PLACEMENT AND RECOVERY OF SEED CACHES BY A SOLITARY RODENT, ORD'S KANGAROO RAT (*DIPODOMYS ORDII*)

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PLACEMENT AND RECOVERY OF SEED CACHES BY A SOLITARY RODENT, ORD'S KANGAROO RAT (*DIPODOMYS ORDII*)

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Date of Graduation

VITA

Jeremy Andrew White, son of Rockey Craig White and Nancy Tinstman Remington, was born 11 June 1975, in Reno, Nevada. He moved to Elko, Nevada, in 1989 and graduated from Elko High School in 1993. After high school, Jeremy enrolled in the University of Nevada at Las Vegas, and in 1997, he received a Bachelor of Science degree in organismal biology from UNLV. After graduation, he moved to Reno and from 1997 to 2000 Jeremy worked as a substitute teacher for Washoe County School District, a lab instructor at Truckee Meadows Community College, and a wildland firefighter for the Bureau of Land Management. Enjoyment from interactions with students at the community college and from exploring the Great Basin Desert and other regions while firefighting, prompted Jeremy to pursue a graduate degree in ecology. He began his graduate work at the University of Nebraska at Omaha in 2000 under the direction of Kenneth N. Geluso who taught Jeremy an appreciation for natural history and ecology and trained him as a field mammalogist. Jeremy completed his M.A. degree in biology in 2003 and went on to obtain his Ph.D. in ecology under Troy L. Best at Auburn University.

DISSERTATION ABSTRACT

PLACEMENT AND RECOVERY OF SEED CACHES BY A SOLITARY RODENT, ORD'S KANGAROO RAT (*DIPODOMYS ORDII*)

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Seed caching is a common behavior that has important ecological consequences for seed-hoarding animals, granivorous competitors, and plants whose seeds are harvested and stored. Despite the significance of this behavior, patterns of storage and recovery of caches for many food-hoarding animals in the wild remain poorly understood. For example, many rodents are prolific and dynamic seed hoarders, storing large quantities of seeds in larderhoards (repeated deposits of seeds in a centralized location) and scatterhoards (small, scattered, subsurface caches), yet few factors that influence placement of caches by rodents have been identified. Furthermore, no study has examined seasonal shifts in placement of caches by seed-storing animals that forage throughout the year. Preliminary investigations revealed that Ord's kangaroo rats

(*Dipodomys ordii*) are active year-round in the Sandhill Region of Nebraska and that these rodents deposit seeds of soapweed yucca (*Yucca glauca*) in both larderhoards and scatterhoards. This unique situation provided an opportunity to investigate use of burrows, seed-caching patterns, and recovery of caches by a solitary rodent in the wild. Ord's kangaroo rats inhabited burrows alone and typically used multiple burrows in summer, but only 1 burrow in winter. Additionally, individuals took yucca seeds directly to burrows in winter (larderhoarding), but distributed seeds into shallowly buried caches in summer (scatterhoarding). Kangaroo rats likely larderhoarded seeds in winter to have convenient access to resources and because few suitable sites were available to scatterhoard seeds in this season. In summer, kangaroo rats placed caches in a clumped arrangement closer to seed sources than to burrows, following the rapid-sequestering hypothesis. In a test of recovery of caches, kangaroo rats did not have a distinct advantage over pilferers in recovering their own scatterhoards of yucca seeds. Although seed caches were recovered quickly, most caches were only partially recovered. Finally, burrows of Ord's kangaroo rats were simple in structure and contained few seeds in summer; reinforcing the observation that larderhoarding was uncommon in this population in summer. Overall, evidence indicates that Ord's kangaroo rats are flexible seed hoarders as they switch patterns of seed storage and use of burrows seasonally. Furthermore, their storage and incomplete recovery of caches has important implications for dispersal of plants in the Sandhill Region.

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INTRODUCTION

Food hoarding is a widespread behavior that has evolved in many groups of animals including arthropods, birds, and mammals (Vander Wall 1990). Many food hoarders store or cache food when it is readily available for consumption during periods of scarcity (Smith and Reichman 1984; Vander Wall 1990). However, other short-term benefits also may promote food-hoarding behavior. For example, cached food allows animals to limit foraging during inclement weather or risk of predation (Vander Wall 1990). In addition, by hoarding food, animals that live in groups may secure resources for their kin, while solitary animals may achieve an advantage over competitors (Vander Wall and Jenkins 2003).

Regardless of the potential benefits of food storing, hoarders must recover more stored food than non-hoarders for this behavior to persist (Andersson and Krebs 1978; Vander Wall and Jenkins 2003). Recovery of stored food by hoarders depends to some degree on distribution of caches. Storage of food at 1 site or a few closely spaced sites where animals make repeated visits to deposit food is called larderhoarding (Smith and Reichman 1984; Vander Wall 1990). Larderhoarders aggressively defend and protect caches from conspecifics and competitors to retain their stored resources. However, if animals are unable to defend their food, then an alternative strategy is scatterhoarding. Scatterhoarders deposit food in small, widely scattered, subsurface caches (Morris 1962;

Vander Wall 1990). For many scatterhoarders, remembering the location of scattered resources is important to successfully recovering stored food (Vander Wall et al. 2006; Vander Wall and Jenkins 2003).

Although most food hoarders are described as either larderhoarders or scatterhoarders, some animals use both caching strategies. Flexibility in food-hoarding patterns is most common in solitary rodents. For example, chipmunks (*Tamias;* Clarke and Kramer 1994; Elliott 1978; Shaffer 1980; Vander Wall et al. 2005; Yahner 1975), red squirrels (*Tamiasciurus hudsonicus*; Hurly and Lourie 1997; Hurly and Robertson 1990), thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*; Devenport et al. 2000), gerbils (*Gerbillus*; Ovadia et al. 2001; Tsurim and Abramsky 2004), North American deermice (*Peromyscus maniculatus*; Vander Wall et al. 2001), and kangaroo rats (*Dipodomys*; Daly et al. 1992; Jenkins and Breck 1998; Jenkins et al. 1995; Preston and Jacobs 2001; Price et al. 2000) use a combination of larderhoarding and scatterhoarding.

Aspects of food-hoarding behavior, including storage and recovery of food, have important ecological implications. However, flexibility in hoarding patterns observed in species of rodents complicates this scenario. For example, studies have suggested that differences in food-hoarding patterns and pilferage ability of heteromyid rodents promote coexistence of similar species (Jenkins and Breck 1998; Leaver and Daly 2001; Price et al. 2000). It certainly is possible that differences in distribution and recovery of stored food may help explain coexistence of similar species that occupy the same environment. Yet, 2 of these studies were conducted in laboratory settings (Jenkins and Breck 1998; Price et al. 2000), and variation in scatterhoarding and larderhoarding might have been a response to artificial environments. For example, studies have demonstrated that food-hoarding rodents used different foraging and hoarding strategies in laboratory settings compared to field studies (e.g., Leaver 2004; Leaver and Daly 1998; Ovadia et al. 2001).

Conflicting results in studies of foraging and hoarding strategies expose our lack of understanding of food-hoarding behavior and arouse some basic questions about food storage in free-living animals. Is variation in food-hoarding behavior a response to artificial situations, or does it exist in nature? If it is prevalent in nature, what factors are involved in the decision to scatterhoard or larderhoard? Before studies connect food hoarding to structuring of rodent communities, we need to understand this behavior more thoroughly. A first step in this process is to investigate variation in food-hoarding behavior by a single species in a natural situation. Therefore, the main body of my research focuses on food-hoarding behavior and recovery of stored food by a solitary rodent, Ord's kangaroo rat (*Dipodomys ordii*), in a natural environment.

Kangaroo rats (*Dipodomys*, Heteromyidae) represent an ideal group in which to investigate aspects of food-caching behavior in a single species. These solitary, nocturnal rodents live in burrows throughout arid and semi-arid habitats in western North America (Schmidly et al. 1993). They are active year-round (Kenagy 1973; O'Farrell 1974; White and Geluso 2007), and typically only emerge from burrows for short excursions on the surface to search for mates and food (Braun 1985; Kenagy 1976; Langford 1983; Schroder 1979). Although they eat green vegetation and insects when available, kangaroo rats mainly forage on seeds (Best and Hoditschek 1982; Best et al. 1993; Lowe 1997; Nagy and Gruchacz 1994; Reichman 1975; Sipos et al. 2002; Tracy and Walsberg 2002). These unique rodents have external, fur-lined, cheek pouches that are used to transport seeds and other items, and many species are known to cache food (Reichman and Price

1993). Large kangaroo rats usually are larderhoarders and smaller ones typically scatterhoard food (Reichman and Price 1993); however, recent studies have demonstrated that at least 6 species (*Dipodomys microps, D. merriami*, *D. ordii*, *D. panamintinus*, *D. deserti*, and *D. spectabilis*) use both caching strategies (Daly et al. 1992; Jenkins and Breck 1998; Jenkins et al. 1995; Preston and Jacobs 2001; Price et al. 2000).

Preliminary investigations revealed that Ord's kangaroo rats in the Sandhill Region of Nebraska distribute seeds into both scatterhoards and larderhoards. *D. ordii* is a medium-sized kangaroo rat that has the largest distribution of any heteromyid, ranging from central Mexico to southern Canada and from the Great Basin Desert to the Great Plains (Garrison and Best 1990; Schmidly et al. 1993). At the eastern edge of their range in the Sandhill Region of Nebraska, Ord's kangaroo rats are abundant and they are the only species of kangaroo rat (Jones et al. 1983). This unique situation presents an excellent opportunity to investigate use of scatterhoarding and larderhoarding by a single species, and to determine effectiveness of recovery of caches by a solitary rodent in the wild. However, along with examining food-hoarding behavior in this population of kangaroo rats, it was important to understand their use of burrows, because these behaviors are inextricably linked.

Evidence suggests that larderhoarders only use 1 burrow and scatterhoarders typically use multiple burrows (Behrends et al. 1986; Daly et al. 1992; Schroder 1979). For example, banner-tailed kangaroo rats (*Dipodomys spectabilis*) are well documented as larderhoarders (Schroder 1979; Vorhies and Taylor 1922). They spend a majority of time on the surface close to their home burrow and defend it from conspecifics and other competitors (Schroder 1979), indicative of central-place foragers. In contrast, Merriam's kangaroo rats (*Dipodomys merriami*) predominantly are scatterhoarders (Daly et al. 1992; Reynolds 1958). These kangaroo rats have large home ranges and move greater distances during the night while using several burrows within their home range (Behrends et al. 1986; Daly et al. 1990). In contrast to these species of *Dipodomys*, limited information exists for patterns of use of burrows by Ord's kangaroo rats (Langford 1983). To more thoroughly understand food-hoarding behaviors of this species, it was crucial to document their patterns of use of burrows in the Sandhill Region. Thus, the 1st chapter of this dissertation focuses on use of burrows by Ord's kangaroo rats.

The 2nd chapter concentrates on food-hoarding behavior of these kangaroo rats. Recently, studies have focused on identifying factors associated with use of different food-caching strategies by a single species (Clarke and Kramer 1994; Daly et al. 1992; Leaver 2004; Leaver and Daly 1998; Preston and Jacobs 2001; Murray et al. 2006; Tsurim and Abramsky 2004). For rodents, many factors seem to influence whether they larderhoard or scatterhoard including age and reproductive condition of individuals (Clarke and Kramer 1994), value of food (Leaver 2004; Leaver and Daly 1998), distance that food is encountered from burrows, (Daly et al 1992; Tsurim and Abramsky 2004), makeup of the competitive environment (Murray et al. 2006), and pilferage of caches (Preston and Jacobs 2001). These studies have demonstrated the dynamic nature of food hoarding in rodents; however, other factors such as season also might be associated with a change in food-hoarding patterns (Jenkins and Breck 1998; Lawhon and Hafner 1981; Price et al. 2000). Surprisingly, no study has investigated whether food-hoarding animals that forage throughout the year switch their method of storage (larderhoarding or scatterhoarding) seasonally in the wild. Therefore, chapter 2 focuses on seed storage and placement of caches by Ord's kangaroo rats in summer and winter.

Chapter 3 is concerned with recovery of caches by Ord's kangaroo rats. An important component of food-hoarding behavior is recovery of stored food. Models on the adaptive value of food hoarding suggest that cachers must recover more stored food than other individuals for this behavior to be advantageous (Andersson and Krebs 1978; Clarkson et al. 1986; Stapanian and Smith 1978; Vander Wall and Jenkins 2003). However, few studies have investigated the recovery advantage of cachers over other individuals (Vander Wall et al. 2006). Furthermore, no study has assessed effectiveness of kangaroo rats in recovering their own caches in the wild. Thus, whether kangaroo rats have an advantage over pilferers in recovering their own seed caches in the Sandhill Region is the focus of this chapter.

In the 4th chapter, structure of burrows of Ord's kangaroo rats and foods stored within their burrows in summer in the Sandhill Region were documented. This chapter on aspects of natural history of these kangaroo rats was important because the method used to investigate food-hoarding behavior only presented a partial picture of this behavior; that is, only the initial location of stored seeds could be determined. Food-hoarding behavior is a dynamic process (e.g., Roth and Vander Wall 2005; Vander Wall and Joyner 1998). Thus, it was possible that individuals moved seeds to burrows after initially caching them in small, subsurface caches, or that individuals frequently scatterhoarded in response to a lack of space inside burrows. By excavating burrows, it was possible to document whether either of these were likely scenarios. Moreover, in the process of characterizing burrows and larderhoards of Ord's kangaroo rats, a novel foraging and caching behavior of this species was documented.

Through the chapters of this dissertation, I explored details of the burrow-use and food-hoarding behaviors of a solitary rodent in a temperate environment. Much of this research, including caching behavior of granivorous animals in winter, has received little attention. It is my belief that the body of work presented herein is an original and meaningful contribution to ecology, and furthers our knowledge of, and appreciation for, granivorous rodents.

LITERATURE CITED

Andersson, M., and J. Krebs. 1978. On the evolution of hoarding behaviour. Animal Behaviour 26:707-711.

Behrends, P., M. Daly, and M. I. Wilson. 1986. Range use patterns and spatial relationships of Merriam's kangaroo rats (*Dipodomys merriami*). Behaviour 96:187-209.

Best, T. L., and B. Hoditschek. 1982. Analysis of cheek pouch contents of Ord's kangaroo rat (*Dipodomys ordii*). The Southwestern Naturalist 27:117-119.

Best, T. L., M. P. Skupski, and R. A. Smartt. 1993. Food habits of sympatric rodents in the shinnery-oak mesquite grasslands of southeastern New Mexico. The Southwestern Naturalist 38:224-235.

Braun, S. E. 1985. Home range and activity patterns of the giant kangaroo rat, *Dipodomys ingens*. Journal of Mammalogy 66:1-12.

Clarke, M. F., and D. L. Kramer. 1994. Scatter-hoarding by a larder-hoarding rodent: intraspecific variation in the hoarding behaviour of the eastern chipmunk, *Tamias striatus*. Animal Behaviour 48: 299-308.

Clarkson, K., S. F. Eden, W. J. Sutherland, and A. I. Houston. 1986. Density dependence and magpie food hoarding. The Journal of Animal Ecology 55:111-121.

Daly, M., L. F. Jacobs, M. I. Wilson, and P. R. Behrends. 1992. Scatter-hoarding by kangaroo rats (*Dipodomys merriami*) and pilferage from their caches. Behavioral Ecology 3:102-111.

Daly M., M. Wilson, P. R. Behrends, and L. F. Jacobs. 1990. Characteristics of kangaroo rats, *Dipodomys merriami*, associated with differential predation risk. Animal Behaviour 40:380-389.

Devenport, J. A., L. D. Luna, and L. D. Devenport. 2000. Placement, retrieval, and memory of caches by thirteen-lined ground squirrels. Ethology 106:171-183.

Elliott, L. 1978. Social behavior and foraging ecology of the eastern chipmunk (*Tamias striatus*) in the Adirondack Mountains. Smithsonian Contributions to Zoology 265:1-107.

Garrison, T. E., and T. L. Best. 1990. Dipodomys ordii. Mammalian Species 353:1-10.

Hurly, T. A. and S. A. Lourie. 1997. Scatterhoarding and larderhoarding by red squirrels: size, dispersion, and allocation of hoards. Journal of Mammalogy 78:529-537.

Hurly, T. A., and R. J. Robertson. 1990. Variation in the food hoarding behaviour of red squirrels. Behavioral Ecology and Sociobiology 26:91-97.

Jenkins, S. H., and S. W. Breck. 1998. Differences in food hoarding among six species of heteromyid rodents. Journal of Mammalogy 79:1221-1233.

Jenkins, S. H., A. Rothstein, and W. C. H. Green. 1995. Food hoarding by Merriam's kangaroo rats: a test of alternative hypotheses. Ecology 76:2470-2481.

Jones, J. K., Jr., D. M. Armstrong, R. S. Hoffmann, and C. Jones. 1983. Mammals of the northern Great Plains. University of Nebraska Press, Lincoln.

Kenagy, G. J. 1973. Daily and seasonal patterns of activity and energetics in a heteromyid rodent community. Ecology 54:1201-1219.

Kenagy, G. J. 1976. The periodicity of daily activity and its seasonal changes in free-ranging and captive kangaroo rats. Oecologia (Berlin) 24:105-140.

Langford, A. L. 1983. Pattern of nocturnal activity of male *Dipodomys ordii* (Heteromyidae). The Southwestern Naturalist 28:341-346.

Lawhon, D. K., and M. S. Hafner. 1981. Tactile discriminatory ability and foraging strategies of kangaroo rats and pocket mice (Rodentia: Heteromyidae). Oecologia (Berlin) 50:303-309.

Leaver, L. A. 2004. Effects of food value, predation risk, and pilferage on the caching decisions of *Dipodomys merriami*. Behavioral Ecology 15:729-734.

Leaver, L. A., and M. Daly. 2001. Food caching and differential cache pilferage: a field study of coexistence of sympatric kangaroo rats and pocket mice. Oecologia (Berlin) 128:577-584.

Leaver, L. A., and M. Daly. 1998. Effects of food preference on scatter-hoarding by kangaroo rats (*Dipodomys merriami*). Behaviour 135:823-832.

Lowe, M. 1997. Diet of Stephens' kangaroo rat, *Dipodomys stephensi*. The Southwestern Naturalist 42:358-361.

Morris, D. 1962. The behaviour of the green acouchi (*Myoprocta pratti*) with special reference to scatter hoarding. Proceedings of the Zoological Society of London 139:701-732.

Murray, A. L., A. M. Barber, S. H. Jenkins, and W. S. Longland. 2006. Competitive environment affects food-hoarding behavior of Merriam's kangaroo rats (*Dipodomys merriami*). Journal of Mammalogy 87:571-578.

Nagy, K. A., and M. J. Gruchacz. 1994. Seasonal water and energy metabolism of the desert-dwelling kangaroo rat (*Dipodomys merriami*). Physiological Zoology 67:1461-1478.

O'Farrell, M. J. 1974. Seasonal activity patterns of rodents in a sagebrush community. Journal of Mammalogy 55:809-823.

Ovadia, O., Y. Ziv, Z. Abramsky, B. Pinshow, and B. P. Kotler. 2001. Harvest rates and foraging strategies of Negev Desert gerbils. Behavioral Ecology 12:219-226.

Preston, S. D., and L. F. Jacobs. 2001. Conspecific pilferage but not presence affects Merriam's kangaroo rat cache strategy. Behavioral Ecology 12:517-523.

Price, M. V., N. M. Waser, and S. McDonald. 2000. Seed caching by heteromyid rodents from two communities: implications for coexistence. Journal of Mammalogy 81:97-106.

Reichman, O. J. 1975. Relation of desert rodent diets to available resources. Journal of Mammalogy 56:731-751.

Reichman, O. J., and M. V. Price. 1993. Ecological aspects of heteromyid foraging. Pp. 539-595 in Biology of the Heteromyidae (H. H. Genoways and J. H. Brown, eds.). Special Publication, The American Society of Mammalogists 10:1-719.

Reynolds, H. G. 1958. The ecology of the Merriam kangaroo rat (*Dipodomys merriami* Mearns) on the grazing lands of southern Arizona. Ecological Monographs 28:111-127.

Roth, J. K., and S. B. Vander Wall. 2005. Primary and secondary seed dispersal of bush chinquapin (Fagaceae) by scatterhoarding rodents. Ecology 86:2428-2439.

Schmidly, D. J., K. T. Wilkins, and J. N. Derr. 1993. Biogeography. Pp. 319-356 in Biology of the Heteromyidae (H. H. Genoways and J. H. Brown, eds.). Special Publication, The American Society of Mammalogists 10:1-719.

Schroder, G. D. 1979. Foraging behavior and home range utilization of the bannertail kangaroo rat (*Dipodomys spectabilis*). Ecology 60:657-665.

Shaffer, L. 1980. Use of scatterhoards by eastern chipmunks to replace stolen food. Journal of Mammalogy 61:733-734.

Sipos, M. P., M. C. Andersen, W. G. Whitford, and W. R. Gould. 2002. Graminivory by *Dipodomys ordii* and *Dipodomys merriami* on four species of perennial grasses. The Southwestern Naturalist 47:276-281.

Smith, C. C., and O. J. Reichman. 1984. The evolution of food caching by birds and mammals. Annual Review of Ecology and Systematics 15:329-351.

Stapanian, M. A., and C. C. Smith. 1978. A model for seed scatterhoarding: coevolution of fox squirrels and black walnuts. Ecology 59:884-896.

Tracy, R. L., and G. E. Walsberg. 2002. Kangaroo rats revisited: re-evaluating a classic case of desert survival. Oecologia (Berlin) 133:449-457.

Tsurim, I., and Z. Abramsky. 2004. The effect of travel costs on food hoarding in gerbils. Journal of Mammalogy 85:67-71.

Vander Wall, S. B. 1990. Food hoarding in animals. The University of Chicago Press, Chicago.

Vander Wall, S. B., and S. H. Jenkins. 2003. Reciprocal pilferage and the evolution of food-hoarding behavior. Behavioral Ecology 14:656-667.

Vander Wall, S. B., and J. W. Joyner. 1998. Recaching of Jeffrey pine (*Pinus jeffreyi*) seeds by yellow pine chipmunks (*Tamias amoenus*): potential effects on plant reproductive success. Canadian Journal of Zoology 76:154-162.

Vander Wall, S. B., E. C. H. Hager, and K. M. Kuhn. 2005. Pilfering of stored seeds and the relative costs of scatter-hoarding versus larder-hoarding in yellow pine chipmunks. Western North American Naturalist 65:248-257.

Vander Wall, S. B., T. C. Thayer, J. S. Hodge, M. J. Beck, and J. K. Roth. 2001. Scatter-hoarding behavior of deer mice (*Peromyscus maniculatus*). Western North American Naturalist 61:109-113.

Vander Wall, S. B., J. S. Briggs, S. H. Jenkins, K. M. Kuhn, T. C. Thayer, and M. J. Beck. 2006. Do food-hoarding animals have a cache recovery advantage? Determining recovery of stored food. Animal Behaviour 72:189-197.

Vorhies, C. T., and W. P. Taylor. 1922. Life history of the kangaroo rat *Dipodomys spectabilis* Merriam. United States Department of Agriculture Bulletin 1091:1-40.

White, J. A., and K. Geluso. 2007. Seasonal differences in onset of surface activity of Ord's kangaroo rat (*Dipodomys ordii*). Journal of Mammalogy 88:234-240.

Yahner, R. H. 1975. The adaptive significance of scatter hoarding in the eastern chipmunk. Ohio Journal of Science 75:176-177.

CHAPTER 1.

USE OF BURROWS BY A SOLITARY RODENT, ORD'S KANGAROO RAT (*DIPODOMYS ORDII*), IN THE NORTHERN GREAT PLAINS

ABSTRACT

Patterns of use of burrows differ among species of kangaroo rats, and for species that inhabit temperate environments, use of burrows may change seasonally. Ord's kangaroo rat (*Dipodomys ordii*) has the largest distribution of any species of *Dipodomys*. However, despite its widespread distribution, patterns of use of burrows have not been investigated in this species. Adult male and female Ord's kangaroo rats were radiocollared during 2 consecutive summers and winters in a temperate environment, the Sandhill Region of Nebraska, to determine number of burrows used in each season, and whether individuals shared burrows during the summer breeding season. Kangaroo rats typically used only 1 burrow in winter, but were still active during cold conditions with heavy snow cover. However, in summer, individuals frequently used multiple burrows. Seasonal patterns of use of burrows exhibited by *D. ordii* are similar to other species of kangaroo rats inhabiting environments with substantial climatic differences between summer and winter. For individuals that used multiple burrows, distances were farther apart in summer than winter, suggesting that Ord's kangaroo rats moved greater distances during the summer breeding season. Interestingly, females used more burrows than

males in summer. Frequent switching of burrows by females might be influenced by reproductive condition, because lactating and recently post-lactating females used more burrows than other individuals. Although both male and female kangaroo rats typically used multiple burrows in summer, they almost never shared burrows. Thus, Ord's kangaroo rats are solitary, similar to most other species of *Dipodomys*.

INTRODUCTION

Burrows serve many important functions for animals that use them. For example, burrows provide shelter from environmental stresses, a refuge from predators, a place to raise young, and a site to store food (Kinlaw 1999; Reichman and Smith 1987). A variety of terrestrial mammals construct and use burrows. Fossorial mammals spend nearly all of their time underground in burrow systems, whereas semi-fossorial mammals spend a majority of time in burrows, but frequently are active on the surface of the ground (Martin et al. 2001). Although semi-fossorial mammals, such as kangaroo rats (*Dipodomys*), commonly are active aboveground, burrows are necessary for their survival and reproduction (Jones et al. 1988).

Kangaroo rats are nocturnal, granivorous rodents of the family Heteromyidae that inhabit arid and semi-arid regions of western North America (Schmidly et al. 1993). These rodents emerge from burrows to search for mates and food, but may only remain on the surface for ≤1 h during the night (Braun 1985; Kenagy 1976; Langford 1983). Characteristics of burrows and patterns of use of burrows are remarkably diverse in the genus *Dipodomys*. For example, banner-tailed kangaroo rats (*Dipodomys spectabilis*) defend exclusive territories around their burrows (Randall 1984). They build complex burrow systems within mounds that may take >2 years to construct (Best 1972). Mounds may persist as long as they are occupied and maintained (Holdenried 1957). Adult banner-tailed kangaroo rats typically inhabit burrows alone where they store seeds that they rely on during periods of food scarcity (Schroder 1979; Vorhies and Taylor 1922). Even when active on the surface, these kangaroo rats rarely stray far from their mound and defend it from conspecifics and other competitors (Schroder 1979). Conversely, Merriam's kangaroo rats (*Dipodomys merriami*) construct relatively simple burrows (Reynolds 1958). Similar to banner-tailed kangaroo rats, adults typically live in separate burrows (Kenagy 1973); however, they do not maintain exclusive territories and are more tolerant of neighbors than *D. spectabilis* (Randall 1993). *D. merriami* usually does not store copious amounts of food within burrows, but disperses seeds into small, subsurface caches (Bienek and Grundmann 1971; Reynolds 1958). In addition, fidelity to burrows is low and individuals commonly use >1 day burrow (Behrends et al. 1986a). Stephens' kangaroo rat (*Dipdomys stephensi*) is more social than other species of *Dipodomys*. These kangaroo rats inhabit burrows that are clustered in complexes; individuals use multiple entrances and sometimes share burrows with other adults (Brock and Kelt 2004).

Different patterns in use of burrows exhibited by species of kangaroo rats seem to reflect varied levels of sociality. However, environmental variables also may influence burrow-use behavior in *Dipodomys*. For example, in east-central California where differences in climate between summer and winter are substantial, kangaroo rats exhibited seasonal variation in patterns of use of burrows (Kenagy 1973). Chisel-toothed kangaroo rats (*Dipodomys microps*) and Merriam's kangaroo rats only used 1 burrow in winter where they constructed a nest, but used up to 3 different burrows during summer (Kenagy 1973). However, in the milder climate of southern California, *D. merriami* commonly used several different day burrows in winter (Behrends et al. 1986a). Different results from these studies suggest that patterns in use of burrows by *Dipodomys* are related to environmental variables. If season affects fidelity to burrows in kangaroo rats, then similar seasonal patterns of use of burrows should be expected in other species that construct relatively simple burrows in temperate environments, such as Ord's kangaroo rat (*Dipodomys ordii*).

Although Ord's kangaroo rat has the largest distribution of any species of *Dipodomys*, little is known about use of burrows by these animals. Burrows of Ord's kangaroo rats in Idaho were relatively simple in structure (Reynolds and Wakkinen 1987). In Utah, Langford (1983) observed that non-scrotal, male *D. ordii* maintained a main burrow and several subsidiary burrows in spring; however, use of burrows in other seasons was not studied. Further, limited information exists on sociality of *D. ordii*. Males seemed to inhabit burrows separately and may have even defended territories (Langford 1983), but whether these kangaroo rats maintained exclusive burrows in the breeding season, or changed patterns in use of burrows seasonally, was not investigated. Thus, the purpose of this research was to document patterns in use of burrows by a population of Ord's kangaroo rat in a temperate environment, the Sandhill Region of Nebraska. I investigated whether Ord's kangaroo rats exhibited different patterns in use of burrows in summer and winter and whether these individuals commonly shared or switched burrows during the summer breeding season.

Northern populations of *D. ordii* experience extremely different conditions from summer to winter and only breed during warmer parts of the year (Jones et al. 1983). In the Sandhill Region of Nebraska, Ord's kangaroo rats were active during winter (White and Geluso 2007), but nightly moves from burrow to burrow and maintenance of multiple burrows may be energetically costly in this season. Individuals were more consistent in initiation of aboveground activity in winter compared to summer (measured by activation of timers on the surface of the ground), suggesting that they were likely traveling from the same burrow each night in winter, while coming from different burrows in summer (White and Geluso 2007). Thus, it was predicted that Ord's kangaroo rats in the Sandhill Region of Nebraska would use multiple burrows in summer, but only 1 burrow in winter. Because previous observations of *D. ordii* indicated that these kangaroo rats were solitary (Langford 1983), it was expected that adults would not share day burrows, but instead would inhabit burrows alone.

MATERIALS AND METHODS

Study site--Research was conducted at Crescent Lake National Wildlife Refuge, Garden Co., Nebraska. This wildlife refuge is located in the Sandhill Prairie Region of Nebraska; a 4.8 million ha area of rolling sand dunes covered in grasses, forbs, and shrubs (Whitcomb 1989). Crescent Lake National Wildlife Refuge consists of 18,616 ha (Whitcomb 1989) located in the southwestern part of the Sandhill Region where many lakes are interspersed among the dunes. Habitats in this region are determined by soils, hydrology, terrain, and vegetation; the major habitat types on the refuge include choppy sands, sands, subirrigated meadows, and marshes. Ord's kangaroo rats were most abundant in choppy sands and sands, so research was conducted exclusively in these habitats. Choppy sands included areas of steeper dunes and sparse vegetative cover, whereas sands habitat consisted of more gradual dunes with greater cover. Conspicuous vegetation of choppy sands and sands habitats included sand bluestem (*Andropogon hallii*), sand muhly (*Muhlenbergia arenicola*), prairie sandreed (*Calamovilfa longifolia*), sand dropseed (*Sporobolus cryptanthus*), needle and thread grass (*Stipa comata*), sunflowers (*Helianthus*), blazing star (*Mentzelia*), sand cherry (*Prunus pumila*), and soapweed yucca (*Yucca glauca*). Soils of the region are composed of sand mixed with 1-4% silt and clay (Whitcomb 1989). Silt and clay impart more cohesion to the soil than pure sand. Cold winters (average minimum temperature for January = -12.8ºC), warm summers (average maximum temperature for July = 31.7ºC) and low humidity are typical in the Sandhill Region and nearly 80% of precipitation falls April-September (Wilhite and Hubbard 1989).

Study animals—Ord's kangaroo rats have the largest distribution of any heteromyid, ranging from central Mexico to southern Canada and from the Great Basin Desert to the Great Plains (Garrison and Best 1990; Schmidly et al. 1993). At the eastern edge of its range in the Sandhill Region of western and central Nebraska, *D. ordii* is the only species of kangaroo rat, and it is abundant (Jones et al. 1983). Other rodents associated with *D. ordii* in the Sandhill Region include the plains pocket mouse (*Perognathus flavescens*), North American deermouse (*Peromyscus maniculatus*), northern grasshopper mouse (*Onychomys leucogaster*), and plains harvest mouse (*Reithrodontomys montanus*).

Use of day burrows.—During 2 consecutive summers and winters (July-August 2006 and 2007; January 2007 and 2008), patterns in use of burrows by kangaroo rats were investigated using radiotelemetry. To determine number of day burrows (burrow that a kangaroo rat remained in during daytime) used by kangaroo rats, individuals were fitted with radiotransmitters and located during the day. Individuals were captured using Sherman live traps (7.6 x 8.9 x 22.9 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida) baited with rolled oats. Several cotton balls were placed in traps during winter. Upon capture, sex, age (adult, subadult, or juvenile), and reproductive condition (non-reproductive, estrous, pregnant, lactating, or post-lactating for females and scrotal or non-scrotal for males) of animals was assessed, and individuals were weighed. Kangaroo rats were fitted with radiotransmitters (model BD-2; Holohil Systems Ltd., Carp, Ontario, Canada) affixed to beaded-chain collars (Harker et al. 1999). Two sizes of radiotransmitters were used to ensure that radiocollars did not exceed 5% of the body weight of kangaroo rats; small models (1.25-g model BD-2) were affixed to individuals <60 g, whereas larger models (1.93-g model BD-2) were used only on individuals ≥60 g.

Two procedures were used for attaching radiocollars to kangaroo rats. The 1st method involved 2 people: 1 person secured the limbs and head of a kangaroo rat while another researcher attached the collar around the neck. This procedure always required 2 people and often took several attempts to determine the correct fit of the collar while the kangaroo rat struggled. Thus, another method of attachment was used, which could be performed by 1 individual and facilitated the attachment process of the collar. This method involved lightly sedating kangaroo rats with isoflurane (Abbott Laboratories, North Chicago, Illinois) until they were immobilized, during which time kangaroo rats could be manipulated to size and attach the collar. To sedate kangaroo rats, ca. 0.1 ml of isoflurane was applied to a cotton ball located in the plastic case of a small syringe. This case functioned as a nose cone to concentrate the anesthetic. The snout of the kangaroo rat was held in the nose cone for ca. 25 s until the animal did not respond to a pinch of the toe. When the animal was unresponsive, the collar was attached. Occasionally, animals awoke during the attachment process at which time they were briefly exposed to the anesthetic again or restrained by another researcher while the collar was attached. After collars were attached to animals that had been sedated, animals were placed back into Sherman live traps or into a large plastic container for ca. 30 min before they were released. Capture and handling procedures of animals in this study were approved by the Institutional Animal Care and Use Committee of Auburn University (IACUC 2003-0571) and followed guidelines of the American Society of Mammalogists (Gannon et al. 2007).

After kangaroo rats recovered from the anesthetic, they were released and tracked for 4-15 days following attachment of the radiotransmitter. Individuals were tracked to burrows during the day by walking concentric 5-m circles around the point of capture with a 3-prong antenna. After the position of the radiotransmitter was located, the entrance to the burrow was identified and marked with wire flags placed nearby. Numbers of burrows used by each individual were recorded and if individuals used multiple burrows, then distances between burrows were measured.

To retrieve radiocollars, either 5 or 10 Sherman live traps baited with rolled oats were set around currently occupied burrows of kangaroo rats. If no kangaroo rat with a radiocollar was captured on the 1st evening, traps were re-baited and set on following nights until individuals were captured. Upon capture of an individual with a radiocollar, the beaded chain was snipped with a pair of wire cutters and the radiocollar assembly was weighed. Collars were weighed after retrieval from kangaroo rats instead of before attachment because the correct size of beaded chain for each animal was determined during the attachment process. Mean weight of small radiotransmitters attached to beaded chains was 2.08 g (n = 17) and mean weight of large radiotransmitters was 2.83 g (n = 29). In addition, reproductive condition and weight of kangaroo rats were recorded. To determine whether radiocollars affected body condition of kangaroo rats, mass of kangaroo rats was compared before and after attachment of radiocollars using a paired *t*-test in SAS (SAS Institute, Inc., Cary, North Carolina). Also, necks of individuals were inspected for chaffing or sores caused by the collar. Some chaffing and sores were observed on the neck of kangaroo rats when collars were removed, even after only 4 days of wear. However, kangaroo rats did not lose mass while wearing radiocollars. Mass of male kangaroo rats was not significantly different before or after wearing radiocollars (paired *t*-test, $t = -1.92$, $P = 0.070$), but female kangaroo rats gained a significant amount of weight while wearing collars (paired *t*-test, $t = -2.90$, $P = 0.008$). Gain in mass by female kangaroo rats likely was influenced by reproductive condition as several kangaroo rats appeared pregnant during removal of collars.

Burrow sharing and switching.—To estimate population density of Ord's kangaroo rats at the study site during summer 2006 and 2007, and to determine whether individuals shared or switched burrows, kangaroo rats that lived in proximity to each other were captured and radiocollared. In both years, a trapping grid was set over 1 ha in choppy sandhills using 100 Sherman live traps with 10-m spacing between traps. Trapping grids were set in different areas in 2006 and 2007 so data would not be gathered on the same individuals. The closest points of these trapping grids were 200 m apart. For both years, traps were checked for 3 consecutive nights; sex, age, and reproductive condition were assessed upon capture, and animals were weighed and marked with numbered ear tags (Monel 1005-1; National Band and Tag Company, Newport, Kentucky). Following the 3rd night of trapping, radiocollars were attached to individuals and they were released at points of capture. These animals were tracked for 7-13 nights, after which, traps were deployed as above to retrieve radiocollars. Number of burrows used by each individual was recorded as well as frequency of burrows that were occupied by 2 kangaroo rats at the same time (sharing burrows) or burrows that were used by 2 individuals at different times (switching burrows). In addition, distances between burrows used by the same individual were measured.

Statistical analyses.—Because it was of interest whether individuals were using the same burrow each night over a short period of time in summer and winter, each individual was categorized as using 1 burrow or >1 burrow. Then proportions of kangaroo rats that used only 1 burrow were compared to those that used >1 burrow between seasons with a Chi-Squared test of independence. To determine whether differences in use of 1 burrow vs. >1 burrow existed for males and females for each season, the Fisher exact test was employed. The Fisher exact test also was used to investigate differences between numbers of burrows used by males and females in summer. This test was used instead of Chi-Squared tests because some expected values were <5. This situation compromises the validity of the Chi-Squared test but does not affect the Fisher exact test (Gould and Gould 2002). To determine if distances between burrows were significantly different between males and females that used >1 burrow, a 2-

factor analysis of variance (ANOVA) with sex of kangaroo rats and year as factors was used. Finally, the Jolly-Seber Method was used to obtain an estimate of population density of kangaroo rats at the study site during summer 2006 and 2007 (Krebs 1989). All statistical analyses except the Jolly-Seber method were conducted using SAS (SAS 9.1, SAS Institute, Inc., Cary, North Carolina) with significance set at $P < 0.05$.

RESULTS

Seasonal use of day burrows.—Over 2 consecutive summers and winters, 69 adult kangaroo rats were radiocollared including 37 females and 32 males (Appendix 3). Of these individuals, 4 kangaroo rats were never recaptured, 2 died shortly after attachment of the collar, and 3 were collared with radiotransmitters that failed shortly after attachment. After eliminating these individuals, 60 different kangaroo rats were radiocollared, tracked for ≥4 days, and recaptured, including 42 in summer (23 in 2006 and 19 in 2007) and 18 in winter (15 in 2007 and 3 in 2008).

Proportions of kangaroo rats that used >1 burrow versus a single burrow were not different in each year for both seasons for males (Fisher exact test: summer 2006 vs. 2007, $P = 0.363$; winter 2007 vs. 2008, $P = 0.250$) or females (Fisher exact test: summer 2006 vs. 2007, $P = 0.180$; winter 2007 vs. 2008, $P = 0.622$). Proportions also were not different between males and females for each season (Fisher exact test: summer, $P = 0.140$; winter, $P = 0.412$); thus, data were combined. The proportion of kangaroo rats that used multiple burrows during 4 consecutive days was significantly greater in summer than winter (Chi-Squared test, $\chi^2 = 7.02$, $d.f. = 1$, $P = 0.008$), as 60% of kangaroo rats used >1 burrow in summer, but only 22% used >1 burrow in winter (Fig. 1).

Of the 42 adult kangaroo rats that were radiotracked during summer, 1 was killed by a barn owl (*Tyto alba*) during the 5th night of the tracking period. However, the other 41 kangaroo rats (24 females and 17 males) were tracked and located in their burrows each day for ≥7 days. Both males and females commonly used multiple burrows during 7 days in summer (65% of males and 79% of females), and proportions of individuals using 1 burrow vs. >1 burrow did not differ between sexes for either year (Fisher exact test: 2006, $P = 0.211$; 2007, $P = 0.397$). However, when examining number of burrows used by each sex, females used significantly more burrows than males in summer 2006 (Fisher exact test, $P = 0.002$), but not in summer 2007 (Fisher exact test, $P = 0.147$; Fig. 2.). Interestingly, kangaroo rats that used the greatest number of burrows (5 individuals that used 4 burrows during 7 nights) were all lactating or recently post-lactating females (Appendix 3).

For adult kangaroo rats that used multiple burrows during 7 nights in summer, distances among burrows varied within sexes for both years (Table 1). Inter-burrow distances were not significantly different between males or females (2-factor ANOVA, $F = 1.94$, *d.f.* = 1, $P = 0.175$) or between years in summer (2-factor ANOVA, $F = 0.31$, *d.f.* = 1, $P = 0.582$). Only 4 kangaroo rats used multiple burrows in winter and mean distance among these burrows was shorter than in summer (12.0 m in winter versus 29.7 m in summer).

Sharing and switching of burrows.—Numbers of Ord's kangaroo rats captured and population estimates derived from these captures were similar in summer 2006 and 2007 (Table 2). Other rodents captured on grids in both years were North American deermice (*Peromyscus maniculatus*) and plains pocket mice (*Perognathus flavescens*).

Eleven adult kangaroo rats in summer 2006 and 9 adults in summer 2007 captured on trapping grids were radiocollared and tracked for ≥7 days. Radiocollared kangaroo rats represented 69% (11 of 16) of the population on the grid in 2006, and 75% (9 of 12) in 2007. Radiotelemetry resulted in 155 radiolocations for these 20 kangaroo rats. Of these radiolocations, only on 1 occasion were 2 kangaroo rats sharing the same burrow.

On 24 July 2007, a post-lactating adult female was in a burrow with a scrotal male. She occupied a different burrow for the previous 6 days, which was 88 m away from the male's burrow. The night after sharing this burrow with the male, she occupied a 3rd burrow that was 24 m from the 1st burrow she occupied and 104 m from the male's burrow. The male occupied his burrow for 7 consecutive days (the 7th day he shared it with the female), moved to a new burrow for 1 day, and moved back to his original burrow for 2 more days. Except for this instance, no radiocollared kangaroo rat used the same burrow at the same time (sharing) or at different times (switching) during tracking periods.

DISCUSSION

Ord's kangaroo rats in the Sandhill Region of Nebraska varied their use of burrows seasonally. As predicted, individuals typically used multiple burrows in summer but only 1 burrow in winter. Similar patterns were reported for *D. microps* and *D. merriami* in a region with extreme climatic differences between summer and winter (Kenagy 1973). This behavior may have important consequences for survival in temperate environments where seasonal fluctuations in climate are extreme.

Seasonal use of burrows.—During winter sessions in the Sandhill Region, kangaroo rats were observed on the surface at temperatures as low as -14.6°C (Appendix 1) with >90% of the ground covered in snow. However, initial trapping attempts during winter resulted in few captures of kangaroo rats. Placement of traps probably affected capture success because foraging runs where kangaroo rats concentrated travel were covered in snow. Thus, traps were placed haphazardly on snow and captures were few although tracks of kangaroo rats were common in snow. However, after entrances to burrows were observed (some of which penetrated through >30 cm of snow) and traps were concentrated near these entrances, capture success improved. Despite initial nights of low capture success, aboveground activity was observed in kangaroo rats almost every night during winter periods, similar to observations by White and Geluso (2007).

Most kangaroo rats only used 1 burrow in winter, and for the few individuals that used multiple burrows in this season, distances among burrows were short. Use of only 1 burrow likely reduces costs associated with maintenance of multiple burrows and travel among burrows. Patterns in use of burrows also might be related to other behaviors, such as food hoarding (Chapter 2). If individuals remain in 1 burrow during winter, then storing seeds in this burrow would give individuals convenient access to resources. However, if individuals leave a burrow with food unoccupied, then this unprotected store of seeds is susceptible to pilferers (Vander Wall et al. 2005). In winter, loss of a larder of seeds could result in death if kangaroo rats are unable to forage on the surface. Although a cessation of aboveground activity was not observed in this study, some populations of Ord's kangaroo rats, as well as populations of other species of *Dipodomys*, limit or cease activity on the surface during cold and snowy conditions (e.g., Gummer 1997;

Holdenried 1957; O'Farrell 1974). In fact, in southern Canada, Ord's kangaroo rats were not active on the surface during heavy snow cover, but remained in burrows and periodically used facultative torpor (Gummer 1997). In addition to caching seeds in burrows for use in winter, Ord's kangaroo rats are capable of using torpor to survive harsh winter conditions; however, this behavior might be restricted to northern Ord's kangaroo rats that are isolated from other populations (Gummer 1997).

In summer, both male and female kangaroo rats commonly used >1 burrow, several of which were >50 m apart (Appendix 4). Although size of home range was not determined in this study, mean distances among burrows were over twice as far in summer (29.6 m) compared to winter (12.0 m). Use of multiple burrows in this population of kangaroo rats might be a response to increased movement and size of home range during the breeding season. Other kangaroo rats move greater distances in breeding seasons including *D. merriami* (Behrends et al. 1986b) and male *D. ingens* (Cooper and Randall 2007). In the Sandhill Region of Nebraska, Ord's kangaroo rats breed April-September (Jones 1964). Additionally, *D. ordii* begins surface activity earlier in relationship to full darkness in summer compared to winter in the Sandhill Region, which likely benefits reproduction (White and Geluso 2007). If Ord's kangaroo rats are spending more time on the surface and traveling greater distances during the summer breeding season, then use of multiple burrows as a refuge from predators would be advantageous as more mobile kangaroo rats are at greater risk from predators (Daly et al. 1990).

Besides using burrows to escape predators on the surface, animals may frequently change burrows to reduce scent that might attract predators to a commonly used burrow

(Behrends et al. 1986a); however, this has not been tested directly. Alternatively, studies have suggested that mammals may commonly change burrows or nest chambers to avoid infestations of ectoparasites that inhabit their burrows (Behrends et al. 1986a; Peinke and Brown 2005; Roper et al. 2002). For example, Brant's whistling rats (*Paratomys brantsii*) changed nesting chambers less frequently after ectoparasites were removed from their bodies (Roper et al. 2002). Both risk of predators and risk of infestations of parasites may contribute to use of multiple burrows in summer by Ord's kangaroo rats.

Although both male and female Ord's kangaroo rats commonly used multiple burrows in summer, females tended to use more burrows than males, especially in 2006 when differences were statistically significant. Surprisingly, kangaroo rats that switched burrows most often were either lactating or recently post-lactating females. Several nursing females switched burrows on most nights in 2006 (4 different burrows during 7 days); thus, these mothers must have moved young to new burrows or left them in an unattended burrow. To attempt to determine if lactating females moved young, 2 lactating females were recorded using night-vision video cameras as they emerged from burrows in summer 2007. Both of these lactating kangaroo rats only used 2 burrows during 7 nights and during nights of recording, juvenile kangaroo rats were never observed leaving burrows on their own or with the aid of females. However, burrows were only recorded for ca. 2 h following sunset and movements could have been missed.

Similar to observations of *D. ordii* in this study, female *D. ingens* also used more burrows than males in the breeding season (Cooper and Randall 2007) and female *D. merriami* switched burrows while lactating (Behrends et al. 1986a). Despite these observations, reasons that nursing kangaroo rats commonly switch burrows are unclear.

Leaving young unattended has been observed in lagomorphs (e.g., Stoddart 1984; Vorhies and Taylor 1933) and was suggested as a possible strategy to reduce risk of predation (Stoddart 1984). A species of jackrabbit may even separate young into different locations and only visit them at night to nurse (Vorhies and Taylor 1933). To my knowledge this behavior has not been observed in solitary rodents.

One reason that lactating kangaroo rats might use multiple burrows is to provide burrows for their young. Kangaroo rats have small litters compared to many rodents of comparable size (Eisenberg 1963, 1993). For example, average litter size of Ord's kangaroo rats in Nebraska is 3 (Jones 1964). Interestingly, 3 lactating kangaroo rats that used 4 burrows during 7 nights in summer 2006 and 1 lactating female that used 6 burrows during 10 nights in summer 2007 (Appendix 3), were not lactating upon recapture to retrieve radiocollars. Furthermore, 2 females that were post-lactating used 4 burrows during 7 nights in summer 2006. These data suggest that females used multiple burrows at the end of lactation, when weaning of juveniles was occurring. In addition, a juvenile kangaroo rat was captured in a trap near another trap with an adult female that had used multiple burrows. When released, the juvenile entered a burrow some distance away that was used by the adult female on a previous day.

Although acquisition of burrows by young kangaroo rats is not well understood (Eisenberg 1993), juvenile kangaroo rats typically do not disperse far from their natal home range (Jones 1993). In fact, some evidence suggests that young kangaroo rats may inherit burrows from their mothers. For banner-tailed kangaroo rats that occupy large mounds, some juveniles remained in their natal burrow after their mothers abandoned it (Jones 1986). Acquiring their mother's burrow resulted in greater survival to reproductive age than juveniles that successfully dispersed (Jones 1986). Movement and use of burrows of female Ord's kangaroo rats and dispersal and establishment of burrows by juveniles requires further study to determine if similar patterns exist in this species.

Solitary behavior.—Ord's kangaroo rats do not share burrows during the breeding season in the Sandhill Region of Nebraska. Twenty different individuals that lived in proximity to each other were tracked and only on 1 occasion were 2 individuals in the same burrow. In this case, a post-lactating female was in a burrow with a scrotal male for 1 night. Additionally, kangaroo rats never used burrows that had been occupied by other individuals on previous nights. Population estimates were similar in each year during the 2-year study (16/ha in 2006 and 12/ha in 2007), but were low compared to a previous year (2005) in the Sandhill Region (Appendix 2). During summer 2005, the population estimate on the same hectare as that in 2006 was 33 kangaroo rats. No apparent reason for the population decline between 2005 and 2006 was determined, but the frequency of sharing burrows might increase during higher populations. This is doubtful however, because burrows do not appear to be a limiting resource in this region. Thus, *D. ordii* inhabits burrows alone, which is consistent with observations by Langford (1983), and similar to other species of *Dipodomys* (Jones 1993; Kenagy 1973; Randall 1993), except *D. stephensi* (Brock and Kelt 2004).

LITERATURE CITED

Behrends, P., M. Daly, and M. I. Wilson. 1986a. Range use patterns and spatial relationships of Merriam's kangaroo rats (*Dipodomys merriami*). Behaviour 96:187-209.

Behrends, P., M. Daly, and M. I. Wilson. 1986b. Aboveground activity of Merriam's kangaroo rats (*Dipodomys merriami*) in relation to sex and reproduction. Behaviour 96:210-226.

Best, T. L. 1972. Mound development by a pioneer population of the banner-tailed kangaroo rat, Dipodomys spectabilis baileyi Goldman, in eastern New Mexico. The American Midland Naturalist 87:201-206.

Bienek, G. K., and A. W. Grundmann. 1971. Burrowing habits of two subspecies of *Dipodomys merriami* in California and Utah. Great Basin Naturalist 31:190-192.

Braun, S. E. 1985. Home range and activity patterns of the giant kangaroo rat, *Dipodomys ingens*. Journal of Mammalogy 66:1-12.

Brock, R. E., and D. A. Kelt. 2004. Conservation and social structure of Stephens' kangaroo rat: implications from burrow-use behavior. Journal of Mammalogy 85:51-57.

Cooper, L. D., and J. A. Randall. 2007. Seasonal changes in home ranges of the giant kangaroo rat (*Dipodomys ingens*): a study of flexible social structure. Journal of Mammalogy 88:1000-1008.

Daly M., M. Wilson, P. R. Behrends, and L. F. Jacobs. 1990. Characteristics of kangaroo rats, *Dipodomys merriami*, associated with differential predation risk. Animal Behaviour 40:380-389.

Eisenberg, J. F. 1963. The behavior of heteromyid rodents. University of California Publications in Zoology 69:1-100.

Eisenberg, J. F. 1993. Ontogeny. Pp. 479-490 in Biology of the Heteromyidae (H. H. Genoways and J. H. Brown, eds.). Special Publication, The American Society of Mammalogists 10:1-719.

Gannon, W. L., R. S. Sikes, and the Animal Care and Use Committee of the American Society of Mammalogists. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammology 88:809-823.

Garrison, T. E., and T. L. Best. 1990. Dipodomys ordii. Mammalian Species 353:1-10.

Gould, J. L., and G. F. Gould. 2002. Biostats basics: a student handbook. W. H. Freeman and Company, New York.

Gummer, D. L. 1997. Effects of latitude and long-term isolation on the ecology of northern Ord's kangaroo rats (*Dipodomys ordii*). M.S. thesis, University of Calgary, Alberta, Canada.

Harker, M. B., G. B. Rathbun, and C. A. Langtimm. 1999. Beaded-chain collars: a new method to radiotag kangaroo rats for short-term studies. Wildlife Society Bulletin 27:314-317.

Holdenried, R. 1957. Natural history of the bannertail kangaroo rat in New Mexico. Journal of Mammalogy 38:330-350.

Jones, J. K., Jr. 1964. Distribution and taxonomy of mammals of Nebraska. University of Kansas Press, Lawrence.

Jones, J. K., Jr., D. M. Armstrong, R. S. Hoffmann, and C. Jones. 1983. Mammals of the northern Great Plains. University of Nebraska Press, Lincoln.

Jones, W. T. 1986. Survivorship in philopatric and dispersing kangaroo rats (*Dipodomys spectabilis*). Ecology 67:202-207.

Jones, W. T. 1993. The social systems of heteromyid rodents. Pp. 575-595 in Biology of the Heteromyidae (H. H. Genoways and J. H. Brown, eds.). Special Publication, The American Society of Mammalogists 10:1-719.

Jones, W. T., P. M. Waser, L. F. Elliott, N. E. Link, and B. B. Bush. 1988. Philopatry, dispersal, and habitat saturation in the banner-tailed kangaroo rat, *Dipodomys spectabilis*. Ecology 69:1466-1473.

Kenagy, G. J. 1973. Daily and seasonal patterns of activity and energetics in a heteromyid rodent community. Ecology 54:1201-1219.

Kenagy, G. J. 1976. The periodicity of daily activity and its seasonal changes in free-ranging and captive kangaroo rats. Oecologia (Berlin) 24:105-140.

Kinlaw, A. 1999. A review of burrowing by semi-fossorial vertebrates in arid environments. Journal of Arid Environments 41:127-145.

Krebs, C. J. 1989. Ecological methodology. Harper and Row Publishers, New York.

Langford, A. L. 1983. Pattern of nocturnal activity of male *Dipodomys ordii* (Heteromyidae). The Southwestern Naturalist 28:341-346.

Martin, R. E., R. H. Pine, and A. F. Deblase. 2001. A manual of mammalogy: with keys to families of the world. Third Edition. McGraw-Hill Publishers, New York.

O'Farrell, M. J. 1974. Seasonal activity patterns of rodents in a sagebrush community. Journal of Mammalogy 55:809-823.

Peinke, D. M., and C. R. Brown. 2005. Burrow utilization by springhares (*Pedetes capensis*) in the Eastern Cape, South Africa. African Zoology 40:37-44.

Randall, J. A. 1984. Territorial defense and advertisement by footdrumming in bannertail kangaroo rats (*Dipodomys spectabilis*) at high and low population densities. Behavioral Ecology and Sociobiology 16:11-20.

Randall, J. A. 1993. Behavioural adaptations of desert rodents (Heteromyidae). Animal Behaviour 45:263-287.

Reichman, O. J., and S. C. Smith. 1987. Burrows and burrowing behavior by mammals. Current Mammalogy 2:197-244.

Reynolds, H. G. 1958. The ecology of the Merriam kangaroo rat (*Dipodomys merriami* Mearns) on the grazing lands of southern Arizona. Ecological Monographs 28:111-127.

Reynolds, T. D., and W. L. Wakkinen. 1987. Characteristics of the burrows of four species of rodents in undisturbed soils in southeastern Idaho. The American Midland Naturalist 118:245-250.

Roper, T. J., T. P. Jackson, L. Conradt, and N. C. Bennett. 2002. Burrow use and the influence of ectoparasites in Brant's whistling rat (*Parotomy brantsii*). Ethology 108:557-564.

Schmidly, D. J., K. T. Wilkins, and J. N. Derr. 1993. Biogeography. Pp. 319-356 in Biology of the Heteromyidae (H. H. Genoways and J. H. Brown, eds.). Special Publication, The American Society of Mammalogists 10:1-719.

Schroder, G. D. 1979. Foraging behavior and home range utilization of the bannertail kangaroo rat (*Dipodomys spectabilis*). Ecology 60:657-665.

Stoddart, L. C. 1984. Site fidelity and grouping of neonatal jack rabbits, *Lepus californicus*. Journal of Mammalogy 65:136-137.

Vander Wall, S. B., E. C. H. Hager, and K. M. Kuhn. 2005. Pilfering of stored seeds and the relative costs of scatter-hoarding versus larder-hoarding in yellow pine chipmunks. Western North American Naturalist 65:248-257.

Vorhies, C. T., and W. P. Taylor. 1922. Life history of the kangaroo rat *Dipodomys spectabilis* Merriam. United States Department of Agriculture Bulletin 1091:1-40.

Vorhies, C. T., and W. P. Taylor. 1933. The life histories and ecology of jack rabbits, *Lepus alleni* and *Lepus californicus* ssp., in relation to grazing in Arizona. University of Arizona, College of Agriculture, Agricultural Experiment Station Technical Bulletin 49:471-587.

Whitcomb, R. F. 1989. Nebraska sand hills: the last prairie. Proceedings of the North American Prairie Conference 11:57-69.

White, J. A., and K. Geluso. 2007. Seasonal differences in onset of surface activity of Ord's kangaroo rat (*Dipodomys ordii*). Journal of Mammalogy 88:234-240.

Wilhite, D. A., and K. G. Hubbard. 1989. Climate. Pp. 17-28 in An atlas of the Sand Hills (A. Bleed and C. Flowerday, eds.). University of Nebraska-Lincoln: Conservation and Survey Division at the Institute of Agriculture and Natural Resources 5a:1-265.

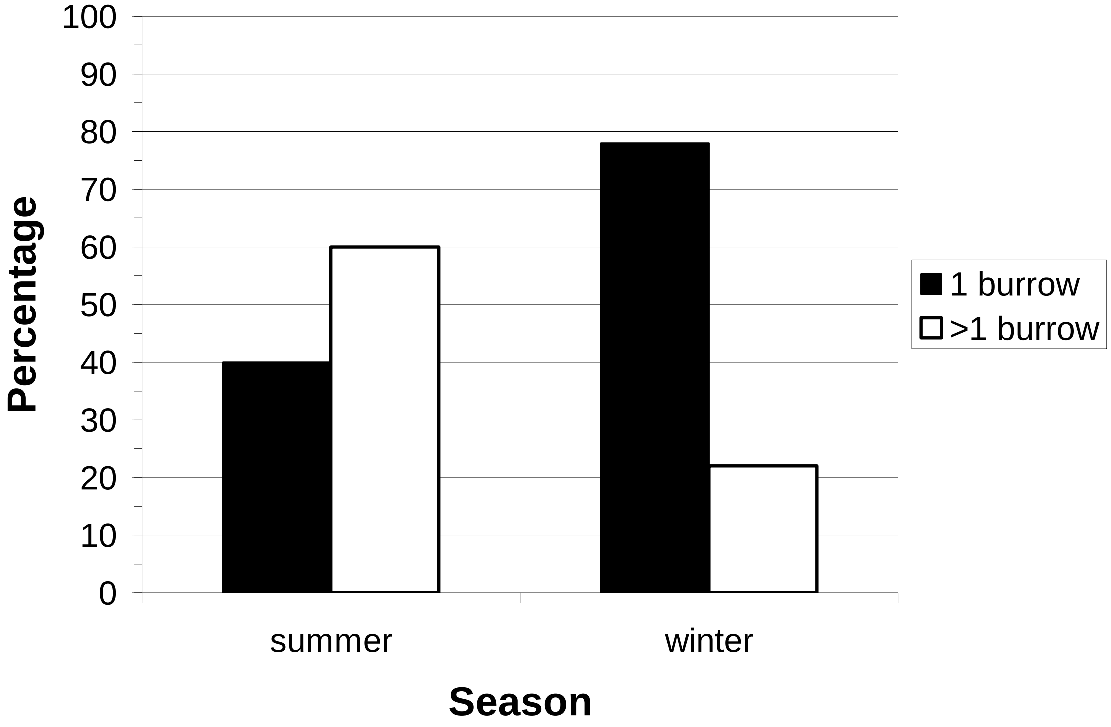

Fig. 1. Percentage of Ord's kangaroo rats (*Dipodomys ordii*) that used 1 burrow or >1 burrow during 4 nights in 2 consecutive summers (July-August 2006 and 2007) and winters (January 2007 and 2008) in the Sandhill Region of Nebraska. Individuals that used >1 burrow either used 2 or 3 burrows during the 4-night tracking period.

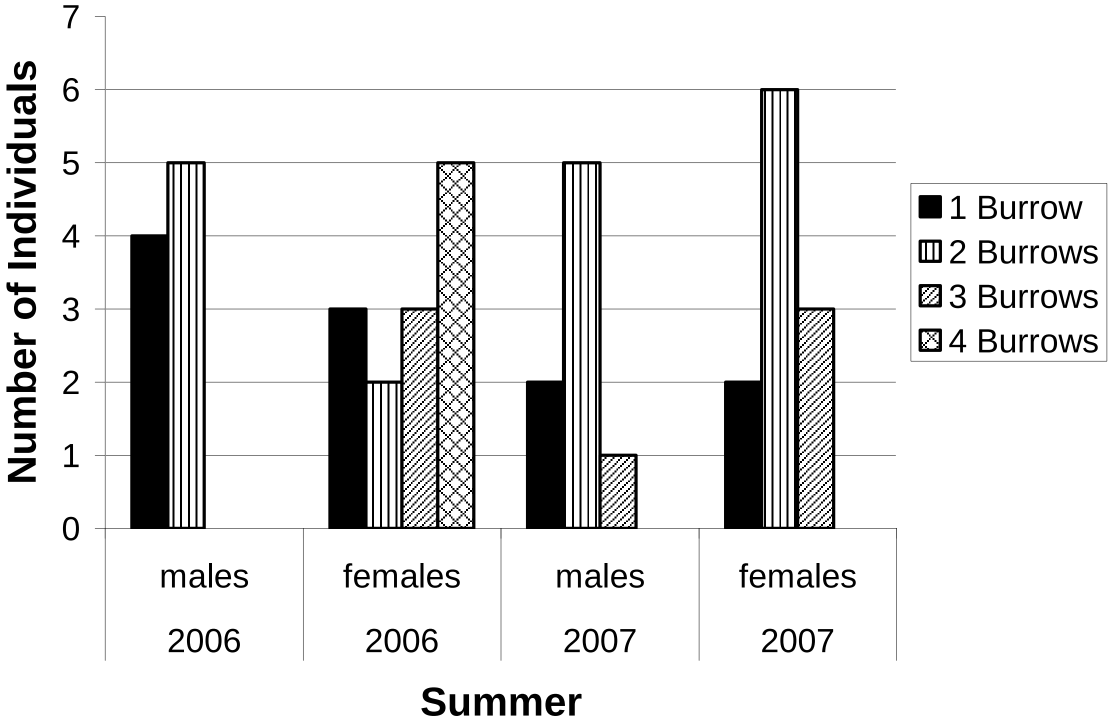

Fig. 2. Number of adult male and female Ord's kangaroo rats (*Dipodomys ordii*) that used 1-4 burrows during 7 nights in the Sandhill Region of Nebraska in summer 2006 and 2007.

Table 1. Distances between burrows of adult Ord's kangaroo rats (*Dipodomys ordii*) that used >1 burrow in summer 2006 and 2007 in the Sandhill Region of Nebraska.

		Distances between burrows (m)			
Year	Sex (*n*)	Mean	*SD*	Min	Max
2006	♀ (10)	26.24	12.65	12.22	52.30
2006	♂ (5)	26.31	19.43	11.05	60.20
2007	♀ (9)	42.19	32.59	12.20	103.53
2007	♂ (6)	19.44	9.76	12.50	38.55
Total	30	29.68	22.08	11.05	103.53

Table 2. Numbers of Ord's kangaroo rats (*Dipodomys ordii*) captured and marked during 3 consecutive nights on 1-ha grids consisting of 100 Sherman live traps spaced 10 m apart in summer 2006 and 2007 in the Sandhill Region of Nebraska. Also reported are estimates of population density for each year using the Jolly-Seber method.

	Numbers of kangaroo rats captured and marked			Estimate of population density (number/ha)
Year	Adults	Subadults	Juveniles	
2006	17	1	2	16
2007	18	0	0	12

CHAPTER 2.

SEASONAL DIFFERENCES IN METHOD OF FOOD HOARDING BY ORD'S KANGAROO RAT (*DIPODOMYS ORDII*) IN THE NORTHERN GREAT PLAINS

ABSTRACT

Method of food storage is a flexible behavior for many food hoarders. Several species of granivorous rodents switch from larderhoarding (concentrating food in a central location) to scatterhoarding (storing food in small, separate, subsurface caches) in response to various factors. However, no study has addressed whether seasonal differences in food-hoarding behavior exist for a rodent that forages year-round in a temperate environment. Thus, objectives of this study were to determine the method of seed storage and placement of caches for Ord's kangaroo rat (*Dipodomys ordii*) in summer and winter in the Sandhill Region of Nebraska. Seeds of soapweed yucca (*Yucca glauca*) covered with powdered fluorescent pigments were used to track individuals to seed caches during 2 consecutive summers and winters. A striking seasonal shift in food-hoarding strategy was observed as Ord's kangaroo rats almost exclusively larderhoarded seeds within burrows in winter, but primarily scatterhoarded seeds in shallow caches in summer. Low nighttime temperatures and snow were common during winter caching trials, so convenient access to food and lack of suitable sites to scatterhoard are likely reasons for larderhoarding in winter. Whereas, spreading

out resources into multiple caches to protect against complete loss of a larderhoard might explain scatterhoarding behavior in summer. Placement of caches was most consistent with the rapid-sequestering hypothesis in summer as caches were clumped near the seed source instead of placed near burrows or widely scattered throughout the home range of individuals. Observations of multiple kangaroo rats at many seed sources in summer suggest that competition for resources is prevalent; thus, rapid depletion of a rich seed source might drive patterns of cache placement in this season.

INTRODUCTION

Food hoarding is a common behavior that allows the hoarder to have some control over food resources in its environment (Gerber et al. 2004; Vander Wall 1990). Distribution of food stored by animals represents a continuous spectrum that ranges from larderhoarding—concentrating resources by making repeated deposits of food in a centralized location such as a burrow, to scatterhoarding—storing food in small, scattered, subsurface caches dispersed throughout an individual's home range (Vander Wall 1990). Throughout this spectrum of cache placement are several distinct patterns including: 1) larderhoarding in 1 location (e.g., a burrow), 2) concentrating scatterhoards in a defensible area such as near a burrow entrance, 3) clustering scatterhoards near a food source, and 4) widely spacing scatterhoards throughout the home range (Jenkins et al. 1995). Although most food-hoarding animals are categorized as either larderhoarders or scatterhoarders, several species of rodents use a combination of these caching strategies (e.g., Clarke and Kramer 1994b; Devenport et al. 2000; Hurly and Robertson

1990; Jenkins and Breck 1998; Price et al. 2000; Shaffer 1980; Vander Wall et al. 2001; Yahner 1975).

Each caching strategy has unique costs and benefits for the hoarder, and several competing hypotheses have been presented to identify the optimal placement of caches in different situations. The larder-defensibility hypothesis predicts that larderhoarding is beneficial for individuals that can protect their stored resources from pilferers (Vander Wall et al. 2005). Concentrating resources in 1 location facilitates aggressive defense of stored items (Dally et al. 2006) and provides convenient access to resources (Jenkins and Peters 1992). Protecting these resources is important however, because unguarded larders are more susceptible to pilferage than scatterhoards of native seeds (Vander Wall et al. 2005). Similar costs and benefits result from scatterhoarding items near a burrow entrance. These caches can be protected more easily than caches distant from the burrow, but hoarders risk losing all of their resources if these clustered caches are pilfered. Thus, individuals that are not able to protect a concentrated store of food may benefit from distributing food into inconspicuous scatterhoards away from the burrow. This behavior protects against complete loss of stored food because resources are spaced out into many different caches (Smith and Reichman 1984). Although scatterhoards distant from the burrow typically are not defended by the hoarder, this method involves more energy and exposure while caching and retrieving seeds (Jenkins and Peters 1992).

Placement of scatterhoards away from the burrow also presents a behavioral challenge. The cache-spacing hypothesis predicts that scatterhoarders should space caches widely throughout their home range. Because animals often demonstrate area-localized searches once a food item is discovered, widely spaced caches are safer from pilferage than highly clumped caches (Clarkson et al. 1986; Daly et al. 1992; Leaver 2004; Stapanian and Smith 1978). However, it may take time to select the desired caching sites, and for individuals that risk losing access to a rich food source, this strategy may be costly. Alternatively, the rapid-sequestering hypothesis predicts that scatterhoarders should cache food in a clumped distribution near the food source (Jenkins and Peters 1992; Jenkins et al. 1995). This strategy will potentially result in higher loss from conspecifics and other pilferers who demonstrate area-localized searches, but animals may deplete a food source more rapidly thereby making food unavailable to non-digging competitors such as ants (Jenkins and Peters 1992).

For species that use a combination of caching strategies, several factors are important in switching from 1 strategy to another. Age may be an important determinant as subordinate individuals of some species hoard food differently than dominant individuals. For example, juvenile eastern chipmunks (*Tamias striatus*) scatterhoard more often than adults, presumably because they cannot adequately defend a larderhoard (Clarke and Kramer 1994b). As juveniles grow older, they larderhoard food in their burrow more often and scatterhoard less frequently. Reproductive condition is another important factor in eastern chipmunks; females with young scatterhoard food more often than other females or males. Scatterhoarding by females with young may reduce the possibility that all hoarded food is consumed by young (Clarke and Kramer 1994b). Besides age and reproductive condition, other factors effect the distribution of stored food by some species. Value of food influences caching behavior of Merriam’s kangaroo rats (*Dipodomys merriami*; Leaver 2004; Leaver and Daly 1998). In addition, pilferage of scattered caches induces a switch from scatterhoarding to larderhoarding in kangaroo rats (Preston and Jacobs 2001). Similarly, composition of the competitive environment influences the distribution of stored food. Merriam's kangaroo rats in an environment consisting of mostly conspecific competitors scatterhoarded more commonly than individuals in an environment of mainly heterospecific competitors (Murray et al. 2006). Distance from where food is discovered to a burrow also seems important as a species of kangaroo rat (*D. merriami*) and gerbil (*Gerbillus allenbyi*) switched from larderhoarding to scatterhoarding when food was encountered far away from their home burrow and travel costs to the burrow were higher (Daly et al. 1992; Tsurim and Abramsky 2004).

These studies provide insight into the dynamic nature of food hoarding; however, other factors also might induce changes in food-hoarding patterns. For example, no study has directly investigated the influence of season on caching behavior of a hoarder that forages throughout the year. Vander Wall et al. (2005) noted that yellow pine chipmunks (*Tamias ameonus*) scatterhoarded exclusively in summer in Nevada, but transferred contents of these caches to a larder in late autumn to prepare for winter. Similarly, Elliott (1978) observed eastern chipmunks commonly scatterhoarding in summer and mainly larderhoarding in autumn as they prepared for winter in the Adirondack Mountains. Both of these species of chipmunks use food stores within burrows as an energy source during hibernation (Elliott 1978; Vander Wall et al. 2005) as yellow pine chipmunks do not forage in winter (Vander Wall et al. 2005) and eastern chipmunks rarely do so (Elliott 1978). Similarly, species of rodents that commonly forage aboveground in winter also might switch their preferred method and placement of food caches seasonally. Thus, in the present study, I investigated whether Ord's kangaroo rats (*Dipodomys ordii*) dispersed cached food differently in summer and winter in a temperate grassland environment, the Sandhill Region of Nebraska.

Conditions in the Sandhill Region provided an excellent situation to investigate seasonal variation in caching behavior. Climate is drastically different in summer and winter in this area. Summers are warm and winters are cold with snow, yet Ord's kangaroo rats are still active in winter in the Sandhill Region (White and Geluso 2007). In addition, both larderhoarding and scatterhoarding have been observed in this population of kangaroo rats (pers. obs.). Finally, *D. ordii* is abundant and it is the only species of kangaroo rat in the region (Jones et al. 1983). Thus, food-hoarding behavior was not confounded by presence of other species of kangaroo rats (Murray et al. 2006). Other granivorous rodents that are known to cache seeds, including North American deermice (*Peromyscus maniculatus*; Vander Wall et al. 2001) and plains pocket mice (*Perognathus flavescens*), occur in the Sandhill Region. However, these rodents were less common than kangaroo rats where the study was conducted (Appendix 2), so it was unlikely that they had a major influence on caching behavior of *D. ordii*.

Because conserving energy is paramount to surviving difficult winter conditions in temperate environments (Gummer 1997), convenient access to food resources in a burrow is desirable. Also, Ord's kangaroo rats typically return to the same burrow night after night in winter in the Sandhill Region (Chapter 1). For these reasons, it was expected that individuals would mainly larderhoard seeds within burrows in winter. However in summer, when kangaroo rats are breeding, scatterhoarding might be the preferred strategy. Kangaroo rats pilfer seeds from each other (Daly et al. 1992; Murray et al. 2006), and Ord's kangaroo rats in the Sandhill Region commonly use >1 burrow during summer (Chapter 1). Adequate defense of a large store of seeds in a burrow in this environment seems unlikely. Although some seeds were in burrows of kangaroo rats in summer in the Sandhill Region (Chapter 4), quantities were small compared to larders constructed by other kangaroo rats (e.g., *Dipodomys venustus*, Hawbecker 1940; *Dipdomys ingens*, Shaw 1934; *Dipodomys spectabilis*, Vorhies and Taylor 1922). Thus, I predicted that a shift in caching strategy would occur between seasons and that individuals would preferentially distribute seeds into inconspicuous scatterhoards in summer.

If scatterhoarding occurred in this population in summer, then 3 potential patterns of cache placement were likely. Caches might be concentrated near burrows, widely spaced throughout the home range of individuals, or clumped near the seed source. Although some species of kangaroo rats cluster caches near burrow entrances (Hawbecker 1940; Shaw 1934), it was expected that Ord's kangaroo rats would not use this strategy because individuals commonly switch burrows in summer in the Sandhill Region, which would leave these concentrated resources vulnerable to pilferage. Merriam's kangaroo rats initially placed caches near seed sources, consistent with the rapid-sequestering hypothesis and then repositioned caches so they were more widely spaced in laboratory arenas (Jenkins and Peters 1992; Jenkins et al. 1995). Based on similar use of burrows by *D. merriami* (Behrends et al. 1986) and *D. ordii* (Chapter 1), I predicted that Ord's kangaroo rats also would initially disperse caches according to the rapid-sequestering hypothesis. That is, caches would be clumped near the source of seeds instead of clumped near burrows or widely scattered throughout the home range of an individual.

MATERIALS AND METHODS

This study was conducted at Crescent Lake National Wildlife Refuge in Garden County, Nebraska. Crescent Lake NWR is located in the Sandhill Region of Nebraska; a 4.8 million ha area of rolling sand dunes covered in grasses, forbs, and shrubs (Whitcomb 1989). Common vegetation on the dunes includes sand bluestem (*Andropogon hallii*), sand muhly (*Muhlenbergia arenicola*), prairie sandreed (*Calamovilfa longifolia*), sand dropseed (*Sporobolus cryptanthus*), needle and thread (*Stipa comata*), sunflowers (*Helianthus*), blazing star (*Mentzelia*), sand cherry (*Prunus pumila*), and soapweed yucca (*Yucca glauca*). Soils of the region are composed of sand mixed with 1-4% silt and clay (Whitcomb 1989). Cold winters (average minimum temperature for January = -12.8ºC), warm summers (average maximum temperature for July = 31.7ºC), and low humidity are typical in the Sandhill Region and nearly 80% of precipitation falls April to September (Wilhite and Hubbard 1989).

Assessment of seed-caching behavior.--Studies of seed caching by Ord's kangaroo rats were conducted during 2 consecutive summers and winters (July-August 2006 and 2007 and January 2007 and 2008). To investigate differences in method of food caching (scatterhoarding or larderhoarding), powdered fluorescent pigments were used (Radiant Color, Richmond, California) to track individuals to seed caches (Longland and Clements 1995). Ten grams of yucca seeds mixed with 1 g of green, yellow, or orange powdered fluorescent pigment were placed in a Petri dish in the center of a cookie sheet lined with sandpaper. The sandpaper was covered with a different color of pigment (e.g., green on seeds and orange on tray); thus, after individuals stepped on the tray to harvest seeds, they left fluorescent footprints on the soil, which could later be followed with a UV light source. When kangaroo rats collected seeds and placed them in their cheek pouches, they transferred the other colored pigment to their forepaws and face and upon deposition of seeds in scatterhoards, they transferred these pigments to the soil. When kangaroo rats took seeds into a burrow to deposit seeds in a larderhoard, both colors of pigment were observed in the entrance of the burrow.

Seeds of the native soapweed yucca (*Yucca glauca*) were selected for use in seed-caching experiments for several reasons. First, yucca is a common and conspicuous plant of the Sandhill Region. Second, yucca seeds seem to be an important food source for Ord's kangaroo rats in the Sandhill Region; kangaroo rats have been observed harvesting yucca seeds from pods, and yucca seeds have been found in traps containing kangaroo rats and in burrows of these animals (Chapter 4). Third, these seeds were readily gathered and cached by kangaroo rats in preliminary food-caching studies in the Sandhill Region. Preliminary studies involved both powdered and unpowdered yucca seeds, which were harvested at a similar rate. Lastly, yucca pods provide a concentrated food source in nature, so a large accumulation of yucca seeds is a natural situation in the Sandhill Region.

Seeds were collected from pods of yucca plants in October 2005, August 2006 and 2007, and January 2007 and 2008. Size of pods and amount of seeds in pods varies. To determine the average amount of seeds in yucca pods, I collected and weighed seeds from 11 pods collected during August 2006. Mean weight of seeds from these pods was 5.34 g (range; 3.08-8.10 g). Ten grams of seeds were used for each seed-caching trial, which approximated the amount of seeds from 2 average-sized pods.

Seed-caching experiments were initiated just after sunset. A small amount of rolled oats (~1 g) was placed at several sites each night with good weather (i.e., no strong winds or rain). Sites selected for assessment of seed-caching behavior displayed signs of activity including presence of burrows, foraging runs, and tracks of kangaroo rats. Oats typically were placed at intersections of foraging runs where tracks of kangaroo rats were present. Piles of oats were checked ca. every 30 min to determine whether kangaroo rats had collected oats. If a pile had been collected, then a seed tray was placed at the site and an observer watched the tray. Sites selected for seed trays were ≥70 m apart, but typically were >100 m apart to prevent the same individuals from gathering seeds from multiple trays. Home ranges of Ord's kangaroo rats vary from 0.43 to 1.36 ha (Garrison and Best 1990), so the radius of a circular home range would vary from 37 to 66 m. Thus, >1 tray probably was not visited by the same individual.

Observers watched the tray with night-vision binoculars (NVB 2.5; Yukon by Sibir Optics, Mansfield, Texas; Night Shadow, American Technologies Corp., South San Francisco, California) from ≥10 m away for ≥30 min and if no kangaroo rat approached the tray, then it was moved to a new location. Also, if a kangaroo rat approached the tray several times and did not gather seeds, then the tray was moved to a new location. When a kangaroo rat began gathering seeds, an observer quietly watched the kangaroo rat cache seeds and return to the tray until all seeds were gone or until the kangaroo rat did not return to the tray for ≥20 min. Total number of trips each individual made to the tray to collect seeds and whether each load was taken into a burrow (larderhoard) or cached in the soil (scatterhoard) was recorded. Most individuals remained in the field of view during observations; however, a few kangaroo rats moved to areas where it was not possible to observe their caching behavior. When individuals took seeds into a burrow, they repeatedly used the same trail and entered the same burrow. Conversely, when individuals made scatterhoards, they typically left the tray in several different directions and often were observed digging a pit in the soil and depositing seeds in the pit. Kangaroo rats were never observed making >1 deposit of seeds to a single scatterhoard.

Observations of kangaroo rats at trays were important for several reasons. First, observations aided researchers in determining the most common method of seed caching by individuals and in finding their seed caches. In addition, it was possible to determine if multiple individuals collected seeds from a tray and if any interactions between kangaroo rats occurred in the area of seed trays. Preliminary studies of powder tracking without observations resulted in difficulty finding seed caches in this sandy environment. Further, captures of multiple individuals with powder on their bodies indicated that several seed trays were visited by >1 kangaroo rat.

After observing individuals collect and cache seeds from trays, fluorescent trails of kangaroo rats were followed using portable ultraviolet lights. If scattered caches were discovered, these caches were carefully uncovered and depth from surface of soil to top of seeds was measured. All seeds were collected to determine weight and number of seeds in each cache. Scattered caches were replaced with about 1 g of seeds in summer 2006 and with the exact number of seeds in 2007 for a study on cache recovery (Chapter 3). Caches were covered with sand and location of each scattered cache was marked with a numbered wire flag placed nearby. If multiple trails led into a burrow, then the burrow also was marked with a wire flag.

Identification of seed cachers—After caches were discovered and marked, 5-20 Sherman live traps (7.6 x 8.9 x 22.9 cm; H. B. Sherman Traps, Inc.; Tallahassee, Florida) were set in the immediate area of the seed tray and caches depending on size of the area traveled by the kangaroo rat. Traps were baited with oats and checked during the night or the following morning. Species, age (adult, subadult, or juvenile), sex, reproductive condition (males—scrotal or non-scrotal; females—estrous, pregnant, lactating, post-lactating, non-reproductive), and weight of each animal were recorded. Individuals also were examined to determine if fluorescent powder was present. Individuals that harvested fluorescent seeds from trays had powder inside their cheek pouches for several days. If multiple individuals were observed collecting seeds from a tray or if multiple individuals with fluorescent powder were captured, then the data were discarded. Multiple individuals with powder were only captured at trays where multiple individuals were observed gathering seeds, except at 1 tray during summer 2007. In this case, 2 trays 100 m apart were deployed on the same evening. Only 1 kangaroo rat was observed harvesting seeds at each tray, but the next day 2 kangaroo rats with powder were captured at 1 tray and no kangaroo rat was captured at the other tray. These data were used in analyses because 1 of the kangaroo rats larderhoarded seeds in a burrow and she was radiocollared and followed to the same burrow after seed-caching trials. Thus, I was confident that she collected seeds from that particular tray.

Distribution of seed caches and burrows.—Distances from seed caches to nearest vegetation were measured. In addition, straight-line distance from each cache to the seed source was measured and a compass reading was taken for each cache in relation to the seed source. Straight-line distances between caches also were measured. If tracks led into a burrow, then distances from the burrow to the seed source and other caches were measured and a compass reading was taken for the burrow in relation to the seed source. Some individuals that cached seeds were fitted with a radiotransmitter (Chapter 1) to determine location of their home burrow or burrows. Individuals were trapped as mentioned above and tracked during the day for ≥4 days after seed-caching trials. Locations of burrows were marked with wire flags and distances between burrows and the seed tray and between burrows and caches were measured at each site.

Statistical analyses.—Each trip to deposit seeds by kangaroo rats was categorized as a scatterhoard or a larderhoard. Chi-squared tests for independence were used to determine whether kangaroo rats made more scatterhoards or trips to larderhoards in summer versus winter for each year. Two analyses were used to characterize relative distribution of scatterhoards made by kangaroo rats. First, a 2-factor analysis of variance (ANOVA) was used to determine whether kangaroo rats cached seeds closer to burrows or seed sources for both years. If >1 cache was discovered, then mean distance from seed tray to caches at each site was calculated, as well as mean distance from burrow to caches. If kangaroo rats used >1 burrow, then the 1st burrow the kangaroo rat occupied after caching trials was used in this analysis. Secondly, a nearest-neighbor analysis (Clarke and Evans 1954) was used to investigate relative dispersion of seed caches. That is, whether seed caches had a clumped, random, or uniform distribution within an individual's home range. Kangaroo rats that made ≥3 caches were used in nearest-neighbor analysis. Area of home range was estimated using mean distance between burrows of kangaroo rats that occupied >1 burrow in summer 2006 and 2007. Mean distance between burrows was 29.7 m (Chapter 1), which was used as the radius to determine home range of kangaroo rats. This estimate is similar to estimates of size of home ranges of Ord's kangaroo rats in other populations (Garrison and Best 1990).

RESULTS

Seasonal differences in food-caching patterns.—During this study, 54 different adult kangaroo rats were observed harvesting and caching seeds, including 39 individuals in summer 2006 and 2007, and 15 individuals in winter 2007 and 2008 (Appendix 5). Individuals varied in amount of seeds they harvested from trays, but mean percentages were similar during summer and winter in both years (summer 2006 = 84%, 2007 = 83%; winter 2007 = 82%, 2008 = 77%). Kangaroo rats that harvested seeds were observed making 160 caches in the soil (scatterhoarding) and 75 trips to deposit seeds within burrows (larderhoarding). In both years, kangaroo rats mainly scatterhoarded seeds in summer, but larderhoarded seeds within burrows in winter (Chi-Squared test; 2006, $\chi^2 = 70.38$, $P < 0.001$; 2007, $\chi^2 = 63.71$, $P < 0.001$: Fig. 3).

Of the 15 kangaroo rats that harvested seeds in winter, 11 larderhoarded seeds in only 1 burrow (4 males and 7 females). These individuals made 1-6 trips from the seed source to their burrow to store seeds. Of the other kangaroo rats, 1 stored seeds in 2 different burrows (female), 2 scatterhoarded and larderhoarded seeds (2 females), and 1 only scatterhoarded seeds (male). Of the 39 adult kangaroo rats that harvested and cached seeds in summer, 21 were males and 18 were females. All 39 individuals scatterhoarded at least some of the seeds they harvested, and 35 individuals only made scatterhoards (1-10 caches). Interestingly, no male larderhoarded seeds in summer, but 4 females larderhoarded some of the seeds they harvested. All of these females made ≥1 scatterhoard and also made 3-6 trips to a burrow to store seeds. One female was lactating and the other 3 were in estrus.

Characteristics of scatterhoards.—Scatterhoards of yucca seeds made by Ord's kangaroo rats in summer varied in size and distance from the seed source, but most caches were large and placed relatively close to the tray (Table 3). When preparing a scatterhoard, kangaroo rats dug a pit in the sand, pushed yucca seeds out of their cheek pouches with their forepaws, and usually covered the seeds by pushing sand over the cache. Most caches were buried shallowly in sand, but a few were left uncovered (mean depth = 14 mm, range 0-40 mm; Appendix 6). Microsite characteristics of caches were recorded in 2007 and caches typically were placed at edges of vegetation (62%; 49 of 79), while some caches were placed in cover (29%; 23 of 79), and a few were in open sand (9%; 7 of 79). Caches were placed near a variety of grasses, forbs, and shrubs, but most caches were placed at the edge of sand muhly (*Muhlenbergia arenicola*), a common grass in upland areas of the Sandhill Region.

Distribution of scatterhoards in summer.—In summer, 22 adult kangaroo rats, including 11 males and 11 females, were radiocollared and tracked to their burrows after caching seeds. Thirteen individuals placed ≥1 cache in the same direction as their burrow in reference to the seed source and 9 did not cache in the direction of their burrow. Although some individuals placed caches in the same direction as their burrow, 92% (12 of 13) of kangaroo rats in 2006, and 67% (6 of 9) in 2007 placed caches closer to seed trays than to burrows. Distances between seed trays and caches also were measured for 18 other kangaroo rats whose burrows were not located. The frequency distribution of burrow-to-cache distances was skewed to the right (Kolmogorov-Smirnov, $P < 0.010$), as was the distribution of seed-source-to-cache distances (Kolmogorov-Smirnov, $P < 0.010$). Because only a few caches were located far from seed trays and burrows, which skewed both distributions, parametric analysis was used to compare these distributions. Scatterhoards were significantly closer to the source of seeds than to burrows in summer ($F = 6.99$, *d.f.* = 1, $P = 0.011$; Fig. 4), while no difference from year to year ($F = 1.13$, *d.f.* = 1, $P = 0.292$) and no interaction occurred ($F = 0.19$, *d.f.* = 1, $P = 0.667$).

To determine relative dispersion of scatterhoards in summer, cardinal directions of caches in relation to the seed source and distances between caches were measured for kangaroo rats that made ≥3 caches in 2006 and 2007. This resulted in inter-cache distances calculated for 71 caches created by 14 kangaroo rats in 2006, and 64 caches made by 13 kangaroo rats in 2007. Mean observed distances between caches of male and female kangaroo rats in each year were smaller than expected for a random distribution. Nearest-neighbor analysis revealed that these scatterhoards were significantly clumped within the home range of both male and female kangaroo rats in both summers (Table 4). Kangaroo rats occasionally cached in wide arcs around the source of seeds (e.g., 249°), but most individuals concentrated scatterhoards in a smaller arc (mean = 116°).

DISCUSSION

Ord's kangaroo rats in the Sandhill Region of Nebraska altered food-caching patterns seasonally; they commonly scatterhoarded seeds in summer, but stored seeds in larderhoards within burrows in winter. The drive to scatterhoard in summer was strong as all kangaroo rats scatterhoarded ≥1 load of seeds in this season. Alternatively in winter, scatterhoarding was uncommon and kangaroo rats took most seeds directly to a burrow. Use of both scatterhoarding and larderhoarding has been observed in kangaroo rats (e.g., Jenkins and Breck 1998; Price et al. 2000), and intensity of hoarding is known to change seasonally for pocket mice and kangaroo rats (Lawhon and Hafner 1981). Additionally, some species of chipmunks hoard more intensively in autumn and either move scattered caches to burrows before winter (Vander Wall et al. 2005) or switch from a combination of scatterhoarding and larderhoarding in summer to almost exclusive larderhoarding in autumn to prepare for winter hibernation (Elliott 1978). Nevertheless, my study is the 1st to demonstrate a seasonal change in method of food storage for any food-hoarding animal that forages throughout the year.

Most males and females larderhoarded seeds in winter and scatterhoarded in summer; however, some variation in caching strategies between males and females was observed in summer. In this season, all males scatterhoarded exclusively, but some females larderhoarded seeds within burrows in addition to scatterhoarding. All 4 female kangaroo rats that larderhoarded seeds were radiocollared after caching trials, and upon release, all entered the burrow where they recently stored seeds. One of these females remained in that burrow for the next 7 days, but the others switched between different burrows. Thus, burrow fidelity was low in summer even for kangaroo rats that larderhoarded seeds. Two of the 3 kangaroo rats that switched burrows returned to their larderhoarding burrow, but the fate of larderhoarded seeds was unknown. It was possible that seeds were consumed, scatterhoarded, moved to another burrow, or left behind in the original burrow.

In other studies, no difference in preference between scatterhoarding or larderhoarding was observed in laboratory arenas between male and female *D. merriami*, but all individuals were non-reproductive (Jenkins and Peters 1992; Jenkins et al. 1995). Larderhoarding in summer in this study might have been influenced by reproductive condition of females because 3 of the 4 larderhoading kangaroo rats were in estrus. Nest-building and larderhoarding has been observed in kangaroo rats just before parturition (Eisenberg 1993; Jones et al. 1983), but these behaviors have not been associated with individuals in estrus. Only 2 kangaroo rats were noticeably pregnant during caching trials and both of these scatterhoarded exclusively. In addition, 10 of 11 lactating and recently post-lactating females only scatterhoarded seeds. Therefore, female kangaroo rats with young scatterhoarded seeds almost exclusively. Female eastern chipmunks with young scatterhoarded more than females without young (Clarke and Kramer 1994b). This switch in caching behavior might have been a strategy for mothers to reserve some resources for their own consumption. This explanation may support observations in female Ord's kangaroo rats; however, so few individuals larderhoarded seeds in summer that reasons for this behavior are still unclear.

Seasonal placement of caches.—Many variables influence placement of caches by food-hoarding animals (e.g., Clarke and Kramer 1994b; Murray et al. 2006; Tsurim and Abramsky 2004) with this study demonstrating that season is an important factor in caching patterns. The striking difference in caching behavior of Ord's kangaroo rats in summer and winter suggests that seasonal placement of caches was important. In winter, caching patterns followed the larder-defensibility hypothesis, whereas in summer, placement of caches was most consistent with the rapid-sequestering hypothesis.

Concentrating resources in a burrow provides convenient access to these items allowing individuals to conserve energy that would be expended during recovery of caches. Recovery of scatterhoards, especially when distant from the home burrow, takes more time and energy than recovery of seeds in larders (Jenkins and Peters 1992). Additionally, scatterhoarding increases exposure to predators and inclement weather as individuals search for and retrieve caches. If weather conditions in the Sandhill Region become harsh enough to prevent kangaroo rats from leaving their burrows, then survival may rely on a sufficient store of food in the burrow. During winter caching trials, temperatures were cold at night reaching -14.6°C (Appendix 1), and snow had accumulated from recent storms. In fact, snow covered >90% of the ground during both winters; it was only absent from some ridge tops, a few south-facing slopes, and some roadsides. Despite these conditions, kangaroo rats were actively foraging and caching seeds. Kangaroo rats also are active during low temperatures and snow in other areas. For example, *Dipodomys microps* and *D. merriami* were active during a light snowstorm and when the temperature reached as low as -19°C in California (Kenagy 1973). But several species of *Dipodomys*, including *D. ordii*, ceased activity on the surface when the temperature was <-15°C and snow covered >40% of the ground in Nevada (O'Farrell 1974). A cessation of activity was not observed in my study; however, with lower temperatures and more snow, which is likely in this region, kangaroo rats might have stayed inside burrows. In this situation, maintenance of a larder of seeds within a burrow would be advantageous.

Although larderhoarding allows kangaroo rats convenient access to resources, this strategy is only beneficial when individuals protect their larder (Smith and Reichman 1984; Vander Wall et al. 2005). Kangaroo rats commonly return to the same burrows in winter in the Sandhill Region, so protection of a food hoard within a burrow in this season would be easier than in summer when individuals commonly used multiple burrows (Chapter 1). In fact, a female was observed chasing another kangaroo rat away from the entrance of her burrow where she had just stored seeds in winter. She returned to this burrow each night for ≥4 consecutive nights after storing seeds there.

Despite my evidence supporting the larder-defensibility hypothesis, Ord's kangaroo rats might have larderhoarded seeds in winter simply because they had no alternative. Kangaroo rats often traveled over snow and frozen sand while transporting seeds, but never scatterhoarded in these substrates. They only were observed making scatterhoards in soft, dry sand, and in both winters, dry sand was uncommon at the study site. Most of the ground was covered with snow or wet sand from recent snowmelt. Wet sand often was pliable during warmer temperatures of the day, but froze at night. The soil in the Sandhill Region is not pure sand, but composed of sand mixed with 1-4% silt and clay (Whitcomb 1989). These properties slow drainage of water from the soil, increasing freezing potential. The surface of snow also hardened at night. Due to solidity of these substrates, kangaroo rats were unable to make or retrieve caches in snow and frozen sand. To my knowledge, caching activity of kangaroo rats and other rodents has not been studied in winter in temperate environments. However, Merriam's kangaroo rats selected caching sites in sandy soils more often than harder, rockier soils in summer (Breck and Jenkins 1997). Perhaps, in my study, Ord's kangaroo rats would have scatterhoarded more frequently in winter in the absence of snow and frozen sand.

In summer, when the soil was friable in the Sandhill Region, scatterhoarding was the preferred strategy of Ord's kangaroo rats. In contrast to winter, placement of caches in summer was consistent with the rapid-sequestering hypothesis. Caches were placed significantly closer to the seed source than to burrows. Furthermore, caches of both male and female Ord's kangaroo rats were concentrated in a small arc from the seed source and were significantly clumped within the estimated home range of individuals.

The range of distances between caches at each site, and between caches and seed source in this study were similar to a field study of Merriam's kangaroo rats (Murray et al. 2006). However, it should be noted that following trails of fluorescent powder becomes increasingly difficult as distance from tray increases, especially in sandy substrates. Caches were located ≤56.4 m from the seed source, but several trails were followed without finding a cache. Mean percentage of seeds recovered from caches of kangaroo rats that exclusively scatterhoarded was 53%. Thus, several scatterhoards went unrecovered and results of cache placement must be interpreted cautiously. However, the clumped placement of caches likely was underestimated because at sites where ≥70% of scatterhoarded seeds were recovered, caches were even more clumped. Thus, in summer, Ord's kangaroo rats typically concentrated caches near the seed source. Benefits of this caching pattern likely include protection from complete loss by spreading resources into many caches and maintaining access to a rich seed patch.

Use of multiple burrows by Ord's kangaroo rats in summer would make it difficult to protect a large accumulation of seeds in a burrow from conspecifics and other competitors (Vander Wall et al. 2005). For example, in summer, a kangaroo rat entered a burrow of another individual although the burrow entrance was plugged with sand. The intruder was chased away, but returned and entered the burrow several more times. The original occupant of this burrow was located in a different burrow the following day and used 6 different burrows during a 13-day period (Appendix 3). Protection of resources within any of these burrows seems unlikely due to constant switching between burrows. Concentrating caches near a burrow entrance would not be advantageous for the same reason. Similar to Ord's kangaroo rats, Merriam's kangaroo rats use multiple burrows (Behrends et al. 1986) and typically do not scatterhoard near burrow entrances (Daly et al. 1992). In contrast, food-hoarding species that defend burrows may concentrate caches near burrow entrances. For example, giant kangaroo rats (*Dipodomys ingens*, Shaw 1934) make shallow caches near burrow entrances. Seeds are cured in these caches before they are moved into a larder within their burrow (Shaw 1934), which is defended (Braun 1985). Eastern chipmunks also placed scattered caches within a defended area near their burrows and were observed chasing away competitors (Clarke and Kramer 1994a). Thus, whether hoarders are able to effectively protect caches may determine where they are placed.

Ord's kangaroo rats are abundant in the Sandhill Region (Appendix 2; Jones et al. 1983), and observations revealed that individuals often used the same foraging areas in this region. Multiple kangaroo rats were observed or captured at 64% (29 of 45) of seed trays where ≥1 individual harvested seeds in summer. Additionally, chasing and fighting were observed at trays. This suggests that competition at seed patches was prevalent, and rapid removal of seeds might be more important than widely spacing caches for protection. However, it was only possible to determine initial location of caches in my study. These caches might have been relocated or moved to burrows after initial placement by kangaroo rats. Merriam's kangaroo rats initially placed caches according to the rapid-sequestering hypothesis and then retrieved caches and repositioned them farther apart in laboratory arenas in agreement with the cache-spacing hypothesis

(Jenkins and Peters 1992; Jenkins et al. 1995). Caches made by Ord’s kangaroo rats in my study were recovered quickly, but it was unknown whether they were moved to a new location by the hoarder (Chapter 3). Thus, similar dynamics of scatterhoarding might be observed in Ord’s kangaroo rats when caches are followed after their initial placement.

Conclusions.—Ord’s kangaroo rats in the Sandhill Region forage throughout the year and vary food-caching patterns seasonally. Placement of caches was consistent with the larder-defensibility hypothesis in winter as most kangaroo rats stored items in their burrow, where they could be more easily defended against pilferers. Also, suitable sites for scatterhoarding in winter were limited as most soil was frozen or covered with snow. In summer, placement of caches followed the rapid-sequestering hypothesis. Kangaroo rats mainly stored seeds in inconspicuous scatterhoards that were clumped near the seed source. Future research should investigate the stimulus for this seasonal shift in behavior.

LITERATURE CITED

Behrends, P., M. Daly, and M. I. Wilson. 1986. Range use patterns and spatial relationships of Merriam's kangaroo rats (*Dipodomys merriami*). Behaviour 96:187-209.

Braun, S. E. 1985. Home range and activity patterns of the giant kangaroo rat, *Dipodomys ingens*. Journal of Mammalogy 66:1-12.

Breck, S. W., and S. H. Jenkins. 1997. Use of an ecotone to test the effects of soil and desert rodents on the distribution of Indian ricegrass. Ecography 20:253-263.

Clarke, P. J., and F. C. Evans. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35:445-453.

Clarke, M. F., and D. L. Kramer. 1994a. The placement, recovery, and loss of scatter hoards by eastern chipmunks, *Tamias striatus*. Behavioral Ecology 5:353-361.

Clarke, M. F., and D. L. Kramer. 1994b. Scatter-hoarding by a larder-hoarding rodent: intraspecific variation in the hoarding behaviour of the eastern chipmunk, *Tamias striatus*. Animal Behaviour 48: 299-308.

Clarkson, K., S. F. Eden, W. J. Sutherland, and A. I. Houston. 1986. Density dependence and magpie food hoarding. Journal of Animal Ecology 55:111-121.

Dally, J. M., N. S. Clayton, and N. J. Emery. 2006. The behaviour and evolution of cache protection and pilferage. Animal Behaviour 72:13-23.

Daly, M., L. F. Jacobs, M. I. Wilson, and P. R. Behrends. 1992. Scatter-hoarding by kangaroo rats (*Dipodomys merriami*) and pilferage from their caches. Behavioral Ecology 3:102-111.

Devenport, J. A., L. D. Luna, and L. D. Devenport. 2000. Placement, retrieval, and memory of caches by thirteen-lined ground squirrels. Ethology 106:171-183.

Eisenberg, J. F. 1993. Ontogeny. Pp. 479-490 in Biology of the Heteromyidae (H. H. Genoways and J. H. Brown eds.). Special Publication, The American Society of Mammalogists 10:1-719.

Elliott, L. 1978. Social behavior and foraging ecology of the eastern chipmunk (*Tamias striatus*) in the Adirondack Mountains. Smithsonian Contributions to Zoology 265:1-107.

Garrison, T. E., and T. L. Best. 1990. Dipodomys ordii. Mammalian Species 353:1-10.

Gerber, L. R., O. J. Reichman, and J. Roughgarden. 2004. Food hoarding: future value in optimal foraging decisions. Ecological Modeling 175:77-85.

Gummer, D. L. 1997. Effects of latitude and long-term isolation on the ecology of northern Ord's kangaroo rats (*Dipodomys ordii*). M.S. thesis, University of Calgary, Alberta, Canada.

Hawbecker, A. C. 1940. The burrow and feeding habits of *Dipodomys venustus*. Journal of Mammalogy 21:388-396.

Hurly, T. A., and R. J. Robertson. 1990. Variation in the food hoarding behaviour of red squirrels. Behavioral Ecology and Sociobiology 26:91-97.

Jenkins, S. H., and S. W. Breck. 1998. Differences in food hoarding among six species of heteromyid rodents. Journal of Mammalogy 79:1221-1233.

Jenkins, S. H., and R. A. Peters. 1992. Spatial patterns of food storage by Merriam's kangaroo rats. Behavioral Ecology 3:60-65.

Jenkins, S. H., A. Rothstein, and W. C. H. Green. 1995. Food hoarding by Merriam's kangaroo rats: a test of alternative hypotheses. Ecology 76:2470-2481.

Jones, J. K., Jr., D. M. Armstrong, R. S. Hoffmann, and C. Jones. 1983. Mammals of the northern Great Plains. University of Nebraska Press, Lincoln.

Kenagy, G. J. 1973. Daily and seasonal patterns of activity and energetics in a heteromyid rodent community. Ecology 54:1201-1219.

Lawhon, D. K., and M. S. Hafner. 1981. Tactile discriminatory ability and foraging strategies of kangaroo rats and pocket mice (Rodentia: Heteromyidae). Oecologia (Berlin) 50:303-309.

Leaver, L. A. 2004. Effects of food value, predation risk, and pilferage on the caching decisions of *Dipodomys merriami*. Behavioral Ecology 15:729-734.

Leaver, L. A., and M. Daly. 1998. Effects of food preference on scatter-hoarding by kangaroo rats (*Dipodomys merriami*). Behaviour 135:823-832.

Longland, W. S., and C. Clements. 1995. Use of fluorescent pigments in studies of seed caching by rodents. Journal of Mammalogy 76:1260-1266.

Murray, A. L., A. M. Barber, S. H. Jenkins, and W. S. Longland. 2006. Competitive environment affects food-hoarding behavior of Merriam's kangaroo rats (*Dipodomys merriami*). Journal of Mammalogy 87:571-578.

O'Farrell, M. J. 1974. Seasonal activity patterns of rodents in a sagebrush community. Journal of Mammalogy 55:809-823.

Preston, S. D., and L. F. Jacobs. 2001. Conspecific pilferage but not presence affects Merriam's kangaroo rat cache strategy. Behavioral Ecology 12:517-523.

Price, M. V., N. M. Waser, and S. McDonald. 2000. Seed caching by heteromyid rodents from two communities: implications for coexistence. Journal of Mammalogy 81:97-106.

Shaffer, L. 1980. Use of scatterhoards by eastern chipmunks to replace stolen food. Journal of Mammalogy 61:733-734.

Shaw, W. T. 1934. The ability of the giant kangaroo rat as a harvester and storer of seeds. Journal of Mammalogy 15:275-286.

Smith, C. C., and O. J. Reichman. 1984. The evolution of food caching by birds and mammals. Annual Review of Ecology and Systematics 15:329-351.

Stapanian, M. A., and C. C. Smith. 1978. A model for seed scatterhoarding: coevolution of fox squirrels and black walnuts. Ecology 59:884-896.

Tsurim, I., and Z. Abramsky. 2004. The effect of travel costs on food hoarding in gerbils. Journal of Mammalogy 85:67-71.

Vander Wall, S. B. 1990. Food hoarding in animals. The University of Chicago Press, Chicago.

Vander Wall, S. B., E. C. H. Hager, and K. M. Kuhn. 2005. Pilfering of stored seeds and the relative costs of scatter-hoarding versus larder-hoarding in yellow pine chipmunks. Western North American Naturalist 65:248-257.

Vander Wall, S. B., T. C. Thayer, J. S. Hodge, M. J. Beck, and J. K. Roth. 2001. Scatter-hoarding behavior of deer mice (*Peromyscus maniculatus*). Western North American Naturalist 61:109-113.

Whitcomb, R. F. 1989. Nebraska sand hills: the last prairie. Proceedings of the North American Prairie Conference 11:57-69.

White, J. A., and K. Geluso. 2007. Seasonal differences in onset of surface activity of Ord's kangaroo rat (*Dipodomys ordii*). Journal of Mammalogy 88:234-240.

Wilhite, D. A., and K. G. Hubbard. 1989. Climate. Pp. 17-28 in An atlas of the Sand Hills (A. Bleed and C. Flowerday, eds.). University of Nebraska-Lincoln: Conservation and Survey Division at the Institute of Agriculture and Natural Resources, 5a:1-265.

Yahner, R. H. 1975. The adaptive significance of scatter hoarding in the eastern chipmunk. Ohio Journal of Science 75:176-177.

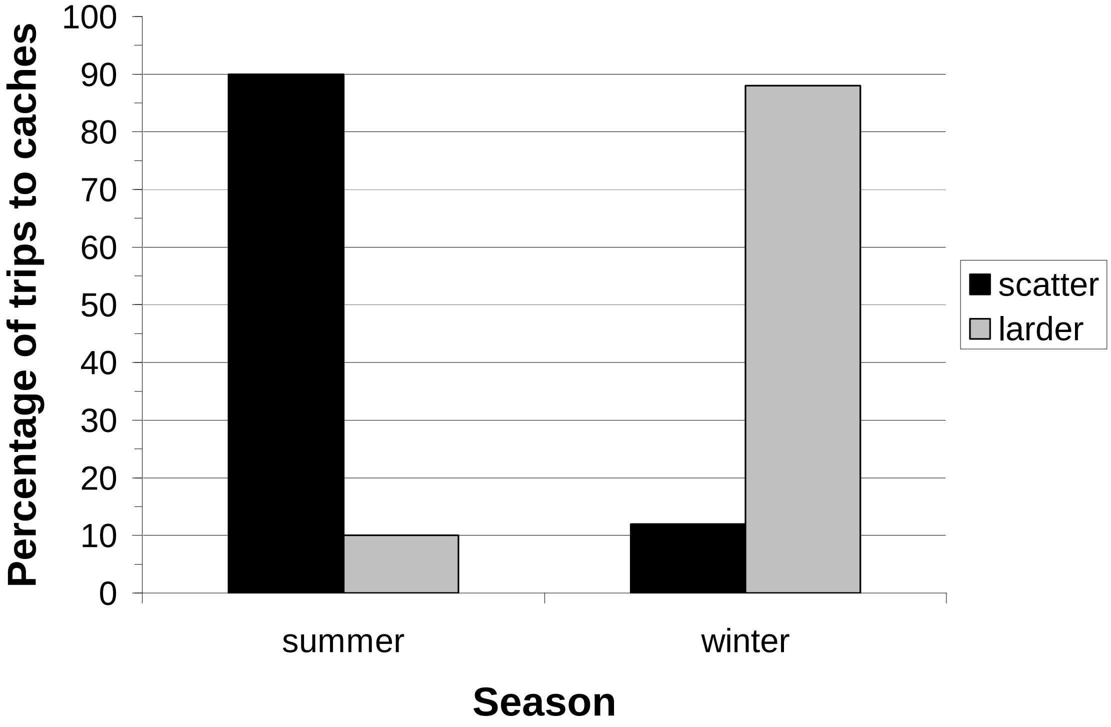

Fig. 3. Percentages of trips made by Ord's kangaroo rats (*Dipodomys ordii*) to deposit seeds in different types of caches (scatterhoards or larderhoards) in the Sandhill Region of Nebraska. Percentages are based on 169 trips made by 39 adult kangaroo rats in summer (July and August 2006 and 2007) and 66 trips made by 15 adult kangaroo rats in winter (January 2007 and 2008).

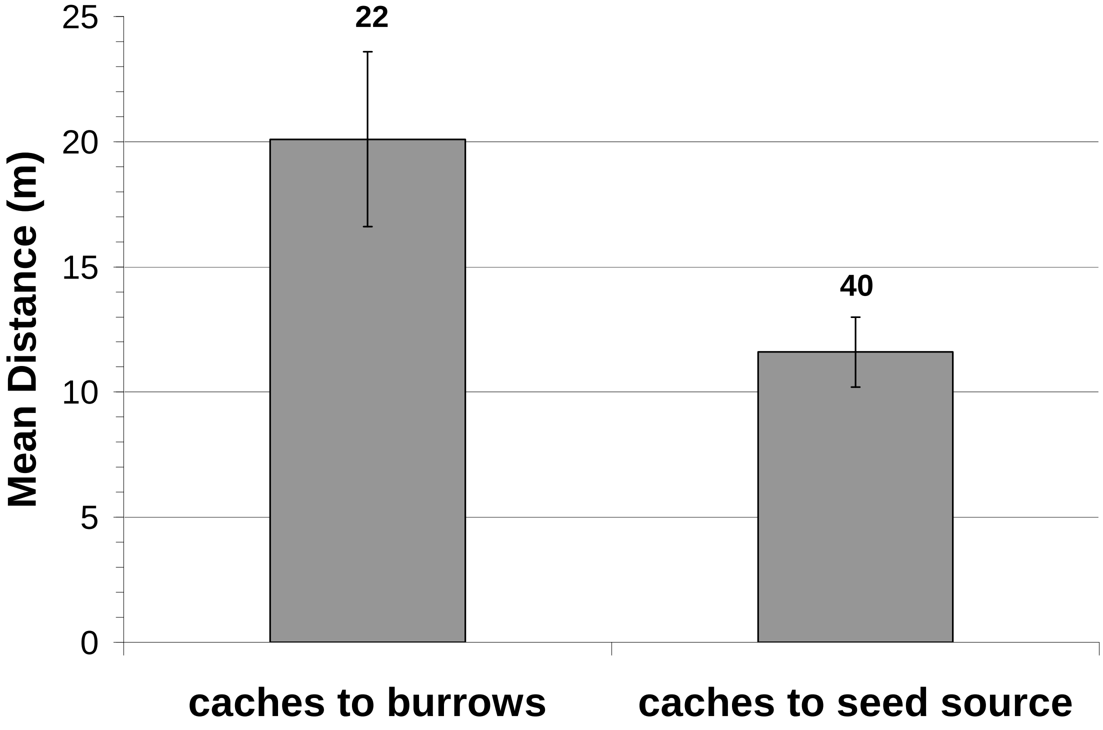

Fig. 4. Comparison of mean distance from scattered seed caches made by Ord's kangaroo rats (*Dipodomys ordii*) to burrows and from caches to source of seeds (seed trays) in the Sandhill Region of Nebraska during summer 2006 and 2007. Burrows of 22 kangaroo rats were located by radiotelemetry.

Table 3. Mean, standard deviation, minimum, and maximum values for size of scatterhoards of seeds of soapweed yucca (*Yucca glauca*) made by Ord's kangaroo rats (*Dipodomys ordii*) and distance from caches to the seed source in summer 2006 and 2007 in the Sandhill Region of Nebraska.

		Size (number of seeds)		Distance (m)	
Year	*n*	Mean (*SD*)	Min-Max	Mean (*SD*)	Min-Max
2006	76	58 (19.7)	6-98	8.83 (4.96)	0.75-25.50
2007	68	62 (21.9)	2-110	11.22 (7.80)	2.10-56.40
Total	144	60 (20.7)	2-110	9.96 (6.54)	0.75-56.40

Table 4. Mean values representing distribution of seed caches made by Ord's kangaroo rats (*Dipodomys ordii*) in summer 2006 and 2007 in the Sandhill Region of Nebraska. Area (2,767 m^2) used in calculation of density was generated using the mean distance between burrows (29.7 m) of kangaroo rats as the radius for the area of the home range. R-values <1 indicate a clumped distribution and C-values >1.96 demonstrate that clumping is significantly different than random at the 0.05 alpha level.

Year	Sex (*n*)	Number of seed caches	Density (caches/2,767 m^2)	RE (expected)	RA (observed)	R (RA/RE)	C
2006	♂ (8)	5	0.0019	11.98	4.56	0.37	2.73
2006	♀ (6)	5	0.0017	12.32	4.23	0.35	2.68
2007	♂ (8)	5	0.0019	11.68	4.91	0.42	2.56
2007	♀ (5)	4	0.0016	12.72	3.65	0.28	2.91

CHAPTER 3.

RECOVERY OF SEED CACHES BY ORD'S KANGAROO RATS (*DIPODOMYS ORDII*): IMPLICATIONS FOR DISPERSAL OF SOAPWEED YUCCA (*YUCCA GLAUCA*)

ABSTRACT

A paired-cache technique was used to determine whether Ord's kangaroo rats (*Dipodomys ordii*) have an advantage in recovering their own seed caches over granivorous pilferers in the Sandhill Region of Nebraska. Scatterhoards of seeds of the soapweed yucca (*Yucca glauca*) made by Ord's kangaroo rats were located using powdered fluorescent pigments. Identical artificial caches were prepared near real caches and each pair was monitored for ≥8 consecutive days. Real caches did not disappear before artificial caches or at a faster rate than artificial caches suggesting that high rates of pilferage occurred in this system. However, moist conditions from frequent rain at the study site, and proximity of real and artificial caches may have enhanced pilferage of artificial caches. Nevertheless, results suggest that Ord's kangaroo rats do not have a distinct advantage over pilferers in recovering seed caches in the Sandhill Region. Although many real and artificial caches were recovered quickly, most caches were only partially recovered. Because overlooked seeds remained at most cache sites and many of

these seeds were viable at the end of the study, Ord's kangaroo rats likely play a significant role in dispersal of soapweed yucca.

INTRODUCTION

An important component of food-hoarding behavior is recovery of stored food. Cached food can either be recovered by the original hoarder, recovered by a pilferer (another animal besides the original hoarder), or remain unrecovered. Models on adaptive value of food hoarding contend that food hoarders must retrieve more of their own stored items than other individuals for this behavior to be advantageous (Andersson and Krebs 1978; Clarkson et al. 1986; Stapanian and Smith 1978; Vander Wall and Jenkins 2003). Successful retrieval of stored food by the hoarder depends to some degree on the distribution of these stored items. For example, larderhoarding animals that concentrate all of their food in a central area have convenient access to their stored resources; however, scatterhoarders that place food in small, inconspicuous caches may have more difficulty retrieving stored food, especially if these caches are widely-spaced (Smith and Reichman 1984). Retrieval of scattered caches entails increased use of energy and increased exposure compared to recovery of larderhoarded items (Jenkins and Peters 1992). Nevertheless, many birds and mammals commonly scatterhoard food throughout their home ranges (Vander Wall 1990). To benefit from these scattered resources, cachers must locate and retrieve these caches before they are exploited by competitors. However, few studies have attempted to quantify the number of caches recovered by the original hoarder versus those discovered by pilferers to assess the hoarder's recovery advantage (Vander Wall et al. 2006a).

One method that has been used to effectively examine the likelihood that a food hoarder would recover more of its own stored food than naïve individuals is the paired-cache technique (e.g., Cowie et al. 1981; Devenport et al. 2000; Macdonald 1976; Vander Wall et al. 2006a; Winterrowd and Weigl 2006). This technique compares the discovery or disappearance of real caches made by hoarders to identical control caches placed nearby. For example, Vander Wall et al. (2006a) offered seeds to yellow pine chipmunks (*Tamias amoenus*), found scatterhoards made by these individuals, and prepared identical artificial caches nearby. Survival of rodent-made caches versus artificial caches provided a measure of the recovery advantage of hoarders over pilferers. Their results suggested that yellow pine chipmunks had a distinct recovery advantage over pilferers by using spatial memory to locate their own caches of seeds of the Jeffrey pine (*Pinus jeffreyi*). The same technique was employed in the present study to determine whether another scatterhoarding rodent, Ord's kangaroo rat (*Dipodomys ordii*), had an advantage over naïve individuals when recovering seed caches in the Great Plains.

Ord's kangaroo rats commonly scatterhoarded seeds in summer in the Sandhill Region of Nebraska (Chapter 2), including seeds of native soapweed yucca (*Yucca glauca*). Similar to chipmunks, some species of scatterhoarding kangaroo rats remember the locations of buried seed caches (Jacobs 1992). In addition, kangaroo rats retrieve scattered caches quickly, and either consume the contents of caches or recache seeds before competitors have much opportunity to locate them (Jenkins and Peters 1992; Jenkins et al. 1995). Speedy retrieval of caches is important because kangaroo rats have an acute sense of olfaction, which enables them to find seeds buried in soil even when they have no knowledge of the location of caches (Geluso 2005; Johnson and Jorgensen

1981; Reichman and Oberstein 1977; Vander Wall et al. 2003). Because kangaroo rats remember the location of buried caches and often retrieve caches quickly, I predicted that Ord's kangaroo rats in the Sandhill Region would have an initial advantage over pilferers in recovering their own seed caches. This recovery advantage was measured by comparing whether real or artificial caches were retrieved 1st and by comparing the rate of recovery for real and artificial caches. If Ord's kangaroo rats have a recovery advantage over pilferers, then they should have retrieved real caches before artificial caches, and real caches should have been recovered significantly faster than artificial caches.

MATERIALS AND METHODS

This study was conducted 2 July-14 August 2007 at Crescent Lake National Wildlife Refuge, Garden County, Nebraska. This wildlife refuge is in the Sandhill Region of Nebraska, an area characterized by rolling sand dunes covered in grasses, forbs, and shrubs (Whitcomb 1989). Crescent Lake National Wildlife Refuge consists of 18,616 ha (Whitcomb 1989) located in the southwestern part of the Sandhill Region where many lakes are interspersed among the dunes. Conspicuous vegetation in the dunes at the study site included sand bluestem (*Andropogon hallii*), prairie sandreed (*Calamovilfa longifolia*), needle and thread (*Stipa comata*), sand muhly (*Muhlenbergia arenicola*), sand dropseed (*Sporobolus cryptanthus*), sunflowers (*Helianthus*), blazing star (*Mentzelia*), sand cherry (*Prunus pumila*), and soapweed yucca (*Yucca glauca*). The sandy soils of the region contain 1-4% silt and clay, which give the soil more cohesion than pure sand (Whitcomb 1989). Climate of the Sandhill Region is characterized by cold winters (average minimum temperature for January was -12.8ºC), warm summers (average maximum temperature for July was 31.7ºC), and low humidity, and nearly 80% of precipitation falls April to September (Wilhite and Hubbard 1989).

Seeds of native soapweed yucca, a common and conspicuous plant of the Sandhill Region, were selected for use in seed-caching experiments for reasons outlined in Chapter 2. Seeds were collected from pods of yucca plants in October 2005, August 2006, and January 2007, and stored for ≥5 months in paper bags or paper containers (cylinders that originally contained rolled oats) before caching trials were initiated. Seeds were sorted prior to food-caching trials so only viable seeds were used. Viable seeds have intact black seed coats, whereas inviable seeds have pale-colored seed coats and lack endosperm (Addicott 1986). Inviable seeds were discarded along with seeds that were damaged by larvae of the yucca moth (*Tegeticula yuccasella*). Seeds were sorted by researchers wearing vinyl gloves and manipulated with utensils so odor of humans would not be transferred to seeds.

Location of scattered seed caches.—To determine location of seed caches made by Ord's kangaroo rats, trails of these bipedal rodents were followed after they collected seeds from trays covered in powdered fluorescent pigments (Lemen and Freeman 1985; Longland and Clements 1995). Seed trays consisted of a cookie sheet lined with sandpaper and a Petri dish affixed to the center of the tray. Ten g of yucca seeds were dusted with either 1 g of yellow or orange fluorescent powder and placed in the Petri dish. The sandpaper on the tray was covered with the other color of fluorescent powder. Using a different color of powder on the tray and seeds aided in finding seed caches among footprints of kangaroo rats. Seed trays were placed at sites that were ≥100 m apart to prevent the same kangaroo rat from collecting seeds at multiple trays. Sites were selected based on signs of activity of kangaroo rats including presence of burrows, foraging runs, and footprints. About 1 g of rolled oats was initially placed at sites and monitored at ca. 30-min intervals. Once oats were harvested by kangaroo rats (based on footprints and tail drags in sand), a seed tray was placed at the site and the tray was observed from ≥10 m away using night-vision binoculars (NVB 2.5, Yukon by Sibir Optics, Mansfield, Texas; Night Shadow, American Technologies Corp., South San Francisco, California). After seed trays were depleted by a kangaroo rat or after 20 min without another visit by a kangaroo rat, seed trays were removed and caches were searched for by following powdered footprints with a portable ultraviolet light. If seed caches were discovered, then they were marked with numbered wire flags.

After locating seed caches by following trails, powdered seeds were collected from caches. The seed cache was carefully uncovered by moving away sand using a spoon. No seed was handled to prevent transmission of human scent, which may increase detection of seeds by foraging rodents (Duncan et al. 2002; Wenny 2002). Depth of seed caches was measured from the soil surface to the top of seeds, number of seeds in caches was recorded, as well as distance of caches to nearest vegetation, and microsite of seed caches (cover—surrounded by dense vegetation, edge of cover, or open). The distance of each cache from the seed tray also was measured (during daylight). Powdered seeds were collected from caches by carefully scooping seeds from the cache with a spoon and filtering sand through a mesh net. After counting seeds, they were replaced with the same number of unpowdered yucca seeds at the same depth as the original cache and covered with sand using a spoon. An identical cache was made containing the same number of seeds at the same depth and in the same microsite as the original cache ca. 30 cm away from the original cache (Vander Wall et al. 2006a). Paired caches were marked by placing a wire flag ca. 30 cm away from both caches so the caches and wire flag formed an equilateral triangle with each side measuring 30 cm. Near each cache, a small twig was placed upright in the sand to aid in locating caches. Both the original and artificial caches were identical except that a kangaroo rat had knowledge of the location of the original cache.

Recovery of seed caches—Seed caches were monitored daily for 8 consecutive days by searching for signs that seed caches were recovered. Signs of digging in sand at the location of seed caches were searched for and, if a cache was disturbed, stray seeds left behind on the surface of the soil and stray seeds that remained buried in caches were looked for. Seeds were counted and returned to their original location (either on the surface or buried in the sand). If seed caches were not recovered within 8 days, then caches were monitored about once a week for several weeks. Number of days that each cache survived in the soil, number of caches partially recovered, and number of seeds remaining in partially recovered caches were determined. At the end of the study, all cache sites were visited and any stray seeds left behind that were still potentially viable were determined by breaking the seed and verifying that endosperm was present inside the seed coat.

After real caches were located and artificial caches were prepared nearby, 10 Sherman live traps (7.6 x 8.9 x 22.9 cm, H. B. Sherman Traps, Tallahassee, Florida) were set at each site to determine identity of kangaroo rats that cached seeds by checking seed pouches for traces of fluorescent powder (Chapter 2). Traps were set 1-5 nights at each site. Although trapping might have delayed recovery of caches by disturbing both hoarders and pilferers, it provided valuable information on which species of rodents were common at sites and, thus, which species were potential pilferers. In addition to trapping, some kangaroo rats that cached seeds were fitted with a radiotransmitter attached to a beaded-chain collar before being released at their points of capture. This procedure was part of another study on use of burrows and food-caching behavior (Chapter 2).

Yucca seeds were harvested by kangaroo rats at 20 different sites during the study and 1-6 caches were discovered at each site. A total of 79 seed caches were made by 21 different kangaroo rats at the 20 sites. At 1 site, a kangaroo rat that made 3 caches died the following day during attachment of a radiocollar, at another site a wire flag was blown away and the paired caches could not be located, and at the same site, 1 cache had already been collected before seeds could be counted. Thus, 74 caches made by 20 kangaroo rats at 19 sites and 74 identical artificial caches prepared nearby were monitored throughout the study. Nine kangaroo rats were radiocollared at their respective sites and 11 kangaroo rats at 10 sites were not collared. Pairs of caches were followed for varying amounts of time; all pairs were monitored for ≥8 days following the night they were made, but some pairs were followed up to 42 days.

Statistical analyses.—Whether real or artificial caches were recovered 1st was determined using Chi-squared analysis. In addition, rate of disappearance of real caches versus artificial caches was compared using survival analysis. Survival analysis is a group of statistical methods used to study timing of events (Allison 1995). In this case, survival analysis was used to determine whether real caches made by kangaroo rats were recovered significantly faster than artificial caches. Survival curves of real caches and artificial caches were generated and compared with Chi-squared statistics using PROC PHREG in SAS (SAS 9.1, SAS Institute, Inc., Cary, North Carolina). The variable of interest was number of days that each cache remained in the soil after it was made. Caches that remained >8 days were right-censored (Allison 1995).

PROC PHREG was selected for analysis of survival data because it uses a robust method called Cox Regression, which can handle discrete measurements of events, including tied data, and it also can cope effectively with clustering using stratification (Allison 1995). In this dataset, it was assumed that caches at a given site were not completely independent of each other because they were made by the same individual. However, treating caches within each site as a distinct cluster reduces bias in the analysis (Allison 1995). For all analyses, significance was set at $P < 0.05$. Because some kangaroo rats were captured and fitted with radiocollars, it was possible that the collar hampered movement, and thus, search and recovery of caches by the original hoarder at these sites. Therefore, recovery of caches at sites where hoarders had radiocollars was examined separately from sites where individuals were not wearing collars.

RESULTS

Characteristics of seed caches made by kangaroo rats.—Kangaroo rats typically prepared caches near the source of seeds, but occasionally traveled far away to cache seeds (Table 3, Chapter 2). Number of seeds in caches varied, but most caches were relatively large (modes = 62 and 74 seeds), and seed caches typically were completely covered by sand, although some caches were left uncovered (Appendix 6). Most caches (62%; 49 of 79) were placed at the edge of vegetation by kangaroo rats, some caches were placed in cover (29%; 23 of 79), and a few caches were made in open sand with no adjacent cover or vegetation (9%; 7 of 79).

Identity of hoarders and potential pilferers at sites.—Kangaroo rats that were observed caching seeds were captured at 17 sites. At the other 3 sites, no kangaroo rat with fluorescent powder was captured, but a kangaroo rat was observed caching seeds at 2 sites, and 2 kangaroo rats were observed caching seeds at the other site. Besides the 17 kangaroo rats that cached seeds, 23 others were captured at the 20 sites. Multiple kangaroo rats were captured at 55% of sites (11 of 20), a single kangaroo rat was captured at 35% of sites (7 of 20), and no kangaroo rat was captured at only 10% of sites (2 of 20). In addition, a total of 8 North American deermice (*Peromyscus maniculatus*) and 1 plains harvest mouse (*Reithrodontomys montanus*) was captured at 6 of the 20 sites. One deermouse was captured at each of 5 sites and 3 deermice and 1 harvest mouse were captured at 1 site.

Recovery of real versus artificial caches.—During the entire monitoring period, 78% (58 of 74) of caches made by kangaroo rats and 69% (51 of 74) of artificial caches were recovered. At the 10 sites where no individual was radiocollared, 66% (29 of 44) of real caches and 66% (29 of 44) of artificial caches were discovered after only 8 nights. At 84% (37 of 44) of paired-cache sites, ≥1 of the caches was discovered after 8 consecutive nights. Caches made by kangaroo rats were recovered 1st at 13 sites, artificial caches were recovered 1st at 9 sites, and both caches were recovered on the same night at 15 sites. At sites where only 1 of a pair of caches was discovered during a night, real caches were not discovered 1st more frequently than expected ($\chi^2 = 0.73$, *d.f.* = 1, $P = 0.394$). In addition, real caches were not removed significantly faster than artificial caches when survival curves were compared ($\chi^2 = 3.46$, *d.f.* = 1, $P = 0.063$; Fig. 5A).

At the 9 sites where hoarders were radiocollared, 53% (16 of 30) of real caches and 27% (8 of 30) of artificial caches were discovered after 8 nights. At 57% (17 of 30) of paired-cache sites, ≥1 of the caches was discovered and caches made by kangaroo rats were recovered 1st at 13 sites, artificial caches were recovered 1st at 3 sites, and both caches were recovered on the same night at only 1 site. At sites where only 1 of a pair of caches was discovered during a night, real caches were discovered 1st more frequently than expected ($\chi^2 = 6.25$, *d.f.* = 1, $P = 0.012$). At these sites, where the hoarder was radiocollared, real caches were recovered significantly faster than artificial caches when survival curves were compared ($\chi^2 = 5.17$, *d.f.* = 1, $P = 0.023$; Fig. 5B).

Frequency of incompletely recovered caches.—Of caches that were retrieved during the study at sites with and without radiocollared kangaroo rats, 76% (44 of 58) of real caches and 65% (33 of 51) of artificial caches were only partially recovered. From 1 to >15 seeds remained buried in the cache or were left on the surface of the ground near the cache, but most partially recovered caches contained 1-3 seeds after recovery (Fig. 6). By the end of the study, 38% (29 of 77) of these partially recovered caches still had ≥1 viable seed buried in the cache or on the surface of the ground near the cache. At least 1 viable seed remained buried at 14 caches, on the surface at 11 caches, and both buried and on the surface at 4 caches.

DISCUSSION

Recovery of caches.—Radiocollars influenced recovery of seed caches by Ord's kangaroo rats because results from sites where individuals were radiocollared differed from sites where individuals were not collared. If radiocollars restricted movement and search for caches by individuals, then I would suspect that fewer real caches would be recovered. However, the opposite was observed; real caches were recovered before artificial caches and at a faster rate than artificial caches at these sites. Reasons for these results are unclear, but some insight might be gained after discussing results at sites where individuals were not radiocollared.

Caches of seeds made by Ord's kangaroo rats (at sites where no individual was radiocollared) were not recovered before artificial caches or at a faster rate than artificial caches. This suggests that kangaroo rats that cache seeds in small, inconspicuous scatterhoards do not have an advantage over granivorous pilferers when recovering their own seed caches. Although kangaroo rats may use spatial memory to return to cache sites (e.g., Jacobs 1992), the disappearance of artificial caches demonstrates that high rates of pilferage occurred in this system. Recent studies of retrieval of caches using the paired-cache technique have shown a distinct advantage in recovery of real caches by yellow pine chipmunks (Vander Wall et al. 2006a) and southern flying squirrels (*Glaucomys volans*; Winterrowd and Weigl 2006). In contrast, this study did not show a distinct difference in rate of recovery of real and artificial caches because many artificial caches also were recovered quickly. Although results of this research on recovery of caches differs from similar research on other rodents, many studies have demonstrated high rates of pilferage on caches prepared by rodents (see review by Vander Wall and

Jenkins 2003). Why then do kangaroo rats in the Sandhill Region put time and energy into caching seeds if they do not have a distinct advantage over granivorous pilferers in recovering these caches?

Vander Wall and Jenkins (2003) introduced a hypothesis of reciprocal pilferage that explained how solitary rodents might benefit from scatterhoarding even when a large portion of their caches are pilfered. They proposed that if caching animals also pilfer caches made by other individuals, then they may recover enough caches for scatterhoarding to persist in a system with high rates of pilferage as long as no animals only pilfer and do not cache. Although individuals are caching for their own benefit, they might lose caches to other kangaroo rats, and alternatively discover caches made by other individuals. Ord's kangaroo rats in the Sandhill Region might represent a population that copes with high rates of theft by reciprocal pilferage for several reasons. First, these kangaroo rats use overlapping foraging areas in the Sandhill Region; multiple individuals often were seen and captured near the same seed tray on the same evening. In addition, individuals typically cached seeds near the source of seeds and were not observed defending cache sites (Chapter 2). Kangaroo rats also have a keen sense of olfaction; they were the most successful rodents at finding caches buried in soil compared to other heteromyids, murids, and sciurids (Reichman and Oberstein 1977; Vander Wall et al. 2003). Because they are so efficient at finding buried seeds, even when they have no knowledge of the location of caches, kangaroo rats probably are good pilferers. In fact, Merriam's kangaroo rats (*D. merriami*) are known to pilfer scatterhoards from each other (Daly et al. 1992; Leaver and Daly 2001; Murray et al. 2006). Based on observations that kangaroo rats often use the same areas for foraging, have a keen sense of smell, and pilfer caches, recovery of caches in this system might be explained by reciprocal pilferage.

One confounding factor that likely influenced detection of caches was the frequency of wet soil resulting from rain during the study. Moisture in soil increases discovery of buried seeds by rodents (Geluso 2005; Johnson and Jorgensen 1981; Vander Wall 1993, 1998, 2000). During my study, it rained on 16 of 44 days and these rain events often saturated the soil (Appendix 1). For example, after 1 rain event, the soil was saturated to a depth of 30 cm on the following day. The wet soil likely increased detection of seed caches by rodents; however, rain was so common that it was not apparent whether caches disappeared more frequently immediately following a rain. Because soil moisture has such a strong influence on detection of buried seeds by rodents, the rate of pilferage observed in this study likely was elevated by soil conditions.

Despite the influence of soil moisture on cache detection, it is possible that Ord's kangaroo rats actually recovered their own seed caches faster than artificial caches, but that this behavior was masked by the experimental design. Data from this study are different from results of cache retrieval in yellow pine chipmunks using essentially the same methods (Vander Wall et al. 2006a). Chipmunks retrieved their own caches more quickly than artificial caches, most likely by using spatial memory to return to cache sites. Because researchers did not check for presence of caches every day, it is unclear how frequently both real and artificial caches were recovered on the same day (Vander Wall et al. 2006a). However, during the initial recovery period in my study, both caches were discovered during the same night at 34% (15 of 44) of paired-cache sites. Olfactory sensitivity of kangaroo rats might be so strong that individuals detected artificial caches when searching for real caches at the same site. Perhaps, kangaroo rats used spatial memory to return to the general area where they cached seeds and subsequently used olfaction to pinpoint the exact location of the cache. This could have resulted in many individuals also locating the artificial cache that was just 30 cm away from the real cache. Thus, use of spatial memory by kangaroo rats to locate and retrieve their own caches might have been masked as a result of discovery of artificial caches by the hoarder using olfaction. This scenario also might help explain results observed at sites where hoarders were radiocollared. If pilferage by other kangaroo rats was uncommon and hoarders were mainly responsible for finding artificial caches, and radiocollared individuals were hampered in their search, then these individuals may not have found as many artificial caches assuming it took longer to locate these caches than their own caches.

Implications for dispersal of soapweed yucca.—Whether the original hoarder or a pilferer recovered caches, many real and artificial seed caches were recovered quickly. Seeds that were recovered from caches could be eaten, recached in scatterhoards, or stored in larders within burrows. Fragments of seed coats found at several caches (20 of 109 recovered caches) indicate that at least some of the recovered seeds were consumed. However, most caches lacked any sign of seeds being eaten at the cache site. In addition, Ord’s kangaroo rats rarely larderhoard seeds in summer in the Sandhill Region (Chapters 2 and 4), so it is unlikely that many seeds were taken into burrows. Thus, most recovered seeds that were taken from caches intact likely were eaten at another location or recached into other scatterhoards. Recaching seeds is common in solitary rodents with caching patterns that have been intensively studied, such as yellow pine chipmunks (Vander Wall and Joyner 1998), eastern chipmunks (*Tamias striatus*; Clarke and Kramer 1994), and Merriam's kangaroo rats (Jenkins and Peters 1992; Jenkins et al. 1995).

Although most caches were recovered, the majority of these caches were not recovered completely. Leaving seeds in caches seemed to be accidental in most cases because the majority of caches contained few seeds after recovery. In addition, some seeds were left exposed on the surface and some were shallowly buried under sand near the cache suggesting that seeds had been tossed out during recovery of the cache. Other seeds were found buried in the original cache, but a pit was still present so the animal did not attempt to conceal the cache. It is unclear how frequently hoarders leave seeds behind at caches, but this behavior has been reported previously. For example, when yellow pine chipmunks recovered caches of Jeffrey pine seeds (Vander Wall 1992) and bush chinquapin nuts (Roth and Vander Wall 2005), they were not reported to have left seeds at cache sites, but when they recovered antelope bitterbrush seeds from caches, they occasionally left seeds (Vander Wall 1995). This behavior apparently was intentional because chipmunks left ≥3 seeds at most caches and seeds were reburied (Vander Wall 1995). Merriam's kangaroo rats also were reported to occasionally have left 1-3 hulled sunflower seeds in caches when recovering scatterhoards in a laboratory arena, but whether this behavior was accidental or intentional was not discussed (Jenkins et al. 1995). Additionally, rodents (probably *P. maniculatus* and *D. ordii*) in eastern Colorado sometimes left 1-2 limber pine (*Pinus flexilis*) seeds at cache sites after recovering scatterhoards, but again it was not discussed whether this behavior was accidental (Tomback et al. 2005).

Perhaps, the number of seeds in caches is important in complete recovery of caches. Studies of scatterhoarding by rodents and birds have used various seeds, and size and shape of seeds likely influences number of seeds placed in caches. If incomplete recovery of caches is a function of size of cache, then seeds might be left behind more often from caches made by kangaroo rats because these rodents make relatively large scatterhoards. Panamint kangaroo rats (*D. panamintinus*) made the largest caches of piñon pine (*Pinus monophylla*) seeds compared to another heteromyid (Great Basin pocket mouse, *Perognathus parvus*), 2 murids, and 2 sciurids in northwestern Nevada (Hollander and Vander Wall 2004). Thus, the frequency of caches that were incompletely recovered in this study likely was partly due to Ord's kangaroo rats making large caches.

Regardless of factors involved in incomplete recovery of caches, this behavior likely is important to dispersal of soapweed yucca. Seeds of *Y. glauca* are described as wind-dispersed (Bare 1979; Dodd and Linhart 1994); these seeds are thin and light and can be carried by wind after the dehiscent pods split open and release seeds. However, seeds of soapweed yucca also are gathered and dispersed by kangaroo rats and possibly by other scatterhoarding animals. In fact, kangaroo rats may play a significant role in the dispersal of *Y. glauca*. These rodents were observed dismantling yucca pods on the ground to harvest seeds before pods completely dried and split. It is not clear whether kangaroo rats climbed yucca stalks to cut pods, but this seems likely because many pods on the ground showed evidence of being chewed from stalks. In addition, Ord's kangaroo rats climb sunflowers in the Sandhills Region and cut seed-filled flowering heads from stems (Lemen and Freeman 1985). Whether kangaroo rats harvest yucca seeds from the surface of the ground or directly from pods, a large amount of yucca seeds are stored in caches, many of which are either neglected or not completely recovered. Neglect of seed caches, or recovery, recaching, and subsequent neglect is important to establishment of seedlings (Roth and Vander Wall 2005; Vander Wall 1994, 1995; Vander Wall and Joyner 1998), but the role of incomplete recovery on reproductive success of plants has received less attention (Vander Wall 1995). Nevertheless, in the present study, incomplete recovery likely is important for seed dispersal because caches with overlooked seeds usually were not revisited and many of these seeds were viable. Although the eventual fate of these seeds is unknown, if they remain viable and are not recovered and eaten, or stored deep underground, then they may germinate and establish seedlings.

Recently, Vander Wall et al. (2006b) discovered that scatterhoarding rodents in the Mojave Desert are important, if not the only, dispersal agents for Joshua trees (*Yucca brevifolia*). Seeds of Joshua trees are contained within indehiscent pods that do not dry and split like pods of soapweed yucca. The only known method for seeds to exit these pods is by rodents dismantling pods and extracting seeds (Vander Wall et al. 2006b). Although pods of the soapweed yucca split and seeds can be initially wind-dispersed, kangaroo rats that gather and cache seeds act as a 2nd phase of seed dispersal. Thus, dispersal of *Y. glauca* is another example of diplochory; the dispersal of seeds by 2 or more phases involving different dispersal agents (e.g., Vander Wall 1992). This process usually is more beneficial for seeds than just 1 mechanism of dispersal (Vander Wall and Longland 2004). Also, Ord’s kangaroo rats are the initial, and possibly only, dispersal agent for seeds harvested directly from pods and cached in scatterhoards. Future studies on fate of seeds of yuccas, as well as other plants, likely will reveal that scatterhoarding animals are important dispersal agents for many plants, even those with seeds that are commonly believed to be dispersed by other mechanisms.

LITERATURE CITED

Addicott, J. F. 1986. Variation in the costs and benefits of mutualism: the interaction between yuccas and yucca moths. Oecologia (Berlin) 70:486-494.

Allison, P. D. 1995. Survival analysis using the SAS system: a practical guide. SAS Institute, Inc., Cary, North Carolina.

Andersson, M., and J. Krebs. 1978. On the evolution of hoarding behaviour. Animal Behaviour 26:707-711.

Bare, J. E. 1979. Wildflowers and weeds of Kansas. Regents Press of Kansas, Lawrence.

Clarke, M. F., and D. L. Kramer. 1994. The placement, recovery, and loss of scatter hoards by eastern chipmunks, Tamias striatus. Behavioral Ecology 5:353-361.

Clarkson, K., S. F. Eden, W. J. Sutherland, and A. I. Houston. 1986. Density dependence and magpie food hoarding. The Journal of Animal Ecology 55:111-121.

Cowie, R. J., J. R. Krebs, and D. F. Sherry. 1981. Food storing by marsh tits. Animal Behaviour 29:1252-1259.

Daly M, L. F. Jacobs, M. I. Wilson, and P. R. Behrends. 1992. Scatter hoarding by kangaroo rats (*Dipodomys merriami*) and pilferage from their caches. Behavioral Ecology 3:102-111.

Devenport, J. A., L. D. Luna, and L. D. Devenport. 2000. Placement, retrieval, and memory of caches by thirteen-lined ground squirrels. Ethology 106:171-183.

Dodd, R. J., and Y. B. Linhart. 1994. Reproductive consequences of interactions between *Yucca glauca* (Agavaceae) and *Tegeticula yuccasella* (Lepidoptera) in Colorado. American Journal of Botany 81:815:825.

Duncan, R. S., D. G. Wenny, M. D. Spitzer, and C. J. Whelan. 2002. Does human scent bias seed removal studies? Ecology 83:2630-2636.

Geluso, K. 2005. Benefits of small-sized caches for scatter-hoarding rodents: influence of cache size, depth, and soil moisture. Journal of Mammalogy 86:1186-1192.

Hollander, J. L., and S. B. Vander Wall. 2004. Effectiveness of six species of rodents as dispersers of singleleaf piñon pine (*Pinus monophylla*). Oecologia (Berlin) 138:57-65.

Jacobs, L. F. 1992. Memory for cache locations in Merriam's kangaroo rats. Animal Behaviour 43:585-593.

Jenkins, S. H., and R. A. Peters. 1992. Spatial patterns of food storage by Merriam's kangaroo rats. Behavioral Ecology 3:60-65.

Jenkins, S. H., A. Rothstein, and W. C. H. Green. 1995. Food hoarding by Merriam's kangaroo rats: a test of alternative hypotheses. Ecology 76:2470-2481.

Johnson, T. K., and C. D. Jorgensen. 1981. Ability of desert rodents to find buried seeds. Journal of Range Management 34:312-314.

Leaver, L. A., and M. Daly. 2001. Food caching and differential cache pilferage: a field study of coexistence of sympatric kangaroo rats and pocket mice. Oecologia (Berlin) 128:577-584.

Lemen, C. A., and P. W. Freeman. 1985. Tracking mammals with fluorescent pigments: a new technique. Journal of Mammalogy 66:134-136.

Longland, W. S., and C. Clements. 1995. Use of fluorescent pigments in studies of seed caching by rodents. Journal of Mammalogy 76:1260-1266.

Macdonald, D. W. 1976. Food caching by red foxes and some other carnivores. Zietschrift für Tierpsychologie 42:170-185.

Murray A. L., A. M. Barber, S. H. Jenkins, and W. S. Longland. 2006. Competitive environment affects food-hoarding behavior of Merriam's kangaroo rats (*Dipodomys merriami*). Journal of Mammalogy 87:571-578.

Reichman, O. J., and D. Oberstein. 1977. Selection of seed distribution types by *Dipodomys merriami* and *Perognathus amplus*. Ecology 58:636-643.

Roth, J. K., and S. B. Vander Wall. 2005. Primary and secondary seed dispersal of bush chinquapin (Fagaceae) by scatterhoarding rodents. Ecology 86:2428-2439.

Smith, C. C., and O. J. Reichman. 1984. The evolution of food caching by birds and mammals. Annual Review of Ecology and Systematics 15:329-351.

Stapanian, M. A., and C. C. Smith. 1978. A model for seed scatterhoarding: coevolution of fox squirrels and black walnuts. Ecology 59:884-896.

Tomback, D. F., A. W. Schoettle, K. E. Chevalier, and C. A. Jones. 2005. Life on the edge for limber pine: seed dispersal within a peripheral population. Ecoscience 12:519-529.

Vander Wall, S. B. 1990. Food hoarding in animals. University of Chicago Press, Chicago.

Vander Wall, S. B. 1992. The role of animals in dispersing a “wind-dispersed” pine. Ecology 73:614-621.

Vander Wall, S. B. 1993. Seed water content and the vulnerability of buried seeds to foraging rodents. The American Midland Naturalist 129:272-281.

Vander Wall, S. B. 1994. Seed fate pathways of antelope bitterbrush: dispersal by seed-caching yellow pine chipmunks. Ecology 75:1911-1926.

Vander Wall, S. B. 1995. Dynamics of yellow pine chipmunk (*Tamias amoenus*) seed caches: underground traffic in bitterbrush seeds. Ecoscience 2:261-266.

Vander Wall, S. B. 1998. Foraging success of granivorous rodents: effects of variation in seed and soil water on olfaction. Ecology 79:233-241.

Vander Wall, S. B. 2000. The influence of environmental conditions on cache recovery and cache pilferage by yellow pine chipmunks (*Tamias amoenus*) and deer mice (*Peromyscus maniculatus*). Behavioral Ecology 11:544-549.

Vander Wall, S. B., and S. H. Jenkins. 2003. Reciprocal pilferage and the evolution of food-hoarding behavior. Behavioral Ecology 14:656-667.

Vander Wall, S. B., and J. W. Joyner. 1998. Recaching of Jeffrey pine (*Pinus jeffreyi*) seeds by yellow pine chipmunks (*Tamias amoenus*): potential effects on plant reproductive success. Canadian Journal of Zoology 76:154-162.

Vander Wall, S. B., and W. S. Longland. 2004. Diplochory: are two seed dispersers better than one? Trends in Ecology and Evolution 19:155-161.

Vander Wall, S. B., J. S. Briggs, S. H. Jenkins, K. M. Kuhn, T. C. Thayer, and M. J. Beck. 2006a. Do food-hoarding animals have a cache recovery advantage? Determining recovery of stored food. Animal Behaviour 72:189-197.

Vander Wall, S. B., T. Esque, D. Haines, M. Garnett, and B. A. Waitman. 2006b. Joshua tree (*Yucca brevifolia*) seeds are dispersed by seed-caching rodents. Ecoscience 13:539-543.

Vander Wall, S. B., M. J. Beck, J. S. Briggs, J. K. Roth, T. C. Thayer, J. L. Hollander, and J. M. Armstrong. 2003. Variation in the olfactory abilities of granivorous rodents. Journal of Mammalogy 84:487-496.

Wenny, D. G. 2002. Effects of human handling of seeds on seed removal by rodents. The American Midland Naturalist 147:404-408.

Whitcomb, R. F. 1989. Nebraska sand hills: the last prairie. Proceedings of the North American Prairie Conference 11:57-69.

Wilhite, D. A., and K. G. Hubbard. 1989. Climate. Pp. 17-28 in An atlas of the Sand Hills (A. Bleed and C. Flowerday, eds.). University of Nebraska-Lincoln: Conservation and Survey Division at the Institute of Agriculture and Natural Resources 5a:1-265.

Winterrowd, M. F., and P. D. Weigl. 2006. Mechanisms of cache retrieval in the group nesting southern flying squirrel, *Glaucomys volans*. Ethology 112:1136-1144.

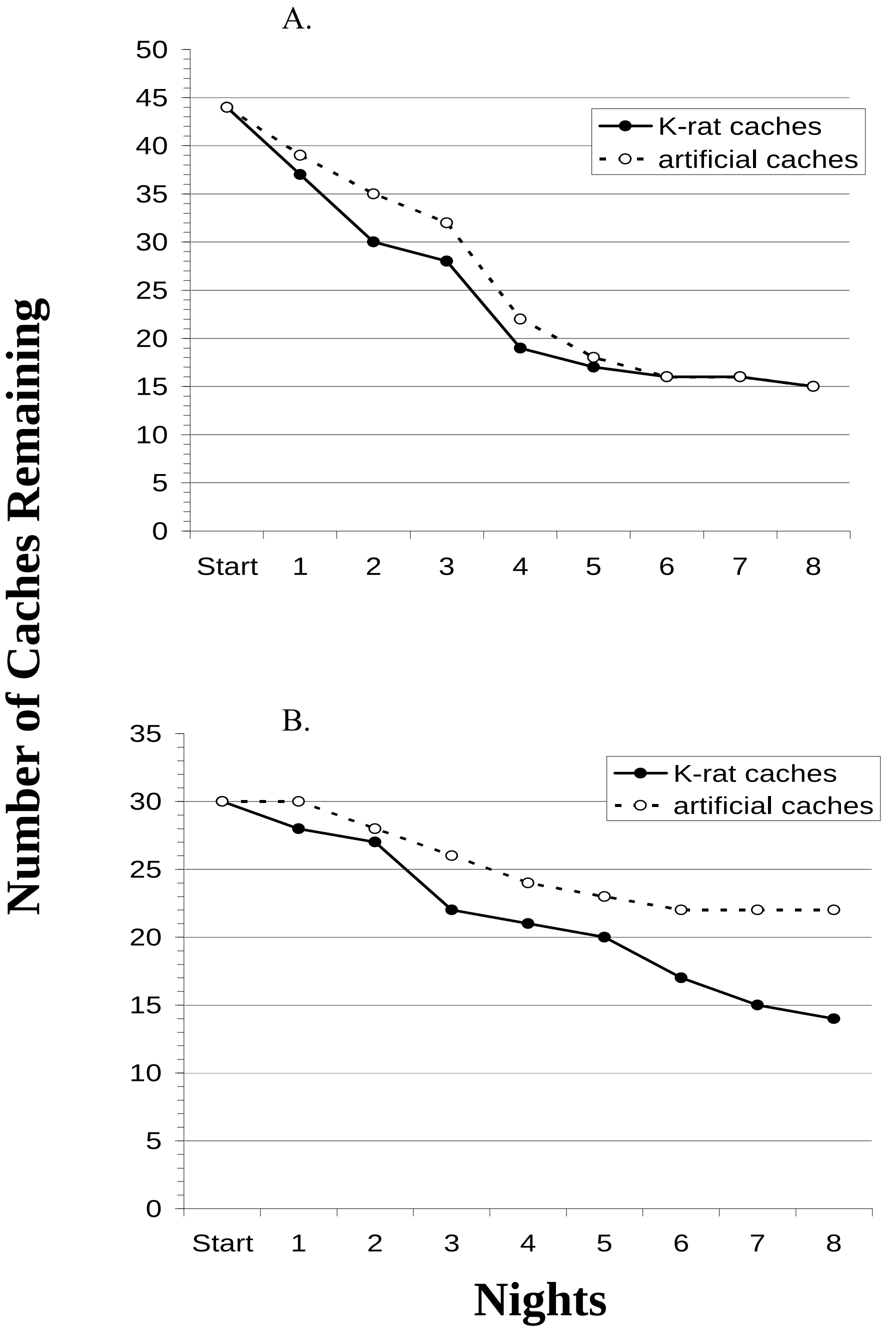

Fig. 5. Survival curves of real caches of seeds of the soapweed yucca (*Yucca glauca*) prepared by Ord's kangaroo rats (*Dipodomys ordii*) and identical artificial caches placed 30 cm away from real caches. Graph A illustrates survival of real and artificial caches at sites where hoarders were not radiocollared, and graph B shows survival of caches at sites where hoarders were radiocollared.

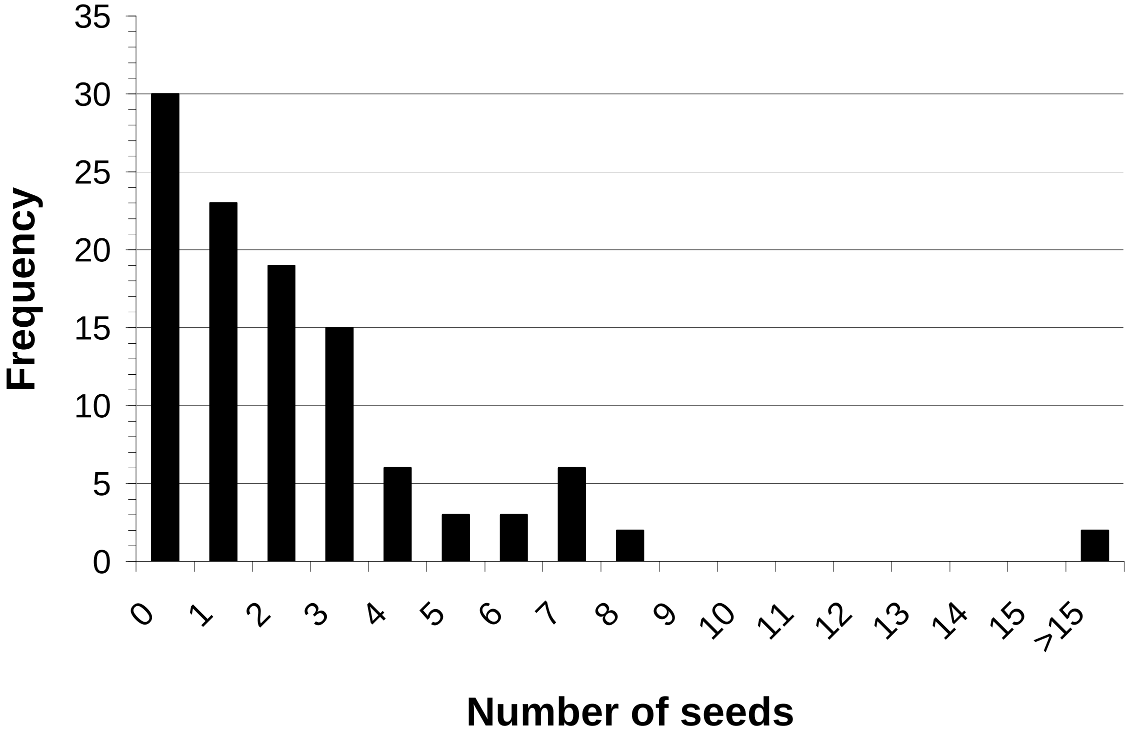

Fig. 6**.** Numbers of seeds of the soapweed yucca (*Yucca glauca*) remaining at cache sites of Ord's kangaroo rats (*Dipodomys ordii*) after seed caches were recovered in the Sandhill Region of Nebraska, summer 2007. Some seeds remained buried in caches and other seeds were left on the surface of the ground near the cache.

CHAPTER 4

STRUCTURE OF BURROWS AND CONTENTS OF FOOD HOARDS OF ORD'S KANGAROO RATS (*DIPODOMYS ORDII*) IN THE SANDHILL REGION OF NEBRASKA

ABSTRACT

Characteristics of burrows and extent of larderhoarding differs among species of kangaroo rats, and limited information exists for burrows and larderhoards of Ord's kangaroo rat (*Dipdomys ordii*). Burrows of *D. ordii* were excavated in summer in the Sandhill Region of Nebraska to determine structure of burrows and contents of food stored within burrows. Burrows of male and female Ord's kangaroo rats were simple in structure, consisting of 1 main tunnel with 1-3 entrances, which were plugged with sand when occupied. Little food was stored within burrows; however, small bundles of cut stems of sand dropseed (*Sporobolus cryptandrus*) were in 80% of excavated burrows. Most stems of sand dropseed contained seeds within the sheath of the stem. This is the 1st documentation of this foraging and caching behavior in *D. ordii* and the 2nd report for the genus. Evidence suggests that Ord's kangaroo rats forage on concentrated resources in the Sandhill Region of Nebraska by harvesting seeds directly from plants. Future research should investigate the frequency of this foraging behavior in kangaroo rats and implications of this behavior on plant communities.

INTRODUCTION

Kangaroo rats are nocturnal, semi-fossorial rodents that inhabit arid and semi-arid regions throughout western North America (Schmidly et al. 1993). Individuals spend most time in burrows and only engage in short-lived bouts aboveground (Braun 1985; Kenagy 1976; Langford 1983; Schroder 1979). Diet of kangaroo rats is composed mainly of seeds (Flake 1973; Lowe 1997; Reichman 1975), and individuals store seeds in burrows, surface caches, or both for future use (Hawbecker 1940; Reynolds 1958; Shaw 1934; Vorhies and Taylor 1922). Structure of burrows differs among species of *Dipodomys*. Some kangaroo rats such as banner-tailed kangaroo rats (*Dipodomys spectabilis*) and giant kangaroo rats (*Dipodomys ingens*) construct large, elaborate mounds with multiple entrances and many chambers for food storage (Shaw 1934; Vorhies and Taylor 1922). While some species, such as Merriam's kangaroo rat (*Dipodomys merriami*), construct comparatively simple burrows without large chambers for food storage (Bienek and Grundmann 1971; Reynolds 1958). Ord's kangaroo rat (*Dipodomys ordii*) is widespread throughout western North America (Garrison and Best 1990); however, few studies have investigated characteristics of burrows inhabited by this species (Reynolds and Wakkinen 1987). Reynolds and Wakkinen (1987) documented burrow structure of *D. ordii* in sagebrush habitat of Idaho, but did not mention whether food was present inside burrows. Thus, objectives of this study were to describe the structure of burrows and contents of food stored inside burrows of *D. ordii* in summer in a temperate grassland region.

Accounts of food hoarding in *D. ordii* in Nevada suggest this species is primarily a larderhoarder (Jenkins and Breck 1998). In addition, observations indicate that individuals defend burrows and possibly territories in Utah (Langford 1983). However, while studying burrow-use and food-hoarding behavior of *D. ordii* in the Sandhill Region of Nebraska, most individuals commonly used >1 burrow (Chapter 1) and scatterhoarded seeds in small, sub-surface caches in summer (Chapter 2). Due to methodical constraints, it was only possible to determine where kangaroo rats initially stored seeds. The possibility existed that individuals quickly recovered caches and deposited seeds within their burrows or that individuals scatterhoarded seeds in response to a lack of space for food storage within burrows. However, because most individuals used >1 burrow, maintaining a large store of seeds inside burrows seemed unlikely in this population. Animals benefit from larderhoarding only if they protect their resources, and an unoccupied burrow with a larder of seeds is susceptible to theft by pilferers (Vander Wall et al. 2005). Therefore, I predicted that burrows of *D. ordii* in summer in the Sandhill Region of Nebraska would be relatively simple in structure with few seeds stored inside.

MATERIALS AND METHODS

Research was conducted at Crescent Lake National Wildlife Refuge in Garden County, Nebraska. This wildlife refuge is located in the Sandhill Region of Nebraska; an area of sand dunes covered in grasses, forbs, and shrubs (Whitcomb 1989). Common vegetation on the dunes includes sand bluestem (*Andropogon hallii*), sand muhly (*Muhlenbergia arenicola*), prairie sandreed (*Calamovilfa longifolia*), sand dropseed (*Sporobolus cryptanthus*), needle and thread (*Stipa comata*), sunflowers (*Helianthus*), blazing star (*Mentzelia*), sand cherry (*Prunus pumila*), and soapweed yucca (*Yucca glauca*). The soils of the region are composed of sand mixed with 1-4% silt and clay

(Whitcomb 1989). Summers are warm (average maximum temperature for July = 31.7ºC) and winters are cold (average minimum temperature for January = -12.8ºC) in the region and nearly 80% of precipitation falls April to September (Wilhite and Hubbard 1989). Ord's kangaroo rats are abundant in the Sandhill Region of Nebraska and they are the only species of kangaroo rat that occurs there (Jones et al. 1983).

To identify patterns of burrow use by Ord's kangaroo rats for a different study, individuals were collared with radiotransmitters attached to beaded-chain collars (Harker et al. 1999). After main burrows of kangaroo rats were identified with radiotelemetry, the structure of selected burrows was examined. Height and width of entrances to burrows were measured when they were located during July-August 2006 and 2007. In addition, 10 burrows were excavated during 15 July-16 August 2007 to measure the length and maximum depth of burrows. Burrows were excavated with a small shovel as tunnels remained intact due to the silt and clay in the soil. Height and width of the main tunnel also were measured for some burrows and number of entrances to burrows was recorded. Presence of a nest or any stored food inside the burrow was noted, and food items were collected and quantified from 4 burrows. Four excavated burrows were recently occupied by 4 males and 6 burrows were recently occupied by 3 females. Three burrows were used by the same female, 2 burrows were used by another female, and 1 burrow was used by the 3rd female.

RESULTS

Day burrows used by Ord's kangaroo rats in summer were simple in structure, usually consisting of 1 main tunnel with a small chamber and entrances at either end of the tunnel (Fig. 7). Most burrows had 1-2 entrances and only 2 burrows had >2 entrances. Occasionally, a tunnel would ascend from the deepest point of the burrow and terminate just below the surface of the soil instead of opening to the surface. True entrances to burrows were inconspicuous as they were small, plugged with sand when occupied, and typically situated in clumps of vegetation instead of open sand. These entrances widened into a main tunnel just below the surface that was about twice the size of the entrance (Table 5; Appendix 7). Side tunnels extending from the main tunnel were in only 3 of the 10 burrows, but small chambers off of the main tunnel were present in 9 of the 10 burrows.

Although a small chamber was present in most burrows, nesting material was only in 2 of the 10 burrows that were excavated in summer. However, seeds and cut stems containing seed heads were stored in most burrows (9 of 10 burrows). The most common items stored in burrows were cut stems (1-3 cm in length) of sand dropseed (*Sporobolus cryptanthus*) that contained seed heads within the sheath of the stem (Fig. 8). Small bundles of these stems were in 8 of the 10 burrows where they were pushed into floors and walls of main tunnels or chambers. Number of stems in bundles collected from 4 burrows was 71-145 stems. Other items in burrows were scattered seeds of soapweed yucca (*Yucca glauca*), sunflower (*Helianthus*), peppergrass (*Lepidium densiflorum*), paspalum (*Paspalum setaceum*), seed heads of sixweeks fescue (*Festuca octoflora*), and seed heads of Schweinitz flatsedge (*Cyperus schweinitzii*).

DISCUSSION

Burrows used by Ord's kangaroo rats in summer in the Sandhill Region of Nebraska were simple in structure, usually only consisting of 1 main tunnel that penetrated to a maximum depth of ca. 0.5 m in the soil. Burrows typically had 1-2 entrances that were small and plugged with sand while kangaroo rats resided in burrows during daytime hours. Length and depth of burrows in the Sandhill Region were similar to those of Ord's kangaroo rats in Idaho (Reynolds and Wakkinen 1987). Burrows of Merriam's kangaroo rats also are simple in structure (Bieniek and Grundmann 1971; Reynolds 1958), but individuals frequently do not plug burrow entrances (Bienek and Grundmann 1971; Kenagy 1973; Soholt 1974).

Not surprisingly, Ord's kangaroo rats did not maintain large stores of food inside burrows in July or early August in the Sandhill Region. Scatterhoarding by these kangaroo rats is common in summer (Chapter 2), and from the lack of stored food inside burrows, individuals likely do not move contents of caches to larderhoards within burrows during this season. However, small bundles of sand dropseed stems were in 8 of 10 excavated burrows. These sections of stems were cut from plants before seed heads emerged from the sheath. This is the 1st report of this behavior in *D. ordii*, but others have observed the same behavior in banner-tailed kangaroo rats (*D. spectabilis*; Herrera et al. 2001; Schroder 1979; Vorhies and Taylor 1922). Bundles of sand dropseed stems stored by *D. ordii* were similar in size (71-145 stems) to those cached by *D. spectabilis* (50 to several hundred; Herrera et al. 2001), although total number of stems in burrows of *D. spectabilis* were much larger (e.g., 680,000 stems; Vorhies and Taylor 1922). Schroder (1979) suggested that by cutting stems and seed heads directly from plants, *D.*

spectabilis can minimize time spent foraging on the surface. Ord's kangaroo rats also may frequently forage on plants before seeds drop. Besides cutting seed-filled stems of sand dropseed, *D. ordii* also chews into yucca pods to collect seeds (Chapter 2) and climbs sunflowers to clip seed-filled heads (Lemen and Freeman 1985). Although individuals did not maintain large stores of seeds inside burrows in summer (number of stems only approximates several pouch loads), Ord's kangaroo rats used concentrated resources similar to *D. spectabilis* (Schroder 1979), and brought small amounts of sand dropseed stems back to burrows in the Sandhill Region.

Common occurrence of seed stems of sand dropseed in burrows of Ord's kangaroo rats suggests that these animals were selective for this grass before seed heads emerged from the sheath. If kangaroo rats sought out this resource, it may negatively impact populations of this grass in the Sandhill Region, especially because *D. ordii* is so common in this area (Appendix 2). Even if individuals do not consume all seeds they gather, clipping and caching seed stems of sand dropseed within burrows likely prevents these seeds from germinating. However, Ord's kangaroo rats commonly bury soapweed yucca (*Yucca glauca*) seeds in scattered caches at depths of 0-4 cm in soil in the Sandhill Region (Chapter 2). Further, individuals occasionally neglect caches or do not completely recover all seeds in caches (Chapter 3). If kangaroo rats cache sand dropseed similarly, and if these seeds germinate from sheaths, then kangaroo rats may have a positive effect on dispersal of this grass. Seeds of sand dropseed were common in seedbanks in the Sandhills and germinated successfully at depths of 0-5 cm in the soil (Pérez et al. 1998). Future research should investigate the frequency of this foraging behavior in kangaroo rats, as well as the fate of these seeds, to determine the effect of this behavior on dispersal and reproductive success of sand dropseed.

LITERATURE CITED

Bienek, G. K., and A. W. Grundmann. 1971. Burrowing habits of two subspecies of *Dipodomys merriami* in California and Utah. Great Basin Naturalist 31:190-192.

Braun, S. E. 1985. Home range and activity patterns of the giant kangaroo rat, *Dipodomys ingens*. Journal of Mammalogy 66:1-12.

Flake, L. D. 1973. Food habits of four species of rodents on a short-grass prairie in Colorado. Journal of Mammalogy 54:636-647.

Garrison, T. E., and T. L. Best. 1990. Dipodomys ordii. Mammalian Species 353:1-10.

Harker, M. B., G. B. Rathbun, and C. A. Langtimm. 1999. Beaded-chain collars: a new method to radiotag kangaroo rats for short-term studies. Wildlife Society Bulletin 27:314-317.

Hawbecker, A. C. 1940. The burrow and feeding habits of *Dipodomys venustus*. Journal of Mammalogy 21:388-396.

Herrera, J., K. L. Ensz, and A. L. Wilke. 2001. Stacking of seeds changes spoilage dynamics of food caches of the banner-tailed kangaroo rat (*Dipodomys spectabilis*). Journal of Mammalogy 82:558-566.

Jenkins, S. H., and S. W. Breck. 1998. Differences in food hoarding among six species of heteromyid rodents. Journal of Mammalogy 79:1221-1233.

Jones, J. K., Jr., D. M. Armstrong, R. S. Hoffmann, and C. Jones. 1983. Mammals of the northern Great Plains. University of Nebraska Press, Nebraska.

Kenagy, G. J. 1973. Daily and seasonal patterns of activity and energetics in a heteromyid rodent community. Ecology 54:1201-1219.

Kenagy, G. J. 1976. The periodicity of daily activity and its seasonal changes in free-ranging and captive kangaroo rats. Oecologia (Berlin) 24:105-140.

Langford, A. L. 1983. Pattern of nocturnal activity of male *Dipodomys ordii* (Heteromyidae). The Southwestern naturalist 28:341-346.

Lemen, C. A., and P. W. Freeman. 1985. Tracking mammals with fluorescent pigments: a new technique. Journal of Mammalogy 66:134-136.

Lowe, M. 1997. Diet of Stephens' kangaroo rat, *Dipodomys stephensi*. The Southwestern Naturalist 42:358-361.

Pérez, C. J. S. S. Waller, L. E. Moser, J. L. Stubbendieck, and Allen A. Steuter. 1998. Seedbank characteristics of a Nebraska sandhills prairie. Journal of Range Management 51:55-62.

Reichman, O. J. 1975. Relation of desert rodent diets to available resources. Journal of Mammalogy 56:731-751.

Reynolds, H. G. 1958. The Ecology of the Merriam kangaroo rat (*Dipodomys merriami* Mearns) on the grazing lands of southern Arizona. Ecological Monographs 28: 111-127.

Reynolds, T. D., and W. L. Wakkinen. 1987. Characteristics of the burrows of four species of rodents in undisturbed soils in southeastern Idaho. The American Midland Naturalist 118:245-250.

Schmidly, D. J., K. T. Wilkins, and J. N. Derr. 1993. Biogeography. Pp. 319-356 in Biology of the Heteromyidae (H. H. Genoways and J. H. Brown eds.). Special Publication, The American Society of Mammalogists 10:1-719.

Schroder, G. D. 1979. Foraging behavior and home range utilization of the bannertail kangaroo rat (*Dipodomys spectabilis*). Ecology 60:657-665.

Shaw, W. T. 1934. The ability of the giant kangaroo rat as a harvester and storer of seeds. Journal of Mammalogy 15:275-286.

Soholt, L. F. 1974. Environmental conditions in an artificial burrow occupied by Merriam's kangaroo rat, *Dipodomys merriami*. Journal of Mammalogy 55:859-864.

Vander Wall, S. B., E. C. H. Hager, and K. M. Kuhn. 2005. Pilfering of stored seeds and the relative costs of scatter-hoarding versus larder-hoarding in yellow pine chipmunks. Western North American Naturalist 65:248-257.

Vorhies, C. T., and W. P. Taylor. 1922. Life history of the kangaroo rat *Dipodomys spectabilis spectabilis* Merriam. United States Department of Agriculture Bulletin 1091, Washington, District of Columbia.

Whitcomb, R. F. 1989. Nebraska sand hills: the last prairie. Proceedings of the North American Prairie Conference 11:57-69.

Wilhite, D. A., and K. G. Hubbard. 1989. Climate. Pp. 17-28 in An atlas of the Sand Hills (A. Bleed and C. Flowerday, eds.). University of Nebraska-Lincoln: Conservation and Survey Division at the Institute of Agriculture and Natural Resources, 5a:1-265.

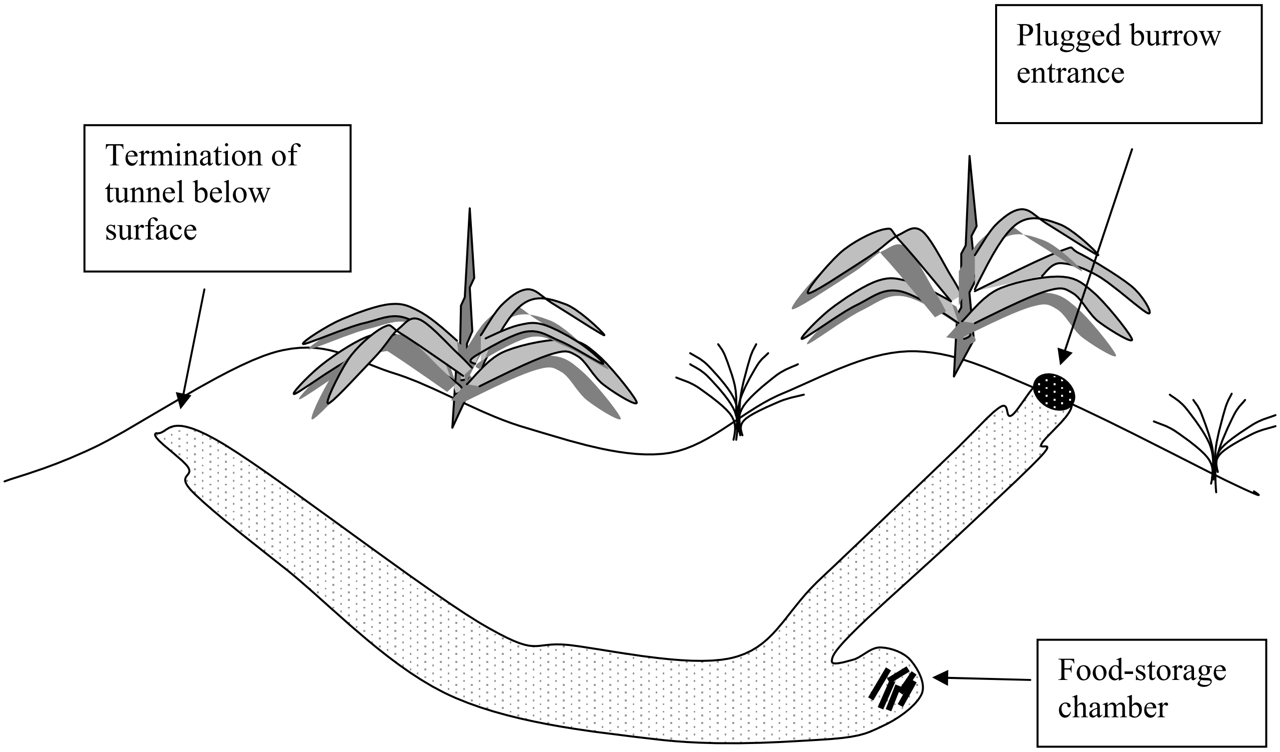

Fig. 7. Diagram of a typical burrow of Ord's kangaroo rat (*Dipodomys ordii*) in summer in the Sandhill Region of Nebraska. Entrances were small, plugged with sand when occupied, and situated in clumps of vegetation instead of open sand. Occasionally tunnels ended just beneath the surface of the soil.

Fig. 8. Cut stems of sand dropseed (*Sporobolus cryptanthus*), with seed heads contained within the stem, were in 8 of 10 burrows of Ord's kangaroo rats (*Dipodomys ordii*) in the Sandhill Region of Nebraska. Burrows were excavated in July and August 2007.

Table 5. Mean size of burrows used by Ord's kangaroo rats (*Dipodomys ordii*) in summer in the Sandhill Region of Nebraska. Measurements of entrances are based on 15 burrows in 2006 and 2007, measurements of length are from 10 burrows in 2007, measurements of maximum depth are from 9 burrows in 2007, and measurements of width and height of the main tunnel are from 4 burrows in 2007.

Entrance (cm)		Main tunnel (cm)			
Width	Height	Width	Height	Length	Maximum depth
3.7	4.1	8.3	8.1	332	46

APPENDICES

Appendix 1. Weather observations recorded during nights of data collection in the Sandhill Region of Nebraska. Information on phase of moon was gathered from the Astronomical Applications Department of the United States Naval Observatory.

Summer 2006

Date	Time (CDT)	Temperature (°C)	Precipitation	Wind	Cloud cover (%)	Phase of moon
6-Jul-06	2113	23.5	light rain	moderate breeze	-	first quarter
7-Jul-06	2025	25.5	none	moderate breeze	75	
8-Jul-06	2030	25.3	none	slight breeze	100	
9-Jul-06	2035	20.3	none	slight breeze	90	
10-Jul-06	2030	23.1	none	slight breeze	15	
11-Jul-06	2028	27.9	none	slight breeze	30	
12-Jul-06	2028	24.7	rain in afternoon	moderate breeze	30	
13-Jul-06	2045	23.7	none	no wind	2	
14-Jul-06	-	no weather data	-	-	-	full moon
15-Jul-06	-	no weather data	-	-	-	
16-Jul-06	-	no weather data	-	-	-	
17-Jul-06	-	no weather data	-	-	-	
18-Jul-06	2045	32.5	none	slight breeze	90	
19-Jul-06	2045	28.4	none	moderate breeze	40	
20-Jul-06	2045	25.5	none	no wind	80	
21-Jul-06	2042	25.9	none	slight breeze	10	
22-Jul-06	2055	23.1	none	slight breeze	15	last quarter
23-Jul-06	2026	29.7	none	moderate breeze	70	
24-Jul-06	-	no weather data	-	-	-	
25-Jul-06	2025	28.8	none	no wind	30	
26-Jul-06	2022	21.1	rain in afternoon	heavy wind	25	
27-Jul-06	-	no weather data	-	-	-	
28-Jul-06	2017	30.1	none	moderate breeze	25	
29-Jul-06	2040	30.8	none	moderate breeze	15	new moon
30-Jul-06	2025	29.1	none	slight breeze	30	
31-Jul-06	2019	25.6	none	heavy wind	95	

Appendix 1 continued.

Summer 2006

Date	Time (CDT)	Temperature (°C)	Precipitation	Wind	Cloud cover (%)	Phase of moon
1-Aug-06	2005	22.4	rain at 2200	slight breeze	40	
2-Aug-06	2023	22.7	none	no wind	10	first quarter
3-Aug-06	2014	27.5	none	moderate breeze	60	
4-Aug-06	2011	28.5	none	slight breeze	20	
5-Aug-06	2036	26.9	none	no wind	65	
6-Aug-06	2037	25.4	none	moderate breeze	30	
7-Aug-06	2047	25.0	none	moderate breeze	55	
8-Aug-06	2032	28.9	none	moderate breeze	0	
9-Aug-06	2028	26.7	none	no wind	50	full moon
10-Aug-06	2017	25.5	none	no wind	5	
11-Aug-06	-	no weather data	-	-	-	
12-Aug-06	2005	20.5	rain in afternoon	moderate breeze	85	
13-Aug-06	-	no weather data	-	-	-	
14-Aug-06	-	22.9	none	heavy wind	50	
15-Aug-06	2017	24.2	none	heavy wind	100	
16-Aug-06	2024	24.8	none	slight breeze	20	last quarter
17-Aug-06	-	no weather data	-	-	-	
18-Aug-06	-	no weather data	-	-	-	
19-Aug-06	-	no weather data	-	-	-	
20-Aug-06	-	no weather data	-	-	-	
21-Aug-06	2007	27.5	none	moderate breeze	65	
22-Aug-06	2010	26.7	none	heavy wind	25	
23-Aug-06	2008	27.2	none	slight breeze	15	new moon
24-Aug-06	2013	25.8	none	moderate breeze	70	
25-Aug-06	-	no weather data	-	-	-	
26-Aug-06	2106	19.3	none	slight breeze	50	
27-Aug-06	-	no weather data	-	-	-	

Appendix 1 continued.

Summer 2006

Date	Time (CDT)	Temperature (°C)	Precipitation	Wind	Cloud cover (%)	Phase of moon
28-Aug-06	2053	14.7	none	no wind	10	
29-Aug-06	2048	18.4	none	moderate breeze	0	
30-Aug-06	-	no weather data	-	-	-	
31-Aug-06	-	no weather data	-	-	-	first quarter

Winter 2007

Date	Time (CDT)	Temperature (°C)	Precipitation	Wind	Cloud cover (%)	Phase of moon
2-Jan-07	2140	0.7	none	slight breeze	75	
3-Jan-07	2027	6.8	light snow	slight breeze	75	full moon
4-Jan-07	1910	1.9	none	slight breeze	85	
5-Jan-07	2255	-6.6	none	no wind	0	
6-Jan-07	1915	-0.2	none	moderate breeze	50	
7-Jan-07	-	no weather data	-	-	-	
8-Jan-07	2055	-0.5	none	heavy wind	0	
9-Jan-07	2205	-4.6	none	slight breeze	0	
10-Jan-07	5	1.8	none	no wind	75	
11-Jan-07	2338	-14.6	none	moderate wind	0	last quarter
12-Jan-07	-	no weather data	-	-	-	

Appendix 1 continued.

Summer 2007

Date	Time (CDT)	Temperature (°C)	Precipitation	Wind	Cloud cover (%)	Phase of moon
2-Jul-07	2317	25.7	none	moderate breeze	100	
3-Jul-07	2220	25.3	none	slight breeze	0	
4-Jul-07	2150	24.0	none	slight breeze	20	
5-Jul-07	2142	21.1	rain in afternoon	no wind	25	
6-Jul-07	2146	25.5	none	moderate breeze	0	
7-Jul-07	2200	24.2	rain at night	slight breeze	25	last quarter
8-Jul-07	2030	-	rain at night	-	-	
9-Jul-07	2148	22.9	rain at night	moderate breeze	20	
10-Jul-07	2150	22.8	rain at night	no wind	75	
11-Jul-07	2150	22.8	none	no wind	75	
12-Jul-07	-	no weather data	-	-	-	
13-Jul-07	2138	20.1	rain in afternoon	no wind	5	
14-Jul-07	2143	22.0	none	slight breeze	10	new moon
15-Jul-07	2135	24.8	none	moderate breeze	0	
16-Jul-07	2152	23.1	none	slight breeze	15	
17-Jul-07	-	no weather data	-	-	-	
18-Jul-07	2144	23.9	rain in afternoon	moderate breeze	85	
19-Jul-07	2154	20.9	none	slight breeze	25	
20-Jul-07	2157	22.7	none	moderate breeze	25	
21-Jul-07	2236	26.3	none	Heavy wind	35	
22-Jul-07	2230	26.1	none	slight breeze	30	first quarter
23-Jul-07	-	no weather data	-	-	-	
24-Jul-07	2147	26.6	none	moderate breeze	0	
25-Jul-07	-	no weather data	rain at night	-	-	
26-Jul-07	2158	23.5	rain at night	slight breeze	100	
27-Jul-07	-		rain	-	-	
28-Jul-07	-		rain	-	-	

Appendix 1 continued.

Summer 2007

Date	Time (CDT)	Temperature (°C)	Precipitation	Wind	Cloud cover (%)	Phase of moon
29-Jul-07	2135	22.3	none	moderate breeze	0	
30-Jul-07	2123	24.7	none	moderate breeze	5	full moon
31-Jul-07	2127	24.6	none	-	10	
1-Aug-07	2126	18.5	none	no wind	20	
2-Aug-07	-	no weather data	-	-	-	
3-Aug-07	2128	thermometer broken	rain	slight breeze	20	
4-Aug-07	-	no weather data	-	-	-	
5-Aug-07	2128	thermometer broken	none	slight breeze	90	last quarter
6-Aug-07	-	thermometer broken	rain in morning	slight breeze	100	
7-Aug-07	2134	thermometer broken	none	slight breeze	100	
8-Aug-07	-	no weather data	-	-	-	
9-Aug-07	-	no weather data	-	-	-	
10-Aug-07	-	thermometer broken	rain in afternoon	-	-	
11-Aug-07	-	no weather data	-	-	-	
12-Aug-07	-	no weather data	-	-	-	new moon
13-Aug-07	-	thermometer broken	rain in afternoon	-	-	
14-Aug-07	-	thermometer broken	rain in afternoon	-	-	
15-Aug-07	-	no weather data	-	-	-	
16-Aug-07	-	no weather data	-		-	

Appendix 1 continued.

Winter 2008

Date	Time (CDT)	Temperature (°C)	Precipitation	Wind	Cloud cover (%)	Phase of moon
3-Jan-08	2130	-8.0	none	no wind	0	
4-Jan-08	2230	-1.4	none	slight breeze	0	
5-Jan-08	1847	3.2	none	moderate breeze	25	
6-Jan-08	-	no weather data	-	-	-	
7-Jan-08	1932	-4.4	none	moderate breeze	0	
8-Jan-08	2030	-7.0	none	no wind	0	new moon
9-Jan-08	2200	-4	none	slight breeze	0	
10-Jan-08	1815	-1.1	none	no wind	100	
11-Jan-08	-	no weather data	-	-	-	

Appendix 2. Captures of small mammals on 1-ha grids containing 100 Sherman live traps with 10-m spacing between traps during 3 summers at Crescent Lake National Wildlife Refuge in the Sandhill Region of Nebraska. Grids were placed in choppy sandhills at the same location in 2005 and 2006 and 200 m away in 2007; *D. ordii* = *Dipodomys ordii*, *P. maniculatus* = *Peromyscus maniculatus*, and *P. flavescens* = *Perognathus flavescens*.

Summer 2005

Trap location	**Species**	**Sex**	**Age**	**Reproductive condition**	**Weight (g)**	**Tag #**	**30-Jul-05**	**31-Jul-05**	**1-Aug-05**
A1	*D. ordii*	♀	adult	non-reproductive	58	41	X	-	-
A2	*D. ordii*	♀	adult	lactating	63	150	X	X	X
A7	*D. ordii*	♂	adult	scrotal	60	176	X	X	X
A10	*D. ordii*	♀	adult	post-lactating	62	194	X	X	X
B9	*P. maniculatus*	♂	adult	scrotal	18	191	X	-	X
B7	*D. ordii*	♀	adult	post-lactating	71	43	X	X	X
C1	*D. ordii*	♂	adult	scrotal	70	185	X	-	X
C6	*D. ordii*	♂	adult	scrotal	76	48	X	-	-
D8	*D. ordii*	♂	adult	scrotal	72	42	X	X	-
D7	*D. ordii*	♂	adult	non-scrotal	63	180	X	X	-
D2	*P. maniculatus*	♂	adult	scrotal	20	119	X	-	X
E2	*D. ordii*	♀	adult	non-reproductive	55	161	X	X	-
E6	*D. ordii*	♂	juvenile	non-scrotal	23	38	X	X	X
F9	*D. ordii*	♀	adult	post-lactating	66	70	X	-	-
H6	*D. ordii*	♀	adult	non-reproductive	67	189	X	-	X
H3	*D. ordii*	♀	adult	lactating	67	58	X	X	X
H1	*D. ordii*	♀	adult	non-reproductive	59	178	X	-	X
I1	*D. ordii*	♂	adult	scrotal	65	193	X	X	X
I4	*D. ordii*	♂	adult	scrotal	62	163	X	X	X
I7	*P. manic*	♂	adult	scrotal	18	188	X	X	X
I8	*P. manic*	♀	subadult	non-reproductive	15	69	X	X	-
I10	*D. ordii*	♀	adult	post-lactating	64	46	X	-	-
J8	*P. manic*	♀	subadult	non-reproductive	15	112	X	-	-
J5	*D. ordii*	♀	adult	non-reproductive	53	122	X	X	X
J4	*D. ordii*	♀	adult	post-lactating	63	167	X	-	X

Appendix 2 continued.

Summer 2005

Trap location	Species	Sex	Age	Reproductive condition	Weight (g)	Tag #	30-Jul-05	31-Jul-05	1-Aug-05
A3	*D. ordii*	♂	adult	non-scrotal	61	168	-	X	X
B9	*P. manic*	♀	subadult	non-reproductive	18	169	-	X	X
B4	*D. ordii*	♀	juvenile	non-reproductive	24	160	-	X	X
C2	*D. ordii*	♂	adult	scrotal	74	103	-	X	-
C10	*D. ordii*	♂	subadult	non-scrotal	36	121	-	X	X
D9	*D. ordii*	♀	subadult	non-reproductive	36	115	-	X	X
D5	*D. ordii*	♂	adult	scrotal	74	113	-	X	X
D1	*D. ordii*	♀	adult	non-reproductive	55	108	-	X	-
E10	*D. ordii*	♀	adult	non-reproductive	59	151	-	X	-
H10	*D. ordii*	♂	adult	scrotal	76	125	-	X	-
H8	*P. manic*	♂	adult	scrotal	17	123	-	X	X
I7	*P. manic*	♂	adult	scrotal	20	107	-	X	X
I9	*D. ordii*	♀	adult	non-reproductive	53	152	-	X	-
J8	*D. ordii*	♂	adult	scrotal	67	166	-	X	-
J2	*D. ordii*	♂	adult	scrotal	70	116	-	X	X
A9	*D. ordii*	♂	adult	scrotal	71	118	-	-	X
C4	*D. ordii*	♀	adult	lactating/pregnant	77	164	-	-	X
E1	*P. manic*	♀	subadult	non-reproductive	15	105	-	-	X
I2	*D. ordii*		adult		59	155	-	-	X
I8	*D. ordii*	♂	adult	scrotal	65	156	-	-	X
J8	*D. ordii*	♀	adult	post-lactating	64	171	-	-	X
J3	*D. ordii*	♀	subadult	non-reproductive	35	174	-	-	X

Summer 2006

Trap location	Species	Sex	Age	Reproductive condition	Weight (g)	Tag #	19-Aug-07	20-Aug-07	21-Aug-07
A1	*D. ordii*	♂	adult	scrotal	74	910	X	X	X
A5	*D. ordii*	♀	adult	lactating	61	911	X	X	X
A9	*D. ordii*	♀	subadult	non-reproductive	44	912	X	X	X

Appendix 2 continued.

Summer 2006

Trap location	Species	Sex	Age	Reproductive condition	Weight (g)	Tag #	19-Aug-07	20-Aug-07	21-Aug-07
B10	*D. ordii*	♀	adult	post-lactating	65	913	X	X	-
C3	*P. flavescens*	♂	adult	scrotal	9		X	-	-
D10	*D. ordii*	♂	adult	scrotal	71	42	X	X	X
D2	*D. ordii*	♂	adult	scrotal	72	103	X	X	X
D1	*D. ordii*	♂	adult	scrotal	69	914	X	X	-
E1	*D. ordii*	♀	adult	non-reproductive	60	915	X	X	-
G10	*P. manic*	♂	adult	scrotal	21	916	X	X	X
H9	*D. ordii*	♀	adult	lactating	67	917	X	X	-
H3	*P. manic*	♂	adult	scrotal	16	918	X	X	X
I2	*D. ordii*	♀	adult	lactating	68	919	X	X	X
J7	*D. ordii*	♂	adult	scrotal	65	156	X	-	X
J4	*D. ordii*	♀	adult	post-lactating	64	167	X	X	X
J1	*D. ordii*	♀	adult	post-lactating	67	920	X	-	X
A10	*D. ordii*	♀	adult	non-reproductive	62	922	-	X	X
C9	*D. ordii*	♀	adult	non-reproductive	63	923	-	X	X
G2	*P. manic*	♀	adult	non-reproductive	19	924	-	X	-
I10	*P. flavescens*	♀	adult	pregnant	11		-	X	-
J6	*P. manic*	♀	adult	non-reproductive	14	925	-	X	X
J3	*P. manic*				19	926	-	X	X
A6	*P. manic*	♂	adult	scrotal	21	927	-	-	X
B10	*D. ordii*	♀	adult	non-reproductive	59	928	-	-	X
C5	*D. ordii*	♀	adult	post-lactating	61	929	-	-	X
D10	*D. ordii*	♂	adult	non-scrotal	60	930	-	-	X
F1	*P. flavescens*	♂	adult		7		-	-	X
G5	*P. manic*	♀	adult	non-reproductive	15	931	-	-	X
H2	*D. ordii*	♀	juvenile	non-reproductive	21	932	-	-	X
H5	*D. ordii*	♀	juvenile	non-reproductive	20	933	-	-	X

Appendix 2 continued.

Summer 2007

Trap location	Species	Sex	Age	Reproductive condition	Weight (g)	Tag #	15-Jul-07	16-Jul-07	17-Jul-07
A2	*D. ordii*	♂	adult	scrotal	62	985	X	X	X
A7	*P. manic*	♂	adult	scrotal	18	986	X	X	X
C8	*D. ordii*	♀	adult	lactating	67	987	X	X	X
B1	*D. ordii*	♂	adult	scrotal	64	988	X	X	-
E1	*D. ordii*	♂	adult	scrotal	67	989	X	-	-
D3	*D. ordii*	♀	adult	estrus	52	990	X	X	-
E8	*P. manic*	♀	adult	non-reproductive	18	991	X	-	X
G8	*D. ordii*	♀	adult	post-lactating	57	999	X	X	X
F5	*D. ordii*	♂	adult	scrotal	60	992	X	X	X
G4	*D. ordii*	♀	adult	estrus	51	996	X	-	-
F1	*D. ordii*	♂	adult	scrotal	75	998	X	-	X
G1	*D. ordii*	♂	adult	scrotal	67	995	X	-	-
I1	*D. ordii*	♂	adult	scrotal	64	1000	X	X	-
J1	*D. ordii*	♂	adult	scrotal	64	993	X	X	X
A7	*P. manic*	♀	adult	non-reproductive	18	850	-	X	-
D8	*P. manic*	♂	adult	scrotal	17	849	-	X	X
I1	*D. ordii*	♀	adult	post-lactating, estrus	62	848	-	X	-
J1	*D. ordii*	♀	adult	post-lactating	61	847	-	X	-
A1	*D. ordii*	♂	adult	scrotal	53	846	-	-	X
B1	*D. ordii*	♀	adult	estrus	50	845	-	-	X
A3	*D. ordii*	♂	adult	scrotal	63	844	-	-	X
A10	*D. ordii*	♂	adult	scrotal	67	843	-	-	X
E8	*P. manic*	♂	adult	scrotal	21	842	-	-	X
F10	*P. flavescens*	♀	adult	lactating			-	-	X

X indicates capture

- indicates no capture

Appendix 3. Number of burrows used by Ord's kangaroo rats (*Dipodomys ordii*) in the Sandhill Region of Nebraska during 2 consecutive summers (2006 and 2007) and winters (2007 and 2008). For age of kangaroo rats; ad = adult and sa = subadult.

Summer 2006

						Days kangaroo rats were tracked to burrows															
Date	**ID**	**Age**	**Sex**	**Reproductive condition**	**Wt. (g)**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
12-Jul-06	2	ad	♀	estrus	60	1	1	2	2	2	2	3	3	3	3	1	**R**				
13-Jul-06	9	ad	♀	post-lactating, estrus	62	1	1	1	1	1	1	1	1	1	1	**R**					
28-Jul-06	31	sa	♀	non-reproductive	44	1	2	2	2	2	3	2	2	2	2	**Dead**					
1-Aug-06	35	ad	♀	lactating	71	1	1	2	1	3	4	3	5	5	**R**						
1-Aug-06	36	ad	♀	estrus	58	1	1	2	2	3	3	3	3	3	**R**						
8-Aug-06	54	ad	♀	post-lactating	56	1	1	1	1	1	1	1	1	**R**							
10-Aug-06	57	ad	♀	lactating	68	1	1	1	1	1	1	1	**R**								
21-Aug-06	167	ad	♀	post-lactating	64	1	2	3	3	4	1	1	**R**								
21-Aug-06	911	ad	♀	lactating	61	1	2	3	3	3	3	4	**R**								
21-Aug-06	912	sa	♀	non-reproductive	44	1	1	1	1	2	1	1	**R**								
21-Aug-06	919	ad	♀	lactating	68	1	2	3	3	3	3	4	**R**								
21-Aug-06	920	ad	♀	post-lactating	67	1	2	3	3	3	4	4	**R**								
21-Aug-06	922	ad	♀	non-reproductive	62	1	1	2	3	3	1	1	**R**								
21-Aug-06	923	ad	♀	non-reproductive	63	1	2	1	1	1	1	1	**R**								
21-Aug-06	928	ad	♀	non-reproductive	59	1	2	2	2	3	3	3	**NR**								
21-Aug-06	929	ad	♀	post-lactating	61	1	2	2	2	2	2	2	**R**								
12-Jul-06	11	ad	♂	scrotal	70	1	1	1	2	2	1	1	1	1	1	**R**					
14-Jul-06	12	ad	♂	scrotal	68	1	2	2	2	2	**killed by barn owl**										
28-Jul-06	28	ad	♂	scrotal	64	1	1	1	1	1	1	1	1	1	1	**R**					
30-Jul-06	33	ad	♂	scrotal	60	1	2	2	2	2	2	2	3	3	2	**R**					
3-Aug-06	38	ad	♂	scrotal	73	1	1	1	1	1	1	1	1	**R**							
7-Aug-06	52	ad	♂	scrotal	61	1	1	1	1	1	1	1	1	**R**							
10-Aug-06	58	ad	♂	scrotal	66	1	1	1	1	1	1	1	**R**								
21-Aug-06	103	ad	♂	scrotal	72	1	2	2	2	2	2	2	**R**								
21-Aug-06	156	ad	♂	scrotal	65	1	1	1	1	1	2	2	**R**								
21-Aug-06	910	ad	♂	scrotal	74	1	2	1	2	2	1	1	**R**								

Appendix 3 continued.

Summer 2007

Date	ID	Age	Sex	Reproductive condition	Wt. (g)	Days kangaroo rats were tracked to burrows															
						1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
3-Jul-07	980	ad	♀	lactating	66	1	1	1	1	2	2	2	**R**								
7-Jul-07	983	ad	♀	lactating	65	1	1	1	1	2	2	2	2	2	3	3	3	3	3	3	**R**
17-Jul-07	845	ad	♀	estrus	50	1	1	1	1	1	1	1	**R**								
17-Jul-07	987	ad	♀	lactating	67	1	1	1	2	3	3	3	4	5	6	4	4	4	**R**		
17-Jul-07	999	ad	♀	post-lactating	57	1	1	1	1	1	1	2	3	3	3	**R**					
17-Jul-07	841	ad	♀	lactating	63	1	2	2	2	3	3	3	1	1	1	**R**					
18-Jul-07	848	ad	♀	post-lactating, estrus	62	1	2	2	3	3	3	3	4	4	4	4	4	**R**			
25-Jul-07	835	ad	♀	estrus	71	1	2	2	1	2	2	1	2	**R**							
25-Jul-07	990	ad	♀	estrus	57	1	1	1	1	1	1	1	**R**								
2-Aug-07	838	ad	♀	post-lactating	67	1	1	1	2	2	1	1	1	1	1	3	3	**R**			
6-Aug-07	833	ad	♀	post-lactating	67	1	2	2	2	2	2	1	**R**								
5-Jul-07	982	ad	♂	scrotal	65	1	1	1	1	1	1	**Dead**									
17-Jul-07	844	ad	♂	scrotal	63	1	1	1	1	2	2	2	**R**								
17-Jul-07	985	ad	♂	scrotal	62	1	2	3	2	3	1	1	**R**								
17-Jul-07	992	ad	♂	scrotal	60	1	2	2	2	2	2	2	3	**R**							
17-Jul-07	843	ad	♂	scrotal	67	1	1	1	1	1	1	1	**R**								
17-Jul-07	998	ad	♂	scrotal	75	1	1	1	1	1	1	1	**R**								
25-Jul-07	834	ad	♂	scrotal	64	1	1	2	2	2	2	2	2	**R**							
6-Aug-07	826	ad	♂	non-scrotal	74	1	2	2	2	2	2	2	**R**								
7-Aug-07	836	ad	♂	scrotal	73	1	1	1	1	2	2	1	**R**								
7-Aug-07	831	ad	♂	scrotal	74	1	2	2	2	2	2	2	**NR**								

Appendix 3 continued.

Winter 2007

						Days kangaroo rats were tracked to burrows															
Date	**ID**	**Age**	**Sex**	**Reproductive condition**	**Wt. (g)**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
5-Jan-07	955	ad	♀	non-reproductive	61	1	1	1	1	1	**R**										
6-Jan-07	959	ad	♀	non-reproductive	63	1	1	2	2	2	**R**										
6-Jan-07	960	ad	♀	non-reproductive	66	1	1	1	1	**R**											
6-Jan-07	962	ad	♀	non-reproductive	65	1	1	1	1	**R**											
6-Jan-07	963	ad	♀	non-reproductive	63	1	1	1	1	**R**											
6-Jan-07	965	ad	♀	non-reproductive	59	1	1	1	1	**R**											
6-Jan-07	968	ad	♀	non-reproductive	53	1	1	1	1	**R**											
6-Jan-07	969	ad	♀	non-reproductive	53	1	2	2	2	**R**											
5-Jan-07	956	ad	♂	scrotal	65	1	1	1	1	**R**											
5-Jan-07	957	ad	♂	scrotal	62	1	1	1	1	1	**R**										
6-Jan-07	958	ad	♂	scrotal	62	1	1	1	1	1	**R**										
6-Jan-07	961	ad	♂	non-scrotal	61	1	1	1	1	**R**											
6-Jan-07	964	ad	♂	scrotal	67	1	2	2	2	**R**											
6-Jan-07	966	ad	♂	scrotal	69	1	1	1	1	**R**											
6-Jan-07	967	ad	♂	scrotal	64	1	1	**radio died**													
6-Jan-07	970	ad	♂	scrotal	67	1	1	1	1	**R**											

Appendix 3 continued.

Winter 2008

						Days kangaroo rats were tracked to burrows															
Date	**ID**	**Age**	**Sex**	**Reproductive condition**	**Wt. (g)**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
4-Jan-08	195	ad	♀	non-reproductive	52	1	1	1	1	1	**NR**										
5-Jan-08	200	ad	♀	non-reproductive	58	1	1	1	1	**R**											
5-Jan-08	627	ad	♀	non-reproductive	64	1	1	1	1	**R**											
7-Jan-08	1982	ad	♀	non-reproductive	52	1	1	1	**Radio died**												
4-Jan-08	628	ad	♂	non-scrotal	68	1	1	1	1	1	**NR**										
5-Jan-08	624	ad	♂	scrotal	67	1	1	1	**Radio died**												
5-Jan-08	625	ad	♂	non-scrotal	76	1	1	1	2	**R**											
5-Jan-08	198	ad	♂	non-scrotal	53	**killed by raptor**															

Numbers indicate which burrow a kangaroo rat was tracked to during each day (e.g., 1 = burrow 1)

R-recaptured

NR-not recaptured

Appendix 4. Distances between burrows of Ord's kangaroo rats (*Dipodomys ordii*) that used >1 burrow during summer and winter in the Sandhill Region of Nebraska. For age of kangaroo rats; ad = adult and sa = subadult.

Summer 2006

					Number of burrows				
ID	**Age**	**Sex**	**Reproductive condition**	**Wt. (g)**	**4 nights**	**7 nights**	**Burrows**	**Distance between burrows**	**Recaptured**
2	ad	♀	estrus	60	2	3	bur 1-2	13.6	y
							bur 1-3	65.0	
							bur 2-3	78.3	
9	ad	♀	post-lactating, estrus	62	1	1	-	-	y
11	ad	♂	scrotal	70	2	2	bur 1-2	60.2	y
12	ad	♂	scrotal	68	2	-	bur 1-2	8.8	n
28	ad	♂	scrotal	64	1	1	-	-	y
31	sa	♀	non-reproductive	44	2	3	bur 1-2	13.8	n
							bur 1-3	62.0	
							bur 2-3	47.9	
33	ad	♂	scrotal	60	2	2	bur 1-2	23.0	y
35	ad	♀	lactating	68	2	4	bur 1-2	25.8	y
							bur 1-3	29.2	
							bur 1-4	58.8	
							bur 2-3	32.6	
							bur 2-4	34.6	
							bur 3-4	49.1	
36	ad	♀	estrus	58	2	3	bur 1-2	22.8	y
							bur 1-3	27.0	
							bur 2-3	49.4	
38	ad	♂	scrotal	73	1	1	-	-	y
52	ad	♂	scrotal	61	1	1	-	-	y
54	ad	♀	post-lactating	56	1	1	-	-	y
57	ad	♀	lactating	68	1	1	-	-	y
58	ad	♂	scrotal	66	1	1	-	-	y
910	ad	♂	scrotal	70	2	2	bur 1-2	11.1	y

Appendix 4 continued.

Summer 2006

					Number of burrows				
ID	**Age**	**Sex**	**Reproductive condition**	**Wt. (g)**	**4 nights**	**7 nights**	**Burrows**	**Distance between burrows**	**Recaptured**
912	sa	♀	non-reproductive	43	1	2	bur 1-2	13.3	y
922	ad	♀	non-reproductive	59	3	3	bur 1-2	13.5	y
							bur 1-3	15.0	
							bur 2-3	11.9	
928	ad	♀	non-reproductive	58	2	3	bur 1-2	17.6	y
							bur 1-3	19.3	
							bur 2-3	36.3	
929	ad	♀	post-lactating	60	2	2	bur 1-2	17.0	n
911	ad	♀	lactating	61	3	4	bur 1-2	21.1	y
							bur 1-3	18.8	
							bur 1-4	15.2	
							bur 2-3	8.4	
							bur 2-4	10.5	
							bur 3-4	6.5	
923	ad	♀	non-reproductive	59	2	2	bur 1-2	28.5	y
103	ad	♂	scrotal	66	2	2	bur 1-2	18.0	y
919	ad	♀	lactating	60	3	4	bur 1-2	8.0	y
							bur 1-3	11.6	
							bur 1-4	10.1	
							bur 2-3	8.0	
							bur 2-4	18.4	
							bur 3-4	17.2	

Appendix 4 continued.

Summer 2006

					Number of burrows				
ID	**Age**	**Sex**	**Reproductive condition**	**Wt. (g)**	**4 nights**	**7 nights**	**Burrows**	**Distance between burrows**	**Recaptured**
920	ad	♀	post-lactating	62	3	4	bur 1-2	8.7	y
							bur 1-3	35.7	
							bur 1-4	20.6	
							bur 2-3	28.0	
							bur 2-4	11.6	
							bur 3-4	17.1	
156	ad	♂	scrotal	61	1	2	bur 1-2	19.3	y
167	ad	♀	post-lactating	60	3	4	bur 1-2	43.1	y
							bur 1-3	47.6	
							bur 1-4	30.3	
							bur 2-3	5.3	
							bur 2-4	14.1	
							bur 3-4	17.9	

Summer 2007

					Number of burrows				
ID	**Age**	**Sex**	**Reproductive condition**	**Wt. (g)**	**4 nights**	**7 nights**	**Burrows**	**Distance between burrows**	**Recaptured**
980	ad	♀	lactating	66	1	2	bur 1-2	20.6	y
983	ad	♀	lactating	65	1	2	bur 1-2	31.9	y
845	ad	♀	estrus	50	1	1	-	-	y
987	ad	♀	lactating	64	2	3	bur 1-2	26.3	y
							bur 1-3	45.1	
							bur 2-3	22.3	
999	ad	♀	post-lactating	59	1	2	bur 1-2	88.4	y
841	ad	♀	lactating	63	2	3	bur 1-2	50.3	y
							bur 1-3	55.0	

Appendix 4 continued.

Summer 2007

					Number of burrows				
ID	Age	Sex	Reproductive condition	Wt. (g)	4 nights	7 nights	Burrows	Distance between burrows	Recaptured
							bur 2-3	38.0	
848	ad	♀	post-lactating, estrus	62	3	3	bur 1-2	146.0	y
							bur 1-3	118.7	
							bur 2-3	45.9	
835	ad	♀	estrus	71	2	2	bur 1-2	13.0	y
990	ad	♀	estrus	57	1	1	-	-	y
838	ad	♀	post-lactating	67	2	2	bur 1-2	31.1	y
833	ad	♀	post-lactating	67	2	2	bur 1-2	12.2	y
982	ad	♂	scrotal	65	1	-	-	-	n
844	ad	♂	scrotal	63	1	2	bur 1-2	12.5	y
985	ad	♂	scrotal	58	3	3	bur 1-2	27.0	y
							bur 1-3	10.5	
							bur 2-3	16.7	
992	ad	♂	scrotal	58	2	2	bur 1-2	19.3	y
843	ad	♂	scrotal	67	1	1	-	-	y
998	ad	♂	scrotal	75	1	1	-	-	y
834	ad	♂	scrotal	64	2	2	bur 1-2	38.6	y
826	ad	♂	non-scrotal	74	2	2	bur 1-2	12.7	y
836	ad	♂	scrotal	73	1	2	bur 1-2	15.5	y
831	ad	♂	scrotal	74	2	2	bur 1-2	11.6	n

Appendix 4 continued.

Winter 2007

ID	**Age**	**Sex**	**Reproductive condition**	**Wt. (g)**	**Number of burrows**		**Burrows**	**Distance between burrows**	Recaptured
					4 nights	**7 nights**			
955	ad	♀	non-reproductive	61	1		-	-	y
956	ad	♂	scrotal	65	1		-	-	y
957	ad	♂	scrotal	62	1		-	-	y
958	ad	♂	scrotal	62	1		-	-	y
959	ad	♀	non-reproductive	63	2		bur 1-2	10.7	y
960	ad	♀	non-reproductive	66	1		-	-	y
961	ad	♂	non-scrotal	61	1		-	-	y
962	ad	♀	non-reproductive	65	1		-	-	y
963	ad	♀	non-reproductive	63	1		-	-	y
964	ad	♂	scrotal	67	2		bur 1-2	8.5	y
965	ad	♀	non-reproductive	59	1		-	-	y
966	ad	♂	scrotal	69	1		-	-	y
967	ad	♂	scrotal	64	-		-	-	n
968	ad	♀	non-reproductive	53	1		-	-	y
969	ad	♀	non-reproductive	53	2		bur 1-2	19.5	y
970	ad	♂	scrotal	67	1		-	-	y

Appendix 4 continued.

Winter 2008

ID	Age	Sex	Reproductive condition	Wt. (g)	Number of burrows 4 nights	 7 nights	Burrows	Distance between burrows	Recaptured
628	ad	♂	non-scrotal	68	-		-	-	n
195	ad	♀	non-reproductive	52	-		-	-	n
200	ad	♀	non-reproductive	58	1		-	-	y
624	ad	♂	scrotal	67	-		-	-	n
627	ad	♀	non-reproductive	64	1		-	-	y
625	ad	♂	non-scrotal	76	2		bur 1-2	9.4	y
198	ad	♂	non-scrotal	53	-		-	-	n
198-2	ad	♀	non-reproductive	52	-		-	-	n

Appendix 5. Captures and observations of Ord's kangaroo rats (*Dipodomys ordii*) at seed trays during 2 summers and winters in the Sandhill Region of Nebraska. For age of kangaroo rats; ad = adult and sa = subadult.

Summer 2006

Tray	Age	Sex	Reproductive condition	Wt. (g)	% gathered	scatter or larder	# of scatters	trips to larder	Comments
1									no caches recovered
2	ad	♀	estrus	60	93	both	2	3	
3									no k-rats observed
4									no k-rats observed
5	ad	♀	estrus	52	91	scatter	4	0	
6									no seeds gathered
7	sa	♀	non-reproductive	42	91	scatter	3	0	
9	ad	♀	post-lacting, estrus	62	93	both	1	6	
10									no seeds gathered
11	ad	♂	scrotal	70	91	scatter	4	0	
12	ad	♂	scrotal	68	36	scatter	1	0	
13									no k-rats observed
14									no k-rats observed
15									no k-rats observed
16									no k-rats observed
17									no k-rats observed
20	-	-	-	-	-	scatter	3	0	2 k-rats cached seeds
21									no k-rats observed
22									no k-rats observed
24									no k-rats observed
25									no k-rats observed
26									
27	ad	♀	pregnant	83	86	scatter	6	0	
28	ad	♂	scrotal	64	67	scatter	1	0	
30	ad	♀	post-lactating	67	91	scatter	4	0	
31	sa	♀	non-reproductive	44	100	scatter	9	0	

Appendix 5 continued.

Summer 2006

Tray	Age	Sex	Reproductive condition	Wt. (g)	% gathered	scatter or larder	# of scatters	trips to larder	Comments
33	ad	♂	scrotal	60	100	scatter	6	0	
35	ad	♀	lactating	71	23	scatter	2	0	
36	ad	♀	estrus	58	91	both	4	4	
37									no caches recovered
38	ad	♂	scrotal	73	100	scatter	4	0	
39									no caches recovered
40	ad	♀	pregnant	85	89	scatter	2	0	
41									no seeds gathered
44									no seeds gathered
45									no seeds gathered
48	-	-	-	-	-	scatter	4	0	2 k-rats cached seeds
52	ad	♂	scrotal	61	83	scatter	5	0	
54	ad	♀	post-lactating	56	100	scatter	5	0	
56									no seeds gathered
57	ad	♀	lactating	68	100	scatter	7	0	
58	ad	♂	scrotal	66	46	scatter	2	0	
59									no seeds gathered
60	ad	♂	scrotal	76	94	scatter	5	0	
61	ad	♂	non-scrotal	67	92	scatter	10	0	
62	ad	♂	scrotal	76	99	scatter	3	0	
64	ad	♂	scrotal	64	97	scatter	5	0	
66									no seeds gathered

Appendix 5 continued.

Summer 2007

Tray	Age	Sex	Reproductive condition	Wt. (g)	% gathered	scatter or larder	# of scatters	trips to larder	Comments
1	ad	♀	lactating	66	98	scatter	5	0	
2	ad	♂	scrotal	67	96	scatter	3	0	
3	ad	♂	scrotal	65	96	scatter	6	0	
4									no seeds gathered
5	ad	♀	lactating	65	99	both	1	4	
6	ad	♂	scrotal	72	98	scatter	6	0	
7									no caches recovered
8									no k-rats observed
9									2 k-rats cached seeds
10									no k-rats observed
11									no caches recovered
12									no seeds gathered
13									no k-rats observed
14	ad	♀	non-reproductive	69	100	scatter	4	0	
15	-	-	-	-	-	scatter	5	0	2 k-rats cached seeds
16	ad	♂	scrotal	68	26	scatter	1	0	
17	ad	♀	post-lactating, estrus	70	97	scatter	5	0	
18	ad	♀	lactating	63	17	scatter	1	0	
19	ad	♂	scrotal	68	98	scatter	5	0	
20									no seeds gathered
21									no seeds gathered
22	ad	♂	scrotal	60	98	scatter	6	0	
23	ad	♀	lactating, estrus	68	99	scatter	3	0	
24									no caches recovered
25									no caches recovered
26	ad	♂	scrotal	64	99	scatter	5	0	
27	ad	♂	scrotal	76	69	scatter	6	0	

Appendix 5 continued.

Summer 2007

Tray	Age	Sex	Reproductive condition	Wt. (g)	% gathered	scatter or larder	# of scatters	trips to larder	Comments
28									no k-rats observed
29									no k-rats observed
31									no k-rats observed
32									no k-rats observed
33									no k-rats observed
34									no k-rats observed
35									no seeds gathered
36									no k-rats observed
37									no seeds gathered
38									no seeds gathered
39	ad	♀	post-lactating	67	97	scatter	1	0	
40	ad	♂	scrotal	74	42	scatter	1	0	
41	-	-	-	-	-	scatter	5	0	no k-rats captured
42	ad	♀	post-lactating	67	72	scatter	5	0	
43	ad	♂	non-scrotal	74	87	scatter	5	0	
44									no seeds gathered
45									no seeds gathered
46									no seeds gathered
47									no seeds gathered

Appendix 5 continued.

Winter 2007

Tray	Age	Sex	Reproductive condition	Wt. (g)	% gathered	scatter or larder	# of scatters	trips to larder	Comments
1									no k-rats observed
2	ad	♀	non-reproductive	59	99	larder	0	5	
3									no k-rats observed
4	ad	♀	non-reproductive	65	59	larder	0	4	
5	ad	♀	non-reproductive	66	97	larder	0	5	
6	ad	♂	non-scrotal	56	94	larder	0	5	
7									no k-rats observed
8	ad	♀	non-reproductive	61	99	larder	0	6	
9	ad	♀	non-reproductive	57	100	both	3	1	
10									no k-rats observed
11									no seeds gathered
12									no seeds gathered
13	ad	♂	non-scrotal	64	12	larder	0	1	
14	ad	♀	non-reproductive	60	99	larder	0	6	

Appendix 5 continued.

Winter 2008

Tray	Age	Sex	Reproductive condition	Wt. (g)	% gathered	scatter or larder	# of scatters	trips to larder	Comments
1									no k-rats observed
2									no k-rats observed
3	ad	♂	non-scrotal	76	100	larder	0	6	
4	ad	♀	non-reproductive	50	100	larder	0	6	
5									no seeds gathered
6	ad	♂	non-scrotal	72	81	larder	0	4	
7									no k-rats observed
8									no k-rats observed
9									no k-rats observed
10	ad	♀	non-reproductive	55	94	both	1	3	
11									no k-rats observed
12									no k-rats observed
13									no k-rats observed
14									no k-rats observed
15									no k-rats observed
16	ad	♀	non-reproductive	49	11	larder	0	2	
17									no k-rats observed
18									no k-rats observed
19									no k-rats observed
20									no k-rats observed
21									no seeds gathered
22	ad	♀	non-reproductive	65	-	larder	0	4	
23	ad	♂	non-scrotal	48	54	scatter	4	0	

Appendix 6. Characteristics of scatterhoards made by Ord's kangaroo rats (*Dipodomys ordii*) during 2 consecutive summers in the Sandhill Region of Nebraska. For age of kangaroo rats; ad = adult and sa = subadult.

Summer 2006

Tray	Age	Sex	Cache	Distance to tray (m)	Size (# of seeds)	Depth (mm)	Dis. to veg. (mm)	Type of veg.	Microsite
2	ad	♀	1	1.40	41	10	30	-	-
			2	3.05	31	20	60	-	-
5	ad	♀	1	5.30	61	5	60	dead grass	-
			2	13.55	75	5	50	sand bluestem	-
			3	9.75	59	5	30	sand muhly	-
			4	10.00	39	3	20	dead grass	-
7	sa	♀	1	0.62	36	10	60	dead grass	-
			2	4.90	31	15	20	dead grass	-
			3	7.45	32	10	40	sunflower	-
9	ad	♀	1	1.80	40	15	30	dead grass	-
11	ad	♂	1	6.90	65	10	50	dead forb	-
			2	14.70	73	15	40	grass	-
			3	8.35	24	10	40	sand bluestem	-
			4	9.25	34	15	25	sand muhly	-
12	ad	♂	1	10.90	53	5	110	grass clump	-
20			1	-	35	20	20	dead grass	-
			2	-	55	20	30	grass	-
			3	-	49	20	25	grass	-
27	ad	♀	1	3.80	62	20	20	grass	-
			2	5.45	58	15	10	ragweed	-
			3	11.15	55	20	10	grass	-
			4	19.20	71	10	0	grass	-
			5	9.70	67	10	0	yucca leaves	-
			6	9.40	2 (collected)	25	80	dead roots	-
28	ad	♂	1	15.80	66	15	20	dead grass	-

Appendix 6 continued.

Summer 2006

Tray	Age	Sex	Cache	Distance to tray (m)	Size (# of seeds)	Depth (mm)	Dis. to veg. (mm)	Type of veg.	Microsite
30	ad	♀	1	6.10	13	5	0	forb	-
			2	6.80	66	10	0	dead grass	-
			3	5.40	37	20	50	sunflower	-
			4	-	2 (collected)	-	-	-	-
31	sa	♀	1	1.70	11	10	35	dead grass	-
			2	3.30	58	5	15	daisy fleabane	-
			3	3.75	9	2	10	grass	-
			4	5.60	64	10	0	dead grass	-
			5	3.80	66	10	0	beneath stem	-
			6	4.20	63	15	15	dead grass	-
			7	4.40	64	15	20	dead grass	-
			8	6.30	64	5	75	ragweed	-
			9	7.20	53	15	15	twigs	-
33	ad	♂	1	5.30	82	15	10	dead grass	-
			2	7.85	74	0	10	sand muhly	-
			3	11.70	75	10	0	sand muhly	-
			4	11.00	73	10	0	grass	-
			5	11.95	75	5	10	grass	-
			6	7.25	2 (collected)	-	20	grass	-
35	ad	♀	1	13.65	43	20	0	grass	-
			2	16.10	49	15	15	twigs	-
36	ad	♀	1	6.95	54	0	0	grass	-
			2	0.75	41	15	0	under twig	-
			3	1.60	55	0	0	grass	-
			4	1.00	0 (collected)	-	-	-	-

Appendix 6 continued.

Summer 2006

Tray	Age	Sex	Cache	Distance to tray (m)	Size (# of seeds)	Depth (mm)	Dis. to veg. (mm)	Type of veg.	Microsite
38	ad	♂	1	10.00	80	15	0	dead yucca	-
			2	11.90	75	10	0	under grass	-
			3	18.30	67	25	80	grass, open sand	-
			4	23.45	1 (collected)	-	-	-	-
40	ad	♀	1	8.80	84	10	0	base of grass	-
			2	23.95	87	15	0	base of grass	-
48			1	-	-	-	-	-	-
			2	-	-	-	-	-	-
			3	-	-	-	-	-	-
			4	-	-	-	-	-	-
52	ad	♂	1	12.70	48	15	0	grass	-
			2	4.50	51	15	30	grass	-
			3	5.60	46	10	20	sand muhly	-
			4	7.20	37	10	0	sand muhly	-
			5	8.20	52	5	0	grass	-
54	ad	♀	1	9.20	62	7	0	sand muhly	-
			2	6.95	56	8	10	stick, dead grass	-
			3	9.50	20	5	0	sand muhly	-
			4	15.10	55	15	0	sage	-
			5	17.70	60	5	10	ragweed	-
57	ad	♀	1	11.40	88	10	0	dead grass	-
			2	10.90	88	10	0	dead grass	-
			3	7.50	79	15	0	under yucca	-
			4	6.30	71	10	10	grass	-
			5	4.10	65	15	0	base of grass	-
			6	5.30	42	15	0	base of forb	-
			7	6.80	77	15	0	sand muhly	-

Appendix 6 continued.

Summer 2006

Tray	Age	Sex	Cache	Distance to tray (m)	Size (# of seeds)	Depth (mm)	Dis. to veg. (mm)	Type of veg.	Microsite
58	ad	♂	1	3.30	44	10	30	dead grass	-
			2	11.60	62	10	20	sand muhly	-
60	ad	♂	1	6.20	72	15	20	sand muhly	-
			2	7.30	89	15	0	grass	-
			3	8.90	66	15	0	sand muhly	-
			4	11.90	84	15	0	sand muhly	-
			5	8.80	70	15	0	sand dropseed	-
61	ad	♂	1	10.50	50	8	30	sand muhly	-
			2	8.70	27	15	110	dead forb	-
			3	6.20	48	5	15	dead muhly	-
			4	5.20	29	5	15	sunflower	-
			5	5.00	52	0	15	grass	-
			6	2.90	47	10	20	sand muhly	-
			7	2.50	6	5	40	forb	-
61	ad	♂	8	3.70	51	10	0	base of grass	-
			9	3.30	49	10	0	sand muhly	-
			10	5.55	30	10	20	ragweed	-
62	ad	♂	1	8.55	85	20	0	sand muhly	-
			2	12.30	83	15	0	sand muhly	-
			3	-	3 (collected)	-	-	-	-
64	ad	♂	1	3.65	37	10	10	prairie rose	-
			2	6.30	82	15	30	grass, open sand	-
			3	16.30	77	20	10	sand muhly	-
			4	25.50	98	15	0	grass	-
			5	-	6 (collected)	-	-	-	-

Appendix 6 continued.

Summer 2007

Tray	Age	Sex	Cache	Distance to tray (m)	Size (# of seeds)	Depth (mm)	Dis. to veg. (mm)	Type of veg.	Microsite
1	ad	♀	1	7.50	42	12	0	grass	Edge
			2	8.50	51	8	60	yucca	Cover
			3	11.40	57	15	0	grass	Edge
			4	11.80	50	5	0	yucca	Edge
			5	12.00	62	15	0	grass	Edge
2	ad	♂	1	7.95	48	10	-	-	Open
			2	10.95	60	17	0	grass	Cover
			3	2.10	48	19	0	sand muhly	Edge
3	ad	♂	1	12.00	64	5	0	grass	Cover
			2	7.85	54	0	0	grass	Cover
			3	8.15	64	5	0	grass	Cover
			4	12.80	62	0	20	sand muhly	Edge
			5	12.85	68	12	0	needle and thread	Edge
			6	12.30	62	5	0	grass and forb	Edge
5	ad	♀	1	22.60	13	7	40	grass	Edge
6	ad	♂	1	5.50	73	15	50	grass	Edge
			2	5.00	61	20	60	yucca and grass	Edge
			3	4.55	62	25	0	sand muhly	Edge
			4	4.20	50	25	0	grass and forb	Edge
			5	3.80	25	35	60	grass	Open
			6	4.05	105	30	0	old yucca	Cover
14	ad	♀	1	8.70	77	15	0	dead grass	Edge
			2	9.50	107	15	0	grass	Cover
			3	10.20	84	18	0	sand muhly	Edge
			4	13.25	110	20	0	sand bluestem	Edge

Appendix 6 continued.

Summer 2007

Tray	Age	Sex	Cache	Distance to tray (m)	Size (# of seeds)	Depth (mm)	Dis. to veg. (mm)	Type of veg.	Microsite
15			1	18.60	82	15	5	grass	Cover
			2	36.50	80	18	40	grass	Edge
			3	17.30	89	25	0	grass yucca	Cover
			4	12.55	69	20	0	yucca	Cover
			5	23.70	88	27	0	grass	Cover
16	ad	♂	1	56.40	91	17	100	needle and thread	Edge
17	ad	♀	1	18.25	82	20	0	grass	Edge
			2	14.70	83	0	0	sand muhly	Cover
			3	12.90	76	12	0	yucca	Edge
			4	17.30	78	15	0	sand muhly	Edge
			5	7.00	67	20	0	yucca	Edge
18	ad	♀	1	15.40	55	0	0	dead grass	Cover
19	ad	♂	1	14.85	83	25	0	grass	Edge
			2	13.35	74	30	0	yucca	Cover
			3	14.45	88	30	0	yucca	Edge
			4	15.25	66	22	0	yucca	Edge
			5	19.45	39	25	0	grass	Cover
22	ad	♂	1	8.80	66	22	40	grass	Open
			2	10.00	67	20	0	sand muhly	Edge
			3	10.45	3	12	15	forb	Open
			4	16.00	55	0	0	sand muhly	Edge
			5	9.10	67	25	0	needle and thread	Edge
			6	8.35	66	23	0	sand muhly	Cover
23	ad	♀	1	23.10	74	12	0	ragweed	Cover
			2	23.40	88	10	0	sand muhly	Edge
			3	12.35	64	20	0	yucca stalk	Cover

Appendix 6 continued.

Summer 2007

Tray	Age	Sex	cache	Distance to tray (m)	Size (# of seeds)	Depth (mm)	Dis. to veg. (mm)	Type of veg.	Microsite
26	ad	♂	1	2.45	71	5	0	needle and thread	Cover
			2	3.30	60	15	0	needle and thread	Edge
			3	7.65	43	15	0	dead grass	Edge
			4	8.60	74	20	0	forb	Edge
			5	7.90	33	10	0	needle and thread	Edge
27	ad	♂	1	19.20	60	17	0	dead grass	Edge
			2	11.10	41	20	0	grass	Edge
			3	8.90	56	25	0	grass and forb	Edge
			4	7.80	53	20	0	needle and thread	Edge
			5	3.80	33	15	0	forb	Edge
			6	-	0 (collected)	-	0	dead grass	Edge
39	ad	♀	1	8.75	63	20	60	sand muhly	Open
40	ad	♂	1	25.20	2	15	0	sparse grass	Open
41			1	11.90	95	25	40	yucca and grass	Edge
			2	4.10	70	10	0	grass	Edge
			3	6.10	86	20	0	grass	Cover
			4	3.30	81	5	0	needle, sand drops	Edge
			5	4.65	59	0	0	sand muhly	Cover
42	ad	♀	1	8.10	59	20	0	grass	Cover
			2	5.10	54	10	0	sand muhly	Cover
			3	5.20	36	25	0	sand muhly	Edge
			4	4.30	52	40	30	grass	Edge
			5	2.30	10	10	0	sand muhly	Edge
43	ad	♂	1	6.75	72	15	30	ragweed	Open
			2	8.25	74	12	0	sand muhly	Edge
			3	8.65	83	20	40	yucca	Edge
			4	7.40	79	20	0	dead grass	Edge
			5	22.20	84	18	0	forb	Edge

Appendix 7. Characteristics of burrows of Ord's kangaroo rats (*Dipodomys ordii*) in summer in the Sandhill Region of Nebraska. For age of kangaroo rats; ad = adult and sa = subadult.

Summer 2006 and 2007

								Entrance (cm)		**Main tunnel (cm)**			
Year	**ID**	**Age**	**Sex**	**Reproductive condition**	**Wt. (g)**	**Burrow**	**# of entrances**	**Width**	**Height**	**Length**	**Max. depth**	**Width**	**Height**
2006	910	ad	♂	scrotal	70	1		4.5	4.0				
2006	912	sa	♀	non-reproductive	43	1		3.4	3.7				
2006	922	ad	♀	non-reproductive	59	1		4.0	4.4				
2006	929	ad	♀	post-lactating	60	1		4.7	4.0				
2006	911	ad	♀	lactating	61	1		3.5	4.2				
2006	103	ad	♂	scrotal	66	1		4.0	3.6				
2006	919	ad	♀	lactating	60	1		3.4	3.7				
2006	920	ad	♀	post-lactating	62	1		3.5	4.0				
2006	167	ad	♀	post-lactating	60	1		3.5	4.5				
2007	982	ad	♂	scrotal	65	1	3	4.0	4.0	595	50	6.0	6.5
2007	987	ad	♀	lactating	67	1	3			390	65		
	987					2	2			330	50		
2007	841	ad	♀	lactating	63	1	1	3.5	4.5	250	40		
	841					2	2			280	45	10.0	8.0
	841					3	2	3.5	3.0	320	35	10.0	7.0
2007	836	ad	♂	scrotal	70	1	1	3.5	5.0	220	45	7.0	11.0
2007	826	ad	♂	non-scrotal	74	1	2	3.5	4.0	130	50		
2007	833	ad	♀	post-lactating	67	1	1	3.2	4.2	265	35		
2007	831	ad	♂	scrotal	74	1	2			540			