

## Behavioural modulation of predation risk: moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys merriami*

MARTIN DALY, PHILIP R. BEHREND<sup>\*</sup>, MARGO I. WILSON &  
LUCIA F. JACOBS<sup>†</sup>

*Department of Psychology, McMaster University, Hamilton, Ontario L8S 4K1, Canada*

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**Abstract.** The temporal and spatial distribution of above-ground activity in Merriam's kangaroo rats, *Dipodomys merriami*, radio-tracked during 10 winters varied in relation to phases of the moon. At the full moon, animals were more likely to be found in their day burrows at scheduled hourly radio fixes, and when they emerged, they stayed closer to home. At partial moon phases, above-ground activity was preferentially allocated to hours when the moon was down. As predicted from an extension of Rosenzweig's (1974, *J. Mammal.*, **55**, 193–199) model of optimal above-ground activity, the suppression of nocturnal activity at the full moon was partially offset by relatively great activity at dusk and dawn, and losses to nocturnal versus diurnal predators were distributed differently over the lunar cycle. Gross predation rates did not differ significantly among moon phases, but the kangaroo rats' relatively crepuscular activity pattern at the full moon both reduced their vulnerability to nocturnal predators, as compared with the new moon phase, and raised their vulnerability to diurnal shrikes.

In various domains of behavioural decision making, animals act as if the risk of predation were a cost to be weighed against expected benefits (Lima & Dill 1990). An example is moonlight avoidance. Nocturnal rodents that forage in relatively open habitats respond to moonlight by reducing activity outside their nests or burrows, and by shifting such activity towards areas of relatively dense cover (e.g. Lockard & Owings 1974; Price et al. 1984; Bowers 1988; Wolfe & Summerlin 1989). Artificial moon-like illumination elicits similar responses (Lockard 1975; Kotler 1984; Brown et al. 1988).

Although these behavioural responses have been assumed to reduce predation risk, no study of moonlight avoidance has incorporated data on actual predation events in the wild. Neither have researchers hitherto assessed the moon's influence on the spontaneous travels of nocturnal rodents in natural habitats, relying instead on measures of activity in enclosures and on visits to artificial food sources. Radio-tracking is a technique by which natural predation events can be detected and related to the behaviour of radio-tracked prey

(Daly et al. 1990), and by which the moon's effects on behaviour can be assessed without experimental interventions.

Kangaroo rats (*Dipodomys*, Heteromyidae) are predominantly granivorous, burrow-dwelling residents of western North American arid and grassy habitats. Kangaroo rats forage more in the open spaces between perennial shrubs than do sympatric granivorous rodents such as pocket mice (Lemen & Rosenzweig 1978; Thompson 1982; Price & Brown 1983), and their bipedal locomotion (Nikolai & Bramble 1983; Thompson 1985) and hypertrophied middle ear cavities (Webster 1962; Webster & Webster 1971) have been interpreted as adaptations to a high level of predation risk in their preferred foraging environment. Crucial decisions for kangaroo rats include the amount of above-ground activity to be undertaken each night and its distribution in time and space (Rosenzweig 1974; Behrends et al. 1986a, b). Daly et al. (1990) analysed 50 predation deaths among 176 radio-tracked Merriam's kangaroo rats, *D. merriami*, and found a strong association between recent surface travels and the risk of predation in both sexes, those animals who were most mobile being most at risk.

Rosenzweig (1974) proposed that the benefits of above-ground activity are likely to exhibit

<sup>\*</sup>Present address: Michael Brandman Associates, San Diego, CA 92130, U.S.A.

<sup>†</sup>Present address: Department of Psychology, University of Utah, Salt Lake City, UT 84112, U.S.A.

diminishing returns as time allocated to such activity increases within nights (e.g. as the most easily collected seeds are depleted and as information on the whereabouts and reproductive condition of conspecifics is updated), while the costs of exposure (predation risk, cold stress and evaporative losses) are likely to continue to rise with positive acceleration because animals can allocate activity preferentially to the lowest-cost times. Hence, there is an optimal amount of time allocated to such activity. With reasonable assumptions, that optimum is likely to decline if the cost curve rises while the benefit curve remains constant (see Rosenzweig's Fig. 1). If moonlight has little influence on the expected benefit curve, but substantially raises the predation risk cost of nocturnal activity, we may predict the following.

(1) Animals will reduce above-ground activity at the full moon as compared with the new moon.

(2) Animals will preferentially allocate above-ground activity to moonless times of the night.

Both of these predictions are upheld by data from captive enclosures (Wolfe & Summerlin 1989) and visits to artificial food sources in the field (Lockard & Owings 1974).

Much less attention has been paid to the issue of variations in predation risk in relation to changing light levels at dawn and dusk (Lima 1988). Many nocturnal rodents emerge from their burrows when light levels are still adequate to support hunting by such predatory birds as shrikes, roadrunners and various hawks and falcons. Self-regulated exposure to risk at these times may also vary with moon phase, not because of the moon's (minor) effect upon light levels at twilight, but because of the moon's influence on the available distribution of low-risk emergence times. In particular, if we assume that phase of the moon has relatively little influence on the predation risk costs of crepuscular activity as compared to its influence on the predation risk costs of nocturnal activity, we may make the following prediction.

(3) Curtailment of nocturnal activity at the full moon should be at least partially compensated by elevated crepuscular activity.

Such crepuscular compensation may be expected even at some cost in elevated predation risk by diurnal predators, because the incremental value of a given amount of crepuscular activity will be higher when nocturnal activity levels are lower. This reasoning also leads to a further, seemingly paradoxical, prediction.

(4) Any elevation of the predation rate, or components thereof, at the full moon will be disproportionately or solely imposed by day-active predators who do not actually exploit moonlight to hunt.

The present study tests these four predictions from radio-tracking data.

## METHODS

We radio-tracked Merriam's kangaroo rats during each of 10 consecutive winters from December 1980 to March 1990 at the Boyd Deep Canyon Desert Research Center near Palm Desert, California, U.S.A. We trapped kangaroo rats and other rodents in Sherman live traps ( $8 \times 9 \times 23$  cm until 1986;  $8 \times 9 \times 30$  cm since 1987) baited with rolled oats. We marked all kangaroo rats individually, by toe clipping until 1988 and by subcutaneous injection of Passive Integrated Transponder tags (Biosonics, Seattle, Washington) since 1989. We implanted SM-1 mouse-style radio transmitters (AVM Instrument, Dublin, California) subcutaneously, under Ketaset anaesthesia in the laboratory. Trapping schedules and our procedures for handling and radio-implanting animals are described in greater detail in Daly et al. (1990).

The study site, centred on a 1-ha grid of 100 trap stations in a  $10 \times 10$  array at 10-m intervals, is situated on an alluvial plain at about 250 m elevation. Labelled markers at 10-m intervals extend in all directions, permitting us to identify quickly any locus with a precision of 1 m. Eleven hectares are thus mapped, encompassing all positions at which we have ever located radio-implanted animals. Zabriskie (1979) described the reserve and its flora in detail; our site is essentially like one he described nearby, at which 14% of the soil surface lay under the canopy of perennial shrubs. Creosote bush, *Larrea tridentata*, is the most common shrub, but the most substantial areas of cover are provided by a few large Palo Verde trees, *Cercidium floridum*, the drooping boughs of which obscure up to about  $20 \text{ m}^2$  of sandy wash.

We determined radio locations (fixes) to a 1-m precision while walking through the study area with radio receivers (LA-12 receiver, AVM; or CE-12 receiver, Custom Electronics, Urbana, Illinois) and hand-held antennae; for a detailed description of the method of locating a signal source, see Madison

et al. (1985). We located each radio-implanted animal daily during daylight, and on tracking nights (usually all those other than trapping nights), we typically located each animal hourly, for anywhere from 6 to 14 consecutive hours. These hourly fixes provide the data base for analyses presented here.

Altogether, 179 individual kangaroo rats bore radios for 6516 radio-animal-nights (RAN), which were categorized into four moon phases as follows.

(1) Full Moon. The 7-day period centred on the date of full moon (1570 RAN).

(2) Waning Moon. Dates between Full and New phases (1679 RAN).

(3) New Moon. The 7-day period centred on the date of new moon (1592 RAN).

(4) Waxing Moon. Dates between New and Full phases (1675 RAN).

During the Waning Moon phase, the night was dark soon after sunset, with the moon rising from behind nearby hills between 2100 and 0330 hours. During the Waxing Moon phase, the night was initially bright until moonset, which occurred almost an hour later than moonrise on corresponding dates of the Waning phase because the western horizon was relatively low.

Analyses of predation risk in relation to moon phase are based on the full data set. Predation events were detected by direct observation of the predator still bearing the kangaroo rat's transmitter emitting a radio signal (8 cases), by the discovery of the discarded transmitter with (18 cases) or without (11 cases) other remains of the victim, or by abrupt disappearance under circumstances inconsistent with radio failure (14 cases). Criteria for concluding that predation had occurred are presented in greater detail in Daly et al. (1990), Table II of which provides further details on the first 50 incidents.

To eliminate variability in the times of sunrise and sunset, portrayal of the influence of moon phase on activity distribution through the night (Figs 1 and 2) is based on a smaller data set of 2386 RAN collected from 128 individuals. These constituted all scheduled hourly fixes collected within 3 weeks of the winter solstice (1 December to 11 January). Because the duration of radio-implantation episodes until predation or radio removal was highly variable and often less than a full lunar cycle, and because fieldwork was scheduled without regard to moon phase, an individual animal in a given year could have been

tracked in one, two, three or all four moon phases. The 2386 RAN were distributed among the four moon phases as follows. (For any pair of moon phases, the particular animals tracked constituted highly over-lapping but non-identical sets, and it is only by chance that the numbers of animals contributing data were identical for full and new moon phases and for waning and waxing phases.)

(1) Full Moon: 3252 fixes from 106 individuals in 561 RAN.

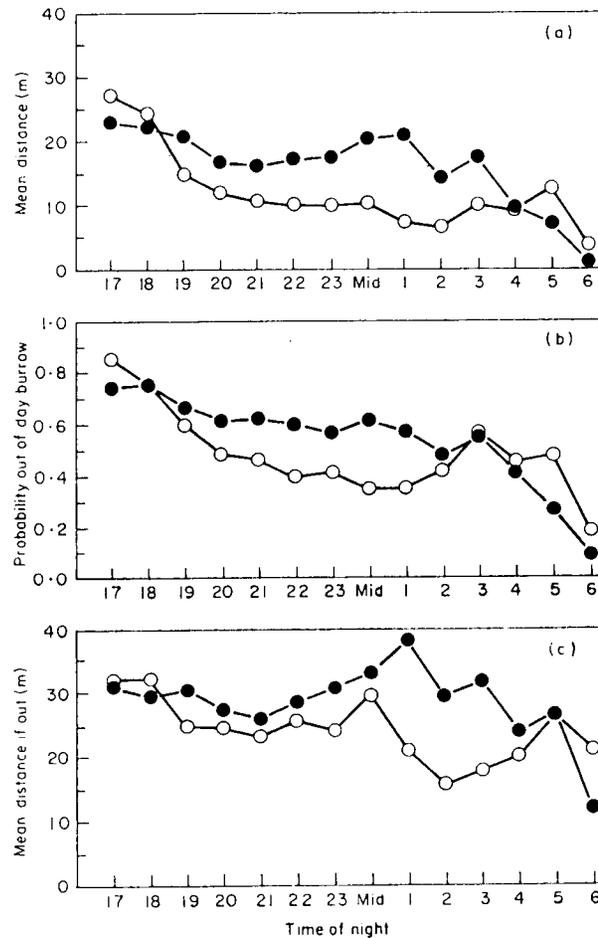
(2) Waning Moon: 2910 fixes from 101 individuals in 529 RAN.

(3) New Moon: 3889 fixes from 106 individuals in 673 RAN.

(4) Waxing Moon: 4043 fixes from 101 individuals in 623 RAN.

For these analyses, the critical data were whether the animal was away from its day burrow at a given scheduled radio fix, and, if so, how far away. (When approached for radio location, kangaroo rats may skulk under a shrub or in a nearby refuge, so fixes do not provide a direct index of the time spent in exposed sites.) Merriam's kangaroo rats on our study site virtually never changed locales during the day, but there was a probability of about 0.22 that the burrows occupied on successive days would be different (Behrends et al. 1986a). On such occasions, the shift of day burrow was considered to have occurred at that point during the night, which would minimize the sum of the distances from home for that night's radio fixes.

Hourly scheduled radio fixes are independent data points in the sense that the average distance between successive fixes for a given animal is not less than the average distance between any two fixes within the same night (Behrends 1984). Individual radio fixes are not independent, however, in the sense that there are differences between animals (e.g. persistent home range size differences), differences between years (e.g. animals were out of their day burrows more and travelled greater distances later in the study after prolonged drought and seed bank depletion), and short-term temporal differences (e.g. a cold spell may have suppressed activity during a particular moon phase in a particular year). Ideally, we would confine statistical comparisons (e.g. of activity at the Full Moon versus the New Moon at each hour of the night) to within animal/within-year contrasts where at least a few (say, three) radio fixes had been collected at each hour at each moon phase; unfortunately, this would eliminate most of the data from the analysis



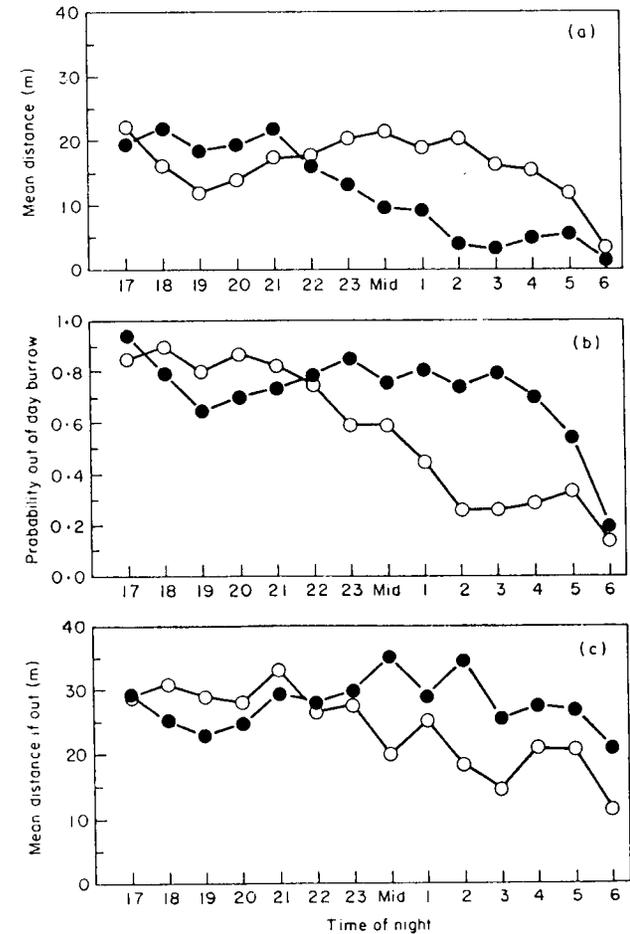
**Figure 1.** Above-ground activity as revealed by animals' locations at scheduled hourly radio fixes, during Full Moon (○) and New Moon (●) phases. All data are from dates within 3 weeks of the winter solstice; sunset occurred within the hour before the 1700-h radio fix and sunrise within the hour after the 0600-h radio fix. (a) The mean distance of animals' radio locations from their day burrows, (b) the probability of being outside one's day burrow and (c) the mean distance away from it when out.

Thus, to evaluate the differences between points in Figs 1 and 2, we present Mann-Whitney *U*-statistics as if each radio fix were independent. Violations of this independence assumption are unlikely to have produced a spurious appearance of pattern in the data, since 10 years of data and over 100 animals contributed to each figure, and since the patterns are smooth and meaningful; nevertheless, statistical tests of these data must be evaluated cautiously in light of their complex multiple non-independences.

## RESULTS

### Inhibition of Above-ground Activity under Moonlight

Above-ground activity was inhibited when the moon was full and high, in accordance with prediction (1). Figure 1 contrasts fixes at the Full Moon versus New Moon phases over the course of the night. For each of the nine hourly fixes designated 19–3, fixes occurred significantly further from home



**Figure 2.** Above-ground activity during Waning (●) and Waxing (○) Moon phases; format as in Fig. 1. During the Waning Moon phase, moonrise occurred between about 2100 and 0330 hours; during the Waxing Moon phase, moonset occurred between about 2200 and 0430 hours.

at the New Moon ( $P < 0.001$  by Mann-Whitney test in each case; Fig. 1a). There was also a downward trend in activity over the night.

Two potentially independent components of this mean distance, the probability of being out at each hour of the night and the mean distance from home if out, contribute, in similar fashion, to the effect of moon phase (Fig. 1b, c).

### Allocation of Activity to Moonless Times of Night

Figure 2 portrays the same information as Fig. 1 for quarter moon phases. In the Waning Moon

phase, activity was strongly concentrated in the early (dark) part of the night. In the Waxing Moon phase, activity was more evenly distributed through the night, with some suppression early under moonlight. The pattern is one of preferential allocation of activity to dark periods, in accordance with prediction (2), superimposed on a general downward trend over the night.

### Crepuscular Compensation

In accordance with prediction (3), the suppression of nocturnal activity under the Full Moon was

**Table 1.** The distribution across moon phases of incidents of predation upon radio-implanted kangaroo rats by diurnal versus nocturnal predators

Moon phase	RAYs*	Known diurnal predators (shrikes)		Known nocturnal predators		Unknown predators	
		N†	Deaths per RAY	N†	Deaths per RAY	N†	Deaths per RAY
Full Moon	4.30	4	0.93	0	0.00	7	1.63
Waning or Waxing	9.18	3	0.33	4	0.44	19	2.07
New Moon	4.36	0	0.00	6	1.38	8	1.84

\*RAY: radio-animal-year. One radio-animal-year = 365.25 animal nights of radio-bearing.

†Number of deaths.

partially offset by increased above-ground activity at dusk and dawn. This compensation is evident in Fig. 1, in which the generally lower activity at the Full Moon phase is reversed at the first two and last two fixes of the night. This double cross-over of the Full Moon and New Moon curves characterizes both the probability of being out and the distance from home if out.

The first evening radio fix (between 1700 and 1800 hours) was recorded in twilight: after sunset but before full darkness. Mean distance from home at the first fix was significantly greater at the Full Moon (27.1 m) than at Waning (19.6 m), New (22.9) or Waxing (22.2) Moon phases ( $P < 0.01$ , Mann-Whitney  $U$ -test for each comparison).

The last morning fix was recorded under a light sky shortly before sunrise, and fainter signs of dawn were typically evident for the preceding fix (between 0500 and 0600 hours) as well. At both fixes, mean distance scores at Full Moon (12.6 and 3.8 m) significantly exceeded corresponding scores for Waning (5.4 and 1.2 m) and New (7.1 and 1.1 m) Moon phases ( $P < 0.01$ , Mann-Whitney  $U$ -test for each comparison), but were not significantly greater than scores at the Waxing Moon (11.7 and 3.2 m).

#### Predation in Relation to Moon Phase

Gross predation rates were not significantly different between moon phases. Eleven kangaroo rats were killed in the Full Moon phase (2.56 deaths per Radio-Animal-Year), 13 in the Waning phase (2.83), 14 in the New Moon phase (3.21), and 13 in the Waxing phase (2.83).

Predators were identified in 17 of the 51 predation incidents. Seven kangaroo rats were killed by a diurnal predator, the loggerhead shrike, *Lanius ludovicianus*, observed at the study site in all

10 years. These cases were identified on the basis of the shrike's characteristic treatment of the victim, whose cranium and upper chest cavity were pecked open and brain and viscera removed. (One was then impaled on a cactus spine.) No other avian predator in the region is known to process prey in this way. Ten other kangaroo rats were killed by a variety of predominantly nocturnal hunters: three by great horned owls, *Bubo virginianus*, three by common whipsnakes, *Masticophis flagellum*, and one each by a red rattlesnake, *Crotalus ruber*, a speckled rattlesnake, *C. mitchelli*, a sidewinder, *Crotalus cerastes*, and a coyote, *Canis latrans*.

Table 1 presents the frequencies and rates of predation by known diurnal predators (shrikes) and nocturnal predators, as a function of moon phase. Shrikes captured kangaroo rats mainly in the Full Moon phase and never in the New Moon phase, with an intermediate rate of predation in the intermediate (Waxing and Waning) phases. Nocturnal predators exhibited precisely the opposite pattern.

Moses (1986, page 417) provides a  $t$ -test approach to the comparison of counted data in ordered categories. By this test, with moon phase ordered Full > (Waxing = Waning) > New, the lunar distributions of predation by shrikes versus known nocturnal predators were significantly different ( $t = 4.54$ ,  $df = 15$ ,  $P < 0.001$ ). Moreover, the lunar distribution of the seven known shrike predations ( $t = 2.70$ ,  $df = 49$ ,  $P < 0.005$ ). These comparisons confirm prediction (4), in that it was diurnal predators that were especially successful at the Full Moon phase.

#### DISCUSSION

Merriam's kangaroo rats modulated predation risk by allocating above-ground activity away from

moonlit periods, confirming predictions (1) and (2). Preferential allocation of activity to the moonless part of the night was superimposed upon a downward trend in activity through the night, such that if the Waxing Moon phase were considered alone, activity would appear to be little affected by moonset (Fig. 2); it is the contrast with the Waning Moon phase that makes moonlight's relevance clear. The decline in activity through the night roughly paralleled declining average temperatures. Nightly lows near the winter solstice typically fall below 10°C and often below 5°C, and comparisons across variably cold nights suggest that it was these cold temperatures that inhibited above-ground activity as the night progressed: the effects of time of night upon mean distance moved between successive fixes were essentially accounted for by the effects of temperature (Behrends 1984).

Kangaroo rats increased their crepuscular activity at the Full Moon, when the danger of such activity relative to that of nocturnal activity was presumably lowest, confirming prediction (3). The absolute danger of crepuscular activity, however, is unlikely to be much affected by moon phase, and the predictable consequence was that the rate of predation by shrikes exhibited the same pattern as did crepuscular exposure: Full Moon > Waxing or Waning > New Moon. Nocturnal exposure exhibited the reverse pattern (New Moon > Waxing or Waning > Full Moon), confirming prediction (1). Predation by known nocturnal predators was similarly maximal at the New Moon and minimal at the Full Moon.

The fact that differential influence of moon phase on diurnal shrikes versus predominantly nocturnal predators was highly significant, on the basis of just 17 cases involving known predators, implies that the genuine effect of moon phase is substantial. Indeed, there were no known shrike predations in the New Moon phase and no known predations by predominantly nocturnal animals in the Full Moon phase. We doubt that such an extreme contrast would persist if the 34 victims of unknown predators could be classified, but they cannot. We might assume that the 14 animals that disappeared abruptly must have been transported beyond detection range and hence further than a shrike could carry them, but we could not then assume that they fell victim to predominantly nocturnal predators, since there is at least one other diurnal/crepuscular predator capable of such transport: greater roadrunners, *Geococcyx californianus*, are frequently seen on our site and

have been observed to prey upon kangaroo rats nearby (J. Foott, personal communication).

Prediction (4) was confirmed in that diurnal predators benefited from the Full Moon more than nocturnal predators. However, our theorizing did not predict that nocturnal predation would actually reverse the moon phase pattern of diurnal predation. Even if kangaroo rats are less active under moonlight, their increased visibility might have kept the predation rate at the Full Moon as high as at the New Moon, or higher. Such was not the case, however. Despite the depredations of shrikes, the overall risk of predation, although not significantly related to moon phase, was actually maximal at the New Moon and minimal at the Full Moon, just the opposite of what might be supposed from simple consideration of the likely influence of moonlight on detectability. Webster & Webster (1971) followed the survival of hearing-impaired *D. merriami* and two control groups by frequent retrapping, and noted that almost all of 13 disappearances occurred near the new moon. Price et al. (1984) cite this result as an anomaly: 'Contrary to what one would expect, their results suggest that kangaroo rats are less vulnerable during moonlit periods, for reasons unknown'. However, because Webster & Webster (1971) released all their experimental and control animals during the waning and new moon phases, and because the study lasted less than a month, disappearance at the new moon was essentially synonymous with almost immediate disappearance, and the apparent relevance of moon phase may have been an artefact. Nevertheless, our gross predation rate data are weakly in the same direction.

But would maximal predation risk at the new moon, if confirmed, actually be contrary to expectation? If a kangaroo rat had a small requisite amount of above-ground activity to engage in monthly, and were free to allocate it to the lowest-risk times, it might be optimal to allocate it all to dark nights: the consequence could be that all predation occurs at the new moon and none at the full moon, even though moonlit nights are riskier per unit of time of exposure. Conversely, if there are new benefits to be garnered from above-ground activity each night, and such benefits reach an asymptote that is affected only by the present night's excursions and not those of previous nights, it could be optimal to budget surface time in such a way that predation became maximal at the full moon. Thus, no expected distribution of total predation over the lunar cycle can be specified without

some empirical or theoretical specification of how the expected benefits of above-ground activity are influenced by prior allocations within and across nights. A complex multi-party game theory may be required, since predators can also re-allocate efforts in response to the behaviour of their prey and since the expected benefits of risky activity will be affected by the activity patterns of both conspecifics and other seed-gathering competitors. In the absence of such a complete theory, it is still possible to predict and demonstrate lunar variation in differential risk from different suites of predators, as demonstrated here.

Moonlight has previously been shown to inhibit kangaroo rats from visiting baited sites in open terrain, but this is the first demonstration of such effects in the absence of artificial lures. It is also the first study to show complementary effects of moonlight on both the time spent outside the day burrow and the average distance away from it, the first to predict and demonstrate crepuscular compensation for nocturnal inhibition of activity, and the first to provide evidence on natural predation events in relation to the lunar cycle.

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