

Basking in the moonlight? Effect of illumination on capture success of the endangered giant kangaroo rat

LAURA PRUGH* AND JUSTIN BRASHARES

Department of Environmental Science, Policy, and Management, 137 Mulford Hall, University of California, Berkeley, CA 94720, USA

* Correspondent: prugh@berkeley.edu

Bright moonlight is thought to increase predation risk for nocturnal rodents and consequently reduce their activity levels and capture rates. We examined the effect of moonlight on the foraging activity and capture success of the federally endangered giant kangaroo rat (*Dipodomys ingens*) in the Carrizo Plain National Monument, California. *D. ingens* is adapted to open grasslands, a habitat type where moonlight should strongly influence its visibility to predators. Using a trapping data set of 11,353 captures from 2007 to 2009 and accounting for factors such as cloud cover, temperature, abundance of the San Joaquin kit fox (*Vulpes macrotis nutica*), plant biomass, trap acclimation, and trap effort, we found a consistently positive effect of moonlight on capture success. In foraging trials we detected no effect of moonlight on giving-up densities or time spent at seed piles. Our results suggest that giant kangaroo rats do not perceive a higher risk of predation in bright moonlight. Nocturnal rodents that rely on early visual detection of predators might benefit from moonlight as much as their predators do, thus resulting in no net change in predation risk. DOI: 10.1644/10-MAMM-A-011.1.

Key words: antipredator strategy, capture, Heteromyidae, lunar cycle, predator-sensitive foraging

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Predator-sensitive foraging can strongly affect population and community dynamics by altering spatial patterns of species abundance, increasing resource heterogeneity, and reducing the foraging efficiency of prey species (Banks 2001; Creel et al. 2009; Hik 1995; Sinclair and Arcese 1995). Bright moonlight is widely believed to increase the risk of predation for nocturnal small mammals (Bowers and Dooley 1993; Brown et al. 1988; Kelt et al. 2004; Kotler et al. 1991), leading to patterns of activity that vary according to the lunar cycle. These fluctuations in the intensity and spatial patterns of mammalian activity are of interest not only because of their effect on community dynamics but also because of their practical implications for studies of nocturnal mammals. For example, studies that require direct behavioral observations, livetrapping, spotlighting, or camera trapping should control for nighttime illumination if it significantly affects behavior and trapping success.

Many mammalian species are active primarily during the night, an activity pattern that may reduce the risk of being detected by visually oriented predators, facilitate temporal partitioning among competitors, and confer thermoregulatory benefits in hot regions (Alterman et al. 1995; Kronfeld-Schor and Dayan 2003; Wright 1982). Illumination intensity on full moon nights is approximately 3 orders of magnitude higher than on new moon nights (Roach and Gordon 1973) and could

strongly affect the foraging efficiency and mortality risk of nocturnal predators and prey. The nocturnal burrowing rodents in the family Heteromyidae (kangaroo rats, kangaroo mice, and pocket mice) are keystone granivores in many deserts and arid grasslands in North America, and early studies examining the effect of moonlight on the activity of nocturnal mammals focused on this group, particularly Merriam's kangaroo rat (*Dipodomys merriami*). Several of these studies found that bright nighttime illumination resulted in habitat shifts toward increased cover and reduced foraging intensity (Bowers 1988; Daly et al. 1992; Kotler 1984). Subsequently, several nocturnal research projects have been designed to conduct trapping during periods of low moonlight, assuming that capture rates will be highest during these periods (Brown and Munger 1985). However, moonlight effects can vary among seasons (Bouskila 1995; Kelt et al. 2004; Lockard and Owings 1974b), years (Brown et al. 1988; Kelt et al. 2004), and species (Kotler et al. 1991; Lockard and Owings 1974a; Price et al. 1984). Some studies of heteromyids and other mammals have reported increased levels of activity during periods of bright moonlight (Erkert 1974; Longland and Price 1991).



These contradictory results among studies highlight our poor understanding of factors that affect the strength and direction of moonlight effects on nocturnal mammals. In this paper, we use a multiseason, multiyear data set to examine the effect of nighttime illumination on the trapping success and foraging activity of the giant kangaroo rat (*Dipodomys ingens*).

The giant kangaroo rat is endemic to California and the largest of the 21 species of kangaroo rats. Once ranging throughout California's Central Valley, the giant kangaroo rat is federally endangered due to habitat loss and is now restricted to 6 remnant populations, the largest of which occurs in the Carrizo Plain National Monument (United States Fish and Wildlife Service 1998). In 2007 we initiated a large-scale study in the Carrizo Plain to optimize habitat management for the giant kangaroo rat and the many other threatened and endangered species that occur there. This study has required an intensive trapping effort over a large area. During 121 trap nights over 3 years we have had 11,353 captures of 3,250 individuals on thirty 1-ha grids. We also monitored foraging intensity on these grids by conducting seed preference trials. Anecdotal evidence has suggested that giant kangaroo rat activity is not influenced by moonlight (Braun 1985), but the similar-sized bannertail kangaroo rat (*Dipodomys spectabilis*) has been shown to decrease activity in open habitats in response to moonlight (Lockard and Owings 1974a).

We examined the effect of moonlight on giant kangaroo rat trapping success and foraging intensity in open grassland sites characterized by various amounts of low vegetation (e.g., bunchgrasses, annual grasses, and forbs) but lacking shrubs and trees. Giant kangaroo rats are generally found in these open habitats (Williams and Kilburn 1991), where foraging individuals are fully exposed and moonlight has a strong potential to increase predation risk from kit foxes (*Vulpes macrotis*) and other predators. We predicted that foraging activity, and consequently trapping success, would decline as the intensity of moonlight increased. Furthermore, we predicted that the suppressive effect of moonlight on giant kangaroo rat activity would be strongest on sites with sparse plant cover and high kit fox abundance, where giant kangaroo rats were most exposed and at risk of predation. We also accounted for other factors that could have affected trapping success, such as cloud cover, temperature, and random spatial variation. Understanding the response of giant kangaroo rats to moonlight will increase our understanding of the relationship between moonlight and predation risk, and it also will help to optimize trapping protocols for this keystone endangered species.

MATERIALS AND METHODS

Study area.—The Carrizo Plain National Monument supports an arid annual grassland that receives an average of 145 mm of precipitation per year, falling almost exclusively as winter rain. Located in the southern San Joaquin Valley of California, the Carrizo Plain is the largest (810 km²) of the few remaining San Joaquin grassland ecosystem remnants (Fig. 1).

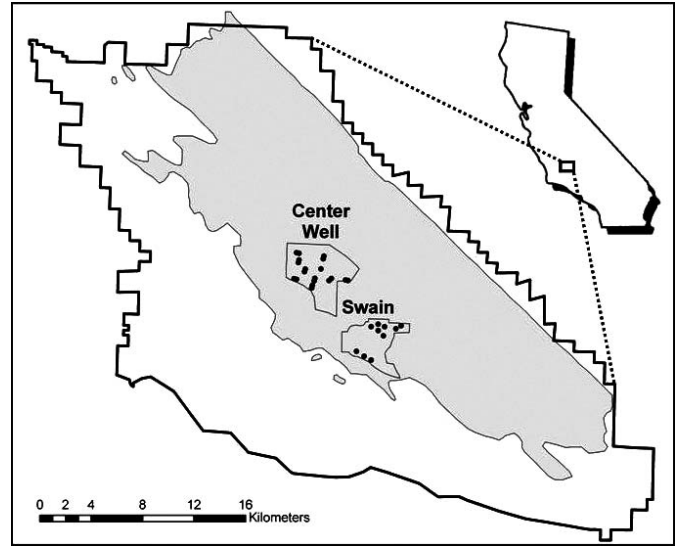


FIG. 1.—The Carrizo Plain National Monument, California (39°15'N, 119°50'W), showing the current distribution of the giant kangaroo rat (*Dipodomys ingens*) in gray and study plots in the Center Well and Swain pastures.

Approximately 556 species of native plants and 110 species of exotic plants occur there. Historically, the Carrizo Plain was dominated by perennial bluegrass (*Poa* spp.) and native annual forbs (Germano et al. 2001). Currently, bluegrass is still present, but the vegetative cover is dominated by European annuals such as red brome (*Bromus rubens*) and red-stemmed filaree (*Erodium cicutarium*).

The rodent guild in the Carrizo Plain is dominated by the giant kangaroo rat but includes other heteromyid rodents, pocket gophers, and ground squirrels. Although federally listed as endangered due to extensive habitat loss, the giant kangaroo rat is locally abundant in the Carrizo Plain, reaching densities of up to 69 individuals/ha (Williams and Kilburn 1991). In the core range of the giant kangaroo rat (where our study plots are located) shrubs are absent and the vegetation consists exclusively of grasses and forbs. In these areas giant kangaroo rats completely dominate the nocturnal rodent community: of 11,357 total captures during our study, only 4 captures were of a species—the short-nosed kangaroo rat (*Dipodomys nitratooides*)—other than giant kangaroo rat. Predators of giant kangaroo rats found in our study area include the San Joaquin kit fox (*Vulpes macrotis mutica*), coyote (*Canis latrans*), American badger (*Taxidea taxus*), long-tailed weasel (*Mustela frenata*), great horned owl (*Bubo virginianus*), short-eared owl (*Asio flammeus*), long-eared owl (*Asio otus*), barn owl (*Tyto alba*), gopher snake (*Pituophis catenifer*), coachwhip (*Masticophis flagellum*), and western rattlesnake (*Crotalus viridis*).

Study plots were located within a pasture (16,302 ha) grazed by cattle and an ungrazed pasture (6,570 ha) in the core range of the giant kangaroo rat (Fig. 1). Stratified randomization was used to place ten 1-ha trapping grids within the ungrazed pasture and twenty 1-ha grids within the grazed pasture. In the grazed pasture 10 of the grids were located

within 1.96-ha cattle enclosures, and 10 were located in areas exposed to annual spring grazing by cattle. Bird spikes were placed on cattle enclosure fence posts to prevent perching by birds of prey, and the fencing did not restrict predator movement. Because cattle grazing had negligible effects on giant kangaroo rat demographics and vegetation structure during our study (2007–2009—Prugh 2009), we did not include grazing as a variable in our models. Instead, we included the unique identifier for each grid (grid ID) as a random variable in models to account for site-specific effects on capture rates of giant kangaroo rats.

Trapping.—Giant kangaroo rats were trapped on all 30 sites for 3–5 consecutive days during 5 mark–recapture sessions that lasted from 3 to 8 weeks each in August–October 2007, April–May 2008, August 2008, April–May 2009, and August 2009. Sherman traps (model XLKR; H. B. Sherman Traps, Inc., Tallahassee, Florida) were placed every 20 m on a 100 × 100-m grid, with each trapline offset such that traps were arranged in a checkerboard ($n = 60$ traps per plot, minimum trap distance along diagonals = 14 m). Two to 5 grids were set on any given trap night. Traps were baited with sterilized parakeet seed (primarily millet) and set at dusk. A crumpled paper towel was added for bedding. In the summer 2007 session traps were checked at dawn. In subsequent sessions traps were checked starting at approximately 2300 h and ending at approximately 0400 h. We recorded the trapping period (i.e., starting and ending times) for each grid. Processing of captured individuals consisted of weighing, tagging with passive integrated transponders and ear tags, measuring skull length, and determining sex and reproductive status. Trapping and handling of kangaroo rats followed guidelines of the American Society of Mammalogists (Gannon et al. 2007), and protocols were approved by the University of California Animal Care and Use Committee.

Calculations and analyses.—Data on moon phase, the fraction of moon illuminated, moon rise and set times, and astronomical twilight start and end times were used to calculate a moonlight index during each night of trapping. These data were obtained from the United States Navy Astronomical Applications Department (<http://aa.usno.navy.mil/data>). The moonlight index was calculated as the fraction of moon illuminated multiplied by the number of hours the moon was visible at night.

We obtained data on other covariates hypothesized to affect capture success of the giant kangaroo rat, including cloud cover, minimum temperature, trapping effort, trap acclimation, kit fox abundance, and vegetative cover (Table 1). Cloud cover was estimated as the proportion of sky covered by clouds during the trapping session for each grid. Minimum nightly temperature was obtained from a weather station in the Carrizo (<http://www.wrh.noaa.gov/sto/getRaws.php?sid=CAZC1&num=48>). Trapping effort was calculated as the number of hours that traps were available on each grid each night. To account for trap acclimation by giant kangaroo rats over time, we added variables for the trapping session number ($n = 5$ sessions) and the night within a trapping session ($n =$

3–5 nights per session). The number of kit fox sightings on each grid each night was used as an index of their abundance. To avoid double-counting, we counted the maximum number of foxes that were seen simultaneously (usually as a family group). Vegetative cover was measured as the average biomass of 8 replicate 25 × 25-cm clip plots on each grid. Clip plots were conducted at peak biomass in April each year.

We constructed general linear mixed models to predict both the number of giant kangaroo rats captured (models referred to as $M_{capt,x}$, where x identifies the specific model) and the proportion of the population captured (models $M_{prop,x}$) on each grid each night. The proportion captured was calculated as the number captured divided by the population estimate for the grid. Population estimates were calculated in program R (R Development Core Team 2009) using the RDHet model (robust design with heterogeneity) in the RMark package (Laake 2009). These estimates were very precise (mean coefficient of variation = 4%, range = 0.03–26%, $n = 150$ estimates). The response variable, number captured, followed a Poisson distribution, and therefore M_{capt} models were run using the lmer modeling procedure with a Poisson family in program R. The proportion captured was normally distributed, and therefore the lme procedure with a Gaussian family was used to run M_{prop} models. We started with full models, including interactions and grid ID as a random effect ($M_{capt,full}$ and $M_{prop,full}$; Table 1), and we used likelihood-ratio tests and the stepAIC function (where appropriate) to select the best models, $M_{capt,best}$ and $M_{prop,best}$ (Zuur et al. 2009). To estimate the amount of variation in capture success explained by these models, we ran general linear models of $M_{capt,best}$ and $M_{prop,best}$ to obtain R^2 values (i.e., the models were run with all factors as fixed effects instead of including grid ID as a random effect).

Foraging experiments.—Seed preference trials were conducted from 11 June to 9 August 2009 (total $n = 117$ trials). Giant kangaroo rat burrow mounds were chosen randomly on each grid ($n = 3–6$ mounds per grid), and small piles of seed heads (0.5 g) from 10 plant species were placed on each mound (total seed mass = 5 g per trial). Samples from giant kangaroo rat surface caches showed that seeds from all plants used in diet trials were consumed under natural conditions (L. Prugh, pers. obs.). Seed heads were gathered within the study area at peak ripeness. Piles were placed on mounds at dusk, collected at dawn, and reweighed. Infrared motion-sensor cameras (model PC90 Professional; Reconyx, Inc., Holmen, Wisconsin) were mounted to record visits to the piles. We used the near video setting so that photos were taken continuously each second as long as motion was detected. Thus, the number of photos taken was a direct measure of foraging time during each trial. Trials not visited by giant kangaroo rats or visited by other species were excluded ($n = 16$ excluded trials). Ant activity at seed piles was rare, as evidenced by a pilot study conducted in 2008 in which control seed piles were placed beneath hardware cloth cages accessible to ants but not to giant kangaroo rats. No evidence of ant activity was found.

TABLE 1.—Description of models used to predict the number of giant kangaroo rats (*Mcapt*) and the proportion of the population (*Mprop*) captured during mark–recapture sessions from 2007 to 2009 in the Carrizo Plain National Monument, California. Y = yes, N = no.

Variables included in <i>Mcapt_{full}</i> and <i>Mprop_{full}</i>	Description	Range of values	Included in <i>Mcapt_{best}</i>	Included in <i>Mprop_{best}</i>
Random effects				
Grid ID	Unique identifier for each trapping grid	1–30	Y	Y
Main fixed effects				
Moonlight index	Fraction illuminated × hours visible	0–8	Y	Y
Night	Trap night within session	1–5	Y	Y
Session	Session number	1–5	Y	Y
Temperature	Minimum nightly temperature (°C)	0–26.1	Y	Y
Trapping effort	Duration of trap availability on each grid (h)	3.4–12	Y	Y
Kit fox abundance	Number of sightings on grids	0–6	Y	N
Clouds	Proportion of sky covered by clouds	0–1	N	N
Plant biomass	Average peak yearly biomass on each grid (g)	2.2–26	N	N
Season	Spring (April) or late summer (August)		N	N
Interactions				
Moonlight index*Session			Y	Y
Night*Trapping effort			Y	Y
Session*Temperature			Y	Y
Session*Effort			Y	Y
Moonlight index*Night			Y	N
Moonlight index*Kit fox abundance			N	N
Moonlight index*Plant biomass			N	N
Moonlight index*Season			N	N
Night*Temperature			N	N

The mass of seeds remaining after a foraging trial was used as a measure of the giving-up density; low giving-up density thus corresponds with high foraging intensity. On average, 56% of seeds were removed from the piles (range = 16–80%), and giant kangaroo rats showed consistent preferences for particular seed types (Prugh 2009), indicating that they foraged selectively at piles. General linear models were used to examine the effect of moonlight on foraging time and giving-up densities using program R (inclusion of grid ID as a random effect was not supported by likelihood-ratio tests; $L = 47.8$, $P = 0.12$). Moon phase was grouped into bright (full, waxing gibbous, and waning gibbous; $n = 50$ trials), half (1st quarter and 3rd quarter; $n = 12$), and dark (new, waxing crescent, and waning crescent; $n = 39$).

RESULTS

Effect of moonlight on trapping success.—Moonlight positively affected capture success for giant kangaroo rats, whether success was measured as the number of giant kangaroo rats caught (Fig. 2A; Table 2; model *Mcapt_{best}*) or proportion of the population caught (Fig. 2B; Table 2; model *Mprop_{best}*). The effect of moonlight on capture success also was positive and significant ($P < 0.01$) in models using the fraction of moon illuminated (irrespective of hours visible) or moon phase as predictors instead of the moonlight index, indicating that results were robust to the type of moonlight measure used in analyses.

Inclusion of grid ID as a random variable was supported by likelihood-ratio tests. This random spatial variation affected the number captured ($L = 104.6$, $P < 0.001$) and also the proportion captured ($L = 5.5$, $P = 0.02$). Model *Mcapt_{best}*

retained all of the predictors that were retained by *Mprop_{best}* (moonlight, trap night, minimum temperature, and session) plus kit fox sightings (Table 1), which negatively affected the number of giant kangaroo rats captured (Table 2). Estimates of all shared predictors had the same sign, indicating general consistency of results (Table 2). Cloud cover, plant biomass, and season did not significantly affect either measure of trap success (Table 1). In general linear models that included all variables as fixed effects, model *Mcapt_{best}* explained 67% of variation in the number of giant kangaroo rats caught, and *Mprop_{best}* explained 51% of variation in the proportion of the population caught. Contrary to our prediction that moonlight would have a stronger negative effect on giant kangaroo rat activity where kit foxes were more abundant and cover was scarcer, the interactions between moonlight and both kit fox sightings and vegetation biomass were not significant (Table 1).

Effect of moonlight on foraging activity.—Moon phase did not affect the amount of seed that giant kangaroo rats removed during seed preference trials ($F_{2,98} = 0.62$, $P = 0.54$; Fig. 3). No effect was detected when moonlight was measured as the fraction of moon illuminated ($F_{1,99} = 0.12$, $P = 0.73$) or the moonlight index ($F_{1,99} = 0.01$, $P = 0.92$). Likewise, moonlight did not affect the duration of foraging bouts at seed piles (moon phase: $F_{2,76} = 0.03$, $P = 0.97$; fraction illuminated: $F_{1,77} = 0.02$, $P = 0.89$; moonlight index: $F_{1,77} = 0.05$, $P = 0.83$).

DISCUSSION

We found a weak but consistently positive effect of moonlight on the capture success of giant kangaroo rats and

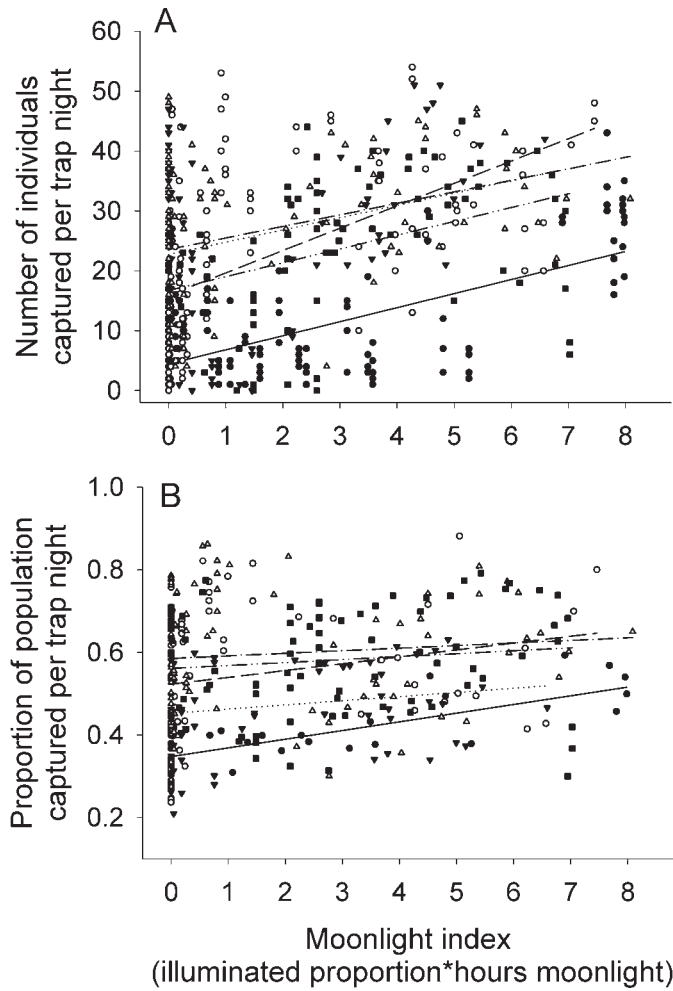


FIG. 2.—Effect of moonlight on A) the number of giant kangaroo rats captured and B) the proportion of the population captured, in the Carrizo Plain National Monument, California. Different lines and symbols correspond to each of the 5 trapping sessions (solid line, filled circle = summer 2007; dashed line, open circle = spring 2008; dotted line, filled triangle = summer 2008; dash-dot-dash, open triangle = spring 2009; dash-dot-dot-dash, filled square = summer 2009).

no effect of moonlight on their foraging intensity. These findings contrast with results from studies of other heteromyid species, which often reported negative effects of moonlight on activity rates (Daly et al. 1992; Lockard and Owings 1974a). However, a closer look at these studies reveals that moonlight effects were often inconsistent. For example, Lockard and Owings (1974a) found that activity of *D. spectabilis* was inhibited by moonlight, but only during the winter (Lockard and Owings 1974b), and activity of *D. nitratoides* was not affected. Brown et al. (1988) found that illumination inhibited foraging by *D. merriami* in only 1 of 2 years, and 2 other heteromyid species shifted habitat usage but did not alter foraging rates. Kelt et al. (2004) found that moonlight effects on the foraging of rodents in Chile varied strongly according to species, season, and year. Longland and Price (1991) reported that activity rates of *D. merriami* were actually 2–5 times higher in the presence of illumination, and activity rates of 3 other heteromyid species were unchanged. Thus, the widespread belief that moonlight inhibits activity of nocturnal heteromyids is not substantiated by strong empirical evidence.

Accurate and precise population estimates are needed to address many ecological and conservation issues, and maximizing capture success while accounting for heterogeneity in capture rates can help to achieve this goal (Lebreton et al. 1992; Pledger and Efford 1998; Tyrrell et al. 2009). In our surveys nighttime illumination significantly increased giant kangaroo rat capture success. This positive influence was consistent among seasons and years. Therefore, a trapping protocol restricting surveys to bright nights would be preferable to trapping on dark nights for giant kangaroo rats. Because decreased capture success could lead to negatively biased or less precise density estimates, use of protocols that maximize capture success is especially important when monitoring endangered species such as giant kangaroo rats. We therefore do not recommend restriction of trapping to dark nights without 1st establishing a negative effect of moonlight on capture of the target species.

To our knowledge, a study demonstrating negative effects of moonlight on capture rates of a nocturnal mammal would

TABLE 2.—Estimates of variables retained in the best models predicting the number of giant kangaroo rats captured ($M_{capt_{best}}$) and the proportion of the population captured ($M_{prop_{best}}$) in the Carrizo Plain National Monument, California. See Table 1 for parameter descriptions.

Parameter	$M_{capt_{best}}$				$M_{prop_{best}}$			
	Estimate	SE	t	P	Estimate	SE	t	P
(Intercept)	2.534	0.159	15.96	< 0.001	-0.009	0.087	-0.11	0.91
Moonlight index	0.184	0.016	11.41	< 0.001	0.026	0.007	3.80	< 0.001
Night	0.368	0.029	12.83	< 0.001	0.212	0.020	10.85	< 0.001
Temperature	0.045	0.004	10.91	< 0.001	0.006	0.003	2.33	0.02
Trapping effort	-0.209	0.017	-12.57	< 0.001	-0.002	0.009	-0.26	0.80
Session	-0.207	0.034	-6.16	< 0.001	-0.043	0.024	-1.77	0.08
Kit fox abundance	-0.041	0.013	-3.11	0.002	—	—	—	—
Moonlight index*Session	-0.039	0.003	-11.22	< 0.001	-0.008	0.002	-3.49	< 0.001
Temperature*Session	-0.013	0.001	-10.37	< 0.001	-0.003	0.001	3.14	0.002
Trapping effort*Night	-0.017	0.004	-4.74	< 0.001	-0.015	0.002	-6.79	< 0.001
Trapping effort*Session	0.090	0.004	20.67	< 0.001	0.022	0.003	7.69	< 0.001
Moonlight index*Night	0.368	0.029	12.83	< 0.001	—	—	—	—

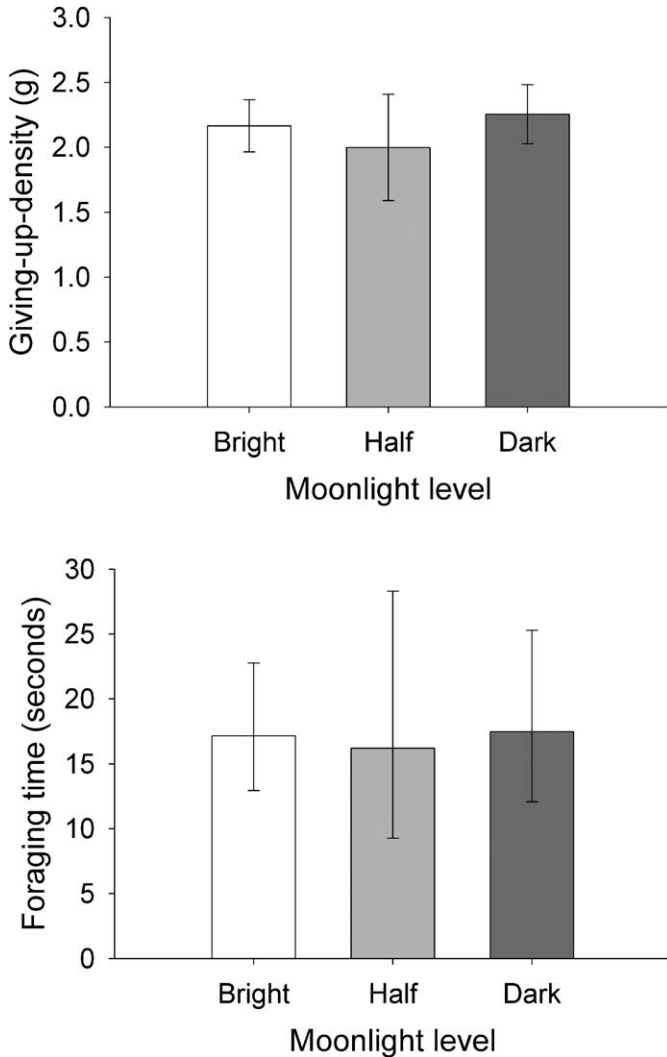


FIG. 3.—Effect of moonlight on foraging intensity of giant kangaroo rats in the Carrizo National Monument, California. Moon phase was grouped into bright (full, waxing gibbous, and waning gibbous, $n = 50$ trials), half (1st and 3rd quarter, $n = 12$ trials), and dark (new, waxing crescent, and waning crescent, $n = 39$ trials). Giving-up density is the amount of seed remaining after a night of foraging (5 g of seed was provided). Error bars show 95% confidence intervals.

be the 1st of its kind. Although many studies have found significant effects of moonlight on mammalian activity and predation rates, we found no other published study that demonstrated a consistent effect of moonlight, either positive or negative, on the capture rate of a nocturnal mammal. No effect of moonlight, or an inconsistent effect over time, was found on capture rates of southern pygmy mice (*Baiomys musculus*) in Mexico (Schnell et al. 2008), prairie voles (*Microtus ochrogaster*) and cotton rats (*Sigmodon hispidus*) in Kansas (Stokes et al. 2001), agile antechinus (*Antechinus agilis*) in Australia (Sutherland and Predavec 1999), snowshoe hares (*Lepus americanus*) in Colorado (Zahratka and Shenk 2008), white-footed mice (*Peromyscus leucopus*) and meadow voles (*Microtus pennsylvanicus*) in Virginia (Bowers and Dooley 1993), *P. leucopus* in New Hampshire (Barry and

Francq 1982), 5 desert rodent species in Arizona (Price et al. 1984), and 33 nonvolant mammal species in Belize (Caro et al. 2001).

Although intuition would suggest that rates of capture in food-baited traps should be positively correlated with rates of foraging activity, no study has demonstrated a direct link. Price (1977) found that relative capture rates of heteromyids in different microhabitats corresponded roughly to the relative use of those areas, but it is not known how closely capture rates track temporal variation in foraging intensity. Capture rates often have been used as a surrogate measure of activity rates (e.g., Price et al. 1984), but this assumed relationship has not been tested with independent data on activity rates and trapping success. We found that moonlight did not affect the foraging intensity of giant kangaroo rats despite finding a positive effect of moonlight on capture rates. This discrepancy, along with the general lack of empirical evidence linking moonlight and trap success despite abundant evidence linking moonlight to activity rates, suggests that capture rates are not closely tied to activity levels. Other factors, such as wariness of individuals or visibility of the traps, may confound the effect of activity level on the probability of capture. In our study capture rates might have increased with illumination because traps were more visible in the moonlight and thus easier for giant kangaroo rats to locate.

The absence of a negative relationship between moonlight and both capture success and foraging activity suggests that giant kangaroo rats do not perceive a higher risk of predation on nights with bright moonlight. The number of giant kangaroo rats captured was significantly lower on grids with relatively high numbers of kit fox sightings, indicating that predator avoidance might have resulted in fewer giant kangaroo rats entering traps. However, the lack of an interaction between moonlight intensity and either kit fox abundance or plant biomass supports the hypothesis that predation risk is not strongly affected by moonlight for this species. This support should be interpreted with caution because giant kangaroo rats have many predators in addition to kit foxes, and all of our sites were relatively open without shrub cover. Nonetheless, kit foxes are one of the most important predators of giant kangaroo rats in this area (S. Etter, California State University, pers. comm.), and sites with high plant biomass had enough vegetation to obstruct predator vision. Our results are consistent with other studies of nocturnal rodents that directly measured components of predation risk. These studies found that the probability of capture by owls did not increase significantly with moonlight (Clarke 1983; Longland and Price 1991).

We propose that moonlight should increase predation risk only for nocturnal prey species that rely on remaining undetected as their primary antipredator strategy. For moonlight to increase predation risk, the benefits of enhanced vision must be greater for predators than for prey. This condition might be met for small rodents that avoid predation by remaining cryptic, but species such as heteromyid rodents have adaptations such as enlarged auditory bullae and large eyes

that facilitate early detection of predators (Webster and Webster 1971). If moonlight enhances vision equally for predators and prey, then predation risk should not change in response to illumination intensity. Kotler (1984) provided evidence consistent with this hypothesis in a study that manipulated habitat cover, illumination, and predator presence for several desert mammal species. The largest kangaroo rat in this study, *Dipodomys deserti*, was the least vulnerable to predation, used open habitats most frequently, and was the least responsive to changes in illumination. The giant kangaroo rat is the largest heteromyid species and thrives in completely open habitats (Germano et al. 2001; Williams and Kilburn 1991). Thus, they may benefit from moonlight as much as their predators do.

In summary, results from our multiseason, multiyear study and a close scrutiny of the literature reveal that moonlight effects on nocturnal small mammals are much more variable than is widely believed. Previous studies are roughly consistent with our hypothesis that differential moonlight effects across species can be explained partially by antipredator strategies. Additionally, our results indicate that the probability of capturing small mammals might not be tied closely to their levels of foraging activity. We therefore caution against the use of capture rate as a surrogate for activity rate. Controlled studies across species are needed for explicit tests of relationships among antipredator strategies, moonlight, activity levels, and capture success.

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