

ABSTRACT

Community Structure, Ecomorphology, Resource Partitioning, Diet: Implications for Conservation of a Forest-Dwelling Bat Community

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Bat communities in southeastern pine forests in Texas are not well studied. However, as bat populations throughout the United States are facing increasing mortality rates due to habitat loss, wind turbine impacts, and white nose syndrome, forest managers are in need of good conservation plans. In this study, I provided some of the information necessary to guide the conservation plan developers in the right direction. I conducted netting surveys at two sites in Sam Houston National Forest, Texas, during summers 2009 - 2011. I captured a total of 382 bats belonging to 8 species: big brown, eastern red, evening, hoary, Mexican free-tailed, Seminole, southeastern bat, and tri-colored bats. I discovered that at least three of these species (big brown, evening, and Seminole bat) exhibit extended seasonal monoestry with parturition and lactation starting earlier and ending later than previously believed. By examining ecomorphology of captured bats, I found that the bat community assemblage (species present and their proportions in community) is impacted by management practices. Annual burns, clearcutting, and planting of pine plantations are altering habitat and changing clutter levels in the forest,

thus managed areas of the forest are made available to higher numbers of clutter-intolerant bat species, while unmanaged areas are restricted to a lower number of species, the ones that are clutter-tolerant. Furthermore, I found that bats at the two sites are exhibiting some temporal partitioning, but that the species involved in this partitioning change on yearly bases and that this partitioning is not linked to food availability. Finally, I employed a new generation sequencing technique (pyrosequencing) to determine the diet of the tri-colored bat. Using this method, I identified prey items belonging to 3 orders and 50 species in a single fecal pellet showing that bats might be more opportunistic eaters at the species than ordinal level. This dissertation provides until now unknown information about the bat community in the southeastern pine forests of Texas on which new studies can build in an effort to construct appropriate conservation plans and preserve bat diversity in the Coastal Plains bioregion.

Community Structure, Ecomorphology, Resource Partitioning, Diet: Implications for Conservation
of a Forest-Dwelling Bat Community

by

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DEDICATION

To my husband Siew-Yee (Charlie) and my daughter River – the loves of my life

CHAPTER ONE

Introduction

The importance of top-order predators in maintaining ecosystem function has been demonstrated in many marine and terrestrial systems (Paine 1966, 1969; Estes and Palmisano 1974; Soulé et al. 1988; Henke and Bryant 1999; McLaren and Peterson 1994). By limiting populations of their prey and/or subordinate competitors, top-order predators can modulate the diversity of a system, and may ultimately increase plant biomass through a series of trophic links (Paine 1980; Pace et al. 1999; Polis et al. 2000; Schmitz et al. 2000; Ripple and Beschta 2003). Species that perform this function are known as keystone predators (Paine 1966, 1969). The identification and conservation of such species, and maintenance of their interactions, is of vital importance in arresting the global loss of biodiversity (Soulé et al. 2003, 2005). Where top-order predators are completely or virtually removed from a system, the effects on species richness and abundance at lower trophic levels can be profound. Previously subordinate predators may increase unchecked, potentially decimating prey populations (Soulé et al. 1988; Crooks and Soulé 1999). Herbivores can become over-abundant, leading to overgrazing on plant populations (McLaren and Peterson 1994). Competitive relationships between prey species may be altered (Paine 1966). In some cases, these effects lead ultimately to community-level trophic cascades (Polis et al. 2000) in which plant biomass is redistributed throughout the system. Insectivorous bats can be considered to be keystone species controlling insect populations at stable levels and as such they are extremely

important for maintenance of ecosystems they live in and we depend on. In addition, bats such as Mexican free-tailed bats (*Tadarida brasiliensis*) play an important role in pest control (Cleveland et al. 2006).

Most of the North American forest bats are relatively small (<30 g), and mostly feed on insects caught in flight (Lacki et al. 2007). Some, such as *Corynorhinus rafinesquii*, Rafinesque's big eared bat, however, are known to occasionally glean invertebrates from the ground or vegetation (Faure and Barclay 1992; Faure et al. 1993; Lacki and Ladeur 2001; Lacki et al. 2007). More than half of North American bat species rely on forests during at least some stage of their lives (O'Shea and Bogan 2003). Today, in North America, forest-dwelling bats are facing increasing hardship due to habitat loss, wind turbine farms, and white nose syndrome (Dixon et al. 2013). Forests have been increasingly exploited for timber and, as a consequence, availability of habitats where these forest-dwelling bats live has been decreasing. This trend of replacement of natural forest habitats with fast growing plantations for timber production will increase as human population needs increase (Wear and Greis 2012, 2013). Wind turbine collisions are contributing to high mortality of migratory bats, many of which are forest-dwelling species (Fraser et al. 2012). Finally, White Nose Syndrome has been spreading throughout United States at alarming rate, devastating bat populations (Dixon et al. 2013). To prevent loss of bat diversity, a better job in development and enforcement of conservation plans needs to be done. The problem is that despite all the effort put forth by scientists to shed light on their roosting and foraging behavior, still very little is known about forest-dwelling bats in particular. Bat ecologists still don't completely understand how these bats choose their day roost sites; how devoted they are to specific roosts or

roosting areas on daily, seasonal, or annual bases; how far away they fly to foraging grounds; what, where, and when they eat; what eats them. Even less is known about how bat communities function and how different species of bats within the community interact within their “shared” habitat.

Fenton (1997) identified possible components of a bat-conservation program, suggesting that the following should be the focus of bat conservation efforts: protection of roosts, food, habitat, and populations. In this dissertation, I investigate three of these components: populations (age structure, gender proportions, and reproductive phenology), habitats (selection of habitat based on ecomorphology, temporal partitioning), and diet.

Population Structure

Community and Demographics

Understanding structure of the bat community in a specific forest enables better overall understanding of how bat communities function and how to protect them in future. It is known that during spring and summer, male and female bats often segregate from each other because of different costs of torpor and different requirements for thermoregulation among them (Hamilton and Barclay 1994; Mattson et al. 1996; Wilkinson and Barclay 1997; Broders and Forbes 2004; Hein et al. 2008). This segregation can occur at various scales at different roosts (Hamilton and Barclay 1994; Kunz and Lumsden 2003), in different parts of a forest (Barclay 1991; Hein et al 2008), or in large-scale geographic ranges (Cryan 2003). For example, Broders and Forbes (2004) studied roosting habits of two bat species (*Myotis septentrionalis* and *Myotis*

lucifugus) common in the Greater Fundy National Park Ecosystem of New Brunswick, Canada. They determined that, due to sexual segregation, these two species form four distinct groups in terms of roost-site selection. As a consequence, a bat community within one forest might be complex mosaic, a mixture of adults and juveniles, males, and reproductive and non-reproductive females in various proportions depending on which species are present in community. For example, if reproductive females are present in the community, the community might be dominated by large aggregation of females forming a maternity colony of up to hundreds individuals. Or, this “maternity colony” might include only a few females (Kunz and Lumsden 2003). For example, evening bat (*Nycticeius humeralis*) maternity colonies in Missouri and Iowa are known to have up to 950 individuals, while colonies in Florida usually contain less than dozen females (Watkins 1972). Furthermore, some forest-dwelling bats are exclusively solitary. Eastern red bats (*Lasiurus borealis*) and hoary bats (*Lasiurus cinereus*) are solitary roosters with the exception of females accompanied by their immature offspring (Constantine 1966).

Investigating the causes of nonrandom associations among group members is critical for understanding the function of group living and the evolution of social behavior (Metheny et al. 2008). Gender, age, and reproductive condition can cause nonrandom associations among group members. For example, Smith et al. (2002) documented associations based on similarity in age and sex for cowbirds. In some mammals, such as spotted hyenas (Holekamp et al. 1997), kinship can be used to predict patterns of association. In addition, members of various fission-fusion mammalian social systems, including African elephants (Archie et al. 2006), African lions (Packer et al. 2001), and spotted hyenas (Van Horn et al. 2004; Wahaj et al. 2004) preferentially

associate with kin. However, Metheny et al. (2008) have recently shown that big brown bats (*Eptesicus fuscus*), even though exhibiting fission-fusion social system, do not preferentially associate with kin.

In this dissertation (Chapter two), I have examined the structure of a single bat community in the pine forest ecosystem of southeastern Texas. I have reported species composition of this bat community, gender and sex proportions for each present species, as well as reproductive phenology. This chapter provides essential information needed for effective conservation plans. In particular, this chapter reports new information on reproductive phenology of three bat species present in this forest that might directly affect management practices.

Ecomorphology

Wing Morphology

Morphology can determine the type of feeding opportunities that are available to an animal (Fenton and Bogdanowicz 2002). Thus, based on external morphology and associated foraging behavior, bats can be placed into one of several distinct groups: aerial foragers, gleaners, and trawlers. Aerial foragers have small hind feet, short calcars, short ears, and narrow tragus, are mostly insectivorous, hunt airborne prey, use high-intensity echolocation calls to detect, track, and evaluate targets (Griffin et al. 1960; Fenton and Bell 1979; Siemers et al. 2001a; Fenton and Bogdanowicz 2002). Gleaners have small hind feet, long ears, wide tragi, and relatively large body size; are often insectivorous; hunt by taking prey from the ground or vegetation; use low-intensity broadband echolocation calls while apparently relying on prey-generated sounds to detect, track, and

evaluate targets (Fenton and Bell 1979; Faure and Barclay 1992, 1994; Fenton and Bogdanowicz 2002). Trawlers have large hind feet, long calcars, and relatively large body; hunt by flying right above water (or flat surface) from which they regularly take prey with their feet; use high-intensity echolocation calls to detect, track, and assess targets (Suthers 1967; Norberg and Rayner 1987; Jones and Rayner 1988; Kalko and Schnitzler 1989; Siemers et al. 2001a, 2001b; Fenton and Bogdanowicz 2002). Some species of trawlers have specialized claws on their hind feet, apparently to minimize drag (Fish et al. 1991).

Though we can often place bats in one of these three groups, it is not unusual to see some bats species within the community that are intermediate in their morphological characteristics. These “intermediate” bats often show plasticity in their foraging behavior, meaning they can change their foraging behavior (Fenton and Bogdanowicz 2002) in order to avoid competition with other bat species.

Habitat structure, choice of food, and foraging behavior have strong influence on flight modes and behavior of flying animals. Even though Findley (1993) stated that most bat faunas are dominated numerically by taxa that are similar in morphology and size, we know that even small differences in wing shape and features can influence flight behavior (Norberg and Rayner 1987). Differences in morphology have implications for foraging and, consequently, for community structure among sympatric taxa (Keast 1968). Therefore, one should expect that dissimilarities in wing morphology among sympatric bat species within a community play an important role in allowing these species to explore different foraging strategies and thus co-exist within the same forest. Several morphological characteristics pertain to wing function: wing length, wing area, wing

loading, aspect ratio, tip length, and tip area ratio. Body mass of a bat is an important determinant as well.

Based on studies conducted by Norberg (1981), Norberg and Rayner (1987), and Fenton and Bogdanowics (2002), it is expected that the most members of family Vespertilionidae, to which the focal bat species in my study areas belong, might be considered average among bats in wing proportions (average wingspan, average or slightly below-average wing loading), and that a typical species is a relatively maneuverable aerial insectivore. However, even with this, some variation should be expected.

Echolocation

Besides the constraints to flight associated with wing morphology, bats also have the challenge of detecting prey, thus wing design and echolocation-call structure tend to form an adaptive complex (Norberg and Rayner 1987; Stoffberg and Jacobs 2004). For example, a gleaning bat should be small, with very low aspect ratio and short, rounded wingtips in order to maneuver in confined space, and their echolocation calls should enable them to distinguish prey from background clutter (vegetation).

Bat echolocation signals are typically in short pulses, lasting from <1 ms to about 50 ms with the intervals between pulses ranging from <5 ms to >100 ms (Fenton et al. 1995). The signals may be short clicks or tonal signals with structured changes in frequency over time also known as frequency modulated or FM signals (Fenton et al. 1995). Based on frequency, bat echolocation calls range from the human-audible (<20 kHz) to the ultrasonic (>20 kHz) and beyond (>200 kHz) range (Fenton et al. 1995). Broadband echolocation calls cover a range of frequencies, while narrowband signals

focus on a smaller range of frequencies. Some narrowband calls are dominated by a single frequency and are also known as constant frequency or CF signals. Clicks are short and broadband, however, tonal signals may be short or long and broadband or narrowband (Fenton et al. 1995). In addition, echolocation signals can be produced at low- or high-duty cycle, illustrating the amount of time that a signal is actually "on" (Fenton et al. 1995).

Short broadband, steep FM components are mostly well-suited for accurate target localization as well as for providing more spectral information and may also have advantages for the classification of different types of vegetation. The longer narrowband shallow FM components are well suited for the detection of small targets at long distances (Neuweiler 1989; Fenton 1990; Schnitzler and Kalko 1998, 2001; Siemers and Schnitzler 2004).

Aerial feeders use echolocation calls that are of long duration (8–25 ms), low (<30 kHz) to medium (30–60 kHz) peak frequency (frequency of maximum intensity), and often dominated by a shallow frequency modulated component (Stoffberg and Jacobs 2004). The narrow bandwidth increases the range at which prey and obstacles are detected (Schnitzler and Kalko 1998).

Gleaners have short (1–3 ms) broadband echolocation calls of low intensity that overcome the masking effects of the emitted call overlapping with echoes that return with very short time delays. This type of call also reduces background echoes, allowing greater resolution of the target (Schnitzler and Kalko 1998; Stoffberg and Jacobs 2004). Barclay (1999) discussed many difficulties in using echolocation calls to identify bats to species. Most importantly, there is variation in call design even at various levels within

each species (Barclay 1999). We see variation within individuals (O'Farrell et al. 1999), variation within population (Brigham et al. 1989; Obrist 1995), and variation among populations (Thomas et al. 1987; Parsons 1997; Gillam and McCracken 2007). Variation occurs among measures such as maximum and minimum frequency and duration, as indicated by O'Farrell et al. (1999), but also in the pattern of change in frequency or shape of call over time (Kalko and Schnitzler 1993; Barclay 1999).

Bartonicka et al. (2007) discussed the importance of plasticity of echolocation calls in individual bats as well as of social calls. Echolocation calls might contain some information on population membership or individual characteristics (Jones 1995; Obrist 1995). Variability of echolocation calls can serve in inter-individual communication within a foraging group or on occasional encounters with another bat (Barclay 1982; Fenton 1986). Success in assigning echolocation calls to each bat (Habersetzer 1981; Masters et al. 1995) suggests that the calls could communicate individual identity and improve recognition of its own echoes. Individual signatures within echolocation calls must contain information on the sender's identity, and receivers must be able to detect those signatures as well as discriminate among them (Bohn et al. 2004).

Alternatively, shifts in echolocation calls might function to minimize jamming effects. If modification of echolocation calls is associated only with jamming avoidance, it can decrease recognition of members of the same colony whether they are related or not (Goodwin and Greenhall 1961; Boughman 1998; Wilkinson and Boughman 1998). Social calls can potentially facilitate individual recognition. High bat densities often result in chases or other manifestations of aggression accompanied by social calls (Fenton 1994). Ratcliffe et al. (2004) suggested that individual signatures can be included in

specific social calls rather than in echolocation calls. Several authors found the increase of social calls when conspecifics are present (Rydell 1986; Wilkinson and Boughman 1998).

Because of all of the potential variation within echolocation calls of any particular species, it is essential that a library of calls includes calls recorded from the geographic area being studied (Barclay 1999), from multiple individuals, as well as from the bats in various environments within the study area (e.g., in forest, in open area, over reflective areas such as water). Variation due to recording differences (e.g., distance between bat and the microphone, the direction that bat is facing) should be taken into account as well (O'Farrell et al. 1999).

In the third chapter of this dissertation, I have attempted to determine effects of management practices on bat community structure by examining the differences in the community between managed and unmanaged areas of Sam Houston National Forest, Texas, and by relating variation in ecomorphology to these different management practices. To achieve this goal, I have sampled bat communities at an unmanaged site (high level of vegetation clutter) and at a managed site (low level of vegetation clutter). I recorded echolocation calls and examined wing morphology of all captured bats at both sites. Analyses of this data might potentially identify a link between bat community structure and variation in vegetative clutter, and offer an understanding of this relationship that can aid in development of management and conservation plans.

Niche Partitioning

Niche Theory

Niche theory emphasizes the role of habitat heterogeneity and niche partitioning as the main factors structuring ecological communities (Hutchinson 1957; MacArthur 1972; Petren 2001; Silvertown 2004; Kadmon and Allouche 2007). Species coexistence is the focus of most ideas on diversity maintenance. Stable coexistence mechanisms function in two major ways: (1) equalizing, which tends to minimize average fitness differences between species, or (2) stabilizing, which tends to increase negative intraspecific interactions relative to negative interspecific interactions. Equalizing mechanisms contribute to stable coexistence because they reduce large average fitness inequalities which might negate the effects of stabilizing mechanisms (Chesson 2000). Stabilizing mechanisms are essential for species coexistence and include mechanisms such as resource partitioning and frequency-dependent predation. The most common meaning of diversity maintenance is coexistence of species with similar ecologies (life histories) in the same region. These species are often termed as “the community” (Chesson 2000). However, these species are also in the same trophic level, so they can be placed in the same guild, a group of species that have overlapping resource requirements (Simberloff and Dayan 1991).

The essential way in which stabilization occurs is most clearly seen with resource competition (Chesson 2000). Interspecific competition that occurs in natural communities is well documented (Connell 1983; Schoener 1983; Gurevitch et al. 1992; Denno et al. 1995; Grover 1997; Glen and Dickman 2008). Competition between mammalian predators often has a strong influence on their abundance and distribution. For example,

African wild dogs *Lycaon pictus* are more abundant in the absence of lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) (Creel 2001; Creel et al. 2001), and red foxes (*Vulpes vulpes*) have extirpated populations of arctic foxes (*Alopex lagopus*) through competitive interference (Hersteinsson *et al.* 1989; Kaikusalo and Angerbjörn 1995). In eastern Australia, the spotted-tailed quoll (*Dasyurus maculatus*), an endangered marsupial carnivore, is thought to be threatened by competition from eutherian carnivores such as the red fox, feral cat (*Felis catus*) and wild dog (*Canis lupus*, Glen and Dickman 2005). This interspecific competition, defined as reciprocal negative effects of one species on another, either directly or indirectly mediated by changes in resource availability (Chase et al. 2002), is one of the most important factors influencing community structure (Cody and Diamond 1975; Tilman 1982; Diamond and Case 1986; Morin 1999), and may lead to niche partitioning, or cause the exclusion of species from the particular community (Gause 1934; Hardin 1960; Levin 1970; Schoener 1983; Bush and Malenke 2008).

In addition to having similar diets, species may occupy niches that overlap in terms of spatial resources (Johnson et al. 1996; Glen and Dickman 2008). For example, guild members may hunt or forage in similar habitats, or use similar structural features in which to shelter and raise young. In such cases, species may partition resources spatially or temporally (Harrison et al. 1989; Johnson and Franklin 1994). Existing knowledge of spotted-tailed quolls, foxes, feral cats and wild dogs indicates overlap in the habitat use of all these species (Catling and Burt 1994, 1997). Structures such as hollow logs and rock crevices may also be used by some or all of these predators as den sites (McIntosh 1963; Thomson 1992; Corbett 1995; Belcher and Darrant 2004; Körtner et al. 2004; Glen and

Dickman 2006). By studying the movements and shelter use by sympatric species, the degree of spatial overlap may be ascertained. Further, by fitting animals with mortality-sensing radio collars, instances of intra guild predation or interspecific killing can be detected (Körtner et al. 2004).

When two species compete, presence of additional potential competitors can influence the relationship between the two original species (Chesson 2000; Kneitel and Chase 2004; Holt and Dobson 2006; van Veen et al. 2006). A common example is the presence of predators which often facilitates the coexistence of competing prey species by suppressing prey populations and during the process preventing competitively superior species from monopolizing resources (Paine 1966; Holt 1977; Holt and Lawton 1994; Abrams 1999; Chase et al. 2002). However, there is still uncertainty about the biological circumstances under which competition between species has a greater or lesser influence on the characteristics of species, their population densities and overall community structure (Chesson and Huntley 1997; Gurevitch et al. 2000).

If species compete for a resource such as space, the possibilities for niche differentiation are limited, so species will generally be constrained to occurring in different habitats or parts of the space that have different characteristics (Connell 1980). In addition, if each species is a superior competitor on a different range of such environmental conditions, then several competing species will be able to coexist at equilibrium. Each will tend to occupy part of a local site where it is the superior competitor (Connell 1980). This could have occurred in two general ways. First, the species may have evolved separately and when they later come together each became established in that part of the site in which it is pre-adapted to do best, excluding inferior

competitors from its habitat. Alternatively, the two species may have coevolved under pressure of competition, diverging from each other so that each then occupied a different part of the site (MacArthur 1972; May 1974; Connell 1980). This phenomenon is usually termed "habitat shift" (Schoener 1974; Connell 1980). In addition, in species that compete for a resource other than space, the divergence is usually visualized as taking place along one or more resource axes. Each species has a resource utilization curve along this axis. For example, one of the axes could be particle size of food, such as seed size in granivores (Connell 1980), or size of insects in insectivorous species.

In Chapter four, I demonstrated that species within a community of forest-dwelling bats exhibit some temporal partitioning at the watering holes. I have found that participants in this temporal partitioning shift and vary on yearly bases, even though the same species are present in the community year after year. In addition, it seems that, at least at my sites, this partitioning is not necessarily a consequence of limited food resources as usually believed by bat ecologists.

Diet

Traditional Approach to Dietary Studies

Diet and dietary adaptations have been the subject of many investigations of the biology of bats. Considering all species of bats, the array of dietary strategies is quite broad. It is thought that diet is a primary dimension along which niches might be partitioned and the structure of a bat community is organized. Understanding the natural history of species and its foraging strategies requires detailed information on food habits (Litvaitis 2000).

One of the ways by which bats might partition niches is by partitioning their food resources. Many studies have investigated the diet of various bat species (i.e., Geggie and Fenton 1985; Jacobs 1999; Menzel et al. 2000); however, seldom do these studies deal with the diets of multiple bat species within a single community (Carter et al. 2003, 2004). Standard procedure for diet studies includes collecting fecal samples of bats or content of their guts. The next step involves soaking each fecal pellet in water or alcohol on a microscope slide, then teasing it apart under a binocular microscope using a pair of dissecting needles (Thabab 2007; Kervyn and Libois 2008). Identification of insect pieces, based on morphology, can be facilitated by the descriptions of Whitaker (1988) and McAney et al. (1991) and by comparison with whole insect specimens collected on the bat's foraging grounds or deposited in entomological collections.

Several authors have evaluated the relevance and limits of this method (Kunz and Whitaker 1983; Robinson and Stebbings 1993). These studies have pointed out that "conventional" fecal analysis allows an estimation of food composition, and that it is valuable for seasonal or geographical comparisons of the diet. But it does not provide the exact composition of the ingested food. Results usually overestimate the proportion of large insects and of those leaving easily identifiable pieces even after ingestion and digestive transit. Soft-bodied insects may be underrepresented. Due to the nature of the "conventional" fecal analysis, we are usually able to identify the prey items only to ordinal or familial level, but only rarely to lower levels.

Novel Approach

Prey identification at order level cannot effectively help determine if the bat species within a single community are exhibiting niche partitioning. The past decade has

brought a wide range of molecular techniques that can shed further light on bat diet. Monoclonal antibodies were until recently the most effective method for gut content identification, but PCR-based techniques have proved to be highly effective and versatile in recent laboratory trials and are likely to rapidly displace all other approaches (Symondson 2002). However, the principal flaw of PCR-based techniques is that they require species-specific primers (Deagle et al. 2005, 2007), but that only few such primers are available. In the past few years, another molecular technique, DNA barcoding of mitochondrial cytochrome c oxidase I (COI), has become available. Results to date indicate that this COI barcode is: (a) easy to recover from diverse taxa, using a limited set of primers; (b) readily aligned for sequence comparisons; and (c) effective in distinguishing among closely related animal species from a variety of invertebrate and vertebrate taxa (Folmer et al. 1994; Herbert et al. 2003; Schwartz et al. 2000; Stoeckle et al. 2005). Currently, the most commonly used method in bat dietary studies was the one developed by Clare et al. (2009). In this method, individual insect fragments are removed from the fecal sample and placed into wells for DNA extraction. Then, DNA extracted from each individual insect fragment is sequenced. This method has provided until now unprecedented insight, at the genus and species levels, into diets of a few bat species: eastern red bats - Clare et al. 2009; little brown bat (*Myotis lucifugus*) – Clare et al. 2011; and Antillean ghost-faced bat (*Mormoops blainvillei*) – Rolfe et al. 2014, and sooty mustached bat (*Pteronotus quadridens*) - Rolfe et al. 2014.

In my dissertation research, I applied an advanced molecular method in efforts to achieve a more-comprehensive description of bat diet than has previously been accomplished. I used pyrosequencing, which analyzes DNA extracted from complete

fecal sample to identify the diet of the tri-colored bat (*Perimyotis subflavus*). Results are presented in Chapter five.

CHAPTER TWO

Structure and Reproductive Patterns in the Summertime Forest-bat Community of Southeastern Texas

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Abstract

Forests of eastern Texas represent the westernmost extent of the southern pine forests and part of the pine belt of the forested Gulf coastal plain. Bat community assemblages in similar forests throughout southeastern United States have been documented in various studies, but only scant data are available for Texas. The purpose of this study was to characterize the assemblage and investigate reproductive patterns of the summer bat community in the austroriparian forest of eastern Texas. Using mist nets, we captured bats during summers 2009-2011 and recorded species, gender, age and reproductive condition. We captured 382 bats of eight species: Seminole *Lasiurus seminolus* (n = 163), evening *Nycticeius humeralis* (n = 86), big brown *Eptesicus fuscus* (n = 57), eastern red *L. borealis* (n = 31), southeastern myotis *Myotis austroriparius* (n = 21), tri-colored *Perimyotis subflavus* (n = 19), Mexican free-tailed *Tadarida brasiliensis* (n = 4), and hoary *L. cinereus* (n = 1) bats. Analysis of reproductive data suggests that three of these species (big brown, evening, and Seminole bats) may be following a reproductive strategy - extended seasonal monoestry (births of single litters spanning a particular season) - different than their previously reported pattern of synchronous monoestry.

Introduction

Southern forests extend through 13 southeastern states from Virginia to Texas (Wear and Greis 2012, 2013). In some regions, forest densities reach >80%. These southern forests are diverse and consist of pines (34%), hardwood types (55%), and oak-pine mixture (11%). Southern forests are divided into five large regions (Wear and Greis 2012, 2013): Coastal Plain, Piedmont, Appalachian-Cumberland, Mississippi Alluvial Valley, and Mid-South. The Coastal Plains are divided into two subsections by the Mississippi Alluvial Valley. Texas pine forests are situated in the Coastal Plains west of the Mississippi River. The Coastal Plains have the highest biodiversity of these forested regions, due to their large geographic extent and the high diversity of habitats. Modeling predicts the Coastal Plains to be the most impacted segment of southern forest by four key factors: population growth; climate change; timber markets; and invasive insects, plants, and diseases (Wear and Greis 2012, 2013). All predictive models (Wear and Greis 2012, 2013) suggest that the Coastal Plains will experience in the next few decades an increase in average annual temperatures by 2.5 – 3.5° C; some models suggest a decrease in precipitation while others predict increased precipitation. This area also is expected to experience increases in human population (urbanization), increased timber production (causing replacement of natural growth pine forests with pine plantations), and increased vulnerability to invasive species and diseases. Together these factors will cause an inevitable decline in biodiversity of this region (Wear and Greis 2012, 2013). Conservation of the biota of this region requires study of the flora and fauna (both surveys and natural history) as predicted changes occur. These studies should provide

better understanding of each affected species and should aid in development of effective conservation plans to prevent loss of these species.

The bat fauna of Texas is rich, including all four bat families (Mormoopidae, Phyllostomidae, Vespertilionidae, and Molossidae) and all but 14 of the 47 bat species occurring in United States (Ammerman et al. 2012). Of the 33 bat species recorded in Texas, 22 use forestland for roosting and foraging (Ammerman et al. 2012). Forests of eastern Texas represent the westernmost extent of the southern pine belt of the forested Gulf Coastal Plain (Wear and Greis 2012, 2013). The bat communities of southern pine forests have been studied previously in at least five states. Morris et al. (2010; May-August) surveyed the managed pine forest in North Carolina using both acoustic sampling and netting. Kilgore (2008; May 2002-May 2004) documented the bat community in managed bottomlands in Alabama. Ford et al. (2006; May-July) conducted acoustic surveys in South Carolina in pine forest managed for red-cockaded woodpeckers *Picoides borealis*. Both Miller (2003; late April-early September) and Welch (2003; June-August) conducted their studies in managed loblolly pine forests in Mississippi. Prior studies of bats in eastern Texas forests have focused on roosting ecology of species of conservation concern, such as Rafinesque's big-eared bat *Corynorhinus rafinesquii* and southeastern myotis *Myotis austroriparius*, or have reported results of broad faunal surveys (Higginbotham and Jones 2001; Michael et al. 1970; Mirowsky et al. 2004; Packard 1966; Schmidly 1983, 1991; Schmidly et al. 1977; Thies 1994; Walker et al. 1996; Yancey and Jones 1996).

We are unaware of any previous studies focusing on the bat community of this ecosystem in Texas. Such a survey is essential and timely as the U.S. Forest Service lacks

detailed data about the bat assemblages in southeastern Texas (D. Jauregui, Sam Houston National Forest, personal communication), and National Wildlife Refuges located in Texas lack well-developed plans appropriate for bat conservation (Dixon et al. 2013). Bats in North America face many challenges due to habitat loss, white nose syndrome, and wind turbine collisions (Dixon et al. 2013); therefore, it is critical that such data are collected to enable development of conservation plans. In addition to compiling inventories, effective conservation plans require knowledge of how bats are using any given area. This demands identification of roost sites, including tree roosts for migrating bats, and maternity colonies and hibernacula (places, usually caves, where bats hibernate over winter), as well as understanding of reproductive patterns and success. Knowledge of timing of bat parturition and lactation is essential as many parts of the Texas pine forest are managed with prescribed burns, and direct smoke and heat exposure might be detrimental for bats (Rodrigue et al. 2001). Thus, the purpose of this study was to characterize the assemblage and investigate reproductive patterns of the summer bat community in the pine forest of eastern Texas.

Study Site

We conducted the study in Sam Houston National Forest, which is located in southeastern Texas and encompasses an area of 65,217 ha (Thomlinson 1995). This forest belongs to the Coastal Plains region of the southern forests, and is composed mostly of coniferous trees <80 years of age (87%), with only 1% of the stands containing trees >100 years of age (Azevedo et al. 2000). Approximately 35% of the forest is occupied either by pine plantations <20 y of age or by recent clear-cuts. The dominant pine is loblolly pine *Pinus taeda*, while shortleaf pine *Pinus echinata* is present in most of the

older stands and dominates some drier sites. Longleaf pine *Pinus palustris* occurs in mixed stands on the eastern side of the forest. A variable mixture of American sweetgum *Liquidambar styraciflua*, southern red oak *Quercus falcata*, post oak *Q. stellata*, white oak *Q. alba*, water oak *Q. nigra*, bluejack oak *Q. incana*, American beech *Fagus grandifolia*, and magnolia *Magnolia* sp. constitutes the canopy, with a well-developed midstory of hardwoods in unmanaged areas. Mixed hardwood forest occurs close to most drainages. At least eight forest-dwelling bat species are expected to summer in these forests (Ammerman et al. 2012; Schmidly 2004): Rafinesque's big-eared bat, big brown *Eptesicus fuscus*, eastern red bat *Lasiurus borealis*, northern yellow bat *L. intermedius*, Seminole bat *Lasiurus seminolus*, southeastern myotis, evening bat *Nycticeius humeralis*, and tri-colored bat *Perimyotis subflavus*.

Suitable mist-netting sites were scarce because most ponds were ephemeral, many drying out by mid-June. We conducted our sampling at two sites where ponds remained water-filled throughout the summer (June – August): Kelly Pond and Henry Lake Creek. Kelly Pond, in Montgomery County (30°30'37"N, 95°39'42"W), was approximately 36 m in diameter, and was surrounded by pine forest canopy except on one side that opened to a clearing. Henry Lake Creek was in San Jacinto County (30°32'31"N, 95°7'29"W), located approximately 55 km east of Kelly Pond. An access road crossed one of the branches of Henry Lake Creek at this site. The road interrupted water flow, forming a slow-moving pool of water similar in size to Kelly Pond. This road section had an open canopy, thus allowing bats to approach the pond, but otherwise was surrounded by dense hardwood canopy.

Methods

We collected field data during the summers of 2009-2011. At Kelly Pond we sampled with either three stacked mist nets (each 2.6 m high and 12 m wide; Avinet Inc., Dryden, NY) or a single large net (7.8 m high and 12 m wide) attached to a single triple-high net system (BatNets.com, Austin, TX). Both net arrangements presented equivalent surface areas. Sampling effort at Kelly Pond was six nights (40 netting-hours) in 2009, six nights (24 netting-h) in 2010, and four nights (23.5 netting-h) in 2011. We netted at Henry Lake Creek, using two triple-high net systems for nine nights (82.5 netting-h) in 2010, and a single triple-high net for four nights (24 netting-h) in 2011. During 2011, both sites were surveyed simultaneously.

We monitored mist nets continuously during all surveys. For each captured bat, we recorded species, age, mass, standard external measurements (lengths of body, forearm, tail, ear, tragus, and hind foot), and reproductive status. We identified each bat as adult or subadult by examining the epiphyseal–diaphyseal fusion of the fourth metacarpal–phalangeal joint (Anthony 1988). Individuals with opened joints were classified as subadults; individuals with closed joints were classified as adults. Furthermore, we determined reproductive status as pregnant, lactating or non-reproductive for females, and as reproductive (scrotal) or non-reproductive for males (Racey 1988). Bats were released within 1 hour of capture. We followed the Guidelines of the American Society of Mammalogists for the use of wild mammals (Gannon et al. 2007) and worked under protocol 10-05 approved by Baylor University Institutional Animal Care and Use Committee and Texas Parks and Wildlife scientific permit (SPR-0706-704).

Reported results represent the combined data sets for both sites for all sampling years (Table S1, Table S2). We computed the proportion of the overall bat community comprised by each species. Bats of each species were grouped according to gender, age and reproductive condition: pregnant females, lactating females, adult non-reproductive females, adult males, and subadults. We compared the reproductive phenology of our most-frequently-captured bat species in eastern Texas forests with reproductive timing in other locations where these species occur.

Results

We captured 382 bats representing eight species (Seminole, evening, big brown, eastern red, southeastern myotis, tri-colored, hoary *Lasiurus cinereus*, and Mexican free-tailed bats *Tadarida brasiliensis*) throughout our study (Table 2.1). During 2009, captures totaled 122 bats of all eight species. During 2010 we captured 136 bats comprising six species, all but hoary and Mexican free-tailed bats. The same six species were also captured during 2011 (124 bats; Table 2.1). Seminole bats dominated the assemblage at both sites in all sampling years, present in nearly twice the number of the next most common species, evening bats (Table 2.1). Together, Seminole and evening bats comprised 65.2% of the bats captured in our surveys. Big brown bats were third most common (13%), with the remaining five species accounting for the final 20% of captures. For Seminole and southeastern myotis, females represented the majority of the bats captured (62% and 67%, respectively), whereas males were in the majority for eastern red, evening, big brown, tri-colored, and Mexican free-tailed bats (67%, 62%, 60%, 58%, and 75%, respectively).

We captured 163 Seminole bats: 20 pregnant females, 34 lactating females, 20 non-reproductive females, 31 adult males, and 58 subadults (Table 2.1). Pregnant bats first appeared in samples during the last week of June and were present continuously through the end of July (Table 2.2). Lactating females, however, were captured nearly a month earlier than the first pregnant bats; lactating bats were present every week from the first sample in late May through the third week in July, a span of seven weeks. The earliest appearance of subadults in our samples was during the last week of June. Though not found in our samples for the first week of July, subadults comprised from half to nearly two-thirds of the samples through the first week of August, when our field seasons ended. Male and female subadults were captured in similar numbers (31 and 27, respectively). Adult males were uncommon in May and early June (only two captures), but their proportions increased from late June through early August, representing up to a quarter of the captures in subsequent weeks. Non-reproductive females were also uncommon, reaching their greatest proportion (26%) during the last week of sampling.

Of the 86 evening bats captured during the survey, adult males represented 60% of all adult evening bats captured, and were present in every weekly sample except for the first week of June (Table 2.1). Most of the males were captured in the last 2 wk of June. Pregnant females ($n = 22$) were captured throughout June and July but were most numerous 15 to 30 June (Table 2.2). Lactating females ($n = 5$) were captured only during a 3-wk interval in June (Table 2.3). Non-reproductive females ($n = 4$) were occasional captures during June, July, and August. Subadults ($n = 8$, all but one male) were captured from mid-June through late July, with 50% of subadults captured during the third week of June.

Males represented almost 58% of big brown bat captures ($n = 57$; Table 2.1). They were present in samples throughout the summer except for the first week of June. Pregnant females ($n = 18$) were captured May through July, and they represented the second most numerous group among big brown bats. The highest capture numbers of pregnant females were on 31 May and during the second week of June. Lactating females ($n = 4$) were only captured in the third week of June. Two male and two female subadults (mid-June) and one non-reproductive female (early August) were captured.

The remaining five species were captured in low numbers during this survey (Table 2.1). We captured 31 eastern red bats, with number diminishing over the three summers: 20 captures in 2009, 8 in 2010, and only 3 in 2011 (Table 2.1). Reproductive females (pregnant and lactating) were captured only during June when they dominated the sample. No non-reproductive adult females were captured. Adult males were captured occasionally throughout the summer. Subadults (all male) represented nearly one-third of captures, and almost all were captured in July of 2009.

Southeastern myotis ($n = 21$) were captured intermittently throughout the summer (Table 2.1). All adult females ($n = 10$) were reproductive. Only four adult males were captured. Subadults (four females and three males) were captured in mid-June. Tri-colored bats ($n = 19$) were captured during every month of sampling (May – August). Pregnant females ($n = 6$) were only captured during the third week of June. No lactating females were captured. Almost 58% of the tri-colored bats captured were adult males. Both subadults were females. Mexican free-tailed ($n = 4$) and hoary ($n = 1$) bats were captured only during summer 2009 (Table 2.1). We captured one Mexican free-tailed bat

(male) on 24 July, three Mexican free-tailed bats (all females) on 7 August, and a single female hoary bat on 12 June.

Discussion

Bat Community Assemblage

Our two pond sites appeared representative of the expected bat community assemblage in Sam Houston National Forest, because we captured all six bat species expected to be present during summer in this type of habitat (big brown, eastern red, Seminole, southeastern myotis, evening, and tri-colored bat). The few other bat species occurring in eastern Texas have habitat requirements not widely present in Sam Houston National Forest. Rafinesque's big-eared bats are known in easternmost Texas (Schmidly 2004) but are rare (Mirowsky et al. 2004; Ammerman et al. 2012); they prefer to roost in hollow water tupelo *Nyssa aquatica* trees (Gooding and Langford 2004) in bottomland hardwood forests (Mirowsky et al. 2004). Northern yellow bats prefer roosting either in Spanish moss *Tillandsia usenoides* hanging from oaks or in palm groves (Webster et al. 1982). Areas broadly surrounding our netting sites lacked tupelo, Spanish moss, and palm groves; thus, we did not expect to find these two bat species in our samples.

Cumulatively, at least nine species of bats have been documented in southeastern forests, with a maximum of eight species found at any particular site (Table 2.3). At least two of these species (evening and tri-colored bats) occur in every sampled community. Their abundance in communities varied substantially, ranging from as high as 28% for both species to as low as 2.8% for evening bats and 1.4% for tri-colored bats, respectively. Eastern red bats, or eastern red-Seminole calls, were also documented in all

of the studies. Abundance of eastern red bats in communities also varied widely. Big brown, southeastern myotis, and hoary bats were documented in five of the seven studies even though both big brown and hoary bats have distributions across the most of the United States (Wilson and Ruff 1999). Hoary bats have been previously reported in southeastern Texas (Schmidly 1994, Ammerman et al. 2012), but they usually only winter in Texas and migrate north for summer. Even though hoary bats were reported in five of seven studies (Table 3), this species was always in low abundance, never constituting >4.3% of the community. Southeastern myotis was not found in the North Carolina study (Morris et al. 2010), which is not surprising as its known distribution extends only into the southern corner of this state (Wilson and Ruff 1999).

Unexpectedly, presence of Seminole bats was confirmed in only three studies other than ours - those conducted in Mississippi (Miller 2003, Welch 2003) and Alabama (Kilgore 2008). In these studies, the Seminole bat was usually the most numerous member of the community with captures ranging from 29% to 42%. The geographic range of Seminole bats extends into North Carolina and Arkansas but the studies conducted there did not report this species' presence.

Mexican free-tailed bats were captured in only two studies - ours (Texas) and Morris et al. (2010; North Carolina), though their range extends into all of the states reported in Table 2.3. The absence of Mexican free-tailed bats in most studies is understandable as these are not considered to be tree-roosting bats; rather, they roost primarily in caves and man-made structures (Schmidly 2004; Ammerman et al. 2012). Some man-made structures (bridges and sheds) are available as potential roosting sites for Mexican free-tailed bats in the vicinity of Kelly Pond site, but we found no occupied

roosts. The nearest caves known to serve as roosts for Mexican free-tailed bats are in the Hill Country of Central Texas, (e.g., Bracken Cave, approximately 320 km from Sam Houston National Forest).

Reproductive Phenology

Our surveys yielded samples of adequate size and temporal coverage to enable consideration of reproductive patterns for several of the study species. Our findings offer new insights for patterning in three species—Seminole, evening and big brown bats. Annual patterns and synchrony of reproduction in bats relate to annual and seasonal climate cycles (Racey and Entwistle 2000). Availability of food resources is one of the main factors affecting timing of parturition (Arlettaz et al. 2001). Insectivorous bats living in temperate zones tend to compress their reproductive activities within summer and fall, corresponding to seasons when insect availability and temperatures are high (Racey and Entwistle 2000). Reproductive cycles of these bats progress as follows: during fall, gametogenesis and mating occur; during winter, development is suspended as most temperate bat species hibernate; during spring, gestation is stimulated by arousal from hibernation; during mid-summer, parturition occurs; and during mid and late summer, lactation occurs (Racey and Entwistle 2000). Due to climatic constraints (mainly temperature and rainfall) which directly impact food availability, most temperate bats are synchronously monoestrous, having one litter per year born during a constrained time period in summer. By comparison, tropical bat species show a wider range of reproductive patterns, including seasonal monoestry, seasonal polyestry, and aseasonal polyestry (Racey and Entwistle 2000).

Extended seasonal monoestry, known in tropical African bat species (Racey and Entwistle 2000), is a strategy with births of single litters spanning a particular season. In such cases, births might extend over a longer period of time than in typical seasonal monoestry as seen for most temperate bat species. It could be beneficial for temperate species to adopt this reproductive pattern in regions where winters are not severe and warm temperatures dominate most of the year. None of the species present in Texas have been reported previously to produce multiple litters (Ammerman et al. 2012), and are not expected to have them as multiple litters are usually present only in areas with multiple rainfall seasons (Racey and Entwistle 2000). However, asynchrony in reproduction might still be beneficial as it might reduce competition for resources (roosts and food) among reproductive females (both pregnant and lactating) and fledglings.

Shifts in the timing of parturition and lactation in most vespertilionid (family Vespertilionidae) bat species have been reported in relation to latitude (Cockrum 1955). Cockrum (1955) also noted that, in vespertilionid bats from temperate climates, it is possible to induce earlier ovulation (and earlier parturition as a consequence) by moving female bats from hibernation into warm laboratories. The reproductive timing of three vespertilionids in our study (i.e., Seminole, evening, and big brown bats) all differed from that previously reported in the literature. We documented an extended season of parturition and lactation lasting ≥ 3 mo, approximately 1 mo longer than previously observed elsewhere. Seminole bats have been considered synchronous breeders, with pregnancy occurring during May and June, and lactation occurring mostly from late May until late June (Cockrum 1955; Jennings 1958; Schmidly 2004; Wilkins 1987). However, we captured lactating females 31 May–21 July, and pregnant females as late as 31 July.

Among past studies concerning the reproductive patterns for Seminole bats, only Miller (2003) reported pregnancy extending into July (mid-July in Mississippi). Given this, our results suggest extended intervals of parturition and lactation that are not as synchronous as previously understood. However, due to lack of data from April and early May, we are uncertain whether parturition in Seminole bats might occur continuously throughout the summer, or if it is completely asynchronous and occurring in multiple waves (for example, one in early May, next in July, etc.).

According to Schmidly (2004), evening bats in Texas give birth in late May and early June. However, in Presidio County, Texas, Dowler et al. (1999) captured a juvenile female on 20 April, suggesting an earlier parturition date (late March or early April). In contrast, pregnant females were captured in Ohio from late April until the end of June (Cockrum 1955) and, in Arkansas, a single pregnant bat was captured on 12 May (Perry et al. 2010). Watkins (1969) reported capture of pregnant evening bats in Missouri on 8 July. We captured pregnant evening bats as early as 1 June and as late as 21 July, and lactating females throughout June, suggesting pregnancy may be more prolonged than reported by Schmidly (2004).

We captured pregnant big brown bats 31 May through 19 July, and lactating females throughout June. Ammerman et al. (2012) reported that parturition in big brown bats in Texas occurs May-June, and lactation continues through July. Thus, our study suggests that Seminole, evening, and big brown bats in southeastern Texas, might have a longer reproductive season than documented for these species elsewhere.

Acoustic surveys conducted in our study area during the November-March period confirm year-around bat activity, although activity levels were lower during winter

compared with summer (Pettit 2011). In southeastern Texas, average temperatures fall below 16 °C (60 °F) only from mid-November to mid-March. During this 4-mo period, nighttime temperatures are often above 4 °C (45 °F) and daytime temperatures tend to approach or exceed 16 °C (60 °F; National Weather Service Forecast Office 2012). This thermal regime might allow bats to enter torpor rather than hibernation (the latter strategy generally followed by bats in colder winters of higher latitudes in the United States). The pattern of warm temperatures and high humidity during summer, enabled by geographic proximity of the Gulf of Mexico, could allow insect populations to prosper from early spring through late autumn, which would likely provide bats with food resource over a longer period than for these species at higher latitudes. As a consequence, parturition in females need not be restricted to a brief interval in mid-summer, but could potentially extend asynchronously through much of the summer. Furthermore, Wear and Greis (2012, 2013) indicated that all predictive models for southern U.S. forests predict temperature increase. It is possible that earlier parturition might be driven in the future, if not already, by global warming.

Our study was conducted near the westernmost extent of the partially managed pine-forest ecosystem that characterizes vast expanses of the southeastern United States. Though we sampled only two sites, this investigation provides the initial report of the bat community assemblage in southeastern Texas. Further, this study provides data revealing reproductive patterns not previously reported for several species found in Sam Houston National Forest. Findings provide limited evidence suggesting that three bat species deviate from synchronous monoestry (the reproductive pattern typical of insectivorous bat species in the temperate zone) in favor of extended seasonal monoestry more often

seen in tropical bat species. We anticipate that these reproductive adaptations might pertain to these species, and perhaps others, widely across the coastal plain of the southeastern United States. Study of historic natural-history records associated with museum specimens and additional studies conducted in similar forests in other states where the influence of the Gulf of Mexico can be felt will be key to evaluating these predictions. Additional studies of this sort will help in obtaining the data needed to formulate comprehensive conservation plans for tree-roosting bats in southeastern Texas and other parts of the austroriparian province.

Supplemental Material

Table S1. Bat capture data collected in Sam Houston National Forest, Texas, at Kelly Pond site over three summers (2009-2011). Table includes bat identification numbers, species, gender (M – male, F – female), reproductive state (R – reproductive, NR – non-reproductive, L – lactating, and P – pregnant), and age (A – adult, or SA – subadult). Species were assigned four letter designations as follows: LABO (*Lasiurus borealis* – eastern red bat), LASE (*L. seminolus* – Seminole bat), LACI (*L. cinereus* – hoary bat), EPFU (*Eptesicus fuscus* – big brown bat), NYHU (*Nycticeius humeralis* – evening bat), MYAU (*Myotis austroriparius* – southeastern myotis), PMSU (*Perimyotis subflavus* – tri-colored bat), TABR (*Tadarida brasiliensis* – Mexican free-tailed bat).

Table S2. Bat capture data collected in Sam Houston National Forest, Texas, at Henry Lake Creek site over two summers (2010-2011). Table includes bat identification numbers, species, gender (M – male, F – female), reproductive state (R – reproductive, NR – non-reproductive, L – lactating, and P – pregnant), and age (A – adult, or SA – subadult). Species were assigned four letter designations as follows: LABO (*Lasiurus*

borealis – eastern red bat), LASE (*L. seminolus* – Seminole bat), LACI (*L. cinereus* – hoary bat), EPFU (*Eptesicus fuscus* – big brown bat), NYHU (*Nycticeius humeralis* – evening bat), MYAU (*Myotis austroriparius* – southeastern myotis), PMSU (*Perimyotis subflavus* – tri-colored bat), TABR (*Tadarida brasiliensis* – Mexican free-tailed bat).

Reference S1. Wear DN, Greis JG, eds. 2012. The Southern Forest Futures Project: summary report. Gen. Tech. Rep. SRS-GTR-168. Asheville, NC: USDA-Forest Service, Southern Research Station. 54 p. Available: <http://www.treesearch.fs.fed.us/pubs/42526> (June 2014).

Reference S2. Wear DN, Greis JG, eds. 2013. The Southern Forest Futures Project: technical report. Gen. Tech. Rep. SRS-GTR-178. Asheville, NC: USDA-Forest Service, Southern Research Station. 542 p. Available: <http://www.treesearch.fs.fed.us/pubs/44183> (June 2014).

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Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Table 2.1. (Table 1 in Debelica-Lee and Wilkins). Summertime bat community composition in Sam Houston National Forest, Texas over a 3-y period (2009-2011). Tabular values report numbers of bats captured by species, site, and year. Capture totals show total number of bats captured at each site by year. Total and percentage columns show cumulative numbers for each species across the whole study.

Bat species	Kelly Pond			Henry Lake Creek			Total	Percentage
	2009	2010	2011	2010	2011			
Seminole	47	24	19	40	33	163	42.7	
Evening	28	6	18	13	21	86	22.5	
Big brown	13	0	2	31	11	57	14.9	
Eastern red	20	6	2	2	1	31	8.2	
Southeastern myotis	3	0	2	10	6	21	5.5	
Tri-colored	6	1	5	3	4	19	5.0	
Mexican free-tailed	4	0	0	0	0	4	1.0	
Hoary	1	0	0	0	0	1	0.3	
Capture Totals	122	37	48	99	76	382	100	

Table 2.2. (Table 2 in Debelica-Lee and Wilkins 2014). Presence of pregnant (P) and lactating (L) Seminole (*Lasiorus seminolus*), evening (*Nycticeius humeralis*), and big brown (*Eptesicus fuscus*) female bats during summertime sampling over a 3-year period (2009-20011) in Sam Houston National Forest, Texas.

		May					June					July										
Bat Species		31	5	7	12	14	16	17	19	21	23	24	26	5	8	12	14	15	19	21	24	26
Seminole											P			P	P	P	P	P				P
		L		L	L			L	L	L		L	L		L			L				
Evening			P		P			P			P	P	P		P				P			
					L							L	L									
Big brown		P	P	P	P			P	P					P	P	P	P		P			
								L		L												

Table 2.3. (Table 3 in Debelica-Lee and Wilkins 2014). Composition of bat communities of southeastern U.S. pine forests documented during summers 2009-2011 in our study (Sam Houston National Forest, TX) and in literature. Table includes type of data collected (captured bats, acoustic sampling), state where study was conducted, total number of bats captured/calls recorded, total number of species, and percentages for each species in respective studies.

Study	Our study	Morris et al. (2010)	Morris et al. (2010)	Kilgore (2008)	Ford et al. (2006)	Miller (2003)	Welch (2003)
Type of data	Bats	Calls	Bats	Bats	Calls	Bats	Bats
State	TX	NC	NC	AL	SC	MS	MS
Total numbers	382	6236	142	174	3251	284	163
Number of species	8	7	5	7	6/7	6	4
Seminole bat	42.8	---	---	29.2	---	16.7	39.3
Evening bat	22.1	2.8	28.2	18.3	11	19.7	27.6
Big brown bat	15.3	24.4	14.1	---	4.8	---	---
Eastern red bat	7.9	60	55.6	12.5	---	53.5	25.1
Southeastern myotis	5.6	---	---	8.5	4.7	0.4	---
Tri-colored bat	5.0	2.6	1.4	28.1	14.6	9.3	8
Mexican free-tailed bat	1.0	8.4	---	---	---	---	---
Hoary bat	0.3	4.3	---	1.1	3.4	0.4	---
Rafinesque's big-eared bat	---	---	0.7	2.3	---	---	---
Eastern red/Seminole bat	---	---	---	---	45.9	---	---
Unknown <i>Myotis</i> spp.	---	1.5	---	---	---	---	---
Unknown bat species	---	---	---	---	15.6	---	---

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CHAPTER THREE

Ecomorphology and Community Structure of Bats in Managed and Unmanaged Texas Pine Forest

Introduction

Managed pine forests dominate the southeastern United States, with a total area of 12.9 million ha in 1999, and are expected to expand to 21.8 million ha by 2040 (Elmore et al. 2005; Miles et al. 2006). These forests, which account for 60% of the timber production in United States (Morris et al. 2010), are often managed by using even-aged systems with short rotations (Hein et al. 2009).

Before European settlement, fires set by Native Americans shaped and maintained most of the western portion of North America's eastern deciduous forest (Boyles and Aubrey 2005). Today, prescribed fires play an important role in restoration of forest ecosystems to their natural state as well as their maintenance, through reduction of understory competition (Boyles and Aubrey 2005; Lacki et al. 2009) and reduction of fuel loads that accumulate during fire-suppression (Lacki et al. 2009). Fires may lead to either positive or negative changes of habitat for birds (Miller and Conner 2007) and mammals (Chamberlain et al. 2002; Lacki et al. 2009). Prescribed burns are used to maintain habitat preferred by red-cockaded woodpeckers (*Picoides borealis*; Rudolph and Conner 1994; Thomlinson 1995; Azevedo et al. 2000; Ford et al. 2002). Fires can cause tree mortality (Aubrey 2004; Boyles and Aubrey 2005) and cavity formation (Aubrey 2004) and thereby promote an increase in roost availability for forest bats (Kurta et al. 1993; Brigham et al. 1997). A previous study has determined that certain bat species

extensively use stands that have been actively treated with fire (e.g., Boyles and Aubrey 2005). Yet, despite the benefits of prescribed burns, direct smoke and heat exposure might be detrimental for bats (Rodrigue et al. 2001).

Bats play a key role in forest ecosystems as nocturnal predators (Miller 2003; Rainho et al. 2010). Habitat degradation and loss represent the greatest threats to bat populations worldwide (Racey and Entwistle 2003; Lacki and Baker 2007). For forest bats, trees serve as day and night roosts, maternity colonies, and hibernacula (Fenton 1997; Hein et al. 2008b). Many studies have shown that roost selection is based on physical properties of the roosting space (Kalcounis and Brigham 1998; Foster and Kurta 1999; Cryan et al. 2001; Baker and Lacki 2006), and that the roost choice is limited by roost availability at local and larger geographic scales (Baker and Lacki 2006). For this reason, researchers emphasize the importance of maintaining various types of snags within managed forests (Baker and Lacki 2006; Arnett and Hayes 2009). Because prescribed burning tends to create or restore favorable cavity-dwelling bat habitat and maintain an open sub-canopy, it might be used as an effective tool for management of roosting habitat for cavity-roosting bats (Boyles and Aubrey 2005), much as it is used for managing habitat for red-cockaded woodpeckers. Additionally, heterogeneity within the forests (presence of old and young trees) and presence of corridors provide sources of insect prey, navigational references, shelter from wind, protection from predators, and roosting sites (Russo et al. 2007; Hein et al. 2008b; Perry and Thill 2008; Perry et al. 2008; Hein et al. 2009).

Fires also can alter forest communities of insects, the food resource of bats in the southeastern pine forests, positively (Coleoptera) or negatively (Lepidoptera) for long

periods of time (Buddle et al. 2006; Moretti et al. 2006; Armitage and Ober 2012). In addition to altering food availability, fire management can impact foraging activity of bats by reducing clutter in forests. Clutter can be defined as background objects, mainly vegetation, which constrains bats' flight and echolocation (Law and Chidel 2002). Based on wing shape and echolocation calls, insectivorous bats can be divided into clutter-sensitive and clutter-tolerant species. Bats with long thin wings (high aspect ratio and high wing loading) and low echolocation call frequencies are less maneuverable, so they have difficulty flying through cluttered, complex habitats and mostly forage in open habitats. Such bats are considered clutter-sensitive species (Norberg and Rayner 1987; Fenton 1990; Loeb and O'Keefe 2006; Loeb and Waldrop 2008; Armitage and Ober 2012). Conversely, bats with low aspect ratio, low wing loading and high-frequency echolocation calls can better maneuver in clutter, so they could forage within the forests as well as in open areas (Norberg and Rayner 1987; Fenton 1990; Loeb and O'Keefe 2006; Loeb and Waldrop 2008; Armitage and Ober 2012). Ecomorphology, or the relationship between wing shapes and echolocation calls, helps predict which of our study species would likely be found in managed forests (reduced clutter) and/or unmanaged forests (high amounts of clutter).

Effects of management practices on bats have been studied with regard to roost availability and selection (e.g., Boyles and Aubrey 2005; Baker and Lacki 2006; Miles et al. 2006; Hein et al. 2008a, b; Perry and Thill 2008; Hein et al. 2009) and in relation to habitat use (Law and Chidel 2002; Elmore et al. 2005; Loeb and Waldrop 2008; Lacki et al. 2009; Morris et al. 2010; Rainho et al. 2010). However, few studies have examined effects of management practices on bat community structure from the perspective of

ecomorphology (Armitage and Ober 2012). Our study investigates effects of management practices on bat community structure by examining the differences in the bat community between managed and unmanaged areas of Sam Houston National Forest, Texas, and by examining the role of ecomorphology in these differences. We predicted that bat species with high wing loading, high aspect ratio and low echolocation call frequencies would occur predominantly in managed, uncluttered parts of the forests, whereas bat species with low aspect ratio, low wing loading, and higher echolocation calls would be more common in unmanaged, more cluttered areas.

Materials and Methods

Study Site

Sam Houston National Forest (SHNF), Texas, located in southeastern Texas, covers an area of 65 217 ha (Thomlinson 1995). The U.S. Forest Service manages the western part of the forest for red-cockaded woodpeckers by thinning, midstory reduction, and prescribed burns (3-year rotations), and by even-aged planting and regeneration of loblolly pine (*Pinus taeda*) stands (Rudolph and Conner 1994). Areas without active red-cockaded woodpecker clusters (primarily eastern part of the forest) are mostly unmanaged.

SHNF is composed mostly (87%) of new growth loblolly pine plantations (Azevedo et al. 2000) and a small proportion of old growth shortleaf pine (*P. echinata*). A mixture of hardwoods, including American sweetgum (*Liquidambar styraciflua*), southern red oak (*Quercus falcata*), post oak (*Q. stellata*), white oak (*Q. alba*), water oak (*Q. nigra*), bluejack oak (*Q. incana*), American beech (*Fagus grandifolia*), and magnolia

(*Magnolia* spp.), as well as longleaf pine (*P. palustris*), represent the majority of trees in eastern part of SHNF (U.S. Department of Agriculture 2008). These mixed hardwoods closely follow most drainages and dominate riparian areas.

We conducted our study at two sites: Kelly Pond (KP), the managed site, in Montgomery Co. (latitude 30°30'36.99"N; longitude 95°39'41.96"W), and Henry Lake Creek (HLC), in San Jacinto Co. (latitude 30°32'31.14"N; longitude 95° 7'29.32"W). The most recent burn at the KP site was 3 months before our study started in 2009, while the HLC site area had not been burned for over 30 years. At the KP site, uncluttered new-growth pine forest surrounded the pond and formed an opening on one side of the pond toward a clearing. Bats actively used this opening to approach the pond, so we placed our mist nets across this opening. At HLC, a low-water crossing created a slow-moving pool of water surrounded by cluttered old-growth mixed hardwoods and shortleaf pine forest. Bats actively used the low-water crossing to approach the pool of water, so we used our nets to close that approach. At HLC, we also used one net across the service road (about 100 m west from the first net) as bats were also using this road as a flight corridor towards the pool of water.

Data Collection

We collected data during the summers of 2009, 2010, and 2011. During summer 2009, we netted at KP over 6 nights for total of 40 netting hours. Each night, we deployed a triple-high netting system (7.8 m high and 12 m wide, BatNets.com) before sunset and kept it opened for as long as bats were active. We netted for 5-9 hours nightly depending on bat activity at the site. We closed nets one hour after the last bat was captured if we could not detect any more bat activity in the area. We used an Anabat SD1 bat detector

(Titley Scientific, Australia) to confirm that bat activity at the site had ceased. During summer 2010, we netted in the same manner as during summer 2009 at Kelly Pond for 6 nights with total of 24 netting hours. Finally, we repeated our netting procedures in summer 2010 for 6 nights (24 netting hours), and in summer 2011 for 4 nights (23.5 netting hours). During summer 2010, we netted at the unmanaged site, HLC, for 10 nights (82.5 netting hours). During summer 2011, we netted for 4 nights (total of 24 netting hours) at HLC with a single triple high net at the edge of water. During 2011, sampling at both sites was conducted simultaneously with separate crews of investigators.

We tended nets continuously and checked them for bats every few minutes. For each captured bat, we recorded species and placed bats into individual holding cups. After 30-45 min, we removed each bat from its cup and recorded age (adult or subadult), reproductive state (pregnant, lactating, reproductive, non-reproductive), mass, total length, tail length, forearm length, ear length, and tragus length. We took digital photographs of bat wings for subsequent measurement in lab. Each bat was placed with wings outstretched on a platform apparatus with light shining from below the bat through a semi-transparent surface, and with a Lumix DMC-z3 digital camera (Panasonic, Japan) mounted above the bat. In lab, photographs were processed using Fiji open source software. Based on Norberg and Rayner (1987), we measured wingspan (B , in m) and wing area (S , in m^2). Using Excel, we calculated final wing parameters, aspect ratio ($A = B^2/S$) and wing loading (Mg/S in Nm^{-2} where M is mass and g is gravitational force), from the recorded measurements.

We used an Anabat SD1 bat detector to record echolocation calls as bats flew along a zipline (Szewczak 2000) or as they were hand-released. To reduce stress, calls of

pregnant females were only recorded from hand release. Bat echolocation sequences with 3 or more call pulses were evaluated for completeness of each call pulse using the RANOISE filter in ANALOOK (v.4.9j 2004). Complete call pulses were further examined with the following parameters extracted for statistical analysis: characteristic frequency (F_c), duration (d), and characteristic slope (S_c). Only complete call pulses were used in order to limit the effects of feeding behavior, echo, and other environmental interference on the analysis.

We followed the Guidelines of the American Society of Mammalogists for the use of wild mammals (Gannon et al. 2007). We worked under Texas Parks and Wildlife scientific permit (SPR-0706-704) and a protocol approved by Baylor University Institutional Animal Care and Use Committee (number 10-05).

Statistical Analysis

All data were analyzed using R (R Development Core Team 2014). Because we had uneven sampling among the years and sites, we converted all of our bat capture numbers into numbers of bats captured per 100 netting hours (Table 3.1). We used chi-square (χ^2) analysis to determine if there were differences in bat community structure for each site among the years (year effect), and if there were differences in bat community structure between the sites (site effect). Because we captured only four Mexican free-tailed bats and one hoary bat (all at Kelly Pond in summer 2009), we excluded these bats from the analysis. We used MANOVA to test for differences among species for echolocation attributes. Preliminary analysis (scatter plot and Box M test) determined that only mean call duration and mean characteristic frequency were not correlated with other call attributes and thus could be used in statistical analysis. Finally, we used ANOVA to

test for differences in wing characteristics among the bats. Aspect ratio data lacked normality, so we log-transformed it. After transformation, aspect ratio data was normal and we were able to use ANOVA for analysis. In cases where statistical differences were found among the bats, we used Tukey's multiple comparison test (*post-hoc*) to determine where the differences were.

Results

We captured a total of 380 bats belonging to 8 species (Table 3.1): *Lasiurus seminolus* (Seminole bat), *L. borealis* (eastern red bat), *L. cinereus* (hoary bat), *Nycticeius humeralis* (evening bat), *Eptesicus fuscus* (big brown bat), *Perimyotis subflavus* (tricolored bat), *Myotis austroriparius* (southeastern myotis), and *Tadarida brasiliensis* (Mexican free-tailed bat).

Chi-square analysis showed that there was a "year" effect for each site ($\chi^2 = 15.59$, $df = 5$, $P = 0.0081$ for HLC site; $\chi^2 = 97.47$, $df = 10$, $P < 0.0001$ for KP site). At HLC site (Table 3.1), smaller bat species such as evening, tricolored, and southeastern myotis bats, were captured at higher rates during summer 2011 than during 2010. At KP site, during summer 2010, we saw the lowest capture rates for all bat species except for Seminole bats. In addition, numbers of captured eastern red bats at KP and HLC sites declined over 3 years of netting from 17.8% to 16% to 4% of bat captures at KP, and from 2% to 1% of captures at HLC (Table 3.2).

Table 3.1. Number of bat captures and captures per 100 netting hours (in parentheses) by site and year, Sam Houston National Forest, Texas. KP denotes Kelly Pond, and HLC denotes Henry Lake Creek.

Bat species	Site, Year, and Hours of Sampling				
	KP2009 (40 h)	KP2010 (24 h)	KP2011 (23.5 h)	HLC2010 (82.5 h)	HLC201 (24 h)
<i>Lasiurus seminolus</i>	47 (118)	24 (100)	19 (81)	40 (48)	33 (138)
<i>Lasiurus borealis</i>	20 (50)	6 (25)	2 (9)	2 (2)	1 (4)
<i>Lasiurus cinereus</i>	1 (3)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Nycticeius humeralis</i>	18 (45)	6 (25)	18 (77)	21 (25)	21 (88)
<i>Eptesicus fuscus</i>	13 (33)	0 (0)	2 (9)	31 (38)	11 (25)
<i>Perimyotis subflavus</i>	6 (15)	1 (4)	5 (21)	3 (4)	4 (17)
<i>Myotis austroriparius</i>	3 (8)	0 (0)	2 (9)	10 (12)	6 (25)
<i>Tadarida brasiliensis</i>	4 (10)	0 (0)	0 (0)	0 (0)	0 (0)
Totals	112 (280)	37 (154)	48 (204)	107 (130)	76 (317)

Chi-square tests also showed that there was a “site” effect for each year ($\chi^2 = 86.33$, $df = 5$, $P < 0.0001$ for 2010; $\chi^2 = 27.66$, $df = 5$, $P < 0.0001$). In 2010 (Table 3.2), Seminole bats (65% of all captures) dominated the KP site, while eastern red (16%) and evening (16%) bats were the second most abundant species. Big brown (0%), tricolored (3%), and southeastern myotis (0%) bats were either not captured or were captured very infrequently. At HLC site, Seminole bats (37% of all captures) dominated the community, but the 2nd most abundant species was big brown (29%), followed by evening (20%) bats. Southeastern myotis (9%) was the 4th most abundant species, while we captured few eastern red (2%) and tricolored (3%) bats. In 2011 (Table 3.2), Seminole (40%) bats dominated KP, closely followed by evening (38%) bats. The tricolored bat (10%) was the 3rd most abundant bat species, while eastern red (4%), big brown (4%),

and southeastern myotis (4%) bats were much less common. Seminole bats (43%) dominated the HLC site, while evening bats (28%) were 2nd most abundant. Big brown (14%) bats were 3rd, southeastern myotis (8%) 4th, and tricolored bats (5%) were the 5th most abundant species. Eastern red bats (1%) were the least frequently captured species at HLC in 2011.

Table 3.2. Percentages of bat species captured at Kelly Pond (KP) and Henry Lake Creek (HLC), Sam Houston National Forest, Texas, during 2010 and 2011.

Bat Species	2010		2011	
	KP	HLC	KP	HLC
<i>Lasiurus seminolus</i>	65	37	40	43
<i>Lasiurus borealis</i>	16	2	4	1
<i>Nycticeius humeralis</i>	16	20	38	28
<i>Eptesicus fuscus</i>	0	29	4	14
<i>Perimyotis subflavus</i>	3	3	10	5
<i>Myotis austroriparius</i>	0	9	4	8

Wing dimensions were determined for 6 of the species captured in the field (Table 3.3). Two classes of body size, as indicated by forearm length, were evident. Three species (big brown, Seminole, and eastern red bat) had forearm lengths of 40 - 46 mm, whereas the others (evening, tricolored, and southeastern myotis) had forearm lengths of <35 mm. Three classes of aspect ratios were represented: >8 (tricolored bat), between 7 and 8 (big brown, eastern red, Seminole, and evening bat), and <7 (southeastern myotis). Based on wing loading, 3 groups of bats were evident: High wing loading (>10 Nm⁻²) was found in big brown and evening bats, medium wing loading (7 - 10 Nm⁻²) in

Seminole, eastern red, and tricolored bats, and low wing loading ($<6 \text{ Nm}^{-2}$) in southeastern myotis.

ANOVA demonstrated significant differences in mean forearm length ($F = 104.54$, $df = 5$, $P < 0.0001$). Tukey's multiple comparison test (*post-hoc*) segregated bats into three distinct groups. The big brown bats (largest mean forearm length) were placed in their own group. Seminole and eastern red bats were grouped together as mid-sized bats by mean forearm length. Finally, evening, tricolored, and southeastern myotis clustered together in third group as the smallest bats. Furthermore, ANOVA demonstrated significant differences in mean aspect ratio ($F = 3.12$, $df = 5$, $P = 0.0097$). Tukey's multiple comparison test (*post-hoc*) placed 6 bat species into 2 overlapping groups (A and B). Tricolored, Seminole and evening bats had the highest mean aspect ratios (>7.7) and were all placed together into group A. Southeastern myotis had the lowest mean aspect ratio (<7.0) and was placed in group B. Big brown and eastern red bats were, as intermediates ($7.0 - 7.7$) in mean aspect ratio, placed in both group A and B.

ANOVA demonstrated significant differences in mean wing loading among bat species ($F = 27.88$, $df = 5$, $P < 0.0001$). Tukey's multiple comparison (*post-hoc*) test generated complex matrix with 4 overlapping groups to which we are referring here as groups A, B, C, or D. Big brown bats had the greatest mean wing loading ($>12 \text{ Nm}^{-2}$) and were placed alone in group A. Next, evening bats had the second highest mean wing loading (approximately 10 Nm^{-2}) and were assigned to group B. Group C comprised of Seminole bats (approximately 9 Nm^{-2}), eastern red bats (approximately 8 Nm^{-2}), and tricolored bats ($6 - 8 \text{ Nm}^{-2}$). Although Seminole bat's mean wing loading falls between

evening and eastern red bats, the large number of Seminole bats ($n = 51$) resulted in a standard error for the difference in mean wing loading between Seminole and evening bats ($n = 17$) small enough that the two species' mean wing load was significant; a similar statement can be made for the difference in the mean wing loading between Seminole and eastern red bats ($n = 5$). Lastly, tri-colored bats were also placed along with southeastern myotis bats (the lowest mean wing loading of all bat species, $< 6 \text{ Nm}^{-2}$) into group D. Pregnancy did not significantly impact mean wing loading in captured bats (ANOVA, $F = 1.05$, $df = 1$, $P = 0.31$).

Table 3.3 Descriptive statistics (mean + SD) for body size and wing characteristics for six species of bats studied at Sam Houston National Forest, Texas.

Species	Body Mass (g)	Forearm Length (mm)	Wingspan (mm)	Wing area (m^2)	Aspect Ratio	Wing Loading (Nm^{-2})
<i>Lasiurus seminolus</i>	9.92±1.71	40.84±2.04	289.12±24.16	0.011±0.002	7.78±1.03	9.09±1.86
<i>Lasiurus borealis</i>	9.31±1.07	40.29±1.80	279.43±18.75	0.011±0.002	7.65±1.82	8.83±1.47
<i>Nycticeius humeralis</i>	8.20±1.36	34.73±2.25	247.17±28.31	0.008±0.002	7.79±1.24	10.40±2.41
<i>Eptesicus fuscus</i>	16.00±0.28	45.84±3.87	304.99±31.48	0.013±0.002	7.44±0.70	12.72±2.14
<i>Perimyotis subflavus</i>	5.55±1.61	33.90±2.13	237.95±14.36	0.007±0.002	8.27±1.44	7.79±1.80
<i>Myotis austroriparius</i>	4.40±1.49	33.70±2.16	228.08±13.14	0.008±0.001	6.77±0.75	5.48±1.61

Based on mean characteristic call frequency, bats were placed into three groups: high mean characteristic frequency ($>40 \text{ kHz}$) with Seminole and eastern red bats; medium mean characteristic frequency (38 - 40 kHz) with southeastern myotis and big brown bat; and low mean characteristic frequency ($<37 \text{ kHz}$) with tricolored and evening bats (Table 3.4). In addition, bats fell into 2 groups based on mean call duration: $\geq 5 \text{ ms}$

(southeastern myotis, tricolored, evening bats) or <5 ms (big brown, Seminole, eastern red bats; Table 3.4). Due to small samples ($n \leq 6$), we eliminated tricolored, southeastern myotis and red bats from further analyses (Table 3.4). Using MANOVA we determined that there was significant difference between the remaining three species for mean characteristic frequency and mean duration ($NumDF = 2$, $DenDF = 62$, $P < 0.0001$).

Table 3.4 Descriptive statistics (mean + SD) for echolocation call characteristics for six species of bats studied at Sam Houston National Forest, Texas.

Bat Species	N	Mean Characteristic Frequency (kHz)	Mean Call Duration (ms)
<i>Lasiurus seminolus</i>	36	41.54±5.55	4.27±1.46
<i>Lasiurus borealis</i>	4	40.90±2.86	4.32±1.64
<i>Myotis austroriparius</i>	6	38.70±5.90	5.66±1.41
<i>Eptesicus fuscus</i>	15	38.01±3.68	4.45±1.27
<i>Perimyotis subflavus</i>	2	36.72±0.48	5.10±2.11
<i>Nycticeius humeralis</i>	15	35.90±7.42	5.99±2.13

Mean characteristic frequencies were 41.52 kHz, 38.00 kHz, and 36.74 kHz for Seminole, big brown, and evening bats, respectively. There was significant difference between mean characteristic frequency values of Seminole and evening bats (Tukey-Kramer test, $df = 62$, $P = 0.0206$), but no difference between mean characteristic frequency values for Seminole and big brown or between evening and big brown bats (Tukey-Kramer test, $df = 62$, $P = 0.1019$; $df = 62$, $P = 0.8119$, respectively). Mean duration of calls was 5.93 ms, 4.44 ms, and 4.27 ms for evening, big brown, and

Seminole bats respectively. Mean duration was significantly higher for evening bats than for either Seminole or big brown bats (Tukey-Kramer, $df = 62$, $P = 0.0047$; $df = 62$, $P = 0.0404$, respectively), but not different between big brown and Seminole bats (Tukey-Kramer test, $df = 62$, $P = 0.9331$).

Discussion

As predicted, we found significant differences in bat community structure between the managed and unmanaged sites, even though the sites shared 6 of the 8 captured species. We found a “site” effect for summers 2010 and 2011. In both years, Seminole bats dominated both sites. Evening bats were the most numerous bats at KP during both years, while at HLC evening bats were 2nd most numerous in 2011, but 3rd most numerous in 2010. Big brown bats were captured in significantly higher proportions at HLC than at KP. Eastern red bats were in decline year to year, but they were captured in higher proportions at KP than HLC. Southeastern myotis and tricolored bats were in low numbers at both sites, but southeastern myotis was in slightly higher proportions at HLC. Finally, we captured Mexican free-tailed and hoary bats only at KP. Both of these species are predicted to be clutter-intolerant (high wing loading and high aspect ratio; Norberg and Rayner 1987), and their presence in our samples only at the managed site was as predicted. Ecomorphological data might explain the “site” effect. Due to prescribed burns, the KP site had open edges and understory, and was dominated by young pine trees. As such, KP is suitable habitat for clutter-intolerant species with high wing loading, high aspect ratio, and low echolocation call frequencies. Because HLC is unmanaged, it had much more vegetative clutter, and a mixture of old growth pine trees

and hardwoods. Consequently, HLC is suitable habitat for clutter-tolerant species with low wing loading, low aspect ratio, and high echolocation call frequencies.

We, as Armitage and Ober (2012), found that southeastern myotis had the lowest wing loading, lowest aspect ratio, and smallest forearm length among species captured at our study sites. This indicates that southeastern myotis are clutter-tolerant. Southeastern myotis had echolocation calls with intermediate mean characteristic frequency and long mean duration, which enabled them to utilize both cluttered and uncluttered areas (Norberg and Rayner 1987). In accordance with expectations, southeastern myotis comprised a smaller proportion (2.5%) of the bat community at the managed site than at the unmanaged site (8.7%). Seminole bats were intermediate in forearm length, wing loading, and high aspect ratio when compared to other bats captured at SHNF. Armitage and Ober (2012) also found that Seminole bats were intermediate in their wing characteristics. Furthermore, echolocation calls of Seminole bats had the highest mean characteristic frequency and shortest mean duration. This combination of wing morphology and echolocation call characteristics suggests that Seminole bats should be generalists, able to use both habitat types. Indeed, they dominated both bat communities, representing overall 45.7% of the community at the managed and close to 40% at the unmanaged area. Menzel et al. (2005) found that the activity of Seminole bats did not differ between cluttered and opened areas in longleaf forests of South Carolina.

Our findings agree with Norberg and Rayner (1987) in that the tricolored bat is a relatively small bat (larger than southeastern myotis but smaller than Seminole) with low wing loading and high aspect ratio. Armitage and Ober (2012) placed tricolored bat into clutter-tolerant group along with southeastern myotis. Tricolored bats had echolocation

calls with high mean characteristic frequency and long mean duration; evening bats were the only bats in this community with lower mean characteristic frequency and longer mean duration. This species was slightly more abundant in the managed site (c. 6.1% of bat community at KP; c. 3.8% at HLC), although it was found in rather small numbers overall. Echolocation features distinguish evening bats from both big brown and Seminole bats. Evening bats had echolocation calls of lowest mean characteristic frequency and longest mean duration, which in combination with high wing loading and high aspect ratio (only big brown bats had higher wing loading) make them the most clutter-intolerant species at SHNF. This is in contrast to Armitage and Ober (2012), who found this species to have low wing loading and aspect ratio and considered them to be clutter-tolerant species. Evening bats represented approximately 22% of the bat community at both sites. The most likely explanation for this is that both sites are providing suitable roosting and foraging sites for evening bats. Hein et al. (2009) discovered that old stands (>40 years) provide suitable roosting habitat for evening bats. The small size (only tricolored and southeastern myotis have shorter forearms) and availability of clutter-free flight corridors through cluttered areas might allow this bat to exploit unmanaged areas of SHNF and the possible roosts it offers. In addition, evening bats are also known to roost in longleaf pine plantations (Menzel et al. 2001), such as found in managed areas.

We also found a significant “year” effect in bat community structure at each site. During 2010, at both sites we saw much lower numbers of evening, tricolored, and southeastern myotis, and slightly lower numbers of Seminole bats in comparison to summer 2009 and 2011. There was no noticeable shift in big brown captures between the

years. Weather might have played a role in this drop in captures. During 2010 sampling season it was raining heavily during every netting trip – either before we started to net, or during netting. Rain might be bigger hindrance to smaller bats (such as tricolored, southeastern myotis, and evening bats) than to intermediate Seminoles or large big brown bats.

Interestingly, there were some differences between our ecomorphology data and that of Norberg and Rayner (1987) concerning eastern red and big brown bats. They found that eastern red bats were larger with much higher wing loading than big brown bats (16 g, 14 Nm⁻²; 15 g, 9.2 Nm⁻², respectively). We found that eastern red bats to be much smaller and have lower wing loading (9.3 g, 8.83 Nm⁻²) than big brown bats (16.0 g, 12.7 Nm⁻²), in agreement with Armitage and Ober (2012) who placed eastern red bats into same group as Seminole bats (intermediate wing loading and aspect ratio). Shump and Shump (1982) specified that eastern red bats vary from 7 to 13 g throughout their range. Eastern red bats in our study area clearly fall into this range, while measurements from Norberg and Rayner (1987) exceed the known upper limit for the weight of this species. Perhaps, eastern red bats reported in Norberg and Rayner (1987) were large pregnant females. Echolocation data might differ among studies because bat echolocation exhibits high plasticity and varies with surroundings (amount of clutter, extent of reflective areas such as water or buildings, presence of other bat species or conspecifics, size of prey items), with purpose (feeding, socializing, navigation), and even with sex and age (Kazial et al. 2001; Wund 2006; Grilliot et al. 2009; Petrites et al. 2009; Gillam et al. 2010). As a result, we determined to use only echolocation data collected at our sites in further discussion regarding echolocation of bat species captured in our study.

Our data, as well as those of Armitage and Ober (2012), imply that big brown bats are clutter-intolerant bats (large size, high wing loading, intermediate aspect ratio, intermediate mean characteristic frequency, intermediate mean duration) and should be more numerous in managed habitat, while eastern red bats (similar in all measurements to Seminole bats: intermediate wing loading, high mean characteristic frequency, and short mean duration) are intermediate in characteristics and should be able to successfully exploit both habitats. However, capture data did not support these expectations in relationship to big brown or eastern red bats. We found that eastern red bats were much more numerous in the managed than unmanaged site (14.2% vs. 1.6%) and that big brown bats were more numerous at the unmanaged site than the managed site (22% vs. 7.6%).

We think that availability of roosting sites and transit corridors through the forest might explain these unexpected results. Large, old pine and hardwood trees and snags with well-developed cavities dominate the unmanaged site. These offer potentially suitable roost sites for large bats that roost in small colonies, such as big brown bats forming maternity colonies. Male big-brown bats are known to occasionally form bachelor colonies or to join female colonies, though they often roost individually during summer (Kurta and Baker 1990). In addition, the unmanaged area, like the managed area, is transected by forest service roads, potentially representing corridors that big brown bats can use to move between roosts and foraging areas without dealing with clutter. Evidence for this contention is that over 90% of big brown bats captured at the unmanaged site were captured in the net that was placed across service road. The majority of clutter tolerant species were captured in the net placed at the edge of the

water. Furthermore, the unmanaged (eastern) part of the forest possesses some open areas (one about 1 km west of HLC netting site) that are remnants of clearcutting conducted by the U. S. Forest Service due to infestations by the southern pine beetle (*Dendroctonus frontalis*) during 1984 - 1985 (Rudolph and Connor 1994). These areas were not re-planted and potentially provide openings in cluttered areas that clutter-intolerant bats might use for foraging.

Eastern red bats are solitary, roosting in groups only when a mother roosts with her pups or when a mating pair roosts together (Constantine 1966). They are also known to roost in foliage, under bark, or in leaf litter, but do not require well-developed cavities as roost sites (Schmidly et al. 1977; Shump and Shump 1982; Schmidly 2004). Eastern red bats were more active in thinned stands and areas with low vegetation clutter than in unmanaged areas of piney forests (Loeb and O’Keefe 2006; Loeb and Waldrop 2008; Armitage and Ober 2012). Contrary to these studies, Menzel et al. (2005) found that *L. seminolus-borealis* were equally active in cluttered and open areas. In addition, Elmore et al. (2005) examined foraging areas of eastern red bats in east-central Mississippi, and determined that the most important features of foraging areas were presence of a reliable water source and suitable roost sites (such as thinned stands). The KP area in SHNF, where the vast majority of eastern red bats were captured, possesses some of these features - low clutter, and thinned stands, likely providing eastern red bats with suitable roosting habitat. However, the amount of water in the pond varied from year to year. During 2011, KP was reduced from being approximately 100 ft to approximately 20 ft in diameter due to drought; this might have contributed to the decline in captures of eastern red bats during our study.

Most of the western portion of the SHNF is managed through clearcutting and even-aged systems with short rotation for timber production, but also with prescribed fires to maintain suitable habitat for the endangered red-cockaded woodpecker. Thus far, no studies have been conducted to determine what impact this type of management might have on forest bats in most southwestern portion of U.S. southeastern piney forests. Our study suggests that these management practices might render the southeastern pine forest better suited to clutter-intolerant species. Yet, presence of unmanaged areas might be essential for some clutter-tolerant species (e.g., southeastern myotis), and even for some clutter-intolerant species (e.g., big brown bats) if flight corridors (e.g., service roads) are available. We suggest that if management practices related to timber production spread into the eastern (non-managed) part of the forest, sections rich in old, large trees (pine and hardwood) and large snags should be preserved. This may provide suitable habitat to a broader range of bat species. Our study also indicates that it is important that studies of this type should be conducted over multiple years in order to better understand bat community structure as data could easily be skewed due to extraneous factors such as extraordinarily dry or rainy seasons.

CHAPTER FOUR

Temporal Niche Partitioning in Six Sympatric Bat Species

Abstract

Although temporal partitioning, whether through exploitation or interference competition, has been recognized as one of the important niche axes, only a few bat community studies have focused on temporal partitioning. Our study investigated temporal partitioning within the insectivorous bat community in the pine forests of southeastern Texas. We hypothesized that since all bat species documented in our study area use the same ponds as foraging and watering sites, they might exhibit some degree of temporal partitioning in order to diminish or avoid direct competition. We recorded and analyzed capture times of bats at the ponds. In addition, we collected insects at the ponds to determine whether temporal partitioning (if present) within the bat community might be due to exploitation competition and driven by food resources. We found that bats did exhibit some temporal partitioning but that bat species involved in partitioning changed on yearly bases. During summer 2009, we found temporal partitioning between evening and Seminole, and evening and tri-colored bats. During summer 2010, we found temporal partitioning between big brown and 4 other bats (evening, Seminole, eastern red, and southeastern myotis). Finally, during summer 2011, temporal partitioning was detected only between big brown and evening bats. In addition, we determined that the temporal partitioning in these bats likely was not related to food resources.

Introduction

The concept of temporal niche partitioning was introduced by MacArthur and Levins (1967). Since then, many studies (e.g., Pianka 1969, 1973, 1975; Schoener 1974, Carothers and Jaksic 1984; Kronfeld-Schor and Dayan 1999; Alanara et al. 2001; Pinter-Wollman et al. 2006) have attempted to empirically and theoretically describe how temporal niche partitioning might have evolved in sympatric species. Carothers and Jaksic (1984) extensively discussed 2 approaches to temporal partitioning. Exploitation competition, a more traditional approach, does not consider time to be a true orthogonal axis of the niche. Here, temporal variation is more of a mechanism that allows partitioning of other niche axes such as habitat and food. In this context, habitat partitioning would occur in cases where multiple organisms use microhabitat at different times, while food partitioning would occur either when a different resource spectrum is available or when a food source, such as insects, is continually renewable (Carothers and Jaksic 1984). Interference competition (Carothers and Jaksic 1984), an alternative approach, suggests that when species are competing for the same resources, the dominant species will displace the subordinate one to different activity times. In this case, direct effects of interference, such as harassment and robbing by competing species, can be eliminated through temporal partitioning.

Although temporal partitioning, whether through exploitation or interference competition, has been recognized as one of the important niche axes (Carothers and Jaksic 1984), only a few bat community studies have focused on temporal partitioning (e.g., Brown 1968; Kunz 1973; Reith 1980; Adams and Thibault 2006). Most studies of sympatric bat species have examined either habitat use and partitioning (Arlettaz 1999;

Duchamp et al. 2004; Baker and Lacki 2006; Brooks and Ford 2006; Yates and Muzika 2006; Perry et al. 2007; Ruso et al. 2007; Perry et al. 2008), or food resource partitioning (Husar et al. 1976; Hickey et al. 1996; Carter et al. 2004; Whitaker Jr. 2004; Ober and Hayes 2008; Feldhamer et al. 2009). Our study investigated temporal partitioning within the insectivorous bat community in the pine forests of southeastern Texas. We hypothesized that since all 8 bat species documented in our study area use the same ponds as foraging and watering sites, they might exhibit some degree of temporal partitioning in order to diminish or avoid direct competition. To test this hypothesis, we recorded and analyzed capture times of bats at the ponds. In addition, we collected insects at the ponds to determine whether temporal partitioning (if present) within the bat community might be due to exploitation competition and driven by food resources.

Materials and Methods

The study was conducted in Sam Houston National Forest (SHNF), Texas, which is located approximately 75 km north of Houston and encompasses an area of 65 217 ha (Cibula and Lucas 1990; Thomlinson 1995). This forest is composed mostly of pine trees <80 years of age (87%), with approximately 1% of the stands containing trees >100 years of age (Azevedo et al. 2000). Approximately 35% of the forest is occupied either by pine plantations <20 years of age or by recent clear cuts. The dominant pine is Loblolly pine (*Pinus taeda*), while *Pinus echinata* (Shortleaf pine) is present in most of the older stands and dominates some drier sites. *Pinus palustris* (Longleaf pine) occurs in mixed stands on the eastern side of the forest. A variable mixture of *Liquidambar styraciflua* (American sweetgum), *Quercus falcata* (Southern red oak), *Quercus stellata* (Post oak), *Quercus alba* (White oak), *Quercus nigra* (Water oak), *Quercus incana* (Bluejack oak), *Fagus*

grandifolia (American beech), and *Magnolia* (Magnolia) constitutes the canopy, with a well-developed midstory of hardwoods in unmanaged areas. Mixed hardwood forest occurs close to most drainages. At least 8 forest-dwelling bat species are expected to summer in these forests (Schmidly 2004; Ammerman et al. 2012): *Corynorhinus rafinesquii* (Rafinesque's big-eared bat), *Eptesicus fuscus* (Big brown bat), *Lasiurus borealis* (Eastern red bat), *Lasiurus intermedius* (Northern yellow bat), *Lasiurus seminolus* (Seminole bat), *Myotis austroriparius* (Southeastern myotis or southeastern bat), *Nycticeius humeralis* (Evening bat), and *Perimyotis subflavus* (tri-colored bat).

Suitable bat-netting sites were scarce in SHNF as most ponds were ephemeral, drying out by mid-June. Our sampling was conducted at 2 sites, which contained ponds that remained water-filled throughout the summer: Kelly Pond and Henry Lake Creek. Kelly Pond is in Montgomery Co., about 25 km west of Interstate 45 (30°30'37"N, 95°39'42"W). Henry Lake Creek, San Jacinto Co. (30°32'31"N, 95°7'29"W), is approximately 55 km east of Kelly Pond. The two sites differed in several ways: Kelly Pond is located in a managed part of the forest, so it is surrounded by young pine plantations with relatively open canopy. Due to prescribed burns conducted by the U.S. Forest Service, understory in this section of the forest is fairly sparse. Kelly Pond is mostly surrounded by pine trees, but on one side opens into a large meadow. Kelly Pond gradually diminishes in size during the summer, as it does not have constant source of water. Henry Lake Creek is located in the non-managed side of the forest. At Henry Lake Creek, a low-water crossing created a slow-moving pool of water surrounded by cluttered old-growth mixed hardwoods and shortleaf pine forest. Henry Lake Creek maintains its size during the summer.

We conducted fieldwork over three summers: 2009, 2010, and 2011. At Kelly Pond we sampled with either 3 stacked mist nets (each 2.6 m high and 12 m wide, Avinet Inc., Dryden, NY) or a single large net (7.8 m high and 12 m wide) attached to a single triple-high net system (BatNets.com, Austin, TX). Sampling effort was 6 nights (40 netting hours) in 2009, 6 nights (24 hours) in 2010, and 4 nights (23.5 hours) in 2011. We netted at HLC, using 2 triple-high net systems for 9 nights (82.5 hours) in 2010, and a single triple-high net for 4 nights (24 hours) in 2011. During 2011, 2 groups of researchers netted simultaneously at both sites.

Nets were monitored continuously. For each captured bat, we recorded capture time, species, age (Anthony 1988), reproductive status (Racey 1988), mass, and standard external measurements (lengths of tail, forearm, ear, tragus, and hind foot). Bats were processed and released within 1 hour of capture. We followed the Guidelines of the American Society of Mammalogists for the use of wild mammals (Gannon et al. 2007). We worked under protocol 10-05 approved by Baylor University Institutional Animal Care and Use Committee and Texas Parks and Wildlife scientific permit number SPR-0706-704.

During 2010, we collected insects at the netting sites using universal black light traps (BioQuip, Rancho Dominguez, CA, USA). Even though sunset time varied from 20:13 to 20:37 throughout the summer, no bats were captured during summer 2009 before 20:30, so we started insect trapping every night at the same time (20:30). We emptied light traps in 1-hour intervals. Insects were killed using ammonium carbonate (BioQuip, Rancho Dominguez, CA, USA) and stored in a freezer until processing. In lab,

using a dissecting microscope, we identified insects to order and measured their body lengths as a proxy for body size.

To determine if there was a site effect (for years 2010 and 2011 as Henry Lake Creek was not sampled in 2009), we used t-tests or, when the assumption of normality was violated, Wilcoxon tests (Zar 1999). As only 2 big brown bats were captured at Kelly Pond and only 3 eastern red bats at Henry Lake Creek, these 2 species were excluded from this analysis. To determine if there was a year effect, for each species we used Kruskal-Wallis tests because the assumption of normality was violated. To determine if there was temporal partitioning in activity times between bat species, we used capture times calculated in minutes after sunset. We used two-sample Kolmogorov-Smirnov tests to determine if activity of 2 species was from the same distribution (Chakravart et al. 1967). When sample number was <3 , species was excluded from pair-wise analysis. In cases where tests showed that species came from same distribution, we interpreted that there was no temporal partitioning. In cases where species came from different distributions, we concluded that species exhibited temporal partitioning. In cases where species came from different distributions, we concluded that species exhibited temporal partitioning. Since non-parametric tests were required parametric adjustments for multiple tests were inappropriate. Consequently, significant p-values should be interpreted in conservative way.

Insect data collected in 2010 was analyzed using Chi-square tests (Zar 1999) to determine if insect assemblages at the 2 sites differed and to determine if the data from two sites could be pooled for further analysis. For each insect order, we used Chi-square tests to determine if insect size was related to their activity time. For this analysis, insects

were placed into following length groups: LG1 (<5 mm), LG2 (5 - 9 mm), LG3 (10 - 14 mm), LG4 (15 - 19 mm), LG5 (20 - 30 mm), and LG6 (>30 mm), except for Ephemeroptera which were grouped in the following manner: LG7 (<10 mm), LG8 (10 - 20 mm), and LG9 (>20 mm).

Results

Bat Data

We captured 382 bats representing 8 species (Seminole, evening, big brown, eastern red, southeastern myotis, tri-colored, hoary, and Mexican free-tailed bats) throughout our study. During 2009, captures totaled 122 bats of all 8 species. We captured 136 bats during 2010, and 124 bats during 2011. Hoary and Mexican free-tailed bats were captured only during the first year. There was no site effect for either Seminole ($df = 104$, $P = 0.548$), evening ($df = 53$, $P = 0.821$), southeastern myotis ($df = 19$, $P = 0.718$), or tri-colored bats ($df = 16$, $P = 0.253$). Due to small sample sizes ($n \leq 3$), big brown and eastern red bats were excluded from site-effect analysis. There was a year effect for big brown bats ($df = 2$, $P = 0.039$) and evening bats ($df = 2$, $P < 0.001$), but not for Seminole ($df = 2$, $P = 0.083$), eastern red ($df = 2$, $P = 0.494$), southeastern myotis ($df = 2$, $P = 0.089$), or tri-colored bats ($df = 2$, $P = 0.157$). We found that, for both evening and big brown bats, activity times differed between 2009 and 2010 ($D = 0.623$, $P < 0.001$; $D = 0.495$, $P = 0.019$, respectively), as well as between 2009 and 2011 ($D = 0.007$, $P = 0.007$; $D = 0.538$, $P = 0.028$, respectively), but did not differ between 2010 and 2011 ($D = 0.278$, $P = 0.265$; $D = 0.323$, $P = 0.275$, respectively). Because 2 species showed a year effect (their capture times varied among years), we analyzed capture times for those

species separately by year. However, since we did not find site effect (activity times for any given bat species did not differ between two sites), we pooled data across the sites.

The 2 lasiurids (Seminole and eastern red bats) were usually the first species to arrive at the pond, with great numbers of these being captured within first 90 min after sunset. Even though Seminole bats represent the majority of the first wave of the bats, they were continuously active for entire sampling interval (Figures 4.1-4.3). Evening bats emerged at the pond later than the lasiurids but earlier than big brown bats, with the majority being captured 50 - 100 min after sunset (Figures 4.1-4.3). Big brown bats were last to appear at the pond, with the majority captured 120 - 150 min after the sunset (Figures 4.1-4.3). Southeastern myotis and tri-colored bat captures were usually scattered throughout the night (Figures 4.1-4.3).

For each year, we performed two-sample Kolmogorov-Smirnov tests to determine if bats showed temporal partitioning at the watering holes. During 2009 (Table 4.1), the only species that exhibited temporal partitioning were Seminole and evening, and evening and tri-colored bats. In 2010 (Table 4.2), we found temporal partitioning between big brown and 4 other species: eastern red bats, Seminole bats, evening bats, and southeastern myotis. During 2011 (Table 4.3), 3 pairs of species exhibited temporal partitioning: big brown and evening bats, big brown and eastern red bats, and eastern red and southeastern myotis.

Insect Data

We captured a total of 7439 insects at Kelly Pond, and 3916 at Henry Lake Creek. Even though there were significant differences ($df = 10$, $P < 0.0001$) between the 2 sites in insect captures regarding taxa present as well as the taxa abundances, Coleoptera

represented around 70% of insect captures (Figure 4.4). At Kelly Pond, the second most numerous were Hemiptera (11.8%), followed by Diptera (6.6%), Lepidoptera (4.4%), and Hymenoptera (1.9%). At Henry Lake Creek, the 2nd most numerous insects were Ephemeroptera (17.2%), followed by Hemiptera (6.7%), Lepidoptera (3.7%), Trichoptera (3.3%), and Diptera (3%).

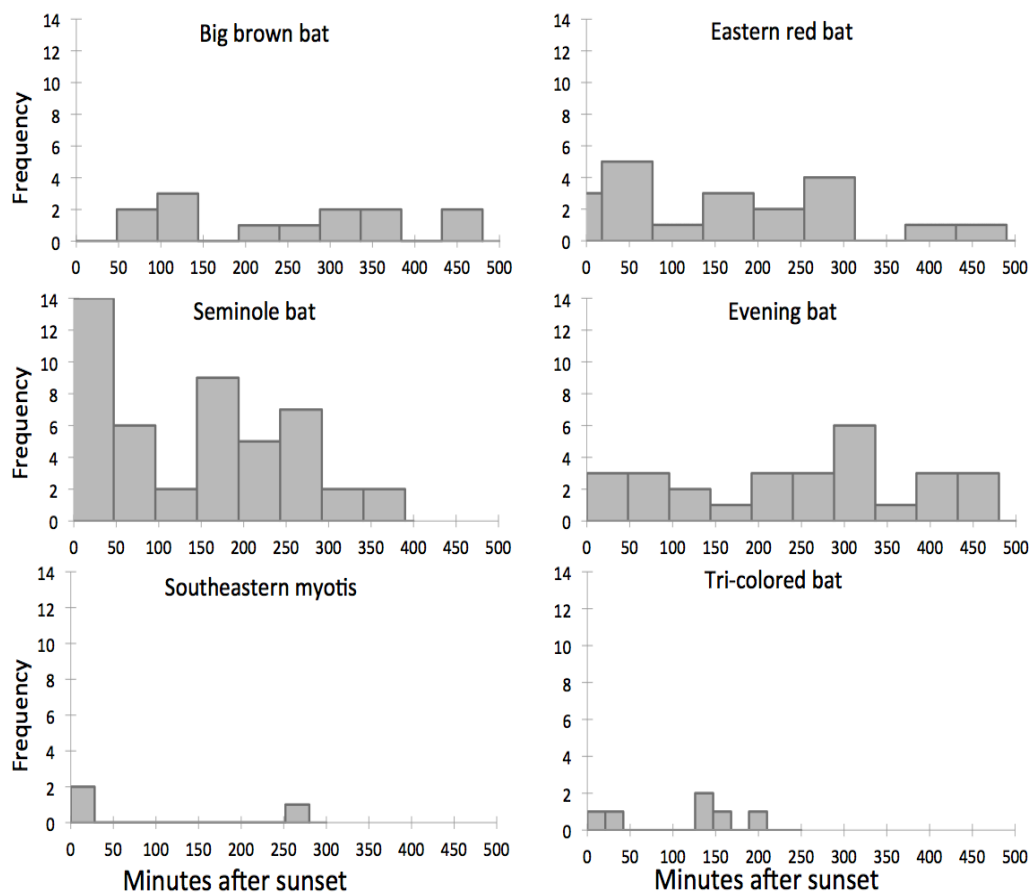


Figure 4.1. Bat captures in relation to time of night for year 2009. Horizontal axis shows capture time in minutes after sunset, and vertical axis shows numbers of captures for each of six species at Sam Houston National Forest, Texas.

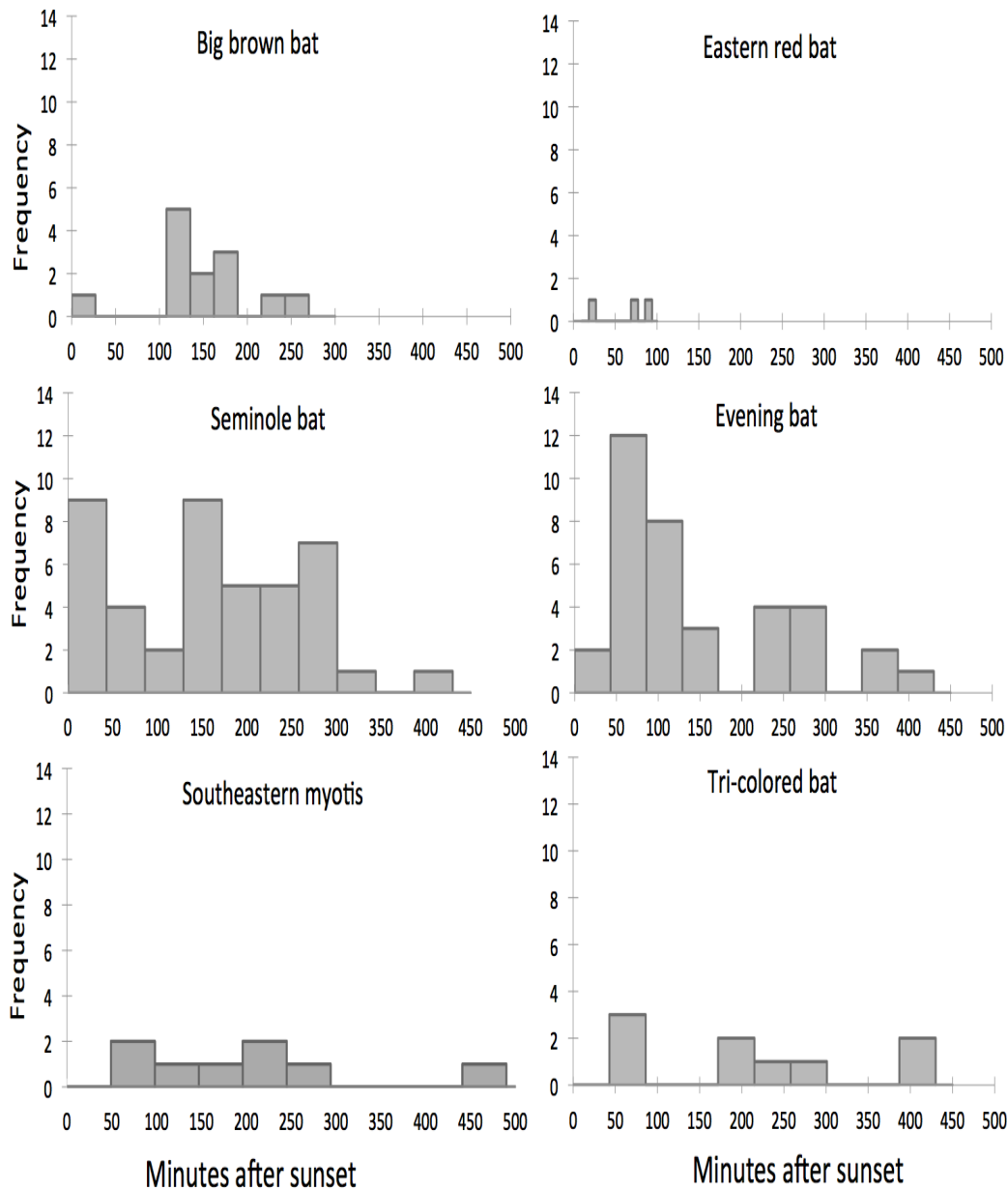


Figure 4.2. Bat captures in relation to time of night for year 2010. Horizontal axis shows minutes after sunset, and vertical axis shows capture numbers for each of six species at Sam Houston National Forest, Texas.

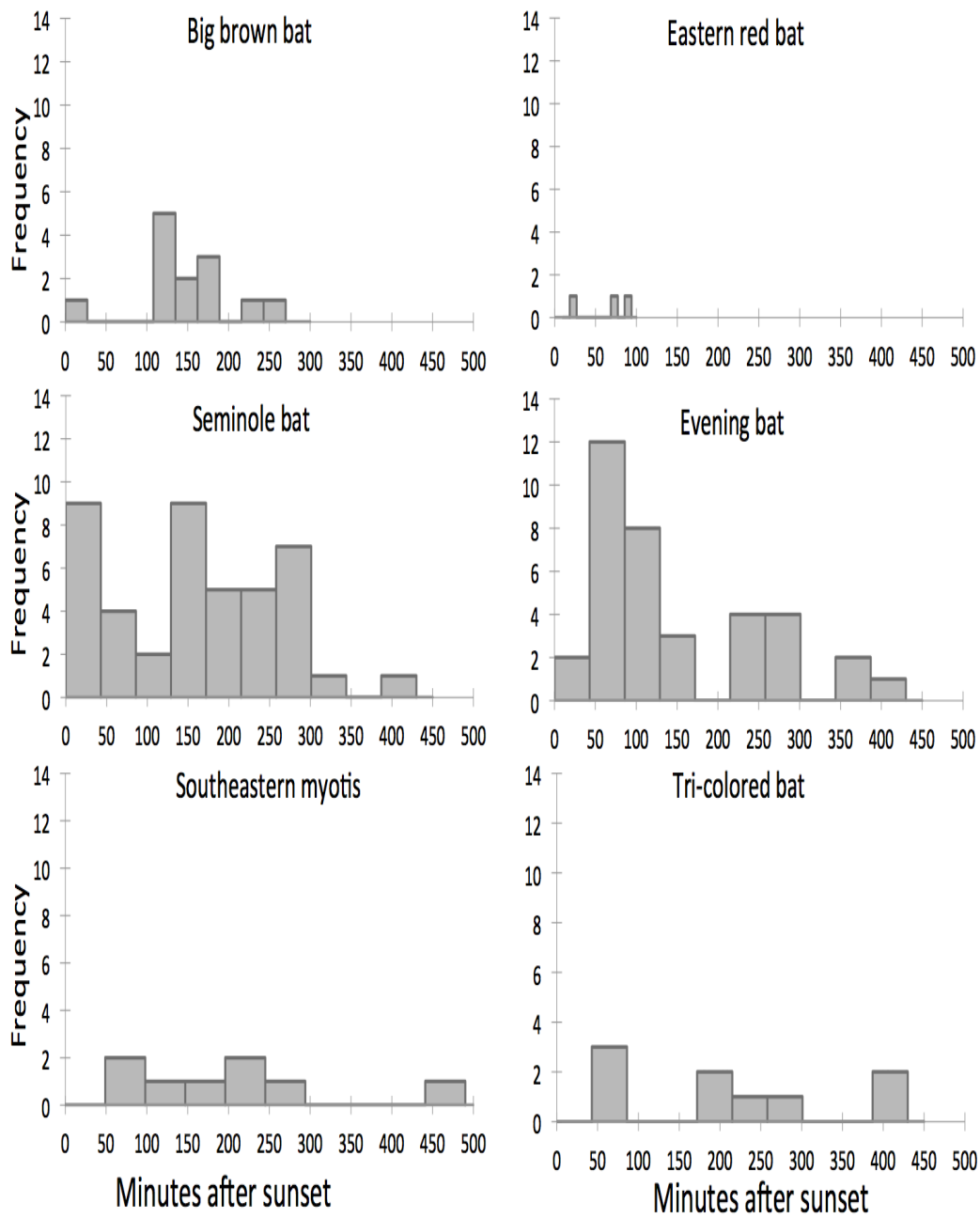


Figure 4.3. Bat captures in relation to time of night for year 2011. Horizontal axis shows minutes after sunset, and vertical axis shows capture numbers for each of six species at Sam Houston National Forest, Texas.

Table 4.1. Results of two-sample Kolmogorov-Smirnov tests (D) for bat capture data collected at Sam Houston National Forest during summer 2009. Where $P > 0.05$, capture times of two bat species compared represent the same distribution (show no temporal partitioning). Where $P < 0.05$ (denoted by *), capture times of bat species compared represent different distributions.

Species compared	D	P -value
Big brown vs. eastern red bat	0.388	0.185
Big brown vs. Seminole bat	0.404	0.071
Big brown vs. evening bat	0.137	0.996
Big brown vs. tri-colored bat	0.615	0.051
Eastern red vs. Seminole bat	0.151	0.906
Eastern red vs. evening bat	0.350	0.114
Eastern red vs. tri-colored bat	0.400	0.355
Seminole vs. evening bat	0.379	0.012*
Seminole vs. tri-colored bat	0.340	0.477
Evening vs. tri-colored bat	0.643	0.018*

At Kelly Pond, insect size as indicated by body length was related to activity times in Coleoptera ($df = 20$, $P < 0.0001$), Hemiptera ($df = 12$, $P < 0.0001$), Diptera ($df = 12$, $P < 0.0001$), Lepidoptera ($df = 16$, $P < 0.0001$), and Hymenoptera ($df = 4$, $P < 0.0001$). Smaller coleopterans were more numerous than larger beetles (Table 4.4). The smallest beetles comprised three-quarters of the coleopterans (LG1, 75.5%), with nearly all of the other beetles in the 5 - 9 mm size range (LG2, 23%).

Table 4.2. Results of two-sample Kolmogorov-Smirnov tests (D) for bat capture data collected at Sam Houston National Forest during summer 2010. Where $P > 0.05$, capture times of two bat species compared represent the same distribution (show no temporal partitioning). Where $P < 0.05$ (denoted by *), capture times of bat species compared represent different distributions.

Species compared	D	P -value
Big brown vs. eastern red bat	0.673	0.024*
Big brown vs. Seminole bat	0.349	0.025*
Big brown vs. evening bat	0.451	0.028*
Big brown vs. southeastern myotis	0.500	0.036*
Big brown vs. tri-colored bat	0.547	0.273
Eastern red vs. Seminole bat	0.404	0.330
Eastern red vs. evening bat	0.277	0.878
Eastern red vs. southeastern myotis	0.333	0.704
Eastern red vs. tri-colored bat	0.333	0.935
Seminole vs. evening bat	0.230	0.448
Seminole vs. southeastern myotis	0.183	0.907
Seminole vs. tri-colored bat	0.365	0.735
Evening vs. southeastern myotis	0.233	0.823
Evening vs. tri-colored bat	0.333	0.868
Southeastern myotis vs. tri-colored bat	0.333	0.901

Table 4.3. Results of two-sample Kolmogorov-Smirnov tests (D) for bat capture data collected at Sam Houston National Forest during summer 2011. Where $P > 0.05$, capture times of two bat species compared represent the same distribution (show no temporal partitioning). Where $P < 0.05$ (denoted by *), capture times of bat species compared represent different distributions.

Species compared	D	P -value
Big brown vs. Seminole bat	0.271	0.451
Big brown vs. evening bat	0.506	0.014*
Big brown vs. southeastern myotis	0.346	0.498
Big brown vs. tri-colored bat	0.513	0.080
Eastern red vs. tri-colored bat	0.667	0.156
Seminole vs. evening bat	0.281	0.090
Seminole vs. southeastern myotis	0.302	0.490
Seminole vs. tri-colored bat	0.295	0.464
Evening vs. southeastern myotis	0.444	0.107
Evening vs. tri-colored bat	0.361	0.242
Southeastern myotis vs. tri-colored bat	0.333	0.638

LG1 coleopterans were highly active between 20:30 and 22:30 (58% of all captures). The smallest hemipterans (LG1) were also mostly captured within first 2 h of trapping and represented 89% of all Hemiptera captures. Approximately two-thirds of Diptera (Table 4.4) captured at Kelly Pond were <5 mm long and were captured in first h of trapping. Almost all (94%) of the Lepidoptera were <10 mm long. The highest activity

for Lepidoptera was just after the sunset (between 20:30 and 21:30). None of the Hymenoptera were >10 mm long. In addition, Hymenoptera <5 mm long captured during first 2 h of trapping represented approximately half of all captured hymenopterans.

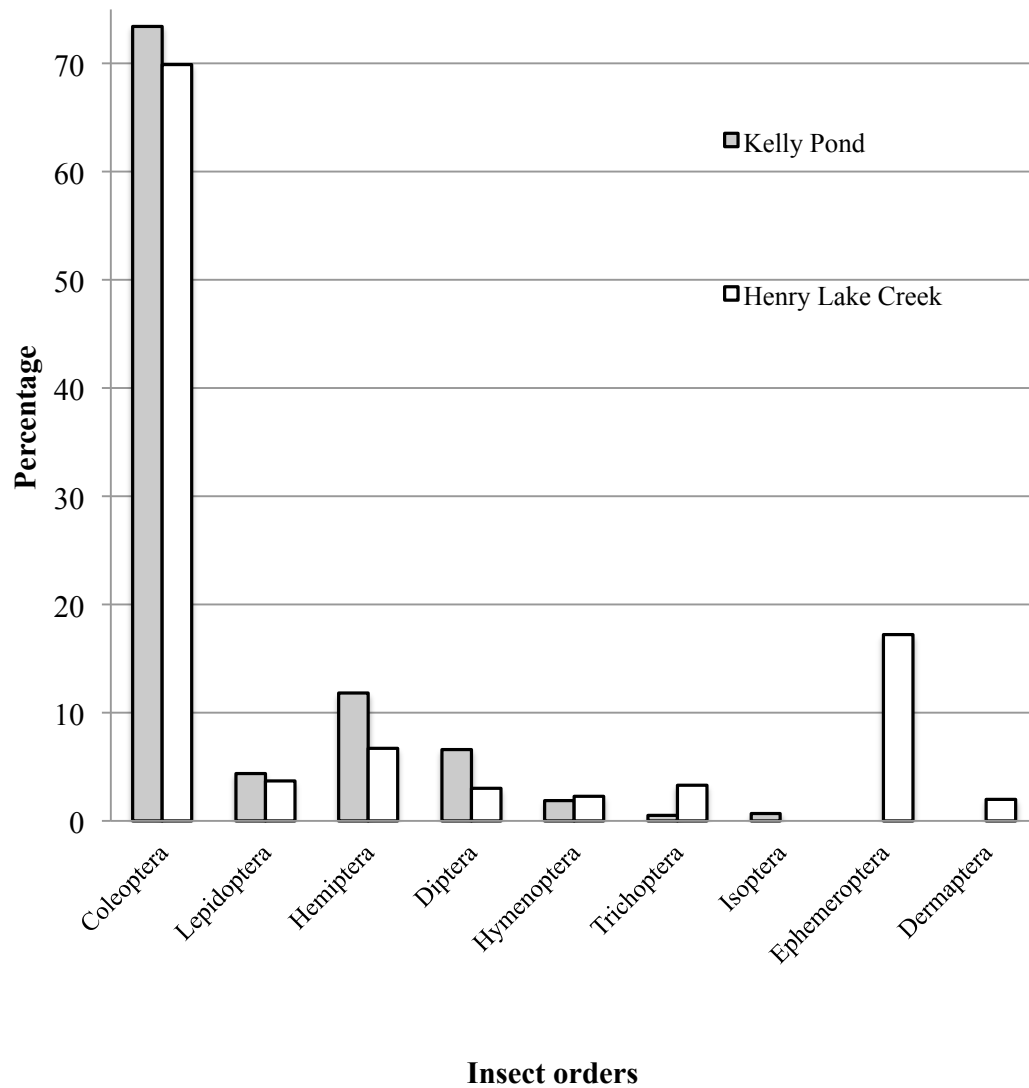


Figure 4.4. Percent captures of each insect order collected from traps at the 2 sites in Sam Houston Nation Forest, Texas, during bat netting session in summer 2010.

Table 4.4. Percent captures at Kelly Pond during summer 2010. Captured insect taxa are organized by capture times and size categories. For Coleoptera, Hemiptera, and Lepidoptera, columns do not add to 100% as all 3 taxa have a small percentage of captures that are >10 mm. LG1 and LG2 columns in Hymenoptera add to 100% as no Hymenoptera captured at Kelly Pond were >10 mm.

Time	Coleoptera (<i>n</i> = 5474)		Hemiptera (<i>n</i> = 906)		Diptera (<i>n</i> = 491)		Lepidoptera (<i>n</i> = 329)		Hymenoptera (<i>n</i> = 144)	
	LG1	LG2	LG1	LG2	LG1	LG2	LG1	LG2	LG1	LG2
20:30-21:30	22.8	6.4	67.7	2.4	71.1	0	39.8	11.2	22.9	13.9
21:30-22:30	35.3	9.1	21.5	3.4	16.1	0.6	21.9	11.6	29.2	6.9
22:30-23:30	12.8	6.9	1.3	1.3	6.3	0.6	0.3	6.1	4.2	11.1
23:30-00:30	2.2	0.6	0.6	0.4	2.4	0.4	0.0	0.9	9.0	0.0
00:30-1:30	2.4	0.3	0.8	0.1	2.0	0	0.3	2.4	2.8	0.0

At Henry Lake Creek, length was related to activity time in Coleoptera ($df = 20$, $P < 0.0001$), Hemiptera ($df = 20$, $P < 0.0001$), Diptera ($df = 12$, $P = 0.0018$), Hymenoptera ($df = 8$, $P = 0.0013$), Trichoptera ($df = 8$, $P = 0.0133$), Lepidoptera ($df = 20$, $P < 0.0001$), and Dermaptera ($df = 2$, $P = 0.0215$). Insects <5 mm long represented large proportions of captured insects (Table 4.5): Coleoptera (82%), Hemiptera (73%), Lepidoptera (51%), Trichoptera (42%), and Diptera (42%). Insects 5 - 9 mm long represented 38% of Lepidoptera, 55% of Trichoptera, and 33% of all Diptera. The majority of Coleoptera, Hemiptera, and Diptera were active late in the evening (between 22:30 and 00:30) while Trichoptera were mostly active between 20:30 and 23:30, and Lepidoptera between 21:30 and 00:30. Small (<10 mm long) Trichoptera were most active within first 2 (<5 mm long) or 3 (5 - 9 mm long) h of trapping. LG2 represented 66% of all captured Hymenoptera, with most captured between 21:30pm and 00:30. The majority (61%) of all Dermaptera were <5 mm long, with 70% of these small dermapterans captured during the first h of trapping. Insects 10 - 20 mm long (LG7) accounted for 56% of captured

Ephemeroptera. Ephemeropterans belonging to all size groups were equally active throughout the night (Table 4.5).

Discussion

Temporal partitioning is often neglected in bat studies or is viewed only as a consequence of resource (food, watering hole, habitat) partitioning (Carothers and Jaksic 1984). The objective of our study was to determine if 8 sympatric bat species within the bat community in southeastern pine forest exhibited temporal partitioning. We found that some bats might have exhibited temporal partitioning (relatively low sample sizes do not allow certainty), and that the species engaging in partitioning may change on yearly bases. Two bat species in this community were most commonly involved in temporal partitioning: evening and big brown bats.

Table 4.5. Percent captures at Henry Lake Creek during summer 2010. Captured insect taxa are organized by capture times and by size categories. The only column adding to 100% is Ephemeroptera because the other orders have representatives in other length groups.

Time	Coleoptera (n = 2738)		Hemiptera (n = 262)		Diptera (n = 119)		Lepidoptera (n = 146)		Ephemeroptera (n = 336)			Trichoptera (n = 129)	
	LG1	LG2	LG1	LG2	LG1	LG2	LG1	LG2	LG7	LG8	LG9	LG1	LG2
20:30-21:30	15.2	2.0	10.9	10.9	8.0	15.8	8.0	10.1	8.0	15.8	8.0	0	0.7
21:30-22:30	12.1	2.4	2.5	2.5	4.5	11.6	3.3	17.8	4.5	11.6	3.3	7.5	13.0
22:30-23:30	15.7	2.8	13.4	13.4	6.3	15.2	8.0	6.2	6.3	15.2	8.0	20.5	16.4
23:30-00:30	35.9	5.2	38.7	38.7	2.1	13.4	3.6	7.8	2.1	13.4	3.6	23.3	7.5
00:30-1:30	3.7	2.6	0	0	0	0	0.3	0.8	0	0	0.3	0	0

During summer 2009, evening bats exhibited temporal partitioning with Seminole and tri-colored bats, although the latter was present in low sample size ($n = 6$). During summer 2010, big brown bats had activity times that differed from Seminole, evening, southeastern myotis, and eastern red bats, although we captured only 8 eastern red bats. Adams and Thibault (2006) found that some *Myotis* species when present at watering holes in larger abundances shifted their activities to earlier in the night. However, we did not find this to hold for either evening or big brown bats. Both of these species showed a year effect, with activity times during summer 2009 differing from the summers 2010 and 2011, and with no difference between summers 2010 and 2011. In both cases capture numbers were similar during summers 2009 and 2011. During summer 2010, big browns had the highest capture numbers while evening bats had the lowest capture numbers. This suggests that shift in activity times of these 2 bats during summer 2009 was not related to changes in their abundances at the sites

To determine if temporal partitioning might be the result of exploitation competition (in this case potentially driven by food resources), we collected insects at the study sites. We found no support for this idea. We found that activity times in some bat species varied on yearly bases, but no bats showed variation based on the netting site. However, we found a strong site effect for insects captured during summer 2010. Not only did these sites differ in proportions of captured insect taxa, they also differed in proportions of captured insects belonging to different size groups as well as in times when different size groups were mostly active. For example, the highest peak of Coleoptera at Kelly Pond site was due to small (LG1) coleopterans active in the first two hours after the sunset, while at Henry Lake Creek, the peak was due to LG1 coleopterans

active between 3 and 4 h after sunset. LG1 hemipterans (approximately 67% of all hemipteran captures) peaked at Kelly Pond within the first hour after sunset, while at Henry Lake Creek hemipterans (approximately 65% of all hemipteran captures) peaked between 3 and 4 h after sunset; yet LG1 and LG2 were present in similar amounts. Similarly, while 71% of dipterans captured at Kelly Pond were LG1 captured within first hour after sunset, at Henry Lake Creek, the majority of captured dipterans were medium sized (LG2) and were equally active throughout the night. Ephemeroptera were the third most abundant insect taxon at Henry Lake Creek, none were present at Kelly Pond.

There are other possible causes for the shifts in temporal partitioning among the bats at these 2 ponds. For example, Carothers and Jaksic (1984) discussed interference competition, an alternative approach suggesting that when species are competing for the same resources, the dominant species could displace the subordinate one(s) to different activity times. In this case, direct effects of interference, such as harassment, robbing, and predation by competing species, can be eliminated through temporal partitioning. If this holds true, then there is a possibility during summers 2009 and 2011 that evening bats were causing temporal partitioning as their abundance increased, while big brown bats caused temporal shifting in activities of other species as its abundance increased.

Finally, we cannot exclude other factors that might have caused changes in temporal partitioning, such as availability of roosts near the netting sites (Adams and Thibault 2006). Evening and big brown bats roost in large tree cavities or man-made structures while eastern red bats and Seminole bats roost individually hidden in foliage (Schmidly 2004; Ammerman et al. 2012). Therefore, differences in activity times at the ponds could be driven by distances that bats had to travel in order to reach the water

sources. However, Adams and Thibault (2006) believe that this might not be a viable explanation as a majority of bats (especially pregnant and lactating females) would choose to roost as close to the water as possible.

Our study shows that temporal partitioning occurs in the insectivorous bat community in the pine forests of southeastern Texas. But, interestingly, the pattern is fluid and might be caused by various environmental factors, perhaps not necessarily by food resources as we hypothesized. These bats might have different preferences for foraging grounds (and prey), however, they still are likely to share the watering holes especially when stable water bodies are as scarce as they are in Sam Houston National Forest, Texas. We believe that more studies of this type need to be conducted in the future to understand the mechanisms behind the observed temporal partitioning. Understanding of this phenomenon could facilitate better understanding of structure and function of bat communities, and to development of effective management plans.

CHAPTER FIVE

Using Next-Generation Sequencing to Determine Diet of the Tri-colored Bat, *Perimyotis subflavus*

Abstract

Diet of bats was traditionally determined by examining gut contents or feces under the microscope. However, this approach usually reveals diet only to the levels of order or family. In recent years, great strides in DNA technologies have led to novel approaches for dietary studies. Using next-generation sequencing (pyrosequencing) of a single fecal pellet from the tri-colored bat (*Perimyotis subflavus*) netted in the pineywoods of eastern Texas, we identified 50 prey species belonging to 3 orders--Lepidoptera (53.8%), Diptera (15.8%), and Coleoptera (18.3%), which accounted for nearly 88% of all identified prey. The remaining 12% of the sample was identified as the tri-colored bat. Previous studies demonstrated that this bat prefers softer prey, but 18% of the sequences in our sample belonged to the coleopteran June bug (*Phyllophaga crinita*). Our study provides rare insight into the diet of tri-colored bats and reveals that this species exhibits a much wider prey base at the species level than previously realized. This project also demonstrates the feasibility of using next generation sequencing as an effective, non-invasive technique to study bat diets.

Introduction

The tri-colored bat is one of the smallest North American bats. It is a common member of bat communities throughout eastern North America and Central America

(Fujita and Kunz 1984). As forest bats in North America are facing mounting challenges to survival, such as habitat loss, wind turbine fatalities, and white nose syndrome (Dixon et al. 2013), it is important to fully understand the natural history of these bats in order to construct effective conservation plans. Habitat (Menzel et al. 2005; Farrow and Broders 2011; Perry 2011; Titchenell et al. 2011) and roost (Perry and Thill 2007; Perry et al. 2008; O’Keefe et al. 2009) preferences of tri-colored bats are well studied. However, only a few studies have investigated dietary habits of this species (Carter et al. 2003; Whitaker 2004). All of the previous accounts of the tri-colored bat’s diet relied on microscopic examination of fecal samples. Although this approach provided valuable information about bat diets, mainly at the levels of order or family of insects, it seldom provided prey identification at the finer scales (e.g., specific level) needed for conservation plans.

In recent years, molecular techniques have been applied to bat dietary studies. Currently, the method most commonly used by bat ecologists is the one developed by Clare et al. (2009), in which individual insect fragments are removed from a fecal sample, and DNA is extracted and sequenced from each fragment. This method has provided a glimpse into the complexity of foraging habits of bats such as eastern red bat (*Lasiurus borealis* – Clare et al. 2009), little brown bat (*Myotis lucifugus* – Clare et al. 2011), Antillean ghost-faced bat (*Mormoops blainvillei* – Rolfe et al. 2014), and sooty mustached bat (*Pteronotus quadridens* – Rolfe et al. 2014). However, as only individually selected insect fragments are chosen for sequencing, some prey items that are more fully digested or prey of small body size might be missed by this method.

Next-generation sequencing (NGS) technologies have recently emerged as useful tools with ecological applications. NGS includes multiple sequencing methods which allow high-throughput sequencing: pyrosequencing - 454 GS FLX; sequencing by synthesis – Illumina MiSeq, Illumina GAIIx, and Illumina HiSeq 2000; ligation and two-base coding - SOLiDv4; dideoxy chain termination – Sanger 3730xl; proton ion detection - Ion Torrent); and single-molecule real time sequencing - PacBio (Liu et al. 2012; Quail et al. 2012). All of these methods provide cost reduction with great increase in output and accuracy (Liu et al. 2012). Proton ion detection and pyrosequencing are proven methods for effectively sequencing DNA samples that are extracted from whole fecal samples. The former has been used to analyze feces from Daubenton's bat (*Myotis daubentonii* – Vesterinen et al. 2013) and pyrosequencing on feces from mammals such as voles (*Microtus oeconomus* and *Myodes rufocanus* - Soininen 2009), Himalayan brown bear (*Ursus arctos isabellinus* – Valentini et al. 2008, 2009), and Australian fur seal (*Arctocephalus pusillus* – Deagle et al. 2009). To our knowledge, no attempt has been made to use pyrosequencing to analyze contents of bat feces. Therefore, the objective of this study was to use pyrosequencing to sequence a complex mixture of COI amplicons from DNA samples extracted from an entire fecal sample to provide a high-resolution (i.e., species level) description of the diet of tri-colored bats.

Methods

An adult male tri-colored bat (*Perimyotis subflavus*) was captured at Henry Lake Creek in Sam Houston National Forest, San Jacinto County, Texas, on 24 June 2011 (Debelica-Lee and Wilkins 2014). A fecal sample was collected, placed into a microcentrifuge vial stored on ice, and later (within 12 h), frozen at -80 °C until DNA

extraction. DNA was extracted using a QIAamp DNA stool mini kit (Qiagen Inc., Valencia, CA) following the instructions provided with the kit. The mitochondrial cytochrome c subunit 1 (COI) gene (710 bp fragment) was amplified using universal DNA primers LCO1490 and HCO2198 primers that have been optimized for identification of Arthropoda (Folmer 1994) and 5 x OmniTaq LA PCR Kit (DNA Polymerase Technology, Inc., Saint Louis, MO). Sample amplification conditions were as follows: 94 °C for 2 min, followed by 40 cycles of 94 °C for 1 min denaturation, 55 °C for 1 min annealing, and 68 °C for 2 min elongation.

Research and Testing Laboratory (Lubbock, Texas) generated the sequence library and sequenced the PCR product using Roche 454 GS_FLX pyrosequencing technologies. Based upon BLASTn+ derived sequence identity percentage, the sequences were identified to the lowest discernible taxonomic levels. Sequences with identity scores greater than 97% identity were resolved to species, 95% - 97% to genus, 90% - 95% to family, 85% - 90% to order, 80 - 85% to class, and 77% - 80% to phylum. Any match below this percent identity was discarded (Bailey et al. 2010; Andreotti et al. 2011).

Results

Altogether, 3813 DNA sequences belonging to 51 species, including tri-colored bat, were identified from the fecal sample. More than half of the sequences belonged to Lepidoptera (53.7%), followed by Coleoptera (18.3%), Diptera (15.8%), tri-colored bat (12%), and unknown Insecta (0.2%). Of 51 prey species, 7 contributed approximately 94% of all identified sequences (Table 5.1): *Rhodostrophia calabra* (Order Lepidoptera), *Chiasmia aestimaria* (Order Lepidoptera - Tamarisk peacock moth), *Cossus cossus* (Order Lepidoptera - goat moth), *Choristoneura conflictana* (Order Lepidoptera - large

Aspen tortrix), *Chymomyza procnemis* (Order Diptera - a fruitfly), *Drosophila medioconstricta* (Order Diptera – a fruitfly), and *Phyllophaga crinite* (Order Coleoptera - June bug). Approximately 25% of identified sequences belonged to known agricultural pests (Table 5.1).

Table 5.1. Diet of a male tri-colored bat captured in Sam Houston National Forest, San Jacinto County, Texas, on 24 June 2011. Percentage values in table represent percent of total number of recovered DNA sequences from the sample. Prey items in bold font are considered to be agricultural pests.

Order	Family	Genus	Species	%
Lepidoptera	Arctiidae	<i>Eucereon</i>	<i>Eucereon consorta</i>	0.446
	Cossidae	<i>Cossus</i>	<i>Cossus cossus</i>	4.301
		<i>Holcocerus</i>	<i>Holcocerus tancrei</i>	0.210
	Crambidae	<i>Ostrinia</i>	<i>Ostrinia orientalis</i>	0.026
	Drepanidae	<i>Drepana</i>	<i>Drepana falcata</i>	0.734
	Gelechiidae	<i>Pectinophora</i>	<i>Pectinophora gossypiella</i>	0.026
	Geometridae	<i>Rhodostrophia</i>	<i>Rhodostrophia calabra</i>	41.254
		<i>Godonela</i>	<i>Chiasmia aestimaria</i>	1.862
	Lycaenidae	<i>Jalmenus</i>	<i>Jalmenus evagoras</i>	0.026
			<i>Jalmenus eubulus</i>	0.052
		<i>Cacyreus</i>	<i>Cacyreus marshalli</i>	0.105
		<i>Plebejus</i>	<i>Plebejus christophi</i>	0.131
		<i>Pseudophilotes</i>	<i>Pseudophilotes</i>	0.052
			<i>abencerragus</i>	
		<i>Chilades</i>	<i>Chilades trochylus</i>	0.079
		<i>Celastrina</i>	<i>Celastrina argiolus</i>	0.026
	Nepticulidae	<i>Acalyptis</i>	<i>Acalyptis lesbia</i>	0.079
	Noctuidae	<i>Helicocheilus</i>	<i>Helicocheilus ionola</i>	0.026
		<i>Heliothodes</i>	<i>Heliothodes diminutivus</i>	0.026
		<i>Schinia</i>	<i>Schinia pulchripennis</i>	0.026
		<i>Leuconycta</i>	<i>Leuconycta diptheroides</i>	0.262
		<i>Feltia</i>	<i>Feltia jaculifera</i>	0.026
		<i>Mechanitis</i>	<i>Mechanitis polymnia</i>	0.026
	Nymphalidae	<i>Thyridia</i>	<i>Thyridia psidii</i>	0.105
		<i>Acraea</i>	<i>Acraea igola</i>	0.026
		<i>Archon</i>	<i>Archon apollinaris</i>	0.026
	Papilionidae			
	Prodoxidae	<i>Tegeticula</i>	<i>Tegeticula elatella</i>	0.026
			<i>Tegeticula baja</i>	0.052
	Pyrilidae	<i>Hypsipyla</i>	<i>Hypsipyla robusta</i>	0.026
	Saturniidae	<i>Rhodinia</i>	<i>Rhodinia fugax</i>	0.026
	Sesiidae	<i>Chamaesphecia</i>	<i>Chamaesphecia proximata</i>	0.367
	Sphingidae	<i>Agrius</i>	<i>Agrius convolvuli</i>	0.918
	Tortricidae	<i>Choristoneura</i>	<i>Choristoneura conflictana</i>	1.862

Table 5.1 Continued

Order	Family	Genus	Species	%
		<i>Ptycholoma</i>	<i>Ptycholoma lecheana</i>	0.026
		<i>Argyrotaenia</i>	<i>Argyrotaenia alisellana</i>	0.131
			<i>Argyrotaenia quercifoliana</i>	0.262
			<i>Argyrotaenia repertana</i>	0.026
			<i>Argyrotaenia coloradana</i>	0.026
		<i>Acroclita</i>	<i>Acroclita subsequana</i>	0.026
	Zygaenidae	<i>Zygaenia</i>	<i>Zygaenia filipendulae</i>	0.026
			<i>Lepidoptera sp</i>	0.157
Coleoptera	Scarabaeidae	<i>Phyllophaga</i>	<i>Phyllophaga crinita</i>	18.07
	Cerambycidae	<i>Monochamus</i>	<i>Monochamus alternatus</i>	0.236
Diptera	Anthomyiidae	<i>Eutrichita</i>	<i>Eutrichota paratunicata</i>	0.026
	Chironomidae	<i>Kiefferulus</i>	<i>Kiefferulus martini</i>	0.393
		<i>Lipiniella</i>	<i>Lipiniella fujiprimus</i>	0.157
		<i>Dicrotendipes</i>	<i>Dicrotendipes pelochloris</i>	0.21
	Drosophilidae	<i>Chymomyza</i>	<i>Chymomyza procnemis</i>	10.333
		<i>Drosophila</i>	<i>Drosophila medioconstricta</i>	4.196
		<i>Drosophila</i>	<i>Drosophila hirtipes</i>	0.105
	Muscidae	<i>Drymeia</i>	<i>Drymeia hamata</i>	0.288
	Sepsidae	<i>Microsepsis</i>	<i>Microsepsis furcata</i>	0.052

Discussion

All previous studies of diets of tri-colored bats were based on the traditional morphological approach to dietary study using microscopy to identify insect fragments in fecal samples (Carter et al. 1998; Carter et al. 2003; Whitaker 2004; Feldhamer 2009). Most of those studies revealed that tri-colored bats feed on a diverse diet including Diptera, Coleoptera, Trichoptera, Hymenoptera, Homoptera, and Lepidoptera. However, other studies (Carter et al. 1998; Feldhamer et al. 2009) reported that tri-colored bats preferred soft-bodied prey (primarily Trichoptera, Diptera, and Lepidoptera) over hard-bodied prey such as Coleoptera. Both Carter et al. (1998) and our study found that although Coleoptera comprise the majority of available taxa at the foraging grounds, they represented a disproportionately small fraction of the diet (Figures 5.1 and 5.2). This was not unexpected as tri-colored bats are small-bodied and have small jaws, making it difficult to handle hard-bodied prey such as beetles. However, 98% of all beetles ($n = 8,195$) captured at our netting sites were small (<10 mm long, unpublished data). This

might explain the relatively high proportions of Coleoptera in the tri-colored bat's diet because insect body hardness increases with body size, so small ("hard-bodied") beetles might require similar bite force as larger ("soft-bodied") moths (Aguirre et al. 2003). Our study confirms that tri-colored bats feed on a wide variety of prey within limited number of prey orders, preferring soft-bodied prey such as Lepidoptera and Diptera (Figures 5.1 and 5.2).

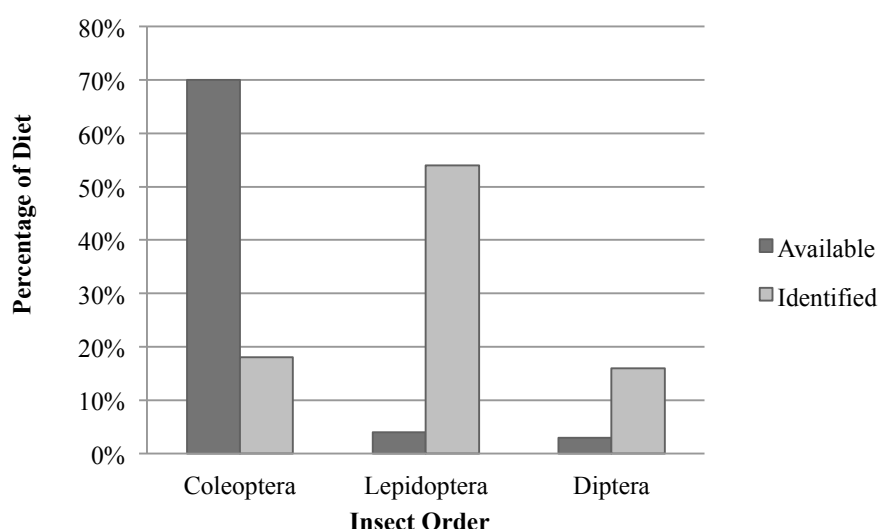


Figure 5.1. Percent abundance of Coleoptera, Lepidoptera, and Diptera available at the netting site compared to the percent abundance of these taxa identified in fecal sample of the tri-colored bat, *Perimyotis subflavus*, in our study.

We recognize that comprehensive understanding of this species' diet requires a larger number of fecal pellets from a larger sample of bats representing both sexes and the range of age classes, and that increased sample size might reveal different feeding patterns than described here. However, even the limited data this study offers is a great

step toward better understanding of the tri-colored bat's diet as a vital element in formation of an effective conservation plan.

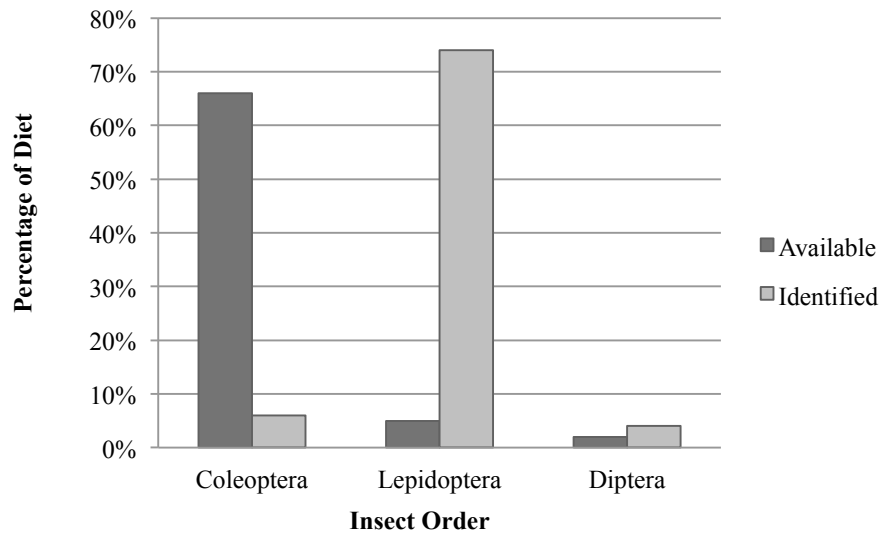


Figure 5.2. Percent abundance of Coleoptera, Lepidoptera, and Diptera available at the netting site compared to the percent abundance of these taxa identified in fecal sample of the tri-colored bat, *Perimyotis subflavus*, in Carter et al. 1998 (McIntosh County, Georgia).

This study clearly demonstrates the superiority of NGS (in this case, pyrosequencing) over the traditional morphological approach to dietary studies as it identified 50 prey species in a single fecal sample. Although pyrosequencing was developed >20 years ago (Ronaghi 2001), and it has been used in dietary studies of some other species of mammals (Valentini 2007; Valentini et al. 2008; Deagle et al. 2009; Soininen 2009; Valentini et al. 2009), this method had not been applied in bat dietary studies until this project. This study demonstrates that NGS, such as pyrosequencing, can be an effective, non-invasive technique for study of bat diets. In the future, this approach

might prove to be superior to other PCR methods as it utilizes DNA extracted from an entire fecal sample.

CHAPTER SIX

Discussion

As bats in North America face increasing perils from habitat loss, wind farms, and white nose syndrome, ecologists need new effective conservation plans (Dixon et al. 2013). However, in many cases, bat ecologists lack data needed to make the best decisions. This dissertation provides new information about a forest-dwelling bat community from southeastern Texas that can be used in the future when considering directions that further conservation efforts might take.

Chapter Two of this dissertation provides evidence of summer presence of at least 6 bat species (big brown, eastern red, evening, Seminole, southeastern myotis, and tri-colored bats). This study offers important new insights into phenology of at least 3 of these bat species: big brown, evening, and Seminole bats. Results indicate that these 3 bats have extended breeding seasons. In contrast to previous data from Texas, we found that parturition season in these species might start in early May if not earlier, and might extend deep into July (Debelica-Lee and Wilkins 2014). These 3 species were previously thought to exhibit seasonal monoestry, a common reproductive mode in temperate bats. In temperate climates, bats go through parturition and lactation during a short period (usually within 2 months) because food resources are in high supply during this period only. However, our study (Debelica-Lee and Wilkins 2014) indicates that Seminole, evening, and big brown bats in southeastern Texas are exhibiting an extended seasonal monoestry. Here, parturition and lactation are extended to a period >2 months. This new

information needs to be taken into consideration when management decisions in southeastern Texas pine forests are made because at least some sections of these forests are managed for red cockaded woodpeckers by annual burns. Rodrigue et al. (2001) indicated that exposure to heat and smoke might be detrimental to bats. If burns are occurring at the time when pregnant females are in the area, fire and smoke might cause distress in these females and, thereby, impact reproductive success.

Chapter Three reported the relationship between bat ecomorphology and community assemblage. Even though the same bat species were present at both study sites, there were some differences in community assemblages. These differences were reflected in the proportions represented by each bat species at the 2 sites. Most likely, types of habitat present at the 2 sites brought about these differences. The Kelly Pond site was surrounded by young pine plantations, and was located in the managed section of the forest with burns conducted every 3 years. Clutter levels at this site were very low. In contrast, the Henry Lake Creek site was not managed and was dominated by old growth pines and hardwoods. Clutter levels at this site were very high. As a consequence, bat species that were clutter-intolerant (as indicated by wing morphology) were present in greater proportions at the Kelly Pond site, and species that were clutter-tolerant were present in greater proportions at the Henry Lake site. Additionally, bat species that were intermediate in their wing morphology and echolocation call structure were found in similar proportions at both sites.

These relationships between ecomorphology and habitat clutter are important to understand when constructing new management plans. Intense management might open habitat to clutter-intolerant species, but could also deter clutter-tolerant bat species

because clear-cutting often removes preferred roosts of these bats (old growth trees with large cavities or snags). Similarly, the decision not to manage forested areas at all (no burns, no clear-cutting, no thinning, etc.) might benefit clutter-tolerant species; however, overall bat species diversity might decline as clutter-intolerant species might be excluded from the habitat.

In Chapter Four, this dissertation explores temporal partitioning as one of the axes that bats might use to partition their resources. I found that temporal partitioning is occurring at our study sites, but that this phenomenon is not consistent within the bat community. During this study, bat species participating in temporal partitioning shifted on yearly bases for yet unknown reasons. Based on data, prey availability did not drive temporal partitioning. In addition, it seems that changes in abundances of each bat species did not affect the partitioning. A better understanding of reasons why temporal partitioning is occurring and why it is not stable is needed in order to fully understand the dynamics of the bat community and how to keep their interactions in balance. Without this understanding, management practices might cause a shift in this balance and tip the scale toward one or another species, potentially causing exclusion of one or more species from the community.

In Chapter Five, I report the diet of tri-colored bats at the species level. All previous studies reporting the diet of this species were constrained by the method used (traditional approach) to ordinal level. In recent years, new generation sequencing methods have emerged and provided ecologists with new tools that add finer resolution (genus and species level) to dietary studies. I have applied one of these new generation sequencing methods (pyrosequencing) in this dietary study of bats. Before my study,

pyrosequencing had been used in studies of seals and some herbivores, but not bats. Using this method, I identified 50 prey species in a single fecal pellet from a tri-colored bat. Identified prey belongs to only 3 orders (Lepidoptera, Diptera, and Coleoptera), but within Lepidoptera this bat consumed a wide array of prey species. In the future, knowledge of detailed prey selection by different bat species might lead toward two different revelations: either bats are completely opportunistic and feed on whatever is most available (depending on their ecomorphology, body size, jaw strength, etc.), or they are extremely selective about what they eat and partition niches along dietary axes. Either way, this knowledge is needed while conservation plans are being developed. If bats are purely opportunistic, then bat diet would become a less important element of a management plans. Habitat changes caused by clearcutting or burns would cause shifts in prey base but would not cause stress to bats. Bats would just simply shift their prey base towards what is available. However, if bats are selective feeders at the species level, potential shifts in prey base due to habitat changes might exclude some bats from community.

This dissertation offers new information about the demography, phenology, ecomorphology, temporal partitioning, and diet (albeit for only a single bat belonging to one species) of a bat community residing in the southeastern pine forest in Texas. The research was conducted at only two sites, thus might not be fully representative of whole forest or the broader Coastal Plains ecosystem. Therefore, before definitive conservation plans are constructed and implemented, further work is needed. A large-scale (increased number of sampling sites), long term (multiple years), year-round (including all seasons) study would provide a more-detailed picture and better understanding of this community.

This type of study would fill the information gaps identified by this dissertation and might offer answers to questions either still unanswered or new questions raised by this dissertation.

It is essential that future research is conducted at large scale. Research needs to include as many sites as possible spread across the Coastal Plains. Bat surveys need to include species inventories; age, gender, and reproductive state of each captured bat; capture or roost emergence times; wing measurements; echolocation calls; fecal samples; and prey availability. This will provide a greater picture regarding some of the questions raised by my study. Some of the questions raised by my dissertation are related to reproductive phenology: Are Seminole, evening, and big brown bats exhibiting extended seasonal monoestry only in southeastern Texas or does this shift in phenology occurs through out the Coastal Plains and beyond? How long is this prolonged parturition and lactation season? When does it start, and when does it end? Are any other bat species exhibiting this shift? Year-around data collection would provide a clear picture as to when first females give birth, and when last females end lactation. Additional climate data would suggest whether the shift towards extended seasonal monoestry is caused by proximity of the Gulf of Mexico and its warmer climate, or if it might be an effect of global warming. If discovered that this shift is only found in proximity to the Gulf of Mexico, then climate change is probably not the cause. However, if it occurs farther north, climate change might be the driving force. In this scenario, climate models could help predict how fast and how far this shift in phenology would spread.

Collecting wing measurements and echolocation calls would allow better understanding of the ecomorphology of bats present in southern parts of North America.

Paired with species inventories and clutter measurements at field sites, effects of management practices on bat communities could be predicted and these practices could be adjusted accordingly. If bat biodiversity is threatened as predicted by Wear and Geist (2012, 2013), forests managers could provide bats with suitable habitats either by clearing clutter from some areas (to attract clutter-intolerant species), or by protecting old growth areas (often rich in clutter) to attract clutter-tolerant species.

As data is collected over multiple years and at multiple sites further questions could be answered. For example, we documented temporal partitioning at the 2 watering holes as well as a year-to-year shift in species participating in temporal partitioning. However, we have not found a link between prey availability or varying abundances of different bat species and these shifts. So, what causes these shifts? Do the same species participate in temporal partitioning at every site in the area or does this also differ from one section of the forest to another? What causes the occurrence of partitioning along the temporal axis? If the actual cause is determined, than we could predict which species might participate in any given year and at any given site. It is important to understand these types of interactions among bat species within the community, because human impact on the habitat might exacerbate these interactions to the point that bat species are not just participating in temporal partitioning but some might also start excluding other species at some sites due to agonistic behavior (harassment, chasing, etc.).

Widespread use of new generation sequencing techniques such as pyrosequencing and proton ion detection will undoubtedly broaden our understanding of bat diets. Prey inventories can be built for various bat species, and we could determine if bats are opportunistic feeders or have preferred prey items. New studies can discern if there are

differences between males and females, adults and subadults. These new studies can also determine whether prey base varies with seasons. Finally, one question that bat ecologists have explored for decades can be answered: do bat species participate in dietary niche partitioning. Many studies based on traditional approaches have shown that such partitioning occurs in some species at the ordinal level. However, in cases where dietary niche partitioning was not found, the reason might be that we just have not looked at this phenomenon at a fine enough (i.e., species level) scale. More complete data sets might demonstrate that bats are highly opportunistic, and therefore that any dietary overlap or dissimilarity might be random.

All of these and many more questions need to be and can be answered through planned and well-executed research. These answers can then be used to build extensive and well-rounded conservation plans that will ensure bat biodiversity to stay intact for decades to come.

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