



# Spacing Behavior of a Non-Larder-Hoarding *Tamiasciurus*: A Study of Mearns's Squirrels in Xeric Coniferous Forests

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## Abstract

In ecosystems with seasonal fluctuations in food supply many species use two strategies to store food: larder hoarding and scatter hoarding. However, because species at different geographic locations may experience distinct environmental conditions, differences in hoarding behavior may occur. Tree squirrels in the genus *Tamiasciurus* display variation in hoarding behavior. Whereas red (*Tamiasciurus hudsonicus*) and Douglas's (*Tamiasciurus douglasii*) squirrels in mesic coniferous forests defend territories centered around larder hoards maintaining non-overlapping home ranges, red squirrels in deciduous forests defend small scatter-hoarded caches of cones maintaining overlapping home ranges. As in other rodent species, variation in hoarding behavior appears to influence the spacing behavior of red and Douglas's squirrels. In contrast, Mearns's squirrels (*Tamiasciurus mearnsi*) in xeric coniferous forests neither rely on larder hoards nor appear to display territorial behavior. Unfortunately, little is known about the ecology of this southernmost *Tamiasciurus*. Using radio-telemetry, we estimated home-range size, overlap, and maximum distance traveled from nest to examine the spacing behavior of Mearns's squirrels. Similar to scatter-hoarding rodents, maximum distance traveled from nest was greater for males during mating season, whereas those of females were similar year round. Although no seasonal differences were detected, male home ranges were three times larger during mating season, whereas those of females were smaller and displayed a minor variation between seasons. Home ranges were overlapped year round but contrary to our expectations, overlap was greater during mating season for both sexes, with no detectable relationship between male home-range size and the number of females overlapped during mating season. Overall, the results appear to support our hypothesis that in the absence of larder hoards, the spacing behavior of Mearns's squirrels should be different from larder-hoarding congeners and more similar to scatter-hoarding rodents.

## Introduction

Food foraging directly affects the energetic balance and nutritional state of animals, which in turn influences growth, reproduction, and other traits closely related to fitness (Quispe et al. 2009). In ecosystems with seasonal fluctuations in food supply, many bird and rodent species cache food as a survival mechanism (Anderson & Krebs 1978; Smith & Reichman 1984; Vander Wall 1990). The spatial patterns of

caching food are classified into two strategies: larder hoarding and scatter hoarding (Hurly & Lourie 1997). Larder hoarders store food in a single large cache within an animal's home range, whereas scatter hoarders disperse their caches across their home range (Vander Wall 1990; Male & Smulders 2007). In contrast to scatter hoarders, larder hoarders display territorial behavior with larders often situated near the territory's center (Orians & Pearson 1979). Nonetheless, because species at different geographic locations

may experience distinct environmental conditions, differences in hoarding behavior may occur (Quispe et al. 2009). As a result, intra- and interspecific variation in hoarding behavior may in turn influence spacing behavior (Layne 1954; Daly et al. 1992; Clarke & Kramer 1994; Gurnell & Anderson 1996; Pratt et al. 2001; Shier & Randall 2004; Jenkins 2011). In kangaroo rats (*Dipodomys*), larder-hoarding species like *Dipodomys spectabilis*, *Dipodomys ingens*, and *Dipodomys deserti* are highly territorial outside the mating season and show little overlap in home range, whereas in scatter-hoarding species like *Dipodomys merriami* and *Dipodomys ordii* home ranges often overlap (Daly et al. 1992; Shier & Randall 2004). Furthermore, because female fitness is more dependent on food and nest resources, whereas male fitness is more dependent on the spatial distribution of females, differences in space use between sexes occur (Hanski et al. 2000; Jones et al. 2003). In polygynous mammals, both larder hoarding and scatter hoarding, males commonly expand their home ranges during mating season to overlap those of females and maximize reproductive success (Clutton-Brock 1989; Cooper & Randall 2007). Thus, social mating systems can be inferred based upon the size of individual home ranges and the degree of spatial overlap between sexes (Cooper & Randall 2007; Harless et al. 2009; Adler 2011).

Tree squirrels in the genus *Tamiasciurus* display variation in hoarding behavior with no sexual dimorphism in territory size (Layne 1954; Smith 1968; Kemp & Keith 1970; Koprowski et al. 2007; Lane et al. 2009). In mesic coniferous forests of western North America, red (*Tamiasciurus hudsonicus*) and Douglas's (*Tamiasciurus douglasii*) squirrels defend food-based territories maintaining non-overlapping home ranges (Smith 1968; Don 1983; Gurnell 1984; Gurnell & Anderson 1996; Koprowski et al. 2007; Lane et al. 2009). Each territory is centered on a large larder hoard of conifer cones, known as a midden (Smith 1968; Shonfield et al. 2012). Males and females larder hoard unopened cones in late summer and autumn to extract the energy-rich seeds later during winter and spring (Descamps et al. 2009). However, in deciduous forests of eastern North America, red squirrels do not rely on middens but are known to defend small scatter-hoarded caches of cones maintaining overlapping home ranges (Hamilton 1939; Layne 1954; Kemp & Keith 1970; Don 1983; Gurnell 1984). Thus, as in other rodent species (Gipps 1985; Ostfeld 1990; Shier & Randall 2004; Adler 2011; Steinwald et al. 2013), variation in hoarding behavior appears to influence the spacing behavior of red and Douglas's squirrels.

In contrast, in xeric coniferous forests of Baja California, Mexico, Mearns's squirrels (*Tamiasciurus mearnsi*) do not store cones in middens (Lindsay 1981; Koprowski et al. 2006), and only one adult male was observed once in 2 yr of radiotelemetry monitoring feeding on a small cache of 20–30 lodgepole pine cones (Ramos-Lara 2012); however, individuals occasionally scatter hoard single food items in branches of trees (Ramos-Lara 2012). Furthermore, the fact that individuals nest communally during summer and that  $\geq 2$  squirrels nest in different cavities of the same tree (Ramos-Lara & Koprowski 2012; Ramos-Lara et al. 2013), which is rare in congeners (Munroe et al. 2009), suggests that this species is non-territorial. Thus, the species provides an excellent opportunity to test the hypotheses on the spacing behavior of *Tamiasciurus* occurring in coniferous forests but without the constraints of defending larder hoards or small caches of cones. Federally listed as threatened in Mexico (Secretaría de Medio Ambiente y Recursos Naturales 2010) and as endangered by the International Union for Conservation of Nature (de Grammont & Cuarón 2008), little is known about the ecology of this southernmost *Tamiasciurus* (Koprowski et al. 2006). Using radiotelemetry, we estimated home-range size, overlap, and maximum distance traveled from nest to examine the spacing behavior of Mearns's squirrels.

Because the spatial movements of Mearns's squirrels are not constrained by larder hoards, we tested the hypothesis that spacing behavior should be different from larder-hoarding congeners and more similar to scatter-hoarding rodents (Ostfeld 1985; Gurnell 1987; Clutton-Brock 1989; Shier & Randall 2004; Adler 2011). In mesic coniferous forests, red and Douglas's squirrels maintain non-overlapping home ranges during non-mating season, whereas during mating season, home ranges between males and males/females overlap but not between females (Smith 1968; Don 1983; Gurnell 1984; Koprowski et al. 2007; Lane et al. 2009). However, based on patterns observed in scatter-hoarding rodents (Ostfeld 1985; Clutton-Brock 1989; Shier & Randall 2004; Cudworth & Koprowski 2010; Adler 2011), we predicted that Mearns's squirrels should exhibit overlapping home ranges year round.

In addition, because the fitness of males and females is limited by food supply during non-mating season (Jones et al. 2003), we predicted smaller home-range sizes and lower overlap between sexes. In contrast, because male fitness is limited by the spatial distribution of females during mating season (Jones et al. 2003), we predicted an increase in male home-range sizes, driven by sexual selection to

overlap a greater number of females, with higher overlap only between males and males/females. Consequently, we also predicted greater distances traveled by males from their nests to maximize reproductive success. On the basis of other rodent species with scramble competition mating systems (Koprowski 2007; Lane et al. 2009; Raveh et al. 2010; Marmet et al. 2012), we predicted that male home-range size should be positively related to the number of females overlapped during mating season. In Eurasian red squirrels (*Sciurus vulgaris*), South American water rats (*Nectomys squamipes*), and some voles (*Microtus*, *Clethrionomys*), females are territorial during breeding season to secure sufficient resources for the successful rearing of litters (Gipps 1985; Wauters & Dhondt 1992; Bergallo & Magnusson 2004). Thus, given that food is a limiting resource in xeric environments, we predicted lower overlap between females during mating season.

## Methods

### Study Area

The study was conducted in the Sierra de San Pedro Mártir (SSPM) National Park located 100 km south-east of Ensenada, Baja California, Mexico (Stephens et al. 2003). The SSPM National Park comprises 65 000 ha of which coniferous forests cover approximately 40 655 ha (Minnich et al. 2000). Forests are composed of Jeffrey pine (*Pinus jeffreyi*), sugar pine (*Pinus lambertiana*), lodgepole pine (*Pinus contorta*), white fir (*Abies concolor*), and limited amounts of quaking aspen (*Populus tremuloides*) and incense cedar (*Calocedrus decurrens*). The most common forest types are Jeffrey pine, Jeffrey pine–mixed conifer, and mixed white fir forests (Stephens et al. 2003). The most striking feature of the mixed-conifer forests is an open park-like aspect that consists of mature trees reaching 30–45 m, with few pole-sized trees and saplings, and an open shrub cover (Bojórquez-Tapia et al. 2004). Elevation averages 2600 m in the north and decreases to 1800 m in the southern portion of the range with the highest peaks over 3000 m (Stephens et al. 2003). Forests have not experienced disturbance from logging, and fires have spread without human interference (Minnich et al. 2000). Summers are dry except for afternoon thunderstorms of the North American monsoon (Minnich et al. 2000).

### Trapping and Telemetry

From May to Nov. 2005, we surveyed approximately 2500 ha of mixed-conifer forest in the margins of the

Vallecitos Meadow (31°00'N, 115°28'W, altitude 2434 m) to detect occurrence of Mearns's squirrels and to establish potential capture sites. The area was explored systematically on foot using a topographic map (Schad 1988). From May to Aug. of 2006 and 2007, we captured a total of 38 adult Mearns's squirrels (20 males and 18 females) placing 41 × 13 × 13 cm live traps (Model 201; Tomahawk Live Trap Co., Hazelhurst, WI, USA) at the base of large-diameter trees, baited with peanuts and peanut butter, covered with tree bark, and checked at 1-h intervals. Captured animals were transferred to a 70 × 45 cm cloth-handling cone (Koprowski 2002) where we collected data on sex, age class, reproductive condition, and body mass. Adult animals (≥240 g) were fitted with radio collars (Model SOM-2190; Wildlife Materials International, Inc., Carbondale, IL, USA) and uniquely numbered monel ear tags (Style #1005-1; National Band and Tag Co., Newport, KY, USA) with 1-cm colored-plastic washers (Style #1842; National Band and Tag Co.) on both ears. We distinguished adults and juveniles based on body mass and reproductive condition (Kunz et al. 1996). All squirrels were released at the capture site after ≤8 min of handling time; no animals were injured during the study. Mean (±SD) number of times adult individuals were recaptured during the study did not differ between males (3 ± 3 individuals, n = 20) and females (4 ± 4 individuals, n = 18; unpaired *t*-test,  $t_{36} = 0.47$ ,  $p = 0.64$ ). Trapping and handling procedures were conducted with approval from The University of Arizona Institutional Animal Care and Use Committee (protocol # 05-038), and with permits from Dirección Forestal y de la Fauna Parque Nacional Sierra de San Pedro Mártir and Dirección General de Vida Silvestre.

We used a 3-element yagi directional antenna (Wildlife Materials International, Inc.) and receiver (Model R-1000; Communications Specialists, Inc., Orange, CA, USA) to locate squirrels from 0700–2000 h at >2-h intervals to avoid spatial autocorrelation (White & Garrott 1990). We tracked squirrels by homing during approximately 1172 h between Apr. and Nov. of 2006 (29.4 h/squirrel radiotracked; males, n = 9; females, n = 6) and 2007 (29.2 h/squirrel radiotracked; males, n = 14; females, n = 11). We did not track squirrels during winter (Dec.–Mar.) due to snow and limited access. Each location was recorded using a global positioning system (eTrex Legend GPS unit; Garmin International, Inc., Olathe, KS, USA). Location error (±6 m) was reduced by tracking squirrels until sighted or by triangulation around the tree when hidden (White & Garrott 1990).

## Data Analysis

We divided years into mating (Jan. through mid-Jul.) and non-mating (mid-Jul. through Dec.) seasons based upon the observation of scrotal males, estrous and lactating females, and emergence of litters (Kunz et al. 1996). We used the home range analysis extension (Rodgers & Carr 1998) for ArcView 3.2a (ESRI, Inc., Redlands, CA, USA) to estimate home-range sizes per individual using 95% and 50% core fixed kernels (FK) with smoothing parameters chosen via least squares cross-validation (Seaman et al. 1999; Powell 2000). Kernel estimators are robust to the presence of autocorrelation, minimizing the problem of independence of relocations (de Solla et al. 1999; Hoset et al. 2008). In addition, we used 95% minimum convex polygons (MCP) to facilitate comparison with other studies. A plot of home-range size vs. number of fixes (telemetry locations) of all individuals reached asymptote between 20 and 25 fixes (Edelman & Koprowski 2006). Thus, we only used individuals with  $\geq 22$  fixes during a season of interest; number of individuals used in each analysis varied due to their number of fixes. Mean ( $\pm$ SD) number of fixes did not differ between males ( $67 \pm 26$  fixes,  $n = 20$ ) and females ( $68 \pm 28$  fixes,  $n = 16$ ; unpaired  $t$ -test,  $t_{34} = 0.20$ ,  $p = 0.84$ ), or between mating ( $47 \pm 20$  fixes,  $n = 27$ ) and non-mating ( $41 \pm 18$  fixes,  $n = 23$ ; unpaired  $t$ -test,  $t_{48} = 1.10$ ,  $p = 0.28$ ) seasons. We used two-way analysis of variance (ANOVA) to examine the effects of sex and season on home-range size.

We used the XTools ArcView extension (DeLaune 2000) to estimate 95% FK home-range overlap and maximum distance traveled from nest between sexes and seasons (Powell 2000). We calculated overlap by measuring the total percentage of an animal's 95% area overlapped by individuals of the same and opposite sex during each season, and by counting the number of individuals with which they overlapped (Pasch & Koprowski 2006). Percentage overlap of all male and female conspecifics overlapping an individual was then averaged for each season (Linders et al. 2004). We examined maximum distance traveled from nest by measuring the linear distance of each individual from its nocturnal nest to the farthest location recorded within each season. When squirrels used more than one nest within the season examined, we selected the nest used for the most nights. We used two-way ANOVA to examine the effects of sex and season on percentage overlap, number of individuals overlapped, and maximum distance traveled from nest. Linear regression was used to explore the relationship between male 95% FK home-range size and

the number of radio-collared females overlapped during mating season (Lane et al. 2009; Cudworth & Koprowski 2010).

All statistical analyses were conducted using SPSS 17.0 (SPSS Inc., IL, USA). When necessary, we log-transformed the variables to better meet the assumptions of parametric tests (Zar 1996); however, means ( $\pm$ SD) reported in the results are from untransformed values.

## Results

During the 2 yr of study, male 95% FK ( $3.9 \pm 3.6$  ha,  $n = 20$ ) was 2.5 times larger than that of females ( $1.6 \pm 1.1$  ha,  $n = 16$ ), male 50% core FK ( $0.6 \pm 0.6$  ha,  $n = 20$ ) was 2.6 times larger than that of females ( $0.2 \pm 0.3$  ha,  $n = 16$ ), and male 95% MCP ( $17.1 \pm 17.4$  ha,  $n = 20$ ) was 3.4 times larger than that of females ( $5.0 \pm 2.3$  ha,  $n = 16$ ). Fixed-kernel home-range size estimates differed between sexes, but not seasons, and without interactions between factors (Table 1). In contrast, 95% MCP differed between sexes and seasons and with interaction between factors (Table 1). Between sexes, male home ranges were 3.8–6.0 times larger than those of females during mating season for all estimators (Fig. 1). Between seasons, although no significant differences were detected, male 95% FK and 50% core FK were 2.7–2.9 times larger during mating season, whereas female 95% FK and 50% core FK were only 1.3–1.5 times larger during mating season (Fig. 1). In contrast, male 95% MCP was 3.7 times larger during mating season, whereas female 95% MCP was only 1.02 times larger during non-mating season (Fig. 1), with interaction between factors (Table 1).

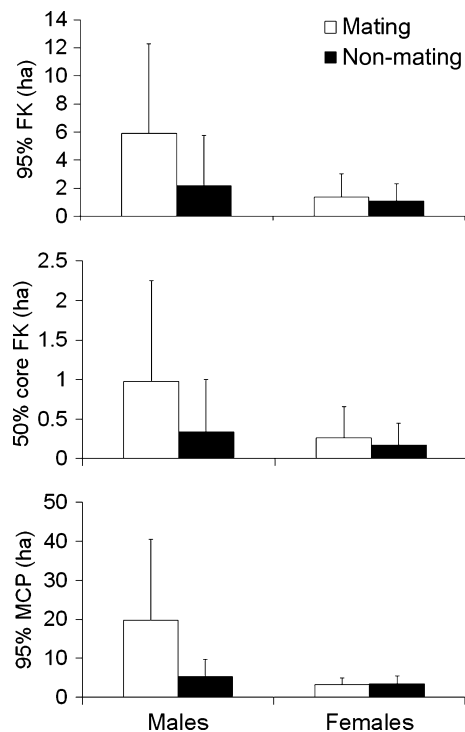
Percentage overlap of male and female 95% FK home ranges by conspecifics differed between seasons, but not sexes, and without interactions between factors (Table 2). Males and females were 2.3–4.3 times more overlapped by conspecifics of either sex

**Table 1:** Two-way analysis of variance used to examine the effects of sex and seasons on home-range size of Mearns's squirrels (*Tamiasciurus mearnsi*) in Baja California, Mexico, from May 2006 to Nov. 2007

	df	95% FK		50% core FK		95% MCP	
		F	p	F	p	F	p
Sex	1, 46	7.44	0.01*	4.26	0.045*	18.5	0.000*
Seasons	1, 46	3.99	0.05	3.12	0.08	6.42	0.02*
Seasons $\times$ sex	1, 46	2.26	0.14	1.56	0.22	6.16	0.02*

FK, fixed kernel; MCP, minimum convex polygon.

Significance ( $p < 0.05$ ) is marked with an asterisk.



**Fig. 1:** Mean ( $\pm$ SD) home-range size estimates of adult male and female Mearns's squirrels (*Tamiasciurus mearnsi*) in Baja California, Mexico, during mating (males,  $n = 14$ ; females,  $n = 13$ ) and non-mating (males,  $n = 15$ ; females,  $n = 8$ ) seasons from May 2006 to Nov. 2007. FK: fixed-kernel. MCP: minimum convex polygon. For results from statistical tests please see Table 1.

during mating season compared with non-mating season (Fig. 2). In other words, overlap between males, females, and males/females was higher during mating season compared with non-mating season (Fig. 2). Furthermore, although no significant differences were detected, females were 1.6 times more overlapped by conspecifics of either sex during mating season compared with males (Fig. 2).

**Table 2:** Two-way analysis of variance used to examine the effects of sex and seasons on percentage of male and female 95% fixed-kernel home ranges overlapped by male and female conspecifics, number of individuals overlapped by male and female conspecifics, and maximum distance traveled from nest by male and female Mearns's squirrels (*Tamiasciurus mearnsi*) in Baja California, Mexico, from May 2006 to Nov. 2007. Degrees of freedom: males = 1, 54; females = 1, 38; distance traveled = 1, 46

	Overlap (%)				Number of individuals				Distance traveled (m)	
	Males <sup>a</sup>		Females <sup>a</sup>		Males <sup>a</sup>		Females <sup>a</sup>		F	p
	F	p	F	p	F	p	F	p		
Sex	0.68	0.41	0.48	0.49	5.82	0.02*	3.66	0.06	4.10	0.049*
Seasons	12.9	0.001*	8.58	0.006*	88.5	0.000*	24.0	0.000*	5.58	0.02*
Seasons $\times$ sex	0.63	0.43	0.12	0.73	3.53	0.07	0.17	0.69	5.54	0.02*

Significance ( $p < 0.05$ ) is marked with an asterisk.

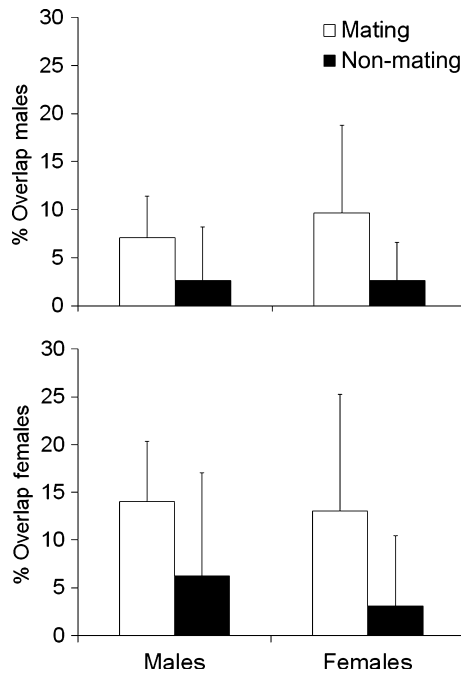
<sup>a</sup>Overlapped by male and female conspecifics during mating and non-mating seasons.

Number of individuals overlapping the 95% FK home ranges of other conspecifics differed between sexes and seasons for males, but only between seasons for females, and without interactions between factors for both sexes (Table 2). Males were overlapped by 7.1 and 6.6 times more males and females, respectively, during mating season compared with non-mating season (Fig. 3). In contrast, females were overlapped by 3.8–12.9 times more conspecifics of either sex during mating season compared with non-mating season (Fig. 3). Male 95% FK home-range size was not related to the number of females overlapped during mating season ( $R^2 = 0.0003$ ,  $F_{1,12} = 0.003$ ,  $p = 0.96$ ,  $n = 14$ ).

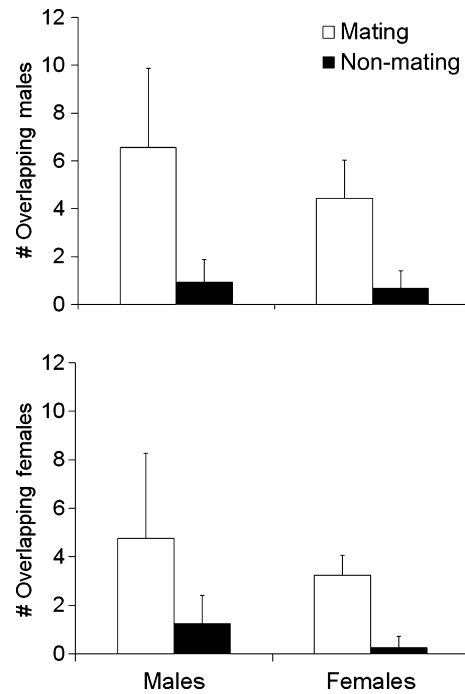
Maximum distance traveled from nest differed between sexes and seasons with interaction between factors (Table 2). Whereas males and females traveled similar distances during non-mating season, males traveled distances 1.9 times greater than those of females during mating season (Fig. 4). Similarly, males traveled distances 2.0 times greater during mating season compared with non-mating season (Fig. 4). In contrast, females traveled similar distances between mating and non-mating seasons (Fig. 4).

### Discussion

Overall, the results appear to support our hypothesis that in the absence of larder hoards the spacing behavior of Mearns's squirrels should be different from larder-hoarding congeners and more similar to scatter-hoarding rodents. In mesic coniferous forests, red and Douglas's squirrels expand their home ranges during summer and autumn, when both sexes travel greater distances to collect unopened cones for their middens, but males also expand their home ranges further to locate estrous females (Smith 1968; Koford 1982; Koprowski et al. 2007; Lane et al. 2009). By

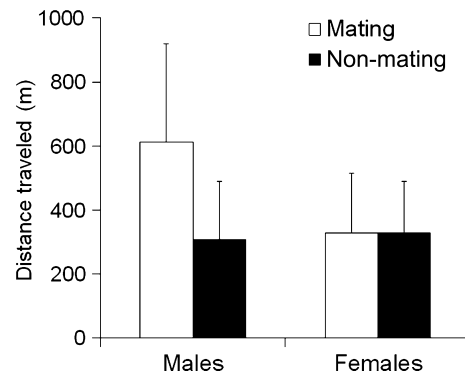


**Fig. 2:** Mean ( $\pm$ SD) percentage overlap of Mearns's squirrels (*Tamiasciurus mearnsi*) 95% fixed-kernel home ranges by male and female conspecifics during mating (males,  $n = 14$ ; females,  $n = 13$ ) and non-mating (males,  $n = 15$ ; females,  $n = 8$ ) seasons in Baja California, Mexico, from May 2006 to Nov. 2007. For results from statistical tests please see Table 2.



**Fig. 3:** Mean ( $\pm$ SD) number of conspecifics overlapping male and female Mearns's squirrels (*Tamiasciurus mearnsi*) 95% fixed-kernel home ranges during mating (males,  $n = 14$ ; females,  $n = 13$ ) and non-mating (males,  $n = 15$ ; females,  $n = 8$ ) seasons in Baja California, Mexico, from May 2006 to Nov. 2007. For results from statistical tests please see Table 2.

contrast, female Mearns's squirrels displayed 95% FK home ranges smaller than those of males, with a minor variation between seasons. However, although no seasonal differences were detected, male 95% FK home ranges were three times larger during mating season and four times larger than those of females during mating season (Fig. 1). Similar space-use patterns for both sexes have been observed in scatterhoarding rodents (Gipps 1985; Ostfeld 1985; Clutton-Brock 1989; Frank & Heske 1992; Wauters & Dhondt 1992; Jones et al. 2003; Bergallo & Magnusson 2004; Shier & Randall 2004; Edelman & Koprowski 2006; Cudworth & Koprowski 2010; Adler 2011; Bonatto et al. 2012). In other words, whereas seasonal variation in home-range size of red and Douglas's squirrels is influenced by sexual activity and food supply due to the maintenance of middens (Wauters & Dhondt 1992; Koprowski et al. 2007), in Mearns's squirrels, seasonal variation appears to be influenced primarily by sexual activity. Mearns's squirrels are described as rare and occurring in limited numbers (Yensen & Valdés-Alarcón 1999), suggesting that females may be spatially dispersed (Cooper & Randall 2007). Thus, like other rodent species with scramble competition mating systems (Koprowski 2007; Lane et al. 2009;



**Fig. 4:** Mean ( $\pm$ SD) maximum distance traveled by adult male and female Mearns's squirrels (*Tamiasciurus mearnsi*) from their nocturnal nests in Baja California, Mexico, during mating (males,  $n = 14$ ; females,  $n = 13$ ) and non-mating (males,  $n = 15$ ; females,  $n = 8$ ) seasons from May 2006 to Nov. 2007. For results from statistical tests please see Table 2.

Raveh et al. 2010; Marmet et al. 2012), only those males that can locate estrous females faster than other male competitors should be favored by sexual selection, as female tree squirrels are commonly in estrus for <1 d and likely <8 h (Koprowski 2007).

Mearns's squirrels exhibited intra- and intersexual overlap in 95% FK home ranges year round similar to scatter-hoarding rodents (Frank & Heske 1992; Lurz et al. 2000; Shier & Randall 2004; Cudworth & Koprowski 2010), including red squirrels in deciduous forests (Layne 1954; Kemp & Keith 1970; Don 1983; Gurnell 1984). Nonetheless, overlap only differed between seasons suggesting that overlap is similar for both sexes within seasons, with lower and higher overlap during non-mating and mating seasons, respectively, between sexes. In red and Douglas's squirrels, the defense of food-based territories restricts overlap to mating season when males travel greater distances in search of estrous females, whereas females maintain non-overlapping home ranges year round (Koford 1982; Koprowski et al. 2007; Lane et al. 2009). In scatter-hoarding rodents, overlap increases when males expand their home ranges during mating season, overlapping other males and females, whereas overlap between females remains lower year round (Ostfeld 1985; Clutton-Brock 1989; Frank & Heske 1992; Shier & Randall 2004; Cudworth & Koprowski 2010). Furthermore, in Eurasian red squirrels, South American water rats, and some voles (*Microtus*, *Clethrionomys*), females defend a territory during breeding season maintaining non-overlapping home ranges with other females (Gipps 1985; Wauters & Dhondt 1992; Bergallo & Magnusson 2004). But contrary to our expectations, overlap between female Mearns's squirrels was higher during mating season despite exhibiting similar home-range sizes and distances traveled from nest year round. An increase in overlap during mating season between female Mearns's squirrels may be due to habitat heterogeneity with females searching more widely for food, but covering areas of similar size as those traveled during non-mating season. In Eurasian red squirrels and root voles (*Microtus oeconomus*), higher overlap between females only occurs when food supply declines and consequently energy requirements increase, particularly during mating season (Lurz et al. 2000; Hoset et al. 2008). Mearns's squirrels also rely on tree cavities for nesting (Ramos-Lara et al. 2013), and both sexes were observed frequently inspecting tree cavities which also may have contributed to increased overlap with other conspecifics, particularly breeding females (Peterson & Gauthier 1985; Hanski et al. 2000).

In areas with high variation in food supply, Eurasian red squirrels and Arizona gray squirrels (*Sciurus arizonensis*) maintain large home ranges year round as a strategy to respond to this variation (Lurz et al. 2000; Cudworth & Koprowski 2010). Mearns's squirrels may have adopted a similar strategy, maintaining

large home ranges and shifting among food types as available (Gurnell 1987; Fletcher et al. 2010), with females increasing overlap during mating season but exhibiting similar home-range sizes year round. Overall, home ranges of Mearns's squirrels are larger than those of congeners (Koford 1982; Bovet 1984; Koprowski et al. 2007; Lane et al. 2009; Munroe et al. 2009). In Arizona, Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) also maintain larger home ranges than those of conspecifics at higher latitudes apparently due to low population densities and poor habitat quality (Koprowski et al. 2007). Female mate choice or epigamic sexual selection, in which females may actively solicit copulations with preferred males (Jones et al. 2003; Solomon & Keane 2007), also might account for a higher overlap during mating season between female Mearns's squirrels. But contrary to the territorial banner-tailed kangaroo rat (*D. spectabilis*), where females expand their home ranges during breeding season to find desired males and to avoid inbreeding (Steinwald et al. 2013), female Mearns's squirrels did not increase home-range sizes and distances traveled from nest during mating season. Nevertheless, higher overlap between sexes during mating season, and the fact that individuals nest communally during summer, support the idea of no territorial behavior in Mearns's squirrels (Munroe et al. 2009; Ramos-Lara 2012; Ramos-Lara & Koprowski 2012). Failure to detect a relationship between male 95% FK home-range size and the number of females overlapped during mating season also may be due to females searching more widely for food, tree cavities, or possibly males, and consequently overlapping numerous males and females.

Maximum distance traveled from nest by males during non-mating season was comparable to those of females during both seasons. A similar spacing behavior has been observed in scatter-hoarding rodents (Bergallo & Magnusson 2004; Linders et al. 2004; Edelman & Koprowski 2006), further supporting the idea of similar resource acquisition during non-mating season between sexes with no sexual dimorphism (Gurnell 1987; Pasch & Koprowski 2006). However, males traveled greater distances during mating season, which also may account for the 95% FK home ranges three times larger observed during mating season. Seasonal variations in home-range size and maximum distance traveled from nest reflect the difference in mating strategies between sexes (Edelman & Koprowski 2006). In mammals, male parental care is rare (Clutton-Brock 1989). Thus, larger home-range sizes and greater distances traveled should allow male

Mearns's squirrels not only to maximize contact with estrous females during mating season, but also to find richer feeding patches during non-mating season to recover energy stores lost to reproduction (Wauters & Dhondt 1998; Koprowski 2007). Whereas the defense of food-based territories restricts the spatial movements of red and Douglas's squirrels (Gurnell 1984; Cooper & Randall 2007), Mearns's squirrels may cover large areas to meet their energy requirements like other non-territorial mammals.

More research on Mearns's squirrels and red squirrels in deciduous forests is needed to discern how variation in hoarding behavior influences spacing behavior and ultimately fitness in *Tamiasciurus* and in other rodent species (Vander Wall 1990; Daly et al. 1992; Shier & Randall 2004; Cooper & Randall 2007). Similarly, more information is still required to understand how local biotic and abiotic factors determine when animals should be larder hoarders or scatter hoarders (Daly et al. 1992; Preston & Jacobs 2005; Quispe et al. 2009).

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