

Do nocturnal rodents in the Great Basin Desert avoid moonlight?

NATHAN S. UPHAM* AND JOHN C. HAFNER

Committee on Evolutionary Biology, University of Chicago, Chicago, IL 60637, USA (NSU)

Department of Zoology, Field Museum of Natural History, Chicago, IL 60605, USA (NSU)

Moore Laboratory of Zoology and Department of Biology, Occidental College, Los Angeles, CA 90041, USA (NSU, JCH)
105 Franklin Avenue, Fortuna, CA 95540, USA (JCH)

* Correspondent: nsupham@uchicago.edu

Rodents make foraging decisions by balancing demands to acquire energy and mates with the need to avoid predators. To identify variations in the risk of predation, nocturnal rodents may use moonlight as a cue of risk. Moonlight avoidance behaviors have been observed in many nocturnal rodent species and are widely generalized to small mammals. However, most prior studies have been limited to 1 species or 1 study site, or occurred in modified habitats. We evaluated desert rodent activity patterns in natural habitats from 1999 to 2006 at 62 study sites across the Great Basin Desert of western North America. Rodent activity was examined by livetrapping in open habitats, using the presence of the sand-obligate kangaroo mouse (*Microdipodops*) as a habitat indicator. Activity patterns were assessed on 69 nights with clear skies and compared to corresponding moonlight values (moon phase and brightness) to evaluate the frequency of moonlight avoidance. Analyses of total activity of all species in the rodent assemblage relative to moonlight showed a distinct nonrandom (triangular-shaped) pattern but no significant correlations. However, individual genera of desert rodents responded differently to moonlight. Only kangaroo rats (*Dipodomys*) displayed significant moonlight avoidance patterns; they were maximally active at significantly different moonlight levels and avoided bright moonlight to a greater extent than co-occurring rodents. Moonlight seemed to limit the activity of kangaroo rats most strongly on bright nights during waxing moon phases and summer seasons, but not significantly during the spring or fall seasons, or during waning moons. Rather than avoiding moonlight, the activity of deer mice (*Peromyscus*), pocket mice (*Perognathus*), and kangaroo mice may be governed by changes in competition with kangaroo rats. Differences in the body size, locomotion, and space use of kangaroo rats relative to other rodents may explain why different moonlight responses were detected, especially if these traits alter how rodents perceive risk from bright moonlight. These findings indicate that moonlight avoidance may be a specialized trait of kangaroo rats rather than a general behavior of nocturnal desert rodents in the Great Basin.

Key words: *Dipodomys*, interspecific competition, lunar cycle, moonlight avoidance, predation risk, quantile regression

© 2012 American Society of Mammalogists

DOI: 10.1644/12-MAMM-A-076.1

Activity patterns are determined by the concomitant need to avoid predators while acquiring food and mates (Abrams 1993; McNamara and Houston 1987). Small mammals aim to avoid predators by limiting exposure to risky situations, and often reduce their activity or shift to safer habitats in response to perceptions of heightened risk (reviewed in Caro 2005). However, antipredator and foraging efforts must be balanced to meet the energetic demands of survival and reproduction (Brown and Kotler 2004; Rosenzweig 1974). This behavioral trade-off emphasizes the adaptive value for prey animals to identify situations of varying risk while also making decisions about when and where to forage (Caro 2005; Lima 1998; Lima and Dill 1990), yet the mechanisms by which prey species

accomplish such a trade-off are not fully understood (reviewed in Stankowich and Blumstein 2005). Small mammals are thought to assess the probability of encountering a predator and succumbing to a fatal attack (the risk of predation sensu Lima and Dill [1990]) by using indirect cues from the environment (Caro 2005; Orrock et al. 2004; Thorson et al. 1998).

For nocturnal rodents, moonlight has been widely investigated as a predation risk cue (Beier 2006; Caro 2005; Lima 1998; Lima and Dill 1990). Studies conducted in laboratory



settings and field enclosures find that several species of owls are more efficient at capturing rodents under simulated full moon conditions (Clarke 1983; Kotler et al. 1988; Longland and Price 1991). Owls may be better able to detect movement when prey shadows are cast against substrate (Kotler 1984b; Lockard and Owings 1974a), resulting in reduced search times as illumination increases (Clarke 1983). This evidence suggests that moonlight increases actual risk of predation from owls and other visual predators, such that rodents should be expected to perceive this risk and then alter their foraging patterns to reduce moonlight exposure on bright nights. This general hypothesis of moonlight avoidance has been tested in an array of nocturnal rodent species, but the greatest support is from studies of North American desert regions where sparsely vegetated habitats are regularly exposed to bright moonlight. These studies most commonly report moonlight behavior as including reduced rodent foraging and aboveground activity (Daly et al. 1992; Kotler 1984a; Lockard and Owings 1974a, 1974b) and shifts in activity from open spaces (i.e., open microhabitats) to areas of greater cover (i.e., bush microhabitats—Brown et al. 1988; Kotler 1984b; Longland and Price 1991; Price et al. 1984). Other responses to moonlight also are reported, although less commonly because radiotracking or direct observation methods are required. They include rodents foraging in shorter but more frequent bouts (Kramer and Birney 2001; Longland and Price 1991; Vásquez 1994), increased vigilance while foraging (Kotler et al. 2010; Vásquez 1994), and foraging closer to known refuges (Daly et al. 1992).

Evidence from rodents for the moonlight avoidance hypothesis is, however, limited in scope and associated with context-dependent caveats. Most previous studies of moonlight avoidance have measured activity at only a single field site (Bouskila 1995; Bowers 1988; Daly et al. 1992; Hughes et al. 1994; Kotler 1984a, 1984b; Kotler et al. 1991, 2010; Lockard and Owings 1974a; Longland and Price 1991; O'Farrell 1974; Price et al. 1984). Moonlight studies often focus on the response of 1 species, with Merriam's kangaroo rat (*Dipodomys merriami*) or other species of *Dipodomys* the most common targets of study in North American deserts, in part because of their high abundance. Except for one study that used successive nights of trapping at bait stations (Prugh and Brashares 2010), kangaroo rats have been found to significantly reduce their activity levels with moonlight, both as the focus of study (Bouskila 1995; Bowers 1988; Daly et al. 1992; Lockard 1978; Lockard and Owings 1974a, 1974b; Schwab 1966) and as members of a rodent assemblage when the activity patterns of multiple species are measured (Justice 1960; Kotler 1984b; O'Farrell 1974; Price et al. 1984). However, some studies found that species coexisting with kangaroo rats respond to moonlight in different ways (Justice 1960; Kotler 1984b; O'Farrell 1974). For instance, pocket mice (*Perognathus*) have been noted to increase their activity under illumination (Kotler 1984b). Desert rodents also may avoid moonlight only during certain seasons and be unaffected by changing moon phases at other times of the year (Bouskila 1995; Lockard 1978; Lockard and Owings 1974b; Meyer and

Valone 1999). Nevertheless, the general notion that all nocturnal rodents, regardless of species or season, may use moonlight as a cue of risk and avoid moonlight activity is a recurrent theme in studies of rodent foraging and antipredator behavior (reviewed in Brown and Kotler 2004; Caro 2005; Lima 1998).

The prevalence of moonlight avoidance behavior by rodents in nature is largely unknown, because of a variety of logistic and project-design challenges (e.g., comparing activity patterns across multiple species, sites, and seasons). However, this information is critical for testing the moonlight avoidance hypothesis. Conclusions about moonlight's importance for determining predation risk and rodent activity have been based on enclosure experiments in the field or laboratory (e.g., Brown et al. 1988; Clarke 1983; Wolfe and Summerlin 1989). These studies have shown that rodents are *capable* of avoiding moonlight in nature, yet the *actual* extent of moonlight avoidance in natural habitats is not well studied. Large-scale assemblage-wide studies conducted over multiple seasons are necessary if we are to determine whether more than a few well-studied species avoid moonlight, and whether moonlight biases trapping results for certain species more than others. Moreover, insights on the frequency of moonlight avoidance in the wild will advance the understanding of how predation risk structures foraging decisions (Brown and Kotler 2004; Meyer and Valone 1999), microhabitat partitioning (Brown and Lieberman 1973; Price 1978; Wondolleck 1978), and interspecific competition (Bowers and Brown 1982; Larsen 1986; Lemen and Freeman 1987).

Here we investigated the extent to which rodent species avoid moonlight in the Great Basin Desert of western North America. Using indicator species to identify similar habitat at multiple sites, we assessed the activity patterns of nocturnal rodents in relation to moonlight over multiple, successive years (Fig. 1). Rodent activity was analyzed in relation to ambient moonlight data to evaluate 2 moonlight avoidance hypotheses. First, if nocturnal rodents, on average, reduce their activity levels with increasing moonlight (e.g., Kotler 1984a), then an inverse relationship is expected between mean rodent activity and moonlight; this statistical interpretation expresses conventional thinking on the topic. Detecting a mean response to moonlight suggests that moonlight is a primary influence on activity. Second, if rodents only respond to moonlight after sufficient moon brightness is reached, then moonlight should set a "limit" or "ceiling" on maximum rodent activity rather than only influencing mean activity (Cade et al. 1999; Thomson et al. 1996). Statistically, this 2nd hypothesis does not assume a mean response and offers an alternative way of viewing moonlight avoidance that has not been considered previously. In this case, moonlight is a subordinate influence on activity relative to the primary influence of unmeasured factors (e.g., temperature, hunger, etc.). In both hypotheses, we focused the initial test on activity across all rodents to determine if nocturnal desert rodents generally avoid moonlight. If so, we expect to detect this pattern on an assemblage-wide basis. We then evaluated the activity of specific rodent

genera to determine if only some rodents avoid moonlight. We analyzed the activity patterns for the most common genera at our study sites: *Dipodomys* (kangaroo rats), *Peromyscus* (deer mice), *Perognathus* (pocket mice), and *Microdipodops* (kangaroo mice). We also compared kangaroo rat activity to the grouped activity of all other desert rodents. Kangaroo rats differ from most other rodents in their bipedal locomotion, large body size, and open-area foraging patterns, and are competitively dominant in many cases (Lemen and Freeman 1987; Price 1978; Reichman and Price 1993). If these traits influence how rodents perceive moonlight-associated risk, then other rodents that use predominantly quadrupedal locomotion and forage near bushes (Djawdan and Garland 1988; Eisenberg 1963) may differ from kangaroo rats in their response to moonlight. We also tested moonlight activity during different seasons and waxing versus waning lunar periods.

MATERIALS AND METHODS

Habitat choice.—We used the presence of kangaroo mice (*Microdipodops*) to identify sites with similar ecological characteristics across the Great Basin. Kangaroo mice have narrow ecological affinities for areas of sandy soil and widely spaced halophytic vegetation (Hafner 1981; Hafner et al. 1996; Hall 1941) so the use of this indicator taxon ensured that only open, sandy habitats were sampled. Any variation in rodent abundance (N) among sites was assumed to occur between seasons and stem primarily from seasonal reproduction rather than spatial heterogeneity in abundance. Given that both N and the probability of entering a trap (p) influence live-trap capture rates (Slade and Blair 2000), within-season comparisons with stable N were assumed to measure p and reliably assess rodent activity.

We performed all fieldwork originally for 2 studies of *Microdipodops* systematics (Hafner and Upham 2011; Hafner et al. 2008), from which we selected 78 nights of trapping when *Microdipodops* was present. Removing 9 nights of trapping where local cloud cover or precipitation was observed, and pooling sites less than 2 km apart, we were left with 69 nights of trapping with clear skies from 62 study sites (Fig. 1). No trapping occurred during nights of partial or total lunar eclipses. All study sites were within the Upper Sonoran Life Zone, at elevations ranging from 1,192 to 2,127 m. A variety of halophytic shrubs was present, including *Artemisia* (sagebrush), *Chrysothamnus* (rabbitbrush), *Atriplex* (saltbush), *Sarcobatus* (greasewood), *Tetradymia* (horsebrush), and *Oryzopsis* (ricegrass). Shrubs did not exceed 1 m in height and were generally 2–3 m apart, providing little cover from moonlight. Predators of rodents at these sites, including long-eared owls (*Asio otus*), coyotes (*Canis latrans*), kit foxes (*Vulpes macrotis*), long-tailed weasels (*Mustela frenata*), and badgers (*Taxidea taxus*), rely on vision to hunt. Heat-sensing Great Basin rattlesnakes (*Crotalus viridis lutosus*) are not noted to frequent sandy habitats (Klauber 1982), and rarely venture into sandy habitats associated with *Microdipodops* (Pierce et al. 1992).

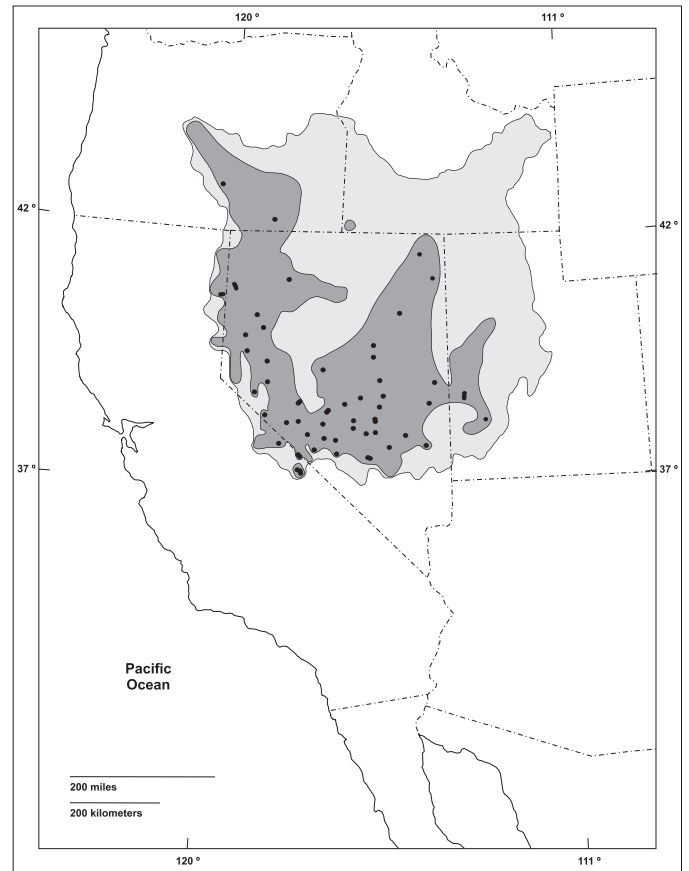


FIG. 1.—Distribution of 62 study sites (black dots) in the Great Basin Desert of western North America (light gray) where nocturnal desert rodents were sampled between September 1999 and September 2006 to examine the prevalence of moonlight avoidance. Sand-obligate kangaroo mice (*Microdipodops*; distribution in dark gray) were utilized as a habitat-indicator taxon for this study: their presence at a site allowed for specific open habitats to be identified across the region. The Great Basin outline and distribution of *Microdipodops* are modified from Cronquist et al. (1972) and Hafner et al. (2008), respectively.

Sampling of rodent activity.—We trapped from September 1999 to September 2006 during the March–October interval each year (range of 24 March–30 October), thereby excluding the winter months when *Microdipodops*, *Perognathus*, and *Chaetodipus* are inactive or less active (Kenagy 1973). Fieldwork was scheduled without bias for moon phase, moon position in the sky, or season. Each night we set ~150 (range 50–400) Sherman folding aluminum live traps (8 × 9 × 23 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida) per site in lines of 50 or 100 traps running through the most uniform areas of open and sandy habitat. We set traps baited with rolled oats for bait about 1 h before sunset and checked them within 1 h after sunrise. Pairs of traps were placed at about 9-m (10-pace) intervals, with traps of a pair 2–3 m apart, and at least 1 m away from the nearest shrub. All traps were thus placed in “open microhabitats” (Price 1978; Price et al. 1984; Thompson 1982). The resulting open-area activity patterns recorded overall changes in aboveground activity level across the

nighttime period. Captured animals were identified to species and released at the site of capture, excepting those retained for the aforementioned systematic studies. All animals were treated in accord with guidelines of the American Society of Mammalogists (Sikes et al. 2011) and Occidental College's Institutional Animal Care and Use Committee.

Rodent activity variables.—We calculated rodent activity each night as the live-trap capture rate (number of captures divided by number of traps set that night). We determined total rodent activity across the assemblage and the activity of each genus.

Moonlight variables.—We obtained local moon phase and position for all trapping nights using MICA 2.0 computer software (United States Naval Observatory 2005). The dates of trapping, latitude and longitude, and elevation were entered for each site, and the program provided information on moonlight conditions for that night. We defined the nighttime period here as spanning from “end civil twilight” (postsunset, sun is 6° below horizon) to “begin civil twilight” (presunrise, sun is 6° below horizon). During this period the atmosphere should have been sufficiently free of solar illumination to allow for moonlight, if present, to be experienced in surface habitats (Janiczek and DeYoung 1987).

We calculated 2 moonlight variables to describe mean moonlight intensity on each trapping night: moon fraction illuminated, and moon lux. Moon fraction illuminated describes the moon's phase during the course of each night on a continuous scale of 0 (new moon) to 1.0 (full moon), and was calculated as the mean value of data generated at 15-min intervals during night-moon hours (i.e., night hours with the moon above the horizon). The 2nd moonlight variable, moon lux, provides information on the moon's illuminance (E_v), or amount of visible moonlight reaching surface habitats, as measured in lux (lx, lumens per meter squared). Moon lux was calculated for each night of trapping from the following illuminance equation: $E_v = [I_0 0.5(1 - \cos(\theta))(R_0/R)^2] \sin(\rho)$, where I_0 is a constant equal to 0.215 lx (illuminance of zenith full moon at the mean earth–moon distance), and R_0 is a constant equal to the mean earth–moon distance of 384,400 km (Austin et al. 1976). The moon's elongation θ (angle between the sun and moon as viewed from earth, in radians), the earth–moon distance R (in km), and the moon's altitude ρ (angle between the moon and horizon, in radians) were entered into the illuminance equation as mean values from 15-min intervals during night-moon hours. On nights near the new moon when the moon did not rise (altitude $< 0^\circ$), a value of zero was entered for moon lux. Calculating moon lux enabled changing moon altitude between seasons to be examined in relation to rodent activity (e.g., in the central Great Basin during fall, full moons pass about 40° higher above the horizon and are nearly 3 times brighter than full moons during summer).

Statistical analyses.—We initially used the G -test for goodness of fit to inspect the distribution of total rodent activity with respect to moonlight for adherence to a random model. Three other statistical approaches were then employed to test our main hypotheses. First, we performed linear

regression analyses to examine the mean responses of activity and moonlight variables. All linear analyses were performed using SYSTAT computer software (version 9—Wilkinson 1998) and the R computer programming language (R Development Core Team 2012). Because most variables showed significant nonnormal distributions (Kolmogorov–Smirnov test with Lilliefors modification), nonparametric statistics were used throughout the study. Functional relationships were examined between pairs of variables using Quenouille's (1952) ordering test, as executed by the methodologically equivalent Kendall's coefficient of rank correlation, tau (Sokal and Rohlf 1995). We determined regression equations for significant functional trends using Kendall's robust line-fit method (Kendall and Gibbons 1990). No more than 4 comparisons were ever included in a single statistical experiment; thus, experimentwise type I error rates were not substantially affected (Chandler 1995). We considered all test statistics biologically significant with 0.05 α -levels, but also noted the conservative Bonferroni correction of $P' = 0.0125$ where appropriate ($P' = 0.05/k$ and $k = 4$ comparisons). Throughout the linear analyses, we used 1-tailed tests that specified the presence of inverse functional relations (i.e., moonlight avoidance) as alternative hypotheses to the null (i.e., no response to moonlight).

Following linear regression, our 2nd approach used circular–linear statistics to evaluate rodent activity in relation to the lunar cycle. We converted each night's moon fraction illuminated into angular estimations of moon phase corresponding to values clockwise around a 360° lunar cycle. The resulting circular variable, termed circular moon phase, used its angular value to differentiate between waxing and waning moon phases, thereby facilitating new comparisons with rodent activity (in contrast, 0.5 moon fraction illuminated may represent waxing 1st-quarter or waning 3rd quarter moons). Circular–linear correlation coefficients (r) were calculated using Oriana software (Kovach 2011) and ranged in value between 0 and 1 (negative correlations were not possible). Evaluating linear activity relative to circular moon phase provided an independent test from simply grouping nights of trapping by waxing or waning moons (Zar 1999).

To contrast the linear and circular models, we also used quantile regression models to investigate if moonlight was related to the upper limits of rodent activity rather than the mean or central tendency. The theory of ecological limiting factors (Cade et al. 1999; Thomson et al. 1996) observes that ecological data are rarely linear and bivariate scatterplots with “triangular” point distributions still contain biologically relevant information at the distributional edges, where changes in the maximum response (y) to a measured habitat factor (x) are often reflected. Quantile regression techniques (Cade and Noon 2003; Koenker 2005) allowed us to model relationships between response variables (rodent activity) and habitat variables (moonlight) from the center (mean) to near the extreme distributional edges. Relationships near the extremes were consistent with limiting factor ceilings for the response variable. Two quantile regression approaches were used; in

each, only comparisons with >50 observations (nights of trapping) were evaluated to ensure reliable parameter estimates.

Models were first built for all quantiles (τ) between 0 and 1 (i.e., 0–100th percentiles) for which finite parameter estimates could be obtained. The model $\ln y = \beta_0 + \beta_1 x + \varepsilon$ was fitted to each quantile using the function “rq()” (part of the “quantreg” package) in R. We chose this model because the nonlinear log-transformation provides stable parameter estimates at high quantiles, and can be back-transformed onto a linear scale for plotting purposes (see Cade et al. 1999). Prior to log-transformation, we added an arbitrary small positive constant (10^{-5}) to any variables that contained zero values (Machado and Santos Silva 2005). The proportion of zeros in a given variable acted as a guideline for determining the lowest reliable quantile estimate (e.g., 20% zeros corresponded to $\tau = 0.20$). For each estimated slope, we calculated a confidence interval (CI) by using default bandwidth weighting (local by quantile) and inverting the quantile rank-score test (Cade and Noon 2003; Cade et al. 1999). The CIs were then used to test the null hypothesis that the estimated slope was not different from zero. Probability values for hypothesis tests were obtained by iteratively adjusting CIs until they excluded zero.

Quantile regression splines at the 95th percentile ($\tau = 0.95$) also were used to model responses to moonlight near the activity maximum (i.e., moonlight optimum) for 4 rodent genera, and compare responses between kangaroo rats and other rodents (Anderson 2008; Koenker 2005). The 95th percentile provides information on maximum responses near the distributional edges without skew toward single outlying values (Anderson 2008). All models were fitted to data using the rq() function along with the function “bs()” (part of the “splines” package in R). We used Akaike’s information criterion corrected for small sample size (AIC_c —Burnham and Anderson 2002) to identify the polynomial degrees of the best-fit (lowest AIC_c) spline models. For each model, we considered the moonlight value at which the model-predicted rodent activity response reached a maximum as the estimated moonlight optimum. We then evaluated the reliability of estimated moonlight optima using bootstrap resampling: 95% CIs were calculated from model reapplication to each of 10,000 bias-corrected bootstrap samples of the original data (using the original polynomial degree). The “sample()” function in R was used to form bootstrap sets (sampling with replacement). We evaluated differences in the moonlight optima of kangaroo rats versus other rodents by comparing 95% bootstrap CIs in the following way: order the bootstrap samples; take “other rodents” minus “kangaroo rats” to obtain the difference in bootstrapped samples (= delta); correct delta for bias; and calculate a 95% bootstrap CI for delta. R scripts for regression spline analyses were provided by M. Anderson (Anderson 2008) and adapted for this study.

Design of comparisons.—We evaluated patterns of moonlight avoidance 1st overall ($n = 69$), and then separately during waxing moon phases ($n = 44$), waning moon phases ($n = 25$), and during seasonal periods corresponding with spring ($n = 21$), summer ($n = 22$), and fall ($n = 26$). Data were

examined according to season by trisecting the actual sampling period into the spring (24 March–5 June), summer (6 June–18 August), and fall (19 August–30 October). Rodents may respond to moonlight differently during these periods (e.g., Alkon and Saltz 1988; Lockard and Owings 1974b), and seasons are expected to differ in terms of the amount and type of food available (Rosenzweig 1974), as well as the timing of behaviors such as reproduction and torpor (Burt et al. 1998; O’Farrell 1974).

RESULTS

Sampling of rodent activity.—Livetrapping activities yielded a total of 10,758 trap-nights and 2,433 animals for analysis (mean trap success 22.6%). Nights of trapping occurred throughout the lunar cycle, with moon fraction illuminated ranging from 0.000 to 0.995 ($\bar{X} = 0.397$). We captured 20 species of nocturnal desert rodents (mean species richness 4.9, range 1–10): 652 deer mice (*Peromyscus maniculatus*), 480 Merriam’s kangaroo rats (*Dipodomys merriami*), 360 little pocket mice (*Perognathus longimembris*), 236 Ord’s kangaroo rats (*Dipodomys ordii*), 177 dark kangaroo mice (*Microdipodops megacephalus*), 131 pallid kangaroo mice (*Microdipodops pallidus*), 111 chisel-toothed kangaroo rats (*Dipodomys microps*), 70 piñon mice (*Peromyscus truei*), 60 Great Basin pocket mice (*Perognathus parvus*), 56 northern grasshopper mice (*Onychomys leucogaster*), 50 desert kangaroo rats (*Dipodomys deserti*), 14 Panamint kangaroo rats (*Dipodomys panamintinus*), 11 western harvest mice (*Reithrodontomys megalotis*), 11 southern grasshopper mice (*Onychomys torridus*), 8 desert woodrats (*Neotoma lepida*), 2 long-tailed pocket mice (*Chaetodipus formosus*), 1 long-tailed vole (*Microtus longicaudus*), 1 montane vole (*Microtus montanus*), 1 sagebrush vole (*Lemmiscus curtatus*), and 1 house mouse (*Mus musculus*). Sampling generally identified a core assemblage of either *P. maniculatus* or *P. longimembris*, and 1 or more kangaroo rat species (most often *D. merriami* and *D. ordii*). The most frequently captured genera were *Dipodomys* (891 captures), *Peromyscus* (722), *Perognathus* (420), and *Microdipodops* (308). Kangaroo rats had much larger body sizes than other desert rodents sampled (35–147 g versus 7–40 g for other rodents, excepting a few large voles and woodrats; masses from Burt et al. [1998]).

Mean trapping and activity statistics were summarized for the overall, waxing, waning, and seasonal periods (Table 1). Mean activity differed between the 3 seasonal periods both for kangaroo rats (Kruskal–Wallis test, $H_2 = 6.812$, $P = 0.033$), and the group of all other rodents (Kruskal–Wallis test, $H_2 = 6.100$, $P = 0.047$), with main differences between fall and spring periods for kangaroo rats (Mann–Whitney $U = 156.0$, $n = 47$, $P = 0.012$), and summer and fall periods for other rodents (Mann–Whitney $U = 404.5$, $n = 48$, $P = 0.014$). Mean sampling effort inadvertently varied significantly between lunar periods (Mann–Whitney $U = 372.0$, $n = 69$, $P = 0.026$), with more trap-nights under waning moonlight. However, all rodent activity variables were independent of sampling effort on given

TABLE 1.—Mean values for trapping statistics and rodent activity measures overall, as well as during designated lunar and seasonal periods ($n = 69$ total nights of trapping), from 62 sites in the Great Basin Desert, trapped from September 1999 to September 2006. Boldface type notes significant differences among means within comparison groups (Mann–Whitney U -tests and Kruskal–Wallis tests).

Category	Overall ($n = 69$)	Waxing ($n = 44$)	Waning ($n = 25$)	Spring ($n = 21$)	Summer ($n = 22$)	Fall ($n = 26$)
No. animals	35.3	28.7	46.9	31.9	39.4	34.5
No. trap-nights	155.9	132.0	198.0	161.8	164.1	144.2
Total rodent activity	0.226	0.226	0.218	0.192	0.251	0.225
<i>Dipodomys</i> activity	0.083	0.090	0.079	0.053	0.069	0.127
All other rodent activity	0.143	0.136	0.139	0.139	0.182	0.098
<i>Peromyscus</i> activity	0.067	0.063	0.063	0.057	0.097	0.039
<i>Perognathus</i> activity	0.039	0.033	0.042	0.045	0.037	0.029
<i>Microdipodops</i> activity	0.029	0.033	0.027	0.028	0.042	0.023

nights ($P > 0.05$). Mean *Microdipodops* activity differed between waxing and waning periods (Mann–Whitney $U = 375.0$, $n = 69$, $P = 0.029$). Kangaroo rat activity was inversely related with *Peromyscus* activity (Kendall's tau = -0.173 , $P = 0.0261$) and with the activity of all other rodents as a group (Kendall's tau = -0.168 , $P = 0.0236$), but not significantly so with other genera (*Perognathus*: Kendall's tau = -0.0595 , $P = 0.252$; *Microdipodops*: Kendall's tau = -0.0106 , $P = 0.454$).

Moonlight on the desert rodent assemblage.—The distribution plot of total rodent activity and moon lux shows a distinct triangular pattern that represents a highly nonrandom distribution (Fig. 2a; gray triangle; $G = 54.88$; $P < 0.001$). Total rodent activity was not inversely related with either moon lux (Kendall's tau = -0.089 , $P = 0.145$) or moon fraction illuminated (Kendall's tau = -0.045 , $P = 0.298$). Circular moon phase and total rodent activity also were uncorrelated ($r = 0.06$, $P = 0.787$). Quantile regression modeling subsequently tested if moonlight influenced rodent activity at other areas of the response distribution ($0.15 < \tau < 0.90$) than the mean. One marginally significant relationship between total rodent activity and moon lux at the $\tau = 0.51$ regression quantile (Fig. 2a; Table 2), along with no relationships with moon fraction illuminated ($0.10 < \tau < 0.90$; $P > 0.05$), suggested that moonlight neither limited the maximum response nor controlled mean activity across the rodent assemblage. No relationships were detected during waxing, waning, or seasonal moons ($P > 0.05$).

Moonlight on desert rodent genera and groups.—Division of the rodent assemblage into genera uncovered significant inverse relationships between *Dipodomys* activity and both of the moonlight variables (Fig. 2b; moon lux: Kendall's tau = -0.177 , $P = 0.018$; moon fraction illuminated: Kendall's tau = -0.139 , $P = 0.050$), although neither was robust under the Bonferroni criterion ($P' < 0.0125$). Quantile regression modeling of *Dipodomys* activity ($0.20 < \tau < 0.90$) also yielded significant regression slopes from $0.55 < \tau < 0.78$ in relation to moon lux (Fig. 2b; Table 2), and from $0.57 < \tau < 0.78$ in relation to moon fraction illuminated (Table 2). In contrast, the activity of rodents other than kangaroo rats, when analyzed as a group, yielded no mean relationships or relationships across regression quantiles with either moon lux (Fig. 2c; $0.15 < \tau < 0.90$; $P > 0.05$) or moon fraction illuminated ($0.10 < \tau < 0.90$; $P > 0.05$). Disaggregating these other rodents into genera found that *Peromyscus*, *Perognathus*,

and *Microdipodops* activity were unrelated to both moonlight variables using the linear model ($P > 0.05$) and the quantile regression model (Figs. 2d–2f; $0.51 < \tau < 0.90$, $0.53 < \tau < 0.90$, and $0.15 < \tau < 0.90$; $P > 0.05$).

Circular–linear analyses yielded significant correlations relative to moon phase for both *Dipodomys* activity ($r = 0.255$, $P = 0.013$) and *Microdipodops* activity ($r = 0.327$, $P < 0.001$), but not for *Peromyscus*, *Perognathus*, or all other rodents as a group ($P > 0.05$). Plots of circular moon phase (Fig. 3) revealed inverse activity patterns among *Dipodomys* and *Microdipodops*, with *Dipodomys* activity mainly decreasing then increasing slightly from new to full to new moon (Fig. 3a) and *Microdipodops* activity increasing then decreasing across the same lunar period (Fig. 3b). These correlations reflected waxing and waning dynamics of the lunar cycle, but were corroborated only by linear relations of *Dipodomys* strongly avoiding waxing moonlight (moon lux: Kendall's tau = -0.258 , $P = 0.008$; moon fraction illuminated: Kendall's tau = -0.221 , $P = 0.021$). *Dipodomys* did not avoid waning moonlight ($P > 0.05$), and *Microdipodops* avoided neither waxing nor waning moonlight ($P > 0.05$).

The summer seasonal period also witnessed a significant correlation between circular moon phase and *Dipodomys* activity ($r = 0.474$, $P = 0.013$) and a near-significant correlation with *Microdipodops* activity ($r = 0.385$, $P = 0.059$). Only the *Dipodomys* correlation was corroborated by significant inverse relationships with both moon lux (Kendall's tau = -0.283 , $P = 0.037$) and moon fraction illuminated (Kendall's tau = -0.263 , $P = 0.050$), although these relationships were not robust after conservative Bonferroni adjustment ($P' < 0.0125$). *Microdipodops* activity was unrelated to either linear moon variable during any season ($P > 0.05$). *Peromyscus* and *Perognathus* activity were not examined by lunar and seasonal periods because these 2 genera had considerably more nights of zero captures overall (30 and 23, respectively) than did *Dipodomys* and *Microdipodops* (8 and 0, respectively).

Ninety-fifth percentile regression spline modeling also found contrasting patterns among kangaroo rats and other rodents in their estimated moonlight optima (Fig. 4). *Dipodomys* activity was characterized by a moon lux optimum at 0.0268 lx (Fig. 4a; 95% CI: -0.0161 – 0.1135 lx, polynomial: 2nd degree), whereas the group of all other rodents displayed a considerably

higher moon lux optimum at 0.0803 lx (Fig. 4b; 95% CI: 0.0242–0.1539 lx, polynomial: 3rd degree). *Perognathus* activity showed a lower optimum of 0.0176 lx (Fig. 4b; 95% CI: –0.0409–0.0887, polynomial: 4th degree), but both *Peromyscus* and *Microdipodops* activity showed similar results to the group of all other rodents, with high optima of 0.0788 lx (95% CI: 0.0035–0.1331, polynomial: 5th degree) and 0.0829 lx (95% CI: 0.0301–0.1339, polynomial: 3rd degree), respectively. Likewise with moon fraction illuminated, *Dipodomys* activity displayed an optimum value at 0.2736 (Fig. 4d; 95% CI: –0.0617–0.9332, polynomial: 5th degree) compared to a substantially higher optimum value of 0.8421 for all other rodents (Fig. 4e; 95% CI: 0.1580–1.0748, polynomial: 4th degree) led by *Peromyscus* and *Microdipodops* with optima of 0.8739 and 0.9949, respectively (95% CI: 0.1632–1.0944, polynomial: 4th degree; and 95% CI: 0.4804–1.0967, polynomial: 2nd degree). *Perognathus* activity again showed a lower optimum value of 0.3781 (95% CI: –0.1803–0.8146, polynomial: 5th degree). When the results from kangaroo rats and all other rodents were compared, 95% CIs on the difference in bootstrapped optima were found to not include zero for either moon lux (Fig. 4c; \bar{X} = 0.0535; 95% CI: 0.0005–0.0932) or moon fraction illuminated (Fig. 4f; \bar{X} = 0.5685; 95% CI: 0.1416–0.8629). Thus, the null hypothesis that all desert rodents have equal moonlight optima was rejected at the 0.05 confidence level. Overall, kangaroo rats displayed a preference for greatest activity at significantly different moonlight levels (less bright, smaller moon fraction illuminated) than did all other rodents.

DISCUSSION

The distinct, triangular-shaped pattern of the distribution plot of total rodent activity and moonlight was a striking and unanticipated finding (Fig. 2a). Such triangular- or wedge-shaped patterns, however, appear somewhat commonly in ecological studies and are interpreted as evidence that the habitat variable (x) imposes an upper limit on the response variable (y) rather than controlling its central tendency. The pattern may stem from unmeasured (and perhaps unknown) habitat factors influencing the response variable (e.g., Cade et al. 1999; Thomson et al. 1996). In this study, total rodent activity appeared to decrease with increased lunar illumination, forming a right triangle. However, quantile regression analyses revealed no significant trends except when the analysis was pared to include only *Dipodomys* activity against moonlight. It appears that kangaroo rats were mainly responsible for the triangular-shaped pattern seen in the plot of total rodent activity and moonlight.

Across desert rodents in the Great Basin, moonlight avoidance was the exception rather than the rule. Only *Dipodomys* displayed significant patterns of moonlight avoidance, whereas other genera, including *Peromyscus*, *Perognathus*, and *Microdipodops*, did not. Moonlight also did not exert an especially powerful influence on kangaroo rat activity. Kangaroo rats essentially halved their activity across the low to

high range of moonlight to produce significant mean relations (Fig. 2b), but relationships with both moon lux and moon fraction illuminated were weakly inverse. Kangaroo rats displayed considerable “noise” in their activity levels on similarly moonlit nights—rather than perceiving a consistent risk cue and responding to moonlight with a steady change in mean activity, kangaroo rats appeared to perceive moonlight as a subordinate influence. We found that kangaroo rats were restricted most on brightly moonlit nights and varied their activity on other nights, such that activity and moonlight were most strongly related at regression quantiles between 0.65 and 0.75 (Fig. 2b; Table 2). These higher quantiles characterize kangaroo rats’ maximum response to moonlight, because models at quantiles greater than 0.90 were unestimatable (confidence intervals extended to infinity). This result indicates that moonlight acts as a limiting factor rather than the main determinant of kangaroo rat activity. Factors not assessed in this study such as ambient temperature, rodent energetic state, and the presence of predators or competitors may provide more powerful influences on rodent activity than lunar illumination (Kotler et al. 2010; Orrock and Danielson 2004, 2009).

Waxing moonlight and summer moonlight appear to influence kangaroo rat activity most strongly, with inverse relationships found during these periods, but not during waning moons or spring and fall seasons. Other studies also found kangaroo rat species to avoid moonlight seasonally, but seasonal responses were fall-only (Bouskila 1995; Meyer and Valone 1999) and winter-only (Lockard 1978; Lockard and Owings 1974b). Summer-only moonlight responses by kangaroo rats also were documented, but in studies restricted to summer sampling (Brown et al. 1988; Kaufman and Kaufman 1982; Kotler 1984a, 1984b). The summer-only avoidance patterns observed in our study might correspond with shifts in the costs or benefits of moonlight activity each season, especially if summer represents the period of lowest profits from reproductive activities (following spring parturitions) and highest resource availability (following spring blooms [Rose-nzweig 1974]). Avoidance of waxing rather than waning moonlight may similarly result from higher perceived predation risk, because waxing moons (the increasing phases from new to full moon) are most prominent during the 1st few hours of the night when nearly all desert rodent species display an activity peak (Hafner 1975; O’Farrell 1974). Waning moons, on the other hand, rise several hours after sunset and remain in the sky during daylight before setting. The waxing moon is also about 20% brighter than corresponding waning phases, presumably from the patches of low-albedo maria on the moon’s surface (Austin et al. 1976; Krisciunas and Schaefer 1991). Reports of avoidance of waxing moonlight in gerbills (*Gerbillus andersoni allenbyi*—Kotler et al. 2010) and Indian crested porcupines (*Hystrix indica*—Alkon and Saltz 1988) agree with our observations and suggest that this response may be common in other rodent groups. Kangaroo rats in the present study may realistically perceive moonlight as riskier during waxing and summer periods than during other times.

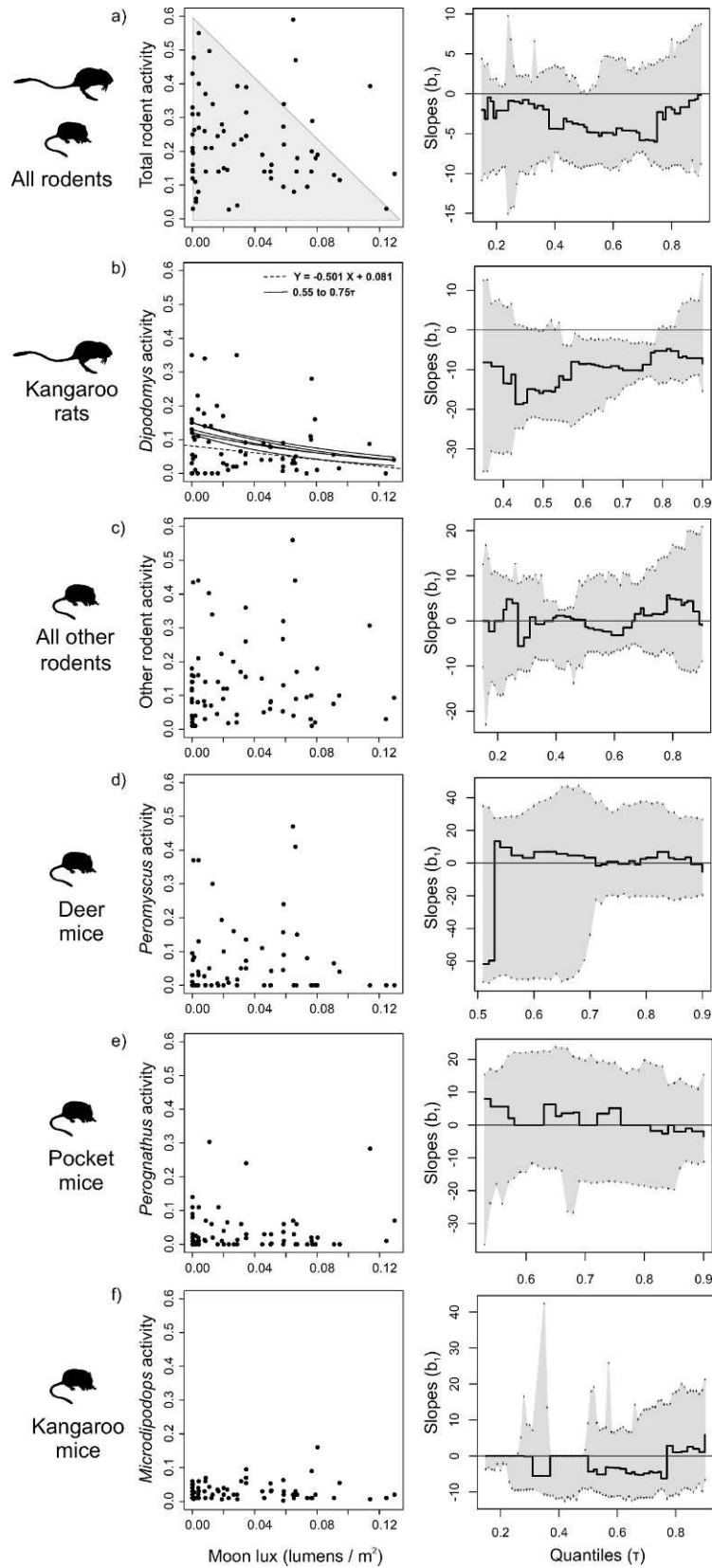


FIG. 2.—Activity patterns of desert rodents (from capture rates) in relation to moon lux, based on 69 nights of trapping at 62 sites in the Great Basin Desert, 1999–2006. a) Total rodent activity was unrelated to moon lux and all other moonlight variables ($P > 0.05$); however, the gray triangle highlights the nonrandom distribution of points. b) Only kangaroo rats displayed significant moonlight avoidance patterns, using both the linear model (dotted line; Kendall's tau = -0.177 , $P = 0.032$) and quantile regression models from $0.55 < \tau < 0.78$ (solid lines every 5th quantile);

Differences in activity patterns between kangaroo rats and coexisting rodents suggest that competitive interactions may be involved. The inverted activity patterns of *Microdipodops* and *Dipodomys* relative to circular moon phase (Fig. 3) suggest that kangaroo mice may increase their activity on certain nights in response to moonlight-avoiding kangaroo rats. Decreases in kangaroo rat activity as the moon waxed coincided with increased kangaroo mouse activity, followed by wavelike trends of increasing and decreasing activity, respectively, after the full moon. Because kangaroo mouse activity was not accompanied by positive linear relationships with moonlight, kangaroo mice may be responding mainly to kangaroo rat foraging competition (and release from this competition) rather than moonlight. *Peromyscus* increased its activity on many of the same nights avoided by kangaroo rats, but *Peromyscus* activity also was not related to moonlight. It is unlikely that the inverse activity of *Dipodomys* with both *Microdipodops* and *Peromyscus* stems from changes in moonlight. Rather, these patterns may result from the well-studied foraging dominance of kangaroo rats over smaller coexisting rodents (reviewed in Reichman and Price 1993).

Kangaroo rats, with their larger bodies, are dominant in competitive interactions with other rodents (Lemen and Freeman 1987; Trombulak and Kenagy 1980), so reduced competition from kangaroo rats during bright moonlit nights may present a stronger influence than moonlight for coexisting rodents. If this is the case, bright moonlight is similar to experimentally removing kangaroo rats, an influence that has been shown to stimulate significantly more open-area foraging by smaller quadrupeds (Wondolleck 1978). Two other studies have captured *P. longimembris* relatively more frequently in open areas under bright moonlight while observing the opposite pattern for kangaroo rats (Kotler 1984b; Price et al. 1984), suggesting that their habitat selection was inversely coupled. O’Farrell (1974:821) observed that “larger, more conspicuous species” avoided moonlight more frequently than “small, cryptic species,” an observation that corresponds to 4 species of *Dipodomys* versus the smaller rodent genera *Peromyscus*, *Perognathus*, *Microdipodops*, and *Onychomys*. Other field studies reported moonlight avoidance by both kangaroo rats and other rodents, but also found species of *Perognathus*, *Microdipodops*, and *Peromyscus* to respond inconsistently to illumination (Brown et al. 1988; Kotler 1984b; Longland and Price 1991). Previous studies detected that *Peromyscus* was inhibited by artificial light equivalent to half the full moon’s intensity (Blair 1943; Clarke 1983; Falkenberg and Clarke 1998), and foraged less under bright moonlight in outdoor settings (Orrock et al. 2004; Wolfe and Summerlin 1989). Our findings instead agree with other reports of lack of a response by *Peromyscus* to moonlight (Kotler

TABLE 2.—Estimates of parameters for significant quantile regression models in Fig. 2 and in the text, including quantile (τ), intercept (b_0), and slope (b_1) for the model $\ln y = \beta_0 + \beta_1 x + \varepsilon$, where y is rodent activity and x is moonlight. Negative relationships at higher quantiles indicate the influence of moonlight as a limiting factor on rodent activity.

τ	b_0	b_1	95% CI of β_1	P^a
Moon lux				
Total rodent activity				
0.51	-1.392	-4.806	-9.096 to -0.110	0.042
<i>Dipodomys</i> activity				
0.75	-1.896	-8.732	-12.529 to -3.099	0.010
0.70	-1.897	-10.192	-14.903 to -2.734	0.004
0.65	-2.040	-9.468	-20.562 to -2.655	0.004
0.60	-2.119	-8.605	-21.924 to -2.416	0.005
0.55	-2.156	-12.577	-23.099 to -3.757	0.028
0.50	-2.217	-15.387	-22.650 to -0.099	0.044
Moon fraction illuminated				
<i>Dipodomys</i> activity				
0.75	-1.897	-0.707	-1.320 to -0.221	0.010
0.70	-1.897	-0.913	-1.295 to -0.236	0.002
0.65	-2.040	-0.777	-1.389 to -0.249	0.003
0.60	-2.099	-1.037	-1.759 to -0.206	0.010

^a Rank-score tests yield P -values for the null hypothesis that: $\beta_1 = 0$.

1984b; Orr 1959). The absence of significant moonlight avoidance by species other than kangaroo rats is not, however, evidence that these rodents do not avoid moonlight; rather, it is an indication that these behaviors may be less widespread than previously assumed.

Analyses of moonlight optima showed significant differences between kangaroo rats and the group of all other rodents. All other rodents were most active under much brighter moonlight conditions than were kangaroo rats; this group preferred near-full gibbous moons (brightness: 0.0803 lx, fraction illuminated: 0.8421; Figs. 4b and 4e), whereas kangaroo rats were most active under young crescent moons (brightness: 0.0268 lx, fraction illuminated: 0.2736; Figs. 4a and 4d). *Microdipodops* and *Peromyscus* activity showed the highest moonlight optima, but the lower *Perognathus* optima were not significantly different from those of the group of all other rodents (Figs. 4b and 4e). Analyses of moonlight optima were consistent with our other findings and reinforce the perspective that kangaroo rats are the only member of the desert rodent assemblage to display moonlight avoidance.

We propose 2 hypotheses to explain why moonlight avoidance was observed only in kangaroo rats. First, kangaroo rats may be more efficient foragers than other desert rodents, gathering more seeds and accumulating larger seed reserves in shorter time, such that they have the luxury of waiting for less

←

see Table 2 for model parameters). These relationships suggest that moonlight limits the maximum activity of kangaroo rats. In contrast, no significant model relationships were displayed across quantiles among c) all other rodents grouped together, d) deer mice, e) pocket mice, or f) kangaroo mice. Slope estimates $b_1(\tau)$ for the quantile regression models (black step function) are significant when their 95% CIs exclude zero (gray cloud with black endpoints).

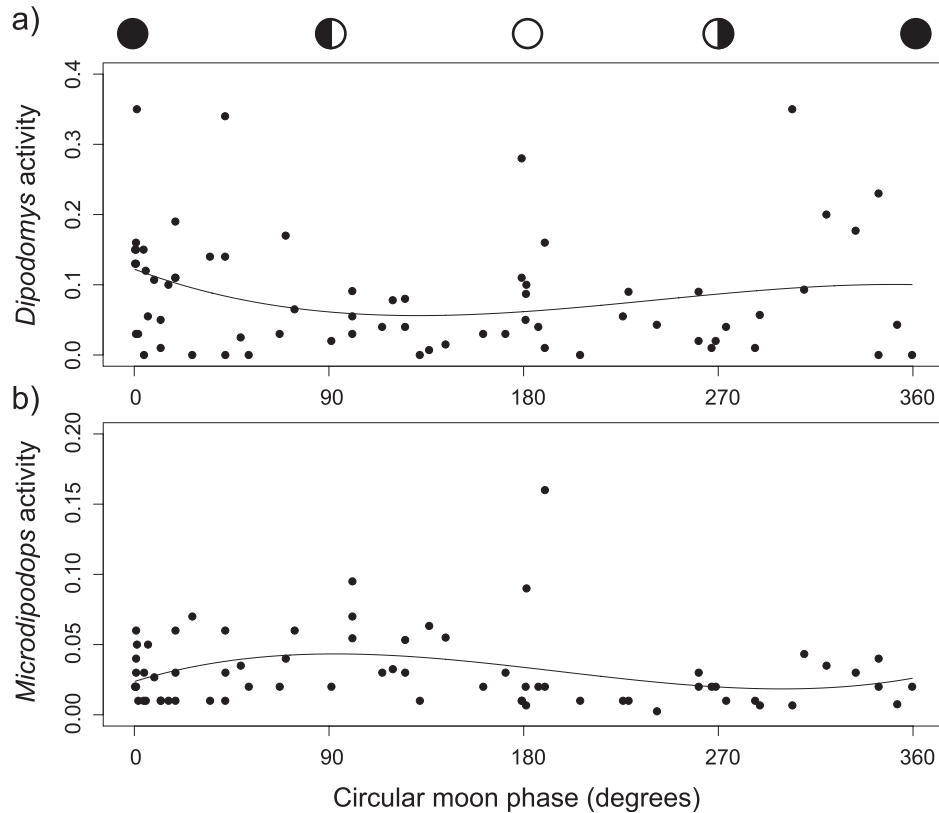


FIG. 3.—Circular-linear analyses of rodent activity relative to circular moon phase, based on 69 nights of trapping at 62 sites in the Great Basin Desert, 1999–2006. Significant correlations were detected for a) *Dipodomys* activity ($r = 0.255$, $P = 0.013$) and b) *Microdipodops* activity ($r = 0.327$, $P < 0.001$). B-spline trend lines (3rd-degree polynomials) were placed through the distribution means to indicate the inverted wavelike trends of activity for *Dipodomys* and *Microdipodops* throughout the lunar cycle. New moons are noted at 0° and 360°, the full moon at 180°, and waxing and waning half moons at 90° and 270°.

bright and presumably less dangerous nights to forage in open areas. Quadrupedal locomotion may require other rodent species to forage in moonlight to meet energetic demands. Kangaroo rats, with their high mobility, are able to gather dispersed seed clumps, whereas many quadrupedal species, being less mobile, seem to forage near shrubs on more evenly distributed seed resources (Thompson 1982). However, quadrupeds are not necessarily less competent foragers than bipeds. Kangaroo rats in laboratory settings tend to accumulate larger seed reserves than quadrupedal species, but not in greater proportion than expected by differences in body mass and metabolic requirements (Jenkins and Breck 1998; Price et al. 2000). Extreme examples of foraging efficiency are known from kangaroo rats in the Sonoran Desert (Lockard and Owings 1974b), but relatively little is known about the quantity of seeds cached by different rodent species from the Great Basin Desert (see Reichman and Price 1993). Higher metabolic costs in small rodents may affect how activity covaries with temperature and moonlight in different species (Orrock and Danielson 2009), but the dearth of detailed information on the actual energetic state of foraging rodents impedes this line of inquiry. The “luxury” hypothesis needs additional investigation before it can be fully assessed.

Alternatively, kangaroo rats may perceive moonlight as indicative of greater predation risk and avoid open areas on brightly moonlit nights as a necessity for survival. Kangaroo rats possess traits that may increase their risk of predation from visual predators: large body size, preferences for open-area foraging, and erratic bipedal hopping movement. Other rodents are not as conspicuous and move more slowly and methodically between foraging sites; hence they may be less noticeable targets. Quadrupedal rodents may show less moonlight avoidance behavior because they experience less actual risk of predation than bipeds if moonlight foraging is no riskier for quadrupeds than other types of foraging, they should expand their open-area foraging when there are fewer active kangaroo rats. Two experiments in the same field enclosure (Kotler et al. 1988; Longland and Price 1991) support this hypothesis. They found that kangaroo rats (*D. merriami*) suffered significantly higher rates of owl predation per unit activity than did Bailey’s pocket mice (*Chaetodipus baileyi*), and were attacked by owls more often on full moon nights than were coexisting quadrupeds, but also escaped more owl attacks than did quadrupeds. Although not conclusive, this evidence argues that uneven moonlight-associated risk contributes to the uneven patterns of moonlight avoidance. This hypothesis

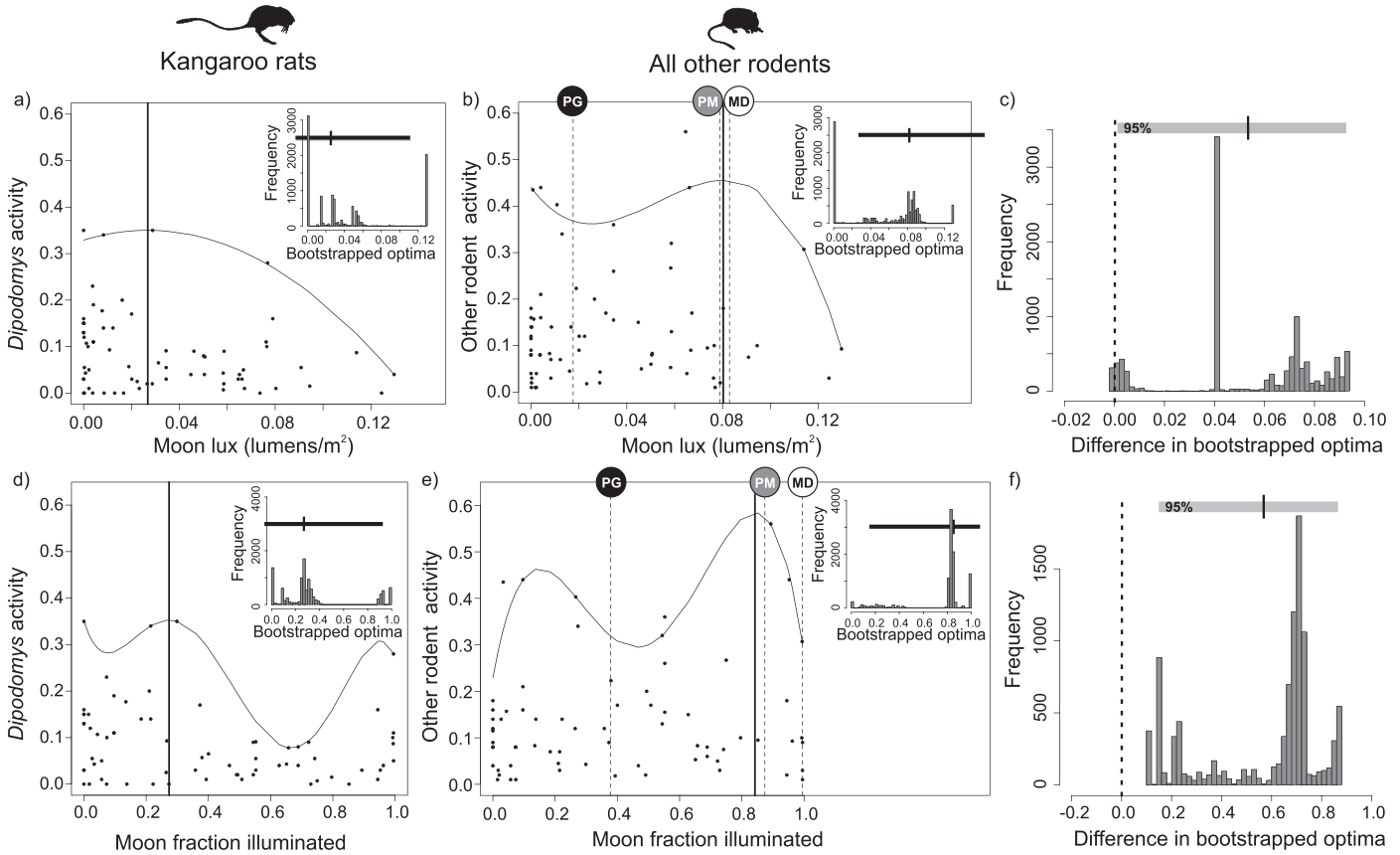


FIG. 4.—Estimation and comparison of moonlight optima for kangaroo rats and all other rodents, based on 69 nights of trapping at 62 sites in the Great Basin Desert, 1999–2006. Regression splines at the 95th percentile were used to model maximum activity in relation to moonlight (curved functions); maximum model values (vertical lines) are interpretable as estimated moonlight optima for rodent activity. For moon lux, a) *Dipodomys* activity was characterized by an optimum at 0.0268 lx and b) activity of the group of all other rodents was characterized by a higher optimum at 0.0803 lx. Bootstrap resampling of these moon lux optima (inset histograms) generated 95% CIs (black bars) for kangaroo rats (−0.0161–0.1135 lx) and all other rodents (0.0242–0.1539 lx). c) Subtracting bootstrap samples of moon lux optima yielded a 95% CI that did not include zero (\bar{X} = 0.0535 lx, 95% CI: 0.0005–0.0932 lx). Similarly for moon fraction illuminated, d) kangaroo rat activity displayed an optimum moon fraction value at 0.2736 (95% CI: −0.0617–0.9332), e) activity of all other rodents displayed a higher optimum of 0.8421 (95% CI: 0.1580–1.0748), and f) the difference in bootstrapped optima yielded a 95% CI that did not include zero (\bar{X} = 0.5685, 95% CI: 0.1416–0.8629). Thus, kangaroo rats and the group of all other rodents had significantly different moonlight optima, with kangaroo rats avoiding bright moonlight to a greater extent. Optima for *Perognathus* (PG), *Peromyscus* (PM), and *Microdipodops* (MD) are overlaid as dotted lines on b) moon lux of 0.0176 lx, 0.0788 lx, and 0.0829 lx, respectively, and e) moon fractions of 0.3781, 0.8739, and 0.9949, respectively (see “Results” for 95% CIs).

challenges research contending that kangaroo rats are a classic example of antipredator morphology with a suite of characters adapted specifically for detecting and escaping predators (e.g., Kotler 1985; Webster and Webster 1971). If kangaroo rats are specially armed with antipredator morphology, it is unclear why they were the only rodents in our study that showed moonlight avoidance (see Hafner [1993] for additional commentary).

Moonlight avoidance is a popular and controversial topic that has attracted interest from a variety of fields. Despite a clear consensus on the way that different rodent taxa respond to moonlight conditions, it appears that standard practice by many mammalogists is to avoid sampling during the full moon (e.g., Casper 1987; Heske et al. 1994; Mares and Rosenzweig 1978). Results presented here question the claimed general applicability of moonlight avoidance (e.g., Caro 2005; Lima 1998).

Specifically, kangaroo rats showed moonlight avoidance but other genera in the rodent assemblage did not. Such results are instructive for field mammalogists working in the Great Basin Desert. For example, studies focusing on *Dipodomys* should avoid periods of higher illumination (especially the latter stages of the waxing moon) but those studies focusing on other species (e.g., *Microdipodops* and *Peromyscus*) may profit by field collecting at times of higher illumination. Our findings await the evaluation of future moonlight studies, but examination of previous studies in North American deserts showed that past evidences of kangaroo rat-only patterns were overlooked. Congruity with past studies highlights the genuine need to reevaluate the conventional wisdom about moonlight avoidance in natural habitats. Although rodent activity is examined here in the cool, high-elevation Great Basin Desert, a fruitful area of research may involve comparing patterns of

moonlight rodent activity among the southern desert regions of North America (Mojave, Sonoran, and Chihuahuan deserts). A key question to be investigated is whether large-bodied, bipedal, and ecologically dominant rodents continue to be affected by moonlight differently than smaller-bodied, quadrupedal, and less-dominant rodents.

ACKNOWLEDGMENTS

Fieldwork for this project was assisted by the diligent efforts of P. M. Hafner. Thanks also to E. Reddington and C. W. Torres as members of the fieldwork team. We thank M. J. Anderson and B. S. Cade for assistance with the quantile regression analyses and M. J. Anderson for providing R scripts. Credit is due to D. J. Webb for helping with the calculation of moon lux, and H. E. Braker, G. G. Martin, D. J. Pondella, and D. R. Prothero for helpful early conversations. Many thanks are due to M. S. Hafner, D. J. Hafner, J. L. Orrock, B. D. Patterson, and N. M. Stewart for improving this manuscript with careful readings. We thank D. H. Van Vuren for providing thoughtful criticism on earlier drafts of this manuscript. This research was supported in part by the Nevada Department of Wildlife (contracts 05–21 and 8-15 to JCH). Funding assistance also was provided by the Moore Laboratory of Zoology at Occidental College, the Committee on Evolutionary Biology at the University of Chicago, and the United States Department of Education (GAANN training program in Evolutionary Environmental Biology; P200A090336). This study was originally based on a thesis submitted by NSU in partial fulfillment of the requirements for degree of Master of Arts in Biology at Occidental College and relies on the long-term field studies of JCH and his students.

LITERATURE CITED

- ABRAMS, P. A. 1993. Optimal traits when there are several costs: the interaction of mortality and energy costs in determining foraging behavior. *Behavioral Ecology* 4:246–259.
- ALKON, P. U., AND D. SALTZ. 1988. Influence of season and moonlight on temporal-activity patterns of Indian crested porcupines (*Hystrix indica*). *Journal of Mammalogy* 69:71–80.
- ANDERSON, M. J. 2008. Animal–sediment relationships re-visited: characterising species' distributions along an environmental gradient using canonical analysis and quantile regression splines. *Journal of Experimental Marine Biology and Ecology* 366:16–27.
- AUSTIN, R. H., B. F. PHILLIPS, AND D. J. WEBB. 1976. A method for calculating moonlight illuminance at the earth's surface. *Journal of Applied Ecology* 13:741–748.
- BEIER, P. 2006. Effects of artificial night lighting on terrestrial mammals. Pp. 19–42 in *Ecological consequences of artificial night lighting* (C. Rich and T. Longcore, eds.). Island Press, Washington, D.C.
- BLAIR, W. F. 1943. Activities of the chihuahua deer-mouse in relation to light intensity. *Journal of Wildlife Management* 7:92–97.
- BOUSKILA, A. 1995. Interactions between predation risk and competition: a field study of kangaroo rats and snakes. *Ecology* 76:165–178.
- BOWERS, M. A. 1988. Seed removal experiments on desert rodents: the microhabitat by moonlight effect. *Journal of Mammalogy* 69:201–204.
- BOWERS, M. A., AND J. H. BROWN. 1982. Body size and coexistence in desert rodents: chance or community structure? *Ecology* 63:391–400.
- BROWN, J. H., AND G. A. LIEBERMAN. 1973. Resource utilization and coexistence of seed-eating desert rodents in sand dune habitats. *Ecology* 54:788–797.
- BROWN, J. S., AND B. P. KOTLER. 2004. Hazardous duty pay and the foraging cost of predation. *Ecology Letters* 7:999–1014.
- BROWN, J. S., B. P. KOTLER, R. J. SMITH, AND W. O. WIRTZ. 1988. The effects of owl predation on the foraging behavior of heteromyid rodents. *Oecologia* 76:408–415.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multi-model inference: a practical information-theoretic approach. 2nd ed. Springer, New York.
- BURT, W. H., R. T. PETERSON, AND R. P. GROSSENHEIDER. 1998. A field guide to mammals: North America north of Mexico. 3rd ed. Houghton Mifflin Harcourt, Boston, Massachusetts.
- CADE, B. S., AND B. R. NOON. 2003. A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment* 1:412–420.
- CADE, B. S., J. W. TERRELL, AND R. L. SCHROEDER. 1999. Estimating effects of limiting factors with regression quantiles. *Ecology* 80:311–323.
- CARO, T. M. 2005. Antipredator defenses in birds and mammals. University of Chicago Press, Chicago, Illinois.
- CASPER, B. B. 1987. Spatial patterns of seed dispersal and postdispersal seed predation of *Cryptantha flava* (Boraginaceae). *American Journal of Botany* 74:1646–1655.
- CHANDLER, R. C. 1995. Practical considerations in the use of simultaneous inference for multiple tests. *Animal Behaviour* 49:524–527.
- CLARKE, J. A. 1983. Moonlight's influence on predator/prey interactions between short-eared owls (*Asio flammeus*) and deer mice (*Peromyscus maniculatus*). *Behavioral Ecology and Sociobiology* 13:205–209.
- CRONQUIST, A., A. H. HOLMGREN, N. H. HOLMGREN, AND J. L. REVEAL. 1972. Intermountain flora, vascular plants of the Intermountain West, U.S.A. Hafner Publishing Co., Inc., New York.
- DALY, M., P. R. BEHREND, M. I. WILSON, AND L. F. JACOBS. 1992. Behavioural modulation of predation risk: moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys merriami*. *Animal Behaviour* 44:1–9.
- DIJAWDAN, M., AND T. GARLAND, JR. 1988. Maximal running speeds of bipedal and quadrupedal rodents. *Journal of Mammalogy* 69:765–772.
- EISENBERG, J. F. 1963. The behavior of heteromyid rodents. University of California Publications in Zoology 69:1–114.
- FALKENBERG, J. C., AND J. A. CLARKE. 1998. Microhabitat use of deer mice: effects of interspecific interaction risks. *Journal of Mammalogy* 79:558.
- HAFNER, J. C. 1981. Evolution, systematics, and historical biogeography of kangaroo mice, genus *Microdipodops*. Ph.D. dissertation, University of California, Berkeley.
- HAFNER, J. C. 1993. Macroevolutionary diversification in heteromyid rodents: heterochrony and adaptation in phylogeny. Pp. 291–318 in *Biology of the Heteromyidae* (H. H. Genoways and J. H. Brown, eds.). Special Publication 10, The American Society of Mammalogists.
- HAFNER, J. C., D. J. HAFNER, AND M. S. HAFNER. 1996. Habitat selection and coexistence of species of kangaroo mice (*Microdipodops*). Pp. 249–259 in *Contributions in mammalogy: a memorial volume honoring Dr. J. Knox Jones, Jr.* (H. H. Genoways and R. J. Baker, eds.). Museum of Texas Tech University, Lubbock.
- HAFNER, J. C., AND N. S. UPHAM. 2011. Phylogeography of the dark kangaroo mouse, *Microdipodops megacephalus*: cryptic lineages

- and dispersal routes in North America's Great Basin. *Journal of Biogeography* 38:1077–1097.
- HAFNER, J. C., N. S. UPHAM, E. REDDINGTON, AND C. W. TORRES. 2008. Phylogeography of the pallid kangaroo mouse, *Microdipodops pallidus*: a sand-obligate endemic of the Great Basin, western North America. *Journal of Biogeography* 35:2102–2118.
- HAFNER, M. S. 1975. Species diversity and community interactions in Mojave Desert rodent communities. M.A. thesis, Occidental College, Los Angeles, California.
- HALL, E. R. 1941. Revision of the rodent genus *Microdipodops*. Field Museum of Natural History, Zoological Series 27:233–277.
- HESKE, E. J., J. H. BROWN, AND S. MISTRY. 1994. Long-term experimental study of a Chihuahuan Desert rodent community: 13 years of competition. *Ecology* 75:438–445.
- HUGHES, J. J., D. WARD, AND M. R. PERRIN. 1994. Predation risk and competition affect habitat selection and activity of Namib Desert gerbils. *Ecology* 75:1397–1405.
- JANICZEK, P. M., AND J. A. DEYOUNG. 1987. Computer programs for sun and moon illuminance with contingent tables and diagrams. Vol 171. U.S. Naval Observatory. Washington, D.C.
- JENKINS, S. H., AND S. W. BRECK. 1998. Differences in food hoarding among six species of heteromyid rodents. *Journal of Mammalogy* 79:1221–1233.
- JUSTICE, K. E. 1960. Nocturnalism in three species of desert rodents. Ph.D. dissertation, University of Arizona, Tucson.
- KAUFMAN, D. W., AND G. A. KAUFMAN. 1982. Effect of moonlight on activity and microhabitat use by Ord's kangaroo rat (*Dipodomys ordii*). *Journal of Mammalogy* 63:309–312.
- KENAGY, G. J. 1973. Daily and seasonal patterns of activity and energetics in a heteromyid rodent community. *Ecology* 54:1201–1219.
- KENDALL, M. G., AND J. D. GIBBONS. 1990. Rank correlation methods. Edward Arnold, London, United Kingdom.
- KLAUBER, L. M. 1982. Rattlesnakes: their habits, life histories, and influence on mankind. 3rd ed. University of California Press, Berkeley.
- KOENKER, R. 2005. Quantile regression. Cambridge University Press, New York.
- KOTLER, B. P. 1984a. Effects of illumination on the rate of resource harvesting in a community of desert rodents. *American Midland Naturalist* 111:383–389.
- KOTLER, B. P. 1984b. Risk of predation and the structure of desert rodent communities. *Ecology* 65:689–701.
- KOTLER, B. P. 1985. Owl predation on desert rodents which differ in morphology and behavior. *Journal of Mammalogy* 66:824–828.
- KOTLER, B. P., J. S. BROWN, AND O. HASSON. 1991. Factors affecting gerbil foraging behavior and rates of owl predation. *Ecology* 72:2249–2260.
- KOTLER, B. P., J. BROWN, S. MUKHERJEE, O. BERGER-TAL, AND A. BOUSKILA. 2010. Moonlight avoidance in gerbils reveals a sophisticated interplay among time allocation, vigilance and state-dependent foraging. *Proceedings of the Royal Society, B. Biological Sciences* 277:1469–1474.
- KOTLER, B. P., J. S. BROWN, R. J. SMITH, AND W. O. WIRTZ II. 1988. The effects of morphology and body size on rates of owl predation on desert rodents. *Oikos* 53:145–152.
- KOVACH, W. L. 2011. Oriana—circular statistics for Windows, version 4. Kovach Computing Services, Pentraeth, Wales, United Kingdom.
- KRAMER, K. M., AND E. C. BIRNEY. 2001. Effect of light intensity on activity patterns of Patagonian leaf-eared mice, *Phyllotis xanthopygus*. *Journal of Mammalogy* 82:535–544.
- KRISCIUNAS, K., AND B. E. SCHAEFER. 1991. A model of the brightness of moonlight. *Publications of the Astronomical Society of the Pacific* 103:1033–1039.
- LARSEN, E. 1986. Competitive release in microhabitat use among coexisting desert rodents: a natural experiment. *Oecologia* 69:231–237.
- LEMEN, C. A., AND P. W. FREEMAN. 1987. Competition for food and space in a heteromyid community in the Great Basin Desert. *Great Basin Naturalist* 47:1–6.
- LIMA, S. L. 1998. Stress and decision-making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior* 27:215–290.
- LIMA, S. L., AND L. M. DILL. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- LOCKARD, R. B. 1978. Seasonal change in the activity pattern of *Dipodomys spectabilis*. *Journal of Mammalogy* 59:563–568.
- LOCKARD, R. B., AND D. H. OWINGS. 1974a. Moon-related surface activity of bannertail (*Dipodomys spectabilis*) and Fresno (*D. nitratoides*) kangaroo rats. *Animal Behaviour* 22:262–273.
- LOCKARD, R. B., AND D. H. OWINGS. 1974b. Seasonal variation in moonlight avoidance by bannertail kangaroo rats. *Journal of Mammalogy* 55:189–193.
- LONGLAND, W. S., AND M. V. PRICE. 1991. Direct observations of owls and heteromyid rodents: can predation risk explain microhabitat use? *Ecology* 72:2261–2273.
- MACHADO, J. A. F., AND J. M. C. SANTOS SILVA. 2005. Quantiles for counts. *Journal of the American Statistical Association* 100:1226–1237.
- MARES, M. A., AND M. L. ROSENZWEIG. 1978. Granivory in North and South American deserts: rodents, birds, and ants. *Ecology* 59:235–241.
- MCMANARA, J. M., AND A. I. HOUSTON. 1987. Starvation and predation as factors limiting population size. *Ecology* 68:1515–1519.
- MEYER, M. D., AND T. J. VALONE. 1999. Foraging under multiple costs: the importance of predation, energetic, and assessment error costs to a desert forager. *Oikos* 87:571–579.
- O'FARRELL, M. J. 1974. Seasonal activity patterns of rodents in a sagebrush community. *Journal of Mammalogy* 55:809–823.
- ORR, H. D. 1959. Activity of white-footed mice in relation to environment. *Journal of Mammalogy* 40:213–221.
- ORROCK, J. L., AND B. J. DANIELSON. 2004. Rodents balancing a variety of risks: invasive fire ants and indirect and direct indicators of predation risk. *Oecologia* 140:662–667.
- ORROCK, J. L., AND B. J. DANIELSON. 2009. Temperature and cloud cover, but not predator urine, affect winter foraging of mice. *Ethology* 115:641–648.
- ORROCK, J. L., B. J. DANIELSON, AND R. J. BRINKERHOFF. 2004. Rodent foraging is affected by indirect, but not by direct, cues of predation risk. *Behavioral Ecology* 15:433–437.
- PIERCE, B. M., W. S. LONGLAND, AND S. H. JENKINS. 1992. Rattlesnake predation on desert rodents: microhabitat and species-specific effects on risk. *Journal of Mammalogy* 73:859–865.
- PRICE, M. V. 1978. The role of microhabitat in structuring desert rodent communities. *Ecology* 59:910–921.
- PRICE, M. V., N. M. WASER, AND T. A. BASS. 1984. Effects of moonlight on microhabitat use by desert rodents. *Journal of Mammalogy* 65:353–356.
- PRICE, M. V., N. M. WASER, AND S. McDONALD. 2000. Seed caching by heteromyid rodents from two communities: implications for coexistence. *Journal of Mammalogy* 81:97–106.

- PRUGH, L., AND J. BRASHARES. 2010. Basking in the moonlight? Effect of illumination on capture success of the endangered giant kangaroo rat. *Journal of Mammalogy* 91:1205–1212.
- QUENOUILLE, M. H. 1952. *Associated measurements*. Academic Press, New York.
- R DEVELOPMENT CORE TEAM. 2012. *R: a language and environment for statistical computing*. R Development Core Team, Vienna, Austria.
- REICHMAN, O. J., AND M. V. PRICE. 1993. Ecological aspects of heteromyid foraging. Pp. 539–574 in *Biology of the Heteromyidae* (H. H. Genoways and J. H. Brown, eds.). Special Publication 10, The American Society of Mammalogists.
- ROSENZWEIG, M. L. 1974. On the optimal aboveground activity of bannertail kangaroo rats. *Journal of Mammalogy* 55:193–199.
- SCHWAB, R. G. 1966. Environmental factors affecting surface activity of the kangaroo rat (*Dipodomys merriami*). Ph.D. dissertation, University of Arizona Tucson.
- 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.
- SLADE, N. A., AND S. M. BLAIR. 2000. An empirical test of using counts of individuals captured as indices of population size. *Journal of Mammalogy* 81:1035–1045.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry, the principles and practice of statistics in biological research*. 3rd ed. W. H. Freeman and Co., New York.
- STANKOWICH, T., AND D. T. BLUMSTEIN. 2005. Fear in animals: a meta-analysis and review of risk assessment. *Proceedings of the Royal Society, B. Biological Sciences* 272:2627–2634.
- THOMPSON, S. D. 1982. Microhabitat utilization and foraging behavior of bipedal and quadrupedal heteromyid rodents. *Ecology* 63:1303–1312.
- THOMPSON, J. D., G. WEIBLEN, B. A. THOMPSON, S. ALFARO, AND P. LEGENDRE. 1996. Untangling multiple factors in spatial distributions: lilies, gophers, and rocks. *Ecology* 77:1698–1715.
- THORSON, J. M., R. A. MORGAN, J. S. BROWN, AND J. E. NORMAN. 1998. Direct and indirect cues of predatory risk and patch use by fox squirrels and thirteen-lined ground squirrels. *Behavioral Ecology* 9:151–157.
- TROMBULAK, S. C., AND G. J. KENAGY. 1980. Effects of seed distribution and competitors on seed harvesting efficiency in heteromyid rodents. *Oecologia* 44:342–346.
- UNITED STATES NAVAL OBSERVATORY. 2005. *MICA: multiyear interactive computer almanac 1800–2050, version 2.0*. Willman-Bell, Richmond, Virginia.
- VÁSQUEZ, R. A. 1994. Assessment of predation risk via illumination level: facultative central place foraging in the cricetid rodent *Phyllotis darwini*. *Behavioral Ecology and Sociobiology* 34:375–381.
- WEBSTER, D. B., AND M. WEBSTER. 1971. Adaptive value of hearing and vision in kangaroo rat predator avoidance. *Brain, Behavior and Evolution* 4:310–322.
- WILKINSON, L. 1998. *SYSTAT for Windows, version 9.0*. SPSS Inc., Chicago, Illinois.
- WOLFE, J. L., AND C. T. SUMMERLIN. 1989. The influence of lunar light on nocturnal activity of the old-field mouse. *Animal Behaviour* 37:410–414.
- WONDOLLECK, J. T. 1978. Forage-area separation and overlap in heteromyid rodents. *Journal of Mammalogy* 59:510–518.
- ZAR, J. H. 1999. *Biostatistical analyses*. Prentice-Hall, Englewood Cliffs, New Jersey.

Submitted 2 August 2011. Accepted 4 July 2012.

Associate Editor was Dirk H. Van Vuren.