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A Comparison of Bat Activity at Low and High Elevations in the Black Hills of Western Washington

Abstract

We examined the differences in activity patterns and community structure of bats between low (< 150 m) and high (\geq 575 m) elevation sites in two habitats of the Capitol State Forest, Washington. Total bat activity averaged four times higher at low elevation sites than at high elevation sites. Feeding activity was almost 20 times higher at low elevation sites. However, the non-myotis group had similar activity levels at high and low elevation, whereas myotis group activity decreased at higher elevations. Different levels of activity between elevations could be the result of differences in insect availability, climatic conditions, and morphology of the bat species.

Introduction

That fewer bats occupy high elevation regions compared to lowland regions is a familiar pattern to many mammalogists. Changes in elevation are ecologically similar to changes in latitude. However, unlike latitudinal patterns in bat diversity that have received considerable attention (Findley and Wilson 1983, Willig and Selcer 1989), elevational gradients have seldom been investigated. An exception to this is a study that examined the variation in bat community attributes along an elevational gradient in the central Andes of Peru (Graham 1983). Graham found that of the 101 species distributed along this gradient, 82 occurred below 400 m and only 10 above 3200 m. He hypothesized that the reduction in insectivorous bat species in the highlands might be explained by a reduction in roost site availability, temperature, or insect abundance.

In the Pacific Northwest, Thomas and West (1991) found no breeding individuals above 300 m in the western Washington Cascade Range. Others have reported decreases in relative abundance of reproductive individuals at high eleva-

tions in south-central British Columbia (Fenton et al. 1980) and the Black Hills of South Dakota (Cryan et al. 2000). Moreover, foraging activity is greater at low elevation sites than at high elevation sites in southern British Columbia (Grindal and Brigham 1999). The authors suggested that foraging opportunities limit bat use of high elevational forests because the cooler conditions may decrease activity of their insect prey while imposing greater thermoregulatory costs.

Apart from the work by Thomas and West (1991), there is no information available concerning elevational patterns in bat activity and species composition in western Washington. The objective of this study was to compare levels of bat activity, weather conditions, and insect abundance between low (< 150 m) and high (\geq 575 m) elevations in two habitats of a Pacific Northwest forest ecosystem.

Methods

The study was conducted at Capitol State Forest (46°57' N, 123°10' W) and Lower Chehalis State Forest (46°83' N, 123°38' W) located in the Black Hills ~24 km west of Olympia, Washington. The forests include more than 34,000 ha of multiple use areas under the stewardship of the Washington State Department of Natural Resources. The forests are a mix of Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*),

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western red cedar (*Thuja plicata*), red alder (*Alnus rubra*), and bigleaf maple (*Acer macrophyllum*). Three pronounced peaks that reach > 800 m in elevation dominate the study area, but the terrain generally lies at < 200 m. Due to prevailing westerly winds and close proximity to the ocean, the area is characterized by rapidly changing weather often resulting in wet conditions.

During summer 1995, activity was monitored at eight sites located within two elevational zones. For purposes of our study, low elevation sites were < 150 m and high elevation sites were \geq 575 m. The high elevation sites were centered on Rock Candy Mountain (718 m), Larch Mountain (810 m), and Capitol Peak (810 m). Two ponds and two clearings were selected for monitoring bat activity within each elevational zone.

Bats were surveyed using remotely deployed ultrasonic detectors (Anabat II bat detectors and delay switches) coupled with tape recorders to record echolocation calls of bats. Two detectors were operated simultaneously, one at low elevation and one at high elevation within the same habitat. These were left in place for two nights before being moved to the next pair of sites. Pond detector stations were located ~1 m from the water's edge facing the pond center. Detector stations located in clearings were placed on stumps ~1 m high and also directed toward the site center. These habitats were sampled from mid-June through late September.

For purposes of this study, a detection was operationally defined as two or more consecutive pulses recorded as a bat flies through the airspace sampled by the microphone. Commuting activity was identified as a steady series of echolocation calls and foraging activity was identified by a distinctive train of pulses with an increasing repetition rate (Griffin 1958). Activity was indexed as the mean number of detections per night within each site. Because bat activity was concentrated within the first 4 hr after sunset, differences in total night length over the sampling period were not considered influential on nightly detection totals.

Recorded detections were analyzed at two levels. First, detections were summed regardless of species to determine the general distribution of detections among sites. Second, detections were grouped into myotis and non-myotis bats based on call characteristics using zero-crossing analy-

sis and signal processing software (Anabat V). The myotis group comprised California myotis (*Myotis californicus*), long-eared myotis (*M. evotis*), little brown myotis (*M. lucifugus*), fringed myotis (*M. thysanodes*), long-legged myotis (*M. volans*), and Yuma myotis (*M. yumanensis*). The non-myotis group comprised big brown bats (*Eptesicus fuscus*), silver-haired bats (*Lasionycteris noctivagans*), hoary bats (*Lasiurus cinereus*), and Townsend's big eared bats (*Corynorhynchus townsendii*). Members of the myotis group are typically small, agile bats that have high frequency, short duration calls. The larger bats of the non-myotis group are characterized as faster, less maneuverable species with low frequency, long duration calls. Separation between these groups, although coarse, does provide insight into ecological differences based on morphology and echolocation call design.

Temperature and wind were monitored at the two elevations using mobile weather stations. Sensors were mounted 1 m above the ground and measurements for each variable were recorded hourly. Throughout the summer, one high and one low elevation site of the same habitat (i.e., pond or clearing) was monitored simultaneously for ~1 wk then rotated to the next pair of sites. Nightly temperature ($^{\circ}$ C) and wind speed (km/hr) were then averaged over all visits within each elevational zone.

We used a sticky trap method and a headlight transect method to provide relative measures of insect abundance at low and high elevations. The sticky trap method consisted of a plastic film wrapped around two tin coffee cans attached end to end. Each set of cans was fastened to a metal rod 2 m above ground level or placed on an inner tube and floated over water. A thin coat of adhesive was applied to the outer surface of the cylinder. Insects landing on the cylinder adhered to the sheet.

A high and low elevation site was sampled concurrently with four sticky traps each. Insects were collected from traps over two consecutive days on eight occasions in each habitat/elevation combination. Insects were classified into large (> 5 mm in length) and small (\leq 5 mm in length) size categories. Ideally, traps would have been cleared simultaneously after every nightly sampling period. Logistical constraints, however, required us to clear traps opportunistically when we visited sites.

Headlight transects were also conducted along two parallel roads located at high and low elevations to sample moth density. The 3.2 km transects were driven ~15-20 min after dusk during which time all moths spotted within the headlights were counted. Both low and high elevation counts were performed weekly.

Because bat activity and insect abundance closely resembled a Poisson distribution, an analysis of deviance (ANODEV) with a log-linear model and Poisson error (GLIM 4.0) (Francis et al. 1993) was used to examine the effect of elevation and habitat on average bat activity and insect abundance (McCullagh and Nelder 1989). The models were overdispersed so that the F-statistic was used to determine significance (Crawley 1993). T-tests were used to compare differences in nightly temperature and wind speed at the two elevations and a paired t-test was used to evaluate differences in moth abundance (SYSTAT 7.0, Wilkinson 1996). Significance was set at $P = 0.05$. We also report mean \pm SE.

Results

We recorded 3206 detections over 122 detector nights. Of the total detections, 2559 were classified in the myotis group, 642 were classified in the non-myotis group, and 5 were unidentifiable. Myotis group activity was significantly associated with habitat and elevation (Table 1), with the highest activity rates found at low elevation ponds (Figure 1). No significant patterns in non-myotis group activity were detected (Table 1, Figure 1).

Nightly activity patterns differed between elevations (Figure 2). At low elevations, a distinct

TABLE 1. Analysis of deviance for mean number of bat detections per night with elevation and habitat type.

Source	df	Deviance	F	P
Myotis group				
Elevation	1	1108.0	14.11	0.020
Habitat	1	1951.0	24.84	0.008
Elevation×Habitat	1	9.111	0.12	0.751
Residual	4	314.21		
Non-Myotis group				
Elevation	1	12.56	0.14	0.732
Habitat	1	230.0	2.47	0.191
Elevation×Habitat	1	25.94	0.28	0.625
Residual	4	372.07		

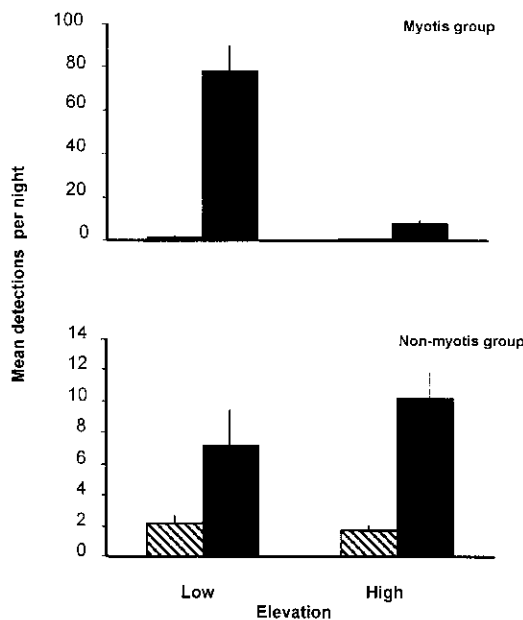


Figure 1. Mean detections per night of myotis and non-myotis bats. Solid bars represent ponds and hatched bars represent clearings. Error bars show standard error.

peak in activity occurred between 2000 and 2300 hr. However, at high elevations the activity was much more protracted throughout the night with no obvious peaks in detection rates.

Of the 3206 detections, 195 were identified as feeding activity. Low ponds had the highest number of feeding attempts per night ($\bar{x} = 6.1 \pm 7.82$). All other sites had less than one feeding attempt recorded per night.

Of the 4676 insects captured using sticky traps, 4125 were small and 551 were large. Overall, insect abundance was greatest at low elevation sites (Figure 3). Small insects were most common in low elevation clearings and no significant difference was detected between high and low elevation ponds (Table 2, Figure 3). We detected no trends in the abundance of large insects caught in sticky traps. Significantly more moths were encountered at low elevation sites ($\bar{x} = 11.30$) than high elevations sites ($\bar{x} = 6.63$; $P < 0.001$) during headlight transects.

On average, nights at high elevation were 2.3°C cooler ($\bar{x} = 11.70^\circ\text{C}$) than at low elevations ($\bar{x} =$

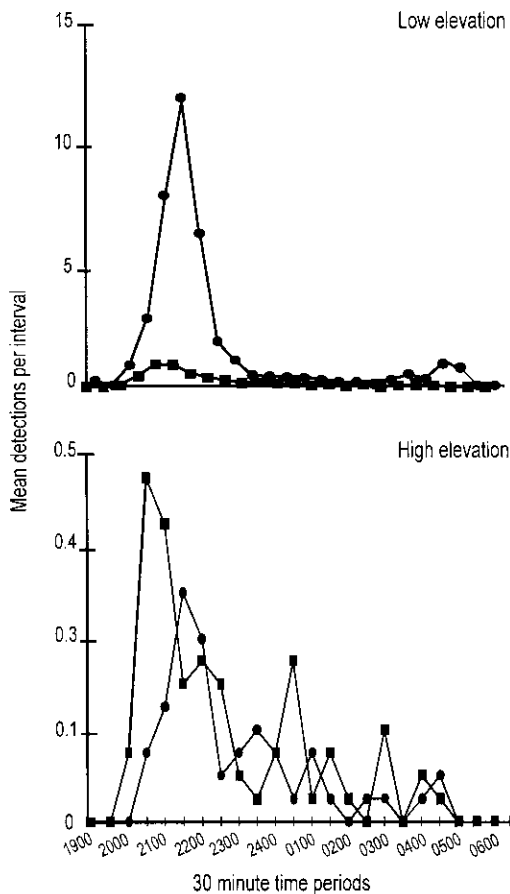


Figure 2. Mean detections per time interval of myotis (•) and non-myotis bats (■) at low elevation and high elevation. Intervals are 30 min time periods beginning at 1900 hr and ending at 0700 hr.

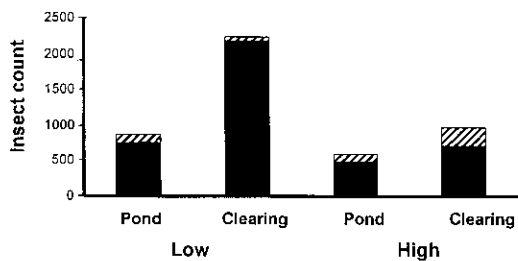


Figure 3. Total number of insects captured by habitat and elevation. Hatched bars represent large insects (>5 mm) and black bars represent small insects (≤ 5 mm).

14.00°C, $P < 0.001$). Similarly, windspeed was 2.9 km/hr greater in the highlands ($\bar{x} = 5.71$ km/hr) than in the lowlands ($\bar{x} = 2.86$ km/hr, $P < 0.001$).

TABLE 2. Analysis of deviance for mean number of insects captured per trapping interval with elevation and habitat type.

Source	df	Deviance	F	P
Small (<5mm)				
Elevation	1	875.9	73.36	0.001
Habitat	1	517.7	43.36	0.003
Elevation×Habitat	1	149.2	12.50	0.024
Residual	4	47.758		
Large (>5mm)				
Elevation	1	28.80	1.29	0.320
Habitat	1	6.928	0.31	0.608
Elevation×Habitat	1	43.45	1.94	0.236
Residual	4	89.503		

Discussion

We found distinct differences in bat activity between elevations and habitats for the myotis group, but not for the non-myotis group. Activity levels of the myotis group were significantly greater at low elevation sites; however, no elevational patterns in non-myotis activity were detected (Figure 1). These elevational differences in activity could be the result of climatic conditions, insect availability or morphological differences between myotis and non-myotis bats.

Cooler and windier nights, such as in the highlands, tend to suppress flight activity of bats (Anthony et al. 1981, O'Farrell 1967, Stebbings 1968) by imposing thermoregulatory stress and by reducing the activity of their insect prey. Barclay (1991) and Cryan et al. (2000) suggest that females move from cool hibernation sites in the mountains to warm maternity colonies at lower elevations where ambient temperature and presumably insect abundance is higher. The absence of reproductive individuals could, therefore, result in lower total bat activity at high elevation sites.

Differences in morphology may also influence the elevational distribution of bats. Because the cost of flight increases with decreasing size, de Jong (1994) hypothesized that smaller bats with slower flight would be restricted from using high elevation habitats where insect abundance was low and long-distance foraging flights were required to find enough food. Such long distance flights would be too energetically expensive for small species but not for larger species. This greater mobility may allow larger-bodied non-myotis bats to use a range of elevations for foraging depending on nightly weather conditions or other factors.

Differences in prey detection capabilities also could influence the activity patterns of bats at different elevations. It has been suggested that large bats are restricted to relatively large prey because their lower frequency calls make it difficult to detect small insects (Barclay and Brigham 1991). The lack of elevational trends in non-myotis group activity (Figure 1) and large insect abundance (Figure 3) is consistent with the hypothesis that larger bat species cover a range of elevations in search of larger insects. However, our study cannot link bat distribution to feeding preferences.

The relationship between bat activity and elevation is complex due to its multi-factorial nature, nonetheless, in this study elevation was associated with bat activity and distribution. Further investigations of species-specific responses to elevation are needed especially in light of the predominance of high elevation reserves in the North-

west Forest Plan (Forest Ecosystem Management Assessment Team 1993). Given this and other studies showing a decrease in bat activity (Grindal and Brigham 1999) or relative abundance (Fenton et al. 1980, Thomas and West 1991, Cryan et al. 2000) with elevation, the effectiveness of these reserves for some bats, especially myotis species, requires further verification.

Acknowledgments

We thank Melanie Bojanowski for her extensive assistance with data collection. We also thank S. D. West, J. K. Agee, D. A. Manuwal, and J. K. Kenagy for commenting on earlier versions of this manuscript. This research was funded in part by the Demonstration of Ecosystem Management Options (DEMO) study, a joint effort of the USDA Forest Service Region 6 and Pacific Northwest Research station.

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Received 7 August 2001

Accepted for publication 19 October 2002