Mortality by moonlight: predation risk and the snowshoe hare

Paul C. Griffin,[a] Suzanne C. Griffin,[a] Carl Waroquiers,[b] and L. Scott Mills[a]
[a]Wildlife Biology Program, University of Montana, Missoula, MT, 59812, USA, and
[b]Institut National Agronomique Paris-Grignon, 16 rue Claude Bernard, Paris, 75231, France

Optimal behavior theory suggests that prey animals will reduce activity during intermittent periods when elevated predation risk outweighs the fitness benefits of activity. Specifically, the predation risk allocation hypothesis predicts that prey activity should decrease dramatically at times of high predation risk if there is high temporal variation in predation risk but should remain relatively uniform when temporal variation in predation risk is low. To test these predictions we examined the seasonably variable response of snowshoe hares to moonlight and predation risk. Unlike studies finding uniform avoidance of moonlight in small mammals, we find that moonlight avoidance is seasonal and corresponds to seasonal variation in moonlight intensity. We radio-collared 177 wild snowshoe hares to estimate predation rates as a measure of risk and used movement distances from a sample of those animals as a measure of activity. In the snowy season, 5-day periods around full moons had 2.5 times more predation than around new moons, but that ratio of the increased predation rate was only 1.8 in the snow-free season. There was no significant increase in use of habitats with more hiding cover during full moons. Snowshoe hares' nightly movement distances decreased during high-risk full-moon periods in the snowy season but did not change according to moon phase in the snow-free season. These results are consistent with the predation risk allocation hypothesis. *Key words:* moonlight, moon phase, movement, predation rate, predation risk, prey behavior. *[Behav Ecol 16:938–944 (2005)]*

Prey animals commonly reduce activity levels in response to stimuli signaling high predation risk, decreasing encounter rates with predators (Lima, 1998a). Optimal prey behavior increases fitness by minimizing exposure to predation, while satisfying energetic needs for survival and reproduction (Ghalambor and Martin, 2001; Rosenzweig, 1974; Sih, 1980). If predation risk is temporally uniform—whether that risk is high or low—then prey should exhibit little variation in anti-predator response (Houston et al., 1993; Lima and Bednekoff, 1999); under uniform predation risk, prey should reduce their activity as much as possible, while still feeding enough to meet metabolic requirements. However, strong temporal variation in predation risk alone should dramatically reduce prey activity levels during very dangerous periods and increase activity during relatively safer periods (Lima and Bednekoff, 1999; Sih et al., 2000). Taken together, these two joint predictions are central to the "predation risk allocation hypothesis" (Lima and Bednekoff, 1999); they have not been tested in wild vertebrates, where reproduction and year-round survival determine fitness.

An alternate hypothesis predicting prey behavioral responses to variation in predation risk is the "minimize μ/g hypothesis" ("μ/f" in Gilliam and Fraser, 1987; Lima, 1998a), where μ is predation risk and g is the foraging rate or associated growth rate. One prediction of this hypothesis is that, given equal foraging quality in different patches, prey species will shift their habitat use to safer habitats. A corollary prediction of this hypothesis as applied to behavior is that, if forage quality is constant, then there should be an incremental increase in antipredator behavior for every incremental increase in predation risk.

Tests of these predictions rely on quantification of temporally variable predation risk and synchronous behavioral responses. Two common behavioral responses to stimuli of increased risk are reduced activity and a shift to safer habitats (Lima, 1998a,b; Lima and Dill, 1990). Laboratory and field-enclosure experiments have assessed the predation risk allocation hypothesis by simulating variable risk with the scent of depredated conspecifics or predators or the nearby presence of predators themselves (Koivisto and Pusenius, 2003; Pecor and Hazlett, 2003; Sih and McCarthy, 2002; Van Buskirk et al., 2002), without directly measuring the risk of predation (but see Lehmann et al., 2004). Field-based experiments that manipulated predator scent or scat (Orrock et al., 2004; Sundell et al., 2004) also have not estimated the predation risk facing prey animals under different conditions. Here, we distinguish predation risk—an individual's probability of being depredated per unit time—from predation rate, which is the actual mortality rate that results as a function of both predation risk and antipredator behavior. If prey behavior could be held constant, then predation rate would be a direct measure of predation risk. However, as a metric of predation risk, the predation rate can be biased low at times when prey reduce movement or move to safer habitats.

Many researchers have used moonlight variation over the 29.5-day lunar cycle as a proxy for risk from predators (reviewed in Lima, 1998a,b; Lima and Dill, 1990; also see Orrock et al., 2004). If predation rates depend on moonlight, then the moon's phase provides regular temporal variation in predation risk. Several studies have manipulated predation risk and/or light conditions in rodents, finding prey responses in movement rate or microhabitat use shifts (Bouskila, 1995; Falkenberg and Clarke, 1998; Kotler, 1984; Kotler et al., 1991, 1994; Longland and Price, 1991; Orrock et al., 2004). Few studies, though, have actually demonstrated that light from the full moon simultaneously increases predation rate and changes prey behavior in the wild (Lima, 1998a). In one exception, kangaroo rats (*Dipodomys merriami* Mearns) were found to have decreased activity and increased predation rates

during the full moon (Daly et al., 1992), but the results were limited to the winter season, when differences in illumination between full and new moons are greatest. In no study has the effects of variable lunar illumination on predation risk been explored in different seasons.

If moon phase is correlated to predation risk, then the relative increase in predation risk during the full moon, as compared with the new moon, should be greater when the full moon's light is particularly bright. The contrast in light levels between new-moon and full-moon phases is greatest in winter in the northern hemisphere, when the moon's path is most directly overhead. Seasonal variation in the moon's path through the night sky changes the variance in ambient moonlight between proximate new moons and full moons. For example, in Montana, on a clear January night the full moon usually rises to ~60° or more above horizontal and has an illumination intensity ≥ ~0.2 lux; in contrast, the full moon is at a shallower angle of only ~20° above horizontal in July, illuminating at ≤ ~0.08 lux (Janiczek and DeYoung, 1987). This seasonal difference in moonlight variance becomes even more pronounced further north, where in some years the moon shines above the horizon for more than 72 h. Moreover, foliage in summer can shade the ground from moonlight, but a lack of deciduous foliage and the high reflectance of snow in some biomes can further increase ambient moonlight at ground level in winter.

Snowshoe hares (*Lepus americanus* Erxleben) are prey for many nocturnal forest carnivores including Canada lynx (U.S. Fish and Wildlife Service, 2000), *Lynx canadensis* Kerr, and most snowshoe hare mortality is due to predation (Boutin et al., 1986; Wirsing et al., 2002). Snowshoe hares forage almost exclusively in twilight and night (Foresman and Pearson, 1999; Keith, 1964; Mech et al., 1966) and may avoid open areas during moonlit nights in winter (Gilbert and Boutin, 1991). Females aged 1 year and older reproduce in up to three or four synchronous birth pulses per summer (Keith, 1990). Other reproductive behaviors are also synchronous because female receptivity to fertilization is highest within days of parturition. The annual survival rates for adults are low (≤32%, Hodges et al., 2001; ≤18%, Wirsing et al., 2002). As a result, current reproduction in a given summer should contribute more to fitness than survival and reproduction in the next summer (sensu Rosenzweig, 1974).

We tested whether snowshoe hares follow both predictions of the predation risk allocation hypothesis in response to measured changes in predation risk associated with moon phase. We measured movement rate and habitat use behaviors and used predation rate as an empirical measure of predation risk. We used a natural experiment (Diamond, 1986) to evaluate the effect of moonlight on snowshoe hare predation rate and behavior in snowy and snow-free conditions. Moon phases and seasons were natural perturbations, and individual snowshoe hares were experimental units whose response in terms of survival, movement, and habitat choice could be evaluated. At the latitude of the study site, variation in moonlight intensity from full to new moon depends on the season, with highest expected variation in moonlight levels in winter, and lowest expected variation in summer. The predation risk allocation hypothesis in this context predicts that, regardless of the average predation risk across the 29.5-day lunar cycle, variation in snowshoe hare antipredator behavior should be low when temporal variation is low for both lunar illumination and predation risk and high when temporal variation is high for both lunar illumination and predation risk. Snowshoe hares are predicted by this hypothesis to have a marked antipredator response if predation risk is only intermittently high. The minimize μ/g hypothesis in this context predicts that antipredator behavior should increase whenever lunar illumi-

nation and predation risk increase. To test predictions of these hypotheses, we estimated predation risk, activity levels, and habitat choice empirically based on observed patterns of predation, movement, and habitat choice in a population of wild snowshoe hares.

MATERIALS AND METHODS

Study sites

Snowshoe hares in the survival analysis were on Richmond Ridge and Spring Creek, two areas encompassing more than 5 km² and separated by ~25 km in Montana's Seeley Lake region (47.3° N, 113.5° W). There are ongoing studies of Canada lynx in the region (Squires and Laurion, 2000); other locally common snowshoe hare predators include coyote (*Canis latrans* Say), bobcat (*Lynx rufus* Schreber), American marten (*Martes americana* Miller) Great horned owl (*Bubo virginianus* Gmelin), and Red-tailed hawk (*Buteo jamaicensis* Gmelin). Fire and forest management here has resulted in a forest vegetation structure mosaic, with variation in canopy cover and forest understory, so that sampled snowshoe hares inhabited multiple structural types found at both sites.

All snowshoe hares in analyses of movement were on Richmond Ridge. Demographic studies that we have conducted since 1998 provided data concerning the timing of reproductive activity in the summers of 2000 and 2001. At Richmond Ridge during this study we observed evidence of parturition on 25 June–1 July 2000, 30 July–8 August 2000, 31 May–3 June 2001, 5–15 July 2001, and 11–19 August 2001. Conditions in the June 2001 full moon were snowy due to an unseasonable 1-day storm on 3 June that deposited >50 cm of snow, an amount >20 times the average total snowfall for the entire month of May and June combined.

Model selection and parameter estimation

We used model selection to assess the parsimony of candidate models to the mortality or movement data based on corrected Akaike's Information Criterion (AICc) values (Burnham and Anderson, 1998). For a given data set, the AICc value for each model quantifies its parsimony, relative to other models considered, because AICc values quantify a tradeoff between the fit of a model and the number of parameters. Lower AICc values imply greater parsimony, and differences in AICc values of less than two imply roughly equal parsimony. Corresponding Akaike weights for each model, which sum to one, reflect the relative strength of evidence in support of that model and its associated parameter estimates, given the data and the models considered. We then estimated parameter values for predation rate and movement distance by model averaging, weighting estimates from each of the models according to their Akaike weight (Burnham and Anderson, 1998).

Predation risk

We monitored survival in 177 adult and large juvenile (≥500 g) radio-collared snowshoe hares for 32 lunar cycles (each of 29.5 days) from August 1999 to April 2002. We checked for survival every 7 days or less, barring logistical problems (e.g., fire-related road closures in summer 2000). Radio-collars were equipped with mortality switches that activated after ~6 h of motionlessness. Of 115 observed mortalities, only three were censored from analyses because predation did not cause death. To assess a simple index of predation risk in snowy or snow-free seasons, we examined the distribution of predation in two broad categories of moon phase: a 14-day period including the full moon and a 15.5-day period including the new moon.

Table 1

Moon phase and dates of intensive snowshoe hare movement observation periods, with sample size of snowshoe hares (n), and snow condition on the ground at that time

Moon phase and dates	n	Snow condition	Maximum lunar illumination
Full, 13–19 July 2000	12	Snow-free	0.084
New, 28 July–3 August 2000	12	Snow-free	0.00093
Full, 6–11 February 2001	7	Snowy	0.20
New, 21–25 February 2001	7	Snowy	0.00016
Full, 7–11 March 2001	9	Snowy	0.19
New, 19–23 May 2001	9	Snow-free	0.00006
Full, 4–8 June 2001	9	Snowy	0.055
New, 18–22 July 2001	9	Snow-free	0.00013
Full, 2–6 August 2001	10	Snow-free	0.073
New, 11–15 January 2002	10	Snowy	0.00006
Full, 25–30 January 2002	7	Snowy	0.23

Maximum lunar illumination (lumens/m^2) during the 5-day period is estimated based on the moon's proximity to the earth and angle above the horizon (Janiczek and DeYoung, 1987), ignoring reflection by snow or shading by cloud cover or vegetation.

Each snowshoe hare's date of death was estimated to be halfway between the dates of its last recorded "live" radio signal and first detected "mortality" signals (the "uncertainty interval"). This time interval was ≤7 days for 51 hares; deaths of these hares can be associated quite precisely with a given point on the lunar cycle. Although using those mortality data alone underestimates true predation rates, deaths of hares with longer intervals cannot as clearly be associated with a particular moon phase. Therefore, hares that died with uncertainty intervals of >7 days were not included in survival rate analyses after the date of their last recorded live radio signal. Patterns of predation rates were qualitatively the same when we analyzed the data with wider uncertainty intervals of ≤10 days based on 77 mortalities (Griffin PC and Mills LS, unpublished data).

Because we measured movement in 5-day periods (see below), we defined risk as the estimated predation rate for a 5-day period, centered either on a full moon or a new moon. A simple index of predation risk, the number of radio-collared hares that die during broad categories for full-moon or new-moon periods in each season may not be an accurate measure of actual risk. To estimate empirical risk (predation rates) we used as data the number of hares that were monitored with radio telemetry each day and the number of hares that died. We used those survival data to test six models against the data, using the known fate model routine in program MARK (White and Burnham, 1999). Program MARK yields AICc values that quantitatively rank model parsimony of multiple models that could explain observed patterns of survival, and also gives maximum likelihood parameter estimates for survival rates based on each model.

We tested six models against our survival data, using program MARK. These models reflected our understanding that variation in moon phase was potentially an influence on predation risk and that such a lunar effect might be more pronounced in the winter. (1) The simplest model, S(.), estimated a single, temporally uniform daily survival rate. (2) S(snow effect) estimated one uniform daily survival rate for all "snowy" days when snow on the ground was widespread and a second uniform daily survival rate for all "snow-free" days without widespread snow. Dates delimiting these seasons were based on our observations and data from U.S. Forest Service Seeley Lake ranger station (~15 km from sites). (3) For S(moon trend), the estimated daily survival rate was a function of a covariate that cycled with moon phase; the covariate for each date was the number of days to the nearest

full moon, ranging from 0 to 15. For every day closer that a day was to a full moon, the moon trend effect could incrementally decrease survival rate. Thus, under model S(moon trend), the daily survival rate 9 days from a full moon could be higher than on the day of the full moon but lower than on the day of the new moon. (4) S(snow effect and moon trend) included separate parameters that allowed for a single year-round effect of moon phase and two different baseline survival rates during snowy versus snow-free conditions. (5) S(moon trend only in winter) only included the effect of a moon trend when the ground was snowy; when the ground was not snowy there was a temporally uniform daily survival rate. (6) S(snow effect and seasonal moon trend) allowed for two different baseline survival rates during snowy versus snow-free seasons and also allowed for different magnitudes of a moon-phase effect in each of those seasons.

We used model averaging to estimate daily survival rates for the 5 days centered on the full or new moon. Survival probabilities are multiplicative, so risk for a 5-day period was one minus the product of those five daily survival rate estimates, expressed as a percentage.

Movement

To examine movement patterns we located 7–12 snowshoe hares once per day and once per night during 5-day observation periods centered on full or new moons (10 locations per animal per 5-day period). To contrast the seasonal effects of moonlight, we limited our observations on movements in two ways: to the 5 days nearest new- and full-moon phases, and to summer and winter (Table 1). In each 5-day period, the nine "movement distances" for each hare were the discrete, linear distances between its consecutive day-to-night and night-to-day locations. Day locations were between 1 h after sunrise and 1 h before sunset. Night locations were between 1 h after sunset and 0.5 h before sunrise. Any missed location for a snowshoe hare reduced the number of sequential movement distances by two. The order of animals located varied between nights.

To control for effects of habitat, sex, and individual variation in movement, we followed the same individual snowshoe hares over multiple moon phases so that moon phases were, in effect, treatments applied to all individuals simultaneously. The sample was chosen from the pool of radio-collared snowshoe hares available at the study site, with attempts to balance the number of males and females and the attempts of sampled

animals in different types of vegetation structure. If individuals died, we located additional snowshoe hares in subsequent moon phases.

Universal Transverse Mercator coordinates for all locations were recorded with handheld global positioning system recorders (<10 m inaccurate). For 933 locations we determined snowshoe hare locations by sight or heard transmitter signals without an antenna, indicating proximity of <15 m (Griffin PC, Olson N, Landro A, and Mills LS, unpublished data). If radio signals indicated that a hare was moving away from us as we approached, we did not record a location for that hare. A smaller number ($n = 132$) of triangulated locations made only in July–August 2000 were estimated using program TelLoc7 (McDaniel G, unpublished data), with uncertainty being estimated using the location error method (Zimmerman and Powell, 1995). Triangulating observers were, on average, within 70 m of the snowshoe hare (SE = 4.8 m), with mean location uncertainty being 46 m (SE = 2.3 m). Exclusion of triangulated locations would not have changed the qualitative results of the study.

The five candidate models for estimating movement distance included: two categorical variables, snow (snowy or snow-free) and moon phase (full or new) and an interaction between snow and moon phase. We used Akaike weights from AICc values to identify the most parsimonious model for movement and tested for variation in movement distances by comparing model-averaged estimates for the expected length of one movement distance under full-moon and new-moon phases in each season. Single measures of movement distance were the dependent variable in mixed-model ANOVAs. The hierarchically nested structure of mixed models allowed us to test for differences in movement distance length in each season and moon phase, while accounting for variation due to individual hares. Individual snowshoe hares ($n = 34$) were treated as a random effect, rather than using each distance from a single animal as independent.

It was not possible to use light meters to quantify light levels at the 1033 hare locations throughout the forested study area. Therefore, each night of full-moon observation periods we recorded relative light level as bright or dark based on visibility of shadows (Gilbert and Boutin, 1991) on a road with no canopy overhead. This distinction is not quantitative, but it is an informative measure of light levels across the entire study site; when moon shadows were not visible in open habitats, it was because clouds prevented direct moonlight from reaching the ground. Full-moon nights with intermittent shadows were considered dark. Even the darkest of full-moon nights were always brighter than any new-moon nights because of the diffuse moonlight that penetrated clouds. We compared the fit of two mixed-model ANOVAs to displacement data from full-moon nights only; one model had an effect of clouds (differentiating bright and dark nights) whereas the simpler model did not.

Habitat use

Snowshoe hares might be expected to avoid open vegetation types during periods when the risk of predation is high (Gilbert and Boutin, 1991). We were able to quantify changes in habitat use that individual hares might have exhibited because we associated each hare location with one of four vegetation structure types found at the site.

The four vegetation structure types represent contrasts in forest stand age (young versus mature) and stem density (dense versus open) based on sampling 11–26 vegetation plots per stand (Griffin PC and Mills LS, unpublished data). The relatively homogeneous forest stand areas ranged from ~5 to ~50 ha. Trees at both study sites were almost exclusively
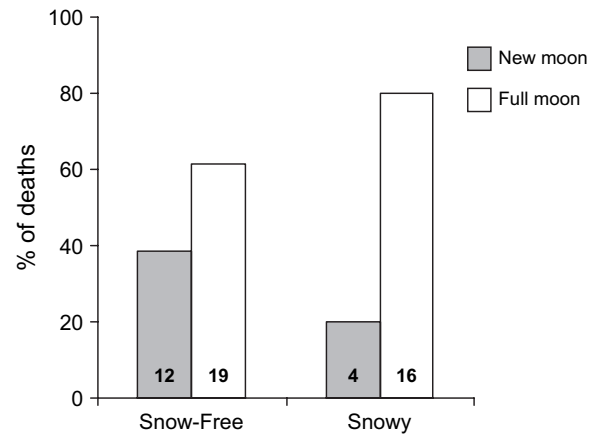

Figure 1
Observed mortality under two moon-phase categories. More snowshoe hares died during the 14 days around full moons (white bars) than the 15.5 days around new moons (gray bars). The number of deaths under the full moon was significantly higher when the ground was snowy (right pair; $n = 20$; $\chi^2 = 7.2$; $p = .0073$) but not when it was snow free (left pair; $n = 31$; $\chi^2 = 1.58$; $p = .21$). The sample size for each moon and season category based on a 7-day uncertainty interval is shown on each bar.

coniferous. We defined forest stands with >5600 saplings/ha as "dense sapling" type. "Open sapling" type of regenerating conifers had <3360 saplings/ha. Saplings were trees >0.5 m tall, but with <10 cm diameter at 1.4 m height. Both "dense mature" and "open mature" stands had tree basal area >13.8 m^2/ha, but dense mature stands had >40% overhead canopy cover, while open mature stands had <30% overhead canopy cover. Open sapling and open mature types had generally less hiding cover but potentially higher hare forage quality because of higher light levels near the ground. Forest stand edges were resolved to ≤15 m uncertainty.

For each hare in the movement analysis, we contrasted the vegetation type of its five nighttime (active) locations in a 5-day full-moon observation period with those from the paired new-moon period. Thus, habitat use could be contrasted within single hares for nights of different moon phase. We used paired t tests to test for a decrease in the number of nighttime locations in open vegetation type use during the full-moon phase, testing snowy and snow-free seasons separately. Individuals who were not alive for both 5-day observation periods in a pair were not included in the analysis.

Seasonal 75% fixed kernel home ranges (Seaman and Powell, 1996) for individual snowshoe hares generally included two or more of the vegetation structure types, so routine movements between foraging habitats with different vegetative structures were possible. Seasonal home range areas were ~5 to ~15 ha in this study (Griffin PC, Landro A, Waroquiers C, and Mills LS, unpublished data), which is consistent with other studies (Hodges, 1999).

RESULTS

The increased proportion of death in days near full moons was higher than expected by chance in snowy, but not snow-free, conditions. Eighty percent of observed predation when the ground was snow covered occurred when the winter moon was half or more full (Figure 1).

The relative increase in predation rate due to the full moon was also greater during snowy conditions than during snow-free conditions (Figure 2). Four models for snowshoe hare survival that had roughly equal parsimony all included an effect of moon phase (Table 2). Two of those, S(moon trend)
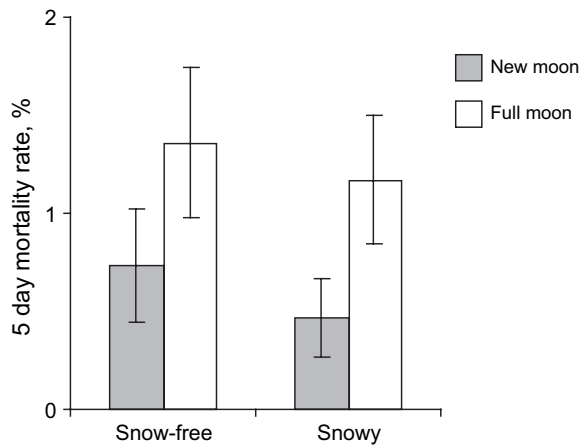
Figure 2
Estimated 5-day predation risk in different moon phases and seasons. Predation risk was higher in the 5 days centered on the full moon (white bars), compared with the new moon (gray bars). Full moons were relatively more risky when the ground was snowy (right pair) than when it was snow free (left pair). Estimates are ± 1 SE.

Figure 3
Estimated movement distances for snowshoe hares under new moons (dark circles) and full moons (open circles) in different seasons. Snowshoe hares reduced movement under full moons when conditions were snowy (right pair) but not when conditions were snow free (left pair). Estimates are ± 1 SE.

and S(snow effect and moon trend), included a moon-phase effect throughout the year, and the two others, S(moon trend only in winter) and S(snow effect and seasonal moon trend), allowed for a different effect of the moon on survival during the snowy season. Model-averaged predation rate estimates indicate that moon phases closer to full increased risk in both seasons, but that increase was dramatically greater in snowy conditions (Figure 2).

The average estimated 30-day predation rate was 4.4% in snowy conditions and 5.8% in snow-free conditions. However, variance in predation rate was greater in snowy conditions. In snowy seasons the estimated predation rate in the 5-day period of a full moon was larger by a factor of 2.5 than in the 5 days of a new moon. In snow-free seasons that increase in predation rate was by a factor of 1.8. To illustrate, in snowy conditions, over the course of six 5-day new-moon periods a hare would be subject to a 2.8% total predation rate, but 6.8% in six 5-day full-moon periods. In contrast, the estimated predation rate over six 5-day new-moon periods in snow-free conditions was 4.3%, and 7.8% for six corresponding full-moon periods.

Table 2
Comparative ranking of six daily survival models for snowshoe hares

Model	ΔAICc	AICc weight	K
S(moon trend)	0.00	0.30	2
S(snow effect and moon trend)	0.30	0.26	3
S(moon trend only in winter)	0.56	0.23	2
S(snow effect and seasonal moon trend)	1.76	0.12	4
S(.)	3.45	0.05	1
S(snow effect)	4.15	0.04	2

There is an effect of moon phase in the four most highly ranked models. Columns show differences in AICc values (ΔAICc) from the highest ranked model, AICc weights, and the number of parameters (K) associated with each model.
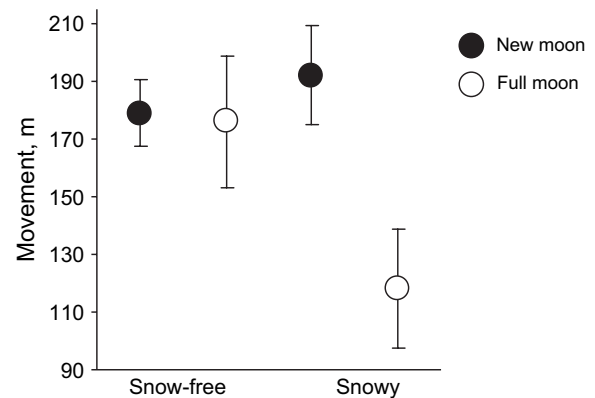
Snowshoe hares moved shorter distances during all winter full-moon observation periods than during winter new-moon periods (Figure 3). Under the most parsimonious model for movement, when the ground was snow covered snowshoe hare movement distances under full moons were 74 m shorter (SE = 27 m) than during new moons—a reduction of ~40% in movement (Figure 3). This model included parameters for snow, moon, and a snow × moon interaction; the Akaike weight was 0.9999, indicating a far better fit than any other candidate model.

In contrast to winter, the full moon in snow-free conditions was not associated with lowered snowshoe hare movement except during the unusually snowy observation period in early June 2001. Instead, summer observation periods with the lowest mean distances moved (July–August 2000 new moon, June 2001 full moon, and July 2001 new moon) and coincided closely with birth pulses. Snowshoe hares of both sexes appeared to decrease movement during 5-day periods near parturition, as compared with nearby periods without parturition.

The light level itself was the likely stimulus for reduced movement in winter. Considering movement only on full-moon nights during snowy conditions, snowshoe hares moved slightly more when clouds darkened the moon based on the criterion of being able to see a shadow in an open area (Gilbert and Boutin, 1991). Despite the fact that some cloudy full-moon nights with rather bright, but diffuse, light were classified as dark, snowshoe hares moved 21.3 m (SE = 11.7 m) more on cloudy (dark) winter full-moon nights than on clear (bright) winter full-moon nights.

Individual snowshoe hares did not significantly decrease their use of open vegetation types in 5-day full-moon observation periods when compared with 5-day new-moon observation periods. There was no significant shift away from dangerous habitats under full moons in either season: snowshoe hares decreased their use of open vegetation types under the full moon by only 0.8% in snow-free periods (SE = 23%; df = 27; one-tailed p = .43) and 5% in snowy periods (SE = 22%; df = 13; one-tailed p = .36). Apparently, changes in movement were the main antipredator response to short-term changes in predation risk.

DISCUSSION

Our observations over 2.5 years from a wild population are consistent with two central predictions of the predation risk

allocation hypothesis (Lima and Bednekoff, 1999), which has heretofore not been tested in a wild prey population facing measured predation risk. First, predation rates were highly variable in winter. Snowshoe hare movement in winter decreased during 5-day observation periods of brightest illumination (and highest relative danger) and increased during the contrastingly darkest, safest 5-day periods. When the ground was snowy, the predation rate increased by a factor of 2.5 in 5 days near the full moon as compared with 5 days near the new moon (Figure 2)—this despite hares' marked antipredator behavior (Figure 3). This suggests that the increase in risk under winter full moons was even greater than the realized increase in predation rates. There was no biologically or statistically significant shift away from "open" vegetation structure types during full moons. Thus, change in habitat use was not apparently an antipredator behavior that snowshoe hares used at times of high predation risk. Because snowshoe hares did potentially decrease their encounter rates with predators by decreasing their movement during times with relatively high predation risk, our winter results are consistent with predictions of both the predation risk allocation (Lima and Bednekoff, 1999) and minimize μ/g (Gilliam and Fraser, 1987; Lima, 1998a) hypotheses.

In winter, temporally predictable, cyclic regularity of low and high risk may facilitate the behavioral response we observed: snowshoe hares moved lesser distances when the risk of predation was intermittently high. During brief periods of reduced winter activity, low food intake or consumption of lower quality food could reduce fitness. However, because survival until the summer breeding season is essential for individuals to have any fitness at all, behaviors that lead to higher winter survival should be favored by natural selection. We speculate that reduced movement in winter full-moon periods could be compensated by foraging relatively more during predictably dark, safe periods when the moon is not high above the horizon. With every day further from the full moon, there are approximately 50 min more darkness during which foraging should be relatively safe, so a few nights of reduced caloric intake could be followed by nights with progressively longer safe feeding periods.

Our summer results are also in line with predictions of the predation risk allocation hypothesis, but this interpretation may be confounded by the timing of snowshoe hare reproduction. Snowshoe hare movements did not vary when temporal variance in predation risk due to moon phase was relatively low. In snow-free periods the full moon did not lead to an increase in the predation rate by as great a factor as during snowy periods (Figure 2). Although predation rate estimates were slightly higher near full moons, we found no consistent reduction in movement or open habitat use in the 5 days closest to the full moon in snow-free periods (Figure 3). This result appears to support the prediction of the predation risk allocation hypothesis that prey should not vary activity levels when temporal variance in predation risk is low. Our summer results do not support the minimize μ/g hypothesis (Gilliam and Fraser, 1987; Lima, 1998a), which predicted some decrease in movement during summer full moons.

It is possible that observed summer activity levels were influenced primarily by reproduction and not by predation risk. The observation that snowshoe hare activity was relatively constant under all moon phases is consistent with the expectation that, at times when reproductive effort can contribute to fitness, animals may be more prone to continued high activity despite risk (Bednekoff, 1996; Houston et al., 1993). Regardless of moon phase, snowshoe hares decreased movements at times near parturition. Female snowshoe hares typically reduce movement around parturition (Hodges, 1999), and males search for and stay near females during the breeding

season (Bider, 1961). Also, independently of moon phase, increased activity 2 weeks before or after parturition may coincide with times when males assess females' spatial distribution and when prenatal and lactating females forage intensively. It is not clear how moon phase and parturition date may be related in snowshoe hares. The annual dates of first conception or parturition in long-term studies (Meslow and Keith, 1968; Stefan and Krebs, 2001) do not universally coincide with new moons. Also, because snowshoe hare gestation is ~35 days, sequential birth pulses must occur in different moon phases over the summer breeding season.

Archibald (1977) suggested that 9–11 year snowshoe hare cycles, which are more regular and pronounced in higher latitude boreal forests (Murray, 2000), may be synchronized in part by lunar phenomena that recur on a 9.3-year interval. This is half the length of the moon's 18.6-year nodal cycle that governs the moon's declination above the horizon, the timing of moonrise and moonset, and the length of time it is visible in the night sky. The brightest full moons closest to any fixed calendar date occur every 9.3 years when the moon reaches a maximum in its declination above the horizon, illumination, and total time above the horizon. The lowest and least bright full moons near the same calendar date also occur predictably every 9.3 years, but 4–5 years after the brightest. The model of Archibald (1977) did not posit a mechanism causing the correlation between the nodal cycle and snowshoe hare population dynamics, but our observations on the seasonality of predation risk and moonlight may be relevant. Snowshoe hare population growth rate is most sensitive to juvenile survival rate, followed by adult survival rate (Haydon et al., 1999). If juvenile and adult snowshoe hares suffer higher predation rates during winters with higher and brighter full moons, then population growth rates for such years should be low relative to years with low-intensity winter lunar illumination. We lack data to test this hypothesis, but suggest that future studies quantify forest moonlight levels and focus on variation in survival rates in winter, when we found strong effects of full moons on snowshoe hare predation rates despite their lower movement rates. Shorter term studies would also benefit from movement data, and ambient light levels quantified for every day of the lunar cycle, facilitating a test for a linear relationship between light levels and snowshoe hare predation and movement rates.

In summary, the predation risk allocation hypothesis predicts that prey will have the most marked antipredator response only when predation risk is intermittently high. Interestingly, the estimated predation rate for snowshoe hares in winter full-moon periods was a value between the estimates for full-moon and new-moon phases in summer. Despite high predation rates in all three of those time periods, we only observed a reduction in movement in the winter full moon—not during either summer moon phase. Summer predation rates were high in all moon phases and relatively invariant—during summer we did not see any change in movement rates in response to moon phase. In contrast, the average winter predation rate was lower, and we only observed reduced movement rates when the predation rate was periodically high. In the safer winter new moons, hares moved distances as large as during either summer moon phase. Our results are consistent with the predation risk allocation hypothesis and suggest that the mediating effect of lunar illumination on many predator-prey interactions could vary seasonally.

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