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Short Communication

Lunar phobia in bats and its ecological correlates: A meta-analysis

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ABSTRACT

Animals show several behavioral strategies to reduce predation risks. Presumably, moonlight avoidance is a strategy used by some nocturnal species to reduce the risk of predation. In bats, some research indicates that foraging activity is negatively correlated with moonlight intensity, a phenomenon better known as lunar phobia. However, the currently available evidence is contradictory because some bat species reduce their activity during nights with more moonlight while the opposite occurs in other species. We quantitatively evaluated the strength and direction of the relationship between moonlight intensity and bat activity using a meta-analysis. We also looked at some ecological correlates of lunar phobia in bats. Specifically, we examined foraging habitat and latitude as potential moderators of the size of the lunar phobia effect. Our results show that, regardless of the method used to evaluate bat activity, the overall relationship between moonlight intensity and bat activity is significant and negative ($r = -0.22$). Species foraging on the surface of the water (piscivores and insectivores; $r = -0.83$) and forest canopy species (i.e., big frugivores; $r = -0.30$) are more affected by moonlight than those with different foraging habitats (understory, subcanopy, open air). Latitude was positively correlated with lunar phobia ($r = 0.023$). The stronger lunar phobia for bats foraging on the water surface and in the forest canopy may suggest that the risk of predation is greater where moonlight penetrates more easily. The significant effect of latitude as a moderator of lunar phobia suggests that there is a weak geographic pattern, with this phobia slightly more common in tropical bats than in temperate species.

Animal activity patterns are shaped to some extent by environmental factors such as temperature, humidity and light availability (Navara and Nelson 2007). These environmental factors constrain foraging and some, like rain, increase energy expenditure (Voigt et al. 2011). The intensity of moonlight is a factor that influences the foraging behavior in nocturnal organisms. For example, nocturnal predators such as fur seals (*Arctocephalus galapagoensis*) are able to dive deeper than usual into the ocean to increase their foraging success during full moon nights (Horning and Trillmich 1999). In contrast, some insects and amphibians reduce the intensity of mating calls in order to avoid predation during full moon nights (Tuttle et al. 1982; Lang et al. 2006). In bats, some behaviors such as changing the stratum of vegetation where they forage or changing their activity schedules (i.e., foraging during the darkest time of night) have been observed when moonlight is intense (Hecker and Brigham 1999; Börk 2006), a phenomenon referred by specialists as “lunar phobia” (*sensu* Morrison 1978).

Some authors have suggested that lunar phobia has a strong negative impact on bat activity. A number of studies have evaluated the relationship between the intensity of moonlight and the number of captures, feeding buzzes (i.e., call sequences produced by bats that attempt prey capture; Griffin et al. 1960) and the size of the activity area. Some of these studies have found that moonlight intensity is negatively correlated with some measures of bat activity (Morrison 1978; Börk 2006; Lang et al. 2006; Esbérard 2007), suggesting that moonlight sensitivity in bats and the corresponding changes in their activity may be an adaptation to reduce the risk of predation. Bats may also reduce their activity due to the indirect effects of moonlight on the availability of prey (Lang et al. 2006). However, other studies have not found any relationship between moonlight intensity and activity (Karlsson et al. 2002; Russo and Jones 2003; Thies et al. 2006; Holland et al. 2011). Therefore, there is no conclusion on whether or not lunar phobia in bats is widespread.

The effect of moonlight intensity on bat foraging activity may be contingent on the foraging habitat and latitude (Morrison 1978; Hecker and Brigham 1999; Karlsson et al. 2002). For instance, moonlight may affect the activity of insectivorous bats foraging in the open air (above the canopy) to a lesser extent than it affects the activity of frugivorous bats foraging in the forest canopy because

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insectivores foraging in the open air are able to fly faster than the frugivores can (Karlsson et al. 2002). On the other hand, moonlight may also improve visibility for the predators of canopy frugivores for which an optimal foraging strategy is to sit and wait for frugivorous bats foraging in mast fruiting canopy trees (Morrison 1980). There is some evidence that the activity of understory insectivores and piscivores is affected negatively by moonlight; however, some evidence suggests that these effects are indirect because the prey of these bats typically reduce the frequency with which they emit communication sounds (which the bats use to locate their prey), as well as their general level of activity during well illuminated nights (Lang et al. 2006; Börk 2006). Regarding latitude, Karlsson et al. (2002) proposed two hypotheses (not mutually exclusive) to explain the lack of lunar phobia they saw in some temperate insectivorous bat species (Vespertilionidae) relative to the apparent regularity of this phenomenon reported for tropical bat species by other authors. The first hypothesis suggests that the greater diversity of predators in tropical ecosystems may increase the risk of predation for tropical bat species relative to their temperate counterparts, and hence one would expect stronger lunar phobia in tropical bats. The second hypothesis suggests that lunar phobia is stronger in tropical than in temperate bats because in the tropics bat communities are dominated by slow-flying bats (frugivores, gleaning insectivores and carnivores), while temperate bat communities are composed mainly of fast-flying bats (open air insectivores; Norberg and Rayner 1987), with tropical species more susceptible to predation than temperate species. However, these two hypotheses remain untested.

Meta-analysis is a powerful tool for evaluating the generalizability of ecological hypotheses tested in different studies (Harrison 2011). It allows us to examine the results of a variety of studies that have explored the same general question, and take differences in statistical power (i.e., sample size) or methodological biases (by using moderator variables) into account (Arnqvist and Wooster 1995; Gurevitch and Hedges 1999). By summarizing results across many different studies, meta-analyses explore statistically the support for a given hypothesis (effect size). The variance among studies can be also addressed by using moderator variables and this allows researchers to look at correlates between effect size and variables other than those examined in the primary studies.

In this research we (i) evaluated the generalizability of the hypothesis of lunar phobia in bats by assessing the relationship between moonlight intensity and bat activity for several bat species and locations. We also (ii) examined the effect of foraging habitat (canopy, subcanopy, understory, open spaces, water surface and open air) and latitude on the size of the effect of lunar phobia. We predict that (i) species that forage in the forest canopy, over the surface of the water and in open spaces will exhibit significantly stronger lunar phobia (i.e., negative effect will be greater) than those foraging in more cluttered habitats (the understory, beneath the canopy); and that (ii) the effect size of lunar phobia will be greater in tropical than in temperate species.

An extensive review of the literature available in Google Scholar and ISI Web of Knowledge electronic data bases was carried out, using “moonlight”, “lunar phobia”, and “bat activity” as keywords. The search was not limited by year or journal. We also searched for studies by consulting the studies cited in the article we had already found. Of the 38 studies we retrieved, we selected those matching the following criteria: (i) the study reports Pearson's coefficient (r) or the data necessary to calculate it; (ii) the authors assessed bat activity over the entire moon cycle and statistical analyses are based on lunar phases and/or their corresponding percentages (full moon = 100%, waxing gibbous = 75%, first quarter = 50%, waxing crescent = 25% and new moon = 0%). Only 11 studies met the selection criteria. In the selected studies lunar phobia was assessed by examining the relationship between percent lunar illumination and bat activity (number of bat captures, number of feeding buzzes, area of activity, and emergence counts). This relationship was usually addressed statistically using a simple linear regression or correlation. We chose the Z transformation of Pearson's product-moment correlation coefficient (hereafter Zr) as the most suitable effect size measure of the strength of this relationship (Borenstein et al. 2009). Zr values were calculated directly from Pearson's product–moment correlation coefficients (r) or from the square root of determination coefficients in regression models (R^2). Three studies (Hecker and Brigham 1999; Karlsson et al. 2002; Singaravelan and Marimuthu 2002) only provided the F statistic as the summarizing statistic, and in these cases r and Zr were calculated with the formula proposed Rosenberg et al. (2000, p. 96–97), where $r = \sqrt{(F/(F + \text{d.f. error}))}$. When r or R^2 were not explicitly available, we calculated them extracting the raw data from the scatter plots, using the DATA THIEF II program (Tummers 2006).

We calculated Zr effect size per species. It has been shown in previous meta-analyses that species are relatively independent units, even when more than one species are reported in the same study (e.g., Aguilar et al. 2006; Carmona et al. 2010; Munguía-Rosas et al. 2011). We weighted effect sizes using the inverse of the variance ($1/N{-}3$) and thus gave more weight in the analysis to more accurate studies. The overall effect size of lunar phobia (i.e., the relationship between moonlight and bat activity in all bat species) was assessed with a random-effects model, for which an average effect size from a population of effects was calculated (Borenstein et al. 2009). We used Cochran's Q as a measure of effect size heterogeneity; calculated as the weighted sum of squared differences between effect size per species and the pooled effect across species (Gurevitch and Hedges 1999). Publication bias was assessed with regression methods as described by Egger et al. (1997) which are more accurate than simple visual examination of the funnel plots.

We evaluated the influence of three moderator variables on the strength of the relationship between moonlight intensity and bat activity: latitude, foraging habitat and the way in which bat activity was recorded. Latitude was given in the majority of studies, and when missing, we easily obtained it by locating the study area on digital cartography using Google Earth (version 6.2). We grouped the foraging habitats of bats into six categories: canopy, subcanopy, understory, open spaces, water surface and open air (following Karlsson et al. 2002; Meyer et al. 2004; Breviglieri 2011; Rex et al. 2011). Open spaces and open-air habitats differ from background cluttered space in the forest. Open-space bat species forage in gaps inside the forest, while open-air species forage several meters above the forest canopy in uncluttered space (Schnitzler and Kalko 2001). The type of bat activity recorded was included as a moderator variable to assess if the way bat activity was measured influences effect size of lunar phobia. The type of bat activity was classified in four categories: number of captures, number of feeding buzzes, inputs and outputs of roost sites, and area of activity. To assess the significance of the moderator variables we also used a random-effects model and the inverse of variance per species as the weighting factor. All analyses were performed using the Metafor package (Viechtbauer 2010) for R 2.12.2 software (R Development Core Team 2011).

We obtained data for 26 bat species from 11 studies, with the exception of four unidentified species for which only family was reported (see Appendix). The foraging habitat for these unidentified species was not used in the analysis as it was not known. The heterogeneity test was significant for all bat species analyzed ($Q = 3589.26$, d.f. = 47, $P < 0.0001$) and therefore a random-effects model is justified. The asymmetry test accepted the null hypothesis of effect size symmetry ($t = 1.701$, d.f. = 46, $P = 0.09$), therefore, there was no evidence of any publication bias in our data set. We found no significant effect of the type of bat activity measured on lunar

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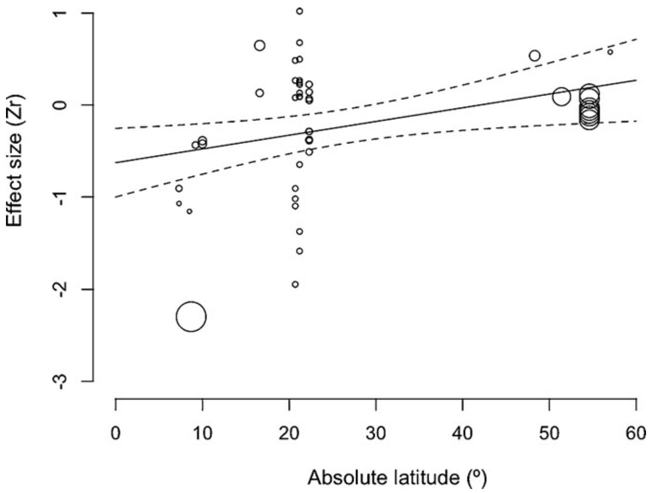

Fig. 1. Relationship between the effect size of lunar phobia (i.e., moonlight intensity vs. bat activity) and north or south latitude (Absolute latitude). Effect sizes were transformed into Fisher's *Z* values. Lines show the fitted regression line and its 95% confidence interval. Bubble size is proportional to the inverse of the variance of the effect size.

phobia (Q_B = 1.4, P = 0.08), meaning there was no bias introduced by the methodological approach.

The results suggest that moonlight is negatively correlated with bat activity, and the overall relationship (back transformed Pearson's r) between these variables was -0.22 ± 0.09 (hereafter, mean and SE; P = 0.02) (see forest plot in the online supplemental material). Although weak, the relationship between latitude and effect size of lunar phobia was significant and positively related ($r = 0.023 \pm 0.009$, P = 0.01; Fig. 1). We found statistically significant differences in the effect size of lunar phobia among the levels of the foraging habitat factor (Q_B = 17.35, P = 0.01). However, only bats that forage over water surfaces ($r = -0.83 \pm 0.44$, P = 0.005) and in the forest canopy ($r = -0.31 \pm 0.14$, P = 0.02) were significantly different from zero.

Lunar phobia in bats has been the topic of debate for several years because there is currently not only evidence supporting (e.g., Morrison 1980; Fleming and Heithaus 1986; Börk 2006; Lang et al. 2006; Esbérard 2007), but also against (e.g., Karlsson et al. 2002; Russo and Jones 2003; Thies et al. 2006; Holland et al. 2011) this phenomenon. However, our rigorous quantitative review of the studies which met the selection criteria suggests that, on average, moonlight intensity has a negative effect on the level of bat activity. Not only does our study provide the first reliable evaluation of the lunar phobia phenomenon, but also suggests that the latter is contingent on foraging habitat, given that the activity of bats foraging over the water surface and over the forest canopy decreased when moonlight was intense (Table 1). Interestingly, our results also suggest that lunar phobia is stronger (i.e., there is a larger negative effect) in tropical bats, while the phenomenon is weak in temperate species (Fig. 1 and Appendix).

Table 1
Results of a random-effects meta-analysis to assess the effect of moonlight intensity on bat activity. Foraging habitat (a factor with 6 levels) was included as a moderator variable in the model. The effect size (*Zr*), the statistics (*Z*) and *P* values per factor level, are shown.

Moderator	Estimate	*Z* value	*P* value
Open air	Zr = 0.09	0.21	0.82
Open space	Zr = −0.24	−0.87	0.38
Canopy	Zr = −0.31	−2.2	0.02
Subcanopy	Zr = −0.10	−0.52	0.6
Understory	Zr = −0.42	−1.1	0.25
Water surface	Zr = −1.23	−2.82	0.005

As predicted, our results indicate that bats that forage over the surface of the water and beneath the forest canopy exhibited significantly more lunar phobia than the bats that forage in more cluttered habitats (see Table 1). The species that forage over water surfaces (*Noctilio leporinus* and *Myotis daubentonii*) feed on fish and flying insects, respectively (Altringham 2011). Bats run a high risk of being preyed upon in these habitats because they are highly visible during well illuminated nights. Another explanation is that moonlight may also increase the ability of the bats' prey to detect the bats, thus reducing capture success, thus moonlight intensity would indirectly reduce bat foraging activity. The species foraging in the forest canopy are usually large frugivores (i.e., *Artibeus* spp. 65–70 g or *Cynopterus sphinx* 34–70 g). A seminal study on lunar phobia with large frugivores detected a decrease in foraging activity that could be attributed to an increased risk of predation (Morrison 1980). Therefore, our results corroborate earlier findings for these bat species. The assumption that bat species that forage in open spaces did not have greater lunar phobia than understory bats and subcanopy bats was not met. This can be explained because some species can change the vertical strata of the forest where they forage (Hecker and Brigham 1999). Additionally, foraging theory tells us that animals are able to change their foraging behavior according to predation risk (Lima and Dill 1990), moving from group to solitary foraging when predation risk increases and, this way these bat species may reduce predation risk even on well lit nights.

The prediction that latitude would be positively related to lunar phobia was correct. Karlsson et al. (2002) proposed that the diversity of predators in ecosystems close to the equator is higher compared to temperate ecosystems. These authors also suggested that most tropical bat species fly slowly (frugivores, gleaning insectivores, carnivores) compared to those that inhabit higher latitudes (open-space insectivores; Norberg and Rayner 1987). These two explanations may be applicable to our results. However, the relationship between latitude and lunar phobia was very weak, perhaps due to the heterogeneity of the data and the lack of studies done for sites located from 25 to 45° latitude in both hemispheres (Fig. 1). This heterogeneity could result from several factors, such as the variation in the density and diversity of predators at the study locations. Accounting for this and other sources of variation, future studies may reveal that the effect size of latitude on lunar phobia in bats is greater that we found here.

Although we provide strong evidence that lunar phobia is common in bat species, we also recognize that we cannot assess causation. Moonlight certainly increases the risk of predation for bats, but intense moonlight also reduces the density of bat prey. Studies evaluating the density of prey available to insectivorous bats have reported a negative relationship between moonlight intensity and insect activity (Lang et al. 2006). Frugivores and nectarivores have UV-sensitive cone photoreceptors that may improve their visual orientation with respect to feeding resources, as well as predator avoidance during well-illuminated nights (Müller et al. 2009). Therefore, lunar phobia in bats is a complex issue for which the trade-off between the risk of predation and foraging success should be taken into account.

It is true that some valuable evidence assessing lunar phobia was not included in our meta-analysis because those studies did not met the selection criteria (see Appendix); however, the selection procedure was established a priori and was applied to all studies independently of the findings of the study (i.e., in favor of or against lunar phobia). In conclusion, lunar phobia is common among bats, especially among those foraging in open habitats, and less important for temperate species. Our study highlighted patterns which will hopefully encourage further work.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.mambio.2012.08.004.

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