotalus atrox*), burrowing owls (*Athene cunicularia*), great-horned owls (*Bubo virginianus*), Cooper's hawks (*Accipiter cooperii*), red-tailed hawks (*Buteo jamaicensis*), badgers (*Taxidea taxus*), coyotes (*Canis latrans*), and feral dogs (*Canis familiaris*). Differences in resource availability, both spatially and temporally, may lead to different levels of sociality within the species, possibly resulting in different levels of sociality observed in this study compared to the previous study by Dunford (1975).

Under various ecological conditions, social organization may vary (Lott 1991); social and behavioral flexibility have been observed in Gunnison's prairie dogs (Travis et al. 1995), raccoons (Gehrt and Fritzell 1998; Ratnayeke et al. 2002), and woodchucks (Maher 2009, 2010). Round-tailed ground squirrels may have behavioral flexibility in dispersal that leads to different levels of social organization (Ratnayeke et al. 2002; Maher 2006; McEachern et al. 2007). Future research that experimentally tests the influence of food and resource abundance, density, habitat saturation, and density-dependent factors leading to delayed dispersal and shared space by female kin might help elucidate the proximate causation and ultimate benefits in this species (Wolff 1993, 1994; Le Galliard et al. 2005).

The rigid definition of sociality and its association with genetic relatedness should be modified to include alternative paths of group formation (i.e. ecological selection hypothesis), where all possible evolutionary costs and benefits of behaviors are considered regardless of degree of relatedness within the group (Hare and Murie 2007). Clustering of rodents may simply be due to high population densities rather than a stable social organization with social relationships and behaviors (Randall 1994, 2008). High densities, such as our population of round-tailed ground squirrels, may have the effect of creating a single aggregate such that kin clusters are not able to form (Hamilton 1964; Armitage 1975). Furthermore, social tolerance may be important for both social and solitary desert rodents because it minimizes the effects of physiological stress and water loss (Randall 2008).

Comparative data from a continuum of kin-structured societies including low to moderately kin-structured aggregates are important in order to delineate how social and fine-scale genetic structures co-vary and may lead to insights about the evolution of sociality in mammal populations (Dobson 1998). Similar levels of agonistic and amicable behavior were found in dyadic interactions among all juvenile Columbian ground squirrel (*U. columbianus*) colony members (Hare 1992) and replicated with evidence for a mechanism of indirect familiarization via chemical cues (Hare 1994). Social and genetic structure may be more common in solitary species than previously considered (Ratnayeke et al. 2002; Hare and Murie 2007; Maher 2009) and therefore it is imperative to compare the fine-scale genetic structure with levels of social behaviors. Social behaviors of ground squirrels may be directed toward maximizing direct fitness (i.e., access to limiting resource, predator alarm calls) and not indirect fitness (Armitage 1988; Fairbanks and Dobson 2010); therefore kin selection would not be necessary to explain the frequency of these behaviors. Furthermore, genetic and observational studies of intraspecific variation in spatial and social relationships may prove useful in resolving the conditions necessary for group formation, conditions that promote philopatry and kin-based sociality.

Ultimately, analyses of genetic relationships within aggregates of individuals may lead to insights to the origin of social behaviors, and environmental conditions that may facilitate group formation and maintenance of simple vertebrate social groups (Slobodchikoff and Shields 1988; Lacey 2000; Qi et al. 2012).

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References

- Alexander RD (1974) The evolution of social behavior. *Annu Rev Syst Ecol* 4:325–383
- Altmann J (1974) Observational study of behavior: sampling methods. *Behaviour* 49:227–267
- Anderson EC, Dunham KK (2008) The influence of family groups on inferences made with the program STRUCTURE. *Mol Ecol Resour* 8:1219–1229
- Armitage KB (1962) Social behaviour of a colony of the yellow-bellied marmot (*Marmota flaviventris*). *Anim Behav* 10:319–331
- Armitage KB (1975) Social behavior and population dynamics of marmots. *Oikos* 26:341–354
- Armitage KB (1981) Sociality as a life-history tactic of ground squirrels. *Oecologia* 48:36–49
- Armitage KB (1988) Resources and social organization of ground dwelling squirrels. In: Slobodchikoff CN (ed) *The ecology of social behavior*. Academic, NY, pp 131–155
- Armitage KB (1999) Evolution of sociality in marmots. *J Mammal* 80:1–10
- Armitage KB (2007) Evolution of sociality in marmots: it begins with hibernation. In: Wolff JO, Sherman PW (eds) *Rodent societies: an ecological and evolutionary perspective*. University of Chicago Press, Chicago, pp 356–367
- Barash DP (1973) The social behavior of the Olympic marmot. *Anim Behav Monogr* 6:171–249
- Barash DP (1974) The evolution of marmot societies: a general theory. *Science* 185:415–420
- Betts BJ (1976) Behaviour in a population of Columbian ground squirrels, *Spermophilus columbianus columbianus*. *Anim Behav* 24:652–680
- Blumstein DT, Armitage KB (1998) Life history consequences of social complexity: a comparative study of ground-dwelling sciurids. *Behav Ecol* 9:8–19
- Blundell GM, Ben-David M, Groves P, Bowyer RT, Geffen E (2004) Kinship and sociality in coastal river otters: are they related? *Behav Ecol* 15:705–714
- Bradbury JW, Vehrencamp SL (1976) Social organization and foraging in emballonurid bats. I: field studies. *Behav Ecol Sociobiol* 2:1–17
- Butler RG (1980) Population size, social behaviour, and dispersal in house mice: a quantitative investigation. *Anim Behav* 28:78–85
- Chesser RK (1991) Gene diversity and female philopatry. *Genetics* 127: 437–447
- Clutton-Brock TH, Lukas D (2012) The evolution of social philopatry and dispersal in female mammals. *Mol Ecol* 21:472–492
- Cockerham CC, Weir BS (1987) Correlations, descent measures: drift with migration and mutation. *Proc Natl Acad Sci U S A* 84:8512–8514
- Connor RC (1995) Altruism among non-relatives: alternatives to the ‘Prisoner’s Dilemma’. *Trends Ecol Evol* 10:84–86

- Cornuet JM, Luikart G (1996) Description and power analysis of two tests for detecting recent population bottlenecks from allele frequency data. *Genetics* 144:2001–2014
- 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
- Drabek CM (1973) Home range and daily activity of the round-tailed ground squirrel, *Spermophilus tereticaudus neglectus*. *Am Midl Nat* 89:287–293
- Dunford CJ (1975) Density limitation and the social system of round-tailed ground squirrels. Dissertation, University of Arizona
- Dunford CJ (1977a) Social system of round-tailed ground squirrels. *Anim Behav* 25:885–906
- Dunford CJ (1977b) Behavioral limitation of round-tailed ground squirrel density. *Ecology* 58:1254–1268
- Ebensperger LA (2001) On the evolution of group-living in the New World cursorial hystricognath rodents. *Behav Ecol* 12:227–236
- Emlen ST (1994) Benefits, constraints and the evolution of family. *Trends Ecol Evol* 9:282–285
- Emlen ST (1995) An evolutionary theory of the family. *Proc Natl Acad Sci U S A* 92:8092–8099
- Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215–223
- Ernest KA, Mares MA (1987) *Spermophilus tereticaudus*. *Mammal Spec* 274:1–9
- Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Mol Ecol* 14:2611–2620
- Excoffier L, Laval G, Schneider S (2005) Arlequin ver. 3.0: an integrated software package for population genetics data analysis. *Evol Bioinform* 1:47–50
- Fairbanks BM, Dobson FS (2010) Kinship does not affect vigilance in Columbian ground squirrels (*Urocitellus columbianus*). *Can J Zool* 88:266–270
- Falush D, Stephens M, Pritchard JK (2003) Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. *Genetics* 164:1567–1587
- Festa-Bianchet M (1981) Reproduction in yearling female Columbian ground squirrels *Spermophilus columbianus*. *Can J Zool* 59:1032–1035
- Garner A, Rachlow JL, Waits LP (2005) Genetic diversity and population divergence in fragmented habitats: conservation of Idaho ground squirrels. *Conserv Genet* 6:759–774
- Gehrt SD, Fritzell EK (1998) Resource distribution, female home range dispersion and male spatial interactions: group structure in a solitary carnivore. *Anim Behav* 55:1211–1227
- Glaubitz JC (2004) CONVERT: a user friendly program to reformat diploid genotypic data for commonly used population genetic software packages. *Mol Ecol Notes* 4:309–310
- Goudet J (1995) FSTAT (version 1.2): a computer program to calculate F-statistics. *J Heredity* 86:485–486
- Greenwood PJ (1980) Mating systems, philopatry, and dispersal in birds and mammals. *Anim Behav* 28:1140–1162
- Griffin AS, West SA (2002) Kin selection: fact and fiction. *Trends Ecol Evol* 17:15–21
- Hall ER (1981) The mammals of North America. Wiley, NY
- Hamilton WD (1964) The genetical evolution of social behavior I and II. *J Theor Biol* 7:1–52
- Hare JF (1992) Colony member discrimination by juvenile Columbian ground-squirrels (*Spermophilus columbianus*). *Ethology* 92:301–315
- Hare JF (1994) Group member discrimination by Columbian ground squirrels via familiarity with substrate-borne chemical cues. *Anim Behav* 47:803–813
- Hare JF, Murie JO (2007) Ecology, kinship, and ground squirrel sociality: insights from comparative analyses. In: Wolff JO, Sherman PW (eds) *Rodent societies: an ecological and evolutionary perspective*. The University of Chicago Press, Chicago, pp 345–355
- Harris MA, Murie JO (1984) Inheritance of nest sites in female Columbian ground squirrels. *Behav Ecol Sociobiol* 15:96–102
- Hartl DL, Clark AG (1997) Principles of population genetics, 3rd edn. Sinauer, Sunderland
- Hoogland JL (1986) Nepotism in prairie dogs (*Cynomys ludovicianus*) varies with competition but not with kinship. *Anim Behav* 34:263–270
- Hoogland JL (1995) The black-tailed prairie dog: social life of a burrowing mammal. The University of Chicago Press, Chicago
- Iverson SL, Turner BN (1972) Natural history of a Manitoba population of Franklin's ground squirrels. *Can Field Nat* 86:145–149
- Koprowski JL (1996) Natal philopatry, communal nesting and kinship in fox squirrels and gray squirrels. *J Mammal* 77:1006–1016
- Koprowski JL (2002) Handling tree squirrels with a safe and efficient restraint. *Wildl Soc Bull* 30:101–103
- Lacey EA (2000) Spatial and social systems of subterranean rodents. In: Lacey EA, Patton JL, Cameron GN (eds) *Life underground: the biology of subterranean rodents*. University of Chicago Press, Chicago, pp 257–293
- Le Galliard J, Ferrière R, Dieckmann U (2005) Adaptive evolution of social traits: origin, trajectories, and correlations of altruism and mobility. *Am Nat* 165:206–224
- Leger DW, Owings DH, Coss RG (1983) Behavioral ecology of time allocation in California ground squirrels (*Spermophilus beecheyi*): microhabitat effects. *J Comp Psychol* 97:283–291
- Lott DF (1984) Intraspecific variation in the social systems of wild vertebrates. *Behaviour* 88:266–325
- Lott DF (1991) Intraspecific variation in the social systems of wild vertebrates. Cambridge University Press, Cambridge
- Loughry WJ (1993) Determinants of time allocation by adult and yearling black-tailed prairie dogs. *Behaviour* 124:23–43
- Maher CR (2006) Social organization in woodchucks (*Marmota monax*) and its relationship to growing season. *Ethology* 112:313–324
- Maher CR (2009) Effects of relatedness on social interaction rates in a solitary marmot. *Anim Behav* 78:925–933
- Maher CR (2010) Mating system and paternity in woodchucks (*Marmota monax*). *J Mammal* 91:628–635
- Matocq MD, Lacey EA (2004) Philopatry, kin clusters and genetic relatedness in a population of woodrats (*Neotoma macrotis*). *Behav Ecol* 15:647–653
- May BT, Gavin A, Sherman PW, Korves TM (1997) Characterization of microsatellite loci in the northern Idaho ground squirrel, *Spermophilus brunneus*. *Mol Ecol* 6:399–400
- McEachern MB, Eadie JM, VanVuren DH (2007) Local genetic structure and relatedness in a solitary mammal, *Neotoma fuscipes*. *Behav Ecol Sociobiol* 61:1459–1469
- McLean IG (1982) The association of female kin in the Arctic ground squirrel, *Spermophilus parryi*. *Behav Ecol Sociobiol* 10:91–99
- Meffert LM, Bryant EH (1991) Mating propensity and courtship behavior in serially bottlenecked lines of the housefly. *Evolution* 45:293–306
- Mesterton-Gibbons M, Dugatkin LA (1992) Cooperation among unrelated individuals: evolutionary factors. *Q Rev Biol* 67:267–281
- Michener GR (1979) The circannual cycle of Richardson's ground squirrels in southern Alberta. *J Mammal* 60:760–768
- Michener GR (1983) Kin identification, matriarchies, and the evolution of sociality in ground-dwelling sciurids. In: Eisenberg JF, Heiman DC (eds) *Advances in the study of mammalian behavior*. Special Publications of the American Society of Mammalogy no 7. American Society of Mammalogists, Shippensburg, pp 528–572.
- Michener GR (1984) Age, sex, and species differences in the annual cycles of ground-dwelling sciurids: implications for sociality. In: Murie JO, Michener GR (eds) *The biology of ground-dwelling*

- squirrels: annual cycles, behavioral ecology, and sociality. University of Nebraska Press, Lincoln, pp 81–107
- Morton ML (1975) Seasonal cycles of body weights and lipids in Belding ground squirrels. *Bull S Calif Acad Sci* 74:128–143
- Munroe KE, Koprowski JL (2011) Sociality, Bateman's gradients and the polygynandrous genetic mating system of round-tailed ground squirrels (*Xerospermophilus tereticaudus*). *Behav Ecol Sociobiol* 65:1811–1824
- Murie JO (1973) Population characteristics and phenology of a Franklin ground squirrel (*Spermophilus franklinii*) colony in Alberta, Canada. *Am Midl Nat* 90:334–340
- Neal BJ (1965) Reproductive habits of round-tailed and Harris antelope ground squirrels. *J Mammal* 46:200–206
- Nei M (1977) F-statistics and analysis of gene diversity in subdivided populations. *Ann Hum Genet* 41:225–233
- Owings DH, Borchert M, Virginia R (1977) The behaviour of California ground squirrels. *Anim Behav* 25:221–230
- Piry S, Luikart G, Cornuet JM (1999) BOTTLENECK: a computer program for detecting recent reductions in the effective population size using allele frequency data. *J Hered* 90:502–503
- Pritchard JK, Wen W (2002) Documentation for Structure software, Version 2.0. University of Chicago, Illinois
- Pritchard JK, Stephens P, Donnelly P (2000) Inference of population structure using multilocus genotype data. *Genetics* 155:945–959
- Qi Y, Noble DWA, Fu J, Martin J (2012) Whiting spatial and social organization in a burrow-dwelling lizard (*Phrynocephalus vlangalii*) from China. *PLoS ONE* 7:e41130
- Queller DC, Goodnight KF (1989) Estimating relatedness using genetic markers. *Evolution* 43:258–275
- Randall JA (1994) Convergence and divergence in communication and social organization of desert rodents. *Aust J Zool* 42:405–433
- Randall JA (2008) Environmental constraints and the evolution of sociality in semi-fossorial desert rodents. In: Wolff JO, Sherman PW (eds) *Rodent societies*. Chicago University Press, Illinois, pp 368–379
- Ratnayeke S, Tuskan GA, Pelton MR (2002) Genetic relatedness and female spatial organization in a solitary carnivore, the raccoon, *Procyon lotor*. *Mol Ecol* 11:1115–1124
- Rayor LS, Armitage KB (1991) Social behavior and space-use of young of ground-dwelling squirrel species with different levels of sociality. *Ethol Ecol Evol* 3:185–205
- Rood JP, Nellis DW (1980) Freeze marking mongooses. *J Wildlife Manage* 44:500–502
- Rousset F (2008) GENEPOP 2007: a complete re-implementation of the GENEPOP software for Windows and Linux. *Mol Ecol Res* 8:103–106
- Sambrook J, Russell DW (2001) *Molecular cloning: a laboratory manual*, 3rd edn. Cold Spring Harbor Laboratory Press, NY
- SAS Institute, Inc (2003) *JMP statistics and graphics guide*. SAS Institute, Cary
- Schwacke L, Schwacke J, Rosel P (2005) RERAT: relatedness estimation and rarefaction analysis tool. Available from: <http://people.musc.edu/~schwackl/>. Accessed on 5 July 2013
- Sherman PW (1981) Kinship, demography, and Belding's ground squirrel nepotism. *Behav Ecol Sociobiol* 8:251–259
- Sikes RS, Gannon WL, The animal care and use committee of the American Society of Mammalogists (2011) Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *J Mammal* 92:235–253
- Slade NA, Balph DF (1974) Population ecology of Uinta ground squirrels. *Ecology* 55:989–1003
- Slobodchikoff CN (1984) Resources and the evolution of social behavior. In: Price PW, Slobodchikoff CN, Gaud WS (eds) *A new ecology: novel approaches to interactive systems*. Wiley, NY, pp 227–251
- Slobodchikoff CN, Shields WM (1988) Ecological trade-offs and social behavior. In: Slobodchikoff CN (ed) *The ecology of social behavior*. Academic, NY, pp 3–10
- Stevens S, Coffin J, Strobeck C (1997) Microsatellite loci in Columbian ground squirrels *Spermophilus columbianus*. *Mol Ecol* 6:493–495
- Streubel DP (1975) Behavioral features of sympatry of *Spermophilus spilosoma* and *Spermophilus tridecemlineatus* and some aspects of the life history of *S. spilosoma*. Dissertation, University of Northern Colorado, Greeley
- Sugg DWCR, Chesser RK, Dobson FS, Hoogland JL (1996) Population genetics meets behavioral ecology. *Trends Ecol Evol* 11:338–342
- Svobodová J, Segelbacher G, Höglund J (2011) Genetic variation in black grouse populations with different lekking systems in the Czech Republic. *J Ornithol* 152:37–44
- Travis SE, Slobodchikoff CN (1993) Effects of food resource distribution on the social system of Gunnison's prairie dog (*Cynomys gunnisoni*). *Can J Zool* 71:1186–1192
- Travis SE, Slobodchikoff CN, Keim P (1995) Ecological and demographic effects on intraspecific variation in the social system of prairie dogs. *Ecology* 76:1794–1803
- Trivers RL (1971) The evolution of reciprocal altruism. *Q Rev Biol* 46:35–57
- Trivers RL (1985) *Social evolution*. Benjamin/Cummings, Menlo Park
- Túnez JI, Guichon L, Centron D, Henderson AP, Callahan C, Cassini MH (2009) Relatedness and social organization of coypus in the Argentinean pampas. *Mol Ecol* 18:147–155
- van Staaden MJ, Michener GR, Chesser RK (1996) Spatial analysis of microgeographic genetic structure in Richardson's ground squirrels. *Can J Zool* 74:1187–1195
- Vestal BM, McCarley H (1984) Spatial and social relations of kin in ground squirrels. In: Murie JO, Michener GR (eds) *The biology of ground-dwelling squirrels*. University of Nebraska Press, Nebraska, pp 404–423
- Waples RS, Gaggiotti O (2006) What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. *Mol Ecol* 15:1419–1440
- Weir BS, Cockerham CC (1984) Estimating F-statistics for the analysis of population structure. *Evolution* 38:1358–1370
- West SA, Pen I, Griffin AS (2002) Cooperation and competition between relatives. *Science* 296:72–75
- Wolff JO (1993) What is the role of adults in mammalian juvenile dispersal? *Oikos* 68:173–175
- Wolff JO (1994) Population regulation in mammals: an evolutionary perspective. *J Anim Ecol* 66:1–13
- Woodell SRJ, Mooney HA, Hill AJ (1969) The behaviour of *Larrea divaricata* (Creosote Bush) in response to rainfall in California. *J Ecol* 57:37–44
- Wrangham RW (1982) Mutualism, kinship and social evolution. In: King's College Sociobiology Group (ed) *Current problems in sociobiology*. Cambridge University Press, England, pp 269–289
- Wrangham RW, Rubenstein DI (1986) Social evolution in birds and mammals. In: Rubenstein DI, Wrangham RW (eds) *Ecological aspects of social evolution*. Princeton University Press, New Jersey, pp 452–470
- Wright S (1931) Evolution in Mendelian population. *Genetics* 16:97–159
- Wright S (1965) The interpretation of population structure by F-statistics with special regard to systems of mating. *Evolution* 19:395–420
- Wright S (1978) Evolution and the genetics of population, variability within and among natural populations. The University of Chicago Press, Chicago
- Zar JH (1999) *Biostatistical analysis*. Prentice-Hall, New Jersey
- Zegers DA (1981) Time budgets of Wyoming ground squirrels, *Spermophilus elegans*. *Great Basin Nat* 41:221–228