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Dispersal, facilitation, and burrow architecture in banner-tailed kangaroo rats

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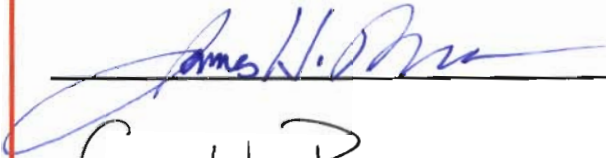
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**DISPERSAL, FACILITATION, AND BURROW
ARCHITECTURE IN BANNER-TAILED KANGAROO RATS**

BY

ANDREW J. EDELMAN

B.S., Biology, Willamette University, 1999
M.S., Wildlife Ecology, University of Arizona, 2004

DISSERTATION

Submitted in Partial Fulfillment of the
Requirements for the Degree of

**Doctor of Philosophy
Biology**

The University of New Mexico
Albuquerque, New Mexico

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ABSTRACT OF DISSERTATION

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ABSTRACT

The largest and most dominant kangaroo rat species in the Chihuahuan Desert is the banner-tailed kangaroo rat (*Dipodomys spectabilis*). This keystone species constructs mounds containing a complex burrow system around which their ecosystem engineering activities are centered. I studied a population of banner-tailed kangaroo rats at the Sevilleta National Wildlife Refuge, New Mexico from 2005-2009. Specifically, I examined how banner-tailed kangaroo rats: 1) modify their mounds in response to seasonal conditions; 2) spatially affect harvester ants (*Pogonomyrmex rugosus*) through ecosystem engineering activities; and 3) differ in timing of natal dispersal between sexes. I used mark-recapture, genetic, experimental, and spatially-explicit methods to address these areas of interest. I observed that kangaroo rats remodeled their mounds seasonally in relation to changes in predation risk, seed spoilage risk, and metabolic costs. My

results documented an additional keystone effect of banner-tailed kangaroo rats in the

Chihuahuan Desert, a facilitatory impact on the spatial structure and dynamics of

harvester ant colonies. I also experimentally determined that physiological cues influence

timing of natal dispersal in males and females differently.

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Chapter 1

Extreme makeover: kangaroo rats remodel burrows in relation to seasonal tradeoffs in thermoregulation, predation, and cache spoilage

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Abstract

Architecture of animal burrows including depth, complexity, orientation, and entrances can enhance specific functions such as food caching and protection from environmental extremes and predators. My objective was to examine how banner-tailed kangaroo rats (*Dipodomys spectabilis*) modify burrow entrances of mounds in response to seasonal variation in temperature, predation risk, and vulnerability of caches to spoilage. For three years, I monitored fluctations of burrow entrances in kangaroo rat mounds in relation to seasonal climate change. I found that number of entrances in mounds was tightly linked with changes in soil temperature and precipitation. As soil temperature decreased, so did the number of entrances. Compared to summer, mounds in winter had approximately 50% fewer entrances and plugged entrances were common. The highest numbers of entrances corresponded to summer months with the greatest amount of rainfall. Seasonal variations in burrow entrances likely reflect tradeoffs between thermoregulation, predation risk, and seed cache preservation. Ambient and burrow air temperatures are

frequently near or below freezing during the winter, requiring a significant increase in metabolic rate for kangaroo rats. Fewer burrow entrances during winter would reduce convective heat loss in mounds, create a warmer microclimate, and result in substantial energy savings. During the summer, thermoregulatory costs are low, but predation risk from snakes increases. Additional burrow entrances would reduce predation risk by increasing escape options. Increases in burrow entrances after large rainfall events would speed evaporation within mounds and reduce spoilage of critical seed caches.

Introduction

Burrows serve many functions for animals; they provide a location for rearing young, sleeping, hibernation, food storage, and protection from predators and environmental extremes (Reichman and Smith 1990, Kinlaw 1999). Architectural features of burrows such as depth, complexity, orientation, and number of entrances can enhance specific functions critical to the occupant's fitness. In particular, burrow architecture across many taxa and habitats plays a major role in thermoregulation (Korb and Linsenmair 1998, 2000, Kleineidam et al. 2001, Bulova 2002). The soil surrounding burrows creates a buffering effect, which shields occupants from diurnal fluctuations in surface temperature and humidity (Burda et al. 2007). Depth and ventilation affect the degree of buffering from surface conditions and can be adjusted by occupants to create microclimates closer to optimum conditions (Roper and Kemenes 1997, Bulova 2002, Shimmin et al. 2002, Roper and Moore 2003). As a result, semi-fossorial animals can avoid physiologically stressful surface conditions of extreme temperatures and water loss

by taking refuge in burrows (King 1980, Reichman and Smith 1990, Prakash 1997, Kinlaw 1999).

Animals may also configure burrows to reduce predation risk. Both comparative and experimental studies indicate that semi-fossorial rodents in habitats with high predation risk have greater burrow complexity and larger numbers of burrow entrances, which likely confuse pursuing predators and aid in escape (Harper and Batzli 1996, Jackson 2000). In addition, many semi-fossorial animals rely on cached food to survive through prolonged periods of scarcity. Burrow architecture can be altered to provide suitable microclimates for food preservation, reducing cache losses from decomposers (Vander Wall 1990). Seasonal variation in climate, predation risk, and caching behavior suggests that burrow architecture may be modified by occupants in response to fluctuations in environmental conditions. However, evidence of seasonal modification is limited to anecdotal observations of plugged burrows during thermally stressful conditions (Luckenbach 1982, Kawamichi 1989, Arnold et al. 1991) or use of burrows at different depths during summer and winter (Bartholomew and Hudson 1961, Ghobrial and Hodieb 1973, Scheibler et al. 2006).

Kangaroo rats (*Dipodomys* spp.) are a model organism for observing variation of burrow architecture in response to seasonal conditions because their burrow environment, physiology, and behavior have been well documented (Genoways and Brown 1993). These nocturnal, non-hibernating rodents inhabit semi-arid ecosystems of western North America (Holdenried 1957, Kenagy 1973, Kay and Whitford 1978, French 1993, Schmidly et al. 1993). One of the largest and most behaviorally complex species in this

genus is the banner-tailed kangaroo rat (*Dipodomys spectabilis*), found in grass- and shrub-lands of the southwestern United States and northern Mexico (Best 1988, Jones 1993). This solitary species constructs and aggressively defends mounds containing a complex burrow system (Schroder 1979). Mounds are typically 4 m in diameter and 30 cm in height with multiple entrances (Fig. 1.1)(Holdenried 1957, Reichman et al. 1985). The burrow system is a labyrinth of tunnels and chambers extending up to 4 stories and > 90 cm in depth (Vorhies and Taylor 1922). Mounds provide thermal refugia for kangaroo rats from extreme surface temperatures that range from near 40ºC during summer to below freezing during the winter. On average, air temperature in burrows is 3-10ºC cooler than surface air temperature (Kay and Whitford 1978). Thermoregulatory costs for kangaroo rats are highest during the winter, when ambient temperature drops below thermoneutrality (Carpenter 1966, Kenagy 1973, Hinds and MacMillen 1985). Within mounds, kangaroo rats larder hoard up to 5 kg of collected seeds to survive periods of resource scarcity. Caching occurs most frequently during spring-fall, when seed availability is highest (Vorhies and Taylor 1922, Monson 1943). Maintaining a low-moisture microclimate within mounds is critical to seed preservation because high-moisture conditions (e.g. after large rainfall event) lead to cache loss due to germination and toxic fungal infections (Reichman et al. 1985, Frank 1988, Valone et al. 1995). A variety of terrestrial and aerial vertebrates prey on banner-tailed kangaroo rats and annual adult survivorship is low (< 50%)(Vorhies and Taylor 1922, Nader 1978, Waser and Jones 1991). Predation risk also varies seasonally because snakes are not active during the colder half of the year. Snakes are one of the few predators that enter mounds in pursuit of kangaroo rats (Randall and Stevens 1987).

My objective was to examine how banner-tailed kangaroo rats modify burrow entrances of mounds in response to seasonal variation in temperature, predation risk, and vulnerability of caches to spoilage. During the winter, thermoregulatory costs for kangaroo rats are high, and risk of predation and cache spoilage are lower. Conversely, during the summer, thermoregulatory costs are low, and risk of predation and cache spoilage are higher. Kangaroo rats would be hypothesized to increase the number of burrow entrances in mounds during summer and reduce them during winter in response to these tradeoffs.

Materials and Methods

Study area

The study area was located at the Sevilleta National Wildlife Refuge, near Socorro, New Mexico, USA (34° 24´ 24.8' N, 106° 36´ 20.5' W, 1600 m elevation). The site encompassed 18 ha of Chihuahuan Desert and short grass steppe vegetation dominated by grama grass (*Bouteloua eriopoda* and *B. gracilis*), burrograss (*Scleropogon brevifolius*), and sand dropseed grass (*Sporobolus cryptandrus*). Soil was classified as deep clayey loam.

Mound census

The study area contained 165 kangaroo rat mounds of varying condition and size. Each mound was mapped and uniquely marked. From March 2005-February 2008 (excluding March, April, and June 2006 and January 2007), I performed a monthly

census of the banner-tailed kangaroo rat population on the study area. Each month, all mounds were assessed for signs of kangaroo rat activity (e.g., fresh digging and feces, burrow entrances free of debris)(Jones 1984). At each, I counted the number of opened and plugged burrow entrances approximately ≥ 5 cm in diameter, the minimum size entrance I observed kangaroo rats to enter. A plugged burrow entrance was a soil-filled area on the mound, which retained the visible outline of the former opening.

All mounds exhibiting active kangaroo rat sign were trapped for 3 consecutive nights. Two to four live traps (Model XLK, H.B. Sherman Traps, Tallahassee, FL, USA) were baited with sweet feed (oats, corn, and barley mixed with molasses) and placed at each mound (Cross and Waser 2000). I opened live traps at dusk and examined them 3-7 hrs after sunset. All individuals were marked with a uniquely numbered Passive Integrated Transponder (PIT) tag (Model 1440ST, Biomark, Boise, Idaho, USA), which was injected subcutaneously. I recorded gender, age, reproductive status, and mass of all captured individuals each month. All animals were handled in accordance with the guidelines of the University of New Mexico Institutional Animal Care and Use Committee (Protocol No. 04MCC00507 and UNM048-TR-100261).

Adult banner-tailed kangaroo rats are solitary and highly territorial. An individual captured most frequently at a mound could reliably be considered the occupant (Schroder 1979, Jones 1984). During this study, I considered a mound occupied by an individual if it was caught at the mound: (1) > 1 month; (2) $\geq$ two times during 3 consecutive months; and (3) more frequently than any other adult (Jones 1984, Waser et al. 2006).

Statistical analysis

All statistical analyses were conducted using R version 2.10.0 (R Development Core Team 2009). Precipitation and mean, minimum, and maximum air and soil temperature at 10 cm were recorded hourly by a data logger (Model CR10X, Campbell Scientific Inc., Logan, Utah, USA) located 6.6 km from study area in grassland habitat (1650 m elevation). Mean soil temperature at 10 cm has been shown to closely match mean burrow air temperature at depths < 30 cm in banner-tailed kangaroo rat mounds (Kay and Whitford 1978). Hourly readings for mean temperature data were averaged and maximum and minimum temperature was determined for each day. For each month, I calculated a time series dataset containing mean daily air temperature and soil temperature at 10 cm (minimum, mean, and maximum), total precipitation, and number of burrow entrances (based on all occupied mounds). To ensure a complete time series for mounds, missing census data (4 months) were estimated by linear approximation between the previous and following months. Data in the time series exhibited significant autocorrelation between consecutive months. Therefore, I used generalized least squares (GLS) regression with autocorrelated errors to examine how number of burrow entrances varied in response to possible explanatory variables. Autocorrelated errors (ρ) were modeled in GLS regression as a first-order autoregressive process, preventing underestimation of standard errors and inflated *P*-values for effects in regression models (Venables and Ripley 2002, Cowpertwait and Metcalfe 2009). I tested for long-term trends individually for each climate variable by comparing the fit of models with (full model) and without a long-term trend component (null model) using a likelihood ratio test. Both the full and null models contained a harmonic seasonal component that allowed

climate variables to change seasonally (Cowpertwait and Metcalfe 2009, Crawley 2009). To choose variables (soil temperature, air temperature, precipitation, and time) that predicted variation in burrow numbers, I performed a backward selection process with cut-off P-values of 0.05 for exclusion in the final regression model.

I examined how individual kangaroo rats varied number of burrow entrances in their mounds between summer (July) and winter (December) by fitting a linear mixed model. Fixed effects were sex, year, and month (July or December) and the random effect was identity of kangaroo rats. Only mounds that were occupied by the same individual during July and December of the same year were included in the model. Effects included in the final model were selected using a backward selection process with cut-off P-values of 0.05 for exclusion. GLS regression and linear mixed models were fitted using the maximum likelihood method for use in likelihood ratio tests and the variable selection process; final models were fitted using the less-biased restricted maximum likelihood method. I used a Pearson chi-square test to compare proportion of mounds with and without plugged burrow entrances between July and December. All data met the assumptions of parametric tests and only two-tailed P-values were reported.

To quantify how variations in ambient temperature would affect metabolic processes, I used published allometric equations for desert heteromyid rodents (Hinds and MacMillen 1985) to estimate basal metabolic rate (BMR) and evaporative water loss (EWL) for banner-tailed kangaroo rats. BMR (ml O_2/g h) was calculated at 5ºC, 15ºC, and thermoneutrality (25-35ºC) using the following equations:

$$BMR_{5º} = 27.938M^{-0.571} \tag{1}$$

$$BMR_{15°} = 15.720M^{-0.508} \tag{2}$$

$$BMR_{TN} = 2.993M^{-0.271} \tag{3}$$

where M is body mass. BMR at 0°C was estimated through linear regression of BMR at higher temperatures. EWL was calculated at 5-25°C and 35° using the following equations:

$$EWL_{5-25°} = 5.267M^{-0.368} \tag{4}$$

$$EWL_{35°} = 4.711M^{-0.211} \tag{5}$$

Mass was fixed at 141.4 g in all equations, the combined mean of male and female banner-tailed kangaroo rats during this study.

In order to estimate the effect of surface conditions on burrow air temperatures in this study, I used the published equation

$$T_B = -2.12 + 0.88T_A \tag{6}$$

for the observed relationship between surface air temperature (T_A) and burrow air temperature (T_B) in banner-tailed kangaroo rat mounds (Kay and Whitford 1978). The equation is based on T_B measured at a variety of depths (10-90 cm) and should be interpreted as an average T_B of the mound. In general, T_B in mounds varies little with depth during winter, but tends to be 2-5°C higher at shallower depths during the rest of the year (Kay and Whitford 1978).

Results

Mean number of burrows in occupied mounds exhibited a strong seasonal pattern,

ranging from a high of 10-12 during the summer months to a low of 4-6 during winter

months depending on the year (Fig. 1.2). Number of occupied mounds each month

ranged from 35 in March 2005 to 103 in August and September 2005 ($\overline{X}$ ± SE = 62.6 ±

3.3 occupied mounds). Fluctuations in mean number of burrow entrances closely

matched variation in soil temperature at 10 cm (Fig. 1.2a) and air temperature (Fig. 1.2b).

The peaks in number of burrow entrances each year corresponded to months when total

precipitation exceeded 60 mm (Fig. 1.2c). Burrow entrances on mounds also tended to

increase slightly in number over time (Fig. 1.2). However, GLS regression models

indicated there were no long-term trends for any climate variables over the duration of

the study. For soil temperature at 10 cm, air temperature, and precipitation GLS

regression models containing only a harmonic seasonal component were a better fit

(Likelihood ratio tests, all $P > 0.71$) than models with a long-term trend component also

included. Across years, estimated burrow air temperatures ranged from a high of 20 to

23ºC during June and July to a low of -2 to 1ºC during December and January (Fig. 1.3).

Burrow air temperatures were slightly below mean surface air temperatures all year, but

the difference between them was greatest at high surface temperatures (Fig. 1.3).

The best-fitting regression model allowed mean number of burrow entrances to

vary with mean soil temperature at 10 cm and precipitation (Fig. 1.4, Table 1.1; residual

standard error = 1.43). During the variable selection process, mean air temperature and

time were not significant effects and were removed from the final regression model.

Mean number of burrow entrances in occupied mounds decreased with mean soil temperature at 10 cm and increased with precipitation. For each 6.5°C (95% CI = 4.8-11.1°C) decrease in soil temperature, number of burrow entrances decreased by an average of about 1, whereas 77 mm (95% CI = 48-333 mm) of precipitation resulted in a mean increase of 1 burrow entrance.

The best fitting linear mixed model contained a significant interaction effect between month and year (Table 1.2), but sex was not a significant effect and was removed from the final model. Total numbers of mounds occupied by the same kangaroo rat during both July and December on site were 46 in 2005, 27 in 2006, and 42 in 2007. Mound owners decreased the number of burrow entrances by an average of 45% to 52% (4-7 burrow entrances) from July to December across all years (Fig. 1.5, Tukey-Kramer test, $P < 0.05$). Number of burrow entrances in July differed among some years with 2007 greater than both 2005 and 2006 (Tukey-Kramer test, $P < 0.05$), but did not differ in December among years (Tukey-Kramer test, $P > 0.05$). Plugged burrow entrances were difficult to detect because kangaroo rats usually covered the area completely with soil, erasing any evidence of the former entrance. However, plugged burrow entrances at mounds occupied by the same individual were almost never detected in July (2%, 2 of 119 mounds) and were more commonly found in December (35%, 41 of 119 mounds) for all years combined ($n = 238$, $\chi_1 = 43.2$, $P < 0.0001$).

Estimated metabolic costs at different ambient temperatures were substantial. Compared to thermoneutrality, estimated BMR of banner-tailed kangaroo rats increased by > 60% at 15°C, > 110% at 5°C, and 140% at 0°C (Fig. 1.6). Evaporative water loss

increased by 115% from 25ºC to 35ºC (Fig. 1.6). Kangaroo rats can minimize both BMR and EWL by remaining at ambient temperatures toward the lower end of thermoneutrality (25ºC).

Discussion

Banner-tailed kangaroo rats modified burrow architecture on a seasonal time scale. These alterations in burrow design closely mirrored variation in air temperature, soil temperature, and precipitation (Fig. 1.2). Decreases in burrow entrances were tightly linked to drops in soil temperature at 10 cm; compared to summer, mounds in winter had half as many openings. Modifications of architecture were intentional, because mounds occupied by the same kangaroo rat differed in burrow openings between winter and summer. Changes in burrow architecture were likely adaptive responses by kangaroo rats to seasonal tradeoffs in thermoregulatory costs, predation risk, and seed spoilage.

Fewer entrances in winter reduce heat loss from air convection and increase the buffering effect of soil creating a more stable and warmer microclimate within burrows (Roper and Kemenes 1997, Bulova 2002, Shimmin et al. 2002, Roper and Moore 2003). At cold surface temperatures, warm air in burrows convectively rises and escapes aboveground and colder air from the surface sinks into burrows reducing the buffering effect of the surrounding soil (Nikol'skii and Savchenko 2002). Thus, kangaroo rats can reduce incursion of cold air into burrows by sealing entrances during the winter months. Winter burrow temperatures of banner-tailed kangaroo rat mounds at lower elevation sites in southern New Mexico averaged 5-10°C (Kay and Whitford 1978, French 1993).

Estimated burrow temperatures at my higher elevation and latitude site were even lower ranging from -2 to 1ºC during December and January (Fig. 1.3) which is below the lower limit of thermoneutrality by about 25ºC (Fig. 1.6). At these temperatures, Estimated BMR of banner-tailed kangaroo rats was about two and half times higher than at thermoneutrality with resulting requirements for increased food consumption for thermoregulation (Fig. 1.6)(Hinds and MacMillen 1985). Modification of burrow architecture to increase burrow temperatures would result in significant energy savings through lower BMR and decrease the rate at which seed caches were depleted. For example, maintaining burrow air temperatures 5ºC warmer than minimum surface air temperatures during the winter would reduce metabolic rate by about 15% (Fig. 1.6).

During the summer, thermoregulatory costs of kangaroo rats are relatively lower than the winter, but evaporative water loss can increase if temperatures are above 25ºC (Fig. 1.6). Burrow temperatures of banner-tailed kangaroo rats at lower elevations were between 25-30ºC, within the thermoneutral zone (Kay and Whitford 1978). At my site, estimated burrow temperatures were lower, ranging from 20-22ºC during June and July (Fig. 1.3). While these temperatures are slightly below thermoneutrality, soil temperatures at 10 cm indicated that burrows at depths < 30 cm would be within the range of 29-33ºC (Fig. 1.2a). Given this range of temperatures, banner-tailed kangaroo rats should be able to move vertically within the burrow system to seek temperatures that minimize both BMR and evaporative water loss (about 25ºC; Fig. 1.6), as observed in other kangaroo rat species (Kenagy 1973).

More burrow entrances on mounds at warm temperatures may be a strategy by kangaroo rats to reduce predation risk, which is greater during warmer periods when snakes are active. From approximately October to early April, large snakes such as the western diamondback rattlesnake (*Crotalus atrox*) are dormant on my study site. Only mammalian and avian predators are active and most of these cannot enter kangaroo rat burrows (personal observation). During the rest of the year, snakes prey on kangaroo rats and enter mounds to pursue them. More burrow entrances during the summer may decrease predation success by providing additional escape routes (Bronner 1992). Banner-tailed kangaroo rats typically flee from snakes by exiting from entrances on the opposite side of mounds from where snakes enter (Randall and Stevens 1987). Other rodent species also exhibit increased burrow complexity when at higher predation risk. In whistling rats (*Parotomys* spp.*)*, species in habitats with higher predation risk had more burrow entrances than species in habitats with lower predation risk (Jackson 2000). Voles (*Microtus* spp.) in pens with predators (including snakes) built more complex burrows with additional entrances than in pens without predators suggesting burrow complexity reduces predation risk (Harper and Batzli 1996).

Peaks in number of burrow entrances corresponded closely with months of high rainfall (> 60 mm) on the study site (Fig. 1.2c). High levels of toxic fungal infections in seed caches within mounds of banner-tailed kangaroo rats often occur after heavy rainfall (Reichman et al. 1985). Kangaroo rats may have attempted to reduce germination and fungal growth in seed caches during wet periods by adding entrances. More entrances would increase passive ventilation of mounds (Vogel and Bretz 1972, Vogel et al. 1973) and speed evaporation of water from burrow soil and caches. Maintaining seed caches are

critical to survival and reproduction of kangaroo rats during periods of resource scarcity, and especially during the winter months (Monson 1943, Vander Wall 1990). Fungal contamination of seed caches with mycotoxins are implicated in the near-extirpation of banner-tailed kangaroo rats following a rainfall event of 129 mm in Arizona (Valone et al. 1995).

There is only scant quantitative evidence on how non-hibernating, semi-fossorial mammals modify burrows in response to seasonal variation in environmental conditions. This is likely due to absence of long-term monitoring of burrow systems. Most detailed studies of burrow architecture are necessarily destructive, eliminating the possibility of comparisons between seasons. Monitoring surface architecture of burrows is a non-destructive technique, which can provide insight into an animal's reaction to variations in climate, predation risk, and other environmental conditions. Kangaroo rats are well known for their physiological and morphological adaptations to arid environments (Brylski 1993, French 1993). My results highlight how behavioral adaptations are also critical to their success at surviving in these extreme habitats.

Acknowledgments

Table 1.1. Parameter estimates of generalized least squares regression model with autocorrelated errors for number of burrow entrances in occupied banner-tailed kangaroo rats mounds from March 2005-February 2008.

Model parameters	Coefficient	95% CI	$F_{1,38}$	P
Intercept	4.43	2.83-6.03	123.71	<0.0001
Soil temperature at 10 cm	0.15	0.09-0.21	32.14	<0.0001
Precipitation	0.013	0.003-0.024	6.33	0.017
Autocorrelation (ρ)	0.80	0.43-0.94		

Table 1.2. Parameter estimates of linear mixed model for number of burrow entrances in mounds of individual banner-tailed kangaroo rats during July and December from 2005-2007.

Fixed effects	Coefficient	95% CI	$F_{1,146}$	P
Intercept	-1422.19	-2753.63– -90.75	709.48	<0.0001
Month	-2269.80	-3832.08– -707.52	227.64	<0.0001
Year	0.71	0.05-1.38	22.11	<0.0001
Month*Year	1.13	0.36-1.91	8.28	0.005

Random effects	SD	95% CI		
Identity	2.36	1.86-3.01		
Residual	2.66	2.37-2.98		
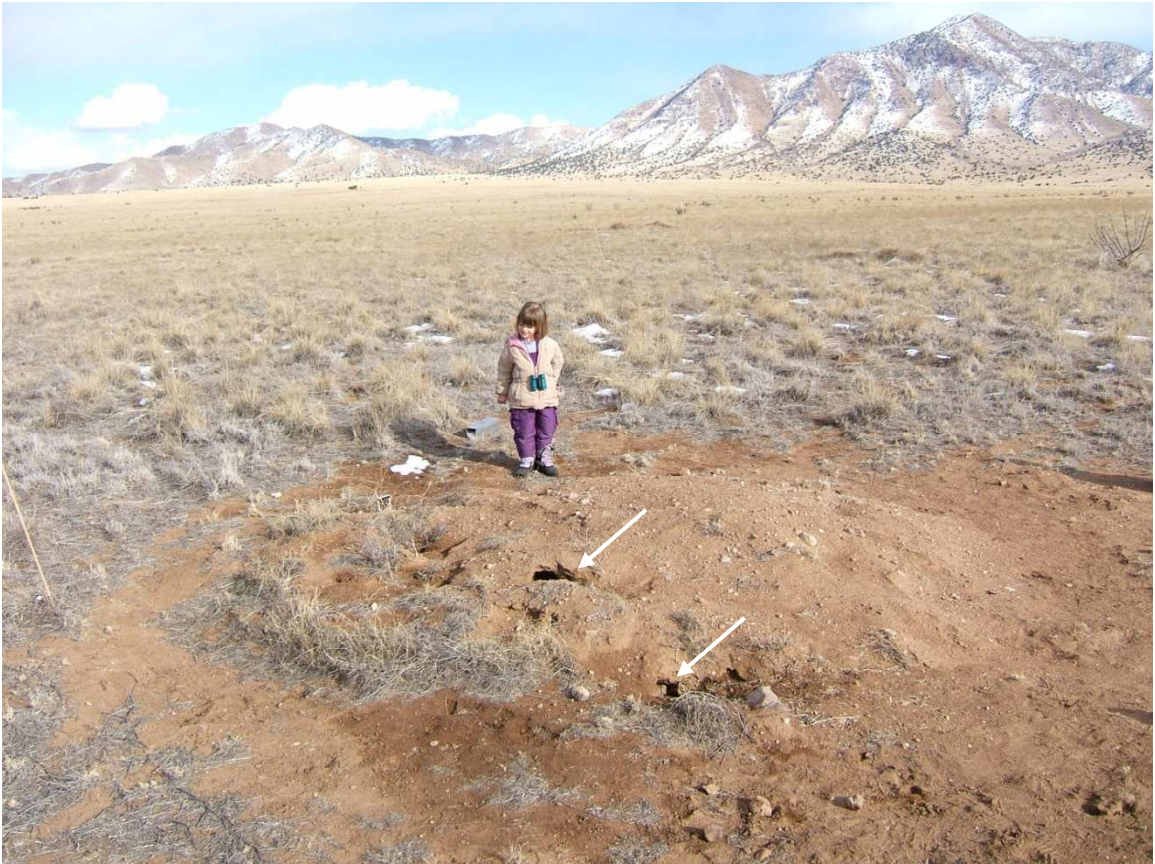
Figure 1.1
Banner-tailed kangaroo rat mound during winter. Visible burrow entrances are marked with white arrows. For scale, the child in the picture is approximately 1-m tall.
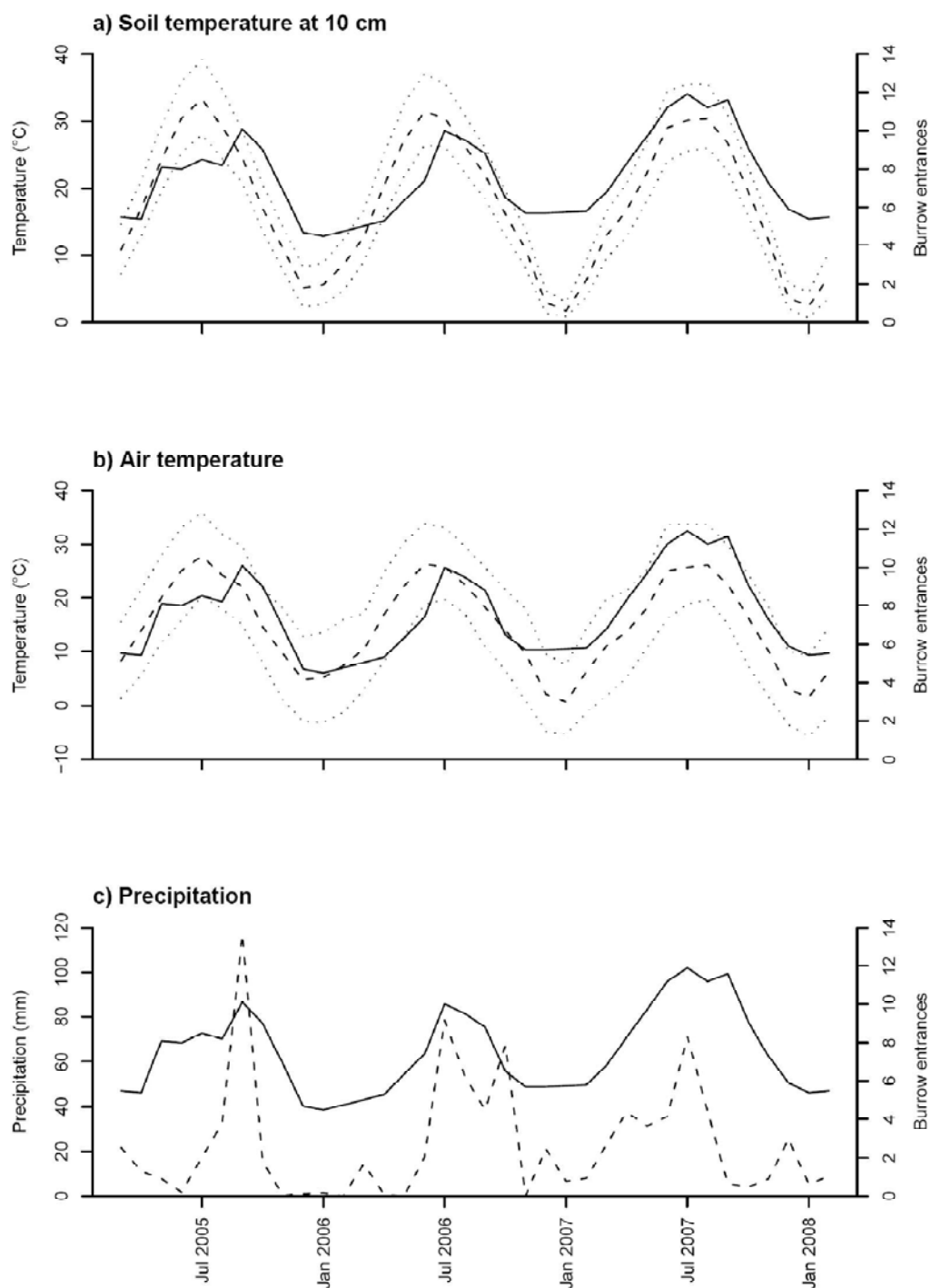
Figure 1.2
Relationship between mean number of burrow entrances (solid line) in occupied banner-tailed kangaroo rat mounds and a) mean daily soil temperature at 10 cm, b) mean daily air temperature, and c) total precipitation each month from March 2005-February 2008. Precipitation and mean daily temperatures are represented by dashed lines and mean daily minimum and maximum temperatures by dotted lines.
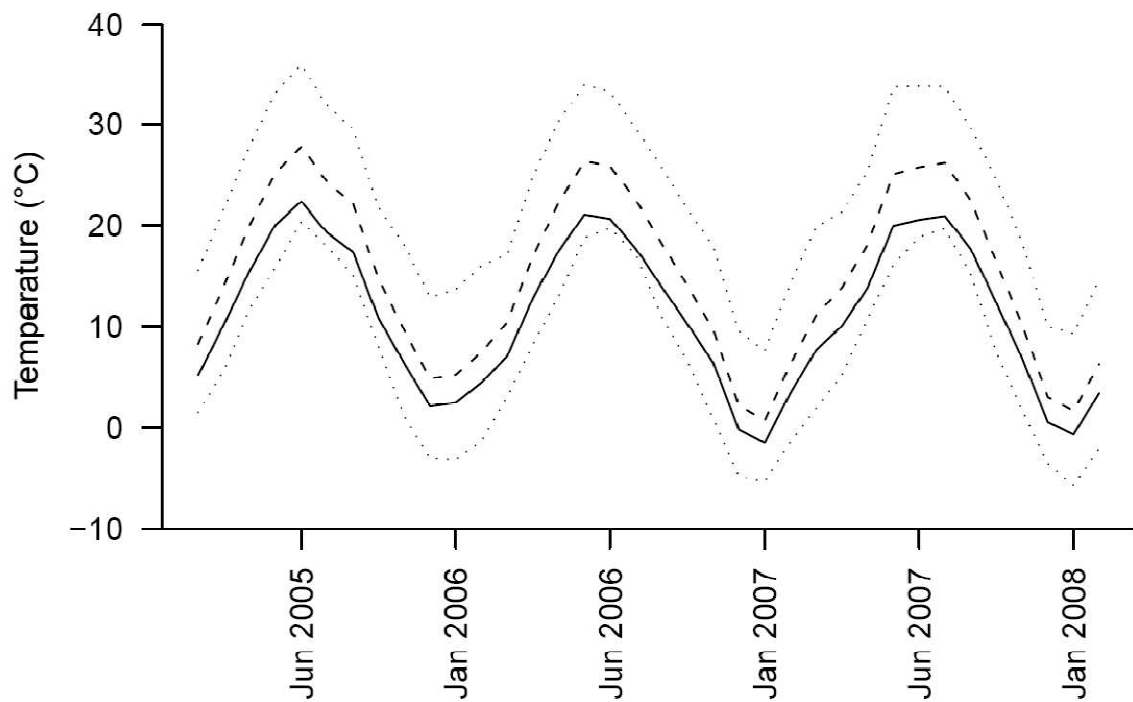
Figure 1.3
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surface air temperatures (dashed line = mean, dotted lines = minimum and maximum)
from March 2005-February 2008. Temperatures are calculated from an equation of the
observed relationship between surface air temperature and burrow air temperature (Kay
and Whitford 1978).
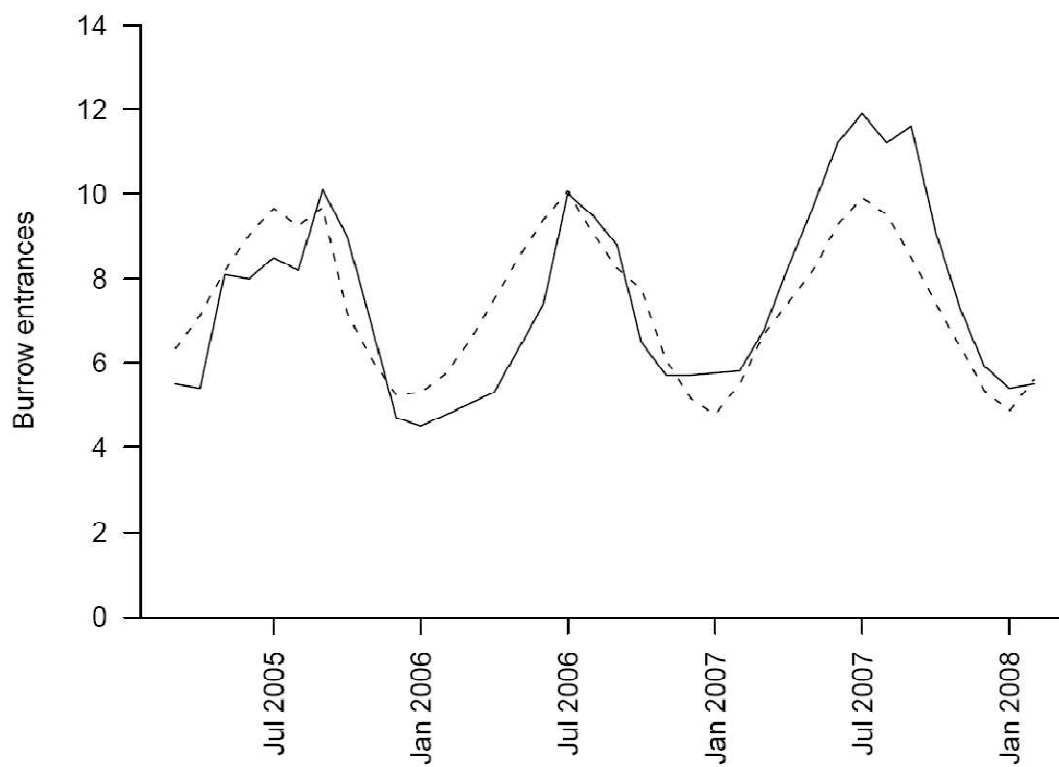
Figure 1.4
Fitted values (dashed line) from generalized least squares regression model compared to observed values (solid line) for number of burrow entrances in banner-tailed kangaroo rat mounds from March 2005-February 2008.
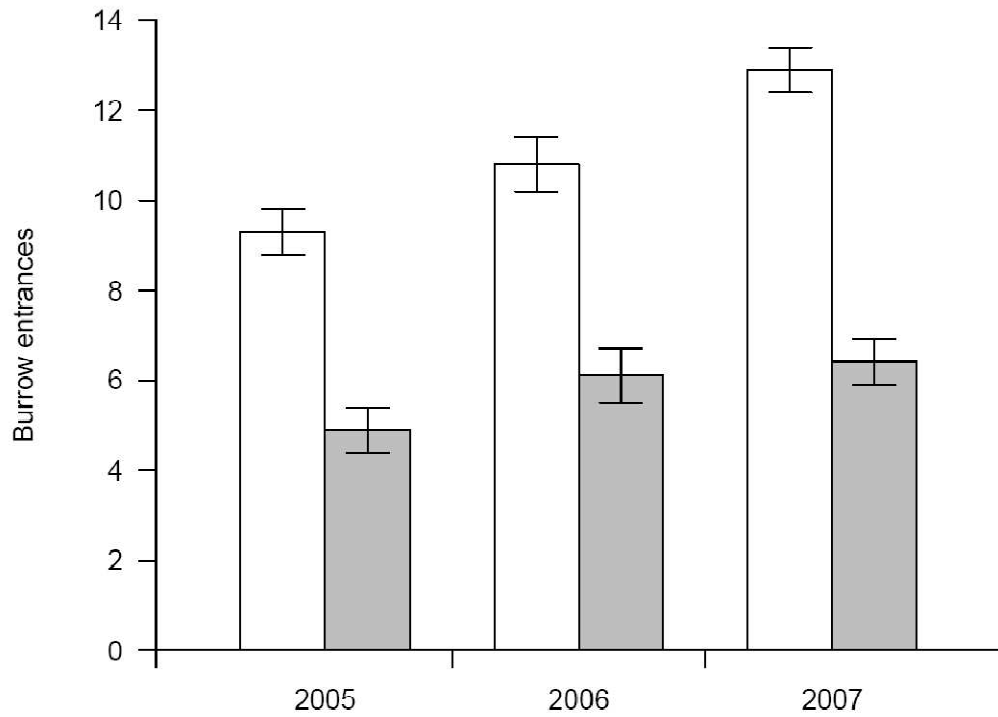
Figure 1.5
Number of burrow entrances (least squares means ± SE) at occupied banner-tailed
kangaroo rat mounds during July (white bars) and December (grey bars) from 2005-2007.
Only mounds occupied by the same banner-tailed kangaroo rat in July and December of
the same year were included.
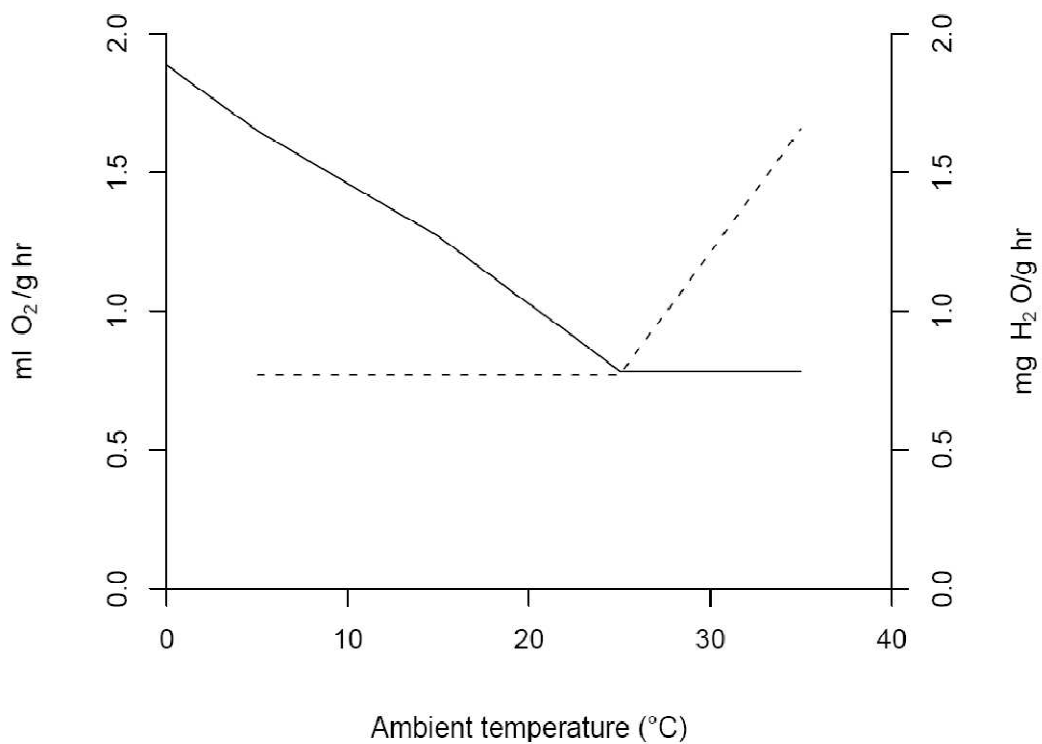
Figure 1.6
Relationship of mass-specific basal metabolic rate (solid line) and evaporative water loss
(dashed line) to ambient temperature for banner-tailed kangaroo rats. Lines are calculated
from allometric equations of desert heteromyid rodents (Hinds and MacMillen 1985)
based on a body mass of 141.4 g. Thermoneutral zone occurs from 25-35ºC.

Chapter 2

Facilitative interactions between keystone rodents and harvester ants in the Chihuahuan Desert

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Abstract

In the Chihuahuan Desert, a keystone kangaroo rat species facilitates harvester ants through ecosystem engineering and foraging. We used spatially explicit techniques and behavioral observations to examine the effects of banner-tailed kangaroo rats (*Dipodomys spectabilis*) on rough harvester ants (*Pogonomyrmex rugosus*). We mapped kangaroo rat mound and harvester ant colonies as well as monitored extinction and founding of ant colonies. We also quantified resource abundance and foraging behavior of harvester ants with respect to distance from kangaroo rat mounds. We tested support for a scale-dependent facilitative interaction by fitting spatial point process models to locations of mounds and colonies. In addition, we built logistic models of colony extinction risk that included spatial effects of mounds and tested their ability to predict spatial patterns of surviving colonies. Best-fitting spatial models exhibited small-scale aggregation (< 10 m) between kangaroo rat mounds and both older and newly-founded colonies, implying a

positive interspecific interaction. Colony extinction risk was affected by colony age, size, and intraspecific competition in both newly founded and older colonies, but proximity to a kangaroo rat mound also decreased extinction risk for newly founded colonies. Seed abundance at the soil surface was greater and foraging time was shorter for colonies near mounds than for those farther away. Our results indicate that kangaroo rats facilitate harvester ants in the Chihuahuan Desert. The scale-dependent effect of mounds on colony founding, extinction, resource abundance, and foraging is likely due to kangaroo rats increasing abundance of ants' preferred food source, small-seeded annuals, around mounds. Colonies within close proximity to an occupied mound have access to more abundant food resources resulting in higher survivorship during the first several years after founding.

Introduction

Facilitation occurs when one species enhances the environment and performance of another species (Bronstein 2009). This positive interaction can arise directly through ecosystem engineering of the abiotic environment (e.g., solar radiation, water, or soil nutrients) or indirectly through effects on secondary species (e.g., suppressing a competitor or increasing abundance of prey) (Stachowicz 2001, Bruno et al. 2003). Species interactions, such as facilitation, are usually scale-dependent reflecting spatial heterogeneity of abiotic and biotic factors (Wiens 1989, Levin 1992). For example, the facilitative effects of nurse plants are highly localized and diminish with distance (Callaway 1995). Species interactions, along with other scale-dependent processes, affect

population dynamics, which in turn influence the distribution of individuals and species across the landscape.

Seed predation and ecosystem engineering activities by kangaroo rats (*Dipodomys* spp.), have disproportionally large effects in the Chihuahuan Desert and arid grassland ecosystems (Brown and Heske 1990, Brown et al. 2001). Long-term experimental research on these keystone rodents has demonstrated the impact of their selective foraging and mound building activities on plant diversity and composition (Davidson et al. 1985, Brown and Heske 1990, Samson et al. 1992, Heske et al. 1993, Guo 1996). However, experiments examining interactions between kangaroo rats and another abundant group of granivores, harvester ants, have yielded only equivocal results (Brown and Davidson 1986, Galindo 1986, Valone et al. 1995). Kangaroo rats are hypothesized to indirectly facilitate harvester ants through their effects on prey species of ants. Kangaroo rats preferentially harvest seeds of large-seeded winter annuals, whereas harvester ants specialize on seeds of small-seeded annuals (Brown and Davidson 1977, Brown et al. 1979, Davidson et al. 1980, Inouye et al. 1980). Large-seeded annuals are superior competitors and removal experiments have shown that kangaroo rats indirectly facilitate small-seeded annuals by suppressing large-seeded annuals (Inouye 1980, Inouye et al. 1980, Davidson et al. 1985, Samson et al. 1992). While abundance of harvester ants' preferred seed species decreases greatly with kangaroo rat removal, the expected decrease in ant abundance does not occur. Lack of response to kangaroo rat removal may be due to harvester ants compensating by utilizing relinquished seed resources (Davidson et al. 1985, Samson et al. 1992).

The largest and most influential kangaroo rat species in the Chihuahuan Desert is the banner-tailed kangaroo rat (*Dipodomys spectabilis*)(Davidson et al. 1980, Brown et al. 2001). This species creates semi-permanent structures around which their ecosystem engineering activities are centered. Banner-tailed kangaroo rats excavate soil to construct mounds (Fig. 1.1a), which are typically 4 m in diameter and 30 cm in height (Holdenried 1957, Reichman et al. 1985). Within the mound is a labyrinth of tunnels and chambers extending up to 4 stories and > 90 cm in depth containing large seed caches (Vorhies and Taylor 1922). Individuals have circular home ranges of about 0.05 ha (12-m radius), with the majority of their active period spent < 6 m from the mound (Schroder 1979). Mounds are occupied for many generations, but only one adult resides in the mound at a time (Holdenried 1957, Schroder 1979, Reichman et al. 1985). Impacts on plant communities by banner-tailed kangaroo rats are highly localized around mounds. Biomass of small-seeded annuals are greatest at distances within 4 m of mounds with highest densities directly on mounds (Guo 1996). Thus, facilitative effects of banner-tailed kangaroo rats on harvester ants would be predicted to decrease with distance from mounds.

Within the ant community, the dominant granivorous ant is the rough harvester ant (*Pogonomyrmex rugosus*). This large-bodied species is ideal for studying the potential facilitative effects of banner-tailed kangaroo rats on harvester ants because colonies are numerous and conspicuous. Each colony builds an underground nest, with a single entrance in the center of a surface disc (averaging 1 m in diameter), which is cleared of vegetation and covered with small pebbles (Fig. 1.1b) (Whitford et al. 1976, Schooley and Wiens 2003). Colonies consist of several thousand workers founded by a single queen (Hölldobler 1976a). Mortality is high for *Pogonomyrmex* founding queens and

young colonies, but established colonies can persist for ≥ 15 years (Johnson 2000, MacMahon et al. 2000). *Pogonomyrmex* forage for seeds in coordinated groups and store collected food in granaries within colonies (Davidson 1977, MacMahon et al. 2000). Foraging activity decreases exponentially with distance from colonies with most foraging occurring < 10 m from colonies (Whitford 1976, De Vita 1979, Crist and MacMahon 1991). Intraspecific aggression between workers of neighboring colonies is common and workers kill founding queens if encountered (Hölldobler 1976b, Johnson 2000).

The hypothesized facilitative effect of banner-tailed kangaroo rats on rough harvester ants is expected to decrease with distance from mounds because ant colonies nearest mounds will benefit most from higher levels of seed resources. Thus, the relationship between kangaroo rats and harvester ants can be viewed as a scale-dependent interaction that decreases in strength with distance from centralized structures. By studying the spatial relationship between these species, we can infer whether facilitation or other interspecific interactions occur (Barot et al. 1999, Fortin and Dale 2005, Tuda 2007). The spatial interaction between kangaroo rats and ants can be examined as a point process, where a stochastic mechanism such as facilitation determines the density (i.e., point pattern) of structures built by these species across the landscape through spatially dependent founding and extinction of ant colonies (Fortin and Dale 2005, Illian et al. 2008). We used point patterns of mounds and colonies to determine whether banner-tailed kangaroo rats facilitated rough harvester ants. Specifically, we tested whether facilitation of harvester ants by kangaroo rats occurred by examining three hypotheses:

1) Kangaroo rat mounds and harvester ant colonies will be spatially aggregated around each other at scales < 10 m.

2) Spatial aggregation will occur because of higher founding and lower extinction rates of ant colonies near mounds.

3) Seed abundance will be greater and foraging time will be lower for colonies close to a mound.

To test these hypotheses, we mapped mounds and colonies built by banner-tailed kangaroo rats and rough harvester ants, respectively, and monitored extinction and founding of ant colonies. We also measured abundance of seed resources and foraging time of colonies that were near and far from mounds. We used two spatially explicit approaches to explore the scale-dependent effects of kangaroo rats on ant populations: 1) comparison of statistical point process models to determine if an interspecific interaction affected distribution of kangaroo rat mounds and existing and newly founded colonies; and 2) logistic models that examined whether colony extinction was spatially dependent on mounds. We followed a deductive model comparison approach by *a priori* selecting biologically appropriate statistical models and parameters based on the known ecology of both species (Mcintire and Fajardo 2009).

Materials and Methods

Study area

The study area was located at the Sevilleta National Wildlife Refuge, near Socorro, New Mexico, USA (34° 24´ 24.8' N, 106° 36´ 20.5' W, 1600 m elevation). The site encompassed an 8.7-ha rectangular plot (397 × 220 m) of Chihuahuan Desert and short grass steppe vegetation dominated by grama grass (*Bouteloua eriopoda* and *B. gracilis*), burrograss (*Scleropogon brevifolius*), and sand dropseed grass (*Sporobolus cryptandrus*).

Mapping

We used a global positioning system (GeoXT, Trimble Navigation Ltd., Sunnyvale, California, USA) to map all banner-tailed kangaroo rat mounds and rough harvester ant colonies on the study site. Coordinates of structures were real-time differentially corrected using a local base station allowing for sub-meter accuracy of mapped locations.

Banner-tailed kangaroo rat mounds were located by walking adjacent 5-m transects throughout the study area during March 2005. From March 2005-February 2008 (excluding January 2007), we performed a monthly census of the banner-tailed kangaroo rat population on the study area. Each month, all mounds were assessed for signs of kangaroo rat activity (e.g., fresh digging and feces, burrow entrances free of debris) (Jones 1984). Any newly built mounds were also mapped at this time. All mounds exhibiting active kangaroo rat sign were trapped for 3 consecutive nights. Two to four live traps (Model XLK, H.B. Sherman Traps, Tallahassee, FL, USA) were baited with

sweet feed (oats, corn, and barley mixed with molasses) and placed at each mound (Cross and Waser 2000). We opened live traps at dusk and examined them 3-7 hrs after sunset. Individuals were marked with a uniquely numbered Passive Integrated Transponder (PIT) tag (Model 1440ST, Biomark, Boise, Idaho, USA), which was injected subcutaneously. All animals were handled in accordance with the guidelines of the University of New Mexico Institutional Animal Care and Use Committee (Protocol No. 04MCC00507 and UNM048-TR-100261).

Adult banner-tailed kangaroo rats are solitary and territorial. Thus, an individual captured most frequently at a mound could reliably be considered the occupant (Schroder 1979, Jones 1984). During this study, we considered a mound occupied during a month by an individual if it was caught at the mound: (1) > 1 month; (2) ≥ two times during 3 consecutive months; and (3) more frequently than any other adult (Jones 1984, Waser et al. 2006). A mound was considered occupied during a year, if it was occupied ≥ 1 month during a 12-month occupancy period. In 2007 and 2008, the occupancy period was July 2006-June 2007 and July 2007-June 2008, respectively. In 2009, the occupancy period was shorter, July 2008-February 2009, because monthly monitoring of mounds ended in February 2009. To compensate for the shorter occupancy period, we visually surveyed all mounds for signs of kangaroo rat activity in September 2009 and included additional occupied mounds ($n = 2$) in the 2009 occupied group. Only occupied mounds were used in analyses because cessation of kangaroo rat activity leads to changes in plant communities around unoccupied mounds (Chew and Whitford 1992, Hawkins and Nicoletto 1992, Guo 1996).

The entire site was surveyed for *P. rugosus* colonies in June-September 2007 and again in August-September 2008. We walked 3-m transects across the study area and visually searched for signs of colonies. New colonies found in 2008 were assumed to have first been established by dispersing queens in the summer 2007 and were not large enough to be detected until the following year (Gordon and Kulig 1996). Surveys were conducted during conditions of high ant activity (e.g., sunny weather and warm surface temperatures). Colonies were identified by the presence of a pebbled disc, nest entrance, and/or presence of workers. *Pogonomyrmex rugosus* workers are easily recognized by their large size (> 8-mm total length) and dark brown head and mesosoma with a lighter colored gaster (MacKay and MacKay 2002). We marked all colonies and measured diameter of colony disc. In August 2008 and September-October 2009, we again checked all marked colonies for activity and measured disc diameter. Colonies were classified as active or inactive based on the presence of *P. rugosus*. In 2007 and 2008, inactive colonies were verified by disturbing the nest entrance to elicit an alarm response from workers (Schooley and Wiens 2003). In 2009, inactive colonies were verified by digging into the disc and looking for workers. In addition, we revisited inactive colonies 1–2 weeks later and repeated the verification process. Inactive colonies were considered to have died between yearly surveys.

Seed abundance and foraging observations

During summer 2008, 30 active harvester ant colonies on the study site were selected for observing foraging time based on a blocked design. All colonies with a disc diameter between 0.7 and 1.1 m were placed in two distance groups, < 10 or > 20 m from an occupied mound. Fifteen colonies were then randomly selected from each distance

group (30 total). Colonies from different distance groups with the shortest distance between them were paired together to reduce spatial variation between groups. We quantified foraging behavior of 8 workers per colony. Foraging observations were conducted only at times of high ant activity, typically warm, sunny weather and before noon. Paired colonies were monitored simultaneously to reduce temporal variation between distance groups, and all observations were completed within a week of each other. At each colony, we randomly selected a worker leaving the nest entrance as our focal individual, followed it, and recorded the total time spent outside the nest on that foraging trip. We did not attempt to distinguish between unsuccessful and successful foraging trips, because workers rarely return to the colony until a food item has been found (Gordon 1993). The distribution of worker foraging times at colonies exhibited strong positive skew. As a result, we analyzed the median instead of the mean foraging time per colony.

Seed abundance in soil surfaces near colonies was quantified for 26 (13 pairs) of the colonies used for foraging observations. From each colony, we took one soil sample by removing the upper 1 cm of the soil surface in an12.5 × 12.5 cm area at 5 m from the nest entrance in a random direction. Soil samples were separated by mechanical sieving (mesh sizes 0.5-2.5 mm) and the smallest seeds were extracted by floatation. Seeds were then dried and sorted using a dissecting scope (Gutiérrez and Meserve 2003). Total mass of dried seeds was determined for each sample. Foraging time and seed number and total mass were analyzed using two-tailed paired t-tests. Seed number and mass were log-transformed prior to testing, but means and SE from untransformed values are presented in results.

Spatial Analysis

Spatial statistics

The spatial relationships among mounds and colonies during 2007 and mounds and new colonies in 2008 were characterized using the bivariate Ripley's *K*-function. This spatial statistic determines the scales at which two point patterns, in this case mounds and colonies, exhibit either complete spatial randomness (CSR), segregation, or aggregation. The bivariate *K*-function totals the number of points of the opposing species within a radius *r* of a focal point (mound or colony):

$$\hat{K}_{12}(r) = A \sum_{\substack{i=1 \\ i \neq j}}^{n_1} \sum_{\substack{j=1 \\ j \neq i}}^{n_2} \frac{\left(w_{ij} \cdot d_{ij}(r)\right)}{n_1 n_2} \tag{1}$$

where $\hat{K}_{12}(r)$ is the observed estimate K at distance r, A is the area of the study plot, n_1 and n_2 are the number of points of each species, w_{ij} is the edge-correction weighting, and $d_{ij}(r)$ is the distance between points i and j and $d_{ij}(r) = 1$ if $d_{ij} \leq r$ and $d_{ij}(r) = 0$ if $d_{ij} > r$ (Ripley 1977). Bivariate Ripley's *K* was calculated for each species separately and combined into one estimate. For ease of interpretation and to stabilize the variance, we used a modified *K*-function, $\hat{L}_{12}(r)$:

$$\hat{L}_{12}(r) = \left(\hat{K}_{12}(r)/\pi\right)^{1/2} - r \tag{2}$$

Biologically, $\hat{L}_{12}(r)$ for two point patterns can be interpreted as exhibiting, with respect to each other, CSR when zero, aggregation when > 0, and segregation when < 0 (Fortin and Dale 2005). $\hat{L}_{12}(r)$ was calculated for distances up to 20 m and a translation edge correction was implemented.

Candidate models

For each observed point pattern, we conducted a formal hypothesis test for the existence of an interspecific interaction between mounds and colonies. We compared the fit of a full model with an interspecific interaction and a null model without an interspecific interaction. The candidate model was chosen based on the known intraspecific interactions that occur within species. Banner-tailed kangaroo rats and harvester ants exhibit strong intraspecific competition, which results in segregated distributions of mounds and colonies through repulsion of conspecifics at short distances (< 30 m for kangaroo rats and < 20 m for harvester ants). Both species also exhibit a hard-core property, meaning that > 1 structure cannot physically exist at the same location (Schooley and Wiens 2001, 2003). This ecological information indicates the suitability of a Gibbs point process model, a flexible class of parametric models that can include interpoint interactions, spatial trends, and dependence on covariates (Stoyan and Penttinen 2000). These models can test for the existence of both negative (e.g., competition) and positive interactions (e.g., facilitation) between points. Gibbs models are specified in terms of conditional intensity, λ (or density), which determines the conditional probability of finding a point at given location based on information provided about the rest of the point process (e.g., interactions, covariates, and marks) (Baddeley

and Turner 2006). We chose the multi-type Strauss hard-core (MSHC) process with spatial covariates as our candidate model. This model allows multiple discrete marks (e.g., mounds and colonies), hard-core properties, and both positive and negative spatial dependence within and between marks. Let $\mathbf{y} = \{(x_1, m_1),\ldots, (x_n, m_n)\}$ denote a multi-type point pattern of a point process in a bounded region $W \subset \mathbb{R}^2$ with a set of M possible marks, where $x_i \in W$ are the points and $m_i \in M$ the corresponding marks. The MSHC model with spatial covariates where $u \in W$ and $k \in M$, has a conditional intensity function of

$$\lambda((u,k),\mathbf{y}) = B_k(u)\prod_i g(k,m_i,\|u - x_i\|) \tag{3}$$

where the interaction between a pair of points u and x with marks k and m is determined by the function

$$g(k,m,\|u - x\|) = \begin{cases} 0 & \text{if } \|u - x\| < h_{km} \\ \gamma_{km} & \text{if } h_{km} \le \|u - x\| \le r_{km} \\ 1 & \text{if } \|u - x\| > r_{km} \end{cases}$$

The four main parameters that define the MSHC model are $B_k(u)$, h_{km}, r_{km}, and γ_{km} (all must be > 0). Function $B_k(u)$ determines the intensity of the process for each mark and includes spatial trends and dependence on covariates at point u. The hard-core distance, h_{km}, specifies the distance between which two points cannot occur. The interaction distance, r_{km}, determines the distance between points in which an interaction occurs and must be > h_{km}. The interaction parameter, γ_{km}, specifies the strength and direction of the

interaction between points. For pairs of points with distances between h_{km} and r_{km} the

interaction parameters are biologically interpreted as attraction when $\gamma_{km} > 1$, no

interaction if $\gamma_{km} = 1$, and repulsion if $0 \leq \gamma_{km} < 1$. The hard-core distances, interaction

distances, and interaction parameters are all symmetrical (e.g., $\gamma_{km} = \gamma_{mk}$) (Baddeley and

Turner 2006).

Model fitting

We used the R package *spatstat* version 1.17-5 to fit non-stationary point process

models with conditional intensity estimated as a log-linear function. The model-fitting

algorithm used a maximum pseudolikelihood method with a translation edge correction

(Baddeley and Turner 1998, 2005). We fitted MSHC models to observed point patterns

of all colonies and occupied mounds during 2007 and occupied mounds and new colonies

during 2008. New colonies were defined as those founded on the study area during 2008,

whereas old colonies were first present during 2007. All points were marked as either

kangaroo rat mounds or harvester ant colonies, denoted as *K* and *A* respectively. The

MSHC model had 11 total parameters; 5 regular parameters ($B_K(u)$, $B_A(u)$, γ_{KK}, γ_{AA}, and

γ_{KA}) and 6 irregular parameters (h_{KK}, h_{AA}, h_{KA}, r_{KK}, r_{AA}, and r_{KA}). Irregular parameters

were estimated using the maximum-likelihood and maximum-pseudolikelihood methods

outlined below. Regular parameters were estimated as part of the model-fitting algorithm.

Depending on the model, functions $B_K(u)$ and $B_A(u)$ included 1-2 spatial covariates. As a

result, these functions took the log-linear form

$$B_k(u) = \exp(\beta_0 + \beta_1 S(u) + \beta_2 Z(u)) \tag{4}$$

where the coefficient parameters unique to each mark are β_0, β_1, and β_2 and $S(u)$ and $Z(u)$ are the covariates at point u. A covariate based on the distance to nearest unoccupied mound, $S(u)$, was included in all models because previous research indicated a negative interaction with occupied mounds (Schroder and Geluso 1975, Schooley and Wiens 2001). Because founding of harvester ant colonies is strongly affected by the presence of existing colonies (Gordon and Kulig 1996, Schooley and Wiens 2003), we added a covariate based on distance to nearest old colony, $Z(u)$, to models including new colonies. We created covariates by dividing the entire study area into 1×1-m pixels and assigning pixel values as the distance from each pixel to the nearest relevant point (e.g., unoccupied mound or old colony).

We used the maximum likelihood method to estimate hard-core distances, which corresponded to minimum interpoint distances (e.g., minimum observed distance between ant colonies). We used the profile pseudolikelihood method with a translation edge correction to estimate interaction distances (Baddeley and Turner 2005, 2006). This method found the interaction distance with the maximum pseudolikelihood between the hard-core distance and a set distance in steps of 0.1 m. We set the upper distance limit in profile pseudolikelihood method as 30 m and 20 m for intraspecific interactions of kangaroo rats and harvester ants, respectively, and 10 m for interspecific interactions. These distances were *a priori* selected based on the hypothesized scale of interactions within and between species.

Model validation

The null model was the same as the full model except there were no interaction terms (γ_{KA}, h_{KA}, and r_{KA}) between points of different species. We performed a Monte Carlo test with the log pseudolikelihood ratio, $\varDelta$, as the test statistic to determine whether to reject the null model (Baddeley and Turner 2006). The Metropolis-Hastings algorithm with 100,000 iterations was implemented to generate 999 simulations of the null model. For each simulation, we fitted the full and null models and calculated $\varDelta$. Finally, we determined the P value of the Monte Carlo test by ranking the observed $\varDelta$ in the set of simulation $\varDelta$'s. We examined the interspecific interaction terms (γ_{KA}, h_{KA}, and r_{KA}) of the best-fitting models to interpret the biological significance of the spatial processes between mounds and colonies. The goodness-of-fit of the best fitting model for each point pattern was examined by comparing the $\hat{L}_{12}(r)$ of the observed point pattern to 95% critical envelopes based on 999 Monte Carlo simulations of the selected model with a translation edge correction (Baddeley and Turner 2005, Perry et al. 2006).

Extinction risk models

Extinction of harvester ant colonies is dependent on colony age, size, and neighborhood characteristics. Older colonies and larger colonies are less likely to go extinct compared to newly founded and smaller colonies (Gordon and Kulig 1996, 1998, Schooley and Wiens 2003). Neighborhood characteristics such as high colony density can also increase extinction risk of colonies (Gordon and Kulig 1998). We used stepwise logistic regression with cut-off P values of 0.05 for inclusion and 0.1 for exclusion to select variables that predicted extinction of 1-year-old and > 1-year-old colonies between

2008 and 2009 (period of highest extinction). One-year-old colonies were those first detected in 2008 and > 1-year-old colonies were the unknown age colonies found during 2007. Thus, variables included in stepwise selection process for 1-year-old and > 1-year-old colony extinction models were disc diameter and influence index. Influence index was a measure of competitive influence calculated as

$$I_f = \sum_{\text{dist}<10\text{m}} D_n / \text{dist}_{nf} \qquad (5)$$

where D_n is disc diameter of a neighboring colony, and dist_{nf} is the distance between a neighboring colony and focal colony (Woods 2000). Disc diameter was used as an index of colony size because it is positively correlated with number of workers in a colony (Wiernasz and Cole 1995, Schooley and Wiens 2003). Due to age differences in foraging ranges (Gordon 1995), we calculated influence index for 1-year-old colonies at distances < 10 m and for > 1-year-old colonies at distances < 20 m. To test the effect of kangaroo rat neighborhood characteristics on colony extinction risk, distance to nearest neighboring mound was included in the stepwise selection process. We used the log-likelihood ratio to evaluate the overall model significance. JMP version 7.0.2 (SAS Institute Inc., Cary, North Carolina, USA) was used to fit logistic regression models.

We tested whether the logistic extinction model or a random extinction model (i.e., null model) was a better predictor of the spatial structure of surviving colonies in 2009. Each model was tested by comparing the univariate version of the homogeneous modified K-function between observed and 95% critical envelopes generated by 999 Monte Carlo simulations of the extinction model. The univariate modified K-function is

calculated and interpreted similarly to the bivariate version except it only characterized the spatial association between colonies. The modified *K*-function was calculated for distances up to 20 m and a translation correction was used to adjust for edge effects. Each Monte Carlo simulation randomly thinned the 2008 point pattern based on an assigned probability of deletion. The resulting number of surviving colonies was the same as the number observed in 2009. Probability of deletion for the random extinction model was equal to the proportion of extinct colonies in 2009 and the same for all colonies, whereas in the logistic extinction model probability of deletion for each colony was the fitted value of the logistic model (Olano et al. 2009). We used *spatstat* to perform spatial analyses and the R-package *ecespa* version 1.1-3 to compute the critical envelopes of the *K*-function from extinction models (De La Cruz 2008).

Results

Demography

Colony density, founding, and extinction varied between years (Table 2.1). The number of colonies on the site increased by 77% from 2007-2008. Colony extinction was very low during 2007-2008, but increased during 2008-2009. Newly-founded colonies experienced higher rates of extinction than older colonies during 2008-2009 (Pearson's chi-square test, $\chi_2 = 24.7$, $P < 0.0001$). Old colonies had a significantly larger disc diameter than new colonies during both 2008 and 2009 (Table 2.1, two-tailed *t*-test, all $P < 0.0001$). Disc diameter increased with age for both existing and newly founded colonies (Table 2.1, paired *t*-test, all $P < 0.001$). The number of kangaroo rat mounds

occupied varied slightly between years: 48 in 2007, 44 in 2008, and 42 in 2009. In total, 56 different mounds were occupied from 2007-2009. The majority of mounds were occupied all three years (65%) and at least two out of three years (84%).

Interspecific spatial patterns

Both existing and newly-founded colonies were aggregated with occupied mounds at small scales as a result of a positive interspecific interaction implying facilitation. In 2007, the full model with a positive interaction between species was a significantly better fit than the null model for mounds and colonies even after controlling for intraspecific interactions and location of unoccupied mounds ($\Delta = 50.4$, $P = 0.001$). Based on the full model's parameters, mounds and colonies were aggregated at small scales ($h_{KA} = 1$ m, $r_{KA} = 5.1$ m, $\gamma_{KA} = 3.65$). Conditional intensities of mounds and colonies were more than three and half times greater at scales of 1-5.1 m around opposing species sites than at larger scales. In 2008, the full model was also a better fit than the null model for mounds and newly founded colonies after controlling for effects of intraspecific interactions and locations of existing colonies and unoccupied mounds ($\Delta = 40.5$, $P = 0.003$). Mounds and newly founded colonies were aggregated around each other with conditional intensities over two times greater at scales of 2.3-8.1 m around opposing species sites ($h_{KA} = 2.3$ m, $r_{KA} = 8.1$ m, $\gamma_{KA} = 2.24$). Comparison of observed $L_{12}(r)$ to 95% critical envelopes for both 2007 and 2008 point patterns confirmed that the full model closely matched the observed spatial pattern (Fig. 2.2). Both the mean simulation and observed $L_{12}(r)$ values exhibited aggregation ($L_{12}(r) > 0$) between species at small scales.

Colony extinction risk

1-year-old colonies had lower extinction risk near kangaroo rat mounds. Three parameters, including one based on spatial relationship to neighboring mounds, were selected in stepwise logistic regression of 1-year-old colony extinction risk from 2008-2009 (Table 2.2). Extinction risk of 1-year-old colonies decreased as disc diameter increased and distance to nearest mound and influence index decreased (Model $P <$ 0.0001). The observed point pattern of 1-year-old colonies in 2009 was most consistent with the logistic extinction model. The observed $L(r)$ function was completely enclosed by the 95% critical envelopes generated by the logistic extinction model (Fig. 2.3a, dashed lines). The simulations of the logistic extinction model exhibited similar levels of small-scale segregation between colonies ($L(r) < 0$) as the observed point pattern. In addition, simulations of the logistic extinction model resulted in a small-scale hard-core property (i.e., minimum distance between points) that was also present in the observed point pattern. The random extinction model was a poor predictor of the observed point pattern of new colonies in 2009, particularly at small-scales (Fig. 2.3a, dotted lines). The observed $L(r)$ function exceeded the 95% critical envelopes generated by the random extinction model several times at distances of 5-10 m and failed to develop a consistent hard-core property. The $L(r)$ function of the random extinction model simulations also tended to produce weaker segregation between colonies than the observed point pattern.

Extinction risk of older colonies was not affected by kangaroo rat mounds. Two parameters were selected as predictors of 2008-2009 extinction risk for > 1-year-old colonies; however, no variables related to neighboring mounds were selected (Table 2.2). Extinction risk of > 1-year-old colonies decreased as disc diameter increased and

influence index decreased (Model $P < 0.0001$). The logistic extinction model was a better predictor of the spatial structure of old colonies in 2009 than the random extinction model (Fig. 2.3b). The observed $L(r)$ function was completely enclosed by the 95% critical envelopes of the logistic extinction model at all scales, whereas it exceeded the envelopes of the random extinction model at distances > 10 m. The simulations of the random extinction model failed to produce as strong segregation between colonies as the observed point pattern and the logistic extinction model.

Seed abundance and foraging time

Distance from an occupied mound affected both seed abundance and foraging of colonies. Seed abundance in the soil surface was 3 times greater at colonies less than 10 m from occupied mounds than colonies located greater than 20 m away (Fig. 2.4a; $t_{12} = -2.72$, $P = 0.019$). Total dried mass of seeds did not significantly differ between distance groups (Fig. 2.4b; $t_{12} = -0.99$, $P = 0.34$), indicating that the increase in seed abundance at colonies near mounds was primarily due to small seeds. Median foraging time was 27% shorter for colonies located less than 10 m from an occupied mound than those located greater than 20 m away (Fig. 2.5; $t_{14} = 5.08$, $P = 0.041$).

Discussion

Our results demonstrated another keystone effect of banner-tailed kangaroo rats in the Chihuahuan Desert; kangaroo rats facilitate the dominant harvester ant, *P. rugosus*. Colony founding, extinction, resource availability, and foraging costs were all spatially dependent on kangaroo rat mounds. Existing and newly founded colonies occurred at

higher densities around mounds at small scales (< 10 m), which was consistent with best-fitting spatial models showing a positive interspecific association, implying facilitation. Extinction of young colonies decreased with increasing proximity to a mound (Table 2.2). Spatial patterns of surviving 1-year-old colonies were accurately predicted by logistic models of extinction risk containing distance to nearest mound (Fig. 2.3). Patterns of colony spacing and dynamics appear to be due to the benefits of being close to areas of high kangaroo rat activity. Abundance of seeds in the soil surface was greater and foraging costs lower for colonies in close proximity to an occupied mound as expected from the facilitation hypothesis. The most parsimonious mechanism for these spatial and behavioral patterns is the indirect facilitation of harvester ants due to impacts of banner-tailed kangaroo rats on seed abundance.

Founding of colonies

The best-fitting model for observed point patterns of mounds and 1-year-old colonies included a positive spatial interaction at distances of 2.3-8.1 m between species. Several possible mechanisms could result in aggregation of newly founded colonies around kangaroo rat mounds at this scale. Founding and early survival of harvester ant colonies are affected by a variety of factors including soil conditions, intraspecific competition, and location of breeding leks. The facilitative effects of kangaroo rats on the abiotic and biotic environment around mounds likely contribute to higher founding and survivorship rates of young colonies. Soils around mounds are typically cleared of vegetation and have more soil nitrogen, salts, and organic matter and finer-textured and looser soils than areas away from mounds (Greene and Murphy 1932, Greene and Reynard 1932). These soil conditions may attract new queens to settle near mounds.

Dispersing *Pogonomyrmex* queens land in areas with bare soil and high surface reflectance (Nagel and Rettenmeyer 1973) similar to the soil characteristics surrounding mounds. While harvester ant colonies did not occur directly on mounds, we observed they were common in areas surrounding mounds (A. J. Edelman, personal observation). Other ant species also favor areas disturbed by burrowing mammals. The western harvester ant (*P. occidentalis*) locates new colonies more frequently on areas disturbed by pocket gophers (*Thomomys talpoides*) than other areas (Hopton 2001). Yellow meadow ants (*Lasius flavus*) colonize European mole hills (*Talpa europaea*), which produce nests that are more resistant to erosion (Mellanby 1973).

The greater resource abundance and lower foraging costs we observed at colonies near mounds likely contribute to the higher density and survivorship of young colonies at these sites. Considerable mortality of newly-founded colonies had probably already occurred by the time 1-year-old colonies were detected. In other *Pogonomyrmex* species, the extinction rate from establishment of a burrow by a founding queen to a colony 1 year of age is close to 99% (Gordon and Kulig 1996). During this vulnerable time period, location near a kangaroo rat mound with higher resource abundance likely provided a significant advantage for colony establishment and contributed to the aggregated pattern between species.

In the closely related *P. barbatus*, 1-year-old colonies are more likely to occur near younger, existing colonies probably because of reduced competition from larger colonies (Gordon and Kulig 1996). Intraspecific competition also appears to affect colony establishment in our study because newly founded colonies tended to be farther away

(paired *t*-test, t_{161} = 3.67, *P* = 0.0003) from nearest-neighboring large colonies > 96 cm in diameter ($\overline{X}$ ± SE = 19.0 ± 0.7 m, *n* =112) compared to nearest-neighboring small colonies ≤ 96 cm in diameter ($\overline{X}$ ± SE = 15.3 ± 0.7 m, *n* = 92). However, we were able to control for the spatial effect of existing colonies on founding in our study by including them as a covariate in the MSHC model. We found that intraspecific spatial interactions alone were unable to account for the aggregation between kangaroo rats and 1-year-old colonies and only a model containing an interspecific interaction between these species could explain observed spatial patterns.

Pogonomyrmex typically breed in centralized leks above tall objects such as hills > 7 m in height and newly founded colonies tend to be clumped around these areas (Wiernasz and Cole 1995). Our study site was relatively flat with no tall objects in the immediate vicinity to indicate possible lekking foci. Kangaroo rat mounds are raised slightly above the surrounding soil surface suggesting they could be used for leks, but they are far shorter than the typical height requirement. Their commonness across the landscape may also make them unsuitable for drawing a significant number of reproductive ants to any one mound to form a lek. Furthermore, use of a few mounds as lek sites would not result in the widespread aggregation of new colonies and mounds that we observed.

Colony extinction risk

Extinction risk of harvester ant colonies has been shown to decrease sharply with increasing age and colony size. In addition, density of other colonies can also increase extinction risk, particularly for small colonies (Gordon and Kulig 1996, 1998, Schooley

and Wiens 2003). We observed the same effects of age and density on extinction risk in our study. Extinction rates were highest in 1-year-old colonies (30%) and survivorship in all colonies was influenced by colony size and competitive effects from neighboring colonies. However, unlike older colonies, survivorship of 1-year-old colonies was also linked to spatial association with mounds. Stepwise logistic regression revealed that extinction risk of these colonies was lower as distance to nearest mound decreased even after controlling for effects of colony size and competition with neighboring colonies (Table 2.2). In addition, this logistic extinction model accurately predicted spatial patterns of surviving 1-year-old colonies (Fig. 2.3). Thus, kangaroo rat mounds impact colonies when young and more susceptible to extinction.

Older colonies have low extinction risk and effects of mounds on annual colony survivorship were absent. Stepwise logistic regression of > 1-year-old colonies did not include distance to nearest mounds in the best-fitting model (Table 2.2). However, older colonies appear to have also gone through the same extinction patterns as experienced by younger colonies. Older colonies were aggregated with mounds and best-fitting spatial models included a significant positive interaction at distances of 1-5.1 m. In addition, spatial models indicated that densities of > 1-year-old colonies were greater than 1-year-old colonies (γ_{KA} was 3.65 vs. 2.24) around kangaroo rat mounds. This difference is likely caused by the additional period of mortality that older colonies have experienced. Further research is necessary to determine if mounds may affect long-term survivorship or reproductive success of colonies.

Some observed founding and extinction events may have actually been colonies that moved locations. In *P. barbatus,* no more than 10% of colonies relocate per year (Gordon 1992). Whether colonies moved or went extinct in our study, the underlying implications remain unchanged. Colonies become aggregated around kangaroo rat mounds over time through dynamics of founding, extinction, or perhaps even relocation.

Facilitation of harvester ants by kangaroo rats

Our results supported the hypothesis that banner-tailed kangaroo rats facilitate harvester ants, due at least in part to effects on prey species. As expected under facilitation, seed abundance was higher in the soil surface near mounds. While we did not categorize seeds by size, the lack of a corresponding increase in total seed mass in samples indicates that the greater numbers of seeds were from small-seeded species that ants preferentially harvest. Kangaroo rats indirectly facilitate harvester ants preferred food source, small-seeded annuals, by selectively foraging on competitively superior large-seeded annuals (Davidson et al. 1985, Samson et al. 1992). Banner-tailed kangaroo rats may also directly facilitate small-seeded annuals through ecosystem engineering effects. Soil on and near mounds is heavily disturbed by kangaroo rats allowing wind-dispersed small-seeded annuals to colonize these gaps earlier than other species (Guo 1996). As a result of foraging and disturbance effects, small-seeded winter annuals are more abundant on and near banner-tailed kangaroo rat mounds than inter-mound areas (Moorhead et al. 1988, Guo 1996). Colonies near mounds appeared to benefit from higher seed availability because we observed that their workers spent less time per foraging trip than those at distant colonies. Reduction in foraging time results in lower metabolic costs to foragers in *Pogonomyrmex* (Fewell 1988).

Kangaroo rats could also directly facilitate harvester ants by increasing accessibility to seeds through larder hoarding. Harvester ants are known to forage for seeds on mounds (Schooley and Wiens 2001), but have not been observed to enter mounds to raid kangaroo rat seed caches. Banner-tailed kangaroo rats may protect against theft via ants by wedging unwieldy seed stems in cul-de-sacs within mounds (Herrera et al. 2001).

The facilitation appears to be unidirectional, with kangaroo rats affecting the distribution of harvester ant colonies, but not vice versa. In the Chihuahuan Desert, no dramatic changes in plant communities or rodent populations were detected when harvester ants were removed (Davidson et al. 1985, Samson et al. 1992). While founding of new harvester ant colonies is common (Schooley and Wiens 2003), new kangaroo rat mounds are rarely built in established populations. Instead, mounds are occupied by different individuals over many generations of kangaroo rats (Holdenried 1957, Parmenter and Van Devender 1995b). Total number and identity of occupied mounds varied little over the study period in comparison to colonies. Thus, the distribution of ant colonies would be expected to respond more quickly than kangaroo rat mounds to variations in environmental conditions.

There is little evidence that kangaroo rats and harvester ants compete strongly and directly for seed resources in the Chihuahuan Desert, as was observed in the Sonoran Desert (Brown et al. 1979). None of the best-fitting point process models included a negative interspecific interaction parameter (e.g., $\gamma_{KA} < 1$) as expected if strong competition existed between species. Furthermore, the logistic extinction model indicated

a positive rather than negative spatial influence of mounds on new colony survival. Differences in seed preferences and activity patterns between kangaroo rats and harvester ants likely reduced the potential of direct competition (Brown and Davidson 1977, Inouye et al. 1980, Davidson et al. 1985, Samson et al. 1992).

Conclusions

Spatial point pattern analysis has rarely been applied to the study of animal spatial patterns and typically inductive pattern analysis has been used. This study is the one of the first applications of a deductive model comparison approach to understanding animal interactions using statistical point process modeling and logistic modeling of extinction spatial patterns. As such, it demonstrates the usefulness of these techniques in teasing apart scale-dependent processes in animal communities. Previous experimental research failed to detect a positive interaction between kangaroo rats and harvester ants (Davidson et al. 1985, Valone et al. 1994) possibly because scale was not explicitly included in analyses.

Banner-tailed kangaroo rats have well-known direct effects on community structure of plants, mammals, arthropods, and reptiles through their ecosystem engineering and selective seed predation (Bowers and Brown 1992, Hawkins and Nicoletto 1992, Brown et al. 1997, Schooley et al. 2000, Brown et al. 2001, Davidson and Lightfoot 2007). Our study adds yet another keystone effect of this species, a facilitatory impact on the spatial structure and dynamics of harvester ant colonies.

Acknowledgments

Table 2.1. Demographic characteristics of harvester ant colonies from 2007-2009.

Year	n	Colonies/ha	Disc diameter (cm) $\overline{X} \pm SE$	Disc diameter growth (cm) $\overline{X} \pm SE$	Extinction (%)
2007	212	25.4	89.3 ± 2.8	-	-
2008	366	42.1	-	-	-
Old colonies[a]	204	23.4	109.4 ± 2.9	18.6 ± 1.7	8 (4%)
New colonies[b]	162	18.6	33.3 ± 2.7	-	-
2009	297	34.1	-	-	69 (19%)
Old colonies[a]	184	21.1	126.6 ± 2.8	11.9 ± 1.5	20 (11%)
New colonies[b]	113	13.0	54.0 ± 3.9	13.1 ± 2.0	49 (30%)

[a] Surviving colonies marked in 2007
[b] Colonies founded in 2007 and first detected in 2008

Table 2.2. Logistic regression models of 2008-2009 extinction risk for 1-year-old ($n =$ 162) and > 1-year-old harvester ant colonies ($n = 204$).

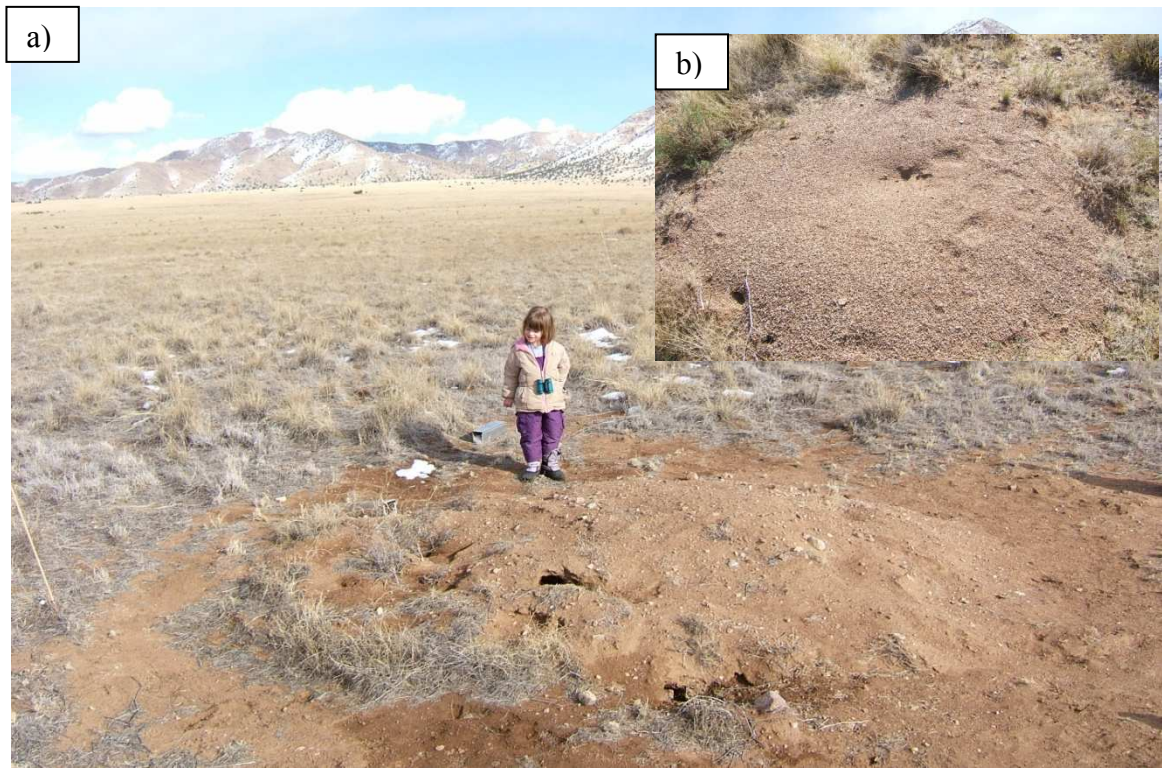| Colony type	Model parameters	Coefficient	SE	*P*
1-year-old colonies	Intercept	1.275	0.451	0.0047
	Disc diameter	-0.029	0.008	0.0002
	10-m Influence index	0.073	0.027	0.0067
	Nearest mound distance	0.037	0.017	0.0271
> 1-year-old colonies	Intercept	1.045	0.866	0.23
	Disc diameter	-0.025	0.006	<0.0001
	20-m Influence index	0.045	0.022	0.044

Figure 2.1
Banner-tailed kangaroo rat mound (a) and rough harvester ant colony disc (b). For scale, the child is 1-m tall and the disc of the colony is approximately 1.5 m in diameter.
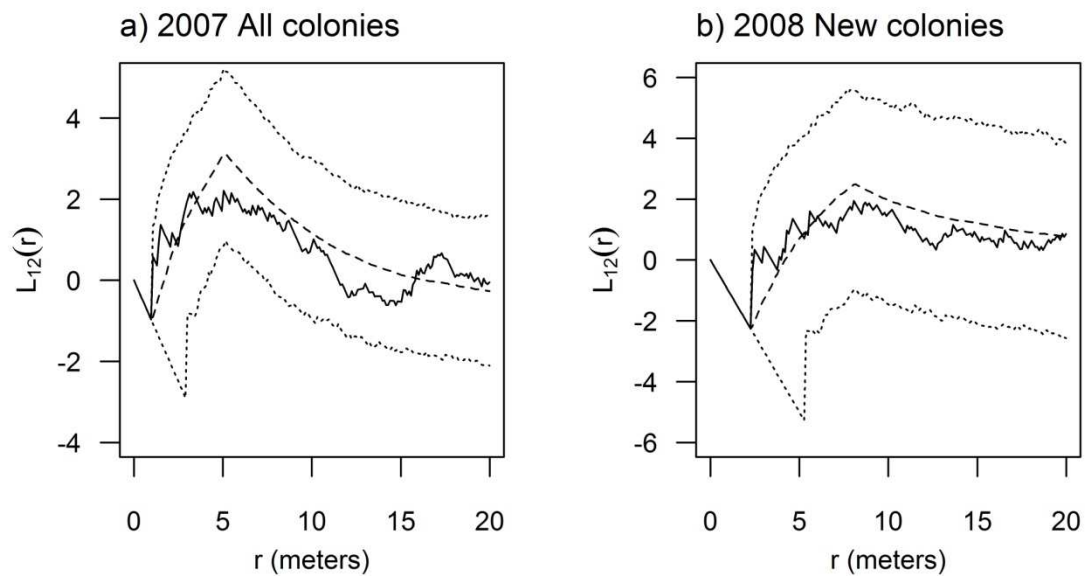
Figure 2.2
Goodness-of-fit of best-fitting spatial models of the relationship between kangaroo rat mounds and harvester ant colonies. Bivariate modified *K*-function of point patterns for: (a) all occupied kangaroo rat mounds and harvester ant colonies during 2007; and (b) all occupied kangaroo rat mounds and newly founded harvester ant colonies during 2008. Solid black line represents the observed and dotted lines are the 95% critical envelopes and dashed lines the means generated from 999 Monte Carlo simulations of the best-

fitting point process model. Biologically, $\hat{L}_{12}(r)$ for two point patterns can be interpreted as exhibiting with respect to each other complete spatial randomness (CSR) when zero, aggregation when > 0, and segregation when < 0.
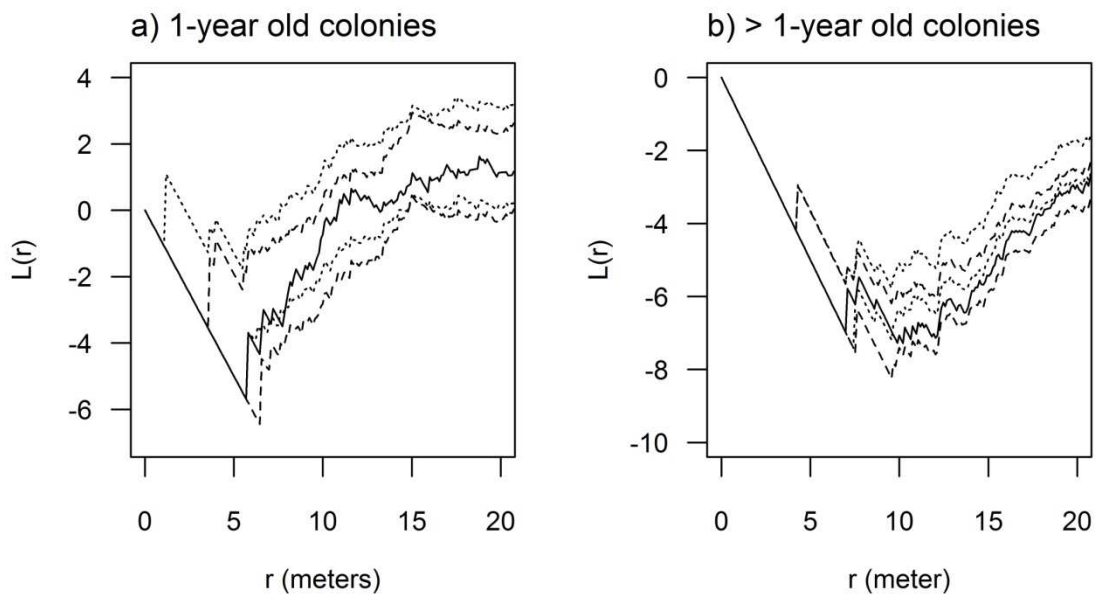
Figure 2.3
Spatial relationship of observed colony locations and locations simulated from extinction risk models. Modified *K*-function of point patterns of harvester ant colonies on the study area during 2009 for: (a) 1-year-old colonies; and (b) > 1-year-old colonies. Solid black lines represent the observed *L(r)* functions. Dotted lines are the 95% critical envelopes of *L(r)* functions generated from 999 Monte Carlo simulations of the random extinction model applied to the 2008 colony and mound pattern. Dashed lines are the 95% critical envelopes of *L(r)* functions generated from 999 simulations of the logistic extinction model applied to the 2008 colony and mound pattern.
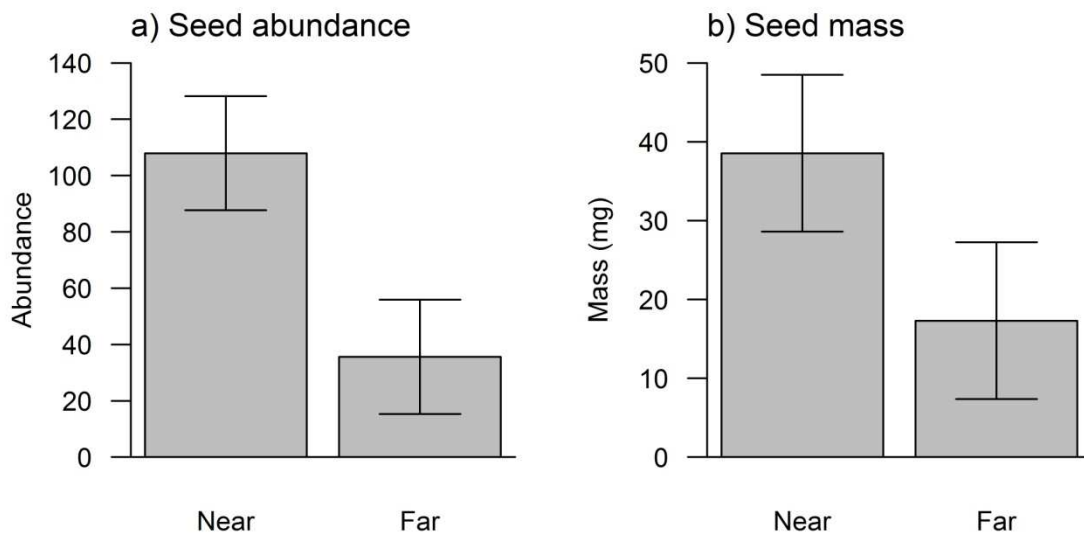
Figure 2.4
 Effects of proximity to a banner-tailed kangaroo rat mound on seed resources in the soil surface around harvester ant colonies. Estimates (± SE) of seed abundance (a) and total dried seed mass (b) from soil samples (156.25 cm^3) taken at the ground surface (1-cm depth) for colonies near (< 10 m) and far (> 20 m) from an occupied mound.
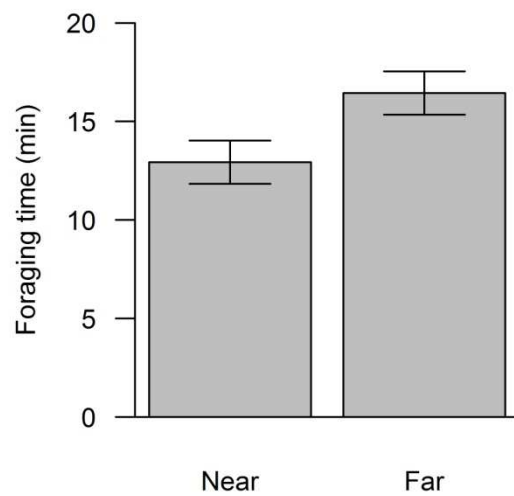
Figure 2.5
Effect of colony location on foraging time of harvester ant workers. Median foraging time ($\overline{\text{X}}$ ± SE) of workers at colonies near (< 10 m) and far (> 20 m) from an occupied banner-tailed kangaroo rat mound.

Chapter 3

Sex-specific effects of size and condition on timing of natal dispersal in kangaroo rats

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Abstract

The effect of proximal cues in eliciting natal dispersal should vary between males and females because of differences in reproductive strategies. I monitored the effect of food supplementation on timing of natal dispersal in banner-tailed kangaroo rats (*Dipodomys spectabilis*), which lack sex-biased dispersal. I provided additional food to a subset of mothers and dependent offspring at their maternal mounds from lactation through natal dispersal. All supplemented offspring, regardless of sex, grew faster, were in better condition, and had higher survivorship than unsupplemented offspring. Food supplementation affected the timing of natal dispersal, but only in males. Sons who received food supplements dispersed almost 2 months earlier than unsupplemented sons indicating that timing of natal dispersal was related to size and condition. Timing of natal dispersal in daughters was unaffected by food supplementation suggesting that size and condition do not affect dispersal behavior. These sex-specific responses to resources match the intersexual differences in reproductive strategies and parental investment

patterns of mammals. My results support the hypothesis that sons remain at the natal site until a certain threshold of size and condition is reached. Male reproductive success is strongly dependent on body size, which affects their ability to find and defend mates. By allowing sons to remain at the natal mound until this threshold is attained, mothers likely increase the fitness of their sons. Daughters appear to disperse at the youngest age possible regardless of size or condition. Female reproductive success is influenced more by securing resources than body size. Thus, dispersing as early as developmentally feasible would allow daughters to secure an existing mound and begin caching food for future reproduction.

Introduction

Natal dispersal, the permanent movement of offspring from the natal site, has substantial effects on the genetic structure, population dynamics, social organization, and spatial distribution of animals (Clobert et al. 2001). Proposed evolutionary causes for natal dispersal include inbreeding avoidance, reduction in intraspecific and kin competition for resources and mates, and environmental stochasticity (Moore and Ali 1984, Waser 1985, Chepko-Sade and Halpin 1987, Lambin et al. 2001, Perrin and Goudet 2001). Males and females can differ in how these evolutionary forces shape the costs and benefits of natal dispersal. As a result, sex-biased dispersal, where one sex disperses farther or more often, is common in many species. Which sex disperses is likely caused by the natal site imparting a greater fitness advantage to the non-dispersing sex (Greenwood 1980, Pusey 1987, Lambin 1994, Clarke et al. 1997).

Proximal causes of natal dispersal are less well understood, but are important to determining how environmental and physiological conditions affect dispersal behavior. A number of variables potentially determine if and when offspring disperse. Dispersal can be triggered or delayed by socioecological factors such as population density, habitat quality, conspecific aggression, and competition or physiological factors including age, condition, size, and hormones (Holekamp 1986, Nunes and Holekamp 1996, Nunes et al. 1997, Smale et al. 1997, Lambin et al. 2001). The effect of socioecological and physiological cues in eliciting dispersal can also vary between males and females because of intersexual differences in reproductive strategies and parental investment (Greenwood 1980, Clutton-Brock 1991, Lambin 1994).

In endotherms without male parental care, timing of natal dispersal in males should be closely related to size and condition, whereas females should be dependent more on factors dealing with resource competition and quality. Male reproductive success is limited by their ability to defend and copulate with mates, and larger males presumably are more competitive and able to mate with more females. Female reproductive success is limited by their ability to convert resources into offspring and larger body size is less important to reproductive success because they produce low, relatively fixed litter sizes (Trivers 1972, Wilson 1975, Crook et al. 1976, Clutton-Brock 1991). Therefore, sons should be under stronger selection to maximize parental investment and achieve a larger body size before independence through increasing the time spent under the parents' care and the amount of resources extracted (Clutton-Brock 1991). While this strategy may result in a parent-offspring conflict, parents should also be more willing to invest in male offspring. Parental investment can have a larger impact on sons' than daughters'

reproductive success as well as their own number of grand offspring produced because of greater variance in male reproductive success (Trivers 1972, 1974, Clutton-Brock 1991). Studying sex differences in timing of dispersal within a species can be difficult because many endotherms have sex-biased dispersal (Nunes et al. 1997). In addition, comparison of parental investment between males and females in species with sex-biased dispersal is complicated by the possibility of differential investment at different life stages (Clutton-Brock 1991).

In mammals, male-biased dispersal is the most dominant form of natal dispersal. However, a small number of mammals, typically solitary, do not exhibit sex-biased dispersal (Greenwood 1980, Waser and Jones 1983). Absence of sex-biased dispersal is hypothesized to occur because of similarity in the influences of socioecological variables on reproductive success of both sexes (Smale et al. 1997). Species lacking sex-biased dispersal are ideal for comparing differences in timing of dispersal and parental investment between sons and daughters.

One well-studied mammal that does not exhibit sex-biased dispersal is the banner-tailed kangaroo rat (*Dipodomys spectabilis*), a solitary species native to desert grasslands of the southwestern U.S. and northern Mexico (Best 1988). This nocturnal rodent aggressively defends territories surrounding a mound that contains a complex burrow system and seed caches (Vorhies and Taylor 1922, Schroder 1979, Randall 1987, 2001). Mounds are constructed through excavation of soil and can persist for > 50 years (Holdenried 1957, Reichman et al. 1985, Parmenter and Van Devender 1995a). Young are usually born in small litters (1-3 offspring) during early spring, weaned at 3-4 weeks

old, and remain with mothers until at least 2 months old, dispersing before reproductive maturity the following winter (Holdenried 1957, Jones 1984, Waser et al. 2006). However, there is considerable variation (2 months to 1 year of age) in timing of dispersal with respect to both age, sex, and body mass (Jones 1984, Waser et al. 2006). Offspring receive substantial parental care after weaning because mothers allow them access to natal mounds and the seed caches within (Jones 1986, Jones et al. 1988). Mounds are critical resources for kangaroo rats, and offspring must obtain a mound to survive and reproduce. New mounds are rarely built, likely because they are costly and time consuming to construct (Best 1972). Both males and females disperse relatively short distances (< 100 m) from natal sites, typically to the closest available mound (Jones 1986). Juveniles sometimes remain at the natal mound into reproductive maturity as a result of inheritance through the death of the mother or by bequeathal through mothers dispersing (Jones 1984). There is likely a minimum age threshold of age or size that offspring must reach before dispersing, because juveniles experimentally forced to disperse at a young age have lower survivorship than juveniles that naturally disperse (Waser 1988). Habitat saturation also affects natal dispersal resulting in shorter dispersal distances (Jones et al. 1988, Waser et al. 2006). While timing of dispersal has not been directly measured in banner-tailed kangaroo rats, juvenile males tend to be trapped at natal mounds later in the year than females (Waser et al. 2006). Banner-tailed kangaroo rats exhibit sexual dimorphism and males actively defend estrus females suggesting that male size contributes to reproductive success (Best 1988, Randall 1991).

My objective was to manipulate resources of banner-tailed kangaroo rat mothers to examine the proximal causes of natal dispersal in males and females. I monitored

timing of dispersal, growth, condition, and survivorship of offspring from mounds with and without experimentally supplemented food supplies. I hypothesized that supplemented offspring compared to control offspring would generally: 1) grow faster; 2) be in better condition; and 3) disperse earlier. Earlier dispersal of supplemented offspring would be predicted if timing of dispersal was determined by size and condition. In addition, I expected timing of dispersal in sons to be more closely dependent on size and condition than in daughters due to relative differences in reproductive strategies and parental investment.

Materials and Methods

Study area

The study area was located at the Sevilleta National Wildlife Refuge, near Socorro, New Mexico, USA (34° 24´ 24.8' N, 106° 36´ 20.5' W, 1600 m elevation). The site encompassed 18 ha of Chihuahuan Desert and short grass steppe vegetation dominated by grama grass (*Bouteloua eriopoda* and *B. gracilis*), burrograss (*Scleropogon brevifolius*), and sand dropseed grass (*Sporobolus cryptandrus*). The study area contained 165 kangaroo rat mounds of varying condition and size.

Mark-recapture and experimental methods

The banner-tailed kangaroo rat population was monitored monthly from March 2005 to February 2008 (excluding January 2007). Each month, all mounds were assessed for signs of kangaroo rat activity (e.g., fresh digging and feces, burrow entrances free of

debris) (Jones 1984). All mounds exhibiting active kangaroo rat sign were trapped for 3 consecutive nights. Two to four live traps (Model XLK, H.B. Sherman Traps, Tallahassee, FL, USA) were baited with sweet feed (oats, corn, and barley mixed with molasses) and placed at each mound (Cross and Waser 2000). I opened live traps at dusk and examined them 3-7 hrs after sunset. All individuals were marked with a uniquely numbered Passive Integrated Transponder (PIT) tag (Model 1440ST, Biomark, Boise, Idaho, USA), which was injected subcutaneously. I recorded gender, age, reproductive status, mass, tail length, and hind foot length of all captured individuals each month. All animals were handled in accordance with the guidelines of the University of New Mexico Institutional Animal Care and Use Committee (Protocol No. 04MCC00507 and UNM048-TR-100261).

Adult banner-tailed kangaroo rats are solitary and highly territorial. An individual captured most frequently at a mound could reliably be considered the occupant (Schroder 1979, Jones 1984). During this study, I considered a mound occupied by an individual if it was caught at the mound: (1) > 1 month; (2) ≥ two times during 3 consecutive months; and (3) more frequently than any other adult (Jones 1984, Waser et al. 2006).

All mounds occupied by adult females in February 2008 ($n = 24$) were randomly assigned to control or treatment groups. Beginning on February 28, 2008, I added 500 ml of mixed seed (millet, cracked corn, and sunflower seeds) weekly to 12 treatment mounds. At the beginning of the experiment, most females had either recently given birth or were in the late stages of pregnancy (16 of 24). The 12 control mounds were visited each week, but no seed was added (i.e., sham treatment). I poured seeds directly into

burrows to avoid removal by other granivore species. Females rapidly transferred seeds into the interior of the mound, typically within a few hours of supplementation (personal observation). I ended food supplementation on July 3, 2008. At this time, > 90% of juveniles had dispersed from natal mounds (32 of 35 offspring).

Gestation in banner-tailed kangaroo rats lasts 3-4 weeks and females rapidly gain 15-20 g prior to birth and lose a similar amount post-partum (Bailey 1931, Holdenried 1957). Pregnancy is only detectable from normal mass fluctuations within the last two weeks of gestation. Thus, based on monthly patterns of mass gain and loss and visible reproductive signs, I was able to establish during which trapping period a female was pregnant. To provide a more refined estimate of birth date for each female, I added a specific number of days to the date of known pregnancy based on the amount of mass gained between trapping periods: 1) < 10 g gained, added 14 days; 2) ≥ 10 g and < 15 g gained, added 7 days; and 3) ≥ 15 g gained, no days added. I calculated age at first capture for each juvenile by subtracting estimated birth date from date of first capture. Age at first capture was used as a measure of the onset of aboveground activity by juveniles. I determined the length of delayed dispersal for all juveniles first captured at an age < 120 days (n = 32) by estimating the maximum possible time spent at the natal mound with mothers. Juveniles differed in completeness of trapping history and philopatry. Therefore, I standardized the time spent at the natal mound among juveniles based on a set of mark-recapture criteria. For juveniles with a continuous trapping history that also dispersed, the date of first capture away from the natal mound was used as the independence date. For juveniles with a discontinuous trapping history (i.e., disappeared or had a time gap between capture at their natal mound and another mound), the census

date after the last capture at the natal mound was used as the independence date. For juveniles that inherited or were bequeathed a natal mound because the mother died or dispersed, I used the census date following the last capture of the mother at the natal mound as the date of independence. The maximum time spent at the natal mound was then calculated by subtracting the juvenile's estimated independence date from its estimated birth date. Dispersal distances were defined as the distance between the natal mound and the first mound where a dispersing juvenile was captured. Individuals that were no longer captured were assumed to have died between trapping periods. Based on telemetry and trapping studies, this assumption has been shown to only slightly underestimate survivorship in banner-tailed kangaroo rats because of their short dispersal distances and high recapture rates (Jones 1986, Cross and Waser 2000). Using this criteria, I estimated survivorship to natal dispersal (first capture away from natal mound) and to December 2008.

Maternity analysis

A total of 44 banner-tailed kangaroo rat juveniles were captured during 2008. Tissue was excised from the ears of each animal upon first capture and dried. Tissue samples of putative mothers and juveniles were then sent to a private laboratory (Wildlife Genetics International, Nelson, Canada) for analysis following standard protocols. All samples were extracted using QIAGEN's DNeasy Tissue kits (Valencia, California, USA) following the manufacturer's instructions. I used 9 microsatellite loci to characterize individuals: DS1, DS3, DS19, DS28, DS46, DS98, DS107, DS109, and DS163 (Davis et al. 2000, Waser et al. 2006). A single base was added to the 5' end of the unlabelled primer of all loci except two (DS107 and DS163) to reduce the risk of

single-base stutter by encouraging complete adenylation of the PCR product (Brownstein et al. 1996). I determined maternity of juveniles using a mixture of exclusion and likelihood-based inference (Waser et al. 2006). Candidate mothers were the 24 adult females of the control and treatment groups. I first used the X-linked marker DS19 to exclude incompatible mothers for each juvenile. Next, I used CERVUS version 3.0.3 to infer maternity based on the 8 autosomal loci (Kalinowski et al. 2007). The genotype error rate was set at 1% in CERVUS. I accepted all mother-offspring matches assigned by CERVUS at the 95% confidence level. I accepted matches at the 80% confidence level if the juvenile was first captured at the putative mother's mound.

Statistical analysis

All statistical analyses were conducted using R version 2.10.0 (R Development Core Team 2009). I used two-tailed versions of Wilcoxon rank sum tests, t-tests, and Fisher's exact tests to compare reproduction of females, dispersal, and survivorship between control and treatment groups. Differences in body measurements at first capture and condition index at capture nearest independence age between control and treatment groups were examined using analysis of covariance (ANCOVA) tests with age at first capture, sex, and interaction effects as covariates. Condition index was measured as the residuals of ordinary least squares regression of log-transformed and standardized body mass and tail length at capture nearest to independence age (Schulte-Hostedde et al. 2005). Time spent at the natal mound with mothers was compared with a two-way analysis of variance (ANOVA) test with treatment group, sex, and an interaction effect. A backward selection process with cut-off p values of 0.05 for exclusion was used to determine if sex and interaction effects were included in final ANOVA and ANCOVA

models. Identity of mothers was originally included as a random factor in models, but was removed because there was no statistically significant improvement in fit and accounted for almost none of the variance.

I used nonlinear regression to fit individual growth curves to capture data grouped by sex and experimental treatment (4 total curves). In order to provide a more complete record of growth at different ages, multiple captures per individual were included in datasets. Iterative least squares criterion was used to fit a modified monomolecular equation

$$M_t = A-(A-B)e^{(-2t/T)} \tag{1}$$

where M_t is mass at age t, A is an asymptotic mass, B is birth mass, and T is time required to complete major part of growth. Generally, T approximates the time period necessary to achieve 90% of A and is a measure of growth rate (Richards 1959, Leberg et al. 1989). The monomolecular growth equation, rather than a sigmoidal-based equation as used for many mammals, was chosen because growth rate in kangaroo rats has been shown to decrease from birth onward (Chew and Butterworth 1959, Butterworth 1961, Lackey 1967). Birth mass was fixed at 8 g based on published data from this species (Holdenried 1957). I used Wald statistics to calculate 95% confidence intervals for parameter and prediction estimates to compare between sexes and experimental groups (Ritz and Streibig 2008).

To examine further how growth varied between groups, I fitted monomolecular growth models which allowed parameters (A and T) to vary by treatment, sex, or both.

Fits of all 13 possible model configurations were compared using residual standard error (RSE) and Akaike information criterion with second order correction for small sample sizes (AICc) which ranks models on goodness-of-fit and minimization of parameters. I selected the model with the lowest AICc (Ritz and Streibig 2008).

Results

Food supplementation of mothers affected whether they reproduced successfully confirming that resources were limiting on control sites, but did not influence other reproductive variables (Table 3.1). Maternity analysis assigned 35 juveniles to mothers on the study area (34 at 95% confidence level, 1 at 80% confidence level). Control and treatment females did not differ in timing of pregnancy, proportion pregnant, proportion producing a second litter, or litter size. Overall, proportion of females that reproduced successfully (i.e., at least one confirmed offspring) was lower for the control than treatment females. Mothers that produced offspring tended to have reduced survival to December 2008 (Fisher's exact test, $P = 0.074$) in the treatment group ($n = 12$) than those in the control group ($n = 7$).

Juveniles from the treatment group grew faster than those from the control group. At first capture, treatment juveniles averaged 25% heavier than control juveniles (Fig. 3.1a; $F_{1,28} = 82.4$, $P < 0.001$) after adjusting for age at capture ($F_{1,28} = 26.1$, $P < 0.001$). Foot and tail length of treatment juveniles averaged 5% ($F_{1,28} = 41.4$, $P < 0.001$) and 11% ($F_{1,28} = 59.3$, $P < 0.001$) longer than control males upon first capture, respectively (Fig. 3.1b), adjusting for age at capture (foot length: $F_{1,28} = 11.6$, $P = 0.002$; tail length: $F_{1,28} =$

37.0, P < 0.001). Sex and interaction effects were not statistically significant for any measurements.

Based on the parameter estimates of different growth curves (Table 3.2, Fig. 3.2), food supplementation increased growth rate of all juveniles, but had no effect on asymptotic mass. Period of major growth (*T*) for females with supplemented natal resources was 50% shorter than non-supplemented females. For males, period of major growth was 29% shorter for supplemented than non-supplemented juveniles. Males, regardless of treatment, had a longer period of major growth than females and grew to a larger asymptotic mass. Asymptotic mass (*A*) did not significantly differ among treatments, but was about 20% greater for males than females, contributing to the additional time necessary for males to reach adult mass. The best fitting nonlinear model allowed asymptotic mass to vary by sex and period of major growth to vary by both sex and treatment (AICc = 1239.95, RSE = 8.5, d.f. = 165) indicating that asymptotic mass was similar between treatments within sexes, but that length of growth period differed among treatments and sexes.

Control juveniles were active aboveground at an earlier age and had lower survivorship while at the natal mound than treatment juveniles indicating they were likely foraging more and at greater predation risk than treatment juveniles. Control juveniles were almost 3 times as likely to be captured at natal mounds prior to dispersal and averaged about 23 days younger at first capture than treatment juveniles (Table 3.1). Almost all treatment juveniles (*n* = 23) survived to disperse, whereas only about half of control juveniles (*n* = 12) survived (Fig. 3.4, Fisher's exact test, P = 0.0033).

Food supplementation affected length of dependency in males, but not females. A significant interaction effect between sex and treatment ($F_{1,28} = 14.6$, $P < 0.001$) indicated that effect of food supplementation on timing of dispersal differed between males and females (Fig. 3.3). One outlier, a control male, was removed from the dataset to improve estimates because he was bequeathed a natal mound at a young age when his mother dispersed. However, statistical significance of the interaction effect was not affected by inclusion of this outlier. Control and treatment females did not differ from each other or from treatment males in the number of days spent at natal mounds (Tukey's test, $P > 0.05$). However, control males stayed at the natal mound an average of 70% longer than treatment males and 77% and 82% longer than control and treatment females, respectively (Fig. 3.3; Tukey's test, $P < 0.05$). Predicted mass at independence from growth models was 16% greater for treatment females and 13% less for treatment males than control juveniles of the same sex (Table 3.2). Food-supplemented juveniles were in better condition than non-supplemented juveniles. Condition index of treatment juveniles ($\overline{X} \pm SE = 0.17 \pm 0.10$) was higher than control juveniles ($\overline{X} \pm SE = -0.32 \pm 0.14$) at capture nearest to age of independence ($F_{130} = 7.6$, $P = 0.01$; age, sex, and interaction effects were not significant).

Experimental groups did not differ in dispersal distance or inheritance of the natal mound. Less than 20% of juveniles inherited or were bequeathed the natal mound in both control and treatment groups (Table 3.1). Dispersal distance did not differ between control and treatment juveniles (Table 3.1). After dispersal, survivorship to December 2008 was similar between control ($n = 6$) and treatment juveniles ($n = 22$) indicating that

food supplementation did not have a long-term effect on mortality (Fig. 3.4, Fisher's exact test, P = 1.0).

Discussion

Males and females exhibited different dispersal behavior in response to resource supplementation (Fig. 3.3). These sex-specific responses match the intersexual differences in reproductive strategies and parental investment patterns of mammals. Timing of male dispersal was earlier in supplemented offspring, which had faster growth and were in better condition than controls (Fig. 3.2). Thus, my results support the hypothesis that size and condition cues are important to triggering dispersal in males. Size and condition likely affect the reproductive success of male kangaroo rats through their ability to find and defend mates. Male banner-tailed kangaroo rats engage in competitive mate searching and direct competition for access to estrus females (Randall 1991). Females did not disperse earlier when food supplemented even though they had faster growth rates and were in better condition (Fig. 3.2). Timing of dispersal in females is predicted to be more influenced by resource quality and competition than body size. Competition for existing mounds was low during this study because population density on the study site was less than half that of high-density years (2.5 vs. 5.7 individuals/ha) and more than half of mounds were unoccupied (unpublished data). Thus, females were able to disperse at the youngest age possible (2-3 months old) in order to secure a mound and begin provisioning it with seed caches. As observed in this study, seed caches are critical to female reproductive success and survivorship of offspring. Mothers with

supplemented seed caches reproduced successfully more often and had higher juvenile survivorship during the dependency period than controls.

The exact timing of dispersal in banner-tailed kangaroo rats appears to be controlled by a mix of cues related to size, age, and condition. Minimum age of dispersal may be set by ontological processes that are not affected by resources. For example, supplemented females did not disperse earlier than control females even though they reached > 80% of adult mass by independence. Thus, other factors such as behavioral development may necessitate a minimum length of dependency before juveniles can live independently. Most juvenile kangaroo rats remained at the natal mound until at least 2 months old and usually closer to 3 months old both in this and other studies (Waser et al. 2006) suggesting that dispersal is generally not feasible before this age. In males, there may be a tradeoff between the effect of size and condition on the timing of dispersal. Although males at food-supplemented mounds dispersed earlier than those at non-supplemented mounds, they also dispersed at a slightly lower percent of adult mass on average. However, their body condition was higher than in controls. Thus, supplemented juveniles may have compensated for the smaller body size through better condition. Dispersing at a younger age when possible may be advantageous to males because they face reduced competition for mounds compared to later dispersing juveniles.

Parental care by banner-tailed kangaroo rat mothers differed between sons and daughters under non-supplemented conditions. Additional parental investment should benefit sons more than daughters because body size has a larger influence on reproductive success in males (Clutton-Brock 1991). Thus, mothers can increase the

reproductive success of sons by allowing them to remain for longer periods at the natal mound. Due to small sample sizes, I was not able to measure whether sons were more costly in terms of fitness to kangaroo rat mothers, but presumably mothers had to relinquish additional resources to support them. Parent-offspring conflict could arise if sons tried to extract more resources than mothers were willingly to provide (Trivers 1974). However, males should not attempt to stay longer than necessary to reach a critical size or condition threshold because obtaining their own mound is essential to survival and reproduction.

Socioecological factors are also known to affect dispersal behavior in banner-tailed kangaroo rats. Habitat saturation causes banner-tailed kangaroo rats to disperse shorter distances (Jones et al. 1988) and delay dispersal longer (unpublished data). During periods of habitat saturation mothers can increase survivorship of offspring by allowing them to remain at natal mounds until a suitable vacancy becomes available (Jones 1984, 1986, Jones et al. 1988). Mounds are a critical resource for kangaroo rats, which can take up to 2 years to construct (Best 1972, Parmenter and Van Devender 1995a); without a suitable mound, kangaroo rats are unable to survive and reproduce. Periods of high density in animal populations often coincide with high food abundance confounding the effects of habitat saturation and resources on timing of dispersal. I was able to decouple the effect of resources from habitat saturation during this experiment because density was well below saturation levels on the study site. These proximate factors appear to affect timing of dispersal differently because habitat saturation caused later dispersal and increased resources resulted in earlier dispersal. The more extreme

instances of delayed dispersal (> 7 months) observed in other studies are probably attributable to habitat saturation (Jones et al. 1988).

Comparison of banner-tailed kangaroo rat dispersal patterns to other mammal species is complicated by the prevalence of sex-biased dispersal. However, sciurids, in particular Belding's ground squirrels (*Spermophilus beldingi*), which exhibit some flexibility in sex-biased dispersal provide the most comparable example (Smale et al. 1997). Similar to male banner-tailed kangaroo rats, food-supplemented male Belding's ground squirrels disperse earlier, but at a comparable mass and condition as control males (Nunes and Holekamp 1996). Unlike banner-tailed kangaroo rats in which both sexes must disperse, female Belding's groups squirrels are often philopatric, but disperse more often when food supplemented, likely because competition for non-food resources increases (Nunes et al. 1997). By examining sex differences in banner-tailed kangaroo rats that lack sex-biased dispersal, I was able to directly compare the effect of food supplementation on dispersal between males and females. My results confirm that differences between sexes in timing of dispersal are likely related to sex-specific reproductive strategies and parental investment patterns common in mammals.

Table 3.1: Effects of food supplementation on female reproduction and juvenile dispersal for banner-tailed kangaroo rats. Means ± SE are presented with sample sizes in parentheses.

Response variable	Control (n)	Treatment (n)	Test statistic	P
Female reproduction				
Percent pregnant	83% (12)	100% (12)	Fisher's exact	0.48
Percent reproduced successfully[a]	58% (12)	100% (12)	Fisher's exact	0.037
Percent producing 2nd litter	0% (12)	25% (12)	Fisher's exact	0.26
Mean Julian day of first pregnancy	65.2 ± 4.4 (10)	66.1 ± 6.1 (12)	$Z = -0.13$	0.90
Litter size	1.7 ± 0.3 (7)	1.6 ± 0.2 (12)	$Z = 0.33$	0.71
Juvenile dispersal				
Age at first capture (days)	69.7 ± 7.4 (11)	83.6 ± 3.8 (21)	$t = 1.86$	0.037
Percent caught at natal mound	82% (11)	29% (21)	Fisher's exact	0.008
Percent philopatric	17% (12)	13% (23)	Fisher's exact	1.0
Median dispersal distance (m)	65.8 ± 17.9 (7)	46.9 ± 14.2 (22)	$Z = -0.05$	0.96

[a]Produced ≥ 1 known offspring

Table 3.2. Parameter estimates from monomolecular growth curves fitted to mass data from captured banner-tailed kangaroo rats in control and treatment groups by sex.

Sex	Group	n^a	Asymptotic mass (g)		Growth period (days)		Predicted mass (g) at independence	
			A	95% CI	T	95% CI	Mass (% adult mass)	95% CI
Female	Control	25 (7)	125.4	119.1-131.6	151.7	127.3-176.1	85.8 (68%)	81.8-89.9
	Treatment	46 (10)	123.2	118.9-127.5	100.9	84.0-117.9	99.8 (81%)	95.6-103.4
Male	Control	23 (5)	159.1	149.1-169.2	241.5	205.9-277.0	114.0 (72%)	110.8-117.2
	Treatment	79 (13)	160.0	154.7-165.2	186.6	167.3-205.8	99.5 (62%)	96.2-102.8

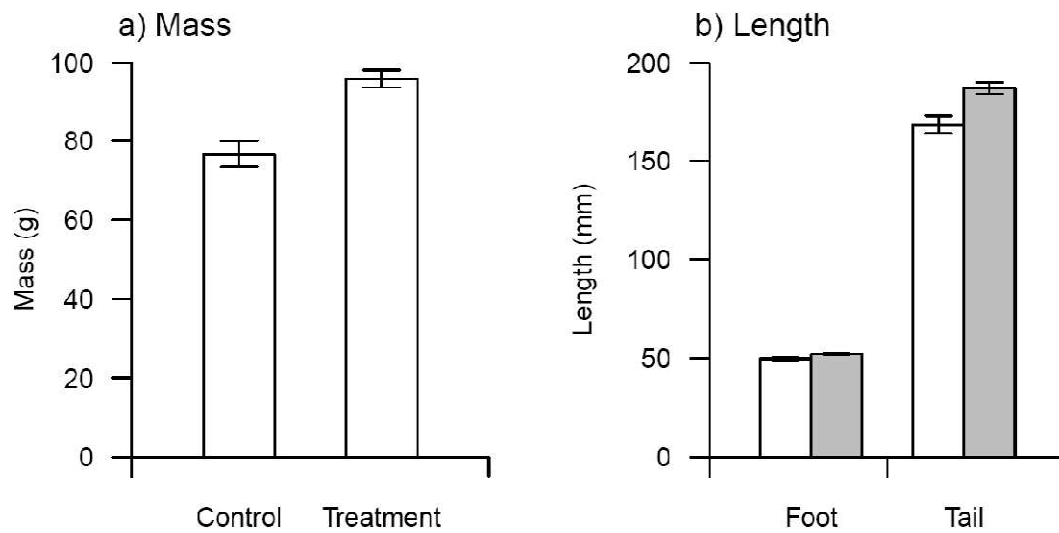[a]Number of captures (number of individuals)

Figure 3.1
Effects of food supplementation on body measurements of juvenile banner-tailed
kangaroo rats. Measurements shown are mass (a) and hind foot and tail length (b, white
bars = control group, shaded bars = treatment group) of control (n = 11) and treatment
groups (n = 21) at first capture (least squares means ± SE adjusted for age at capture
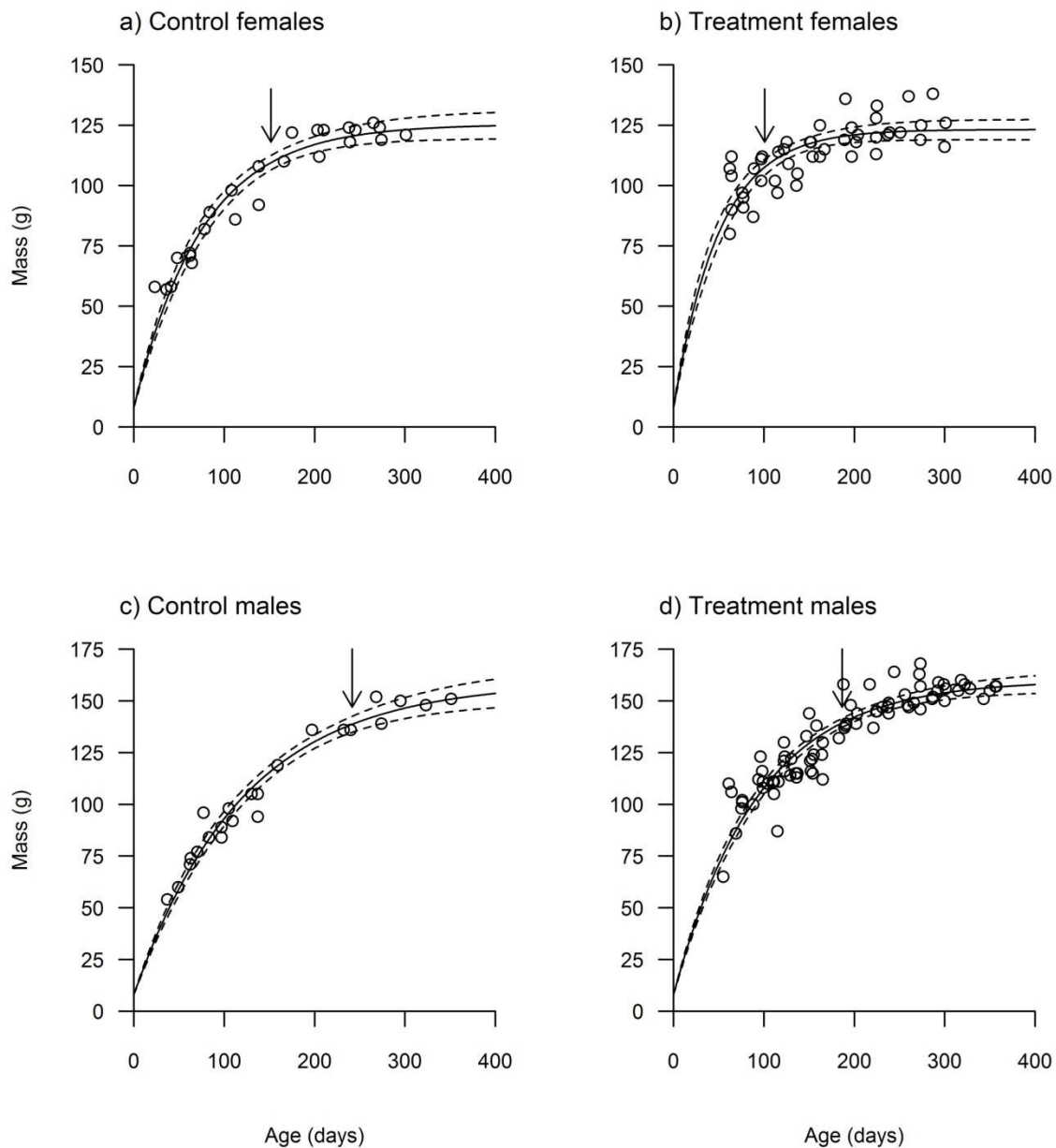through ANCOVA).

Figure 3.2
Growth of banner-tailed kangaroo rats separated by sex and experimental group. Solid lines are monomolecular growth curves fitted to mass data (circles). Dashed lines are 95% confidence intervals. Arrows indicate parameter *T*, age at which approximately 90% of asymptotic mass was reached. Parameter estimates of growth curves are presented in Table 3.2.
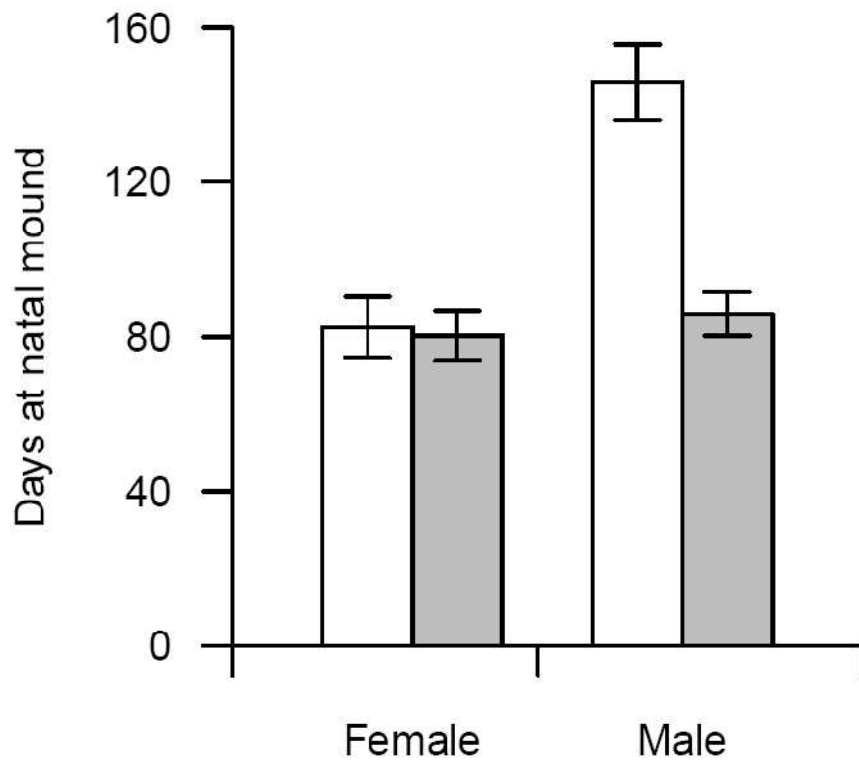
Figure 3.3
Effects of food supplementation on length of dependency for female and male juvenile banner-tailed kangaroo rats. Estimated days spent at natal mound with mother (least squares means ± SE) for control (white bars) and treatment groups (shaded bars) are shown. Samples sizes are: control females = 6, control males = 4, treatment females = 9, and treatment males = 12.

Figure 3.4
Proportion of juvenile banner-tailed kangaroo rats that survived to natal dispersal and to December 2008 in control (white bars) and treatment groups (shaded bars).

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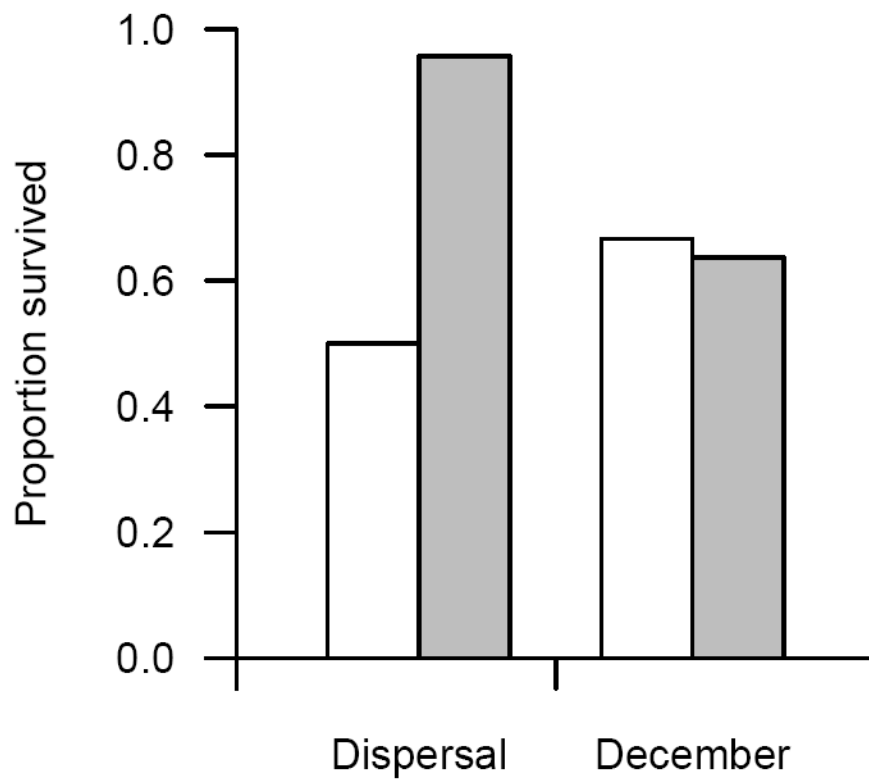
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