

Female mobility and the mating system of the banner-tailed kangaroo rat (*Dipodomys spectabilis*)

MOLLY C. STEINWALD, BRADLEY J. SWANSON, JACQUELINE M. DOYLE, AND PETER M. WASER*

Science Education and Research Department, Phipps Conservatory and Botanical Gardens, Pittsburgh, PA 15213, USA (MCS)

Department of Biology, Central Michigan University, Mt. Pleasant, MI 48858, USA (BJS)

Department of Biological Sciences, Purdue University, West Lafayette, IN 47907, USA (JMD, PMW)

* Correspondent: waserpm@purdue.edu

Like some species of pika (*Ochotona*) and tree squirrel (*Tamiasciurus*), the banner-tailed kangaroo rat (*Dipodomys spectabilis*) is a solitary, philopatric larder-hoarder that practices unisexual territoriality. Seeking to understand how this unusual combination of traits might influence the mating system, we used systematic trapping at mounds (burrows) and spool-and-line tracking to examine male and female visits to each other. Where genetic data exist, unisexual larder-hoarders such as *D. spectabilis* have been found to be polygynandrous. We asked whether the fact that females sometimes mate with more than 1 male is a passive side effect of imperfect mate defense by males, or whether females actively engage in behaviors that encourage multiple mating. During the nonbreeding season, adults of both sexes were rarely captured at mounds other than their own. In contrast, during the breeding season females as well as males were significantly more likely to be captured away from their home mounds, most often at mounds belonging to adults of the opposite sex. Spool-and-line tracking during the breeding season confirmed these results. Consistent with the expectation that they engage in competitive mate searching, adult males visited adult females' mounds significantly more than expected by chance and without regard to age, size, or relatedness. More surprisingly, adult females exhibited similar behavior, expanding their home ranges and disproportionately visiting the mounds of large adult males during the nights preceding estrus. Increased (and apparently directed) female mobility during the days preceding estrus may serve as a means of shaping the pool of competing mates and is worthy of more attention in this and other, ecologically similar species.

Key words: competitive mate searching, genetic bet-hedging, inbreeding avoidance, kangaroo rat, mate choice, mobility, polygynandry, spool-and-line tracking

© 2013 American Society of Mammalogists

DOI: 10.1644/13-MAMM-A-124

In the banner-tailed kangaroo rat (*Dipodomys spectabilis*), males and females live singly in nonoverlapping home ranges, each centered on a den comprising a large dirt mound that is defended from conspecifics of both sexes (Schroder 1979; Randall 2007). This pattern of unisexual territoriality, presumably related to the species' larder-hoarding habit, is unusual among mammals, the best-known examples being some populations of red and Douglas squirrels (*Tamiasciurus hudsonicus* and *T. douglasii*—Smith 1968; Koford 1982; Lane et al. 2009) and North American pikas (*Ochotona princeps* and *O. collaris*—Smith and Ivins 1984; Zgurski and Hik 2012). The larder-hoarding whistling rat (*Parotomys brantsii*) also may show this pattern; at low population densities, both males and females defend space against adults without regard to sex (Jackson 1999).

Monogamy or polygyny might be expected in these species, because association with a larder-hoard ties females to a single, reliable location that is presumably economical for a male to defend. Yet where data are available, mammals with unisexual territoriality are polygynandrous (Waser and DeWoody 2006; Lane et al. 2008; Zgurski and Hik 2012). Here, we track visits by male *D. spectabilis* to females, and vice versa, to ask how male and female movement patterns interact to produce a polygynandrous mating system.

Where females' locations are spatially fixed and estrus is synchronized, most models predict male mate competition to



be in the form of combat, sparring, and exclusion (Emlen and Oring 1977; Waterman 2007). However, in *Tamiasciurus* and *D. spectabilis*, estrus is short and often asynchronous (Randall 1991; Koprowski 2007). In such species, it has been suggested that competitive mate searching, in which males attempt to rapidly locate (and thus be the 1st to mate with) estrous females, can supplement or take the place of physical contests as a means of maximizing male reproductive success (Dobson 1984; Schwagmeyer 1995). Short periods of estrus may also favor mate-guarding, including passive mate-guarding in the form of copulatory plugs (Dunham and Rudolf 2009).

For mammals with unisexual territoriality, one hypothesis might thus be that the strong attachment of females to their mounds makes them economically defensible, so that the mating system is shaped primarily by male mate competition. Some data from *D. spectabilis* are consistent with this view. For example, Randall (1991) observed copulations at females' mounds, and concluded that "males always come to the female's mound to mate." Competitive mate searching and scramble competition can both occur. When local population density is high and female cycles are asynchronous, multiple males visit and attempt both pre- and postcopulatory mate-guarding, competing aggressively in the vicinity of females' mounds (Randall 1987a, 1991). Males deposit a conspicuous copulatory plug (Randall 1991, 2007; McCreight et al. 2011).

Nevertheless, genetic data from *Tamiasciurus* and *Ochotona* have demonstrated high levels of multiple mating by females as well as by males (Lane et al. 2008; Zgurski and Hik 2012). Behavioral observations, parentage analysis, and genetic analysis of copulatory plugs all demonstrate that some female *D. spectabilis* mate with > 1 male (Randall 1991; Waser and DeWoody 2006; McCreight et al. 2011).

Multiple mating by females might arise in several ways. A 1st hypothesis would postulate that females gain no advantage from multiple mating, although females might mate multiply if no one male can completely exclude his competitors. In a study of multiply mating female *Tamiasciurus*, for example, Lane et al. (2008, 2009) found no evidence for any of the usual benefits of multiple mating, suggesting that female mating behavior is a "passive response to selection on multifemale mating in males" (Lane et al. 2008:1927).

An alternative to the hypothesis that polygynandry is a passive side effect of mate competition is that females proactively encourage it, as expected if they gain advantages from selective or multiple mating (e.g., Klemme et al. 2007; Lane et al. 2009). Females might exert mate choice by advertising their reproductive state, actively circumventing mate competition, or at least shaping the pool of male competitors. Mating with multiple males dilutes the effects of mating with low-quality males and potentially opens the door to postcopulatory mate choice ("bet-hedging"—Bergeron et al. 2011). Females also might solicit matings with high-quality males, for example, those that are older, larger, or less related to them. Some data from *D. spectabilis* also are consistent with this alternative hypothesis. For example, the species is philopatric, so that on average, a female is related to her

nearest male neighbor by $r = 0.17$ (Winters and Waser 2003; Busch et al. 2009). Nevertheless, her offspring are sired by her sons or littermate siblings, who grow up in proximity with her, far less often than expected by chance (Waser et al. 2012). Patterns of parentage are consistent both with inbreeding avoidance via discrimination against familiar kin and with genetic bet-hedging (Winters and Waser 2003).

We know little, however, about the tactics that female *D. spectabilis* might use to exert mate choice. Direct observations of mating patterns are limited because *D. spectabilis* spends all day and most of each night underground, and often mates there (Schroder 1979; Randall 1991). As in other *Dipodomys* species, the night of behavioral estrus is difficult to predict from visual indicators (swollen vulva), although males can discriminate between urine from estrous and anestrus females (Wilson et al. 1985; Randall 1986, 2007). Females may have several litters per breeding season but behavioral estrus is brief, lasting a night or less (Randall 1991).

Here, we attempt to distinguish between our 2 hypotheses by documenting male and female visits to each others' mounds. First, we examine patterns of visitation inferred from livetrapping data during biannual censuses. We then use spool-and-line tracking during the breeding season to ask whether females selectively visit mounds of potential mates, and if so, whether they focus their visits in ways that might potentially shape the pool of competing males. In parallel, we examine mound visitation by spool-carrying males. If the mating system is driven solely by male mate competition we would expect female movement patterns to remain uninfluenced by estrous state. Males engaged in competitive mate searching should actively visit female mounds in order to monitor their estrous state, but females should remain equally sedentary during breeding and nonbreeding seasons, or during anestrus and proestrus.

In contrast, if polygynandry involves not only male competition but also bet-hedging or mate choice by females, or both, we would expect estrus-related increases in visits by females to males, or differential visitation of males that are older, larger, or less related to the female, or both.

MATERIALS AND METHODS

Study site and census trapping.—Our "Rucker" study site is located on private free-range cattle ranchland in southeastern Arizona (31°37'N, 109°5'W). The habitat is classified as desert grassland, and areas preferred by banner-tailed kangaroo rats tend to be open, characterized by short grasses and forbs and by patches of bare ground (Waser and Ayers 2003). Each year from 1990 to 2007, using census procedures described by Jones (1984), we carried out biannual censuses as part of a long-term study of demography and genetics of *D. spectabilis* (Busch et al. 2009; Sanderlin et al. 2011). We trapped at all mounds for 3 nights to determine sex, reproductive state, age (in years), and body mass (± 2 g). The locations of all mounds were measured with a laser theodolite (± 1 m). All animals received numbered ear tags at 1st capture, and the birth years of

all animals were known at the start of this study. We categorized age as “juvenile” (< 1 year old) or “adult” (reproductively mature and 1–6 years old); females < 1 year old but entering their 1st estrous cycle were categorized as “subadult.” We used the protocol of Jones (1984) to determine which adult owned (was the most frequent user of) each mound. Because some animals used > 1 mound, we defined each animal’s primary residence as the mound in which it usually spent the day (Jones 1984).

To infer patterns of movement from livetrapping, we compared the spatial distribution of captures of adult males and females between March (breeding season) and August (nonbreeding season) censuses, 1990–2007. For each adult trapped at least twice during a census, we derived 2 indexes of mobility. First, we determined the percentage of its captures during which it was trapped at its primary residence. We then determined the mean distance between successive captures. Whenever an adult was trapped at a mound other than its own, we recorded the mound owner. Finally, because our trapping protocol does not produce a standard measure of home-range size, we report “95% capture radius”; 95% of individuals were always captured this distance or less from their primary residence.

Spool-and-line tracking.—In May 1998, May 1999, and February 2001, we monitored visits by kangaroo rats to mounds other than their own via spool-and-line tracking (Key and Woods 1996; Steinwald et al. 2006). Every 3–4 days, we trapped at all mounds occupied by adults, allowing us both to apply thread spools to target animals and to monitor changes in female reproductive state. Swelling of the vulva indicates proestrus (Wilson et al. 1985). Because swelling lasts several days with considerable individual variation (Randall 2007), our categorization of females as “proestrous” indicates they are within 1–5 days of mating. Females without swollen vulvas, and those we judged to be pregnant based on unusual body mass or palpation, were considered to be anestrus.

To reduce risk to the target animals (Steinwald et al. 2006), we avoided trapping the same individual on 2 successive nights. To minimize the possibility of entanglement, we did not attach spools to females trapped on what we judged to be their estrous night. Hence, all females with spools were judged to be either anestrus or proestrous, but not mating. We also avoided attaching spools to females known to be pregnant and those with small juveniles, and we did not simultaneously spool animals whose mounds were located within 25 m of each other. In selecting animals to track, we focused on adults but included a small number of subadult females that were entering their 1st estrous cycle.

We used 1 × 3-cm cocoon spools (Culver Textiles Corporation, West New York, New Jersey; Imperial Threads, Inc., Northbrook, Illinois), each consisting of 180 m of nylon thread, weighing about 1.7 g and having no inner bobbin. We dyed the thread bobbins 10 different colors using fabric dye (Rit Dyes, Inc., Indianapolis, Indiana) to distinguish the thread trails of different animals spooled on the same night. We wrapped each spool with medical tape and glued it to the

subject’s fur middorsally with Skin-Bond medical glue (Smith and Nephew, Inc, Bartlett, Indiana). The process of spool attachment took less than 10 min and is described in more detail in Steinwald et al. (2006). We released the kangaroo rat while holding the trailing thread, and all animals ran to their mounds immediately upon release. We observed 4 adults carrying spools (2 males and 2 females) from release to dawn with night-vision goggles. Animals with spools reemerged from their mounds within 48–56 min, and subsequently moved, foraged, foot-drummed, and sand-bathed as described for animals without spools (Randall 1984, 1987b; Steinwald 2004). Spooling’s disruption of normal behavior thus appeared to be minor and short-term; it had no subsequent effect on the experimental individual’s survival, body mass, or willingness to enter traps (Steinwald et al. 2006).

When weather was cold and wet, we checked traps and attached spools at about 2200 h, giving experimental *D. spectabilis* time to reemerge and leave thread trails the same night ($n = 17$). When conditions were mild, we checked traps and attached spools at about 0400 h; kangaroo rats carrying spools remained in their mounds until the following night ($n = 118$). We collected thread “tracks” either the afternoon after attaching spools (if attached at about 2200 h) or 24 h later (if attached about 0400 h). Collecting the thread within these time periods ensured that the data represented 1 night of each animal’s movement. We combined the 2 data sets after finding no difference in number of visits (Mann–Whitney $U = 1,160$, $P = 0.27$) or distance moved during visits ($U = 1,161$, $P = 0.28$). All procedures followed guidelines of the American Society of Mammalogists (Sikes et al. 2011) and were approved by the Purdue University Institutional Animal Care and Use Committee.

Thread data collection.—We categorized aboveground kangaroo rat activity as “at the primary residence” when it was < 3 m from its mound center. Movements away from the primary residence were divided into “visits” if they approached within 3 m of another mound center and otherwise as “forays.” Beginning at the mound where a kangaroo rat was released, we followed its thread trail to completely retrace its movements, and then collected the thread. For each visit to another mound, we recorded the visit distance as the straight-line distance between the originating mound and the visited mound.

Statistical analyses.—Because the distance between successive capture locations within a census was most often 0, we used Kruskal–Wallis tests to compare rates of movement between sexes and seasons. We attached spools to individual *D. spectabilis* up to 4 times, and animals sometimes visited > 1 mound per night. We therefore used repeated-measures analyses to examine the effect of the sex and estrous state of animals with spools on the distances moved during forays and visits to other mounds. Statistical analyses were performed using SAS version 9.2 (SAS Institute Inc. 2008). Specifically, we used Proc MIXED after log-transformation to ensure normality for distances moved, and Proc GENMOD (which assumes the data are Poisson-distributed) for numbers of forays or mound visits per night. Either 1st-order autoregressive or

compound symmetry was used to model the covariance structure, depending on whichever provided the best fit based on Akaike Information Criterion (AIC) and quasi-AIC (QAIC) fit statistics. After failing to find significant differences in movement behavior between years, we combined data from all 3 years.

To assess whether visits by *D. spectabilis* to neighboring mounds were random with regard to mound ownership, we performed randomization tests (programs written in DBASE III by PMW). These tests asked whether animals carrying spools visited other mounds at random within 125 m of their primary residence. We chose the 125-m limit because the maximum distance *D. spectabilis* has been observed to travel from its primary residence in previous studies was 49 m (radio-tracking—Schroder 1979), 122 m (mark-recapture—Winters and Waser 2003), 125 m (visual observations—Randall 1991), and 102 m (these spool-and-line data). To avoid pseudoreplication in randomization tests, we created a single “average” record for each individual. For example, if a female that was tracked on 3 nights visited a total of 4 mounds, 2 of which were owned by adult males, we scored her as visiting 0.5 males per visit.

The randomization program worked as follows. For each individual that we spooled the program 1st identified each mound within 125 m of the individual’s primary residence, its distance from the primary residence, and the identity and characteristics of its owner. It then used a random number generator to select 1 mound among this set of available mounds and recorded the characteristics of the randomly chosen mound’s occupant as determined for that particular tracking night. This procedure was repeated until it generated a list of 1 random visit choice for every spool-carrying animal in the analysis. The entire process was iterated 1,000 times.

The probability of visiting a mound declined as the negative exponential function of the ranked distance to that mound (nearest mound = rank 1), and a preliminary analysis showed that the effects of distance overwhelmed any other patterns in the data (Waser and DeWoody 2006). To control for the effects of distance, we fit negative exponential functions to the observed distributions of visit distance. We then weighted probabilities of mound choice by these functions in our simulations. In other words, our randomization tests simulated hypothetical animals that visited mounds according to their distance from “home” but were oblivious to the nature of the mound owner.

Our 1st round of randomization tests asked whether animals with spools chose to visit mounds without regard to ownership. We compared the mean number of times that animals carrying spools visited mounds owned by adults of the opposite sex with the mean of 1,000 random choices by the same animals. For animals that visited mounds occupied by opposite-sexed adults, we performed a 2nd randomization test to ask whether those adults were chosen randomly with regard to age, body mass, and genetic relatedness. As described in more detail elsewhere (Waser and DeWoody 2006; Busch et al. 2009), *D. spectabilis* was genotyped at up to 9 microsatellite loci. We

estimated dyadic relatedness using program ML-Relate (Kalinowski et al. 2006). In the 2nd set of tests, we compared the mean age, body mass, or relatedness characterizing observed mound visits to the means for 1,000 random choices by the same animals. The probability that the observed visits would occur by chance was calculated as the proportion of simulations with a result as extreme, or more extreme, than that observed in the data.

RESULTS

Mobility as indicated by capture locations.—During March and August censuses, 1990–2007, we trapped 532 adult males and 535 adult females 4,740 times. During August (nonbreeding season) censuses, adults of both sexes were rarely captured away from their primary residences (males, 110 of 1,301 captures, 8%; females, 142 of 1,213 captures, 12%). Probabilities of capture away from the primary residence were similar between sexes ($P = 0.06$, Fisher exact test). The 95% capture radius was 17 m for males and 20 m for females (median nearest-neighbor distance during this study was 35 m). The distances moved between captures did not differ significantly between males and females (male range 0–54 m, female range 0–48 m; $U_{357,363} = 52,930.5$, $P = 0.08$). There was no tendency in either sex to focus their visits on mounds that were owned by opposite-sexed animals, either adult or juvenile (all $P > 0.05$, binomial tests).

During March (breeding season) censuses, *D. spectabilis* was much more likely to be captured while visiting other mounds (males, 294 of 1,057 captures, 28%; females, 282 of 1,169 captures, 24%). This increase in movement from the nonbreeding to the breeding season was highly significant for both sexes (both $P < 0.001$, Fisher exact tests). Proportions of captures away from the primary residence were similar between sexes ($P = 0.10$, Fisher exact test). The 95% capture radius was 55 m for males and 35 m for females.

During breeding season censuses, *D. spectabilis* also moved further between captures. Compared to censuses during the nonbreeding season, the increase in distance moved between captures was significant for both males ($U_{357,441} = 30,116.5$, $P < 0.001$) and females ($U_{363,407} = 40,386.5$, $P < 0.001$). Males were particularly mobile (male range 0–189 m, female range 0–120 m; $U_{441,407} = 38,882$, $P < 0.001$).

During breeding-season censuses, adult kangaroo rats away from “home” were most likely to be trapped at mounds owned by members of the opposite sex. Of 380 captures of adult males at mounds owned by other adults, 317 were visits to females (83%; $P < 0.001$, binomial test). Of 29 adult male captures at mounds owned by young animals, 21 were visits to subadult females (72%; $P = 0.02$, binomial test). During the breeding season, females as well as males were often captured visiting a member of the opposite sex. When an adult female visited a mound that was not her own, it usually belonged to an adult male (208 of 278 captures, 75%; $P < 0.001$, binomial test).

Forays and visits characterized by spool-and-line tracking.—We attached spools to 33 adult male, 36 adult

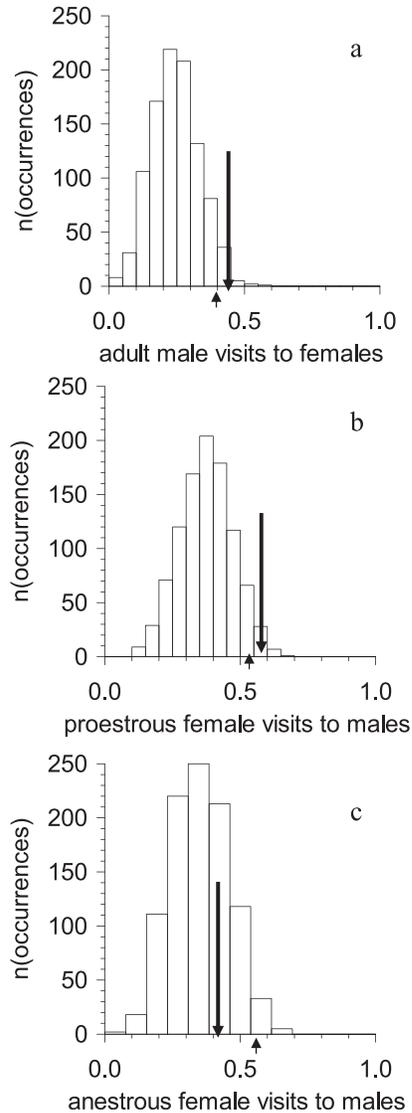


Fig. 1.—Randomization tests show that both a) adult males ($n = 20$, $P = 0.04$) and b) proestrous females ($n = 21$, $P = 0.04$) were significantly more likely to visit mounds occupied by adults of the opposite sex than expected given the spatial distribution of mound ownership. In contrast, c) anestrus females visited adult males no more often than expected by chance ($n = 12$, $P = 0.39$). The x-axis is the proportion of visits to mounds that are owned by adults of the opposite sex; histogram bars give the number of times (out of 1,000 iterations of the test) that spool-carrying animals would have visited that proportion of opposite-sexed adults had they chosen at random from the mounds in their vicinity. Downward-pointing arrows indicate the observed proportion of visits, whereas triangles denote the minimum proportion of visits required for $P < 0.05$.

female, and 10 subadult female *D. spectabilis* a total of 135 times. Of the 46 females, 30 were tracked at least once when proestrous and 26 at least once when anestrus.

Kangaroo rats deposited nearly half of all aboveground thread within 3 m of their mounds (males $44\% \pm 6\% SE$ [$n = 56$], females $50\% \pm 6\%$ [$n = 81$]). A few animals (12 of 79) evidently spent the entire night in the immediate vicinity of the

mound. A majority, however, made at least 1 foray > 3 m away from it. Most forays were short, and none approached within 10 m of any neighboring mound. Males and females did not differ either in the number of forays per night (median 1, range 0–3 for both sexes; $\chi^2_1 = 1.53$, $P = 0.22$) or in foray length (median 4 m, range 0–29 m for females; median 4 m, range 0–66 m for males; $F_{1,42.8} = 0.01$, $P = 0.93$).

In addition to forays, most animals (20 of 33 adult males, 20 of 36 adult females, and 6 of 10 subadult females) visited at least 1 nearby mound. As with forays, the distribution of distances traveled to visit other mounds was right-skewed. Most visits were to adjacent mounds, but some individuals (6 of 20 adult males that visited mounds, 7 of 20 adult females, and 1 of 6 subadult females) moved well past their nearest neighbors (up to 3 times the median nearest-neighbor distance for males 2.5 times the distance for females). Adult females and males visited similar numbers of mounds per night (median 1 for both sexes; $\chi^2_1 = 0.32$, $P = 0.58$) and traveled similar distances (median visit length 23 m, range 11–38 m for females; median 22 m, range 8–69 m for males; $F_{1,33.5} = 0.69$, $P = 0.41$).

Both females and males visited the mounds of opposite-sexed adults more than any other category, including their own secondary mounds. Randomization tests showed that adult males were more likely to visit mounds occupied by adult females than expected given their local availability (observed/expected number of visits = 1.7 [Fig. 1a]). Similarly, proestrous females disproportionately visited the mounds of adult males (observed/expected = 1.5 [Fig. 1b]). Anestrus females, however, did not disproportionately visit the mounds of adult males (observed/expected = 1.1 [Fig. 1c]).

Movements by males to adult females' mounds were very direct, and often utilized well-worn paths ("runways") between the mounds. Adult males carrying spools were tracked to 1 or more females' mounds on 23 nights. On most nights, including all 10 when the 1st female visited was proestrous, males visited only a single female's mound (sometimes more than once). On 3 of 4 nights when the 1st visited female was anestrus, the male went on to visit a 2nd female's mound.

Twelve of the 20 males that visited a female's mound were spooled again later during the same week; 2 of these visited the same female (in both cases, the female was anestrus on the 1st night). Most, however, visited different females (up to 3) on different nights.

Randomization tests did not demonstrate any tendency for males to selectively visit mounds owned by females that were larger, older, or less related to them (Table 1).

Patterns of female visitation to males were similar to those of males to females. Adult or subadult females carrying spools visited mounds owned by males on 24 nights. Most females that visited males' mounds visited just 1 per night (sometimes more than once), but 3 of 17 went on to visit a 2nd male. Six of the 20 females that visited a male were spooled on multiple nights during the course of a week; 5 repeatedly visited the same male. Comparing the sexes, we found that females made as many visits per night to males as vice versa (median number

Table 1.—Randomization tests indicate that male and anestrous female *Dipodomys spectabilis* visited members of the opposite sex without regard to their age, body mass, or relatedness. In contrast, proestrous females preferentially visited larger males. Data are from adult males or adult and subadult females that visited at least 1 mound belonging to an opposite-sex adult. The Bonferroni-adjusted experiment-wide $\alpha' = 0.017$.

	Observed	Expected	<i>P</i>
Adult males (<i>n</i> = 14)			
Female characteristic			
Mean age (years)	1.1	1.4	0.18
Mean mass (g)	127	126	0.35
Mean relatedness	0.06	0.10	0.06
Proestrous females (<i>n</i> = 16)			
Male characteristic			
Mean age (years)	1.4	1.7	0.21
Mean mass (g)	143	139	0.01
Mean relatedness	0.10	0.11	0.49
Anestrous females (<i>n</i> = 5)			
Male characteristic			
Mean age (years)	2.0	1.8	0.48
Mean mass (g)	136	136	0.49
Mean relatedness	0.01	0.06	0.24

of visits per night by both sexes = 0, range 0–2; $\chi^2_1 = 0.32$, $P = 0.57$). We detected no differences in the distances traveled by the 2 sexes to visit each other (female median 24 m, range 9–76 m; male median 34 m, range 9–102 m; $F_{1,20.9} = 2.86$, $P = 0.11$). However, estrous state influenced females' rates of visiting males. Subadult and adult females approaching estrus visited at higher rates (proestrous female median number of visits per night = 1, range 0–3; anestrous female median = 0, range 0–2; $\chi^2_1 = 3.95$, $P = 0.05$). Of the 30 females that were tracked when proestrous, 14 visited 1 or more males (15 different individuals). Of the 26 females tracked when anestrous, only 5 visited males (5 individuals).

For females, randomization tests demonstrated no female selectivity with regard to male age or relatedness. Anestrous females were not selective with regard to male body mass. However, proestrous females tended to visit males that were slightly larger than expected by chance (Table 1).

DISCUSSION

Both capture locations and spool-and-line tracking show that male mobility increases and that males target females during breeding season visits, as anticipated if males are engaged in competitive mate searching. But (based on our 95% capture radii) females also expand their home ranges during the breeding season, and visits to males become particularly frequent and selective during the nights immediately preceding estrus. The results thus favor the hypothesis that female choice or bet-hedging, as well as imperfect male mate defense, contribute to polygynandry in *D. spectabilis*.

Increased male mobility during the breeding season.—Males leave their primary residence more often and move farther between recaptures during breeding censuses than

during nonbreeding censuses. Their 95% capture radius during the nonbreeding season is approximately one-half the distance between nearest neighbors, but during the breeding season it triples. When they are trapped outside their usual home range during the breeding season, males are most often visiting females.

These results are consistent with published observations (Randall 1984, 1991) and are reinforced by spool-and-line data. During the breeding season, males carrying spools visited females as much as 100 m away; a circular area of 100-m radius would, on average, include the residences of 5.3 females. Males carrying spools disproportionately visited females; visits were not confined to nearest neighbors, and males visited particular females repeatedly, at least until they came into estrus. Visits targeted both adult and subadult females, apparently without regard to body mass, age, or relatedness. These observations suggest that each male in this population monitors the estrous condition of most or all nearby females every few nights, that is, that mate searching is an important component of male–male competition. In this regard, male *D. spectabilis* are similar to male *Tamiasciurus* (and many other sciurids), which increase home-range size and overlap with female home ranges during the breeding season (e.g., Waterman 2007; Lane et al. 2009; Cudworth and Koprowski 2010).

Female mobility, reproductive advertisement, and mate choice.—Previous radiotracking and observational studies (Schroder 1979; Randall 1991) did not lead us to anticipate the extent to which females expand their home ranges during the breeding season. Randall (1984) reported that female *D. spectabilis* sometimes visit males' mounds; examination of our trapping data shows that their probability of doing so increases dramatically during the breeding season, showing a pattern very similar to that of males. Females are more often captured away from their mounds, double their 95% capture radius, move farther from night to night, and more often visit males during the breeding season than during the nonbreeding season. Spool-and-line tracking further shows that females can be nearly as mobile as males and that their mobility is tied to reproductive state. Both a female's visitation rate and her tendency to visit the mounds of males are higher during the nights immediately preceding estrus. Estrous females carrying spools were tracked to the mounds of males up to 74 m away; within this radius, the average female has 3.5 male neighbors.

In many rodents, increased estrogen increases activity levels, as reviewed by Morgan et al. (2004). More specifically, increased mobility as a female approaches estrus may be a common characteristic of *Dipodomys* mating systems. Behrens et al. (1986) found that aboveground activity by female *D. merriami* increased markedly during the period immediately prior to and during estrus. Cooper and Randall (2007) reported that home ranges of radiotagged female *Dipodomys ingens* did not significantly increase in size during the breeding season, but the small sample size (7 females) and associated probability ($P = 0.08$) suggest that breeding-season ranges might prove to be larger with increased sample size

In tree squirrels with overlapping male and female home ranges, female home-range size and mobility remain stable or even decrease during the breeding season (Edelman and Koprowski 2006; Pasch and Koprowski 2006; Cudworth and Koprowski 2010). However, populations of *Tamiasciurus* with unisexual territoriality demonstrate a pattern more like that of *D. spectabilis*: female home-range size doubles during the breeding season (Lane et al. 2009). Data from pikas with unisexual territoriality are lacking, because breeding generally occurs under the snow, but Smith and Ivins (1984) observed female *O. princeps* entering male territories to breed at their hay piles. In these species, as well as in *D. spectabilis*, a question worth further investigation is the extent to which such behaviors are proactive. Do females increase home-range size, mobility, or male visitation before mating begins? If estrous females move farther in response to male pursuit, do they direct their movements toward the home ranges of particular males? Species with unisexual territoriality provide an especially good prospect for answering such questions, because females rarely enter male home ranges except in a reproductive context.

The magnitude and timing of females' visits to males allow us to reject our 1st hypothesis, that multiple mating by female *D. spectabilis* is a passive consequence of males' inability to exclude their competitors. Visits increase several days before behavioral estrus (we did not attach spools on estrous nights), suggesting that females are proactively informing males of their impending state. In *Tamiasciurus* (and many other sciurids—Koprowski 2007), females provoke male scramble competition on their estrous day by advertising their state with olfactory, visual, and acoustic signals. Females also may influence the outcome of male competition by soliciting matings, by evasive maneuvers during chases, and by steering chases to locations that are relatively secluded (Koprowski 2007). No evidence exists for mating chases in *D. spectabilis*, but increased mobility and visiting of males during the days preceding behavioral estrus make it clear that polygynandry cannot be a simple consequence of imperfect male mate defense.

It remains unclear whether polygynandry in this species simply dilutes the effects of mating with low-quality males (bet-hedging) or whether females are actively choosing to visit males with characteristics desirable to them. We detected no preference by females to differentially visit less-related males, even though avoidance of close maternal relatives is suggested both by the identity of males represented in copulatory plugs (McCreight et al. 2011) and by patterns of parentage (Waser and DeWoody 2006; Waser et al. 2012). On the other hand, we did detect a tendency for females to preferentially visit larger males. The magnitude of this tendency is small, but it is much clearer in proestrous than anestrous females. In either case, examination of spool-and-line data suggests a possibility worth more attention: that in species with unisexual territoriality, proestrous females can actively seek out males, thereby increasing the number of partners with which they mate or influencing which males engage in competition.

ACKNOWLEDGMENTS

We thank J. Sanderlin, S. Hoffmann, J. Winters, and D. Hitt for help in the field; and A. Smith, S. Boutin, J. Lane, J. Zgurski, R. Swihart, R. Howard, and several anonymous reviewers for input into the writing. This work was partially supported by the National Science Foundation (DEB 9616843).

LITERATURE CITED

- BEHREND, P., M. DALY, AND M. J. WILSON. 1986. Aboveground activity of Merriam's kangaroo rats (*Dipodomys merriami*) in relation to sex and reproduction. *Behaviour* 96:210–226.
- BERGERON, P., D. RÉALE, M. M. HUMPHRIES, AND D. GARANT. 2011. Evidence of multiple paternity and mate selection for inbreeding avoidance in wild eastern chipmunks. *Journal of Evolutionary Biology* 24:1685–1694.
- BUSCH, J. D., P. M. WASER, AND J. A. DEWOODY. 2009. The influence of density and sex on patterns of fine scale genetic structure. *Evolution* 63:2302–2314.
- COOPER, L. D., AND R. A. RANDALL. 2007. Seasonal changes in home ranges of the giant kangaroo rat (*Dipodomys ingens*): a study of flexible social structure. *Journal of Mammalogy* 88:1000–1008.
- CUDWORTH, N. L., AND J. L. KOPROWSKI. 2010. Influences of mating strategy on space use of Arizona gray squirrels. *Journal of Mammalogy* 91:1235–1241.
- DOBSON, F. S. 1984. Environmental influences on sciurid mating systems. Pp. 227–249 in *The biology of ground-dwelling squirrels* (J. O. Murie and G. R. Michener, eds.). University of Nebraska Press, Lincoln.
- DUNHAM, A. E., AND H. W. RUDOLF. 2009. Evolution of sexual size monomorphism: the influence of passive mate-guarding. *Journal of Evolutionary Biology* 22:1376–1386.
- EDELMAN, A. J., AND J. L. KOPROWSKI. 2006. Seasonal changes in home ranges of Abert's squirrels: impact of mating season. *Canadian Journal of Zoology* 84:404–411.
- EMLEN, S. T., AND L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215–223.
- JACKSON, T. P. 1999. The social organization and breeding system of Brants' whistling rat (*Paratomys brandtsii*). *Journal of Zoology (London)* 247:323–331.
- JONES, W. T. 1984. Natal philopatry in bannertailed kangaroo rats. *Behavioral Ecology and Sociobiology* 15:151–155.
- KALINOWSKI, S. T., A. P. WAGNER, AND M. L. TAPER. 2006. ML-Relate: a computer program for maximum likelihood estimation of relatedness and relationship. *Molecular Ecology Notes* 6:576–579.
- KEY, G. E., AND R. D. WOODS. 1996. Spool-and-line studies on the behavioural ecology of rats (*Rattus* spp.) in the Galapagos Islands. *Canadian Journal of Zoology* 74:733–737.
- KLEMM, I., J. A. ECCARD, AND H. YLÖNEN. 2007. Why do female bank voles, *Clethrionomys glareolus*, mate multiply? *Animal Behaviour* 73:623–628.
- KOFORD, R. R. 1982. Mating system of a territorial tree squirrel (*Tamiasciurus douglasii*) in California. *Journal of Mammalogy* 63:274–283.
- KOPROWSKI, J. L. 2007. Alternative reproductive tactics and strategies of tree squirrels. Pp. 86–95 in *Rodent societies: an ecological and evolutionary perspective* (J. O. Wolff and P. W. Sherman, eds.). University of Chicago Press, Chicago, Illinois.
- LANE, J. E., S. BOUTIN, M. R. GUNN, AND D. W. COLTMAN. 2009. Sexually selected behaviour: red squirrel males search for reproductive success. *Journal of Animal Ecology* 78:296–364.

- LANE, J. E., S. BOUTIN, M. R. GUNN, J. SLATE, AND D. W. COLTMAN. 2008. Female multiple mating and paternity in free-ranging North American red squirrels. *Animal Behaviour* 75:1927–1937.
- MCCREIGHT, J., J. A. DEWOODY, AND P. M. WASER. 2011. DNA from copulatory plugs can give insight into sexual selection. *Journal of Zoology (London)* 284:300–304.
- MORGAN, M. A., J. SCHULKIN, AND D. W. PFAFF. 2004. Estrogens and non-reproductive behaviors related to activity and fear. *Neuroscience and Biobehavioral Reviews* 28:55–63.
- PASCH, B., AND J. L. KOPROWSKI. 2006. Sex differences in space use of Chiricahua fox squirrels. *Journal of Mammalogy* 87:380–386.
- RANDALL, J. A. 1984. Territorial defense and advertisement by footdrumming in bannertail kangaroo rats (*Dipodomys spectabilis*) at high and low population densities. *Behavioral Ecology and Sociobiology* 16:11–20.
- RANDALL, J. A. 1986. Preference for estrous female urine by male kangaroo rats (*Dipodomys spectabilis*). *Journal of Mammalogy* 67:736–739.
- RANDALL, J. A. 1987a. Observations of male competition and mating in Merriam's and bannertail kangaroo rats. *American Midland Naturalist* 117:211–213.
- RANDALL, J. A. 1987b. Sandbathing as a territorial scent-mark in the bannertail kangaroo rat, *Dipodomys spectabilis*. *Animal Behaviour* 35:426–434.
- RANDALL, J. A. 1991. Mating strategies of a nocturnal, desert rodent (*Dipodomys spectabilis*). *Behavioral Ecology and Sociobiology* 28:215–220.
- RANDALL, J. A. 2007. Environmental constraints and the evolution of sociality in semifossorial desert rodents. Pp. 369–379 in *Rodent societies: an ecological and evolutionary perspective* (J. O. Wolff and P. W. Sherman, eds.). University of Chicago Press, Chicago, Illinois.
- SANDERLIN, J. S., P. M. WASER, J. HINES, AND J. D. NICHOLS. 2011. On valuing patches: estimating contributions to metapopulation growth with reverse-time capture–recapture modeling. *Proceedings of the Royal Society London, B. Biological Sciences* 279:480–488.
- SAS INSTITUTE INC. 2008. SAS. Version 9.2. SAS Institute Inc., Cary, North Carolina.
- SCHRODER, G. D. 1979. Foraging behavior and home range utilization of the bannertail kangaroo rat (*Dipodomys spectabilis*). *Ecology* 60:657–665.
- SCHWAGMEYER, P. L. 1995. Searching today for tomorrow's mates. *Animal Behaviour* 50:759–767.
- SIKES, R. S., W. L. GANNON, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92:235–253.
- SMITH, A. T., AND B. L. IVINS. 1984. Spatial relationships and social organization in adult pikas: a facultatively monogamous mammal. *Zeitschrift für Tierpsychologie* 66:289–308.
- SMITH, C. C. 1968. The adaptive nature of social organization in the genus of tree squirrels, *Tamiasciurus*. *Ecological Monographs* 38:31–63.
- STEINWALD, M. C. 2004. Following the bannertail: a study of home range utilization and the mating system of *Dipodomys spectabilis* using spool-and-line tracking. M.S. thesis, Purdue University, West Lafayette, Indiana.
- STEINWALD, M. C., B. J. SWANSON, AND P. M. WASER. 2006. Effects of spool-and-line tracking on small mammals. *Southwestern Naturalist* 51:71–78.
- WASER, P. M., AND J. M. AYERS. 2003. Microhabitat use and population decline in banner-tailed kangaroo rats. *Journal of Mammalogy* 84:1031–1043.
- WASER, P. M., AND J. A. DEWOODY. 2006. Multiple paternity in a philopatric rodent: the interaction of competition and choice. *Behavioral Ecology* 17:971–978.
- WASER, P. M., A. PFEIFER, AND M. BERNING. 2012. Mechanisms of kin discrimination inferred from pedigrees and the spatial distribution of mates. *Molecular Ecology* 21:554–561.
- WATERMAN, J. 2007. Male mating strategies in rodents. Pp. 27–41 in *Rodent societies: an ecological and evolutionary perspective* (J. O. Wolff and P. W. Sherman, eds.). University of Chicago Press, Chicago, Illinois.
- WILSON, M., M. DALY, AND P. BEHREND. 1985. The estrous cycle of two species of kangaroo rats (*Dipodomys microps* and *D. merriami*). *Journal of Mammalogy* 66:726–732.
- WINTERS, J. B., AND P. M. WASER. 2003. Gene dispersal and outbreeding in a philopatric mammal. *Molecular Ecology* 12:2251–2259.
- ZGURSKI, J. M., AND D. S. HIK. 2012. Polygynandry and even-sexed dispersal in a population of collared pikas, *Ochotona collaris*. *Animal Behaviour* 83:1075–1082.

Submitted 20 May 2013. Accepted 22 July 2013.

Associate Editor was Loren D. Hayes.