

Characteristics of kangaroo rats, *Dipodomys merriami*, associated with differential predation risk

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Abstract. Between 1980 and 1990, 176 adult Merriam's kangaroo rats were subcutaneously implanted with radio transmitters and tracked for a total of 6316 animal-days at a California site, prior to and during reproductive seasons. Thirty-six animals are known to have been killed by predators, and 14 who disappeared abruptly are also presumed victims. These 50 cases permit various analyses of differential predation risk. Males incurred a predation rate (4.22 deaths per animal-year) more than twice that of females (2.01); this sex difference in mortality was apparently absent or reversed after the breeding season. Both male and female victims travelled significantly greater distances between successive radio-locations shortly before their deaths than surviving same-sex animals tracked contemporaneously. Rather than being selective for the feeble, predation on kangaroo rats is selective for the mobile.

Predation must constitute a major selection pressure on the behaviour of small mammals. Foraging decisions, exploration, dispersal, territorial defence, mating and nepotistic strategies all have cost/benefit structures that are affected by the fact that behavioural alternatives expose animals to variable risks of predation. However, because naturally occurring predation is generally unpredictable, and because it is more often observed in studies focusing on the predators than the prey, there is seldom information on the correlates of differential risk to members of the prey species, especially the behavioural correlates.

It is widely supposed that predation operates selectively against individuals who are very young or old, weak, diseased, injured, parasite-ridden or otherwise defenceless. In general, however, studies confirming differential predation upon the relatively feeble concern large prey species whose principal anti-predator tactics consist of either long-distance flight or active defence (e.g. Mech 1970). In the case of small mammals whose principal defence is crypticity or escape to a nearby refuge, it is not clear that a similar pattern of selective predation prevails. In a study of radio-telemetered snowshoe hares, *Lepus americanus*, for example, Brand et al. (1975) found little or no evidence that predation was concentrated upon those in poor condition.

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Nor should we necessarily expect predation to be selective for the feeble in the case of small mammals. Instead, the likeliest victims may often be those healthy, large, dominant adults for whom the prospective fitness benefits of present reproductive efforts are sufficient to offset the costs in elevated exposure to risk. Two studies of predation on rodents in small enclosures provide some fuel for such conjectures: Roberts & Wolfe (1974) found that a cat, *Felis catus* (but not a hawk, *Buteo jamaicensis*), captured trios of cotton rats, *Sigmodon hispidus*, in the order of most to least dominant, and Cushing (1985) found that a weasel, *Mustela nivalis*, captured an oestrous deer mouse, *Peromyscus maniculatus*, before her dioestrous neighbour in more than 90% of trials. We have found only one relevant field study, namely Madison's (1978) analysis of six cases of snake predation on radio-implanted voles, *Microtus pennsylvanicus*; despite having information on just three victims of each sex, Madison was able to show that predation risk was significantly associated with lactation in females and with large body size in males.

This paper is based on analyses of naturally occurring incidents of predation on Merriam's kangaroo rats, *Dipodomys merriami*, implanted with radio-transmitters, during the course of a long-term study of various aspects of the species' behavioural ecology and sociobiology. Kangaroo rats (*Dipodomys*; Heteromyidae) have been the objects of considerable ecological research, mostly concerned with issues of interspecific competition

and coexistence among desert granivores. The general conclusion from a variety of studies of microhabitat partitioning is that kangaroo rats, more than sympatric granivorous rodents such as pocket mice, *Perognathus* and *Chaetodipus* spp., exploit the open ground between perennial shrubs (Lemen & Rosenzweig 1978; Thompson 1982; Price & Brown 1983). Several characteristics of kangaroo rats appear to reflect the selective consequences of a high level of predation risk in their preferred foraging environment. Webster (1962, also Webster & Webster 1971) makes a convincing case that the hypertrophied middle-ear cavities of kangaroo rats are adapted for predator detection and evasion. Similarly, bipedal locomotion in kangaroo rats and other desert rodents exploiting open microhabitats, once considered an adaptation for energetically efficient locomotion, now seems better explained as providing speed and agility in an anti-predator context (Garland 1983; Nikolai & Bramble 1983; Thompson 1985). Another presumed anti-predator adaptation of kangaroo rats is moonlight avoidance (Lockard & Owings 1974; Price et al. 1984; Brown et al. 1988). Despite considerable interest in and discussion of predation upon kangaroo rats in these several contexts, however, information about spontaneous acts of predation in the field has hitherto been lacking.

METHODS

Study Site

This research was conducted at the University of California's Boyd Deep Canyon Reserve, approximately 3 km south of Palm Desert, California, U.S.A. The study site, located on the upper alluvial plain of Deep Canyon at an elevation of about 250 m, is centred on a 1-ha trapping grid, consisting of 100 trap stations in a 10 × 10 array at 10-m intervals. This grid of Cartesian coordinates extends, in the form of labelled stone cairns or stakes at 10-m intervals, in all directions around the trapping grid, permitting researchers to identify quickly any locus in the mapped area with a precision of 1 m. Extension of the mapped study area has been undertaken as required to encompass all the positions at which animals radio-implanted after trapping on the central trapping grid have ever been radio-located. The fully mapped area presently covers about 11 ha.

Zabriskie (1979) described the reserve and its flora in detail. Essentially similar to our site is one

that he described at an elevation of 240 m, where 14% of the soil surface lay under the canopy of perennial shrubs of some 14 species, of which creosote bush, *Larrea tridentata*, was the most common. Local substrate is a mixture of pebbly 'desert pavement' and sandy washes up to 40-m wide, with occasional rocky patches and a few substantial boulders.

Kangaroo rats on our study area almost never change locales during daylight hours, remaining in a 'day burrow'; the probability that the day burrow used on one day will not be the same as that used on the previous day is about 0.22 (Behrends et al. 1986a). The distance between successive day burrows is typically about 10–20 m, and rarely exceeds 50 m.

Trapping and Radio Implantation Procedures

Kangaroo rats and other rodents on the study site were captured in Sherman live traps measuring 8 × 9 × 23 cm until 1986, and 8 × 9 × 30 cm since 1987, baited with rolled oats. Each of the 100 trapping stations on the central grid is the site of a single trap, left in place during periods of continuous researcher presence at the site. These research periods have typically begun in late November or December and continued for 1 to 7 months.

Trapping was conducted on 4–6 consecutive nights at the beginning of each research period, to assess survival of previously marked animals, to mark those newly captured, and to select and radio-implant appropriate animals for tracking (those captured regularly and not solely on the periphery of the grid). A trapping night typically entailed opening and baiting the 100 traps at dusk, and returning 2–5 h later to process captured animals and close the traps. Captured rodents were weighed, sexed and assessed for reproductive condition, and then released at their capture sites, unless scheduled for radio implantation or removal. All *D. merriami* were distinctively marked by toe-clipping.

For radio implantation and removal, animals were transported 2 km by car to the laboratory, and were lightly anaesthetized with a weight-dependent dose of Ketaset (0.001 ml/g). Transmitters were implanted subcutaneously just lateral to the dorsal midline, and the requisite incision was closed with two to four small wound clips. The implanted package consisted of an SM-1 mouse-style transmitter (AVM Instrument, Dublin, California) with

internal antenna, soldered to a 1.35-V or 1.5-V mercury battery. The transmitter and battery were coated with dental acrylic (to make a hard package that would survive most of the talons, beaks and jaws likely to be encountered) and then sealed with beeswax, yielding a package weighing 2.7 ± 0.2 g. After recovery from the anaesthesia, kangaroo rats were released in darkness at their point of capture, usually about 3 h after implantation.

After radio implantation, the trapping effort varied from year to year (primarily according to our changing interest in precise determination of female reproductive condition), but seldom exceeded 2 nights per week. During prolonged research periods, subjects had to be reimplanted with fresh batteries one to three times; sometimes rather than trapping the whole grid of 100 traps, we placed several traps around a particular animal whom we wished to inspect or reimplant, which usually led to capture and removal of the traps within 1 h. At the end of research periods, 1–3 nights of trapping the 100-trap grid, plus strategic placement of a few traps off the grid, sufficed to recover radios from all but two survivors.

Radiotelemetry Methods

We determined radio-locations by walking through the study area carrying a hand-held antenna and a radio receiver (LA-12 receiver, AVM; or CE-12 receiver, Custom Electronics of Urbana, Urbana, Illinois); for a detailed description of the method of locating a signal source, see Madison et al. (1985). Locations were recorded as Cartesian co-ordinates to a 1-m precision.

On tracking nights (usually all those other than trapping nights), we located each radio-implanted animal each hour, for 6–14 consecutive hours. The numbers of animals tracked contemporaneously ranged from 4 to 26. These hourly locations provided the data base for the measure of activity used in this paper: the mean hourly distance, which is the mean of the distances between pairs of successive hourly radio locations, including both the distance from the day burrow to the first nocturnal fix and that from the last nocturnal fix to the subsequent day burrow. (Note that this hourly distance measure represents the minimum distance moved in the hour, and is therefore only a coarse index of travels; for example, successive locations at a single site yield a distance of zero, but do not imply that the animal has not moved.) More frequent

Table 1. Seasonal distribution of radio-tracking effort and predation incidents; totals for 1980–1990

Month	Predation victims	Animal-days	Predations per animal-year
November	15	566	9.7
December	18	2053	3.2
January	5	1074	1.7
February	3	865	1.3
March	2	378	1.9
April	3	278	3.9
May	1	228	1.6
June	1	645	0.6
July	2	229	3.2

locations and continuous scheduled focal-animal samples of behaviour were also collected on various schedules, but these data are not used here.

Seasonal Distribution of Data Collection

Radio-tracking effort has been unevenly distributed over the calendar year (Table 1), with the consequence that seasonal variations in the activity of kangaroo rats and their predators have been unevenly sampled. In particular, rattlesnakes *Crotalus ruber* and *C. atrox*, and sidewinders, *C. cerastes*, are almost completely inactive at our site from December to March, and 69% of our animal-days are from those 4 months.

In eight Novembers for which we have trapping data, small non-scrotal testes have characterized all males. Males typically exhibit testicular development by mid-December. Females begin oestrous cycling (Wilson et al. 1985) in late December or January; these dates are more variable for females than for males and more variable between than within years. Females can wean three litters in a single reproductive season, but probably rarely do so. Reproductive activity continued into July 1985 and 1988. Although we have collected no radio or trapping data between mid-July and mid-November in any year, we infer from the complete absence of subadult animals in November and December that reproduction ends by August.

RESULTS

The Radio-tracked Animals

Between December 1980 and January 1990, we radio-tracked 176 individual *D. merriami* rats,

89 males and 87 females, for durations ranging from a single day (a male killed by a sidewinder within 24 h of being radio-implanted) to 280 days (a female tracked at intervals from December 1981 to February 1985). The 176 animals were tracked for a total of 6316 animal-days, during which time 36 were known victims of predators: remains of 25 victims were found and the transmitter was found in the other 11 cases. (Though a few animals shed transmitters through reopened skin wounds, especially in the first 2 years of the study and especially after carrying the radio for at least 3 weeks, we did not consider it plausible that any of these 11 had shed their transmitters, mainly because all had been closely examined shortly before disappearing.) A further 14 disappeared abruptly, and were presumed to have been victims on the basis of circumstantial evidence; none had exhibited the slowing signal emission rate characteristic of a failing battery, and all had been easily and reliably trappable until disappearance. These 50 known or presumed predations represent a rate of 2.89 deaths per radio-animal-year. Table II presents a brief characterization of each of these 50 cases, for reference in the analyses to follow.

Predation incidents often occurred in bursts, apparently as a result of the locally intensive depredations of individual predators. Victims 28, 29 and 30 (Table II), for example, were all slain within 1 week; they were taken to three different Palo verde trees, *Cercidium floridum*, in the same vicinity, and were probably all victims of one or two great horned owls, *Bubo virginianus*, present on the study site every night of that week. Similarly, two of the three known victims of common whipsnakes, *Masticophis flagellum*, victims 13 and 17, were killed 12 days apart, by what appeared to be the same individual. Predation victims 35 and 36 were both killed between midnight and dawn on the night of 24 November 1987, and victims 37 and 38 were killed between midnight and dawn on the next night; all four may well have been taken by a single predator. Victim 44 was killed by a shrike, *Lanius ludovicianus*, at dawn on 25 November 1988, and victims 45 and 46 were apparently taken by the same predator at dusk of the same day. Because of this temporal clumping, predation incidents cannot be treated as independent events, so that appropriate statistical comparisons are generally those between predation victims and their surviving contemporaries.

Activity Level and Predation Risk

In 43 of the 50 cases of predation, we collected tracking data, consisting of hourly radio locations during nocturnal sessions of at least 6 h duration, on 1, 2 or 3 of the 3 nights immediately preceding the predation incident (see Table II).

Comparisons of the radio-tracking data for predation victims and their surviving contemporaries show that predation is selective with respect to movement. The mean hourly distance moved was greater than the median value among contemporaneously tracked animals for 29 predation victims and was below the median for 11 victims ($P=0.003$ by one-tailed sign test); the mean hourly distances of three victims fell at the median value. When comparisons are confined to same sex animals, 28 victims had mean hourly distances above the contemporaneous median and 10 below ($P=0.003$), while five fell at the median. Thus, there was a strong association between risk of predation and recent surface travels, those animals who were most mobile being most at risk.

This association between mobility and predation risk is significant within each sex considered separately. Among 19 female victims for whom recent tracking data were available, 13 had mean hourly distances above the contemporaneous female median and five below ($P=0.048$ by one-tailed sign test), while one value equalled the median. Among 24 male victims, 15 were above the median and five below ($P=0.021$); four equalled the median. In 7 of 19 cases in which a female was preyed upon, the victim was the single most active radiotagged female at the time (see Table II); given the numbers of females being tracked, 2.7 would be expected by chance. Ten of 24 male victims were each the single most active tracked male at the time of death; 5.2 would be expected by chance.

A few predation victims were dramatically more mobile than any of their contemporaries. Immediately before being captured by a coyote, *Canis latrans*, for example, victim 1 moved a mean hourly distance of 101 m, while 17 surviving contemporaries averaged 16 m with a maximum of 34 m; victim 1 was furthermore the only animal to have moved after dawn on the previous day. Similarly, victim 25's mean hourly distance of 58 m was more than 8 SD above the mean of 3.6 m among his 21 surviving contemporaries. In the 43 comparisons of recent movement data among victims and their contemporaries, no non-victim was ever such an outlier as either victim 1 or 25.

Table II. The 50 predation incidents; victim's 'activity rank' based on mean hourly distance moved between radio-locations relative to animals tracked contemporaneously

	Sex	Date	Evidence*	Victim's activity rank/number of animals tracked contemporaneously		Predator		Sex	Date	Evidence	Victim's activity rank/number of animals tracked contemporaneously		Predator
				Both sexes	Same sex						Both sexes	Same sex	
1.	M	Dec. 80	a	1/18	1/12	Coyote	26.	F	Jun. 85	a	7/13	5/9	Red rattlesnake
2.	M	Dec. 81	b, d	1/6	1/4	?	27.	M	Nov. 85	b, c	1/11	1/4	?
3.	M	Jan. 82	b, c	2/5	1/3	?	28.	M	Dec. 85	b, c	4/13	1/4	?
4.	M	Jan. 82	b, e, f	2/4	2/2	?	29.	F	Dec. 85	e, l	4/14	2/9	Great horned owl
5.	F	Jan. 82	b, c	No data		?	30.	F	Dec. 85	e, l	8/13	5/8	Great horned owl
6.	M	Feb. 82	b, d	6/8	1/3	?	31.	M	Dec. 85	e, g	1/13	1/5	Loggerhead shrike
7.	F	Mar. 82	e, g	7/8	5/6	Loggerhead shrike	32.	F	Dec. 85	b, e	4/12	3/8	?
8.	F	Mar. 82	b, c	3/8	1/6	?	33.	M	Dec. 86	b, c	11/11	6/6	?
9.	M	Apr. 82	d	1/9	1/3	?	34.	M	Dec. 86	b, e	1/12	1/5	?
10.	F	Apr. 82	a	4/8	3/6	Common whipsnake	35.	M	Nov. 87	b, d	No data		?
11.	M	Apr. 82	a	3/11	3/5	Sidewinder	36.	M	Nov. 87	b, d	No data		?
12.	F	May 82	e, h, i	1/7	1/4	?	37.	M	Nov. 87	b, d	No data		?
13.	M	Nov. 82	a	No data		Common whipsnake	38.	M	Nov. 87	b, e	No data		?
14.	F	Nov. 82	b, c, f	6/11	2/6	?	39.	F	Nov. 87	e, g	8/13	4/6	Loggerhead shrike
15.	M	Nov. 82	e, i, j	4/10	3/5	?	40.	M	Dec. 87	b, d	3/14	2/9	?
16.	M	Nov. 82	b, c	2/11	2/6	?	41.	F	Jul. 88	e, g	4/10	1/7	Loggerhead shrike
17.	F	Nov. 82	a, i	2/13	1/6	Common whipsnake	42.	M	Jul. 88	a	2/9	2/3	Speckled rattlesnake
18.	M	Dec. 82	e, f, g, k	10/12	6/7	Loggerhead shrike	43.	F	Nov. 88	b, d	No data		?
19.	F	Dec. 82	b, d	2/12	1/6	?	44.	M	Nov. 88	e, g	3/11	2/5	Loggerhead shrike
20.	M	Dec. 83	a	8/13	3/6	Great horned owl	45.	M	Nov. 88	e, g	6/11	4/5	Loggerhead shrike
21.	M	Dec. 83	b, d	10/12	3/5	?	46.	F	Nov. 88	m	9/14	8/10	Shrike?
22.	F	Feb. 84	b, d	10/10	10/10	?	47.	F	Dec. 88	b, c	2/14	1/10	?
23.	M	Jan. 85	b, d	3/25	3/11	?	48.	F	Dec. 88	b, c	4/10	2/6	?
24.	F	Jan. 85	b, c	5/25	1/14	?	49.	M	Dec. 88	e, g, n	9/13	4/5	Shrike?
25.	M	Feb. 85	b, c	1/22	1/9	?	50.	F	Dec. 88	b, c	5/11	2/8	?

*Key to Evidence column: (a) Predator observed directly, transmitting radio signal of ingested victim. (b) Abrupt disappearance between scheduled radio fixes (probable predator: bird or mammal). (c) Neither transmitter nor remains found. (Hence 'presumed' rather than 'known' predation.) (d) Transmitter found without remains of victim. (e) Remains of victim found with transmitter. (f) Killed after dawn. (g) Partially eaten in manner characteristic of shrike (removal of heart, brain and some other viscera). (h) Intact in burrow; snake-bite victim? (Hence 'presumed' rather than 'known' predation.) (i) Died in own day burrow. (j) Found in tunnel with head missing. (k) Impaled on a cactus thorn. (l) Cached intact high in a Palo verde tree; apparent talon holes atop head and under chin. (m) Cached intact in mistletoe with spine severed below cerebellum, apparently by single beak blow. (n) Apparent shrike kill, but carried atypically far from home range and eaten at atypically large perch.

Table III. Predation incurred by females versus males

	Animal-days	Known predation victims		Known + presumed victims	
		Number	Per animal-year	Number	Per animal-year
Females	3807	13	1.25	21	2.01
Males	2509	23	3.35	29	4.22

Table IV. Predation incurred in relation to reproductive condition

	Animal-days	Known predation victims		Known + presumed victims	
		Number	Per animal-year	Number	Per animal-year
Females					
Reproductive	1628	5	1.12	8	1.79
Non-reproductive	2179	8	1.34	13	2.18
Males					
Reproductive	1632	12	2.69	17	3.80
Non-reproductive	877	11	4.58	12	5.00

Differential Predation by Sex

Table III contrasts predation upon male versus female kangaroo rats. Given that males incurred 39.7% of the total time (animal-days) at risk of predation and females 60.3%, the probability that 23 or more of the 36 known victims would have been males by chance is 0.003 and the probability that 29 or more of the 50 'known plus presumed' victims would have been males by chance is 0.007 (binomial tests). 'Known plus presumed' predation rates upon males have surpassed those upon females in every one of the 9 years (November–July) of the study in which any predation events occurred ($P=0.002$ by sign test).

Differential Predation by Reproductive Condition

Kangaroo rats were categorized as either in or out of 'reproductive condition'. For males, the criterion of reproductive condition was either a conspicuous development of the androgen-dependent (Lepri & Randall 1983) dorsal sebaceous gland, or testes at least 8 mm in length (which, if withdrawn into the abdominal cavity, were forced into the scrotum by gentle manual pressure for measurement). Females were considered to be in reproductive condition if they exhibited oestrous cycling (see Wilson et al. 1985) or had recently done so, or

were conspicuously pregnant or lactating. According to these criteria, both females and males were preyed upon at slightly but not significantly higher rates when out of reproductive condition (Table IV).

As noted above, temporal clumping of predator activity adds noise to comparisons like those in Table IV, so that victims should be compared with non-victim contemporaries. Unfortunately, risk to reproductive versus non-reproductive animals cannot be assessed by such simultaneous comparisons because the study animals were in or out of reproductive condition in virtual synchrony, at least within sexes. However, males varied over time and between individuals in testicular development as measured by testis length, and activity measures are positively correlated with testis length across individual males in at least some breeding seasons (Behrends et al. 1986b); moreover, males known to have attained matings on our study site have consistently been males with relatively large testes as compared to their contemporaries (unpublished data). We thus compared the most recent testis length measure of each 'reproductive' male victim to those of all contemporaneously tracked 'reproductive' male survivors; results are directionally consistent with the hypothesis that activity associated with reproductive condition elevates risk, but not significantly so: 10 known or presumed predation

victims had larger than median testes and five had smaller ($P=0.15$; one-tailed sign test); one fell at the median and relevant measures were unavailable for one other.

The reproductive states of female victims were too variable for summary characterization and statistical comparison. Two animals (victims 12 and 26) were both in advanced states of pregnancy when last captured 5 days before their deaths, so both were probably killed near the date of parturition. Victim 5 had been in oestrus 17 days before her death and was therefore either pregnant or cycling. Victim 41 was about 17 days postpartum and lactating when killed by a shrike. Victim 10 had a copulatory plug 6 days before being killed by a whipsnake, and victim 39 had been in oestrus (but apparently did not copulate) 3 days before being killed by a shrike. Other 'reproductive' females (victims 7 and 8) were too infrequently captured and inspected to guess their condition when killed. Many more data will be needed to determine how risk varies in relation to particular reproductive states.

Differential Predation by Body Weight

Predation victims tended to be neither especially heavy nor especially light. Among the 29 known or presumed male victims, 11 were above the median body weight of contemporaneously tracked males, 14 were below it, and four fell at the median. Among the 21 females, 11 were heavier than the female median, eight lighter and two at the median. The absence of excess mortality of underweight individuals suggests that predation is not concentrated upon the feeble, but it is perhaps noteworthy that the sole animal originally captured with a serious deformity or injury was soon preyed upon: victim 10 was completely lacking one forepaw, and was killed by a whipsnake 45 days after initial capture and 11 days after radio implantation.

There was a slight tendency for kangaroo rats killed when in reproductive condition to be relatively heavy (13 above the contemporaneous same-sex median body weight, nine below, three at the median), and for those killed when not in reproductive condition to be relatively light (nine above the median, 13 below, three at the median). This pattern was not significant (one-tailed $P=0.18$ by Fisher's exact test), but suggests the hypothesis that kangaroo rats may modulate vulnerability behaviourally, such that animals with the greatest

energy reserves incur the least risk outside the reproductive season (when foraging is the principal reason for risk-taking) and the greatest risk when sociosexual agendas become paramount. A larger data set will be needed to confirm or reject this hypothesis.

DISCUSSION

Predation upon *D. merriami* is not selective for the feeble, but for the mobile. Prey species like kangaroo rats can reduce risk by minimizing surface activity, but by so doing they also reduce their foraging and mating opportunities. We have previously shown that reproductive condition is associated with greater mobility in both sexes (Behrends et al. 1986b), and we now find that mobility is strongly associated with elevated predation risk; furthermore, there was a slight though non-significant tendency for male predation victims to be individuals with larger than average testes. These facts suggest that risk-taking and resultant mortality are concomitants of reproductive effort. The hypothesis that predation risk is exacerbated by reproductive efforts in small mammals gains support from Madison's (1978) demonstration of elevated risk of snake predation upon reproductively active voles. It is therefore surprising that we found no hint of greater predation rates upon kangaroo rats in reproductive condition (Table IV). We tentatively attribute this anomaly to the non-independence of the predation incidents, but more data are needed to settle the matter.

In mating systems in which male fitness variance exceeds that of females ('effective polygyny'), the large fitness prize available to the most successful males selects for high mating effort (Williams 1966; Trivers 1972; Low 1978). In the case of mammals, this often means that home-range size and mortality are both greater for males than for 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 (but not those with testes regressed) traversed areas many times as large, overlapping with several females and with one another, and apparently incurred elevated predation risk (inferred from disappearances) by so doing. Such excess male mortality (at least in adulthood and perhaps among juveniles, too) probably characterizes most mammals (Trivers 1985).

Kangaroo rats, including *D. merriami*, are solitary dwellers, and over-dispersed in suitable habitat (e.g. Kenagy 1973; Behrends et al. 1986a; Randall 1989). There is no evidence of pair formation or paternal care in any member of the family Heteromyidae, and kangaroo rats of both sexes have been observed to mate polygamously in the field (Randall 1987 for *D. spectabilis* and *D. merriami*, and our unpublished observations for *D. merriami*). These facts suggest that *Dipodomys* spp. have a typically mammalian, effectively polygynous mating system, so that the sex difference in predation risk found in the present study (Table III) is unsurprising. The story is complicated, however, by the fact that several major retrapping studies indicate that sex differences in ranging behaviour are smaller and less reliable in the genus *Dipodomys* than in many other rodents (reviewed by Behrends et al. 1986a), and that the life tables of male and female kangaroo rats are surprisingly similar (Fitch 1948; Holdenried 1957; Chew & Butterworth 1964; M'Closkey 1972; McClenaghan 1984; Jones 1986; Zeng & Brown 1987a, b).

Longland & Jenkins (1987) sexed the pelvic bones found in great horned owl pellets in Nevada, and found some evidence of male-preferential predation upon *D. ordii*. Such data imply that the sexes differ in how they expose themselves to risk, but they cannot reveal sex differences in mortality. If equal numbers of females and males are weaned, for example, then an excess of one sex among those taken by owls implies that there must be an excess of the other sex dying in some other way, and tells us nothing about sex differences in life expectancy.

The data from retrapping studies cannot distinguish mortality from dispersal beyond trapability. In an analysis of the survival of *D. merriami* at an Arizona site, Zeng & Brown (1987a) claim to have solved this problem by using the distances between successive captures of individuals to calculate an estimate of the likelihood of dispersing and then subtracting dispersal from disappearances. The resultant 'accurate estimate of death rate' was 0.217 per year for females and 0.205 for males, an insignificant difference. We doubt that this method yields a more accurate estimate than the simple disappearance rates, since Zeng & Brown offer no evidence in support of their assumption that inter-capture distances are directly related to the probability or distance of dispersal (i.e. of relatively permanent shifts in home burrow sites or utilized ranges), and their estimates of survival are not

believable. According to the above death rates, 48% of the females and 50% of the males alive at time x would be expected to survive until time $x + 3$ years, for example, whereas in fact only three of 339 marked females and none of 443 males on their site are known to have survived 3 years (Zeng & Brown 1987b). In any case, this 8-year study of 782 marked *D. merriami* yielded statistically indistinguishable mortality schedules for females and males, as had all previous studies.

Similarly, the survival of males has apparently differed little from that of females at our site. Twenty of 135 females marked on the main trapping grid between 1981 and 1988 were known to be alive 1 year after first capture (14.8%), as compared to 16 of 145 males (11.0%). Four females and four males are known to have lived more than 2 years on our site, and two females are known to have lived more than 3 years.

Such similar year-to-year survivorship of females and males suggests that sex-differential mortality of the magnitude found during radio-tracking (Table III) cannot always prevail. One possibility is that the radios themselves elevate mortality risk more for males than for females, but there is no reason to suppose that this is so; if anything, radios should be slightly less burdensome for males, who are slightly larger (cf. Webster & Brooks 1980). A more likely hypothesis is that excess male mortality is especially characteristic of the season when most of our radio data were collected (i.e. just before and during the breeding season) and that the sex difference disappears or is reversed late in or after the breeding season. This possibility gains indirect support from the fact Behrends et al. (1986b) found that the travels of male *D. merriami* surpassed those of females only when the animals were in breeding condition.

Rosenzweig (1974) proposed a model to generate the 'optimal aboveground activity' of kangaroo rats. He assumed that predation risk will always be higher outside the burrow, and our observation of heavier predation upon relatively mobile individuals supports his assumption; other probable costs of surface activity are energetic and evaporative losses. Rosenzweig suggested that the countervailing benefits of surface activity include the immediate energetic gains of foraging, the more distal gains of territorial defence, and mating opportunities. Because most studies of the ecology of kangaroo rats have been concerned with the problem of what sort of specializations permit granivorous rodent

species to coexist, however, the social utility of above-ground activity has been overlooked since Rosenzweig's paper. Reichman (1983), for example, on the assumption that a well-adapted kangaroo rat should minimize surface time within the constraints of maintaining energy balance, deems it a puzzle that *D. merriami* do not make a single brief excursion nightly and return home only when their cheek-pouches are full; many other papers on *Dipodomys* ecology similarly embed the unexamined and unlikely assumption that surface activity has the sole function of foraging (e.g. Schroder 1979; Thompson 1982). But energy balance does not equal fitness, and the effects of reproductive condition upon surface activity (Behrends et al. 1986b), especially the extensive and risky travels of scrotal males and estrous females, suggest that a more satisfactory cost-benefit account of kangaroo rat surface activity will have to incorporate sociosexual benefits.

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