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The influence of regional climate and nightly weather conditions on activity patterns of insectivorous bats

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We examined the influence of average climatic conditions and nightly weather variations using bat detectors on the summer activity of bats. Average summer precipitation was the principal climate variable correlated with differences in bat activity along a latitudinal array of sites, with the highest activity levels occurring at sites located in montane rain shadows. On a nightly basis, the occurrence of rain and low temperatures had strong negative correlations with flight activity. However, the variation in nightly activity at a site that was explained by weather was relatively small. Our results suggest that the use of long-term climatic data offers potential to predict variations in bat activity among sites. Such information may be useful in recognizing conservation priorities for the management of bats in the Pacific Northwest where topography is complex and climate conditions are variable.

Key words: bats, climate, activity patterns, bat detector, Pacific Northwest

INTRODUCTION

Being small endothermic animals, temperate insectivorous bats may be particularly sensitive to climatic conditions because much of their energy is used to maintain a stable body temperature (Lewis, 1993). Unfavorable conditions of rain and low temperatures impose additional energetic costs to insectivorous bats by increasing thermoregulatory stress and decreasing activity of their insect prey (Racey and Speakman, 1987). Therefore, the ability to avoid unfavorable conditions by entering periodic torpor is essential for occupancy of temperate zones by small insectivorous bats (Findley, 1993). However, for pregnant females, torpor slows fetal development and may delay parturition (Racey and Swift, 1981). Delayed parturition in temperate regions may result in a significant decrease in the survival rate of females and young due to insufficient preparation for winter (Grindal *et al.*, 1992). Therefore, climate should have a major influence on the distributions of reproductive female bats (Thomas and West, 1991; Lewis, 1993) and densities of bats in general.

Understanding how climatic factors influence bat activity can provide insight into limitations on bat distributions, particularly at higher latitudes and in mountainous regions where environmental conditions may be extreme and variable. The most thorough examination of this relationship requires investigations on a temporal scale from the short (nightly weather variations) to the long (average climatic conditions) term. In this paper, we examine the influence of climatic conditions on bat activity at two spatio-temporal scales. We used data obtained from a number of concurrent echolocation surveys in the Pacific Northwest to assess the influence of average climatic conditions on bat activity at a regional scale (43°11'N to 48°32'N). In addition, a time series analysis at a single foraging site was performed to examine the influence of nightly weather conditions on bat activity at a local scale.

Materials and Methods

Regional Scale

During 1992–1996, indices of bat activity were obtained from multiple surveys in mature coniferous forest stands located in Oregon and Washington. These surveys were conducted in thirteen blocks of one to six sites each (total of 64 sites, Fig. 1) located within four physiographic provinces (Franklin and Dyrness, 1973): the Puget Trough, Southern Washington Cascade Range, Columbia Basin, and the Oregon Cascade Range. Except for the Teanaway study area (located in the Columbia Basin), the sites consisted of upland forest habitats dominated by mature Douglas-fir (*Pseudotsuga menziesii*). The Teanaway study area had an overstory comprised primarily of grand fir (*Abies grandis*), but was similar in age and stand structure to that of the Douglas-fir dominated sites. Additional site details are provided by Erickson (1998).

Species of bat potentially occurring in the study area included *Myotis californicus, M. evotis*, *M. lucifugus*, *M. thysanodes*, *M. volans*, *M. yumanensis*, *Eptesicus fuscus*, *Lasionycteris noctivagans*, *Lasiurus cinereus*, and *Corynorhinus townsendii* (Christy and West, 1993). We used the average number of detections (defined as the sequence of pulses recorded as a bat flies through the airspace sampled by the detector) per night at each site as an index of activity. Sites were sampled for 1–3 yrs and bat activity (calls per night) was averaged over years and sites to yield a single mean for each block (Table 1). The combined bat activity data represent activity patterns for the entire bat community, and may not be representative of the activity patterns of the individual species.

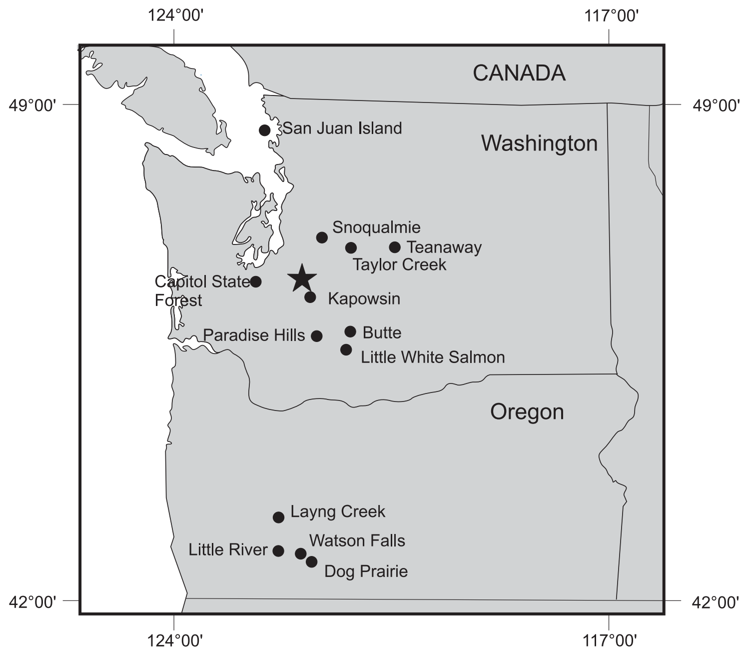

Fig. 1. Study sites where bat activity was recorded in the regional climate and nightly weather analyses. Circles indicate the location of the 13 study blocks used in the regional climate analysis. The star shows the location of a pond where bat activity was recorded and used in the nightly weather analysis

Remotely deployed ultrasonic detectors (Anabat II bat detectors and delay switches, Titley Electronics, Ballina, NSW, Australia) coupled with tape recorders were used to detect and record bat echolocation calls along with time announcements entered at the time of detection. At each site, the detector was placed 1 m from the ground and oriented 30° up from horizontal. Detector locations were chosen within small forest openings to reduce potential bias by recording in a similar microhabitat configuration. The same location was used each time the site was sampled.

Several detectors were operated simultaneously at sites within Oregon and Washington. At a site, a detector was left in place for two consecutive nights then moved to another site. Each site was visited at least three times for a minimum of six nights sampled. Sampling began in mid-June or early July and continued through mid-September. Visitation was spaced evenly throughout the sampling period to account for differences in activity related to reproduction, lactation and fledging of young (Christy and West, 1993). Detectors became active at dusk and remained operational for approximately 8 h. Because most of the bat activity is concentrated within the first four hours following sunset, differences in total night length over the sampling period were not considered influential on nightly detection totals. No sites were sampled in heavy rain due to the decrease in bat activity associated with precipitation (Erkert, 1982).

Climate data were obtained from the PRISM (Parameter-elevation Regressions on Slopes Model) mapping project of the USDA Natural Resources Conservation Service, Water and Climate Center. This analytical model uses point data and a digital elevation model to interpolate climatic variables from weather stations to grid points (Daly *et al*., 1994). The weather station data consists of three datasets: the National Climatic Data Center 1961–1990 'normals' dataset, the NRCS SNOTEL (SNOwpack TELemetry) network dataset and supplemental datasets submitted by the individual State Climatologists or Regional Climate Centers.

Gridded ASCII files generated by the PRISM model were imported into ArcInfo (ESRI, Redlands, CA) and monthly and annual climatic data were obtained for each study block. As most of the annual bat activity occurs during the summer months, climatic variables from May, June, July and August were used for analyses (Christy and West, 1993). Cooling degree-days and heating degree-days (calculated as the number of degrees that the mean daily temperature was above 18°C, and below 18°C, respectively), were summed from May through August, and minimum temperature and total monthly precipitation were averaged over this same time period. These four variables along with the mean date of the first fall freeze and last spring freeze were used in a stepwise multiple regression with forward selection using SYSTAT 7.0 (significance levels set at $\alpha = 0.05$; Wilkinson, 1996). Mean detections of bats per night were calculated for each block to serve as the dependent variable. A log transformation was used when calculating these means. To reduce the influence of age-related structural differences among sites, stand age was forced into the model as the first variable of the forward selection.

TABLE 1. Location, detection rates per night ($\bar{x} \pm$ SE) and number of years sampled in each of the 13 study blocks in Washington and Oregon

Site	Detection Rates	Years Sampled
Oregon		
Dog Prairie	4.1 ± 9.97	2
Watson Falls	7.9 ± 11.22	2
Little River	8.2 ± 10.39	2
Layng Creek	4.9 ± 6.43	2
Washington		
Little White Salmon	17.8 ± 29.58	2
Paradise Hills	1.6 ± 2.86	2
Butte	2.5 ± 11.04	2
Capitol State Forest	6.9 ± 14.87	2
Kapowsin	3.9 ± 4.94	2
Taylor Creek	3.6 ± 3.13	1
Snoqualmie	5.3 ± 6.55	1
Teanaway	18.8 ± 23.70	3
San Juan Island	25.8 ± 35.03	1

Local Scale

Using the ultrasonic detection techniques described previously, bat activity was monitored at night from mid-June through mid-September at one pond in 1996. The pond was a bat foraging site located in an intensively managed forest in the southwestern Cascade Range, Washington (Fig. 1). The detector was placed 2 m from the pond edge with the microphone tilted 30° up from horizontal and aimed towards the pond center. Unlike the regional scale analysis, ultrasonic monitoring of the foraging site occurred in all weather conditions including rain. A rain shelter was erected to keep raindrops from directly contacting the equipment and to muffle any rain noise that might interfere with the detection of bats.

Local weather conditions were measured continuously throughout the sampling period using a mobile weather station (Weather Wizard III, Davis Instruments, Hayward, California) placed adjacent to the pond. Weather variables measured were: average, minimum and maximum nightly temperatures, hourly average minimum and maximum nightly temperatures, average temperature during the afternoon preceeding the current night's sample, and the occurrence of wind and precipitation. Additional variables measuring solar radiation (average mega-joules of solar radiation per hour of the afternoon preceding the current night's sample), hourly average dew point, hourly average relative humidity, and average barometric pressure (midnight to midnight) were obtained from weather stations located ca. 12 km (Charles Lathrop Pack Experimental and Demonstration Forest) and 53 km (Sea-Tac Airport, National Oceanic and Atmospheric Association) from the pond.

Weather variables were summarized for 2000–0630 h (time of bat activity) and for 1300–1700 h (time preceding the night of detection). The potential number of weather variables available was large and highly correlated so analysis began with a process of variable reduction. Highly correlated variables were either summarized using principal components analysis (PCA) or all but one of the variables was removed from each highly correlated set. Minimum nightly temperature, average minimum nightly temperature, maximum nightly temperature, average maximum nightly temperature, and average nightly temperature were summarized using the first factor from a PCA. Except for solar radiation, afternoon measurements (1300–1700 h) correlated highly with night measurements (2000–0630 h) and were eliminated from further analysis.

Because bat activity decreased as fall approached, a transformation was used to detrend the data (i.e., remove the general downward trend in the series). The detrended variable was then normalized with a log transformation. The serial dependence of the time series data was further evaluated by examining auto-correlations and cross-correlations of bat activity and the independent variables. Variables with significant auto-correlations were differenced to achieve stationarity (replace each value by the difference between it and the previous value; Wilkinson, 1996). Similarly, cross-correlations were examined between bat activity and the weather from the previous night (Wilkinson, 1996).

We used partial correlations to assess the independent effects of each weather variable on nightly activity levels (e.g., the effect of nightly precipitation on bat activity, holding all other variables constant). Stepwise multiple regression, using forward selection, was then applied to measure the combined effect of the independent variables on bat activity. Analyses were performed using SYSTAT 7.0 with significance levels set at $\alpha = 0.05$, unless otherwise stated.

Results

Regional Scale

Bat activity was highest on San Juan Island, Washington (Table 1). Activity was least at Paradise Hills and Butte, Washington, which had fewer than three calls per night. Due to high correlations, last spring freeze estimate, which was highly correlated with first fall freeze estimate ($r = -0.894$, $n = 15$, $P < 0.001$), and heating degree days, which was highly correlated with average minimum summer temperature ($r = -0.850$, $n = 15$, $P < 0.001$) were dropped from the analysis. To decrease the influence of stand-level effects, stand age was forced into the model as the first variable of the regression ($F_{1,\ 11} = 0.05$, $P >> 0.05$). After entering stand age, average summer precipitation was the only significant variable ($F_{1,\ 10} = 17.51$, $P < 0.01$). This association was negative and alone explained 64% (based on r^2) of the variation in bat activity among the 13 blocks (Fig. 2). However, San Juan, Teanaway, and Little White Salmon, had large individual influences on the multiple

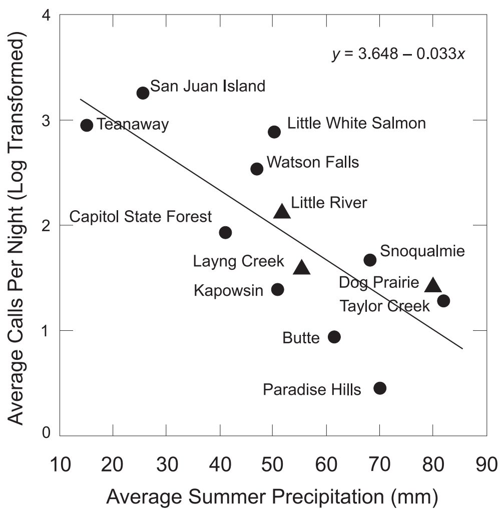

Fig. 2. The relationship between average calls per night and average summer precipitation for the 13 study blocks used in the regional climate analysis. Circles represent Washington sites and triangles represent Oregon sites

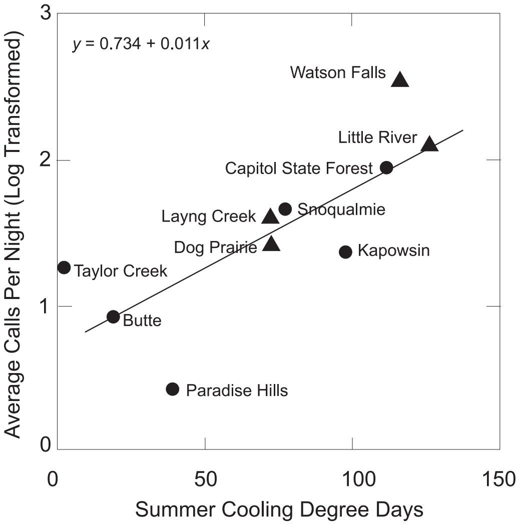

FIG. 3. The relationship between average calls per night and cooling degree days for the subset of 10 study blocks used in the regional climate analysis. Circles represent Washington sites and triangles represent Oregon sites

regression results (Fig. 2) probably because they are each near a mountain range that caused a rain shadow. To address differences in bat activity among the more climatically similar blocks, the latter three blocks were omitted in a second regression. After entering stand age ($F_{1, 8} = 0.70$, $P >> 0.05$), cooling degree days was the only significant variable ($F_{1, 7} = 9.047$, $P < 0.05$). This association was positive and alone explained 60% of the variation in bat activity among the 10 blocks (Fig. 3).

Local Scale

Ultrasonic monitoring took place on 70 nights during mid-June through mid-September, 1996. We detected 3,110 echolocation calls at the pond, with an average (± SE) of 44 ± 65.4 calls recorded per night. Only four nights had no activity. We recorded large night-to-night fluctuations in activity throughout the sampling period (Fig. 4). In general, the first detection occurred 90 min after sunset, and the following 4 h contained 93% of the total detections for each night.

The number of bat detections on a given night was not correlated with activity from the previous night, nor with weather conditions on the previous night. The best predictor of bat activity was mean night temperature, which was positively associated with activity ($F_{1, 67} = 22.27$, $P < 0.001$). There

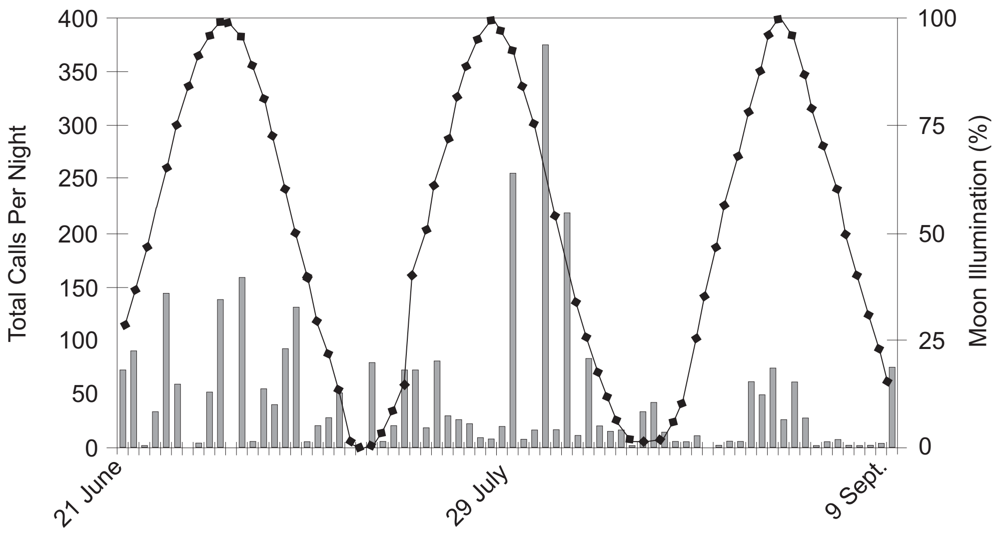

FIG. 4. Number of bat detections (bars) recorded each night from June to September 1996, in relation to moon phase (diamonds)

was a negative association with rain ($F_{1, 66} = 7.71$, $P < 0.01$), and a positive association with the amount of moon illumination ($F_{1, 65} = 4.06$, $P < 0.05$). These three variables explained 37% of the variation in nightly bat activity.

The local weather variables were highly correlated, so partial correlation analysis was used to assess the independent effects of each weather variable. Only night time temperature was statistically significant at the 0.05 α level ($P < 0.001$). Both rain ($P = 0.07$) and moon illumination ($P = 0.08$) had significant partial correlations at the 0.1 α level.

Discussion

Regional Scale

Thomas and West (1991) documented regional differences in activity and demography of bat populations in their study of unmanaged forests in the Pacific Northwest. Bat activity was two times higher in the Oregon Coast Range than in the western Washington Cascades. In Washington, few captured bats were female and no reproductive females were captured > 300 m in elevation. This contrasted sharply with the Oregon Coast Range where pregnant and lactating females were numerous (Thomas and West, 1991). As a result of these regional differences, Thomas and West (1991) recommended that management priority for bats be given to the Oregon Coast Range and mountains to the south.

We found detections of bats were highest in areas with lowest precipitation and warmest temperatures. Such conditions were predominately found in rain shadows of mountain ranges such as at the Teanaway and Little White Salmon blocks and the San Juan Island block (Teanaway and Little White Salmon are located on the leeward side of the Cascade Range, and San Juan Island is located in the rain shadow of the Olympic Mountains). If results from this study paralleled those of Thomas and West (1991), our southern blocks should have had higher activity levels than those to the north. However, the difference in activity that we found was not significant, and was much less than that found between the western Washington Cascades and the Oregon Coast Range by Thomas and West (1991). It appears that the average climatic conditions of blocks was a better predictor of bat activity than latitude. Although latitude may be a general indicator of bat activity, climatic conditions at a given location can apparently alter any general latitudinal pattern.

Local Scale

Results from the local weather analysis suggested that low activity levels were caused by the occurrence of rain and low temperatures. However, these variables only accounted for 37% of the nightly variation in bat activity at a given site. Nightly activity patterns may also be strongly influenced by nonmeteorological factors. Because many bats are opportunistic foragers (Fenton and Morris, 1976), increased insect abundance due to sporadic hatches may periodically elevate local bat activity. The addition of volant young to the population may also result in an increase in bat activity of an area (Maier, 1992). We found that additional variation in nightly bat activity was explained by the percentage of moon illuminated. Bat activity was positively correlated to increasing moon illumination (Fig. 4). Bats adjusting their use of habitats to minimize predation risk could explain this increase in activity. To avoid predators, some bats may shift their foraging from more open habitats (i.e., clearcuts, fields, lakes) to more sheltered areas during periods of bright moonlight (Reith, 1982). Our study site was surrounded by tall trees, which may have provided shadows not available in the more open foraging areas where bats are more likely to be silhouetted against the night sky. Alternatively, moonlight may change the distribution of some insects, which would increase foraging opportunities resulting in increased bat activity levels at a particular site (Hecker and Brigham, 1999). Therefore, in addition to weather, it is likely that non-meteorological factors contribute to activity patterns on a night-to-night basis.

Although short-term weather conditions explained relatively little variation in nightly activity of bats at a particular site, long-term climatic conditions explained a large portion of the variance in average activity levels among blocks. Because of the correlation between bat activity and climate, climatic profiles may be useful in predicting the relative activity levels of bats among different sites. Such information would be useful in conservation efforts by determining the most appropriate locations for monitoring or surveying projects. In addition, the use of climate and weather variables as co-variates may increase the power of monitoring efforts to detect changes in bat activity over time or space.

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