analysis without significantly affecting intestine weight or length. If the source of carcasses is unknown, then an analysis of small intestine weight, either as a measure of intestine size or to examine the effects of dietary, seasonal, sex, or age differences, should be treated with caution. If the same information can be gained by examining intestine length, this is preferred. Nevertheless, the results of studies from carcasses of unknown origin should always be interpreted with care, regardless of whether intestine length or intestine weight is reported. Also, length and weight changes in the intestine of live birds are not always correlated, so it should not be assumed that they are comparable measures of gross intestinal morphology (Kehoe et al. 1988).

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Sexually differentiated effects of radio transmitters on predation risk and behaviour in kangaroo rats *Dipodomys merriami*

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In a 12-year study involving 191 radio-tracked Merriam's kangaroo rats and 337 subcutaneous radio implantations, females were killed by predators at a rate of 0.0054 per radio-bearing night and males at a rate of 0.0116. Both the mortality rate and the sex difference therein declined over the course of several nights after radio implantation. Females reduced their excursions from the day burrow for the first few nights after radio implantation, whereas males exhibited little if any such inhibition of movement. This sexually differentiated behavioural response to the transmitters is a likely source of the sexually differentiated mortality patterns.

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Au cours d'une étude de 12 ans pendant lesquels 191 Rats-kangourous de Merriam ont été suivis par radio et ont subi au total 337 greffes sous-cutanées d'émetteurs radio, les femelles avaient un taux de mortalité dû aux prédateurs de 0,0054 et les mâles, de 0,0116 par nuit de port d'émetteur. Le taux de mortalité et son caractère dimorphique ont diminué progressivement au cours des nuits de port de radio émetteur. Les femelles ont fait moins d'excursions hors de leur terrier de jour au cours des premières nuits après l'installation de l'émetteur, alors que les mâles n'ont pas manifesté d'inhibition de leurs déplacements ou alors très peu. La réaction différente des mâles et des femelles à la présence d'un émetteur est une cause possible des patterns différents de mortalité chez les mâles et les femelles.

[Traduit par la rédaction]

Introduction

Radio tracking provides a unique window on the behaviour of cryptic animals in the field. The value of this technique is compromised, however, if the transmitters affect the study animals, especially if researchers are unaware of such effects.

The most popular technology for radio tracking small mammals (weighing less than about 60 g) entails attaching a 1- to 3-g package containing a radio transmitter and battery to the animal, by collar (e.g., Webster and Brooks 1980; Ormiston 1985; Schroder 1987; Pouliquen et al. 1990; Douglass 1992), subcutaneous implantation (e.g., Rawson and Hartline 1964; Daly et al. 1990), intraperitoneal implantation (e.g., Smith 1980; Madison et al. 1985; Gaulin and FitzGerald 1988), or gluing to the fur (e.g., Brooks and Banks 1971). Researchers addressing the question of possible impacts of such radio packages (e.g., Smith 1980; Webster and Brooks 1980; Madison et al. 1985; Ormiston 1985; Pouliquen et al. 1990; Douglass 1992) have generally found only slight, transient effects on behaviours such as wheel running or open-field activity, and no detectable effects on survival. None have reported sexually differentiated effects of radio-transmitter attachment.

Unfortunately, most studies have lacked either the numbers of subjects or the time necessary to achieve the statistical power that would impart a high probability of detecting even quite large (e.g., twofold) effects on such rare events as predation death, so the conclusion that radio attachment does not affect survival is premature (see White and Garrott 1990, pp. 28−35). Here we present evidence of sexually differentiated effects of radio transmitters on behaviour and on predation incurred by kangaroo rats during a 12-year study.

Methods

We radio tracked nocturnal desert-dwelling Merriam's kangaroo rats (*Dipodomys merriami*) at the Boyd Deep Canyon Desert Research Center, Palm Desert, California, for parts of each year from December 1980 to December 1991. For a description of the Boyd Reserve see Zabriskie (1979), and for a detailed description of our study site and field methods see Behrends et al. (1986a) and Daly et al. (1990).

During this study, there were 337 episodes in which a radio-transmitter package was subcutaneously implanted in a kangaroo rat and it was released in the field and radio tracked. Subject animals were captured in Sherman traps on a 1-ha square grid of 100 trap sites (see Daly et al. 1990 for trapping regimes) and transported 1.3 km to the laboratory, where radios were implanted under ketamine anaesthesia (0.8 mL/kg). We wetted a small area of fur about 2 cm lateral to the dorsal midline, made an incision about 3 cm long, inserted the transmitter, adjusted its position to avoid pressing on the spine, and applied sulfa powder to the wound and closed it with two to four small wound clips. The intraperitoneally injected anaesthesia took full effect in less than 5 min, and the operation then consumed about 4 min. Animals were typically upright and active in their holding cages within 30 min after the initial injection.

We used "mouse-style" transmitters (AVM Instrument Company,

Dublin, Calif., and Custom Electronics, Urbana, Ill.) soldered to a hearing-aid battery, "potted" in epoxy and thinly coated in beeswax to make a smooth package weighing 2.0−3.6 g. Subjects of the 337 implantation episodes were 191 individual kangaroo rats, 73 of whom were implanted more than once. When initially implanted, females weighed 34.7 ± 0.1 g (mean ± SE; range 28−45; $n = 97$) and males weighed 38.2 ± 0.1 g (range 30−46; $n = 94$). The radio package's weight constituted a mean of 7.4% (range 5−11%) of the animal's body weight.

In 242 of the 337 implantation episodes, the animal was released on the night of implantation, between 1 and 3 h after recovering from anaesthesia; in the other 95 episodes, release was delayed until the next evening, between 16 and 23 h after implantation. Durations of radio-bearing by individual kangaroo rats ranged from a minimum of less than 6 h between release and death by predation to a maximum of 281 radio-nights and 9 implantation episodes over a 39-month period. The mean duration of the 337 episodes (i.e., time from implantation to radio removal or death) was 19.8 days.

Behavioural measures in our study were derived from daily location of the radio-bearing animals' day burrows, from scheduled hourly nocturnal locations, and from direct observation under dim headlamp illumination during scheduled focal follows (Behrends et al. 1986a, 1986b; Daly et al. 1990).

Results

Fifty-two kangaroo rats were predation victims while bearing a radio (Table 1). Males suffered more than twice the death rate of females ($p = 0.004$ by binomial test). The identity of the predators, characteristics of the victims, and circumstances of predation are described in Daly et al. (1990, 1992).

Rates of death by predation varied as a function of the time since radio implantation, with both sexes, but especially males, being especially vulnerable during the first few nights (Fig. 1). Combining the sexes, the predation rate of 0.0137 per night during the first 4-day block significantly exceeded the rate of 0.0063 for all subsequent days ($p = 0.008$ by binomial test); moreover, the predation rate of 0.0101 during the second 4-day block was more than twice the rate of 0.0053 for all subsequent days ($p = 0.057$ by binomial test).

It is difficult to assess the effects of bearing a radio on behavioural measures in the absence of comparable data from animals without radios. As with predation, however, the influence of the radio is apparent in the form of changes over time after radio implantation. Kangaroo rats, especially females, exhibited some initial suppression of aboveground activity when newly radio implanted (Fig. 2). For females there were 160 implantation episodes in which nocturnal radio data were collected in each of the first two 4-day blocks. The proportion of scheduled hourly nocturnal locations in which the female was away from her day burrow increased between blocks in 103 cases, decreased in 48 ($p < 0.001$ by one-tailed sign test), and remained unchanged in 9; moreover, this proportion increased monotonically across six 4-day blocks (one-tailed

Table 1. Summary statistics on kangaroo rats radio tracked at a California field site, 1980–1991

|	Females	Males
No. of kangaroo rats radio tracked	97	94
No. radio implanted more than once	46	27
No. of radio-implantation episodes	198	139
Total animal-nights bearing a radio in the field	4 081	2 590
Mean duration of implantation episodes (days)	20.6	18.6
No. of nocturnal hourly radio locations	15 434	10 418
No. of deaths by predation while bearing a radio	22	30
Predation rate per radio-bearing night	0.0054	0.0116
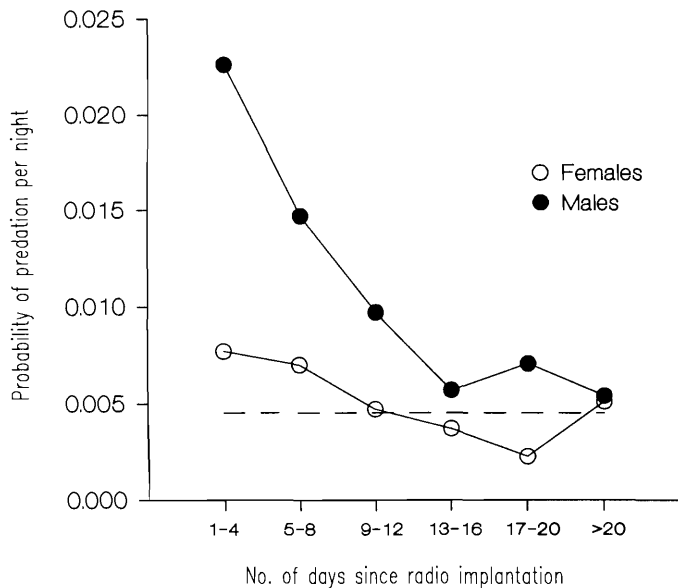
Fig. 1. Predation rates upon radio-implanted kangaroo rats as a function of the victim's sex and of the time elapsed since radio implantation. The figure is based on 52 predation deaths and 337 radio implantations between 1980 and 1991. The broken line represents the estimated predation rate on unimplanted animals (see text).
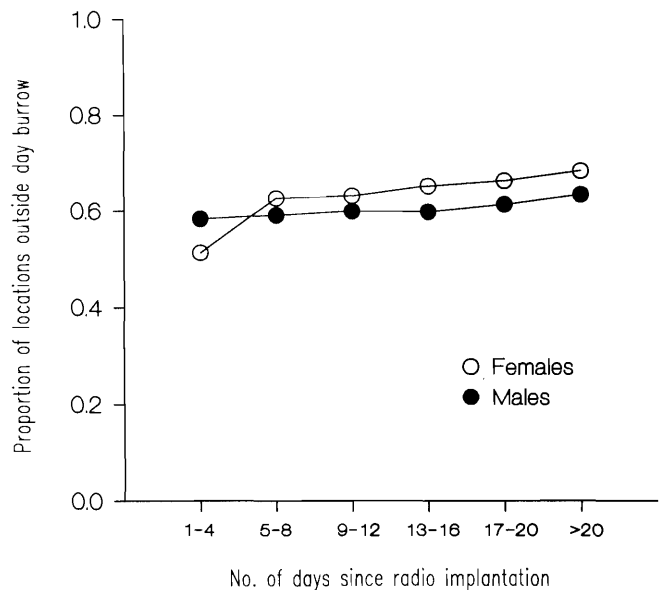

Fig. 2. The probability that a radio-implanted kangaroo rat would be outside its day burrow at the time of a scheduled nocturnal radio location, as a function of sex and time elapsed since radio implantation. The figure is based on 25 852 nocturnal radio locations (scheduled no more than once per hour) and 337 radio implantations between 1980 and 1991.

$p = 0.001$, using rank correlation as a trend test). A similar response was less pronounced in males. The proportion of locations outside the day burrow increased from the first to the second 4-day block in 61 cases, decreased in 49 ($p = 0.15$ by one-tailed sign test), and remained unchanged in 4; this proportion also increased significantly across 4-day blocks (one-tailed $p = 0.008$, using rank correlation as a trend test). The 103:48 division between females who increased versus decreased their extra-burrow activity differs significantly from the corresponding 61:49 division of the males ($\chi^2 = 4.44$, df $= 1$, $p = 0.03$).

Discussion

Estimation of the overall impact of radios on survival depends on estimation of the death rate incurred by control animals. A gross estimate is provided by the observed year-to-year survival of kangaroo rats when not radio implanted. During annual winter trapping seasons (within 5 weeks of the winter solstice), there were 153 instances in which kangaroo rats were trapped on our grid in a given year and released unimplanted, so they might have survived until the next winter.

Fifteen of 72 females (0.208) of 20 of 81 males (0.247) were recaptured the next year. These proportions constitute minimum estimates of the numbers of females and males actually surviving from year to year, for although there is no evidence that adult *D. merriami* disperse or become trap-shy, so that survivors would have gone undetected, these possibilities cannot be eliminated. The daily survival rates that would produce "annual" survival (actually an average requisite survival of 330 days) rates of 0.208 and 0.247 are 0.9953 and 0.9958, respectively (i.e., $0.208 = 0.9953^{330}$, and $0.247 = 0.9958^{330}$). Hence the estimated daily "death" (disappearance) rates for unimplanted animals are 0.0047 ($1.0 - 0.9953$) for females and 0.0042 ($1.0 - 0.9958$) for males, a nonsignificant difference. Other data sets confirm nearly identical survivorship of the sexes in this species (e.g., Zeng and Brown 1987), and remarkably similar male and female life tables appear to be characteristic of the genus *Dipodomys* (see references in Daly et al. 1990).

Combining the sexes, the observed daily death rate for radio-implanted kangaroo rats (0.0078) was 1.7 times the estimated daily death rate of nonimplanted animals (0.0045).

According to this estimation procedure, excess mortality was incurred mainly by males: the observed death rate of radio-bearing females (Table 1) was only 1.1 times that estimated for nonimplanted females, whereas the observed death rate for radio-bearing males was 2.7 times that estimated for non-implanted males. Such estimation of the excess risk associated with radio implantation is problematic for several reasons, however. Daily death rates are unlikely to be invariant through-out the year; radio-implanted animals were often those most reliably trapped and (or) centrally located rather than a random subset; and unimplanted animals may survive better than retrapping data reveal. Conclusive evidence for an effect of radios is therefore not to be found in the gross predation rate but rather in the temporal pattern of changing predation risk shown in Fig. 1.

We doubt that the temporal patterns portrayed in Figs. 1 and 2 can be attributed to trauma from the implanting procedure. Extensive laboratory experience indicates that the effects of ketamine anaesthesia have fully dissipated within a few hours at most, and incisions heal in less than a day, yet postimplantation effects extended at least into the second 4-day block. One possibility is that this temporal pattern reflects a gradual process of kinaesthetic accommodation to the subcutaneous transmitter load, with attendant gradual recovery of maximal speed and agility. (As open-habitat foraging specialists, kangaroo rats probably rely less on crypticity and more on agility to escape predators than do most rodents; see Nikolai and Bramble 1983.) Our subcutaneous implants usually settled into position away from the animal's midline, so the load's asymmetry may have exacerbated the task of accommodating to it. If this is so, other transmitter attachment procedures that distribute the load more symmetrically might permit more rapid accommodation. However, collars have sometimes been found to suppress activity for several days after attachment, too (e.g., Hamley and Falls 1975; Webster and Brooks 1980). The hypothesis of gradual kinaesthetic accommodation can be assessed with captive animals, but this will require finer behavioural measures than have hitherto been employed.

Researchers eager to affirm the utility of radio tracking are often tempted to assert the null hypothesis that the procedure is neutral (White and Garrott 1990). Pouliquen et al. (1990), for example, concluded that "there were no adverse effects... on survival" on the basis of a study involving fewer than 200 animal-days of radio bearing in the field, and Douglass (1992) suggested that "telemetry techniques seem to have little negative effect on survival of rodents" on the basis of even fewer animal-days. However, predation is a sufficiently infrequent event that even quite large effects upon the rate at which it occurs could escape detection by such procedures. For example, in the present study, radio-implanted kangaroo rats incurred one predation death per 128 animal-days of radio bearing; if this represented a doubling of predation risk (a very large effect), one would need a data set containing thousands of animal-days with versus without radios to demonstrate the effect significantly. Thus, the fact that the present study demonstrated effects of radio implantation on death rates, while others have demonstrated no such effects of radio collaring, cannot be taken to imply that collars are relatively benign. More study is needed.

The sex difference shown in Fig. 1 seems to imply that radios raise the predation risk solely or more extremely in the case of males. Daly et al. (1990) noted that the sex difference in the mortality of radio bearers seemingly contradicts sur-

vivorship data from both this and other studies of *D. merriami*. Doubting that the radios could be more burdensome to the larger sex, Daly et al. (1990) hypothesized that death rates of males exceed those of females before and early in the breeding season, when our radio-tracking efforts have been concentrated, and that sex-differential mortality is reversed later. However, the present analyses suggest that excess male mortality may indeed reflect a differential influence of radios after all, at least in part: females manifest an increased cautiousness while adjusting to the novelty of an implanted radio, whereas males show little such effect (Fig. 2). This sexually differentiated behavioural response to the transmitters is a likely source of the sexually differentiated mortality patterns portrayed in Fig. 1.

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