7-3-2013 12:00 AM

Structure of an Ensemble of Insectivorous Bats

Matthew A. Emrich
The University of Western Ontario

Supervisor
Brock Fenton
The University of Western Ontario

Graduate Program in Biology
A thesis submitted in partial fulfillment of the requirements for the degree in Master of Science

Structure of an Ensemble of Insectivorous Bats

(Thesis format: Monograph)

by

Matthew A. Emrich

Graduate Program in Biology

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science

The School of Graduate and Postdoctoral Studies
The University of Western Ontario
London, Ontario, Canada

Abstract

Ensembles of species show distinct characteristics that may permit resource partitioning but few studies focus on more than one or two traits. Using seven sympatric Jamaican bats, I examined features which could allow for spatial, temporal, behavioural and dietary partitioning including wing morphology, echolocation characteristics, flight behaviour, habitat use, and diet. Using acoustic arrays I compared activity patterns at different sites to determine temporal and spatial partitioning and generated flight paths to determine flight speeds. From captured bats I measured wing morphology to examine morphological differences and did genetic analysis of guano to determine dietary partitioning. Morphology, call structure and flight speeds suggested division into cluttered, edge and open foraging habitats. Species sharing habitats partitioned them in time. I found little dietary overlap among species or between seasons. In summary, the ensemble exhibited partitioning in all five dimensions I examined, suggesting multi-dimensional features may aid in ensemble resource division.

Keywords

Insectivorous Bats, Ensemble, Resource Partitioning, Spatial Partitioning, Temporal Partitioning, Behavioural Partitioning, Dietary Partitioning, Flight Speeds, Jamaica, *Molossus molossus*, *Tadarida brasiliensis*, *Mormoops blainvillii, Pteronotus parnellii*, *P. quadridens*, *P. macleayii*, *Macrotus waterhousii.*

Acknowledgments

I thank Dr. Brock Fenton for taking me on as a graduate student and for his support and assistance throughout the entire process. It was through his enthusiasm and guidance that I discovered the amazing world of bats and had opportunities to travel the world.

I thank the Windsor Research Center for partially funding my research including my stay in Jamaica and my field assistants. I am grateful to Dr. Susan Koenig for her guidance, support and her help as a field assistant. I also thank Michael Schwartz for his guidance, technical help and for providing me with transport. I thank Wayne Francis for his work as my field assistant and Sugarbelly for his great cooking. I must also thank Lily Bolt for taking me into her home and treating me like family and Colin Hayward for his help as a field assistant and for keeping my spirits up. I also thank the National Environment and Planning Agency (NEPA) for giving me permission to conduct my research.

I thank Dr. Elizabeth Clare for performing the genetic analyses used in my thesis. Her help saved me from spending countless hours sorting through piles of guano and manually identifying insect remains.

I thank Dr. Liana Zanette, who served as my advisor and provided me with guidance throughout my project and for reading my thesis before submission. I also thank Dr. Jack Millar who provided guidance as my advisor and served on my thesis defence committee. I am grateful to Dr. Sheila Macfie for serving on my proposal defence committee and Dr. Amanda Moehring and Dr. Jim Staples for serving on my Thesis defence committee.

I thank Dr. Liam McGuire, for helping me develop my project, analyze my data and for editing my thesis. His critical review of my project at every stage helped me build a

stronger story. I would like to thank Dr. Amanda Adams for teaching me how to perform and analyze acoustic recordings, for her constant guidance and for her editing skills. I must also thank the other members of my lab for their help, support and their friendship, especially Erin Fraser, Colin Hayward, Rachel Hamilton, Meredith Jantzen, Leslie Reynolds, Lindsey Clairmont and Toby Thorne.

Finally I thank my friends and family, especially my parents, Jack and Audrey Emrich, for their constant support and financial aid through this major life change.

Table of Contents

List of Tables

List of Figures

List of Appendices

Chapter 1 – Introduction

1.1 Communities and Ensembles

Biological communities consist of variable numbers of species interacting across temporal and spatial domains (Ricklefs, 2007). To be considered a community, all taxonomic groups within the area, both autotrophs and heterotrophs, must be included (Patterson *et al*., 2003). All of the species either directly or indirectly influence one another (Ricklefs, 2007). Due to the complexity of the system, it becomes too costly, time consuming and taxonomically challenging to analyze species interactions in complete biological communities (Patterson *et al*., 2003). Some studies have attempted to examine them (Paine, 1980), but their analyses were performed on simple systems omitting some members of the communities. For more complex systems, the study of subsets is often the most logical approach (Patterson *et al*., 2003).

There are different levels to consider for subsets of communities (Patterson *et al*., 2003). An assemblage is a group of species sharing a taxonomic level. All mammals would be considered an assemblage (Fauth *et al.*, 1996). A guild represents species that share a functional characteristic such as a common diet (Fauth *et al.*, 1996). An ensemble is a subset that combines the two previous definitions, i.e., the assemblage and the guild, by including species that share common taxonomic classification and functional characteristics (Fauth *et al.*, 1996). Sympatric insectivorous bats would fall under the category of an ensemble. Which subset one chooses to study depends on both the complexity of the system and the question being asked. For biological hot spots, areas with increased endemic fauna, such as the Caribbean islands (Myers *et al*., 2000), examining species ensembles becomes the first step in understanding the complex interactions that allow communities to achieve a high level of biodiversity.

1.2 Partitioning

Two main hypotheses are invoked to explain interspecific competition. They are competitive exclusion and neutral theory of biodiversity and biogeography (Gatti, 2012). The neutral theory of biodiversity and biography argues that a community can be diverse

without differentiation of the resources and environmental conditions a population requires over its lifetime, in other words their niches (Hubbell, 2008; Russell *et al.*, 2010). The principle of competitive exclusion conversely argues that species co-exist through variation in the niches they occupy (Hardin, 1960). Levine and HilleRisLambers (2009) provided experimental evidence supporting the competitive exclusion principal which they suggest is the main mechanism involved in maintaining species diversity. Interspecific competition is believed to be the most important factor in determining the number of species in an ensemble (Ramesh *et al*., 2012). Species may reduce competition by using different resources, such as shelter, food or space or alternately, they may use the same resource in different ways, referred to as resource partitioning (Russell *et al.*, 2010). Morphological, behavioural, spatial, temporal and dietary factors have all been suggested as mechanisms involved in partitioning resources (Schoener, 1974). By increasing the dimensionality, i.e. the number of mechanisms involved in partitioning, an ensemble can increase the number of niches available and support a higher diversity of species (Schoener, 1974).

1.3 Ecomorphology as a Means of Partitioning

Morphology limits an organism's range of behaviours (Swartz *et al*., 2003). Ecomorphology combines observations of morphology and behaviour to determine how an organism exploits its environment (Swartz *et al*., 2003). Apparent differences in morphology have been observed across all major taxonomic groups and have resulted in unique methods of partitioning. Morphology may influence how an organism is able to forage. For example, Werf *et al.* (1993) noted that monocot plants with large roots systems outcompeted species with small roots by growing above ground biomass at a increased rate. Aldridge and Rautenbach (1987) suggested wing morphology determined both speed and manouevrability in bat flight. Morphology can also be an indicator of where a species can forage. Albertson (2008) and Losos (1990) observed morphological differences associated with spatial partioning in cichlids and *Anolis* lizards respectively. Finally, morphology can influence the diet of an organism. Hayward and Garton (1988) suggested that differences in wing parameters of an ensemble of owls resulted in dietary partitioning among species. Spencer (1995) and Barton *et al.* (2011) hypothesized that

morphology correlated to dietary partitioning in both Bovidae and beetles, respectively. These examples illustrate an overall trend observed in many ecomorphological studies. Morphology alone, however, cannot account for all means of partitioning, especially in ensembles with morphologically similar species.

1.4 Spatial, Dietary and Temporal Partitioning

Schoener (1974) proposed spatial partitioning as the most common form of resource partitioning and many studies, from a range of organisms, support this point of view. Spatial partitioning can give species access to different resources. Weltzin and McPherson (1997) reported that some plant species accessed ground water at different depths in the soil. The spatial scale used may also influence partitioning. Kadye and Chakona (2012) reported a fish assemblage, with both large and fine scale partitioning in different sections of the river and at different water depths. Buckley and Roughgarden (2005) reported landscape scale partitioning of anole species, as well as small-scale differences in perch height. The habitat preference of prey items is also an influence. Ramesh *et al.* (2012) reported large carnivores partitioning space in relation to their prey's habitat use. Lack of spatial partitioning can result in resource partitioning as well. Takahashi *et al.* (2005) observed that spatial aggregation of an insect community decreased competition between species using common resources.

Diet is the second most invoked aspect of partitioning (Schoener, 1974) and has been observed in many systems (Dial, 1988; Spencer, 1995; Platell *et al*., 2010; Steenweg *et al*., 2011 Ramesh *et al*., 2012). Steenweg *et al.* (2011) and Dial (1988) reported dietary partitioning in sympatric sea birds and woodrat species, respectively. Dietary partitioning may be achieved through morphological differences between species. Platell *et al.* (2010) reported that differences in the jaw structures of three sympatric fish decreased prey overlap. Competition among species may also partition diet by limiting foraging behaviour. Inouye (1978) reported that when competitors were removed, bumblebees increased their dietary breadth. Dietary partitioning may not always occur, however. Farrell *et al.* (2000) reported that of four sympatric carnivores, jaguar and pumas had overlapping diets.

Schoener (1974) argued that temporal partitioning is the least employed means of partitioning and, as such, is uncommon. However, evidence demonstrates its real or potential importance (Cotton 1998; Weltzin and McPherson 1997; Kronfeld-Schor and Dayan 1999; Gutman and Dayan 2005; Gordon *et al.,* 2010; Veen *et al.,* 2010; Razgour *et al.* 2011a; Kadye and Chakona 2012; Ramesh *et al.,* 2012). Temporal partitioning ranges from fine scale temporal activity to large scale seasonal variation. On a daily scale, an assemblage of 13 lizards was reported exhibiting varied temporal activity (Gordon *et al.,* 2010). Hummingbirds temporally partitioning flower resources, with smaller birds using flowers either early or late in the flowering period when nectar production was reduced (Cotton, 1998). On a seasonal scale, weevils varied dormancy cycles when multiple species were consuming the same species of acorn (Venner *et al,* 2011). Competition between species may also limit foraging time. Gutman and Dayan (2005) noted an increase in foraging, from diurnal to both diurnal and nocturnal, when one species of spiny mouse was removed from a two mouse system. Seasonal differences in habitat structure can also influence interactions between species. During periods of flooding, fish assemblage compositions change (Kadye and Chakona, 2012).

1.5 Bats as Model Organisms

In the tropics, an increase in the number of ecological niches allows communities to support higher species diversity (Ricklefs, 2007). For mammals, species richness in the tropics is mostly due to the diversity of bats (Buckley *et al*., 2010). Bats, especially insectivorous species, often have a high diversity of morphologically similar sympatric species (Nicholls and Racey, 2006). Bats avoid competition by partitioning resources in at least one niche dimension (Arlettaz *et al*., 1997; Fukui *et al*., 2009, Siemers and Swift, 2006), though in some instances there is no evidence of resource partitioning among species (Andrianaivoarivelo *et al*., 2006). Bat ensembles are excellent model systems which can assist in the study of various species interactions. Their diversity, large colony sizes, congregation in a central location and our passive monitoring techniques permit morphological, dietary, spatial and temporal data collection. Extensive literature on bat ecology and multiple guild associations within the order (insectivores, frugivores, piscivores, nectivores and carnivores) (Patterson *et al*., 2003) are also excellent tools to

study these interactions. The ecological roles bats play within a community, such as pest control, pollination and seed dispersal, also make them an economically important species to examine (Patterson *et al*., 2003). As a result, studies of bats may lead researchers to glean a better understanding of ecological diversity and interactions within communities (Patterson *et al*., 2003).

1.6 Ecomorphology in Bats

Wing morphology is one of the most important factors determining where and how bats fly (Aldridge and Rautenbach, 1987), and can best be described in terms of aspect ratio (AR), forearm length, wing tip index (I) and wing loading (WL) (Jacobs and Barclay, 2009). Combinations of the above characteristics also affect flight behaviour. This can result in different foraging strategies (Jacobs and Barclay, 2009), and flying styles (Vaughan, 1970). Varied techniques of flying give bats greater access to diverse habitats and prey (Vaughan, 1970). Species with high aspect ratios can fly faster and for longer distances but in turn have reduced manoeuvrability (Norberg and Rayner, 1987). This flying style is used by bats who feed in open habitats, either above the tree canopy or in clearings (Vaughan, 1970). Bats with low aspect ratios fly slowly exhibiting high manoeuvrability thus allowing them to forage in dense vegetation (Vaughan, 1970). Large wing tip indices, indicating rounded wings, coincide with slow speed flight and hovering (Norberg and Rayner, 1987). Long forearm lengths aid in attaining greater speeds (Norberg and Rayner, 1987). High wing loading allows for greater flight speeds but little manoeuvrability (Jacobs and Barclay, 2009). While morphology may confer the ability to access these habitats, bats must also possess the ability to orient the habitat in darkness, and most bats do this with echolocation (Kalko, 1995).

1.7 Echolocation in Bats

Different echolocation strategies provide differential access to habitats which vary in physical parameters (Fenton, 1990). The structure of an echolocation call provides information on a bat's potential foraging locations (Fenton, 1990). One character to consider is duty cycle, the percentage of time that calls are emitted (Schnitzler and Kalko, 2001). Bats using high duty cycle (HDC) echolocation appear specialized for detecting

fluttering targets in cluttered habitats (areas of dense vegetation) (Fenton *et al*., 2012). The *Pteronotus parnellii* complex (Clare *et al.*, 2013) is the only group of HDC echolocators among bats of the New World (Fenton *et al*., 2012). All other laryngeally echolocating bats use low duty cycle echolocation (LDC) (Fenton *et al*., 2012). LDC bats can produce low or high intensity calls. Generally, bats that are active in cluttered habitats, e.g., *Macrotus waterhousii*, use low intensity echolocation calls, reducing their detectability (Kalko, 2004). These bats may locate prey using prey-generated sounds rather than echolocation (Fenton, 1990). The use of high intensity echolocation calls by LDC bats increases the range from which echoes can return, thus providing better access to foraging opportunities in edge and open habitats (Brinkløv *et al*., 2009, Surlykke and Kalko, 2008). Species foraging in open environments use narrowband calls consisting of shallow, long duration FM, frequency modulated, sweeps (Fenton, 1990). Such signals give low spatial resolution but travel greater distances (Simmons, 1973). Species using edge environments employ a combination of narrowband and broadband calls (Fenton, 1990). This method provides good range resolution and descriptive information of the prey (Simmons, 1973, Schnitzler and Kalko, 2001).

1.8 Methods to Measure Partitioning in Bats

Echolocation is an active system, meaning that bats use echoes of sounds they produce to collect information about their surroundings, from obstacles to food. In addition, the system is often flexible, allowing bats to respond to echo feedback by changing the characteristics of their calls. This allows researchers/biologists to assess patterns of habitat use and activity of bats by acoustically monitoring their echolocation calls (Adams *et al*., 2012). As an added benefit, echolocation calls vary among species allowing species identification based solely on call characteristics, although this is not true for all species (Fenton and Bell, 1981; Murray *et al*., 2009). There are disadvantages to acoustic monitoring. Not all bats produce calls of the same intensity and directionality and as a result, some species will be overrepresented or underrepresented in any survey (Adams *et al*., 2012, Brinkløv *et al*., 2011). Another disadvantage is that acoustic surveys provide no information about population numbers (Adams *et al*., 2012). Acoustic monitoring provides measures of habitat use, time of activity, and flight speeds in an

undisturbed, natural setting (Adams *et al*., 2012). By using a microphone array, the slight variation in call detection times across multiple microphones can be used to triangulate a bat's position (Surlykke *et al*., 2009). By using the bat's travel distance between calls and the time it took to travel the distance, the bat's flight speed can be calculated (Surlykke *et al*., 2009).

The traditional method of studying diets in bats has relied on visual identification of insect remains present in the guano or stomach (Findley and Black, 1983; Hickey *et al*., 1996; Fukui *et al*., 2009; Andrianaivoarivelo *et al*., 2006; Feldhamer *et al*., 2009; Mancina *et al*., 2012). Visual identification of insect remains classifies species to ordinal or in the best case, family level. This method lacks the precision required to address predictions about resource partitioning (Bohmann *et al*., 2011). New techniques in genetic sequencing using DNA barcoding have allowed species identification of insect remains, providing the level of precision required to address resource partitioning in bats (Bohmann *et al*., 2011; Razgour *et al*. 2011b).

1.9 Spatial, Temporal and Dietary Partitioning in Bats

Many studies have shown habitat preference as a means for resource partitioning in bat ensembles (Kunz, 1973; Saunders and Barclay, 1992; Arlettaz, 1999; Nicholls and Racey, 2006; Razgour *et al*., 2011a). Although morphology and echolocation have been shown to influence foraging habitat in bats, spatial partitioning can occur without their influence. Species lacking morphological and echolocation differentiation have been observed partitioning space (Arlettaz, 1999; Nichools and Racey, 2006). Habitat type can also influence patterns of species use. Frugivores were observed having different activity patterns in selectively logged and successional forests (Bumrungsri *et al.,* 2007). Patriquin and Barclay (2003) examined the habitat use in relation to different tree harvesting methods and observed different patterns of activity in relation to each method. In arid environments different species associate with different pond sizes (Razgour *et al.*, 2011a). Williams *et al.* (2006) suggested that the introduction of non-native habitats could increase species richness by diversifying habitats. Habitat can even be partitioned within a site. Differences in activity at ground level, in the canopy, and above the canopy have been report (Menzel *et al.*, 2005). Not all studies support spatial partitioning

however (Mancina *et al.*, 2012). In these instances, other factors such as dietary partitioning may also play a role.

Most studies examining dietary partitioning in bats have focused on a few closely related species within an ensemble (Hickey *et al*., 1996; Arlettaz *et al.*, 1997; Siemers and Swift, 2006; Andrianaivoarivelo *et al*., 2006; Fukui *et al*., 2009; Bohmann *et al.*, 2011). Few studies have examined a larger portion of an ensemble (Findley and Black, 1983; Lopez and Vaughan, 2007; Feldhamer *et al*., 2009; Mancina *et al.*, 2012). Results, however, are inconsistent, with some showing partitioning (Findley and Black, 1983; Hickey *et al*., 1996; Fukui *et al*., 2009) and others showing no evidence of it (Andrianaivoarivelo *et al*., 2006; Burles *et al.*, 2008; Feldhamer *et al*., 2009; Bohmann *et al.*, 2011). Genetic analyses have been successful in comparing diets between two sympatric species (Bohmann *et al*., 2011; Razgour *et al*. 2011b), but have yet to examine resource partitioning at an ensemble level.

Some bat ensembles partition temporal domains (Kunz, 1973; Adams and Thibault, 2006; Razgour *et al*., 2011a), but few studies have supported this approach. Jones and Rydell (1994) reviewed emergence times of bat species and noted differences based on diet and foraging strategies. Hickey *et al.* (1996) showed differences in foraging times in two sympatric species. Studies supporting temporal partitioning have mostly focused on temporal activity of bats visiting water resources in arid environments. In arid environments, bats visit water holes at different times (Adams and Thibault, 2006). Partitioning can occur across larger temporal domains as well. Shifts in foraging activity occur between seasons (Razgour *et al.*, 2011a; Bumrungsri *et al.*, 2007). Communities lacking any evident limiting resources show little temporal partitioning (Saunders and Barclay, 1992). Adams and Fenton (in review) noted the lack of a unified method of identifying periods of high activity and proposed that the use of a space-time statistic may reveal temporal partitioning overlooked in the past.

1.10 Multidimensional Partitioning

Most biological studies simplify system dynamics by examining one or two dimensions of partitioning in a small subset of an ensemble. This oversimplifies the complex

interactions within an ensemble and may overlook important means of partitioning and how these means interact with one another (Levine and HilleRisLambers 2009). Ross (1986) examined 37 studies on resource partitioning in fish. He observed that the dimensionality of partitioning increases with the diversity of the assemblage. He also observed increased temporal partitioning as relatedness of species decreased. Bearzi (2005) took a similar approach on the family Delphinidae and noted dolphins using spatial, temporal and dietary partitioning among species. Fasola (1993) examined a sympatric newt community and observed partitioning between prey, habitat, water depth and season. Jacob and Barclay (2009) examined two morphologically similar bats for resource partitioning and observed variation in diet, morphology and echolocation parameters, but no spatial or temporal partitioning. Mancina (2012) examined multiple dimensions of partitioning in four related bats and found variation in diet, temporal activity, morphology and echolocation parameters.

In this study, I examined 7 species, of the possible 14 known from Jamaica. I expected that examining the majority of species across multiple dimensions of partitioning, would provide better understanding of interactions among species in an ensemble, as well as interactions between the different methods of partitioning

1.11 Statement of Purpose

I investigated multi-dimensional resource partitioning in an ensemble of 7 insectivorous bats. I tested predictions from the hypothesis that differences in wing morphology and echolocation behaviour would coincide with differences in habitat use and diet. I took morphological measurements of all bat species, documenting variations in echolocation and flight behaviour, patterns of habitat use, as well as diet, and tested the following predictions:

1) Species with similar morphologies would exploit similar habitats (open, edge, cluttered) corresponding to their wing morphology and echolocation behaviour.

2) Species exploiting similar habitats would show different temporal peaks in activity and/or would show different flight speeds.

3) Species in the ensemble would have little dietary overlap.

Chapter 2 – Materials and Methods

2.1 Study Site

I worked in the Windsor region at the northern edge of Cockpit Country, Jamaica (18°21'N, 77°38'W, elevation 100-500 m). The forest type is wet limestone, with an average canopy height of 15-20 m and a poorly developed understory (Koenig, 2001). The period between December and March is considered to be the dry season in the area, where May to November is wet season (McNab, 1976). I selected this region because the Great Windsor Cave is a roost inhabited by a large and diverse population of bats (Vogel, 1997). Jamaica's bat fauna includes insectivores (14), frugivores (2), nectarivores (4) and piscivores (1) (Nowak, 1994). In the Windsor region the insectivorous bat ensemble includes *Molossus molossus* (velvety free-tailed bat), *Tadarida brasiliensis* (Mexican free-tailed bat) (Molossidae), *Mormoops blainvillii* (Antillean ghost-faced bat), *Pteronotus parnellii* (Parnell's mustached bat), *P. quadridens* (sooty mustached bat), *P. macleayii* (Macleay's mustached bat) (Mormoopidae), *Macrotus waterhousii* (Waterhouse's leaf-nosed bat) (Phyllostomidae) and *Chilonatalus micropus* (Cuban funnel-eared bat) (Natalidae).

2.2 Morphological Measurements

I used mist nets (2.5 m x 10 m, 32 mm mesh size; Ecotone, Gdynia) and harp traps (Forest Strainer, Bat Conservation and Management Inc., Carlysle; custom built 1.5 m x 1.5 m harp trap) between 13 July and 6 August 2011 and between 12 May and 9 June 2012, both considered to be wet season. I selected sites with the highest levels of activity as indicated by acoustic monitoring, increasing my efforts at the lower and upper entrances of the Great Windsor Cave. I did not place mist nets and harp traps near sites which were being acoustically monitored. These were left up either for the entire night or between 2 and 6 hours and were checked every 15 (mist nets) or 5 minutes (harp traps). I held the bats in cloth bags for a maximum of 2 hours and released pregnant females immediately upon capture.

I recorded: a) body mass (M) using a digital scale (±0.1 g), b) time of capture, c) species, d) sex and age (sub-adult and adult), e) state of testes, nipples and whether or not the bat was pregnant or lactating based on visual inspection, f) percent abdomen distension, g) presence or absence of guano in the bag, h) head length, forearm length (fl), length of hand wing (l_{hw}), length of arm wing (l_{aw}), and body width (bw). I photographed both the wing and tail membrane when extended against a sheet of graph paper (metric quad 5 mm) (Figure 6 in Appendix I). All linear measurements were made three times with electronic calipers and the mean in millimetres was recorded. I identified species and sex from morphology.

I calculated total surface area (S) and the surface area of the hand wing (S_{hw}) and arm wing (S_{aw}) (see Figure 7 in Appendix I for visual representations) using Paint version 6.1 (Microsoft, USA) and ImageJ (National Institutes of Health, USA). In Paint, I divided the wing and tail membrane photos into four parts-- hand wing, arm wing, body and tail membrane. In ImageJ, I set the program's scale to match that of the graph paper in the photos. I converted these photos into a binary image which pixelated the wing section black and the background white. I ran a particle analysis to calculate $S_{hw,}$ S_{aw}, body area (S_b) and tail membrane (S_t) in mm^2. I added all the values together and multiplied by two to get S (mm^2). I calculated total wingspan ($B=2(l_{hw}+ l_{aw})+bw$) in mm, wing loading ($WL=Mg/S$) in N/m^2, aspect ratio ($AR=B^2/S$), tip length ratio ($T_l=l_{hw}/l_{aw}$), tip area ratio ($T_s=S_{hw}/S_{aw}$) and tip shape index ($I=T_s/(T_l-T_s)$) based on recommendations by Norberg and Rayner (1987). I arbitrarily classified wing characters into classes based on values presented in Jennings *et al*. (2004) in order to make ecomorphological predictions.

Sexual dimorphism influences habitat use and diets (Radford and du Plessis, 2003, Pinet *et al.*, 2012, Nudds, 1984, Safi *et al.*, 2007, Shine *et al.*, 2003). To account for this, I examined sexual dimorphism within each species, except in *P. macleayii* and *P. quadridens* where there was an uneven sex representation in sampling. I used an independent sample, non-parametric, Kruskal-Wallis test with a Bonferroni correction in xLSTAT, due to non-normal distribution of measurements and multiple tests respectively. I used sex as the group and head length, forearm length, length of hand wing, length of arm wing, body width, wingspan, total surface area, aspect ratio, wing

loading, tip length ratio, tip area ratio and tip shape index as the test fields. If a species was shown to be sexually dimorphic in any of these traits, I separated the sexes for all morphological analyses.

I used an independent sample, non-parametric, Kruskal-Wallis test with a Bonferroni correction in xLSTAT, due to non-normal distribution of measurements and multiple tests respectively, to explore morphological differences among species. I used species as the group and head length, forearm length, length of hand wing, length of arm wing, body width, wingspan, total surface area, aspect ratio, wing loading, tip length ratio, tip area ratio and tip shape index as the test fields. I also ran a Conover-Inman test to do a pairwise comparison between species and rank them based on differences. I ran a principal component analysis (PCA) in xLSTAT to group species according to forearm length, wing loading, aspect ratio and wing tip index.

2.3 Acoustic Monitoring

I acoustically monitored bat activity between 30 May and 4 July 2011. Acoustic monitoring was employed to determine spatial partitioning among species using habitat use data, temporal partitioning among species using periods of peak activity, and behavioural partitioning using flight speed data.

To determine habitat use, I acoustically monitored 9 sites within 1 km radius of the Great Windsor Cave, representing cluttered, open, or edge settings. To classify habitats as one of the three habitat types, I conducted a literature review of how habitats were classified in the past and conducted a 15 m radius habitat assessment of each site. I recorded latitude, longitude, elevation, slope, distance to the cave's lower and upper entrance, percent of each type of ground substrate, percent of each type of understory vegetation, canopy density, circumference at breast height for each tree with a circumference ≥15 cm, height of tree, height of first branch and vine. To calculate latitude, longitude, elevation, area of the patch and distance to both entrances, I used a Garmin eTrex Vista H (Garmin International, Inc., Olathe, KS, USA) GPS unit. I calibrated elevation using a known elevation in the area. The GPS unit was accurate to within 10 m. I calculated canopy density by taking the mean of North, South, East and

West densitometer calculations based on manufacturer's instructions (number of squares reflecting less than 50% of sky, multiplying by -1.04 and adding 100) at the center of a site. To measure the 15 m radius and the circumference at breast height, I used a meter tape. Percent of site composed of each type of substrate (soil, herbaceous plants, leaf litter, woody debris, rock and water), percent of understory composed of each type of vegetation (seedling, herbs, 3-fingered plants, grass, fern and other) and tree heights were independently estimated by both my field assistant and myself, and the mean was taken.

I ran a PCA in xLSTAT to compare the sites and determine habitat classifications (open, edge and cluttered). The characteristics included in the analysis were elevation, slope, average canopy density, area of site covered in trees, percent of site covered in soil, herbaceous plant material, leaf litter, woody debris, rocks, water, percent of understory covered in seedlings, herbs, 3-finger plants, grass, fern and other. Average canopy density, area of site covered in trees, percent of site covered in leaf litter and percent of understory covered in seedlings were the best indicators for the level of clutter. Percent of site covered in water was used to define sites as edge in addition to the level of clutter.

The first site for acoustic monitoring was the front yard of a home. It was approximately 0.3 ha and the grass, which represented 100% of the sites ground cover, was regularly cut. Site 2 was a cliff face that overlooked tree canopy. Site 3 was an area that had been cleared for cultivation but has since been abandoned. It was approximately 0.08 ha and was composed mostly of ferns. Site 4 was a section of river located in a cluttered habitat. Site 5 was a section of river located in an open habitat. Site 6 was the boundary of a cluttered forest and an open pasture. Site 7 was a small patch, 0.3 ha, of forest surrounded by roads and open habitats. Site 8 was a sloped hillside along a forest trail. Site 9 was a forested plateau located between the peaks of two hills.

To record activity and flight paths, I deployed two back-to-back four microphone arrays using eight Avisoft Bioacoustic CMPA microphones (Avisoft Bioacoustics, Berlin, Germany) attached to two Avisoft UltraSoundGate 416 interfaces (Avisoft Bioacoustics, Berlin, Germany) which was based on previous work by Surlykke *et al*.

(2009). In each array, the microphone was 1 m from the next in an upside down T configuration (Figure 8 in Appendix II). The UltraSoundGate was connected to a Dell PP04X laptop computer which continuously recorded from dusk until dawn using Avisoft Recorder USG software (Avisoft Bioacoustics, Berlin, Germany). I recorded files 1 minute in length, with a 250 kHz sampling frequency, a gain of 5 and an 8 bit format. I recorded at each site for at least five nights.

Previously my colleagues in the Fenton lab created a call library for bats in the area by allowing bats to fly on a zipline and recording the calls. Using this library, I identified six of the eight insectivorous species in the ensemble. *C. micropus* and *M. waterhousii* were not detected in acoustic surveys, but all other species, *M. molossus*, *M. blainvillii*, *P. parnellii*, *P. quadridens*, *P. macleayii* and *T. brasiliensis* had distinctive calls.

I analyzed echolocation recordings using CallViewer 18, a MatLab (The MathWorks, Nadick, MA, USA) based program designed to analyze echolocation calls (Skowronski and Fenton, 2008). I used the Quick Summary feature of the program to automatically identify files with calls. If the summary determined that at least one microphone had two or more calls, I manually examined the file. I visually assessed bat presence by examining the spectrograms of channel 1 (the highest microphone off the ground and the most likely to pick up a call) and separated the files based on species.

I randomly selected 10 acoustic files for each species to determine call parameters in CallViewer 18. I selected the call with the highest intensity on each file and ran the auto-detection feature to determine call length (ms), maximum and minimum frequencies (kHz). I calculated the bandwidth (kHz) by subtracting the minimum from the maximum frequency. I recorded the mean and standard deviation for each of the features and determined habitat preference based on work by Fenton (1990). For *M. waterhousii*, calls from free flying bats were not detected in the survey, so acoustic measurements were taken from bats flying on a zipline used to create the call library. I analyzed calls from 2 bats on the zipline, 5 calls from each, with each analyzed call coming from a different pass.

To analyze habitat use, I used the activity index (AI) proposed by Miller (2001). An activity index examines relative bat activity while removing the bias of repeated visits (Miller, 2001). A species AI on a given night is the number of one minute files with echolocation calls from that species. I used xLSTAT to compare species activity among sites by running a nonparametric Kruskal-Wallis test with a Bonferroni correction and a Conover-Inman pairwise comparison, due to some habitats having low activity which created non-normal distributions. I used species as the group and site AI as the test fields to determine species habitat use. I calculated the relative habitat use by taking the species AI on a given night and dividing it by the total AI for that species. Using relative AI, I performed a PCA analysis in xLSTAT to separate species based on habitat use.

I examined temporal activity by converting time stamps on each acoustic file to minutes after sunset (Dateandtime.info, 2011) and creating a frequency table of bat detection (number of nights the species was present during the one minute time period). I used SaTScan v.9.1.1 (SaTScan, Boston, USA) to identify peak activity times for locations and species. Although SaTScan was originally designed to detect disease clusters in space and time, by identifying elevated infection rates compared to background levels, the principals can be translated to see patterns elsewhere (Kulldorff, 2010). I used the program to detect increased levels of activity at a given time across all sites. I created a case file, for each species with the site, time from 50 minutes before sunset to 798 minutes (≈13 hrs.) after sunset (1 minute intervals), and frequency of bat detection at a given time across the five nights. I did a space-time retrospective analysis, with a space-time permutation probability model, time aggregation to 1 and scanned for areas of high and low rates. The output identified periods of peak activity by comparing levels of activity across all sites and determining the probability that one peak in activity, either high or low, was greater than peaks in other locations. For each site I used species with the highest habitat use based on the Kruskal-Wallis analysis, and created a Gantt chart with periods of high and low activity. If temporal partitioning was occurring, I would expect to see differences in high and low peak activity among species.

To determine flight behaviour and speeds, I reconstructed flight paths based on echolocation calls. I selected recordings with a sequence of calls, between 3 and 30

depending on the species, the clarity of the call, and whether the calls were recorded on all four microphones. On two of the five nights, I used a portable ultraviolet light to increase insect abundance near the array and therefore attract bats to the area (Bell, 1980). On the same two nights, I used Robomoth, a motor rotating a piece of tape at the end of a thin metal rod which simulates the fluttering of a moth wing, to attract bats closer to the array (Lazure and Fenton, 2011). I ran a Kruskal-Wallis test to compare activity levels on nights with and without ultraviolet lights and Robomoth, to determine if activity patterns were influenced by the modification of the habitat. If there were no significant differences, all nights were included in habitat use analyses.

I used a MatLab based program, (Moonshine, Lasse Jakobsen, University of Southern Denmark) to recreate the bats' flight paths (detailed methods are presented in Appendix II). To calculate the maximum and minimum instantaneous speeds required to travel between two consecutive fixes in a flight path, I used 20% of the highest and lowest speeds attained in any flight path and calculated the mean. To calculate the maximum and minimum total flight path speeds, based on total distance travelled in a flight path over total time, I used the mean value for 30% of the highest and lowest total flight path speeds. To calculate predicted speeds, I used Flight version 1.1 (Pennycuick, 2008) and found the optimal maximum and minimum speeds bats can achieve based on their morphology. Although the program was designed mainly for birds, the same principals can be applied to bats (Pennycuick, 2008). The program calculates maximum range speed and minimum power speeds based on energetic requirements, using mass, wingspan and wing surface area.

I used xLSTAT to compare speeds among species and accepted all values of $p<0.05$ as being significant. I used an independent sample, non-parametric, Kruskal-Wallis test, due to non-normal distribution of measurements and used a Conover-Iman test with a Bonferonni correction to do a pairwise comparison between species and then separated them into groups. I used species as the group and maximum and minimum instantaneous speeds, maximum and minimum average speeds and maximum and minimum predicted speeds as the test fields.

2.4 Analysis of Diet

Guano samples were collected to determine dietary differences between species by means of DNA barcoding. Susan Koenig collected guano samples between December 2010 and March 2011 (dry) catching at the cave entrances and May to June 2011 (wet) by setting a tarp under a *M. waterhousii* roost in the roof of a building and collected guano in the morning. There were only one to three bats in the roost on any given night and only *M. waterhousii* used the roost. I collected guano samples from July to August 2011 (wet). In December 2010 to March 2011 and July to August 2011, bats were actively captured using techniques presented in Section 2.2 and guano was extracted from holding bags once bats were released. For individuals where full morphological measurements were not taken, at least species, sex and age were recorded. I stored all guano samples in 1.5 ml microcentrifuge tubes properly labeled to reflect species and sample number, and immediately froze them after trapping.

Dietary analysis was performed to determine the amount of resource partitioning among species. All genetic sequencing and analyses were performed by Elizabeth Clare (University of Bristol, Bristol, United Kingdom). For each species, she selected eight (*M. blainvillii*, *M. molossus*) or 16 (*P. parnellii*, *T. brasiliensis*, *M. waterhousii*, *P. macleayii*) guano samples (based on capture success in the two different seasons) for a total of N = 80 analyzed guano samples. She also selected an equal number of samples from males and females. For each sample, she homogenized the guano by vortexing and inverting the microcentrifuge tube, to ensure it was well mixed, and then extracted DNA from 50% of this material. For DNA extractions she used the QIAmp DNA Stool Mini Kit (Qiagen, UK) according to manufacturer's instructions with the modifications indicated by Zeal *et al*. (2011) and with the following additional modifications; 1) she used only half of an InhibitEX tablet for each sample and 2) she extended the first centrifuge step (Zeal step 4) to 3 minutes to aid in pelleting the particulate material. Extracted DNA was stored at -20 °C prior to DNA amplifications.

She tested all DNA extractions using unmodified primers ZBJ-ARTF1c and ZBJ-ArtR2c from Zeal *et al*. (2011) to confirm extraction success. She then amplified each sample using fusion primers designed for the Roche FLX sequencer as described by

Bohmann *et al*. (2011). These primers consisted of a Lib-L, the key sequence, a unique DNA sequence (MID) and the original primer sequence as required and described by the Liverpool Center for Genomic Research (University of Liverpool). In our design, identical MID sequences were used for each set of eight samples, thus for species with n=8 samples analyzed, a single MID sequence was used and for those with n=16 two different MID tags were used (one for the early season captures and the other for the late season captures).

PCR reactions were carried out following the amplification reaction described by Bohmann *et al*. (2011) in a 20µl reaction containing 2µl of template DNA using Qiagen multiplex PCR kits (Qiagen, UK) as described with the following modifications. She did not use either Q solution (from the kit) or BSA (as suggested by Bohmann *et al*. 2011). All PCR products were visualized on a 1.5% agarose gel. Approximately equal molar quantities were pooled by MID sequence and then size selected and purified using a QIAquick Gel Extraction kit (Qiagen, UK). Each pool was quantified using a Qubit dsDNA BR Assay Kit (low sensitivity with a Qubit Fluorometer (Invitrogen life technologies)).

Exactly equal amounts of PCR product were mixed, dried and rehydrated to give a final product of 100µg of PCR product in 10µl of molecular grade water. Sequencing of the product was conducted at the Liverpool Center for Genomic Research (University of Liverpool) using a ¼ plate, Lib-L chemistry on a Roche 454 GS FLX+ sequencing system (Roche Applied Sciences).

She analyzed sequences using the Galaxy platform (https://main.g2.bx.psu.edu/root; Goecks *et al*. 2010; Blankenberg *et al*. 2010; Giardine *et al*. 2005) and Bioedit (T. Hall, http://www. Mbio.ncsu.edu/bioedit/bioedit.html). She screened all recovered sequences for rare haplotypes (represented by <2 copies) and sequences much longer (>250bp) or shorter (<150bp) than expected length (230bp amplicon+primer). She collapsed the remaining sequences into unique haplotypes and then aligned these haplotypes using clustal W in Bioedit. She then removed primers and edited the alignment manually. She clustered the sequences into molecular operational

taxonomic units (MOTU) in the program jMOTU (Jones *et al*. 2011) and tested thresholds from 1-10bp. A graph of recovered MOTU vs. threshold and a neighbour joining tree suggests that a 6bp cut-off was most appropriate in this data set (see Razgour *et al*. 2011b) effectively identifying operational taxonomic units without obviously "oversplitting taxa". She extracted representative MOTU using PostgresSQL and compared representative sequences for each MOTU to similarity database of COI sequences retrieved from Genbank (http://www.ncbi.nlm.nih.gov/genbank/). She used a basic local alignment search (BLAST) of this database to retrieve BLAST scores (e-value cut-off 0.0001). These scores were visualized in MEGAN (Huson *et al*. 2011) using default settings and a "Min Score" of 1. Hits were restricted to ordinal-level taxonomy.

Sørensen Similarity Index and Hamming distances were used to compare similarities in diet among seasons and species. The Sørensen Similarity Index is an ecological index for presence and absence data (McCune and Grace, 2002). The formula to calculate it is

$$QS = \frac{2C}{(A+B)} = \frac{2n(A \cap B)}{n(A)+n(B)}$$

where C is number of shared prey, A and B are total number of prey consumed for each of species A and B (McCune and Grace, 2002). This index considers the number of insects consumed by each species and overlap between diets (McCune and Grace, 2002). Values range from 0 and 1, with 0 representing no dietary overlap and 1 representing full dietary overlap (McCune and Grace, 2002). This index only considers the prey consumed by the two species in question, and not the entire pool of available prey. To examine the entire pool of available prey, she used Hamming Distances. The Minimum Hamming Distance is a computer science metric used on binary data to calculate the minimum number of changes required to convert one string of binary data into another (Hamming, 1950). This analysis differs from the Sørensen Similarity Index because it considers prey items avoided as well as shared prey (Hamming, 1950). In this analysis, common prey item shared in diets and common prey items avoided are considered to be the same choice and are weighted equally (Hamming, 1950). Values range from 0 (all common dietary choices) to 616 (no common dietary choices) (Hamming, 1950) and values were

computed online using SIMCAL (http://www.miislita.com/searchito/binary-similarity-calculator.html).

Chapter 3 – Results

3.1 Morphological Results

I recorded morphological measurements for 114 individuals of 7 species. Patterns of variation in morphology (Table 1) reflected those reported in other studies. Although the species I studied, except *M. blainvillii*, were sexually dimorphic in at least one characteristic (Table 1), this topic is not pursued in this thesis because I had no way to track the consequences of sex through the other data sets I used. Interspecific differences were observed in some wing features but not in others (Table 1). Using the approach of Jennings *et al.* (2004), I classified characters from very low to high. For aspect ratio, values >7.3 were high, values =6.1-7.3 were intermediate and values <6.1 were low. For wing loading values >10.3 were high, values =7.5-10.3 were intermediate, values 6.45-7.5 were low and values ≤6.45 were very low. For tip shape index values ≥1.9 were high, values =1.3-1.9 were intermediate and values ≤1.3 were low. I added a fourth class to classify wing tip index because ranges differed among studies. Wing tip indices ≤0.9 were considered very low. Aspect ratios for mormoopids (*P. parnellii*, *P. quadridens*, *P. macleayii* and *M. blainvillii*) were intermediate, those for molossids (*M. molossus* and *T. brasiliensis*) were high and those for *M. waterhousii* were low. The wing loadings for mormoopids were very low, except for *P. parnellii* which had a low wing loading. *M. waterhousii* had intermediate wing loading and the molossids had high wing loading. The wing tip index of molossids, *P. quadridens* and *M. blainvillii* were very low, *P. parnellii* and *P. macleayii* were low and *M. waterhousii* were intermediate.

Species	Sex	n	Mass (g)	Forearm Length (mm)	Aspect Ratio	Wing Loading (N/m^2)	Tip Shape Index
Pteronotus parnellii	M	14	14.1±1.4 C	**52.54 ±0.71 B**	**6.4±0.4 DE(2)**	7.4±1.0 F(1)	1.2±0.2 A(1)
Pteronotus parnellii	F	11	13.6±1.0 C	**53.31 ±0.61 AB**	**6.8±0.3 CD(2)**	7.6±0.6 F(2)	1.3±0.2 A(1)
Pteronotus quadridens	M and F	7	6.7±0.3 F	38.29 ±0.76 F	6.6±0.6 CDE(2)	6.3±0.5 G(0)	0.9±0.2 BC(0)
Pteronotus macleayii	M	9	7.1±0.5 F	43.04 ±0.79 CD	7.1±0.7 BC(2)	5.9±0.9 G(0)	1.2±0.2 AB(1)
Molossus molossus	M	11	**18.1±0.9 B**	38.46 ±0.63 F	**8.0±0.4 AB(3)**	**16.1±1.0 AB(3)**	**0.5±0.0 D(0)**
Molossus molossus	F	10	**19.3±1.3 AB**	37.85 ±0.77 F	**8.4±0.4 A(3)**	**18.7 ±1.2 A(3)**	**0.7±0.1 CD(0)**
Tadarida brasiliensis	M	8	**10.0±0.6 DE**	39.63 ±0.76 E	8.5±0.5 A(3)	**10.3±1.1 CD(3)**	0.8±0.2 C(0)
Tadarida brasiliensis	F	8	**11.6±1.0 D**	40.09 ±0.65 DE	8.7±0.6 A(3)	**12.0±1.1 BC(3)**	0.8±0.1 C(0)
Macrotus waterhousii	M	10	21.0 ±1.8 A	**52.63 ±0.90 B**	5.8±0.3 G(1)	9.0±0.8 DE(2)	1.3±0.3 A(1)
Macrotus waterhousii	F	10	20.5±1.6 A	**53.75 ±1.10 A**	5.9±0.4 FG(1)	8.6±0.8 E(2)	1.5±0.5 A(2)
Mormoops blainvillii	M	10	9.6±0.9 E	45.79 ±1.20 C	6.2±0.2 EF(2)	5.6±0.6 G(0)	0.8±0.0 C(0)
Mormoops blainvillii	F	6	9.0±0.9 E	46.52 ±0.97 C	6.3±0.1 EF(2)	5.3±0.5 G(0)	0.7±0.0 C(0)

Table 1: Morphological measurements of seven insectivorous bat species in the Windsor region, Jamaica with standard deviation. Numbers in bold represent sexual dimorphic characters within a species based on a Kruskal-Wallis analysis. If the morphological character of multiple species were statistically the same based on a Kruskal-Wallis analysis with a Bonferonni and Conover-Iman pairwise comparisons, they were grouped together and given the same letter under the value of the measurements. If two species have different letters, their values are statistically different for that character. Relative size of wing characters is represented by the number in brackets. Very low values are represented by 0, low values by 1, intermediate values by 2 and high values by 3.

The PCA comparison of morphologies among species showed trends when dimensionality was reduced (Figure 1). PC1 in this analysis accounts for 69% of the variation and shows strong factor loadings for forearm length, wing loading, aspect ratio and wing tip index (Table 2). PC2 represents 18% of the variation and shows strong factor loadings for wing loading and wing tip index. Based on Norberg and Rayner (1987) species with low WL and AR and high I values would reflect flight in cluttered environments, species with high WL and AR and I values equal to 1 flight in open environments and species with intermediate WL and AR values would use edge environments. This suggests that species towards the right on the PC1 axis are more likely to use cluttered environments, species in the center edge and species to the left use open habitat.

Based on body size classification (Table 1) and PCA analysis (Figure 1), I expected four distinct groups with respect to habitat preference. Species in the first group should forage most in open habitats (*M. molossus* and *T. brasiliensis*). Species in the second group should forage mainly in edge environments (*P. quadridens* and *M. blainvillii*). Species in the third group should forage in cluttered environments (*P. parnellii* and *M. waterhousii*). The final group should show little preference to any habitat type and includes *P. macleayii*. These groups also should show different echolocation behaviour reflecting the physical challenges presented by each habitat type (Fenton, 1990).

Table 2: Factor loadings of the first two principal components of wing morphology characteristics of 7 insectivorous bat species. PC1 represents forearm length, wing loading, aspect ratio and wing tip index and PC2 represents wing loading and wing tip index.

	PC1	PC2
Forearm Length (mm)	0.901	0.220
Aspect Ratio	-0.869	0.288
Wing Loading (N/m^2)	-0.778	0.499
Tip Shape Index	0.759	0.580

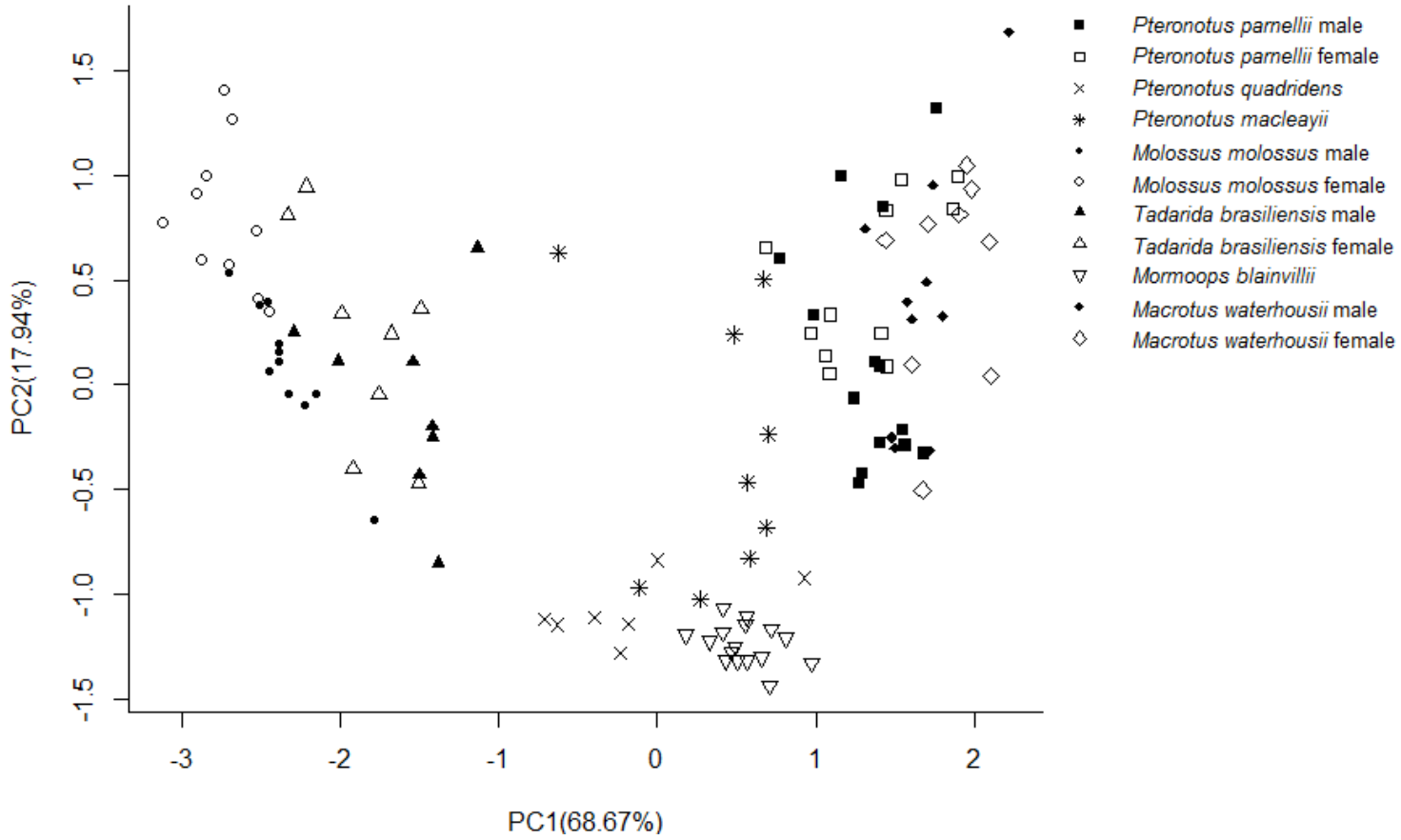


Figure 1: PCA analysis of wing morphology (Table 2) of 7 insectivorous bats in Jamaica. PC1 represents forearm length, wing loading, aspect ratio and wing tip index. The further right a species is on the PC1 axis the higher its wing tip indexes and forearm lengths are and the lower its wing loadings and aspect ratio are. PC2 represents wing loading and wing tip index with species further up on the PC2 axis having high values for these features.

3.2 Echolocation Call Parameter Results

Call duration, duty cycle, intensity and bandwidth suggest habitat differentiation based on call parameters (Table 3). Based on Fenton (1990) I determined expected foraging habitat based on call parameters. High duty cycle and low intensity calls appear to be specializations for foraging in cluttered environment, although they are not used together. Narrowband calls are specialized for foraging in open habitats, whereas broadband calls are used in either edge or cluttered habitats. Species with call parameters specialized for clutter include *P. parnellii* and *M. waterhousii.* Differences in duty cycles and call intensities can allow dietary partitioning between these two species based solely on call parameters (Fenton, 1990). The narrowband calls of *M. molossus* and *T. brasiliensis* suggest specialization for open environments. Broadband calls with low duty cycle and high intensity suggest *P. quadridens, P. macleayii* and *M. blainvillii* are specialized for edge habitats.

3.3 Predicted Habitat Use Based on Echolocation and Morphology

Morphology and echolocation suggest similar placement of the 7 insectivorous species in three generalized habitat types (open, edge and clutter). The only species with contradicting placement was *P. macleayii*, whose morphology suggested no habitat specialization and whose call parameters suggesting a specialization for edge habitats. *P. macleayii* use of edge fits call features because edge calls are designed to deal with the physical challenges presented in both open and cluttered habitats. This leads to four distinct expected foraging groups which may aid in the partitioning of resources. The first group forages in open habitats includes *M. molossus* and *T. brasiliensis*. The second group forages in edge habitats includes *P. quadridens* and *M. blainvillii*. The third group forages in cluttered environments includes *P. parnellii* and *M. waterhousii*. The final group with no preference to any habitat type includes *P. macleayii*. The specialization suggested by morphology and call parameters should be reflected in habitat use analyses.

Table 3: Call parameters of 7 Jamaican insectivorous bats based on call analysis of free flying and bats on a zipline. Habitat association was determined by comparing call features to work done by Fenton (1990).

Species	n	Duration (ms)	Fmax (kHz)	Fmin (kHz)	Duty Cycle	Intensity	Bandwidth	Predicted Habitat Association
Pteronotus parnellii	10	29.03±4.42	61.18±1.13	49.12±2.81	High	High	Broadband	Cluttered
Pteronotus quadridens	10	4.49±0.792	80.03±1.43	60.84±1.51	Low	High	Broadband	Edge
Pteronotus macleayii	10	4.80±1.21	70.65±1.81	54.69±1.15	Low	High	Broadband	Edge
Mormoops blainvillii	10	2.95±1.13	66.65±1.87	44.09±3.64	Low	High	Broadband	Edge
Molossus molossus	10	6.48±1.80	40.97±3.46	33.54±4.43	Low	High	Narrowband	Open
Tadarida brasiliensis	10	7.69±0.68	56.79±5.43	33.79±1.84	Low	High	Narrowband	Open
*Macrotus waterhousii**	10	1.91±0.71	73.65±6.62	46.19±2.68	Low	Low	Broadband	Cluttered

* Call parameter were analyzed for individuals on a zipline.

3.4 Habitat Assessment

PCA for habitat assessment confirmed the classification of sites (Figure 2). The first two principal components (PC1 and PC2) represented 36.5 and 20.4% of total variance. In PC1, the factor loadings (Table 4) with the highest absolute values are area of tree cover, canopy density and percent seedling coverage. PC2 represents percent soil cover, negative elevation, slope and percent water. PC1 loadings suggest that PC1 represents the amount of clutter in the habitat. Sites located on the right of the graph correspond to sites that are cluttered, sites in the center to edge habitats and sites on the left open. PC2 loadings suggest that PC2 corresponds to peaks and valleys in the cockpits. Habitat assessment classifications compared similarly to visual classifications, those identified as cluttered habitats placed similarly along the PC1, suggesting that appropriate definitions for these sites. Edge sites grouped together along the PC2 axis suggesting proper classification as well. Two of the three open sites were placed at the extreme of the PC1 axis representing an uncluttered environment (Site 1 and 3) and the third placed near the PC2 axis representing edge (Site 2). Site 2 was classified as open because it was located on a cliff overlooking the area above the tree canopy. Although there was some cluttered space on one side of the array, I only used data from the side overlooking the tree canopy. The quantification of habitat use supports preliminary classification of sites. In knowing this we can determine that the site preference observed in the acoustic survey is representative of species using the generalized classification of habitats.

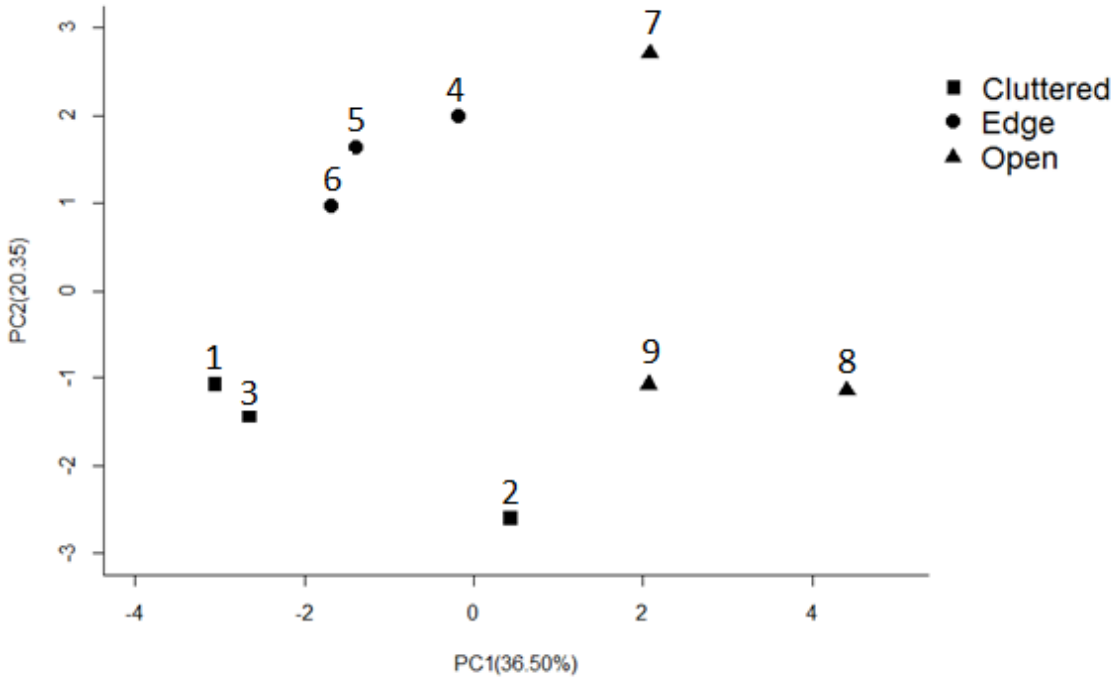


Figure 2: PCA of habitat assessments of sites 1 to 9. Sites to the right of the PC1 axis represent cluttered habitats, sites in the center edge and sites to the left open. Sites above zero for PC2 represent peaks and sites below represent valleys.

Table 4: Factor loadings of the first 2 principal components of habitat assessment of sites. PC1 represents amount of clutter and PC2 represents elevation.

	PC1	PC2
Elevation(ft.)	0.576	-0.779
Soil (%)	-0.084	0.944
Herbaceous (%)	-0.741	-0.443
Leaf litter (%)	0.621	-0.276
Woody Debris (%)	0.698	-0.010
Rock (%)	0.737	-0.110
Water (%)	-0.208	0.524
Seedling (%)	0.847	0.238
Herbaceous (%)	0.462	0.632
3-Finger (%)	0.320	0.096
Grass (%)	-0.279	0.233
Fern (%)	-0.424	-0.262
Other (%)	0.000	0.000
Slope (°)	0.478	-0.598
Average Canopy Density	0.886	0.165
Area of tree (m^2)	0.908	0.151

3.5 Habitat Use

Over 46 nights I recorded a total of 30911 minutes of acoustic data [10500 one minute files (34%) contain bat calls (files having multiple species were counted multiple times)]. Bats were most active in edge, cluttered and then open habitats. *P. parnellii* had the highest level of activity and *P. quadridens* had the lowest. Activity levels varied between species and sites (Table 5).

Pteronotus parnellii was most active and foraged in cluttered environments, *P. macleayii* had no preference, and the other 4 species were most active and foraged in edge and open environments (Table 5). Patterns of species activity in different habitats were dimensionally reduced using PCA (Figure 3). The first two principal components (PC1 and PC2) were retained in the analysis accounting for 48.3 and 19.3% of the total variance respectively. Factor loadings are presented in Table 6 PC1 had sites 3, 7, 8 and 9 with the highest positive loadings and sites 1, 5 and 6 with the highest negative loadings and PC2 had sites 2, 3 and 4 with the highest positive loading. Predictions made for habitat use based on morphology and call structure were supported for *P. parnellii, P. macleayii, P. quadridens* and *M. blainvillii*. My predictions that *M. molossus* and *T. brasiliensis* would forage most often in open areas were not supported as these bats were most active and foraged in edge environments. The edge sites these species preferred, however, occurred towards the open portion of the PC1 axis in habitat assessment and open areas were present at each site. The high level of overlap in morphology, call structure and habitat use suggest another means of partitioning would be required to account for the level of resource partitioning observed in the dietary analysis. This could have been accomplished through temporal partitioning.

Table 5: Activity indexes (number of one minute files with species present in a given night) recorded for each species at each site and habitat type. Letters next to the activity indexes represent grouping based on a Kruskal-Wallis test with a Bonferonni correction and a Conover-Iman pairwise comparisons. Numbers in bold represent sites with the highest activity for a given species and numbers that are underlined have the lowest activity. Activities indexes with different letters are statistically different from one another. Activity indexes with multiple letters are not statistically different from at least 2 groups.

	Site									Habitat Totals					
Species	1	2	3	4	5	6	7	8	9	Open	Edge	Clutter	Total	H8	p
Pteronotus parnellii	39D	303C	684BC	80D	39D	86D	**845AB**	**1153A**	**1198A**	1026	205	3196	4427	41.19	<0.0001
Pteronotus quadridens	**47AB**	8C	17C	**85A**	**140A**	**121A**	9C	22BC	23BC	72	346	54	472	36.24	<0.0001
Pteronotus macleayii	35ABC	**153A**	**137A**	59ABC	**125A**	**79AB**	2C	**101A**	22BC	325	263	125	713	26.96	0.001
Molossus molossus	**48AB**	60BC	10BC	5BC	**395A**	**199A**	1C	0C	0C	118	599	1	718	33.61	<0.0001
Tadarida brasiliensis	291BC	143CD	17D	2E	**944A**	**351AB**	1E	0E	0E	451	1297	1	1749	42.47	<0.0001
Mormoops blainvillii	19CD	**101AB**	97B	**242A**	**143AB**	**110AB**	2D	59BC	7D	217	495	68	780	35.20	<0.0001
Unknown	51	81	63	280	559	323	69	94	121	195	1162	284	1641		
Total	530	849	1025	753	2345	1269	929	1429	1371	2404	4367	3729	10500		

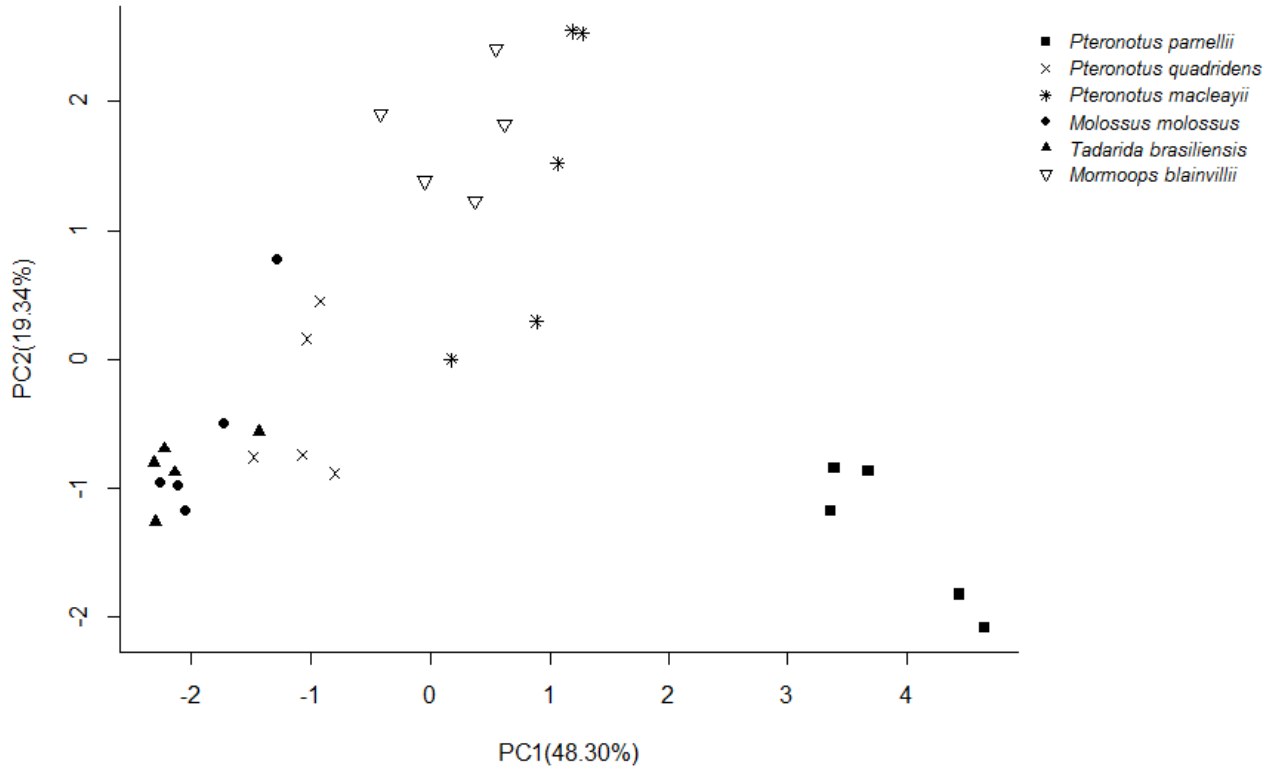


Figure 3: PCA of habitat use (Table 6) of 7 insectivorous bats in Jamaica. Species to the right of the graph were associated with sites 3, 7, 8 and 9 and species to the left 1, 5 and 6. Species toward the top of the PC2 axis were associated with sites 2 and 4.

Table 6: Factor loadings for the first 2 principal components of habitat use at sites.

Site	PC1	PC2
1	-0.634	-0.285
2	0.167	0.677
3	0.700	0.514
4	0.009	0.656
5	-0.719	-0.119
6	-0.795	-0.149
7	0.831	-0.482
8	0.966	-0.074
9	0.810	-0.483

3.6 Temporal Division of Habitat

Temporal patterns of activity (high and low) varied among species (Table 7). At sites with high levels of activity for multiple species, I found temporal variation in both high and low activity (Figure 4). Sites 3, 7 and 9 were not included in Figure 4 because of the high degree of spatial rather than temporal partitioning (had only 1 species using it as preferred habitat). Sites lacking spatial partitioning showed high level of temporal partitioning and as the number of species using a site increased, so did the amount of partitioning.

Table 7: Periods (minutes after sunset) of high and low activity for species at a given site based on a space-time scan statistic. It compares activity levels across all sites and determines if increased levels of activity differ from background levels for a given species.

		Sites								
	Species	1	2	3	4	5	6	7	8	9
High Activity	*Pteronotus parnellii*	-	21-384	21-384	-	-	-	566-665	633-674	21-384
	Pteronotus quadridens	-	-	-	631-644	598-614	14-36	-	649-667	-
	Pteronotus macleayii	-	44-84	-	442-616	442-616	442-616	-	638-658	(-)1-11
	Molossus molossus	490-603	(-)18-15	(-)18-15	-	-	605-634	-	-	(-)18-15
	Tadarida brasiliensis	324-391	(-)20-38	(-)20-38	(-)20-38	-	41-144	-	(-)20-38	(-)20-38
	Mormoops blainvillii	-	278-460	278-460	205-286	85-192	-	-	616-651	278-460
	Other	-	-	-	47-101	115-538	47-101	-	-	0-70
Low Activity	*Pteronotus parnellii*	60-254	524-674	524-674	-	-	-	60-254	22-72	524-674
	Pteronotus quadridens	631-667	17-68	17-68	17-68	631-667	-	631-667	17-68	17-68
	Pteronotus macleayii	629-658	-	24-240	629-658	629-658	629-658	629-658	24-240	24-240
	Molossus molossus	618-634	-	-	46-230	-	46-230	618-634	-	-
	Tadarida brasiliensis	20-84	86-507	-	183-596	-	183-596	-	-	-
	Mormoops blainvillii	-	85-234	85-234	005-32	194-420	005-32	-	85-234	85-234
	Other	-	181-588	-	(-)21-16	(-)21-104	(-)21-16	-	-	181-588

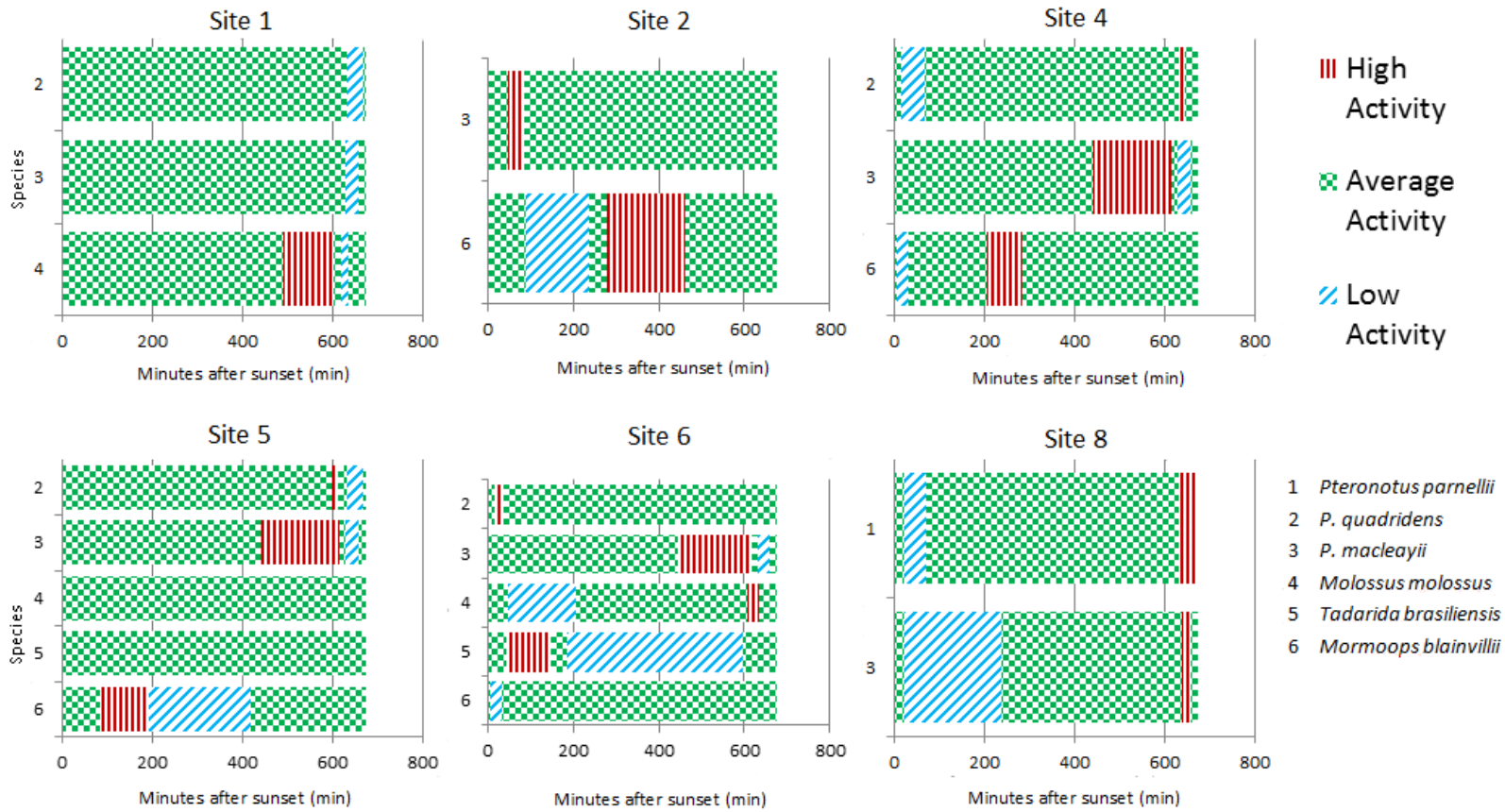


Figure 4: Temporal activity patterns of species throughout the night at their most used sites, based on Table 7. Periods represented by the green checkered pattern are background activity levels based on activity patterns at all sites for a given species. Red vertical and blue diagonal lines represent periods of high and low (respectively) activity compared to activity at all other sites and times.

3.7 Flight Behaviour

Flight paths speeds, optimal flight speeds based on energetic requirements of flight and flight path manoeuvrability are presented in Table 8, and there were no significant differences among any of the manoeuvrability indices (H4=2.869 p=0.580). Maximum instantaneous speeds did not differ among species, except *T. brasiliensis* which flew faster than all other species. Maximum average speeds and minimum instantaneous speeds showed a picture similar to that portrayed by habitat preference, suggesting that *P. parnellii*, which foraged in clutter, was the slowest and *T. brasiliensis*, that foraged in the open, and *M. blainvillii*, which foraged in edge habits, were the fastest. I observed few differences among average minimum speeds. Predicted speeds that were calculated based on morphological characters showed few statistical differences compared to speeds calculated using acoustic data. The ensemble of species show differences in morphology, call structure, flight speeds, spatial preference and temporal activity. Together, these differences provide the ensemble with mechanisms that could result in partitioning in diet.

Table 8: Calculated and predicted speeds (m/s) of 5 insectivorous bat species in Jamaica with standard deviations. Based on a Kruskal-Wallis analysis with a Bonferonni correction, speeds in bold are statistically different from another speed in the same category (maximum and minimum) with the number in brackets representing which value it is significantly different from (1=Instantaneous, 2=Average, 3=Predicted). Letters under speeds represent ranking of the species in relation to other members of the ensemble based on a Conover-Iman test. Group A have the highest values. Multiple group association signifies no statistical difference among groups group.

Species	n	Maximum Instant Speed (m/s)	Maximum Average Speed (m/s)	Predicted Maximum Speed (m/s)	Minimum Instant Speed (m/s)	Minimum Average Speed (m/s)	Predicted Minimum Speed (m/s)	Average Total Path Speed (m/s)	Manoeuvrability Index
Pteronotus parnellii	17	**10.8±1.0(2)** **B**	**8.6±0.6(1,3)** **C**	**11.4±0.2(2)** **A**	**3.4±0.8(2,3)** **C**	**5.1±0.8(1)** **A**	**5.8±0.2(1)** **A**	6.9±1.5 B	0.27
Pteronotus quadridens	14	**11.2±0.7(2)** **B**	**9.1±1.0(1)** **BC**	10.8±0.2 CD	**4.0±0.7(2,3)** **BC**	**5.8±1.1(1)** **A**	**5.3±0.1(1)** **B**	7.6±1.5 AB	0.36
Pteronotus macleayii	18	**11.0±1.0(2)** **B**	**9.4±0.4(1)** **BC**	10.5±0.1 D	**4.3±0.9(2)** **B**	**5.8±0.5(1)** **A**	5.1±0.1 B	7.5±1.5 AB	0.4
Tadarida brasiliensis	8	**12.9±0.6(2,3)** **A**	**10.7±0.0(1)** **AB**	**11.2±0.2(1)** **B**	5.6±1.19 A	7.2±1.8 A	5.9±0.2 A	9.4±1.7 A	0.39
Mormoops blainvillii	11	11.9±0.9 B	11.5±0.6 A	10.9±0.2 C	**4.8±0.88(2)** **A**	**7.0±0.4(1,3**) A	**5.3±0.2(2)** **B**	9.0±2.0 A	0.15

3.8 Use of Ultraviolet Lights and Robomoth

I used ultraviolet lights and robomoth, to manipulate actual insect density (lights) or perceived density (fluttering targets – robomoth). I designed these site manipulations to determine if bat activity (approaches to the arrays) would change (Bell, 1980, Lazure and Fenton, 2011). Bats flying closer to the array allowed more accurate reconstruction of flight paths. Although there were no statistical differences between nights with and without the modifications (Table 9), echolocation calls had higher intensities on nights with the manipulation suggesting bats flew closer to the array. The bats appeared to respond to changes in real or perceived density of prey. Bell (1980) reported an increase in bat activity on nights with and without ultraviolet light and proposed that ultraviolet lights generated a swarm of insects in an environment where insects although abundant were patchy in space, time and quality. This did not happen in my experiments, with habitat use not being affected by ultraviolet light, suggesting that insect populations were evenly distributed in space. It may be possible that low sample size explains no statistically significant differences and more sampling periods may detect differences not observed in this study

Table 9: Results of a Kruskal-Wallis analysis comparing nights with and without an ultraviolet lights and robomoth. No significant difference was found at any site (α=0.05).

Site	Test Statistic	df	Significance
2	2	1	0.157
4	2	1	0.157
6	3	1	0.083
7	0.333	1	0.564
8	0.333	1	0.564
9	0.333	1	0.564

3.9 Dietary Analysis

DNA barcode analysis of the diets of *P. parnellii, P. macleayii, M. molossus, T. brasiliensis, M. blainvillii* and *M. waterhousii* illustrated interspecific variations in diet (Table 10). The consistency of the number of raw sequences across groups suggests successful methods of quantification. Although I had twice as many sequences for *M. waterhousii* as for the other species, this bat's diet fell within a similar range. The number of raw sequences did not correlate to the number of haplotypes or the number of MOTU, suggesting enough sequencing was done and that further sequencing would not have increased the number of MOTU. The total number of MOTU, representing number of species in the diets of the analyzed bats was 616. Of those a total of 216 were unique to the early season, 312 were unique to the late season and 88 were shared across seasons. *P. parnellii* and *P. macleayii* ate the highest numbers of species.

Table 10: Sequencing outcomes and estimates of dietary breadth.

Species	Season	Raw Sequences	Haplotypes	MOTU at 6bp
Macrotus waterhousii	Late	15103	4642	58
Macrotus waterhousii	Early	16150	7032	92
Tadarida brasiliensis	Late	11968	5566	37
Tadarida brasiliensis	Early	9764	4700	56
Pteronotus parnellii	Late	11999	6629	152
Pteronotus parnellii	Early	11392	6621	99
Pteronotus macleayii	Late	9861	6626	104
Pteronotus macleayii	Early	10146	6221	82
Molossus molossus	Late	11269	5301	48
Mormoops blainvillii	Late	11449	5898	64

The Sørensen Similarity Index and Minimum Hamming Distances show little dietary overlap among species (Table 11). The Sørensen Similarity Index shows that the diets of most species differed between seasons. The highest overlap occurred in *M. waterhousii*. The comparison among species shows that the amount of dietary overlap was very low. *P. macleayii* showed the highest amount of overlap between themselves and other species. This amount of overlap reflects dietary diversity. *M. waterhousii* had the most unique diet. Higher levels of overlap among species usually occurred in different seasons (*P. parnellii* and *P. macleayii*; *P. parnellii* and *M. molossus*; *T. brasiliensis* and *M. blainvillii*; *T. brasiliensis* and *P. macleayii*), showing seasonal partitioning of resources. Minimum Hamming Distance suggests that the diets of the species were similar because they are closer to 0 than to 616. This analysis considers the prey consumed by the entire ensemble and suggests sharing of similar prey absent from their diets (shared avoidance), which is expected if prey items are partitioned. Results from both analyses show that resources are partitioned among bats of the ensemble.

MOTU analysis provides taxonomic classification of prey species (Figure 5). The dominant prey items consumed by the bats were insects in the orders Lepidoptera, Diptera and Coleoptera. *P. parnellii* ate the widest diversity of *Lepidoptera*, as well as other insects. *P. macleayii* ate the widest range of taxonomic groups. These results support data in Table 10 revealing that *P. parnellii* and *P. macleayii* have the widest niche breadths by diet. My results supported my predictions that differences in morphology, call structure, flight speeds, spatial preference and temporal activity coincide with dietary partitioning.

Table 11: Estimates of dietary overlap among bat species. Species are denoted by the first letters of their genus and species name. Number following species name represents season (1=wet, 2=dry). The letters next to Mw represent different sampling periods.

Sørensen Similarity Index (*QS*)											
Minimum Hamming Distances		**Mw1a**	**Mw1b**	**Tb1**	**Tb2**	**Pp1**	**Pp2**	**Pm1**	**Pm2**	**Mm**	**Mb**
	Mw1a		**0.40**	0.03	0.02	0.15	0	0	0	0.02	0.05
	Mw1b	**99**		0.02	0.06	0.20	0.05	0.05	0.04	0.07	0.09
	Tb1	93	124		**0.07**	0.05	0.08	0.09	0.03	0.13	0.02
	Tb2	112	139	**87**		0.09	0.03	0.13	0.08	0.06	0.11
	Pp1	180	199	179	191		**0.09**	0.12	0.03	0.07	0.10
	Pp2	157	180	126	151	**229**		0.16	0.10	0.13	0.09
	Pm1	162	185	129	140	228	173		**0.15**	0.11	0.07
	Pm2	140	167	115	128	226	163	**160**		0.08	0.04
	Mm	104	129	75	98	186	129	136	120		0.07
	Mb	116	141	99	108	196	149	156	140	104	

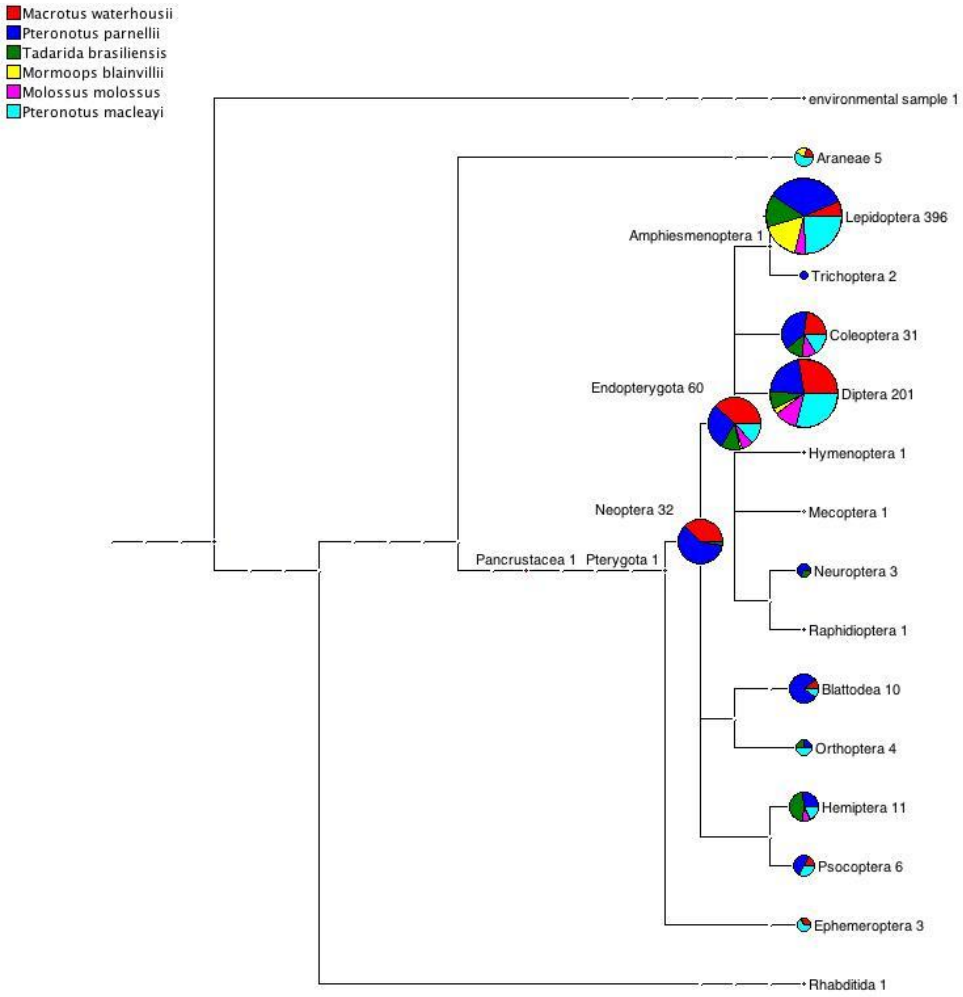


Figure 5: The proportion of MOTU assigned by BLAST to a given taxonomic node for each predator. Values at nodes represent the number of BLAST assignments. The size of the pie chart for a given taxonomic group is proportional to the number of MOTU found in that group, which is the number next to the pie chart. There is a high rate of false positive assignments of COI at higher taxonomic levels thus any one assignment should be treated cautiously. However higher node assignments can be loosely interpreted as support for a given node. A higher number of node assignments translates into higher confidence that that a given node is actually present in the diet (for example, it is highly unlikely that there are 396 false positive assignments at the Lepidoptera node thus we can be confident that Lepidoptera are present in the diet and likely in high proportion).

Chapter 4 – Discussion

4.1 Purpose Revisited

I began this study with three main predictions: a) that species with similar morphologies would forage in similar habitats based on their wing design and echolocation calls; b) that species foraging sympatrically would partition the space in time or through behaviour; and finally, c) there would be minimal overlap among the diets of species. My results support all three predictions to various degrees. These findings suggest ecomorphological differences and spatial, temporal, behavioural and dietary partitioning within an ensemble of insectivorous bats are interrelated.

4.2 Interactions Among Morphology, Call Structure and Foraging Habitat

Aldridge and Rautenbach (1987) proposed that morphology determines ideal foraging habitat for bats. They argued the most important features to consider were associated with wing features, especially aspect ratio, wing loading and wing tip index. Numerous studies since then have supported their findings (Saunders and Barclay 1992; Fenton and Bogdanowicz 2002; Swartz *et al.* 2003; Saldamendi *et al.* 2005; Bumrungsri *et al.* 2007; Jacobs and Barclay 2009). Ecomorphological associations based on wing morphology can also be applied to birds (Hertel and Balance, 1999; Pennycuick, 2008; Vanhooydonck *et al.*, 2009). Aldridge and Rautenbach (1987) expanded this view by introducing echolocation call structure to the concept. They suggested species with low frequency and narrow band calls would forage in open environments. High frequency broadband calls would allow foraging in cluttered habitats. The use of constant frequency, HDC calls would also permit foraging in cluttered habitats (Fenton *et al.* 2012). Numerous studies since have supported these findings and it is generally accepted that morphology and echolocation are good indicators of habitat use (Saunders and Barclay 1992; Fenton and Bogdanowicz 2002; Swartz *et al.* 2003; Saldamendi *et al.* 2005; Bumrungsri *et al.* 2007; Jacobs and Barclay 2009). However, there are certain caveats to these indicators. Bininda-Emonds and Russell (1994) noted differences in morphological measurements between museum and live specimens. This difference can result in misclassification of

foraging habitats. For example Norberg and Rayner (1987), predicted *P. parnellii* would forage in open habitats. I suggest, as well as others that examined the morphology and habitat use for *P. parnellii* (Mancina *et al*., 2012; Jennings *et al*, 2004), the species is more suited to cluttered environments. Bininda-Emonds and Russell (1994) proposed introducing a standardized method of measuring wing features. In recent years, most studies have focused on live specimens. Even with standardized methods, variations can be observed. Specifically, my measurements of wing features differ from those reported elsewhere from the same species on different islands (Mancina *et al*., 2012; Vaughan *et al*, 2004). This could reflect taxonomic differences (Clare *et al*., 2013). The benefits of echolocation as indicators of habitat use appear to be limited to the order Chiroptera. Echolocation in oilbirds is primarily employed to locate their nests in darkened caves (Konishi and Knudsen, 1979) and certain cetaceans employ it to increase their field of view in aquatic environments where vision is limited (Thomas, 2004). Consequently, these uses provide little differentiation in habitat selection.

4.3 Partitioning Through Call Structure

The echolocation behaviour of *M. waterhousii* and *P. parnellii* suggest capacity for operating in clutter. The HDC echolocation behaviour of *P. parnellii* appears adapted to detect fluttering prey in clutter (Lazure and Fenton 2010; Fenton *et al*. 2012). *M. waterhousii* uses low intensity, LDC echolocation, which is well suited to operating in clutter (Bell, 1982). In clutter they may rely on prey-generated signals to find their food source (Bell, 1985). This is the most likely reason why they were not detected in the acoustic survey. While the echolocation behaviour of both of these species appear well suited for foraging in clutter, my data lend support to the proposal that echolocation behaviour can reflect capacity for resource partitioning. I determined this by showing little dietary overlap between the species (Table 11), with *P. parnellii* eating more moths than *M. waterhousii*, although they did not specialize on Lepidoptera (Figure 4). Even though few studies have investigated partitioning through echolocation in other orders, Barrett-Lennard *et al.* (1996) observed different examples of this behaviour in orca whales depending on their diet. They noted that populations preying on mammals

produced fewer echolocation calls than those consuming fish. This suggests intraspecific resource partitioning through the use of echolocation may also occur among non-bats.

4.4 Defining Habitats

Defining a habitat is a complex issue (Racey and Entwistle, 2003). What humans perceive as a habitat often differs from what a habitat assessment might suggest and what a bat might perceive as a habitat. A habitat assessment is a quantification of a habitat based solely on measurable factors. Although this method is generally accepted within the scientific community, there is no way of knowing whether the species in question perceives the habitat by using these measurable characteristics. Historically, habitats that bats forage in have been defined as cluttered, edge or open (Racey and Entwistle, 2003). I used the same classifications for habitats, but a habitat is usually more complex than such a limited classification. Habitats can be combinations of the different habitat types. Environments with water have classically been defined as edge (Racey and Entwistle, 2003), but the area above the water can also be deemed as cluttered, open or edge environments. This was obvious at sites 4 (cluttered) and 5 (open), both designated edge habitats, although they had different levels of clutter above the water. Water habitats had the highest level of activity and may be best defined as a distinct habitat type regardless of vegetation. These sites showed different levels of activity and were preferred by many different species. We also see that species are not necessarily confined to a single habitat type and sometimes use multiple sites with varying habitat characteristics. It may therefore be more appropriate to define habitats on a continuum basis and not an ordinal one.

4.5 Spatial Partitioning

My results are generally consistent with spatial partitioning observed in other studies (Weltzin and McPherson 1997; Gabor *et al.*, 2001; Buckley and Roughgarden 2005; Takahashi *et al.* 2005; Schick *et al.* 2011; Gable *et al.* 2012; Kadye and Chakona 2012; Ramesh *et al.* 2012). Habitat preference has been found to be a means of partitioning in bats as well. Alettaz (1999) examined habitat partitioning in two sympatric radio-tracked insectivorous bats with similar morphology and echolocation behaviours. He observed

partitioning despite the similarities. Saunders and Barclay (1992) examined the same phenomenon using capture data and found similar results. Bumrungsri *et al*. (2007) cited similar patterns in frugivorous species. Razgour *et al.* (2011a) noted habitat partitioning in an ensemble of bats using acoustic methods. Although I found many common sites used among species, I found each species exhibited a unique level of activity when all sites were considered. *P. parnellii* inhabited the most uncommon set and used cluttered sites, which matches predictions made based on call structure and morphological analysis. The most commonly used sites among species were ones classified as edge, supporting previous studies (Racey and Entwistle, 2003; Jantzen and Fenton, 2013). *P. macleayii* showed high levels of activity in the widest range of habitats, supporting previous predictions from wing morphology (Mancina, 2005). Mancina *et al*. (2012) found no spatial partitioning among mormoopids in Cuba, whereas I found the same mormoopids had different combinations of preferred habitats. One possible explanation for the discrepancy is variations in acoustic equipment. Mancina *et al*. (2012) used Anabat detectors which can be less effective at detecting bat echolocation calls than the Avisoft system which is the detectors I used (Adams *et al*., 2012). My data were also assessed from 9 sites, compared to their 3.

4.6 Temporal Partitioning

My results are generally consistent with temporal partitioning observed in other studies (Ross 1986; Cotton *et al.* 1998; Gutman and Dayan 2005; Adams and Thibault 2006; Burles *et al.* 2008; Gordon *et al.* 2010; Veen *et al.* 2010; Razgour *et al.* 2011a; Venner *et al.* 2011; Kadye and Chakona 2012; Ramesh *et al.* 2012). Temporal partitioning may be more common than Shoener (1974) originally proposed. I observed temporal partitioning on a nightly as well as seasonal basis. In bat ensembles, this type of partitioning has only been shown in environments with limiting resource (Adams and Thibault, 2006; Razgour *et al*., 2011a). When resources were not limited, there were no signs of temporal partitioning (Saunders and Barclay, 1992; Hickey *et al*., 1996). My study contradicts this by supporting temporal partitioning in an environment with no obvious limiting resources.

Kunz (1973) noted an increase in activity in five bat species between 2 and 3 hours after sunset. This pattern masks the effects of temporal activity by undermining smaller scale peaks. I used the program SaTScan, a new method for examining temporal activity, and found temporal variations that may have been unobserved in previous studies. SaTScan is designed to discover statistical significances of disease outbreaks across space and time. The same principals used by the software to analyze the occurrence of diseases can also be applied to determine peak activity (Adams, submitted). The statistical analysis examines activity across all sites and determines whether the peak of activity at one site is statistically different from the peaks observed in all other sites. By using this method, I remove the bias of time, with high activity due to key events in the night (i.e. sunset and sunrise) that have been shown to affect levels of activity (Kunz, 1973). The analysis is able to detect periods of low activity as well. Although my analysis focused on the activity patterns of bats, this same method can be used to detect activity patterns for any organism where presence and absence data is available with a time stamp. This method would be especially beneficial for species that have increased or decreased levels of activity due to daily abiotic factors such as sunrise or sunset.

4.7 Flight Speeds

A classic way of measuring flight speeds involves catching bats, releasing them and timing how long it takes them to travel a given distance (Hopkins *et al*., 2003). This method assumes that the bat travelled in a straight line after release. The flight path also begins from a motionless position, which means the bat is not traveling at its maximum speed throughout the entire flight. Finally, the bat may not perform natural flight behaviour after being handled. New techniques using acoustic monitoring permit passive recording of flight paths with minimal disturbance to the bat (Jakobsen and Surlykke, 2010). By using acoustic monitoring we see a section of a bat's flight path and a more realistic travel distance. Finally, the bat is not being manipulated and should therefore be flying naturally. Based on this, we would expect to see faster and more accurate speeds. Hopkins *et al*. (2003) reported flight speeds for *P. parnellii* ranging from 2.4m/s to 8.5 m/s using the catch and release method. My speeds ranged from 3.8 m/s to 9.4 m/s. For average path speed, Hopkins *et al*. (2003) found values of 4.9 m/s and 5.3 m/s for males

on two separate days and 3.6 m/s for females, quite different from the 6.9 m/s I found. Hayward and Davis (1964) employed the same catch and release technique to calculate the speed of *T. brasiliensis*. They reported flight speeds from 3.1 m/s to 4.7 m/s compared to my 5.9 m/s to10.7 m/s. Williams *et al.* (1973) used radar to calculate speeds of commuting *T. brasiliensis* and calculated 1.9 m/s to 28.3 m/s and an average speed of 11.1 m/s, much faster than the speeds I obtained. Although flight speed has been investigated in multiple bat and bird species, to my knowledge no study has examined resource partitioning based solely on flight speed.

4.8 Dietary Partitioning

Results of dietary partitioning in this study are generally consistent with those from other studies. However, I found more dietary specialization among all species than reported in other orders (Inouye, 1978; Dunbar, 1978; Dial, 1988; Farrell *et al.,* 2000; Platell *et al.,* 2010; Steenweg *et al.,* 2011). In bats, Whitaker *et al.* (1999) and Andrianaivoarivelo *et al*. (2006) observed dietary differences across seasons. My data supports this view, with only 88 species of insects evident in the diets in both wet and dry seasons. There were more species of insects found in the diet of bats only in the wet (312) compared to the dry season (216). This is most likely due to an increase in insect abundance during the wet season (McNab, 1976). The dietary overlap in *M. waterhousii* can be explained by the early season for *M. waterhousii* being between May and June, whereas the early season for the other species was between December and March. This suggests that early and late time periods of *M. waterhousii* should not be compared to those of the other species.

Dietary partitioning has been observed in sympatric bats using traditional methods of visual identification of insect remains (Findley and Black, 1983; Hickey *et al*., 1996; Fukui *et al*., 2009), but new genetic sequencing techniques show less evidence of resource partitioning (Bohmann *et al*., 2011; Razgour *et al*. 2011b). My results contradict some earlier results achieved through DNA barcode analysis by showing a high degree of dietary partitioning among species. Similar results were obtained for composition of diets with all three studies showing Lepidoptera and Diptera the most diverse orders in the analysis. According to competitive exclusion, two species can co-exist in a stable

environment only if the niches they fill differ in some measure (Hardin, 1960). I demonstrated partitioning along several niche dimensions by species in an ensemble of insectivorous bats. But I have no evidence of competition between species, even in the dry season when insect abundance was low (McNab, 1976) we found little overlap in diet. This suggests prey availability might not be a limiting factor within the ensemble, which is also evident in a lack of increased bat activity with increasing insect abundance (ultraviolet light experiments). Both of these results suggest insects are not a limiting resource.

4.9 Bat Ensembles

Each dimension of resource partitioning explored in my research could be considered separately and has been treated this way in multiple studies (Findley and Black, 1983; Norberg and Rayner, 1987; Hickey *et al*., 1996; Andrianaivoarivelo *et al*., 2006; Feldhamer *et al*., 2009; Fukui *et al*., 2009; Bohmann *et al*., 2011; Razgour *et al*. 2011b). However, as the number of dimensions increases, interactions among the separate components emerge, providing a clearer understanding of the structure of an ensemble. Ecomorphological studies suggest that morphology determines how a bat flies and where it can fly (Norberg and Rayner, 1987), and this has been demonstrated experimentally (Aldridge and Rautenbach 1987). This introduces one level of niche partitioning. This was supported with the PCA for morphology matching the PCA for habitat preference, but the story was more complicated. Where a bat flew also determined what echolocation strategy was required. This introduced a second level of partitioning, with different echolocation behaviours giving species access to different prey items as was seen between *P. parnellii* and *M. waterhousii*. Morphology also influenced the speed with which the bats flew, which is another dimension used in partitioning. *T. brasiliensis* foraged with multiple species in edge environments, but flew faster than every other species. Sites with multiple species foraging in them were also partitioned in time. Each species I examined had unique patterns of high and low temporal activity at each site. The combination of all these types of partitioning resulted in each species having access to different prey items which was reflected in dietary analysis. Although previous studies suggested resource partitioning and the means by which it occurs (Findley and Black,

1983; Hickey *et al*., 1996; Fukui *et al*., 2009), these studies focused on only a few pieces of a much bigger puzzle. In doing so, integral biological processes involved in both niche partitioning and resource partitioning can be overlooked, resulting in oversimplifying complex interactions or concluding that partitioning was not occurring when another dimension would support it.

4.10 Future Research

Although I examined multiple levels of partitioning, I did not assess partitioning at all levels. For example, Jacobs and Barclay (2009) noted a difference in roosting behaviour of two sympatric bats, with one species using tree roosts and the other using buildings. In the Windsor region, seven of the eight insectivorous species roost in the Great Windsor Cave and *M. molossus* roosts in buildings, providing a level of partitioning. There may be spatial partitioning within the cave as well, which can be addressed in future research. Intraspecific partitioning may also be occurring. Nudds and Kaminski (1984) and Radford and du Plessis (2003) observed resource partitioning in relation to sexual dimorphism in birds. Although I observed sexual dimorphism, I was unable to detect intraspecific partitioning patterns due to the sampling techniques used, i.e. acoustic monitoring. This dimorphism may play a role in intraspecific resource partitioning, but few bat studies have examined this. Safi et al. (2007) observed differences in ecology and behaviour between sexual dimorphic *Vespertilio murinus*. In a dietary analysis, Rolfe and Kurta (2012) observed dietary differences in male and female *P. parnellii*. Niche partitioning has been observed in other vertebrate groups as well. Knip et al. (2012) found sharks to partition space based on sex. Studies on birds have shown differences in diet based on behaviour (Pinet et al., 2012). Age may also play a key role in intraspecific partitioning. Several studies have shown a trend of bats having relatively high wing loading at birth, which significantly decreases during the rapid growth phase in their first month (Hughes *et al*., 1995; Adams, 2008). Upon first flight, which is typically 21 days after birth, bats are still a fraction of their adult size (Adams, 2008). In *Myotis lucifugus*, an insectivorous bat native to North America, the area of a juvenile's wing upon first flight is 60% of its adult size (Adams, 2008). With morphology playing a large role in habitat partitioning, it stands to reason that morphological differences between age

classes will influence habitat use. Buchler (1980) found adult *Myotis lucifugus* exiting roosts earlier than juveniles, suggesting temporal partitioning. Adams (1996, 1997) found adult *Myotis lucifugus* shifted from using open habitats when juveniles were still roosting, to cluttered environments when the juveniles began foraging. Interspecific competition may not play a role at this site. In four years, only three individuals of other species were caught. Because the niche space may have been relatively open, intraspecific partitioning may have been higher than in more diverse ensemble. The acoustic method I used is not able to distinguish between juvenile and adult, or male and female calls, therefore I was not able to assess intraspecific habitat partitioning. This may explain the differences observed between predicted habitat use through morphology and echolocation call structure, and measured habitat use, from acoustic monitoring. Future research would be required to test this hypothesis.

The methods I used were designed to assess resource partitioning in bats, but the concepts can be modified for other vertebrate species. Mellinger *et al.* (2007) reviewed acoustic monitoring techniques in cetaceans and noted a use for species identification and determination of spatial and temporal activity patterns. Acoustic information may even provide more data in other species than it does in bats. Barrett-Lennard *et al.* (1996) observed echolocation differentiation based on diet, either fish-eating or mammal eating, for sympatric *Orcinus orca* populations. Gasc *et al*. (2013) used species specific territorial songs to determine community diversity in birds. Although this technique provides information on community diversity and spatial and temporal habitat use, it may be highly variable especially between mating and non-mating seasons. For species that do not readily use vocalizations, similar techniques can be used such as video surveillance. Ramesh *et al.* (2012) used camera traps to examine spatial and temporal partitioning in large carnivores. This method can also be used on a wide range of species (O'Connell *et al*, 2010) and although providing different data, similar techniques to those used in this study can assist in analyzing spatial and temporal patterns. DNA barcoding has been employed to analyze diets of a wide range of organisms (Valentini *et al.* 2009), from insects (Staudacher, 2011) to bears (Valentini, 2008), and herbivores (Abdeljalil *et al.* 2012) to carnivores (Chaves *et al.*, 2012). It has even been utilized to examine the diets of

extinct species (Geel *et al.* 2010; Gould *et al.* 2010). DNA barcoding allows species identification of dietary remains, providing the fine scale resolution required to determine partitioning.

4.11 Recommendations

There have been relatively few studies on multi-dimensional resource partitioning in vertebrates (Ross, 1986; Hayward and Garton, 1988; Fasola, 1993; Feldhamer *et al.*, 1993; Kitchen *et al.*, 1999; Bearzi, 2005; Platell *et al.*, 2010; Kamler *et al,*. 2012) and even less so in bats (Aldridge and Rautenbach, 1987; Saunders and Barclay, 1992; Jacobs and Barclay, 2009; Estrada-Villegas *et al.*, 2012; Mancina *et al.*, 2012). Examining multiple dimensions is apt to give a more comprehensive picture than those which only focused on a few factors. In bats, if examining every level of partitioning is not possible I recommend focusing on morphology, diet and temporal activity. Morphology can provide predictions of habitat preference and speed. Temporal activity can allow for separation of species sharing common habitats, and diet can determine if bats are partitioning food resources.

I also suggest using DNA barcoding techniques to determine diets in any vertebrate species, as opposed to visually identifying guano remains. It provides the fine scale resolution required to determine dietary partitioning. Quantitative genetic analysis of guano samples may benefit related studies by quantifying the importance of prey in diet. The dietary overlap observed in this study may have been underestimated, if a shared prey item had high proportions in the diets of multiple species. Finally, I would suggest analyzing temporal data with SatSCan to determine partitioning. This method of analysis provides an objective, statistical method of determining peaks in activity, and although originally designed to measure disease outbreaks, its methodology can be employed on a wide range of organisms and questions.

Chapter 5 - Conclusions

1) Species in the ensemble of insectivorous bats I studied showed resource partitioning based on dietary analysis which may reflect multiple dimensions of niche partitioning including morphological, behavioural, spatial and temporal partitioning. The multiple levels of partitioning seen in this study may aid in maintaining diversity in bats and other ensembles as well, allowing the existence of diverse communities.

2) In the Windsor region of Jamaica, bat activity was highest at sites with water.

3) New methods of analyzing temporal activity may show patterns previously overlooked.

4) New methods of measuring flight speeds in bats may provide more accurate results than traditional methods.

5) The diets of species in the ensemble varied greatly between species and across seasons within a species.

6) The bats I studied ate mainly moths and flies (Lepidoptera and Diptera).

References

Abdeljalil, M., Baamrane, A., Shehzad, W., Ouhammou, A. and Abbad, A. (2012) Assessment of the Food Habits of the Moroccan Dorcas Gazelle in M'Sabih Talaa, West Central Morocco, Using the trnL Approach. PloS one, 7.

Adams, A.M., Jantzen, M.K., Hamilton, R.M. and Fenton, M.B. (2012) Do you hear what I hear? Implications of detector selection for acoustic monitoring of bats. Methods in Ecology and Evolution, 3, 992–998.

Adams, A.M. and M.B. Fenton. Identifying peaks in bat activity: a new application of the space-time scan statistic. Journal of Applied Ecology, submitted.

Adams R. A. (1996) Size-specific resource use in juvenile little brown bats, Myotis lucifugus (Chiroptera: Vespertilionidae): is there an ontogenetic shift? Canadian Journal of Zoology, 1210, 1204–1210.

Adams R.A. (1997) Onset of volancy and foraging patterns of juvenile little brown bats, Myotis lucifugus. Journal of Mammalogy, 78, 239–246.

Adams, R. A. (2008) Morphogenesis in Bat Wings: Linking Development, Evolution and Ecology. Cells Tissues Organs, 187, 13–23.

Adams, R.A. and Thibault, K.M. (2006) Temporal resource partitioning by bats at water holes. Journal of Zoology, 270, 466–472.

Albertson, R.C. (2008) Morphological Divergence Predicts Habitat Partitioning in a Lake Malawi Cichlid Species Complex. Copeia, 2008, 689–698.

Aldridge, H. and Rautenbach, I. (1987) Morphology, echolocation and resource partitioning in insectivorous bats. The Journal of Animal Ecology, 56, 763–778.

Andrianaivoarivelo, A.R., Ranaivoson, N., Racey, P.A. and Jenkins, R.K.B. (2006) The diet of three synanthropic bats (Chiroptera: Molossidae) from eastern Madagascar. Acta Chiropterologica, 8, 439–444.

Arlettaz, R. (1999) Habitat selection as a major resource partitioning mechanism between the two sympatric sibling bat species *Myotis myotis* and *Myotis blythii*. Journal of Animal Ecology, 68, 460–471.

Barrett-Lennard, L.G., Ford, J.K.B. and Heise, K. A. (1996) The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales. Animal Behaviour, 51, 553–565.

Barton, P.S., Gibb, H., Manning, A.D., Lindenmayer, D.B. and Cunningham, S. A. (2011) Morphological traits as predictors of diet and microhabitat use in a diverse beetle assemblage. Biological Journal of the Linnean Society, 102, 301–310.

Bearzi, M. (2005) Dolphin sympatric ecology. Marine Biology Research, 1, 165–175.

Bell, G.P. (1980) Habitat use and response to patches of prey by desert insectivorous bats. Canadian Journal of Zoology, 58, 1876–1883.

Bell GP (1982) Behavioral and ecological aspects of gleaning by a desert insectivorous bat Antrozous pallidus (Chiroptera: Vespertilionidae). Behavioral Ecology and Sociobiology, 10, 217–223.

Bell GP (1985) The sensory basis of prey location by the California leaf-nosed bat Macrotus californicus (Chiroptera: Phyllostomidae). Behavioral Ecology and Sociobiology, 16, 343–347.

Bininda-Emonds, O. and Russell, A. (1994) Flight style in bats as predicted from wing morphometry: the effects of specimen preservation. Journal of Zoology, 234, 275–287.

Blankenberg, D., Von Kuster, G., Coraor, N., Ananda, G., Lazarus, R., Mangan, M., Nekrutenko, A. and Taylor, J. (2010) Galaxy: a web-based genome analysis tool for experimentalists. Current Protocols in Molecular Biology, 19-10.

Bohmann, K., Monadjem, A., Noer, C.L., Rasmussen, M., Zeale, M.R.K., Clare, E., Jones, G., Willerslev, E. and Gilbert, M.T.P. (2011) Molecular Diet Analysis of Two African Free-Tailed Bats (Molossidae) Using High Throughput Sequencing. PloS one, 6, e21441.

Brinklov, S., Jakobsen, L., Ratcliffe, J.M., Kalko, E.K. V and Surlykke, A. (2011) Echolocation call intensity and directionality in flying short-tailed fruit bats, *Carollia perspicillata* (Phyllostomidae). Journal of the Acoustical Society of America, 129, 427–435.

Brinklov, S., Kalko, E.K. V and Surlykke, A. (2009) Intense echolocation calls from two "whispering" bats, *Artibeus jamaicensis* and *Macrophyllum macrophyllum* (Phyllostomidae). Journal of Experimental Biology, 212, 11–20.

Buchler E.R. (1980) The development of flight, foraging, and echolocation in the little brown bat (Myotis lucifugus). Behavioral Ecology and Sociobiology, 6, 211–218.

Buckley, L.B., Davies, T.J., Ackerly, D.D., Kraft, N.J.B., Harrison, S.P., Anacker, B.L., Cornell, H. V, Damschen, E.I., Grytnes, J.A., Hawkins, B.A., McCain, C.M., Stephens, P.R. and Wiens, J.J. (2010) Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. Proceedings of the Royal Society B-Biological Sciences, 277, 2131–2138.

Buckley, L.B. and Roughgarden, J. (2005) Lizard habitat partitioning on islands: the interaction of local and landscape scales. Journal of Biogeography, 32, 2113–2121.

Bumrungsri, S., Leelapaibul, W. and Racey, P. (2007) Resource partitioning in sympatric Cynopterus bats in lowland tropical rain forest, Thailand. Biotropica, 39, 241–248.

Burles, D.W., Brigham, R.M., Ring, R. a. and Reimchen, T.E. (2008) Diet of two insectivorous bats, *Myotis lucifugus* and *Myotis keenii*, in relation to arthropod abundance in a temperate Pacific Northwest rainforest environment. Canadian Journal of Zoology, 86, 1367–1375.

Chaves, P.B., Graeff, V.G., Lion, M.B., Oliveira, L.R. and Eizirik, E. (2012) DNA barcoding meets molecular scatology: short mtDNA sequences for standardized species assignment of carnivore noninvasive samples. Molecular Ecology Resources, 12, 18–35.

Clare E., Adams A. (2013) Diversification and reproductive isolation: cryptic species in the only New World high-duty cycle bat, Pteronotus parnellii. BMC evolutionary biology, 13, 26.

Cotton, P. (1998) Temporal partitioning of a floral resource by territorial hummingbirds. Ibis, 140, 647–653.

Dial, K. (1988) Three sympatric species of *Neotoma*: dietary specialization and coexistence. Oecologia, 76, 531–537.

Dunbar, R.I.M. (1978) Competition and niche separation in a high altitude herbivore community in Ethiopia. African Journal of Ecology, 16, 183–199.

Estrada-Villegas, S., McGill, B.J. and Kalko, E.K. V. (2012) Climate, habitat, and species interactions at different scales determine the structure of a Neotropical bat community. Ecology, 93, 1183–93.

Farrell, L.E., Roman, J. and Sunquist, M.E. (2000) Dietary separation of sympatric carnivores identified by molecular analysis of scats. Molecular Ecology, 9, 1583–90.

Fasola, M. (1993) Resource partitioning by three species of newts during their aquatic phase. Ecography, 16, 73–81.

Fauth, J., Bernardo, J. and Camara, M. (1996) Simplifying the jargon of community ecology: a conceptual approach. The American Naturalist, 147, 282–286.

Feldhamer, G.A., Carter, T.C., John, O., The, S., Midland, A. and Whitaker, J.O. (2009) Prey Consumed by Eight Species of Insectivorous Bats from Southern Illinois. The American Midland Naturalist, 162, 43–51.

Feldhamer, G., Klann, R., Gerard, A. and Driskell, A. (1993) Habitat partitioning, body size, and timing of parturition in pygmy shrews and associated soricids. Journal of Mammalogy, 74, 403–411.

Fenton, M. (1990) The foraging behaviour and ecology of animal-eating bats. Canadian Journal of Zoology, 68, 411–422.

Fenton, M.B. and Bell, G.P. (1981) Recognition of species of insectivorous bats by their echolocation calls. Journal of Mammalogy, 62, 233–243.

Fenton, M. and Bogdanowicz, W. (2002) Relationships between external morphology and foraging behaviour: bats in the genus *Myotis*. Canadian Journal of Zoology, 80, 1004–1013.

Fenton, M.B., Faure, P.A. and Ratcliffe, J.M. (2012) Evolution of high duty cycle echolocation in bats. Journal of Experimental Biology, 215, 2935–2944.

Findley, J. and Black, H. (1983) Morphological and dietary structuring of a Zambian insectivorous bat community. Ecology, 64, 625–630.

Fukui D, Okazaki K, Maeda K (2009) Diet of three sympatric insectivorous bat species on Ishigaki Island, Japan. Endangered Species Research, 8, 117–128.

Gable, J., Crowder, D., Tobin, D., Steffan, S. & Snyder, W. (2012) Niche engineering reveals complementary resource use. Ecology, 93, 1994–2000.

Gabor, T., Hellgren, E. and Silvy, N. (2001) Multi-scale habitat partitioning in sympatric suiforms. The Journal of Wildlife Management, 65, 99–110.

Gasc, A., Sueur, J., Jiguet, F., Devictor, V., Grandcolas, P., Burrow, C., Depraetere, M. and Pavoine, S. (2013) Assessing biodiversity with sound: Do acoustic diversity indices reflect phylogenetic and functional diversities of bird communities? Ecological Indicators, 25, 279–287.

Gatti, R. (2012) The evolution of biodiversity: state of knowledge, recent developments and new hypotheses. economologos.com, III.

Geel, B. Van and Guthrie, R. (2011) Mycological evidence of coprophagy from the feces of an Alaskan Late Glacial mammoth. Quaternary Science Reviews, 30, 2289–2303.

Giardine, B., Riemer, C., Hardison, R.C., Burhans, R., Elnitski, L., Shah, P., Zhang, Y., Blankenberg, D., Albert, I., Taylor, J., Miller, W., Kent, W.J. and Nekrutenko, A. (2005) Galaxy: A platform for interactive large-scale genome analysis. Genome Research, 15, 1451–1455.

Goecks, J., Nekrutenko, A., Taylor, J. and Galaxy, T. (2010) Galaxy: a comprehensive approach for supporting accessible, reproducible, and transparent computational research in the life sciences. Genome Biology, 11, R86.

Gordon, C.E., Dickman, C.R. and Thompson, M.B. (2010) Partitioning of temporal activity among desert lizards in relation to prey availability and temperature. Austral Ecology, 35, 41–52.

Gould, B. and León, B. (2010) Evidence of a high-Andean, mid-Holocene plant community: An ancient DNA analysis of glacially preserved remains. American Journal of Botany, 97, 1579–1584.

Gutman, R. and Dayan, T. (2005) Temporal partitioning: an experiment with two species of spiny mice. Ecology, 86, 164–173.

Hamming, R.W. (1950) Error detecting and error correcting codes. Bell System Technical Journal, 29, 147–160.

Hardin, G. (1960) The competitive exclusion principle. Science, 131, 1292–1297.

Hayward, B. and Davis, R. (1964) Flight speeds in western bats. Journal of Mammalogy, 45, 236–242.

Hayward, G. and Garton, E. (1988) Resource partitioning among forest owls in the River of No Return Wilderness, Idaho. Oecologia, 75, 253–265.

Hertel, F. and Ballance, L. (1999) Wing ecomorphology of seabirds from Johnston Atoll. Condor, 101, 549–556.

Hickey, M.B.C., Acharya, L. and Pennington, S. (1996) Resource partitioning by two species of vespertilionid bats (*Lasiurus cinereus* and *Lasiurus borealis*) feeding around street lights. Journal of Mammalogy, 77, 325–334.

Hopkins, H.L., Sanchez-Hernandez, C., Romero-Almaraz, M.D., Gilley, L.M., Schnell, G.D. and Kennedy, M.L. (2003) Flight speeds of four species of Neotropical bats. Southwestern Naturalist, 48, 711–714.

Hubbell, S. P. (2008). The unified neutral theory of biodiversity and biogeography (MPB-32) (Vol. 32). Princeton University Press.

Huson, D.H., Mitra, S., Ruscheweyh, H.J., Weber, N. and Schuster, S.C. (2011) Integrative analysis of environmental sequences using MEGAN4. Genome Research, 21, 1552–1560.

Inouye, D. (1978) Resource partitioning in bumblebees: experimental studies of foraging behavior. Ecology, 59, 672–678.

Jacobs, D. and Barclay, R. (2009) Niche differentiation in two sympatric sibling bat species, *Scotophilus dinganii* and *Scotophilus mhlanganii*. Journal of Mammalogy, 90, 879–887.

Jakobsen, L. and Surlykke, A. (2010) Vespertilionid bats control the width of their biosonar sound beam dynamically during prey pursuit. Proceedings of the National Academy of Sciences of the United States of America, 107, 13930–13935.

Jantzen, M. and Fenton, M. (2013) The depth of edge influence among insectivorous bats at forest-field interfaces. Canadian Journal of Zoology, 292, 287–292.

Jennings, N. V, Parsons, S., Barlow, K.E. and Gannon, M.R. (2004) Echolocation calls and wing morphology of bats from the West Indies. Acta Chiropterologica, 6, 75–90.

Jones, M., Ghoorah, A. and Blaxter, M. (2011) jMOTU and Taxonerator: Turning DNA Barcode Sequences into Annotated Operational Taxonomic Units. PloS one, 6, e19259.

Jones, G. and Rydell, J. (1994) Foraging Strategy and Predation Risk as Factors Influencing Emergence Time in Echolocating Bats. Philosophical Transactions of the Royal Society B: Biological Sciences, 346, 445–455.

Kadye, W.T. and Chakona, A. (2012) Spatial and temporal variation of fish assemblage in two intermittent streams in north-western Zimbabwe. African Journal of Ecology, 50, 428–438.

Kalko, E. (1995) Insect pursuit, prey capture and echolocation in pipestirelle bats (Microchiroptera). Animal Behaviour, 50, 861–880.

Kalko, E. K. V. (2004) Neotropical leaf-nosed bats (Phyllostomidae):"Whispering" bats or candidates for acoustic survey. Proceedings of a Workshop on Identification and Acoustic Monitoring of Bats, M. Brigham, G. Jones, and EKV Kalko, eds. Austin, TX: Bat Conservation International.

Kamler, J.F., Stenkewitz, U., Klare, U., Jacobsen, N.F. and Macdonald, D.W. (2012) Resource partitioning among cape foxes, bat-eared foxes, and black-backed jackals in South Africa. The Journal of Wildlife Management, 76, 1241–1253.

Kitchen, A.M., Gese, E.M. and Schauster, E.R. (1999) Resource partitioning between coyotes and swift foxes: space, time, and diet. Canadian Journal of Zoology, 77, 1645–1656.

Knip, D.M., Heupel, M.R. and Simpfendorfer, C. a. (2012) Habitat use and spatial segregation of adult spottail sharks *Carcharhinus sorrah* in tropical nearshore waters. Journal of Fish Biology, 80, 767–84.

Koenig, S.E. (2001) The breeding biology of Black-billed Parrot Amazona agilis and Yellow-billed Parrot *Amazona collaria* in Cockpit Country, Jamaica. Bird Conservation International, 11, 205–225.

Konishi, M. and Knudsen, E. (1979) The oilbird: hearing and echolocation. Science, 204, 425–427.

Kronfeld-Schor, N. and Dayan, T. (2003) Partitioning of time as an ecological resource. Annual Review of Ecology, Evolution, and Systematics, 34, 153–181.

Kulldorff, M. (2010) Information Management Services, Inc. (2005) SaTScanTM v6. 0: Software for the Spatial and Space-Time Scan Statistics.

Kunz, T.H. (1973) Temporal and Spatial Components of Bat Activity in Central Iowa. Journal of Mammalogy, 54, 14–32.

Lazure, L. and Fenton, M.B. (2011) High duty cycle echolocation and prey detection by bats. Journal of Experimental Biology, 214, 1131–1137.

Levine, J.M. and HilleRisLambers, J. (2009) The importance of niches for the maintenance of species diversity. Nature, 461, 254–7.

Lopez, J.E. and Vaughan, C. (2007) Food niche overlap among neotropical frugivorous bats in Costa Rica. Revista de Biología Tropical, 55, 301–13.

Losos, J. (1990) Ecomorphology, performance capability, and scaling of West Indian Anolis lizards: an evolutionary analysis. Ecological Monographs, 60, 369–388.

Mancina, C. (2005) *Pteronotus macleayii*. Mammalian Species, 1–3.

Mancina, C.A., Garcia-Rivera, L. and Miller, B.W. (2012) Wing morphology, echolocation, and resource partitioning in syntopic Cuban mormoopid bats. Journal of Mammalogy, 93, 1308–1317.

McCune, B., Grace, J.B. and Urban, D.L. (2002) Analysis of Ecological Communities. MjM Software Design Gleneden Beach, Oregon.

McNab, B. (1976) Seasonal fat reserves of bats in two tropical environments. Ecology, 57, 332–338.

Mellinger, D., Stafford, K. and Moore, S. (2007) Fixed passive acoustic observation methods for cetaceans. Oceanography, 20, 36–45.

Menzel, J., Menzel, M. and Kilgo, J. (2005) Effect of habitat and foraging height on bat activity in the coastal plain of South Carolina. Journal of Wildlife Management, 69, 235–245.

Miller, B.W. (2001) A method for determining relative activity of free flying bats using a new activity index for acoustic monitoring. Acta Chiropterologica, 3, 93–105.

Murray, K., Fraser, E. and Davy, C. (2009) Characterization of the echolocation calls of bats from Exuma, Bahamas. Acta Chiropterologica, 11, 415–424.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B. and Kent, J. (2000) Biodiversity hotspots for conservation priorities. Nature, 403, 853–858.

Nicholls, B. and Racey, P. (2006) Habitat selection as a mechanism of resource partitioning in two cryptic bat species *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus*. Ecography, 29, 697–708.

Norberg, U.M. and Rayner, J.M.V. (1987) Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Philosophical Transactions of the Royal Society of London B Biological Sciences, 316, 335–427.

Nowak, R. M. (Ed.) (1994) Walker's bats of the world. JHU Press.

Nudds, T. and Kaminski, R. (1984) Sexual size dimorphism in relation to resource partitioning in North American dabbling ducks. Canadian Journal of Zoology, 62, 2009–2012.

O'Connell, A. F., Nichols, J. D., & Kāranta, K. U. (2010) Camera traps in animal ecology. Springer.

Paine, R. (1980) Food webs: linkage, interaction strength and community infrastructure. Journal of Animal Ecology, 49, 666–685.

Patriquin, K. and Barclay, R. (2003) Foraging by bats in cleared, thinned and unharvested boreal forest. Journal of Applied Ecology, 40, 646–657.

Patterson, B.D., Willig, M.R. and Stevens, R.D. (2003) Trophic Strategies, Niche Partitioning, and Patterns of Ecological Organization (eds TH Kunz and MB Fenton). The University of Chicago Press, 536-579.

Pennycuick, C. J. (2008). Modelling the flying bird (Vol. 5). Academic press.

Pinet, P., Jaquemet, S., Phillips, R. a. and Le Corre, M. (2012) Sex-specific foraging strategies throughout the breeding season in a tropical, sexually monomorphic small petrel. Animal Behaviour, 83, 979–989.

Platell, M.E., Hesp, S.A., Cossington, S.M., Lek, E., Moore, S.E. and Potter, I.C. (2010) Influence of selected factors on the dietary compositions of three targeted and co-occurring temperate species of reef fishes: implications for food partitioning. Journal of Fish Biology, 76, 1255–1276.

Racey, P.A. and Entwistle, A.C. (2003) Conservation Ecology of Bats (eds TH Kunz and MB Fenton). The University of Chicago Press, 680-743

Radford, A. and du Plessis, M. (2003) Bill dimorphism and foraging niche partitioning in the green woodhoopoe. Journal of Animal Ecology, 72, 258–269.

Ramesh, T., Kalle, R., Sankar, K. and Qureshi, Q. (2012) Spatio-temporal partitioning among large carnivores in relation to major prey species in Western Ghats. Journal of Zoology, 287, 269–275.

Razgour, O., Korine, C. & Saltz, D. (2011a) Does interspecific competition drive patterns of habitat use in desert bat communities? Oecologia, 167, 493–502.

Razgour, O., Clare, E.L., Zeale, M.R.K., Hanmer, J., Schnell, I.B., Rasmussen, M., Gilbert, T.P. and Jones, G. (2011b) High-throughput sequencing offers insight into mechanisms of resource partitioning in cryptic bat species. Ecology and Evolution, 1, 556–70.

Ricklefs, R.E. (2007) History and diversity: Explorations at the intersection of ecology and evolution. American Naturalist, 170, S56–S70.

Rolfe, A.K. and Kurta, A. (2012) Diet of Mormoopid Bats on the Caribbean Island of Puerto Rico. Acta Chiropterologica, 14, 369–377.

Ross, S. (1986) Resource partitioning in fish assemblages: a review of field studies. Copeia, 1986, 352–388.

Russell, P.J., S.L. Wolfe, P.E. Hertz, C. Starr, M.B. Fenton, H. Addy, D. Maxwell, T. Haffie and K. Davey. (2010) Biology: Exploring the Diversity of Life. Thomson Brooks/Cole.

Safi, K., König, B. and Kerth, G. (2007) Sex differences in population genetics, home range size and habitat use of the parti-colored bat (*Vespertilio murinus*, Linnaeus 1758) in Switzerland and their consequences for conservation. Biological Conservation, 137, 28–36.

Saldamendi, E., Aihartza, J., Goiti, U., Almenar, D. and Garin, I. (2005) Echolocation calls and morphology in the Mehelyi's (*Rhinolophus mehelyi*) and Mediterranean (*Rhinolophus euryale*) horseshoe bats: implications for resource partitioning. Journal of Mammalogy, 16, 149–158.

Saunders, M. and Barclay, R. (1992) Ecomorphology of insectivorous bats: a test of predictions using two morphologically similar species. Ecology, 73, 1335–1345.

Schick, R., Halpin, P., Read, A., Urban, D., Best, B., Good, C., Roberts, J., LaBrecque, E., Dunn, C., Garrison, L., Hyrenbach, K., McLellan, W., Pabst, D., Palka, D. and Stevick, P. (2011) Community structure in pelagic marine mammals at large spatial scales. Marine Ecology Progress Series, 434, 165–181.

Schnitzler, H. and Kalko, E. (2001) Echolocation by insect-eating bats. Bioscience, 51, 557–569.

Schoener, T.W. (1974) Resource partitioning in ecological communities. Science, 185, 27–39.

Shine, R., Shine, T. and Shine, B. (2003) Intraspecific habitat partitioning by the sea snake *Emydocephalus annulatus* (Serpentes, Hydrophiidae): the effects of sex,

body size, and colour pattern. Biological Journal of the Linnean Society, 80, 1–10.

Siemers, B.M. and Swift, S.M. (2006) Differences in sensory ecology contribute to resource partitioning in the bats *Myotis bechsteinii* and *Myotis nattereri* (Chiroptera: Vespertilionidae). Behavioral Ecology and Sociobiology, 59, 373–380.

Simmons, J. A. (1973) The resolution of target range by echolocating bats. The Journal of the Acoustical Society of America, 54, 157–173.

Skowronski, M.D. and Fenton, M.B. (2008) Model-based automated detection of echolocation calls using the link detector. Journal of the Acoustical Society of America, 124, 328–336.

Spencer, L. (1995) Morphological correlates of dietary resource partitioning in the African Bovidae. Journal of Mammalogy, 76, 448–471.

Staudacher, K., Wallinger, C., Schallhart, N. and Traugott, M. (2011) Detecting ingested plant DNA in soil-living insect larvae. Soil Biology and Biochemistry, 43, 346–350.

Steenweg, R.J., Ronconi, R.A. and Leonard, M.L. (2011) Seasonal and Age-Dependent Dietary Partitioning between the Great Black-backed and Herring Gulls. Condor, 113, 795–805.

Surlykke, A., Boel Pedersen, S. and Jakobsen, L. (2009) Echolocating bats emit a highly directional sonar sound beam in the field. Proceedings of the Royal Society B: Biological Sciences, 276, 853–60.

Surlykke, A. and Kalko, E.K. V. (2008) Echolocating bats cry out loud to detect their prey. PloS one, 3, e2036.

Swartz, S.M., Freeman, P.W. and Stockwell, E.F. (2003) Ecomorphology of Bats: Comparative and Experimental Approaches Relating Structural Design to Ecology (eds TH Kunz and MB Fenton). The University of Chicago Press, 257-300

Takahashi, K., Tuno, N. and Kagaya, T. (2005) The relative importance of spatial aggregation and resource partitioning on the coexistence of mycophagous insects. Oikos, 109, 125–134.

Thomas, J. A., Moss, C.F. and Vater, M. (2004). Echolocation in bats and dolphins. University of Chicago Press.

Valentini, A. (2008) Non-invasive Diet Analysis Based on DNA Barcoding: The Himalayan Brown Bears (*Ursus arctos isabellinus*) as a Case Study.

Valentini, A., Pompanon, F. and Taberlet, P. (2009) DNA barcoding for ecologists. Trends in Ecology and Evolution, 24, 110–7.

Vanhooydonck, B., Herrel, A., Gabela, A. and Podos, J. (2009) Wing shape variation in the medium ground finch (*Geospiza fortis*): an ecomorphological approach. Biological Journal of the Linnean Society, 98, 129–138.

Vaughan, T.A. (1970) Flight patterns and aerodynamics. Biology of Bats 1 (ed W.A. Wimsatt), pp. 195–216. Academic Press, New York.

Veen, T., Sheldon, B.C., Weissing, F.J., Visser, M.E., Qvarnström, A. and Saetre, G.-P. (2010) Temporal differences in food abundance promote coexistence between two congeneric passerines. Oecologia, 162, 873–84.

Venner, S., Pélisson, P.-F., Bel-Venner, M.-C., Débias, F., Rajon, E. and Menu, F. (2011) Coexistence of insect species competing for a pulsed resource: toward a unified theory of biodiversity in fluctuating environments. PloS one, 6, e18039.

Vogel, P. (1997) Summary of bat surveys of Windsor Cave, 18-21 July 1997. Retrieved from the Windsor Research Centre (Jamaica).

Werf, A. Van der, Nuenen, M. Van, Visser, A. and Lambers, H. (1993) Contribution of physiological and morphological plant traits to a species' competitive ability at high and low nitrogen supply: a hypothesis for inherently fast. Oecologia, 94, 434–440.

Weltzin, J.F. and McPherson, G.R. (1997) Spatial and temporal soil moisture resource partitioning by trees and grasses in a temperate savanna, Arizona, USA. Oecologia, 112, 156–164.

Whitaker, J.O., Issac, S.S., Marimuthu, G. and Kunz, T.H. (1999) Seasonal variation in the diet of the Indian pygmy bat, *Pipistrellus mimus*, in southern India. Journal of Mammalogy, 80, 60–70.

Williams, T., Ireland, L. and Williams, J. (1973) High altitude flights of the free-tailed bat, *Tadarida brasiliensis*, observed with radar. Journal of Mammalogy, 54, 807–821.

Williams, J., O'Farrell, M. and Riddle, B. (2006) Habitat use by bats in a riparian corridor of the Mojave Desert in southern Nevada. Journal of Mammalogy, 87, 1145–1153.

Zeale, M.R.K., Butlin, R.K., Barker, G.L.A., Lees, D.C. and Jones, G. (2011) Taxon-specific PCR for DNA barcoding arthropod prey in bat faeces. Molecular Ecology Resources, 11, 236–244.

Appendices A: Morphology

Figure 6: Example of wing membrane photograph used to calculate wing surface areas.

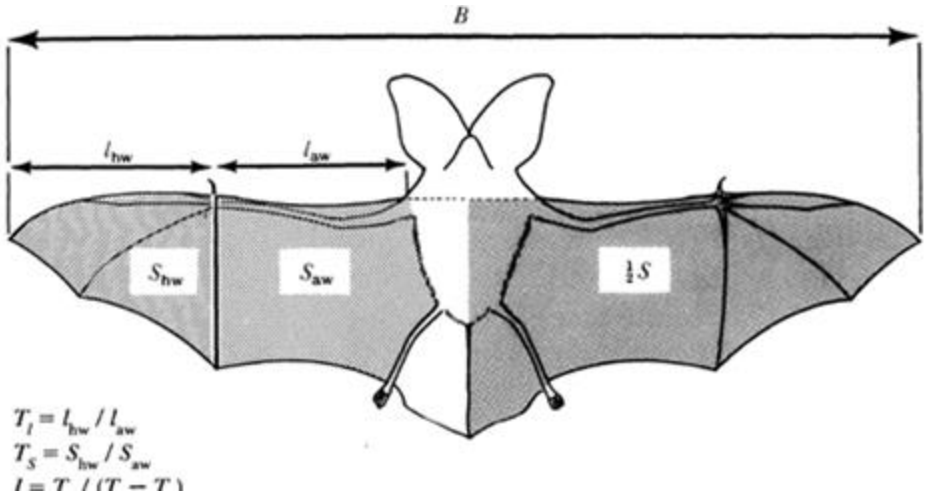


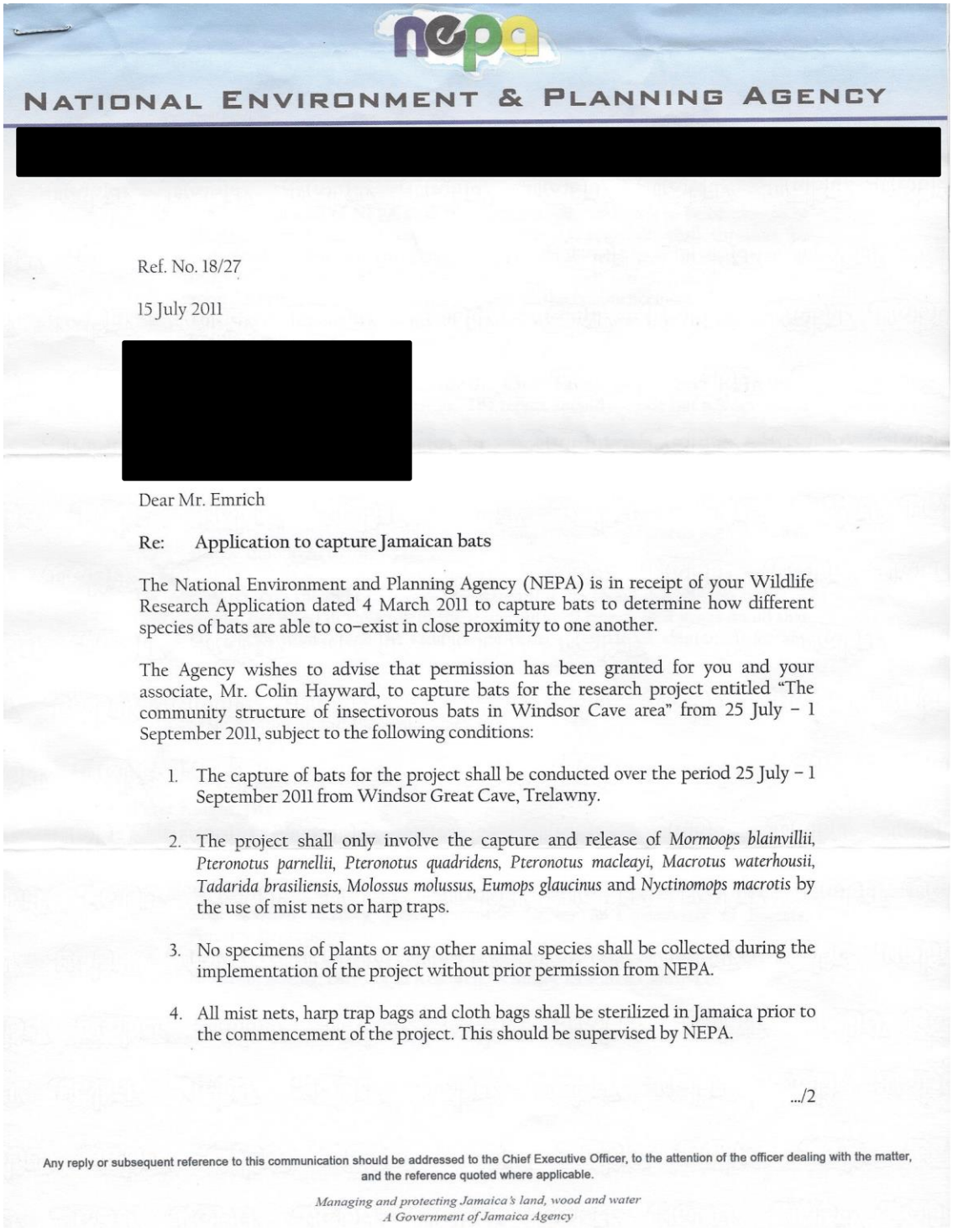
Figure 7: Definition of morphological quantities used in this paper to bat wings. The wingspan B, is measured from tip to tip of extended wings; S is the wing area, including the tail membrane (when present) and the area of the body between the wings, but excluding the projected area of the head; aspect ratio and wing loading are defined from these quantities with body mass M and gravitational acceleration g = 9.81 m s^{-2}. S_{hw} and S_{aw} are the areas of the hand- and arm-wings, that is the area distal to the fifth digit and between the fifth digit, the body and the legs. l_{hw} and l_{aw} are the corresponding lengths. These quantities are used to define the tip length and tip area ratios, T_l and T_s and the wingtip shape index, I (figure adapted from Norberg and Rayner, 1987).

Appendices B: Acoustics

Using Avisoft SASLab Pro (Avisoft Bioacoustics, Berlin, Germany), the acoustic file was shortened to include only the calls of the flight path. To create the paths I used the program Moonshine, a MatLab based program designed to generate flight paths (Lasse Jakobsen, University of Ulm, program creator). I loaded a text file containing the coordinates of the arrays microphones and set channel 3 to be analyzed, the microphone in the center of the array. Temperature and humidity data was collected every 30 minutes using a HOBO U30 Weather Station with S-THB-M00x Temperature/RH Smart Sensor (Onset, MA, USA). The weather data at the time closest to the acoustic file's time stamp was used in the flight path analysis. The threshold level used in the analysis varied between files but was always set to a level that included as many echolocation calls as possible, while omitting background noise. The C-width, the window of time the program searches for the same call among channels once a call is detected, was set to 2.5 ms. Next I ran the analysis which generated a text file containing the 3-dimensional coordinate of where the bat was when it produced the call. I calculated the distance traveled and speed between each point. Using Matlab I generated a 3-dimensional graph of the bats flight.

Figure 8: Two, four microphone acoustic arrays set up back to back at Site 3.

Appendices C: Permits



NATIONAL ENVIRONMENT & PLANNING AGENCY

[redacted]

Ref. No. 18/27

15 July 2011

[redacted]

Dear Mr. Emrich

Re: Application to capture Jamaican bats

The National Environment and Planning Agency (NEPA) is in receipt of your Wildlife Research Application dated 4 March 2011 to capture bats to determine how different species of bats are able to co-exist in close proximity to one another.

The Agency wishes to advise that permission has been granted for you and your associate, Mr. Colin Hayward, to capture bats for the research project entitled "The community structure of insectivorous bats in Windsor Cave area" from 25 July – 1 September 2011, subject to the following conditions:

1. The capture of bats for the project shall be conducted over the period 25 July – 1 September 2011 from Windsor Great Cave, Trelawny.

2. The project shall only involve the capture and release of *Mormoops blainvillii*, *Pteronotus parnellii*, *Pteronotus quadridens*, *Pteronotus macleayi*, *Macrotus waterhousii*, *Tadarida brasiliensis*, *Molossus molussus*, *Eumops glaucinus* and *Nyctinomops macrotis* by the use of mist nets or harp traps.

3. No specimens of plants or any other animal species shall be collected during the implementation of the project without prior permission from NEPA.

4. All mist nets, harp trap bags and cloth bags shall be sterilized in Jamaica prior to the commencement of the project. This should be supervised by NEPA.

.../2

Any reply or subsequent reference to this communication should be addressed to the Chief Executive Officer, to the attention of the officer dealing with the matter, and the reference quoted where applicable.

Managing and protecting Jamaica's land, wood and water
A Government of Jamaica Agency

5. A member of staff of NEPA shall participate in the fieldwork to be conducted at Windsor Great Cave. A copy of the fieldwork schedule shall therefore be submitted to Ms. Andrea Donaldson, at NEPA who may be contacted at telephone numbers [redacted] or e-mail [redacted] two weeks prior to the commencement of the project. This should include the names of persons who will assist in the capture and handling of bats during the project.

6. A project report shall be sent to the Chief Executive Office of NEPA by 1 December 2011 at [redacted] The report should include but not limited to the following: a list of species collected and observed, total number of each species collected and the location of collection sites (latitude and longitude coordinates). A final report on the findings of the project shall be submitted to NEPA and the JCDT by 1 March 2012.

7. Copies of all articles and publications arising from the specimens collected shall also be submitted to this Agency.

The Agency reserves the right to revoke the permit if it has found that the researcher or their associate has acted in violation of the terms outlined herein, or if it has found that any of the species from which the samples are being collected are threatened for any reason.

Yours sincerely
National Environment and Planning Agency

[redacted]

Peter Knight, JP
Chief Executive Officer

/mc

c. Mrs. Marilyn Headley, Chief Executive Officer & Conservator of Forests, Forestry Department
Dr. M. B. Fenton, Emeritus Professor of Biology, University of Western Ontario
Dr. Susan Koenig, Director of Research, Windsor Research Centre Ltd.

NATIONAL ENVIRONMENT & PLANNING AGENCY

[redacted]

Ref. #: 18/27

9 May 2012

[redacted]

Dear Mr. Emrich

Re: Application to capture Jamaican bats

The National Environment and Planning Agency (NEPA) refers to your Wildlife Research Application dated 4 March 2011 to capture bats to determine how different species of bats are able to co-exist in close proximity to one another and to our permission letter dated 15 July 2011. The Agency also acknowledges receipt of your e-mail dated 1 May 2012 requesting an extension to this research.

Please be advised that this letter supersedes the permission letter dated 15 July 2011 granted to you and your associate, Mr. Colin Hayward to capture bats for the research project entitled "The community structure of insectivorous bats in Windsor Cave area" from 25 July to 15 December 2012, subject to the following conditions:

1. The capture of bats for the project shall be conducted over the period 25 July – 15 December 2012 from Windsor Great Cave, Trelawny.

2. The project shall only involve the capture and release of *Mormoops blainvillii, Pteronotus parnellii, Pteronotus quadridens, Pteronotus macleayi, Macrotus waterhousii, Tadarida brasiliensis, Molossus molussus, Eumops glaucinus* and *Nyctinomops macrotis* by the use of mist nets or harp traps.

3. No specimens of plants or any other animal species shall be collected during the implementation of the project without prior permission from NEPA.

.../2

4. All mist nets, harp trap bags and cloth bags shall be sterilized in Jamaica prior to the commencement of the project. This should be supervised by NEPA.

5. The species *Mormoops blainvilli* is not to be held in cloth holding bags for fecal collection but placed in a small, fine-mesh-sided holding box, with a hanging perch.

6. A member of staff of NEPA shall participate in the fieldwork to be conducted at Windsor Great Cave. A copy of the fieldwork schedule shall therefore be submitted to Ms. Andrea Donaldson, at NEPA who may be contacted at telephone numbers [redacted] two weeks prior to the commencement of the project. This should include the names of persons who will assist in the capture and handling of bats during the project.

7. A project report shall be sent to the Chief Executive Office of NEPA by 31 March 2013 at [redacted] The report should include but not limited to the following: a list of species collected and observed, total number of each species collected and the location of collection sites (latitude and longitude coordinates). A final report on the findings of the project shall be submitted to NEPA and the JCDT by 30 June 2013.

8. Copies of all articles and publications arising from the specimens collected shall also be submitted to this Agency.

The Agency reserves the right to revoke the permit if it has found that the researcher or their associate has acted in violation of the terms outlined herein, or if it has found that any of the species from which the samples are being collected are threatened for any reason.

Yours sincerely
National Environment and Planning Agency

[redacted]

Peter Knight, JP
Chief Executive Officer

/ad

c. Mrs. Marilyn Headley, Chief Executive Officer & Conservator of Forests, Forestry Department
Dr. M. B. Fenton, Emeritus Professor of Biology, University of Western Ontario
Dr. Susan Koenig, Director of Research, Windsor Research Centre Ltd.

AUSPC

From: [redacted]
Sent:
To:
Cc:
Subject: eSirius Notification - Annual Protocol Renewal APPROVED by the AUS 2008-003-04::3

Western

2008-003-04::3:

AUP Number: 2008-003-04
AUP Title: Behavioural Ecology of Bats

The YEARLY RENEWAL to Animal Use Protocol (AUP) 2008-003-04 has been approved.

1. This AUP number must be indicated when ordering animals for this project.
2. Animals for other projects may not be ordered under this AUP number.
3. Purchases of animals other than through this system must be cleared through the ACVS office. Health certificates will be required.

REQUIREMENTS/COMMENTS
Please ensure that individual(s) performing procedures on live animals, as described in this protocol, are familiar with the contents of this document.

The holder of this Animal Use Protocol is responsible to ensure that all associated safety components (biosafety, radiation safety, general laboratory safety) comply with institutional safety standards and have received all necessary approvals. Please consult directly with your institutional safety officers.

Submitted by: Thompson, Sharla H
on behalf of the Animal Use Subcommittee

[redacted]

[redacted]

Curriculum Vitae

Name: Matthew Emrich

Post-secondary Education and Degrees:
McGill University
Montreal, Quebec, Canada
2007-2010 B.Sc.

The University of Western Ontario
London, Ontario, Canada
2011-2013 M.Sc.

Related Work Experience
Teaching Assistant
The University of Western Ontario
2011-2013

Presentations:

Emrich, M.A. 2012. Ensemble Structure of Sympatric Insectivorous Bats. 42nd Annual North American Symposium on Bat Research, San Juan, Puerto Rico.

Emrich, M.A. 2012. Ensemble Structure of Sympatric Insectivorous Bats. Bat Research Meeting Cuba-Canada, Havana, Cuba.

Emrich, M.A. 2011. Flight Patterns of Sympatric Insectivorous Bats in Jamaica. 41st Annual North American Symposium on Bat Research, Toronto, Ontario.