SPATIOTEMPORAL ACTIVITY PATTERNS
OF
MERRIAM KANGAROO RATS (*DIPODOMYS MERRIAMI*)

By

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ABSTRACT

Using radiotelemetry, the spatiotemporal surface activity patterns of the Merriam kangaroo rat (Dipodomys merriami) were studied in relation to several physiological and ecological factors. It was found that males were more active than females during the breeding season but not otherwise. Females' surface activity varied in relation to reproductive condition with estrous females most active, pregnant and lactating females intermediate, and anestrous females least active. D. merriami home range sizes were sexually monomorphic in all seasons and ranged in size from 0.03 to 1.16 ha. The majority of activity, however, was restricted to an area of about 0.03 ha. Animals exhibited substantial range overlap with females overlapping males more than other females. No difference was apparent for males. Ranges remained relatively stable in location with only a few animals making substantial shifts. Day burrows, of which animals used several, were regularly distributed so that nearest-neighbors tended to be at maximal distances. As with spatial overlap, females' nearest-neighbors tended to be males.

These findings contribute to the natural history of D. merriami and to the study of small mammal social systems. These findings also suggest that this species may have a more complex social structure than heretofore thought.

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Chapter I

Precis

This thesis examines the behavior patterns of free-ranging Merriam kangaroo rats (Dipodomys merriami) emphasizing the socio-ecological approach to the study of mammalian social systems. In this brief chapter I will present the rationale and underlying assumptions of this study and a precis of the chapters to follow.

Until recently the natural behavior patterns and social systems of small, free-ranging mammals such as rodents were relatively unknown due to their often cryptic and usually nocturnal habits. The development of radiotelemetry, however, made it feasible to concurrently monitor the spatio-temporal patterns of a small population of individuals, thus providing a crucial data base for the study of social structure. As a result of this technological breakthrough, several studies have provided new insight into the diversity of the spatiotemporal activities and social behavior in several rodent species (e.g. Brooks and Banks, 1971; Banks, Brooks, and Schnell, 1975; Mineau and Madison, 1977; Madison, 1978a,b,c; Schroder, 1979).

The Merriam kangaroo rat is a burrow-dwelling, nocturnal rodent of the family Heteromyidae ubiquitous in the arid southwest of North America. This species' physiological adaptations to the desert environment and its role in desert community ecology are well-studied, yet little is known about its intraspecific behavior in relation to physiological and environmental factors. Furthermore, virtually nothing is known about how individual behavioral variation in this species may reflect different adaptive strategies by animals differing in sex, reproductive condition, and age- or size-class or how different strategies function in the context of this species' social organization.

The structure and function of mammalian social systems has long been an important problem for workers in animal behavior, but only recently has significant theoretical progress been made linking Darwinian natural selection to the formation of various types of systems. A promising avenue of research is the socio-ecological approach which, as outlined by Crook, Ellis, and Goss-Custard (1976), considers social structure to be the product of the complex interactions between the adaptive behavioral strategies of individuals for resource exploitation, predator avoidance, and mating and rearing of progeny. The type of social system exhibited by any particular species or, indeed, a local population will be limited by intrinsic (species) and extrinsic (environmental) parameters. The former may include the intensity and duration of parental care, risk of predation, body size, mobility, and foraging and feeding patterns while the latter may include spatial and temporal distribution and/or density of resources and the density and/or distribution of potential predators.

The socio-ecological approach is comparative by nature; inter- and intraspecific variations in social systems are interpreted as adaptations to different ecological circumstances. This method has been used to identify significant relationships between social structures and intrinsic and extrinsic parameters in primates (Crook, 1970; Clutton-Brock, 1974), birds (Crook, 1964), African antelope (Jarman, 1974), and Saharan gerbils (Daly and Daly, 1975). This thesis is not a socio-ecological analysis of D. merriami social organization *per se*, but rather provides basic information which should contribute to subsequent socio-ecological analyses of small mammal social systems. A more detailed application of the socio-ecological approach to kangaroo rat social systems will presented in later chapters.

In the following chapters I will describe several aspects of Merriam kangaroo rat natural history and spatio-temporal activity patterns in relation to a variety of physiological and environmental factors. Where the data warrant, the attempt will be made to generate conceptual statements or hypotheses about the factors influencing behavior in terms of theories of life history tactics and/or socio-ecology. Obviously the natural behavior of most animal species is under multifactorial control and these factors are often difficult to separate, especially in a field situation. A strength of the socio-ecological approach, however, is that it considers the entire ecological milieu as providing the context for behavioral adaptation and, as a consequence, the organism is viewed as a compromise design. Also, it is hoped that by assuming multifactorial control of behavior excessive reductionism, which may occur when behavior is partitioned and considered out of its ecological context, will be avoided (See Gould and Lewontin, 1979 and Mayr, 1983 for arguments about the study of adaptation and the problems of biological reductionism).

Chapter 2 presents a general review of the literature on kangaroo rats regarding their morphological and behavioral adaptations to desert existence and their habitat and resource use. In this chapter, I discuss several topics including body size, mobility, possible mechanisms for predator avoidance, physiological regulation, habitat preferences, and foraging and feeding habits. This information lays the groundwork for later discussions of spatiotemporal patterns and social structure. Parenthetically, it should be noted here that statements about the relationships between behavioral patterns, for example predator avoidance and social structure, do not imply phylogenetic causality. Rather, it is assumed that the different selection pressures impinging on an individual form a complexly interwoven feedback system. Although it is difficult to specify causal patterns, consistent relationships between some behaviors should be apparent. For example, kangaroo rats are highly mobile and thus have the capacity for large home or cruising ranges. Hence, mobility has ramifications for how animals space themselves, how they exploit their habitat, and whether resources, including potential mates, are economically defendable.

Chapter 3 contains the methods for the laboratory and field studies discussed in Chapters 4 through 7. This chapter includes descriptions of the animals used, the field study sites, equipment, and procedures for data collection. A separate methods chapter is included to avoid redundancy between chapters and to provide a convenient reference for the reader.

In Chapter 4 I describe the reproductive activity of Merriam kangaroo rats in the laboratory and the field. The mating and rearing habits of this species including the reproductive physiology, growth and development, sexual maturation, and initial emergence from the natal burrow are considered in the context of life history tactics. How these reproductive traits may reflect adaptation to existence in an unpredictably fluctuating environment is discussed.

Chapter 5 focuses on the spatiotemporal activity patterns of this species with particular emphasis on how patterns of surface activity including relative distances moved and time on the surface are related to sex and reproduction. These relationships will be considered from a cost-benefit perspective in which behavior (e.g. surface activity) is assumed to vary in net benefit (or cost) in accordance with factors such as risk of mortality, resource availability, or reproductive state. An interesting question, for example, is whether reproductively active animals take more "risks" than non-reproductive animals through increased surface activity and presumably greater exposure to predators or climatic stresses. Another concern of this chapter is whether individuals have such different surface activity patterns that a description of so-called "species-typical" ranging behavior is misleading.

Chapter 6 examines the temporal patterns of D. merriami surface activity. I also consider the influence of several environmental factors on surface activity including moonlight, air temperature, and precipitation in this chapter. For example, natural selection may operate on surface activity under moonlight if moonlight increases the risk of predation. The evidence for a moonlight effect on kangaroo rats, however, is equivocal (Lockard and Owings, 1974b; Schroder, 1979). I present evidence supporting the notion that these animals should be sensitive to moonlight. Air temperature should influence surface activity if animals are sensitive to the energetic costs of surface activity (e.g. thermoregulation).

In Chapter 7, I turn to the spatial relationships between conspecific individuals. The primary concern here is how individuals space themselves; how ranges are used, the extent of spatial overlap in ranges, and how range parameters vary in relation to such factors as sex, reproduction, and season. Included in this chapter are some descriptions of observed social encounters between conspecifics in the field and their relevance to questions about the degree of intraspecific aggression and territoriality.

In Chapter 8 I attempt to collate the diverse findings of this thesis and present a general description of _D. merriami_ socio-ecology. The relationships between reproduction parameters (i.e. life history tactics), social behavior, and ranging behavior are discussed.

Chapter II

A General Review

Introduction

Many aspects of the natural history of kangaroo rats (*Dipodomys* spp.) and their physiological, morphological, and behavioral adaptations to harsh and unpredictable desert environments have been studied. This genus and the family *Heteromyidae* in general have been of particular interest to workers in physiology, evolutionary biology, and ecology with the result that these rodents stand among the most thoroughly studied in North America. This chapter includes a synopsis of what is known about the general habits of kangaroo rats in the field, a brief selective review of kangaroo adaptations to arid and semiarid habitats, and a selective review of the literature concerning their putative role in desert community ecology. The information presented in this chapter provides a general background from which to examine data presented later.

Distribution and General Description of Kangaroo Rats

There are 21 extant kangaroo rat species distributed throughout the arid and semiarid regions of western North

America and northern Mexico (Burt and Grossenheider, 1976). This genus is generally considered to be desert-adapted (e.g. needing little or no free water to survive) but the various species are found in a range of habitats with respect to rainfall and flora, from the relatively wet Pacific Coast Range (e.g. _D. agilis_ and _D. venustus_) to the extremely hot and arid Colorado and Sonoran Deserts (e.g. _D. merriami_ and _D. deserti_) (Burt and Grossenheider, 1976). Nonetheless, kangaroo rats are a relatively homogeneous group morphologically, physiologically, and behaviorally. Both the common name 'Kangaroo rat' and the genus name '_Dipodomys_', which derives from the Latin _dipodia_ meaning 'two feet', accurately describe the outstanding feature of this genus. These animals possess relatively large rear legs which enable them to move bipedally in a saltatory fashion across open ground. But kangaroo rat species and other quadrupedal and bipedal heteromyid species (e.g. pocket mice and kangaroo mice respectively) also share several other characteristics. All are primarily granivorous (with the exception of _D. microps_ which feeds on saltbush leaves, _Atriplex confertifolia_, when available; Kenagy, 1972,1973b; Csuti, 1979), nocturnal, and burrow-dwelling in their habits and all possess external fur-lined cheek pouches used for transporting seeds and other foods (e.g. green vegetation or insects) back to their home burrows or shallow food caches established nearby.

Field studies indicate that kangaroo rats are active on the surface throughout the year despite the fact that soil surface temperatures may range from 0 to 50°C during their active periods. Pocket mice (Perognathus spp.) and kangaroo mice (Microdipodops spp.), on the other hand, become dormant or torpid in the winter months in response to cold stress or poor food resource conditions (Carpenter, 1966; Kenagy, 1976a, 1973a; O'Farrell, 1974). There is some evidence, however, that D. merriami too may enter torpor during extreme cold in the field (Mullen, 1971) and this state has been induced by cold stress and food deprivation in the laboratory (Yousef and Dill, 1971).

D. merriami, the subject of this thesis, is the smallest member (30-50 g) of the genus Dipodomys which includes species as large as 180 g (D. ingens). D. merriami, found in the driest regions of this genus' range, is one of the most widely-distributed kangaroo rats. For this reason, and because it is one of the kangaroo rat species with the capacity to thrive on a diet of dry seeds only, D. merriami, is the best-studied member of this genus.

Morphological Adaptations of Kangaroo Rats

Bipedalism: Bartholomew and Caswell (1951) suggested that saltatorial bipedal locomotion by rodents inhabiting a sparse environment is advantageous for reasons related to foraging efficiency and predator avoidance. Saltatorial locomotion enables an animal to move across open, sparsely vegetated ground much more quickly (at least 32 km/h for D. merriami, Kenagy 1973a) than quadrupedal locomotion. Consequently, an animal can move between widely scattered food patches efficiently and minimize the amount of time spent in open areas and the time spent engaged in foraging activities. Presumably this adaptation reduces predation risk and exposure to climatic stress. Its powerful rear legs also enable the kangaroo rat to elude predators including owls, shrikes, snakes, and coyotes by leaping and ricocheting off the substrate, rocks, and shrubs in an erratic manner. It seems clear that bipedalism serves some adaptive function(s) for desert existence because nearly all bipedal hopping mammals are inhabitants of arid environments. But whether the hypothesized adaptive functions of bipedalism are the actual ones remains untested.

In contrast to explanations for bipedalism based on foraging efficiency and predator avoidance, it has been suggested that bipedalism confers savings in the energetic costs of locomotion (Dawson and Taylor, 1973). It is well established in quadrupeds that running speed and oxygen consumption (VO_2) are positively correlated up to the attainment of maximum aerobic capacity. For bipedal hopping mammals, however, there is some evidence that VO_2 becomes independent of speed prior to attainment of maximum aerobic capacity resulting in energy savings at higher speeds (Dawson and Taylor, 1973; Dawson, 1975). Thus in certain desert communities where competition for food resources may be severe, animals capable of exploiting scattered food patches as a result of lower locomotion costs should be at a selective advantage.

Thompson et al. (1980), however, failed to demonstrate that bipedal hopping by kangaroo rats conferred energetic savings. This failure to demonstrate the energetic advantages of bipedal hopping must be treated with caution, though, because of the theoretical and methodological difficulties associated with this study. Although the theoretical difficulties are beyond the scope of this discussion, Thompson (1980) points out that the standard equations used to predict VO_2 from body size may have been inadequate for this genus. Furthermore, difficulties were encountered in training kangaroo rats to hop on the standard type of treadmill used for metabolism studies resulting in measurements for a very limited range of speeds. For instance, at speeds greater than 6.2 km/h for D. deserti and 3.3 km/h for D. merriami subjects began to break stride and "ride" the treadmill. Thus the obtained measures of VO_2 are of questionable validity. Hence, it remains unknown whether bipedalism is a cost-efficient mode of locomotion in the field.

Auditory Specialization: A distinctive feature of kangaroo rats is a large cranium resulting from their relatively large metatarsal bullae. Kangaroo rats possess an enlarged middle-ear cavity, which through the increased size of the tympanic membrane, mechanically enhances low frequency sound sensitivity. The increased size of the tympanic membrane reduces its damping effect and thus resonance is facilitated. Webster (1962) determined D. merriami peak auditory sensitivity to be at 1400, 1800-2200, and 2600 cps. Webster also investigated the potential adaptive value of low frequency sound sensitivity in kangaroo rats by exposing animals with bilaterally reduced middle-ear cavity volumes and intact controls to two natural predators: an owl and a sidewinder rattlesnake. All deafened animals were killed by the predators whereas two of the four intact controls successfully avoided the owl and all eluded the snake. Interestingly, none of the deafened animals attempted to escape from the predators. Control tests indicated that this lack of escape behavior resulted from surgical deafening rather than deficits in locomotion. To support the hypothesis that low frequency sensitivity may be an adaptation for predator avoidance, Webster showed that the sounds of attacking owls in flight contained frequencies around 1200 cps and those of a striking rattlesnake contained frequencies around 2000 cps. These frequencies fall within the range of D. merriami peak auditory sensitivity.

It is conceivable that low frequency sensitivity by kangaroo rats may serve a social function also. Kenagy (1976b) observed footdrumming by D. microps in the field and D. merriami sometimes footdrum in captivity (Per. Obs.). What communicative function, if any, footdrumming serves in the field remains unknown.

Physiological Adaptations

Water and Heat Regulation: Kangaroo rats are perhaps most famous for their water conservation capabilities. A series of studies culminating in a major review of the water metabolism of desert mammals by Schmidt-Nielsen (1964) indicated that kangaroo rats (D. merriami as the main subject) conserved water in several ways. They conserve water behaviorally by occupying burrows during daylight hours, thus avoiding high temperatures which would otherwise force them to expend water for heat regulation (e.g. through panting, sweating, or salivation and self-licking). Subsequent studies by Carpenter (1966) on D. merriami and D. agilis and Kenagy (1973a) on D. merriami and D. microps showed that maximum temperatures in the nest chamber or wherever the animal happens to be resting in the burrow system probably do not exceed the lower end of thermoneutrality (about 30°C for kangaroo rats; Dawson, 1955). The lower critical temperature of thermoneutrality may shift upward several degrees between winter and summer and thus allow for some fluctuations in burrow temperatures without causing temperature stress (Hayworth and Behrends, unpublished data). A more direct physiological adaptation by kangaroo rats to water stress and heat is that their evaporative water loss is much lower than that of other mammals when corrected for mass, e.g. 50% that of the white rat (Schmidt-Nielsen and Schmidt-Nielsen, 1952; Soholt *et al.*, 1977). This is probably due to their relatively low basal metabolic rate which is only 70% of that predicted for a mammal of the same mass (Dawson, 1955; McNab, 1979,1970). Additionally, the kangaroo rat produces low volumes of highly concentrated urine and its feces are much lower in moisture content in comparison to the white rat's (Schmidt-Nielsen and Schmidt-Nielsen, 1952; Schmidt-Nielsen, 1964). Finally, since kangaroo rats inhabiting extremely arid regions (e.g. *D. merriami*, *D. spectabilis*, and *D. deserti*) are so efficient in conserving water, much of their water requirements are satisfied by oxidative or metabolic water in conjunction with the moisture content of the seeds and herbaceous material they consume (Schmidt-Nielsen, 1964). Schmidt-Nielsen determined that only under very low humidity conditions (<10%) would kangaroo rats suffer negative water balance, an unusual condition in even the hottest and driest deserts.

Kangaroo rat species are distributed throughout a diverse range of habitats, from the mesic Pacific Coast Range to the xeric desert. Consequently, one might expect interspecific differences in the capacity to tolerate water stress. Indeed, Sork (1978) demonstrated that different species exhibited varying abilities to concentrate urine in a way negatively correlated with available vegetation. Moreover, studies have shown that sympatric species which differ in their feeding ecologies also utilize water differently. Investigators looking at tritiated water turnover rate in the laboratory (Yousef _et al_., 1974) and in the field (Mullen, 1971) found that the folivore, _D_. _microps_, had a 60% greater water turnover rate than the granivore, _D_. _merriami_. _D_. _microps_ urine concentration is the lowest reported for the genus and these animals will succumb within a month if placed on a diet of dry seeds without free water or succulent vegetation, unlike _D_. _merriami_ who thrive indefinitely on the same regime (Kenagy, 1973b).

Heteromyid Community Ecology and Foraging Behavior

Information about the natural ranging and foraging behavior of kangaroo rats is scant because detailed field observations are difficult to carry out. What little is known about these animals comes from studies of desert community ecology which focus on the mechanisms of successful coexistence by several heteromyid species (e.g. Brown, Reichman, and Davidson, 1979). A brief examination of this literature is presented (1) to establish the basic patterns of kangaroo habitat and resource use and (2) to point out some of the weaknesses of indirect, nonobservational field techniques traditionally used to draw inferences about the behavior of these animals.

Desert ecosystems have proven to be useful for testing theories of how competition for resources by morphologically and behaviorally similar species may shape and/or maintain animal communities. The question posed by competition theorists is how desert granivores partition resources so that several species manage to coexist (Brown _et al._, 1979). This point is important for this thesis because interspecific competition may set limits on the extent of intraspecific phenotypic variation. A central idea of community ecology is that severe interspecific competition will lead to and maintain relatively specialized phenotypes capable of exploiting resources at a high level of efficiency (Rosenzweig, 1981). Conversely, relaxation of competition should result in ecological or niche release in species which are flexible phenotypically or have retained enough genetic variation to produce phenotypes capable of exploiting newly available resources.

In most parts of their range, kangaroo rats are sympatric (geographical co-occurrence) with at least two or three and sometimes as many as six or seven potential competitors, usually pocket mice (Perognathus spp.) and often other kangaroo rat species. There are three reasonably well-established characteristics of heteromyid communities which are consistent with competition-based hypotheses about interspecific coexistence: (1) a structured scale of body mass differences between species, (2) habitat partitioning, and (3) resource partitioning. It will be apparent that these characteristics, though different in their focus, are highly interrelated.

Body Mass Relationships: In heteromyid communities there are consistent differences in the body masses of different species which follow a mass ratio of 1.5 between a species and the next heaviest member of the community (Bowers and Brown, 1982). This relationship may reflect the successful partitioning of food resources by animals of different body mass and, consequently, different energetic requirements. An implication of this relationship is that competition should restrict intraspecific phenotypic variation in body mass and prevent invasion of an existing community by species too similar in mass to residents.

Habitat Partitioning: Bartholomew and Caswell (1951) suggested that saltatorial bipedal locomotion by kangaroo rats was an adaptation for traversing sparsely vegetated areas quickly to minimize predation risk. Recent investigations of habitat partitioning by heteromyid communities support the hypothesis that kangaroo rats utilize open areas and that quadrupedal pocket mice utilize areas around the dense canopy of shrubs. The evidence for habitat partitioning by these two genera is based on two field techniques: (1) live-trapping in different microhabitats (ecologically different areas within a habitat as defined quantitatively or qualitatively by vegetation type or density, soil differences, etc.) and (2) providing seeds labelled with a tracer (e.g. dye or isotopes) in different microhabitats and determining utilization by different species.

Studies have demonstrated that several kangaroo rat species (e.g. *D. deserti*, *D. merriami*, *D. ordii*, and *D. spectabilis*) are likelier to be trapped in open, sparsely vegetated areas and that, in general, pocket mice are likelier to be trapped around shrubs or in more densely vegetated habitats (Rosenzweig and Winakur, 1969; Brown, 1973; Brown and Lieberman, 1973; Rosenzweig, 1973; Congden, 1974; Schroder and Rosenzweig, 1975; Lemen and Rosenzweig, 1978; M'Closkey, 1980; Price, 1978a; Thompson, 1982a,b). Experimental manipulations of vegetative cover demonstrate increases in kangaroo rats and decreases in pocket mice when vegetation is removed and the opposite when vegetation is augmented (Rosenzweig, 1973; Price, 1978a).

Natural observations and experimental studies of seed utilization also support the notion that kangaroo rats utilize open areas and pocket mice utilize areas with denser vegetation. Based on the seed contents of cheek pouches and the assumption that this measure reflects microhabitat use, M'Closkey (1980) determined that D. merriami utilized microhabitats without large shrubs. Wondolleck (1978) placed dyed seeds in four different microhabitats and found that D. merriami concentrated on seeds from open microhabitats whereas pocket mice took seeds placed around vegetation. Lemen and Rosenzweig (1978) placed seeds marked with various isotopes in different microhabitats and found that D. ordii avoided dense grass.

If different heteromyid species do coexist in part because of habitat partitioning, an important question is whether competition serves as a proximate mechanism to maintain habitat partitioning or whether, as a consequence of competition, microhabitat selection has become a relatively permanent feature of the species. One technique to test whether the presence of potential competitors restricts a species from utilizing other microhabitats is to remove or add competitors in a controlled environment and monitor the subsequent presence of a species in the different microhabitats. Price (1978a) found that heteromyid species shifted their presence in microhabitats in the predicted directions when competitors were added or removed. That is, in the absence of typical competitors, animals expanded their activity to previously little-used microhabitats. This evidence suggests that at least some heteromyid species may be facultative habitat selectors and that competition may serve proximally to separate species. The study by Price was conducted in a large outdoor enclosure where the population densities of the different species were carefully controlled and immigration by outside animals was eliminated. A study of habitat utilization and competition by sympatric _D_. _merriami_ and _D_. _ordii_ conducted by Schroder and Rosenzweig (1975), in which immigration control was not possible, yielded a different result. Before removal of segments of the population of one of the two species on different sites, _D_. _ordii_ were mainly trapped in overgrazed grassland areas and _D_. _merriami_ in immediately adjacent creosote-shrub associations (a much sparser habitat). After removal of a substantial proportion of one of the two species, there was no evidence of habitat invasion by the unmanipulated species. The manipulation simply resulted in an influx of previously untrapped and presumably transient conspecifics.

These conflicting results are not surprising in light of the methodological differences between the two studies. But the differences also point out the difficulty in generalizing about the role of interspecific competition in maintaining communities. Factors such as intraspecific competition, species diversity, and habitat diversity are important considerations. The role of competition, if indeed, it is an important factor in structuring and maintaining communities, is likely to vary from community to community. At this point, it is reasonable to assume that heteromyid species have diverged morphologically and behaviorally to the extent of being relatively specialized habitat selectors. Under relaxed ecological conditions, however, these species may utilize marginal habitats; i.e. they may be rather opportunistic when the costs are low.

All of the studies cited thus far conclude that kangaroo rats utilize open areas and pocket mice restrict themselves to areas around shrubs. The evidence seems compelling since there are no contrary results from studies using trapping or seed utilization techniques. However, evidence based on these field methods may indicate only that kangaroo rats are likelier than pocket mice to traverse open areas and that seeds fortuitously encountered in transit are utilized. There is no direct evidence, based on these studies, that kangaroo rats preferentially utilize open areas. To the contrary, Thompson (1982a) directly observed the foraging activities (slow, quadrupedal locomotion, digging, and gleaning) of free-living D. deserti, D. merriami, and the much smaller Perognathus longimembris (7-9 g). The foraging activity of the kangaroo rats was only slightly less confined to areas around the protective canopy of shrubs compared to the pocket mouse (75% vs. 89%). Kangaroo rats did tend to traverse open areas more than the pocket mice but these movements were between shrubs. Thompson suggests that the morphological differences between kangaroo rats and pocket mice are reflected by their foraging differences. The greater body size of the kangaroo rat necessitates movements between shrubs in search of high yield food patches whereas the smaller pocket mouse is energetically satisfied by foraging around a few shrubs. These data must be treated with caution too, however, because Thompson approached to within 10-20 meters of the focal animal for his observations. The close presence of a human observer may bias the spatial activity of the animal (Pers. Obs.). Furthermore, it is difficult to discriminate between behaviors such as sniffing and gleaning by a free-ranging kangaroo rat or pocket mouse from a distance of 10-20 meters (Pers. Obs.). Unfortunately, Thompson did not establish the reliability of his observations.

Resource Partitioning: Another possible mechanism for the coexistence of heteromyid communities is that different species may concentrate on different food types or dispersions. Analysis of seeds collected from the cheek pouches of wild-trapped heteromyids indicated a positive correlation between the size of the seed and heteromyid body mass (Brown and Lieberman, 1973). This result made intuitive sense because the energetic cost of homeothermy increases with mass and, on average, larger seeds should contain more energy. Lemen

(1978) reevaluated this relationship by using the same seed samples and correlating seed weight rather than size with heteromyid body mass. He found no correlation between the two variables. Two more recent studies have shown that, on the basis of cheek pouch analysis, heteromyids do collect seeds of particular sizes but the distributions vary in relation to their availability in particular microhabitats rather than to body mass (Stamp and Ohmart, 1978; M'Closkey, 1980). Furthermore, there is evidence that heteromyids select seeds on the basis of their net energetic value, but again this is not necessarily related to seed size (Soholt, 1973; Reichman, 1975,1977). The energetic aspects of seed selection will be discussed more fully later.

Evidence from both the field and the laboratory indicates that kangaroo rats preferentially utilize substantial seed clumps and that pocket mice concentrate on smaller seed clumps and scattered dispersions. Isotope-labelled seeds placed in clumps in the field by Lemen and Rosenzweig (1978) were more readily collected by D. ordii than were scattered seeds. Similarly, D. spectabilis and D. merriami preferentially utilized clumped dispersions of isotope-labelled seeds placed in the field (Frye and Rosenzweig, 1980). Bowers (1982), through direct observations of the foraging behavior of free-living D. merriami, P. formosus, and P. longimembris, obtained data consistent with the prediction that Dipodomys utilize seed clumps and Perognathus utilize scattered seeds. D. merriami moved farther between stops to dig and glean and stayed longer when they did stop. The pocket mice, on the other hand, moved more slowly and continuously and appeared to be continually gleaning or filtering the surface soil. Bower's observational techniques, however, are subject to the same criticisms directed toward Thompson (1982a).

Laboratory studies confirm that kangaroo rats are likelier to utilize clumped seed dispersions and are better at locating buried seed clumps than pocket mice. Lockard and Lockard (1971) demonstrated that D. deserti could detect seed clumps buried beneath the sand at depths to 20 cm. Reichman and Oberstein (1977) compared the detection and recovery abilities of D. merriami and P. amplus for seed clumps of various sizes buried at different depths. D. merriami were more accurate in locating seed clumps as indicated by digging loci and they dug deeper when a clump was located. Furthermore, the pocket mouse was likely to enter torpor when clumps were buried at the greater depths. Price (1978b) allowed individual D. merriami and individuals of three pocket mice species to forage in isolation overnight in a large room with scattered seeds, 1-g clumps, and 3-g clumps available. The D. merriami preferentially utilized the large seed clumps and the pocket mice concentrated on the small seed clumps and scattered dispersion.

Two laboratory studies have examined the effects of direct competition by naturally sympatric species on seed utilization. Hutto (1978) found that directly-competing D. ordii and P. flavus could coexist indefinitely when scattered seeds were available but the kangaroo rat excluded the pocket mouse from obtaining seeds when only seed clumps were available. Trombulak and Kenagy (1980) carried out a similar set of experiments with pairwise combinations of D. deserti, D. merriami, Microdipodops pallidus (pale kangaroo mouse), and P. longimembris. When the different species foraged alone, none showed a significant preference for clumped or scattered seeds. Direct competition resulted in all but P. longimembris preferentially utilizing the clumped seed dispersion and invariably the smaller of the two competitors got less food than when it foraged alone.

These studies support the notion that kangaroo rats preferentially exploit clumped seed dispersions and are probably able to do so because of their greater mobility and social dominance over pocket mice. Due to their smaller body mass and, hence, lower energetic costs, pocket mice can afford to concentrate on scattered seeds without suffering energetic deficits. As a consequence, these animals can probably meet their energetic needs within a relatively small area, thus eliminating the energy and predation costs associated with high mobility. Kangaroo rats, because of their superior size and mobility, have greater energetic demands which must be met by concentrating on more profitable clumps of seeds.

At present, resource partitioning as a function of the different energetic demands of heteromyid species is considered to be the best candidate for a mechanism which could shape and maintain heteromyid community structure.

Food Selection: An important consideration for any organism is diet selection, a problem that has received considerable theoretical treatment in the past (Emlen, 1966; Schoener, 1971; Pyke, Pulliam, and Charnov, 1977). In theory, an organism should select the diet that provides the maximum net yield of some relevant resource (e.g. energy or some important nutrient). Furthermore, the inclusion of a particular item in the diet should not depend on its availability but rather on the availability of the more preferred items.

Some of the studies cited earlier used cheek pouch contents to infer seed selection by heteromyids, with the general result that seed types are selected rather opportunistically; that is, in proportion to their availability in particular microhabitats (Lemen, 1978; Stamp and Ohmart, 1978; M'Closkey, 1980). Reichman and Oberstein (1977) suggest that different seed types may clump differentially, perhaps on the basis of size, weight, shape, or modes of dispersal. If heteromyids do indeed partition the habitat and/or resources based on their clumpedness, one could account for differential seed selection among species.

Preliminary data on natural seed densities in various Sonoran Desert microhabitats (e.g. around shrubs, sandwashes, rocks, and depressions) indicate differential seed densities with some of the highest densities found in open areas (Reichman and Oberstein, 1977). On the other hand, Thompson (1980) found that seed densities in the Mojave Desert were higher beneath shrubs than in the open. However, different vegetation, sampling procedures, season of census, weather patterns, topography, etc. could easily account for these differences. The point is that resource distributions will vary between habitats and thus, foraging dynamics will be expected to vary as well.

Despite earlier cited results based on cheek pouch contents which suggest that kangaroo rats do not select particular seed types within a microhabitat, there is ample evidence to the contrary. In general, a kangaroo rat's diet consists primarily of seeds of grasses, forbs, and shrubs, greenery to a lesser extent (although up to 60% when available), and insects in small amounts (Tappe, 1941; Chew and Chew, 1970; Chapman, 1972; Alcoze and Zimmerman, 1973; Bradley and Mauer, 1973; Flake, 1973; Soholt, 1973; Reichman, 1975,1977). To a large extent, the seed types selected depend on their availability in different habitats, but there is some indication that energetically superior seeds are preferred (Soholt, 1973; Reichman, 1977). Reichman (1975), for example, looked at seed selection and diet of D. merriami trapped in a Sonoran Desert habitat in relation to the available resources. An analysis of cheek pouch and stomach contents revealed that 75-85% of the animal's diet was comprised of seeds (mostly of forbs and, to a lesser extent, of grasses and shrubs) and 15-25% consisted of greenery and insects. Furthermore, preferred seeds were ingested in relatively greater proportions than their occurrence in random soil samples. Reichman (1977) determined that collected seeds were also energetically superior to those in random soil samples and that ingested seeds were energetically superior to those collected. But D. merriami also collected and ingested some relatively unavailable and energetically inferior seeds suggesting that energy value may not be the only relevant dimension for seed selection. Although Reichman (1975,1977) considers D. merriami to be a food generalist, these data indicate discrimination of food items both in situ during foraging and later during actual ingestion. There is some evidence that D. deserti also discriminate between potential food items based on their energetic value. Lockard and Lockard (1971) presented D. deserti commercial seeds differing in carbohydrate, protein, and lipid content in a laboratory setting with the result that seeds high in carbohydrate were significantly preferred.

One difficulty which arises in attempting to predict food selection in heteromyid species is how to determine the salient properties of the resource which influence foraging decisions. The degree to which different seed types clump in dispersal may determine the net energetic rewards to be gained. In other words, utilization of a large clump of energetically inferior seeds may be more profitable than searching for more dispersed energetically superior seeds. Clearly this situation will yield variable food preference hierarchies that are not simply related to the energetic value of individual seeds.

To further complicate the issue of food selection, the risk of obtaining seeds may influence the degree of in situ seed discrimination. Hay and Fuller (1981) determined the preference hierarchies of *D. merriami* and *P. fallax* for naturally available seeds and then placed preferred and non-preferred seeds in separate containers either under the protective canopy of shrubs or in presumably riskier open areas. The ratio of preferred to non-preferred seed removal by rodents was significantly higher in the open areas than under the shrub canopies. One interpretation of this result is that the higher cost of obtaining seeds in the open precluded foraging for less-preferred food items. On the other hand, an animal can "afford" to be relatively indiscriminate in selecting food when foraging under the protective canopy of a shrub.

Clearly the question of food selection by kangaroo rats is complex and must take into account the food types available, their energy and nutrient values, their distribution parameters, and the risk of obtaining them. It makes intuitive sense, however, that kangaroo rats should collect seeds that are generally available on the surface if sorting and discrimination of seeds during foraging significantly increases the risk of mortality due to predators or climatic stresses. If diet selection is truly important to these animals, perhaps it should occur when the animal is ingesting the seeds in the relative safety of its burrow (Reichman, 1975).

Conclusion

In this chapter I have discussed a variety of issues concerning the adaptations of kangaroo rats to desert existence as well as their role in desert community ecology. This chapter illustrates the wide breadth of studies on kangaroo rats, but it is apparent that serious gaps in our knowledge still exist. The data concerning behavioral and physiological adaptations to water and heat stress are reasonably straightforward and well-accepted by the scientific community. On the other hand, whether bipedal locomotion functions to minimize travel time and so reduce predation risks or whether it serves to conserve energy at high speeds has not been resolved. Despite the many field studies of kangaroo rats, little is known about their social organization or individual behavioral strategies. In the past, ecologists have primarily concentrated on the energetic relationships between surface activity (i.e. range patterns and habitat use) and foraging-feeding patterns while tending to neglect other presumably costly surface activities (in terms of time, energy expenditure, and risk) such as reproduction and social interactions. Behavioral ecologists and sociobiologists are becoming increasingly aware, however, that reproduction and social behavior (e.g. competition for mates, mate choice, and nepotism) are important considerations for how an animal budgets its time and energy. Unfortunately, generalizations about the social organization of kangaroo rat species have been based, in large part, on ecological studies using field methods inadequate for addressing such questions (e.g. capture-mark-recapture techniques). These limitations have led to the conclusion that kangaroo rats, in addition to being solitary, are asocial creatures with relatively simple and uninteresting social systems. While it may be true that kangaroo rats are relatively asocial compared to some gregarious rodents (e.g. many sciurids), such a generalization overlooks the possibility of more subtle and interesting social relationships.

Chapter III

General Methods

In this thesis I will present information about the behavior patterns and social organization of D. merriami stemming from both laboratory and field studies. Laboratory studies were undertaken in 1978 to establish basic information about the reproductive physiology and behavior, growth and development, and maternal behavior of D. merriami. Since 1980 three separate field studies consisting of intensive radio-tracking in conjunction with regular trapping have been conducted to investigate the free-ranging behavior of D. merriami. We have been interested in how sex, reproduction, and environmental factors including season, weather, and meteorological events are related to variations in ranging behavior. In the course of these field studies we have accumulated information about predation and home range stability as well.

This chapter is composed of two major parts: (1) a description of the methods used for the laboratory studies of reproduction, growth and development, and maternal behavior and (2) a description of the field methods used for the study of the free-ranging D. merriami.

Laboratory Studies of Reproduction

Breeding Cycles

As will be discussed in Chapter 4, the information about the breeding cycles of kangaroo rats has been rather scattered and unreliable up to this point despite the fact that these animals possess some interesting reproductive traits. As a result, we have carried out long-term studies of the breeding cycles of *D. merriami*, the results of which are presented in Chapter 4. It will also be apparent that this information is important for interpreting the field study results presented in Chapters 5 through 7.

Animals: Fourteen *D. merriami* females wild-trapped in the Great Basin Desert near Big Pine, Inyo County, California in 1978-1979 were used. All were adults when captured and had been maintained in the laboratory 1-7 months before observations began.

The animals were housed individually in clear plastic cages (33 X 28 X 17 cm) with sand substrate and a half-liter cardboard tube or can provided as shelter. They were maintained on mixed wheat, sunflower seed, and rolled oats and water *ad libitum* and provided with fresh lettuce or spinach daily. A reversed 13L:11D light cycle prevailed and ambient air temperature was maintained at approximately 22°C.

External Genitalia: Females were examined for 204 consecutive days between March and September 1979. Although paired with males when vulvar swelling occurred, no females copulated during this observation period.

External spring calipers were used to measure the diameter of the vulva to the nearest .5 mm. In addition, a descriptive catalog was developed to characterize the external appearance of the vulva. The degree of vulvar tumescence was nominally characterized as flat (F), medium (M), or swollen (S), or transitional (FM or MS). The vaginal orifice was categorized as open or closed. Differing vaginal discharges noted included (1) sloughed, dried, and flaky substance only at the vaginal opening or occasionally in quantities covering much of the vulvar region, (2) a "vaginal cast" of sinew-like sloughed material mucous-like in color that exuded from the vaginal orifice, (3) a copulatory plug confusable with a vaginal cast but which lacks the well-defined ridges of the cast and is not secreted, and (4) fresh or dried blood. Simultaneous but independent observation and recording of appropriate descriptors for the same animals by three people resulted in an overall concordance of 82% for these nominal categories.

Estrous Cycle Length: To determine the inter-estrous intervals, the day of estrus was defined according to a hierarchy of criteria: (1) day of copulation, (2) if no copulation occurred, the day of maximal vulvar swelling, (3) if two days of maximal swelling occurred then the day the vaginal orifice was open and/or the day of greatest vulvar diameter, (4) if no maximal swelling, then maximal vulvar diameter provided a value at least 2.5 mm greater than the minimum measure at last cycle.

Development and Growth

Information about the development and growth of young is basic to understanding a species' life history. Important developmental questions addressed here include the course and speed of growth and development, the age at which the young become relatively independent of the mother (e.g. weaning age, emergence from the natal burrow), and the age of sexual maturity of females. The results of these studies are also presented in Chapter 4.

Development: Twelve *D. merriami* litters (34 individuals) from ten females wild-trapped near Big Pine, Inyo County or near Palm Springs, Riverside County, California were observed.

Five litters from females already pregnant when captured were observed between March and July 1978 at the University of California, Riverside. Mothers and their litters were housed in "burrow boxes" 53 cm across, 37 cm front to back, and 92 cm high. A 53 X 32 cm platform was situated 31 cm deep in the burrow box resulting in a burrow area 61 X 53 X 5 cm. Boxes were constructed from plywood and clear plexiglas facing which allowed a view of the burrow area.

Animals were maintained on wheat seed and water _ad libitum_ and provided fresh lettuce three times weekly. A 12L:12D reversed light cycle prevailed and ambient air temperature was maintained at approximately 22°C.

Seven litters observed in July and August 1980 were from five females housed at McMaster University in the manner described in the previous section on breeding cycles. Pregnancies in these females were from laboratory copulations. Observations were made with the mother and her litter in their home cage.

Observations were generally carried out within six hours of the onset of the dark cycle under a red light. Daily observations of 15 min duration were conducted for the first 25 days postpartum, at which time the pups were weaned but left together. After day 25 postpartum, observations were made at five day intervals until day 50, at which time the pups were separated and observations were terminated. The mother was not separated from the pups during observations to avoid disturbance. In the first few days postpartum a single pup from the litters housed in the plastic cages was unsystematically selected to check for tooth eruption. Otherwise the pups were not handled by the observer.

Observations were recorded manually on a checklist with categories for the development of morphological characteristics, locomotion, grooming, digging, feeding, and social interactions (see Appendix A for list and description of characteristics). The checklist developed by Daly (1971) for the observation of golden hamsters was easily modified for kangaroo rats.

Individuals within a litter were not uniquely marked or sexed so a characteristic was considered present if exhibited by at least one pup. As such, each litter was treated as a statistical unit.

<u>Growth Measurements</u>: Twenty-four pups (10 males and 14 females) from 12 litters produced by ten females were used. These animals were housed in the same manner as described above in the section on breeding cycles. The pups were weaned and separated at 25 days postpartum.

From day 1 postpartum (approximately 24 hrs following birth) individually marked pups were removed one at a time for measurements of several morphological features. Measurements were made with a metric ruler to .5 mm. Total body length from snout tip to tail tip and ear length were measured for 25 days postpartum. Tail length and hind foot length were monitored for up to 80 days postpartum (tail breakage was a common problem) and body weight to .5 g was recorded for 120 days postpartum. Only animals surviving at least 120 days postpartum were included in the results.

Age at Female Sexual Maturity: Forty-six laboratory-born females housed as described above were examined daily from day 18 postpartum for the onset of sexual maturity as indicated by external genitalia (see above methods).

Three social groupings were established: (1) 22 pups were weaned and housed separately at day 25 postpartum, (2) 10 pups were weaned at day 25 but remained with littermates an additional 15 days, and (3) 14 pups were weaned and housed separately at day 40 postpartum.

Nest Attendance by the Mother: Four of the five litters housed in burrow boxes as described above were used in this study. Observation was via video monitor in a separate room with the camera mounted on a remote-controlled revolving pedestal encircled by the burrow boxes. Observations were carried out three times weekly until weaning at 25 days postpartum. Each litter was observed at least ten days. Sessions began between four and ten hours from the onset of the dark cycle and observations were made under a red light. The location of the mother and the pups was recorded as either on the nest or surface at 5 min intervals for two hours yielding a total of 24 samples per session.

Field Methods

Before describing the methods used in the field studies, it is useful to review, compare, and contrast live-trapping and radiotelemetry techniques. It will be apparent that these techniques have their strengths and weaknesses with respect to their effects on the natural movements of animals and the validity of their results.

Until the advent of sophisticated radiotelemetry systems in the early 1960's (see Cochran and Lord, 1963), the study of movements by small mammals including activity, home range, migration, immigration, and emigration was difficult due to the often cryptic nature of these animals. Field workers have used a variety of techniques to study animal movements including direct observation, tracking, radioactive markers, dyes for urine and feces, photographic devices, live-trapping, and radio-tracking (see Sanderson, 1966). Live-trapping and, more recently, radiotelemetry are probably the most common methods in present use.

Live-trapping: The use of live-traps to study small mammal movements is very simple; an animal is captured, marked for future identification, released at the point of capture, and subsequently recaptured. At the time of capture, the animal is usually sexed, weighed, and inspected for reproductive condition. Usually a trapping grid is established with one or more traps placed at permanent stations located at specific intervals. Trapping is generally carried out on a predetermined schedule over a relatively long time period. For example, trapping several days per month for one or more years yields information about short- and long-term range patterns including changes in the size and stability of ranges in relation to season, reproductive condition, and population structure and/or density. Live-trapping may also be used to investigate circadian cycles in natural populations by checking traps frequently over 24 hour periods (e.g. Kenagy, 1973a,1976a). As was discussed extensively in Chapter 2, live-trapping is a primary method used by ecologists to examine aspects of interspecific competition including microhabitat and resource utilization.

Despite the many kinds of questions addressable with live-trap data, the technique suffers several serious limitations, at least two of which stem from the possible adverse effects of trapping on the animal's natural movements. Foremost is that an animal's further movements are constrained. A nocturnal creature captured early in the evening, for instance, may be restricted from normal movements for at least several hours if not the entire night. The effects of confinement on the captured animal's subsequent ranging behavior and the ranging behavior of conspecifics during its absence have not been evaluated. Second, if trapping is carried out too frequently, the regular provisioning of animals may lead to unnatural changes in movement patterns. An animal with a "homesite" relatively far from the trapping-grid, for example, may encounter a trap during an unusually long excursion and, as a consequence, shift its range to include a portion of the trapping-grid.

Problems associated with the interpretation of trapping data have received much more treatment in the literature than the problems cited above (see, e.g., Mohr and Stumpf, 1966; Jennrich and Turner, 1969; Metzgar, 1972, 1973a; Koeppl, Slade, and Hoffmann, 1975; Van Winkle, 1975; Anderson, 1982). Since the practice of establishing permanent trap stations on a grid limits the number of spatial positions at which an animal can be recorded, inferential techniques for estimating range size and use must be used. Statistical home range estimates, for example, often assume that ranges are elliptical in shape and that the animal's center of activity lies at the geometric mean of the range (see, e.g. Jennrich and Turner, 1969). This assumption of normality is probably not justified in many species since topography, resource distribution, and inter- and intraspecific interactions will strongly influence an animal's range utilization patterns (see Metzgar, 1973b, however). A non-parametric alternative is the utilization density map described by Anderson (1982) which makes no assumption about the underlying distribution of space use and does not assume an elliptical range shape. The consensus of studies comparing different home range analyses is that no one technique is adequate to examine the range patterns of all species (see Mohr and Stumpf, 1966; Jennrich and Turner, 1969; Anderson, 1982).

Another difficulty in interpreting movements indicated by trapping data is that such movements may only be relevant to food-getting. Unless other biologically relevant stimuli are placed in traps (e.g. odors of conspecifics), one cannot be certain that ranging and other activities unrelated to foraging are reflected in the trapping data.

Radiotelemetry: Radiotelemetry systems used to track the movements of small mammals are quite simple. Miniature radio transmitters which emit easily-localizable, pulsating signals are implanted or affixed to the animal by means of a collar or harness. The transmitter frequencies are individually-tuned so that a multiple-channel receiver can be used to discriminate among many individuals. The recording systems are of two general types: (1) portable systems in which the observer physically approaches the focal animal and (2) remote systems in which at least two antennae are mounted on spatially-separated towers and an animal's location is found by triangulation. Simply, the antennae are rotated until the peak radio signal is received, a compass direction for each tower is recorded, and the intersection of the directional vectors from the towers is taken to be the animal's location. The remote system is particularly useful for frequent sampling of the locations for a large number of relatively sedentary animals. Its resolution or accuracy, however, is inferior to that of the portable system. Furthermore, highly mobile animals such as kangaroo rats, may move entirely out of the receiver's range. Portable systems, though quite labor intensive, have several advantages in addition to their potentially greater accuracy. The most significant advantage of the portable system, perhaps, is that animals can be visually observed once located, thus leading to information about surface activity that cannot be gained using remote systems.

Radiotelemetry is superior to trapping in general because it yields more data, a focal animal can be located anywhere within its range at any time, activity cycles (e.g. circadian rhythms) can be studied by frequent time sampling, home burrows and nests can be located, and social interactions (e.g. proximity, cohabitation, etc.) can be monitored. Furthermore, descriptive rather than inferential data analysis techniques are more feasible when a large number of data points are available.

The major disadvantage of radiotelemetry is that animals must be handled more extensively than for trapping. This procedure often requires anesthesia and sometimes surgery, in the case of subcutaneous or peritoneal implants. Moreover, the extra weight and sometimes cumbersome attachment of a transmitter may restrict natural movements and activity patterns. Hamley and Falls (1975), for example, demonstrated a decrease in running on an activity wheel by transmitter-carrying voles even though their ranging behavior seemed normal on the basis of trap data. Ten days were required for animals to recover to their previous baseline activity levels. Most investigators, however, do not consider the presence of a transmitter to be a serious hindrance if it is attached properly and its weight does not exceed 10% of the animal's weight.

Radiotelemetry has proven invaluable in several studies of rodent spatiotemporal ranging and habitat utilization patterns. For instance, Schroder (1979) studied Dipodomys spectabilis foraging and home range utilization. Brooks and Banks (1971) demonstrated range differences in the collared lemming (Dicrostonyx groenlandicus) in relation to sex and reproductive condition. Banks, Brooks, and Schnell (1975) conducted a similar study of the brown lemming (Lemmus trimucronatus). Mineau and Madison (1977) and Madison (1978c) investigated the ranging, habitat utilization patterns, and social interactions of the white-footed mouse (Peromyscus leucopus). Madison (1978a,b,1980,1981) has conducted extensive studies on the movements, habitat use, social structure, maternal behavior, and predation susceptibility of the meadow vole (Microtus pennsylvanicus). Cranford (1976) examined dusky-footed woodrat (Neotoma fuscipes) home range and habitat utilization.

In the remainder of this chapter I describe the methods used to carry out similar field studies of the behavior of free-ranging D. merriami.

Study Areas

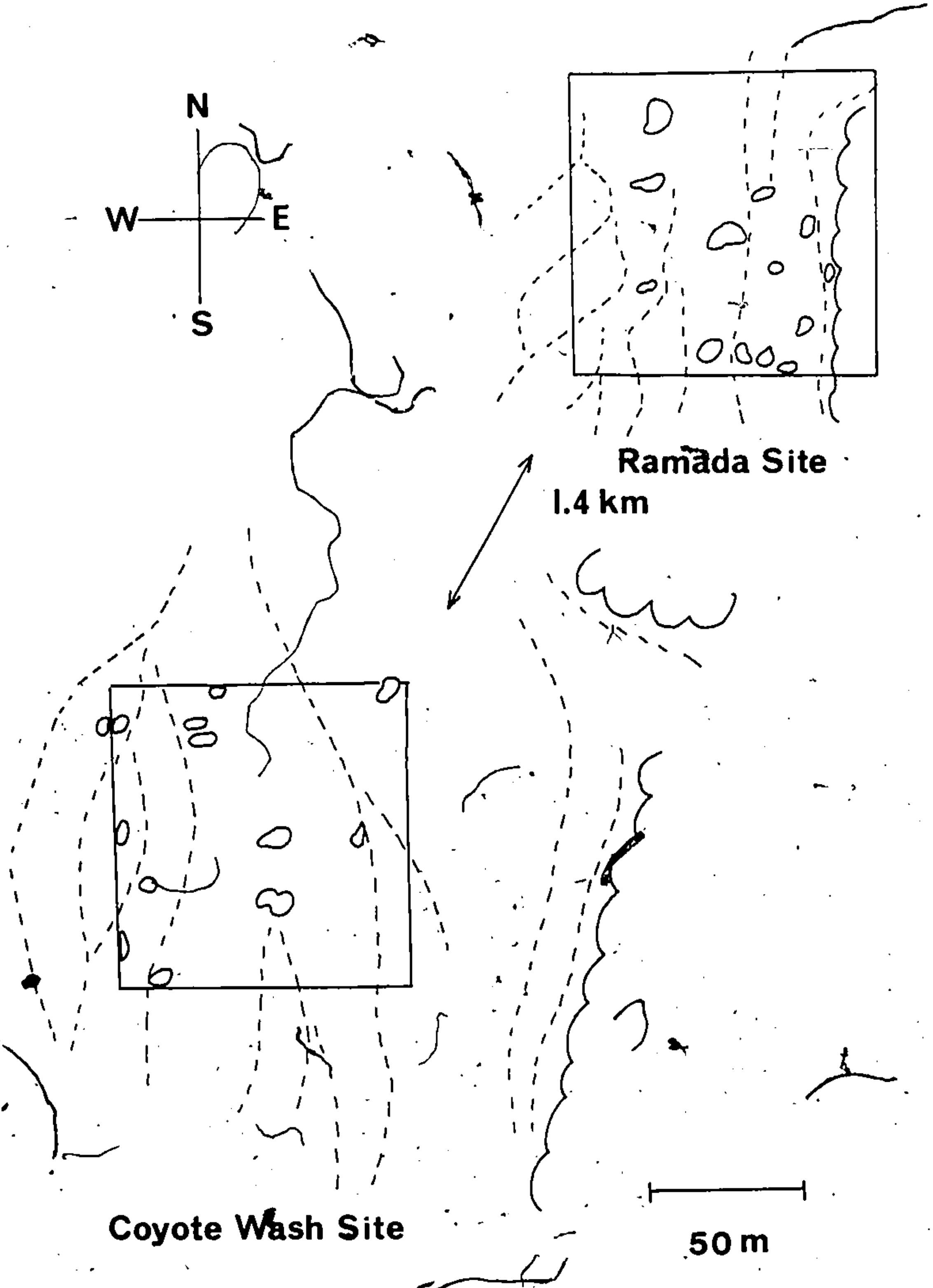
Field work was carried out on two study sites, designated the Ramada site and the Coyote Wash site, located 1.4 km apart on a north-south axis on the upper alluvial plain within the confines of the Boyd Deep Canyon Reserve (el. 300 m) approximately three kilometers south of Palm Desert, Riverside County, California. We changed field sites in December 1981 because the Ramada site was designated as an undergraduate teaching area and, thus, was no longer a suitable site for longitudinal studies. Radio-tracking in conjunction with trapping was carried out on the Ramada site between November 27 and December 22, 1980 (study period 1). Similar work was carried out on the Coyote Wash site between December 11, 1981 and May 25, 1982 (study period 2) and November 11 and December 22, 1982 (study period 3).

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 only 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.

Due to the close proximity of the two study sites, their topographic and floral characteristics are similar. Figure 3.1 depicts the main topographic features of the two sites. Both contain interspersions of sandy washes, hummocks and rocky strips. Plant surveys at an elevation of 240 m summarized by Zabriskie (1979) show that 14 perennial shrub species 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 indigo bush (Dalea schottii), burrobush (Ambrosia dumosa), sweetbush (Bebbia juncea), brittlebush (Encelia farinosa), cheesebush (Hymenoclea salsola), desert lavender (Hyptus emoryi), and chuparosa (Beloperone californica). Large perennial species which may be arbitrarily classified as tree or shrub include palo verde (Cercidium floridum), smoke tree (Dalea spinosa), and cat's claw (Acacia gregii). Five cactus genera occur in the area with the pencil cholla (Opuntia ramosissima) as the most common species.

The Deep Canyon alluvial plain also contains at least 93 annual species with cryptantha (Cryptantha genus) and evening-primroses (Cammissonia genus) as the dominant genera. However, the most abundant species are the woody

Figure 3.1. The Ramada and Coyote Wash study sites. Dotted lines indicate sand washes, scallops indicate ridges, closed circular figures are large palo verde trees, and the rectangles represent the perimeters of the trapping-grids.


N
W
E
S
Ramada Site
1.4 km
Coyote Wash Site
50 m

plantain (Plantago insularis) and the introduced abu-mashi (Schismus barbatus). Most of the annuals germinate 5-14 days following fall and winter rains and flower in the spring but some species germinate and flower in the summer following rainfall.

General Trapping Procedures: One hectare 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 X 9 X 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 within an hour of dusk, baited with rolled oats, and checked either four to five hours later or the next morning.

In addition to D. merriami, all captured rodents including pocket mice (Perognathus spp.), the desert woodrat (Neotoma lepida), and the cactus mouse (Peromyscus eremicus), were weighed, sexed, and inspected for reproductive condition. Females' external genitalia were examined and classified in the manner described in the previous section for cycle lengths. Assignment of pregnancy was straightforward in most cases. In study period 2, 23 females captured on the Coyote Wash site were determined or suspected to be pregnant. In 13 of the 23 cases pregnancy was confirmed because the female was captured before and after parturition, indicated by an abrupt weight loss ($\bar{x} = 4.7 \pm 2.9$ g) and the development of red, distended nipples. In four cases females were captured only during the lactation period. Six females showed signs of pregnancy but were not captured during lactation. In one case the female's weight increased from 34 to 40 g in one week and in another weight increased from 38 to 45 g in 30 days in combination with the appearance of protruding nipples. Finally, four females were suspected to be pregnant on the basis of weights of 40, 43, 47, and 50 g compared to the average anestrous female weight of 35.5 g (± 2.5 g). Males captured on the Ramada site in 1980 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 1982 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 between testes length in males possessing scrotal sacs). In the fall of 1982 the length of the expressed testes was measured with calipers to the nearest .5 mm. Furthermore, in the 1982 study periods hind foot length and tail measurements were taken and the size and activity of the male's dorsal gland was noted. Rodents captured on the Ramada site in 1980 were ear-tagged for identification but rodents captured on the Coyote Wash site in 1982 were toe-clipped due to the problem of animals losing their eartags.

The intensity of trapping varied between study periods so each is described separately. In the fall of 1980 trapping was primarily conducted to capture subjects for radio implantation, subsequent hormone treatments (to be discussed in Chapter 5), and for radio retrieval. In the winter and spring of 1982 trapping was conducted on a weekly basis except when animals were needed for radio implantation or particular animals requiring examination were not captured on the regular trapping night. In the fall of 1982 trapping was conducted once every three days on average to ensure that an estrous cycle (swelling and subsidence) would not be missed.

Radiotelemetry Procedures

Animals: Sixty adult (i.e. $>$ 30 g) *D. merriami* including 32 males and 28 females were radio-tracked for periods ranging from 1 to 84 days in the three study periods between November 1980 and late December 1982. A complete description of the subject populations and the data collected for individuals will be presented in the results section of Chapter 5.

Equipment: Standard radiotelemetry equipment was used (AVM Instrument Co., Dublin, California) including SM-1 mouse-style transmitters with an internal antenna and individually-tuned frequencies around 151 mHz, an LA-12 multiple-channel receiver, and a hand-held Yagi antenna. The transmitters were powered by 1.35 volt mercury batteries rated to last two months. For the first and part of the second study periods, the transmitter-battery unit was encapsulated in epoxy and then dipped in beeswax yielding an implant unit weighing about 3.8 g. Due to problems with application of the epoxy (lumps and small gaps) and the difficulty of its removal for battery replacement, dental acrylic was subsequently used for initial encapsulation of the radio unit. The virtues of acrylic are that it flows more evenly, sets faster, and can easily be "washed away" in an agitated acetone bath in order to recover and re-use the transmitter. Furthermore, acrylic-encapsulated units weigh less than 3 g. Transmitters have a signal range of 30 to 60 m at ground level depending on the slope and rockiness of the terrain.

For radio-implantation, animals captured 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 to the right or left of 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 approximately hourly during the night. In the first and second study periods 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 the third study period each animal was located hourly throughout the dark period yielding a total of 15 locations per night. In the first study period radio-tracking was carried out on consecutive nights between November 27 and December 22, 1980. In the second study period radio-tracking was generally carried out four nights per week between December 15, 1981 and May 20, 1982. In the third study period radio-tracking was conducted two out of every three nights between November 11 and December 22, 1982. 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^2. 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 in most cases.

The two study sites were mapped as grids with 10 m^2 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. Several other observations were recorded along with hourly radio locations: (1) the microhabitat (e.g. shrub species or open ground) in which the animal was located, (2) the air temperature, (3) the presence or absence of the moon, and (4) miscellaneous comments about weather conditions (e.g. wind, rain, or cloud cover).

Data analysis methods will be deferred to the relevant chapters.

Chapter IV

Kangaroo Rat Reproduction

Introduction

Life in the desert presents an organism with a special set of problems to solve for survival and reproduction. A variety of morphological and behavioral adaptations for desert existence possessed by kangaroo rats were discussed in Chapter 2. In this chapter the reproductive characteristics of the Merriam kangaroo rat and some of its congeners are examined. Rather than simply describe the species-typical reproductive patterns of kangaroo rats, I will assume that individuals are decision-makers or "strategists" with respect to reproduction and, furthermore, that individuals vary on parameters potentially related to reproduction such as age, physical condition, social standing, or quality of territory or range. In the following chapters I will attempt to relate the reproductive tactics of Merriam kangaroo rats to their socio-spatial behavior patterns.

To provide a general theoretical framework from which to examine the reproductive tactics of kangaroo rats, it is useful to draw upon life history theory (see Gadgil and Bossert, 1970 and Stearns, 1976 for excellent reviews).

This body of theory combines the study of reproduction, ecology, and genetics with the aim of understanding how combinations of reproductive traits are related to ecological circumstances. A reproductive trait is a set of coadapted traits designed by natural selection to solve an ecological problem (Stearns, 1976). As a decision-maker, the basic problem for any organism is how to partition time, energy, and effort between somatic growth and reproduction over its lifetime so that its contribution of genes to future generations is maximized. An economic metaphor which, perhaps, makes the point more cogently is that allocation for the reproductive processes should be such that it maximizes the rate of reproductive profit on investment (Williams, 1966a). The four traits most often addressed by life history theory are (1) at what age to first breed, (2) how often to breed, (3) what size brood to produce, and (4) what size offspring to produce.

At present, life history theory is still in its infancy, beset with poorly defined concepts, abstruse quantification, and weak empirical support (see Hirshfield and Tinkle, 1975; Stearns, 1976,1977; Horn, 1978). Nonetheless, this body of theory has provided several useful concepts, predictions and a general classificatory description of reproductive traits and ecological circumstances which tend to [illegible] together.

A fundamental concept of life history theory is the relative reproductive value of different age classes which Fisher (1958) defined as the value of future progeny, in terms of units of biological fitness, of an organism at any age. Although this concept has been modified by different authors (see Stearns, 1976) it remains essentially the same as Fisher's original definition. For example, Stearns (1976) defines reproductive value as the present value or average number of future offspring a female at age x can expect to have over the rest of her lifetime given a specified population growth rate. It should be intuitively clear that any instantaneous measurement of reproductive value will depend on a multitude of intrinsic and extrinsic factors including age, size, mortality risk, current reproductive effort, physical condition, and season (Pianka and Parker, 1975). The importance of this concept is that reproductive behavior should vary between individuals in relation to their reproductive value which, in turn, depends on the interaction of the factors stated above.

At this point it is useful to introduce the notion of reproductive effort to clarify the relationship between reproductive value and reproductive tactics. Reproductive effort is simply the organism's investment of resources (energy, nutrients, time, etc.) in reproduction over a specified time interval (Williams, 1966b; Pianka and Parker, 1975; Stearns, 1976). One difficulty is that, in a sense, all investments by an organism for survival may be considered to benefit reproduction so that assigning costs to activities directly concerned with reproduction can be problematic (see Williams, 1966b). The problems of interpretation notwithstanding, reproductive effort in organisms without parental care is usually measured as the ratio of reproductive tissue to somatic tissue. Extensive comparisons between conspecific lizards and other reptiles on this measure have been carried out recently (Hirshfield and Tinkle, 1975; Pianka and Parker, 1975; Stearns, 1976,1977). In organisms with parental care, reproductive effort may be divided into mating and parental effort (Low, 1978). However, the costs associated with mating effort (e.g. courtship, risk of predation, transmission of disease) and parental effort (e.g. nuture and/or defense of offspring) are not easily quantified so many estimates of reproductive effort are at best ordinal. Despite these problems, the notion of reproductive effort has heuristic value for considerations of individual reproductive tactics.

To consider the relationship between reproductive value and reproductive effort, it is necessary to partition reproductive value into its two components, namely present versus future progeny. The latter term represents the organism's residual reproductive value in the next age category multiplied by its probability of survival to the next interval (Pianka and Parker, 1975). It is generally assumed that reproductive effort and residual reproductive value should vary inversely as a consequence of their mutual feedback (e.g. Williams, 1966a,b; Gadgil and Bossert, 1970; Pianka and Parker, 1975; Stearns, 1976,1977; Snell and King, 1977). It should be apparent that increases in reproductive effort will lower residual reproductive value due to the investment of energy and other resources and the likely increase in the risk of mortality due to poor physical conditi[illegible]r exposure to disease or predators. The extreme case is semelparity in which the organism uses all of its available resources for breeding and dies shortly thereafter, as in some Pacific salmon (Williams, 1966b; Gadgil and Bossert, 1970). In this case high reproductive effort reduces residual reproductive value to zero. Additionally, in species where residual reproductive value reaches some low value as a result of past reproductive effort or some other factors including age-specific fecundity (e.g. menopause) selection should result in increased reproductive effort with age. When residual reproductive value is low the organism has no reason to allocate reproductive effort in a conservative manner.

A comparison of reproductive tactics by organisms occupying different ecological niches reveals that certain combinations of traits tend to occur together. MacArthur and Wilson (1967) coined the terms r- and K-selection to describe two combinational extremes in reproductive tactics. In population biology r is the intrinsic rate of increase in a population unencumbered by ecological constraints (e.g. population saturation, predators, etc.) and K is the carrying capacity or saturation level of a specified environment. r-selected organisms exhibit early sexual maturity, many small young, and large reproductive effort (often semelparous) whereas K-selected organisms show later sexual maturity, a few large young, a long life, and smaller reproductive effort (usually iteroparous). Furthermore, r- and K-selected organisms tend to occur with certain ecological circumstances. r-selection is usually associated with variable and/or unpredictable climates, catastrophic and density independent mortality, fluctuating population densities, and variable intra- and interspecific competition (Pianka, 1970). K-selection, on the other hand, is generally associated with fairly constant and/or predictable climates, directed and density-dependent mortality (e.g. juvenile mortality generally exceeds adult mortality), fairly constant population sizes at or near carrying capacity (K) and generally severe intra- and interspecific competition (Pianka, 1970). It is clear that r-selection places a premium on immediate and high productivity whereas K-selection, in association with a saturated environment, favors the channeling of resources into growth and maintenance and the production of a few, extremely fit offspring (Pianka, 1970).

Discussions using the terms r- and K-selection often lead to confusion because authors sometimes fail to state clearly whether they consider r- and K-selection to represent the two extremes of causal forces leading to the different combinations of reproductive traits or whether the terms are simply descriptive labels. In this thesis I will use r- and K-selection only as descriptive labels for the discussion of the reproductive traits and tactics of kangaroo rats.

Kangaroo Rat Reproduction

Environment: An important limiting factor for reproduction by many organisms is resource availability. It is generally the case that animals must be in good physical condition for successful reproduction to occur. From the above discussion, it is clear that an animal's decision to reproduce must be based in part on the likelihood of successful reproduction if it is assumed that present reproductive effort lowers residual reproductive value. Hence, in iteroparous organisms faced with poor environmental conditions for breeding the best decision may be to forego reproduction until conditions improve. For example, in iteroparous species highly dependent upon the availability of resources for successful reproduction one may expect to find rather opportunistic breeding habits. It will be shown that kangaroo rats tend to be opportunistic breeders in relation to climate and resource conditions.

Deserts are usually characterized as having harsh and often unpredictable climates, an important consideration for the germination, ripening, and seed shedding of annual plants. It is well established that the germination of annual plants is dependent upon the appropriate combination of moisture and temperature (Beatley, 1969; Mayer and Poljakoff-Mayber, 1982). Beatley (1969) determined that the production of winter annuals in the Mojave Desert, a *D. merriami* habitat, is under the control of precipitation between September and December with at least 25 mm required for annual germination. If 15-25 mm of rain falls in this interval only scattered plants germinate. Furthermore, if no rain falls annuals simply do not germinate and perennials become dormant. There are inter- and intraspecific differences in responses by annuals to moisture and temperature as well. Went (1957; cited in Mayer and Poljakoff-Mayber, 1982) found that winter annuals germinated when moistened at lower temperatures (10°C) while summer annuals only germinated when moistened at higher temperatures (26-30° C). Mayer and Poljakoff-Mayber (1982) discuss the possibility that desert-adapted annual species possess some sort of inhibitors which act as rain gauges and prevent germination under suboptimal conditions for seedling survival (although they admit that this possibility remains controversial).

The timing of precipitation and the production of annuals are similar for the Deep Canyon Reserve and the

Mojave Desert so it is expected that my subject population is subjected to resource conditions similar to those described by Beatley (1969).

Population Fluctuations: If kangaroo rat populations are resource-limited, population fluctuations in association with differing climatic conditions should be apparent. These fluctuations may occur as a result of increased mortality, inhibition of reproductive activity, emigration, or suppressed immigration.

There are few longitudinal studies on kangaroo rats which provide data suitable for examining the correlation between climatic factors and population changes and fewer yet which establish the factors responsible for the population fluctuations. The few studies which have been carried out over sufficient time periods do, however, seem to establish a relationship between ecological parameters and population densities.

Reynolds (1958) conducted trapping over a 12 year period on a sample area of approximately 30,000 acres in southern Arizona. Over this time period annual precipitation varied between 170 and 380 mm, annual plant production between 9 and 81 kg/acre, and perennial plant production between 13 and 91 kg/acre (Reynolds does not state how these estimates were arrived at). Likewise the population of <u>D. merriami</u> fluctuated widely from a low of 1.4 animals/acre to a high of 7.0 animals/acre. The density of animals in general was not well correlated with annual precipitation or the overall production of annual plants. A breakdown of the type and timing of precipitation, however, indicated that population increases did tend to occur in relation to rain adequate for average and above-average winter and summer annuals production. In two separate years, for example, winter population levels were high following better than average summer annual production. Populations declined with heavy or late winter snowfalls and torrential summer downpours. It seemed to be the case that population densities did, in general, track the availability of food resources over the years of this study.

Beatley (1969) monitored D. merriami populations in the Mojave Desert over a five year period and found additional evidence for variations in populations associated with climatic patterns. Her findings were similar to those of Reynolds with summer population levels down when autumn rainfall was nil and subsequent winter annual germination was sporadic. Conversely, when autumn rains were extraordinarily good, there was a concomitant increase in rodent populations the following summer. Chew and Butterworth (1964) noted a similar rise and fall in D. merriami populations in relation to precipitation in the Mojave Desert. In their study, however, population changes tended to lag about a year behind the weather patterns.

A relationship between population densities and the production of vegetation is apparent. Most studies indicate that there is a primary effect of climate and consequent resource variability on reproduction. It is not known, however, whether this relationship reflects a specific adaptation to desert existence by kangaroo rats.

Mortality and dispersal should be important determinants of rodent population densities and they certainly are important considerations for the treatment of reproductive tactics (see discussion section below). Unfortunately, the relative contributions of mortality and dispersal to disappearances from kangaroo rat populations are not known. These animals are reported to live as long as 93 months in captivity (Egoscue, Bittmenn, and Petrovich, 1970) but life expectancies in the field, based on the sparse data available appear to be much shorter. French, Maza, and Aschwanden (1967) constructed survivorship curves for _D. merriami_ and _D. microps_ based on a 2.5 year trapping study on fenced (i.e. free of dispersal effects) and unfenced plots. The survivorship curves are not true life tables for three reasons: (1) the lifespan of an individual was defined as the time between its first and last appearance in the trapping record, (2) many animals were of adult size when the study began, and (3) it was impossible to estimate mortality rates for the period between birth and first capture. However, these data are useful for examining juvenile and adult mortality and disappearances. The mean life expectancy on fenced plots was 4.3 months for D. merriami and 4.9 months for D. microps. While 50% of both species survived six months, only 18% survived one year and 3-4% survived more than 30 months. Furthermore, it appears that juvenile mortality exceeds adult mortality since survivorship was lower on the plot with proportionally more juveniles. On the unfenced plot, disappearances (a combination of mortality and dispersal) were much more dramatic. For both kangaroo rat species only 18% of the animals remained after four months and 1-5% after 10 months. French et al. (1967) suggested that dispersal and kit fox predation accounted for the increase in disappearances from this plot.

Two other long-term trapping studies obtained similar results for the disappearance of kangaroo rats from a local population. Holdenreid (1957), based on a two year period of regular trapping, reported that 12% of adult bannertail kangaroo rats (D. spectabilis) remained in the trapping area over the first year. Of the animals in the population at the end of the first year, 22% remained in the area through the second year of trapping. The actual disappearance rate due to dispersal and mortality was lower, though, because these figures include animals which died in traps. Chew and Butterworth (1964) found that 12-19% of D. merriami remained on their trapping area over a one year period based on a 29 month study. Furthermore, they estimated that the disappearance rate was less than 10% per month for May through September but was greater than 20% per month for October through April. They assumed that the high disappearance rate for the winter months was attributable to high juvenile disappearance and the harshness of winter.

Although these studies only crudely estimate survivorship, it is apparent that the chance of surviving from one breeding season to the next is rather low. Hence, it would make sense for individuals to expend a great deal of reproductive effort when breeding conditions are good and it is expected that sexual maturation should be relatively rapid so that individuals may breed in their natal year. However, better data on survivorship and reproductive effort for different age groups are needed to examine reproductive tactics. A possible bias may exist in these estimates of survivorship as well. There may be a tendency to conduct trapping studies in the better habitats where population levels, reproduction, and turnover rates are atypically high and, hence, survival unusually low. The populations of lower density habitats may be more stable and have higher survival.

Reproductive Activity in the Field

Seasonality: The peak breeding season for all kangaroo rat species studied occurs from mid-winter through spring with occasional smaller peaks in late summer and early fall

(Duke, 1944; Fitch, 1948; Quay, 1953; Pfeiffer, 1956; Holdenreid, 1957; Reynolds, 1960; Beatley, 1969; Bradley and Mauer, 1971,1973; Kenagy, 1973a; Reichman and Van De Graaff, 1973,1975; Van De Graaff and Balda, 1973; Flake, 1974). Reproductive activity in male D. merriami (Reynolds, 1960; Kenagy, 1973a) and D. microps (Kenagy, 1973a), as indicated by the presence of scrotal testes, begins before and extends beyond the reproductive activity of females so that active males are available when females begin cycling. The literature suggests that virtually all adult individuals are capable of reproduction during the peak breeding season but that only some individuals may be in reproductive condition during smaller peak periods (e.g. Kenagy, 1973a).

Precipitation and Green Vegetation: A controversial question concerning reproduction by kangaroo rats is what factor or combination of factors triggers reproductive activity, especially in females. In Chapter 2 I discussed the adaptations of kangaroo rats to cope with water stress. It was pointed out that several kangaroo rat species can survive without access to free water. The added physiological stress of pregnancy and lactation, however, may require females to ingest free water to avoid a negative water balance. The most likely source of free water for many desert species is green vegetation. Thus it has been suggested by several investigators that precipitation and/or green vegetation is necessary for the initiation of reproductive activity by kangaroo rats. Some early studies had noted that reproductive activity declined severely in association with drought (Chew and Butterworth, 1964; French et al., 1967) and subsequent studies have examined the relationship between reproduction, precipitation, and vegetation in more detail (e.g. Beatley, 1969; Bradley and Mauer, 1971,1973; Kenagy, 1973a; Van De Graaff and Balda, 1973; Reichman and Van De Graaff, 1975; Soholt, 1973,1977).

The point was made earlier that the absolute amount of annual precipitation and production of annual plants was not strongly correlated with changes in D. merriami population densities (Reynolds, 1958). This finding suggests that the initiation of reproduction should be associated only with the appropriate amount and timing of precipitation and annual plant production. For example, Kenagy (1973a) found that reproductive activity in female D. merriami closely followed moderate rainfall in the late fall and early winter but not large rainfalls. He also noted that this reproductive activity was associated with the great proliferation of previously germinated annual plants and considerable new germination. Based on five years of data, Beatley (1969) concluded that autumn rains sufficient for germination of winter annuals (see above discussion) were necessary for spring reproduction by D. merriami.

In addition to noting the relationship between the production of winter annuals and reproduction, other workers have investigated the feeding habits of kangaroo rats in and out of the breeding season. Analysis of stomach contents and reproductive condition indicate that D. merriami include a greater proportion of green vegetation in their diet during the breeding season (Bradley and Mauer, 1973; Soholt, 1973,1977; Reichman and Van De Graaff, 1975).

The weakness of these correlational studies is their inability to establish causal relationships between precipitation, vegetation, and reproduction. It is not known whether precipitation itself triggers reproductive activity in such a way that the production of annuals coincides temporally with the initiation of pregnancy and/or lactation or whether germinating annuals contain some sort of nutrient or some estrogenic substance necessary for the onset of reproduction.

There is experimental evidence that herbaceous vegetation and/or free water is important for successful reproduction. Soholt (1977) examined the consumption of herbaceous vegetation and water by D. merriami during gestation and lactation and found that water consumption by anestrous and pregnant females was similar but that lactating females increased their water consumption 225% on average. This increased water consumption drops off at about 23-24 days postpartum, which coincides with my observations of the timing of weaning in this species (see results below). Furthermore, water consumption was related to litter size and, in fact, two females each weaned a single pup without increasing their water consumption. Soholt concluded that the consumption of herbaceous material or water is necessary to support lactation but not for the initiation of reproduction or support of pregnancy.

The trigger for reproduction in kangaroo rats remains unknown but it is probably some cue predictive of normal production of winter annuals. It would appear on the basis of Beatley's data (1969) that a certain amount of rainfall between September and December or something associated with the germination of annual plants (e.g. nutrients or some estrogenic substance) are the best candidates.

Fecundity: In the discussion of life history tactics presented earlier, I stated several important questions concerning reproduction including when to breed, how often, and at what age. The information on kangaroo rats regarding these issues is scattered but reasonably consistent within and between the few species examined. I previously discussed the seasonality of breeding in the preceding section. But how often does a female breed within a season? With a gestation period of 30-33 days and lactation lasting three to four weeks (see results below), a female first breeding in late December or early January could conceivably wean three litters by mid-June. Furthermore, as will be shown, females are sexually mature in two to three months, and thus a female born in January or early February could breed in her natal season.

At least three previous field studies have provided evidence for multiple breeding by females within a season. Holdenreid (1957) observed one female D. spectabilis to be pregnant three times within a season and once the next season. The inter-brood interval for this female was 42-49 days between the first and second litters and 37-42 days between the second and third litters. Bradley and Mauer (1971) reported that second litters for D. merriami females that had been marked and retrapped were common on their Mojave Desert field site.

The data concerning the age of first breeding are a bit more suspect, mostly due to the practice of estimating ages by weight. Seasonal flucuations in weight may be so great that adults could be categorized as juveniles if this criterion alone is used (Pers. Obs.). Nonetheless, Reynolds (1960) reports breeding by females in their natal year and Bradley and Mauer (1971) estimated that sexual maturity occurs at less than two months of age based on evidence of placental scars and estrus. Up to this time there has been no direct evidence of first-year females successfully breeding. As will be shown in the results section, there is now unequivocal evidence for breeding by first-year females.

The evidence is good that multiple litters may be produced within a breeding season, probably in association with high production of winter annuals. There are no data, however, concerning the relationship between population density and reproductive output. It would be interesting to determine whether high population densities and, presumably, fewer opportunities for juveniles to establish themselves lead to a suppression of breeding. There is, for example, a substantial body of literature on socially- and chemosignal-induced breeding suppression and delayed maturation in house mice (e.g. Vandenbergh, Drickamer, and Colby, 1972; Drickamer, 1974,1977,1979,1982; Vandenbergh, 1975; Massey and Vandenbergh, 1980).

Laboratory Breeding

It is generally desirable to study the reproductive behavior of a species under naturally varying conditions if one is interested in reproductive tactics. Unfortunately it is very difficult to determine certain reproductive traits in burrow-dwelling mammals from field observations. This obstacle and the historical difficulty of breeding kangaroo rats in captivity have, until the present study, resulted in little information about reproduction in this genus. In this section I review the sparse literature on aspects of kangaroo rat reproduction in captivity including breeding cycles, copulatory patterns, gestation length, litter size, and development. More definitive information about reproduction in *D. merriami* will then be presented.

Breeding Cycles: Several authors have noted a relationship between sexual activity in female kangaroo rats and distinct morphological changes in the size and appearance of the vulvar region (Day, Egoscue, and Woodbury, 1956; Pfeiffer, 1956,1960; Holdenreid, 1957; Chew, 1958; Eisenberg and Isaac, 1963; Butterworth, 1961a; Chew and Butterworth, 1964; Behrends, 1981). Pfeiffer (1960) administered estrogen (.01 mg/day for 3 days) and/or progesterone (2.5 mg/day for 3 days) to female *D. ordii* with the result that estrogen caused vulval swelling and a reduction in the thickness of the clitorine urethral epithelium while progesterone inhibited the action of estrogen. Pfeiffer suggested that under normal hormonal conditions the vulva swells during proestrus follicular development and remains enlarged for long periods of proestrous growth. The vulva decreases in size after ovulation and remains small and closed in anestrous females.[1]

Temporal patterns for breeding cycles in kangaroo rats have not been reliably established, primarily due to the difficulty of maintaining reproductively active animals in captivity. Chew (1958) reported that *D. merriami* females exhibited swollen and open vaginas for an average length of six days (range = 3-11 days) and that the average breeding cycle was 25 days (range = 13-45 days). However, these data were collected on few animals over relatively short time periods.

__Copulatory Patterns__: Kangaroo rats have been difficult to breed in captivity although scattered reports of attempts exist (Allan, 1944; Butterworth, 1961a; Eisenberg and Isaac, 1963; Eisenberg, 1967) and at least one observation of a copulation by __D. microps__ in the field is reported (Kenagy, 1976b). Behrends (1981) provides the most complete description of the copulatory patterns of a kangaroo rat species. __D. microps__ were paired under controlled conditions when females exhibited vulvar swelling. Pre-copulatory behavior by both the male and the female is often characterized by aggression, including defensive posturing, ventral-ventral fighting, and biting. If the female is sexually receptive this initial aggression usually subsides within 10-15 min of pairing and the female remains stationary in the lordotic position and allows the male to approach and attempt to mount. Mutual circling, allogrooming, and sniffing or licking of the perineal area by the male may also occur. In this species there is a single continuous mount of 1-6 min duration with repeated intravaginal thrusting until ejaculation. Soon after copulation a hard gelatinous copulatory plug develops in the female's vagina. In the 20 copulations observed by the author, eight included second ejaculations. Four litters were produced from the 12 single ejaculations and three litters were produced from the eight double ejaculations. Whether second copulations occur under natural conditions is not known. Kenagy (1976b) reported no subsequent interaction between a male and female D. microps after a single copulation in the wild. The fact that litters were produced by females that had copulated only once in a test session verifies that multiple ejaculations are not necessary for fertilization nor for adequate progestational stimulation for implantation and successful pregnancy.

Anecdotal reports in the literature (see Eisenberg and Isaac, 1963) indicate that copulatory patterns are similar in other kangaroo rat species although there does seem to be variation in the degree of intraspecific aggression associated with pre-copulatory behavior.

Gestation Length and Litter Size: Laboratory studies have established the gestation length of several kangaroo rat species to be about 29-33 days (Day *et al*., 1956; Butterworth, 1961a; Eisenberg and Isaac, 1963) although Chew (1958) reports a gestation length for D. merriami of 17-23 days. The reason for this large discrepancy is not clear, but Chew's estimate is certainly in error.

All field and laboratory studies report modal litter sizes in kangaroo rats of two or three with a range of one to five (Fitch, 1948; Doran, 1952; Day *et al*., 1956; Holdenreid, 1957; Reynolds, 1960; Chew and Butterworth, 1959; Lackey, 1967; Bradley and Mauer, 1971; Flake, 1974).

There are scattered observations of growth and development of kangaroo rats (Culbertson, 1946; Fitch, 1948;

Doran, 1952; Holdenreid, 1957; Chew and Butterworth, 1959; Reynolds, 1960; Butterworth, 1961b; Lackey, 1967) but most suffer from small sample sizes and a lack of systematic observation. Because I have collected substantial data on the growth and developmental trends in kangaroo rats, I will defer treatment of this topic to the results section.

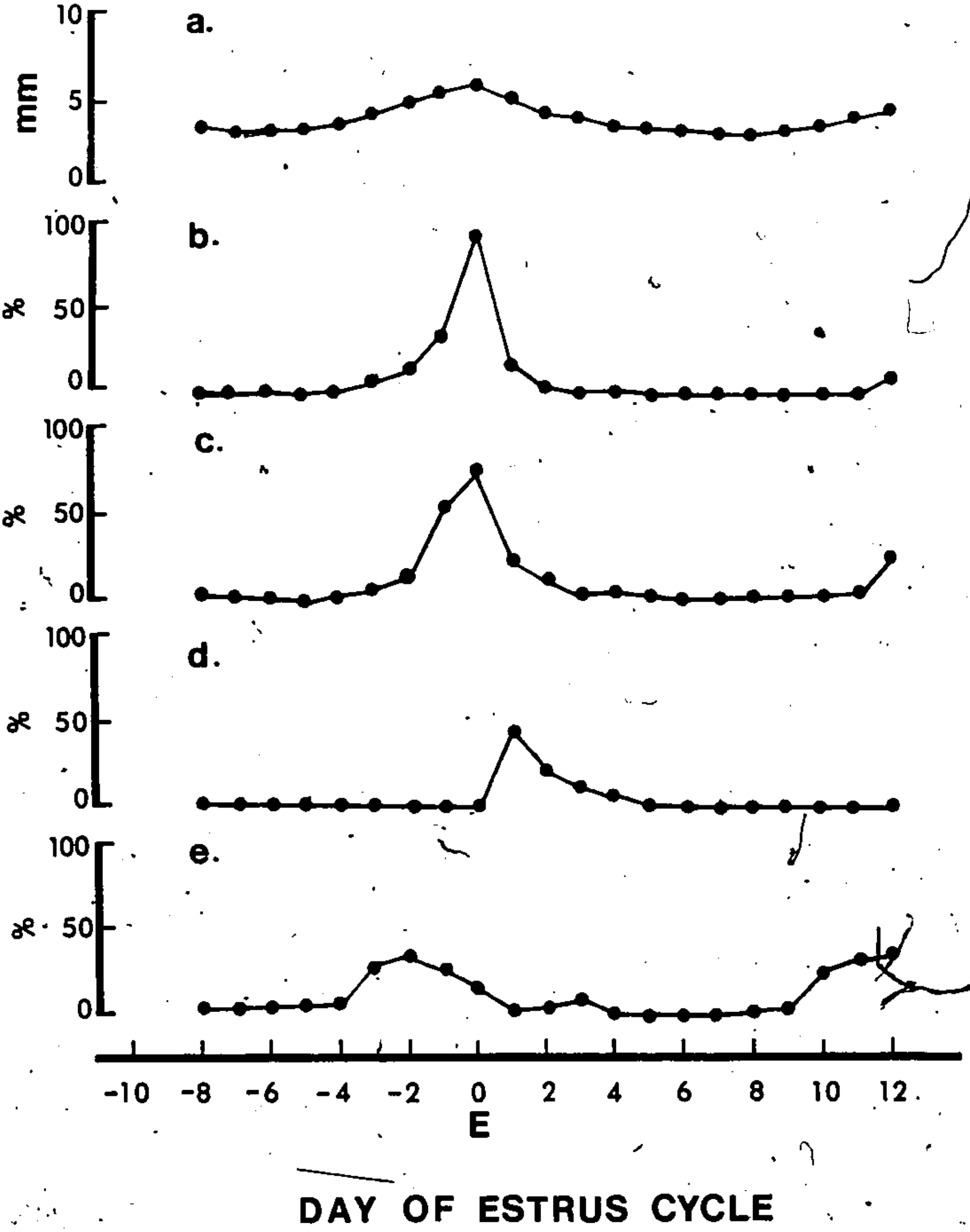
Although one can glean from the literature a substantial amount of anecdotal information on the reproduction of kangaroo rats in the field and captivity, there is a lack of convincing quantitative data and several glaring inconsistencies, especially in regard to breeding cycles and gestation length. In response to the paucity of reliable information, Margo Wilson, Martin Daly, and I have conducted several laboratory studies and observations of the reproductive behavior of D. merriami and D. microps including investigations of the changes in external genitalia in females, vaginal cytology, ovarian histology, effects of hormone replacements, maternal behavior, and growth and development. These data are presented in detail elsewhere (Wilson, Daly, and Behrends, in prep; Daly, Wilson, and Behrends, in press; Behrends, in prep); thus I will restrict my discussion here to laboratory observations relevant to our field studies on free-ranging D. merriami including the length of breeding cycles, the efficacy of female external genitalia for assessing reproductive state, maternal behavior, and growth and development. In addition, I will present data on the reproductive activity of free-ranging D. merriami gathered in the course of the radiotelemetry studies. In the discussion section I will comment on the reproductive traits of D. merriami from the life history theory perspective.

Results of Breeding Studies

External Genitalia: A total of 106 estrous cycles were recorded for 13 females between March and September 1979. The daily changes in appearance of external genitalia are shown in Figure 4.1. Vaginal opening and maximal vulvar swelling were limited to 1 or 2 days of the cycle at estrus. The presence of a vaginal cast was limited to 1 day after estrus and the presence of blood occurred reliably 1-3 days before estrus.

D. merriami did not begin breeding in the laboratory until June 1980 so there were no copulations recorded for the time period when the external genitalia of the females were monitored daily. However, for the period between June 1980 and December 1982 we have data on the appearance of the external genitalia on 66 days of copulation (behavioral estrus) for 31 females. At behavioral estrus the external genitalia were characterized by medium to maximal vulvar swelling, a perforable vaginal orifice, and no discharge. The diameter of the vulva was measured in six animals with

Figure 4.1. Daily changes in the appearance of D. merriami external genitalia over the estrous cycle. a. Vulvar diameter. b. Percent of individuals medium-swollen or swollen. c. Percent of individuals with an open vaginal orifice. d. Percent of individuals with a filamentous discharge. e. Percent of individuals with a blood discharge. E represents the day of estrus.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12
DAY OF ESTRUS CYCLE

two at 5.5 mm, three at 6.0 mm, and one at 6.5 mm (anestrous females generally measure 2-3 mm). In mating tests, three of these six females copulated.

Estrous Cycle Length: A hierarchy of criteria (see methods in Chapter 3) was used to select a female for mating and to define vaginal estrus and inter-estrus intervals. Two independent observers selected the same day for vaginal estrus for 79% of the 119 estrous periods used to define estrous cycle length. Although none of these females copulated, the data are similar for the appearance of the external genitalia of females that copulated between June 1980 and December 1982. The reliability of the estrous cycle length is illustrated in Figure 4.2. The modal cycle length of 106 cycles for 13 females was 13 days (Figure 4.3).

Ovarian histology (for details see Wilson et al., in prep) indicated that the formation of corpora lutea after ovulation does not depend on stimulation during copulation; in *Dipodomys* ovulation and formation of corpora lutea evidently occurs spontaneously.

Gestation Length and Litter Size: Due to the practice of checking females for litters once a day it is possible that an estimate of gestation length could exceed the actual period by one day if a female delivered soon after the daily check. The modal gestation length for 65 pregnancies in

Figure 4.2. Representative estrous-cycle lengths for *D. merriami* females. Open circles indicate days on which the vagina was perforate. The height of the curve indicates the degree of vulvar swelling. Numbers between maximal swelling points are the number of days between maximal swellings (i.e. the cycle length).

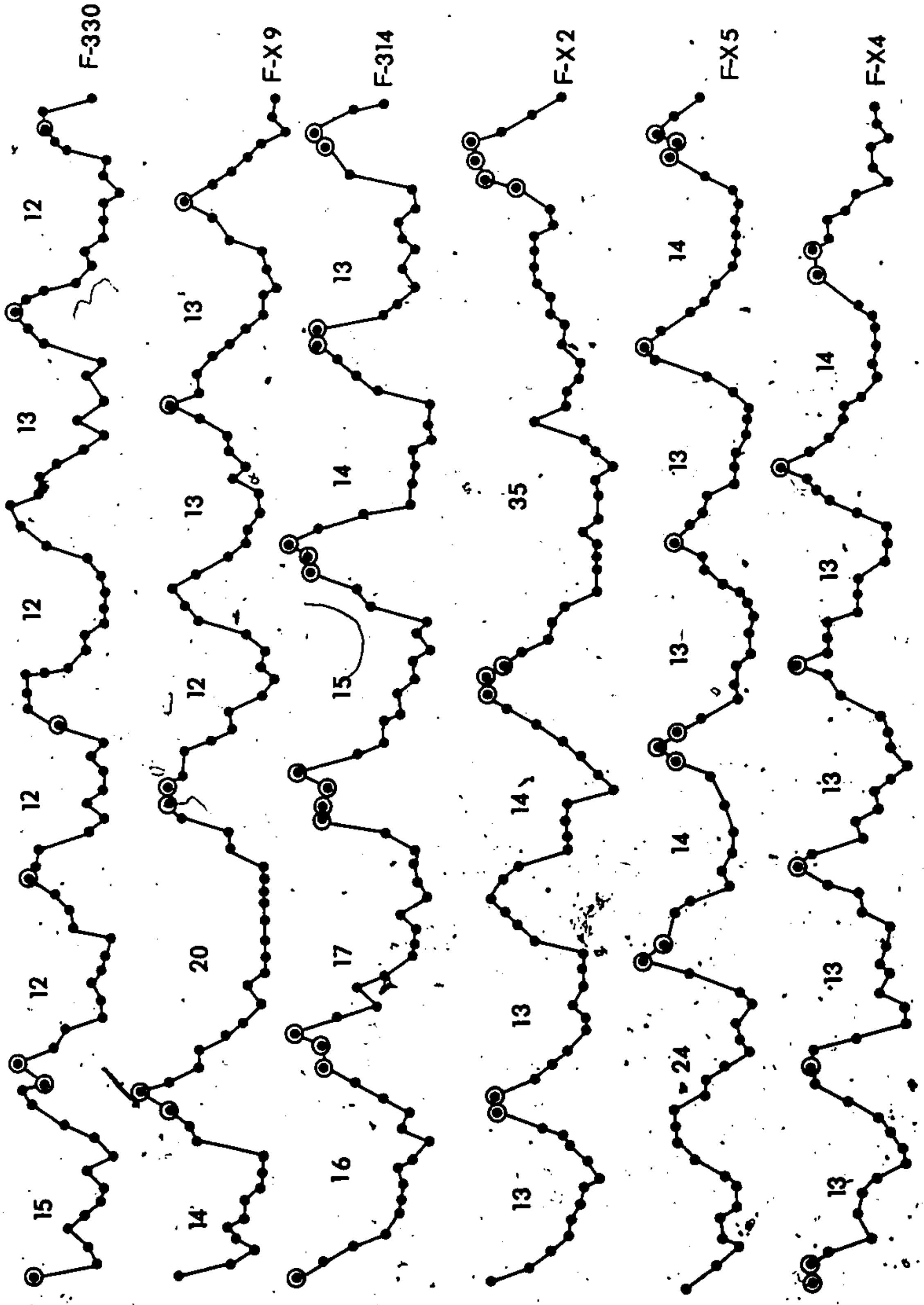
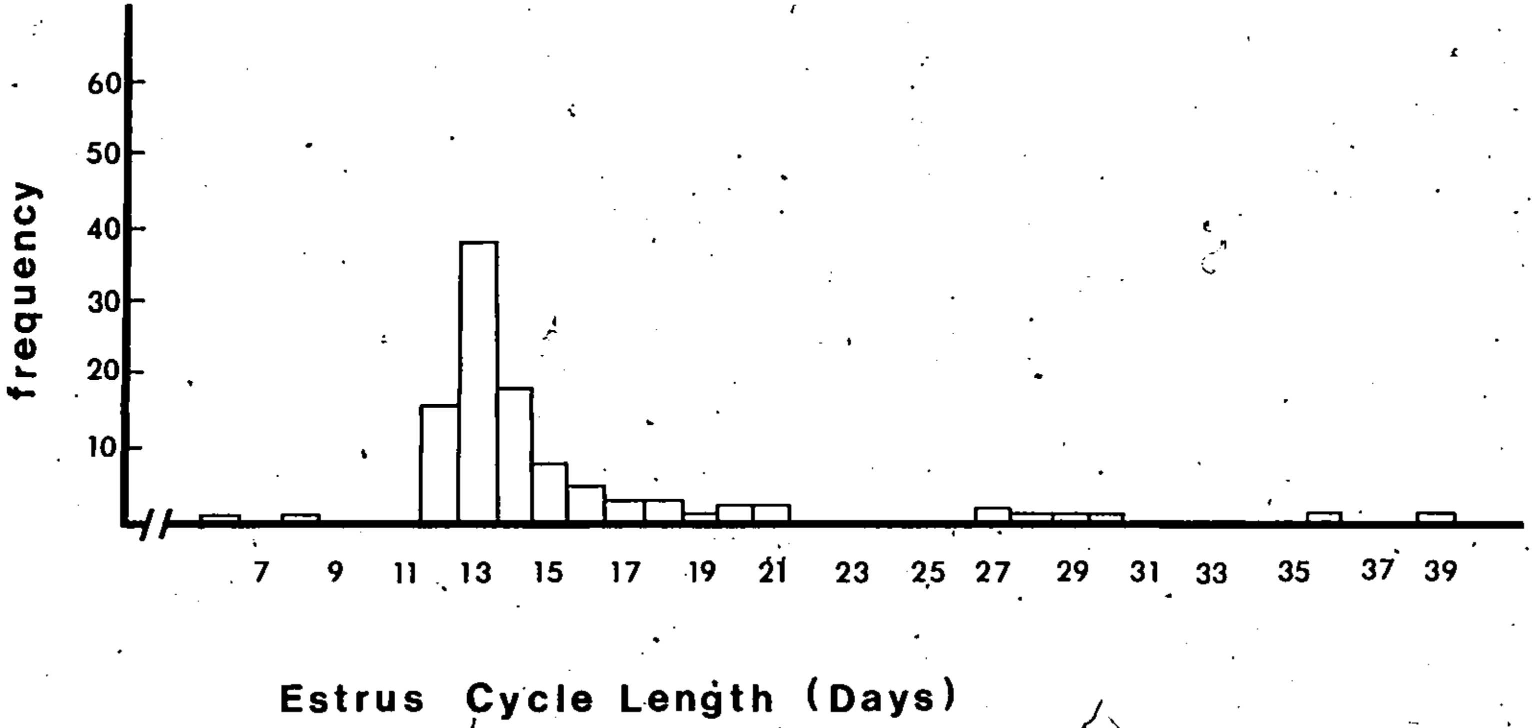

F-330
12
13
12
12
12
15
F-X9
13
13
12
20
14
F-314
13
14
15
17
16
F-X2
35
14
13
13
F-X5
14
13
13
14
24
F-X4
14
13
13
13
13

Figure 4.3. Estrous cycle lengths for D. merriami females.


frequency
60
50
40
30
20
10
7
9
11
13
15
17
19
21
23
25
27
29
31
33
35
37
39
Estrus Cycle Length (Days)

which the date of copulation was certain was 33 days (Table 4.1).

Between April 1978 and April 1983, 322 D. merriami pups were born to 51 females in 129 deliveries for a mean litter size of 2.50 (Table 4.2). Of these, ten wild-conceived litters ($\bar{x} = 3.70$) were significantly larger ($\underline{t}_{127df} = 4.75$; $\underline{p} < .001$) than 119 laboratory-conceived litters ($\bar{x} = 2.39$). The lower productivity of laboratory matings cannot be attributed to inbreeding since related animals were not mated.

Development: The appearance of some representative developmental landmarks is found in Table 4.3. Pups are born hairless but pelage appears within a few days and animals are fully furred by 10-12 days postpartum. If the mother is present and not disturbed, the pups remain in the nest for the first seven days. Development tends to proceed rapidly from about day 10 postpartum. At this time the pup's eyes and ears begin to open, locomotion and grooming attempts come under progressively finer motor control, and the pups begin to sit up, manipulate, and ingest solid food. Between days 15 and 20, the pups exhibit grooming behavior including complex sequences of scratching and grooming of the head, body, and tail. At this time the pups exhibit their first crude attempts to sandbathe, incorporating both ventral and side rubs. Forepaw digging in combination with a hind foot

Table 4.1. Duration of gestation for *D. merriami*.

	Duration of Gestation (Days)			
	32	33	34	35
# Pregnancies	22	31	11	1

Table 4.2. Litter sizes for _D. merriami_.

	Litter Size					
	1	2	3	4	5	6
Lab-conceived	13*	59	35	11	1	0
Wild-conceived	0	0	5	4	0	1

* Values are frequencies

Table 4.3. Developmental landmarks for *D. merriami* juveniles.

Characteristic	$\bar{x}$ Days of Age	Range
Pelage	3.7	2-5
Lower Incisor	7.5	5-10
Upper Incisor	8.7	6-12
Flank Scratch	10.6	7-16
Head Groom	13.7	10-18
Body Groom	14.0	13-15
Tail Groom	16.6	11-24
Eyes Open	12.0	10-14
Eat Solid Food	11.7	9-15
Dig and Kick	19.4	14-30
Sandbathe	19.2	13-35
Bipedal Hop	14.3	11-18
Face-Face Sniff with Sib	16.3	11-23
Chase Mother	19.5	15-25
Weaned	23.0*	
Ears Open	15.3	12-18

* Approximate Age

kick used for burrowing also appears about this time. Social interactions become more directed at this time with face-face sniffing, pawing, ventral-ventral wrestling, chasing, and biting. By days 20-25 postpartum the pups exhibit a range of behavioral characteristics similar to those observed in adults. Weaning probably occurs between 20 and 25 days although this determination is difficult due to the limited sample period each day.

Growth: The body mass growth curves for 24 pups of both sexes for the first 120 days postpartum is presented in Figure 4.4. The measurement for the instantaneous percentage rate of growth is according to Chew (1958) where

$$k = ((\ln m_2 - \ln m_1)/(t_2 - t_1))100$$

in which $\ln m_1$ and $\ln m_2$ are the natural logarithms of the measurements at time period 1 (t_1) and time period 2 (t_2). Growth rate is highest at an average of 8% per day for days 1-20 postpartum and then abruptly declines after that point. Weight at birth is about 10% of weight at day 120, 50% at day 23, 74% at day 52, and 90% at day 80.

A breakdown of individual pup mass and litter mass based on litter size (Table 4.4) indicates that there is an inverse relationship between litter size and individual pup size although these differences are not testable statistically due to small sample sizes for litters with three or four pups. Not surprisingly, litter mass increases

Figure 4.4. Body mass growth curve for male and female *D. merriami* up to 120 days of age. The values of k for different intervals are given beneath the growth curve (see text for calculation and interpretation of k).

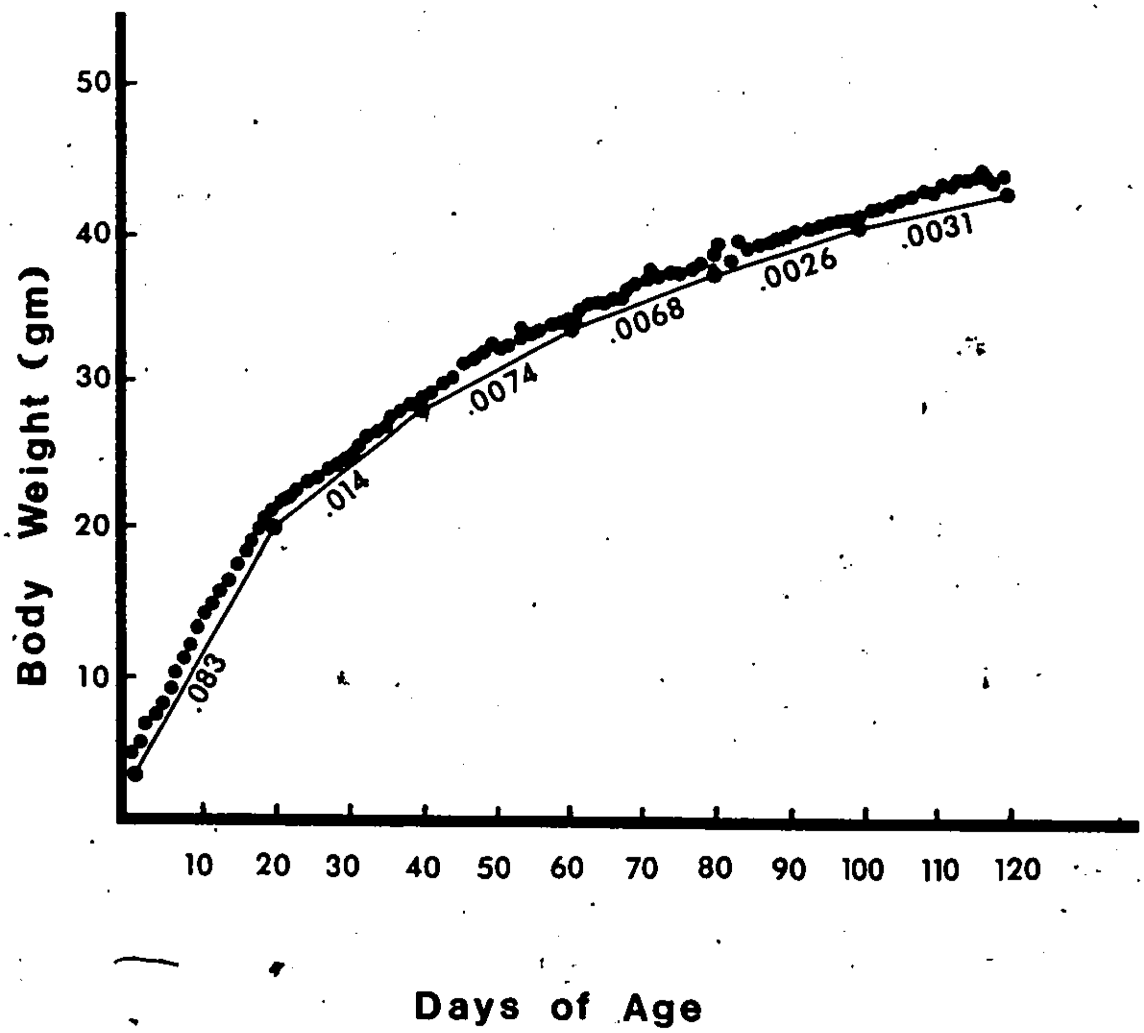

Body Weight (gm)
50
40
30
20
10
10
20
30
40
50
60
70
80
90
100
110
120
.083
.014
.0074
.0068
.0026
.0031
Days of Age

Table 4.4. D. *merriami* litter and individual pup weights.

Litter Size	# of Pups	$\bar{x}$ Day 1 Pup Weight	$\bar{x}$ Day 1 Litter Weight
2	18	4.59*	9.20
3	6	4.29	12.89
4	4	4.04	16.16

* Weight in grams

with litter size.

The growth curve for tail length is presented in Figure 4.5. The tail grows throughout a kangaroo rat's lifespan, albeit slowly in adulthood, and may reach lengths of 15-16 cm in the field (Chew, 1958). The pattern of tail growth here is very similar to that for body weight with an 8% increase per day on average for days 1-20 postpartum. Using 15 cm as the adult tail length, animals achieved 93% of tail growth by day 80 postpartum.

The growth rate of the hind foot, depicted in Figure 4.5, is strikingly different. Ninety-two percent of the adult size is achieved by day 20 postpartum.

Nest Attendance: The mean percentage of observations of the mother attending the nest within a session (i.e. at or on the nest) are presented in Figure 4.6. Nest attendance was very high for the first five days postpartum and then generally decreased over the following 20 days. Although not shown in the graph, the increased time off the nest was related to an increase in the percentage of samples during which the female was observed on the surface feeding. Food intake by the dam was not measured so it is not known whether the surface feeding reflected a greater intake or simply a change of location.

The mean percentage of samples within a session for which at least one pup was on the surface is also shown in

Figure 4.5. The growth curves for tail and hind foot for _D. merriami_ up to 80 days of age. ● = tail and ○ = hind foot. The values for k for tail length are given beneath the curve (see text for calculation and interpretation of k).

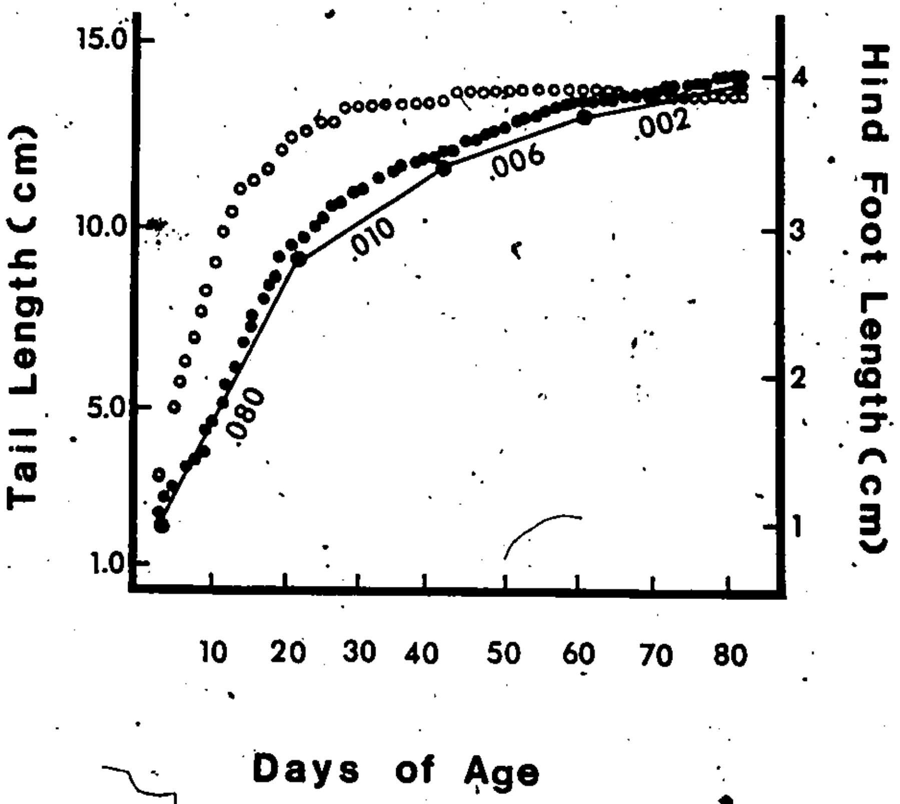

Tail Length (cm)
Hind Foot Length (cm)
Days of Age
15.0
10.0
5.0
1.0
4
3
2
1
10
20
30
40
50
60
70
80
.080
.010
.006
.002

Figure 4.6. The percentage of observations in which the mother (●) was on the nest and at least one pup (○) was off the nest. Vertical bars represent one standard deviation.

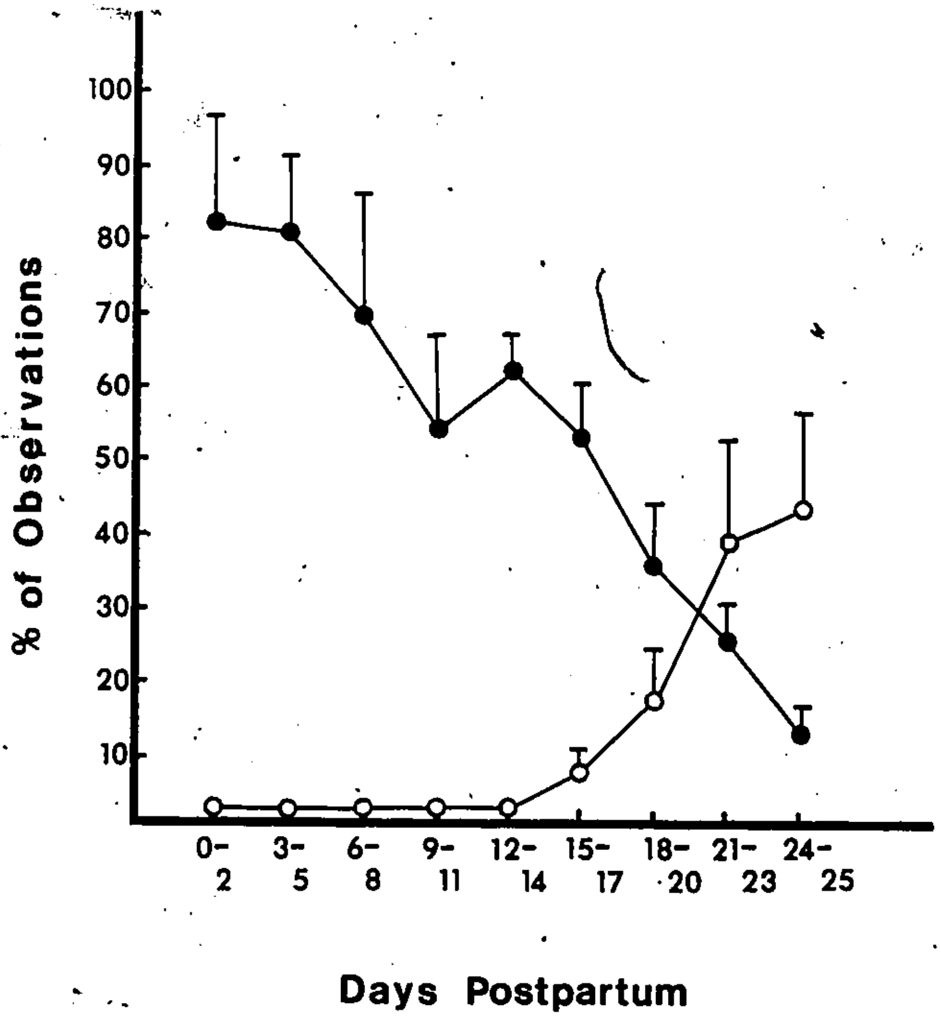
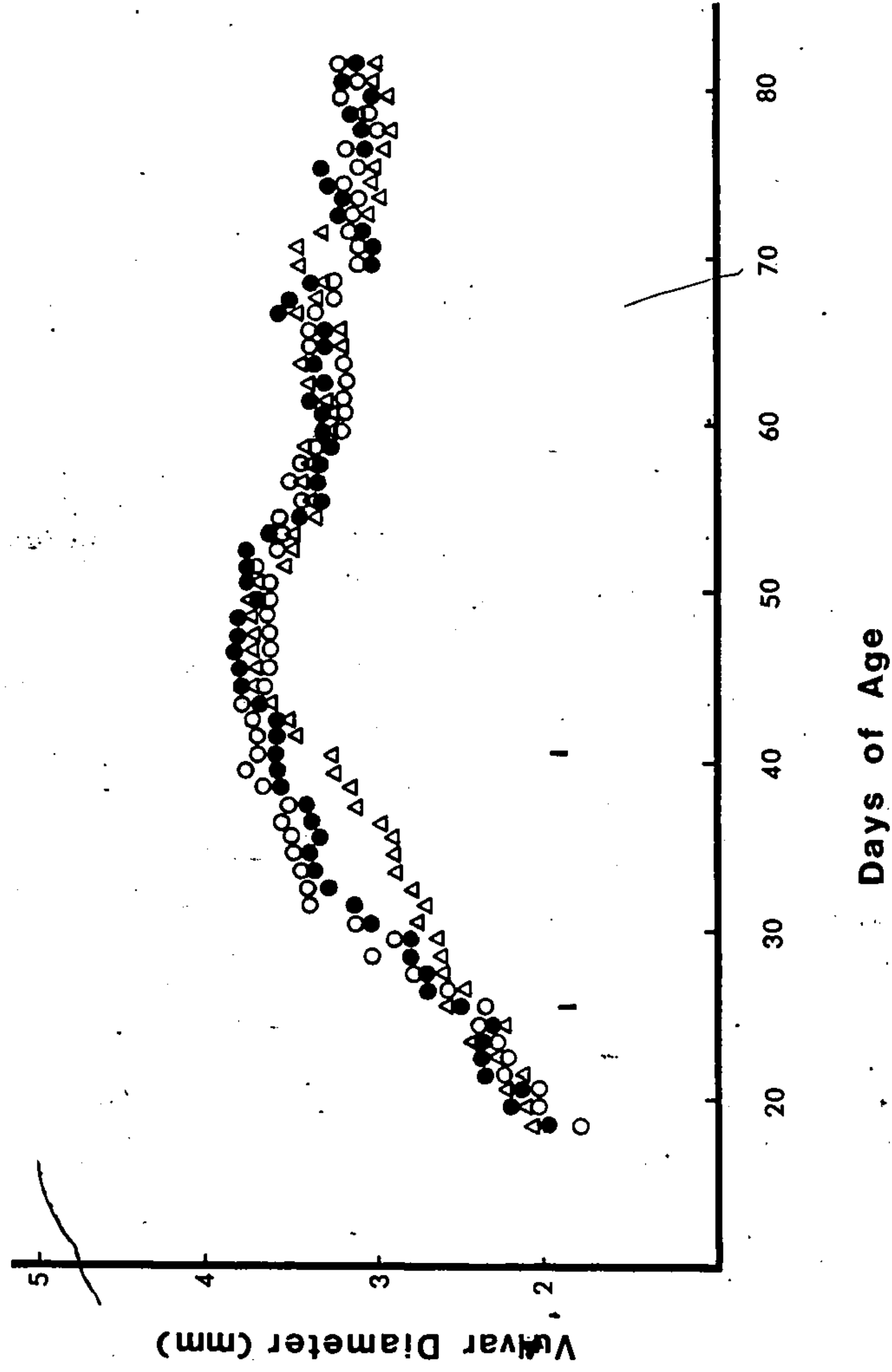

% of Observations
100
90
80
70
60
50
40
30
20
10
0-2
3-5
6-8
9-11
12-14
15-17
18-20
21-23
24-25
Days Postpartum

Figure 4.6. Pups were not observed to leave the burrow until about day 15 postpartum, after which activity increased dramatically. There was, expectedly, an inverse relationship between the percentage of samples in which a female was attending the nest and the surface activity of the pups.

Sexual Maturation: Forty-four females were examined for onset of sexual maturity and subsequent estrous cycles from 18 days of age to an average of 138 days of age (range = 64-194 days). Examinations were terminated when females were presumed to be pregnant. Vaginal openings first occurred at 74 days of age on average (range = 71-77 days, n = 28) and maximal vulvar swelling occurred at 58 days of age on average (range = 24-92 days, n = 39). The early vulvar swellings were associated with a persistent crusty and/or flaky discharge. The onset of adult-like estrous cycles occurred later, 89 days of age on average (range = 73-105 days, n = 11) and the first subsequent inter-estrous interval was 18 days later on average (range = 12-24 days, n = 10). Four females first gave birth on day 97, 155, 167, and 172 days of age, the earliest fertile mating occurring on day 64.

Separation of the pups from their mother on day 40 rather than day 25 apparently retarded the growth in diameter of the female pups' external genitalia (Figure 4.7). There was no apparent effect of separating the littermates at the time of weaning (25 days) compared to 15 days later.

Figure 4.7. Vulvar diameters of juvenile female _D_. _merriami_ under three social conditions. Condition 1 (o): Pups were weaned and housed separately at 25 days of age. Condition 2 (●): Pups were weaned at 25 days of age and housed separately at 40 days of age. Condition 3 (Δ): Pups were weaned and housed separately at 40 days of age.


Vulvar Diameter (mm)
2
3
4
5
20
30
40
50
60
70
80
Days of Age

Furthermore, the sex composition of the litter had no apparent effects.

We have established several basic parameters of Dipodomys reproduction and development in the laboratory. The significance of these observations will be presented more fully in the main discussion of this chapter following the results of the field observations of reproductive activity. Suffice to mention here that these data also provide important practical information for the interpretation of field observations. The characterizations of female external genitalia and inter-estrous intervals are useful for the assignment of reproductive condition to wild-trapped females. In Chapter 5, I present data on the ranging activities of females in relation to reproductive condition and thus accurate evaluation of reproductive state is critical.

Field Breeding Activity

Animal Captures: A summary of animal captures on the two study sites between November 1980 and December 1982 is presented in Table 4.5. The number of individuals marked on the Coyote Wash site includes 14 individuals captured off the trapping-grid when traps were set around the day burrows of radio-implanted animals. All subsequent analyses will include only animals captured on the regular trapping-grid.

Table 4.5. Animal captures 1980-1982

Site	# Traps	*D. merriami*			*Perognathus*	*Neotoma*	*Peromyscus*
		Male	Female	?			
Ramada Fall 1980	1312	95 (16)*	60 (12)	3	245	39	9
Coyote Wash 1982	4562	307 (45)	322 (41)	6	686	11	0

* Numbers in parentheses indicate the number of individuals.

? Indicates that an animal escaped before its sex was determined.

The community structures of the two study sites were quite different with more cricetid rodents (i.e. *Neotoma* and *Peromyscus*) occurring on the Ramada site. Slightly more male than female *D. merriami* were marked on both sites. Monthly data on captures and the recruitment of new individuals to the Coyote Wash site trapping-grid (Table 4.6) reveals only small fluctuations in the overall trapping population size. However, the monthly differences from January to May 1982 in the number of newly marked individuals approach significance ($\chi^2_{5df} = 8.06$, $.10 < p < .05$). Ten of the 11 new individuals captured in January, February, and March were of adult size (>35 g) and ten of the 17 new individuals captured in April and May were probably juveniles (<28 g). The greater turnover rate of individuals in April and May may reflect the intensification of intraspecific competition resulting from the influx of juveniles. Another possibility is that predator density increases around this time (especially snakes which become more active with spring rises in temperature) and thus provide the opportunities for immigration by conspecifics. A breakdown and explanation of the different fates of individuals captured on the Coyote Wash grid from December 1981 to December 1982 is provided in Table 4.7. There was no sex difference for any fate category. Although it is impossible to estimate survivorship and longevity in the field from these data, it is possible to compare males and females on the number of days they were

Table 4.6. Monthly trapping-grid captures.

	1980 Dec	1981 Dec	1982 Jan	Feb	Mar	Apr	May	Nov	Dec
Male	16	15	14	10	9	11	11	14	10
Female	12	10	12	13	11	12	11	15	13
# New		25	7	2	2	9	8	17	2
% Turnover			27	9	10	39	36	59	9

Table 4.7. Fates of *D. merriami* at Coyote Wash site.

Fate	Female	Male	Definition
Disappear	14	18	Never retrapped
Snake	2	2	
Other	5	5	Animal found dead or implant found
Accidental	3	3	Human intervention
Survive	11	9	Alive when study 3 terminated

in the trapping population, defined here as the interval between the first and last capture (or last radio location in the case of radio-implanted animals). For females the median number of days in the population was 42 (range = 1-377 days, n = 35) and for males, 41 days (range = 1-335, n = 37).

Reproductive Activity: The percentage of captured individuals in reproductive condition on a monthly basis is illustrated in Figure 4.8. With the exception of November 1980, most males were reproductive during the months the populations were sampled. By contrast, females were reproductively inactive in the fall with the exception of December 1981. During this month, 50% of the captured females showed evidence of cycling and from January the majority of females showed evidence of reproductive activity until termination of the study in late May. A summary of the breeding activity for regularly-caught females (Table 4.8) shows that the majority of females bred at least once and it is likely that most were capable of breeding twice or more within the season. The mode of one litter is probably an artifact of fewer captures of those females.

Inter-brood Interval: It was necessary to use anecdotal information to estimate the minimum inter-brood intervals because of the large time gaps between successive captures

Figure 4.8. The percentage of captured *D. merriami* individuals in reproductive condition (see text of Chapter 3 for details of assigning reproductive condition) during different months on the Ramada and Coyote Wash sites. ○ = females, ● = males.

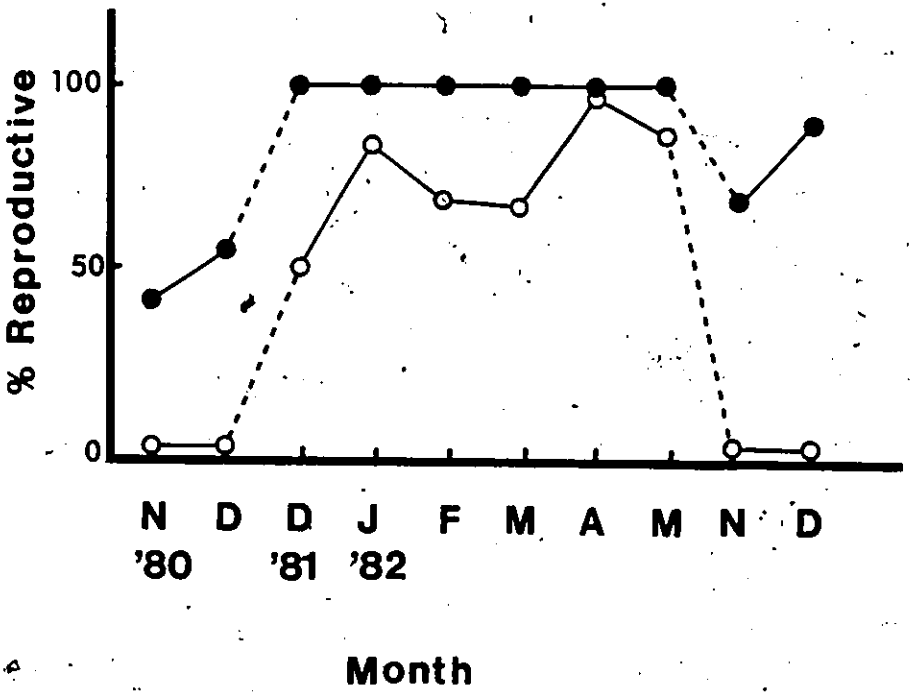

% Reproductive
100
50
0
N '80
D
D '81
J '82
F
M
A
M
N
D
Month

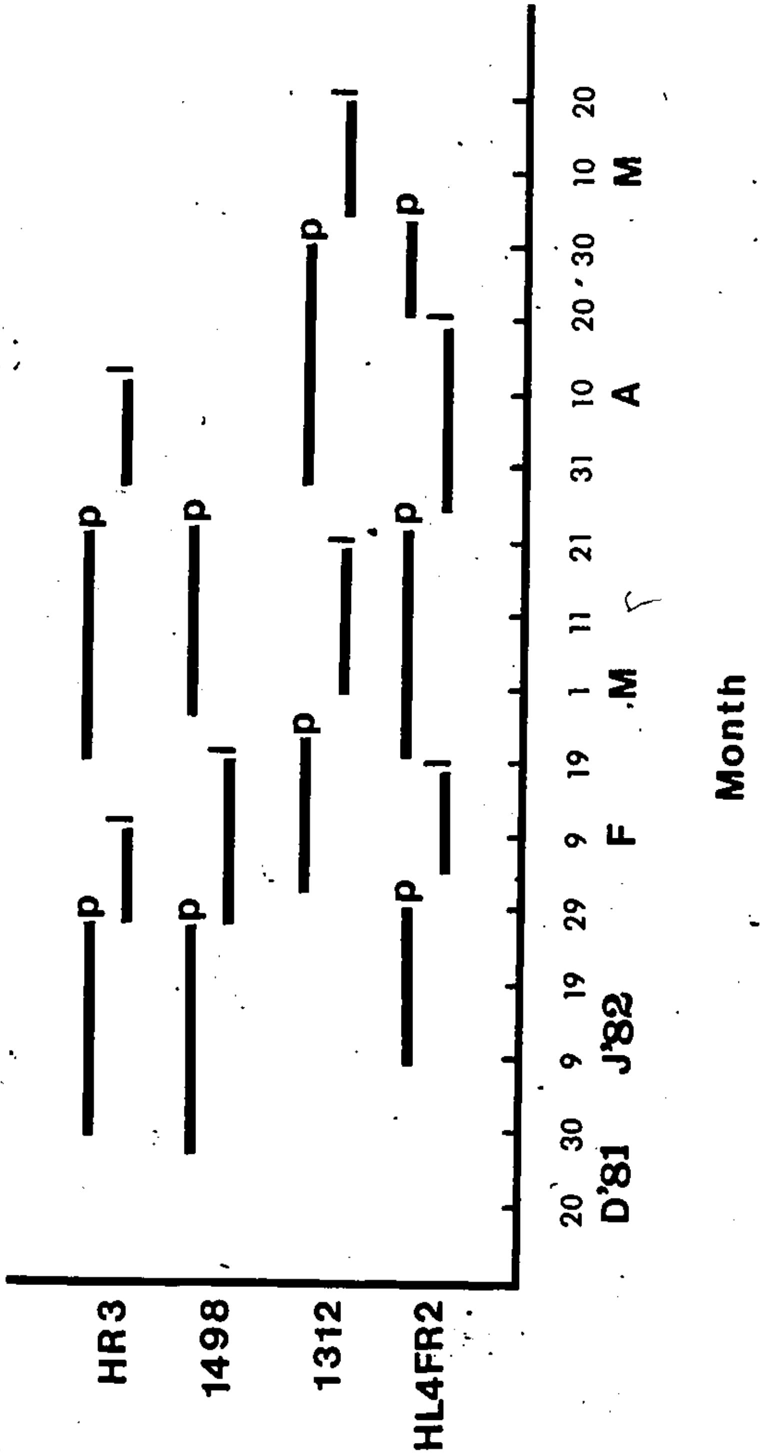
Table 4.8. Reproductive activity of D. merriami females during study period 2.

	# of Pregnancies		
	1	2	3
# of Females	13	4	1
Median # of Captures	4	15.5	7

for many females. The data from three females indicate that a female is capable of producing successive litters at 50-60 day intervals from weaning. For example, female HL4FR2 weighed 37 g and was lactating on February 17 and weighed 44 g on March 19 (Figure 4.9). This 30 day interval from lactation to late pregnant weight was among the shortest observed. Furthermore, this female was lactating until at least April 21 and subsequently weighed 41 g on May 6 suggesting that she was pregnant a third time. Female 1498 was lactating until about February 19 and subsequently weighed 47 g on March 15, an interval of only 24 days from late weaning to late pregnant weight (Figure 4.9).

Juvenile Breeding: The field data demonstrate that females may breed in their natal season. Of five presumably juvenile females marked (see below for this determination), two exhibited clear signs of reproductive activity. A female estimated to be born in the last week of January became pregnant at approximately 40-50 days of age and successfully carried a litter to full term, as evidenced by lactation. Another 23 g female had a swollen vagina and copulatory plug on April 29. Apparently this female did not become pregnant because she exhibited vaginal bleeding on May 15 and May 19 and a closed, swollen vagina with discharge on May 25. This 20-25 day inter-estrous interval was not unlike those observed in laboratory-raised juvenile females.

Figure 4.9. Temporal aspects of breeding by four frequently captured *D. merriami* females during study period 2. p = pregnant and l = lactating.


HR3
1498
1312
HL4FR2
p
l
20
30
9
19
29
9
19
1
11
21
31
10
20
30
10
20
D'81
J'82
F
M
A
M
Month

Age at Emergence: In two cases female pups, whose approximate dates of birth were known from their mothers' capture records, were observed making excursions from the natal burrow with their mothers. In both cases the pups were 20-25 days of age when first observed on the surface. One pup weighed 21 g at approximately 23 days of age and the other 24 g at approximately 30 days of age. These values agree with those for laboratory-raised pups at the same age (Figure 4.4) indicating that field weights up to 25 g may be used to assess the age of juveniles. Assessing the age of field animals weighing over 25 g from the laboratory standard is dubious, however. We have recorded weights under 30 g in known adults in the field whereas laboratory animals on ad libitum diets do not drop below this weight once it has been obtained. On the assumption that weights less than 25 g provide a useful estimate of age, we have also captured juveniles of approximately 19, 25, 29, and 33 days of age.

The use of tail length to estimate ages in the field proved to be impractical because of the difficulty of accurate measurement and the common occurrence of tail breakage in the Sherman traps.

Body Weight: Table 4.9 presents the average body weights for adult males and females during the three study periods. Males are significantly heavier than females without accounting for

Table 4.9. Mean body weights (g) of *D. merriami*.

Study Period	Male	Female
1	35.7 (3.31)	34.1 (3.40)*
2	38.4 (4.40)	37.5 (3.64)
3	36.5 (2.70)	33.0 (1.52)
Overall	36.9 (3.85)	35.2 (4.00)

* Standard deviations are in parentheses

reproductive condition ($\underline{t}_{104df} = 2.74$; $\underline{p} < .01$).

It is generally believed that animals must be in good physical condition to breed. One common metric of physical condition is body weight. Females were heaviest during the breeding season (i.e. study period 2) but this difference was, in part, due to the heavier weights of pregnant and lactating females (Table 4.10). For instance, within the breeding season females were significantly heavier during lactation compared to non-reproductive periods ($\underline{t}_{9df} = 3.27$; $\underline{p} < .01$). The difference in non-reproductive female body weights between the different study periods was not clear-cut. Although non-reproductive females in the second study period were not significantly heavier than non-reproductive females in the first study period, they were significantly heavier than non-reproductive females on the same site in the third study period ($\underline{t}_{33df} = 3.52$; $\underline{p} < .01$)

A positive relationship exists between reproductive condition and body weight in males as well. Due to small sample sizes, it was not possible to compare the body weights of scrotal and non-scrotal males within each study period and, hence, control for environmental factors such as resources, climate, season, and population differences. Combining the data for three study period, however, revealed a significant difference ($\underline{t}_{54df} = 3.50$; $\underline{p} < .01$) in body weight

Table 4.10. Body weights (g) of *D. merriami* females at different reproductive stages.

	Non-reproductive	Pregnant	Lactating
Mean	35.5 (2.50)	40.9 (2.50)	38.1 (2.80)
Sample Size	17	16	14

between scrotal ($\bar{x}$ = 38.2 ±3.9 g), and non-scrotal ($\bar{x}$ = 34.9 ±2.9 g) males.

Climate and Reproduction: It is interesting to note that Deep Canyon received 25 mm of rain for the months July to November in the fall of 1981, the year that 50% of the females exhibited breeding activity in December. On the other hand, 58 mm of rain fell in 1980 and 116 mm fell (including 91 mm on one day in September) in 1982 over the same time period. In December of these years no females were in reproductive condition. Unfortunately we were not in the field beyond December to record the onset of the breeding season these years. It may be the case that excessive rainfall interferes with the normal germination of annuals or whatever cue happens to trigger reproduction. It is also possible that flooding actually washes away much of the seed crop. Nonetheless, the relationship between the optimal amount and timing of rainfall for good annual plant germination (Beatley, 1969) and the earliest breeding recorded over the three study periods is interesting and consistent with Beatley's evidence for a relationship between precipitation, green vegetation, and reproductive activity. It was noted, however, that surface growth of herbaceous vegetation was not necessary for the successful rearing of offspring. For instance, female 1314 gave birth to at least one offspring in late January and successfully weaned the pup by mid-February (see earlier results) when annual vegetation had not yet appeared. It is possible that this female obtained free water from sub-surface growth or perennial leaves, however.

Discussion

A comparison of the reproductive tactics of mammals reveals a diversity of patterns which defies taxonomic or ecological categorization. Mammals solve very similar problems of reproduction in a variety of ways (see Conaway, 1971; Weir and Rowlands, 1973).

Rodents in general possess several traits which indicate that they are relatively "r-selected" mammals. In most rodent species the life expectancy of an individual attaining maturity in a natural population is probably rather short, perhaps on the order of only a few months. Consequently, a general characteristic of an r-selected rodent should be the capacity to produce many offspring over a short period of time. _D. merriami_, though typical for a rodent its size with respect to some reproductive traits, possesses some traits which indicate that it is relatively "K-selected".

Conaway (1971) and Weir and Rowlands (1973) suggest that short estrous cycles should be associated with high turnover prey species; that is, rapid recovery from a non-pregnant cycle should be strongly selected for in species with short life expectancies. The non-pregnant estrous cycle of D. merriami, however, is relatively long at 11-14 days compared to several small rodents including Rattus species, the house mouse, and the golden hamster which have cycles ranging from four to eight days (Conaway, 1971). The physiological explanation for the difference is straightforward. Our studies reveal that D. merriami has spontaneous corpus luteum formation after spontaneous ovulation, a pattern similar to the guinea pig (Wilson et al., in prep). It has been demonstrated in many mammal species that secretion of progesterone from the corpus luteum inhibits a return to the estrous condition (Weir and Rowlands, 1973). Corpus luteum formation in the aforementioned myomorph rodents, on the other hand, requires the stimulation of mating. If, for example, a sterile mating occurs in these species, a luteal phase or "psuedo-pregnancy" of 9-12 days follows, after which estrus is reinstated.

Exactly why D. merriami has a spontaneous luteal phase as opposed to a phase induced by stimulation, from an evolutionary view, is more obscure. A provocative argument is that spontaneous corpus luteum formation phyletically preceded the induced pattern which arose in a later period in high turnover prey species (Weir and Rowlands, 1973). An observation consistent with this hypothesis would be that kangaroo rats and other rodents with spontaneous corpus luteum formation have longer life expectancies in natural populations than do rodents with induced corpus luteum formation. As pointed out in the introduction, however, documentation of survivorship in natural kangaroo rat populations and other rodent species is poor. Thus it is difficult to examine the relationship between population turnover and cycle length across species. Furthermore, questions pertaining to the phylogeny of estrous cycle length are clouded, for at least two reasons. Firstly, observations of non-pregnant cycles in natural populations are rare even though these same species may exhibit quite regular cycles in the laboratory. Conaway (1971) and Weir and Rowlands (1973) make the point that under natural conditions the estrous cycle may not normally be involved in reproductive activities and, therefore, selection pressure would not have acted on its length. Secondly, even if one could demonstrate high turnover in species with spontaneous corpus luteum formation, the question as to whether the species possessed the physiological preadaptations or genetic variability to develop the pattern of induced corpus luteum formation would remain.

Another way in which some rodent species (e.g. many microtines, cricetids, and murids; Conaway, 1971) enhance their reproductive output is by a postpartum estrus. In these species the female becomes sexually receptive within hours of parturition and apparently even between the delivery of offspring (stated in Weir and Rowlands, 1973 without giving a specific reference). Although delayed implantation or embryonic diapause may occur with postpartum estrus, the inter-brood interval is significantly shortened. Consequently, this strategem allows a female to produce a large number of offspring over a short period of time. For some species there may be a limited period of time in which the chances for survival of the offspring are maximized. Furthermore, a postpartum estrus would lead to rapid replacement if a litter is lost early.

There is no evidence for a postpartum estrus in D. merriami from our laboratory and field observations. Observations of external genitalia and inter-brood intervals of 50-60 days under natural conditions indicate that females come into estrus in late lactation or shortly thereafter and estrus occurs at three to four weeks postpartum in the laboratory as well.

Comparative mammalian development is a complex topic due to the variety of factors which may influence developmental rates including the absolute size of the female, the degree of encephalization of the young, the relative metabolic rate of the female, and the structure of the placenta (Eisenberg, 1981). Although it is beyond the scope of this chapter to treat this topic in great detail, I will show that D. merriami exhibits developmental patterns similar to other rodents of its size on two measures presented by Eisenberg (1981).

In mammals generally, gestation length tends to increase with increases in body size (Kihlström, 1972), but the condition of the young at birth may be highly variable; ranging from altricial and requiring substantial parental care to precocial and requiring little or no parental care. To control for the condition of the young at birth, Eisenberg (1981) considers the relationship between adult body size and gestation length plus the number of days to eye opening (Figure 4.10). Clearly D. merriami falls well within the developmental range for myomorph and sciuromorph rodents.

It is also well established that the number of days required to reach adult body size increases with adult body size (Eisenberg, 1981). Figure 4.11 shows that the postnatal growth rate of D. merriami falls between the smaller Baiomys and the larger Neotoma and Spermophilus. Although its growth rate at the earlier stages is slightly faster than the smaller Ochrotomys, it is clear that the postnatal growth pattern of D. merriami is typical for a rodent its size.

Observations of behavioral development, including locomotion, grooming, and social interactions, indicate that laboratory-raised D. merriami are probably quite independent of their mother by three to four weeks of age, about the time of weaning. The timing of reduced maternal nest attendance

Figure 4.10. A comparison of D. merriami with selected myomorph and sciuromorph rodents with respect to the relationship between body weight ($\log_{10}$) and gestation length + days to eye opening. The polygon represents the outermost (i.e. range) of points for different species (from Eisenberg, 1981).

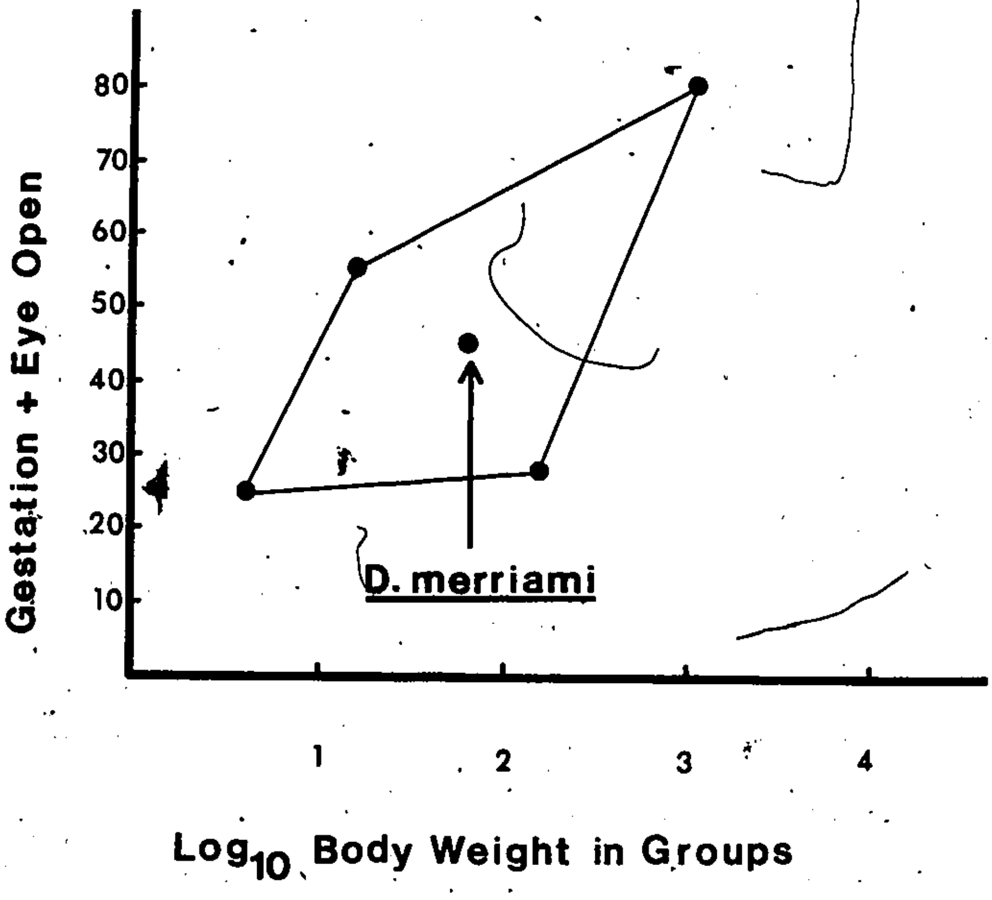
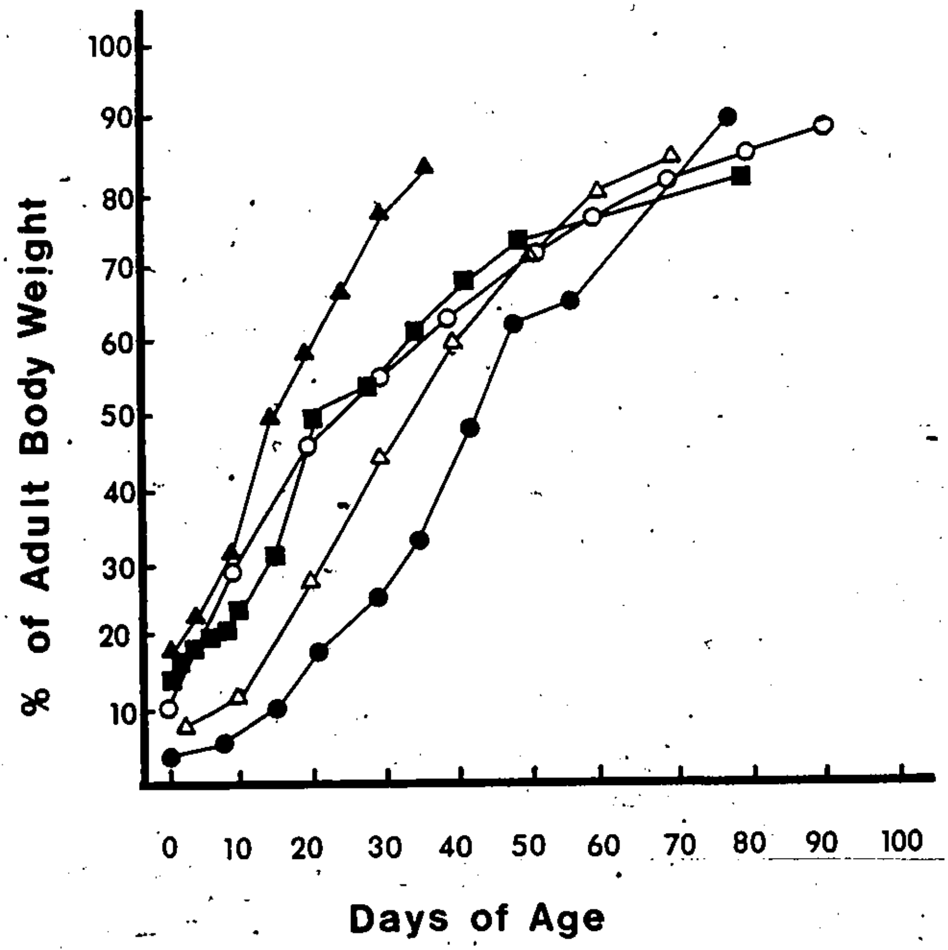

Gestation + Eye Open
80
70
60
50
40
30
20
10
D. merriami
1
2
3
4
Log10 Body Weight in Groups

Figure 4.11. A comparison of the *D. merriami* body weight curve to the weight curves for selected rodent species. ○= *D. merriami*, ●= *Spermophilus* (>500 g), Δ = *Neotoma* (100-150 g), ▲= *Baiomys* (9-12 g), and ■= *Ochrotomys* (22-25 g). (from Eisenberg, 1981).



100
90
80
70
60
50
40
30
20
10
% of Adult Body Weight
0
10
20
30
40
50
60
70
80
90
100
Days of Age

and the pups' emergence from the burrow boxes is consistent with this conclusion. The two field observations of excursions from the natal burrow by a female and her pup and age estimates for several captured juveniles indicate that pups emerge at three to four weeks of age and begin making independent excursions at four or five weeks of age (see also Jones, 1982).

Laboratory and field data demonstrate that females may become sexually mature at less than two months of age. Consequently females may breed in their natal season. Although I have documented one first year female bringing a litter to full term, whether this is a common occurrence is not known.

Conclusion

I began this chapter with a brief discussion of life history theory which assumes that a reproductive tactic is comprised of a set of coadapted traits designed by natural selection to solve an ecological problem (Stearns, 1976). The primary "decisions" animals must make regarding reproduction are at what age to breed, how often to breed, what size brood to produce, and what size offspring to produce. Some relatively definitive answers to these questions have been provided by the preceding results and discussion. D. merriami possess some relatively conservative reproductive traits compared to some other high turnover prey species. For instance. the relatively long estrus cycle, the probable lack of a postpartum estrus, and small litters suggest that this species, and very likely the entire genus, either has not been subjected to selection pressure for high reproductive output or is subjected to environmental factors which limit reproductive potential. Obviously the phylogeny of reproductive traits is difficult to establish and the assumption that reproductive traits possessed by this species are indeed adaptations to desert existence is tenuous. A detailed comparison of the reproductive traits of kangaroo rats with those of non-desert genera of the same family (i.e. Liomys and Heteromys) is needed.

Progress toward a full understanding of the life history of D. merriami is impeded by the lack of information about survivorship in natural populations and age-graded fecundity and how these factors interact with ecological circumstances (e.g. population density, resource availability, or predator density). An important question requiring this type of information, for example, is what the costs of reproduction are in terms of physiological decrements or increased risk of predation. Likewise, is it better to invest less in reproduction as a young female and to invest more with age (see discussion of reproductive value and effort in introduction)?

The literature and our field observations indicate that kangaroo rats are solitary creatures. Males and females do not share burrows nor do males care for young. It is possible that mating constitutes the only significant interaction between conspecifics. As a spontaneous ovulator, behavioral estrus in D. merriami may last for only a few hours two or three times a breeding season at intervals of 50 to 60 days. Furthermore, if females mate promiscuously there would be, perhaps, little advantage to maintaining specific social relationships. On this basis, one might predict that D. merriami should be quite asocial. On the other hand, litters are small and there is evidence that juvenile mortality exceeds adult mortality (French *et al.*, 1967), hence there are probably few juveniles available for recruitment to existing populations. Consequently, populations may have relatively low turnover and stable age-class structures (i.e. once adulthood is reached and a stable home range is established, animals may be quite long-lived). Under these conditions the opportunity for a stable social structure and distinct social relationships should exist. For instance, the maintenance of specific social relationships through direct social contact, spatial proximity, or olfactory communication (e.g. scent-marking by sandbathing) may be important to reproductive activities in regard to mate choice and/or intrasexual competition. The maintenance of specific social relationships may be important for non-reproductive activities; for example, with respect to competition for food, burrows, or territories. Furthermore, the opportunity for nepotistic behavior may exist in species with low turnover and a stable social structure (see, e.g., Jones, 1982; Sherman, 1981).

Chapter V

Determinants of Surface Activity Variation

Animals must budget their time and energy for activities which contribute both directly and indirectly to reproductive success. For kangaroo rats, some of these activities, including foraging, sandbathing, and social interactions, must be carried out aboveground. Thus a kangaroo rat must "decide" when to emerge from the relative safety of its burrow, how much time to spend aboveground, and how to allocate its time aboveground to different activities. These behavioral decisions are important if one assumes that individuals incur certain costs (e.g. energy expenditure, predation risk, or climatic stresses) and gain certain benefits (e.g. energy, nutrients, or mates) as a result of their aboveground activity. In theory, one should be able to measure the tradeoff between these costs and benefits and determine the ultimate net payoff in terms of units of biological fitness. A factor which should be an important determinant of the costs and benefits of surface activity is an individual's reproductive potential or capacity (which may be related to sex, reproductive condition, social class, etc.). Since reproductive potential varies between individuals and, indeed, for the same individual at different times, it follows that the costs and benefits of surface activity will vary as well. It is assumed that these differences will be reflected by variation in several indices of surface activity including the proportion of time spent aboveground, the distance moved over specified time periods, home range size, and habitat utilization patterns.

The focus of this chapter is the relationship between such individual characteristics as sex, reproductive condition, and size-class and the surface activity of free-ranging D. merriami as determined by radiotelemetry. It is first necessary, however, to review several somewhat diverse topics which provide the theoretical and informational framework for the presentation of the radiotelemetry data in this chapter and the chapters to follow. Since a major aim of our studies is to elucidate the socio-ecology of D. merriami, a brief outline of this approach will be presented. Next, the observed variation in surface activity by kangaroo rats in relation to sex, reproduction, season, and moonphase will be interpreted in terms of a cost-benefit analysis. Third, I will discuss studies pertaining to the free-ranging patterns and spatial relationships exhibited by three kangaroo rat species including D. merriami.

Socio-ecology

Socio-ecologists assume that a population's social structure is the product of complex interactions between individual behavior patterns for mating, rearing of progeny, resource exploitation, and predator avoidance. In order to simplify the analysis of social systems, Crook et al. (1976) consider these behavior patterns to be "functional subsystems", despite their non-independence. How animals carry out these subsystem activities is determined by both intrinsic (species) and extrinsic (environmental) parameters. The former may include the intensity and duration of parental care, susceptability to predators, body size, mobility, and foraging and feeding patterns. The latter may include the spatiotemporal distribution and/or density of food resources and potential predators. An important task of a socio-ecological analysis is the assignment of these parameters to the behavioral subsystem(s) to which they are important. For instance, mobility may be relevant to mating, resource exploitation, and predator avoidance, but not to the rearing of offspring. The ultimate goal of the socio-ecological approach is to incorporate intrinsic and extrinsic parameters into a model of the structure and function of social systems. One of the goals of this thesis is to elucidate the relationships between activity patterns, social relationships, and intrinsic and extrinsic parameters.

The remainder of this section is a summary of the information about kangaroo rats pertinent to the socio-ecological approach broken down into the subsystems described by Crook _et_ _al_. (1976). Since many of the factors important to a species' socio-ecology are highly interrelated, some redundancy in the concepts presented below will be apparent.

Mating: The male-female pair-bond in _Dipodomys_ is apparently short in duration, perhaps only spanning the time necessary for a very brief courtship (15-30 min in duration) and mating (1-6 min in duration). For instance, Kenagy (1976b) observed no subsequent interactions between a male and female _D_. _microps_ after a single copulation in the field. It is not known whether _D_. _merriami_ have a polygynous or promiscuous mating system. Likewise, how mate choice operates in this species remains to be determined.

Rearing: Like most mammals, male kangaroo rats apparently do not invest in their offspring after copulation. Females, on the other hand, appear to invest quite heavily in their offspring until weaning at approximately three weeks postpartum (see Scholt, 1978). Our field observations (see Chapter 4) suggest that the mother-offspring bond in _D_. _merriami_ does not persist much beyond four or five weeks postpartum. Two juvenile females dispersed distances of approximately 100 to 200 m from their natal burrows while the dams did not move. We have no information about dispersal by juvenile males in our study population, but males in a southern Arizona population apparently disperse at least to the same extent as females (Jones, 1982). It is not known whether close relatives maintain differential social contact compared to non-relatives after dispersal.

Resource Exploitation and Predator Avoidance: Three parameters important to social systems (Crook *et al.*, 1976) are common to both the resource exploitation and predator avoidance subsystems: (1) group size, (2) group stability, and (3) refuge or cover utilization. A fourth parameter relevant to the resource exploitation subsystem is range exclusivity. From all the evidence, *D. merriami* live, forage, and avoid predators solitarily. With respect to the third parameter, this burrow-dwelling species may be termed a temporary refuge-user; individuals spend the daylight hours and several hours at night in relatively safe and benign burrows while certain activities including foraging, sandbathing, and social interactions are carried out aboveground.

Range use and the spatial relationships of *D. merriami* are not well documented. A review of the trapping data (Maza, French, and Aschwanden, 1973; O'Farrell, 1978,1980) and radiotelemetry data to be presented later indicate that animals' ranges may overlap quite extensively although individuals may maintain a relatively exclusive "core area" around their home burrow.

Intrinsic (Species) Parameters: Crook *et al*. (1976) list five intrinsic parameters which may set important constraints on the type of social structure that a species can develop: (1) the duration and intensity of the mother-infant bond, (2) the susceptability of the species to predators, (3) body size, (4) mobility of the species with respect to speed of movement and areal range capacity, and (5) the species-typical foraging and feeding patterns.

The intensity of the mother-infant bond has important ramifications for social structure. The presence of offspring, for example, may very well affect a female's interactions with conspecifics of either sex (e.g. defense of natal burrow). In addition, the duration of the mother-infant bond may dictate how often a female breeds during the reproductive season. Since *D. merriami* young mature rapidly and disperse during their natal season, the female may have the opportunity for multiple breeding. The likelihood of estrous females being available at various times throughout the breeding season should influence ranging patterns, spatial relationships, social status or dominance relationships, intrasexual competition, and mate choice.

The susceptability of a species to predation and its modes of defense will also have important ramifications for social structure. As small, relatively defenseless rodents, *D. merriami* are probably highly susceptable to predators, although previous data on predation are quite sparse (see

French *et al.*, 1967). It seems likely that predation is a selection pressure which limits the amount of time animals spend aboveground and, consequently, the frequency, duration, and intensity of social interactions. Furthermore, there should be selection against social aggregations if these aggregations increase the detectability of the potential prey without aiding in their defense against predators.

In several respects, body size may be an important determinant of social behavior. For instance, body size in conjunction with resource distribution and/or density will determine the area needed to meet energetic demands. In Chapter 2 it was suggested that interspecific competition between pocket mice and kangaroo rats, and the larger size of the latter, forced kangaroo rats to specialize on widely dispersed clumps of seeds. Consequently, kangaroo rats may require rather large and, perhaps, overlapping home ranges which may, in turn, lead to frequent encounters between conspecifics. Under such circumstances, one might expect the development of certain social responses which modulate encounters (e.g. discrimination between neighbors and strangers). Another way in which body size is important to social structure is through inter- and intrasexual size relationships. Sexual dimorphisms in body size are apparently intimately tied to mating systems (Ralls, 1977) and intrasexual size differences (e.g. related to age-class or differential access to food resources) have obvious implications for intrasexual social relationships, dominance, competition for resources, and so forth. D. merriami show only a slight degree of sexual dimorphism in body size (Chapter 4). Moreover, once individuals reach maturity, within-sex variations in size are similar for males and females. This suggests that larger body size in males confers no great advantage with respect to reproductive success. Male-male competition leading to differential access to females and mate choice, if indeed they are operative in this species, are probably not strongly related to differences in body size.

The mobility of a species should influence the number of conspecifics an individual may potentially encounter in its ranging activities. Kangaroo rats are highly mobile animals due to their powerful rear legs and bipedal locomotion. Although bipedalism in kangaroo rats has been postulated to serve foraging, predator avoidance (Bartholomew and Caswell, 1951), and energy savings functions (Dawson and Taylor, 1973; Dawson, 1975), this high mobility also provides the potential for individuals to monitor and/or interact with several conspecifics over short time periods. The degree of mobility or ranging of D. merriami will be a major focus of the results section.

As mentioned before, D. merriami inhabit environments with fluctuating resource distribution and/or density. Consequently, large foraging ranges may not be economically defendable in the sense that one would not expect animals to waste time and energy or risk injury or death in aggressive encounters over food resources. On the other hand, this species does establish small surface caches around home burrows which should be defendable. Thus the likelihood of aggressive encounters between conspecifics might be distance-graded; encounters in the immediate vicinity of an individual's home burrow would be aggressive whereas encounters occurring at mutually distant locations would be relatively passive. The results concerning spatial relationships and social interactions between individuals will be presented in Chapter 7.

Extrinsic (Environmental) Parameters: At least two extrinsic parameters are thought to influence social structure: (1) the spatiotemporal distribution and density of food resources and (2) the distribution, density, and mode of hunting by potential predators (Crook *et al.*, 1976). An implication of environmental influences on social relationships is that different populations of the same species may exhibit quite different social systems (Lott, in press). For instance, a local population inhabiting an area with abundant, evenly dispersed food resources may exhibit relatively exclusive, well-defined territories. Individuals may be familiar and/or interact only with adjacent territory-holders. On the other hand, populations inhabiting areas with sparse, patchily distributed food resources may exhibit large, overlapping home ranges which are not economically defendable. As will be shown in Chapter 7, this seems to be the case for D. merriami. In this situation, individuals may very well be socially familiar with several conspecifics. Although it is likely that kangaroo rats live in a variety of habitats ranging between the two extremes, it is difficult to evaluate the relevant resource conditions of the different habitats. As a consequence, detailed examinations of the relationship between resource conditions and social structure have not been carried out.

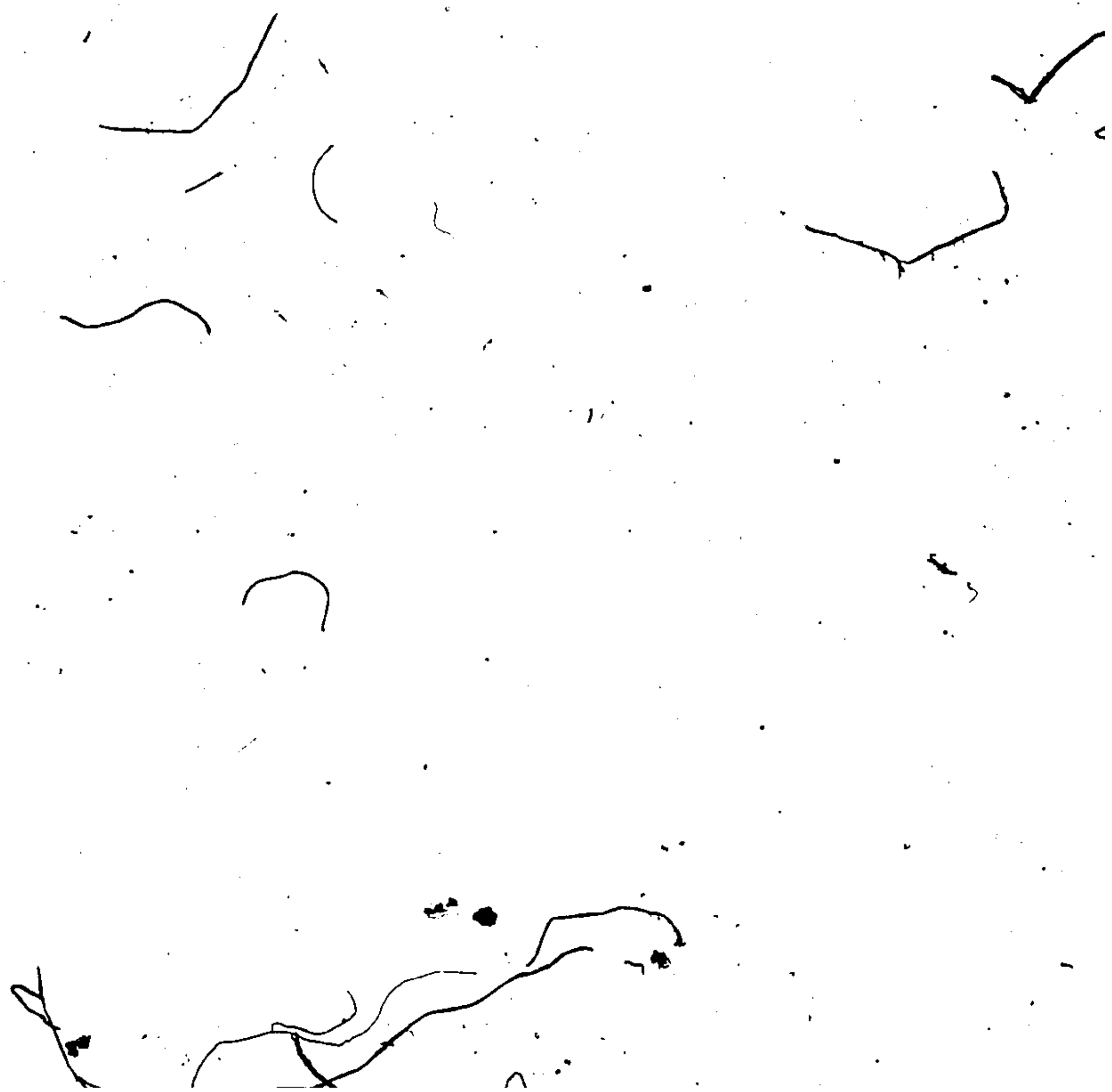
The effects of predation on social structure remain unstudied as well. D. merriami are faced with a variety of avian and terrestrial predators. On our study sites, for example, kangaroo rats must contend with great horned owls, loggerhead shrikes, coyotes, three rattlesnake species, and several non-venomous snake species. Kangaroo rats may reduce their risk from some of these predators by limiting the duration of their aboveground activity, especially to the nocturnal predators which take prey on the surface. Other predators, for example the coachwhip snake, probably take kangaroo rats in their burrows and, hence, may not exert significant selection pressure on the aboveground behavior of these animals.

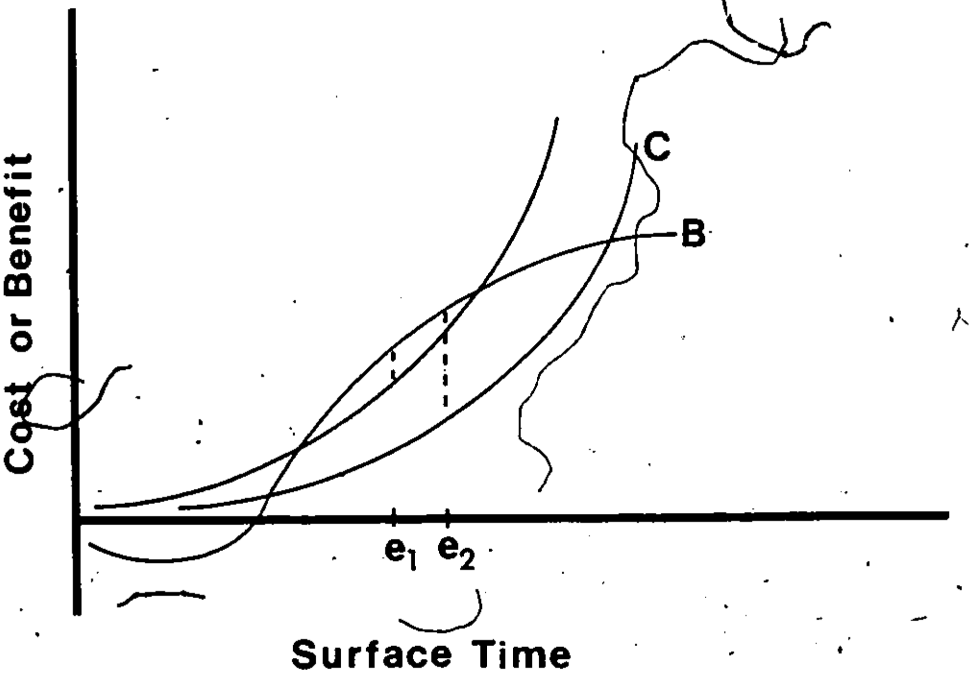
Individual Tactics

To reiterate, the data presented in this chapter address questions concerning the relationship between surface activity and individual characteristics. For heuristic purposes, it is useful to return to the perspective of the individual as a "decision-maker" where the behavior maximizing the net benefit in terms of some biological currency is chosen (see, e.g., Maynard Smith, 1976; McFarland, 1977; Parker, 1978; Pyke, Pulliam, and Charnov, 1978). Too little is known about the behavior of D. merriami to apply optimality models with any quantitative rigor, but a cost-benefit perspective provides a useful heuristic for considering the function of behavior. Rosenzweig (1974) developed a qualitative graphical cost-benefit model of the aboveground activity of D. spectabilis. The impetus for this model was a report by Lockard and Owings (1974) that D. spectabilis were inactive during moonlight hours in the fall and winter but became indiscriminate in the spring. Lockard and Owings suggested that D. spectabilis were active during moonlight on the shorter spring nights in order to meet their energetic requirements. According to Rosenzweig (1974) this explanation was inadequate because at no time were animals active during the entire dark period of nights with moonlight. In response, Rosenzweig presented several alternatives in the form of graphical models to account for changes in aboveground activity seemingly related to moonlight. The general model

(Figure 5.1) is based on an elementary cost-benefit analysis where the concave function represents the mortality risk due to predators or climatic factors such as cold or heat and the sigmoidal function represents reproductive capacity. Animals must spend some minimum amount of time aboveground to meet their basal energetic demands. After the exposure time where the benefit curve rises above the horizontal axis, the animal has to decide how much time to spend aboveground engaging in other important activities. By increasing their time aboveground, however, animals increase their risk of mortality due to predators and/or climatic stresses. According to the model there exists an optimal exposure time, E_i, that maximizes reproductive success; exposure times greater or less than E_i yield submaximal returns on investment. From this general model, it is easy to generate plausible explanations or predictions about the variation between individuals or for the same individual at different times. For instance, seasonal differences in predation risks may affect aboveground activity. Predation by snakes is highest in the spring and summer so the cost of aboveground activity per unit time during this period will be higher relative to fall and winter (assuming that mortality due to other predators does not decrease). Consequently, the optimal exposure time will shift to the left of the fall and winter E_i and aboveground activity should decrease. On the other hand, animals may be subjected to pressures for increased aboveground

Figure 5.1. Cost-benefit curve for surface activity by a fossorial rodent. The concave function represents mortality risk and the sigmoidal function represents reproductive capacity (i.e. the benefit function). e_1 and e_2 represent optimal exposure times with different cost functions (see text for a detailed discussion). (from Rosenzweig, 1974)




C
B
Cost or Benefit
e_1
e_2
Surface Time

activity which counteract pressures for a reduction of activity. During the reproductive season it may be necessary to spend more time aboveground to acquire mates or meet the increased energy demands of reproduction. Clearly, a thorough understanding of the conflicting demands confronting a animal is necessary to generate adequate cost-benefit curves.

Field Studies of Dipodomys Social Structure

Few studies have expressly addressed questions pertaining to kangaroo rat social organization in the natural environment. Schroder and Geluso (1975) examined the home mound dispersions of *D. spectabilis* and Schroder (1979) used radiotelemetry to determine the home range and habitat utilization patterns of this same species. Home ranges and spatial relationships have been determined for *D. microps* and *D. merriami* using capture-mark-recapture techniques by Maza *et al.* (1973) and O'Farrell (1978,1980). A generalization stemming from these studies is that kangaroo rats have a closed-dispersed social structure; individuals occupy regularly dispersed home burrows and utilize home ranges in a manner minimizing range overlap and, presumably, confrontations with conspecifics. Laboratory observations of intra- and interspecific social behavior tend to support this generalization. Although there are interspecific differences, between- and within-sex paired-encounters tend to be aggressive and occasionally fatal except under breeding conditions (Eisenberg and Isaac, 1963; Blaustein and Risser, 1976; Behrends, 1981). It has not been demonstrated, however, that the high degree of intraspecific aggression observed in the laboratory occurs in natural circumstances and/or serves as a mechanism for territorial defense or social dominance.

The existence of a closed-dispersed social structure need not imply that socio-spatial relationships are static. Space use and inter-individual relationships will vary as a function of several factors including breeding condition, season, resource density and distribution, and population density. The variance in ranging behavior and spatial relationships by three kangaroo rat species have been investigated using trapping techniques and radiotelemetry. Maza et al. (1973) carried out a seven year trapping program in which heteromyid populations on three separate 9 ha enclosures were censused monthly. Despite the questionable validity of trapping for estimating absolute home range size and activity patterns (Chapter 3), these data are useful for examining the effects of sex and season on behavior. Maza et al. report that 39% of the captures for male and female D. merriami lay within a 37 m radius of the individual's center of activity (i.e. one standard deviation based on a normal model) whereas for D. microps these values were 27 m for males and 25 m for females. A breakdown of ranging patterns by season revealed that D. merriami of both sexes had larger summer than winter ranges. Furthermore, the longest excursions were by reproductive male D. merriami in the spring. Differences in ranging patterns between D. merriami and D. microps were noted by Kenagy (1973a) as well. Individual D. merriami were likelier to be captured on two different quadrats 62 m apart (28 times by 11 individuals) than D. microps (only once).

By trapping a grid several nights every month for a year, O'Farrell (1978,1980) was able to investigate dynamic changes in intraspecific spatial relationships in relation to sex, reproductive condition, and season. O'Farrell concluded that male-male spatial overlap was greatest during reproductive activity in the winter and spring. To a lesser extent, the pattern of male-female overlap was similar. Home range sizes, shapes, and orientations, as determined by principal components analysis (i.e. yielding elliptical home ranges), differed seasonally as well. O'Farrell suggests that these seasonal differences in range overlap, shape, and size, reflect changes in the population structure (e.g. the influx of juveniles), resource density and distribution, and reproductive behavior.

Radiotelemetric data on the ranging patterns and spatial relationships of D. spectabilis collected by Schroder (1979) are markedly different from those based on trapping for D. microps and D. merriami. Schroder found that D.

spectabilis confined much of their surface activity to a small range of about 0.05 ha around a centrally-located home mound. In fact, only 20% of the radio fixes found animals more than six meters beyond their home mound. Members of this species are probably territorial because they maintained very exclusive home ranges. An interesting finding was that male areal home ranges were twice as large as female ranges. In further contrast to the findings for D. merriami and D. microps, there was little apparent seasonal variation in D. spectabilis home ranges. Comparisons between species based on different field methods must, however, be treated with caution. Upon comparison of the radiotelemetry and trapping techniques for estimating the spatial overlap of particular individuals, Schroder found that analyses based on trapping data overestimated spatial overlap.

Several points can be made from these field studies. First, Schroder's (1979) study makes it clear that radiotelemetry and trapping may yield quite different home range and activity results for the same individual. As was discussed in Chapter 3, radiotelemetry eliminates many of the biases in estimating surface activity and home range parameters associated with trapping data. Second, it is apparent that interspecific differences in ranging and spatial relationships exist. The implications of these findings for interspecific differences in kangaroo rat social structure remain unknown. That species differ on these surface activity measures is, perhaps, not surprising in light of the interspecific differences in body size, foraging and feeding ecologies, and geographical distribution (Chapter 2). These factors, in conjunction with differences in resource distribution, will influence activity and habitat utilization patterns. Exactly how these intrinsic and extrinsic factors interact to yield the observed interspecific variation cannot be evaluated on the basis of the aforementioned studies.

The variation in ranging and spatial relationships by D. merriami in relation to sex, reproductive condition, and season is particularly interesting. An implication of these results is that individuals behave differently with changes in their physiological state, resource conditions, and the density and behavior of conspecifics. Unfortunately Maza et al. (1973) and O'Farrell (1978,1980) did not present their findings in sufficient detail to examine individual behavioral strategies.

The Present Study

The remainder of this chapter focuses on the surface activity patterns of D. merriami in relation to study period, sex, reproductive condition, and size-class as revealed by radiotelemetry. The approach taken here is that inferences can be made about a species' social structure by examining the activity patterns of individuals. If, for example, some males range more widely than others, one might hypothesize that these differences reflect dominance relationships or differential access to resources such as food, territories, or mates.

In the interest of simplicity, the analyses presented here are restricted to relatively straightforward indices of activity including (1) the mean distance moved between successive radio fixes ($\bar{D}$), (2) the average deviation from an individual's nightly center-of-activity (SD-COA), (3) the percentage of radio fixes an animal was determined to be on the surface (%AG), and (4) the distance between an animal's nightly center-of-activity and its day burrow location (COA-DB). Since these indices are based on time interval samples rather than continuous observation, they are not to be taken as absolute measures of activity. Nonetheless, these measures are useful for relative comparisons of activity by different individuals or the same individual at different times. One seeming difficulty which may become apparent in the analyses to follow is that in some cases groups will differ statistically on one measure but not another. Although these activity measures tend to be correlated, they are, in fact, sensitive to different aspects of behavior. Moreover, they may be differentially affected by the sampling procedure. The average move between successive fixes, for example, is a straightforward and easily calculable statistic which serves well as a relative index of activity. It is also useful for examining temporal behavior patterns. Madison (1978a), however, found that this statistic was sensitive to changes in the sample interval. A resultant limitation of this measure is that comparisons can only be made when the sample intervals are similar. The deviation around a nightly center-of-activity, on the other hand, is relatively impervious to changes in the sample interval (Madison, 1978a). A statistic summarizing the proportion of radio fixes finding the animal on the surface provides very different information from the movement indices. Some animals with relatively low movement scores were frequently observed on the surface around their home burrows. The "percentage aboveground" statistic discriminates between sedentary surface-active individuals and sedentary surface-inactive individuals. Finally, the statistic concerning the distance between an animal's center-of-activity and its day burrow is interesting because it provides information about how animals distribute their activity spatially with respect to the safety of their home burrow. This statistic may thus be useful for examining "risky" behavior.

Data Analysis

Data Selection: Data collected in study periods 1 and 2 were selected for analysis using the same criteria. For nights when data were collected between dusk and midnight, the preceding day location and all of 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 study period 3, in which data were collected throughout the night, the preceding day location and the subsequent night locations were included in the analyses. Summary statistics for animal movements and surfa[illegible]ctivity were generated on both a per night and overall basis. These statistics were also generated for females at different reproductive stages (see Chapter 3 for general methods of assignment of anestrus, estrus, pregnancy, and lactation). For the analysis of movements and activity 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 any of the summary statistics and the number of nights an animal was tracked ($\bar{D}$, $r = -.08$; S[illegible]A, $r = -.04$; %AG, $r = .21$; COA-DB, $r = -.14$; all p[illegible]

Mean Distance Moved: The mean distance moved (in meters) by an animal between successive radio fixes ($\bar{D}$) is found by the simple formula

$$\bar{D} = ((x_t - x_{t-1})^2 + (y_t - y_{t-1})^2))^{\frac{1}{2}}/n$$

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.

Standard Deviation around the COA: The center-of-activity (COA) is the mean x and y coordinates for n radio locations. The standard deviation around COA is found by the following formula

$$\text{SD-COA} = (((x_i - \bar{x})^2 + (y_i - \bar{y})^2)/n)^{\frac{1}{2}}$$

where $\bar{x} = \sum x_i/n$ and $\bar{y} = \sum y_i/n$.

% Observed Aboveground: An animal was scored as aboveground if it was visually observed or if there were changes in the direction of the peak radio signal indicating movement. The denominator for the calculation of this statistic was the number of night locations (i.e. not including day burrow determinations).

Distance Between COA and Day Burrow: The distance between an animal's center-of-activity and its day burrow (COA-DB) was calculated on a per night basis and a grand mean (i.e. a mean of means) was generated for the overall statistic for the reason that animals regularly change day burrows. This distance was found with the formula

$$\text{COA-DB} = ((\text{COAX} - \text{DBX})^2 + (\text{COAY} - \text{DBY})^2)^{\frac{1}{2}}$$

where COAX and COAY are the x and y coordinates for the COA and DBX and DBY are the x and y coordinates for the day burrow.

Results

A summary of the radio-tracking data collected over the three study periods and included in the analyses below is presented in Table 5.1. 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 were reported elsewhere; Daly, Wilson, and Behrends, 1981). The data for hormonally manipulated animals are omitted from Table 5.1 and all subsequent analyses in this thesis so that all comparisons are among hormonally unmanipulated animals.

Throughout the studies, an attempt was made to collect equivalent amounts of data from particular individuals (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. As stated above, however, the movement and activity indices used here are relatively unaffected

Table 5.1. Summary of radiotelemetry data collected.

	Nov-Dec 1980		Dec-May 1982		Nov-Dec 1982		Total
	M	F	M	F	M	F	
Sample Size	12	9	13	11	10	9	60
Mean # of Fixes	92.4	59.1	72.5	155.4	199.7	202.2	134.1
Mean # of Nights Radio-tracked	12.1	7.5	10.8	24.4	14.4	14.4	14.4

M = Male, F = Female

by the number of data points. (The number of locations becomes important for measures of range size and utilization parameters, see Chapter 7). 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 11-592 and 1-64, respectively. In total, the data used for the analyses below represent 8500 animal hours and 920 animal days.

General Activity Patterns: Kangaroo rats 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 (see Chapter 6 for a discussion of temporal activity patterns). Individuals may return to their day burrows several times throughout the night, perhaps to store food, reduce energetic costs, or avoid predators. Animals usually return to their day burrows permanently before dawn, although occasionally an animal moved following the dawn check (some predations, probably by loggerhead shrikes, occurred after the dawn check).

Study Period: Average movements and activity by animals broken down by study period are summarized in Table 5.2. With the sexes combined, there were significant differences between study periods in several instances. Animals in study period 1 moved less than those in study period 2 (for $\bar{D}$, $\underline{t}_{43df} = 2.21$, $\underline{p} < .05$; for SD-COA, $\underline{t}_{43df} = 2.19$, $\underline{p} < .05$; both two-tailed tests) and those in study period 3 (for $\bar{D}$, $\underline{t}_{38df} = 4.97$, $\underline{p} < .001$; for SD-COA, $\underline{t}_{38df} = 3.71$, $\underline{p} < .001$; both two-tailed tests). Study period 1 animals were also on the surface significantly less than study period 2 animals ($\underline{t}_{43df} = 2.63$, $\underline{p} < .02$, two-tailed test, arcsin transformation) and study period 3 animals ($\underline{t}_{38df} = 7.26$, $\underline{p} < .001$, two-tailed test, arcsin transformation). Finally, study period 1 animals located their COA's closer to their day burrows than either study 2 animals ($\underline{t}_{43df} = 3.06$, $\underline{p} < .01$, two-tailed test) or study period 3 animals ($\underline{t}_{38df} = 4.26$, $\underline{p} < .001$, two-tailed test). Likewise, study period 2 animals moved less than study 3 animals (for $\bar{D}$, $\underline{t}_{41df} = 3.12$, $\underline{p} < .01$ and for SD-COA, $\underline{t}_{41df} = 2.20$, $\underline{p} < .05$, both two-tailed tests) and were observed on the surface less ($\underline{t}_{41df} = 3.93$, $\underline{p} < .001$, two-tailed test, arcsin transformation).

Sex: The movement and activity measures broken down by sex over the three study periods are provided in Table 5.3. For study period 1, in which females were non-reproductive, only the means for COA-DB were significantly different ($\underline{t}_{18df}$ =

Table 5.2. Overall summary (sexes combined) of _D. merriami_ surface activity where $\bar{D}$ = hourly move, SD-COA = the standard deviation around a center-of-activity, %AG = the percentage of samples in which the animal was observed or determined to be moving aboveground, and COA-DB = the distance between an animal's day burrow and its nightly center-of-activity. Standard deviations are in parentheses here and throughout.

Study Period	$\bar{D}$	SD-COA	%AG	COA-DB
1	10.9 (8.0)	12.4 (9.8)	9.8 (6.9)	7.0 (3.4)
2	16.8 (9.7)	18.5 (8.9)	18.4 (12.2)	13.7 (9.3)
3	27.5 (12.8)	25.9 (13.1)	31.0 (8.0)	15.9 (9.4)

Table 5.3. Surface activity of *D. merriami* broken down by sex and study period.

Study Period		$\bar{D}$	SD-COA	%AG	COA-DB
1	Male	11.5 (9.8)	13.1 (12.8)	11.8 (5.8)	6.3 (2.6)
	Female	10.1 (5.2)	11.5 (3.9)	10.6 (9.1)	9.4 (3.7)
2	Male	20.4 (11.3)	21.7 (10.7)	18.4 (14.3)	15.1 (11.8)
	Female	14.1 (4.7)	15.1 (4.4)	18.4 (9.4)	11.8 (4.3)
3	Male	28.9 (15.1)	27.7 (16.4)	30.4 (9.4)	15.4 (8.2)
	Female	25.9 (10.4)	24.7 (8.8)	31.8 (8.6)	15.9 (9.4)

2.12, $p < .05$, two-tailed test) with female COA's located significantly farther from day burrows than male COA's. Although males and females in study period 1 did not differ in their average $\bar{D}$ or SD-COA, within male variance was significantly greater than within-female variance on the movement measures ($F_{max,11df} = 3.55$, $p < .05$ for $\bar{D}$ and $F_{max,11df} = 10.8$, $p < .01$ for SD-COA). There was no apparent difference between males and females in the proportion of time spent on the surface ($t_{19df} = 1.32$, $p > .05$).

In the second study period (the breeding season), animals were not only more active on the surface than those in the first study period, but males moved relatively more than did females based on $\bar{D}$ ($t_{22df} = 1.72$, $p < .05$, one-tailed test) and SD-COA ($t_{22df} = 1.83$, $p < .05$, one-tailed test). The average move between radio fixes for males was 45% greater than the average move by females and the average male SD-COA was 42% greater than the average female SD-COA. Moreover, for each of the measures, with the exception of %AG, between male-variance was greater than between-female variance ($F_{max,12df} = 5.78$, $p < .01$ for $\bar{D}$; $F_{max,12df} = 26.0$, $p < .01$ for SD-COA; $F_{max,12df} = 7.53$, $p < .01$ for COA-DB). $\bar{D}$ for males ranged from 4.8 m to 38.7 m while the $\bar{D}$ range for females was only 8.8 m to 23.5 m. Despite the differences in movement indices, the average percentage of samples on the surface by males and females was similar.

In study period 3, as in study period 1, all females were non-reproductive and some males lacked scrotal testes. The overall movements of animals were greatest during this study period, but there were no differences between the sexes on any of the measures with respect to average values or within-sex variance.

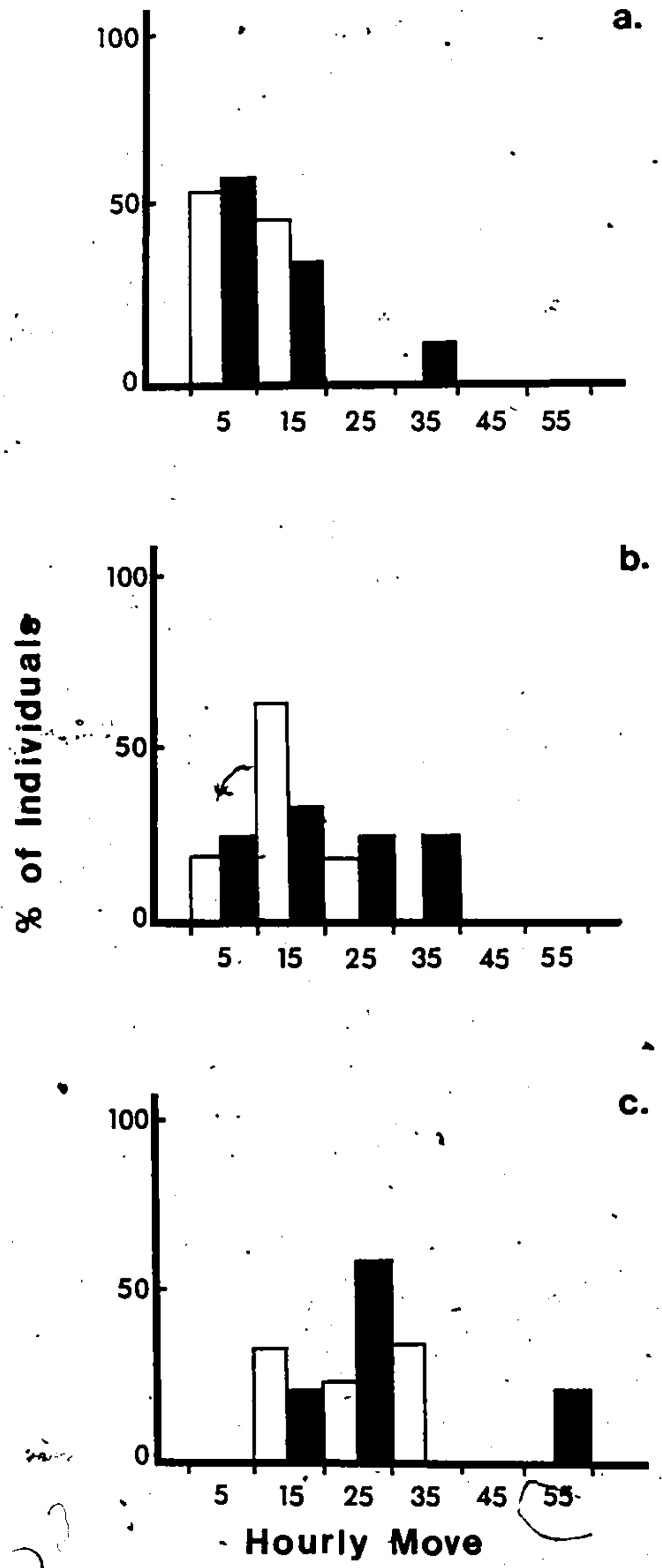
A summary of the results for $\bar{D}$ broken down by sex and study period is depicted in Figure 5.2. On the one hand, when females were non-reproductive and there was variability in male reproductive condition, as in study periods 1 and 3, the $\bar{D}$'s were similar for the two sexes. In the breeding season (study period 2), on the other hand, the $\bar{D}$'s for males and females were different. Figure 5.2 also illustrates that throughout the three study periods, males had the largest $\bar{D}$'s.

Reproductive Condition: The $\bar{D}$'s for study period 2 females in different reproductive stages are summarized in Table 5.4. Despite small sample sizes, t-tests for dependent groups revealed that movement by females varied in relation to their reproductive condition. Movements, as indicated by $\bar{D}$, were three times greater on average for females in estrus compared to anestrus ($t_{3df} = 3.63$, $p < .05$, two-tailed test). Likewise, females moved more during pregnancy than anestrus ($t_{4df} = 2.21$, $p < .05$, two-tailed test) and also during lactation compared to anestrus ($t_{3df} = 3.48$, $p < .05$, two-tailed test). Although the differences were not statistically significant, $\bar{D}$ tended to be greater for estrus compared to

Table 5.4. Hourly moves of *D. merriami* females at 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	26.1
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

Figure 5.2. The percentage of D. merriami individuals in different average hourly move categories. Values in the abcissa are the midpoints of the interval. a = study period 1, b = study period 2, and c = study period 3. Males are solid bars and females are open bars. For example, in study period 1 approximately 55% of the males had average hourly moves between 1 and 10 m.

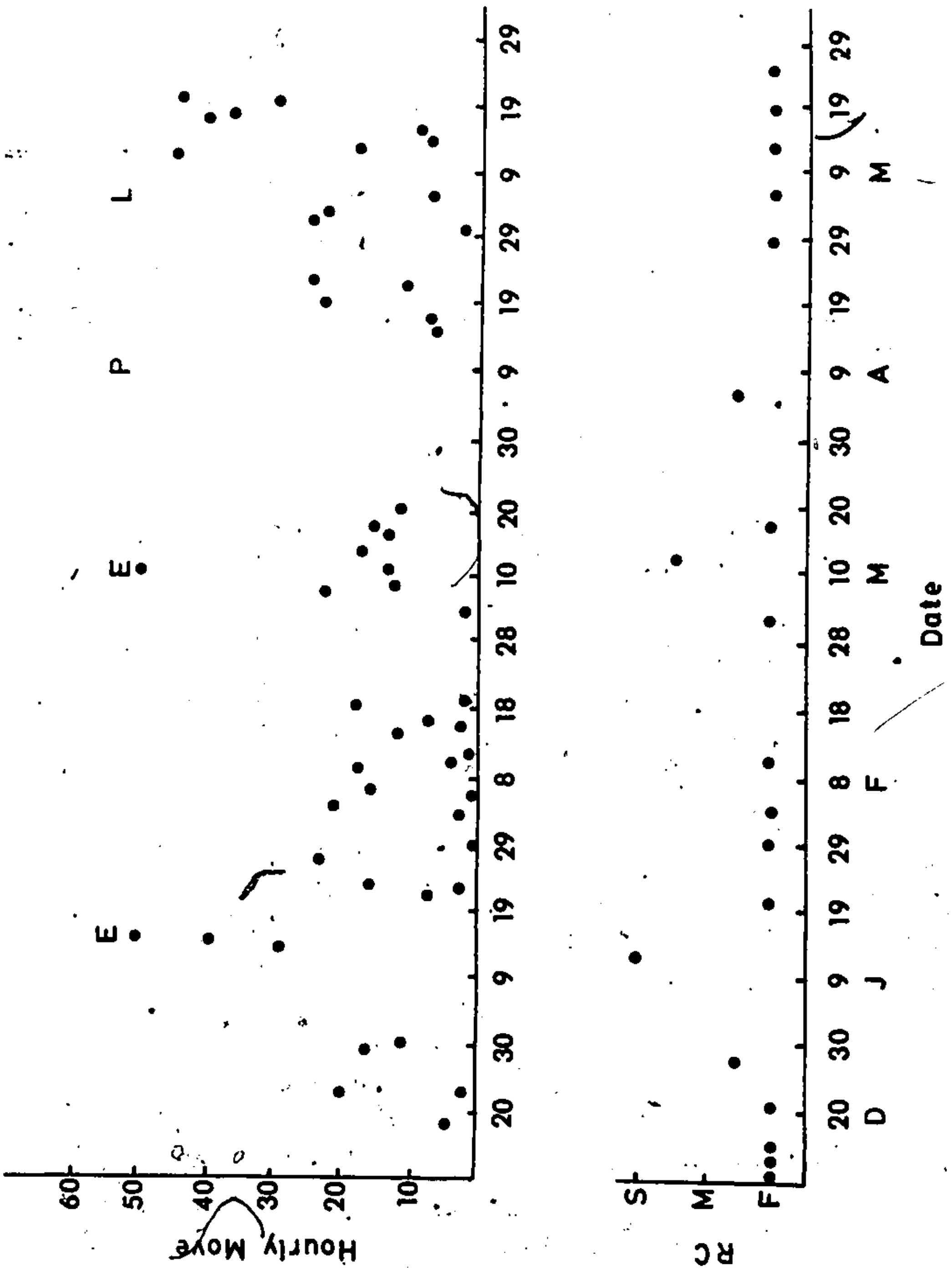

a.
b.
c.
100
50
0
% of Individuals
5
15
25
35
45
55
Hourly Move

pregnancy ($t_{3df} = 2.00$, $.10 > p > .05$, one-tailed test) and estrus compared to lactation ($t_{3df} = 2.18$, $.10 > p > .05$, one-tailed test) as well. The same comparisons with the %AG measure yielded similar results: anestrus vs. estrus ($t_{3df} = 7.70$, $p < .01$, two-tailed test), anestrus vs. pregnant ($t_{4df} = 5.30$, $p < .01$, two-tailed test), and anestrus vs. lactation ($t_{3df} = 6.89$, $p < .01$, two-tailed test). Anestrous females were generally on the surface for less than 10% of the samples while females in reproductive condition were observed aboveground on 25% of the samples, on average.

Figure 5.3 depicts the most complete set of data on a single female's movements through different reproductive stages. Despite the substantial variation in $\bar{D}$ from night to night, there were dramatic increases in movement around periods of estrus. These levels of movement were matched only when this female was lactating and, presumably, foraging more as a result. Furthermore, this particular female, whose average day burrow move was 15 m when anestrous, pregnant, and lactating, had day burrow moves of 100 m and 95 m during two estrus periods. On both occasions, this female returned to her previous day burrow area one or two days after estrus.

Unfortunately, only data from the third study period are usable for examining the relationship between testicular development in males and surface activity. In the first and second study periods the evaluation of male reproductive condition was subjective (see Chapter 3 for methods) whereas

Figure 5,3. The upper graph is a summary of the nightly hourly moves ($\bar{D}$) by female 1485 throughout study period 2. E = estrus, P = pregnant, and L = lactating. The lower graph depicts the female's reproductive condition over the same time period in the manner described in Chapter 3.


Hourly Move
60
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testes length was measured to the nearest 0.5 mm in the third study period. A summary of average testes length and activity measures is found in Table 5.5. There were significant positive correlations between average testes length and $\bar{D}$ (r = .79, $p < .02$) and between testes length and SD-COA (r = .78, $p < .02$). There was, however, no linear relationship between testes length and %AG.

Body Weight: For males, physical factors which may, in part, account for the substantial variation among individuals are not clear-cut. Over the three study periods there was only a mild positive relationship between body weight and $\bar{D}$ (r = .28, $p < .05$, one-tailed test). This statistic should be viewed with caution, however, due to the difference in this relationship between the three study periods. In the first study period, the relationship was only slightly positive (r = .10) and in the second study period this relationship was, in fact, slightly negative (r = -.11). Only in the third study period was there a reasonably convincing positive relationship between body weight and $\bar{D}$ (r = .57, $p < .05$). The results were quite different for the %AG measure. The overall correlation between %AG and body weight was only -.03. But again, a breakdown of this relationship by study period revealed striking differences; for study period 1 r = .13, for study period 2 r = .13, and for study period 3 r = -.68 ($p < .05$, two-tailed test).

Table 5.5. Surface activity of individual study period 3 male *D. merriami* in relation to body weight and reproductive condition.

Male	Body Weight (gm)	Testes Length (mm)	$\bar{D}$	SD-COA	%AG
HL1	32.2	5.0	18.2	17.7	33.8
HR2	33.7	6.6	26.2	27.6	39.0
HL3FL3	38.7	8.2	22.3	26.0	30.2
12	41.0	9.0	24.1	28.0	19.9
HR4	34.7	9.3	27.2	28.7	32.1
HR1FL4	36.7	9.3	11.6	12.3	22.4
HL4	34.7	9.5	25.4	25.2	45.7
HL3FL2	38.2	11.1	21.7	20.2	29.5
13	39.7	14.0	55.3	67.4	36.9
HL2FR2	42.2	14.5	57.4	57.3	14.4

For females, there was no relationship between non-pregnant body weight and $\bar{D}$ ($r = -.25$, $p > .05$) or %AG ($r = -.19$, $p > .05$) over the three study periods. In addition, a breakdown by study period revealed no significant linear relationships between body weight and $\bar{D}$ or %AG.

The Risk of Surface Activity: One of the assumptions of the cost-benefit model of surface activity presented in the introduction was that the risk of mortality should increase with increases in surface exposure time. One prediction from this assumption is that an animal's tenure in a population should be negatively related to its level of surface activity. To test this assumption, I selected animals first trapped on the Coyote Wash site in December 1981 or January 1982 and which were subsequently radio-implanted. Only animals trapped during this period were used in order to avoid confounding the results with animals entering the trapping population at a later date. I then correlated the animals' overall $\bar{D}$'s with the number of days they were in the trapping population (i.e., the number of days from first capture to last capture or last radio-tracking day). The results of this analysis showed a rather surprising positive correlation between tenure and $\bar{D}$ although the correlation did not deviate significantly from 0 ($r = .44$, $p > .05$, one-tailed test). Furthermore, of the 13 animals used for this analysis, the nine who disappeared during the study period (i.e. preyed upon, lost transmitter, or were never recaptured) had a $\bar{D}$ of 10.8 m (±3.4), whereas the four animals which remained until the end of the study period had an average $\bar{D}$ of 19.3 m (±8.7). This difference is probably biased by the generally higher activity levels recorded in the spring, but the point remains that animals who disappeared were not more active than those remaining at the end of the study period.

Another way to test the relationship between surface activity and risk is to look for an increase in activity by an animal shortly before it is preyed upon or disappears from the population. This analysis was suitable for six of the eight known predation cases (Chapter 4); that is, movements (D) were recorded for the day of predation. A comparison of an animal's average $\bar{D}$ with its $\bar{D}$ on the day of predation showed that of the six animals, one was more active on the day of predation, four were less active, and one was equally active. For cases of disappearance (including known predations), 15 animals over the three study periods met the criterion of disappearing the same day for which there was movement data. Of these animals, eight were more active on the day of disappearance, six were less active, and one was equally active.

Discussion

The data presented in this chapter and in the remainder of this thesis represent the most complete information about the daily surface activity of kangaroo rats collected to date. As the first concerted effort to establish basic information about the surface activities and socio-spatial relationships of D. merriami, the data concerning certain relationships are suggestive but require further study. It is also apparent that certain factors could have been investigated more carefully through experimental manipulation (e.g. resource availability), but priority was given to collecting data under naturally varying conditions. I take some freedom in this discussion to speculate about the function of certain observed behavior patterns and, in doing so, I hope to identify questions deserving further study.

Reproduction

Time and movements aboveground could be positively related to reproduction for several reasons. Foremost, during the breeding season animals may spend more time aboveground and range more widely in order to gain access to mates. How animals gain access to mates, however, may take a variety of forms. For example, regularly visiting opposite-sexed conspecifics and establishing social familiarity may be important for mating in some solitary species, as seems to be the case for the Mongolian gerbil (Daly, 1977). For males in particular, it may be advantageous to visit several females frequently enough to monitor their reproductive condition. Estrous females, on the other hand, may ensure mating by spending more time aboveground, scent-marking to attract males, or visiting particular males. In general, intraspecific and intrasexual competition, for example, for food resources, burrow sites, territories, and mates (in the case of intrasexual competition), should be particularly keen during the breeding season. An increase in the intensity of competition could result in more patrolling and defense of territories which probably requires a substantial commitment of time and energy to surface activity.

Non-social factors may influence aboveground activity during the breeding season as well. Pregnant and lactating D. merriami ingest significantly more dry food and herbaceous material than non-reproductive females (see later discussion). Since D. merriami do not hoard large amounts of food, it is expected that reproductive females would spend more time aboveground foraging.

From the above considerations, one would expect animals to be more active on the surface during the breeding season than during non-breeding periods. The data, however, do not bear out this prediction. Although animals in the second study period (the breeding season) were significantly more active than the non-breeding animals in the first study period, they were significantly less active than the non-breeding animals in the third study period. Despite the relationship between reproduction and aboveground activity within the breeding season (see results above and discussion below), variation over longer time periods (e.g. between seasons or years) appears to be dependent upon some other factor or set of factors, for example, population density, weather patterns, and resource conditions. I will discuss these factors in a later section of this chapter.

<u>Sex Differences</u>: As was remarked in Chapter 4, male *D. merriami* most likely do not invest in their offspring beyond the contribution of sperm. Free from parental investment, defined by Trivers (1972) as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parents' ability to invest on other offspring." (pg. 139), males are expected to direct their reproductive effort toward inseminating as many females as possible. Moreover, since females are the nurturant sex and, thus, have a limited reproductive capacity, they are a limited resource for which males must compete. Obvious characteristics related to intrasexual competition for mates (e.g. sexual size dimorphism, special weaponry) have not evolved in kangaroo rats and this genus does not possess any obvious secondary sexual characteristics which could serve as the

basis for mate selection. It seems that if males do compete for females, competition must occur in a more indirect way. Perhaps males who establish social contact and visit females on a frequent basis enjoy the greatest reproductive success. Similar patterns of visitation of females by males on a regular basis and/or around the time of estrus have been described for some solitary-living rodent species. For instance, Daly and Daly (1974) describe a social system in free-living Saharan gerbils (Psammomys obesus) whereby females establish burrow sites in patchily-distibuted vegetation (their primary food source) and males inhabit vegetationally poor burrow sites that are, nevertheless, located near several females' burrows. Thus, it is possible for a male to visit several females on a regular basis. Similarly, Madison (1980) reported that while female meadow voles (Microtus pennsylvanicus) maintained exclusive home ranges from other females, males' ranges overlapped and, furthermore, males temporarily inhabited the ranges of estrous females. Finally, Brooks and Banks (1971) determined that male collared lemmings (Dicrostonyx groenlandicus) 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 on the surface, one would expect the patterns of the two sexes to vary in relation to the females' reproductive condition. Indeed the results show that ranging patterns were sexually dimorphic only during the breeding season with males moving more than females. These results provide circumstantial evidence that movement patterns within the breeding season are in some way related to the different reproductive strategies of males and females. In order to interpret this divergence in ranging, more information about how mate selection operates in this species is necessary. With respect to the male's role, however, possible reasons for this difference include the regular visitation of females, either to maintain social familiarity or to monitor the females' reproductive condition, increased patrolling of home ranges in order to maintain their range or prevent rival males from visiting females, or simply spending more time on the surface to increase one's chance of encountering a receptive female. Some of these alternatives will be addressed in Chapter 7 when I deal with spatial relationships.

A common finding on the ranging behavior of solitary rodents is that males range more widely than do females, although this dimorphism is not always restricted to the reproductive season, as seems to be the case with D. merriami and a Saharan gerbil, Meriones libycus (Daly and Daly, 1975). Species in which a sexual range dimorphism exists include the collared lemming (Brooks and Banks, 1971), the fat sandrat (Daly and Daly, 1974), the brown lemming (Lemmus trimuncronatus; Banks et al., 1975), the dusky-footed woodrat (Neotoma fuscipes; Cranford, 1976), the white-footed mouse (Peromyscus leucopus; Mineau and Madison, 1977), the bannertail kangaroo rat (D. spectabilis; 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 and Madison, 1983).

Reproductive Condition: The observation that ranging patterns were only sexually dimorphic during the breeding season suggests that surface activities reflect different reproductive strategies by males and females. Nevertheless, this information tells us little about individual behavioral strategies. For example, if the assumption that males compete for access to females is true, which factors distinguish successful and unsuccessful males? Likewise, females at different reproductive stages are faced with different physiological and environmental demands. Estrous females must carry out activities that ensure mating success. Pregnant and lactating females must contend with the increased energy, nutrient, and water demands of reproduction and, perhaps, with threats to their offspring by conspecifics and predators. Non-reproductive females, on the other hand, may "bide their time" and thus avoid costly behavior until they have breeding opportunities. Thus males and females alike must make important "decisions" about the timing, duration, and intensity of surface activity such that they "choose" the behavior that will maximize some net benefit, be it energy from foraging or the number of viable offspring from reproductive behavior. In the same manner as Rosenzweig (1974), I will assume that surface activity reflects "decisions" that have ramifications for reproductive success (in principle, this assumption is testable by assessing the relative fitness of individuals which behave differently, but in practice this is an extremely difficult undertaking).

The results clearly demonstrated that females' surface activity varied in relation to reproductive condition. The most striking observation was the dramatic increase in surface activity by females in 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 do diestrous rats (Birke and 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, Andrews, and Best, 1977), and estrous rats patrol mazes more rapidly and enter illuminated mazes more frequently (Martin and Böttig, 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-marking locations. Increases in ambulation by estrous females have been observed in the field as well. Calhoun (1962) reported that female rats move more on the night of proestrus and suggested that these females might be scent-marking to attract males. Brooks and 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 day burrows were located when the males were radio-implanted two weeks later). Visual observations of this female during this period of estrus found her to be in close proximity (e.g. under the same creosote bush) to at least two unidentified animals for approximately one-half hour. At no other time have animals been observed to be in such close proximity for this length of time. The unidentified animals may well have been the males subsequently found to have burrows nearby. It is not clear what function surface activity by estrous females serves, but the episode just described suggests that females may actually seek out males during estrus. This activity would not preclude the possibility of males visiting females since social familiarity based on prior interactions may be important for subsequent mating. Alternatively, females may be scent-marking to advertise their sexual state or they may simply be on the surface more to maximize the chance of encountering a male. With a relatively long estrous cycle of 11-14 days and a restricted breeding season, females probably cannot afford to miss mating opportunities.

Pregnant and lactating females also showed elevated surface activity compared to their anestrous 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 and Banks (1971) estimated the home range 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 (1978a) 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 mammal species including male collared lemmings in the laboratory (Mallory and Brooks, 1978). 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 do anestrous females under laboratory conditions (Behrends, unpublished data) and lactating D. merriami consume more vegetative matter than do anestrous and pregnant animals (Soholt, 1978). 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. It would also be interesting to know whether increased foraging activities and, hence, time away from the natal burrow, increase the offsprings' risk to infanticide by conspecifics or predation. 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 and Chapter 7), but future food resources may be a concern for competing conspecifics. Thus, there may be a 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 (Chapter 4) 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 budget 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. This finding suggests that males are subjected to somewhat different exigencies than are females and may reflect differential access by males to resources such as food, burrows, territories, or mates. These differences may, in turn, be related to a male's age (and perhaps tenure of a territory), size, social status, or hormonal state (which may interact with other physical factors). At this point in our studies we cannot look beyond simple correlations between ranging patterns and physical factors because we do not know what functional difference, if any, exists between the different ranging patterns. For example, some males may range widely to visit females whereas others may do so because they occupy ranges of inferior resource quality.

One obvious factor which may influence the ranging behavior of males, as it does in females, is reproductive condition. Experimental studies have shown that testosterone has the effect of enhancing search behavior in chicks (Andrews, 1972), increasing persistence in food selection by chicks (Andrews, 1978), and increasing persistence in runway tasks by mice (Archer, 1977). Based on these findings, one might expect testicular _D. merriami_ to exhibit range patterns different from their non-reproductive counterparts. The best data for looking at this relationship are from the third study period since these males exhibited substantial variation in testicular development and ranging behavior (see Table 5.5). As was reported in the results, there were significant positive correlations between testes length and $\bar{D}$ and SD-COA. The following examples demonstrate just how striking the differences between males were. Male 13's testes measured 14 mm in length versus the average of 9.6 mm for all males. His average hourly move was 55 m versus an average by males of 29 m and 23% of his hourly moves were over 100 m versus the male average of 4% (including a single move of 250 m). Similarly, male HL2FR2's testes measured 14.5 mm, his average move was 57 m and 12% of his moves were over 100 m, including a move of 184 m. On the other hand, male HL1, who exhibited no evidence of testicular development, had an average move of 18.2 m and had no moves over 50 m. In fact, 80% of HL1's moves were under 31 m.

Clearly there are factors which differentiate males from one another. Whether hormonal state is of critical importance is difficult to evaluate on the basis of correlational data. These data suggest that reproductive condition and, presumably, level of testosterone are important factors influencing aboveground activity. On the other hand, males implanted with testosterone-secreting capsules in study period 1 did not range significantly more than unmanipulated, but reproductively intact, males (Daly *et al.*, 1981). Furthermore, variation among males during the breeding season, when all males were apparently in reproductive condition, indicates that other factors must be important to the ranging behavior of males.

Body Weight: Another physical factor which could conceivably be related to aboveground activity is body weight. For instance, weight may be positively correlated with such factors as age, social status, or differential access to resources. Whether body weight should be positively or negatively correlated with aboveground activity, however, is not immediately obvious. For example, older animals or those with higher social status may occupy better quality ranges and, thus, would not have to range as widely for resources. On the other hand, such animals may spend more time patrolling their ranges, perhaps either to visit opposite-sexed conspecifics or to exclude competitors. The data do not reveal any clear relationship between body weight and ranging. Despite the overall positive relationship between body weight and ranging behavior, the study-to-study differences prevent any general conclusions.

Risk-taking and Ranging

An important assumption of the cost-benefit approach to the aboveground activity of kangaroo rats is that the risk of mortality should increase with longer exposure time (see Figure 5.1 and explanation in the introduction). As was demonstrated in the results, however, the data presented here do not support that assumption. On the other hand, the small number of known predation instances limits one's conclusions about this relationship. I considered predations as a single factor rather than considering each type of predation separately (i.e. snake vs. shrike, and so forth). Surely different predators call for different kinds of anti-predator strategies. For example, limited surface activity may be effective against avian predators but not against some snake predators. Clearly, much more data are needed to examine the impact of different predators in relation to the surface activity of kangaroo rats.

Study Period

There were clear differences in the aboveground movement and activity patterns of animals between study periods. Factors which conceivably could account for these differences include reproduction, population density, weather patterns, and resource availability. I discussed the role of reproduction in the previous section. In the following sections, I discuss how environmental factors may influence the behavior of _D. merriami_ in general. I then compare the study periods with respect to these factors and the observed activity patterns.

To examine the possible influence of environmental factors on surface activity, I will compare data from the first and third study periods. These data were collected over similar seasonal periods (i.e. November and December) and no breeding was evident in either study. Weather data were recorded at the Boyd Center (a U.S. Weather Service station) located only 1.4 km and 2.8 km from the two study sites. Since food resources on the two study sites were not directly assessed, I depend on the rainfall data from the Boyd Center and the relationship between desert annual production and rainfall established in earlier field studies (e.g. Beatley, 1969) to make inferences about resource availability.

Population Density: Population density may affect ranging behavior in at least two distinct ways. First, when population density is high, competition may result in food shortages. Under these conditions, animals may be forced to forage more widely. On the other hand, if population density is high but food is plentiful and economically defendable, one might find smaller, more exclusive ranges or territories and a concomitant decrease in surface activity.

In addition to intraspecific competition for resources, kangaroo rats probably compete with pocket mice, other rodent species, ants, and birds throughout much of their geographical range (Brown *et al*., 1979). For this reason, the entire biomass of granivores inhabiting or temporarily exploiting (e.g. some birds) an area is probably the population variable most relevant to ranging behavior. Unfortunately we do not have population data on non-rodent granivores. As a result, estimates of granivore density and thus potential competition must be based on trapping data, in this case nightly trapping success and the number of different individuals captured. On average, 34% of the available traps contained rodents during study period 1 of which 10% were occupied by *D. merriami*, 20% by pocket mice, 3% by woodrats, and less than 1% by cactus mice. In study period 3, 38% of the traps contained rodents on average with a breakdown of 16% *D. merriami* and 22% pocket mice. Despite the greater diversity of rodent species on the Ramada site ($\chi^2_{3df} = 67.5$, $p < .01$), the average nightly trap success was not significantly different for the two study sites. With respect to *D. merriami*, however, significantly more individuals were captured on a nightly basis in study period 3 compared to study period 1 ($p < .05$, Mann-Whitney *U* test), despite the fact that the overall numbers of different individuals captured on the two sites were similar; 28 individuals on the Ramada site in December 1980 and 29 and 23 individuals on the Coyote Wash site in November and December of 1982, respectively. Unfortunately, some confounds exist in these data which make it difficult to draw comparisons between the two study sites. For instance, the lower trapping success of *D. merriami* on the Ramada site, despite similar numbers of individuals, may reflect the lower activity levels of animals that were observed in this population. On the other hand, individuals may have been spaced more widely, resulting in less frequent visits to the trapping grid by some more distant individuals.

On the basis of these data, it is difficult to assess the relationship between rodent population density and the ranging behavior of *D. merriami*. As it stands from the overall trapping success measure, however, it would appear that the difference in activity between the study periods was not strongly related to population densities.

Weather: Estimates of kangaroo rat activity under different weather conditions based on trapping data indicate that these animals are relatively impervious to cold and/or severe weather conditions. Animals may be active on the coldest winter nights with temperatures falling well below 0°C and the occasional snowfall (Kenagy, 1973a; O'Farrell, 1974). However, a more sensitive method of monitoring surface activity such as radio-tracking might reveal changes in activity patterns in relation to weather factors, especially if animals are sensitive to the energetic costs (e.g. thermoregulation) of surface activity (see Chapter 6 for a detailed examination of this relationship).

On nights animals were radio-tracked, the mean minimum temperature at the Boyd Center was 10.4°C for November-December 1980 and 11.2°C for November-December 1982 ($\underline{t}_{14df} = .84$, $\underline{p} > .05$). Therefore the difference in surface activity between the two study periods cannot be accounted for by differences in the average minimum air temperature. This finding, however, does not imply that air temperature exerts no control whatsoever over surface activity. In study period 1 there was a positive relationship ($\underline{r} = .36$) between air temperature and $\bar{D}$, but there was no relationship between these variables for study period 3 ($\underline{r} = -.06$). This discrepancy may partly be explained by the relatively small range in minimum air temperatures in study period 3 (7-14°C) compared to the range in study period 1 (4-19°C). On the other hand, other factors (e.g. food resources) in study period 3 may have been more important than air temperature to animals' activity budgets.

Precipitation may influence the aboveground activity of kangaroo rats for at least two reasons. First, it would seem to be important for a small mammal to keep its fur dry for insulation. Second, kangaroo rats may not be able to forage efficiently when the substrate is wet since their foraging involves filtering the soil for small seeds. This difficulty may persist for several days following heavy rainfall. But it appears that precipitation cannot account for the observed differences in activity patterns between the study periods either. There was no measurable rainfall during the first study period. On the other hand, Boyd Center received 7.5 cm of rain over the course of the third study period. If anything, the predicted direction of differences in surface activity would be opposite to those observed. Rainfall does inhibit surface activity on a night-to-night basis however: on a night when animals were radio-tracked during a rainstorm, the $\bar{D}$ was 10.4 m, the lowest nightly average for the study period (Chapter 6).

Resources: It is difficult to evaluate the role food availability may have had in influencing surface activity since food density and distribution were not directly assessed during the study periods. The vegetational characteristics of the closely-situated sites were similar. For example, each 1 ha trapping-grid had 24 palo verde trees and the Ramada site had 78 creosote bushes versus 93 for the Coyote Wash site. One possibility is that, as a result of different amounts and timing of rainfall, the two study sites differed in their food production over periods preceding the studies. This hypothesis is not testable from the data available but a few speculations based on the observed rainfall patterns can be made. From September to December of 1979, the time when moisture is necessary for the germination of winter annuals, only 3 mm of rain fell at the Boyd Center, well below that needed for good germination (Beatley, 1969). This lack of rainfall should have depressed winter annual seed production in 1980. But in July and August of 1980, Boyd Center received 25 mm of rain, perhaps resulting in good summer annual production and ensuring an adequate food supply for the animals in the fall. From September through November of 1981, Boyd Center received 25 mm of rain, the optimal amount reported by Beatley (1969) for good winter annual production in the Mojave Desert. Hence, winter annual seed production in 1982 should have been good. In September of 1982 a severe thunderstorm struck the region around Boyd Center and, with a deluge of over 90 mm of rain in one day, triggered a flash flood on the Coyote Wash site. It is not known what specific effects the flood had on the food supply, but it seems plausible that seeds were washed away and much of what remained germinated. The flora of Deep Canyon was unusually lush in November and December of 1982 with reports of the presence of annual species that had not been seen before (Burke, personal communication) and the observation that there was unusually good germination of palo verde trees (Mitchell, personal communication). Thus, animals in the fall of 1982 could have been faced with a shortage of food which, consequently, would have led to increases in their surface activity to meet energy-nutrient demands.

The aforementioned factors (i.e. reproduction, population density, weather, and resources) probably do play a role in the observed seasonal and yearly differences in surface activity, but the nature of their influence remains unknown. The main point is that variability over the long term exists and that no single factor appears to be sufficient to account for the variation. Long-term variation in surface activity probably requires a multifactorial explanation and much more longitudinal data are required to address these kinds of questions.

Conclusion

In this chapter, we have seen that the aboveground activity of D. merriami can vary substantially from season-to-season and from year-to-year. Moreover, these differences are not singularly related to reproductive condition, population density, weather patterns, or resource availability. Rather, the aboveground activity of these animals probably results from the complex interaction of these factors and possibly others not considered here. A long-term study on the same site is necessary to evaluate the influence of these factors on surface activity. It should also be possible to manipulate such factors as resource availability and population density to determine their effects on surface activity. The very fact of inter-study differences is important, however, because they clearly demonstrate that descriptions of so-called "species-typical" behavioral patterns based on short-term field studies or those with inadequate methodology (e.g. trapping techniques) are suspect.

A more substantial contribution of the information presented in this chapter, in regard to considerations of behavioral strategies, is the observation of sexual dimorphism in the ranging patterns of D. merriami only during the breeding season. This finding indicates that ranging patterns probably serve functions beyond the acquisition of food resources and, consequently, that some aspects of ranging may be related to the different reproductive strategies of the two sexes and, moreover, of individuals. That female ranging varies significantly with reproductive condition is further evidence for this. The variance in male ranging behavior may also reflect different behavioral strategies. One may speculate that the greater within-sex variance in ranging by males compared to females during the breeding season is somehow related to the greater variability of males' access to mates and, hence, reproductive success.

Chapter VI

Relationships Between Physical Factors and Surface Activity

Innumerable laboratory studies have demonstrated that the daily activity patterns of captive small mammals are influenced by several environmental factors including the time of day, incident and ambient light, ambient air temperature, and humidity (see Kenagy, 1973a, 1976a, for example). Presumably, small free-living mammals too are sensitive to variations in environmental parameters and modify their behavior accordingly. Unfortunately, however, comparatively few studies of small mammals have been able to demonstrate convincing relationships between behavior in the natural environment and environmental factors. The lack of experimental control and methodological and inferential limitations inherent in most field studies (see Chapter 3) have contributed to this difficulty.

Throughout this thesis I have assumed that animals make behavioral "decisions" which reflect the cost-benefit relationships of their activity (refer to discussion in Chapter 5). Several environmental factors could conceivably influence the cost-benefit relationships of kangaroo rat activity either by affecting predation risks or energetic relationships. Those to be discussed here include moonlight, temperature, and precipitation. Some studies investigating the responses of small mammals to these environmental factors provide evidence that in many cases animals behave in ways consistent with predictions from cost-benefit models of activity.

Following a brief selected review of these studies, data concerning D. merriami surface activity in relation to moonlight, time of night, temperature, and precipitation will be presented.

Moonlight

Suppression of activity under moonlight may be a means by which small nocturnal mammals reduce their losses to predators. For example, owls, which are important predators of nocturnal rodents, probably hunt more effectively under moonlight than in total darkness. Dice (1945) demonstrated experimentally that barred, long-eared, and barn owls located dead prey (thus eliminating auditory cues) more readily under low light levels than in total darkness. Likewise, Clark (1983) using a flight chamber, simulated moon phases, and live deermice as prey, found that the hunting effectiveness of short-eared owls increased with a waxing moon and that search and capture time were significantly reduced under simulated full moonlight.

Moonlight avoidance has been reported for some kangaroo rat species including the Tulare kangaroo rat, D. heermanni (Tappe, 1941), D. spectabilis (Lockard and Owings, 1974a,b; Lockard, 1975,1978) and D. merriami (O'Farrell, 1974). In contrast, other studies have failed to indicate moonlight avoidance by kangaroo rats including D. spectabilis (Schroder, 1979), D. merriami (Chew and Butterworth, 1964), and D. nitratoides (Lockard and Owings, 1974a).

A series of field studies by Lockard and Owings provides perhaps the most convincing demonstration of moonlight avoidance by any species of rodent. D. spectabilis activity was monitored by automatically recording the visitation of animals to seed dispensers placed in the field. Lockard and Owings (1974b) and Lockard (1978) found a striking reduction in visitations under moonlight during long winter nights when dark hours were also available for foraging. However, D. spectabilis were active during moonlight in the spring. This seasonal difference led Lockard and Owings to suggest that animals were forced into moonlight activity on the shorter nights in the spring in order to meet their energetic demands. In contrast to these findings, Schroder (1979) failed to observe moonlight avoidance in any season by radiotelemetered D. spectabilis. If, however, D. spectabilis in the Lockard and Owings studies were indeed foraging during moonlight in order to meet energetic demands, it is conceivable that the D. spectabilis observed by Schroder (1979) were faced with food shortages in the winter and thus forced to forage under moonlight as well.

It makes sense that D. spectabilis, as larder hoarders with large food supplies in their home mounds, would avoid unnecessary surface activity under moonlight when predation risks may be higher. D. merriami, as scatter hoarders, do not have large food stores in their burrows (Jones, 1982) and thus may be required to forage during moonlight to meet their energetic demands. On the other hand, D. merriami are much smaller than D. spectabilis (35-45 g versus 100-150 g) and, thus, have lower energetic demands which may be met without resorting to moonlight activity.

Until the present study, the evidence for moonlight avoidance by D. merriami has been equivocal. Chew and Butterworth (1964) found no evidence for moonlight avoidance by D. merriami based on trapping data. However, O'Farrell (1974), although providing no quantitative data, states that "When the moon was present activity was low, but if a cloud were to pass in front of the moon activity immediately increased." (pg. 817). It is not clear whether this statement is based on trapping data or anecdotal observation. In any case, solid quantitative measures of moonlight activity by D. merriami have not been reported.

It should be noted that moonlight (natural and simulated) has been observed to suppress the activity of several other small mammal species including cactus mice, *Peromyscus eremicus* (Owings and Lockard, 1971), deermice, *Peromyscus maniculatus* (Clark, 1983), harvest mice, *Reithrodontomys megalotis* (Pearson, 1960), grasshopper mice, *Onychomys leucogaster* (Jahoda, 1970,1973), meadow voles, *Microtus pennsylvanicus* (Doucet and Bider, 1969), a neotropical fruit bat, *Artibeus jamaicensis* (Morrison, 1978), and masked shrews, *Sorex cinereus* (Vickery and Bider, 1978).

Temporal Activity and Temperature

Information about a species' temporal activity patterns is crucial for understanding its energy/activity budgets. The temporal activity patterns of kangaroo rats are particularly interesting because heteromyids have developed certain foraging specializations (e.g. cheek pouches and hoarding behavior) which presumably serve to minimize the amount of time spent away from the burrow (Kenagy, 1973a). Variations in temporal activity patterns should reflect changes in resource conditions. For example, when resources are scarce or energetic demands are higher, animals must spend more time on the surface foraging. Indeed, Lockard (1978) found that *D. spectabilis* were active on the surface during daylight hours following several months of severe drought. However, it is likely that temporal activity patterns do not vary merely in response to changes in food resources. Ample evidence has been presented in this thesis that D. merriami surface activity entails more than the acquisition of food to meet energetic demands.

An interesting study of D. merriami nocturnal activity was carried out by Reynolds (1960) in which activity was monitored in the field by movements across a treadle positioned at the entrance of a nest box. In this study, D. merriami made frequent trips throughout the night with peak activity occurring about two hours after sunset and about two hours before sunrise. Animals seldom spent more than about 35 minutes out of any hour away from their nest boxes even at peak activity.

Two studies in which trapping was conducted over successive periods within a night revealed rather different temporal activity patterns by two separate D. merriami populations. Kenagy (1973a) found that D. merriami activity (inferred by the relative numbers of animals entering traps) increased over successive quarters of the night. This finding was unexpected since it meant that D. merriami were most active during the coldest part of the night when energetic costs should be highest. Conversely, O'Farrell (1974) found that D. merriami activity levels were generally greater in the early part of the night. In addition, O'Farrell found that temporal activity varied in relation to season and sex. In the winter, animals entered traps at about the same rate throughout the night and there was no difference between males and females. In the spring and summer, activity was greatest in the early part of the night with males more active than females throughout the night. In the fall, a pattern similar to the spring-summer pattern was observed but there was a smaller difference between males and females.

This finding of two fundamentally different nocturnal activity patterns by two separate _D. merriami_ populations is interesting. On both study sites _D. merriami_ are sympatric with _D. microps_. Kenagy suggested that _D. merriami_ are more active later in the night in order to avoid confrontations with the larger and socially dominant _D. microps_. Why the same interaction was not apparent on O'Farrell's study site is not clear. It is possible that the two sites have different community structures and, consequently, different levels of interspecific competition. For instance, the two sites may differ in the relative densities of _D. merriami_ and _D. microps_ populations or in the utilization of different microhabitats. Nonetheless, it is apparent that _D. merriami_ alter their nocturnal patterns in relation to season and perhaps social factors.

Taken together, findings from the different studies suggest that _D. merriami_ temporal activity patterns are relatively labile. Generalizations about activity patterns should be avoided in the absence of specific information about resource conditions and inter- and intraspecific interactions.

Ambient air temperature is a potentially important determinant of nocturnal activity. During extremely cold or hot temperatures, the metabolic costs of surface activity will be significantly higher than those associated with activity during milder temperatures. Animals should therefore modify their surface activity, for example, by reducing surface time or by avoiding microhabitats with more severe climatic conditions (e.g. open windy areas or low spots where cold, moist air may collect).

Unfortunately, trapping studies provide relatively poor information about the responses of animals to temperature. Traps generally are not checked frequently enough to detect fine-tuned responses to temperature fluctuations occurring throughout the night. However, there is evidence that _D. merriami_ are active on the surface at temperatures down to -19°C and as high as 30°C (Kenagy, 1973a). Animals may also be active during and shortly after light snowfalls (Kenagy, 1973a) although O'Farrell (1974) reported that animals were inactive when there was more than 40% snow cover. Kangaroo rats have insulating fur on the bottom of their rear feet and thus may be relatively impervious to extreme cold if they minimize the duration of their surface bouts.

Radiotelemetry is a more useful technique for monitoring nocturnal activity and responses to temperature changes. It will be shown in the results that temperature, at least in the range recorded in the present study, is not an important determinant of surface activity.

Precipitation

Humidity and rainfall may differentially influence the activity patterns of different small mammal species. Species exhibiting enhanced activity with high humidity or light rain include the masked shrew (Vickery and Bider, 1978), the harvest mouse (Pearson, 1960), the grasshopper mouse (Jahoda, 1970,1973) and the oldfield mouse, _Peromyscus polionotus_ (Gentry and Odum, 1957). The response of animals may also depend on the intensity and timing of rain with respect to the animals' typical daily activity patterns. Grasshopper mouse activity is suppressed in heavy rain (Jahoda, 1970,1973) and masked shrew activity is greatest when rain shortly precedes nocturnal activity (Vickery and Bider, 1978).

For carnivorous or insectivorous animals such as the grasshopper mouse and the masked shrew, high humidity and light rainfall may be associated with increases in the abundance of prey. Activity under humid or rainy conditions may also be advantageous during the winter since temperatures are generally milder.

For kangaroo rats, trapping success is generally lower on rainy nights. Tappe (1941), rather surprisingly, found that _D. heermanni_ did not enter traps on rainy nights (0 rats in 300 trap nights in the rain!). Similarly, O'Farrell (1974) found that trap activity by *D. merriami* and *D. microps* was suppressed by rainfall. Kenagy (1973a), on the other hand, found that while *D. merriami* were somewhat suppressed, both *D. merriami* and *D. microps* were active in all four quarters of a night with continuous moderate rainfall.

As primarily granivorous rodents (with the exception of *D. microps*; Kenagy, 1972,1973b; Csuti, 1979), it seems that foraging by kangaroo rats would be hindered by rainfall since seeds must be gleaned from the soil. Rainfall also releases some rather pungent odors from many desert plants which may mask the odor of seeds and thus make them more difficult to detect. *D. microps*, which were not deterred by the rain in the Kenagy (1973a) study, feed on saltbush and thus would not be affected by rainfall.

The Present Study

The studies cited above provide coarse analyses of relationships between environmental factors and surface activity. Radiotelemetry, with the advantage of providing more continuous monitoring of unrestrained animals, should provide a finer-grained analysis of these relationships.

Analyses

<u>Moonlight Avoidance</u>: The hypothesis that moonlight inhibits the surface activity of *D. merriami* was tested by comparing the hourly movements of individuals for moonlit and dark periods in the following way. Data for analysis were drawn from nights with at least two hours of moonlight and two hours of dark within the sample interval. The average movement by an individual under moonlight was calculated from the pooled hourly moves for the two hours preceding moonset or following moonrise. Similarly, the average move for dark periods was calculated from the pooled hourly moves for the two hours preceding moonrise or following moonset. The difference between the means were then tested using Student's *t*-test for correlated groups.

The relationship between the inhibitory effects of moonlight and the intensity of moonlight was examined by correlating the fraction of the moon illuminated on a given night with the mean difference between moonlight and dark surface activity for that night. Difference scores were calculated by first finding for each individual the mean hourly move for the two hour moonlight and two hour dark periods, respectively, on tracking nights used in the above analysis. Grand means (i.e. a mean of means) for moonlight and dark period movements were then generated from the individual means for each night and the difference between the moonlight and dark movement means was found.

Temporal Patterns: Temporal activity patterns were established by determining the mean move per hour by an individual at each hour of the night. The means for individuals were pooled within each study period to provide a description of populational temporal behavior patterns for a particular season and night length. The data from study periods 1 and 3 were tested for sex differences and trends using ANOVA with one between-groups factor (sex) and one within-subjects factor (hour of night).

Temperature Effects: The analysis of the effects of air temperature on surface activity presented in Chapter 5 failed to reveal a consistent linear relationship between average hourly movement and minimum nightly air temperature ($\underline{r}$ = .36 for study period 1 and $\underline{r}$ = -.06 for study period 3). Nonetheless, the possibility remains that, over the course of a night, animal movements vary in relation to hour-to-hour changes in ambient air temperature. To confound matters, however, there is a strong negative relationship between air temperature and the number of hours past sundown (e.g., $\underline{r}$ = -.96 for study period 3). In addition, as will be shown in the results, there was a negative linear trend in surface activity over the course of the night in study period 3. Hence, the data were tested to determine whether time of night and temperature had separate and/or interactive effects.

Data from study period 3 were used for analysis because that period provided a substantial data set collected simultaneously for several individuals of both sexes over a relatively short period of time; i.e., 21 tracking nights in 35 days. Each hourly movement for an individual was categorized by hour of the night and air temperature. For simplification, the dark period was broken down into four intervals: 1700 to 2000 hr, 2100 to 2400 hr, 0100 to 0400 hr, and 0500 to 0700 hr. Air temperature was collapsed into two categories: warm ($>11^{\circ}C$) and cold ($\leq 11^{\circ}C$). Means for each time-temperature category were found for each individual and then subjected to ANOVA with one between-groups factor and two within-subjects factors (hour and air temperature).

Results

Moonlight: Moonlight had a clear inhibitory effect on the movements of animals. For both study periods 2 and 3 animals moved 8 m less on average during moonlit periods versus dark periods (15.9 m vs. 24.0 m for study period 2, $t_{18df} = -2.45$, $p < .025$, one-tailed test and 24.9 m vs. 32.9 m for study period 3, $t_{15df} = -2.72$, $p < .01$, one-tailed test). Males and females responded similarly to the presence of moonlight. In study period 2, 6 of 10 females and 6 of 9 males were less active during moonlight versus dark. In study period 3, 6 of 8 females and 7 of 8 males were less active during moonlight.

Whether the reduction of surface activity by animals under moonlight is positively related to the intensity of moonlight is equivocal. There was no linear correlation between the difference scores (i.e. between moonlight movement and dark movement) and the fraction of the moon illuminated for study period 2 ($\underline{r} = -.09$, see Figure 6.1). On the other hand, this correlation was significant for study period 3 ($\underline{r} = .73$, $p < .05$, see Figure 6.1). The data from study period 3 are more suitable for calculating a correlation because samples were from a wider range of fraction illuminated values. From Figure 6.1, however, it is difficult to see how a wider range of illumination values for study period 2 would have changed the results since five difference scores in the 60-80% illumination range were negative.

Temporal Patterns: In general, surface activity occurred throughout the night in all three study periods (Figure 6.2 a-f) but there was variation in the relative levels of activity. For study period 1, analysis of variance (Appendix B) revealed temporal activity differences ($\underline{F}_{13,208df} = 3.32$, $\underline{p} < .01$) with a trend that departed significantly from linearity. Figure 6.1a shows that these animals exhibited temporal bimodality in their surface activity with peaks after dusk and again around midnight. Animals in study

Figure 6.1. The relationship between the fraction of the moon illuminated and the moonlight-dark surface activity difference score (see text for explanation). ○ = study period 2, ● = study period 3. $r = -.09$ for study period 2 and $r = .73$ for study period 3 ($p < .01$).

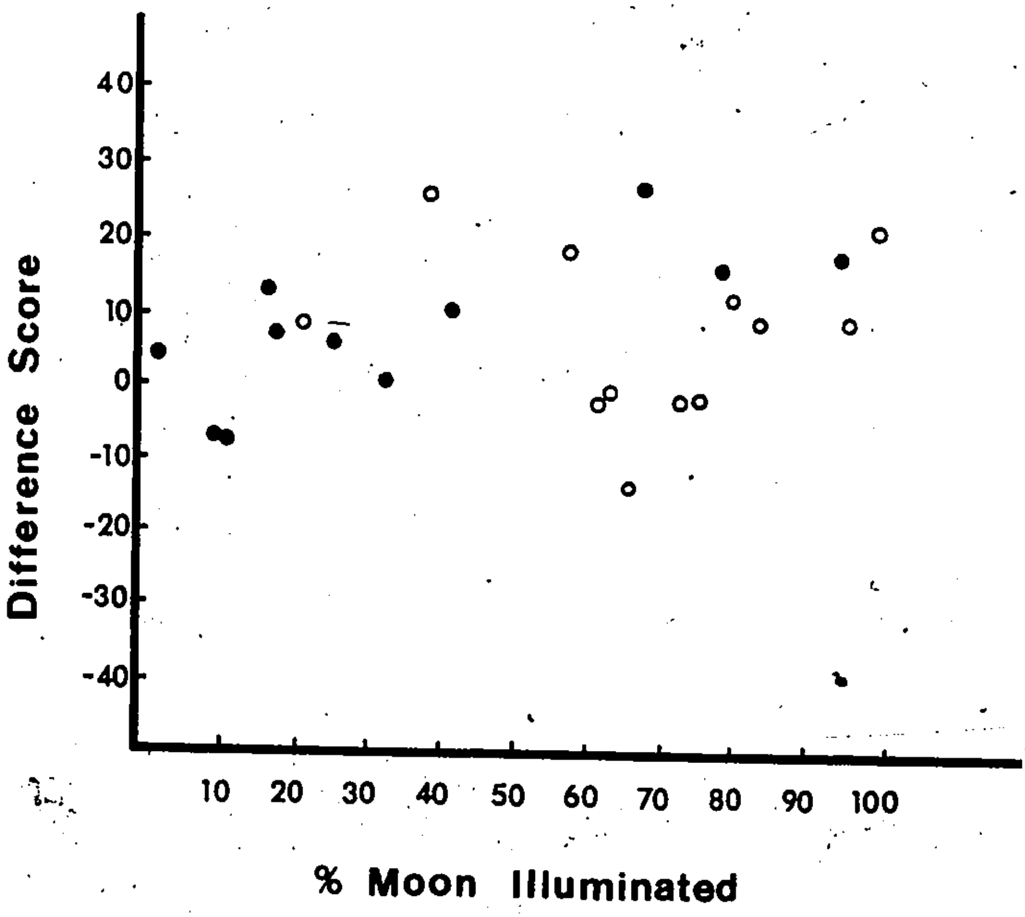
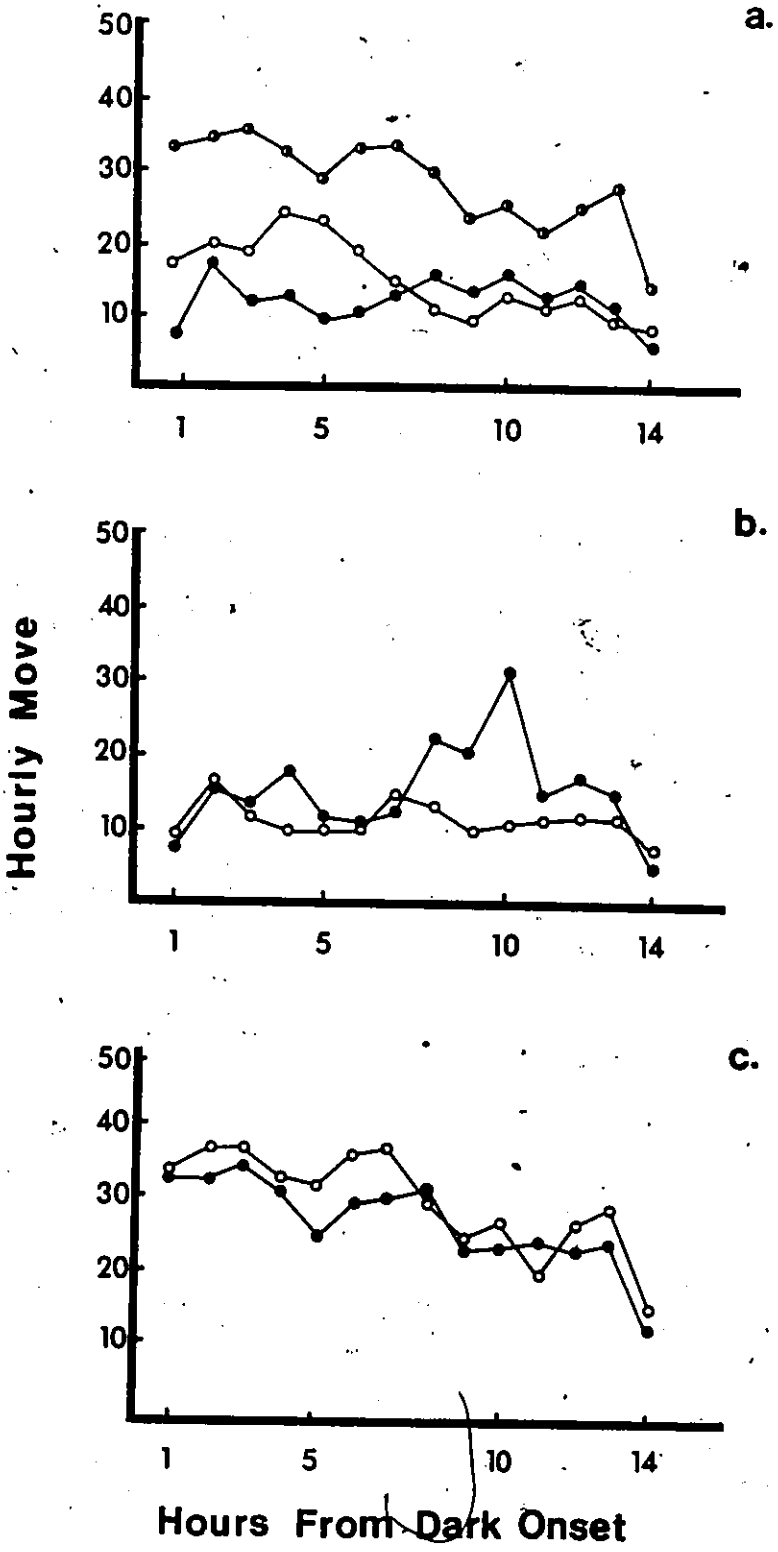
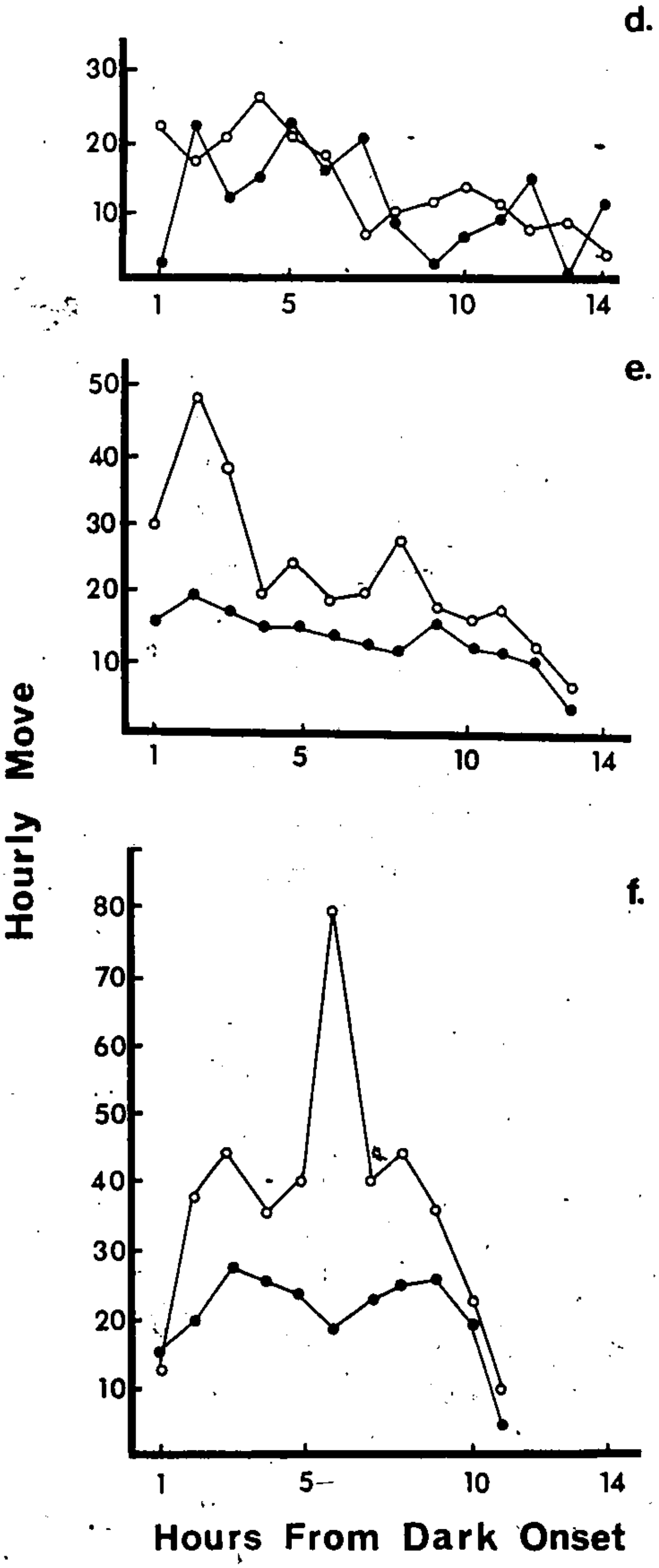

Difference Score
40
30
20
10
0
-10
-20
-30
-40
10
20
30
40
50
60
70
80
90
100
% Moon Illuminated

Figure 6.2. Average hourly moves $(\bar{D})$ throughout the night. a. male-female combined, ● = Dec. 1980, ○ = Dec. 1981 to Jan. 1982, ◐ = Nov. to Dec. 1982. b. Dec. 1980, ○ = male, ● = female. c. Nov. to Dec. 1982, ○ = male, ● = female. d. Dec. 1981 to Jan. 1982, ○ = male, ● = female. e. Feb. to March 1982, ○ = male, ● = female. f. April to May 1982, ○ = male, ● = female.

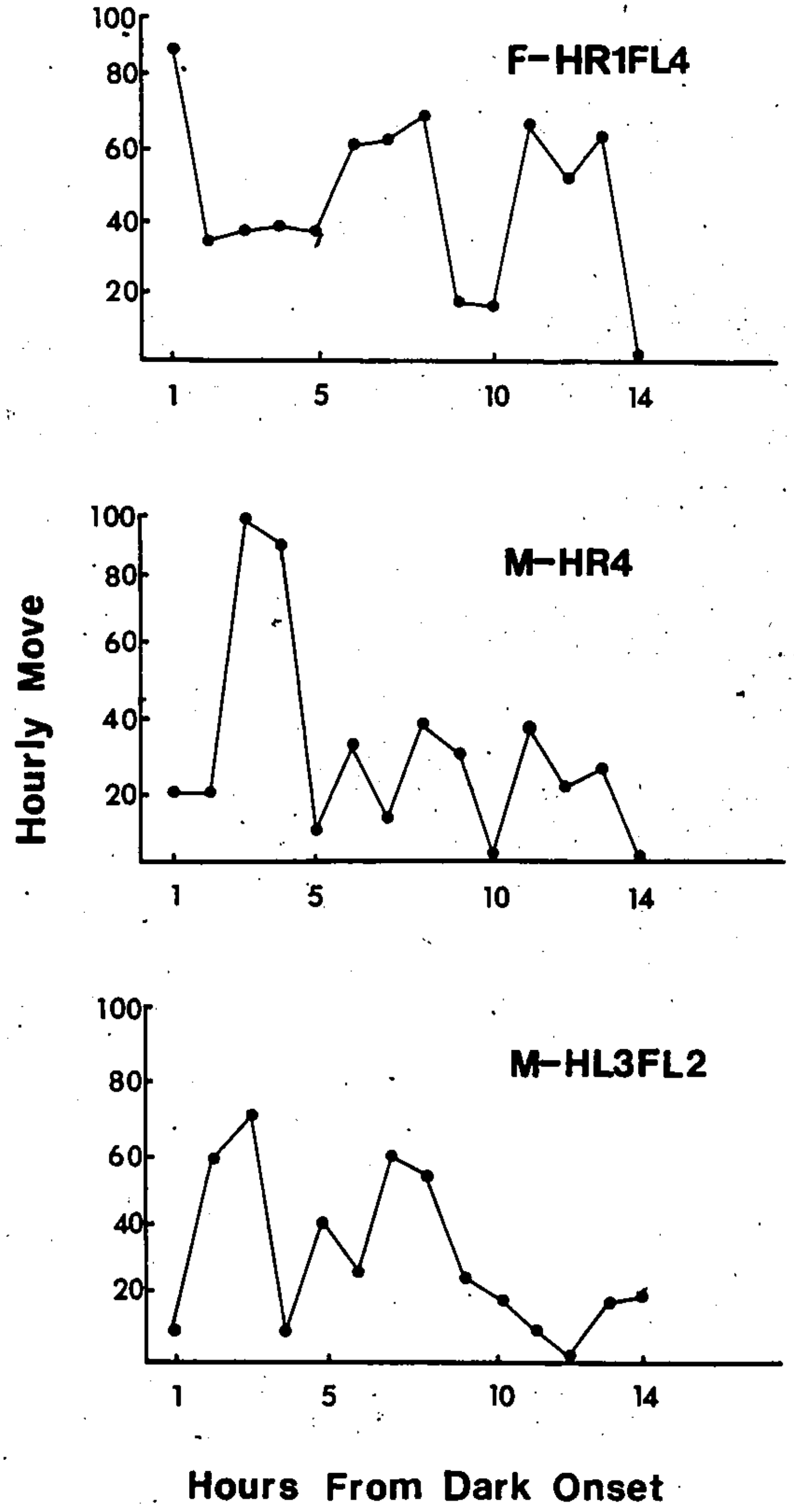

a.
b.
c.
50
40
30
20
10
1
5
10
14
Hourly Move
Hours From Dark Onset


d.
30
20
10
1
5
10
14
e.
50
40
30
20
10
1
5
10
14
f.
80
70
60
50
40
30
20
10
1
5
10
14
Hourly Move
Hours From Dark Onset

3 also exhibited variation in their activity over the course of the night ($F_{13,182df} = 5.56$, $p < .01$) but in this case there was a significant linear trend ($F_{lin,13,182df} = 63.3$, $p < .01$). Figure 6.2a shows that activity levels in this population were highest shortly before dark with smaller peaks occurring just before midnight and again shortly before dawn. The temporal patterns of study period 2 animals during the winter depicted in Figure 6.2d,e were similar to study period 3 animals but these data were not analyzed statistically due to the small sample sizes for these periods. The temporal patterns of study period 2 animals during the spring months (Figure 6.2f) are different from the fall and winter patterns. Animals were continuously active from shortly after dusk to shortly before dawn, perhaps in response to factors such as warmer air temperatures, shorter nights, or some social or reproductive considerations.

The above analyses describe the temporal patterns seen in the population on a whole. To examine the temporal patterns of individuals, three study period 3 animals were selected at random and one single-night sample from each was selected at random for illustrative purposes. Figure 6.3a-c shows that the temporal patterns described for study period 3 animals hold for individuals as well. Despite the variation among individuals, these single-night samples exhibit a variable but decreasing trend in movements throughout the night similar to the pooled data presented in Figure 6.2a.

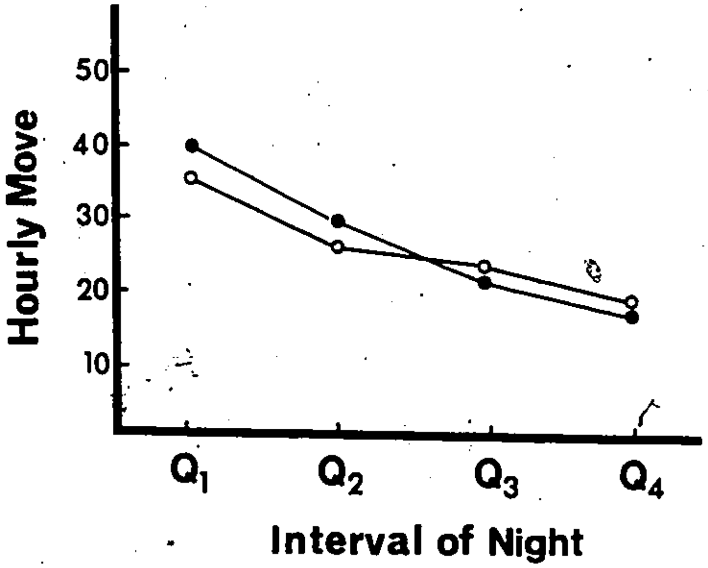
Figure 6.3. Hourly moves ($\bar{D}$) over a randomly selected night by a randomly selected individual from study period 3 (see text for details). Female HR1FL4 on Dec. 21, 1982, Male HR4 on Nov. 20, 1982, and Male HL3FL2 on Nov. 22, 1982.


F-HR1FL4
M-HR4
M-HL3FL2
Hourly Move
100
80
60
40
20
1
5
10
14
Hours From Dark Onset

Sex Differences in Temporal Activity: Analysis of variance (Appendix B) revealed a significant sex by time of night interaction in study period 1 ($F_{13,208df} = 1.93$, $p < .05$). Females were relatively more active in the early morning hours than the males (Figure 6.2b). However, for the same season and under similar populational reproductive conditions in study period 3, there was no sex difference (Figure 6.2c). Although the data were not statistically analyzed, from February through May there was a sex difference in activity but the temporal patterns of the two sexes appear to be very similar (Figure 6.2d-e).

Temperature Effects: The analysis of temperature effects on surface activity as a function of sex and time of night indicates that, at least in study period 3, temperature was not an important factor. In accordance to the results reported in the previous section, time of night was a significant factor for surface activity (ANOVA, $F_{3,36df} = 11.6$, $p < .01$). As Figure 6.4 indicates, a mild interaction exists between temperature and time of night ($F_{3,36df} = 2.03$, $.25 > p > .10$). If such an interaction were verified, it would indicate that animals mass their surface activity over shorter periods of time when faced with cold temperatures whereas activity is more evenly distributed throughout the night when temperatures are warmer.

Figure 6.4. The average hourly move ($\bar{D}$) at different quarters of the night at warm (○, >11°C) and cold (●, ≤11°C) temperatures (see text for explanation).


Hourly Move
50
40
30
20
10
Q_1
Q_2
Q_3
Q_4
Interval of Night

Precipitation: Surface activity during or immediately following rainfall is reduced rather dramatically. For study period 2, movements were monitored on four nights with rain occurring either before or during the sample period. On these nights, 12 of 13 animals exhibited $\bar{D}$'s that were below their average $\bar{D}$. On average, hourly moves were reduced 50% on nights with rainfall. The results were similar for the single night animals were tracked during rain in study period 3. Twelve of 12 animals showed reduced $\bar{D}$'s compared to their average $\bar{D}$ with an average reduction of 60%.

Discussion

The surface activity of *D. merriami* varies in relation to moonlight, time of night, and precipitation. As discussed in the introduction, these environmental factors have potential importance to the cost-benefit relationships of surface activity.

Moonlight Avoidance: The finding that *D. merriami* move less under moonlight agrees with an earlier anecdotal report of moonlight avoidance by this species (O'Farrell, 1974) and the findings for *D. spectabilis* by Lockard and Owings (1974a,b) and Lockard (1978). The data were insufficient, however, to determine whether there was a seasonal component to *D*.

merriami moonlight avoidance similar to that observed in D. spectabilis.

The seasonal nature of D. spectabilis moonlight avoidance (Lockard and Owings, 1974a,b; Lockard, 1978) suggests that this behavior is facultative and may depend on the availability of resources and/or the time available for foraging. This may account for the apparent lack of moonlight avoidance reported elsewhere for D. merriami (Chew and Butterworth, 1964) and D. spectabilis (Schroder, 1979).

Rosenzweig (1974) proposed an alternative explanation for the seasonal nature of D. spectabilis moonlight avoidance based on a more general cost-benefit model. By assuming that the potential benefits of surface activity (in terms of reproduction) were higher in the spring, Rosenzweig suggested that D. spectabilis were insensitive to moonlight in the spring due to the greater opportunities for reproduction. If this hypothesis were true, study period 3 animals (i.e. non-breeding) in the present study should have exhibited relatively greater suppression under moonlight than study period 2 animals (i.e. breeding). This was not the case. For study period 2 animals there was a 34% reduction in movement under moonlight while the reduction for study period 3 animals was only 24%. Furthermore, if reproductive potential is an important determinant of surface activity under moonlight, the sex with the greater potential (presumably males in kangaroo rats; see discussion in Chapter 5) should be less affected by moonlight. There was no sex difference in the suppression of surface activity under moonlight.

Despite the apparent absence of seasonal and sex differences in the avoidance of moonlight by D. merriami, these questions certainly deserve further study. The data were not adequate to make detailed comparisons of moonlight activity by animals differing in sex and reproductive condition. Laboratory studies of activity by animals exposed to simulated moonlight would be more feasible than field studies to investigate these questions. As an example, Martin and Böttig (1980) found that estrous laboratory rats entered illuminated mazes more frequently that diestrous rats.

An unresolved issue concerns the function of moonlight avoidance. Although the assumption that moonlight avoidance serves to reduce the predation risk of small prey is supported by at least one laboratory study (Clark, 1983), at present there is no direct evidence that this is the case under natural circumstances.

Temporal Activity Patterns: The temporal activity patterns of D. merriami in the present study were similar to those reported by O'Farrell (1974), but somewhat different from the patterns reported by Kenagy (1973a). In the fall and winter months the greatest activity occurred in the early hours of the night with smaller peaks occurring 5-7 hours after dusk and 1-2 hours before dawn. In April and May of study period 2, animals were active throughout the night with no apparent lulls. If one assumes that animals are sensitive to the higher energy costs of surface activity in the face of cold temperatures, these temporal patterns make sense. During the fall and winter, temperatures are warmest in the early evening while in the spring air temperatures are relatively mild throughout the night. However, when the effects of ambient air temperatures and time of night were examined together for study period 3, air temperature was not a significant factor.

Seasonal variation in D. merriami temporal activity patterns could possibly result from changes in the availability of resources and the time available for foraging. Long fall and winter nights may allow an animal sufficient time to forage and still spend several hours in its burrow. On shorter spring nights an animal may have to be on the surface foraging most of the dark hours. In addition, it is during the late winter and spring that females' energetic demands will be higher due to reproduction.

The sex difference in surface movements reported for study period 2 animals in Chapter 5 is reflected in their temporal patterns as well (Figure 6.2e,f). Males were more active than females at all hours of the night from February through May of 1982. There was no consistent sex difference in temporal activity of the non-breeding periods of studies 1 and 3. The interaction between sex and season with respect to temporal activity is similar to the pattern for D. merriami reported by O'Farrell (1974).

Taken together, the evidence from this study and earlier studies (O'Farrell, 1974; Kenagy, 1973; Lockard, 1978) suggests that the labile temporal activity patterns of kangaroo rats are probably influenced by both endogenous and exogenous factors including sex, energetic demands, resource conditions, and interspecific competition. The most striking example of adjustments in activity by kangaroo rats in response to environmental factors is the diurnal activity of D. spectabilis following several months of drought (Lockard, 1978). The demonstrated flexibility of temporal activity by kangaroo rats raises important questions about the proximate control of these behavioral adjustments. One possibility is that relatively slow-acting and long-term adjustments occur as a result of hormonal changes. An alternative, but not necessarily exclusive, possibility is that animals are constantly processing external information in order to assess environmental conditions such as resources, inter- and intraspecific competition, and the availability of mates. The latter possibility assumes that a more complex cognitive process is in operation than the former. It would be interesting to examine the cognitive abilities of these animals given the behavioral flexibility they exhibit in the field (see, e.g., Daly, Rauschenberger, and Behrends, 1982).

Precipitation: In agreement with trapping studies of kangaroo rat activity by Tappe (1941) and O'Farrell (1974), *D. merriami* in the present study were significantly less active on rainy nights compared to dry nights. This stands in contrast to several small mammal species which exhibit elevated levels of activity with high humidity and rain (Gentry and Odum, 1957; Pearson, 1960; Jahoda, 1970,1973; Vickery and Bider, 1978). The significance of kangaroo rat avoidance of rain is unknown but some possibilities include problems with foraging, predator avoidance, or thermoregulation. Unfortunately, too few data are available on *D. merriami* activity under different intensities of rainfall to determine whether animals respond differentially.

Conclusion

The results of this chapter indicate that *D. merriami* modify their surface activity in response to several environmental factors including moonlight, time of night, season, and precipitation.

Surface activity is suppressed under moonlight and may be a means by which animals reduce their losses to predators. However, there is presently no direct evidence that predation risk is higher under moonlight.

There was an interaction between temporal activity patterns and season. In the fall and winter, activity was highest in the early part of the night with lulls and smaller activity peaks later in the night. In the spring, activity was high throughout the night. Variations in temporal patterns with regard to season and sex may occur in response to changing resource conditions, energetic demands, the amount of time available for foraging, and reproductive activities.

These results suggest that D. merriami make short- and long-term adjustments in surface activity in response to both endogenous and exogenous factors.

Chapter VII

Range Use and Spatial Relationships

A primary method used by field workers to study the social structure of small, free-ranging mammals is to assess spatial patterns (e.g. home range size and use) and inter-individual spatial relationships including the spatial distribution of homesites, territories, and ranges. There is ample evidence that spatial patterns and inter-individual spatial relationships are important factors for the social behavior of many species (see Brown and Orians, 1970 and the discussion in Chapter 5). Recall, for example, the finding by Daly and Daly (1974) that male fat sandrats inhabit resource-poor burrow sites which are nevertheless located near several females' burrow sites. The finding by Brooks and Banks (1971) that male collared lemmings maintain no consistent center-of-activity but rather have several rest areas in their range near female homesites is also a good example of a relationship between spatial patterns, social behavior, and reproduction.

I previously reviewed the literature pertaining to the spatial relationships of free-ranging kangaroo rats in

Chapter 5. In the following section of this chapter I will outline the rationale and methods for the analyses used to examine the spatial patterns and inter-individual spatial relationships of D. merriami. These include home range size, range use patterns, spatial overlap, and day burrow distribution and use patterns. This section will be followed by the results and a discussion of D. merriami socio-spatial behavior.

Analyses

Minimum Home Range: Some of the techniques used to estimate home ranges were discussed in Chapter 3. Since there is no single accepted statistical technique for estimating home ranges, and due to the difficulty of satisfying the underlying assumptions of these methods, I will present the home range data in a very descriptive manner. Given the large number of radio fixes collected for most animals, it is likely that the ranges described below are very close to the animals' actual ranges.

Home range is generally defined here as the areal sum of the quadrats (see below for an explanation of the mapping system) in which the animal was radio-located plus the areal sum of the minimum number of quadrats the animal would have had to traverse in order to reach disjunct quadrats in which locations were recorded.

The calculation of home range is very straightforward. Each study site was mapped as a two-dimensional grid (i.e. x-y coordinates) with each quadrat $10\ m^2$ in size. To find the home range, the different quadrats occupied by an animal are mapped and counted and the minimum number of intervening quadrats needed to reach distant quadrats is determined. Home range (in hectares) is determined from the following equation

$$HR = Q/100$$

where Q = the number of quadrats occupied plus the minimum number traversed. An example of a home range for a male is depicted in Figure 7.1. This male was radio-located in 16 different quadrats with three having no adjacent occupied quadrats. This male would have to have traversed at least six additional quadrats, and thus the home range is 0.22 ha.

Only animals with more than 50 night fixes were included in this analysis since within each study period home range tended to increase to an asymptote with 50-60 fixes.

Detailed statistical comparisons between study periods were not carried out on home range for several reasons. First, there was a significant positive correlation between the number of night fixes and home range for all animals with more than 50 night fixes ($r = .48$, $p < .001$). However, there was also a reasonably consistent positive correlation between average hourly move and home range size when broken down by sex and study period (Table 7.1). Since

Figure 7.1. A sample home range for a study period 1 male. This male was radio-located in the quadrats which enclose a solid circle. Open quadrats represent the minimum quadrats the animal would have had to traverse to reach disjunct quadrats. Home range = 0.22 ha.

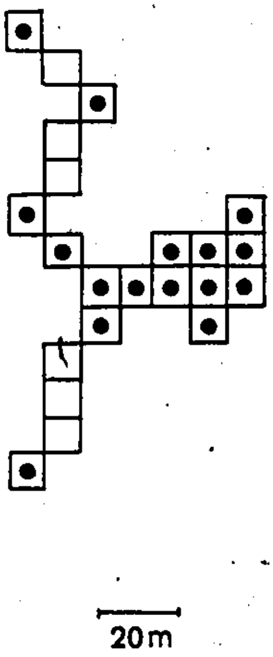

20m

Table 7.1. Pearson correlation coefficients for the relationship between mean hourly move and home range size.

	Study Period		
	1	2	3
Male	.86	.68	.87
Female	.86	.45	.26

the average number of fixes per animal increased with each study period (see Table 5.1), the correlation between the number of fixes and home range size may be an artifact stemming from the inter-study differences in surface activity. Nonetheless, inter-study comparisons have to be treated with caution. Second, and related to the previous problem, animals in different study periods were radio-tracked for varying lengths of time with different protocols. Thus the same number of radio fixes for two animals may be collected over different time periods and, conversely, animals followed over comparable lengths of time may have different numbers of fixes. Third, extensive inter-study comparisons of movement patterns (i.e. $\bar{D}$ and SD-COA) were presented in Chapter 5. The reasonably strong positive correlations between $\bar{D}$ and home range for the two sexes within each study period suggest that further comparisons would be redundant. For these reasons, I will focus mainly on variations in home range within each study period.

Range Use: An important supplement to the description of an individual's or a population's home range area is information about how the individual (or population) distributes its activity in space and time. For instance, an individual may distribute activity over its home range uniformly or it may maintain a center of intense activity with a decreasing probability of using areas progressively farther from the core area (e.g. a bivariate normal distribution). A simple description of home range area is inadequate to distinguish these two range patterns and therefore an index which assesses the relative occupational density of quadrats is necessary. Such a range index may be based on the actual duration of the time spent in a quadrat or the number of location samples in a quadrat. I use cluster analysis, similar to that used by Madison (1978a), which describes the relative concentration of an individual's activity within its home range based on the percentage of the total number of fixes located in each quadrat. The concentration of activity will be described in terms of (1) primary clustering (PC) defined as the percentage of the total number of fixes that were in the quadrat with the highest frequency, (2) secondary clustering (SC) defined similarly but with the second highest frequency, and (3) tertiary clustering (TC) defined similarly but with the third highest frequency. These cluster scores are useful for making inter-study comparisons as well as intra-study comparisons since the correlation between PC, for example, and the number of night fixes does not deviate from 0 ($\underline{r} = -.20$).

Range-use patterns, as indicated here by the cluster analysis, should be relevent to several ecological factors including resource abundance and distribution, inter- and intraspecific competition (e.g. for space, food, or mates), and the type, density, and distribution of predators (see

Brown and Orians, 1970 for an excellent review of these issues). With respect to kangaroo rats, cluster patterns should provide information relevant to foraging behavior. For example, one might expect hoarding animals to bring food back to a central location (i.e. a central place forager) for processing and feeding and thus spend a large proportion of time around their burrows. Cluster patterns may also reflect the social behavior of kangaroo rats. If males are indeed patrolling their ranges in order to exclude rival males and/or to visit females, then the cluster scores for males should be lower than for females.

Range Overlap: A useful measure for investigating the likelihood of social interactions between small mammals is range overlap. Overlap measures indicate which animals are likely to interact either directly or indirectly (e.g. through scent-marking) under various conditions (e.g. reproductive versus non-reproductive seasons). O'Farrell (1980), for instance, concluded that D. merriami male-male spatial overlap was greatest during reproductive activity in the winter and spring. On the other hand, Schroder (1979) found that D. spectabilis maintained relatively exclusive home ranges throughout the year, including the reproductive season.

The overlap results reported here are based on the average proportion of an individual's home range shared with a conspecific. Using set theory notation, overlap was calculated with the equation

$$OL = Q_i \cap Q_j / Q_{itot}$$

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

<u>Day Burrow Distribution and Use</u>: A potentially important consideration for many animals which establish stable territories or home ranges is the choice of a homesite which provides protection from predators and other environmental stresses. For some species the home site or the area around the homesites may be a limiting resource for which animals must compete. This situation might occur where the number of suitable homesites is limited or where relevant resources are patchily distributed. For example, <u>D. spectabilis</u> homesites consist of elevated mounds requiring two to three years to construct and substantial effort to maintain, but which also provide large storage space for hoarded food and protection from flooding (Jones, 1982). Jones suggests that these mounds are a potentially limiting resource for which competition is severe and which, in fact, may be matrilineally passed on to offspring. Jones also suggests

that burrows are not a limiting resource for D. merriami based on the evidence that these individuals continually moved to new burrows. Upon excavation, Jones found that D. merriami burrows are simple, typically consisting of a single chamber 10 to 20 cm in diameter, 5 cm high, and generally less than 30 cm in depth. This evidence does not imply, however, that D. merriami choose burrow sites randomly since the location of a burrow or set of burrows relative to food resources or conspecifics may be an important consideration.

The dispersion of occupied burrows should provide some clues about social structure. If burrows are aggregated, the potential for social interactions should be high. If, on the other hand, burrows are uniformly dispersed so that nearest-neighbor distances are large, the potential for social interactions may be relatively low. Such a finding would imply active repulsion or avoidance.

Results

Home Range

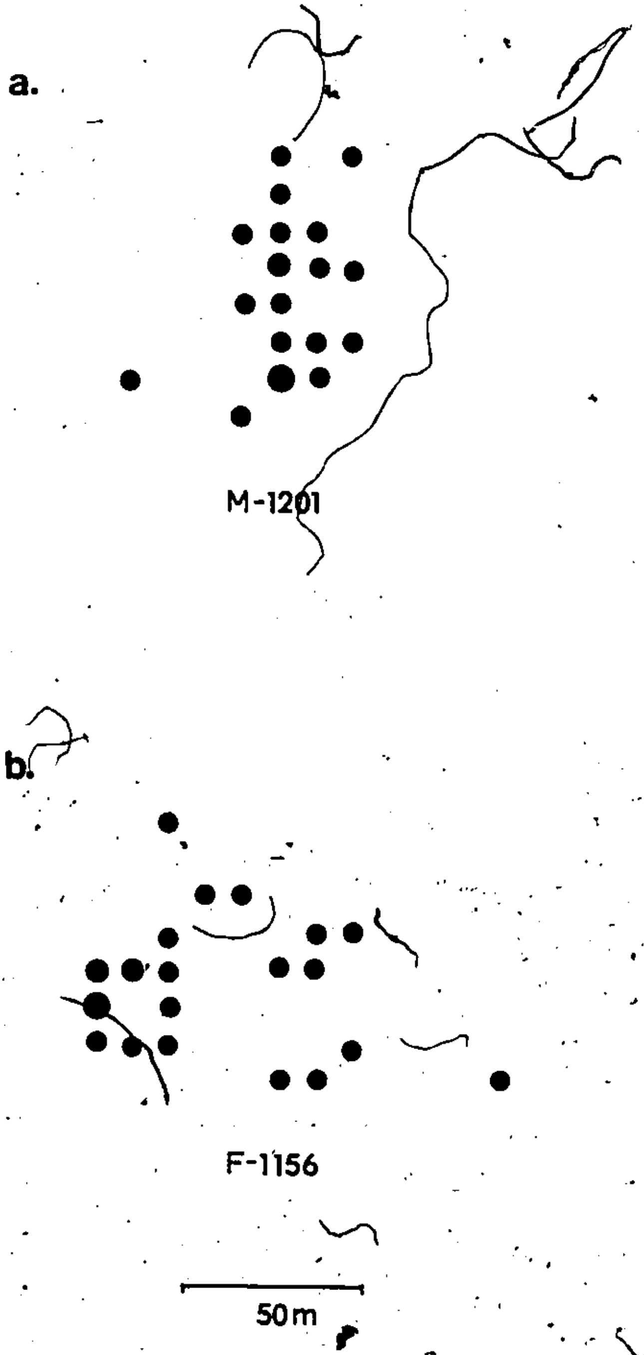
The results presented in Table 7.2 indicate that home ranges were smallest in study period 1 with an overall (i.e. sexes combined) average size of 0.19 ha, somewhat larger in study period 2 at 0.31 ha, and largest in study period 3 at 0.48 ha. The inter-study home range differences reported here thus exhibit a pattern similar to the inter-study differences in hourly moves (see Table 5.2). The results given in Table 7.2 provide no evidence whatsoever of a sex difference in home range in any of the study periods ($\underline{t}_{16df}$ = .91 for study period 1, $\underline{t}_{18df}$ = .71 for study period 2, and $\underline{t}_{16df}$=.91 for study period 3).

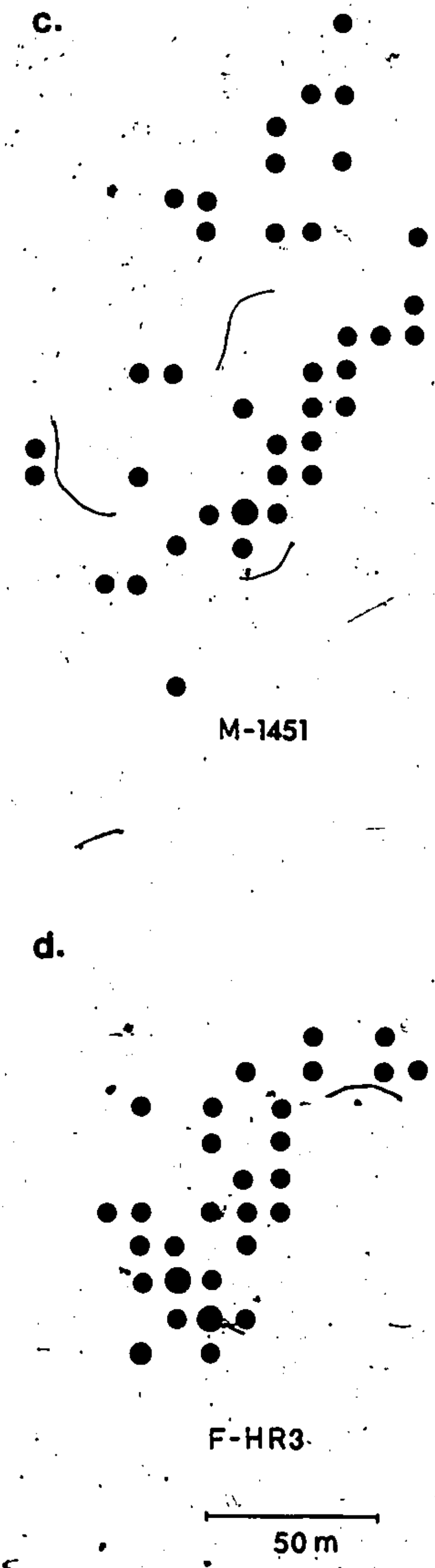
As with the movement patterns described in Chapter 5, individuals exhibited substantial variation in home ranges within each study period. In study period 1 the range in home range was 0.04 to 0.32 ha, in study period 2 the range was 0.13 to 0.56 ha, and in study period 3 the range was 0.24 to 1.16 ha. To illustrate the variance between individuals' spatial patterns with respect to home range and the general dispersion of activity further, Figures 7.2a-f depict the ranging pattern of a randomly selected male and female from each study period. Each individual appears to utilize one to three quadrats intensively (see cluster analysis below) and a varying number of other quadrats to a lesser extent. Clearly

Table 7.2. The average home range sizes (in hectares) broken down by sex and study period.

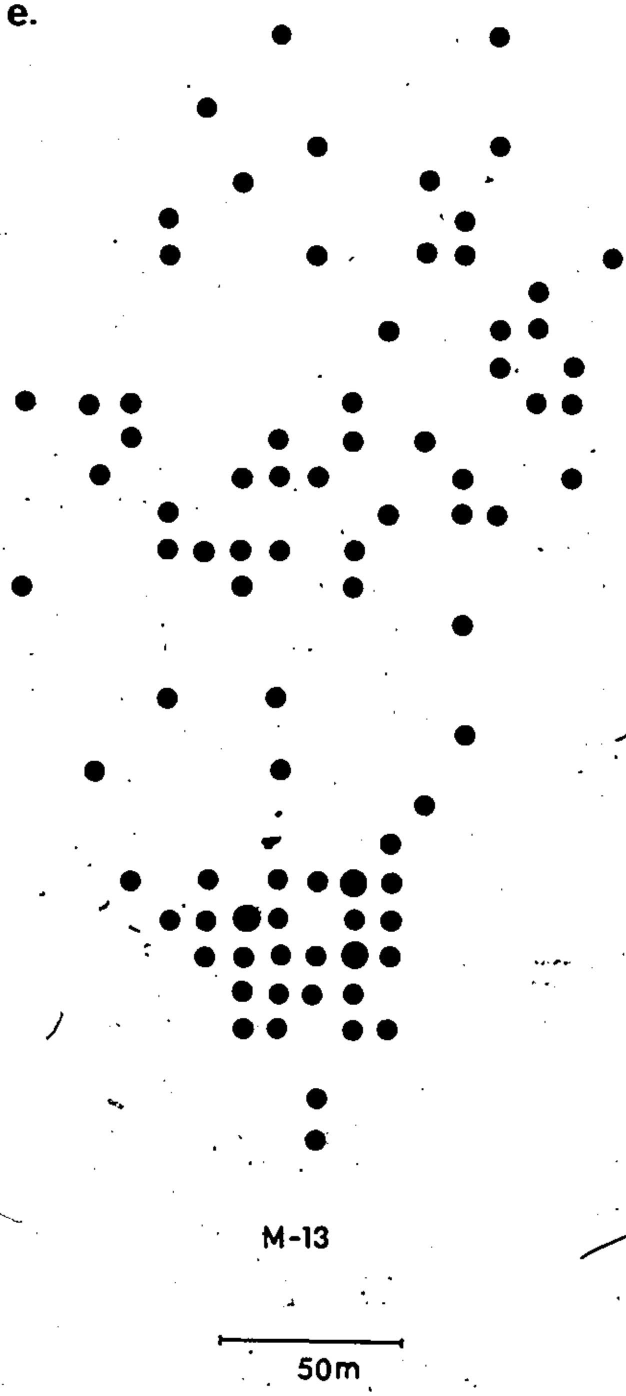
	Study Period		
	1	2	3
Male	.18 (.08)	.33 (.14)	.52 (.27)
Female	.21 (.06)	.29 (.11)	.43 (.14)

Figure 7.2 a-f. Maps of quadrats in which randomly selected animals from each study period were radio-located. The size of the circles indicates the relative frequency that the animal was located in the quadrat. a,b are from study period 1; c,d are from study period 2; and e,f are from study period 3.

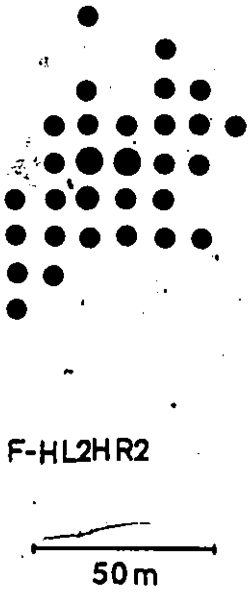

a.
M-1201
b.
F-1156
50 m


c.
M-1451
d.
F-HR3
50 m

e.



f.



the activities of some individuals are much more dispersed than others even within study periods (e.g. male 13 vs. female HL2HR2).

There is some evidence that range size is related to male reproductive condition based on a positive correlation between testes size of study period 3 males and range size (r = .58). The sample size is too small to test this relationship statistically, however, and the data for male reproductive condition in study periods 1 and 2 were inadequate to examine this relationship. Unfortunately, the data on variations in female reproductive condition are too scant to relate to home range sizes. Based on the enhanced surface activity by females in relation to reproductive events and the generally positive relationship between hourly moves and range size, however, one would predict that female home ranges vary in relation to reproduction as well.

Cluster Analysis

Animals on both the Ramada and Coyote Wash sites maintained relatively stable core activity loci within their home ranges regardless of the length of time an animal was radio-tracked. Table 7.3 shows that on average 30-50% of nocturnal activity (including subterranean activity) was restricted to a single 10 m^2 quadrat. In fact, the majority (50-76%) of all nocturnal activity was confined to only three quadrats or an area of 0.03 ha. Figures 7.2a-f further

Table 7.3. Overall cluster scores for _D. merriami_ for the three study periods where PC = primary cluster, SC = secondary cluster, and TC = tertiary cluster.

Study Period	PC	SC	TC
1	49.6 (13.4)	16.8 (7.1)	8.7 (4.1)
2	28.6 (10.5)	15.7 (5.4)	9.5 (3.9)
3	29.1 (9.4)	12.7 (5.1)	7.5 (3.3)

illustrate this finding by showing that each individual maintained 1-3 areas of intense use and occupied other quadrats much less frequently.

The high degree of clustering by D. merriami in part reflects the extensive use of day burrows throughout the night. For 45 of 52 animals, the quadrat with the highest cluster score was also the quadrat with the most frequently used day burrow.

There was some evidence for inter-study differences in clustering. The mean primary cluster score (PC) for study period 1 animals (Table 7.3) was significantly higher than the PC score for study period 2 animals ($\underline{t}_{34df} = 5.20$, $\underline{p} < .001$, two-tailed test) or study period 3 animals ($\underline{t}_{32df} = 5.20$, $\underline{p} < .001$, two-tailed test). Study period 2 and 3 animals did not differ in PC nor were there any inter-study differences in SC or TC.

There was no clear evidence on the basis of cluster analysis that males and females use their home ranges differently. The data presented in Table 7.4 indicate that the cluster patterns for males and females are similar with the exception that study period 1 males had a higher average SC score than females ($\underline{t}_{16df} = 2.22$, $\underline{p} < .05$, two-tailed test) and study period 3 females had a higher average TC score than males ($\underline{t}_{14df} = -2.19$; $\underline{p} < .05$, two-tailed test).

Table 7.4. Cluster scores for *D. merriami* broken down by sex and study period.

Study period		PC	SC	TC
1	Male	48.9 (11.6)	19.4 (6.9)	8.3 (3.5)
	Female	50.6 (16.8)	12.8 (5.6)	9.4 (5.2)
2	Male	30.4 (11.8)	15.6 (6.6)	7.7 (3.7)
	Female	27.1 (9.8)	15.7 (4.7)	11.0 (3.6)
3	Male	26.8 (6.0)	14.2 (2.9)	7.2 (3.3)
	Female	31.4 (11.9)	11.3 (6.5)	7.8 (3.6)

Range Shift

Range use may also be investigated by determining center-of-activity (COA) changes over time. An animal with a high degree of site attachment (i.e. occupying the same territory or range over a long period of time) should exhibit nightly variations in its COA which are independent of the time span over which the animal is radio-tracked. To make this determination, I compared each animal's total COA shift, defined here as the distance between its first and last nightly COA, with its average weekly COA shift. The results indicate that *D. merriami* have a relatively high degree of site attachment for periods of up to at least six months. Table [illegible]5 shows that total COA shifts ranged from a low of 7.1 m over an average of two weeks by study period 1 males to a high of 24.3 m over an average of five weeks by study period 2 males. A 25 m COA shift by animals with excellent ranging capabilities (e.g. male 13's several hourly moves over 200 m) would seem relatively small. More importantly, the total COA shifts by these animals were not significantly larger than their weekly shifts with the exception of study period 2 females ($\underline{t}_{7df} = 2.91$, $\underline{p} < .05$, two-tailed test). Four animals, including three males and one female from study period 2 were subsequen[illegible]re-implanted with transmitters in study period 3. Wit[illegible]exception of male 13 whose COA shifted 121 m, the animals inhabited the same general area. Female 1500's COA shift was 15 m, male 12 shifted 36 m, and

Table 7.5. Center-of-activity shifts (meters) on a weekly and overall basis for male and female *D. merriami* during different study periods.

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

male HL3FL2 shifted 43 m.

Within study periods there were sex differences in weekly COA shifts for periods 1 and 2. Females in study period 1 had significantly greater shifts than males ($\underline{t}_{16df}$ = 2.35, $\underline{p} < .05$, two-tailed test). Males in the breeding season (study period 2) clearly exhibited the most erratic ranging behavior from week to week (see Table 7.5). This difference is primarily due to the activity of four males who exhibited some drift in their home ranges (see also day burrow results below). Of these four males, male 6 had an average weekly COA shift of 45 m, male HL3FL2 had a 35 m shift, and male 12 had a 39 m shift. The average weekly COA shift by the remaining eight males of 15 m was similar to the other weekly averages given in Table 7.5.

Range Overlap

Range overlap among conspecifics can be difficult to evaluate if range size and use and/or population densities fluctuate significantly. However, the data just presented suggest that individual range use patterns are consistent over time. Furthermore, this statistic can provide essential information about the potential for social interactions. The spatial overlap results presented here should be regarded as minimum estimates of actual intraspecific overlap since we did not radio-implant all animals on the study sites. It is therefore likely that some animals without transmitters had home ranges that were interspersed among the ranges of radio-implanted animals. This likelihood would lead to biased estimates of the absolute proportion of an individual's range overlapping with conspecifics. Hence, for comparative purposes, I calculated for each individual a mean score for spatial overlap with conspecifics of the same sex, the opposite sex, and the sexes combined. This spatial overlap score is expressed as a percentage of the total number of quadrats in which the individual was radio-located.

Table 7.6 gives the results for spatial overlap broken down by study period and sex. It is evident from the combined overlap scores that the difference in spatial overlap between study periods and between the sexes were small despite the changes in breeding condition between study periods. A noteworthy finding was that females tended to overlap more with male conspecifics than female conspecifics. This difference was significant for study period 1 females ($\underline{t}_{5df} = 2.70$, $\underline{p} < .05$, two-tailed test) with similar, but not statistically significant trends for study periods 2 ($\underline{t} = 1.71$) and 3 ($\underline{t} = 1.45$). Combining the data over study periods, however, revealed that female-male overlap was significantly greater than female-female overlap ($\underline{t}_{21df} = 3.22$, $\underline{p} < .01$, two-tailed test). A similar relationship was apparent in study period 1 with male-female overlap significantly greater than male-male overlap ($\underline{t}_{7df} = 2.53$, $\underline{p} < .05$, two-tailed test). However, this difference was not apparent in study periods 2

Table 7.6. The mean percent of home range overlap by D. *merriami* broken down by sex and study period.

Study Period	Overall	Same Sex	Opp. Sex
1 Male	15.1 (12.3)	14.5 (13.9)	20.4 (16.1)
Female	12.8 (3.5)	8.5 (3.5)	14.8 (4.5)
Combined	14.3 (9.9)	11.9 (10.9)	18.0 (12.0)
2 Male	13.8 (4.8)	13.4 (7.3)	13.3 (6.4)
Female	12.6 (3.7)	11.6 (2.0)	14.8 (4.6)
Combined	13.9 (4.2)	12.3 (4.6)	14.2 (5.2)
3 Male	11.1 (3.5)	11.3 (6.7)	12.3 (3.9)
Female	12.3 (4.0)	8.8 (6.7)	12.9 (4.6)
Combined	11.7 (3.7)	10.0 (6.6)	12.6 (4.1)

and 3 males.

Most individuals of both sexes overlapped to some degree with several conspecifics. The median number of conspecifics overlapping with any single individual was 5 (range = 1-14). The median number of same-sexed conspecifics overlapping was 2 (range = 1-7) and the median number of opposite-sexed conspecifics overlapping was 3 (range = 1-7).

There were no cases of overlap among animals' PC, SC, or TC quadrats. However, in several cases the cluster quadrats for different individuals were adjacent. In study period 1 there were two cases of adjacent female-female SC's, one adjacent female PC-male TC, one adjacent female SC-male PC, and one adjacent female SC-male SC. In study period 3, there was one adjacent female SC-male SC and one adjacent female PC-female SC. In general, overlapping quadrats between any two individuals were in areas that were little-used by at least one of the animals.

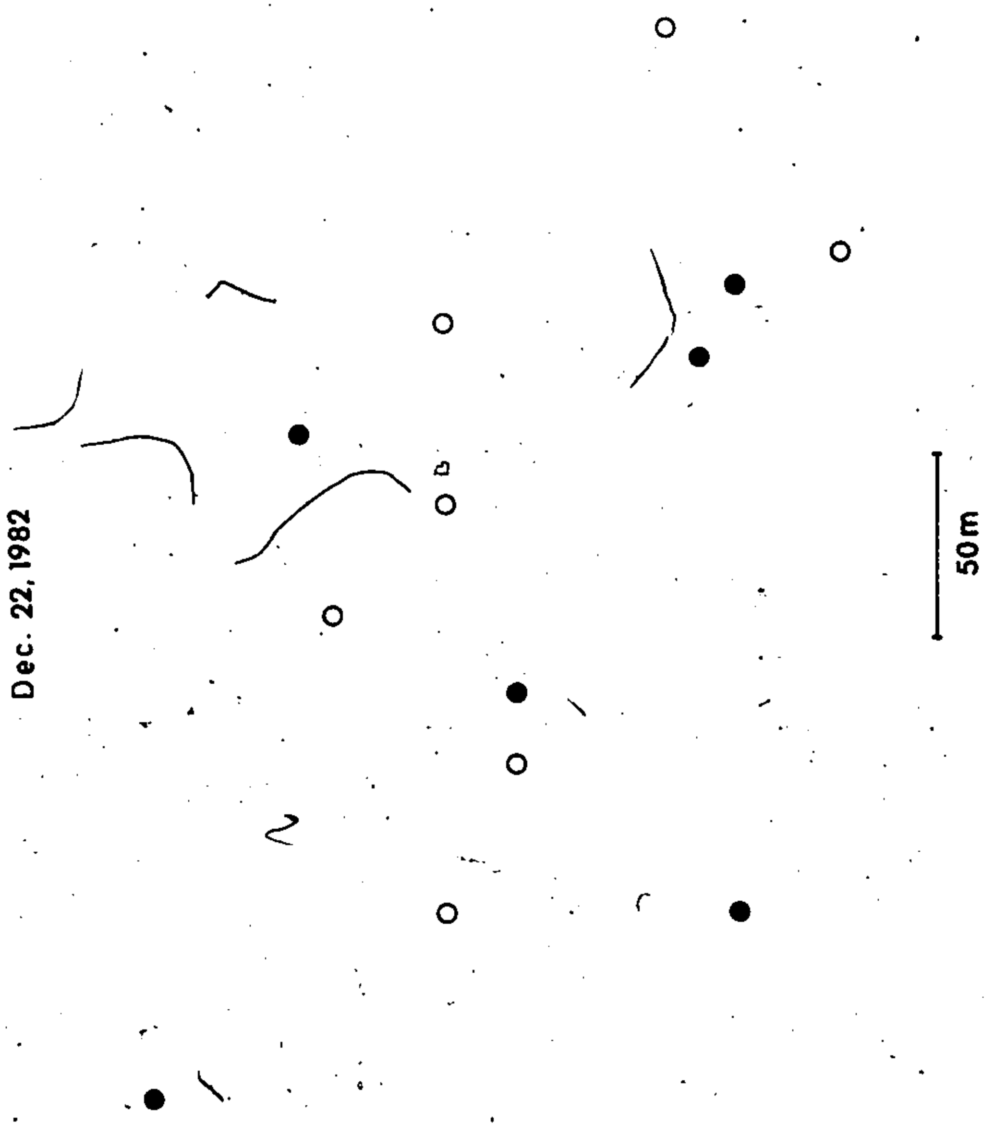
Day Burrow Distribution

A means of gaining insight into the socio-spatial relationships of animals is to examine the spatial distribution of their homesites, or in the case of kangaroo rats, day burrow sites. As a solitary species, it is expected that D. merriami should select day burrow sites in a non-random fashion so that nearest-neighbor distances are large. Such a strategy would result in a uniform distribution of day burrow sites.

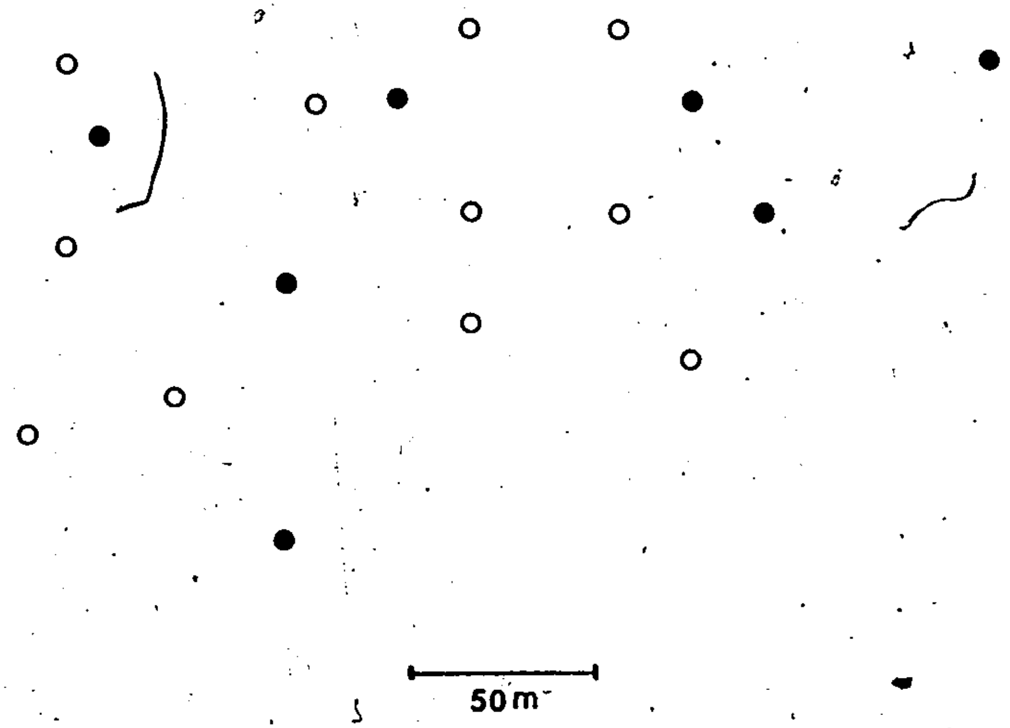
In order to test whether D. merriami day burrows are more uniformly distributed than random, I compared the mean nearest-neighbor distance between day burrow sites observed in study periods 1 and 3 with the mean nearest-neighbor distance generated from a computer simulation utilizing a random dispersion model. The day burrow locations were from one randomly selected day each from study period 1 and 3 (there were probably few animals without radio implants that were interspersed during these study periods). The analyses were based on 18 animals for study period 1 and 12 animals for study period 3 (a female whose nearest-neighbor was 95 m away was considered to be an outlier and thus was omitted). The computer simulation was designed to generate a mean nearest-neighbor distance to the nearest 0.1 m using a random dispersion model and the grid size and day burrow density as parameters. The simulation program generated a random set of grid (i.e. x-y) coordinates without replacement, the nearest-neighbor for each coordinate pair was found, and the mean of the nearest neighbor distances was calculated. This procedure was carried out 100 times to generate a mean of the sampling distribution of means for nearest-neighbor distances.

Figures 7.3a,b depict the day burrow locations for the two randomly selected days from study period 1 and study period 3. The mean nearest-neighbor distance for study period 1 on December 15 was 34.8 m (±12.7) which was

Figure 7.3 a,b. Day burrow locations for male (○) and female (●) D. merriami on two randomly selected days each from study period 1 (Dec. 15, 1980) and study period 3 (Dec. 22, 1982).


Dec. 22, 1982
50m

Dec. 15, 1980



significantly larger than the expected mean of 25.7 m ($t_{17df} = 3.04$, $p < .005$, one-tailed test). The mean nearest-neighbor distance for December 22 of study period 3 was 40.9 m (±17.7) which was significantly larger than the expected mean of 30.9 m ($t_{11df} = 1.95$, $p < .05$, one-tailed test). This evidence supports the notion that D. merriami day burrows are uniformly distributed and that individuals space themselves in a manner which reduces intraspecific interactions.

It was shown earlier that sex was relevant to spatial overlap patterns with female-female overlap significantly less than female-male overlap. It is possible that sex might also be a relevant factor for the spatial distribution of day burrows. To examine this possibility, the nearest-neighbor distances to the day burrows of same-sex and opposite-sex conspecifics were compared for each individual using the day burrow data from the same days in the preceding analysis. Since there were more males than females on both days, randomly selected males were excluded from the analysis so that there was an equal number of potential nearest-neighbors of each sex. Otherwise nearest-neighbor distances would be biased toward the more numerous sex. The results of this analysis are given in Table 7.7. It is apparent that nearest-neighbors tend to be of the opposite sex, but the results are only significant for females ($t_{12df} = 1.81$, $p < .05$, one-tailed test). One interpretation of these results is that females attend more to the day burrow locations of conspecific

Table 7.7. Average nearest-neighbor distances (meters).

	Study Period 1		Study Period 2	
	Male	Female	Male	Female
Male	54.4	42.6	56.7	48.3
Female	45.1	57.2	53.9	70.4

females than to male day burrow location whereas males do not appear to discriminate.

Day Burrow Use

There are several aspects of day burrow use addressed in this section including the number of day burrows occupied over a given period of time, the number of moves between day burrows, whether old day burrows are reused, the distance between successive day burrows, and whether individuals have "favorite" day burrow sites.

The data used to investigate day burrow use come from a subset of animals from study periods 1 and 3. Day burrows from these two study periods were recorded daily throughout the studies with the exception of one day in study period 3. Animals that were radio-tracked throughout most of a study period were selected yielding 16 animals radio-tracked from 1 to 22 days for study period 1 and nine animals radio-tracked from 32 to 40 days for study period 3.

In general, each individual used several day burrows over the relatively short periods of time the animals were radio-tracked. However, in most cases only one or two day burrows were used with high frequency. In many instances, an individual used a particular day burrow for several consecutive days, switched to a new burrow for one or two days, and then returned to the original day burrow. The combined results given in Table 7.8 bear out these general

Table 7.8. Summary of day burrow use by *D. merriami*.

Study Period		Sample Size	# Days Tracked	# Day Burrows	# Moves	Ratio*	Mean Move
1	Male	11	18.1 (2.7)	3.5 (1.3)	4.6 (2.7)	1.6 (.4)	11.9 (5.1)
	Female	5	19.0 (2.5)	4.0 (1.9)	6.0 (3.9)	1.9 (1.2)	16.4 (9.2)
3	Male	5	35.8) (3.8)	5.4 (2.7)	8.6 (4.9)	1.8 (.3)	24.9 (16.1)
	Female	4	37.5 (3.0)	4.5 (2.6)	9.0 (7.4)	1.9 (.7)	12.8 (3.4)
	Combined	25	24.9 (9.3)	4.2 (1.9)	6.4 (4.5)	1.7 (.6)	15.7 (9.9)

* Ratio = # Moves/# Day Burrows for each individual.

conclusions. On average, each individual used approximately four different day burrows (range = 1-8) over a 25 day period (range = 15-40). However, indivdiduals did not use different day burrows with equal frequency. For each individual, one day burrow was used 64% of the days on average (range = 27 to 100%) and two day burrows accounted for 86% of use on average (range = 54-100%). Table 7.8 shows that the average ratio of the number of day burrow moves to the number of different day burrows used by each individual is greater than one indicating that animals tended to return to or recycle previously used day burrows. In fact, only three of the 24 animals who switched day burrow locations never returned to a previous location.

There were no apparent differences in the way males and females utilized day burrows in either study period (Table 7.8) with respect to the number of day burrows used, the tendency to reuse previous day burrows, or the intensity in which one or two particular day burrows were used. Considering the differences in the number of days animals were followed in the different study periods, there do not appear to be any study differences on these measures either.

The average day burrow move was relatively small for these two study periods at 15.7 m (range = 3.6 to 53.2 m). There was no difference on this measure between males and females in study period 1 ($\underline{t}_{14df}$ = 1.02) or study period 3 ($\underline{t}_{7df}$ = 1.63, $\underline{p} > .05$).

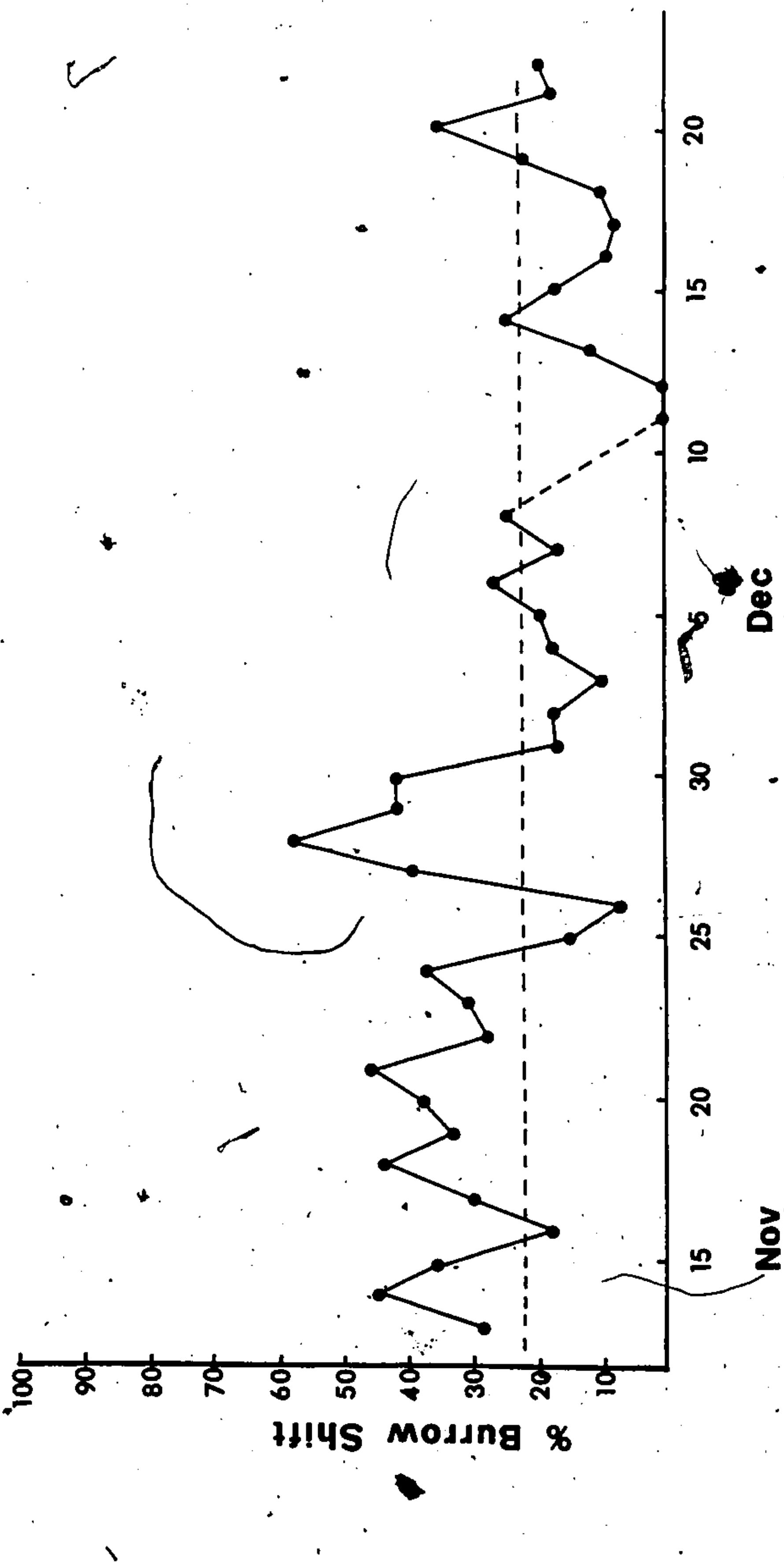
An interesting finding in study period 3 was that animals made more day burrow moves in November than December. The median proportion of animals moving on any given day in study period 3 was 0.22. Figure 7.4 illustrates that on 14 of 17 days in November, a greater number of individuals had day burrow moves than expected (p = .005, binomial test). In contrast, on 16 of 20 days in December, fewer individuals had day burrow moves than expected (p = .005, binomial test).

Though it is not clear what proximate factors trigger day burrow moves in general, there were several specific day burrow moves apparently related to reproduction, dispersal, range shifts, and social interactions.

Unusually large day burrow moves by one female, 1485, were associated with estrus. As mentioned in Chapter 5, this particular female, whose average day burrow move was 15 m when anestrous, pregnant, and lactating, had day burrow moves of 100 m and 95 m, respectively, during two estrus periods. On both occasions, this female returned to her previous day burrow area one or two days after estrus.

Females continue to change day burrows throughout late gestation and lactation, presumably moving their offspring to the new day burrow sites since there was no evidence that females terminated lactation around the time of the moves. For instance, female 1485 had a 28 m move 5-10 days preceding parturition and a 20 m move no more than 7 days postpartum. Female 1312 showed a similar pattern with a

Figure 7.4. The proportion of D. merriami that switched day burrows each day in study period 3. The dashed horizontal line is the median proportion (.22) of animals moving day burrows on a given day.

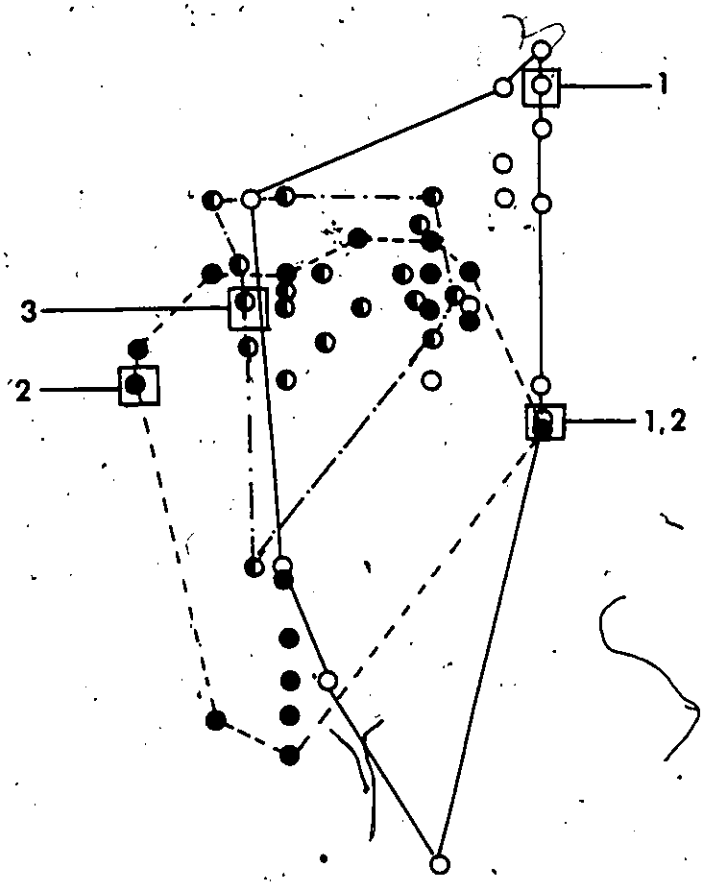

% Burrow Shift
100
90
80
70
60
50
40
30
20
10
15
Nov
20
25
30
5
Dec
10
15
20

62 m move at most 12 days before parturition and a 36 m move no more than 5 days postpartum. Female 1500 had a 25 m move followed by a 24 m move the following day no more than 7 days preceding parturition and an 8 m move no more than 7 days postpartum. Finally, female 1 had a 51 m move within 3 days of parturition (it is not known whether the move occurred before or after parturition) and a 20 m move no more than 14 days postpartum.

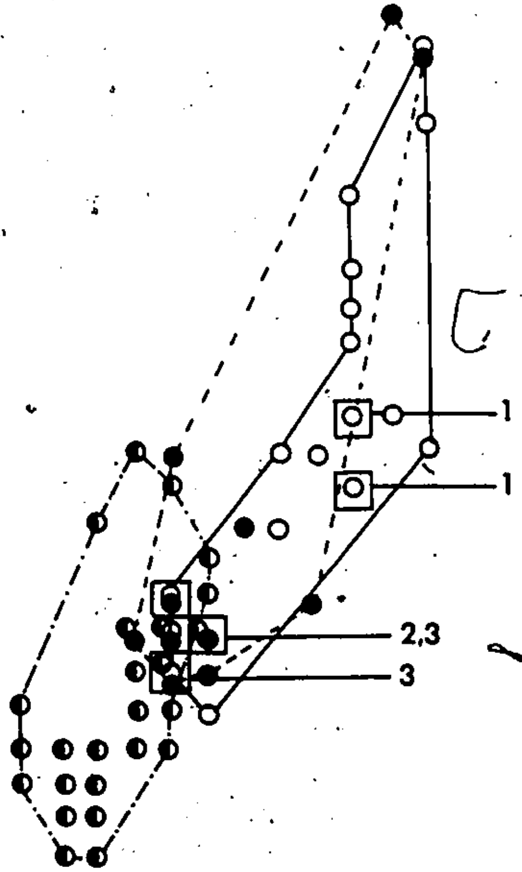
Some day burrow moves by adult males in April and May of study period 2 were unusually large. Male 6, for example, had a day burrow move of 102 m, male 1451 had moves of 88, 91, and 48 m, male HL3FL2 had moves of 87, 110, and 84 m, and male 12 had a move of 76 m. Of these males, male 6, male HL3FL2, and male 12 had major COA shifts (see earlier results in this chapter) indicating that these day burrow moves were related to home range shifts. Figures 7.5a,b illustrate the association between day burrow moves and range shifts for male HL3FL2 and male 12. Male HL3FL2's range progressively shifted west over a one month period with a concomitant reduction in size. The change from a rather erratic ranging pattern to a compact and consistent range suggests that this male may have been in the process of establishing a day burrow and range area. Further support for this possibility is that this male was first captured on the grid only 5 days before radio-implantation on April 17. The range shift pattern exhibited by male 12 indicates that long-term

Figure 7.5 a,b. Home ranges for two males from study period 2 for 7-10 day intervals. Squares enclosing symbols indicate burrow locations and numbers indicate the interval in which the day burrow was used. a: Interval 1 (o) April 18-25; Interval 2 (●) April 26-May 5; Interval 3 (◉) May 10-20. b: Interval 1 (o) April 14-23; Interval 2 (●) April 24-May 5; Interval 3 (◉) May 10-17.

a. M-HL3FL2



b. M–12



residents may also have substantial range shifts. This male was initially captured on January 20, 1982 and thus had been a grid resident for almost three months when he exhibited a large range shift. However, as indicated by the COA shift results presented earlier, range shifts of such magnitude were unusual occurrences with most animals having only small COA shifts over relatively long periods of time.

One set of day burrow moves in study period 3 suggests that social considerations may influence day burrow locations and use patterns. Female HL2 was killed by a coachwhip snake on November 25, which then remained in the burrow until December 3. Subsequently, on December 8, male HL3FL3 moved 53 m to female HL2's former day burrow. On December 10, female HL2HR2 moved 24 m to male HL3FL3's former day burrow and was located there five of the next nine days, including December 19. On December 20 male HL3FL3 was again in his former day burrow which had just been occupied by female HL2HR2 the previous day. On occasion animals have been located in the former day burrows of other animals, but this was the only case in which the shared day burrow was reoccupied by the former owner.

Discussion

Home Range

Home range was defined by Burt (1943) as the area, usually around a homesite, over which an animal normally travels in search of food. Despite this seemingly simple definition, home range is a rather onerous concept which has generated much debate about its measurement and meaning. One point of contention is the time course over which home range should be measured. For example, should home range be calculated on a weekly, monthly, seasonal, or annual basis? Another difficult issue is what movements should be included in the calculation of a home range. The occasional long sally probably should not be considered a part of an animal's "normal" home range, but what is meant by a long sally is not always agreed upon. This question led to the formulation of probabilistic descriptions of home range (e.g. 95% probability ellipses) which were discussed in Chapter 3 (see also, e.g., Jennrich and Turner, 1969). It has become increasingly clear that debates about the proper or single-most effective way to collect and describe home range data are fruitless. Each investigator must decide which methodology will most accurately convey the behavioral phenomena under study.

Questions concerning the function of home range have brought about a more fundamental split among workers. On the one hand, many ecologists consider home range size and use patterns to primarily reflect the organism's energy demands (e.g., McNab, 1963; Harestad and Bunnell, 1979; Mace and Harvey, 1983). On the other hand, the worker interested in social behavior may consider home range to reflect socio-spatial interactions (see Brown and Orians, 1970 for a review). Certainly most investigators would agree that ranging patterns reflect the interaction between energetic demands, food density and distribution, and social and reproductive exigencies. This perspective can be subsumed under the socio-ecological approach outlined in Chapter 5.

In the introduction of this chapter, I defined home range as the area in which the animal was radio-located plus the minimum area the animal must have traversed to reach distant locations. I have thus included long sallies in home range under the assumption that unusual movements have some biological relevance. Since the major focus here is the association between home range and socio-spatial relationships rather than the relationships between range size and energetic demands, I feel that the inclusion of long sallies is justified.

The average seasonal range size of 0.37 ha (range = 0.03 to 1.16 ha over all study periods) agrees well with the average annual home range size of 0.49 ha (range = 0.05 to 2.35) for D. merriami in Nevada calculated from retrapping data by O'Farrell (1978). However, O'Farrell calculated home range sizes using principal components analysis (i.e. 95%

probability ellipses). Thus, simple comparisons between the two sets of results must be viewed with caution.

Despite the variance among individuals, home range sizes fall within the same order of magnitude. This probably does in fact reflect a basic relationship between energetic demand, range size, and food supply. However, one is still left with the question of why individuals exhibit such great variation in home range size. Certainly some of this variation can be accounted for by differences in habitat quality, but the evidence that some individuals make many long sallies over the home ranges of several conspecifics (e.g. male 13 overlapped with 14 radio-implanted conspecifics in study period 3) indicates that factors unrelated to foraging are probably important as well. The positive correlation between testes size and home range in study period 3 males suggests the possibility that males in reproductive condition may range more widely to visit females or to monitor the location of conspecifics in general. This possibility raises questions about factors related to reproduction including social familiarity, mate choice, and dominance patterns.

Sexual dimorphism in home range size was not apparent (see discussion of the significance of range dimorphism in Chapter 5). Even though this finding agrees with O'Farrell (1978), it was surprising in light of the difference in movements between males and females during the breeding season (see Chapter 5). Apparently males move about their home ranges more widely than females rather than ranging farther afield. The differential sensitivity of home range and movement measures to sex-related differences point to the weakness of home range size as an indicator of ranging dynamics.

As indicated by cluster analysis, animals tend to spend most of the night in and around their day burrows with periodic sallies to more distant locations. This distribution of activity is generally consistent with the expected activity distribution of a central place forager. Food provisioning experiments in the field (Daly, Wilson, and Behrends, unpublished data) show that upon discovery of rich food sources, animals pouch approximately 2 g of food (rolled oats) and immediately transport the food to their current day burrow. Several trips are made in quick succession (5 or 6 trips in 15-20 min for 10 g of food in this experiment) until the food is depleted. It is likely that under normal circumstances animals make several foraging trips each night and spend part of the remaining nocturnal hours feeding in the safety of their burrow. As a scatter hoarder, D. merriami also establish small surface food caches in the vicinity of their burrows (Pers. Obs.), but it is not known how important these caches are as long-term food stores. It seems that severe losses of food from these caches would occur from raids by conspecifics and pocket mice.

Despite the movement differences between males and females during the breeding season, the two sexes had similar range use patterns. Based on the cluster scores, there was no evidence that males patrol their ranges more than females.

Differences in clustering between study period 1 and study periods 2 and 3 provide further evidence that study period 1 animals were more sedentary than study period 2 or 3 animals. Study period 1 animals were radio-tracked on a different study site making comparisons with study periods 2 and 3 difficult. However, as discussed in Chapter 5, there were no consistent differences in weather patterns including temperature differences or precipitation that could account for the inter-study differences.

It is noteworthy that some individuals were found in the same general area from season to season and from year to year. This finding, along with the conservative reproduction of this species and the evidence that juvenile mortality exceeds adult mortality (French et al., 1967), implies that social communities may be relatively stable over seasons and perhaps even years. Long-term stability in communities should provide the opportunity for complex social structures to evolve with social familiarity, mate choice, kin relationships, and dominance patterns as potentially important factors (see Chapter 8). At the least, it seems, stable home ranges should provide the opportunity for repeated social interactions between individuals with the result that neighbors become socially familiar.

Range Overlap

The degree of intraspecific range overlap provides indirect information about the likelihood of social interactions. O'Farrell (1980) reported that individual D. merriami overlap was greatest during the breeding season. Moreover, he found that male-male overlap was greatest, male-female overlap intermediate, and female-female overlap least. Unfortunately no statistics supporting these findings were reported.

There was substantial intraspecific range overlap in the present study, but the patterns were different from those reported by O'Farrell. There were no seasonal differences in the degree of overlap and no difference between opposite-sex and male-male overlap. Similar to O'Farrell's findings, however, overlap between females was significantly less than overlap between the sexes.

Apparently D. merriami tolerate substantial range overlap with conspecifics, a not atypical mammalian pattern (Brown and Orians, 1970). The extensive range overlap of D. merriami stands in marked constrast to the rather exclusive ranges of D. spectabilis (Schroder, 1979). Brown and Orians (1970) point out that due to the relative lack of mobility of many mammals, the cost of defending a foraging range probably outweighs the benefits gained. Thus, the large overlapping ranges of D. merriami may in part reflect the exploitation of scattered, economically undefendable resources.

Estimating the likelihood of direct physical encounters among overlapping individuals is difficult on the basis of these data. However, the lack of spatial overlap among individuals' core areas suggests that direct encounters probably occur at a relatively low rate. Nonetheless, on several occasions, individuals have been observed visiting the areas around conspecifics' day burrows. On many occasions, two, and, on one occasion, three individuals have been observed in close proximity (1 to 5 m) under a shrub, creosote bush, or palo verde tree. Sometimes encounters are aggressive, usually with one animal chasing the other, but at other times the animals are passive and seem oblivious to the close presence of a conspecific. These observations of aggressive interactions suggest that D. merriami may maintain territories (i.e. defended areas; Burt, 1943) around their day burrows and core activity areas, but these data are too sparse to make any conclusive statements.

The relative lack of spatial overlap between females compared to the overlap between the sexes or between males is not uncommon in solitary rodents (see, e.g., Daly and Daly, 1975; Madison, 1980) and suggests that there is relatively less direct social interaction between females. The likelihood of mutual avoidance by females is reinforced by the demonstration that for females, the nearest male day burrows were significantly closer than the nearest female day burrows. Males, on the other hand, tended to overlap females as much as males, with the exception of study period 1 when male-male overlap was significantly less than male-female overlap (Table 7.6). Moreover, males exhibited no specific sex-related day burrow distribution patterns. These results are quite different from O'Farrell's finding that the greatest degree of overlap was between males.

One may speculate that a relevant dimension for a female's choice of a day burrow location and use of a home range is the spatial location of conspecific females. Males, despite their similar uniform spacing, do not appear to choose their day burrows or have overlap patterns that are related to the sex of nearby conspecifics.

With respect to day burrow distribution in general, it is clear that individuals space themselves in a regular manner, as indicated by the nearest-neighbor analysis. A regular distribution of D. spectabilis mounds was also noted by Schroder and Geluso (1975). The implication of this sort of day burrow distribution is that animals space themselves to avoid mutual interactions. Well spaced day burrows may be important for minimizing costly conflicts over resources (in terms of time, energy, and risk of injury or predation). Despite the regular spacing of day burrows, however, D. merriami exhibit much more range overlap than D. spectabilis. For D. merriami, uniform day burrow distribution may not be for mutual avoidance per se, but rather for minimizing interactions between conspecifics in areas where the cost of such interactions are particularly high (e.g. loss of food stores or disruption of reproductive activities). As was discussed in Chapter 5, individuals may be aggressive around their burrows and core activity areas, but relatively passive in other parts of their range.

Day Burrow Use

It is interesting that individuals tended to use several day burrows and, moreover, usually returned to previously used burrows. No external factors triggering day burrow moves were apparent, although it was noted that day burrow moves occurred together in study period 3. No individual characteristics seemed to be related to unusually frequent or distant moves with the exception of long moves by an estrous female and several males apparently in the process of range shifts. Day burrow move patterns were similar for males and females over study periods 1 and 3.

Though the factors responsible for day burrow moves are unknown, these moves seem important. The fact that several lactating females switched day burrows, presumably at some risk to their pups, indicates that this is so. Of course, lactating females may be switching day burrows for some reason unrelated to those normally operating such as reducing the pups' risk to infanticidal conspecifics (see

Sherman, 1981). One possibility is that animals switch day burrows to avoid nest parasites. The only evidence to support this idea is that D. merriami are relatively free of ticks, fleas, and mites compared to pocket mice (little information is available on burrow use by pocket mice, but they do go torpid for months at a time; Kenagy, 1973a). Since D. merriami do not store large amounts of seeds in their burrows (Jones, 1982), perhaps the least costly way to avoid parasites is to vacate a burrow for a period of time. Another possible reason for frequent day burrow shifts is to avoid certain predators (e.g. snakes) which may be attracted to the strong odor of a heavily used burrow. Finally, the day burrow shifts may be a way of avoiding raids on smaller burrow food hoards by conspecifics, pocket mice, or ants. Scatter hoarding by these animals may be related to competition with other granivores as well.

Conclusion

The data presented in this chapter include basic information on the home range size and use patterns of D. merriami. Despite the season to season and year to year variations, ranges were sexually monomorphic. Range use patterns were very similar for the two sexes as well with the majority of nocturnal activity occurring in and around an individual's day burrow.

The investigation of spatial relationships revealed some interesting results. Spatial range overlap varied in relation to sex. Females establish day burrows and ranges that serve to isolate them from conspecific females whereas males do not appear to discriminate.

The relative stability of home range areas, the substantial degree of spatial overlap, and yet, the regular distribution of day burrows suggests that _D_. _merriami_ social structure may be more complex than heretofore thought. These animals are by no means gregarious, but at the same time, they are not particularly asocial. Direct social encounters are not uncommon (not to mention indirect communication, e.g., through olfactory cues) and, thus, social familiarity and dominance patterns may be important for both community stability and reproduction. These issues will be discussed more fully in Chapter 8.

Chapter VIII

Summary and Conclusions

This thesis has examined several aspects of *D. merriami* natural history including reproduction, ranging behavior, and socio-spatial relationships. This summary chapter contains a general description of *D. merriami* behavior based on the findings presented in the previous chapters. I will also identify several unresolved issues that are important for understanding the socio-ecology of this species.

The most outstanding social attribute of *D. merriami* is their solitary nature which is exemplified by the uniform distribution of their day burrows. That is, day burrows tend to be located at maximal distances from nearest-neighbors. This spatial distribution may serve to minimize intraspecific interactions with regard to competition for space and resources. However, there is some evidence that social factors also influence these spatial relationships. It was found, for example, that the nearest-neighbors for females tended to be males.

Despite the uniform distribution of day burrows, there is substantial spatial overlap of D. merriami ranges with most individuals overlapping with several conspecifics. As with day burrow locations, range overlap appears to be partly influenced by social factors since females overlap more with conspecific males than other females. Males show no such discrimination. Although little overt aggression has been observed in the field and these animals are relatively unaggressive toward conspecifics in laboratory pairings, individuals probably maintain relatively exclusive core activity areas near their burrows. The core areas of individuals (as defined in Chapter 7) never overlapped with the core areas of conspecifics.

The ecological significance of the socio-spatial relationships of D. merriami is not completely understood. It is generally accepted that abundant, evenly distributed food resources will give rise to uniform spacing and territorial defense of space and resources by animals (Brown and Orians, 1970). On the other hand, as Brown and Orians point out, when resources are scattered and/or economically undefendable, substantial overlap may occur. If this is the case, intraspecific variation in spatial overlap in relation to variations in food availability and distribution should be demonstrable. At present, the relationship between resource conditions and spatial patterns has not been investigated.

The reproductive traits of D. merriami are ostensibly rather conservative compared to some other rodent species (notably myomorphs including Rattus species, the house mouse, and the golden hamster). Our laboratory studies have shown that females have an 11-14 day estrous cycle, no postpartum estrus, and small litters. On the other hand, the speed of morphological and behavioral development of offspring is similar to other rodents of comparable size and dispersal occurs at about four to six weeks. Consequently, a female may breed several times within the reproductive season. Furthermore, sexual maturation is fairly rapid with females capable of breeding in their natal season. Generally, D. merriami appear to be opportunistic breeders in relation to environmental conditions, particularly with respect to the production of green vegetation (see introduction of Chapter 5).

The type of mating system exhibited by D. merriami remains unanswered by direct evidence. Since these animals do not pair-bond for reproductive purposes, monogamy is ruled out. On the other hand, these animals are not strongly sexually dimorphic in body size or ranging behavior nor do they possess any obvious secondary sexual characteristics indicative of strong sexual selection in their evolutionary history and, hence, a high degree of polygyny.

As with spatial relationships, ecological conditions may be an important determinant of the mating system of a species. Emlen and Orians (1977) point out that the degree of polygyny of any species depends in part on the "economic monopolizability" of several mates; i.e. the degree to which multiple mates or the resources necessary to gain mates are economically defendable. For *D. merriami*, it is likely that resources (including mates) are too widely scattered to be defendable from potential rivals. Hence, strong sexual dimorphisms in body size and ranging behavior have not arisen.

What, then, is the nature of the mating system of *D. merriami* and what proximate factors determine who mates and with whom? The information collected over the last three years has not provided direct answers to these questions but some interesting possibilities exist. The following discussion is meant to identify some of the factors potentially important for the sociobiology of this species and to direct future research.

First of all, it is apparent that the majority of adult females reproduce during the breeding season. This is a typical mammalian pattern in which the majority of females reproduce at some point in their lifetime. For males, however, only the establishment of paternity can verify reproductive success. So, even though all of the adult males in the breeding season were apparently capable of reproduction as indicated by scrotal testes, whether all enjoyed reproductive success remains unknown.

Some behavior patterns exhibited by males suggest that this species, like most mammals, is at least mildly polygynous. Throughout the field studies, the variance between males in surface activity was greater than the variance between females. Even during the breeding season when male ranging behavior was significantly greater than female ranging, several males had movements less than or similar to females while a few males made extremely long moves. Unfortunately, no consistent individual characteristics were associated with the differences between males. During the breeding season, the biggest moves were by the smaller males while in the following non-breeding study period just the reverse was true. Nonetheless, these differences between males may be in some way related to differential access to females.

In the absence of strong sexual dimorphisms, what other factors might bring about differential breeding success by males? One such factor might be social familiarity. It was shown in Chapter 7 that individuals' home ranges remain relatively stable over time thus providing the opportunity for complex social relationships to develop. Perhaps a male's "worth" as far as a female is concerned is related to his ability to establish and maintain a stable home range and that the relevant factor for mate choice is simply social familiarity. Such a system would be consistent with our findings of sex differences in range overlap and the tendency of some males to make many long sallies. Of seeming importance to the issue of mate choice is also the striking increase in ranging by estrous females.

Clearly the factors involved in intrasexual competition and mate choice require further clarification. However, the variation observed in the ranging behavior of males and females suggests that mating is probably not random (i.e. promiscuous) and that D. merriami are at least mildly polygynous.

An important issue concerning the sociobiology of a species is the extent to which relatives interact after the dispersal of young and, thus, the potential for nepotism (i.e. discriminative behavior which enhances the inclusive fitness of a relative). Evidence from our studies indicates that nepotism may not play an important role in the social behavior of D. merriami as it appears to in some other sciuromorph rodents (e.g., Sherman, 1980). A mother and daughter had day burrows that were located over 200 m apart and showed no range overlap.

Conclusion

The field and laboratory studies presented in this thesis have provided some definitive and provocative information about the behavior of D. merriami. As one of the most ubiquitous rodents of the arid regions of North America, but whose habitat in many areas is being destroyed in favor of development, D. merriami is a worthy subject for study. It is hoped that the information presented here will be useful for the further clarification of rodent social ethology and socio-ecology. The findings of this thesis provide further evidence that so-called "solitary" species are not always particularly asocial and may indeed exhibit quite interesting and complex social structures.

Appendix A

Rodent Development Checklist

Morphology:

Hair-none
    vibrassae
    back
    belly
    color?
Nails-toes, fingers clearly differentiated?
Eyes-open?
Ear-stages until open?
Teeth-incisors?
    molars?

Locomotion and Gross Body Movements:

Body twitch	whole-body twitches
Limb twitch	limb twitches
Limb Xtend	single limb extensions
Finger spread	finger spreading
Toe spread	toe spreading
Pull forward c̄ FP	pulling self forward with forepaws
Push forward c̄ HF	pushing self forward with hind feet
Alt stride s̄	alternating hind foot strides?
c ft. hold	(with or without use of foothold)
Root under sib	rooting under sibling
c̄ FP	with or without use of forepaws
c HF	with or without use of hindfeet
Crawl on sib	crawling over siblings
Self rite c̄ thrash	self-righting by irregular thrashing about
c̄ / roll	self-righting by diagonal roll over shoulder
c̄ fwd roll	self-righting by forward roll between legs
Walk clear ground	walking keeping body clear of ground
c head turns	walking with or without side-to-side head movements
Trot	alternating 'trot' gait
Gallop	'gallop' gait (hind feet together, fore together)
Run	run (high speed walk)
Dash	dash (very quick short run)
Hop	hop (quadrupedal saltation)
Bipedal hop	bipedal hop
Nest exit	nest departure
Wall rear	rearing up wall
open rear	open rear (= no forepaw support)

Freeze	freeze alert
Grooming:	
Scr air	scratch without contact
Scr flank	scratch flank
Scr shoulder	scratch shoulder
Scr crown	scratch top of head
Scr chk/eye	scratch cheek or eye
Scr+bodtwist	scratch with body twist toward scratching foot
Scr+footlick	scratch with foot-licking
Scr bout	scratching bout with succession of places scratched
Scr pit	scratch armpit with arm-lift
FPG	forepaw grooming
snout	snout groom (2-handed wiping of snout tip)
Pawlick	paw-licking
FPG to eye	forepaw grooming below eye
FPG eye-ear	forepaw grooming between eye and ear
FPG over ear	forepaw grooming above ear
Nonsync HG	asymmetrical head-grooming (paws out of synchrony, pulling over one side more that other)
FPG situp	forepaw grooming sitting up without support
BGM	body grooming with mouth
flank	
thigh	
foot	
ft.+FPhold	foot holding with forepaws (to mouth it)
ft.+2FPhold	foot holding with two forepaws (to mouth it).
Groom Bouts	
Scr + FPG	scratching with forepaw grooming
Scr + BGM	scratching with body grooming with mouth
FPG + BGM	forepaw grooming with body grooming with mouth
All 3	
Tail groom (FP+M)	Tail grooming with paws and mouth
Sandbathing	
Ventral rub	rub ventrum on sand
Side rub	rub side on sand
Yawn	
Str body	stretch whole-body
alt.FP	stretch forepaws alternately
simult.FP	stretch forepaws simultaneously
Diagonals	stretch diagonals
Yawn + stretch	yawn and stretch together

BSR (bearskinrug)	'bear-skin-rug'
Shake body	shake whole-body
head	shake head
+dash	shake + quick dash

Digging:

Nest Build NB	mouthing nest material (NP = nest paper)
Mouth NP	mouthing it and holding it
Hold NP	
Shred NP	shredding or chopping it
Manip NP	arranging it with forepaws
Pat NP	patting down
	bumping with snout & forepaws into nest wall
Long FPD NP	Dragging nest-material under self with long forepaw strokes
+ exit	" " " " while leaving the nest
FPD altntng	forepaw digging in substrate
simult?	(alternating or simultaneous?)
HF apart	hindfeet firmly planted apart
HF kick	hindfoot kicks
simult?	simultaneous?
FPD + HF kick	integrated bout of forepaw digging and hindfoot kicks
Burrow	burrow under nest material
Peek-a-boo	peeking from under nest material

Eating:

Mouthing	mouthing (objects) food
Hold c FP+mouth	holding it down with forepaws and mouthing
Eat	clear ingestion
Eat+situp	eat sitting up
Hold food	holding food in forepaws
Steal food	steal food from sibs
Hoard food	carry food to nest to eat
Protect food	protecting food from sibs by turning back to them and evasion
Carry food	dragging food about
Pouch food	stuffing pouches with food (objects)
Drink	drinking, prolonged bout?
pickup+drop food	picking up and dropping food
pile food	piling food

Elimination:

Defecate	defecate without maternal assistance
Urinate	urinate without maternal assistance (further refinements, e.g. urine posture, extraction of feces, etc.)

Social Interactions:

Face-face pawing	face to face pawing
Face-face sniffing	face to face sniffing
Nose-nose sniffing	mutual nose to nose sniff
Sniff flank	sniff flank
Sniff A-G	sniff ano-genital area
Play fights	
mutual swat	mutual swatting
V-V wrestle	rolling together ventral-ventral wrestle
Pounce	play pounce
+bite	with biting?
+mutual bite?	with mutual flank biting
+chases	with chases
Defense Posture	defensive posture-- turning on back
+ears fwd	ears forward?
+hiss	hiss?
Suckling	
out of nest	suckling attempt out of nest
successful?	
Sniff mom's A-G	sniff mom's ano-genital region
Sniff mom ear+nip	sniff, nip mom's ears
Sniff mom mouth	sniff, corner of mom's mouth
Playfight mom	play-fight, chase, etc, with mom
Chase mom	
Groom sib	mutual grooming (or unilateral) with sibling
Groom mom	mutual groomimg (or unilateral) with mom
Mounts?	

Appendix B

Analysis of Variance

Study Period 1

Source	SS	df	MS	F
A (sex)	801.5	1	801.5	2.30 ns
Subj. w. groups	5570.8	16	348.2	
B (time of night)	2476.9	13	190.5	3.32 **
AB	1435.6	13	110.4	1.93 *
B X Subj. w. groups	11923.1	208	57.3	

* $p < .05$

** $p < .01$

ns = not statistically significant

Study Period 3

Source	SS	df	MS	F
A (sex)	58.4	1	58.4	2.89 ns
Subj. w. groups	282.6	14	20.2	
B (time of night)	8157.2	13	627.5	5.56 **
AB	330.8	13	25.4	0.22 ns
B X Subj. w. groups	20531.3	182	112.8	

** $p < .01$

ns = not statistically significant

Study Period 3- Effects of Time and Temperature

Source	SS	df	MS	F	
A (sex)	1.9	1	1.9	0.002	ns
Subj. w. groups	14367.0	12	1197.2		
B (temperature)	21.3	1	21.3	0.78	ns
AB	7.8	1	7.8	0.29	ns
B X Subj. w. groups	325.7	12	27.1		
C (time of night)	5860.6	3	1953.5	11.60	**
AC	86.1	3	28.7	0.17	ns
C X Subj. w. groups	6074.3	36	168.7		
BC	222.0	3	74.0	2.03	ns
ABC	53.0	3	17.7	0.48	ns
BC X Subj. w. groups	1313.7	36	36.5		

** $p < .01$

ns = not statistically significant

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