ABSTRACT

Bat Activity in Forest Margins: Canopies, Edges, Seasonality, and Competition

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Forest edges provide open space that bats often use to travel and forage. As another type of margin, forest canopies provide similar structural space for bat activities. Such margins may supply bats in forests with the structural resources they require, such that some species could compete over edge space as a preferred habitat type. This project examined the role of forest canopies and edges as an important habitat type for bats through the observation and examination of bat activity levels. Bat communities in the Rocky Mountains of northern Utah (summers 2008-2009) and the pineywoods of eastern Texas (fall 2009 and spring 2010) were observed through the use of Anabat SD1 bat detectors. Activity levels of bats in Utah were much higher in forest edges than in canopies. This phenomenon appears to have a strong seasonal component, during which period competition over edge resources intensifies between high and low frequency guild bats. In the pineywoods of eastern Texas, bat activity levels also differ between canopies and edges, but bats in this habitat seem to shift seasonally between margin types. These shifts may coincide with seasonal migrations of some bat species. Future research would

further investigate seasonality in bat activity, and better define the role of clutter in bat activity in forest margins.

Bat Activity in Forest Margins: Canopies, Edges, Seasonality, and Competition

by

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A Dissertation

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DEDICATION

To Kami,

I could not have done it without your love and support

To Emily, Jack, Xiri, and Paisley,

Daddy's coming home now

CHAPTER ONE

Introduction

Edge Habitat

Many species appear in literature as edge specialists, including white-tailed deer

(Williamson and Hirth 1985), cowbirds (Gates and Giffen 1991), and tiger sharks

(Heithaus et al. 2006). Several scientists include bats in this group, as bats maintain high

activity levels in forest edge habitats (Crome and Richards 1988, Gaisler and Kolbac

1992, Grindal and Brigham 1999, Hogberg et al. 2002). Some researchers have also

examined vertical strata as a component of animal distribution in a temperate forest

(Kalcounis et al. 1999, Menzel et al. 2005, Henry et al. 2004), with some suggesting that

the highest level of forest strata, the forest-sky interface itself, acts as edge habitat for

many bat species (Grindal and Brigham 1999). This study examines bat activity in forest

canopies and edges. The main purpose is to increase understanding of the rate at which

bats use forest margins, as well as to identify how interactions between bats might be

reflected in rates of use of these two types of forest margins.

History of Edge in Ecology

Early examinations of edge habitats compared the number of animal species in

edges to the number of similar species in interiors (Lay 1938), or on the distribution of

species relative to the amount of edge habitat (Beecher 1942). Lay's work focused on

forests, discussing edges in terms of forest clearings and interfaces between forests and

meadows. He used the terms "edge" and "margin" interchangeably, but favored margin, probably due to the connotation of a wider space than the term "edge" implies.

Lay noted that birds in general seemed to make use of margins around clearings at a higher rate than interior habitats, evidenced by higher overall abundance of individuals and greater species richness. Not all bird species were found in edges, as some he termed "interior species" were not observed in margin habitat. However, more species were found in the edges surrounding forest clearings than anywhere else in the forest. He also noted (citing "abundant evidence") that some mammals "are attracted to" forest margins surrounding clearings (Lay 1938).

Beecher's (1942) definition of edge habitat was subtly different from Lay's approach, defining edge as "…the amount of border around any plant community in a given complex of communities. It is measured as closely as possible along the "zone of tension" or ecotone between adjacent communities." Beecher's use of the phrase "zone of tension" here actually denotes a boundary – it is a line drawn between two habitat types. This zone likely refers to the interaction between the differing habitat types that share a particular border, with the interaction creating the gradient effect, or "ecotone." Though "gradient" still finds common use for small-scale edge descriptions, modern discussions of edge using Beecher's "ecotone" usually refer to large-scale habitat changes over a scale of kilometers instead of meters (Winemiller and Leslie 1992).

Edge and Fragmentation

Modern ecologists often associate the term "edge" with the phenomenon of habitat fragmentation, where disturbance events cause contiguous habitat to become interrupted and patchy in distribution. These disturbance events may include human

activities (Saunders et al. 1991, Murcia 1995) as well as landscape-level processes related to hydrology, soil distributions, and weather patterns (Harrison 1997, Hargis et al. 1999). Bat habitat ecologists have found that human-caused habitat fragmentation is generally exploited by forest bat species (Crome and Richards 1988, Grindal and Brigham 1999, Patriquin and Barclay 2003).

Edge Effects

Edge characteristics differ by habitat type, though they typically share characteristics of both adjoining habitats (zone of tension - Beecher 1942). Human-created edges often affect interior habitats by introducing processes, conditions, and organisms that previously were not present. For example, forest remnants adjacent to areas where humans have removed trees exhibit decreased soil moisture due to increased solar radiation; greater windthrow (tree falls from wind) and windborne particle deposition due to greater amounts of exposed surface area; and water flow changes across denuded landscapes, often contributing to increased erosion, and nutrient flow changes (Saunders et al. 1991, Murcia 1995). These processes, conditions, and species interactions are generally referred to as "edge effects" in the scientific literature (Beecher 1942, Saunders et al. 1991, Murcia 1995), though other types of edge effects may exist.

Beecher (1942:3) used the term "edge effect" to describe the effects of edge propagation on related wildlife. He described edge effect as "[t]he influence of…animal constituents on the population density that is exerted when the ratio of edge in any plant community is increased relative to its area." This definition is useful for explaining effects of edge as they relate to population density, though it does not explain many other factors contributing to the role of edges in a system. Such interactions change the

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character, and even definition, of edge habitat on a per-taxon, or per-species basis. For

example, edges may increase predation along an agriculture-forest interface, though

predators only make superficial incursions to the forest edge (Angelstam 1986).

Similarly, what to some species is an edge to be exploited may serve as an impenetrable

barrier to other species, depending on the ability of a species to pass through an edge and

the spatial configuration of the habitat (Stamps et al. 1987).

Few studies have asked how traditionally accepted edge effects compare to the

conditions in sky-canopy forest edges, likely due to logistical or practical difficulty. This

sky-canopy interface may act as edge habitat, as it shares characteristics of both forest

canopy and sky. For bats, sky-canopy margins assumedly act as edge habitat because of

the combination of open space for flying and trees for foraging (Grindal and Brigham

1999, Kalcounis et al. 1999, Menzel 2005), though this phenomenon has never been

thoroughly examined. Additionally, scientists have never compared bat activity levels in

forest edge habitat to forest canopy activity levels.

Edge Contrast

Wiens et al. (1985) suggest that habitat edges compare well to biological

membranes. Similar to membranes, edges vary in permeability to different substances

and particles, including organisms. This variation in permeability arises from properties

of the membrane (edge). Properties potentially affecting permeability include thickness

of the membrane (edge width), amount of difference between habitats on both sides of

the membrane (edge contrast), components of the membrane (edge structure), and

physical density of the membrane (edge density). Thus, ecological edges, as an analog to

biological membranes, can be impermeable to some organisms and "leaky" to others (Wiens et al. 1985).

Some studies involving edge habitat refer to habitat edges in terms of this concept of permeability: hard vs. soft edges. Hard edges (Stamps et al. 1987) originally represented an edge impermeable to organisms of a particular species (Garcia et al 1998, Holmquist 1998, Ries and Debinski 2001, Stamps et al. 1987). Recently, any high-contrast boundary between edge types, with sharply defined zones of tension, has the label of hard edge (Collinge and Palmer 2002, Coxson and Stevenson 2007, Desrochers et al. 2003, Lopez-Barrera and Newton 2005, Lopez-Barrera et al. 2006, Lopez-Barrera et al. 2007, Malt and Lank 2007, Reynoso and Linera 2007, Wermelinger et al. 2007). However, definitions of such edges vary widely depending on the organisms and systems in question (Wiens et al. 1985, Stamps et al. 1987). The proposed study considers edges from the forest landscape scale.

In forests, hard edges usually result from tree-clearing events, such as avalanches, landslides, severe storms, fire, flooding, or sylviculture. In addition, hard edges can form along the edges of abrupt edaphic and hydrologic changes. Though many current high-contrast forest edges appear naturally, hard edges are often associated with human activities (Coxson and Stevenson 2007). Human-created edges tend to be longer and of higher contrast than natural edges, cutting across multiple landscape elements and interrupting the interactions that formed the original heterogeneous landscape (Matlack and Litvaitis 1999).

More difficult to define, soft edges originally represented an edge permeable to organisms and process flows (Stamps et al. 1987, Garcia et al 1998, Holmquist 1998,

Ries and Debinski 2001). Recently, soft edge has become a term describing a low-contrast gradient of change between one habitat type and another (Desrochers et al. 2003, Lopez-Barrera and Newton 2005, Lopez-Barrera et al. 2006, Lopez-Barrera et al. 2007, Malt and Lank 2007, Reynoso and Linera 2007, Wermelinger et al. 2007). In forests, soft edges appear as encroachment boundaries or regrowth areas, as forest plant species slowly extend the forest boundaries, or recover areas lost to other processes (e.g., hard-edge creation events).

As with any other landscape-level process or metric, the degree of softness or hardness depends on the scale of analysis. Lay's (1938) and Beecher's (1942) definitions of edge were on a scale of a few meters or less, whereas the ecotones discussed by Winemiller and Leslie (1992) could cover kilometers. One method uses characteristics of internal forest habitat, defining where edges begin and end relative to amounts of interior forest characters. The line of separation between these interior and edge habitats constitutes a "zone of tension" (Beecher 1942). A second method uses a ranking system to assign certain degrees of softness or hardness to each section of edge habitat (Rittenhouse et al. 2008). Such a ranking system requires a quantitative method of describing edge structure, though such a ranking system does not yet exist.

Edge in the Proposed Study

The proposed study uses a simple definition of edge: edges are interfaces between habitat types. Lay's (1938) use of the term "margin" is the most descriptive for how the term applies to this project, as it connotes a space between one habitat type and another that extends for some distance into both neighboring habitats where conditions are affected by the neighboring habitat. Additionally, this study will use the concept of hard

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and soft edges as defined by the degree of contrast between habitat types, invoking the "edge density" terminology of Rittenouse et al. (2007).

Clutter

Examples of forest edge habitat normally include a transition from forest to non-forest habitats. Often drastic, changes in the habitat structure occur throughout the transition from one habitat type to another. Bat biologists commonly refer to this habitat structure and the resulting effects on bat echolocation in forest edges as "clutter" (see below for references).

Definition of Clutter

Defining "clutter" can be problematic, as use varies by context, and vice versa. One dictionary definition of clutter is "a disorderly heap or assemblage; litter" ("clutter" Dictionary.com 2011). The amount of space taken up by leaves and branches easily qualifies for this definition. Bat studies often reference this physical aspect of clutter (Brigham et al. 1997, Broders et al. 2004, Carter and Feldhamer 2005, Ford et al. 2006, Gillam and McCracken 2007, Humes et al. 1999, Kunz and McCracken 1996, Law and Chidel 2002, Law and Chidel 2006, Lloyd et al. 2006, Loeb and O'keefe 2006, Menzel et al. 2005, Saunders and Barclay 1992, Sedgeley 2006, Sleep and Brigham 2003).

Another dictionary definition used in bat biology is related to acoustic clutter: "an echo or echoes…that do not come from the target and can be caused by such factors as atmospheric conditions, objects other than the target, chaff, and jamming of the…signal" ("clutter" Dictionary.com 2011). Many studies of bat echolocation use this definition of acoustic clutter (Neumann and Schuller 1991, Masters and Raver 1996, Wiegrebe and Schmidt 1996, Masters et al. 1997, Kalko et al. 1998, Rydell 1998, Tougaard et al. 1998,

Jensen and Miller 1999, Rydell et al. 1999, Siemers and Schnitzler 2000, Arlettaz et al. 2001, Jensen et al. 2001, Eklof et al. 2002).

To add to the confusion, in the context of bat echolocation, a "disorderly heap" of branches and leaves (Broders et al. 2004), or even water (Rydell et al. 1999) can produce "an echo or echoes …that do not come from the target." Thus, which definition of "clutter" applies can quickly become muddled. Further complicating usage, several definitions apply to the same situation, depending on how clutter informs a study.

Bat researchers have to deal with both of these definitions, as many species of bat echolocate, and all deal with "disorderly heap[s]" in the form of cave, rock, or tree roost, forest, or any other kind of obstacle interpretation and navigation. Many users of the term "clutter" do not define the term *a priori*, instead requiring the reader to infer the meaning in context. For studies of bat response to acoustic clutter, which kind of clutter the researcher is referring to can be particularly difficult, as leaf clutter results in acoustic clutter for the echolocating bat (Broders et al. 2004). Terms such as "clutter-adapted species" normally refer to a species with a suite of characteristics that allow for utilization of physically cluttered environments (Aldridge and Rautenbach 1987, Law and Chidel 2002, Broders et al. 2004, Ford et al. 2005, Menzel et al. 2005, Law and Chidel 2006, Lloyd et al. 2006, Loeb and O'keefe 2006, Sleep and Brigham 2003). Though a reader might also infer this to mean an "acoustic clutter-adapted species" as much as a "physical clutter-adapted species", or both, it is interesting to note that 8 of the 9 papers cited above using the term "clutter-adapted" or similar, infer or state a physical clutter definition. The remaining paper uses an acoustic definition of clutter (Aldridge and Rautenbach 1987).

Bat-Clutter Interaction

Bat activity and physical clutter are negatively related (Saunders and Barclay 1992, Brigham et al. 1997, Grindal and Brigham 1997, Humes et al. 1999, Law and Chidel 2002, Broders et al. 2004, Carter and Feldhamer 2005, Law and Chidel 2006, Lloyd et al. 2006, Loeb and O'keefe 2006). Though some scientists have speculated that high bat activity levels in physically uncluttered habitats may be the result of roost preference (Carter and Feldhamer 2005, Loeb and O'keefe 2006), it is also reasonable that roost selection is the result of high levels of bat activity in more open habitats. Most of these studies attempt to relate physical clutter levels to bat activity levels using qualitative indices of physical clutter (Law and Chidel 2002). Studies of this type do little to inform about how bats detect and interact with physical clutter, though they do suggest associations between bat species and habitat types.

Unsurprisingly, bat activity and acoustic clutter also share a negative relationship (Rydell et al. 1999, Jensen et al. 2001, Eklof et al. 2002, Gillam and McCracken 2007). Though physical clutter begets acoustic clutter, studies of acoustic clutter better inform of a bat's ability to perceive physical clutter. For instance, in Sweden, ghost moths (*Hepialus humuli*) hovering in mating displays over grass (Mallet 1984, Andersson et al. 1998) would be easy targets for foraging bats were the moths not staying within the clutter echoes, the "clutter overlap zone." Bat capture success of hovering moths within the clutter overlap zone was near zero (Rydell 1998), indicating a relationship between clutter (physical or acoustic) and bat predation of these moths. These echoes project a short distance from background physical clutter, and are easily calculated, based on the assumption that bats at physical clutter boundaries call from close enough to avoid

problems with sound attenuation (0.5 x speed of sound x signal duration – Jensen et al.

2001). If ghost moths ever emerge from the safety of the clutter overlap zone to contest

another male's display, display for a female, or move to a new position, they immediately

become subject to bat attacks (Andersson et al. 1998, Rydell 1998). It is interesting to

note that laboratory studies done with trained bats have found that some bat species

readily distinguish targets within the clutter overlap zone (Siemers and Schnitzler 2000,

Siemers et al. 2001), though this phenomenon is not supported in field observations

(Siemers and Schnitzler 2000, Eklof et al. 2002).

Clutter Navigation

A bat's ability to interact with clutter by echolocation directly relates to a bat's

ability to navigate a physically clutter-dense edge habitat. Bat wing morphology is

highly correlated with the echolocation call design, maneuverability, and habitat use of a

bat species (Aldridge and Rautenbach 1987, Norberg and Rayner 1987). Scientists

believe that wing design heavily influences the ability of a bat to navigate its environment

(Aldridge and Rautenbach 1987, Norberg and Rayner 1987). Measurements of wing

characteristics, using metrics such as loading (ratio of wing area to body mass – Saunders

and Barclay 1992), aspect ratio (wing shape index –Norberg and Rayner 1987), and

wingtip shape index (Norberg and Rayner 1987), help create profiles of maneuverability

and habitat use. Higher wing loading positively correlates with minimum flight speed

and negatively correlates with maneuverability, or tight turns, and agility, or quick turns

(Norberg and Rayner 1987). Aspect ratio positively correlates with flight efficiency

(Norberg and Rayner 1987). Wingtip shape index, derived from measurements of

relative wing tip shape, indicates pointed (high values) or rounded (low values) wing tips

(Norberg and Rayner 1987). Pointed wing tips might relate to hovering ability (Findley et al. 1972), and therefore to a slower, more maneuverable flight style.

Echolocation call design also affects a bat's ability to interact with its environment. Bat biologists split echolocation techniques into two classes: frequency modulated (FM), and constant-frequency (CF) signals (Simmons et al. 1979). Whereas FM calls provide detailed information about target shape, size, and distance, CF calls provide only information on target presence and movement (Saunders and Barclay 1992, Simmons et al. 1979). More-maneuverable bats use FM calls and usually forage close to or amongst clutter. Less-maneuverable bats use CF calls and tend to forage in open areas (Fenton 1990). Combinations of echolocation and wing adaptations result in more or less clutter-tolerant bats (Aldridge and Rautenbach 1987). For example, high wing aspect ratio, low wing loading, and pointed wing tips with a wide band FM echolocation design would strongly suggest a clutter-tolerant bat (Aldridge and Rautenbach 1987).

Competition

According to evolutionary theory, interactions between and within groups of organisms play a critical role in the action of natural selection. Such interactions between organisms often result in conflict over shared resources, or competition, where the fitness of one organism is reduced in the presence of another. According to Gause's law of competitive exclusion, two species competing for the same resources (e.g., space, food, roosts) cannot coexist in perpetuity, all else remaining constant (Gause 1932). Thus organisms sharing habitats must adjust their life strategies to account for the presence of competing organisms.

Species that share similar niches may utilize one or more competition strategies. These may include segregation of habitats or other resources (Schoener 1974, Steinmetz et al. 2011), or shifting the timing of activities (Carothers and Jaksic 1984, Lee and McCracken 2004, Reith 1980). Where one species is larger than other species, the larger organisms often exclude the smaller organisms from a shared resource (Alford and Crump 1982, Kotler 1984, Lemke 1984, Steinmetz et al. 2011), presumably due to the relative advantage of mass in physical confrontations.

Competition in Bats

Bat ecologists have long been aware of antagonistic interactions between bats (Lemke 1984, Reith 1980). For example, Lemke (1984) observed long-nosed bats (*Glossophaga soricina*) defending clusters of agave (*Agave desmettiana*) flowers until the nectar load dropped below approximately 50%. Once nectar loads were low enough in flowers in the preferred territory, *G. soricina* no longer defended depleted food resources. The previously territorial bats then switched to a "trapline" foraging strategy (visiting plants of up to 5 different species in a fairly linear fashion, as if checking traps).

Interactions between insectivorous bat species are more difficult to observe directly, mainly due to the difficulty of observing bat behavior during the night. Reith (1980) observed a long, low-intensity foraging period in silver-haired bats (*Lasionycteris noctivagans*) when netted at the same location and time as big brown bats (*Eptesicus fuscus*). When netted without *E. fuscus* present, *L. noctivagans* foraged much more intensely and for a shorter time, suggesting that interactions between the two species caused some competitive exclusion of *L. noctivagans*.

Bat Competition and Edges

Edge habitat may provide a preferred resource for bats in the form of open space for navigation and flight. Some authors have observed bats foraging more often in forest edges than in forest interiors (Brigham et al. 1997, Grindal and Brigham 1999, Law and Chidel 2002), suggesting that edge habitat is a preferred resource for bat species. Organisms that might otherwise have little contact with each other often interact when two or more different species attempt to occupy the same patch of preferred habitat (Alford and Crump 1982, Kotler 1984, Steinmetz et al. 2011). For example, Steinmetz et al. (2011) noted that a shared preference for groves of fruit trees led to competitive interactions between Asiatic black bears (*Ursus thibetanus*) and sun bears (*Helarctos malayanus*). Note that the larger black bears usually excluded the smaller sun bears from access to the preferred groves of fruit trees (Stenmetz et al. 2011), just as the larger and more aggressive big brown bats disrupted the smaller silver-haired bats from their normal foraging patterns (Reith 1980). Because forest edges may provide a preferred habitat type for bat species in forests, an examination of bat activity in forest edges may allow observation of competition between bat species in much the same way as groves of fruit trees do for bear species in Asia.

Identification of Problems and Study Objectives

Due to the importance of edge habitat for forest bat species (Grindal and Brigham 1999), and how little is yet known of the relative magnitudes of bat activity in forest canopies and edges in North American forests (Kalcounis et al. 1999), the role of clutter in bat use of edges remains poorly understood. Additionally, any interactions between forest bat species in edges could be representative of behavior in preferred habitats, and

thus, would provide an opportunity to examine interspecific competition over a preferred resource in bats. Observation of bat activity levels in forest canopies and edges in different habitat types would help determine general patterns of activity, further define the role of clutter in bat-forest interactions, indirectly identify competitive interactions of bats over a preferred resource, and provide natural history information about the bat communities studied.

This study was implemented under the following objectives: 1) Identify the importance of forest canopies to bat species relative to edges by examining the rates at which bats use both margin types. 2) Determine the role of vegetative clutter distribution in bat use of forest margins through comparison of bat activity levels to metrics representative of vegetative clutter. 3) Verify the importance of edge habitat to forest bats through observation of competitive interactions between bat species. 4) Describe any temporal patterns of bat activity in forest margins.

Research on these topics was conducted in the aspen forest of the Rocky Mountains of Utah and in the pineywoods of eastern Texas. Chapter two examines bat activity levels in canopies and edges of aspen forest in Utah, with an evaluation of the role of clutter levels on bat activity in forest margins. Chapter three utilizes other aspects of the Utah data to identify the importance of edge habitat for forest bats through the examination of temporal and seasonal activity patterns of bats in edges. Chapter four reports the results of repeating methodologies from chapters two and three in the pineywoods of eastern Texas, with intent to compare and contrast canopy and edge activity of bats, as well as to identify seasonal patterns of activity in forest margins. The dissertation concludes in chapter five with an assimilation of the findings, synthesis of

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results for a better understanding of forest edge activity in bats, and identification of

future directions for research.

CHAPTER TWO

Canopy and Edge Activity of Bats in Aspen Forest

Abstract

Characteristics of edges affect species in adjacent habitats. Forest canopies may provide edge-like habitat for bats, though bat response to edge orientation has not been well examined. We sampled bat activity in aspen forest canopies and edges in Heber Valley, UT during summer 2009 using Anabat detectors. CART analysis of echolocation characteristics (e.g., frequency, duration) identified 2 guilds based on characteristic frequency (i.e., high and low frequency). We used linear regression to compare characteristics of canopy and edge vegetation (e.g., tree height, DBH) to bat activity levels. Activity levels of high-frequency bats did not respond differentially to edge vegetation; low frequency bat activity seemed to respond to canopy height. Activity levels of high frequency bats were significantly higher than low frequency bats in both edges and canopies. We detected significantly more bat activity in forest edges than in forest canopies, indicating the importance of edges to bats in forests.

Introduction

Ecosystems consist of mosaics of habitat types, with habitats interfacing at edges. Researchers have long understood that habitat edges produce effects on components of adjacent habitat types (Beecher 1942; Saunders et al. 1991). Edge effects may include abiotic effects like higher solar radiation (Saunders et al. 1991) and the resulting changes

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in microclimate (Gehlhausen et al. 2000; Murcia 1995). There may be direct biological effects, such as increasing vegetation density near forest edges (Malcolm 1994), or indirect biological effects like the tendency for red-backed voles (*Clethrionomys californicus*) to be much less common near forest edges than interiors (Mills 1995). Bat species also respond to edges in forests. Studies of bat activity levels in forest ecosystems demonstrate that many species forage preferentially along forest edges compared to foraging in forest interiors (Adams et al. 2009; Grindal and Brigham 1999).

Edges, as viewed in studies cited above, are generally considered as vertically oriented interfaces between habitat types. However, for volant species such as bats, canopies also comprise edges but with a more-or-less horizontal orientation. One objective of this study was to examine bat activity levels at both traditional vertical edges and at the canopy interface of treetops with open sky. Bats use canopies as well as traditional edges for foraging and commuting (Grindal and Brigham 1999; Kalcounis et al. 1999, Menzel et al. 2005). Though edge activity has been investigated by the previous authors, relationships between canopy and edge activity have not been well-examined.

The other main objective of this study involved closer examination of traditional vertical edges. Abrupt changes in habitat structure are considered high contrast or hard edges, while more gradual transitions are considered low contrast or soft edges (Ries and Sisk 2008). Terrestrial vertebrates respond differently to boundaries of different contrast (Desrochers et al. 2003; Fletcher and Koford 2003). For some animals, high contrast edges constitute poor habitat – boundaries they could not or would not cross (flying squirrels – Descrochers et al. 2003; bobolinks – Fletcher and Koford 2003). For other species, such edges provide ideal or high-quality habitat (meadow voles – Bowers et al.

1996; butterflies – Ries and Sisk 2008). Variation in structural contrast relates to vegetative clutter in the edge, an important characteristic of forest edges often used to predict bat activity (Crome and Richards 1988).

Bat ecologists generally refer to the structure inherent in forest edge boundaries as "clutter." Clutter can be a physical condition, such as "a disorderly heap or assemblage; litter" (Dictionary.com 2010), and is defined this way in many studies of bat-vegetation interaction (Brigham et al. 1997, Broders et al. 2004, Law and Chidel 2002, Lloyd et al. 2006, Menzel et al. 2005, Saunders and Barclay 1992, Sleep and Brigham 2003). Such physical clutter in forest canopies and edges limits bats' flight and maneuverability, and may act as a barrier along which bats commute and forage (Grindal and Brigham 1999). Grindal and Brigham (1999) further suggested that forest canopies may provide a similar exclusionary edge effect for bats because although oriented horizontally rather than vertically, the canopy can offer as much vegetative clutter as forest edges. Previous studies of associations between bats and forest characteristics, particularly for clutter, suggest that some forestry metrics help predict bat activity levels in forest edges (e.g., tree height – Adams et al. 2009; Jung et al. 1999).

Some bat species have a suite of physical and acoustic characteristics that allow them to be tolerant of clutter and that correlates strongly with their method of prey acquisition (i.e., aerial hawking, gleaning, etc. – Aldridge and Rautenbach 1987; Norberg and Rayner 1987). Clutter-tolerant species tend to use frequency-modulated signals (i.e., cover a wide range of frequencies in a single call pulse) with short durations (Norberg and Rayner 1987). Clutter-intolerant species tend to use constant-frequency signals (i.e., cover a short range of frequencies) with long durations (Norberg and Rayner 1987). In

spite of these adaptations, bat activity levels for both clutter-tolerant and clutter-intolerant species vary inversely with clutter levels (Adams et al. 2009; Schnitzler and Kalko 2001; Sleep and Brigham 2003). Sleep and Brigham (2003) demonstrated that even clutter-tolerant species avoided cluttered areas, while Schnitzler and Kalko (2001) found that though clutter-tolerant species could utilize more cluttered habitats, they often used habitats with more open space. Both clutter-tolerant and clutter-intolerant bat species adjust their echolocation behavior in the presence or absence of clutter (increasing call duration and decreasing frequency range in open space, or decreasing call duration and increasing frequency range in cluttered space; Schnitzler and Kalko 2001). This plasticity in habitat exploitation allows some bat species to flutter in and out of habitat edges, using space immediately adjoining edge for nightly activities. Behavioral shifts in echolocation characteristics also provide a means by which bat-clutter interactions can be detected, particularly in the case of habitat edge use by bats (Schaub and Schnitzler 2007).

This investigation of how bat activity levels vary between canopies and edges and with different arrangements of clutter in forest boundaries examined several null hypotheses: We tested the hypothesis that bats use forest canopies at the same rate as forest edges. We further hypothesized that bat activity levels would not differ with respect to the orientation of physical clutter in edges. For the orientation and the clutter predictions above, we hypothesized that there would be no differences in responses of clutter-tolerant and clutter-intolerant species of bats.

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Materials and Methods

Field work spanned 4 summers (2006-2009). Bat netting was conducted during all four summers. Echolocation and forestry-metrics data were collected during a pilot study (summers 2006-2008) and for the formal study (10 July through 27 August 2009).

The study area was in Heber Valley, Wasatch County, Utah, at the confluence of the north-south Wasatch mountain range and the east-west Uinta range. The valley is formed by the Wasatch Range to the west and the Uinta range to the east. The aspen (*Populus tremuloides*) forest of north-central Utah provides a contiguous canopy and low-diversity plant community that simplifies analysis of bat-vegetation interactions. Bat capture sites were within the Timber Lakes housing development consisting mostly of densely-forested 0.4 hectare (1 acre) properties with vacation homes. Long-term, passive echolocation sampling was performed in the 3,500 hectare Heber Valley Camp, privately-owned property immediately south of the Timber Lakes development. Elevations of both sampling areas ranged between approximately 2,500 m and 3,000 m.

In both the Heber Valley Camp and the Timber Lakes development, quaking aspens dominate the forest tree community, with some Douglas fir (*Pseudotsuga menziesii*). Herbaceous vegetation less than 1 m in height dominates the understory, with aspen tillers and fir seedlings representing occasional woody vegetation in forest interiors. All non-forest habitats—primarily bluebell (*Mertensia* spp.) and horse nettle (*Agastache urticifolia*) meadows—consisted of leafy vegetation less than 1 m in height, except near forest stands where aspen tillers became a major component.

Bats were captured in mist nets to determine identities of species comprising the bat community and to catalogue echolocation signals for each species encountered. Nets

were placed over or near water approximately 1 km from the closest echolocation monitoring site, and less than 4 km from the most distant monitoring site. Nets were opened at dusk and closed between 2300 h and 0100 h. Captured bats were identified to species using external features (Barbour and Davis 1969; Durrant 1952), and then released by hand after nets had been closed. As we released bats we recorded their echolocation signals with an Anabat SD1 bat detector (Titley Electronics, Ballina, New South Wales, Australia); calls of one *Myotis evotis* were recorded while flying on a zip line prior to hand release. We used echolocation signals collected in this manner to build a library of local echolocation call sequences to identify passively-collected signals of free-flying bats. Bats were netted under Utah Division of Wildlife Resources permit number 4COLL7570, and animals were handled according to ASM guidelines (Gannon et al. 2007) under Baylor University IACUC protocol number 06-03.

Bat activity levels were sampled in two different habitat margins, edge and canopy. We sampled 6 sites in each habitat for at least 10 days per site (Gorresen et al. 2008, Hayes 2000). Edge sites ($n = 6$) were chosen based on a clear demarcation between contiguous aspen forest and open habitat. Canopy sites ($n = 6$) were situated at least 20 m from any edges or gaps in the canopy. Due to weather and animal interference, detectors at 2 canopy sites did not produce usable recordings. Gorresen et al. (2008) used a minimum between-detector distance of about 120 m to avoid "double counting" of bats. All detectors in this study were at least 150 m from any other concurrently-sampling detector. Elevations of sampling sites differed by as much as 500 m; the most distant sampling sites were 2.5 km apart.

Bat echolocation signals were recorded in canopies and edges with 4 Anabat SD1 bat detectors. Microphones were directed toward vegetation to limit reception only to bats active in edge space (Larson and Hayes 2000; Schaub and Shnitzler 2007). Detectors were set in a paired design, with one edge and one canopy microphone set approximately 150 m from each other, with 2 pairs operating per night. Edge detector microphones were situated approximately 1 m above the ground and 2 m from edge vegetation, i.e., 2 m from the point at which aspen tiller growth ended. Canopy microphones were attached to fiberglass antennae (Wonderpole, American Flag and Banner Company, Salem, Oregon, USA) affixed to tree boles, with the microphones positioned approximately 2 m above the forest canopy (approximately 15-27 m above the ground, depending on canopy height). Detectors were set to automatically begin recording at 2000 h (56 minutes before sunset at study beginning, 5 minutes before sunset at study end) and to stop recording at 0630 h (27 minutes after sunrise at study beginning, 27 minutes before sunrise at study end) the following morning, for 10.5 detection hours per night per site. During summer 2009, detectors were deployed at each of 10 sites (4 canopies, 6 edges) for 14 to 18 nights per site. Bat activity levels were reported as the number of echolocation call files recorded per detector per night (i.e., calls per detector-night).

As detector microphones are subject to environmental degradation from rain and other sources of moisture if unprotected, they must be weatherproofed (Britzke et al. 2010). The various methods of weatherproofing result in some change to microphone performance. Corben (2006) found that wrapping microphones in a thin film of plastic wrap produced a 0-15 dB loss in signal strength depending on frequency. Reflector

plates (Britzke et al. 2010) result in a similar loss in sensitivity. For this study, bat detector microphones were protected by covering them in a thin film of plastic wrap. All detector microphones were weatherproofed in the same manner for the duration of the study. Larson and Hayes (2000) recognized that microphone sensitivity varies with each detector. Thus, bat detectors were calibrated by turning the sensitivity dial to the point where microphone feedback began, then turning the dial back just enough to stop receiving feedback (Larson and Hayes 2000).

Passively-collected echolocation data were downloaded from data cards and evaluated for complete call pulses. Echolocation call sequences with 3 or more call pulses (i.e., high frequency sound identifiable as bat echolocation signals) and 1 or more complete call pulses (i.e., call pulses uninterrupted by echo, atmospheric conditions, etc.; identified using the RANOISE filter in ANALOOK, v.4.9j 2004) were further examined with the following parameters extracted for each call pulse: maximum frequency, minimum frequency, characteristic frequency (F_c), duration, and characteristic slope. Only complete call pulses were used in order to limit the effects of feeding behavior, echo, and environmental interference on the analysis. Similarities between periods (i.e., seasonal shifts) of bat activity identified qualitatively were verified by use of Kolmogorov—Smirnov tests (Fuller 1976, Pedro and Taddei 2002). Kolmogorov—Smirnov tests, a type of empirical cumulative distribution function (ECDF) technique, are useful for comparing stationary time series data where a temporal pattern should be preserved, or where data do not meet the assumptions of more rigorous tests (e.g., normality—Fuller 1976).

Bat echolocation detectors do not have the ability to identify an echolocation sequence as belonging to an individual bat, so multiple call files collected in succession might belong to one or more bats. Repeat sampling in this way may potentially lead to pseudoreplication—violating the assumption of independence required for many statistical tests—in data sampled by bat detectors (Hurlbert 1984). Many studies encounter pseudoreplication in attempts to identify individual or groups of call files to species, where call data is randomly subsampled by sampling site or bat call (Kofoky et al. 2009, Russo et al. 2009, Teixeira and Jesus 2009, Adams et al. 2010, Armitage and Ober 2010, Obrist et al. 2011, Ramasindrazana et al. 2011). However, to answer questions about bat activity levels in specific habitat types, the effects of pseudoreplication can be overcome by treating groups of bat call files as indices of activity per unit time (Miller 2001, McCracken et al. 2008). Though activity patterns may show some bias during times of highest activity (Miller 2001), assignment of bat activity values to temporal categories (e.g., minute, hour, or nightly intervals) reduces bat activity data to an index that can be evaluated using statistical techniques that are sensitive to repeat measures (Hayes 2000, Miller 2001, McCracken et al. 2008).

In order to identify the effects of pseudoreplication in the current study, all passively-collected bat call data were assigned to sampling intervals of 1, 5, and 10 minutes (Miller 2001, Armitage and Ober 2010). Sampling intervals of 1 and 5 minutes have been used in previous studies (Miller 2001, Armitage and Ober 2010), but the 10 minute sampling interval was included to provide a larger number of sampling intervals for comparison. If a sampling interval contained at least one bat call file, a record of activity was registered for that sampling interval. Nightly bat activity levels subsampled

at 1, 5, and 10-minute intervals were then compared to continuously sampled data (unadjusted for pseudoreplication) by pairwise Kolmogorov—Smirnov tests, adjusted for multiple comparisons by Bonferroni corrections (Fuller 1976).

Each bat echolocation call sequence was identified to the level of call frequency guild. Guilds were determined using classification and regression tree (CART) analysis using R (v.2.11.1 2010), a method shown to function well in straightforward analyses of echolocation data for simple bat communities (Preatoni et al. 2005). Additionally, CART analysis is robust to repeat measures (Hurlbert 1984, Adams et al. 2010). For comparison we used sequences collected from individuals of each species either known (by capture) to be active in the study area, or whose distribution includes the study area (Durrant 1952). A library of bat calls from known species was used to determine which classifying variables would be used for analysis. Based on the results of CART analysis, we assigned bat calls recorded passively in the study area to guild groups. Individual echolocation variables of members assigned to echolocation guilds were compared using Mann—Whitney tests. Bat activity levels of guilds in canopies and edges were also compared using Mann—Whitney tests, adjusted for multiple comparisons via Bonferroni corrections.

To quantify clutter, the following forestry metrics were assessed within 5 m of each detector: stem density, the number of trees of thumb diameter or greater within a 5 m radius (Erickson and West 2003); diameter at breast height (DBH) for tree stems thumb diameter or greater, often used as a correlate to tree size or forest age (Loeb and Waldrop 2008); canopy base height (CBH), the height above the ground where canopy leaf growth begins – used in fire ecology as a measure of clutter (fuel) beneath the

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canopy (lower values mean more clutter – Cruz et al. 2003); canopy height, the maximum

height of trees in edge sample (Adams et al. 2009, Jung et al. 1999); edge depth, the

distance from the leading edge of forest vegetation to the point at which tree height

reaches the approximate height of interior canopy trees; and edge slope, i.e., canopy

height/edge depth, a measure of structural contrast (Bowers et al. 1996, Ries and Sisk

2008). Edge depth was only measured for edge sites. Vegetation parameters in canopy

and edge habitats were compared using Mann—Whitney tests. Determination of the

vegetation characters of edges that provide the greatest influence on bat activity levels

was performed through linear regression of all vegetation parameters to the amount of

local bat activity (JMP®, Version 7. SAS Institute Inc., Cary, NC, 1989-2007). All other

statistical analyses were performed in R (v.2.11.1 2010).

Relative amounts of edge and canopy space were also examined to determine if

activity densities could explain any differences between bat activity in edges and

canopies. The amount of canopy space was estimated using satellite imagery (Google

Earth 2011), where polygons were fitted to each forest patch, and polygon areas

determined. The amount of edge space was estimated by multiplying the length of the

polygon edges fitted during canopy estimation by the average maximum heights of each

edge, as measured for comparison to bat activity. These measures should be considered

very rough estimates, but serve as comparison values.

Results

Mist netting resulted in 27 bat captures: 5 *Myotis evotis* (long-eared myotis; 2

female, 3 male) and 22 *Myotis volans* (long-legged myotis; 17 female, 5 male). These

individuals served as a source of the known-identity reference calls used in this study.
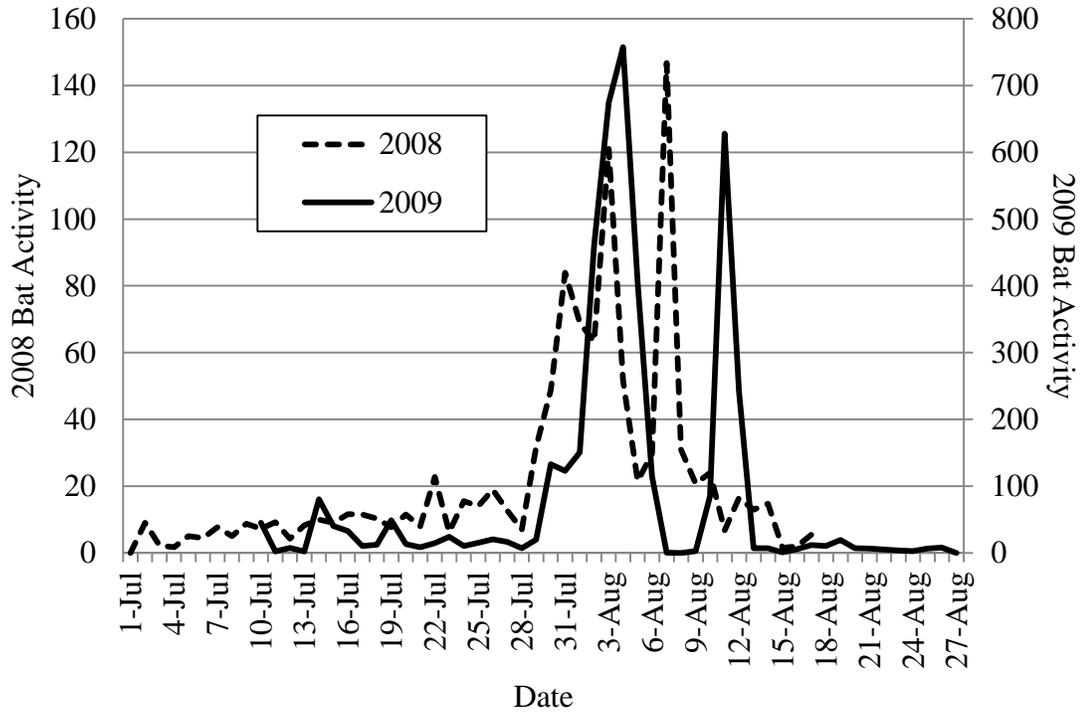
Figure 2.1. Bat activity from edges and canopies of aspen woods in Heber Valley, Utah from pilot data collected during summer 2008 (1 July – 17 August) and formal data collected during summer 2009 (10 July – 27 August). Bat activity measured in total call files per detector per night. Activity spike appears near end of July and persists until middle of August in both years. Left and right y-axis scales differ because activity levels were much higher in 2009.

Bat detectors were operated for a total of 162 detector nights, representing 1,701 detector hours.

Bat Activity Level Sampling

Figure 2.1 depicts nightly bat activity levels during the summertime. Activity levels varied between 0 and 118 call files per detector-night for much of summer 2009 (Fig. 2.1). However, during mid-summer (30 July - 13 August 2009), bat activity increased nearly tenfold that of the early summer and late summer activity levels (up to 1051 call files per detector-night). This period of high activity corresponded with a similar peak of activity during approximately the same period the previous year (Fig.

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2.1), though activity levels were lower during preliminary sampling in summer 2008. Bat activity patterns during this period of high activity were significantly different than activity patterns during early and late summer (Kolmogorov—Smirnov $D = 0.7333$, $P < 0.0001$, $n = 48$).

This period of high activity coincided with the sampling of only 2 edge sites and 1 canopy site. Few concurrent samples (edges, $n = 2$) precluded the use of the linear regression method used to compare vegetation metrics to bat activity levels for these sites. Additionally, the application of any other statistical method would serve only to establish the relationship represented by a single line drawn between two points. Thus, subsequent analyses were restricted to only the data collected before and after the high activity period (before 30 July and after 13 August).

Pseudoreplication Analysis

None of the bat activity patterns by sampling intervals differed significantly from continuously collected activity data over the entire summer (Table 2.1). Because of an elevated activity level during a 2-week period at the beginning of August, the same analysis of longer sampling intervals was run for just this 2-week period to be certain the lower values of the early and late summer bat activity did not obscure the potential

Table 2.1. Results of Kolmogorov—Smirnov tests comparing bat activity at 3 time intervals to continuous sampling. Comparisons were made within the entire summer, early/late, and the midsummer periods. This analysis produced no significant difference between any sub-sampled intervals and continuous sampling.

Sampling Interval	Entire Summer	Early/Late Period	Midsummer Period
1 min.	$P > 0.95$	$P > 0.95$	$P > 0.95$
5 min.	$P > 0.95$	$P > 0.95$	$P = 0.76$
10 min.	$P > 0.95$	$P > 0.95$	$P = 0.28$

effects of pseudoreplication in the high activity data. During the 2-week, high activity

period, none of the sampling intervals showed a significant difference from the

continuous sample ($P > 0.28$). As the effects of pseudoreplication seem to be controlled

for this dataset, all tests were run on continuously sampled bat echolocation data.

Bat Call Analysis

CART analysis of echolocation parameters extracted from a library of call files of

species known or suspected to be present in the study area provided a small tree with only

2 ecologically-meaningful categories (Kalcounis et al. 1997), distinguished solely by F_c.

Call pulses with an F_c higher than 33.795 kHz were assigned to a high frequency guild,

and call pulses with an F_c lower than 33.795 kHz were assigned to a low frequency guild.

Call files containing pulses from multiple bats belonging to separate guilds ($n = 32$) were

split into two files. For the early/late summer sampling period, the high frequency guild

produced 901 call files (832 in edges, 69 in canopies), and the low frequency guild

produced 280 call files (263 in edges, 17 in canopies). Echolocation characteristics

differed somewhat between bats in high and low F_c guilds (Table 2.2). As expected from

CART analysis results, F_c differed significantly between high and low frequency guilds

($U = 252280$, $P < 0.0001$). All other echolocation characteristics also differed

significantly between high and low frequency guild bat call files (maximum frequency –

$U = 244061$, $P < 0.0001$; minimum frequency – $U = 252202$, $P < 0.0001$; duration – $U =$

11413.5, $P < 0.0001$; characteristic slope – $U = 231562.5$, $P < 0.0001$).

Passive detectors in canopy and edge sites detected 1,181 call files during 34

nights from 10 July – 26 August 2009. Bat activity levels were highest in forest edges at

1,095 total call files, a rate of 8.41 ($\pm$ 1.51 *SE*) calls per detector-night. Canopy activity

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Table 2.2. Descriptive statistics ($X \pm SE$) for variables collected from passively-collected echolocation sequences from canopy and edge sites, assigned to low or high frequency F_c call guild, Heber Valley, Utah, early/late summer 2009. Bats of the high-frequency guild tended to produce higher-pitched, shorter calls than bats in the low-frequency guild. Echolocation parameters include the following: F_c = characteristic frequency, F_{max} = maximum frequency, F_{min} = minimum frequency; d = duration; S_c = characteristic slope.

Guild	Habitat	F_c (kHz)	F_{max} (kHz)	F_{min} (kHz)	d (msec)	S_c
Low Freq.	Combined	26.40	30.19	26.17	8.00	20.84
	$n = 280$	±2.80	±7.71	±2.59	±2.91	±31.53
	Canopy	26.00	29.07	25.86	6.49	16.63
	$n = 17$	±2.86	±6.17	±2.84	±1.76	±24.59
	Edge	26.43	30.19	26.18	8.09	21.12
	$n = 263$	±2.81	±7.80	±2.58	±2.94	±31.95
High Freq.	Combined	40.65	52.65	39.71	3.71	89.91
	$n = 901$	±2.80	±6.57	±2.28	±0.86	±41.22
	Canopy	41.56	53.22	40.34	3.45	97.61
	$n = 69$	±2.78	±7.42	±2.18	±0.73	±49.70
	Edge	40.57	52.60	39.66	3.73	89.27
	$n = 832$	±2.79	±6.50	±2.29	±0.87	±40.41

levels were much lower, with a total of 86 call files, a rate of 0.65 (± 0.16 *SE*) calls per detector night. Significantly more bat calls per detector night, regardless of guild, were recorded in edges than in canopies ($D = 0.5758$, $P < 0.0001$, $n = 66$).

Activity levels of high frequency guild bats were significantly higher than activity levels of bats in the low frequency guild (Kolmogorov—Smirnov $D = 0.5758$, $P < 0.0001$, $n = 68$). Both high frequency guild calls ($D = 0.7273$, $P < 0.0001$, $n = 66$) and low frequency guild calls ($D = 0.5455$, $P = 0.0001$, $n = 66$) were more abundant in forest edges than in forest canopies. In forest canopies, activity levels of bats in the high frequency guild were higher than activity levels of bats in the low frequency guild ($D = 0.3333$, $P = 0.05$, $n = 66$). However, activity levels of high frequency guild bats were

greater than low frequency guild bat activity levels in forest edges ($D = 0.6061$, $P <$ 0.0001, $n = 66$).

Within the high-frequency guild, maximum frequency ($U = 31053$, $P = 0.26$) and characteristic slope ($U = 32070$, $P = 0.11$) did not differ between canopy and edge habitats (Table 2.2). However, F_c ($U = 34860.5$, $P = 0.003$), duration ($U = 23426.5$, $P = 0.01$), and minimum frequency ($U = 33374$, $P = 0.02$), differed significantly for high frequency guild bats between canopies and edges. Echolocation parameters of bats in the low frequency guild differed only in shorter call durations ($U = 1556$, $P = 0.04$) in edges compared to canopies. All other call characteristics for low frequency guild bats did not differ between canopies and edges (e.g., F_c, $U = 2270.5$, $P = 0.92$; maximum frequency, $U = 2261$, $P = 0.94$; minimum frequency, $U = 2266.5$, $P = 0.92$; characteristic slope, $U = 2052$, $P = 0.57$).

Vegetation Structure Analysis

Canopy and edge vegetation structure differed significantly in several key ways (Table 2.3). Edges ranged from very deep (30 m) to shallow (8 m), producing a mean edge width of 16.50 m ($\pm$ 9.98). Trees in canopy sites tended to be taller than trees in edges ($U = 8289$, $P < 0.0001$). Dividing the mean maximum height by the mean edge width produced a mean slope of 1.33 ($\pm$ 0.57) in edge sites, though slope ranged between 0.67 and 2.00. Woody vegetation in most of the sampling areas consisted primarily of *P. tremuloides*, though a few *P. menziesii* were present. Stem densities did not differ significantly between edge and canopy sites ($U = 11$, $P = 0.49$). Both DBH ($U = 7405$, $P < 0.0001$) and canopy base height ($U = 7343$, $P < 0.0001$) were significantly greater in canopies than in edges.

Table 2.3. Descriptive statistics ($X \pm SE$, where appropriate) for characteristics of vegetation sampled in 5 m radius of bat detectors in Heber Valley, Utah, early/late summer 2009.

Sampling Sites	Edge Slope	Stem Density (stems/m^2)	Height (m)	DBH (m)	CBH (m)
Canopies					
BKC1	NA	0.34	10.44 ± 2.01	0.20 ± 0.05	7.00 ± 1.44
BKC2	NA	0.32	20.08 ± 4.55	0.28 ± 0.10	10.40 ± 4.31
NNC1	NA	0.23	20.11 ± 5.07	0.28 ± 0.07	15.80 ± 4.77
TVC1	NA	0.52	18.63 ± 5.00	0.52 ± 1.80	12.36 ± 5.51
All Canopies	NA	0.35 ± 0.12	17.32 ± 4.63	0.32 ± 0.14	11.39 ± 3.68
Edges					
BKE1	1.50	0.24	9.21 ± 2.25	0.23 ± 0.12	5.16 ± 2.12
BKE2	0.67	0.04	17.67 ± 2.08	0.29 ± 0.01	6.33 ± 3.21
NNE1	1.11	0.60	5.81 ± 4.44	0.10 ± 0.05	1.95 ± 2.42
NNE2	2.00	0.17	11.15 ± 6.43	0.14 ± 0.07	3.77 ± 2.31
All Edges	1.32 ± 0.57	0.26 ± 0.24	10.96 ± 4.99	0.19 ± 0.09	4.30 ± 1.88

When nightly bat activity was regressed against forestry variables for edge sites, the frequency guilds manifested different levels of interaction with height, but not with other variables (Table 2.4). For the low frequency guild, canopy height ($P = 0.044$) was the only important predictor for the level of bat activity. Activity of bats in the high frequency guild responded to none of the forestry metric variables ($P \geq 0.503$ for all variables; Table 2.4).

Discussion

The hypothesis that bats in the study area use forest canopies and edges at equal rates was not supported by these results. Rather, bat activity levels were greater in edges than in canopies.

Bat activity levels did not seem to vary directly with most measures of clutter in forest edges. However, activity levels of low frequency guild bats varied negatively with

Table 2.4. Linear regression models of the effects of edge vegetation structure on bat activity levels for high and low frequency guild bats in Heber Valley, Utah, early/late summer 2009. Canopy height was the only significant predictor of activity for low frequency bats. High frequency bat activity did not respond significantly to any vegetation variables.

Guild	Vegetation Metric	Coefficient	SE	t-Ratio	P
High Freq.	DBH	43.578	5.374	0.84	0.503
	Stem density	47.703	7.300	0.68	0.579
	Canopy height	-1.140	0.178	-0.67	0.585
	Slope	2.294	0.395	0.60	0.617
	CBH	4.548	0.925	0.51	0.669
Low Freq.	Canopy height	-1.222	0.178	-5.72	0.044
	DBH	7.197	5.374	1.12	0.400
	Stem density	6.121	7.300	0.70	0.569
	CBH	0.705	0.925	0.63	0.602
	Slope	0.250	0.395	0.53	0.659

canopy height (Table 2.3), indicating that edges of various heights may be used differently by some species of bats. This finding is consistent with the hypothesis that edge habitats serve as flight corridors and navigation landmarks for low frequency guild bats (Grindal and Brigham 1999, Limpens and Kapteyn 1991).

Guilds also differed in the amount of interaction with edge vegetation, as evidenced by adjustments in echolocation call characteristics (Schaub and Schnitzler 2007). Considering elevated edge activity levels in forest bats (Adams et al. 2009; Grindal and Brigham 1997), an examination of the Ries and Sisk (2008) model suggests that open edge space on one side of forest edges aligns in a complementary way with resources on the side cluttered with vegetation. The most likely resource provided for bats by cluttered space is prey, as insects are more numerous in forest interiors than in or beyond forest edges (Grindal and Brigham 1997, Kilgo 2005), though other possibly

relevant resources and benefits could include predator avoidance, interspecific interactions and roost site access.

High frequency guild bats did not respond to variation in edge structure (Table 2.1), likely because the species in this guild typically avoid open space and preferentially forage in and along edge vegetation (Faure and Barclay 1994; Manning and Jones 1989; Warner and Czaplewski 1984). Members of the high frequency guild ($F_c > 33.795$ kHz) include species adapted to navigate high-clutter (*M. evotis*) to background-clutter (*M. volans*) habitats (Norberg and Rayner 1987; Schnitzler and Kalko 2001). *M. evotis* is primarily a gleaning bat, though it is known to engage in aerial hawking of moths (Faure and Barclay 1994), with short, broadband, frequency modulated (FM) echolocation calls (Faure and Barclay 1994; Norberg and Rayner 1987). *M. volans* also possesses echolocation call characteristics of a bat that forages against background clutter, with broadband, FM echolocation calls (Norberg and Rayner 1987, Warner and Czaplewski 1984), though the calls of *M. volans* tend to be less frequency-modulated than the calls of *M. evotis*. The echolocation behavior detected in this study affirms what is known of the natural history of these small, maneuverable bats: they are adapted to spend much of their time in close proximity to the high-clutter environment of forest edges.

Bats in the low frequency guild did not seem to interact directly with clutter (i.e., edge vegetation) as often as high frequency bats, though the negative response to canopy height suggests that bats in the low frequency guild may be more sensitive to changes in clutter distribution and arrangement than high frequency bats. All echolocation signals were collected within 5 m of edge vegetation, well within the detection radius of the bat detectors (Larson and Hayes 2000), thus suggesting that low frequency guild bats were

active within a few meters of edge vegetation. The three low frequency guild species potentially represented in this community – big brown bats (*Eptesicus fuscus*), silver-haired bats (*Lasionycteris noctivagans*), and hoary bats (*Lasiurus cinereus*) – are adapted for flight in open-space, such as found external to or along cluttered habitat types. Bats in the low frequency guild tend to avoid cluttered environments (Schnitzler and Kalko 2001), and use mostly lower-slope, more constant frequency (CF) echolocation calls at lower frequencies ($F_c < 33.795$ kHz), a pattern of echolocation behavior characteristic of *E. fuscus, L. cinereus,* and *L. noctivagans* (Barclay et al. 1999; Kurta and Baker 1990; Norberg and Rayner 1987; Thomas et al. 1987).

Bat echolocation behavior differed significantly between forest canopies and edges in the study area. For bats in the low frequency guild, even though activity levels differed significantly between canopies and edges, echolocation behavior largely did not. Low frequency guild bats responded to both habitat types similarly, differing only in the durations of each call pulse between forest canopies and edges. This echolocation evidence suggests that low frequency bats in the study area likely maintained consistent distance from vegetation in canopies and edges, indicated by consistent frequency characteristics in both habitats (Table 2.1).

However, high frequency guild bats seemed to increase their distance from vegetation in edges, using lower frequencies and longer call durations than they did in forest canopies. High frequency bats may be using peripheries of forest patches as sources of prey (Grindal and Brigham 1997). However, higher frequency and shorter duration call pulses from high frequency bats suggest that they fly closer to vegetative clutter in canopies, perhaps even within the canopy. Because bats are opportunistic

foragers, this difference in clutter response might indicate pursuit of prey, as insect abundance decreases from forest interiors to edges (Grindal and Brigham 1999; Kilgo 2005).

The pattern of insect abundance between forest canopies and interiors has not been well-examined for temperate forests. However, forest canopies provide close access to forest interiors at relatively low levels of ambient clutter, potentially providing a source of prey along the canopy-sky boundary (Kalcounis et al. 1999). Benoit-Bird and Au (2003) reported an analogous behavior in another echolocating predator: spinner dolphins (*Stenella longirostris*) using an acoustic boundary layer (i.e., water layers with different temperature, current and density characteristics than adjacent layers) to confine foraging activities and capture prey. Bats of both guilds in the study area may be utilizing forest edge habitats in a similar way, trapping insects as they become distinct from background echoes and physical clutter of forest edges (Eklöf et al. 2002).

The mid-summer period of elevated activity likely coincides with significant events in the life histories of the species in this bat community. A similar mid-summer elevation in bat activity levels has been observed in other ecosystems (O'Farrell and Bradley 1970; Sendor 2002), but the timing and motivation for the behavior has not been well-established. O'Farrell and Bradley (1970) observed a similar pattern of activity during the hottest, driest part of the summer in a Nevada desert, where high activity levels occurred over a water source. Sendor (2002) encountered high mid-summer activity levels in pipistrelle bats (*Pipistrellus pipistrellus*) swarming around a year-round roost at Marburg Castle, Marburg, Germany. Behavioral anomalies such as has been encountered in the current study may represent a seasonal migration, regional or long-

distance (Barbour and Davis 1969; Hayes 1997); feeding behavior (Fukui et al. 2006); juvenile recruitment (Anthony et al. 1982; Koehler and Barclay 2000; Kunz and Anthony 1982; Tuttle 1976); and reproductive behavior (Cryan 2008; O'Farrell and Bradley 1970; Phillips 1966; Sendor 2000). Any of these phenomena would cause a significant behavioral change in addition to the marked increase in activity. Thus, any understanding reached as a result of the analysis of data from the early/late period may not apply to bat-forest interactions during the midsummer period. Future work on this little-studied phenomenon of mid-summer activity increase would benefit from a targeted sampling design, focused on a better understanding of bat-clutter interactions during this very busy season for these forest bats.

High frequency guild activity levels were significantly higher than low frequency guild activity levels in forest edges and canopies. This large difference in activity levels between canopies and edges may be simply an effect of the amount of available canopy space relative to the amount of available edge space. Investigations of use of shallow water versus deep water by fish in lake ecosystems may present a useful model for future investigations of this phenomenon. Vadeboncoeur et al. (2011) reported that more than 93% of lake fish inhabit shallow, littoral zones in lakes, though most fish exploit benthic resources. Schindler and Scheuerell (2002) found that lake environments were strongly coupled by fish exploiting multiple resources. These evidences suggest that though littoral zones support the highest densities of fish activity, more fish may be found in the much more abundant benthic or pelagic lake zones. Analogous to this littoral/benthic/pelagic fish activity model, approximations of the overall space available for bat activity in canopies relative to edges provide evidence that could decrease the

apparent importance of edge space for bat use of forests. For instance, canopy space in

the forest patches sampled was approximately 3 to 6 times greater than edge space in the

same patches. Canopies may provide a forest margin type less dense in bat activity

relative to forest edges, but the importance of forest canopy for bat use may not be as

trivial as these results may imply. However, the results of this investigation seem to

promote edges as preferred, more densely utilized regions for bats in alpine aspen forest.

Future analyses of similar habitats would certainly help to further define the role of

canopies in forest bat ecology.

CHAPTER THREE

Evidence of Temporal Partitioning By Echolocating Bats in Alpine Forest Edges

Abstract

Species with similar resource requirements may partition habitats or resources to coexist in the same geographic area. Some communities of organisms maintain habitat partitions through regular interactions between community members. This activity pattern was examined in a bat community composed of two echolocation guilds (high and low frequencies) in the edges of aspen forest in Heber Valley, Utah. Bat activity data were collected with Anabat SD1 bat detectors in 6 edge sites from 10 July – 26 August 2009. Two distinct activity periods were identified: a low activity period during early/late-summer 2009 (10 – 29 July, 14 – 26 August), and a period with much higher activity during mid-summer (30 July – 13 August). Bats in the high frequency guild had significantly higher levels of activity than low frequency guild bats during the early/late-summer period, but low frequency guild bats produced nearly twice the activity level of high frequency bats during the mid-summer period. High and low frequency guild bats demonstrated relatively little interaction during the early/late-summer period, whereas high frequency guild bats seem to avoid low frequency guild bats during mid-summer.

Introduction

Species with similar resource requirements may coexist by partitioning habitats or habitat resources (Kotler and Brown 1988; Schoener 1974). Interactions between organisms are assumed as the basis for many of these evolved relationships, resulting in

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species adapted to occupy specific niches within a landscape (Alford and Crump 1982; Crome and Richards 1988). Habitat partitioning can also result from competition over shared, preferred resources, where preference is manifested in abundance, fitness, or simple choice (Steinmetz et al. 2010).

Competitive interactions often follow the pattern of larger organisms exerting dominance over smaller organisms. Multiple studies provide examples of this phenomenon, typically with the result of the larger organism aggressively excluding smaller individuals from a preferred resource. Alford and Crump (1982) found antagonistic interactions between size classes of southern leopard frogs (*Rana utricularia*), where the largest tadpoles excluded smaller tadpoles from habitats with more food resources. Kotler (1984) found that larger-bodied kangaroo rats (*Dipodomys merriami*, *D. microps*) excluded smaller-bodied pocket mice (*Perognathus longimembris*) from preferred microhabitats around desert shrubs. Steinmetz et al. (2011) identified interactions between Asiatic black bears (*Ursus thibetanus*) and sympatric sun bears (*Helarctos malayanus*) only in habitats with large numbers of fruit trees, where larger black bears forced the smaller sun bears to subsist primarily on arthropods. No interactions were detected between bear species in less-favorable habitats, indicating that interactions represented competition for a resource both species favored (Steinmetz et al. 2011).

This pattern of competitive interaction has also manifested in bat communities. Reith (1980) discovered a shift in the temporal activity patterns of smaller silver-haired bats (*Lasionycteris noctivagans*) when they were sympatric with the larger big brown bats (*Eptesicus fuscus*). Some bat species even exhibit antagonistic interactions

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intraspecifically. Such is the case with Hawaiian hoary bats (*Lasiurus cinereus semotus*), as some individuals produce a characteristic antagonistic call while chasing conspecifics away from a preferred feeding resource: lights where insects swarmed (Belwood and Fullard 1984). Additionally, Lemke (1984) found that long-nosed bats (*Glossophaga soricina*) displayed antagonism through territorial defense of clusters of agave (*Agave desmettiana*), the source of their preferred food resource from conspecifics.

We evaluated the hypothesis that bat echolocation guilds partition temporally when activity levels of the bat community are high, though they do not partition at low activity levels. This suggests that the bat community in the study area partitions resources based on a shared-preferences system of niche differentiation. In this case, niches overlap to the extent that resource partitioning occurs by way of competitive dominance (Steinmetz et al. 2010). We predicted that the occurrence of partitions can be explained by the likelihood of one bat encountering a bat of another species or guild. This suggests that little evidence of interaction between guilds would exist during a period of low activity density, but that smaller, high frequency guild bats would avoid larger, low frequency guild bats when activity density is high. We predicted that this interaction would result in a temporal shift in nightly activity by high frequency bats only during periods of high activity levels by both frequency guilds.

Materials and Methods

Study Site

Bat activity data were collected during summer 2009, from 10 July through 27 August. The study area was in Heber Valley, Wasatch County, Utah. We netted bats within the Timber Lakes vacation housing development summers 2007-2009. Passive

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echolocation sampling efforts were concentrated in sections of the 3,500 hectare Heber Valley Camp, a church camp immediately adjacent to the Timber Lakes development. Elevations of both sampling areas ranged between approximately 2,500 m and 3,000 m.

Bats were captured in mist nets to determine identities of species comprising the bat community and to catalogue echolocation signals for each species encountered. Nets were placed over or near water approximately 1 km from the closest echolocation monitoring site, and less than 4 km from the most distant monitoring site. Nets were opened at dusk and closed between 2300 h and 0100 h. Captured bats were identified to species using external features (Barbour and Davis 1969; Durrant 1952), and then released by hand after nets had been closed. As bats were released, we recorded their echolocation signals with an Anabat SD1 bat detector (Titley Electronics, Ballina, New South Wales, Australia); calls of one *Myotis evotis* were recorded while flying on a zip line prior to hand release. We used echolocation signals collected in this manner to build a library of local echolocation call sequences to identify passively-collected signals of free-flying bats. Bats were netted under Utah Division of Wildlife Resources permit number 4COLL7570 and were handled according to ASM guidelines (Gannon et al. 2007) under Baylor University IACUC protocol number 06-03.

Quaking aspens (*Populus tremuloides*) represented the predominant tree species in the study area, with Douglas fir (*Pseudotsuga menziesii*) sparsely distributed among the aspens. Undergrowth in aspen stands was largely herbaceous, less than 1 m in height, with aspen tillers and fir seedlings representing occasional woody understory. Open habitat adjacent to forest edges consisted primarily of bluebell (*Mertensia* spp.) and horse nettle (*Agastache urticifolia*).

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Bat Detection

Bat activity levels were sampled using Anabat SD1 bat detectors (Titley Electronics, Ballina, New South Wales, Australia). Bat detector microphones were directed toward vegetation to limit reception only to bats active in edge space (Larson and Hayes 2000), and to restrict recordings of echolocation behavior only to habitats more likely to contain consistent, edge-specific behaviors (Schaub and Schnitzler 2007). Microphones on edge detectors were situated in open meadow habitat, ~2 m from woody edge vegetation, with the microphones directed towards edge at an angle of approximately 30 degrees from horizontal. Gorresen et al. (2008) used a minimum between-detector distance of about 120 m to avoid "double counting bats." All detectors in this study were at least 150 m from any other concurrently-sampling detector. Elevations of sampling sites differed by as much as 500 m; the most distant sampling sites were 2.5 km apart. Detectors automatically began recording at 20:00 (56 minutes before sunset at study beginning, 5 minutes before sunset at study end) and stopped recording at 6:30 (27 minutes after sunrise at study beginning, 27 minutes before sunrise at study end) the following morning, for 10.5 detection hours per night per site. During summer 2009, detectors were deployed at 6 edge sites, 11 to 18 nights per site, for a total of 158 detector nights representing 1659 detector hours.

Bat Community Analysis

Each bat echolocation call sequence was identified to the level of call frequency guild. Guilds were determined by classification and regression tree (CART) analysis using R (v.2.11.1 2010), a method shown to function well in straightforward analyses of echolocation data for simple bat communities (Preatoni et al. 2005). For comparison we

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used sequences collected from individuals of each species either known (by capture) to be active in the study area, or whose distribution includes the study area (Durrant 1952). A library of bat calls from known species developed by C. Corben was used to determine which classifying variables would be used for analysis. Based on the results of CART analysis, we assigned bat calls recorded passively in the study area to guild groups (i.e., high frequency, low frequency, with 33.795 kHz as the division between groups).

Bat Activity Patterns

Nightly bat activity data were refined to the number of call files per detector (site), averaged across detectors operated concurrently per night ($n = 1$ or 2), and separated into seasonal or nightly time periods (e.g., early/late-summer, hours after sunset, etc.). Levels of nightly activity were compared between and within periods (i.e., early/late, mid-summer) and guilds (i.e., high, low) by Kolmogorov—Smirnov tests (R Development Core Team 2010), adjusted for multiple comparisons by Bonferroni corrections. Kolmogorov—Smirnov tests compare stationary time series data between two samples (Fuller 1976, Pedro and Taddei 2002).

Hourly activity data were evaluated as the mean number of call files per hour after sunset per detector-night. Passively-collected echolocation data were downloaded from data cards and evaluated for complete call pulses. Echolocation call sequences consisted of 3 or more call pulses (i.e., high frequency sound identifiable as bat echolocation signals) and 1 or more complete call pulses (i.e., call pulses uninterrupted by echo, atmospheric conditions, etc.; identified using the RANOISE filter in ANALOOK, v.4.9j 2004). Only complete call pulses were used in order to limit the effects of feeding behavior, echo, and environmental interference on the analysis. Hourly bat activity

levels, separated by guild and by seasonal activity period, were also compared between

and within periods and guilds by Kolmogorov─Smirnov tests.

Bat activity data should not be treated as directly representative of population

density because calls of individual bats may be recorded different numbers of times

depending on how often a particular bat passes by a recording microphone (Hayes 1997).

However, the relative importance of a resource can be revealed by the frequency with

which bat activity is detected around that resource (Hayes 1997). We used the rate of

detection (i.e., number of bat call files per detector night) for comparison between periods

of different length (i.e., early/late-summer period $n = 33$, mid-summer period $n = 15$).

Differences between observed and expected bat activity values were compared using a

Fisher's exact test (R Development Core Team 2010), with the expectation that

interactions between guilds would manifest as deviations from expected models of

activity.

Results

Mist netting resulted in 27 bat captures: 5 *Myotis evotis* (long-eared myotis; 2

female, 3 male) and 22 *Myotis volans* (long-legged myotis; 17 female, 5 male). These

individuals served as a source of the known-identity reference calls used in this study.

Bat detectors collected 10,647 unique call files over 48 nights, for a mean of

221.8 (73.3 *SE*) call files per night, resulting in 137.3 (46.8 *SE*) files per detector-night.

Over the course of the entire summer, 1,741 ($X = 8.5$, 36.3 *SE*) call files contained call

pulses from only high frequency guild bats, whereas 2,720.5 ($X = 93.0$, 20.3 *SE*) had

pulses from only low frequency guild bats, and 1,064 ($X = 22.2$, 10.2 *SE*) contained call

pulses from bats in both guilds. Nightly activity levels of bats, regardless of guild,

differed greatly between early/late- and mid-summer periods, with bat activity nearly 10 times higher during the mid-summer period (Table 3.1).

Activity levels within high and low frequency guilds differed between activity periods, with significantly greater activity levels for both high ($D = 0.6727$, $P < 0.0001$) and low ($D = 0.5758$, $P = 0.0005$) frequency bats during the mid-summer activity period. High frequency bat activity was significantly greater than low frequency guild activity in the early/late-summer period ($D = 0.6364$, $P < 0.0001$), though low frequency guild activity levels differed marginally from high frequency guild activity levels in the mid-summer period ($D = 0.4000$, $P = 0.05$).

Hourly activity levels during early/late-summer were significantly greater for high frequency guild bats ($X = 2.8$ call files per hour, $SE = 0.5$) than for low frequency guild bats ($X = 0.9$ call files per hour, $SE = 0.3$; $D = 0.7778$, $P = 0.009$; Table 3.1). The high frequency guild in the early/late-summer activity period (Fig. 3.1) had a bi-modal pattern of activity with an early peak (2 hours after sunset) and a late peak (7 hours after sunset). Low frequency guild bats showed a steady increase in activity until a peak 1 hour later than high frequency bats (8 hours after sunset).

Hourly activity levels of high frequency bats ($X = 26.5$ call files per hour, $SE = 4.6$) and low frequency bats ($X = 42.4$ call files per hour, $SE = 6.6$) were not significantly

Table 3.1. Hourly bat activity (call files per detector night, per hour after sunset) and nightly activity (call files per detector night), by guild and activity period ($X \pm SE$) in aspen forest edges in Heber Valley, Utah, summer 2009.

Period	Guild	Hours	Hourly Activity	Nights	Nightly Activity
Early/late summer	High	9	2.8 ± 0.5	33	12.1 ± 2.4
	Low	9	0.9 ± 0.3	33	3.5 ± 1.4
Mid-summer	High	9	26.5 ± 4.6	15	89.4 ± 21.2
	Low	9	42.4 ± 6.6	15	173.7 ± 54.7
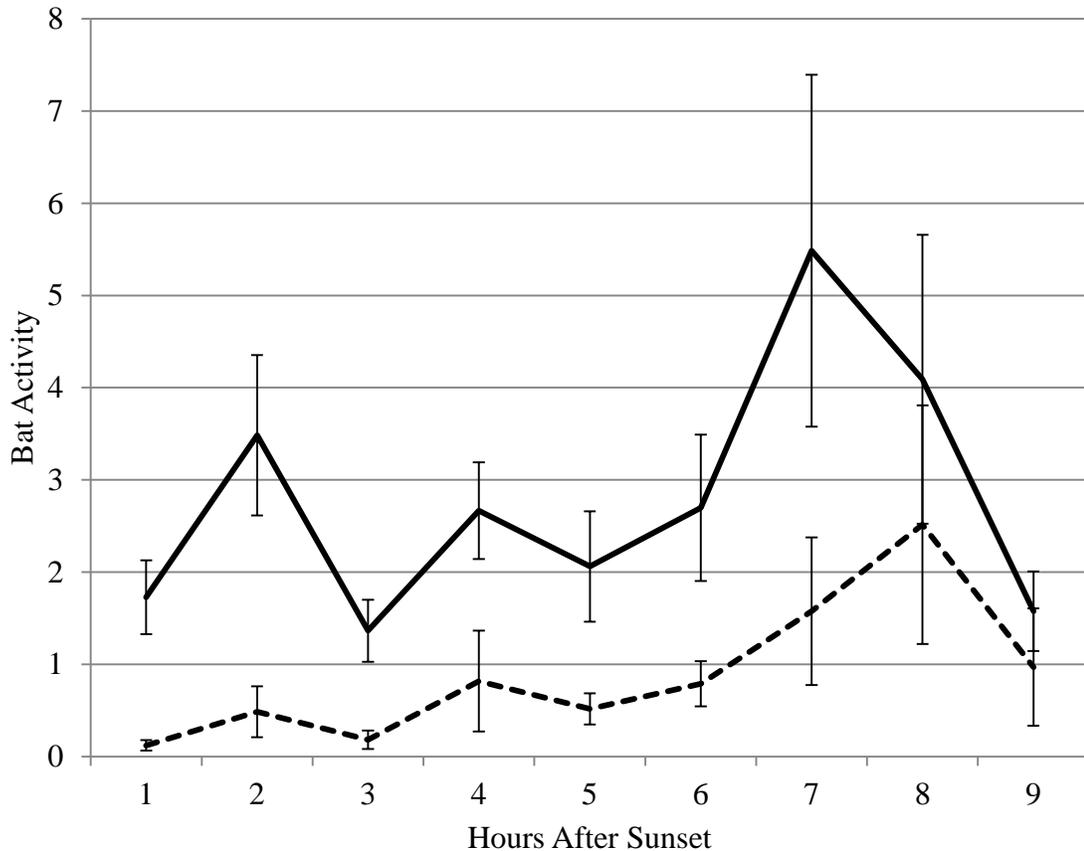
Figure 3.1. Early/late-summer 2009 activity levels for high frequency (solid line) and low frequency (dashed line) bat guilds, Heber Valley, Utah. Mean number of bat call files per hour per detector night over 33 nights (10 July – 29 July; 14 August – 27 August) plotted against time after sunset. Error bars = *SE*.

different over the entire night during the mid-summer activity period ($D = 0.5556$, $P = 0.12$). Activity levels of high frequency guild bats ($\bar{X} = 32.5$ call files per hour, $SE = 10.2$) and low frequency guild bats ($\bar{X} = 30.0$ call files per hour, $SE = 12.0$) also did not differ for the first few hours after sunset ($D = 0.25$, $P > 0.99$). However, late night activity levels of high frequency guild bats ($\bar{X} = 20.6$ call files per hour, $SE = 2.3$) were significantly reduced relative to low frequency guild bat activity ($\bar{X} = 52.8$ call files per hour, $SE = 4.8$; $D = 1.000$, $P = 0.01$). Hourly activity during the mid-summer activity period (Fig. 3.2) for bats in the high frequency guild peaked at 2 and 4 hours after sunset,
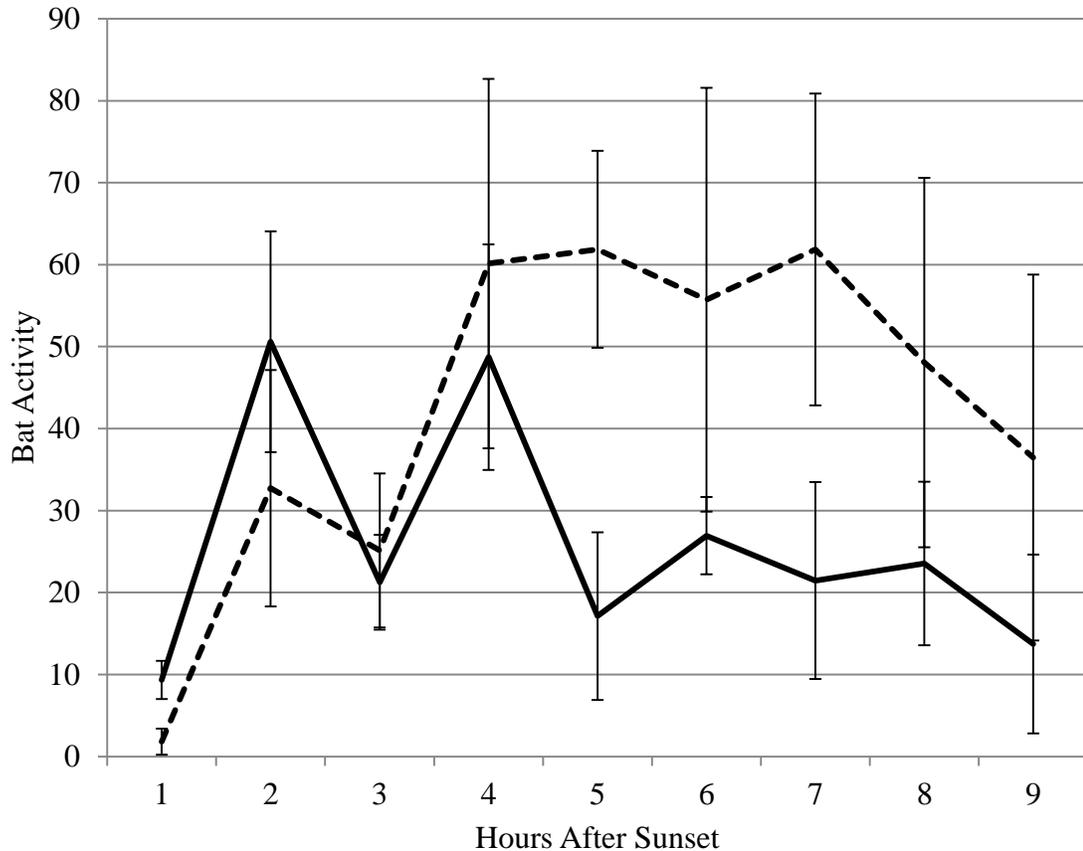
Figure 3.2. Mid-summer 2009 activity levels for high frequency (solid line) and low frequency (dashed line) bat guilds, Heber Valley, Utah. Mean number of bat call files per hour per detector night over 15 nights (29 July – 13 August) plotted against time after sunset. Error bars = *SE*.

dropping by about half for the remainder of the night. Low frequency guild bats followed roughly the same nightly pattern as high frequency guild activity, but did not drop at the second peak (4 hours after sunset). Low frequency guild activity remained elevated until approximately 7 hours after sunset, steadily decreasing thereafter until dawn.

Total nightly bat activity during the early/late-summer activity period comprised an average of 17.56 (3.2 *SE*) call files per night. Of these files, an average of 12.1 (2.4 *SE*) call files per night included signals from only high frequency guild bats. During the same period, an average of 3.5 (1.4 *SE*) call files per night contained only low frequency

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bat signals. High and low frequency guild bats were present in an average of 1.0 (0.3 *SE*) call files per night. Thus, both guilds were represented singly in 15.6 call files per night (2.8 *SE*), and both guilds were represented together in an average of 1.0 (0.3 *SE*) call files per night.

Total nightly bat activity during the mid-summer activity period comprised an average of 400.7 (127.5 *SE*) call files per night. Of these files, an average of 89.4 (21.2 *SE*) call files per night included signals from only high frequency guild bats. During the same period, an average of 173.7 (54.7 *SE*) call files per night contained only low frequency bat signals. High and low frequency guild bats were present in an average of 68.8 (29.9 *SE*) call files per night. Thus, both guilds were represented singly in 263.1 call files per night (72.7 *SE*), and both guilds were represented together in an average of 68.8 (29.9 *SE*) call files per night.

Activity levels of high and low frequency guild bats differed more than expected by chance between the early/late-summer and mid-summer periods (Table 3.2; Fisher's exact test, *d.f.* = 1, *P* < 0.0001).

Table 3.2. Contingency table for the Fisher's Exact Probability Test of inter-guild interactions between high- and low-frequency bats in aspen forest in Heber Valley, Utah, during the early/late and the mid-summer intervals of 2009. High = only high frequency guild represented in a call file; Low = only low frequency guild represented in a call file; Both = both guilds represented in a call file. Values are the average number of call files per detector-night of each period.

Period		High	Low	Both	Obs. Row Total	P
Early/late	Obs.	12.1	3.5	1.0	16.6	< 0.0001
(*n* = 33)	Exp.	4.8	8.4	3.3		
Mid	Obs.	89.4	173.7	68.8	331.9	
(*n* = 15)	Exp.	292.2	168.7	66.4		
Obs. Column Total		101.5	177.2	69.8	348.5	

Discussion

The findings indicate that the bat community in the aspen forest of Heber Valley, Utah showed little habitat partitioning during the early/late-summer period. Though hourly activity levels differed significantly between guilds, the patterns of activity overlapped heavily (excepting the early peak in high frequency guild activity – Fig. 3.1). Additionally, the rate at which two bats occupied the same space at the same time over the course of a night was slightly less than 1 time per night. Compared to the occurrence of single detections, this low level of multiple detections shows little evidence of interaction between high and low frequency guilds in Utah's aspen forest during the early/late period. High and low frequency bats had few opportunities to encounter each other, so few interactions between the guilds occurred. This allowed both guilds to operate independently of each other during periods of low activity density, producing few signs of habitat partitioning during the early/late-summer period (Fig 3.1).

Differences between mid-summer and early/late-summer activity patterns support the hypothesis that bats of high and low frequency guilds partitioned edge habitat temporally during the mid-summer period. Though hourly activity levels of high and low frequency guild bats did not differ significantly during the first few hours of the night during the mid-summer period, the significant difference in activity levels during the later hours of the night (Fig. 3.2) suggests some avoidance of encounters between guilds by high frequency guild bats. Reith (1980) observed a similar difference in the activity patterns of *L. noctivagans* when the larger and more aggressive *E. fuscus* was sympatric. Much higher rates of multiple bat call detection indicate that both guilds encountered each other much more during a single night in the mid-summer period than in the

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early/late-summer period. Higher encounter rates support the prediction that guilds

interacted more during the mid-summer period, when activity densities were highest.

Interestingly, though guilds did interact more during the mid-summer activity

period, they did not interact as often as elevated activity levels suggested they would.

Call files with calls from both guilds during the mid-summer period were significantly

less-numerous than expected by chance (Table 3.2), suggesting avoidance of interactions

between members of these guilds. High frequency guild bat activity was much lower on

average than low frequency guild activity during the mid-summer period. Other studies

on competition (Alford and Crump 1982; Kotler 1984; Steinmetz et al. 2011; Reith 1980)

have found that larger individuals tend to act aggressively toward smaller individuals. In

this study, the larger, low frequency guild bats are perhaps interacting aggressively with

smaller, high frequency guild bats. Evidence indicates that high frequency guild bats

(i.e., smaller, more maneuverable species) likely avoided interaction with low frequency

guild bats (i.e., larger, less maneuverable species) during the mid-summer period. As

edge habitat may constitute a preferred resource for bats in Utah's high-elevation aspen

forest (Pettit and Wilkins, in litt.), our data supports the hypothesis that smaller, high

frequency bats may be avoiding the larger, low frequency guild bats, effectively being

excluded from a preferred resource during periods of high activity of both guilds.

In Heber Valley, Utah, it is unclear why nightly bat activity levels increase so

greatly in this high-elevation aspen forest during late July and early August. Elevated

mid-summer bat activity levels have been reported in other studies (O'Farrell and

Bradley 1970; Sendor 2002). Additionally, sampling in the study area for consecutive

years (2008-2009) has revealed a similar increase in bat activity in separate locations (~ 1

km) for the same period (Pettit and Wilkins, in litt.). High bat activity during the mid-summer period might be explained by several phenomena, including an influx of long-distance or regional migrants (Barbour and Davis 1969; Hayes 1997); feeding behavior (Fukui et al. 2006); juvenile recruitment (Anthony et al. 1982; Koehler and Barclay 2000; Kunz and Anthony 1982; Tuttle 1976); and reproductive behavior (Cryan 2008; O'Farrell and Bradley 1970; Phillips 1966; Sendor 2000).

Further research is required to more fully expose underlying phenomena and promote greater understanding of factors affecting forest bats, particularly in light of the evidence presented here of increased competition between bat guilds during this increase in mid-summer bat activity. Any of the hypotheses explaining the increase bat activity levels could also help explain an increase in competition for preferred resources. Thus, understanding the reasons for the dramatic increase in bat activity during early August will help explain the patterns of competition between bats in the high and low frequency guilds.

CHAPTER FOUR

Seasonality in Bat Use of Forest Canopies and Edges in Southern Pine Forest

Abstract

Forest edges provide open, uncluttered habitat in which bats navigate and forage. Forest canopies may provide a similar kind of habitat for bat activity in forests, though the relationship between forest canopies and forest edges has not been well-examined. Bat activity levels were sampled in forest canopies and edges in Sam Houston National Forest, Texas, during fall 2009 and spring 2010 using Anabat SD1 bat detectors. CART analysis of echolocation characteristics identified 4 guilds based on characteristic frequency (e.g., high, mid, low frequency). Overall, activity levels of bats did not differ between forest canopies and edges. However, bat activity levels in canopies and edges differed seasonally. Additionally, activity levels in canopies and edges differed somewhat between guilds, both between canopies and edges, and between seasons. Hoary bats were detected mostly in forest canopies, and primarily during spring 2010.

Introduction

What we generally refer to as forest usually consists of a patchwork of habitat types, with individual habitat types interfacing at edges. Such boundaries often take on the characteristics of both adjacent habitats, a phenomena referred to as "edge effects" (Beecher 1942; Saunders et al. 1991). Edge effects may be abiotic, as in higher solar radiation (Saunders et al. 1991) or changes in edge microclimate, relative to forest interiors (Gehlhausen et al. 2000; Murcia 1995). Biological effects may manifest in two

ways: direct biological effects, such as increasing vegetation density near forest edges (Malcolm 1994), or indirect biological effects, like decreasing tendency for red-backed voles (*Clethrionomys californicus*) to be found near forest edges (Mills 1995). Bat species also respond to forest edges, likely due to the presence of obstructive vegetation, or clutter (Brigham et al. 1997, Sleep and Brigham 2003). Many bat species forage preferentially along forest edges (Adams et al. 2009; Grindal and Brigham 1999).

Edges are generally considered as vertical interfaces, particularly in forest habitats. However, forest canopies may also provide edge-like habitat, but with a more horizontal orientation (Grindal and Brigham 1999, Kalcounis et al. 1999). Bats use both canopies and traditional edges for nightly activities (Grindal and Brigham 1999; Kalcounis et al. 1999, Menzel et al. 2005, Pettit and Wilkins, in litt.). Though edge activity has been investigated by all of the previous authors, relationships between canopy and edge activity are little studied. The main objective of this study was to compare bat activity levels at traditional vertical edges with activity levels at the canopy interface between treetops and the sky.

One of the variables in forest edges that bats respond to most directly is generally referred to as "clutter." Physical clutter (i.e., leaves, branches, and other obstructive material) is indicated in many studies of bat-clutter interactions as having a direct, negative relationship with bat activity (Brigham et al. 1997, Broders et al. 2004, Law and Chidel 2002, Lloyd et al. 2006, Menzel et al. 2005, Saunders and Barclay 1992, Sleep and Brigham 2003). Such physical clutter limits flight, maneuverability, and access to interior forest habitats. It may also act as a barrier or landmark along which bats commute and forage (Grindal and Brigham 1999, Limpens and Kapteyn 1991). Grindal

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and Brigham (1999) suggested that the same exclusionary effect on bat activity in forest edges might also manifest in forest canopies because the canopy also offers an interface cluttered with vegetation. Other authors have supported this proposal (Kalcounis et al. 1999, Menzel 2005, Pettit and Wilkins, in litt.), though none have yet provided evidence to support the hypothesis that forest canopies provide edge-like habitat.

This study examines bat activity in both forest canopies and traditional forest edges. Per the findings of Pettit and Wilkins (in litt.) in aspen forests in the Rocky Mountains in Utah, bat activity levels in the pineywoods of eastern Texas were expected to differ between canopies and edges, with higher activity levels in edges. Bat activity levels should also differ between seasons, though higher activity levels in edges should manifest across seasons. Within canopies, edges, and seasons, bat activity levels were expected to remain consistent within the bat echolocation guilds identified in the study. Additionally, echolocation characteristics were expected to differ between canopies and edges depending on the foraging strategy of each guild.

Materials and Methods

Field work was conducted fall 2009 (23 October – 22 November) and spring 2010 (2 April – 20 May). The study area was in Sam Houston National Forest (SHNF), Montgomery and Walker Counties, Texas. Sections of the forest sampled for bat activity were dominated by loblolly pine (*Pinus taeda*) in the overstory. Some edge sites contained oak (southern red oak – *Quercus falcata*, post oak – *Q. stellata*, white oak – *Q. alba*, water oak – *Q. nigra*, or bluejack oak – *Q. incana*) and sweet gum (*Liquidambar styraciflua*). Yaupon holly (*Ilex vomitoria*), sapling *P. taeda* and *Quercus* spp. comprised most understory vegetation.

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Following the methods of Pettit and Wilkins (in litt.), bat activity levels were sampled in two types of habitat margins, edge and canopy. In fall 2009, 4 canopy sites and 4 edge sites were sampled for 11 to 21 days per site (Gorresen et al. 2008, Hayes 2000). In spring 2010, 5 canopy sites and 6 edge sites were sampled for 13 to 21 days per site. Edge sites were chosen based on a clear demarcation between contiguous forest and open habitat. Canopy sites were situated at least 20 m from any edges or gaps in the canopy. Due to microphone corrosion, detectors at 1 canopy site and 2 edge sites did not produce usable recordings during fall 2009. Gorresen et al. (2008) used a minimum between-detector distance of about 120 m to avoid "double counting" of bats. All bat detection sites in this study were at least 150 m from any other site; the most distant sampling sites were 24 km apart.

Bat echolocation signals in canopies and edges were recorded with 4 Anabat SD1 bat detectors. Microphones were directed toward vegetation to limit reception only to bats active in edge space (Larson and Hayes 2000; Schaub and Schnitzler 2007). Detectors were set in a paired design, with 1 edge and 1 canopy microphone set approximately 150 m from each other, and 2 pairs operating per night. Edge detector microphones were situated approximately 1 m above the ground and 2 m from edge vegetation, i.e., ~2 m from the point at which tree growth ended. Canopy microphones were attached to fiberglass antennae (Wonderpole, American Flag and Banner Company, Salem, Oregon, USA) affixed to tree boles, with the microphones positioned approximately 2 m above the forest canopy (approximately 15-35 m above the ground, depending on canopy height). Detectors were set to automatically begin recording at 2000 h (97 minutes after sunset at study beginning, 13 minutes before sunset at study

end) and to stop recording at 0630 h (exactly at sunrise at study beginning, 65 minutes after sunrise at study end) the following morning, for 10.5 detection hours per night per site. Bat activity levels were reported as the number of echolocation call files recorded per detector per night (i.e., calls per detector-night).

As detector microphones are subject to environmental degradation from rain and other sources of moisture if unprotected, they must be weatherproofed (Britzke et al. 2010). The various methods of weatherproofing result in some change to microphone performance. Corben (2006) found that wrapping microphones in a thin film of plastic wrap produced a 0-15 dB loss in signal strength depending on frequency. Reflector plates (Britzke et al. 2010) result in a similar loss in sensitivity. For this study, bat detector microphones were protected by covering them in a thin film of plastic wrap. All detector microphones were weatherproofed in the same manner for the duration of the study. Larson and Hayes (2000) recognized that microphone sensitivity varies with each detector. Thus, bat detectors were calibrated by turning the sensitivity dial to the point where microphone feedback began, then turning the dial back just enough to stop receiving feedback (Larson and Hayes 2000).

Passively-collected echolocation data were downloaded from data cards and evaluated for complete call pulses. Echolocation call sequences with 3 or more call pulses (i.e., high frequency sound identifiable as bat echolocation signals) and 1 or more complete call pulses (i.e., call pulses uninterrupted by echo, atmospheric conditions, etc.; identified using the RANOISE filter in ANALOOK, v.4.9j 2004) were further examined with the following parameters extracted for each call pulse: maximum frequency, minimum frequency, characteristic frequency (F_c), duration, and characteristic slope.

Only complete call pulses were used in order to limit the effects of feeding behavior, echo, and environmental interference on the analysis.

Occupancy Modeling

Occupancy modeling (MacKenzie et al. 2002; Royle and Nichols 2003; Gu and Swihart 2004; MacKenzie 2005; MacKenzie 2006) was considered for analyzing patterns of activity in this study. For datasets where establishing the presence of a species in a habitat type is essential, but where probabilities of detection are below 1, occupancy modeling can be an invaluable technique.

MacKenzie (2006) enumerates 4 major assumptions of this technique: 1. Occupancy status does not change over the course of the survey season; 2. Probability of occupancy remains constant across sites, or any differences are modeled using covariates; 3. Probability of detection remains constant across all sites, or differences can be modeled by covariates; and 4. Species detections and histories of detection are independent.

Of these, assumptions 2 and 3 are most problematic. The probability of detection has not yet been reliably tied to any useful covariates for any of the bat species captured. Inconsistency in patterns of bat activity in the study area, and no reliable method of modeling that activity, suggest that assumptions 2 and 3 of occupancy modeling would likely be violated.

In addition to problems with meeting all the necessary assumptions, the best purpose of occupancy analysis, estimating the presence of a particular species in a specific habitat type (MacKenzie et al. 2002), is not the main focus of the study. It has been established by capture methods that bats are active in SHNF in large numbers. This

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project has detected bat activity in both forest canopies and edges, but endeavors to establish relative amounts of activity in parts of the forest rather than presence or absence. Occupancy analysis is of limited utility in answering questions of magnitude of use of habitat types, and thus would be an inefficient way of examining the data.

Kolmogorov—Smirnov Test

Similarities between periods (i.e., seasonal shifts) of bat activity were examined by use of Kolmogorov—Smirnov tests (Fuller 1976). Two-sample Kolmogorov—Smirnov tests are often used to make comparisons between changes in ecological variables over time, particularly where datasets violate assumptions required for more powerful statistical methods (Castro-Arellano et al. 2009, Furey et al. 2010, Kneeshaw and Bergeron 1998, Necknig and Zahn 2011, Pedro and Taddei 2002, Walli et al. 2009, Wiens and Milne 1989).

Each bat echolocation call sequence was identified to the level of call frequency guild. Guilds were determined using classification and regression tree (CART) analysis using R (v.2.11.1 2010), a method shown to function well in straightforward analyses of echolocation data for simple bat communities (Praetoni et al. 2005). For comparison we used call sequences collected from individuals of each species either known to be active in the study area (by capture; A. Debelica-Lee, pers. comm.), or whose geographic distribution includes the study area (Schmidly 2004). A library of bat calls from known species, provided by C. Corben, was used to determine which classifying variables would be used for analysis. Based on the results of CART analysis, bat calls recorded passively in the study area were assigned to guild groups. Guild activity levels of bats in canopies and edges in fall 2009 and spring 2010 were also compared using pair-wise

Kolmogorov—Smirnov tests, adjusted for multiple comparisons with Bonferroni

corrections. Echolocation variables were compared between guilds using pair-wise

Mann—Whitney tests, also adjusted for multiple comparisons with Bonferroni

corrections. All statistical analyses were performed in R (v.2.11.1 2010).

Results

Bat Activity

Overall, bat detectors collected data over 81 calendar nights, 32 nights in fall

2009 (23 October – 22 November) and 49 nights in spring 2010 (2 April – 20 May). In

fall 2009, canopy detectors recorded 36 total call files (0.7 ± 0.3 call files per detector-

night) and edge detectors recorded 535 total call files (16.5 ± 4.3 call files per detector-

night). In spring 2010, canopy detectors recorded 980 total call files (12.6 ± 3.3 call files

per detector-night) and edge detectors recorded 92 total call files (1.1 ± 0.3 call files per

detector-night).

Over both seasons, bat activity levels were significantly different between

canopies and edges. In fall 2009, bat activity levels in canopies were significantly lower

than bat activity levels in edges (Fig. 4.1; $P = 0.001$), and activity levels of bats in edges

were significantly higher in fall 2009 than in spring 2010 ($P = 0.001$). However, in spite

of high activity in the canopy during the first two weeks of sampling in spring 2010 (Fig.

4.2), bat activity levels were not significantly different between canopies and edges

during spring 2010 ($P = 0.38$). Also, canopy activity levels of bats in fall 2009 were not

significantly different from canopy activity levels of bats in spring 2010 ($P = 0.79$).

Analysis of the library of known call files by CART identified 4 groups based

exclusively on characteristic frequency (F_c; Table 4.1). Schmidly (2004) cites 12 bat
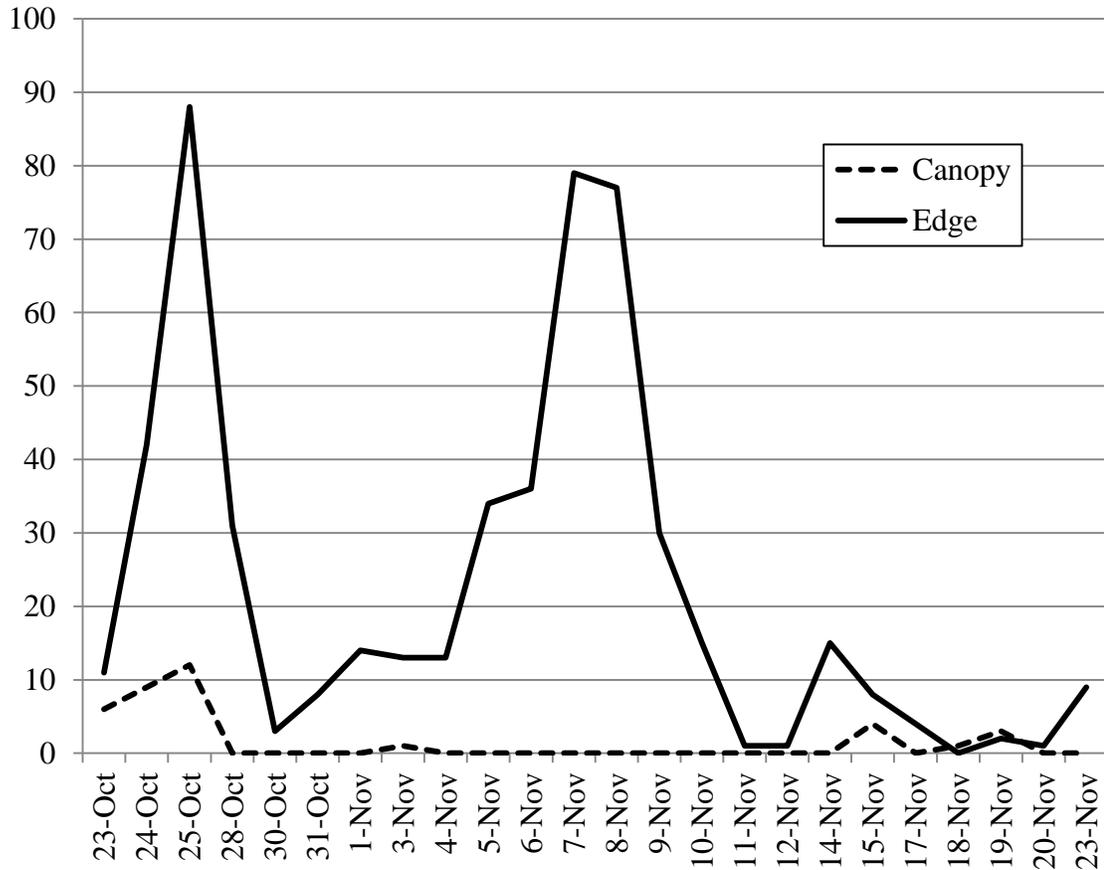
Figure 4.1. Nightly activity levels of bats (number of call files per detector) 23 October –
22 November 2009 in pine forest (*Pinus taeda*) canopies and edges, Sam Houston
National Forest, Texas.

species to be found in Walker or Montgomery counties, including the 10 bat species

reported from capture, and 2 additional bat species predicted to include these counties as

part of their range. A companion study by A. Debelica-Lee at SHNF during 2009-2011

yielded only 8 species from > 230 individuals captured. Echolocation characteristics

allow these 8 species to be classified into 4 frequency guilds: The high frequency guild

likely contained echolocation calls primarily from red bats (*Lasiurus borealis*), Seminole

bats (*Lasiurus seminolus*), tricolored bats (*Perimyotis subflavus*), evening bats

(*Nycticeius humeralis*), and southeastern myotis (*Myotis austroriparius*). The mid

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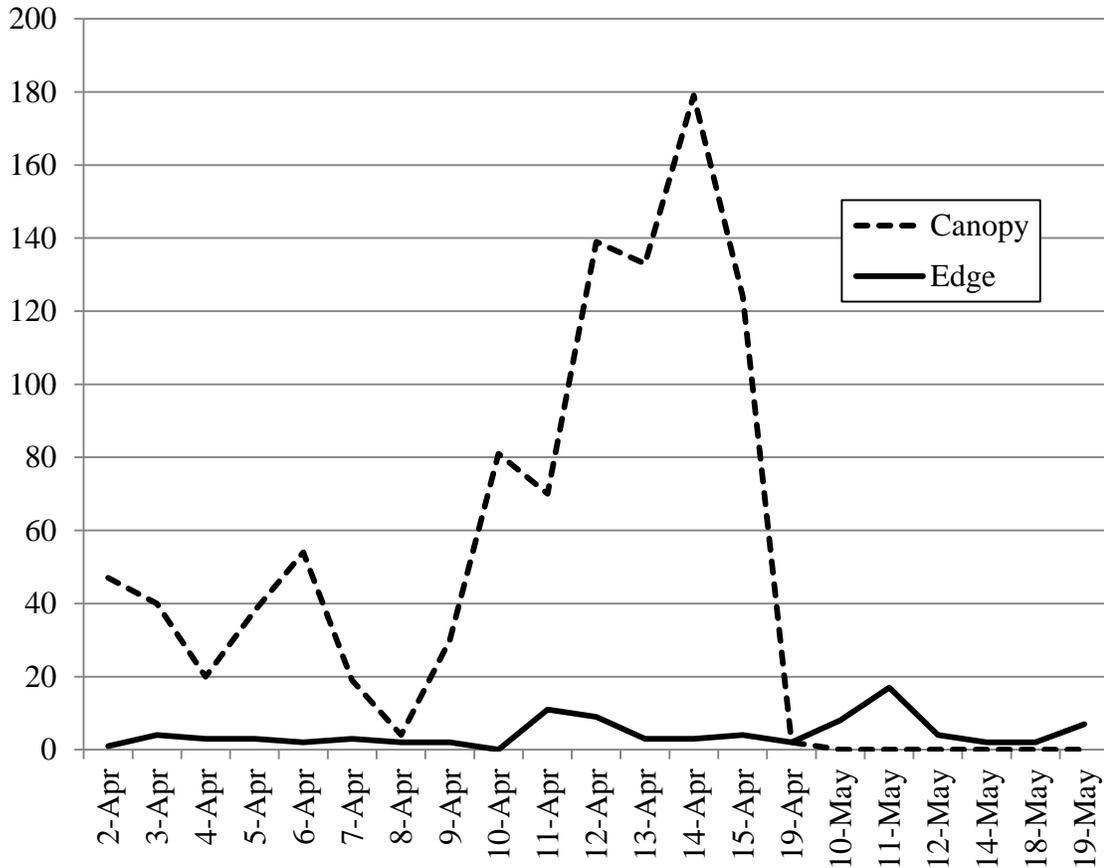
Figure 4.2. Nightly activity levels of bats (number of call files per detector) 2 April – 20 May 2010 in pine forest (*Pinus taeda*) canopies and edges, Sam Houston National Forest, Texas.

frequency guild likely contained echolocation calls primarily from *E. fuscus*, though *T. brasiliensis* may have contributed some call files in this range. The low frequency guild likely contained mostly *T. brasiliensis*, though some hoary bats (*Lasiurus cinereus*) and very few *E. fuscus* may have contributed to this group as well. The hoary guild likely consisted entirely of call files produced only by *L. cinereus*.

During the first 3 weeks of sampling during fall 2009 and the first 2 weeks of sampling during spring 2010, activity levels were consistently higher than during the remainder of both sampling periods (Figs. 4.1-4.2). An examination of only these high-activity periods using the same methods as used for analyzing the entire dataset

Table 4.1. Activity levels of bats in multiple guilds, as identified by CART analysis, shown with respective mean nightly activity levels, Sam Houston National Forest, Texas. Fall period spanned 23 October to 22 November 2009; spring period from 2 April to 20 May 2010. CART analysis identified groups based entirely on characteristic frequency (F_c). Bat activity levels reported as call files per detector-night $\pm$ *SE*.

Guild	F_c (kHz)	Fall 2009		Spring 2010	
		Canopy	Edge	Canopy	Edge
High	> 32.955	0.25 ± 0.13	7.80 ± 2.34	6.45 ± 1.66	0.78 ± 0.22
Mid	24.980—32.955	0.35 ± 0.17	3.93 ± 1.04	1.90 ± 0.48	0.17 ± 0.06
Low	20.500—24.980	0.08 ± 0.06	5.52 ± 1.43	1.58 ± 0.52	0.08 ± 0.04
Hoary	< 20.500	0	0.54 ± 0.33	2.63 ± 0.99	0.10 ± 0.04

(Kolmogorov—Smirnov tests, adjusted for multiple comparisons by Bonferroni corrections) produced results that differed somewhat from the activity results produced by a more complete analysis. Edge activity did not differ between fall 2009 and spring 2010 for all guilds detected ($P = 0.20$), though canopy activity was much higher for all guilds in spring 2010 than in fall 2009 ($P = 0.0002$; Fig. 4.3). Edge activity was much higher than canopy activity during fall 2009 ($P = 0.008$). However, canopy activity was higher in spring 2010 than it was in fall 2009 ($P = 0.002$). Hoary guild activity was mostly restricted to forest canopies, and only during the first two weeks of April. These results are possibly good indicators of bat activity in parts of SHNF, but were not replicated across more than 2 sample sites. Thus, any conclusions drawn from the results of this simple examination of early sampling in both fall 2009 and spring 2010 should be interpreted cautiously.

Bats in the high frequency guild ($F_c > 32.955$ kHz) were significantly more active in fall 2009 edges than in canopies ($P = 0.0005$), and were significantly more active in fall 2009 edges than in spring 2010 edges ($P = 0.005$). However, there was no significant difference between high frequency bat activity in canopies and edges during spring 2010.

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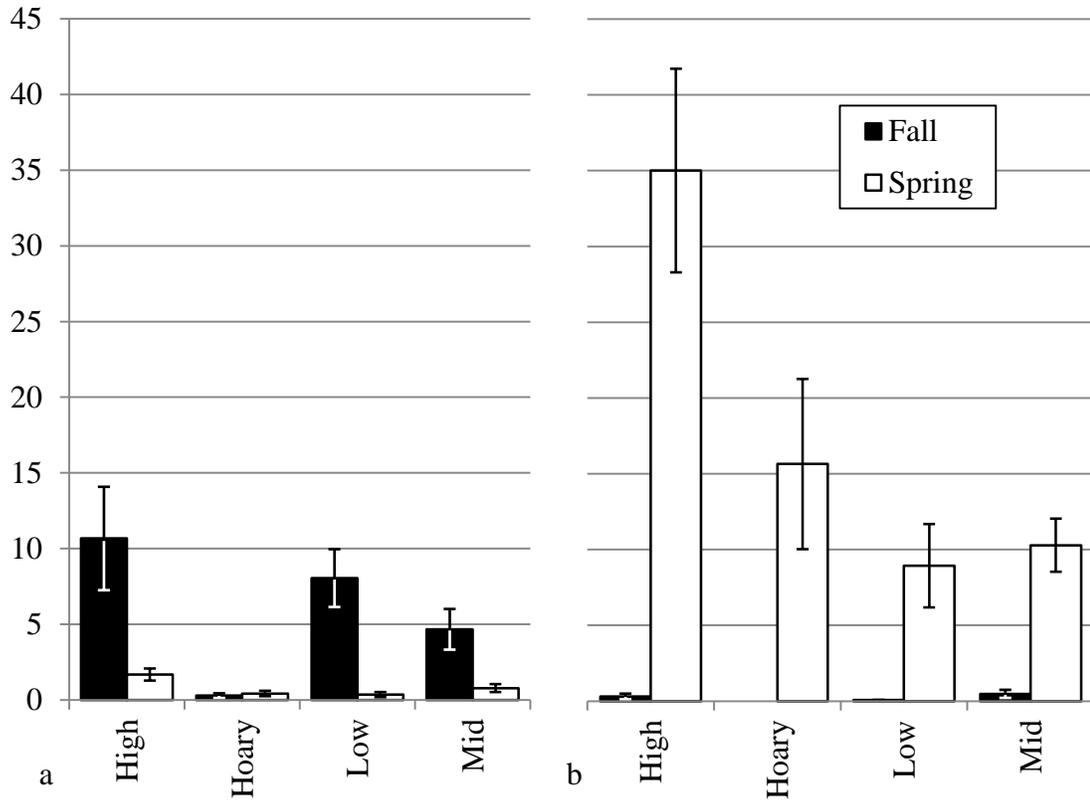
Figure 4.3. Bat activity levels (number of call files per detector-night) by frequency guild during most-active periods only, 23 October – 12 November 2009 (fall) and 2 April – 15 April 2010 (spring), Sam Houston National Forest, Texas. Bat activity levels in edges are shown in a., and bat activity levels in canopies are shown in b. Error bars = *SE*.

Bats in the mid frequency guild (24.980 kHz $< F_c <$ 32.955 kHz) were more active in edges during fall 2009 than spring 2010 ($P = 0.01$). However, there were no significant differences in the activity levels of bats in the mid frequency guild between canopies and edges during fall 2009 ($P = 0.13$), or spring 2010 ($P = 0.64$). Also, canopy activity levels of bats in the mid frequency guild did not differ significantly between fall 2009 and spring 2010 ($P > 0.95$).

Bats in the low frequency guild (20.500 kHz $< F_c <$ 24.980 kHz) were more active in edges during fall 2009 than in spring 2010 ($P = 0.01$). In fall 2009, low frequency guild bats were also more active in edges than in canopies ($P = 0.005$). However, bats in

the low frequency guild had similar activity levels in canopies during fall 2009 and spring

2010 ($P > 0.95$), and no difference in activity levels between canopies and edges in

spring 2010 ($P > 0.95$).

Activity levels of bats in the hoary guild ($F_c < 20.500$ kHz) were not significantly

different between edges or canopies, between or within seasons ($P > 0.95$), in spite of

increased activity during the first sampling period in spring 2010. No call files from bats

in the hoary guild were collected in canopies during fall 2009.

Bat Echolocation Characteristics

Pair-wise Mann—Whitney tests comparing values for the five echolocation call

attributes revealed no differences within each guild in fall or winter, between canopy and

edge activity ($P > 0.05$). Additionally, most guilds did not differ in canopy or edge

activity levels between seasons. The few exceptions to this pattern are detailed below;

significance is indicated at $P < 0.05$ (Table 4.2).

Echolocation behavior of bats in the low frequency guild in canopies was not

significantly different from any guild in forest edges. Echolocation behavior of bats in

the mid frequency guild in canopy differed in most measured attributes from other guilds

in edge, except for in frequency range and characteristic slope in the high frequency and

hoary guilds, and pulse duration in the high frequency guild. Echolocation behavior of

bats in the high frequency guild in canopy differed significantly for echolocation

characteristics (e.g., characteristic frequency, maximum frequency, minimum frequency)

from other guilds in edge, however the duration of call pulses was significantly different

between high frequency guild bats in canopies and low frequency guild bats in edges. No

Table 4.2. Mean echolocation characteristics by guild, by season and edge type (canopy or edge), Sam Houston National Forest, Texas. Fall period spanned 23 October to 22 November 2009; spring period from 2 April to 20 May 2010. Guilds determined by CART analysis of characteristic frequency (F_c; Table 1). No members of the hoary guild were detected in canopies during Fall 2009.

Guild	Echol. Charac.	Fall 2009 Canopy Mean	SE	Fall 2009 Edge Mean	SE	Spring 2010 Canopy Mean	SE	Spring 2010 Edge Mean	SE
High	Dur	5.14	± 1.75	5.30	± 1.45	4.53	± 1.04	4.30	± 0.97
	F_{max}	45.33	± 5.99	46.92	± 5.97	46.21	± 5.52	45.11	± 4.56
	F_{min}	40.04	± 2.63	40.01	± 3.24	37.61	± 2.97	37.07	± 2.56
	F_{range}	5.28	± 3.51	6.91	± 3.92	8.59	± 4.53	8.05	± 4.66
	F_c	40.26	± 2.58	40.10	± 3.25	37.84	± 2.99	37.32	± 2.48
	S_c	23.89	± 18.66	29.37	± 16.56	43.54	± 26.30	48.63	± 32.33
Mid	Dur	5.66	± 0.88	6.55	± 1.69	5.50	± 1.48	5.54	± 1.18
	F_{max}	32.67	± 2.01	31.74	± 4.11	38.30	± 5.92	35.64	± 5.95
	F_{min}	27.13	± 0.78	26.71	± 1.66	29.13	± 2.51	28.02	± 2.16
	F_{range}	5.54	± 1.75	5.04	± 3.30	9.17	± 5.62	7.62	± 4.87
	F_c	27.50	± 1.39	26.92	± 1.69	29.46	± 2.38	28.22	± 2.13
	S_c	36.00	± 13.65	29.55	± 17.10	50.85	± 35.48	39.73	± 18.34
Low	Dur	8.05	± 3.06	8.94	± 2.04	6.58	± 1.32	8.31	± 1.54
	F_{max}	24.06	± 1.43	25.79	± 2.45	26.59	± 5.44	24.61	± 2.51
	F_{min}	22.82	± 1.55	23.21	± 1.11	21.32	± 1.20	22.00	± 1.73
	F_{range}	1.24	± 0.53	2.58	± 1.95	5.27	± 4.88	2.61	± 1.59
	F_c	23.08	± 1.61	23.30	± 1.09	21.49	± 1.21	22.01	± 1.73
	S_c	6.47	± 6.77	13.88	± 7.75	27.54	± 17.61	18.47	± 10.32
Hoary	Dur	N/A		9.97	± 2.91	6.69	± 1.11	8.21	± 4.00
	F_{max}	N/A		22.82	± 2.54	23.28	± 2.29	22.07	± 0.57
	F_{min}	N/A		20.02	± 0.31	19.81	± 0.46	19.50	± 0.62
	F_{range}	N/A		2.79	± 2.37	3.46	± 2.26	2.56	± 1.08
	F_c	N/A		20.06	± 0.31	19.88	± 0.45	19.52	± 0.64
	S_c	N/A		17.46	± 8.40	26.86	± 9.75	23.45	± 10.53

comparison could be made for echolocation behavior for hoary guild bats in canopies, as no hoary guild bat calls were detected in the canopy during fall 2009.

Within each guild, echolocation characteristics did not differ significantly during spring 2010. However, guilds differed in at least 2 echolocation characteristics when compared with each other during this same season. Echolocation behavior of bats in the high frequency guild in canopies differed significantly from echolocation behavior of bats in edges in the hoary guild, though high frequency guild behavior in canopies differed by all but frequency range and characteristic slope with bats in edges in the low or mid frequency guilds. High frequency guild bat behavior in edges was significantly different from behavior in all other guilds, except for frequency range and characteristic frequency produced by bats in the mid frequency guild. Bats in the hoary guild in canopies displayed similar echolocation behavior to bats in the low frequency guild in edges and low frequency guild bat behavior in canopies was similar to echolocation behavior of bats in the hoary guild in edges in all ways but in characteristic frequency and minimum frequency. Most frequency characteristics were similar between bats in the mid frequency guild, active in canopies, and low frequency guild bats in edges. Frequency characteristics were also similar between low frequency guild bats, active in canopies, and bats in the mid frequency guild, active in edges, with only pulse duration, frequency range, and characteristic slope differing between them.

In canopies, echolocation behavior differed little between seasons for each guild. However, bats in the high frequency guild differed significantly in pulse duration between seasons, and bats in the mid frequency guild differed in frequency characters from fall to spring, excepting frequency range. Additionally, behavior of bats in the low

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frequency guild did not differ from any other guild between fall and spring. Bats in the mid frequency guild in fall differed in most ways from all guilds in spring, including the mid frequency guild, except for in frequency range and characteristic slope for high, low, and mid frequency guilds, and in pulse duration for mid and low frequency guilds in spring. Bats in the high frequency guild in fall also differed significantly in most frequency characteristics and pulse duration from other guilds in spring. High frequency guild bats did not differ in frequency range or characteristic slope. Due to the absence of hoary guild activity during the fall season in canopies, no comparison could be made.

In forest edges, the pattern of within-guild similarity generally continued across seasons. Additionally, echolocation behavior for bats in the hoary and low frequency guild did not differ between seasons. However, echolocation behavior of bats in the high frequency guild differed by duration, characteristic frequency, and minimum frequency. Bats in the hoary guild differed only in characteristic frequency between seasons. In general, guilds differed from each other in most echolocation characteristics. If any similarity existed, typically it occurred in pulse duration, frequency range, and characteristic slope.

Discussion

Bat activity levels in SHNF did not differ significantly between canopies and edges overall (except, perhaps, in situations like those encountered in the site sampled during the first 2-3 weeks of each season), so the hypothesis that bat activity levels are higher in forest edges was not supported. These findings differ from an analysis of bat activity levels collected in canopies and edges of aspen forests in north-central Utah (Pettit and Wilkins, in litt.) where edge activity was greater than canopy activity.

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However, the results support the predictions of other authors (Grindal and Brigham 1999, Kalcounis et al. 1999) that canopies may serve as another form of forest edge for bats.

Lack of agreement with the findings of Pettit and Wilkins (in litt.) may be explained by the greater diversity of feeding and flight niches in piney woods habitat type available in SHNF compared to the relative paucity of niches available in Utah's alpine aspen forest (Schoener 1974). The limitation on availability of niches in alpine aspen forest is evident in the small number of species (3-5) and guilds (2) of bats identified in the Utah forest (Pettit and Wilkins, in litt.) relative to the number of bat species (8-9; A. Debelica-Lee, pers. comm.) and guilds (4) found in SHNF. One of the factors possibly relating to differences in number of niches in these two ecosystems relates to the insect fauna available as diets for insectivorous bats. In the warm, moist lowland pine forest of SHNF, a diverse array of insects is available nearly year-round. The local climate of the arid, alpine aspen forest of north-central Utah offers a shorter period of warm weather for insect activity, thereby limiting the diversity of niches available to insectivorous bats.

Differences in structural complexity between these two habitats also may contribute to differences in diversity of the respective bat communities. Flight space between branches in canopies is more open in pine canopies relative to aspen canopies. Bat activity shows a negative relationship with vegetative clutter, even among bats adapted to navigate more cluttered environments (Brigham et al. 1997, Sleep and Brigham 2003). Because forest canopies are more open in SHNF pine forests than they are in Utah's aspen forest, bats may be exploiting the extra space for flight and forage (Schnitzler and Kalko 2001). More openness in forest canopies may allow access for bats to more prey resources closer to forest interiors, where insect abundance is high

(Grindal and Brigham 1999, Kilgo 2005). In SHNF, bats may be skimming through the more open forest canopies, snatching insects as they become distinct from background echoes and physical clutter of vegetation (Eklöf et al. 2002).

Evidence weakly supported the hypothesis that bat activity levels differ between seasons. High activity levels in forest edges during fall 2009 do not persist through spring 2010. The highest activity levels recorded in a similar study by Pettit and Wilkins (in litt.) found that bat activity was highest in forest edges, and that those levels could reach incredibly high values during brief intervals of the summer. In that case, high activity levels were attributed to the height of the edge and relative openness of the habitat adjacent to the edges (Pettit and Wilkins, in litt., Schnitzler and Kalko 2001).

Evidence did not support the hypothesis that bat activity levels in canopies and edges do not differ by guild. Because guild membership was determined entirely by the characteristic frequency of each call sequence, a metric previously connected with a bat species' foraging strategy (e.g., gleaning, aerial hawking, etc. – Norberg and Rayner 1987), differences in activity levels between guilds likely reflect foraging behavior of bat species represented in each guild. Thus, guild-specific variation in nightly patterns of activity may reflect changes in prey availability (Fukui et al. 2006, Vinson and Hawkins 1998), or even sensitivity of some bats to foraging activities of other bats (Gillam 2007).

Evidence weakly supported the hypothesis that bats in the various guilds change echolocation characteristics depending on whether they are in canopies or in edges. Within-guild similarities in echolocation characteristics between canopies and edges in each individual season do not support this hypothesis. However, differences in echolocation characteristics between seasons do support this hypothesis. Bat species

using these habitat interfaces are likely responding similarly to interface orientation or the position of vegetation in the forest within each season. Differences in echolocation characteristics between the two seasons may be attributable to changes in atmospheric conditions in the forest, bat community composition, or prey availability.

Differences in echolocation behavior of the high and mid frequency guilds between seasons (and the missing echolocation behavior for the hoary guild fall 2009) in forest canopies may indicate changes in the species composition of these guilds during different seasons due to migration of guild member species. Some species in the high frequency guild are long-distance migrants (*L. borealis* – Cryan 2003, Shump and Shump 1982a; *N. humeralis* – Watkins 1972), one of the species in the mid frequency guild is long-distance migrant (*T. brasiliensis* – Wilkins 1989), and the only species in the hoary guild also is a long-distance migrant (*L. cinereus*).

In spite of similarity in activity levels between seasons in forest canopies, bats in the hoary guild were only present in substantial numbers for the first two weeks in April 2010 (Fig. 4.3). As hoary bats are the only bat species known by capture to be present in the study area that regularly echolocate at a mean frequency below 20 kHz (Barclay et al. 1999, Schmidly 2004), it is possible that the observed rise in hoary guild activity in canopies during spring 2010 represents the migration of hoary bats over SHNF. Observation of hoary bats, a long-distance migrant, in southeastern Texas during this time period is consistent with what is known of the timing of hoary bat migrations (Cryan 2003, Findlay and Jones 1964, Shump and Shump 1982b). Further sampling by mist net during early spring in SHNF should result in more concrete capture data for this large, migratory bat.

In conclusion, this study in eastern Texas has demonstrated that forest edges provide useful habitat for bats in pine forests during fall and spring, the seasons when sampling was conducted. Examination of forest edges year-round may further elucidate the importance of season in bat habitat use. This analysis also began to reveal how canopies in the southeastern pine forests provide more complex bat activity patterns than do the aspen forests of the Rocky Mountains, likely due to a more complex community structure. Which interfaces bats use seems to depend on factors other than simply whether the interface is vertical (edge) or horizontal (canopy). Additionally, as some bat species (e.g., *L. cinereus*) seem to be found only in canopies during certain seasons, it is recommended that acoustic monitoring of canopies not be neglected in comprehensive surveys of forest bat communities.

CHAPTER FIVE

Summary and Conclusions

Conclusions

Results of the research constrained within the bounds of this dissertation project provided insight on bat activity in forest edges and canopies. These studies also identified edge habitat as a preferred resource for forest bats, as evidenced by competition between bat echolocation guilds during times of elevated activity.

The conclusions of research presented in Chapter two revealed high activity levels in forest edges relative to canopies during short alpine summers of the aspen forests in north-central Utah. Bat activity did not seem directly connected to traditional measures of clutter, though echolocation guilds responded in predictable ways to vegetation in forest edges. Larger-bodied species, using low-frequency echolocation calls, tended to interact little with edge vegetation, as evidenced by the consistency in echolocation parameters between canopy and edge spaces. Smaller-bodied species, using high-frequency echolocation calls, often interacted with edge vegetation, as evidenced by changes in echolocation characteristics between canopy and edge spaces. Edge and canopy activity levels represented previously unknown information on bat activity in forest habitats, though the echolocation behavior of bats in call frequency guilds reflected what is already established in the natural history literature on bats.

Competition over preferred resources, a facet of bat ecology that has received little attention, found some exposure in Chapter three. Bats in high and low frequency guilds had few, if any, competitive interactions in forest edges during stretches of low

activity. However, during a two-week period of high activity, high frequency guild bats seemed to avoid interaction with low frequency guild bats. This example of density-dependent competition provided insight to how bat communities partition temporally and spatially, and allowed better understanding of bat competition over preferred resources.

Finally, the findings from Chapter four presented a more nuanced understanding of bat activity in forest margins. The richer bat community in Sam Houston National Forest, Texas seemed to be more active in forest canopies than the simple bat community of Heber Valley, Utah. However, this pattern of activity in forest margins shifted drastically from fall to the spring of the following year. This seasonal shift coincided with the fall migration flights of large, migratory bat species (e.g., hoary bats). Additionally, the relatively complex bat community of Sam Houston National Forest likely reflects a large variety of competitive niches, motivating some species to switch between use of edges and canopies during different seasons of the year. Though seasonal shifts in habitat use have been identified previously in bat communities of North American forests, examination of this pattern in forest margins has been neglected.

Future Investigations

Though these studies have provided great insight into factors surrounding bat use of forest margins, many questions still remain:

Seasonality in bat activity levels in both study areas needs further investigation. Though some species are known to be migratory, and many are known to hibernate in well-established hibernacula, very little is known about seasonal, regional movements in most bat species.

For the pineywoods of southeast Texas, a comprehensive, year-round monitoring program—including use of bat detectors in both forest canopies and edges, with simultaneous mist-netting over nearby ponds—would greatly improve understanding of the seasonality of patterns of foraging for the bat community.

In Heber Valley, Utah, seasonality of bat activity occurs in a particularly intriguing manner, with regard to the 2-week period of extremely high bat activity in the middle of the summer. It is unclear why nightly bat activity levels increase so greatly during late July and early August. Elevated mid-summer bat activity levels have been reported in other studies (O'Farrell and Bradley 1970; Sendor 2002), though not in the same community or ecosystem. However, sampling in the study area for consecutive years (2008-2009) has produced a similar increase in bat activity in separate locations (~ 1 km apart) for the same period (Chapter two).

High bat activity during the mid-summer period might represent the following phenomena.

An Influx of Migrating Bats

Bats on a long-distance migration might use the study area for a few days, then continue along their migratory route. Of the species suspected to be in the study area, silver-haired bats (*Lasionycteris noctivagans*) and hoary bats (*Lasiurus cinereus*) both are known to migrate long distances (Barbour and Davis 1969). Both *L. noctivagans* and *L. cinereus* have echolocation calls that would overlap heavily with those of the non-migrant, big brown bat (*Eptesicus fuscus*) also suspected to live in the study area. Additionally, as bat activity directly relates to temperature (Brooks 2009; Hayes 1997; Kunz 1974; O'Farrell and Bradley 1970), elevated bat activity may represent the infusion

of species in both high and low frequency guilds from lower elevations during warmer parts of the season.

Feeding Behavior As Bats Exploit Seasonal Insect Emergences

Bats respond to insect emergences by increasing local foraging activity (Fukui et al. 2006), though there can be a delay of at least one night between the beginning of the emergence and the increase in bat activity (Kennard 2008). Tracking of concentrations of insects might become important as bats begin to augment fat storage reserves in preparation for winter hibernation or migration. Big brown bats (*E. fuscus*) near St. Paul, MN, for example, reach their highest weights just prior to entering hibernation, usually near the end of September or beginning of October (Beer and Richards 1956). Bats in the study area may experience a shorter foraging season than what is available for bats in Minnesota, so it is possible that bats during this period are putting more effort in foraging activities to increase fat reserves in preparation for hibernation.

Juvenile Recruitment

In temperate forests, juvenile bats of both frequency guilds usually fledge between late June and early July (Anthony et al. 1982; Koehler and Barclay 2000; Kunz and Anthony 1982; Tuttle 1976). Late July may represent a time of elevated activity for young bats in this high-elevation aspen forest as they become volant and join in nightly foraging and prepare to disperse.

Reproductive Behavior

Netting over water in a high-elevation (1360 m) desert habitat 24 km north of Las Vegas, Nevada, O'Farrell and Bradley (1970) found that western pipistrelles, *Pipistrellus*

hesperus (*Parastrellus hesperus*), had a similar period of elevated activity June-August, peaking in July by a factor of 10 over activity September-May. As most individuals they captured were reproductive females (i.e., pregnant or lactating), and more males than females were captured September-May, they attributed the increase in *P. hesperus* activity over water to the metabolic demands of reproduction.

Some bat species participate in intraspecific swarming as a part of mating behavior, where adult males chase females in a geographically constrained area until both land and copulate (Thomas et al. 1979). The location of these swarms may be hibernacula (Thomas et al. 1979), or some other location (Sendor 2000). Mating swarms have not been observed for most species represented in high and low frequency guilds, leaving much unknown of bat reproductive behavior in the wild.

Males and females of most hibernating bat species separate during the maternity period, often roosting separately for the entire summer. Several authors have described conditions supporting the hypothesis of reproductive behavior for high edge activity levels during this period (Davis et al. 1968; Long 1940; Phillips 1966; Sendor 2002). For instance, communally roosting male and female bats (*E. fuscus*, *Pipistrellus pipistrellus*) often do not share roosts during summer months (Long 1940; Phillips 1966; Sendor 2002). Male *E. fuscus* had the highest sperm counts, largest testes, and longest epididymides (Phillips 1966), and Sendor (2002) found that the few adult males participating in swarming behavior near a maternity roost were at reproductive peak during July and August. This indicates, in spite of separate roosting habits, that mid-summer should be a time of heightened reproductive activity for bats in temperate biomes.

The most likely interpretation of the available information is that many bats engage in copulation mid- to late-summer at sites other than at or inside roosts. Bats may be engaging in reproductive behavior while foraging, particularly in areas where defined boundaries (i.e., edge habitats) provide recognizable landmarks (Cryan 2008, Cryan and Brown 2007).

Impacts of Clutter on Bat Activity

Also of interest, clutter remains one of the most important, but least quantifiable, variables related to bat habitat ecology. Future work in this area, perhaps through the use of a device like the LAI-2200 (LI-COR, Lincoln, NE, USA), should promote the use of simple, affordable, fine-scale, repeatable measures for estimating the amount of vegetative material a bat would need to navigate. Such measures would vastly improve the study of bat-clutter interactions that are currently based on qualitative, rough-scale estimations. These and other questions and problems need to be addressed so that bat ecology in forests may be better understood and compared across multiple systems.

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