



Original Investigation

Spatial relationships between burrows of an insular population of *Dipodomys merriami*

Jorge Vázquez, Sergio Ticul Álvarez-Castañeda*

Centro de Investigaciones Biológicas del Noroeste, Mar Bermejo 195, AP 128, La Paz, Baja California Sur, 23090, México

ARTICLE INFO

Article history:

Received 16 June 2010

Accepted 20 May 2011

Keywords:

Burrows

Dipodomys merriami

Mexico

San José Island

Spatial relationships

ABSTRACT

For semi-fossorial rodents, descriptions of the distribution and use of burrows can advance in understanding the spatial and social organization of their population. This study describes the use and spatial relationships between burrows of the kangaroo rat (*Dipodomys merriami insularis*), a subspecies that is possibly on the verge of extinction. Individuals were captured and recaptured in an area of 79.8 hectares located at San José Island, Gulf of California, Mexico, during both the breeding (BRED, from March to May) and the non-breeding (NON-BRED, from October to November) seasons of 2008. Our results show that females and males use a median of 1–2 burrows; factors such as age class, season and frequency of captures account for the number of burrows used by individuals. Few individuals shared their burrows (9.2% during BRED and 1.1% during NON-BRED). The burrows showed a clumped spatial distribution in both sampling periods. The spatial relationship between burrows is characterized by the fact that animals of opposite sex are closer to each other than same-sex individuals, and this spatial relationship between nearest-neighbor burrows is influenced by age class. Our results show that *D. m. insularis* displays burrow use and spatial organization patterns similar to those observed in other populations of *D. merriami*.

© 2011 Deutsche Gesellschaft für Säugetierkunde. Published by Elsevier GmbH. All rights reserved.

Introduction

For semi-fossorial animals, burrows are used as shelter from predators and adverse environmental conditions, as well as for breeding and food storage (Reichman and Smith 1990). Burrows are often the activity centre of individual home ranges and the space that individuals defend against conspecifics (Randall, 1993). These characteristics of burrow usage have profound social implications for the population. Thus, the description of burrow distribution and use can advance the understanding of the spatial and social organization of a population. Kangaroo rats (*Dipodomys*) are semi-fossorial nocturnal mammals adapted to dry habitats (Reichman and Price 1993; Vaughan et al., 2000). Members of this genus use burrows for food storage (especially seeds), shelter, breeding and protection from sun and predators (Reynolds, 1958). The burrows of this species range from a simple construction consisting of a series of interconnected underground tunnels with one or more openings (such as in *D. merriami*, Reynolds, 1958; Daly et al., 1992) to conspicuous mounds characterized by a labyrinth of multi-storied tunnels (such as in *D. spectabilis*, Best, 1972).

Adult *Dipodomys* are solitary, with each animal maintaining an exclusive burrow (Randall, 1993; Schroder and Geluso 1975). The

frequency of contacts between conspecifics depends on the species. Larger species such as *D. spectabilis*, *D. deserti* (Schroder, 1979), and *D. ingens* (Randall et al., 2002) are highly territorial, with little overlapping of their home ranges. However, smaller species such as *D. merriami* and *D. ordii* exhibit frequent overlap of home ranges (Randall, 1989, 1991). The sex, reproductive condition and dispersal status of individuals can influence their spatial relationships. For example, species such as *D. merriami* and *D. heermanni* commonly maintain an extensive home range overlap between male pairs as well as between males and females, but only a slight overlap between female pairs (Behrends et al., 1986; Jones, 1989; Shier and Randall, 2004). Individuals of *D. spectabilis*, *D. deserti* (Schroder, 1979), and *D. ingens* (Randall et al., 2002) show a lesser home range overlap during periods of low reproductive activity, with increased overlap in *D. merriami* and *D. ordii* when individuals are dispersing (Randall, 1989, 1991). For species with common home range overlap, opposite-sex neighbor burrows are closer to each other than those of same-sex animals (*D. merriami*, Behrends et al., 1986; *D. heermanni*, Shier and Randall, 2004). Hence, the spatial distribution of burrows can be used as an approximate measure of the spatial relationships between individuals of *Dipodomys* (Brock and Kelt, 2004).

Merriam's kangaroo rat, *D. merriami*, is widely distributed across the Baja California peninsula (Álvarez-Castañeda et al. 2009). Recently, populations inhabiting the islands of Margarita and San José off the coast of the Baja California peninsula were included

* Corresponding author. Tel.: +52 612 123 8486; fax: +52 612 125 3625.

E-mail address: sticul@cibnor.mx (S.T. Álvarez-Castañeda).

as distinctive subspecies of *D. merriami* (*D. m. margaritae* and *D. m. insularis* respectively; Álvarez-Castañeda et al. 2009), providing an opportunity to contribute with information to understand how insularity has influenced spatial organization. In this study we focus in *D. m. insularis*, a subspecies considered threatened by the Mexican government (Norma Oficial Mexicana, 2002) and as “critically endangered” by the IUCN (2009). Recent information suggests that *D. m. insularis* is restricted to an area of only 30 km² in the southwestern coast of San José Island, with the population having been drastically reduced in size and being close to extinction (Álvarez-Castañeda and Ortega-Rubio 2003; Espinosa-Gayosso and Álvarez-Castañeda 2006). In spite of the interest generated by the conservation status of this subspecies, both the social organization and the spatial relationship between individuals of this subspecies remain unknown. Therefore, knowledge of the spatial distribution of burrows and patterns of burrow occupancy are a key first step toward understanding the population dynamics and social structure of these animals, which are essential for developing appropriate conservation plans (Caro, 1998).

This study describes the spatial pattern of active burrows of *D. m. insularis* and explores the factors that influence spatial relationships between burrows of neighboring individuals in this population. The hypothesis tested is whether the spatial arrangement of neighboring animals differs between opposite- versus same-sex pairs of animals. The specific objectives were: (1) to determine whether burrow use is influenced by season, sex, and age of kangaroo rats, and (2) whether spatial relationships differ in relation to season, sex and age of kangaroo rats. In addition to providing the first quantitative data of burrow use in *D. m. insularis*, our analyses generate important data about the breeding and social structuring of this highly vulnerable population of the kangaroo rat.

Material and methods

Field site and study animals

The study population of *D. merriami insularis* is located in a 79.8 ha (1050 m × 760 m) area in San José Island, Gulf of California, México (24.9291 to 24.9227N, 110.635–110.6294W and 24.933–24.9258N, 110.6294–110.6236W; Fig. 1). Individuals were live-trapped from March to May and from October to November 2008. The sampling periods included the rainy and dry seasons, respectively (Salinas-Zavala et al. 1990). Reproductive individuals of *D. m. insularis* are found during February and March (Best and Thomas 1991). In this study, we found the highest prevalence of reproductive individuals from March to May, and juveniles and subadults during October and November. Thereafter, we made the first sampling period occurred during the breeding season (BRED) and the second one during the non breeding season (NON-BRED). The vegetation type at the study site is a desert shrub, in which the dominant species are: *Fouquieria diguetii*, *Jatropha cinerea*, *Bursera microphylla*, *Simmondsia chinensis*, *Cercidium pininsulare*, *Stenocercus gummosus* and *Cyrtocarpa edulis* (Espinosa-Gayosso and Álvarez-Castañeda 2006). The mean annual temperature is 21–23 °C and mean annual rainfall was 100–150 mm, with most of the precipitation occurring during the summer (Cody et al. 1983). To capture kangaroo rats, metal box traps measuring 30 cm × 10 cm × 10 cm (HB Sherman traps, Inc., Tallahassee, FL) baited with rolled oat were set out. These were checked once a day (in the morning) during each trapping session. Twenty six transect lines of 160 traps/line were established; transect lines were separated by 30 m, and traps within each line were separated by 5 m. Transect lines were distributed so as to cover the whole study site. Traps were set along three transect lines during three BRED or two NON-BRED nights,

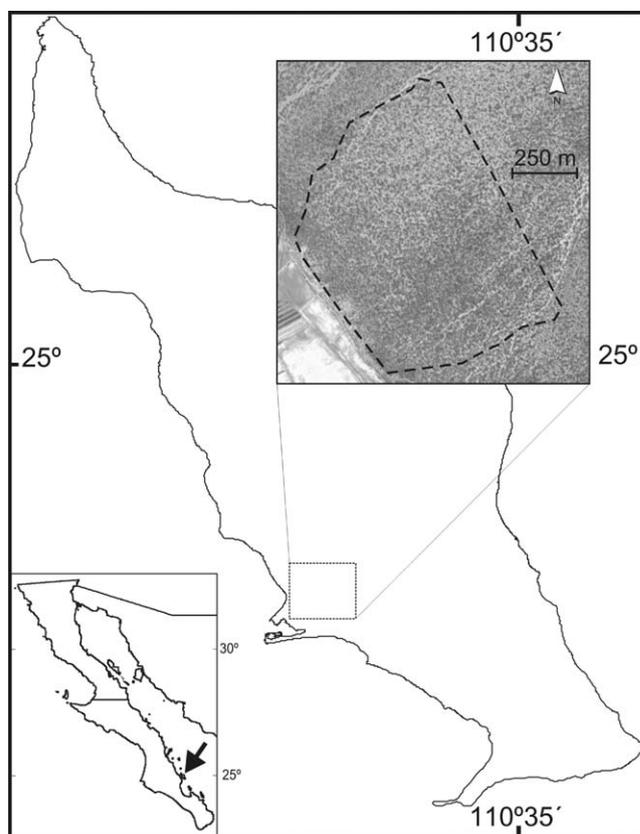


Fig. 1. Study population of *Dipodomys merriami insularis* in San José Island, Baja California Sur, Mexico. The study site encompassed an area of 79.8 ha.

after which they were moved to an adjacent line; this procedure was repeated until all 26 lines were trapped. The reduction in trapping effort to two nights during NON-BRED was decided because we observed that individuals that were frequently captured (up to 15 times) during BRED showed weakness and a reduction in body weight.

For each individual captured, sex and age class were defined; additionally, body weight (using a scale with a precision of 1.0 g) and body length (from the nose tip to the base of the tail, to the nearest 0.1 mm) were measured. Since methods for accurately estimating the age of live *D. m. insularis* are not currently available, we used body weight, fur condition, and reproductive status to define three age categories: juveniles, subadults and adults. Juveniles (females and males) were defined as having soft pelage and weighing less than 28 g, since the minimum weight of a reproductive male (descended testis) was 28.5 g. Juveniles were all non-reproductive, males without descended testes and females that were neither pregnant, lactating nor in estrus. Subadults were defined as having soft juvenile pelage and weighing more than 28.5 g. Subadult males were either non-reproductive or had descended testes measuring less than 12.6 mm in length, and females were neither pregnant nor lactating but some were in estrus. Adults had rough adult pelage and weighed at least 36.1 g, given that the minimum weight of a reproductive female was 36.1 g. Adult males had testes longer than 12.6 mm and females were either reproductive or not. Minimum trappability (Krebs and Boonstra 1984) and recapture rates were calculated for each sex, age class, and sampling period. Each individual captured had one ear tagged (# 1005-1, National Band and Tag Co. Newport, KY, USA) with a number before being released at the point of capture. Handling procedures conformed to the recommendations of the American Society of Mammalogists (Gannon et al. 2007).

Burrow location

Since we could not determine the exact limits of the burrow system, we used the location of the main burrow entrance as a proxy of the burrow system. Thus, the main burrow entrance was defined as the one most frequently visited by an individual. This approach could have biased the analyses because we do not know where the animals were underground, but presumably the main entrance is an important location and is deemed a reasonable approximation for assessing spatial relationships. The burrows used by captured animals were identified using a cocoon bobbin with a 150 m-long filament (Danfield threads, Inc. Winsted, CT, USA) adhered to the individual's back with instant glue (KRAZY® KOLA LOKA®). After releasing a kangaroo rat, we followed the filament until it entered a burrow. Once the burrow was located, we removed the package attached to the kangaroo rat by pulling the filament in order to disintegrate the rest of the bobbin. Each main burrow entrance was marked with a stake and a steel plate on which the date and identification number of the individual that had entered the burrow were noted. The owner of each burrow was assumed to be the individual that entered that burrow with the highest frequency, which ranged from 1 to 4 times in both sampling periods. As for burrows where only one individual entered, it was assumed to be an individual that did not enter any other burrow. Burrows where individuals entered but with no signs of kangaroo rat activity, such as footprints or removed sand, were not included in the data analysis. The locations of main burrow entrances were recorded using a hand-held GPS (Lowrance ifinder Expedition C) with a typical position accuracy of 3 m.

Data analyses

Data analyses are presented as follows: first, we describe the pattern of burrow use; then we analyze whether the pattern of burrow use is influenced by season, sex or age class; and whether the spatial relationship between nearest neighbors vary with season, sex or age class.

To describe the pattern of burrow use by *D. m. insularis*, the following parameters were individually evaluated: (1) number of non-shared burrows that an individual entered, (2) frequency of burrow sharing, and (3) spatial distribution of burrows. All analyses of burrow locations were based on main burrow entrances. It was assumed that two or more animals shared a burrow when the same individuals were found repeatedly (more than twice) at a single burrow or if no other burrows were found for those animals.

To determine if the main burrow entrances were randomly distributed, a "Nearest Neighbor Analysis" (Clark and Evans 1954) was performed using the extension ver.1.0 in Arc View version 3.2a (ESRI Web site). This method compares the mean distance of each main burrow from its nearest neighbor with the mean distance expected for a set of points randomly dispersed at the same density. The ratio of the observed mean distance to the expected distance (R) provides an indication of how the observed distribution deviates from random. An " R " greater than 1 indicates an even distribution, whereas a value close to "0" indicates a clustered distribution. For further details please refer to the script developed by Colin Brooks (Nearest Neighbor Script, v.1.8 available on ESRI Web site). Separate analyses were run for burrow locations of all individuals (females and males), females only, and males only.

The data on number of burrows showed a right-skewed distribution and could not be transformed. Therefore, to determine which factors influence the pattern of burrow use, a generalized linear model (GLM) with a Poisson error distribution (Poisson distribution produced the minimum deviance; Crawley, 2007) was used to test the effect of sex, age class, season (BRED, NON-BRED), capture frequency (low = 1–3 captures, medium = 4–6, and high \geq 6), and their

interactions (sex \times season, sex \times age class and age class \times season) on the number of burrows used by each individual. We confirmed that the residuals of all parametric models approximated to the normal distribution by visually checking probability plots and by using the Shapiro–Wilk test (Faraway, 2006).

Spatial relationships between burrows were described for the entire study area by calculating distances between nearest-neighbor burrows (locations separated by the shortest linear distance between them) for animals of the same or opposite sex. The distance (m) between the entrances of each burrow was calculated using the ArcView 3.2a extension `dmatrix_en.avx` for ArcView (Maoh, 2001).

The mean distance between burrows for same- and opposite-sex pairs of females and males in each sample period were compared. Neither data set met the assumption of normality required by parametric statistics. Thus, we used *Kruskal–Wallis tests* to identify significant differences between groups, followed by Dunn's tests to identify pairwise differences, as needed.

The spatial relationship between nearest-neighbor burrows of same-sex animals with respect to opposite-sex individuals was estimated by a distance index estimated for each individual by dividing the distances between nearest neighbor burrows of same-sex by the distance between individuals of opposite sex. To determine which factors influence the spatial relationship between nearest neighbor burrows of same-sex animals with respect to that of opposite-sex animals, a GLM with a Gamma error distribution (Gamma distribution produced the minimum deviance; Crawley, 2007) was used to test for the effect of season, sex, and age class on the distance index. The distance index showed a strong right-skewed distribution and the transformations did not normalize this distribution. Therefore, a GLM with a Gamma error distribution was fitted in order to investigate relationships between variables.

The statistical analyses about the influence of season, sex, and age class on the pattern of burrow use and the spatial relationships between burrows were carried out with R for Windows version 2.11.1 (R Development Core Team, 2008).

Results

We captured 302 individuals (145 females and 158 males) over the course of this study. During the BRED season we captured 179 individuals (85 females and 94 males) with a median of 2 recaptures per individual (range 1–15); during NON-BRED, 176 individuals (85 females and 91 males) were captured with a median recapture frequency of 1 (range 1–9). We found that the mean frequency of captures was 3.06 ± 0.18 during the BRED season and 1.68 ± 0.07 during NON-BRED. This difference was statistically significant ($U = 9971.5$, $P < 0.0001$). The trappability rate varied from 43.9% (in adults) to 72.3% (in subadults) during the BRED season, and from 32.5% (in subadults) to 67.6% (in adults) during the NON-BRED season. Of the individuals captured during the BRED season, 13 (7.2%) were juveniles, 16 (8.9%) subadults, and 148 (82.3%) adults; of those captured during NON-BRED, 46 (30%) were juveniles, 79 (44.9%) subadults, and 56 (31.8%) adults. Of the individuals captured during the BRED season, the recapture rate during the NON-BRED season was 15.0% for juveniles, 12.5% subadults, and 33.1% adults. The numbers, trappability rate, and recapture rate for animals captured in each sample period are given in Table 1.

Burrow use patterns

One hundred and forty two individuals (69 females and 73 males) were assigned to at least one burrow during the BRED season. In most cases, only one main burrow entrance was identified for each female (range 1–6) and male (1–4). During the BRED

Table 1
Age class, sex, trappability and recapture rate of *Dipodomys merriami insularis* individuals captured (including recaptures) during the breeding (BRED) and non-breeding (NON-BRED) seasons of 2008.

Sampled period	Juveniles	Subadults	Adults	Total
BRED				
Females (n)	7	11	65	85
Males (n)	6	5	83	94
Total (n)	13	16	148	179
Trappability rate (%)	69.6	72.3	43.9	
Median number of burrows for females (range)	1 (1–2)	1 (1–2)	2 (1–6)	
Median number of burrows for males (range)	1 (1)	1.5 (1–2)	1 (1–4)	
NON-BRED				
Females (n)	21	41	28	85
Males (n)	25	38	28	91
Total (n)	46	79	56	176
Trappability rate (%)	48.5	32.5	67.6	
Recapture rate (%)	15.4	12.5	33.1	
Median number of burrows for females (range)	1 (1–2)	1 (1–2)	1 (1–2)	
Median number of burrows for males (range)	1 (1–3)	1 (1–3)	1 (1–2)	

Table 2
Summary of GLMs (with Poisson error distribution and log link) calculated to examine the effect of sex, age, season and frequency of captures on the number of burrows used in *Dipodomys merriami insularis*.

Variable	Deviance	df	P
Sex	0.69	1	0.401
Age	6.27	2	0.043
Season	5.69	1	0.016
Captures	22.45	2	<0.0001
Sex × season	1.52	1	0.216

season, both sexes had a median of 1 burrow. During the NON-BRED season, 168 individuals (82 females and 86 males) were assigned to at least one burrow. In most cases, only 1 burrow was assigned to each female and male (median = 1; range 1–3). Table 1 shows the median and range of the number of burrows used by each sex and age class during the two sampling seasons.

The 142 kangaroo rats captured during the BRED season, and for which a home burrow could be identified, had a total of 207 active burrows (95 for females and 112 for males). Nineteen burrows (9.2%) were shared by two individuals; no burrow was shared by more than two animals. Of these 19 burrows, eleven (57%) were shared by 2 adults of opposite sex, 2 (10%) by an adult female with a subadult male, and 6 (30%) by an adult female with a juvenile. The 168 individuals captured during the NON-BRED season, and for which home burrows could be identified, had 265 active burrows (123 females and 142 males). Three burrows were shared (1.1%): one was shared between an adult male and a juvenile female; another, by an adult female and a juvenile male; the third, by two subadults of opposite sex. The main burrow entrances displayed a clumped spatial distribution for all individuals and for both sexes separately during the BRED (all individuals: $n = 138$, $R = 0.2$, $r_i = 0.011$; females: $n = 66$, $R = 0.14$, $r_i = 0.004$; males: $n = 73$, $R = 0.15$, $r_i = 0.005$) and the NON-BRED (all individuals: $n = 158$, $R = 0.21$, $r_i = 0.014$; females: $n = 77$, $R = 0.14$, $r_i = 0.005$; males: $n = 81$, $R = 0.14$, $r_i = 0.006$) seasons.

Factors associated with burrow use patterns

Age class, season and capture frequency all exerted significant effects on the number of burrows used by individuals (GLM: $n = 300$, $P = 0.016$; Table 2). Individuals in the medium and high capturing categories used more burrows than those in the low capturing category. Adult individuals used more burrows than subadults, and more burrows were assigned to each individual during the BRED season (Fig. 2).

Table 3
Mean nearest-neighbor distances among pairs of burrows for female-female, male-male and female-male categories of all individuals captured during the breeding (BRED) and non-breeding (NON-BRED) seasons. n , sample size; SE, Standard error. Different letters in each sampling period mean that there were significant differences (A posteriori Dunn's test was used to test for pair-wise differences $P < 0.05$).

Pairs of individuals	BRED			NON-BRED		
	n	Mean (m)	SE	n	Mean (m)	SE
All individuals	133	37.7	1.9	161	42.3	1.3
Female–female	67	58.1 ^a	2.5	84	60.6 ^{ab}	3.1
Male–male	66	58.5 ^a	3.1	77	60.5 ^a	2.8
Female–male	67	40.5 ^b	4.3	84	48.8 ^b	2.3

Spatial relationships between burrows

Mean distances between main burrow entrances for nearest neighbors of all individuals, same-sex and opposite-sex pairs are shown in Table 3. Opposite-sex burrows were significantly closer than those of same-sex pairs during the BRED season, and than those of male-male pairs during the NON-BRED season ($n = 443$, $H = 34.5$, $P < 0.0001$).

Age class had significant effects on the distance index of spatial relationship between nearest neighbor burrows of same-sex pairs with respect to opposite-sex individuals (GLM: $n = 294$, $P = 0.018$). Adults displayed a higher distance index relative to subadults ($P = 0.041$). Distance index did not vary respect to breeding and non-breeding seasons ($P = 0.3$) nor in the age classes respect to both seasons ($P = 0.8$).

Discussion

Characterizing the use of burrows by *Dipodomys merriami insularis* (*sensu* Álvarez-Castañeda et al. 2009) provides us with an understanding of spatial relationships between individuals. Our results reveal that members of this subspecies typically use 1–2 different burrows, with a low frequency of burrow sharing, and a clumped spatial distribution of burrows. Factors such as age class, season and capture frequency influenced the number of burrows used by individuals. The spatial organization is characterized by the fact that animals of opposite sex are closer to each other than same-sex individuals; also, this spatial relationship between nearest-neighbor burrows is influenced by age class.

The present study was based on a capture-recapture sampling method. A changing trappability rate and a low recapture rate were observed in this study. The trappability rate showed a reduction of 21.1% for juveniles and 39.8% for subadults between sampling periods, and an increase of 23.7% for adults. The mean recapture

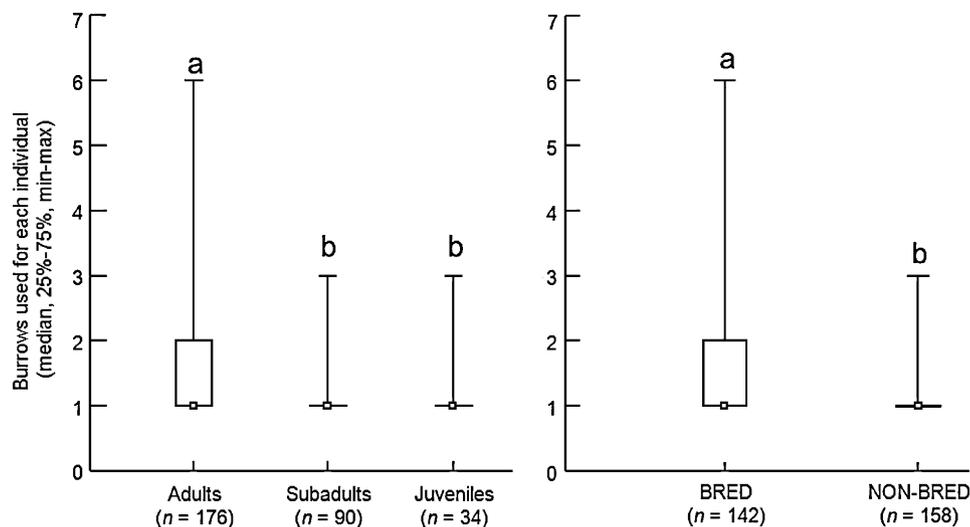


Fig. 2. Effects of age class (left) and season (right) on the number of burrows used by the individuals of *Dipodomys merriami insularis*. Sampling periods were during breeding (BRED) and non-breeding (NON-BRED) season. Different letters mean that there were significant differences ($P < 0.05$).

rate was lower than 33.1%, which suggests a high mortality and/or emigration of individuals. Therefore, the detection of spatial organization patterns can be influenced by a low capture efficiency.

Patterns of burrow use by the kangaroo rat at San Jose Island

This is the first record of the number of burrows used per individual in *D. merriami* from Baja California. In the population studied, individuals used 1–2 burrows. The maximum number of burrows per individual reported here is slightly lower than the highest number recorded (up to 8 burrows) for this species (Behrends et al., 1986; Jones, 1989). Other species, such as *D. spectabilis* (Jones, 1984; Winters and Waser, 2003) and *D. ingens* (Cooper and Randall, 2007), use 1–3 burrows per individual, similar to our results. Subadult individuals occupied slightly fewer burrows per individual than juveniles and adults (Fig. 2). Settled individuals of *D. merriami* can use several burrows but most often use only one or two (Behrends et al., 1986). Subadults probably are individuals not completely settled that use fewer burrows because they have excavated fewer burrows. We found that juveniles and adults used a similar number of burrows, suggesting that juveniles have more burrows than subadults because they are using their mothers' burrows. All individuals used more burrows during the BRED season (Fig. 2), which suggests a higher mobility of animals – possibly an outcome of the reproductive activity – as observed in other populations of *D. merriami* (Behrends et al., 1986). Individuals in the low-capture category used fewer burrows and were influenced by the capture effort. Therefore, increasing the capture effort could contribute to validate our results.

Our results show that, similar to the findings reported for mainland populations of *D. merriami*, a low frequency of burrow sharing was observed (Randall 1987, 1993). The relatively high frequency of burrow sharing by adults during BRED could be explained by the stage in the reproductive cycle of *D. m. insularis*. In isolated mainland populations of *D. merriami*, adult females share their burrows with males for reproductive purposes (Randall 1987, 1993). We suspect that this is also the case in our study population. By contrast, burrow sharing during the NON-BRED season involved adult females and possibly their offspring (juvenile or subadults), as occurs in females of *D. merriami* (Zeng and Brown 1987).

The spatial distribution of burrows was clumped for both females and males during both sampling periods. This result contrasts with the distribution of burrows in species that seem

to minimize intraspecific interactions by spatial means, as *D. spectabilis* (Schroder and Geluso 1975; Schroder 1979; Schooley and Wiens 2001) and *D. ingens* (Cooper and Randall, 2007). The distribution pattern of burrows observed in our study resembles the distribution of burrows observed for mainland populations of *D. merriami*, which exhibit frequently overlapping female and male home ranges (Jones, 1989; O'Farrell, 1980; Behrends et al., 1986; Randall, 1993; Perri and Randall, 1999). Therefore, we can expect that if the home range of *D. m. insularis* overlaps, this could result in a clumped spatial distribution of burrows. The absence of seasonal changes in the spatial distribution of burrows of *D. m. insularis* could be explained as a large intraspecific overlapping of home ranges yearlong as occurs in *D. merriami* (O'Farrell, 1980).

Spatial relationships between burrows

We found that the mean distance between burrows of nearest neighbors was similar to the one in mainland populations of *D. merriami* (Behrends et al. 1986) but slightly larger than those found in the medium-sized species *D. heermanni arenae* (Shier and Randall 2004) and the large-sized *D. nelsoni*, *D. spectabilis zygomaticus*, *D. s. cratodon* (Best et al. 1988), and *D. ingens* (Cooper and Randall 2007). Our results suggest that nearest-neighbor distances are apparently not related to mean body size in *Dipodomys*. Different habitats and individual density, rather than body size, are likely to contribute to these interspecific differences.

In our study, burrows belonging to opposite-sex animals were closer than those of same-sex animals, an outcome that is consistent with previous studies of *D. merriami* (Behrends et al., 1986) and *D. heermanni* (Shier and Randall, 2004). The closer burrows of opposite-sex neighbors and the overlapping home ranges between sexes suggest a higher spatial tolerance between individuals of opposite sexes than between females in *D. merriami* (Behrends et al., 1986; O'Farrell, 1980; Randall, 1993; Perri and Randall, 1999) and *D. heermanni* (Shier and Randall, 2004). The latter supports that female burrows are significantly closer to males' than to other females' (Shier and Randall, 2004). Thus, our results suggest that females and males have more spatial tolerance than same-sex individuals, and that both sexes could have less intra-sexual spatial tolerance, especially during the BRED season.

Our analysis of the spatial relationships between individuals reveals that the distance between burrows of same-sex nearest neighbors with respect to opposite-sex (calculated by the distance

index) is influenced by age class. Namely, adult individuals had a higher distance index than subadults, which indicates that adult individuals had burrows closer to burrows of opposite-sex than same-sex neighbors. Although in another population of *D. merriami* the breeding season also influenced the mobility of individuals (O'Farrell 1980), in this study the season did not appear to influence the spatial distribution pattern of burrows. Probably, the breeding season does influence the mobility of *D. merriami insularis* but not the spatial organization of their burrows.

Our results showed that *D. merriami insularis* displays patterns of burrow use and spatial organization similar to those observed in other populations of this species. Thus, these results contribute to understanding the reduced variation in the social organization of this kangaroo rat, a fact that should be considered in conservation planning for this endangered taxon.

Acknowledgements

We are grateful to M.L. Rodríguez, A.T. Haro, C. I. Gutierrez and M. De La Paz for their valuable aid in the field, to W. Lidicker, E. Lacey, P. Cortés, P. Cruz and F. Aguilar for their comments during the study and the revision of the manuscript, and to D. Dorantes and S. Sánchez Colón for his tutoring in English. This study was done with research grants from the Consejo Nacional de Ciencia y Tecnología (CONACYT grants SEMARNAT-2002-C01-0193 and 39467Q).

References

- Álvarez-Castañeda, S.T., Ortega-Rubio, A., 2003. Current status of rodents on islands in the Gulf of California. *Biol. Conserv.* 109, 157–163.
- Álvarez-Castañeda, S.T., Lidicker Jr., W.Z., Ríos, E.R., 2009. Revision of the *Dipodomys merriami* complex in the Baja California Peninsula, Mexico. *J. Mammal.* 90, 992–1008.
- Behrends, P., Daly, M., Wilson, D.I., 1986. Range use patterns and spatial relationships of Merriam's Kangaroo rats (*Dipodomys merriami*). *Behaviour* 96, 187–209.
- Best, T.L., 1972. Mound development by a pioneer population of the banner-tailed kangaroo rat. *Dipodomys spectabilis baileyi* Goldman, in eastern New Mexico. *Am. Midl. Nat.* 87, 201–206.
- Best, T.L., Inness, C., Shull, K.D., 1988. Mound structure in three taxa of Mexican kangaroo rats (*Dipodomys spectabilis cratodon* D. s. *zygomatiscus* and *D. nelsoni*). *Am. Midl. Nat.* 119, 216–220.
- Best, T.L., Thomas, H.H., 1991. *Dipodomys insularis*. *Mammal. Species* 374, 1–3.
- Brock, R.E., Kelt, D.A., 2004. Conservation and social structure of Stephens' kangaroo rat: implications from burrow-use behavior. *J. Mammal.* 85, 51–57.
- Caro, T., 1998. The significance of behavioral ecology for conservation biology. In: Caro, T. (Ed.), *Behavioral Ecology and Conservation Biology*. Oxford University Press, New York, pp. 369–393.
- Clark, P.J., Evans, F.C., 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* 35, 445–453.
- Cody, M.L., Moran, R., Thompson, H., 1983. The plants. In: Case, T.J., Cody, M.L. (Eds.), *Island Biogeography in the Sea of Cortez*. University of California Press, Berkeley, pp. 49–97.
- Cooper, L.D., Randall, J.A., 2007. Seasonal changes in home ranges of the giant kangaroo rat (*Dipodomys ingens*): a study of flexible social structure. *J. Mammal.* 88, 1000–1008.
- Crawley, M.J., 2007. *The R Book*. The John Wiley & Sons, Ltd., Chichester, England, 511–526.
- Daly, M., Behrends, P.R., Wilson, M.I., Jacobs, L.F., 1992. Behavioral modulation of predation risk moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys merriami*. *Anim. Behav.* 44, 1–10.
- Espinosa-Gayosso, C.V., Álvarez-Castañeda, S.T., 2006. Status of *Dipodomys insularis*, an endemic species of San José Island, Gulf of California Mexico. *J. Mammal.* 87, 677–682.
- Faraway, J., 2006. *Extending the Linear Model with R*. Chapman and Hall/CRC, New York.
- Gannon, W.L., Sikes, R.S., Animal Care and Use Committee of the American Society of Mammalogists, 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *J. Mammal.* 88, 809–823.
- IUCN (International Union for Conservation of Nature and Natural Resources), 2009. 2009 IUCN Red list of threatened species. www.iucnredlist.org (accessed November 2009).
- Jones, W.T., 1984. Natal philopatry in bannertailed kangaroo rats. *Behav. Ecol. Sociobiol.* 15, 51–155.
- Jones, W.T., 1989. Dispersal distance and the range of nightly movements in Merriam's kangaroo rats. *J. Mammal.* 70, 27–34.
- Krebs, C.J., Boonstra, R., 1984. Trappability estimates for mark-recapture data. *Can. J. Zool.* 62, 2440–2444.
- Maoh, H., 2001. Distance Matrix of Point Features (dmatrix.en.avx) extension for ArcView 3.2a. Available at: <http://arcscrippts.esri.com/details.asp?dbid=10408>.
- Norma Oficial Mexicana (2002): Protección ambiental—especies nativas de México de flora y fauna silvestres—categorías de riesgo y especificaciones para su inclusión, exclusión o cambio—lista de especies en riesgo. NOM-059-ECOL-2001. Diario Oficial de la Federación, Norma Oficial Mexicana, México City, Mexico.
- O'Farrell, M.J., 1980. Spatial relationships of rodents in a sagebrush community. *J. Mammal.* 61, 589–605.
- Perri, L.M., Randall, J.A., 1999. Behavioral mechanism of coexistence in sympatric species of desert rodents, *Dipodomys ordii* and *D. merriami*. *J. Mammal.* 80, 1297–1310.
- Randall, J.A., 1987. Field observation of male competition and mating in Merriam's and banner tail kangaroo rat. *Am. Midl. Nat.* 117, 211–213.
- Randall, J.A., 1989. Neighbor recognition in solitary desert rodent (*Dipodomys merriami*). *Ethology* 81, 123–133.
- Randall, J.A., 1991. Sandbathing to establish familiarity in the Merriam's kangaroo rat, *Dipodomys merriami*. *Anim. Behav.* 41, 267–275.
- Randall, J.A., 1993. Behavioural adaptations of desert rodents (Heteromyidae). *Anim. Behav.* 45, 263–267.
- Randall, J.A., Hekkala, E.R., Cooper, L.D., Barfield, J., 2002. Familiarity and flexible mating strategies of a solitary rodent, *Dipodomys ingens*. *Anim. Behav.* 64, 11–21.
- R Development Core Team, 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0, <http://www.R-project.org>.
- Reichman, O.J., Price, M.V., 1993. Ecological aspects of Heteromyid foraging. In: Genoways, H.H., Brown, J.H. (Eds.), *Biology of the Heteromyidae*. Special Publications No. 10. The American Society of Mammalogists, Utah, pp. 539–574.
- Reichman, O.J., Smith, S.C., 1990. Burrows and burrowing behavior by mammals. In: Genoways, H.H. (Ed.), *Current Mammalogy*. Plenum Press, New York/London, pp. 197–244.
- Reynolds, H.G., 1958. The ecology of the Merriam kangaroo rat (*Dipodomys merriami* Mearns) on the grazing lands of southern Arizona. *Ecol. Monogr.* 28, 111–127.
- Salinas-Zavala, C.A., Leyva-Contreras, A., Lluch-Belda, D., Díaz-Rivera, E., 1990. Distribución geográfica y variabilidad climática de los regímenes pluviométricos en Baja California Sur, México. *Atmósfera* 3, 217–237.
- Schooley, R.L., Wiens, J.A., 2001. Dispersion of kangaroo rat at multiple scales in New Mexico, USA. *Landscape Ecol.* 16, 267–277.
- Schroder, G.D., 1979. Foraging behavior and home range utilization of the bannertail kangaroo rat (*Dipodomys spectabilis*). *Ecology* 60, 657–665.
- Schroder, G.D., Geluso, K.N., 1975. Spatial distribution of *Dipodomys spectabilis* mounds. *J. Mammal.* 87, 748–756.
- Shier, D.M., Randall, J.A., 2004. Spacing as a predictor of social organization in kangaroo rats (*Dipodomys heermanni arenae*). *J. Mammal.* 85, 1002–1008.
- Vaughan, T.A., Ryan, J.A., Czaplewski, N.J., 2000. *Mammalogy*, fourth ed. Harcourt College Publishers, Philadelphia.
- Winters, J.B., Waser, P.M., 2003. Gene dispersal and outbreeding in a philopatric mammal. *Mol. Ecol.* 12, 2251–2259.
- Zeng, Z., Brown, J.H., 1987. Population ecology of a desert rodent: *Dipodomys merriami* in the Chihuahuan desert. *Ecology* 68, 1328–1340.