DOES MOONLIGHT CHANGE VERTICAL STRATIFICATION OF ACTIVITY BY FOREST-DWELLING INSECTIVOROUS BATS?

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We hypothesized that bats would not change total nightly activity in response to the lunar cycle but would exhibit a shift in habitat among vertical levels (different degrees of spatial complexity and light penetration) of temperate rainforest with changing levels of lunar light. As predicted, we found no evidence that activity of bats varied directly with intensity of moonlight. However, activity changed depending on height within the forest, and there was a significant interaction between moonlight and height. The shift between vertical levels was not expected if risk of predation was an important selective pressure, because activity was highest in the canopy and lowest at the level of shrubs on bright nights. The most likely explanation for interaction between height and moonlight is that bats adjust use of microhabitats to match distribution of prey.

Key words: Vespertilionidae, bats, echolocation, activity, habitat use, moonlight, British Columbia

Biological rhythms often are influenced by external cues that synchronize various behavioral and physiological systems. Illumination is especially important from a behavioral perspective in organisms ranging from invertebrates to mammals (Pittendrigh, 1993). One component of illumination important to many nocturnal mammals is the lunar cycle. Rodents have been the foci of most studies on moonlight-mediated patterns of behavior in mammals, and most research has focused on reactions to lunar light as antipredator responses. Longland and Price (1991) found that heteromyid rodents were subject to greater predation by great horned owls (Bubo virginianus) when illumination was high and when in open habitats. Similarly, Brown et al. (1988) showed that when barn owls (Tyto alba) were introduced to an experimental enclosure, heteromyid rodents significantly decreased activity and shifted remaining activity into habitats with more cover, even though less food was available. Some studies (e.g., Dickman, 1992) even have used lunar illumination as an index of predation pressure.

Visually oriented nocturnal birds may be particularly constrained by lunar illumination due to risk of crashing into obstacles. Nocturnal and crepuscular birds increase activity during bright periods of the lunar cycle (Brigham and Barclay, 1992; Mills, 1986). In contrast, many visually navigating frugivorous bats are least active on bright nights (Fleming, 1988; Law, 1997; Morrison, 1978), which is expected if predation from visual predators were a major selective pressure. An exception is the red fig-eating bat (Stenodermata rufum) which does not alter activity in response to changes in lunar illumination; however, it presumably evolved on an island (Puerto Rico) in the absence of visually oriented nocturnal predators (Gannon and Willig, 1997).

For echolocating insectivorous bats, different levels of light throughout the lunar cycle should be irrelevant with respect to navigation, and changes in intensity of light should not directly affect activity by these
bats. However, some studies anecdotally report that lunar illumination suppresses activity by increasing risk of predation (Fenton et al., 1977; Padgett and Rose, 1991). In contrast, Negraeff and Brigham (1995) showed that overall levels of activity by little brown bats (Myotis lucifugus) were not related to percentage of the moon’s face illuminated (an index to amount of moonlight). Likewise, Rydell (1991) found no effect of moonlight on overall activity by northern bats (Eptesicus nilssonii). However, neither study rigorously assessed the possibility that bats maintained similar overall activity but shifted to different microhabitats with changing lunar light. A limited study (2 h of monitoring on each of 7 nights) by Reith (1982) suggested that insect-eating bats sometimes adjust activity to fly more in shadow on moonlit nights. This supports the habitat-shift hypothesis.

Our purpose was to assess if overall activity of bats differed with respect to lunar illumination and if bats exhibited a more subtle behavioral response to moonlight in the form of a shift between habitats. A shift in habitats could result from either perceived risk of predation or changing distribution of insects (prey). Specifically, we predicted that if forest-dwelling bats avoided highly illuminated areas due to perceived risk of predation, activity on bright nights should be concentrated at lower heights within the forest, where less light would penetrate, thus hampering visual predators. Conversely, we expected that more activity would occur in the canopy on dark nights.

**Materials and Methods**

**Study area.**—The study took place at three sites in temperate rain forest on Vancouver Island, British Columbia, Canada. Site A was in coastal forest of Douglas fir (Pseudotsuga menziesii) at the Department of National Defense Ammunition Depot at Rocky Point on the southernmost tip of the island (48°20’N, 123°38’W). Common species of tree were Douglas fir, western red cedar (Thuja plicata), grand fir (Abies grandis), arbutus (Arbutus menziesii), garry oak (Quercus garryana), and red alder (Alnus rubra—Meidinger and Pojar, 1991). The forest was open, with low spatial complexity and many gaps in the canopy; maximum height of trees was ca. 65 m.

Site B was in the Carmanah Valley (48°38’N, 124°30’W), a watershed that was classified as the very wet hypermaritime subzone of coastal forest of western hemlock (Tsuga heterophylla). Western hemlock and Sitka spruce (Picea sitchensis) were the most common species of tree (Meidinger and Pojar, 1991). That site had a thick layering of branches in the canopy and subcanopy, resulting in the least penetration of light of all sites. There also was thick shrubby vegetation that made walking difficult. Maximum height of trees was ca. 90 m.

Site C was near the town of Bamfield (48°48’N, 125°12’W) in wet, hypermaritime, coastal forest of western hemlock. Sitka spruce was the dominant species of tree (Meidinger and Pojar, 1991), with a maximum height of ca. 80 m. Trees at this site also had a thick layering of branches in the canopy and subcanopy but were more widely spaced than those at site B. All sites were old-growth (>200 years old) rainforest that had never been logged or managed.

**Measuring activity of bats.**—Species of bat potentially occurring at the study sites included Myotis lucifugus, M. californicus, M. evotis, M. keenii, M. yumanensis, M. volans, Lasiurus cinereus, Lasionycteris noctivagans, Corynorhinus townsendii, and Eptesicus fissus (Nagorsen and Brigham, 1993). We used total number of recorded bat passes per night as an index to total nightly activity of bats. To detect and record echolocation calls, we used bat detectors, delay switches (Anabat II—Titley Electronics, Ballina, New South Wales, Australia), and a voice-actuated tape recorder (RadioShack CTR-76—Barrie, Ontario). The delay switch turned on the tape recorder only when calls were detected to maximize amount of time the system could be left unattended (Bradshaw, 1997). Although echolocation calls of some species of bat are detected more easily than those of others due to differences in intensity, that bias likely had minimal effect because we were sampling the entire community rather than a single species. Detectors were not deployed on nights with heavy rain.

A detector, delay switch, tape recorder, and
12-V battery were packed in a plastic box (26 by 35 by 10 cm) with the microphone of the detector pointing parallel to the ground through a hole in the side of the box. We hoisted those units into the canopy using pulleys anchored to the highest branch possible on a mature tree. Maximum height of trees varied among sites (ca. 65–90 m), with the highest detector unit ≤8 m from the top of the tree. On any given night, we deployed three detectors at one site: one in the canopy, a second halfway between the pulley and the ground (subcanopy), and a third ≤2 m from the ground (shrub). Each night, all microphones were pointed in one, randomly determined, cardinal direction. For each "detector-night," we recorded the number and time of occurrence of all sequences of echolocation during true night. We did not analyze echolocation calls by species or groups of species because discrimination among calls from bats potentially encountered in our study (especially various Myotis) was unreliable. Also, we were most interested in response to moonlight by the community of bats, as opposed to individual species.

Environmental variables.—We measured intensity of moonlight using a light meter intended for use in photographic darkrooms (Beseler PM2L—Charles Beseler Company, Linden, NJ). The high-resolution light meter was calibrated at the factory but did not indicate standard units of light (i.e., lumens); instead, it measured light in arbitrary units ranging from 0 (no light) to 50 (full moon directly overhead, cloudless sky). We took hourly measurements of light beginning after nautical twilight in the evening and ending when nautical twilight began in the morning. Nautical twilight occurs when the sun is 0°–12° below the horizon, below which, solar light has a negligible effect on total illumination (Mills, 1986). Times of the beginning and end of nautical twilight were taken from astronomical tables calculated by the Dominion Astrophysical Observatory (Victoria, British Columbia, Canada). Illumination was measured at ground level in the largest available clearing (>10 m in diameter and ≤2 km from the sampling site), which presumably was representative of the maximum amount of light reaching the top of the forest. Logistically, it was not possible to measure levels of light at the same sites as detectors were deployed. We also recorded minimum nightly ambient temperature, degree of cover by clouds (on a scale of 0–3, with 0 being clear and 3 being completely overcast), speed of wind (on a scale of 0–3, with 0 being completely calm and 3 being winds >50 km/hr), and presence of fog or precipitation.

Statistical analyses.—Our data were not normally distributed, so we used square-root and logarithmic transformations (Zar, 1996). After transformation, data were close to normal (Shapiro–Wilks’ test, W = 0.9506, P > 0.01), so we used parametric analysis of variance (Zar, 1996). To assess effects of height in the forest and light on activity of bats, we performed a two-way factorial analysis of covariance, with height of detector and type of forest (categorical variables) as main effects and intensity of light (continuous variable) as a covariate (Zar, 1996). Post-hoc Tukey’s HSD tests were conducted when analysis of covariance was significant (Zar, 1996). To investigate environmental effects, we conducted multiple correlation analysis with activity as the dependent variable and height of detector, intensity of light, velocity of wind, minimum nightly ambient temperature, percent cover by clouds, and presence of fog and precipitation as independent variables (Zar, 1996). Data are presented as $\bar{x} \pm 1 SE$, and the criterion of rejection was 0.05 for all statistical tests.

RESULTS

We simultaneously sampled activity of bats at three vertical levels on 33 nights between 31 May and 26 August 1995. Samples were collected on 10 nights at three trees at Rocky Point, 17 nights at four trees in the Carmanah Valley, and 6 nights at three trees near Bamfield.

Using analysis of covariance, we found that nightly activity of bats did not differ among types of forest ($F = 0.27, d.f. = 2, 83; P = 0.77$) or with intensity of light ($F = 0.32, d.f. = 1, 83; P = 0.99$); however, levels of activity differed with height of the detector ($F = 5.61, d.f. = 2, 83; P = 0.015$). Tukey’s tests showed that there was less activity in the canopy than in the subcanopy ($P = 0.04$) or shrub level ($P = 0.02$), but activity did not differ between the shrub and subcanopy level ($P = 0.90$). There were no interactions between type of forest and height of detector ($F = 1.10, d.f. = 4, 83; P = 0.39$) or between type of for-
est and intensity of light ($F = 0.12; \text{d.f.} = 2, 81; P = 0.88$). There was an interaction between intensity of light and height of detector ($F = 2.94; \text{d.f.} = 2, 81; P = 0.01$) suggesting that bats shifted habitat with changing lunar illumination. Activity of bats in shrubs and the subcanopy decreased as lunar illumination increased, although only slightly. However, opposite to our prediction, activity in the canopy increased as light increased (Fig. 1). Temperature (range = $7.9$–$14.7^\circ\text{C}$), speed of wind (range: 0–2), cloud cover, and presence or absence of rain or fog were not correlated with total activity by bats.

**DISCUSSION**

The community of bats on Vancouver Island did not exhibit an overall reduction in activity in response to the lunar cycle. This corroborates results of Reith (1982), Rydell (1991), and Negraeff and Brigham (1995). Together, these studies strongly suggest that overall activity of insect-eating bats is not directly influenced by moonlight in contrast to anecdotal reports (Fenton et al., 1977; Padgett and Rose, 1991).

The most interesting result of our study, however, was the significant interaction between height of detector and moonlight on activity of bats. This interaction indicates that lunar light does have a subtle influence on activity of bats, but not one suggesting that bats' responses to moonlight are mediated by perceived risk of predation. If predation were a significant factor, we expected bats to shift activity into areas of the forest with greater spatial complexity and less light (closer to the ground), in a manner analogous to rodents (Daly et al., 1992; Kotler et al., 1991). In contrast, we found that bats were more active on bright nights in the canopy, which presumably is a spatially less complex habitat with more penetration by light. That we found no evidence for a shift between microhabitats that could be explained by predation may not be surprising, given the rarity of records for predation on bats in the north temperate zone, especially in cluttered areas such as forests (Baker, 1962). Flying bats are difficult to catch, and owls, which are likely the only potential predators of bats, are probably not agile enough to catch them on a regular basis (Baker, 1962).

Another factor that could account for the interaction between height and moonlight is the distribution of flying insects. Studies of the influence of the lunar cycle on patterns of activity in insects have produced conflicting results. For example, noctuid moths exhibit no change in activity attributable to lunar light (Hardwick, 1972), but other insects, such as pink bollworms (*Pectinophora gossypiella*), are more active at certain times in the lunar cycle (Beasley and Adams, 1994; Williams and Singh, 1951). Williams and Singh (1951) argue that insects' patterns of activity relative to the lunar cy-
cle appear specific to the individual site, species, or perhaps even community.

Studies of the height of activity by insects in relation to moonlight have produced more consistent results. Williams et al. (1956) suggested that insects alter their flying altitude in response to changing illumination. That hypothesis was tested in East Africa by Brown and Taylor (1971), who found that the altitude of flight of most insects, except lepidopterans, changed with the lunar cycle. Schaefer (1976) used radar to track moths and found that density above the canopy was correlated highly with captures of moths in light traps within the canopy, except on 2 nights with bright moonlight when captures were reduced by a factor of eight. Schaefer's (1976) results suggested that, although moths remained active, they altered flight with respect to habitat in response to lunar light. Likewise, McGechie (1989) used catches by a trap to show that activity of moths was correlated with nocturnal illumination. Thus, we argue that the most likely explanation for the interaction of height and moonlight is that bats adjust use of microhabitats to match distribution of prey.

Minimum nightly ambient temperature, wind speed, cloud cover, and presence of rain or fog were not correlated with activity of bats, which may be due to the physical nature and microclimate of rainforest and our sampling protocol. Temperature and wind did not fluctuate greatly, and we did not sample during heavy rain.

Our evidence shows that moonlight has no overall effect on activity by temperate, insectivorous bats, but there is a subtle behavioral shift in where activity of bats is concentrated, depending on levels of lunar light. The shift between microhabitats is not consistent with the hypothesis that bats face increased risk of predation with increasing light. It is more likely that activity of bats is affected by changes in use of microhabitats by flying insects, perhaps mediated by the lunar cycle. This hypothesis remains to be evaluated with precise data on diet and availability of insects in relation to the lunar cycle.

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