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LONG-DISTANCE MOVEMENTS OF JUVENILE MOHAVE GROUND SQUIRRELS, *SPERMOPHILUS MOHAVENSIS*

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ABSTRACT—We studied movements of 36 juvenile Mohave ground squirrels (*Spermophilus mohavensis*) during their first active season, until immergence into hibernation, a period that lasted from late May to late August. For all radiocollared individuals, the mean greatest distance between any 2 locations was 1,520 m for males (range 110 to 6,230 m) and 505 m for females (range 105 to 3,862 m). Eleven individuals (6 females, 5 males) with known litter affiliations were followed from their initial capture until inactive underground: males moved a mean distance of 2,920 m (range 0 to 6,230 m), and females moved a mean distance of 753 m (range 0 to 3,862 m) between their natal area and hibernation site. Ten individuals (8 males, 2 females) moved distances >1 km. Individuals making long-distance movements were likely to have traversed habitat that would be considered marginal for adult Mohave ground squirrels. Long-distance movement by juveniles might be critical for connecting local populations and recolonizing sites after local, drought-related extirpation.

RESUMEN—Estudiamos los desplazamientos de 36 jóvenes de la ardilla de tierra de Mohave (*Spermophilus mohavensis*) durante su primera temporada activa hasta que comenzaron la invernada, o sea durante el periodo de finales de mayo a finales de agosto. Para todos los individuos con radiotransmisores al cuello, la mayor distancia media entre cualquiera de dos lugares fue de 1,520 m para los machos (rango 110 a 6,230 m) y de 505 m para las hembras (rango 105 a 3,862 m). Once individuos (6 hembras y 5 machos) con conocidas afiliaciones de camada fueron seguidos desde su captura inicial hasta su inactividad subterránea: los machos se desplazaron una distancia media de 2,920 m (rango 0 a 6,230 m) y las hembras una distancia de 753 m (rango 0 a 3,862 m) entre su área natal y el sitio de la invernada. Diez sujetos (8 machos, 2 hembras) se desplazaron una distancia de >1 km. Los individuos que se desplazaron una larga distancia probablemente cruzaron hábitat que se consideraría subóptimo para los adultos de la ardilla de tierra de Mohave. Los desplazamientos de distancia larga de las ardillas jóvenes pueden ser decisivos para conectar las poblaciones locales y para volver a colonizar los sitios después de la extinción local debido a la sequía.

Movement capabilities of a species influence landscape-scale patterns of habitat use and genetic structure of populations (Dobson, 1994; Price et al., 1994; Diffendorfer et al., 1995; Peacock, 1997). Movement patterns might help to identify possible travel corridors between populations. Movements of different age and sex classes of mammals are often quite different (Gaines and McClenaghan, 1980; Greenwood, 1980; Holekamp, 1984*a,* 1986). For example, in ground squirrels, movements during the mating season (Dobson, 1984; Schwagmeyer, 1988) and natal dispersal (Dobson, 1982; Holekamp, 1984*a,* 1984*b*; Wiggett and Boag, 1989*b*; Waterman, 1992; Olson and Van Horne, 1998; Byrom and Krebs, 1999) are usually sex-biased, with males making more extensive movements. We studied the movements of juvenile Mohave ground squirrels (*Spermophilus mohavensis*) during the time of year when dispersal or other exploratory movements would be likely to occur: between emergence from the natal burrow and entry into first hibernation (Holekamp, 1984*a*).

The Mohave ground squirrel is a small (adult post-hibernation mass of 100 to 150 g), herbivorous rodent found in desert-scrub habitats of the western Mojave Desert (Best, 1995).

The active season for adults usually extends from February through July, with the rest of the year spent in dormancy (Bartholomew and Hudson, 1960). The single annual mating season occurs immediately after emergence from hibernation in February and early March. Young are usually born in late March and early April, and lactation can continue through mid May. Litters generally first appear above ground from late April to mid May. The species is frequently described as uncommon and having a patchy distribution (Burt, 1936; Zembal and Gall, 1980), and it is listed as threatened under the California Endangered Species Act. Within the geographic range of the species, patchy distribution might be related to landscape factors, such as the basin-and-range topography of the western Mojave Desert, soil type, shrub size and density, and plant community composition. Particular shrub species that are patchily distributed can be an important part of the diet (Best, 1995). Mohave ground squirrels would be expected to exhibit metapopulation dynamics in which local populations differ in productivity and persistence through drought periods. We observed drought-related local extirpation from 1989 to 1992 at one of our study sites. Despite extensive searching for suitable habitat and trapping at several locations near the site, no nearby populations were located. Recolonization occurred in 1993, following 2 consecutive years of higher rainfall and ground squirrel reproduction at other sites in the region. These events suggested that data on the dispersal movements of juvenile males and females might help to explain local distribution patterns.

There is no published information on movements in *S. mohavensis,* although dispersal has been studied in a number of other ground squirrels (Holekamp, 1984*a,* 1984*b*; Ortega, 1988; Wiggett and Boag, 1989*a*; Wiggett et al., 1989; Waterman, 1992; Olson and Van Horne, 1998; Byrom and Krebs, 1999). Hafner (1992) and Hafner and Yates (1983) hypothesized that low mobility might be one of several possible explanations for the persistence of a stable contact zone between *S. mohavensis* and *S. tereticaudus,* a closely related, allopatric species. As part of a study of habitat use and population dynamics in *S. mohavensis,* we studied the movements and home range of adult Mohave ground squirrels (Harris and Leitner, 2004). We found that adults rarely move distances >200 m during the postmating season, and that home-range sizes of adult females vary depending on rainfall and plant productivity. We also found that adult males move longer distances during the mating season than the postmating season, whereas female movements are similar in the mating and postmating seasons. In this paper, we present the results of radiotelemetry observations of movements by juvenile Mohave ground squirrels during their first summer.

METHODS—*Study Site*—We conducted our study in the Coso Range, a desert mountain range about 20 km east of the Sierra Nevada in the northwestern Mojave Desert, Inyo County, California (36°04′N, 117°48′W). Elevation of the study site was 1,400 to 1,500 m, and slopes ranged from 2 to 15%. Alluvial soils at the study site were loamy, coarse sands. The vegetation was a mixed desert-scrub community including spiny hopsage (*Grayia spinosa*), fourwing saltbush (*Atriplex canescens*), shadscale (*A. confertifolia*), cheesebush (*Hymenoclea salsola*), Cooper's boxthorn (*Lycium cooperi*), and winterfat (*Krascheninnikovia lanata*). This community is typical of the transition between Mojave and Great Basin desert biomes (Beatley, 1975). The rugged uplands between alluvial basins were rocky or gravelly, with a sparse cover of shrubs, often including California buckwheat (*Eriogonum fasciculatum*) and needle-leaved rabbitbrush (*Chrysothamnus teretifolius*). Mean annual precipitation (1949 through 1999) was 163 mm at Haiwee Power Plant (elevation 1,160 m), 15 km to the northwest of the study site. Winter rainfall predominated, with 79% of annual precipitation received between 1 October and 31 March over the 51-y period of record.

Studies took place on a 47-ha site located in an alluvial basin southeast of Cactus Peak. A 22-ha portion of the site, with trap stations placed at 50-m intervals in an 8 by 15 array, was used exclusively for radiotelemetry studies in 1990 and from 1994 through 1997 (Harris and Leitner, 2004). Juvenile Mohave ground squirrels were radiocollared on this portion of the study site in 1995. A 25-ha portion of the site, with trap stations at 25-m spacing in a 21 by 21 array, was used for demographic studies from 1988 through 1996. We radiocollared juvenile Mohave ground squirrels on this portion of the study site during 1997. Radiocollared animals freely used both portions of the study area.

Capture Procedures—Ground squirrels were captured with Pymatuning (10 by 11 by 39 cm) or Sherman (8 by 9 by 30 cm) traps baited with a commercial horse feed and placed under shrubs at each trap

station. Traps were set in early morning, checked at mid-day and late afternoon, and then closed for the night. All captured ground squirrels were weighed, and their sex, age, and reproductive condition recorded. Adults could be distinguished from juveniles by body mass and pelage. Adult females were examined for evidence of pregnancy or lactation to facilitate the location of litters. We marked ground squirrels for permanent identification with passive integrated transponder (PIT) tags implanted subcutaneously between the scapulae with a 12-gauge hypodermic needle (Schooley et al., 1993). Additional traps were used as needed to capture particular previously collared animals to obtain information about the condition of animals and body mass, collect fecal samples, or capture juvenile ground squirrels at their natal burrows.

Radiotelemetry Procedures—We radiocollared 13 juvenile Mohave ground squirrels in 1995 (9 females, 4 males) and 23 juveniles in 1997 (12 females, 11 males). These 2 years of successful reproduction were separated by a drought year in which there was no evidence of pregnancy and no juveniles were observed. Juvenile ground squirrels generally began to appear near their natal burrows in mid May. We equipped juveniles with PIT tags at the first capture and with radiocollars when they reached a body mass of about 80 g. All captured juveniles that met this weight criterion were equipped with radiocollars. This weight criterion was adopted in part to ensure that the radiocollar could accommodate any size increase due to growth. The dates on which juveniles were radiocollared differed between the 2 years of study (7 to 9 June in 1995 and 19 May to 3 June 1997) due to differences in birth dates of juveniles between the 2 years. Radiotelemetry continued until mid August, when most surviving juveniles had entered hibernation.

We equipped juvenile Mohave ground squirrels with 5-g transmitters (Model SM1, AVM Instrument Co., Livermore, California) with flexible collars fitting around the neck of the animal. The fit of collars was such as to allow some space for growth. We attempted to recapture radiocollared juveniles to obtain body mass data and to examine the fit of collars. Radiocollared Mohave ground squirrels were located using portable receivers (Model LA-12, AVM Instrument Co.) and hand-held two-element Yagi antennas (Telonics, Inc., Mesa, Arizona). On 16 July and 9 August 1997, we used an aircraft provided by the California Department of Fish and Game to locate juveniles that had made long-distance movements. Animals detected from the air were later located on the ground. Ground locations were determined by following radio signals until a squirrel was either seen or localized in a burrow within 5 m by signal strength and direction. On the study site, each location was recorded by measuring compass bearing and distance of the animal from the nearest trap station. Locations off the study site were determined using a Garmin Model 12XL GPS receiver (Garmin International, Inc., Olathe, Kansas). Distances between locations, or between distant locations and the point of origin of an animal on the study site, were calculated using the program CALHOME (Kie et al., 1996). We attempted to locate each juvenile Mohave ground squirrel twice per day during its diurnal active period: once in the morning and once in the afternoon.

A ground squirrel was judged to be hibernating if it was located by radiotelemetry in the same burrow on 3 or more consecutive days. To confirm that it was inactive, several baited traps were placed in the immediate vicinity of the burrow. Because this method was generally quite effective in capturing nonhibernating, radiocollared Mohave ground squirrels, lack of capture success was considered to be another indication that the animal had entered hibernation. On each subsequent radiotelemetry session, all dormant animals were checked to determine that there had been no movement. This method cannot exclude the possibility that an animal had died underground, though in no case did the individuals judged to have entered hibernation seem to be in poor condition prior to the observed inactivity. During the following spring, we attempted to recapture those individuals for which hibernation sites were known so we could remove radiocollars, but were able to recover only 2 animals in this manner. Because this time period exceeded the battery life of radiotransmitters, it was difficult to relocate animals that had moved away from the study grid.

We recovered some radiocollars with evidence suggesting that the radiocollared individuals had been taken by an avian or mammalian predator. These indications included some combination of blood or tooth marks on the collar or discovery of the collar at a potential raptor or raven perch site. We considered these individuals to have been probable victims of predation, in contrast to those cases in which a signal could no longer be detected, which we categorized as disappearance. These individuals either moved out of detection range or had radios that failed.

Measures of Movement—We determined the distance between natal area and hibernation site for those individuals that survived to hibernation and were associated with a known litter. We established litter associations by observing and capturing juveniles at natal burrows or by patterns of association between individuals. In 1995, we were able to observe juveniles in the first few days after emergence from natal burrows. Most of the radiocollared juveniles in 1995 were captured while still active in a small area surrounding the natal burrow. Individuals were often in close association with siblings and their

TABLE 1—Distances (m) moved and fates of juvenile Mohave ground squirrels (*Spermophilus mohavensis*) in California during 1995 and 1997. The litter affiliation and fate of each animal is shown, if known. Dispersal distance is the distance between natal area and hibernation site. Maximum distance is the maximum distance between any 2 locations for each animal.

Animal	Sex	Year	Litter	Dispersal distance	Maximum distance	Fate
F152	F	1997	5		198	Died
F030	F	1995	1		213	Disappeared
F346	F	1995	1		304	Disappeared
F988	F	1995	2		175	Disappeared
F264	F	1997	5		130	Disappeared
M156	M	1995	1		110	Disappeared
M607	M	1995	3		662	Disappeared
M145	M	1997	6		110	Disappeared
M274	M	1997	4		1,778	Disappeared
F115	F	1995	2	75	118	Hibernation
F740	F	1995	1	380	513	Hibernation
F878	F	1995	3	100	218	Hibernation
F898	F	1995			195	Hibernation
F951	F	1995			263	Hibernation
F066	F	1997	7	3,862	3,862	Hibernation
F101	F	1997	6	0	158	Hibernation
F203	F	1997			188	Hibernation
F294	F	1997	4	100	382	Hibernation
M780	M	1995	3	1,400	1,455	Hibernation
M165	M	1997	7	4,548	4,548	Hibernation
M172	M	1997	7	6,230	6,230	Hibernation
M184	M	1997	6	390	655	Hibernation
M192	M	1997	7	2,031	2,031	Hibernation
M333	M	1997			1,664	Hibernation
F760	F	1995	2		111	Predation
F092	F	1997	5		295	Predation
F123	F	1997			625	Predation
F254	F	1997	6		105	Predation
F285	F	1997	4		168	Predation
F304	F	1997	4		1,913	Predation
F343	F	1997	6		478	Predation
M180	M	1995	1		358	Predation
M025	M	1997			165	Predation
M113	M	1997	7		1,937	Predation
M222	M	1997			90	Predation
M308	M	1997	4		1,256	Predation

mother. Eleven of 13 juveniles could be associated with 1 of 3 litters. In contrast, because emergence from the natal burrow occurred earlier in 1997, we did not observe juveniles in the first few days of emergence. Nevertheless, patterns of association of individuals during daily activity, and common occupancy of nocturnal burrows, allowed us to associate 18 of 23 radiocollared juveniles with 1 of 4 different litters.

In addition to determining the distance between natal area and hibernation site, we also determined the greatest distance between any 2 locations for each individual. This distance simply gives an indication of the maximum movement potential of an individual. Differences in movement measures between males and females were tested using a *t*-test on log-transformed movement data.

RESULTS—*Fates of Individuals*—Litter affiliations were established for 29 juveniles. Eleven of these were determined to have entered hibernation at the end of their first active season (Table 1). Nine of the other 18 that had known

litter affiliations probably were taken by predators, 8 disappeared and were never relocated, and 1 was found dead in a Joshua tree (*Yucca brevifolia*). Some of these individuals made long-distance movements prior to disappearance or predation. Seven individuals did not have a clear litter affiliation; 4 of these entered hibernation and 3 were probably taken by predators, in some cases after long-distance movements.

Distance from Natal Area to Hibernation Site—For those 11 animals that had both a known litter affiliation and hibernation site, the mean distance from natal area to hibernation site (Table 1) was 1,738 m (range 0 to 6,230 m). The mean distance for males was 2,920 m (range 390 to 6,230 m, $n = 5$), and the mean distance for females was 753 m (range 0 to 3,862 m, $n = 6$, $t = 2.29$, $df = 9$, $P < 0.05$). Five individuals moved distances greater than 1 km (4 of 5 males, 1 of 6 females). With the single exception of an individual that moved 3,862 m, distances from natal area to hibernation site for females were <500 m. Three females were the only individuals with known litter affiliations that hibernated and never moved >200 m between consecutive locations.

Maximum Distances Moved—The mean maximum distance between any 2 locations (Table 1) was 1,520 m for males (range 110 to 6,230 m) and 505 m for females (range 105 to 3,862 m, $t = 2.58$, $P = 0.01$, $df = 34$). In 4 cases, the maximum distance was the same as the distance from natal area to hibernation site. For 13 individuals, the greatest distance between consecutive locations was the only such movement >200 m; 8 individuals had multiple movements >200 m. In some cases, these movements occurred during multiple round-trips between the natal area and a remote location. Eight of 15 males moved distances >1 km, whereas 2 of 21 females made such movements ($\chi^2 = 8.37$, $df = 1$, $P < 0.05$).

Relationship of Long-distance Movements to Topography—With a single exception, juveniles that moved >1 km moved out of the alluvial basin in which the study area was located. In all cases, the most direct pathway would have required passing over rocky terrain with less shrub cover than the study area. Two individuals that moved in a westerly direction from the study site crossed dirt roads to reach their final known locations. Four individuals that moved in a northerly direction from the study site were found near the edge of an extensive, barren playa. Three of these animals seemed to have stopped when they reached the playa, while the fourth seemed to have moved northeastward along the edge of the playa for several hundred meters to reach its final known location.

Discussion—We found that juvenile Mohave ground squirrels can move relatively long-distances during their first summer, prior to hibernation. Ten individuals made movements >1 km (range 1,000 to 6,230 m). These distances are straight-line distances from point of origin on the study site to the last known location. Twenty-one individuals had maximum movement distances >200 m (11 of 15 males, 10 of 21 females). Such movements are relatively uncommon in adults, with the exception of males during the mating season (Harris and Leitner, 2004).

In all but one case, individuals that moved >1 km simply disappeared from the study site on a particular day and were found later at a distant location. Therefore, they had moved out of radio reception range (approximately 400 to 500 m) within one day. Thus, these individuals reached their final known locations without evidence of exploratory movements to these locations. A few other juveniles made regular daily movements of several hundred meters but returned to their natal areas at night, but exploratory behavior was not observed in all juveniles. It is possible that short exploratory movements might have been made between the times that individuals were located on a given day. Sudden dispersal movements within a period of 1 to 2 days have also been noted for *S. columbianus* (Wiggett et al., 1989) and *S. parryii* (Byrom and Krebs, 1999). This behavior contrasts with the gradual increase of home range followed by a fissioning of new and old home range described for *S. beldingi* (Holekamp, 1984*a*).

Natal dispersal in Mohave ground squirrels seems to be male-biased, as it is in most other ground squirrel species (Dobson, 1982; Holekamp, 1984*a*, 1984*b*; Wiggett and Boag, 1989; Waterman, 1992; Olson and Van Horne, 1998; Byrom and Krebs, 1999). Both the maximum distance between any 2 locations, and the distance from natal area to hibernation site were

significantly greater for males than females. Eight of the 10 individuals that made movements >1 km were males.

Long-distance natal dispersal has been recorded in several other species of ground squirrels. A maximum natal dispersal distance of 9.6 km has been documented for *S. richardsonii* (Quanstrom, 1971), a distance of 8.5 km was reported for an individual of *S. columbianus* (Wigget and Boag, 1989), and a distance of 3.9 km was reported for an individual of *S. variegatus* (Ortega, 1988). Dispersal distances >1 km also have been reported for *S. beldingi* (Holekamp, 1984*b*) and *S. townsendii* (Olson and Van Horne, 1998). However, Holekamp (1984*a*) found that dispersal distances in most ground squirrels were <1 km, and that no ground squirrel species that had been studied to date had a mean dispersal distance >0.55 km. A later study of *S. columbianus* (Wigget and Boag, 1989; Wigget et al., 1989) found that individuals dispersing among a set of fragmented colonies had mean dispersal distances of 2.0 km for males and 1.8 km for females. Olson and Van Horne (1998) reported a mean dispersal distance for *S. townsendii* of 515 m, with a maximum dispersal distance of 1,076 m. Byrom and Krebs (1999) reported mean dispersal distances for *S. parryii* of 120 m for females and 515 m for males. Although our sample of individuals from known litters that made long-distance movements during their first summer was small, the distances moved, combined with the long-distance movements of several other individuals, suggest that Mohave ground squirrels might have a greater dispersal distance than most other ground squirrel species.

Our results suggest that many, if not most, juvenile Mohave ground squirrels disperse in their first summer. We cannot rule out the possibility that some of the individuals that remained in or near their natal area might have made significant movements during their second summer. Dispersal in the first summer is prevalent in ground squirrels (Holekamp, 1984*a*), although yearling dispersal is found in *S. columbianus* (Festa-Bianchet and King, 1984; Wiggett and Boag, 1989; Waterman, 1992). Several other species, including *S. beldingi* (Holekamp, 1984*b*), *S. elegans* (Pfeifer, 1982), *S. richardsonii* (Michener and Michener, 1977), and *S. tridecemlineatus* (Rongstad, 1965; McCarley, 1966), exhibit some yearling dispersal, though most individuals disperse in their first summer. Among those species that disperse in their first summer, most make dispersal movements between 4 and 12 weeks after emergence from the natal burrow (Holekamp, 1984*a*). We were able to determine a dispersal date for 3 individuals in 1995 (8 through 10 June) and 10 in 1997 (25 May through 1 June). These observations suggest that juvenile Mohave ground squirrels disperse during the early portion of the 4-week to 12-week post-emergence interval observed for other species.

Juveniles that moved long-distances were likely to have traveled through habitats considered marginal for permanent occupancy (Fig. 1). For example, all juveniles that moved >1 km probably traveled through habitat with rocky or gravelly soils, and over elevation changes of several hundred meters. However, several juveniles did not cross a barren playa that they encountered in their movements. A reasonable conclusion from these observations is that large unvegetated areas might constitute barriers to dispersal, but that rough terrain and rocky soils might be traversed if some shrub cover is available. This behavior seems to be in contrast to that of many rodent species, which tend to remain in habitat suitable for adults while dispersing (Holekamp, 1984*b*; Garrett and Franklin, 1988; Wiggett and Boag, 1989). Despite having traveled long-distances, those individuals that moved >1 km did not seem to sustain a higher predation rate: 3 of 10 (30%) individuals making such movements were preyed upon, whereas 9 of 26 (34.6%) individuals that did not make such movements were preyed upon. This observation seems to contradict the common assumption that dispersers suffer a higher rate of predation (Gaines and McClenaghan, 1980), although data from other ground squirrel species are equivocal. Byrom and Krebs (1999) reported a maximum survival rate of 40% for dispersing *S. parryii*. They also found that risk of mortality for *S. parryii* was higher with greater dispersal distance and that males had higher mortality rates than females. However, Olson and Van Horne (1998) found no difference in mortality rate between dispersing and philopatric individuals for *S. townsendii,* and Wiggett et al. (1989) concluded that risk of predation was not high for dispersing *S. columbianus,* though they did not directly contrast mortality rates of

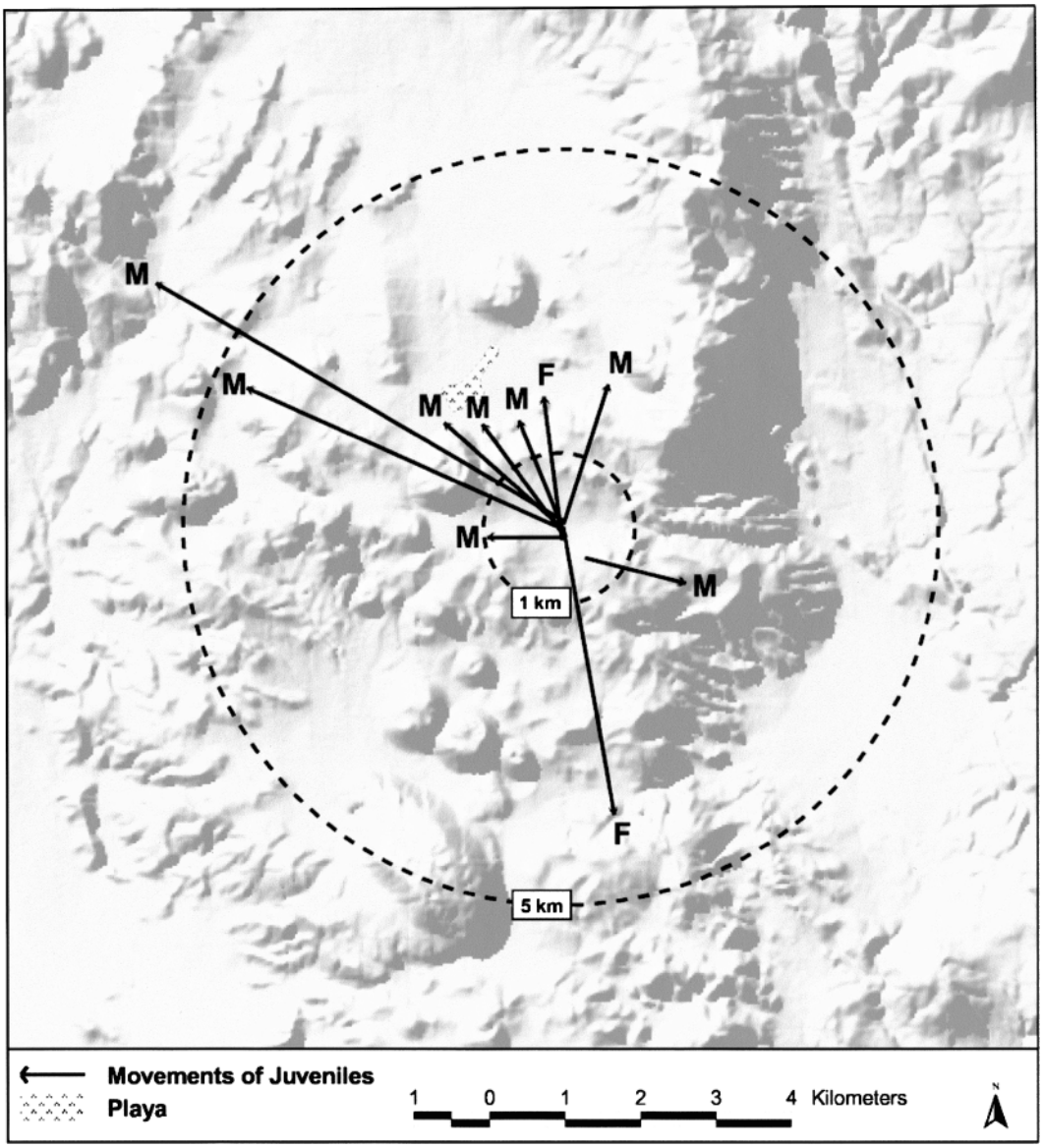

FIG. 1—Long-distance movements (>1 km) of juvenile Mohave ground squirrels (*Spermophilus mohavensis*) in relation to topography. The sex of the individual is shown at the terminus of each arrow. A radius of 1 km is shown from the center of the trapping grid in which the ground squirrels were captured and equipped with radio transmitters.

dispersers with non-dispersing individuals. Nunes and Holekamp (1996) concluded that juvenile *S. beldingii* disperse after reaching a threshold body mass and that this behavior might delay dispersal until the animal is better prepared for the demands of dispersal, including avoiding predation. In addition, the apparently short period of time during which individuals made long-distance movements might have reduced predation rate (Harrison, 1992).

Our observations of movements by juvenile Mohave ground squirrels suggested that this species is relatively mobile compared to other ground squirrel species, particularly those in

grasslands or mesic habitats (Holekamp, 1984*a*). Bowman et al. (2002) suggested that home range might be a better predictor of dispersal distance than body size. The Mohave ground squirrel seems to be consistent with this hypothesis, as its home range might be larger than those of ground squirrels of similar size. Postmating home ranges of females ranged from a median of 0.29 to 1.90 ha among 5 years of study (Harris and Leitner, 2004). Dispersal distance in mammals generally is less than 5 home range diameters (Harrison, 1992). Mohave ground squirrels would seem to have unusually long dispersal movements by this standard as well.

Although long-distance movements were male-biased, the small proportion of females that make such movements could have great significance for recolonization of sites that had suffered local extinction. The ability of juveniles to travel long-distances is a potential mechanism for achieving gene flow between local populations. Such movements could connect populations that are separated by habitat that is not suitable for permanent occupancy. The recolonization of sites after local, drought-related extirpation can be explained readily by juvenile movements from sites with populations that have persisted through drought. Long-distance movements by juveniles might have adaptive value to this patchily distributed, uncommon species.

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