Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles

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Summary

1. The risk of predation strongly affects mammalian population dynamics and community interactions. Bright moonlight is widely believed to increase predation risk for nocturnal mammals by increasing the ability of predators to detect prey, but the potential for moonlight to increase detection of predators and the foraging efficiency of prey has largely been ignored. Studies have reported highly variable responses to moonlight among species, calling into question the assumption that moonlight increases risk.

2. Here, we conducted a quantitative meta-analysis examining the effects of moonlight on the activity of 59 nocturnal mammal species to test the assumption that moonlight increases predation risk. We examined patterns of lunarphilia and lunarphobia across species in relation to factors such as trophic level, habitat cover preference and visual acuity.

3. Across all species included in the meta-analysis, moonlight suppressed activity. The magnitude of suppression was similar to the presence of a predator in experimental studies of foraging rodents (13·6% and 18·7% suppression, respectively). Contrary to the expectation that moonlight increases predation risk for all prey species, however, moonlight effects were not clearly related to trophic level and were better explained by phylogenetic relatedness, visual acuity and habitat cover.

4. Moonlight increased the activity of prey species that use vision as their primary sensory system and suppressed the activity of species that primarily use other senses (e.g. olfaction, echolocation), and suppression was strongest in open habitat types. Strong taxonomic patterns underlay these relationships: moonlight tended to increase primate activity, whereas it tended to suppress the activity of rodents, lagomorphs, bats and carnivores.

5. These results indicate that visual acuity and habitat cover jointly moderate the effect of moonlight on predation risk, whereas trophic position has little effect. While the net effect of moonlight appears to increase predation risk for most nocturnal mammals, our results highlight the importance of sensory systems and phylogenetic history in determining the level of risk.

Key-words: foraging efficiency, giving-up density, illumination, indirect effects, lunar cycles, moonlight, nocturnality, phylogenetic meta-analysis, predation risk, risk-sensitive foraging

Introduction

Predation influences the ecology and evolution of mammals via both direct mortality and behavioural responses to the threat of death (Creel 2011). Fear of predation can impact population and community dynamics to a greater extent than predation itself (Schmitz, Beckerman & O'Brien 1997; Creel & Christianson 2008), and factors that affect these behavioural responses can therefore have far-reaching impacts. Sublethal behavioural effects of predation include altered movement and activity patterns (Brown 1999; Lima & Bednekoff 1999), grouping behaviour (Creel & Winnie 2005), fecundity (Creel *et al.* 2007) and stress (Clinchy, Sheriff & Zanette 2013), which can

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reduce population growth rates and substantially alter community interactions (Brown, Laundre & Gurung 1999; Creel & Christianson 2009). The risk of predation for prey species and the foraging efficiency of both prey and predators may cycle with lunar phase, and these predictable and dramatic fluctuations may therefore have strong effects on the behaviour and ecology of nocturnal animals (Price, Waser & Bass 1984; Kotler, Brown & Hasson 1991; Embar, Kotler & Mukherjee 2011; Packer *et al.* 2011).

Nocturnality is widely thought to be the ancestral activity cycle of mammals, and adaptations to nighttime activity have therefore been a driving force in mammalian evolution (Crompton, Taylor & Jagger 1978; Heesy & Hall 2010). Approximately 44% of extant mammals are classified as nocturnal, while 26% are primarily diurnal and 29% are crepuscular or cathemeral (Jones *et al.* 2009). Cycles in moonlight may therefore affect the behaviour of a large proportion of mammalian species. Nocturnal species experience monthly fluctuations in ambient light levels that range over three orders of magnitude, from 0·0009 lux on moonless nights to 0·2 lux on clear, full moon nights (Bowden 1973). Although many studies have examined the influence of illumination on the activity of nocturnal mammals, these effects have not been synthesized across species. Thus, we have a poor understanding of the strength, variability and patterns of moonlight effects on the behaviour and population dynamics of nocturnal mammals. Most importantly, we lack a general understanding of how strongly moonlight affects predator-sensitive foraging.

Optimal foraging theory predicts that animals balance a trade-off between the marginal fitness gains obtained from foraging and the associated risk of predation (Charnov 1976; Brown 1988). Studies of nocturnal rodent foraging behaviour were instrumental in the development of this theory (e.g. Lockard & Owings 1974; Rosenzweig 1974; Kotler 1984; Price, Waser & Bass 1984; Bowers 1988; Brown *et al.* 1988). These studies often used nocturnal illumination level and habitat cover as proxies for predation risk, and they often found that nocturnal rodents foraged less intensely when conditions were riskier (i.e. on full moon nights and in open habitats where prey species were theorized to be more visible to predators). However, subsequent studies have reported higher levels of activity for some rodent species during bright nights (e.g. Longland & Price 1991; Bouskila 1995; Prugh & Brashares 2010). Studies of other taxonomic groups, such as nocturnal primates, also report positive effects of moonlight on activity levels (e.g. Wright 1989; Bearder, Nekaris & Buzzell 2002; Nash 2007). These conflicting results indicate that the relationship between moonlight and predation risk may not always be positive, or that the benefits of improved vision may outweigh the increased risk of predation for some species.

Moonlight enhances vision in nocturnal mammals, which leads to the following two predictions: (i) mammals that detect prey visually, such as most nocturnal carnivores, will detect prey more often as light levels increase and (ii) mammalian prey species that detect predators visually will be better able to detect predators as light levels increase. The assumption that moonlight increases predation risk is based on the first prediction but ignores the second. For moonlight to increase predation risk, it must increase vulnerability to a greater extent than it increases the ability of prey to detect and avoid predators. Thus, nocturnal illumination may actually reduce predation risk if nocturnal predators rely on the cover of darkness to successfully attack prey (Packer *et al.* 2011). Additionally, prey species that use vision to forage may have improved foraging efficiency with moonlight, and these gains may outweigh any increases in the risk of predation. The net effect of moonlight on the activity level of nocturnal mammals should therefore be determined by the relative importance of its benefits (improved detection of food and predators) and costs (increased vulnerability to predation).

Here, we conducted a quantitative meta-analysis examining the effect of moonlight on the activity level of mammals from around the world. We synthesized data from 58 studies of 59 species that examined the effect of illumination on the activity of nocturnal mammals. We quantified the net effect of moonlight on activity level across taxa and examined factors associated with lunarphilia or lunarphobia. Using this data set, we tested the following hypotheses:

1 *Predation risk hypothesis.* If the dominant effect of moonlight is to increase predation risk, we expected species at lower trophic levels to be less active and species at higher trophic levels to be more active with moonlight, regardless of visual acuity. Using the subset of studies that experimentally manipulated predator presence, we expected the suppressive effect of illumination on prey species to be strongest in the presence of predators.

2 *Visual acuity hypothesis.* If the dominant effect of moonlight is to increase foraging efficiency and detection of predators, we expected prey species relying primarily on vision to locate food and predators to be more active with moonlight and species relying primarily on other senses (e.g. olfaction, touch, echolocation) to be suppressed or unaffected by moonlight. We expected predators to be less active with moonlight due to reduced success rates, regardless of visual acuity.

3 *Habitat-mediated predation risk.* If moonlight increases predation risk by aiding detection of prey, the suppressive effect of moonlight on the activity of prey species should decrease as habitat cover increases. Using the subset of studies that experimentally manipulated habitat cover, we expected the suppressive effect of illumination on prey species to be strongest in open areas.

In addition to testing the above hypotheses, we examined other factors that may have influenced the effect of

illumination on activity, such as evolutionary history (i.e. phylogeny or taxonomic group), the type of activity measured and the type of illumination used (natural moonlight or artificial illumination). Together, these analyses increase our understanding of the role that moonlight plays in the behaviour and ecology of nocturnal mammals.

Materials and methods

BUILDING THE DATABASE

Published studies examining the effect of nighttime illumination on mammalian activity were located using ISI Web of Science searches on 25 April 2012. The following search terms were used: (moon* or illumination or lunar or giving up densit* or GUD) and mammal*, and results were restricted to articles in English within the environmental sciences and ecology subject areas. This search resulted in 502 articles, and relevant studies cited by papers found with these searches were also examined (e.g. studies published in book chapters). Studies were included in the meta-analysis if they provided a test statistic (e.g. *F*-test, *t*-test, or correlation coefficient) for the effect of illumination on the activity level of a nocturnal terrestrial mammal. All statistics were converted to correlation coefficients prior to analysis using standard conversion formulas (Zar 2009). Studies reporting *F*-statistics with a numerator degrees of freedom greater than one were excluded, because conversion of these values to correlation coefficients can inflate effect sizes (Hullett & Levine 2003). Correlation coefficients (*r*) were standardized using Fisher's *z*-transformation (Borenstein *et al.* 2009):

$$z = 0 \cdot 5 * ln\left(\frac{1+r}{1-r}\right)$$

We conducted weighted analyses, in which effect sizes were weighted by the inverse of the variance for each effect size. The inverse of the variance of Fisher's *z* is $\frac{1}{n-3}$ (Borenstein *et al.* 2009). The grand mean effect size and test of heterogeneity

among studies were conducted using the 'metafor' R package (Viechtbauer 2010). To facilitate interpretation of effect size magnitudes in figures, mean Fisher's *z*-values were back-transformed to correlation coefficients.

For each study, we recorded the location, biome and type of illumination used. For each species, the following taxonomic and life-history information was recorded: order, family, body mass, group size, diet, trophic level, primary sensory mode (visual or non-visual), habitat cover preference and locomotion mode (see Table 1 for life-history trait and study characteristic categories used). Data were obtained from the PanTHERIA data base (Jones *et al.* 2009) and supplemental literature searches.

Assessment of the primary sensory mode was necessarily a coarse and subjective measure. Most mammals employ multiple senses to detect food and predators, and information regarding the relative importance of these senses was difficult to obtain. However, variation in the relative use of senses certainly does occur, and we used information from species accounts as well as knowledge about the morphology of the species (e.g. eye-to-head size ratios, rostrum lengths) to create our 'best guess' as to whether the species relies primarily on vision or other senses. For example, flying foxes (*Pteropus sp.*) use vision to a much greater extent than Microchiropteran bats that rely on echolocation, and primates have relatively poor senses of smell and hearing compared with their visual acuity. Despite its limitations, we feel this trait (sensory mode) captures important information that is not otherwise available.

For each effect size (test statistic), the following information was recorded: the measure of activity that was used as the response variable (giving-up density, duration of activity, capture rates in live traps or habitat shift), degrees of freedom (numerator and denominator) and direction of effect (suppression or enhancement of activity). Illumination was reported either as a categorical variable (e.g. full vs. new moon) or as a continuous variable (e.g. proportion of moon illuminated).

PHYLOGENETICALLY CONTROLLED ANALYSES

Phylogenetic generalized least squares (PGLS) models were used to examine the effect of species traits on sensitivity to moonlight

Table 1. Life-history traits and study characteristics recorded for species and studies included in the meta-analysis

	Description
Life-history trait	
Body mass	Average body mass (g) of adults
Social group size	Number of individuals in a group that spends the majority of their time in a 24-h cycle together where there is some indication that these individuals form a social cohesive unit, measured over any duration of time
Cover preference	Preferred level of habitat cover: 1 = open, 1·5 = open/bush, 2 = grass, 2·5 = open/forest or grass/bush, 3 = bush, 3·5 = bush/forest, 4 = forest
Diet type	Carnivore, insectivore, herbivore/frugivore, granivore or omnivore
Locomotion	Arboreal (primates), flight (bats), quadrupedal and bipedal
Primary sensory mode	Visual (primarily uses vision) or non-visual (primarily uses other senses such as olfaction or echolocation)
Trophic level	(1) herbivore (primarily consumes plant material), (2) omnivore (consumes plants and animals) and (3) carnivore (primarily consumes vertebrates and/or invertebrates)
Study characteristics	
Biome	Boreal forest, desert, grassland, savanna, scrub, temperate forest, tropical forest
Continent	Africa, Asia, Australia, North America, Europe, South America
Duration	Length of the study (days)
Illumination type	Natural moonlight or artificial lights

after controlling for phylogenetic relatedness. The species-level phylogenetic tree of nearly all extant mammals constructed by Bininda-Emonds *et al.* (2007) was pruned to the species in our meta-analysis using the 'ape' package in program R (Paradis, Claude & Strimmer 2004). We tested for a phylogenetic signal in the effect of illumination by calculating Pagel's λ (Pagel 1999) using the 'caper' package in program R (Orme *et al.* 2012). An intercept-only PGLS model was used to obtain a maximum likelihood estimate of Pagel's λ, which ranges from 0 (no phylogenetic signal) to 1 (strong phylogenetic signal). Using this estimate of λ, weighted PGLS models were run to test our hypotheses using the 'ape' package with 'corPagel' as the correlation structure. Effect sizes and weights for each species were averaged.

GENERALIZED LINEAR MIXED MODELS

To avoid averaging across studies and to examine study-specific factors that may have affected the detection of moonlight effects, weighted generalized linear mixed models (GLMMs) were conducted using the 'lme' function in program R. 'Study' was included as a random effect, and species or study traits were included as fixed effects in all models. Models were weighted by the inverse of the variance in the estimate of Fisher's *z*. Models were constructed to address each of our hypotheses. In addition, a multiple regression model to examine the importance of other factors that may have explained variation in moonlight effects among studies was constructed (Table 1). Body mass and social group size were log-transformed prior to analyses.

GIVING-UP DENSITY EXPERIMENTS

Additional analyses were performed using the subset of studies that conducted giving-up density (GUD) experiments on rodents (*n* = 16 studies of 17 species). The giving-up density (GUD) is the resource density at which a forager abandons a food patch (Brown 1988), and this metric is often used to examine the response of foragers to predation risk. All studies reported paired GUD estimates on 'new moon' and 'full moon' nights (sometimes using artificial lights to simulate the illumination level of a full moon), and most studies also used predator exclosures or enclosures and brush piles to manipulate the presence of predators and habitat cover. These treatments resulted in 83 paired effect size measurements across all study-species-treatment combinations.

The difference in giving-up densities among dark and bright nights was calculated as:

$$\text{Moon effect} = \left(\frac{\text{GUD}_{new} - \text{GUD}_{full}}{\text{Seed}_i} \right) * 100$$

where GUD_{new} is the giving-up density on new moon nights, GUD_{full} is the giving-up density on full moon nights, and Seed_i is the amount of seed initially offered, measured in grams of seed. Giving-up density is inversely related to foraging activity level; a higher GUD indicates that more seed remained uneaten and the animal foraged less intensely. Thus, a positive moon effect indicates that a higher percentage of seed remained uneaten on new moon nights, and moonlight therefore enhanced foraging activity, whereas a negative moon effect indicates that a higher percentage of seed remained uneaten on full moon nights, and moonlight

therefore suppressed activity. Because studies reported standard errors for only 35 of the 87 pairs of GUD estimates, the average moon effect was calculated using raw mean differences rather than standardized mean differences (Borenstein *et al.* 2009). A GLMM was used to examine the effect of life-history and study traits on the moon effect, with study entered as a random effect.

To examine interactions among habitat cover, predator presence and illumination, a GLMM was constructed with predator (present/absent), habitat (open/cover), illumination (full/new moon) and interaction terms as fixed effects, study as a random effect, and the proportion of seeds remaining (GUD/seed_i) as the response variable. Predators used in studies included owls (3 studies), foxes (1 study), snakes (2 studies) or multiple unspecified species (10 studies).

Results

Our data set consisted of 118 effect sizes from 58 studies (Table S1, Supporting information) examining the effect of nocturnal illumination on the activity of 59 mammalian species (Table S2, Supporting information). Across all mammals, illumination suppressed nocturnal activity, with a grand mean effect size (correlation coefficient, *r*) of −0·28 (*n* = 118, 95% CI = −0·22 to −0·35). There was significant heterogeneity among studies (tau^2 = 0·20, Cochran's Q = 1755·8, *P* < 0·0001).

PHYLOGENETICALLY CONTROLLED ANALYSES

There was a significant phylogenetic signal in the effect of illumination on nocturnal activity (Fig. 1; λ = 0·58, *P* = 0·0008, *n* = 59). Phylogenetic generalized least squares models did not support any of our proposed hypotheses, and none of the examined life-history traits explained significant variation in effect sizes among species (Table 2).

GENERALIZED LINEAR MIXED MODELS

Phylogenetically controlled analyses required averaging effect sizes and weights in cases where species were included in multiple studies, thus reducing the sample size from 118 to 59. We therefore conducted generalized linear mixed models (GLMMs) without phylogenetic structure to avoid averaging effect sizes. Taxonomic order was included in models to partially account for phylogenetic relatedness. GLMMs supported the visual acuity hypothesis and did not support the predation risk hypothesis (Table 3). As predicted by the visual acuity hypothesis, illumination generally increased the activity of prey species relying on vision as their primary sensory system and suppressed the activity of prey species relying primarily on non-visual senses (Fig. 2). Moonlight appeared to decrease rather than increase the activity of carnivores and insectivores, regardless of their sensory mode (Fig. 2).

The effect of illumination was related to habitat cover preference, such that moonlight tended to decrease the activity of species occurring primarily in open habitats
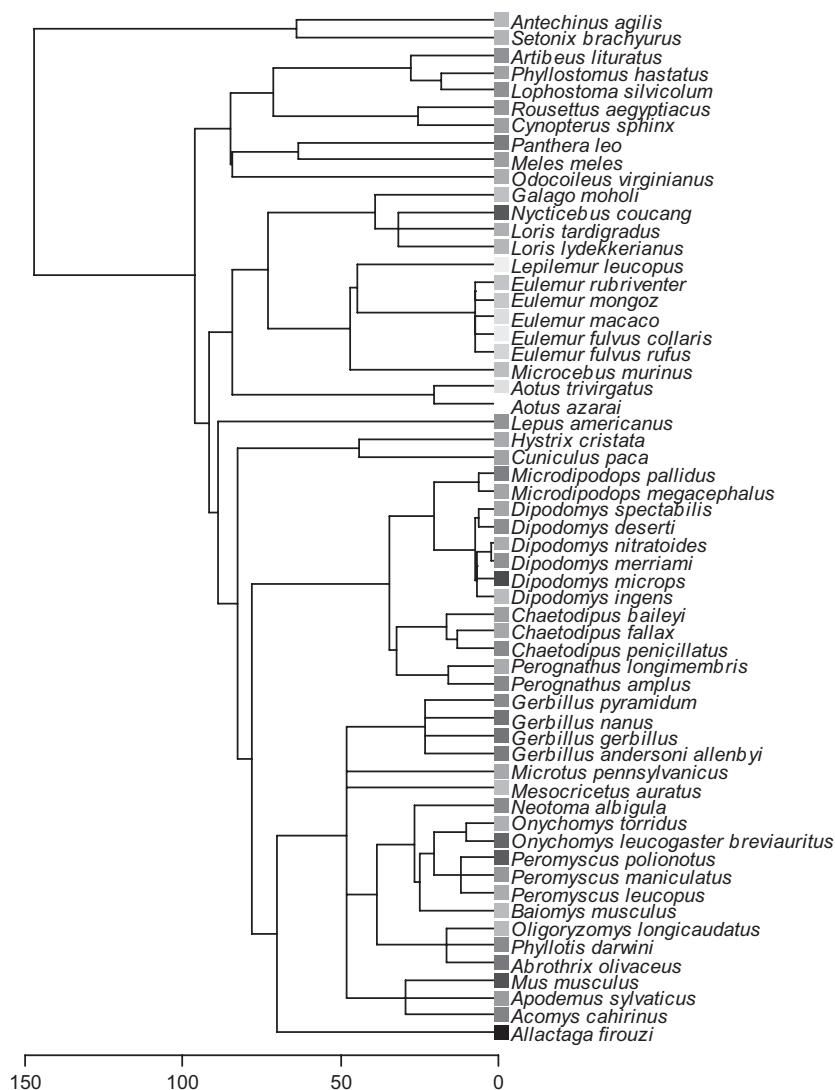
Antechinus agilis
Setonix brachyurus
Artibeus lituratus
Phyllostomus hastatus
Lophostoma silvicolum
Rousettus aegyptiacus
Cynopterus sphinx
Panthera leo
Meles meles
Odocoileus virginianus
Galago moholi
Nycticebus coucang
Loris tardigradus
Loris lydekkerianus
Lepilemur leucopus
Eulemur rubriventer
Eulemur mongoz
Eulemur macaco
Eulemur fulvus collaris
Eulemur fulvus rufus
Microcebus murinus
Aotus trivirgatus
Aotus azarai
Lepus americanus
Hystrix cristata
Cuniculus paca
Microdipodops pallidus
Microdipodops megacephalus
Dipodomys spectabilis
Dipodomys deserti
Dipodomys nitratoides
Dipodomys merriami
Dipodomys microps
Dipodomys ingens
Chaetodipus baileyi
Chaetodipus fallax
Chaetodipus penicillatus
Perognathus longimembris
Perognathus amplus
Gerbillus pyramidum
Gerbillus nanus
Gerbillus gerbillus
Gerbillus andersoni allenbyi
Microtus pennsylvanicus
Mesocricetus auratus
Neotoma albigula
Onychomys torridus
Onychomys leucogaster breviauritus
Peromyscus polionotus
Peromyscus maniculatus
Peromyscus leucopus
Baiomys musculus
Oligoryzomys longicaudatus
Phyllotis darwini
Abrothrix olivaceus
Mus musculus
Apodemus sylvaticus
Acomys cahirinus
Allactaga firouzi

150   100   50   0

Fig. 1. Phylogenetic tree of the 59 mammal species included in the analysis, based on the supertree constructed by Bininda-Emonds *et al.* (2007). Branch lengths scale to millions of years before present, shown on bottom axis. Greyscale blocks at each tip show the effect of moonlight on activity (average Fisher's *z*-value). Dark blocks = moonlight suppressed activity, light blocks = moonlight increased activity. Strength of colour block indicates the magnitude of the effect size (very dark = strong suppression, very light = strong enhancement).

and increase the activity of species occurring in forested habitats (Fig. 3). This relationship did not differ detectably between trophic levels (Table 3).

The model including all life-history and study traits identified sensory mode, habitat cover preference and locomotion mode as factors affecting the response of species to moonlight (Table 3). Order could not be included in the same model as locomotion because of covariation (e.g. all primates used an arboreal mode of locomotion and all chiropterans used flight). Order was a significant factor in all other models (Table 3), as expected due to the strong phylogenetic signal detected in PGLS models. Primate activity was enhanced by illumination, whereas the activity of rodents, lagomorphs, carnivores and bats was suppressed (Fig. 4).

GIVING-UP DENSITY EXPERIMENTS

Moonlight increased the giving-up density (GUD) of foraging rodents by a mean of 6·4% (95% CI = 3·9–8·9%, n = 87), indicating that foraging was suppressed.

The proportion of seed eaten (i.e. the inverse of the GUD) was significantly lower with illumination ($F_{1,119} = 14\cdot3$, $P = 0\cdot0002$), with predators ($F_{1,119} = 28\cdot8$, $P < 0\cdot0001$) and in open habitats ($F_{1,119} = 241\cdot4$, $P < 0\cdot0001$). Without moonlight, rodents consumed 49% of seeds (GUD = 51% remaining), whereas they consumed 42·4% (GUD = 57·6%) with moonlight. Thus, moonlight suppressed rodent foraging activity by an average of 13·6% (calculated as the change, 6·4%, divided by consumption without moonlight, 49%). Similarly, the presence of a predator reduced foraging by 18·7% (Fig. 5a). The absence of habitat cover reduced foraging intensity by 40% (Fig. 5b). Interactions with illumination were not significant (Fig. 5; illumination*predator $F_{1,119} = 1\cdot4$, $P = 0\cdot25$, illumination*habitat $F_{1,119} = 0\cdot64$, $P = 0\cdot43$). The moon effect was not significantly related to any of the life-history or study traits examined (Table 4). None of the rodents included in the GUD analyses were categorized as relying primarily on vision, and all were classified as granivores or omnivores (trophic levels 1 or 2).

Table 2. Results of three weighted phylogenetic generalized least squares (PGLS) models examining the effect of moonlight on the activity level of nocturnal mammals. Average effect sizes (Fisher's z-values) and weights (inverse variances) for each species (n = 59) were used in each model, and a phylogenetic error structure was used. Model 1 tests the predation risk and visual acuity hypotheses (see Introduction). Model 2 tests the habitat-mediated predation risk hypothesis (see Introduction). Model 3 examines the effects of life-history traits on the response to moonlight. See Table 1 for a description of traits

Factor	Num DF	Den DF	F-value	P-value
PGLS model 1: Predation risk and visual acuity hypotheses				
(Intercept)	1	55	0·06	0·81
Sensory mode	1	55	0·99	0·33
Trophic level	1	55	0·03	0·86
Sensory*trophic	1	55	2·72	0·10
PGLS model 2: Habitat-mediated predation risk hypothesis				
(Intercept)	1	55	0·12	0·73
Cover preference	1	55	0·33	0·57
Trophic level	1	55	0·37	0·54
Cover*trophic	1	55	0·61	0·44
PGLS model 3: All factors				
(Intercept)	1	47	0·08	0·78
Locomotion	3	47	1·18	0·33
Sensory mode	1	47	0·14	0·71
Cover preference	1	47	0·30	0·59
Diet	4	47	0·67	0·62
Body mass	1	47	0·13	0·72
Group size	1	47	1·14	0·29

Table 3. Results of weighted generalized linear mixed models examining the effect of moonlight on the activity of nocturnal mammals. Study was entered as a random effect in each model, and effect sizes (Fisher's z-values) were weighted by the inverse of their variances (n = 59 studies, 118 effect sizes). Model 1 tests the predation risk and visual acuity hypotheses (see Introduction). Model 2 tests the habitat-mediated predation risk hypothesis (see Introduction). Taxonomic order was included as a factor in Models 1 and 2 to partially account for phylogenetic relatedness. Model 3 examines the effects of life-history and study traits on the response to moonlight. See Table 1 for a description of traits

Factor	Num DF	Den DF	F-value	P-value
GLMM 1: Predation risk and visual acuity hypotheses				
(Intercept)	1	56	14·12	0·0004
Sensory mode	1	51	8·37	0·006
Trophic level	1	51	1·03	0·31
Sensory*trophic	1	51	0·42	0·52
Order	7	51	2·53351	0·03
GLMM 2: Habitat-mediated predation risk hypothesis				
(Intercept)	1	56	14·25	0·0004
Cover preference	1	51	9·03	0·004
Trophic level	1	51	0·23	0·63
Cover*trophic	1	51	0·0004	0·98
Order	7	51	2·68	0·02
GLMM 3: All factors				
(Intercept)	1	54	13·59	0·001
Cover preference	1	45	8·61	0·005
Sensory mode	1	45	4·25	0·04
Locomotion	3	45	4·29	0·01
Study duration	1	54	0·40	0·53
Illumination type	1	54	0·80	0·37
Body mass	1	45	0·08	0·78
Group size	1	45	0·15	0·70
Activity measure	5	45	0·40	0·85
Diet	4	45	0·61	0·66

GLMM, generalized linear mixed models.

Discussion

Moonlight has generally been thought to increase predation risk by enhancing the ability of predators to detect prey (Kotler, Brown & Hasson 1991; Nash 2007), thus leading to reduced activity or shifts in prey microhabitat use in the presence of bright moonlight (Lockard & Owings 1974; Daly *et al.* 1992; Orrock, Danielson & Brinkerhoff 2004). Our results demonstrate that moonlight has highly variable, yet not idiosyncratic, effects on activity across nocturnal mammal species. There was a strong phylogenetic signal in the effect of moonlight on activity: primate activity was enhanced by illumination, whereas the activity of rodents, lagomorphs, chiropterans and carnivores was suppressed (Figs 1 and 4). Sample sizes were low for all taxonomic orders aside from primates and rodents, so these patterns should be interpreted with caution. Moonlight suppressed the activity of most nocturnal mammals in our analysis, indicating the net effect of illumination may indeed often increase predation risk. Foraging trials showed that moonlight suppressed rodent foraging intensity, and the magnitude of suppression was similar to the presence of a predator (13·6% and 18·7% suppression, respectively). Contrary to the predation risk hypothesis, however, and consistent with the hypothesis that moonlight improves the ability of prey to detect predators and/or forage efficiently (the visual acuity hypothesis), the activity of many prey species increased with moonlight, whereas the activity of carnivores and insectivores tended to be suppressed.

SENSORY SYSTEMS

The net effect of moonlight was positive for prey species relying primarily on vision to forage and detect predators (i.e. activity increased with moonlight), whereas it was negative for prey species relying primarily on other senses (Fig. 2). Species that rely primarily on vision may be more efficient at locating food in the presence of moonlight, and they may also experience lower predation risk because their ability to detect predators should increase. In developing a theoretical framework to predict the relative magnitude of predation risk effects, Creel (2011) identified group size, body mass, the degree of foraging specialization and whether direct mortality is additive or compensatory as important factors. Social group size ranged from 1 to 2000 individuals and body mass ranged from 8 to 158 624 g among species included in our meta-analysis (Table S2, Supporting information), but these traits did not affect the response of species to moonlight. While body and group size may influence the overall magnitude of direct predation rates and risk effects, these factors do not appear to moderate the impact of moonlight
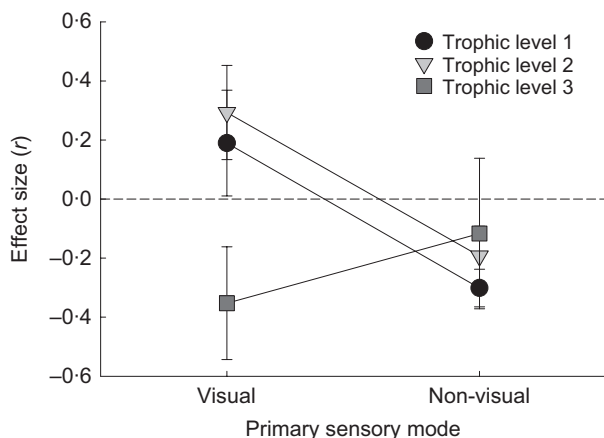
Fig. 2. Effect of primary sensory mode and trophic level on the response of nocturnal mammals to moonlight. Primary sensory mode was categorized as visual or non-visual (e.g. olfaction, echolocation) for each species. Trophic level 1 = herbivores, granivores, frugivores, 2 = omnivores, 3 = insectivores, carnivores. Effect sizes were calculated as Fisher's *z*-values, and means were back-transformed to correlation coefficients for ease of interpretation. Negative values indicate suppressed activity and positive values indicate increased activity with moonlight. Standard error bars are shown.

Fig. 4. Response of nocturnal mammals to moonlight by taxonomic order. Negative values indicate suppressed activity and positive values indicate increased activity with moonlight. Sample sizes and standard error bars are shown.

Fig. 3. Effect of habitat cover preference on the response of nocturnal mammals to moonlight. Preferred level of habitat cover: 1 = open, 1·5 = open/bush, 2 = grass, 2·5 = open/forest or grass/bush, 3 = bush, 3·5 = bush/forest, 4 = forest. Negative values indicate suppressed activity and positive values indicate increased activity with moonlight. Sample sizes and standard error bars are shown.

Fig. 5. Effect of moonlight on the foraging activity of nocturnal rodents (a) with predators present vs. absent and (b) in open habitat vs. cover. The giving-up density (GUD) is the proportion of seeds remaining after a night of foraging; higher GUD values indicate lower foraging intensity (i.e. more seeds remained uneaten). Standard error bars are shown.

on risk levels. Our results instead highlight the importance of considering the sensory systems of predators and prey.

Visual sensitivity and acuity varies widely among nocturnal species, sparking debate about the role of nocturnality in the evolution of mammalian vision (Tan *et al.* 2005; Zhao *et al.* 2009). Ancestral mammals are believed to have been nocturnal, and many extant nocturnal species have lost function in opsin genes required for colour vision (Heesy & Hall 2010). However, many nocturnal primates retain functional opsin genes, and this
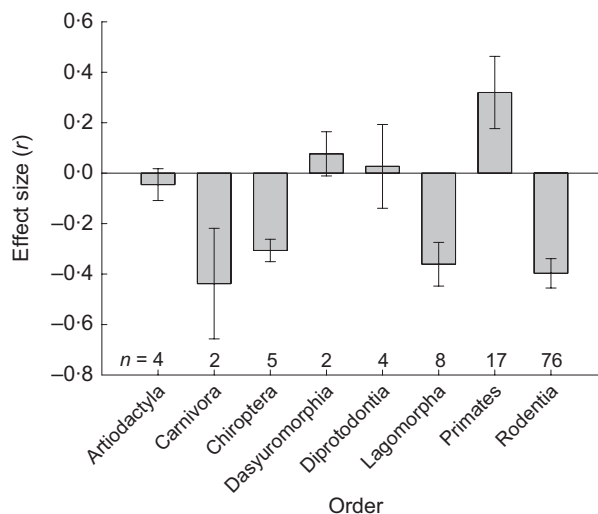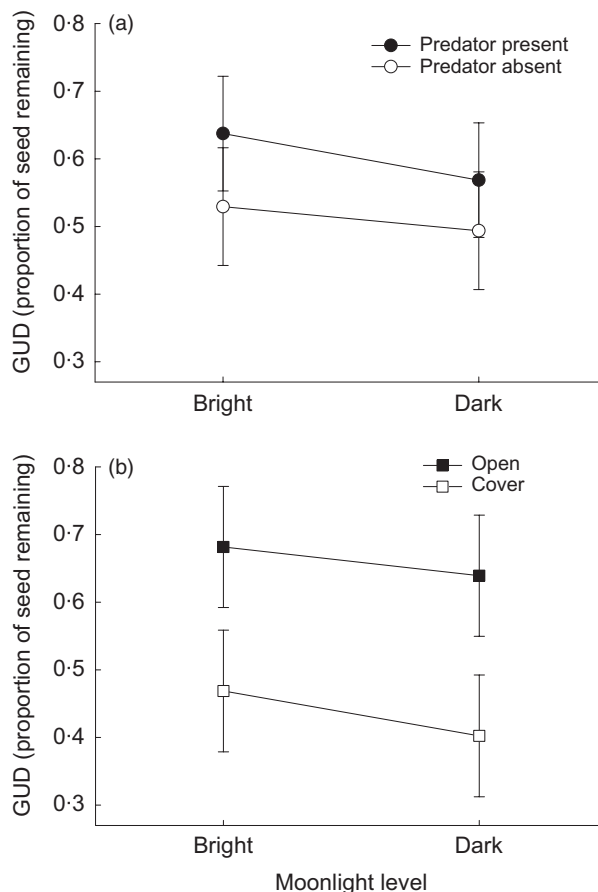
Table 4. Results of a generalized linear mixed model examining the effect moonlight on the foraging activity of nocturnal rodents, as measured by giving-up-density (GUD) trials. Study was entered as a random effect in each model, and effect sizes were constructed as raw mean differences in GUD values on full moon and new moon nights ($n = 16$ studies, 87 effect sizes). Biome = desert, scrub or temperate forest, diet = granivore or omnivore, locomotion = bipedal or quadrupedal, family = Cricetidae, Muridae, or Heteromyidae

Factor	Num DF	Den DF	*F*-value	*P*-value
(Intercept)	1	67	17·16	0·0001
Body mass	1	67	0·59	0·44
Cover preference	1	67	3·02	0·09
Illumination type	1	10	0·21	0·65
Biome	2	10	0·29	0·76
Diet	1	67	3·18	0·08
Locomotion	1	67	0·13	0·72
Family	2	10	1·14	0·36

finding has been interpreted as evidence that primate ancestors were diurnal (Tan *et al.* 2005). A recent study questioned this interpretation, reporting that many bat species also retain functional opsin genes despite evidence of nocturnality for the past 65 million years (Zhao *et al.* 2009). Nocturnal arboreal primates rely heavily on vision for foraging and locomotion (Charles-Dominique 1977), and their visual acuity may therefore be higher than expected for nocturnal species (Bearder, Nekaris & Curtis 2006). Colour vision may be more important to nocturnal mammals than previously realized (Kappeler & Erkert 2003; Zhao *et al.* 2009), and we suggest that lunar cycles could play an important role in maintaining selection for functional opsin genes.

In this study, we categorized species as relying primarily on visual or non-visual sensory systems based on species accounts in the literature. Because most species employ multiple sensory organs to detect food and predators, this categorization is admittedly coarse. Additionally, the sensory capabilities of a given species' predators and prey may also be important in determining the net effect of moonlight on its activity level, but we were unable to include this information in our analyses. For example, bats may be less active with moonlight because their insect prey are less active, not because they are more at risk of predation (Lang *et al.* 2006). We were therefore surprised to find such a strong effect of our binary sensory categorization on the response of species to moonlight. Future studies that include more detailed information about the visual acuity of nocturnal predators and prey would be useful in clarifying the importance of this trait in moderating predation risk and foraging efficiency.

TROPHIC LEVEL

The activity level of species in higher trophic levels did not increase with moonlight, contrary to the predation

risk hypothesis. Only two carnivores were included in our analysis (European badger, *Meles meles*, and African lion, *Leo panthera*), but the activity of both species was strongly suppressed by moonlight (Fig. 4; Cresswell & Harris 1988; Packer *et al.* 2011). A study of the viverrid *Arctictis binturong*, which could not be included in the quantitative meta-analysis, reported that this carnivore was also less active with moonlight (Grassman, Tewes & Silvy 2005). In addition to these carnivores, the highest trophic level in our analyses also included four insectivores (a bat, a marsupial and two rodents; Table S2, Supporting information). Despite its intuitive appeal, trophic level may be a poor index of predation risk. Most predators are susceptible to predation themselves, and our results indicate that predation risk may not necessarily decrease as one moves up the food chain.

Although the mammalian carnivores and insectivores in our analyses were less active with moonlight, nocturnal avian predators such as owls may be more active (Nelson 1989; Kotler, Brown & Hasson 1991; Mougeot & Bretagnolle 2000). Many mammalian predators rely on stealth and ambush to capture prey, whereas avian predators may rely more on speed, and this difference could lead to opposite effects of moonlight on mammalian and avian predators. Despite the potential for increased predation risk from avian predators, moonlight strongly increased the activity of nocturnal primates (Fig. 4). All primates in our analysis were frugivores or omnivores (Table S2, Supporting information) and subject to predation by avian and mammalian predators (Charles-Dominique 1977, 1980; Cheney & Wrangham 1987; Nash 2007).

HABITAT COVER

Consistent with the habitat-mediated predation risk hypothesis, we found that the suppressive effect of moonlight was stronger in more open habitat types across all species (Fig. 3). This pattern was most dramatic in the difference between species that occur in forested habitats (cover index 4) compared with other species. Because all primates in our analysis occurred in forested habitats, this pattern may have been driven by phylogeny rather than an effect of habitat on predation risk. However, six of the 20 species in this cover class were non-primates (an ungulate, four bats and a marsupial; Table S2, Supporting information), and suppression steadily increased as cover class decreased (Fig. 3). In addition, seven of nine species in our meta-analysis shifted their habitat use towards denser cover in response to moonlight (Kotler 1984; Dickman 1992; Sutherland & Predavec 1999; Griffin *et al.* 2005). A shift in habitat use due to increased predation risk carries costs in terms of decreased foraging efficiency (Lima & Dill 1990; Labeelund *et al.* 1993), and monthly habitat shifts in response to bright moonlight may therefore substantially decrease net energy gains of nocturnal species over the course of their lifetime.

In the giving-up density (GUD) analyses, habitat cover had a stronger effect on the foraging intensity of rodents than predator presence or illumination did. On average, rodents removed 40% more seed from trays under habitat cover than in the open. While this strong preference was likely a response to predation risk, it is possible some rodents preferred habitat cover for other reasons, such as competition avoidance (Heske, Brown & Mistry 1994). Contrary to the habitat-mediated predation risk hypothesis, there was no interaction between illumination and habitat among GUD studies. Thus, the suppressive effect of moonlight on rodents was not stronger in open areas, as was found in the overall analyses.

PHYLOGENETIC PATTERNS

Phylogenetic relatedness is increasingly acknowledged as an important factor to consider when conducting meta-analyses involving multiple species (Chamberlain *et al.* 2012). However, software packages that are available to run phylogenetic analyses allow only one entry per species. This limitation is problematic for data sets such as ours, in which multiple effect sizes were recorded for many of the species. The results from our phylogenetic models differed substantially from our generalized linear models; species traits identified as important in non-phylogenetic models were not significant factors in phylogenetic models. It is unclear how much of this difference was due to problems associated with averaging effect sizes and weights in the phylogenetic analyses or a failure to fully account for phylogenetic structure in the non-phylogenetic models. Taxonomic order was included as a factor in all non-phylogenetic models, and significant effects of sensory mode and habitat cover preference remained. Therefore, these are likely important traits in moderating the effects of moonlight, whether they occur due to shared evolutionary history or common selective pressure.

OTHER FACTORS INFLUENCING MOONLIGHT EFFECTS

We expected other factors, such as locomotion mode, study duration, illumination type, activity type, diet, body mass and group size, to influence the response of species to illumination. Although locomotion was a significant factor in the overall analysis, this was entirely due to differences between species that use arboreal locomotion (primates) and other modes (flight, quadrupedal and bipedal). Previous research suggested that quadrupedal rodents may be more susceptible to predation than bipedal species and therefore more sensitive to moonlight (Kotler 1984; Longland & Price 1991). However, we found no difference between quadrupedal and bipedal species in either the overall analysis or the subset of rodent GUD studies. We also expected studies using artificial illumination to find stronger effects and that the type of activity measured would influence effect sizes. For

example, activity was measured by various techniques including direct observations, GUD experiments and capture success during live-trapping. Even when examining this factor in univariate analyses that did not control for phylogeny, activity measure did not affect the response to moonlight. Thus, observed patterns do not appear to be artifacts of different study designs. Traits that may be important in determining overall predation rates, such as body and group size (Sinclair, Mduma & Brashares 2003), do not appear to affect species' responses to moonlight.

Conclusions

Moonlight has long been assumed to increase predation risk of nocturnal mammals (Lockard & Owings 1974), but the possibility that increased illumination could benefit nocturnal prey through improved detection of predators and foraging efficiency has been largely ignored. We found that moonlight did indeed suppress the activity of many nocturnal species, but the activity of a substantial number of nocturnal prey species was enhanced by moonlight. Our results suggest that moonlight may play an important role in sustaining relatively high levels of visual acuity in some nocturnal mammals The magnitude of moonlight effects on activity level was large enough to indicate that lunar cycles likely have a major impact on the foraging rates and habitat use of many species. Population models that account for moonlight effects are needed to reveal how strongly lunar cycles may impact the demographic rates of nocturnal species. Additionally, studies designed specifically to tease apart the effect of moonlight on the foraging efficiency and predation risk of predators and prey would substantially improve our understanding of the mechanisms through which moonlight affects activity levels. Overall, our synthesis shows that moonlight strongly affects the ecology and evolution of nocturnal mammals, and further study examining its role will be illuminating.

Data accessibility

Data available from the Dryad Digital Repository (Prugh & Golden 2013).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Summary information about studies included in the meta-analysis.

Table S2. Summary information about species included in the meta-analysis.

Appendix S1. References for studies included in the meta-analysis.