Influence of Riparian Vegetation on Bats at Multiple Spatial Scales

Holly K. Ober and John P. Hayes

Animals may make habitat selection decisions in a hierarchical fashion, considering different spatial scales at each stage. The relevance of multiple spatial scales has been demonstrated in habitat selection studies of a variety of vertebrate taxa, yet research on bat foraging activity has typically focused on a single, fine spatial scale. If bats consider different spatial scales when making habitat selection decisions, use of a multi-scale approach to investigate foraging activity by bats could be more informative than the single-scale approach typically employed.

We hypothesized that vegetation was most likely to influence bats at three spatial scales: the watershed, nightly activity area, and stream reach. We reasoned that vegetation composition at the scale of the watershed could influence selection of nightly activity areas, that vegetation composition at the scale of the nightly activity area could influence selection of stream reaches, and that vegetation cover, composition, or structure at the stream reach scale could influence bat habitat selection at this scale.

The primary goal of this study was to determine which relationships between vegetation and bats were strongest, so that land managers planning vegetation manipulations might better predict the influence of their actions on bat activity patterns. Our specific objectives were to determine:

1) which vegetation characteristics were most closely related to bat activity at each of three spatial scales,
2) whether the effect of vegetation characteristics at one spatial scale on bat activity influenced the effect of vegetation characteristics on bat activity at other spatial scales,
3) which of the three spatial scales explained the greatest amount of variability in bat activity, and
4) whether these patterns varied among species.

METHODS

Over the course of three summers we monitored bat activity in 118 second- and third-order stream reaches randomly selected throughout the Oregon Coast Range. We investigated 41 stream reaches in 2002, 37 new stream reaches in 2003, and 40 new stream reaches in 2004. In addition, we resampled eight of the stream reaches from a single watershed first visited in 2002 the following two years to assess inter-annual variability in bat activity.

We assessed bat activity by passively recording echolocation calls of free-flying bats. We recorded echolocation calls at each stream reach once during each 2-week period between mid-June and early September, for a total of four visits per stream reach in 2002 and five visits per stream reach in 2003 and 2004. Echolocation calls of bats were recorded from sunset until sunrise using calibrated, automated Anabat II detectors. We used a blocked sampling design, simultaneously monitoring 5–8 stream reaches within a given watershed each night. It is not possible to distinguish the number of individuals that produced calls, so we used recordings to obtain an index of bat use of each stream reach rather than to estimate the number of bats in that stream reach.

We used Analook (v4.9j) to view recorded bat echolocation call sequences. We quantified bat activity by determining the number of minutes per night during which echolocation calls were recorded. It was not possible to categorize all echolocation calls to species due to similarities in the calls of closely related species of bats. Instead, we categorized calls according to phonic groups of species having similar call characteristics so that all echolocation calls were categorized into one of six groups: *Myotis californicus* and *M. yumanensis* (California myotis and Yuma myotis); *M. lucifugus* and *M. volans* (little brown myotis and long-legged myotis); *M. evotis* and *M. thysanodes* (long eared myotis and fringed myotis); *Eptesicus fuscus, Lasionycteris noctivagans* and *Lasiurus cinereus* (big brown, silver-haired, and hoary bat); *Corynorhinus townsendii* (Townsend's big eared bat); or unidentifiable bat calls.

We sampled vegetation along a 30 m length of stream extending 10 m downstream and 20 m upstream of each echolocation detector, and extending 30 m from the stream edge upslope on both sides of the stream. We estimated vegetative species richness, cover, and composition, as well as the area of open flight space over the stream channel created by vegetation bordering and overhanging the stream reach. We estimated vegetation characteristics at the nightly activity area and watershed scales using the Coastal Landscape Analysis and Modeling (CLAMS) database on vegetation.

Table 1. Relationships between riparian vegetation and activity of bats predicted by *a priori* hypotheses.

Hypothesis	Spatial scale	Predicted relationship
Resource diversity	stream reach	Bat activity will increase as vegetative species richness increase
Resource abundance	stream reach	Bat activity will increase as vegetative cover increases
Resource quality	stream reach	Bat activity will increase as deciduous vegetative cover increases
Open flight space	stream reach	Bat activity will increase as open space above the stream channel increases
Stream surface obstruction	stream reach	Bat activity will decrease as shrubs overhanging the stream channel increase
Vegetation composition	nightly activity area	Bat activity will increase as deciduous vegetative cover increases
Vegetation rarity	nightly activity area	Bat activity will increase as the divergence in vegetation composition between the stream reach and the surrounding area increases
Vegetation composition	watershed	Vegetation composition throughout entire watershed will influence relationships between smaller-scale vegetation patterns and bat activity
Vegetation composition	watershed	Riparian vegetation composition throughout entire watershed will influence relationships between smaller-scale vegetation patterns and bat activity

We proposed several competing hypotheses to explain potential mechanisms underlying associations between vegetation and bats. We hypothesized that vegetation at the stream-reach scale could influence bat foraging activity through one of two pathways: (1) by determining the distribution of insect prey, or (2) by imposing structural restrictions on potential flight paths of bats, limiting their ability to acquire prey. We formulated candidate models to reflect each of these hypotheses, as well as those pertaining to watershed and nightly activity area spatial scales (Table 1). Multilevel models (hierarchical linear models) allow the structure of data to be taken into account when sample units are nested within larger units and explanatory variables exist for the description of the smaller and the larger units. We used multilevel models because several stream reaches were embedded within each watershed, and we had explanatory variables to describe both the stream reaches and the watersheds. We used model selection to rank all candidate models according to the weight of evidence for each.

RESULTS AND DISCUSSION

We monitored bat activity over 5,540 hours during 604 detector nights. Bat activity varied among stream reaches and species. The number of minutes during which activity of any phonic group occurred per stream reach per night varied from 4 to 371 (Table 2). The majority of identifiable calls (>99%) were from bats in the genus *Myotis*. The data for Townsend's big eared bat were too sparse to permit accurate modeling, so this phonic group was dropped from further analyses.

One of our objectives was to determine whether small-scale (stream reach), intermediate-scale (nightly activity area), or large-scale (watershed) factors explained the greatest proportion of variability in bat activity so we could assess the degree of concordance between the scale of typical forest management operations and the scale of vegetation characteristics most relevant to bat activity patterns. More variation in activity existed among stream reaches within watersheds (70-100%) than among watersheds (0-30%) for all phonic groups. Furthermore, variables at the stream-reach scale consistently explained more variation in activity than did variables at the nightly-activity-area scale. Thus, of the factors explored in our analyses, we conclude that stream-reach scale vegetation factors had greater influence on bat activity than did factors measured at either of the two larger spatial scales along streams in the Oregon Coast Range. It is not surprising that activity of bats was most strongly associated with patterns of vegetation heterogeneity at the smallest spatial scale we investigated: the high vagility of bats enables them to investigate and respond to habitat heterogeneity at fine spatial scales.

Table 2. Number of minutes during which activity occurred per stream reach per night for bats in riparian areas of the Oregon Coast Range, summers 2002-2004.

Bat phonic group	$\bar{x}$	SE	Range
California myotis and Yuma myotis	44.2	4.23	0-275
Little brown myotis and long-legged myotis	17.2	2.17	0-120
Long-eared myotis and fringed myotis	2.5	0.27	0-20
Big brown, silver-haired, and hoary bat	0.2	0.07	0-7
Townsend's big eared bat	0.3	0.05	0-3
all bats	89.4	6.18	4-371

Another of our objectives was to determine whether the influence of vegetation characteristics at one spatial scale on bat activity affected the influence of vegetation characteristics on bat activity at other spatial scales. Watershed-scale attributes generally had a relatively weak influence on bat activity. However, for the phonic group containing California myotis and Yuma myotis, 30% of the variation in bat activity was among watersheds, and watershed-scale riparian buffer vegetation composition explained 18% of this variation. In other words, watershed-scale vegetation conditions influenced the effect of stream-reach scale vegetation conditions for this phonic group, but did not do so for the remaining phonic groups. In general, neither or the two watershed-scale variables we measured explained appreciably more variation in bat activity than the other, which limits our ability to predict whether or not upslope forest management operations might influence bat activity within riparian areas.

Our final objective was to determine which of our original hypotheses regarding relationships between bat activity and vegetation characteristics best explained the observed data. Across the entire bat community as a whole, none of our original hypothesis performed overwhelmingly better than the others, indicating that bats respond to vegetation in a species-specific manner.

California myotis and Yuma myotis

The stream surface obstruction hypothesis predicts that bat activity increases as the amount of shrub foliage overhanging a stream reach decreases, due to the increased availability of foraging space for bats that feed along the surface of the water. The model reflecting this hypothesis ranked as most likely given the data for the phonic group containing California myotis and Yuma myotis: activity of these species increased as deciduous shrub cover decreased.

Both the Yuma myotis and the California myotis forage directly over water, often very close to the surface of streams and lakes where they feed on insects of aquatic origin flying within close proximity to the water surface. Obstructions at the surface of the water would hinder the ability of foraging bats to capture insects. Foliage from salmonberry, the most abundant deciduous shrub in riparian areas throughout the study region, often overhangs the banks of streams, limiting bat access to the surface of the water along stream margins. Thus, deciduous shrub cover was the most influential vegetation factor for activity of these bat species.

Little brown myotis and long-legged myotis

The flight space hypothesis predicts that bat activity increases as the amount of open airspace directly above the stream channel increases, due to reduced interference on bat flight patterns from vegetative clutter. The model reflecting this hypothesis ranked as most likely given the data for the phonic group containing little brown myotis and long-legged myotis: activity of these species increased as open airspace directly above the stream channel increased.

The long-legged myotis is the fastest flying species in the Myotis genus in western Oregon, and tends to forage using rapid, direct flight patterns near the forest canopy or in the open. The rapid flight of this species likely limits the foraging success and efficiency of these bats within cluttered habitats where quick, tight turns are required. The other species in this phonic group, the little brown myotis, is a slower, more agile flier that tends to forage along the margins of vegetation as well as over water, often in close proximity to the ground or the surface of water. It is unfortunate that we were unable to discern differences in calls between species that occupy such disparate ecological niches, because combining these two species into a single phonic group likely obscured the finer details of associations each species has with vegetation characteristics. However, an affinity for open areas while foraging seems to be a common characteristic of these two species, and has also been reported in other geographic areas.

Long-eared myotis and fringed myotis

The resource abundance hypothesis predicts that prey abundance increases as the availability of food resources for phytophagous insects increases, which in turn leads to increased bat activity. The model reflecting this hypothesis emerged as most likely given the data for the phonic group containing long-eared myotis and fringed myotis: activity of these species increased as canopy cover increased.

These species fly relatively slowly and forage close to the canopy, often among the trees. They use a combination of aerial-hawking and substrate-gleaning to obtain food. Substrate-gleaning and hovering are relatively expensive modes of foraging, and therefore are profitable only when energy returns from prey are relatively high. Given the affinity of these bats for the canopy, an increase in the volume of canopy foliage likely provides increased foraging substrates from which to obtain prey, which may in turn increase their foraging efficiency.

Big brown, silver-haired, and hoary bat

We recorded relatively little activity of bats in the phonic group containing big brown, silver-haired, and hoary bats, and therefore modeled presence/absence of these bats rather than number of minutes of activity per night. These low activity levels likely reflect the limited foraging these species do in the airspace measured by our echolocation detectors. All three of these species tend to avoid flying in cluttered habitats due to the physical hindrance their long wings impose on making quick turns in small spaces. As the three fastest flying species in western Oregon with the lowest frequency echolocation calls, these bats are morphologically adapted to detect insects in open habitats at long range: vegetative clutter precludes foraging success. Due to the constraints on foraging imposed by their morphology, these species are more likely to forage either in higher-order streams characterized by expansive open space above the water channel or above the forest canopy.

Activity of these species increased as canopy cover decreased. These bats likely selected stream reaches with large open flight spaces, which were those where branches from trees located on opposite sides of the stream did not interdigitate. Such streams necessarily had limited canopy layer.

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

We began this investigation with the expectation that local riparian vegetation characteristics would either influence bat foraging habitat selection by regulating the distribution of their insect prey or by posing limitations to the locations in which bats could forage. Although other portions of this research project demonstrated associations between vegetation and nocturnal insect abundance, as well as associations between nocturnal insect abundance and bat activity, the analysis reported here indicates that associations spanning from vegetation to bats along these nutritional pathways were weak. Bats from only one phonic group (long-eared myotis and fringed myotis) responded to vegetation characteristics in a manner consistent with the insect prey distribution explanation. Bats from the three other phonic groups (California myotis and Yuma myotis; little brown myotis and long-legged myotis; and big brown, silver-haired, and hoary bat) were more strongly associated with vegetation characteristics in a manner consistent with the structural hindrance explanation, which suggests that vegetation influences bats most strongly by imposing restrictions on potential flight paths of bats, limiting the ability of bats to acquire insect prey.

Vegetation features measured at the stream-reach scale were more influential to bat activity than vegetation features measured at larger spatial scales. This suggests that small-scale riparian forest management operations have the capacity to influence bat foraging activity patterns.

We recommend that land managers planning to manipulate riparian vegetation consider the associations we found between bat activity and shrub cover, canopy cover, and open space above the stream channel. Given the diversity of responses to small-scale vegetation characteristics among bat species in this region, the best strategy for the achievement of biodiversity conservation goals may be maintenance or creation of a diversity of riparian vegetation conditions.

STUDY TIMELINE

This project was initiated in fall 2001. Data were collected 2002-2004, and analyzed 2005-2006. The final report in the form of a Ph.D. dissertation will be on file with the CFER office winter 2007.

The Cooperative Forest Ecosystem Research (CFER) program was developed to facilitate sound management of forest ecosystems, with emphasis on meeting priority research information needs of the Bureau of Land Management (BLM) and the Oregon Department of Forestry (ODF) in Western Oregon.

The information contained in this document is preliminary in nature and has not been peer-reviewed. The data are not guaranteed to be correct or complete. Users are cautioned to consider carefully the provisional nature of the information.

The CFER program cooperators provide financial support, faculty and staff to conduct research and information exchange, study sites, assistance with project installations, and in-kind support as needed.

Program cooperators include: