RANGE USE PATTERNS AND SPATIAL RELATIONSHIPS OF MERRIAM'S KANGAROO RATS (DIPODOMYS MERRIAMI)

by

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Merriam's kangaroo rat (*Dipodomys merriami*; Rodentia: Heteromyidae) is a nocturnal, burrow-dwelling rodent, widespread in the arid southwest of North America. Kangaroo rats are characterized by their large, powerful rear legs which enable them to move bipedally across open ground in a saltatory fashion and by their external, fur-lined cheek pouches which are used to transport seeds, green vegetation, and occasionally insects back to their home burrows or to surface caches.

Kangaroo rats have been the objects of a great deal of ecological, anatomical, and physiological research. Indeed, REICHMAN & BROWN (1983) introduce a collection of recent reviews of heteromyid research with the suggestion that kangaroo rats and their allies are better known with respect to "comparative anatomy, physiology, behavior, ecology, and evolution" than any other mammalian group. However, what is known about the behaviour of these nocturnally active, burrow-dwelling rodents is largely inferred from indirect evidence, especially from trapping data, and presents certain anomalies with respect to current theories of sexual selection and territoriality.

Among solitary rodents, males are commonly observed to range more widely than females. Thus, for example, in two species of Saharan gerbils (*Psammomys obesus* and *Meriones libycus*), DALY & DALY (1975a, b) found that mature females occupied small, non-overlapping ranges while sexually active males traversed areas several times as large, overlapping with

several females and with one another. Similar sex differences have been documented in diverse taxa including voles (MADISON, 1980), lemmings (BROOKS & BANKS, 1971) and many others. The conventional interpretation of such ranging patterns is that they reflect sexually differentiated reproductive strategies. Males of solitary species, making no parental investment (TRIVERS, 1972), expend their reproductive effort in the pursuit of mating opportunity, competing with other males for access to females. In several mammalian taxa, this competition involves direct combat, with the result that males have evolved great body size and/or specialized weaponry; within such taxa, sexually monomorphic species are likely to be monogamists, exhibiting biparental care of the young and a lesser male variance in reproductive success compared to related species that are sexually dimorphic and effectively polygynous. In the Rodentia, however, morphological sex differences are seldom dramatic, even in species that lack paternal investment and are therefore likely to have effectively polygynous breeding systems. Male-male competition is more of a scramble competition and less of a confrontational contest in such rodents, and the effects of sexual selection show up in ranging patterns more than in morphological dimorphism. The association between home range dimorphism and mating system is nicely illustrated by comparisons within genera, such as the large range dimorphism of the promiscuous *Microtus pennsylvanicus versus* sexual monomorphism in the monogamous *M. pinetorum* (GAULIN & FITZGERALD, in press). That the males of species with range dimorphism indeed expend reproductive effort is indicated by the fact that the expected lifespan of a mature male is substantially shorter than that of a mature female (*e.g.* Saharan gerbils; DALY & DALY, 1975a, b), and by the elevated risk of predation that is associated with reproductive condition in males (*e.g.* voles; MADISON, 1978a).

How kangaroo rats fit into this scheme is a conundrum. All available evidence suggests that they live solitarily as adults, and are rather antisocial. In captivity, encounters staged between or within sexes tend to be aggressive, although some smaller *Dipodomys* species, including *D. merriami*, do not always or even usually fight. Many field studies, involving retrapping, opportunistic observation, and excavation of burrows, indicate that adult kangaroo rats live solitarily in regularly dispersed home burrows, rarely approaching one another's core areas. Recent studies utilizing radiotelemetry (SCHRODER, 1979; JONES, 1982; this paper) confirm that adult kangaroo rats indeed dwell separately. Monogamy and male parental effort thus seem improbable, and we would expect a high level of male mating effort instead. As in most rodents, sexual dimor-

phism in body size is slight: in studies of several species, for example, males have consistently been found to be significantly heavier than females but usually by less than 10%.

So far, kangaroo rats sound like typical solitary rodents, in whom we would expect to find a large sex difference in home range size. However, home ranges typically exhibit either no sex difference (*D. merriami*: ALLRED & BECK, 1963; CHEW & BUTTERWORTH, 1964; MAZA, FRENCH & ASCHWANDEN, 1973; *D. microps*: ALLRED & BECK, 1963; MAZA, FRENCH & ASCHWANDEN, 1973; *D. agilis*: MACMILLEN, 1964; *D. elator*: ROBERTS & PACKARD, 1973) or male ranges larger than those of females but less than twice as large (*D. merriami*: BLAIR, 1943; O'FARRELL, 1978; REYNOLDS, 1960; YORK, 1949; *D. ordii*: BLAIR, 1943; *D. spectabilis*: SCHRODER, 1979). Surprisingly, FITCH (1948) found considerable evidence of larger movements by females than by males in *D. heermanni* (a species regret-tably little known); these data may reflect a sex difference in home range or in dispersal or both. The BLAIR and O'FARRELL studies suggest that range dimorphism in *D. merriami* may be seasonal, but the relevance of reproductive activity, if any, is unclear. Also surprising for a solitary ro-dent, but consistent with the lack of range dimorphism, is the fact that long-term retrapping studies (FITCH, 1948; HOLDENRIED, 1957; CHEW & BUTTERWORTH, 1964) provide no evidence whatever of sex differences in survival.

It appears, then, that male kangaroo rats do not expend costly mating effort scrambling after females in the manner of gerbils, voles and lem-mings. But the evidence is not conclusive. The bulk of it comes from retrapping studies, which may provide a biased view of range use. SCHRODER (1979), for example, reported that radiotelemetry and trap-ping produced contrasting pictures of the spatial behavior of *D. spectabilis*. Trapping picks up a disproportionate number of excursions; more time is spent near home than the distribution of captures would suggest. And it was only in his radio data, not his trapping records, that SCHRODER could discern a sex difference in home range. The present study applies radiotelemetry techniques to a second species, *D. merriami*, for whom the evidence on range dimorphism from retrapping studies has been incon-sistent.

Besides the issue of sex differences, kangaroo rat range use presents a further challenge to theory, with respect to territoriality and home range overlap. On the basis of energetic considerations, one would expect solitary animals to be evenly dispersed in suitable habitat, minimizing in-traspecific competition and costly travels by mutual repulsion and by the

exploitation of familiar, exclusive territories (BROWN & ORIANS, 1970). The first *Dipodomys* species to have been studied by radiotelemetry, namely the bannertail kangaroo rat (*D. spectabilis*), evidently does just that. Bannertails construct large mounds around their burrows, to which they hoard substantial quantities of seed (VORHIES & TAYLOR, 1922). SCHRODER & GELUSO (1975) demonstrated that bannertail mounds are spaced more evenly than a random scatter. SCHRODER (1979) found that radiotagged individuals spent 78% of their nocturnal active period within just 6 m of the home burrow, and that regularly utilized ranges exhibited negligible overlap.

Merriam's kangaroo rat, however, does not appear to behave similarly. *D. merriami* do not build elaborate burrows, do not hoard large caches, and, perhaps for these reasons, do not exhibit the home site fidelity of *D. spectabilis* (JONES, 1982). Retrapping studies are inconsistent with respect to the extent of home range overlap that is revealed: some suggest that ranges overlap little (REYNOLDS, 1960; O'FARRELL, 1978), but others utilizing more intensive trapping (BLAIR, 1943; YORK, 1949) indicate that each individual's home range is likely to overlap those of several conspecifics of both sexes.

It seems likely that there will be ecologically interpretable differences in ranging behaviour within the genus *Dipodomys*. SCHRODER (1979), for example, attributed the sedentariness and exclusive ranges of his radiotagged *D. spectabilis* to their exploitation of energy-rich seed heads. For species such as *D. merriami* that glean scattered, loose seeds, he proposed that "home ranges might be larger and indefensible", and that without the seasonal hoarding of large caches, attachment to a single home burrow might be lacking. The present study verifies this conjecture.

In this paper, we present data collected by radiotelemetry in order to characterize the home range behavior of *D. merriami*: home range size and use patterns, spatial overlap, temporal and spatial patterns of the use of different day burrows, and any differences between the sexes in these matters.

Methods

Study areas.

Field work was carried out on two study sites, designated the Ramada site and the Coyote Wash site, located 1.6 km apart on a north-south axis on the upper alluvial plain within the confines of the Boyd Deep Canyon Reserve (el. 300 m) approximately three kilometers south of Palm Desert, Riverside County, California. The lower ecological zones of Deep Canyon are part of the warm and arid Colorado Desert (< 125 mm of precipitation per year) which encompasses much of southern California, Arizona, and northern Mexico. The dominant flora of the area include creosote bush (*Larrea tridentata*),

sweetbush (*Bebbia juncea*), cheesebush (*Hymenoclea salsola*), palo verde (*Cercidium floridum*), and cholla cactus (*Opuntia* spp.). (See BEHRENDS *et al.*, 1986, for a complete description of the study sites).

Radiotracking in conjunction with trapping was carried out on the Ramada site from November 27 to December 22, 1980 (study period 1) and on the Coyote Wash site from December 11, 1981 to May 20, 1982 (study period 2) and from November 11 to December 22, 1982 (study period 3).

Animals.

Sixty adult (*i.e.* > 30 g) *D. merriami*, 32 males and 28 females were radio-tracked for periods ranging from 1 to 84 days over the three studies. (See BEHRENDS *et al.*, 1986, for a complete description of the trapping procedures and processing of the animals.) The criteria by which animals were selected for different analyses are described below.

Equipment.

Standard radiotelemetry equipment was used (AVM Instrument Co., Dublin, California) including SM-1 mouse-style transmitters with an internal antenna and individually-tuned frequencies around 151 mHz, an LA-12 multiple channel receiver, and a hand-held Yagi antenna. The transmitters were powered by 1.35 volt mercury batteries rated to last two months. The transmitter-battery unit was encapsulated in acrylic and sealed with beeswax yielding an implant unit weighing less than 3.0 g. Transmitters had a signal range of 30 to 60 m at ground level depending on the slope and rockiness of the terrain.

For radio-implantation, animals captured (Sherman live traps) on the study site were transported to the laboratory at the research center and lightly anesthetized with a weight-dependent dose of Ketaset (0.001 ml/g). Transmitters were implanted subcutaneously just lateral to the dorsal midline. Usually animals were returned to their point of capture within 1-3 hours following surgery. If bleeding occurred the animal was kept overnight, closely monitored, and returned to the field the next evening. No animal was kept out of the field more than 24 hours.

Data collection.

Systematic radiotelemetry data were collected by locating each radio-implanted animal once per hour. The use of radio-fixes at hourly intervals achieves a sort of sequential independence of data points, in that the probability that an animal will be at the same site for successive fixes is not different from the probability for any random pair of fixes from the same night. In the first and second studies, six or seven radio fixes were collected for each animal per night either from dusk until midnight or midnight until dawn on an alternating basis. In study period 3, each animal was located once per hour through the dark period yielding a total of 15 radio fixes per night. In study period 1, radio-tracking was carried out over 25 consecutive nights between November 27 and December 22, 1980. In study period 2, radio-tracking was generally carried out four nights per week between December 15, 1981 and May 20, 1982. In study period 3, radio-tracking was carried out two out of every three nights between November 11 and December 22, 1982. The burrows occupied during daylight hours ("day burrows", in which animals almost invariably remained from dawn until dusk) were located every day a worker was in the field throughout the studies. (See BEHRENDS *et al.*, 1986, for details of the radiotelemetry procedures).

The two study sites were mapped as grids with 10 m × 10 m quadrats to the extent of the animals' ranges. Each radio fix was recorded as an x and y coordinate pair (*i.e.* a Cartesian coordinate) to a one meter level of precision. Several other microhabitat and weather data were recorded along with the hourly radio fixes, but are not treated in this report.

Data analyses.

Minimum home range.

For present purposes, home range is defined as the areal sum of the $(10 \text{ m})^2$ quadrats in which the animal was radio-located plus the areal sum of the minimum number of quadrats the animal would have had to traverse in order to reach disjunct quadrats in which locations were recorded. To find the home range, the different quadrats occupied by an animal were mapped and counted and the minimum number of intervening quadrats needed to reach disjunct quadrats was determined and added to the sum of occupied quadrats. Home range values are expressed in hectares. (Each separate quadrat used by the animal thus contributes 0.01 ha to the home range estimate.)

   Only animals with more than 50 night fixes were included in the home range analysis since within each period home ranges tended to increase to an asymptote with 50-60 fixes. Direct statistical comparisons of the home ranges of animals in the different study periods were not made, since the animals were radio-tracked for varying lengths of time with different protocols. For instance, the same number of radio fixes for two animals might have been collected over different time periods, or, conversely, animals followed over comparable lengths of time might have different numbers of radio fixes.

Range use.

"Clustering" indices, similar to those used by MADISON (1978b), are used here to describe the relative concentration of an individual's activity within its home range. The concentration of activity is described in terms of the percentage of the total number of nocturnal radio fixes that were in the quadrat with the highest frequency, in the two most frequented quadrats, and in the three most frequented quadrats. These clustering indices are useful for comparing range use within and between study periods, since the indices were not correlated with either the number of radio-fixes or the duration of radio-tracking.

Range overlap.

Range overlap scores for an individual are based on the average proportion of that individual's home range shared with a conspecific. Using set theory notation, overlap was calculated as

$$OL = Q_i \cap Q_j) / Q_{i \text{ tot}}$$

where $Q_i \cap Q_j$ = the number of quadrats shared by individuals i and j over the time period that both were radio-tracked, and $Q_{j \text{ tot}}$ = the total number of quadrats occupied by individual i over the time period that both were radio-tracked.

Results

A summary of the radio-tracking data collected over the three studies is provided in Table 1. For males, the range in the number of radio-fixes for different individuals was 14-430 and the range for the number of nights radio-tracked was 2-40. For females, these values were 11-592 and 1-64, respectively. In total, the data used for the analyses below represent 8500 animal hours and 920 animal days.

Home range.

The results presented in Table 2 indicate that home ranges were smallest in study period 1 with an overall (*i.e.* sexes combined) average size of

TABLE 1. Summary of radiotelemetry data collected

| | Study period | | | | | | |
| | 1 Nov.-Dec. 1980 | | 2 Dec.-May 1982 | | 3 Nov.-Dec. 1982 | | |
	Male	Female	Male	Female	Male	Female	Total
Sample size	12	9	13	11	10	9	60
Mean number of fixes	92.4	59.1	72.5	155.4	199.7	202.2	134.1
Mean number of nights tracked	12.1	7.5	10.8	24.4	14.4	14.4	14.4

TABLE 2. Mean home range size (in hectares) broken down by sex and study period

| | Study period | | |
	1	2	3
Females	.21 (.06) n = 7	.29 (.11) n = 10	.43 (.14) n = 8
Males	.18 (.08) n = 11	.33 (.14) n = 8	.52 (.27) n = 8

Standard deviation in parentheses. The table includes only animals for which at least fifty nocturnal radio locations were obtained.

0.19 ha, somewhat larger in study period 2 at 0.31 ha, and largest in study period 3 at 0.48. These substantial differences are not readily attributed to season. The extreme values (study periods 1 and 3) represent the same season (Nov.-Dec. 1980 *vs* 1982), and in both years, adult males had begun to exhibit scrotal testes but no females were in reproductive condition. In study period 2 (Dec. 1981 to May 1982), reproduction commenced somewhat earlier, and animals of both sexes were in reproductive condition throughout. (See BEHRENDS *et al.*, 1986, especially Figure 1, for greater detail on reproductive condition of the animals.)

There is no evidence of a sex difference in home range in any of the study periods ($t_{16 \, df} = 0.91$ for study period 1, $t_{16 \, df} = 0.71$ for study period 2, and $t_{14 \, df} = 0.91$ for study period 3).

Individuals exhibited substantial variation in home ranges within each study period. In period 1, home range size varied from 0.04 to 0.32 ha, in

period 2 from 0.13 to 0.56 ha, and in period 3 from 0.24 to 1.16 ha. To illustrate the variance among individuals in home range use, Fig. 1 depicts the ranging pattern of a randomly selected animal of each sex from each study period. Each kangaroo rat utilized one to three quadrats intensively (see "clustering", below) and a varying number of other quadrats to a lesser extent. Clearly the activities of some individuals were much more dispersed than those of others even within study periods.
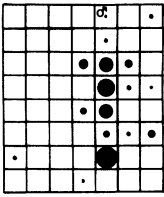
Clustering.

Animals on both the Ramada and Coyote Wash sites maintained relatively stable core activity loci within their home ranges regardless of the length of time an animal was radio-tracked. Table 3 shows that on average 27-51% of nocturnal activity (including subterranean activity) was restricted to a single 10 m² quadrat. In fact, the majority (48-77%) of all nocturnal activity was confined to only three quadrats or an area of 0.03 ha. Fig. 1 further illustrates this finding by showing that each individual maintained 1-3 areas of intense use and occupied other quadrats less frequently.

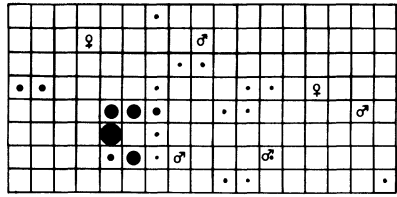TABLE 3. Clustering of activity within preferred areas of the home range

Study period		Mean proportion of radio fixes in which the animal was located within:		
		its most preferred quadrat	one of its two most preferred quadrats	one of its three most preferred quadrats
1	Females	.506	.634	.728
	Males	.489	.683	.766
2	Females	.271	.428	.538
	Males	.304	.460	.537
3	Females	.314	.427	.505
	Males	.268	.410	.482

The high degree of clustering by *D. merriami* in part reflects the occupation of day burrows for several hours per night. For 45 of 52 animals, the

Fig. 1. Illustrative range use patterns of one randomly selected male and female from each of the three study periods. Each square represents a quadrat 10 m². The areas of the black circles within quadrats are proportional to the number of radio fixes on which the animal was located in that quadrat. Male and female symbols show the quadrats containing the principal day burrows of other radio-implanted animals. HR is the minimum home range size in hectares.

♂ 1201
93 radio fixes
HR = 0.20 ha

♀ 1156
73 radio fixes
HR = 0.31 ha

♂1451
137 radio fixes
HR = 0.48 ha

♀ HR3
152 radio fixes
HR = 0.31 ha

♂ 13
270 radio fixes
HR = 1.16 ha

♀ HL2HR2
287 radio fixes
HR = 0.31 ha

quadrat with the highest cluster score was also the quadrat with the most frequently used day burrow.

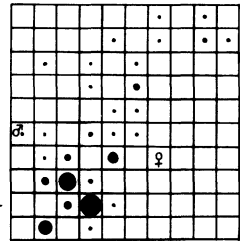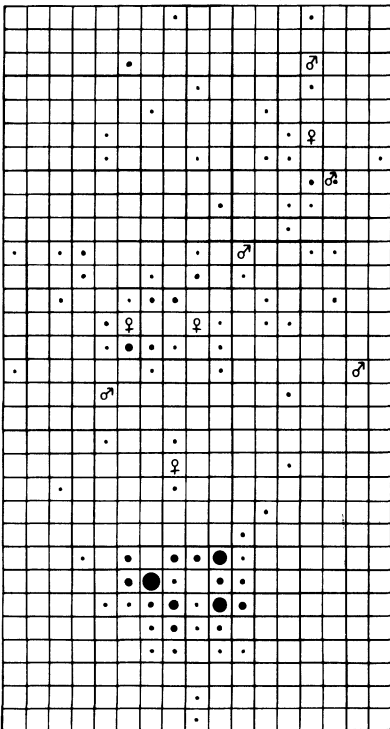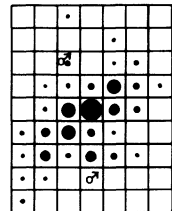There was some evidence for inter-study differences in clustering. The proportion of locations occurring in the most preferred quadrat (Table 3) was significantly higher for study period 1 than for study period 2 ($t_{34\,df}$ = 5.20, p < .001,) or study period 3 ($t_{32\,df}$ = 5.20, p < .001,). Study periods 2 and 3 did not differ. (All tests are two-tailed unless otherwise stated.)

There was no clear evidence on the basis of cluster indices that males and females used their home ranges differently. The data presented in Table 3 indicate that the cluster patterns for males and females were similar.

Range use may also be investigated by determining center-of-activity (COA) changes over time. An animal with a high degree of site attachment (*i.e.* occupying the same territory or range over a long period of time) should exhibit small variations in its COA from night to night, without the COA drifting over the time span over which the animal is radio-tracked. To determine whether animals used the same general home range over long periods of time, the distance between an animal's first and last nightly COA for the entire period of time it was radio-tracked was compared with its weekly COA shift. The results indicate that *D. merriami* have a strong degree of site attachment for periods of time up to at least six months. Table 4 shows that COA shifts ranged from a low of 7.1 m over an average of two weeks by males in study period 1 to a high of 24.3 m over an average of five weeks by males in study period 2. More importantly, the total COA shifts by these animals were not significantly larger than their weekly shifts with the exception of females in study period 2 ($t_{7\,df}$ = 2.91, p < .05, two-tailed test). Four

TABLE 4. Mean centre-of-activity shift (meters) on a weekly and overall basis, broken down by sex and study period

| | Study period | | | | | |
| | 1 | | 2 | | 3 | |
	Weekly	Total	Weekly	Total	Weekly	Total
Females	15.5	16.5	12.7	23.5	11.1	13.7
	(11.1)	(12.3)	(3.9)	(9.2)	(6.9)	(12.0)
Males	8.0	7.1	22.3	24.3	15.0	14.0
	(5.1)	(4.4)	(14.1)	(23.8)	(7.6)	(7.9)

Standard deviation in parentheses.

animals (three males and one female) from study period 2 were subsequently re-implanted with transmitters in study period 3. With the exception of male 13 whose COA shifted 121 m, the animals inhabited the same general area. Female 1500's COA shift was 15 m, male 12 shifted 36 m, and male HL3FL2 shifted 43 m.

Within study periods there were sex differences in weekly COA shifts between periods 1 and 2. Females in study period 1 had significantly greater shifts than males ($t_{16 \ df} = 2.35$, $p < .05$). Males in the breeding season (study period 2) clearly exhibited the most erratic ranging behavior from week to week (Table 4). This difference is primarily due to the activity of four males who exhibited some drift in their home ranges (see also day burrow results below). Three of these four had average weekly COA shifts of 35 m or more, exceeding the maximum recorded in any other group. The remaining males in study period 2 had a mean weekly COA shift of 15 m, similar to the other weekly averages in Table 4.

Range overlap.

The range overlap results presented here should be regarded as minimum estimates of actual intraspecific overlap since we did not radio-implant all animals on the study sites. It is therefore likely that some animals without transmitters had home ranges that were interspersed among the ranges of radio-implanted animals, although radios were given to those individuals who were repeatedly trapped in one area of the grid during preliminary trapping, in an attempt to minimize this problem.

For each radio-tagged individual, we calculated the spatial overlap with each radio-tagged neighbor as the proportion of all the quadrats in which the focal animal was radio-located that were also quadrats where the neighbor was ever radio-located. (Note that occasional use of common areas can thus lead to substantial overlap scores, even if intensively used core areas are exclusive.)

Table 5 gives the results for spatial overlap broken down by study period and sex. It is evident from the combined overlap scores that the differences in spatial overlap between studies and between the sexes were small despite the changes in breeding conditions between studies. A noteworthy finding was that females tended to overlap more with male conspecifics than with female conspecifics in all study periods.

Most individuals of both sexes overlapped to some degree with several conspecifics. The median number of radio-implanted conspecifics

TABLE 5. Degree of home range overlap as a function of sex

	Number with radios	Same-sex animals overlapping		Opposite-sex animals overlapping	
		Number: Mean (range)	Mean maximum overlap	Number: Mean (range)	Mean maximum overlap
Period 1					
Males	12	2.2 (0-5)	16.5	1.7 (0-4)	18.3
Females	7	1.7 (0-3)	9.4	2.8 (2-4)	21.0
Period 2					
Males	9	1.4 (0-3)	14.3	2.4 (0-5)	13.4
Females	11	1.5 (0-3)	9.7	2.6 (1-5)	21.4
Period 3					
Males	10	3.8 (1-7)	17.7	3.4 (0-7)	16.2
Females	8	1.6 (1-3)	12.1	4.3 (2-7)	24.3

"Number" refers to the number of other radio-tagged individuals whose home ranges overlapped that of the focal animal. "Maximum overlap" is the percentage of the focal kangaroo rat's home range that was overlapped by the one animal whose range most overlapped the focal animal's.

Note that for females, but not males, maximum overlap with same-sex animals is consistently less than with opposite-sex animals.

overlapping with any single individual was 5 (range = 1-14). The median number of same-sexed conspecifics overlapping was 2 (range = 0-7) and the median number of opposite-sexed conspecifics overlapping was 3 (range = 0-7).

There were no cases of overlap among animals' primary, secondary or tertiary quadrats. However, in a few cases, the intensively used quadrats of different individuals were adjacent: in three cases, two females had adjacent quadrats of intense use (*i.e.* within each female's three preferred quadrats), and in four cases a female and a male exhibited similar proximity. In general, however, those quadrats that entered into the home ranges of two individuals were in areas that were little-used by one or both of the animals.

Day burrow distribution.

As a solitary species, it is expected that *D. merriami* should select day burrow sites in such a way that nearest-neighbor distances are larger than in a random distribution. In order to test this hypothesis, we compared the mean nearest-neighbor distances between day burrow sites with the mean nearest-neighbor distance generated from a computer simulation

utilizing a random dispersion model. One day was randomly selected for analysis from each of study periods 1 & 3. (We then had the largest number of simultaneously radio-implanted animals, and also had implanted all individuals trapped repeatedly on one side of the trapping grid, so that the presence of undetected animals among the known day burrow distribution should have been minimized.) Eighteen animals entered into the analysis for period 1, 12 for period 3. The rectangular area of the simulation grid was delimited by the actual maximum and minimum x- and y-coordinates of the observed day burrows. The actual loci of the burrows located on the boundaries were then included in each simulated distribution, with the remaining burrow sites randomly situated within the rectangle. The simulation was repeated 100 times in order to generate "expected" nearest-neighbor distances with which to compare observed differences.

The mean nearest-neighbor distance for the study period 1 analysis was 34.8 m, which proved significantly larger than the expected mean of 28.9 m ($t_{17\ df} = 1.97$, $p < .05$, one-tailed test). For the study period 3 analysis, the mean nearest-neighbor distance (40.9 m) was again larger than the expected mean generated by simulation (37.4 m), but not significantly so ($t_{11\ df} = 0.68$).

It was found (Table 5) that sex is relevant to spatial overlap patterns with female-female range overlap less than female-male overlap. It is possible that sex might also be a relevant factor for the spatial distribution of day burrows. To examine this possibility, nearest-neighbor distances to the day burrows of same-sex and opposite-sex conspecifics were compared for each kangaroo rat, using the day burrow data from the same days as in the preceding analysis. Since there were more males than

TABLE 6. Mean distance (m) from individual's day burrow to the day burrows of nearest neighbours of same and opposite sex

	Nearest same-sex neighbour	Nearest opposite-sex neighbour
Study period 1		
Females	57.2	45.1
Males	54.4	42.6
Study period 3		
Females	70.4	53.9
Males	56.7	48.3

Nearest-neighbour analyses include equal numbers of same-sex and opposite-sex neighbours; see text for fuller explanation.

females on both days, randomly selected males were excluded from each analysis so that the nearest neighbor should be equally likely to be of one sex as the other. The results of this analysis are given in Table 6. It is apparent that nearest neighbors tend to be of the opposite sex, but the results are only significant for females ($t_{12\ df} = 1.81$, $p < .05$, one-tailed test).

Day burrow use.

When radiotracked for several days, Merriam's kangaroo rats frequently move from one day burrow site to another. To investigate day burrow use, we employed data from a subset of animals from study periods 1 and 3 (the periods when day burrows were recorded daily with the exception of one day in period 3). Only animals that were radio-tracked throughout most of the study period were considered, namely 16 who were tracked for 15 to 22 days in study period 1, and 9 who were tracked for 32 to 40 days in study period 3.

Twenty-four of 25 animals used two or more day burrows during these brief tracking periods. In most cases, only one or two day burrows were used with high frequency. In many instances, an individual used a particular day burrow for several consecutive days, switched to a new burrow for one or two days, and then returned to the original day burrow (Table 7). Only three of 24 animals who changed day burrow locations never returned to a previous location. On average, each individual used approximately four different day burrows (range = 1-8) over a 25 day period (range = 15-40). However, individuals did not use different day burrows with equal frequency. For each individual, one day burrow was

TABLE 7. Use of day burrows by those kangaroo rats tracked throughout most of study periods 1 and 3

	Mean number of days radio-tracked	Mean number of different day burrows occupied	Mean number of moves	Mean move (Distance between successively occupied day burrows)
Study period 1				
Females (n = 5)	19.0	4.0	6.0	16.4 m
Males (n = 11)	18.1	3.5	4.6	11.9
Study period 3				
Females (n = 4)	37.5	4.5	9.0	12.8
Males (n = 5)	35.8	5.4	8.6	24.9

used on 64% of the days on average (range = 27-100%) and two burrows accounted for 86% of use on average (range = 54-100%).

There were no apparent differences in the utilization of day burrows by males and females with respect to the number used, returns to former sites, or the intensity of use of favorite day burrows. When animals occupied different burrows on successive days, the average distance between them was 15.7 m (range 3.6-53.2 m) and there was again no sex difference ($t_{14\,df} = 1.02$ for study period 1 and $t_{7\,df} = 1.63$ for study period 3; both $p > .05$).

The probability of a day burrow move varied temporally, most notably within study period 3, when the probability that a given animal would move on a given day was 0.34 in November, but fell to 0.15 in December (Fig. 2).
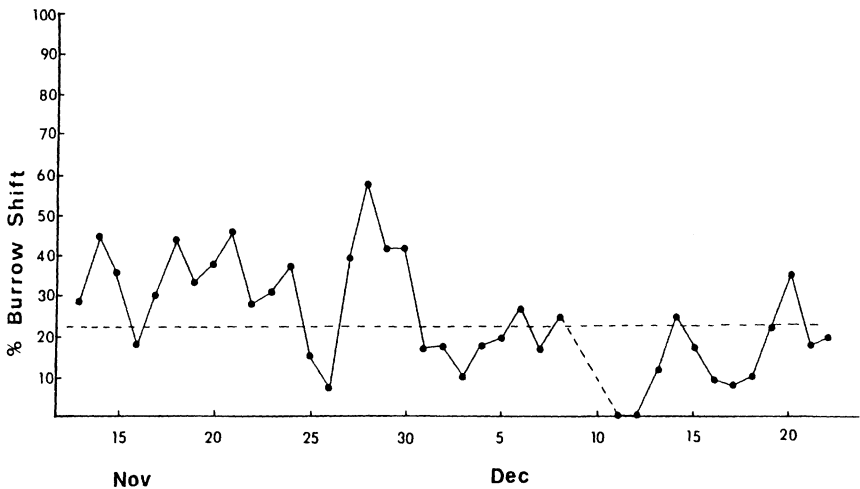

Fig. 2. The proportion of radio-implanted kangaroo rats that switched day burrows on each day of study period 3. The dashed line is the median proportion (0.22) for the entire period.

In study period 2, when females were reproductively active, day burrows were not located daily over several weeks as in the other study periods. However, day burrow locations for two or more successive days were frequently recorded, so some analysis of day burrow moves is possible. Day burrow moves were not more frequent in the breeding season, but when they occurred, they often covered much greater distances than those in study periods 1 and 3.

Unusually large day burrow moves by one female in study period 2 were apparently associated with estrus. This animal, whose average day burrow move was 15 m when anestrous, pregnant, or lactating, had day burrow moves of 100 m and 95 m, respectively, during two estrus periods. On both occasions, she returned to her previous day burrow area one or two days after estrus (see BEHRENDS et al., 1986).

Females continued to change day burrows during late pregnancy and even lactation, presumably moving their offspring to the new day burrow sites. Female 1312, for example, moved her day burrow 62 m more than halfway through a pregnancy, and moved again, a distance of 36 m, within the first five days postpartum. Periodic examinations of this individual, and of other females who behaved similarly, showed that lactation continued for the normal duration of more than three weeks, and hence that these moves were not associated with the loss of a nursing litter.

Some day burrow moves by adult males in April and May of study period 2 were unusually large. Male 6, for example, made a day burrow move of 102 m; male 1451 made moves of 88, 91 and 48 m; male HL3FL2 made moves of 87, 110 and 84 m; and male 12 made a move of 76 m. By way of comparison, the largest of 129 day burrow moves recorded in study periods 1 and 3 was 53 m. Home ranges were largest in study period 3, smallest in study period 1, and intermediate in size in study period 2 (Table 2), and yet all the largest day burrow moves by animals of both sexes occurred in study period 2, the breeding season.

Three of the four males who moved long distances during study period 2 also made major center-of-activity shifts, indicating that these day burrow moves reflected home range shifts. Fig. 3 illustrates the association between day burrow moves and range shifts for two males. Male HL3FL2 exhibited a progressive range shift, and was apparently an immigrant to the area. Male 12, by contrast, had been an adult resident of the trapping grid for at least 90 days when he exhibited a large range shift.

One set of day burrow moves in study period 3 suggests that there is competition for preferred day burrow sites despite their apparent abundance. On November 25, female HL2 was killed by a coachwhip snake which then remained in her burrow until December 3. On December 8, a male (HL3FL3) moved 53 m to occupy the predated female's former day burrow. On December 10, a female (HL2HR2) moved 24 m to occupy the day burrow vacated by male HL3FL3 two days earlier. She continued to use that burrow until December 19, but on December 20 male
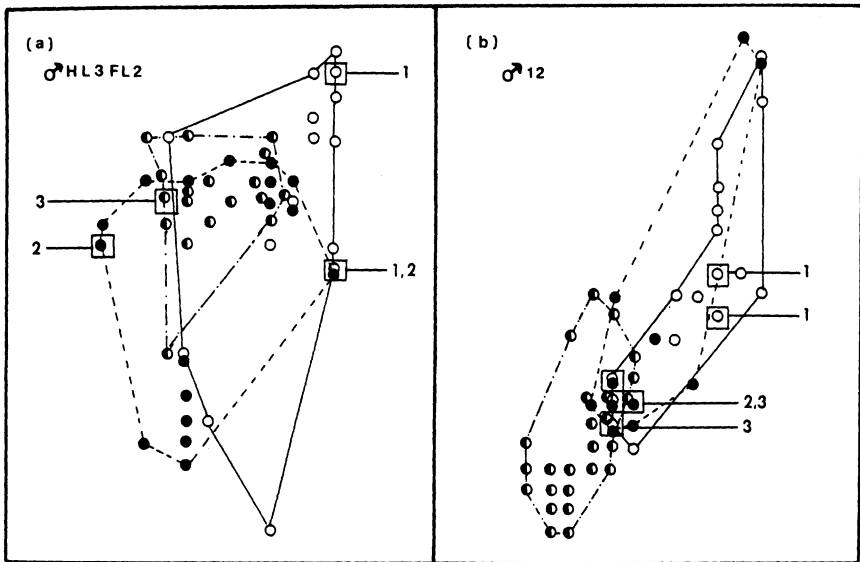
Fig. 3. Changes in the home ranges of two males during study period 2 (the breeding season), between intervals of 7-10 days. Circles represent radio locations. Squares enclose day burrow locations. Numbers indicate the interval in which each day burrow was used: a) Interval 1 (○) = April 18-25, Int. 2 (●) = April 26-May 5, Int. 3 (◐) = May 10-20; b) Int. 1 (○) = April 14-23, Int. 2 (●) = April 24-May 5, Int. 3 (◐) = May 10-17.

HL3FL3 reoccupied it, and the female returned to the use of earlier bur-rows. On several occasions, we have located radio-implanted animals in the former day burrows of departed animals, but this was the only case in which the burrow in question was reoccupied by the former owner.

Discussion

Home range.

In the introduction, we defined home range as the area in which the animal was radio-located plus the minimum area the animal must have traversed to reach disjunct locations. We have thus included long sallies in the home range, unlike many mammalogists, an inclusion which seems to us appropriate because our main concern is socio-spatial rela-tionships rather than the relationship between range size and energetic demands.

In comparison to previous trapping studies of *D. merriami*, home ranges in the present study are rather small, despite the considerably greater data base afforded by radiotelemetry (Table 8). Different methodologies

TABLE 8. Home range and density estimates from geographically
scattered studies of *D. merriami*

Study	Locale	Mean female home range (ha)		Mean male home range (ha)	Approximate density (resident adults/ha)
YORK 1949	Texas	1.4		2.6	1
BLAIR 1943	New Mexico	1.4		1.6	2
O'FARRELL 1978	Nevada	—	0.49	—	3
this study	California	0.31		0.33	6
REYNOLDS 1960	Arizona	0.16		0.19	8

and habitats probably both contribute to these differences. Yet despite
disparate methods, and although the bases for density estimates are weak
and inconsistent, the data in Table 8 indicate that home range size and
density of animals are inversely related. The question of why individuals
within studies exhibit large variation in home range size remains. Some
of this variation might be accounted for by differences in habitat quality,
but that seems unlikely to be the whole story. BLAIR (1943), who pub-
lished extensively on rodent home ranges, found a 7.5-fold variation
among *D. merriami* ranges in uniform habitat, and remarked ''The range
of variation in home range size is greater than in any other small mam-
mal of which I know'' (p. 27). Why this should be remains a mystery, but
the fact that some individuals make many long sallies over the home
ranges of several others (*e.g.* male 13 overlapped with 14 radio-implanted
conspecifics in study period 3) indicates that ranging probably has other
functions than just foraging (see BEHRENDS *et al.*, 1986, for a discussion of
ranging variation).

Sexual dimorphism in home range size was not apparent in the present
study. But if male home ranges were not larger than those of females,
males nevertheless made greater average moves between successive
radio-fixes during the breeding season than did females (BEHRENDS *et al.*,
1986).

Merriam's kangaroo rats spent most of the night in core areas near
their day burrows, with occasional long distance sallies (often to points
more than 100 m away). Their activity was not so spatially concentrated,
however, as that reported for *D. spectabilis* by SCHRODER (1979). The 29%

(study period 2) to 50% (study period 1) of time spent within the preferred quadrat (a square of area 100 m²) is notably less than the 78% of time that SCHRODER's bannertails spent within 6 m of their home burrows (a circle of area 112 m²). Merriam's kangaroo rats are clearly not such territorial central place foragers as bannertails; in fact, *D. merriami* scatter hoard, primarily near their day burrow areas, but also much more widely.

We have radio-tracked several individuals in successive years and one female in 3 winters over a duration of 29 months. Although the average lifespan of kangaroo rats in the field is undoubtedly short, the maximum lifespan in captivity is over 7 years (EGOSCUE, BITTMEN & PETROVICH, 1970; pers. observ.). By contrast, most well known rodent species (mainly myomorphs: rats, mice, hamsters, gerbils, voles, lemmings) senesce and die in 2 to 4 years. Kangaroo rats (and desert-dwelling myomorphs; see EGOSCUE *et al.*, 1970) thus appear to be relative K-strategists or "bet-hedgers" (STEARNS, 1977), exhibiting relatively long potential lifespan and conservative reproductive tactics (small litter size and long gestation in comparison to like-sized myomorphs; see DALY, WILSON & BEHRENDS, 1984). These considerations, the fact that juvenile mortality exceeds adult mortality (FRENCH, MAZA & ASCHWANDEN, 1967), and some evidence that individuals disperse little between birth and adulthood (JONES, 1982) all suggest some long-term stability in social communities, which might permit such complex social phenomena as tolerance by individual familiarity, mate selection (the exceptional travels of females in estrus are particularly intriguing), stable dominance relations, and post-weaning nepotism. The apparent asociality of kangaroo rats notwithstanding, these possibilities deserve exploration.

Range overlap.

The degree of intraspecific range overlap provides indirect information about the likelihood of social interactions. O'FARRELL (1980) reported that individual *D. merriami* overlap was greatest during the breeding season. Moreover, he found that male-male overlap was greatest, male-female overlap intermediate, and female-female overlap least. There was substantial range overlap in the present study, but the patterns differed from those reported by O'FARRELL. There were no seasonal differences in the degree of overlap and no difference between opposite-sex and male-male overlap. A finding similar to O'FARRELL's however, was that the overlap between females was significantly less than the overlap between males and females.

Apparently *D. merriami* tolerate substantial range overlap with conspecifics, not an uncommon mammalian pattern (BROWN & ORIANS, 1970). The extensive range overlap of *D. merriami* stands in marked contrast, however, to the rather exclusive ranges of *D. spectabilis* (SCHRODER, 1979). BROWN & ORIANS (1970) point out that due to the relative lack of mobility of many mammals the cost of defending a foraging range probably outweighs the benefits gained. Thus the large, overlapping ranges of *D. merriami* may in part reflect the exploitation of scattered, economically undefendable resources.

Estimating the likelihood of direct physical encounters among overlapping individuals is difficult on the basis of these data. However, the lack of spatial overlap among individuals' core areas suggests that direct encounters probably occur at a relatively low rate. Nonetheless, although our hourly radio fixes indicate virtually no such intrusions, we have directly observed individuals visiting the areas around conspecifics' day burrows, usually for brief durations. On many occasions, two and, on one occasion, three adults have been observed in close proximity (1 to 5 m) under a small shrub, a creosote bush, or a palo verde tree. Typically, encounters are aggressive, usually with one animal chasing the other, but at other times the animals are passive and seem oblivious to the close presence of a conspecific. These observations of aggressive interactions suggest that *D. merriami* may maintain territories (*i.e.* defended areas, BURT, 1943) around their day burrows and core activity areas, but we do not have adequate data to compare aggressivity in different parts of the home range.

The relative lack of spatial overlap between females compared to the overlap between the sexes or between males is not uncommon in solitary rodents (see, *e.g.*, DALY & DALY, 1975a, b and MADISON, 1980), and suggests that there is relatively less direct social interaction between females. The likelihood of mutual avoidance by females is reinforced by the demonstration that for females, the nearest male day burrows were significantly closer than the nearest female day burrows. Males, on the other hand, tended to overlap with males as much as with females. Moreover, the locations of males' day burrows did not appear to be related to the sex of their nearest neighbors. A regular distribution of *D. spectabilis* day burrow mounds was noted by SCHRODER & GELUSO (1975). The implication of this sort of day burrow distribution is that kangaroo rats space themselves to avoid mutual interactions. Well-spaced day burrows may be important for minimizing costly conflicts over resources (in terms of time, energy, and risk of injury or predation). The evidence for

regular spacing of *D. merriami* day burrows was equivocal, however. Day burrows were shown to be dispersed in study period 1 but not in study period 3. The finding that *D. merriami* have substantial range overlap suggests that this species may be less averse to the proximity of conspecifics than *D. spectabilis* (and indeed *D. merriami* is less aggressive during staged captive encounters). However, the lack of overlap around core areas indicates that little interaction may occur in those areas where the cost of interactions may be particularly high (*e.g.* direct competition for food resources, raids on food caches by conspecifics, or disruption of reproductive activities). Consequently, individuals may behave agonistically around their day burrows but be relatively tolerant of conspecifics in less densely used parts of their ranges.

Day burrow use.

Individuals tended to use several day burrows and, moreover, usually returned to previously used burrows. No external factors triggering day burrow moves were apparent, although it was noted that there were periods when moves were more or less frequent (Fig. 3; see also KENAGY, 1973), and that long moves by kangaroo rats of both sexes occurred in the breeding season. No individual characteristics seemed to be related to unusually frequent or distant moves with the exception of long moves by an estrous female and several males apparently in the process of range shifts.

Although the factors responsible for day burrow moves are unknown, these moves appear to be important. The fact that several lactating females switched day burrows, presumably at some risk to their pups, indicates that this is so. Of course, lactating females may be switching day burrows for some reason unrelated to those affecting other animals, such as to reduce the pups' risk from infanticidal conspecifics (SHERMAN, 1981). One possibility is that animals switch day burrows to escape parasites that infest their nests. The only evidence to support this idea is that *D. merriami* on our study area are relatively free of ticks, fleas, and mites compared to pocket mice (little information is available on burrow use by pocket mice, but some species go torpid for months at a time; KENAGY, 1973). Since *D. merriami* do not store large amounts of seeds in their burrows (JONES, 1982), perhaps the least costly way to confound parasites is to vacate a burrow for a period of time. Another possible reason for frequent day burrow shifts is to avoid certain predators (*e.g.* snakes or mammals) which may be attracted to the strong odor of a heavily used burrow. Finally, the day burrow shifts may be a way of

avoiding raids on smaller burrow food hoards by conspecifics, pocket mice, or ants. These and other hypotheses may be testable by developing models predicting the frequency and temporal patterning of day burrow shifts under each hypothesis.

Summary

Radiotelemetry was used to investigate the home range patterns and inter-individual spatial relationships of Merriam's kangaroo rat (*Dipodomys merriami*). Sixty adult *D. merriami* (32 males and 28 females) were radio-tracked for varying lengths of time over three study periods between November 1980 and December 1982, on two desert habitat sites located near Palm Desert, California. Analyses of home range size and utilization patterns, range overlap with conspecifics, and day burrow distribution and use patterns were carried out.

Home range varied between 0.03 ha and 1.16 ha with substantial inter-study differences but no apparent sex differences. Animals maintained relatively stable core activity loci within their ranges which were centered around frequently occupied day burrows. However, long sallies of 100 m or more away from core areas were not uncommon. The examination of shifts in animals' centers-of-activity (COA) over long periods of time indicated that animals maintained relatively stable home ranges over seasons and even years although a few individuals did exhibit COA shifts of more than 100 m. There was substantial home range overlap, with individuals overlapping the ranges of up to 14 radio-implanted conspecifics. The home ranges of pairs of neighboring females overlapped less than did those of males or pairs of opposite sex, and the average nearest-neighbor distance between the day burrows of males and females was significantly smaller than the average nearest-neighbor distance between females. Thus in kangaroo rats, as in other ''solitary'' rodents, females maintain territorial spacing to a greater degree than do males.

D. merriami utilized several day burrows with moves occurring once every four days on average. However, most animals used only one or two day burrows frequently. The largest moves coincided with reproductive activity, and in particular with the day of estrus. The findings are discussed with respect to their implications for *D. merriami* social structure, and for comparative studies within the genus *Dipodomys* and within the order Rodentia.

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