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# ABOVEGROUND ACTIVITY OF MERRIAM'S KANGAROO RATS (*DIPodomys MERRIAMi*) IN RELATION TO SEX AND REPRODUCTION

by

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(With 2 Figures)  
(Acc. 1-V-1985)

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Kangaroo rats (*Dipodomys*; Rodentia: Heteromyidae) are predominantly granivorous, nocturnally active, solitary, burrow-dwelling rodents of arid and semi-arid regions in the North American southwest.

Kangaroo rats, in comparison with sympatric granivores (especially pocket mice), acquire more of their food in unvegetated open areas, and less under the canopy of shrubs (*e.g.* PRICE, 1977). Foraging in open desert is risky, and kangaroo rats appear to be specialized for the task. The bipedalism of many desert rodents, once believed to conserve energy, is now considered an anti-predator adaptation (see THOMPSON *et al.*, 1980), and large tympanic bullae give *Dipodomys* an exceptional capacity to detect and evade owls and snakes (*e.g.* WEBSTER & WEBSTER, 1971). Kangaroo rats also reduce risk by moonlight avoidance (LOCKARD & OWINGS, 1974; PRICE, WASER & BASS, 1984). Even so, kangaroo rats are preyed upon while they are abroad. Confirmed predators of radio-tagged kangaroo rats on our study area, for example, include great horned owls (*Bubo virginianus*), sidewinders (*Crotalus cerastes*), and loggerhead shrikes (*Lanius ludovicianus*) who catch late-active animals in the rising light before dawn; other confirmed predators, namely coyotes (*Canis latrans*), and coachwhip snakes (*Coluber* sp.) are capable of taking

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kangaroo rats in their burrows as well as in transit, but it is clear that surface activity is riskier than sitting home.

ROSENZWEIG (1974) proposed a model to generate the "optimal above-ground activity" of kangaroo rats. He assumed that predation risk will always be higher outside the burrow, and that there may be other (*e.g.* energetic and evaporative) costs of exposure. If costs vary by time of night (due to moonlight, for example, or temperature), then animals should be preferentially active at low-cost times, so that cost is likely to be a positively accelerated function of time spent aboveground. Benefits of aboveground activity (*e.g.* energy accrual, mating opportunities, territorial defense), however, are apt to show diminishing returns with increased surface time, and so the net benefit (benefit minus cost) will be maximal at some intermediate (optimal) amount of exposure. Though lacking the data to test his model precisely, ROSENZWEIG showed how it might account for seasonal changes in moonlighting. We are no closer to a rigorous test. Of interest here is the suggestion that benefits of aboveground activity are not merely energetic but also social, and that they might therefore change in the reproductive season, a point forgotten in later studies of kangaroo rat ecology.

Kangaroo rats have been the objects of a large corpus of ecological research, most of it inspired by the problem of how ecologically similar species manage to coexist (for reviews, see ROSENZWEIG, 1977; BROWN, REICHMAN & DAVIDSON, 1979; PRICE & BROWN, 1983). Within this body of research, the unlikely assumption has arisen (apparently unnoticed) that aboveground activity has the sole function of foraging. Thus, for example, the first published radiotelemetry study of kangaroo rats (SCHRODER, 1979) was entitled "Foraging behavior and home range utilization...", though the data consisted solely of radio-locations. For other discussions that assume that surface activity must be foraging activity, see REICHMAN (1983) and THOMPSON (1982).

Aboveground activity must surely have social as well as foraging benefits, but the effect of social agendas upon time budgets and travels is unknown. A likely place to begin investigation is to look for differences in surface activity of males *vs* females and of animals varying in reproductive condition. Sex differences in ranging behavior have been linked to reproductive strategies in some rodents. MADISON (1980) reported, for example, that male meadow voles had overlapping home ranges which temporarily overlapped those of estrous females, whereas females excluded one another. BROOKS & BANKS (1971) found that male collared lemmings had no consistent center-of-activity, but rather had several rest

sites near female home sites. Female ranges have also been shown to vary as a function of reproductive condition in woodrats (CRANFORD, 1976) and voles (MADISON, 1978a).

Kangaroo rats do not exhibit the dramatic sex difference in home range size that is seen in some other solitary, burrow-dwelling rodents, though the ranges of males are often somewhat larger than those of females (review in BEHREND *et al.*, 1986). Individual differences in home range are exceptionally large (BLAIR, 1943), however, and may prove intelligible in terms of social or reproductive status. Home range sizes does not differ between the sexes on our study area (BEHREND *et al.*, 1986). However, the analyses in this paper will show that males and females use their ranges somewhat differently and that reproductive activity affects ranging.

## Methods

### *Study areas.*

Field work was carried out on two study sites, designated the Ramada and the Coyote Wash sites, 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. Radio-tracking 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), November 11 to December 22, 1982 (study period 3) and January 18 to March 12, 1984 (study period 4).

The lower ecological zones of Deep Canyon are part of the warm and arid Colorado Desert which encompasses much of southern California, Arizona, and northern Mexico. Monthly temperatures range from a mean maximum of 39°C in July to a mean minimum of 9°C in December. This area receives an average yearly rainfall of 120 mm (range 25-305 mm from records since 1961) from generally predictable winter rains and unpredictable and often torrential storms in the late summer and early fall.

Both field sites contain interspersions of sandy washes, hummocks, and rock strips. Vegetation is both denser and more variegated than in much *D. merriami* habitat. Plant surveys at an elevation of 240 m are summarized by ZABRISKIE (1979), who found 14 perennial shrub species to cover 14% of the ground. The evergreen creosote bush (*Larrea tridentata*) is the dominant shrub species and accounts for 29% of the vegetative cover. Other important perennial species are drought-deciduous and include *Dalea schottii*, *D. spinosa*, *Ambrosia dumosa*, *Bebbia juncea*, *Encelia farinosa*, *Hymenoclea salsola*, *Hyptis emoryi*, *Beloperone californica*, *Acacia gregii* and *Cercidium floridum*. Five cactus genera occur on the site with *Opuntia ramosissima* the most common species.

The Deep Canyon alluvial plain also contains at least 93 annual species with *Cryptantha* and *Cammissosonia* the dominant genera, though *Plantago insularis* and *Schismus barbatus* are the most abundant species. Most of the annuals germinate 5-14 days after fall and winter rains and flower in the spring, but some germinate and flower after summer rains.

### *Trapping procedures.*

One-hectare square grids were established on the Ramada site in 1979 and the Coyote Wash site in 1981. On each trapping-grid single Sherman live-traps (8 × 9 × 23 cm) were

placed at trap stations established at 10 m intervals yielding a total of 100 trap stations per site. In general, the traps were set in the hour before dusk, baited with rolled oats, and checked either four to five hours later or the next morning. All captured *D. merriami* were weighed, sexed, and inspected for reproductive condition. Female *D. merriami* have an 11-14 day estrous cycle, the stage of which is roughly discernible by examination. The vulva swells gradually as estrus approaches and the vagina is but briefly open, followed by a visible discharge of sloughed-off epithelial cells for 3-4 days post-estrus (WILSON, BEHREND'S & DALY, 1985). Diagnosis of pregnancy and lactation was straightforward. During the breeding season, all reproductive radio-implanted females were captured before and after parturition, which was indicated by an abrupt loss of weight and the appearance of red, distended nipples. Males captured on the Ramada site in study period 1 were judged to be in reproductive condition if they exhibited a scrotal sac. To better characterize male reproductive condition, males captured on the Coyote Wash site in study period 2 were judged to be in reproductive condition if the testes were expressible by palpating the lower abdomen (presence of a scrotal sac is probably a reliable criterion for reproductive potential but there is substantial variation among testis lengths in males possessing scrotal sacs). In study period 3 the length of the expressed testes was measured with calipers to the nearest 0.5 mm. Rodents captured on the Ramada site in study period 1 were ear-tagged for identification but rodents captured on the Coyote Wash site in periods 2, 3, and 4 were toe-clipped due to the problem of animals losing their eartags.

The intensity of trapping varied between study periods so that each is described separately. In period 1, grid trapping was conducted primarily to capture subjects for radio implantation. Focal trapping (that is, the surrounding of a radio-located animal with two to four traps, which usually led to the animal's capture within a few hours) was conducted for the retrieval of radios and for hormone manipulation of some animals. In period 2, grid trapping was conducted on a weekly basis except when animals were needed for radio implantation, and focal trapping when particular animals requiring examination were not captured on the regular trapping night. In period 3, grid trapping was conducted once every three days on average to ensure that an estrous cycle (swelling and subsidence) would not be missed. In period 4, focal trapping of radiotelemetered females was conducted once every three days during anestrus periods and on successive nights during estrous periods.

#### *Animals.*

Sixty-seven adult (*i.e.* > 30 gm) *D. merriami* (32 males and 35 females) were radio-tracked for periods ranging from 1 to 117 days in the four study periods between November 1980 and mid-March 1984. Most individuals were tracked only in a single study period. One female was radio-tracked in periods 2, 3, and 4, three males were tracked in periods 2 and 3, and one female was tracked in periods 3 and 4.

#### *Equipment.*

Standard radiotelemetry equipment was used (AVM Instrument Co., Dublin, California) including SM-1 mousestyle 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 dental acrylic and sealed with beeswax yielding a package weighing about 3.0 g. Transmitters had a signal range of 30 to 60 m at ground level depending on the terrain.

For radio implantation, animals captured 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. In study periods 1 and 2, six or seven locations were collected for each animal per night either from dusk until midnight or midnight until dawn on an alternating basis. In period 3, each animal was located hourly throughout the dark period yielding a total of 15 locations per night. In period 4, each animal was located hourly for the first seven hours after dusk. In period 1, radio-tracking was carried out over 25 consecutive nights. In periods 2 and 4, radio-tracking was carried out on an average of four nights per week. In period 3, radio-tracking was conducted two out of every three nights. Day burrows were located every day a worker was in the field throughout the studies.

The procedure for locating an animal was simple. Once an animal's radio signal was received, the observer walked toward the signal source scanning the area ahead with the aid of a dim headlamp. If the animal was not visually detected the observer continued until the signal was of a strength indicating that the animal was within about 2 m. At this point the observer would move approximately 5 m to face the signal source at a 90° angle from the original position in order to triangulate the animal's location. Using this procedure an animal could be located to within approximately 1 m<sup>2</sup>. If the strength and/or direction of the radio signal varied persistently during close approach the animal was considered to be aboveground and moving. If visual contact was not made, an approximate location was recorded with the signification that the animal was moving. The error associated with these situations was probably not greater than 5 m.

The two study sites were mapped as grids with (10 m)<sup>2</sup> quadrats to the extent of the animals' ranges. Each radio location was recorded as an x and y coordinate pair (*i.e.* a Cartesian coordinate) to a one meter level of precision.

#### *Data analysis.*

The surface activity measure reported here is the mean distance moved in meters between successive hourly radio fixes, called mean hourly distance (MHD).

$$MHD = \Sigma \{[(x_t - x_{t-1})^2 + (y_t - y_{t-1})^2]^{1/2}\} / n$$
 where x and y are the Cartesian coordinates for the study site grid, t denotes the present location, and t-1 denotes the immediately preceding location. n is the number of locations used for the summary statistic. Since this index is based on time interval samples rather than continuous observation, it is not to be taken as an absolute measure of activity. (In particular, successive radio fixes at the same site will yield a distance of 0, but do not necessarily imply that the animal has not moved.)

In study periods 1, 2, and 4, nightly MHD's were based on successive hourly fixes plus the adjacent daylight fix. That is, for nights when data were collected between dusk and midnight, the preceding day location and all the subsequent night locations were used. For nights when data were collected between midnight and dawn, all night locations plus the following day location were used. For period 3, in which data were collected throughout the night, the preceding day location and the subsequent night locations were included in the nightly MHD calculations. Summary statistics for animal movements were generated on both a per night and an overall basis. These statistics were also generated for females at different reproductive stages. For the analysis of movements by estrous females, only the day of maximal vulvar swelling and the two days surrounding maximal swelling were used. For statistical purposes, each animal's data were weighted equally because there was no correlation between MHD and the number of nights an animal was radio-tracked ( $r = -.08$ ).

The protocol for data collection was significantly different for period 4 compared to the three previous studies: (1) Animals were radio-tracked only through the first seven hours

of the night when activity was greatest. (2) Only during this study period were animals radio-tracked on the same nights on which they were trapped. (Subsequent analysis showed that trapping has an inhibitory effect on movements later in the night.) (3) Only females were radio-implanted. For these reasons, the period 4 results are not comparable statistically with the earlier results but will be cited in reference to specific points.

**Results**

Reproductive activity.

The percentage of radiotelemetered individuals in reproductive condition (*i.e.* estrous, pregnant, or lactating females, and males with scrotal testes) on a monthly basis is illustrated in Fig. 1. With the exception of study period 1, most males had scrotal testes during the months the populations were sampled. During study period 4, no males were radio-implanted but all captured males had scrotal testes. By contrast, females were reproductively inactive in the fall with the exception of December 1981.

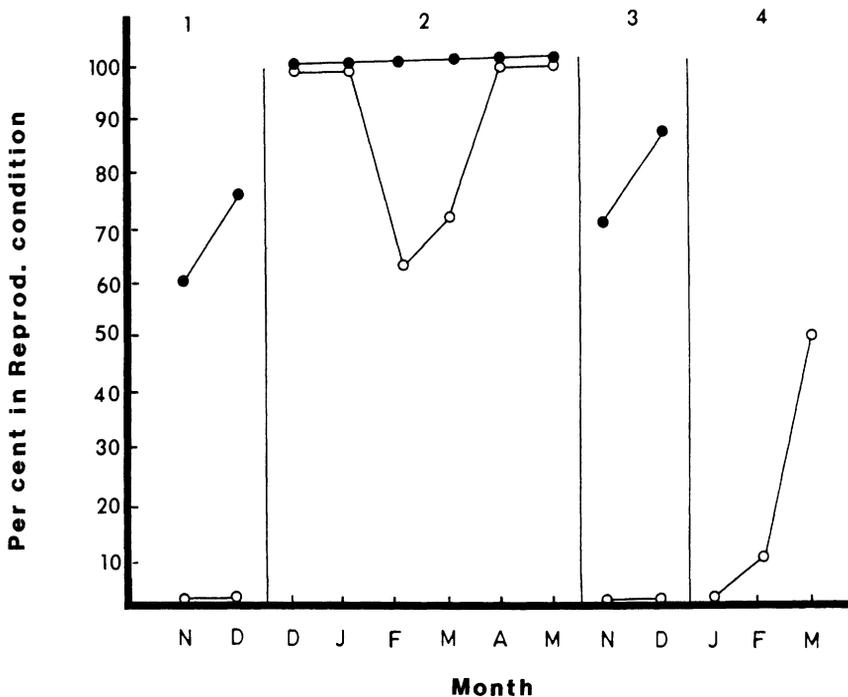


Fig. 1. The percentage of radiotelemetered kangaroo rats in reproductive condition (*i.e.* scrotal males and cycling, pregnant, or lactating females) by month. Numbers in the upper part of the figure indicate the study period. Closed circles are males, open circles females.

## Radio-tracking data.

A summary of the radio-tracking data collected over the four studies and included in the analyses below is presented in Table 1. In study period 1, four females and three males were implanted with hormone-secreting silastic capsules midway through the study to examine the influence of hormonal state on movements (these data have been reported elsewhere; DALY, WILSON & BEHREND, 1981). The data for hormonally manipulated animals are omitted from Table 1 and all subsequent analyses so that all comparisons are between hormonally unmanipulated animals.

TABLE 1. Summary of radiotelemetry data collected over the four study periods

		Sample size	Mean # fixes	Mean # nights tracked
Study				
1	Male	12	92.4	12.1
	Female	13	59.1	7.5
2	Male	13	72.5	10.8
	Female	11	155.4	24.4
3	Male	10	199.7	14.4
	Female	9	202.1	14.4
4	Female	11	226.9	28.4
Total		67	141.4	16.1

Throughout the studies, an attempt was made to collect similar amounts of data on different animals (*e.g.* by radio-implanting several individuals over a short time period), but there was substantial variation among individuals due to disappearances, predation, equipment failure, and two surgery-related deaths. For males, the range in the number of locations for different individuals was 14-430 and the range for the number of nights radio-tracked was 2-40. For females, these values were 11-856 and 1-97, respectively. In total, the data used for the analyses below represent 10,996 animal hours and 1232 animal days.

## General activity patterns.

*D. merriami* are not strictly nocturnal creatures, but rather show a degree of crepuscular activity as well. Animals generally emerge from their day burrows around dusk and on many occasions could be spotted visually without the aid of a head lamp. Animals may be active at any hour of the night, but the heaviest concentration of activity tends to occur in the

three to four hour time span following the onset of darkness (BEHREND, 1984). Individuals may return to their day burrows several times throughout the night, and usually return permanently before dawn, although a few moves occurred after the dawn check.

### Study period.

Average movements (MHDs) by animals are broken down by study period in Table 2. With the sexes combined, there were significant differences between studies. Animals in study period 1 moved less than those in period 2 ( $t_{47}$   $df = 2.21$ ,  $p < .05$ ; all tests are two-tailed unless otherwise indicated) and less than those in period 3 ( $t_{42}$   $df = 4.97$ ,  $p < .001$ ). Likewise, study period 2 animals moved less than study period 3 animals ( $t_{41}$   $df = 3.12$ ,  $p < .01$ ).

TABLE 2. The mean distance in meters moved between successive hourly fixes (MHD) broken down by study period and sex

	Study period			
	1	2	3	4
Male	11.5 (9.8)	20.4 (11.3)	28.9 (15.1)	—
Female	10.1 (5.2)	14.1 (4.7)	25.9 (10.4)	14.6 (3.1)
Combined	10.9 (8.0)	16.8 (9.7)	27.5 (12.8)	

Standard deviations are in parentheses.

### Sex.

The MHDs broken down by sex over periods 1, 2, and 3 are also provided in Table 2. Although males and females in period 1 (when no females were in reproductive condition) did not differ in their average MHDs, between-male variance was significantly greater than between-female variance ( $F_{11,12}$   $df = 3.55$ ,  $p < .05$ ). In period 2 (the breeding season), animals were not only more active on the surface than those in period 1, but males moved more than females ( $t_{22}$   $df = 1.72$ ,  $p < .05$ , one-tailed test). The average move between radio fixes by males was 45% greater than the average move by females. Between-male variance was again greater than between-female variance during study period 2 ( $F_{12,10}$   $df = 5.78$ ,  $p < .01$ ): MHDs for males ranged from 4.8 m to 38.7 m while the range for females was only 8.8 m to 23.5 m. In study period 3, as in

study period 1, all females were non-reproductive and some males lacked scrotal testes. The overall MHDs of animals were greatest during this period, but there was no difference between the sexes.

#### Reproductive condition.

The MHDs for females in different reproductive stages (study period 2 only) are summarized in Table 3. Despite small sample sizes, t-tests for dependent groups revealed that movement by females varied in relation to their reproductive condition. MHDs were three times greater on average for females in estrus compared to anestrus ( $t_3$   $df = 3.63$ ,  $p < .05$ ). Female movements were also greater during pregnancy than during anestrus ( $t_4$   $df = 2.21$ ,  $p < .05$ ) and during lactation than during anestrus ( $t_3$   $df = 3.48$ ,  $p < .05$ ). Although the differences were not statistically significant, MHDs tended to be greater for estrus compared to pregnancy and estrus compared to lactation as well.

TABLE 3. Average hourly moves (in meters) of *D. merriami* females in different reproductive stages

Female	Non-reprod.	Estrous	Pregnant	Lactating
1500	3.5	12.3	14.6	14.8
1485	10.4	34.3	12.5	26.1
1314	8.9	—	8.5	14.0
1312	—	—	12.5	16.1
1	11.1	—	14.1	15.8
1498	—	28.9	8.3	12.8
HR3	8.2	26.6	20.3	12.9
1497	4.6	11.6	—	—
HL4FR2	—	—	26.2	13.3

Fig. 2 depicts the most complete set of data on a single female's movements through different reproductive stages. Despite the substantial variation in MHD from night to night, there were clear increases in movements around periods of estrus. These levels of movement were matched only when this female was lactating and, presumably, foraging more as a result.

This particular female, whose average day burrow move (when a move was made) was 15.0 m during anestrus, pregnancy and lactation, made day burrow moves of 100 m and 95 m during two brief estrus periods. (*D. merriami* typically use several day burrows, BEHREND *et al.*, 1986.) On both occasions, this female returned to her previous day burrow area one or two days after estrus.

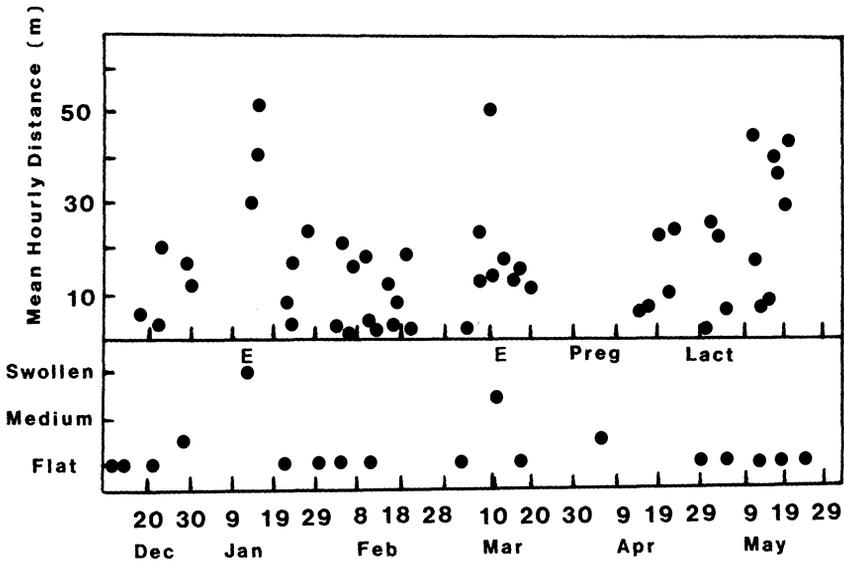


Fig. 2. Nocturnal activity of female 1485 over a 5-month period as a function of reproductive condition. The upper graph depicts her average hourly move (MHD, in meters) on nights when she was radio-tracked. The lower graph depicts her reproductive state as evidenced by the degree of vulvar swelling. E = estrus. Preg = pregnancy. Lact = lactation. Note the movement peaks associated with estrus.

Only two of five females exhibited elevated MHDs during estrus in study period 4. However, if these data are combined with study period 2 animals, there remains a tendency for females to be more active on the surface during estrus ( $t_8 \text{ df} = 1.91, p < .05$ , one-tailed test). In addition, two study period 4 females again made their longest day burrow moves during estrus. One female, whose average day burrow move was 14.1 m, made a 56 m move; the other, whose average day burrow move was 17.8, made a 35 m move. Unfortunately both these females' transmitters failed before it could be determined whether they returned to their previous day burrows.

For males, physiological and morphological factors which may account for the substantial variation among individuals are not clear-cut. Only data from study period 3 are adequate for examining the relationship between testicular development in males and surface activity. A summary of average testis length in relation to MHD is found in Table 4. There was a significant positive correlation between MHD and testis length ( $r = .79, p < .02$ ). Over periods 1-3 combined, there was a mild positive relationship between body weight and MHD ( $r = .28, p < .05$ , one-tailed

test). This statistic should be viewed with caution, however, due to the difference in this relationship among the three study periods. In period 1, the relationship was only slightly positive ( $r = .10$ ) and in period 2 this relationship was slightly negative ( $r = -.11$ ). Only in period 3 was there a reasonably convincing positive relationship between body weight and MHD ( $r = .57$ ,  $p < .05$ ). For females, there was no relationship between body weight and MHD ( $r = -.25$ ,  $p > .05$ ).

TABLE 4. The average hourly moves in meters (MHD) of study 3 males in relation to body weight and testes length

Male	Body weight (g)	Testes length (mm)	MHD
HL1	32.2	5.0	17.7
HR2	33.7	6.6	26.2
HL3FL3	38.7	8.2	22.3
12	41.0	9.0	24.1
HR4	34.7	9.3	27.2
HR1FL4	36.7	9.3	11.6
HL4	34.7	9.5	25.4
HL3FL2	38.2	11.1	21.7
13	39.7	14.0	55.3
HL2FR2	42.2	14.5	57.4

## Discussion

Aboveground activity proves to vary considerably as a function of sex and reproductive state, and there may be several reasons why. Competition for food, burrow sites, territories, and mates may all be particularly keen during the breeding season. An increase in the intensity of competition could result in more patrolling and defense of territories. Were surface time determined solely by foraging needs, we might instead expect it to decrease in the breeding season since kangaroo rats breed when resources are abundant (BEATLEY, 1969); however, pregnant and lactating *D. merriami* eat considerably more than non-breeding females (SOHOLT, 1977; BEHREND, unpubl. data), and since they do not establish large hoards in their home burrows, reproductive females may have to spend more time foraging.

In the present study, surface activity differences between seasons are not straightforwardly associated with reproduction. Although animals in study period 2 (the breeding season) were significantly more active than the non-breeding animals in period 1, they were significantly less active than the non-breeding animals in period 3. Despite the relationship be-

tween reproductive state and aboveground activity *within* the breeding season, variation between seasons or years evidently depends on other factors. Possibilities include population density, weather patterns, and resource availability.

As solitary animals, *D. merriami* males apparently do not invest in their offspring beyond the contribution of sperm. Free of parental investment, males might be expected to exhibit high levels of mating effort and intrasexual competition. However, sexually selected characteristics (*e.g.* major sexual size dimorphism or sex-specific weaponry) are not conspicuous in solitary rodents, including *Dipodomys*. Males will fight with one another, but they are not evidently specialized for intrasexual combat: as in many small rodents, females seem to be at least as effective fighters as males.

Perhaps males who establish social contacts and visit several females on a frequent basis enjoy the greatest mating success. DALY & DALY (1974), for example, describe a social system in free-living Saharan gerbils (*Psammomys obesus*) whereby females establish burrow sites in patchily-distributed vegetation (their primary food source), while males choose vegetationally poor burrow sites that are handy to the home burrows of several females, and visit them on a regular basis. Similarly, while female meadow voles maintain exclusive home ranges from other females, males' ranges overlap with one another and, temporarily, with the ranges of estrous females (MADISON, 1980). Finally, BROOKS & BANKS (1971) determined that male collared lemmings maintained no consistent center-of-activity, but rather had several rest areas near female home sites. Apparently males were able to visit females every 1-2 days.

If male *D. merriami* do indeed compete indirectly for access to females in some way that is reflected by their ranging patterns, either by visiting females or simply spending more time aboveground, one would expect the patterns of the two sexes to vary in relation to the females' reproductive condition. Indeed the MHD results show that ranging patterns were sexually dimorphic only during the breeding season with males moving more than females.

A common finding in solitary-living rodents is that males range more widely than females, although these dimorphisms are not always restricted to the reproductive season, as seems to be the case with *D. merriami* and a Saharan gerbil, *Meriones libycus* (DALY & DALY, 1975). Species in which a sexual range dimorphism exists include the collared lemming (BROOKS & BANKS, 1971), the fat sandrat (DALY & DALY, 1974), the brown lemming (BANKS *et al.*, 1975), the dusky-footed woodrat (CRANFORD,

1976), the white-footed mouse (MINEAU & MADISON, 1977), the banner-tail kangaroo rat (SCHRODER, 1979), and the meadow vole (MADISON, 1980). Thus, there is mounting evidence for a general pattern of sexual dimorphism in the ranging behavior of small, solitary rodents. This stands in marked contrast to the sexually monomorphic home ranges of the monogamous oldfield mouse (*Peromyscus polionotus*; BLAIR, 1951) and pine vole (*Microtus pinetorum*; FITZGERALD & MADISON, 1983).

Merriam's kangaroo rats do not exhibit the dramatic sex differences in home range size that characterize many solitary rodents, but that is not for want of male travels. One male's home range in the breeding season, for example, overlapped the ranges of 14 radio-implanted conspecific adults (and probably many more without radios). Sex differences in home range are instead inconsistent because females also overlap with several conspecifics and because there is exceptional variance in home range size within both sexes (BLAIR, 1943).

The results from the breeding season clearly demonstrated that females' aboveground activity varied in relation to reproductive condition. The most striking observation was the dramatic increase in surface activity by females during estrus. This finding accords well with those of laboratory investigations of the relationship between hormonal state and behavior in female rats and guinea pigs. For instance, FINGER (1969) showed that running wheel activity by female rats was greatest during estrus. More recent studies have shown that estrous rats ambulate more and defecate less in open field tests than diestrous rats (BIRKE & ARCHER, 1975), both estrous rats and guinea pigs show longer object investigation (BIRKE, 1979), estrous rats are less distractable (*e.g.* less likely to shift attention) in maze tasks and food selection experiments (BIRKE, ANDREW & BEST, 1979), and estrous rats patrol mazes more rapidly and enter illuminated mazes more frequently (MARTIN & BOTTIG, 1980). BIRKE (1979) suggested that spending more time investigating objects in the environment at estrus serves the function of finding males, for example by spending more time at scent-marked locations. Increases in ambulation by estrous females have been observed in the field as well. CALHOUN (1963) reported that female rats move more on the night of proestrus and suggested that these females might be scent-marking to attract males. BROOKS & BANKS (1971) noted that female collared lemmings ranged more widely during postpartum estrus, as did the female meadow voles studied by MADISON (1978).

A very interesting observation in the present study was the dramatic day burrow moves by female 1485 around estrus. Moreover, during the

first estrus period this female moved to a day burrow that was near the day burrows of three males (these burrows were located when the males were radioimplanted two weeks later); direct observations during this estrous period found her under a creosote bush with at least two unidentified animals for approximately one-half hour. At no other time have we observed kangaroo rats in such close proximity for this length of time. It is not clear what function increased surface activity by estrous females serves, but the episode just described suggests that females may actually seek out males during estrus. It is tempting to speculate that long movements reflect active strategies of mate selection by females, whether to avoid inbreeding with closely related neighbors (see JONES, 1982) or to select for some desired quality. This activity would not preclude the possibility of males visiting females since social familiarity based on prior interactions may be important for subsequent mating.

Pregnant and lactating females also showed elevated surface activity compared to the anestrus condition. This finding is quite different from patterns found in some other rodent species. Female dusky-footed woodrats, for instance, had their smallest home ranges during the breeding season (CRANFORD, 1976). BROOKS & BANKS (1971) estimated the home ranges of female collared lemmings to be about 0.16 ha with no distinct center-of-activity before mating and during the first two weeks of gestation but only 0.02 ha from late gestation to weaning (with the exception of a resurgence around postpartum estrus). A similar pattern was noted for female meadow voles by MADISON (1978) with ranging decreasing around parturition, remaining suppressed through early lactation, and then increasing toward weaning (also with a resurgence around postpartum estrus). MADISON suggested that this movement reduction by meadow voles in late pregnancy and early lactation may combine with more intense use of local food resources to result in energy savings for females. He also suggested that diligent nest attendance in early lactation may function to protect the helpless offspring from infanticidal attacks by conspecifics, a situation well documented in several mammalian species, including male collared lemmings in the laboratory (MALLORY & BROOKS, 1978).

All of the above rodent species, in which ranging decreases during lactation, are herbivores who feed primarily on the vegetative parts of plants and breed when such resources are superabundant. Increased activity during pregnancy and lactation by *D. merriami* may be related to the increased energy, nutrient, and water demands of reproduction. Pregnant and lactating *D. merriami* consume more solid food than anestrus females

under laboratory conditions (BEHREND, unpubl. data) and lactating *D. merriami* consume more greenery (SOHOLT, 1977). Since *D. merriami* do not establish large food caches in their burrows, it is reasonable to assume that their foraging requirements are greater during pregnancy and lactation with the result that females must spend more time aboveground. Just why they do not lay in large stores (as do some other kangaroo rat species), at least in anticipation of reproduction, remains unknown. It would also be interesting to know whether increased foraging activities and, hence, time away from the natal burrow, increase the offspring's risk from conspecifics or predators. Infanticide by female conspecifics has been reported for Belding's ground squirrels by SHERMAN (1981) and may be related, as he suggests, to the infanticidal female's potential competition with another female's offspring for future breeding sites and food resources. Competition for burrows may not be a concern for *D. merriami* since burrows are simple affairs and quite ubiquitous (see JONES, 1982), but future food resources may be a concern for competing conspecifics. Thus, there may be risk to offspring associated with aboveground activity during early lactation which could necessitate a compromise between foraging and nest attendance. Laboratory observations of nest attendance by female *D. merriami* (BEHREND, 1984) indicate that females spend most of their time at the nest until the pups' eyes open and they begin ingesting solid food, but this may be an artifact resulting from the readily available food supply. More data on the reproductive females' activity budgets are needed.

A noteworthy finding in these studies was that within-sex variance was consistently higher for males than for females, and significantly so during the breeding season. At least some of this within-sex variability is attributable to reproductive condition, as was clearest in study period 3 (Table 4) when a significant positive correlation between testis length and surface travels was found.

The results for both sexes thus suggest that the extent to which kangaroo rats suffer the predation risk and other costs of surface activity cannot be understood simply in terms of foraging needs.

### Summary

Sixty-seven male and female Merriam's kangaroo rats (*Dipodomys merriami*) were radio-tracked over four study periods between November 1980 and mid-March 1984 on two study sites near Palm Desert, Riverside County, California. Animals were located once per hour yielding data representing 10,996 animal hours and 1232 animal days. The reproductive condition of animals during the tracking periods was also monitored. This paper describes the general surface activity patterns of *D. merriami* in terms of the mean

distance moved in meters between successive hourly fixes (called MHD) with particular emphasis on movements in relation to sex and reproductive condition.

It was found that during non-breeding periods (study periods 1 and 3), males and females exhibited similar surface movement patterns, although during period 1, between-male variance was significantly greater than between-female variance. During the breeding season (study period 2), however, males moved significantly more from one hour to the next than did females, and again between-male variance was significantly greater than between-female variance. Movements were also found to be related to reproductive condition in both females and males. During study period 2, females that were estrous, pregnant, or lactating moved significantly more than when they were non-reproductive. One female in study period 2 and two females in study period 4 moved their day burrows over exceptional distances precisely at the time of estrus. In study period 3, there was a significant positive correlation between testis length in males and surface movements.

These results indicate that surface activity by *D. merriami* reflects different behavioral strategies by individuals in relation to sex and reproduction; and that analyses which attempt to balance the costs of surface activity must consider the social functions of such activity and not simply the foraging returns.

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