



Social organization in a North African ground squirrel

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Research on sociality in temperate ground-dwelling squirrels has focused on female philopatry and other life history trade-offs, which are influenced by constraints in the duration of the active growing season. Temperate ground-dwelling squirrels that experience high predation pressure, are large in body size, and have a short active season, show a more complex social organization. In contrast, African ground squirrels are active year-round, suggesting that instead of a short active season, distinct selective pressures influence their social organization. We examined the social organization of Barbary ground squirrels, *Atlantoxerus getulus*, and compared the social organization of temperate and African ground-dwelling sciurids. Anecdotal accounts on Barbary ground squirrels' social organization suggested that they were either solitary or gregarious, or live in small family groups. We recorded the group size, composition, cohesion, and genetic relatedness, of the population on the arid island of Fuerteventura, Spain. Our data indicate that females live in small (1–8) all-female kin groups separate from adult males, and that unrelated adult males share sleeping burrows with immature individuals of either sex. We observed sex-biased dispersal with males primarily the dispersing sex and females primarily philopatric. Females sleep solitarily during gestation and lactation and nest either communally or singly after juvenile emergence. During the day, males and females can be active in the same area. Barbary ground squirrels are social because the squirrels share sleeping burrows and show spatiotemporal overlap. Barbary ground squirrels' social organization resembles that of the closely related Cape ground squirrel rather than that of the temperate ground-dwelling sciurids, although the former are more temperate, seasonal breeders. In addition to describing the social organization of a previously unstudied species, this paper sheds light on the ecological drivers of sociality, and the evolution of distinct social organizations in ground-dwelling sciurids.

Key words: fission–fusion, group-living, home range, invasive species, Marmotini, nonhibernating, rodents, sexual segregation, tolerance, Xerini

Spatiotemporal distribution and social interactions among conspecifics help to characterize a species' grouping pattern (Lacey and Sherman 2007). For example, solitary species do not share space with conspecifics, species that form aggregations do so but do not, or rarely, interact with one another (Parrish et al. 1997; Munroe and Koprowski 2014), and species that live in social groups share space and interact with conspecifics of different ages and sexes (e.g., overlapping home ranges, performing social behaviors, and communicating—Hamilton 1964; Alexander 1974; Wilson 1975; Armitage 1981; Ebensperger 2001; Silk 2007). Accordingly, sociality is defined as “any set of organisms, belonging to the same species that remain together for a period of time interacting with one another to a distinctly greater degree than with other

conspecifics” (Wilson 1975). Thus, sociality includes social organization (i.e., group size, composition, cohesion, and genetic relatedness—Kappeler 2019) and social interactions among conspecifics (i.e., social structure—Hinde 1976). Selective pressures leading to grouping may be genetic (Hamilton 1964), phylogenetic (Sobrero et al. 2014), ecological (Emlen 1982), or sociobiological (Armitage 1981; Blumstein and Armitage 1998), and these pressures are not mutually exclusive (Thierry 2008).

Comparative studies are useful to decouple drivers of sociality to understand the selective forces behind particular social organizations. However, measures of sociality often differ among studied taxa, making comparisons difficult (Gromov 2017). In addition, the classification scheme for sociality may

vary depending on whether the researcher bases the characterization on sociobiological (female philopatry, mating system, life history), ecological, or phylogenetic aspects. Finally, no consensus exists on how to characterize sociality (Kappeler et al. 2019; but see Prox and Farine 2020). For example, the four currently characterized levels of primate social organization are based on mating system (Schaik and Hooff 1983), while the five levels in antelopes are influenced by ecology and mating system (Jarman 1974).

Social organization in temperate ground-dwelling squirrels (rodent family Sciuridae, tribe Marmotini) is categorized into five distinct levels, but these are not always coincident among authors (Armitage 1981; Michener 1983). Michener (1983) characterized the levels from asocial, single-family female kin clusters, female kin clusters/male territoriality, polygynous harems/male dominance, and egalitarian polygynous harems, and argued that female philopatry characterizes a species' social organization. Armitage (1981) also defined five levels, ranging from solitary-living to living in colonies with both males and females living individually, or females living separately with male territoriality, harem (females share burrows and male territoriality), and multi-harem colonies, and reasoned that the social organization is primarily defined by a species' life history strategy. Further, Blumstein and Armitage (1998) found that species with reproductive skew, later maturity, smaller litters, and higher juvenile survival showed greater levels of sociality, supporting the role that life history plays in a species' social organization. However, the overall tendency is for agreement that female matrilineal kin groups characterize the level of sociality for these ground squirrels (Armitage 1981; Michener 1983; Blumstein and Armitage 1998; Hare and Murie 2007).

Comparative studies of diurnal, semifossorial, temperate ground-dwelling squirrels suggest that levels of sociality are higher for squirrels that experience high predation pressure, are larger in body size and absolute brain size, and have a shorter active season (Armitage 1981; Hoogland 1981; Michener 1983; Blumstein and Armitage 1998; Hare and Murie 2007; Matějů et al. 2016). Ground-dwelling squirrels that live in a nutrition-deprived habitat due to environmental pressures (e.g., short active season) may show a delay in juvenile dispersal (Barash 1974; Armitage 1981, 2017; Michener 1983, 1984). In addition, these harsh climatic conditions increase levels of sociality in sciurids because the species that hibernate in groups derive thermoregulatory benefits (Arnold 1990). Thus, living in a harsh environment (long, cold winters) influences temperate ground-dwelling squirrels' social organization, but a short active season may not be relevant to explain grouping in ground-dwelling squirrels living in environments without this constraint.

The African ground squirrels (tribe Xerini)—a sister tribe to the temperate ground-dwelling squirrels—are diurnal, semifossorial rodents with a year-round active season (Happold 2013). Different selective pressures, such as a low amount and unpredictable timing of rainfall (Shenbrot 2014) rather than a short temperate growing season, may influence their social organization. For example, the Cape ground squirrel, *Xerus*

inauris, is a social species that does not fit the sociality index of the temperate ground squirrels (Waterman 1995). Although similar to temperate ground squirrel species, female Cape ground squirrels live in matrilineal groups (Waterman 1995). Male Cape ground squirrels group with unrelated males to gain access to reproductive females that can come into estrus year-round (Waterman 1997), a situation different from that in any temperate ground squirrel species. Few data are available for the other species in this genus, but at least three of the five species appear to be solitary (Happold 2013). The small-bodied Barbary ground squirrel *Atlantoxerus getulus* is potentially the only other social species in the tribe Xerini: anecdotal information published on the social organization either reports that the species is gregarious (Machado 1979), or that their group composition varies within their endemic range from solitary to living in small family groups of 2–3 individuals (Gouat and Yahyaoui 2001). However, no comprehensive study has yet focused on the Barbary ground squirrel's social organization.

In this context, we first examined Barbary ground squirrels' social organization and compared their social organization with that of temperate ground-dwelling squirrels to ascertain similarities and differences. We also undertook comparisons between Barbary ground squirrels (more temperate and seasonal breeders—van der Marel 2019) and the closely related Cape ground squirrels (because Barbary ground squirrels are also active year-round—Machado and Domínguez 1982). If matrilineal kin groups are the foundation for female grouping patterns, as in other ground squirrel species, then we predict that females are the philopatric sex and that they will live in small, cohesive family groups. If males follow the temperate ground squirrel pattern, then males will be the dispersing sex and will not group. If males follow the Cape ground squirrel pattern, then they will be the dispersing sex and male group formation will occur among unrelated males, i.e., the observed relatedness will not differ from expected relatedness. Second, we aimed to compare our results with the social organization characteristics of other ground-dwelling sciurids to develop a more comprehensive framework for the evolution of sociality in ground-dwelling sciurids.

MATERIALS AND METHODS

Barbary Ground Squirrel Social Organization

Species, study sites, and climatic data.—We studied an invasive population of Barbary ground squirrels, *A. getulus*, on the island of Fuerteventura, Canary Islands, Spain. This species is the only species currently recognized in the genus (Kryštufek et al. 2016) and is native to Morocco and parts of Algeria (Aulagnier and Thévenot 1986). The Barbary ground squirrel is active year-round, diurnal (Machado and Domínguez 1982; van der Marel et al. 2019), small-bodied (< 250 g—Machado and Domínguez 1982; Roth and Thorington 1982); a seasonal breeder (van der Marel 2019); and possibly an obligate rock-specialist (Nutt 2007). Since the first introduction of two individuals from Morocco to Fuerteventura in 1965 (Machado 1979), the population has grown to an

estimated population density of 296 squirrels/ha; no additional introductions have been reported since their initial arrival (López-Darias 2007).

We selected three study sites for this study, each 0.73 ± 0.03 (mean \pm SE) km distant from the others: Site 1: $28^{\circ}35'58.1''\text{N}$, $13^{\circ}59'49.15''\text{W}$; Site 2: $28^{\circ}35'36.81''\text{N}$, $13^{\circ}59'48.71''\text{W}$; and Site 3: $28^{\circ}35'38.51''\text{N}$, $14^{\circ}00'01.41''\text{W}$ (Piquet et al. 2018; van der Marel et al. 2019). The sites do not represent three distinct populations of squirrels: we observed that males from different sites searched for females in estrus in the other sites during the mating season (A. van der Marel, pers. obs.), and we found no genetic differentiation among sites (Supplementary Data SD1). We defined the mating season as the period when females in any of our sites were in estrus.

Fuerteventura is a volcanic island characterized by arid climate with year-round temperatures of $\sim 20^{\circ}\text{C}$ and low rainfall (average < 100 mm/year) and semidesert rocky habitats similar to those of their natural range (Machado 1979; López-Darias and Lobo 2008; López-Darias et al. 2008). Ravines caused by erosion and numerous man-made rock walls and dams that fence properties and form terraces for land cultivation characterize the sites and the island (López-Darias and Lobo 2008). The rock structures function as shelters and lookout perches for the squirrels (López-Darias and Lobo 2008; van der Marel et al. 2019).

Trapping and marking.—We trapped Barbary ground squirrels in the mornings and afternoons approximately once a week from March through July 2014, and January through July 2015 and 2016. These months encompassed three breeding seasons. We captured squirrels using live traps (Tomahawk Live Trap Co., Hazelhurst, Wisconsin; $13 \times 13 \times 40$ cm) baited with peanut butter. In addition to checking the traps every 45–60 min, we covered the traps with cardboard and placed them strategically to avoid direct sunlight, thus minimizing heat-induced stress. To reduce stress during handling, we transferred the squirrels into a conical handling bag (Koprowski 2002). For individual identification, we implanted a sterile 0.1 g, 2.1×12 mm passive integrated transponder (PIT) tag (Avid Identification Systems, Inc., Norco, California) subcutaneously on the back between the middle and right stripe of adult squirrels and gave the adults a unique dorsal dye mark (Melchior and Iwen 1965). Juveniles (individuals newly emerged from their nest burrow up to 6 months of age) received ear tags (#1005 Size 1 Monel, National Band and Tag Co., Newport, Kentucky) with differently color-coded thread attached. Upon first capture, we also collected DNA samples (2–3 mm tissue of the tail tip stored in 95% ethanol—Griffin et al. 2003). We determined the sex of the squirrels based on the appearance of the external genitalia, and classified animals as subadults or adults by looking at the swelling of the nipples for females and the development of the scrotum for males. Subadult males were those males that have reached adult body size but had nondescended testes during the breeding season, while adult males had descended testes during the breeding season. Subadult females were those females that had small nipples, as the nipples elongate and swell after their first successful parturition (Waterman 1996).

Behavioral observations.—To determine social organization, we collected observational data during the study period. We used binoculars (Zwallow 8 \times 42; Vogelbescherming, Zeist, The Netherlands) to observe squirrels from approximately 50 m from roads and nearby elevated areas. We collected observational data from first emergence in the morning until immergence into sleeping burrows in the evening. Every 10 min, we recorded the identity, location, and activities of all squirrels using scan sampling (Altmann 1974); specific recorded behaviors followed Waterman (1995). To note down the observations, we used Numbers (Apple, Cupertino, California) and “Prim8” software (McDonald and Johnson 2014) on an iPod (Apple, Cupertino, California) and an Android phone (Motorola Droid A850), respectively. We recorded the locations of the squirrels using an adjusted Cartesian grid of 10×10 m using the centers of the main rock walls or dams that crossed the site as our zero points. From those zero points, we marked every 10 m on the rock walls and other rock outcroppings in each wind direction with differently colored spray paint. We recorded the zero points in Universal Transverse Mercator (UTM) units with a GPS (Garmin GPSmap 78; Garmin International, Inc., Olathe, Kansas) using the EPSG:4083 REGCAN95/UTM zone 28N coordinate system, and referenced all other points in space using the Cartesian grid relative to those zero points.

Group size, composition, and cohesion.—We defined a social group as individuals sharing sleeping burrows with one another, which also is used as social group definition in other semifossorial rodent species (Waterman 1995, 1997; Hayes et al. 2009; Davis et al. 2016). We included only observations with complete information about immergence into sleeping burrows at night or emergence in the morning from the same burrow entrance. We measured the level of stability of the female social groups (group cohesion) using an association index of individuals that shared a sleeping burrow for the night. We used all males within a site as our sample size for male group cohesion, as males varied regularly in their sleeping associations. We were unable to obtain calibration data, i.e., group and individual identification errors; we therefore used the simple ratio index, SRI, as suggested by Hoppitt and Farine (2017). This index measures the proportion of time two individuals shared a sleeping burrow to the total time they were observed. The SRI varies from one (two individuals were always observed together) to zero (they were never observed together).

Throughout the day, patterns of group formation and sexual segregation might differ from those present at night (Radespiel et al. 2001). We therefore also calculated the mean percentage of adult males and females in a 60-m radius within a 10-min scan using all our scan samples. The 60-m radius is the distance a ground squirrel can see when on the ground (see van der Marel et al. 2019 for description and justification of the 60-m radius). We excluded days that females were in estrus from this analysis. We also used nearest neighbor dyads (either individuals observed within 1 m of each other or individuals that were observed in the same location during a scan excluding scans on days that females were in estrus) to analyze grouping patterns during the day.

Density and spatiotemporal overlap.—We measured the size of the three sites by walking around the rock walls that bordered the ravines and stony plains with a GPS (Garmin GPSmap 78, Garmin International Inc., Olathe, Kansas) and treated the linear distance as the perimeter of the site. We considered the rock walls as the edge of the site, because the ground squirrels rarely ventured out onto the stony plains, except for males during the mating season (A. van der Marel, pers. obs.). The squirrels therefore are clustered around the rock walls that fence properties and form terraces for land cultivation, particularly in small ravines (López-Darias and Lobo 2008; Rihane et al. 2019). We established our field sites in 2014, but increased the size of the sites in 2015 to include more social groups (Table 1). We estimated densities each year by dividing the number of adults by the size of the study sites, which we adjusted with the expansions.

To determine home ranges and home range overlap, we used the locations of both males and females from our 10-min scan samples outside of the mating season, only selecting individuals with more than 20 observations for final calculations. We observed males from March through August 2014 (mean \pm SD = 125.5 \pm 92.1 observations). For females, we divided the nonmating season into two different periods: a pre-juvenile emergence period from March to May 2014 (60.3 \pm 23.7, mean \pm SD, observations) and a post-juvenile emergence period from May to August 2014 (75.9 \pm 52.7 observations) and April to July 2015 (39.1 \pm 15.9 observations), because female African ground squirrels sleep solitarily with their offspring during lactation, i.e., during the pre-juvenile emergence period (Waterman 2002). We calculated home ranges using a kernel density estimator (Worton 1989; Signer and Balkenhol 2015). As bandwidth parameter, we used the reference bandwidth because it works best with clustered data (Signer and Balkenhol 2015). For contour levels, we used a 50% contour level (hereafter kde50) to measure core areas and a 95% contour level (kde95) to prevent overestimation of the home ranges (Laver and Kelly 2008). To calculate the kde95 overlap among females and males outside the mating season, we used the utilization distribution overlap index (UDOI). This index measures home range overlap of two individuals while taking the probability distribution of the individuals' space use into account (Fieberg and Kochanny 2005). The UDOI index can range from 0% overlap (0) to more than 100% overlap (> 1). The latter may occur if there is substantial overlap between the utilization

distributions of two individuals and if their utilization distributions are nonuniformly distributed.

We trapped sites regularly after juvenile emergence to measure natal philopatry and dispersal of juveniles. Upon arrival the following field season, newly trapped individuals either were immigrants, or some unmarked juveniles from the previous field season due to our inability to trap all newly emerged juveniles before we left the field at the end of the summer.

Genetic relatedness.—We extracted DNA from 189 tissue samples using the Chelex extraction protocol (Detwiler et al. 2012). We describe microsatellite characterization in Supplementary Data SD1. We excluded primers with error rates of over 50% or with potential null alleles ($N = 7$) and individuals typed at fewer than six loci ($N = 4$). We genotyped our samples from 2014 ($N = 171$) using 11 microsatellite loci to determine kinship (Supplementary Data SD2). We used the program Genecap version 1.2.2 to check our data set for double and problematic genotypes with the matching sibling probability set to lower than 0.05 (Wilberg and Dreher 2004). We then carried out a Pearson's correlation of observed and expected relatedness estimates using a simulated data set of 1,000 individuals with the same locus characteristics to assess the best of seven distinct estimators (Van De Castelee et al. 2001; Wang 2011; Taylor 2015).

Statistical analysis.—All statistical analyses were undertaken in R version 3.5.1 (R Development Core Team 2012) unless stated otherwise. Data for all 3 years were pooled except when stated to the contrary. We used nonparametric tests if the assumptions of a normal distribution and homogeneous variances were violated. We report the mean \pm SE unless stated otherwise; alpha was set to 0.05 for statistical analyses. Figures were made with the R packages "ggplot2" version 3.0.0 (Wickham 2009) and "Survival" version 2.43-1 (Therneau and Grambsch 2000; Therneau 2015).

We tested whether males were more likely to share sleeping burrows with other males or with adult females or subadults of either sex using a binomial exact test with an assumed probability of 0.5. For group size measurements, we combined different group compositions. We tested for group size differences per season for males and females separately using a Mann-Whitney U -test.

To calculate the SRI of adult ground squirrels, we used the package "asnipe" version 1.1.11 (Farine 2018). We tested for

Table 1.—The size of the sites per year in ha, the total number of adults and subadults Barbary ground squirrels (N), and their density (individuals/ha) per site and year on Fuerteventura Island, Spain.

		Site 1			Site 2			Site 3		
		ha	N	ind/ha	ha	N	ind/ha	ha	N	ind/ha
2014	Females	1.19	10	8.42	5.73	21	3.66	2.39	15	6.27
	Males		13	10.94		14	2.44		13	5.44
	Total		23	19.36		35	6.11		28	11.71
2015	Females	2.31	20	8.66	5.73	29	5.06	4.47	20	4.48
	Males		14	6.06		24	4.19		14	3.13
	Total		34	14.73		53	9.25		34	7.61
2016	Females	2.31	25	10.83	5.73	38	6.63	4.47	19	4.25
	Males		16	6.93		24	4.19		16	3.58
	Total		41	17.76		62	10.80		35	7.84

SRI differences between sexes and among seasons (mating and nonmating period) and their interaction term using a generalized linear mixed model (GLMM) for a zero-inflated beta distribution using a zero-inflated beta regression in the package “*gamlss*” version 5.1-2 (Rigby and Stasinopoulos 2005). Males and the mating season were set as the reference values. We used site as our random effect. We then analyzed female SRI across seasons (mating, pre-, and post-juvenile, emergence period) with a zero-inflated beta regression with site as random factor. We used residual diagnostics to validate the model. We carried out a likelihood-ratio (LR) test between the model and a null model using the “*lmtest*” package version 0.9-36 (Zeileis 2002).

We used the “*adehabitatHR*” package version 0.4.15 (Calenge 2006) to measure home ranges and home range overlap. We log-transformed our home range estimates to meet the normal distribution assumption. As we only selected individuals with more than 20 observations, we did not have data for males and females per season for each year and each site. We therefore carried out paired *t*-tests on our 50% and 95% kernel density estimator contour levels to test for size differences in female home ranges between the pre- and post-juvenile emergence period in 2014, and an unpaired *t*-test between male and female home ranges in the nonmating period. We also carried out an unpaired *t*-test to test for sex differences in home range overlap. We used the Kaplan–Meier approach on juvenile persistence within their natal site using the “*Survival*” package, version 2.43-1 (Therneau and Grambsch 2000; Therneau 2015).

We used the package “*Related*” version 1.0 in R version 3.4.1 for our relatedness estimation (Pew et al. 2015; R Development Core Team 2012). We calculated “observed” average relatedness separately within female and male social groups. We then generated “expected” average relatedness values by shuffling individuals of the same sex among groups using 1,000 randomization steps while keeping the size of the groups constant (Pew et al. 2015). If average relatedness within social groups was random, then observed relatedness would not differ from that expected by chance. If average relatedness was not random, then observed relatedness would be greater than expected by chance. Next, we log-transformed observed relatedness to meet the normal distribution assumptions and performed a linear regression on average relatedness and adult group size.

Ethical note.—It was not possible to record data blind because our study involved focal animals in the field. Research on live animals followed ASM guidelines (Sikes et al. 2016), and was approved by the University of Manitoba Animal Care and Use Committee, protocol no. F14-032, and the government of Fuerteventura, Cabildo Insular de Fuerteventura no. 14885.

Ground-Dwelling Sciurids’ Social Organization Comparison

We compared social organization characteristics of the Barbary ground squirrels with those of other African ground squirrels (excluding long-clawed ground squirrel, *Spermophilopsis leptodactylus*) and a subset of North American ground-dwelling sciurids following the selection of Armitage (1981) and Michener (1983). In our comparison table, we added female

body weight in grams (data derived from Hayssen 2008). We also included the sociality index developed by Armitage (1981) with the following levels: 1 = solitary-living; 2 = living in colonies with both males and females living individually; 3 = females living separately with male territoriality; 4 = harem (females share burrows and male territoriality); and 5 = multi-harem colonies. In addition, we included the sociality index developed by Michener (1983), which included the following levels: 1 = asocial; 2 = single-family female kin clusters; 3 = female kin clusters/male territoriality; 4 = polygynous harems/male dominance; and 5 = egalitarian polygynous harems. We then followed the social organization framework developed by Prox and Farine (2020). This framework labels eight different variables within three categories: organization, group composition, and group cohesion, and describes social organization to enable comparative analyses to decouple drivers of sociality (Prox and Farine 2020). We slightly adjusted the framework developed by Prox and Farine (2020). In their organization category, we also included the following three variables: primary units, tolerance levels, and levels of organization. Similar to the framework, we used solitary-living, pair-living, family-living, and group-living, as our primary units. As our tolerance levels, we had *open*, which meant that individuals can move freely between primary units and aggression is rare; *tolerant*, where individuals can mix, but where low levels of agonistic interactions are observed; and *intolerant*, with territorial individuals or groups. We changed the variable called “organizational levels” by Prox and Farine (2020) to “overlap,” which consist of either *no overlap* (0), where solitary individuals or groups do not have overlapping home ranges; and *overlap* (1) for species where there is considerable home range overlap and tolerance toward neighboring individuals or groups, such as for solitary individuals living in aggregations or family groups living in colonies; we excluded multilevel societies as a level. The second category, group composition, consisted of offspring membership, sex ratio, and group size. Offspring membership consisted of a level where offspring disperses before they reach sexual maturity (*short* instead of limited); a level with generations of overlap (*extended*); and a level with a philopatric sex, where offspring stays in the family group or close to their natal area (*philopatric*). We added a fifth level in sex ratio, as Prox and Farine (2020) did not include multimale and multifemale groups. Sex ratio consisted of only male (1); single female, multimale (2); multimale, multifemale (3); single male, multifemale (4); and only female (5) groups. If only 1 or 5 was noted, then the other sex was living solitarily. The size of the primary unit (group size) was either 1 (solitary); pair small (up to six individuals); and large (more than six individuals). For the third category, group cohesion (temporal category in Prox and Farine 2020), we excluded seasonal variation as most ground-dwelling sciurids show little seasonal variation in social organization, although males and females of some species may share their sleeping burrow in the mating season (Nesterova et al. 2011). We excluded cyclical as a level for group stability, but included: *fluid*, where group membership may fluctuate regularly; *stable* (long-lasting), where group membership changes

only a number of times in an individual's life; and *permanent*, where group membership does not change for adults.

RESULTS

Group size, composition, and cohesion.—Prior to pregnancy, females shared sleeping burrows with 3.5 ± 0.3 [1–8] females ($n = 32$ burrow sharing events of nine different social groups). After their day of breeding but before their parturition date, females isolated themselves from their group members until juvenile emergence. Females varied in postlactation behavior as 87 of a total of 146 mothers (58.8%) moved their litter to a communal burrow, while 41.2% nested singly with their litters. On average 2.6 ± 0.2 [2–6] mothers and 8.7 ± 0.9 [2–25] juveniles were present in each communal group ($n = 33$ groups). Female group sizes prior to pregnancy were larger than group sizes for communally breeding females (Mann–Whitney U -test: $U = 3,286$, $P < 0.001$).

Males shared sleeping burrows with 3.4 ± 0.1 [1–16] individuals ($n = 545$ observed burrow sharing events). The majority of these male sleeping groups (76.9%, 95% $CI = [0.73–0.80]$) were comprised solely of adult males (2.7 ± 0.1 males, $n = 419$). Although on days of estrus ($n = 42$), but also during nonmating periods ($n = 13$), 3.3 ± 0.3 [1–10] males shared sleeping burrows with 3.3 ± 0.3 [1–8] females, totaling 6.9 ± 0.5 individuals ($n = 55$ sleeping burrow sharing events). In addition, adult males shared sleeping burrows with subadults of either sex during the nonmating period in 2014 (total group size 4.7 ± 0.3 individuals, 2.8 ± 0.1 [1–7] adult males and 1.9 ± 0.1 [1–4] subadults of either sex, $n = 71$), the only year when we observed subadults (with the exception of one subadult in 2016—van der Marel et al. 2019). Males shared sleeping burrows more frequently with other males ($n = 419$) than with adult females or subadults of either sex ($n = 126$; binomial test: two-tailed $P < 0.001$). Over all 3 years, male group sizes were larger in the mating season, i.e., the period when females in any of our sites were in estrus (6.0 ± 0.4 , $n = 72$ burrow sharing events), compared to the nonmating season (3.0 ± 0.1 , $n = 470$ burrow sharing events; Mann–Whitney U -test: $U = 25,853$, $P < 0.001$). Throughout the day, male and female social groups were not always segregated, as we observed both adult males and females within 60 m in $50.2 \pm 6.2\%$ ([41.8–62.2%]; $n = 3$ sites) of our 10-min scans. Using the nearest neighbor dyads ($n = 265$ dyads), we found that female–female dyads occurred 30.9%, male–male dyads 38.5%, and female–male dyads 30.6% of the time. When we excluded subadults ($n = 137$ dyads), most dyads were between males (69.3%) compared to females (13.9%) and mixed sex (16.8%). When we selected for adults that were observed in the same location during a scan ($n = 186$ dyads), we found that female–female dyads occurred 59.1% and male–male dyads 40.9% of the time, but no mixed-sex dyads were observed.

Group cohesion (SRI) differed significantly between the sexes and across seasons (LR test: $\Lambda = 118.2$, $P < 0.001$; Fig. 1A). Female SRI differed between the mating season and the pre- and post-juvenile emergence periods (LR test:

$\Lambda = 26.2$, $P < 0.001$; Fig. 1B). Overall, social groups consisted of a small number of adult females sharing sleeping burrows, except during gestation and lactation, and adult males sharing sleeping burrows with other adult males as well as with subadults of either sex when they were present. Male group composition fluctuated regularly resulting in lower SRI for males compared to females. Males and females were observed in the same area throughout the day.

Density and spatiotemporal overlap.—Overall density was 9.98 ± 0.31 individuals/ha calculated over all three sites and years. Density and rainfall was 9.24 individuals/ha and 93.3 mm in 2014, respectively, 9.68 individuals/ha and 164.9 mm in 2015, and 11.03 individuals/ha and 176.5 mm in 2016. Table 1 provides the number of individuals in a site, and the density per site and year. Home ranges for both males and females were clustered around rock walls, dams, ravines, and abandoned cultivated areas. Both the core area (kde50) and the 95% contour (kde95) home range of females did not significantly differ in size between the pre-juvenile emergence season (kde50: $2.78 \pm$

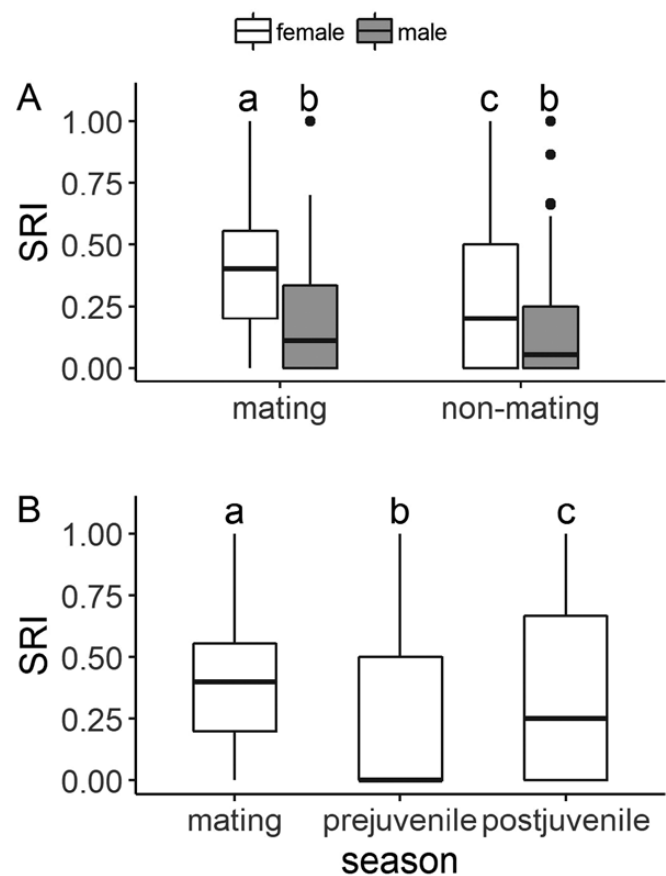


Fig. 1.—Simple ratio index (SRI) as a measure of group cohesion (A) between male and female Barbary ground squirrel groups between the mating and nonmating season; and (B) across seasons for female social groups. The dark line is the median, the box edges (mating, prejuvenile emergence, and postjuvenile emergence season) are the upper and lower quartiles, while the whiskers are 50% from the median, and the closed circles are the outliers, calculated as the values smaller or larger than 1.5 times the box length (i.e., upper–lower quartile). Means sharing a letter are not significantly different.

0.54 ha; kde95: 11.64 ± 1.89 ha) and the post-juvenile emergence season (kde50: 2.15 ± 0.36 ha, paired t -test: $T_{16} = -1.59$, $P = 0.13$; kde95: 9.51 ± 1.26 ha, $T_{16} = -1.25$, $P = 0.23$; $n = 17$ for both). During the nonmating season, male home ranges (kde50: 3.01 ± 0.29 ha; kde95: 13.87 ± 1.71 ha; $n = 23$ for both) were significantly larger than female home ranges (kde50: 2.39 ± 1.77 ha, t -test: $T_{58.68} = 2.51$, $P = 0.01$; kde95: 10.43 ± 0.96 ha, $T_{46.41} = 2.61$, $P = 0.04$; $n = 42$ for both).

The UDOI was significantly larger within female social groups ($103.0 \pm 13.0\%$, $n = 9$ female social groups excluding days of estrus) than within male social groups ($88.0 \pm 13.0\%$, $n = 5$ male groups; $t_{15.6} = -2.15$, $P < 0.05$). Male home ranges ($n = 41$ males) overlapped female home ranges by $17.0 \pm 3.0\%$ ($n = 56$ females).

Juvenile disappearance was highest within their first month of emergence (Fig. 2). Male juveniles disappeared from their natal site at a significantly higher rate than female juveniles (Fig. 2; Kaplan–Meier test: $P < 0.001$). After 6 months postweaning, no male juveniles remained at their natal site. On average 84.7 ± 6.1 days after first emergence, we observed or trapped 5.2% of 236 emerged male juveniles in a different site than their natal site. Of all the newborn females that survived into adulthood (32.4% of 204 emerged female juveniles were trapped the following field season), the majority remained in the area in which they were born because only five females dispersed to nearby areas. At the beginning of the field seasons, we captured individuals that were immigrants ($n = 50$) and, of these, 64.0% were adult or subadult males.

Overall, females had a greater home range overlap but smaller home ranges than males. Male home ranges overlapped female home ranges. Males were the dispersing sex, whereas females were the philopatric sex.

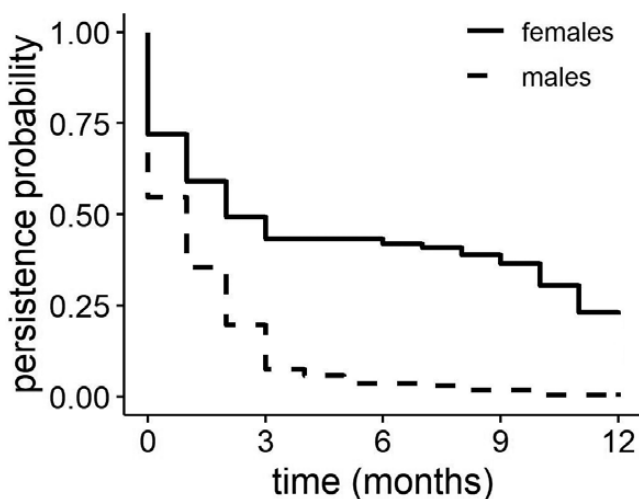


Fig. 2.—Persistence probability using the Kaplan–Meier approach of newly emerged female (solid line) and male (dot dashed line) juvenile Barbary ground squirrels within their natal site on Fuerteventura, Spain. Males disperse from their natal site, resulting in a steeper decline of persistence within the natal site for male, in comparison to female juveniles ($P < 0.001$). As females are philopatric, the figure also reveals females' first-year mortality.

Genetic relatedness.—Of seven relatedness estimators (Milligan 2003; Wang 2007), the dyadic likelihood estimator (DyadML) showed the highest correlation between the observed and expected values of our simulated data set. Observed average relatedness (r) within female social groups ($n = 48$ females in nine social groups) was 0.32 ± 0.07 (range 0.03–0.67), which was higher than expected from a randomly shuffled population (expected $r = 0.17$, $P < 0.002$; Fig. 3). However, when relatedness was independently analyzed per group, four of the nine female social groups did not differ from random ($r = 0.26$, 0.18, 0.19, and 0.03, $P = 0.09$, 0.44, 0.38, and 0.58, respectively). The average relatedness within male social groups ($n = 46$ males in six groups) was 0.20 ± 0.02 (range 0.14–0.28), which was not higher than expected by chance ($r = 0.17$, $P < 0.18$; Fig. 3), and none of the male groups differed from random. We found neither a relationship between female group size and average relatedness (linear regression: adj. $R^2 = -0.14$, $P = 0.91$), nor for males (adj. $R^2 = -0.09$, $P = 0.49$). In sum, females showed high relatedness within a group, whereas males were not related. Yet, female group relatedness was not always higher than male group relatedness or the relatedness of a randomly shuffled population.

DISCUSSION

Barbary Ground Squirrel Social Organization

We showed that Barbary ground squirrels, the only species in *Atlantoxerus*, the North African ground squirrels, are social because they share sleeping burrows, and show spatiotemporal overlap and cohesiveness. Barbary ground squirrels show sexual segregation by sharing sleeping burrows with individuals of the same sex. However, we found that same-sex and mixed-sex dyads occurred throughout the day. These daytime results may be underestimated because we did not record all individuals

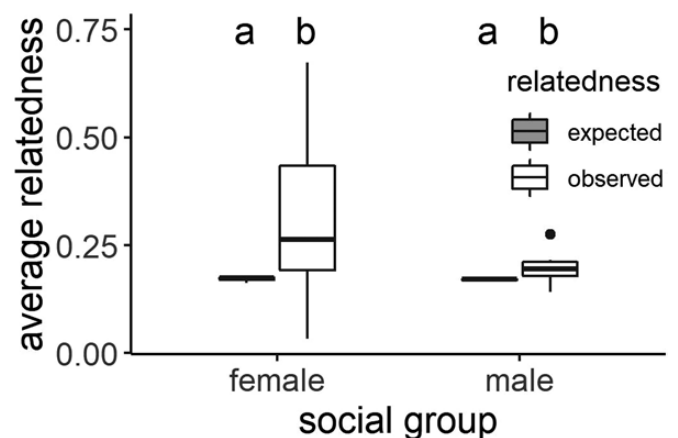


Fig. 3.—Boxplot of the relatedness for the different categories of animals examined—female group mates, male group mates, and randomly selected Barbary ground squirrels. The dark line is the median, the box edges are the upper and lower quartiles, while the whiskers are 50% from the median, and the closed circles are the outliers, calculated as the values smaller or larger than 1.5 times the box length (i.e., upper–lower quartile). Means sharing a letter are not significantly different.

within 1 m of each other. Matrilineal kin groups are the primary foundation for female grouping patterns similar to other temperate and African ground squirrels (Table 2; Michener 1983; Waterman 1995), although not all-female groups showed a higher relatedness than a randomly shuffled population. Males are the dispersing sex and form groups with other unrelated

males and subadults of either sex, when they are present. The male grouping pattern is unlike the temperate ground squirrel pattern, but similar to the closely related Cape ground squirrel, *X. inauris* (Table 2; Waterman 1995, 1997). Thus, the social organization is more similar to the closely related Cape ground squirrel than temperate ground-dwelling squirrels.

Table 2.—Social organization characteristics of a subset of diurnal, semifossorial temperate ground-dwelling sciurids (family Sciuridae, tribe Marmotini) and African ground squirrels (family Sciuridae, tribe Xerini). Headings are defined below the table.

Species	Mass	Index 1981	Index 1983	Organization			Group composition			Group cohesion	Refs
				Primary unit	Tolerance	Overlap	Offspring	Sex ratio	Group size	Stability	
Temperate ground-dwelling sciurids											
<i>C. gunnisoni</i>	470.16	3	4	Family (clan)	Intolerant	1	F: philopatric, M: extended	3 or 4	Small	Permanent	1–4
<i>C. leucurus</i>	923.54	3	2	Family (clan)	Intolerant	1	F: philopatric, M: extended	4	Small	Permanent	5–6
<i>C. ludovicianus</i>	881.28	5	5	Family (coterie)	Intolerant	1	F: philopatric, M: extended	3 or 4	Large	Permanent	7–8
<i>M. flaviventris</i>	2,791.69	4	4	Family	Intolerant	1	F: philopatric, M: extended	3 or 4	Large	Permanent	9–10
<i>M. monax</i>	2,754.36	1	1	Solitary	Intolerant	0	F: philopatric, M: short	na	1	na	11–12
<i>M. olympus</i>	3,120.00	4	5	Family	Tolerant	1	F: philopatric, M: extended	4	Small	Permanent	13–14
<i>O. beecheyi</i>	508.52	2	2 or 3	Solitary	Tolerant	1	F: philopatric, M: short	na	1	na	15–16
<i>C. lateralis</i>	159.68	1	1	Solitary	Intolerant	0	Short	na	1	na	17–18
<i>I. tridecemlineatus</i>	142.78	2	1 or 2	Solitary	Intolerant	0	Short	na	1	na	19–20
<i>P. franklinii</i>	424.86	1	1	Solitary	Intolerant	0	Short	na	1	na	21–22
<i>U. armatus</i>	347.32	2	2	Solitary	Tolerant	1	F: philopatric, M: short	na	1	na	23–24
<i>U. beldingi</i>	265.24	2	2	Solitary	Tolerant	1	F: philopatric, M: short	na	1	na	25–26
<i>U. columbianus</i>	441.39	4	3	Solitary	Tolerant	1	F: philopatric, M: short	na	1	na	27–29
<i>U. elegans</i>	284.29	2	2	F: family, M: solitary	Intolerant	1	F: philopatric, M: short	5	Small	Stable	30–31
<i>U. parryi</i>	524.28	3	3	Family	Intolerant	1	F: philopatric, M: short	4	Small	Stable	32–34
<i>U. richardsonii</i>	273.43	2	2	Solitary	Tolerant	1	Short	na	1	na	35–38
<i>U. townsendii</i>	183.28	2	1 or 2	Solitary	Tolerant	1	Short	na	1	na	39–40
<i>X. tereticaudus</i>	142.09	2	2	Solitary	Tolerant	1	Short	na	1	na	41
African ground squirrels											
<i>A. getulus</i>	225.00			F: family, M: group	F: tolerant, M: open	1	F: philopatric, M: short	F: 5, M: 1	F: small, M: small	F: stable, M: fluid	42
<i>X. inauris</i>	579.73			F: family, M: group	F: tolerant, M: open	1	F: philopatric, M: extended	F: 5, M: 1	F: small, M: small	F: stable, M: fluid	43
<i>X. erythropus</i>	741.68			Solitary/pairs	Tolerant	1	Short	na	1 or pair	na	44–46
<i>X. princeps</i>	665.20			F: family, M: solitary	Tolerant	0	F: philopatric, M: short	na	1 or pair	Stable	47
<i>X. rutilus</i>	252.00			Solitary	Tolerant	1	F: philopatric, M: short	na	1 or pair	Stable	48

Species: subset of temperate ground-dwelling sciurid species from Armitage (1981) and (Michener 1983). The long-clawed ground squirrel, *Spermophilopsis leptodactylus*, is excluded from the African ground squirrels. *Mass*: female body mass (g) from Hayssen (2008). *Index 1981*: sociality index from Armitage (1981); 1 = solitary-living, 2 = living in colonies with both males and females living individually, 3 = females living separately with male territoriality, 4 = harem (females share burrows and male territoriality), and 5 = multi-harem colonies. *Index 1983*: sociality index from Michener (1983); 1 = asocial, 2 = single-family female kin clusters, 3 = female kin clusters/male territoriality, 4 = polygynous harems/male dominance, and 5 = egalitarian polygynous harems. *Organization*—*Primary unit*: solitary-, pair-, family-, or group-living. *Tolerance*: type of interactions between primary units; *open* (individuals can move freely between primary units and aggression is rare), *tolerant* (individuals of different primary units can mix, but low levels of agonistic interactions are observed), and *intolerant* (no mixing of primary units, territorial individuals or groups). *Overlap*: 0 = no overlap (solitary individuals or groups without overlapping home ranges); 1 = overlap (species where there is considerable home range overlap and tolerance toward neighboring individuals or groups, such as for solitary individuals living in aggregations or family groups living in colonies). *Group composition*—*Offspring*: duration that offspring stays in the primary unit; *short* (offspring disperses before they reach sexual maturity), *extended* (overlapping generations), or *philopatric* (offspring stays in the family group or close to their natal area). *Sex ratio*: number of adult females and males present in the primary unit; 1 = only males; 2 = single female, multimale; 3 = multimale, multifemale; 4 = single male, multifemale; 5 = only females. *Group size*: the size of the primary unit; 1 (solitary), pair, small (up to six individuals), and large (more than six individuals). *Group cohesion*—*Stability*: temporal stability of primary unit membership; *fluid* (group membership fluctuates regularly); *stable* (long-lasting, group membership stays the same for prolonged periods of time); and *permanent* (group membership does not change for adults). *References (refs)*: 1–4 (Rayor 1988; Hoogland 1999; Verdolin and Slobodchikoff 2009; Hoogland et al. 2012); 5–6 (Hoogland 1981; Hoogland et al. 2013); 7–8 (Armitage 1981; Hoogland 1981); 9–10 (Armitage 2012; Blumstein 2013); 11–12 (Bronson 1964; Maher 2009); 13–14 (Barash 1973; Armitage 1981); 15–16 (Owings et al. 1977; Boellstorff and Owings 1995); 17–18 (Ferron 1985; Jesmer et al. 2011); 19–20 (Wistrand 1974; Streubel and Fitzgerald 1978); 21–22 (Murie 1973; Hare 2004); 23–24 (Balph and Stokes 1963; Eshelman and Sonnemann 2000); 25–26 (Turner 1972; Sherman 1981); 27–29 (Murie and Harris 1978, 1988; Festa-Bianchet and Boag 1982); 30–31 (Clark and Denniston 1970; Zegers 1981); 32–34 (Carl 1971; McLean 1982; Lacey and Wiczorek 2001); 35–38 (Michener 1979, 1983; Davis 1982, 1984); 39–40 (Alcorn 1940; Sharpe and van Horne 1998); 41 (Munroe and Koprowski 2014); 42 this study; 43 (Waterman 1995); 44–46 (Ewer 1966, 1968; Linn and Key 1996); 47 (Herzig-Straschil and Herzig 1989); 48 (O'Shea 1976).

In our study, Barbary ground squirrels showed a higher level of sociality than the gregariousness described by Machado and Domínguez (1982), and were more similar to what has been reported for a southern population (southwestern Anti-Atlas) within their natural range (Gouat and Yahyaoui 2001). For that region, groups consisted of a single female with her offspring or multiple females and their offspring, and at least one male was sometimes present (Gouat and Yahyaoui 2001). However, a robust comparison is not possible because data only are available for the reproductive period, the groups only were observed during the day, and no other details about male group composition and burrow sharing were provided (Gouat and Yahyaoui 2001). Gouat and Yahyaoui (2001) did not report that variability in social organization differed by habitat, suggesting that social organization may be similar independent of location; however, their sampling was limited. Thus, social organization may be similar for the individuals that were introduced on Fuerteventura, which came from Sidi-Ifni (Machado 1979), an even more southerly located area in Morocco than the Anti-Atlas.

Female Barbary ground squirrels primarily nest in small cohesive matrilineal groups similar to other ground squirrels (Table 2; Michener 1983; Waterman 1995) and other mammal species (Greenwood 1980; Lukas and Clutton-Brock 2011). Females in these matrilineal kin groups may accrue both indirect and direct fitness benefits (Hamilton 1964; Lacey and Sherman 2007). However, not all-female Barbary ground squirrel groups show high relatedness, possibly due to immigration or the small number of females per group, which could make it difficult to detect significant departures from background relatedness in some groups. During gestation and lactation, all pregnant females sleep solitarily in isolated/parturition burrows, which often has been observed in ground squirrels (Hoogland 1995; Waterman 1996, 2002; Michener 2002). Once lactation ends, juveniles emerge and females either nested only with their offspring (41%) or merged their litters with the litters of other females (59%). Thus, adult females appear to be facultative communal nesters, a behavior common in rodents (Hayes 2000; Ebensperger et al. 2004). Also for Barbary ground squirrels in their natural range, social organization varied during the reproductive season, with females either nesting singly or communally (Gouat and Yahyaoui 2001). Temperate ground squirrels show no alternative tactics after weaning, but in some highly social species, reproduction may be suppressed and the nonreproducing females may provide alloparental care, i.e., cooperative breeding (Hoogland 1983; Michener and Murie 1983; Blumstein and Armitage 1999). Cape ground squirrels also have no alternative tactics: instead all females bring their litters to the adult female group after weaning, and cooperative breeding may be present (Pettitt and Waterman 2011). The absence of alternative tactics in Cape ground squirrels is possible because they are asynchronous year-round breeders (Waterman 1996), whereas Barbary ground squirrels are synchronous breeders with a distinct breeding season (van der Marel 2019). The distinct breeding season of Barbary ground squirrels is more similar to temperate ground-dwelling squirrels, where a short active season constrains breeding. However,

the social organization of the highly social temperate ground-dwelling squirrels differs from Barbary ground squirrels in that typically, one male is associated with the social group, or that associations of males are usually between related individuals (Table 2; Hoogland 1981, 1986).

Female and male Barbary ground squirrels have segregated sleeping burrow associations except when subadult females are present or during days of estrus, when both males and females occasionally were observed to enter and leave the same burrow entrance. Different selective pressures, including the localization of females in estrus, social preference, differences in activity, burrow maintenance, predator avoidance, or avoidance of sexual harassment, may explain social sexual segregation, which is seen across the animal kingdom (Waterman 1995; Ruckstuhl and Neuhaus 2002, 2005; Senior et al. 2005; Romey and Wallace 2007; Ruckstuhl 2007; Schneider and Kappeler 2016; Whiteside et al. 2017). Possible benefits for same-sex relationships or associations of the dispersing sex are to reduce contest competition when a species has a linear dominance hierarchy with dominance being a predictor of the outcome (Lehmann and Boesch 2009), or due to the spatial distribution of resources (Lehmann and Boesch 2009; Wakefield 2013). In addition, male grouping may prove beneficial in the context of comparative mate choice, i.e., females may compare potential mates with the other males present in the group (Bateson and Healy 2005). Male associations also may be present around females in estrus (Koprowski 1993). Sometimes, males also share sleeping burrows with females before their day of estrus as a premating behavioral tactic (Nesterova et al. 2011), which could explain the result that some males share sleeping burrows with adult females during the mating season. However, the presence of males could be costly for the females in terms of fitness (Hayes et al. 2019), and could potentially explain why sleeping burrow associations between adult males and adult females are not common in Barbary ground squirrels (only 10% of burrow sharing associations). Dispersed males not only associate with other adult males but also with subadults of either sex, which is atypical for most mammals (Solomon 2003). Sharing of sleeping burrows by males and subadults particularly occurs during the period that pregnant and lactating females isolate themselves in parturition burrows. In Cape ground squirrels, multiple unrelated males also share sleeping burrows (Waterman 1995, 1997), but dispersed males never grouped with females or subadults (Waterman 1995). Subadult Barbary ground squirrels are not always present, but unfavorable conditions, such as lower amounts of rainfall, could potentially influence the age of maturity as subadults were mainly present in the year with the lowest amount of rainfall.

Comparison of Ground-Dwelling Sciurids' Social Organization

We used the recently developed social organization framework to compare the social organization of both African and North American ground-dwelling sciurids because such a framework enables comparative analyses (Prox and Farine 2020). However, our results differ from the data used by Prox and Farine (2020) for the following four ground-dwelling squirrels, *A. getulus*, *C. ludovicianus*, *C. gunnisoni*, and *U. beldingi*. For

example, Prox and Farine (2020) categorized Barbary ground squirrels as having an individual primary unit consisting of one female and multiple males, whereas we found that male groups and female kin groups were segregated. Thus, we show the importance of understanding the basic biology of species that can be used in comparative analyses to decouple the drivers of evolution of sociality.

The social organization patterns of African and North American ground squirrels are found along a continuum from solitary to highly social species (Table 2), but we found some differences between the two tribes. One of the differences is that for the more social temperate species, males either sleep with related males or with females and their offspring and show territoriality. In the more social African species, unrelated males group together, and show fluidity and very little aggression (tolerance level in Table 2). Female ground squirrels either sleep solitarily but may show spatial proximity and tolerance to closely related females, live in pairs, or live in matrilineal kin groups with, occasionally, associated males. The matrilineal kin groups in temperate ground squirrels show more stability and less tolerance to neighboring groups in contrast to more fluidity and tolerance in kin groups in African ground squirrels. African ground squirrels are active year-round, whereas the majority of North American species have a short active season and hibernate, except for black-tailed prairie dogs (Armitage 1981; Hoogland 1981). As a consequence of a short active season, North American ground-dwelling sciurids have a distinct breeding season. African ground squirrels can breed year-round (Happold 2013) with the exception of Barbary ground squirrels, which do not breed in the summer and fall months (van der Marel 2019). Active season duration and body size do not explain social organization in African ground squirrels, as it does in North American ground-dwelling sciurids (Armitage 1981; Michener 1983; Blumstein and Armitage 1998; Hare and Murie 2007), because both a small- and medium-sized African ground squirrel are highly social (males and females share sleeping burrows and show tolerance to conspecifics; Table 2). Even though sociality levels of temperate ground-dwelling squirrels are more continuous than categorical (Armitage 1981; Michener 1983), Barbary ground squirrels do not fit this sociality index because of their year-round activity, the sharing of space by males and females throughout the day, and their social segregation during the night into same-sex sleeping associations (Table 2). We show that unstandardized measures of social organization do not always work to characterize the social organization for closely related species, where different selective pressures influence social organization.

Not only do we find differences in social organization between the two tribes (Table 2), but the data summary in Table 2 also shows that the more social species in both tribes have overlap in generations in common (offspring extended in Table 2). In North American species, overlap in generations is a factor of the harsh environment the species inhabit because juveniles cannot gain enough mass to survive their first

hibernation period by themselves (Armitage 1981; Michener 1983; Blumstein and Armitage 1998; Hare and Murie 2007). In Cape ground squirrels, age, social organization of the natal group, and reproductive suppression or opportunities in the natal group influence the decision of natal males to disperse (Scantlebury et al. 2008). However, the delay of dispersal is one of the differences in the social organization between Cape and Barbary ground squirrels because Barbary ground squirrel males disperse before reaching sexual maturity.

Our research provides insight into the basic biology of the invasive population of Barbary ground squirrels, which is useful to manage the population or plan actions for their control. The social organization of Barbary ground squirrels, which is a temperate region, small-bodied species that breeds seasonally but is active year-round, resembles that of Cape ground squirrels, because males share sleeping burrows with other unrelated adult males and females live in small cohesive kin groups. Thus, the selective pressures explaining social organization in temperate ground-dwelling sciurids, including a short active season and body size, do not explain social organization in African ground squirrels. Our results contribute to the development of a comprehensive framework for the evolution of sociality in ground-dwelling sciurids.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Characterization of microsatellite loci in the invasive Barbary ground squirrel.

Supplementary Data SD2.—Microsatellite characteristics of loci developed for Barbary ground squirrels (*Atlantoxerus getulus*) on Fuerteventura, Spain.

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