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## The Role of Morphology in Diet and Flower Visitation by Five Species of Cuban Flower-Visiting Bats

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A thesis submitted in partial fulfillment of the requirements for the degree in Master of Science  
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THE ROLE OF MORPHOLOGY IN DIET AND FLOWER VISITATION BY FIVE  
SPECIES OF CUBAN FLOWER-VISITING BATS

(Thesis format: Monograph)

by

Lindsey Clairmont

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

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## Abstract

Pollinator and flower morphology are important factors in structuring the plant-pollinator relationship. A pollinator's morphology may influence aspects of its diet. Flower-visiting bats are important pollinators but very little is known about what influences their interactions with food plants. I examined the role of morphology in the partitioning of food resources for five species of flower-visiting Cuban bats. I analyzed cranial traits and body size to examine differences among species and to determine the degree of morphological specialization for flower-feeding for each species. I also collected dietary data from guano and used acoustic monitoring to assess bat activity at flowers. I found evidence of partitioning of plant resources among the bat species, although evidence of limiting resources was not observed. Morphological similarity between species did not predict dietary overlap. However, species differing in their morphological specialization for flower-feeding consumed resources and visited food plants at different frequencies.

## Keywords

Flower-visiting bats, flower visitation, food resource partitioning, ecomorphology, specialization, nectarivory, Cuba, *Artibeus jamaicensis*, *Brachyphylla nana*, *Erophylla sezekorni*, *Monophyllus redmani*, *Phyllonycteris poeyi*.

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## Chapter 1 - Introduction

### 1.1 Understanding Plant-Pollinator Interactions

Mutualistic interactions are relationships among different species where each individual involved in the relationship derives a benefit. Some of the most ecologically and economically important mutualistic interactions occur between flowering plants and their pollinators (Kearns *et al.* 1998). More than 90% of the approximately 250,000 described species of angiosperms are pollinated by animals (Nabhan and Buchmann 1997). These pollinators are most commonly insects that belong to the order Hymenoptera (wasps and bees), Lepidoptera (butterflies, moths and skippers), Diptera (flies) or Coleoptera (beetles) (Nabhan and Buchmann 1997). Vertebrates represent a smaller, but equally important group of animal pollinators. Vertebrate pollinators include birds, such as Trochilidae (hummingbirds), Nectariniidae (sunbirds) and Meliphagidae (honeyeaters), bats such as those belonging to Phyllostomidae and Pteropodidae, and some non-flying mammals (e.g. marsupials and rodents) (Fleming and Muchhala 2008). Both invertebrate and vertebrate pollinators facilitate the pollination of angiosperms by foraging for resources within flowers. The resources supplied at the flowers are most commonly nectar (a source of carbohydrates, micronutrients and some free amino acids) (Ziegler *et al.* 1964; Hiebert and Calder 1983) and/or pollen (a source of protein and lipids) (Howell 1974a). Through foraging within flowers, an animal's body contacts the plant's male reproductive organs (stamens), causing pollen to be transferred from the site of production on the anther, to the animal's body. The pollen contains the plant's sperm cells which the pollinating animal will then inadvertently transfer to the female reproductive organs (stigma) of a flower on the same, or another plant, as the animal travels from flower to flower foraging for resources.

To understand how we can manage and maintain plant-pollinator communities, we first need to identify factors that determine the structure of plant-pollinator interactions within a specific habitat (Kearns *et al.* 1998). Previous studies have shown that many different factors can influence the community structure of pollinators including the abundance and diversity of flowers and flower resources. For example, floral

abundance positively affects pollinator abundance in bee communities (Heithaus 1974; Potts *et al.* 2003) and pollinator diversity in butterfly communities (Steffan-Dewenter and Tschardt 1997). Additionally, Potts *et al.* (2003) found that the overall structure of Mediterranean bee communities in a post-fire regenerating habitat depended on the variety of different nectar resources available in a given habitat. Morphology of both plants and their pollinators can also play an important role in the structure of plant-pollinator communities within a specific habitat. For example, flowers that differ in corolla morphology attract different hummingbirds (Snow and Snow 1972; Colwell 1973; Feinsinger and Colwell 1978) and different sphingid moths (Haber and Frankie 1989). Likewise, pollinators that exhibit divergent morphologies within a community pollinate different types of flowers. This has been demonstrated for hummingbirds (Brown and Bowers 1985; Feinsinger and Colwell 1978), sphingid moths (Agosta and Janzen 2005) and butterflies (Corbet 2000).

## 1.2 Ecomorphology in Plant-Pollinator Interactions

Morphological differences among species often indicate ecological differences (Schoener 1974). Ecomorphology is the study of the relationship between the morphology of an organism and their ecology (Karr and James 1975). Floral ecomorphology and pollinator, or flower-visitor ecomorphology concerns the relationship between flower morphology and pollinator morphology (Olesen *et al.* 2007). A flower's morphology will affect different aspects of the plant-pollinator relationship, such as the number and types of flower visitors it can receive. Morphological characteristics such as flower shape, corolla tube length and corolla color can all affect flower visitation by pollinators. For example both flower color and flower shape can significantly affect flower visitation by hummingbirds and bees (Sutherland and Vickery, 1993; Schemske and Bradshaw 1999). Additionally, corolla tube length has a direct effect on the species of hawkmoths that were able to pollinate the South African iris (*Gladiolus longicollis*; Alexandersson and Johnson 2002).

Similarly, a pollinator's morphology can affect the flowers that it visits. Harder (1985) found that glossa length, body mass and wing length in bees were accurate

predictors of which plant species a bee species would visit within a habitat on a particular day, to some degree. Additionally, bee species with long glossae tended to feed from a greater number of plant species (Harder 1985). Likewise, long-tubed flowers are visited primarily by long-tongued hawkmoths (Haber and Frankie 1989), butterflies (Corbet 2000) and bees (Heinrich 1976; Ranta and Lundberg 1980; Borrell 2005). Similarly there is a high degree of association between flower-visiting birds of a certain bill length and flowers of a given morphology (e.g. knob, cup, tube) (Brown and Hopkins 1995). Body size can also be an important morphological trait affecting flower visitation, as Muchhala and Jarrín-V (2002) found that larger bat species visited larger flowers more often and smaller bat species preferred smaller flowers. Pollinator morphology can affect the efficiency of foraging at different flowers. For example, flower-visiting bats with greater tongue and rostrum lengths have higher nectar extraction efficiencies at long-tubed flowers than bats with shorter tongues and rostrum lengths (Gonzalez-Terrazas *et al.* 2012). This was also found to be true for hummingbirds of longer bill lengths (Montgomerie 1984).

### 1.3 Generalists and Specialists in Flower Visitation

Studies of pollination mutualisms have revealed a continuum of interactions. These interactions range from highly specific to very general. Figs and fig wasps are an example of a highly specific mutualism, where each fig species is thought to have only one or two species of fig wasp pollinators and each fig wasp species pollinates only one species of fig (e.g. Wiebes 1979; Cook and Rasplus 2003). Conversely there are many generalised plant-pollinator relationships as well, such as those that occur between some desert columnar cacti and their pollinators, where several cactus species are pollinated not only by multiple species of pollinators but also by multiple taxonomic groups (e.g. birds, bats and bees) (Fleming *et al.* 2001).

One way that many studies have characterized specialization or generalization in a plant or pollinator is through morphology. Many flowers possess morphological features thought to reflect their pollinators (Müller 1883). This is the result of adaptation to the use of different pollinator groups and is associated with attracting and facilitating

pollination within each taxonomic group (Fenster *et al.* 2004). The collection of floral traits associated with a specific group of pollinators is called a “pollination syndrome”. Pollination syndromes have been recognized for most major taxonomic groups of pollinators including bees (“melittophily”), wasps (“sphecophily”), butterflies (“psychophily”), moths (“phalaenophily”), hawkmoths (“sphingophily”), carrion flies (“sapromyiophily”), flies (“myiophily”), beetles (“cantharophily”), birds (“ornithophily”), bats (“chiropterophily”) and non-flying mammals (Ollerton and Watts 2000). Each pollination syndrome is described on the basis of flower size, morphological features, color, scent and nectar characteristics and timing of anthesis (Ollerton *et al.* 2009). Vogel (1954), Faegri and van der Pijl (1979) and Proctor *et al.* (1996) provide a detailed description of each pollination syndrome and I will present a few examples here for context and comparison.

Bee pollinated (melittophilous) flowers may be a variety of colors including white, red, yellow, purple, ultraviolet, green, or blotched and streaked with more than one color (Heinrich 1974). Typical bee-pollinated flowers also have “nectar guides” which consist of patterns on petals that orient the bees for access to floral nectar (e.g. Medel *et al.* 2003). In contrast, bat-pollinated (chiropterophilous) flowers are often plain and inconspicuously coloured (white, cream or green) (e.g. von Helversen and Winter 2003). In bee-pollinated flowers, anthesis and scent production is diurnal and nectar is present in small volumes, strong and sweet smelling and found as deep as 15 mm (Vogel 1954). In contrast, bat pollinated flowers are typically night blooming, opening at dusk and closing at dawn, with dilute nectar which is present in large volumes and produced throughout the night (e.g. von Helversen and Winter 2003). Scents are also released nocturnally with flower volatiles containing sulfur or disulfide compounds (von Helversen *et al.* 2000). Bee-pollinated flowers are small and shapes are typically platform shaped, bilaterally symmetrical, variable in petal number (either lobed or unlobed) or “brush”- form (e.g. Vogel 1954; Heinrich 1974). In contrast, bat pollinated flowers are often exposed on long stems or hanging down from branches (e.g. von Helversen and Winter 2003). Wide open-form bell shaped or “brush”-form flowers are typical (e.g. von Helversen and Winter 2003). In both cases, the pollination syndrome characteristics reflect the biology of the pollinators. For example, while bees use visual cues such as nectar guides in colors

significant to their color vision sensitivity (e.g. Kevan *et al.* 2001) to locate nectar rewards, neotropical bats, which rely largely on echolocation for orientation typically feed from dull colored flowers with shapes that efficiently reflect and magnify echolocation calls over wide angles, advertising flower location to approaching bats (von Helversen *et al.* 2003; Simon *et al.* 2011). It should be noted that the use of pollination syndromes in predicting plant-pollinator interactions is not necessarily reliable, and the syndromes themselves do not reflect any one plant and real plants in nature exhibit a variable combination of these traits (Ollerton and Watts 2000; Ollerton *et al.* 2009).

Pollinators themselves can also be specialized morphologically. Morphological specialization in pollinators is often associated with the ability to feed efficiently from floral resources. In insects, many morphological adaptations for flower visitation and nectar/pollen feeding are associated with the mouthparts. The most specialized nectar-feeding species have elongated proboscides/glossae modified for suction to extract nectar even from flowers with long corollas (e.g. Nilsson 1988; Johnson and Steiner 1997). This particular specialization has been noted in species of Coleoptera, Hymenoptera, Diptera and Lepidoptera (Krenn *et al.* 2005). Other species may be specialized for pollen-feeding through various adaptations. For example, some bees have pollen-removing hair on the proboscis, used for collecting pollen from tube-shaped flowers with hidden anthers (Thorp 1979; Thorp 2000). Similarly, a long tentacle appendage found on the mouthparts of yucca moths (Prodoxidae) collects pollen from anthers (Pellmyr 2003). Morphological specializations in flower-visiting birds often include longer bills and precise bill shapes corresponding to shapes of tubular corollas on certain food plants (e.g. Stiles 1975). In bats, morphological specialization for flower visitation is associated primarily with elongated rostrums and elongated tongues equipped with brush-like papillae (von Helversen and von Helversen 1975; von Helversen and Winter 2003). These morphological features are thought to be adaptations to a nectarivorous diet as the tongue papillae facilitate nectar extraction via capillary action while rostrum elongation provides room for a longer tongue and allows the bat access to more flowers with a greater range of corolla lengths (Freeman 1995; Harper *et al.* 2013). Many morphologically specialized flower-visiting bats also have modified cranial characteristics associated with reduced

dentition and bite force which reflect a diet composed largely of liquid nectar (Freeman 1995; Nogueira *et al.* 2009).

## 1.4 Food Resource Partitioning

The use of different resources by different species living in sympatry can reduce interspecific competition (Schoener 1974). This concept is derived from the competitive exclusion principle (Hardin 1960), which states that the coexistence of species depends on the occupation of different niches. Niche differentiation can be achieved by partitioning different resources such as food (Schoener 1974). Partitioning of food resources by sympatric species has been reported in many different groups of animals and ecosystems (e.g. Reynolds and Meslow 1984; Toft 1985; Smythe 1986; Ross 1986). As such, it is not surprising that food plant partitioning has also been found to be an important factor in the structure of several different plant-pollinator communities. Partitioning of floral resources has been demonstrated among pollinators such as bees (e.g. Heinrich 1976; Ranta and Lundberg 1980; Graham and Jones 1996) and hummingbirds (Abrahamczyk and Kressler 2010). Although there is a large body of literature on partitioning of flowers by bee species, there is a significant lack of information on this subject for other groups of pollinators.

Food resource partitioning may be achieved by different means including morphology and competition. As we can see from the discussion of ecomorphology in flower visitors above, a flower-visitor's morphological characteristics such as tongue, bill or proboscis length can influence the flowers that it visits for food and which flowers are energetically efficient for it to feed from. It has even been suggested that corolla elongation may have, in some cases, evolved as a means of partitioning flower visitors (Rodríguez-Gironés and Santamaría 2006; Rodríguez-Gironés and Santamaría 2007). Alternatively food resource partitioning can be achieved by interference competition via aggressive foraging behavior. This method of resource partitioning has been observed among species of bees (Nagamitsu and Inoue 1997) and between hummingbirds and butterflies (Primack and Howe 1975).

## 1.5 Bats as Flower Visitors

Bats are at least partially responsible for the pollination of no less than 500 species of neotropical plants, making them an important part of tropical communities (Vogel 1969). A recent review (Fleming *et al.* 2009) reported that flower-visiting bats (Phyllostomidae and Pteropodidae) forage from at least 528 different plant species belonging to 67 different families in 28 orders of angiosperms. Even if we discount the large number of plants that rely on bats for pollination, they would still be an important pollinator group as they are able to transport pollen over long distances, greater than any other pollinator, which can be an important factor in preventing inbreeding and maintaining successful reproduction in plant species with low population densities and spatially isolated individuals (Heithaus *et al.* 1974; Gribel and Lemes 1999; Ward *et al.* 2005). Despite their importance as pollinators, there is very little literature about the community structure of flower-visiting bats and their food plants.



## 1.6 Statement of Purpose

Flower-visiting bats exhibit a large degree of variation in their morphological specialization for feeding (Freeman 1995). Evidence from other groups of flower-visitors suggests that sympatric pollinators exhibiting morphological divergence will exploit different plant resources (Feinsinger and Colwell 1978; Brown and Bowers 1985; Corbet 2000; Agosta and Janzen, 2005). I hypothesized that morphological differences among sympatric flower-visiting bat species will translate into different plant-based diets.

Specifically I tested the following two predictions:

- 1) Species which share similar morphological features will also share similar diets. Morphologically distinct species will have less dietary overlap than morphologically similar species.
- 2) Morphological flower-feeding specialist species will use food resources differently than generalist species.

I tested these predictions by analyzing morphological and dietary data collected from a community of five sympatric flower-visiting bat species in Cuba. I also used acoustic monitoring to assess bat activity at flowers.

Understanding how a flower-visitor's morphology can influence its interactions with food plants can help us to understand why a particular species consumes the plants that it does. In turn this may help us to predict which plants may be important for a particular flower-visiting species of a given morphology and which morphological groups of flower-visitors are more/less effective as pollinators. The diet of a particular species will vary depending on many factors including the time of year and which plants are available in a given area so determining the plants that are important to a given species needs to be determined both during different seasons and across a wide variety of habitats. These types of studies are time consuming and labour intensive. By being able to understand why certain plants may be important to a pollinator based on its morphological traits we may be able to make predictions about plant-pollinator interactions which can be used to facilitate conservation efforts of both plants and their pollinators.

## 1.7 Study Species

Cuba is home to five species of bats which are known to visit flowers for food; these species are *Artibeus jamaicensis*, *Brachyphylla nana*, *Erophylla sezekorni*, *Monophyllus redmani* and *Phyllonycteris poeyi* (Figure 1). *Artibeus jamaicensis* is considered to be primarily frugivorous specializing in eating figs (*Ficus*), which can form up to 78% of the annual diet of this species at some sites (Handley and Leigh 1991). This species has morphological attributes characteristic of specialized phyllostomid frugivores (Freeman 2000). *A. jamaicensis* also consumes pollen and nectar to a lesser extent and is considered to be an opportunistic flower visitor (e.g. Heithaus *et al.* 1975, Ortega and Castro-Arellano 2001). Insects are not considered to be a large part of the diet of *A. jamaicensis* as reports of insect consumption by this species are scarce (Ortega and Castro-Arellano 2001). *B. nana* is omnivorous consuming pollen, nectar, fruit and insects although fruit and pollen/nectar compose the majority of its diet (Gardner 1977, Silva 1979, Silva and Pine 1969). *Brachyphylla*'s cranial morphology reflects this omnivorous diet as the genus exhibits features characteristic of phyllostomid frugivores, nectarivores and insectivores (Griffiths 1985, Freeman 1995, Freeman 2000, Monteiro and Nogueira 2011). *E. sezekorni* is a generalist nectarivore based on its morphological characteristics as compared to other phyllostomid nectarivore species (Freeman 1995) although previous studies have found that *E. sezekorni* consumes fruit, pollen/nectar and insects at nearly equal frequencies (Soto-Centeno and Kurta 2006). *M. redmani* also has a generalist nectarivore morphology (Freeman 1995) and a diet composed primarily of pollen/nectar and insects, with fruit consumed to a much lesser extent (Soto-Centeno and Kurta 2006). Likewise, *P. poeyi* has a generalist nectarivore morphology as well (Freeman 1995) and consumes pollen/nectar as its primary food source, and fruit and insects to a lesser extent (Mancina 2010).

The study species represent a range in size from the large *A. jamaicensis* (36-48 g; Ortega and Castro-Arellano 2001) and *B. nana* (27-41 g; Silva 1979) to the small *M. redmani* (6-10 g; Soto-Centeno and Kurta 2006). *E. sezekorni* and *P. poeyi* are intermediate in size with weights of 16-21 g (Soto-Centeno and Kurta 2006) and 15-29 g (Mancina 2010), respectively. *B. nana*, *E. sezekorni*, *M. redmani* and *P. poeyi* all roost in

caves. Alternatively, *A. jamaicensis* has been known to use hollow trees, foliage and buildings as well as caves for roost sites (Silva 1979, Ortega and Castro-Arellano 2001).

All five study species belong to the family Phyllostomidae, with *B. nana*, *E. sezekorni*, *M. redmani* and *P. poeyi* belonging to the primarily nectarivorous subfamily Glossophaginae and *A. jamaicensis* belonging to the primarily frugivorous subfamily Stenodermatinae (Baker *et al.* 2003, Datzmann *et al.* 2010). *Brachyphylla*, *Erophylla* and *Phyllonycteris* form a monophyletic clade where *Phyllonycteris* and *Erophylla* are sister taxa and *Brachyphylla* is more basal (e.g. Carstens *et al.* 2002; Jones *et al.* 2002; Dávalos 2004; Dávalos *et al.* 2012). There is some disagreement on this subject; for example, Datzmann *et al.* 2010 place *Erophylla* as the basal taxon and many earlier studies do not include the *Brachyphylla-Erophylla-Phyllonycteris* clade as part of Glossophaginae (e.g. Wetterer *et al.* 2000). *Monophyllus* belongs to a clade with a sister-group relationship to *Brachyphylla-Erophylla-Phyllonycteris* (Baker *et al.* 2003, Datzmann *et al.* 2010).



**Figure 2: Skull morphology of the five flower-visiting bats of Cuba.** A) *Artibeus jamaicensis* (78590♀), B) *Brachyphylla nana* (63160♂), C) *Erophylla sezekorni* (63166♂), D) *Monophyllus redmani* (44595♀) and E) *Phyllonycteris poeyi* (78764♀). Photographs were taken with a Nikon D800 by Brock Fenton using specimens obtained from the Royal Ontario Museum (Toronto, Ontario, Canada). Scale bar is equal to 1 cm.

## Chapter 2 – Materials and Methods

### 2.1 Study Area

I collected data from June through August 2012 at four sites in western Cuba around Havana: 1) the National Botanic Garden in Havana, 2) the cave “La Candela” in the rural locality of “Segundo”, 3) the cave “Numancia” in the rural locality of “Compostizo” and 4) the cave “Indio” in the rural locality of “La Jaula”. I made acoustic recordings of bat calls at flowers in the National Botanic Garden.

### 2.2 Morphological Analysis

#### 2.2.1 Field Specimens

I captured bats throughout the night (21 00 to 6 00 hours) in mist nets set at locations surrounding flowering trees at site 1, and within caves or near cave entrances at sites 2-4 (Table 1). I identified the species of captured bats using the key of morphological characteristics identified by Silva (1979). I recorded the sex and age (juvenile or adult) of all individuals. I determined sex by the presence of external genitalia and age by examining cartilaginous zones at the tips of the metacarpals using a flashlight; this area is translucent in subadults (Anthony 1988).

I compared morphology among the five species of bat in two ways. First, in the field I measured and recorded the forearm length, head length, snout width and snout length for all adults captured. All measurements were made with electronic digital calipers to the nearest 0.02 mm. I measured forearm length by moving the forearm at a 30° angle from the corpus and the digits at a 30° angle from the forearm, then measuring the greatest length of the forearm with calipers positioned at a 90° angle to the forearm. Head length and snout length were measured as the greatest distance from the mid region of the posterior head or the most anterior point of the tear duct, respectively, to the anterior dorsal tip of the nose. Snout width was measured as the greatest distance across the snout just below the nose. Forearm length is a predictor of overall body size, and body size and cranial morphology (snout size and shape) can influence the types of flowers that

**Table 1: Locations and dates of bat captures in sites around Havana, Cuba in 2012.**

<b>Site</b>	<b>Type</b>	<b>Location</b>	<b>Dates at site</b>	<b>Bat Species Captured</b>
1	National Botanic Garden	Havana	July 5 -11, 16, 23-24	<i>Artibeus jamaicensis</i> , <i>Erophylla sezekorni</i> , <i>Monophyllus redmani</i> , <i>Phyllonycteris poeyi</i>
2	Cave ("La Candela")	Rural locality of "Segundo"	July 13-15	<i>B. nana</i> , <i>M. redamni</i> , <i>P. poeyi</i>
3	Cave ("Numancia")	Rural locality of "Compostizo"	July 20-21	<i>M. redmani</i> , <i>P. poeyi</i>
4	Cave ("Indio")	Rural locality of "La Jaula".	July 19-20, August 6	<i>B. nana</i> , <i>E. sezekonri</i> , <i>P. poeyi</i>

different bat species can visit (Freeman 2000; Winter and von Helversen 2003). I repeated these measurements twice on the first five bats processed and these measurements differed by no more than 0.5 mm for measurements of forearm length and head length and no more than 0.3 mm in measurements of snout width and snout length so measurements beyond these were not repeated.

### 2.2.2 Museum Specimens

To more precisely determine the morphological differences among the bat species and to look at aspects of morphological specialization for flower-feeding which can only be observed from skeletons, I collected 9 linear measurements from the skulls of each of the five species of flower-visiting Cuban bats. Specimens were obtained from voucher specimens in the Royal Ontario Museum and the number of skulls sampled per study species were as follows: 13 (*A. jamaicensis*), 7 (*B. nana*), 6 (*E. sezekorni*), 6 (*M. redmani*) and 7 (*P. poeyi*). These specimens all originated from Cuba (Appendix A). I chose measurements that differentiate between phyllostomid nectarivorous and frugivorous species (Freeman 1995) and which reflect overall skull size and shape (Freeman 1988; Freeman 1995; Dumont 2004). The measurements which differentiated between phyllostomid nectarivorous and frugivorous species included rostrum length, width across the canines, palatal breadth, palatal length, length from the dentary condyle to the most posterior tooth in the lower tooth row (length from dentary condyle to M3), dentary thickness and a space index as defined by Freeman (1995) (Freeman 1988, Freeman 1995). To clarify, rostrum length is a measurement similar to that of 'snout length' in the live field caught specimens, but the different terminology is meant to differentiate between the measurements made on live specimens versus skulls. The space index measures the sum of the distances between upper post-canine teeth as well as the medial gap between canines, divided by the length of the upper toothrow (Freeman 1995). Species with higher space index values are thought to be more specialized nectarivores (Freeman 1995). Another morphological feature that can differentiate between frugivorous and nectarivorous species is tongue length, which I did not measure, however tongue length is highly correlated with rostrum and palate length in nectar-feeding bats (Winter and von Helversen 2003). Measurements which were taken to

estimate overall skull size and shape were skull length, zygomatic breadth and temporal height (Freeman 1988, Freeman 1995, Dumont 2004). Specific information on how these measurements were made can be found in Appendix B. The species included in this study cover a wide range of different body sizes so to determine relative specialization for nectarivory I calculated size-adjusted measurements for all of the values which differentiate between nectarivorous and frugivorous species (except for the space index). I did this by dividing each measurement by the geometric mean of all measurements from that individual and then taking the natural logarithm of the resultant value (Darroch and Mosimann 1985; Falsetti *et al.* 1993; Jungers *et al.* 1995; Dumont *et al.* 2004).

### 2.2.3 Data Analysis

I examined the morphological differences among bat species for all field-collected and museum-collected measurements (including raw and size-adjusted values) using an independent sample, non-parametric, Kruskal-Wallis test with a Bonferroni correction and Conover-Inman pairwise comparison due to non-normal distribution of measurements. I also tested for sexual dimorphism in all raw morphological measurements (field-collected and museum-collected) using a Kruskal-Wallis test with a Bonferroni correction to compare measurements between males and females of the same species. This analysis revealed very little sexual dimorphism after Bonferroni correction (only one trait in three of the five species) so the results present pooled data from both sexes. I used a principal component analysis (PCA) using a Pearson's correlation matrix on raw field-collected and museum-collected morphological values to differentiate between species based on their morphological measurements. I also ran a second PCA on the size-adjusted museum-collected cranial measurements associated with differentiating between feeding specializations and the space-index to compare the degree of morphological specialization for flower-visitation for each species. All analyses were completed using xLSTAT (Addinsoft, New York, NY, USA).

## 2.3 Dietary Analysis

To determine the different characteristics of the diets of each bat species I collected fecal samples from all bats captured; this was accomplished by placing the bat in a clean,



labeled cloth bag for 30 minutes to 3 hours until a fecal sample had been obtained. I placed each fecal (guano) sample in a plastic 1.5 mL microcentrifuge tube with beads of silica gel to dry the samples. Analysis of pollen present in the fecal matter of bats can give an accurate depiction of the diets of flower-visiting bats because the bats ingest pollen present on their fur picked up from visiting flowers (Howell 1974a). I also collected pollen from plant species flowering around each of the study sites to use as a reference collection. I used a piece of tape to pick up pollen from the anthers of flowers and attached the tape to a piece of filter paper which was labeled with the plant species. All fecal and pollen samples were stored in a -20 °C freezer from the time of collection until the time of processing.

I homogenized dried guano samples using a mortar and pestle. I then spread the contents evenly in a thin layer within a 6 cm diameter plastic Petri dish and swabbed this with a 5 mm x 5 mm cube of basic fuchsin gelatin which stains pollen red or pink (Beattie 1971). I also used 5 mm x 5 mm cubes of basic fuchsin gelatin to swab the tape and filter paper containing the pollen of the reference plant species. I then melted the cube on a glass slide using a hot plate on low heat and covered with a glass coverslip. I used a Zeiss Axio Imager A1 AX10 microscope to view the pollen present in each sample (400 X magnification). I counted and photographed each pollen grain exhibiting a distinct morphology using a Nikon D800 with a DD20ZNT – 2.0 X digital SLR large format camera coupler or a Sony XCD-X700 Digital Interface and D10ZNC – 1.0 X C-mount coupler with Northern Eclipse V8 imaging software. I also noted the presence of fruit pulp and insect remains in samples.

I calculated the number of different pollen species present per guano sample to estimate the number of number of species of flower the individual had visited that night (Geiselman 2010). This measurement will be referred to as ‘nightly pollen species’ for simplicity (Geiselman 2010). I was able to determine the number of different species present due to morphological differences among pollen grains, but not necessarily the species name belonging to each different pollen morphotype. I then used a Kruskal-Wallis analysis with a Bonferroni correction and Conover-Inman pairwise comparisons to

examine the differences in the number of flower species visited per night among bat species.

I calculated the diversity of pollen species present in each guano sample collected using Simpson's Diversity Index (D) (Simpson 1949):

$$D_s = \sum_{i=1}^s \frac{n_i(n_i - 1)}{N(N - 1)}$$

where  $n_i$  is the number of pollen grains of the  $i^{\text{th}}$  species that were found in a guano sample,  $N$  is the total number of pollen grains present in that sample and  $s$  is the total number of pollen species present in that sample. Results are presented as 1-D so that larger values represent higher diversity.

I compared the evenness of resource use for each bat captured by calculating Pielou's Evenness Index ( $J'$ ) for the pollen species present in each guano sample (Pielou 1966):

$$J' = \frac{H'}{H_{max}} = \frac{-\sum_{i=1}^S p_i \ln p_i}{\ln S}$$

Where  $p_i$  is the proportion of pollen grains of species  $i$  in the guano sample and  $S$  is the total number of species. I then compared the indices between species with an ANOVA and Tukey's range test for multiple pair-wise comparisons, as recommended by Magurran (2004).

I also looked at the mean dietary overlap (%) within and between species by generating a dissimilarity matrix using Manhattan distance (Luo and Fox 1996):

$$0.5 \sum |p_i - q_i|$$

Where  $p$  and  $q$  are the proportions of dietary items  $i$  in two different individuals. I then converted the matrix to proportional similarities by subtracting each value from 1 so that each value ranged from 0 to 1, indicating zero to complete similarity respectively. I then calculated a dietary similarity index for within and among bat species by determining the average of all relevant pair-wise comparisons. I also used a non-metric multi-dimensional scaling analysis to visualize the dietary similarity within and among bat species. This used the similarity matrices previously mentioned, generated using Manhattan distance.

To test prediction one, that species with similar morphologies will have more similar diets than species with very different morphologies, I determined the correlation between morphology and diet with a nonparametric Mantel test, using 10 000 randomizations, after generating dissimilarity matrices using Manhattan distance. The first matrix conveyed diet dissimilarity among species and was generated from the dietary item proportions. The second matrix conveyed morphological dissimilarity and was generated from the principal component scores obtained from the PCA of raw cranial morphological measurements obtained from the museum specimens. All statistical analyses were performed using the statistical software xLSTAT.

## 2.4 Acoustic Monitoring of Flower Visitors

To determine how each bat species used floral resources, and to test for differences among species, I identified bats visiting the flowers of five different plant species (Table 2, Figure 2) by placing ultrasonic bat detectors (Batcorder 2.0; ecoObs, Nürnberg, Germany) at flowers. These species of plants were chosen because they were flowering during the study period and their flowers either bloomed nocturnally, or remained open at night, making them accessible to the bats. The bat detectors use an algorithm-linked triggering mechanism to save echolocation call data onto secure digital high capacity cards (500 kHz, 16 bit). Call data are stored as audio files where each file contains a pass, or a series of echolocation calls, from bats as they fly past the recording device within the recording range (Figure 3). Recording is triggered by an echolocation call event and continues until no further calls are recognized within a chosen time interval (800 ms). The Batcorders were set to record from sunset to sunrise for 7 nights per plant species at

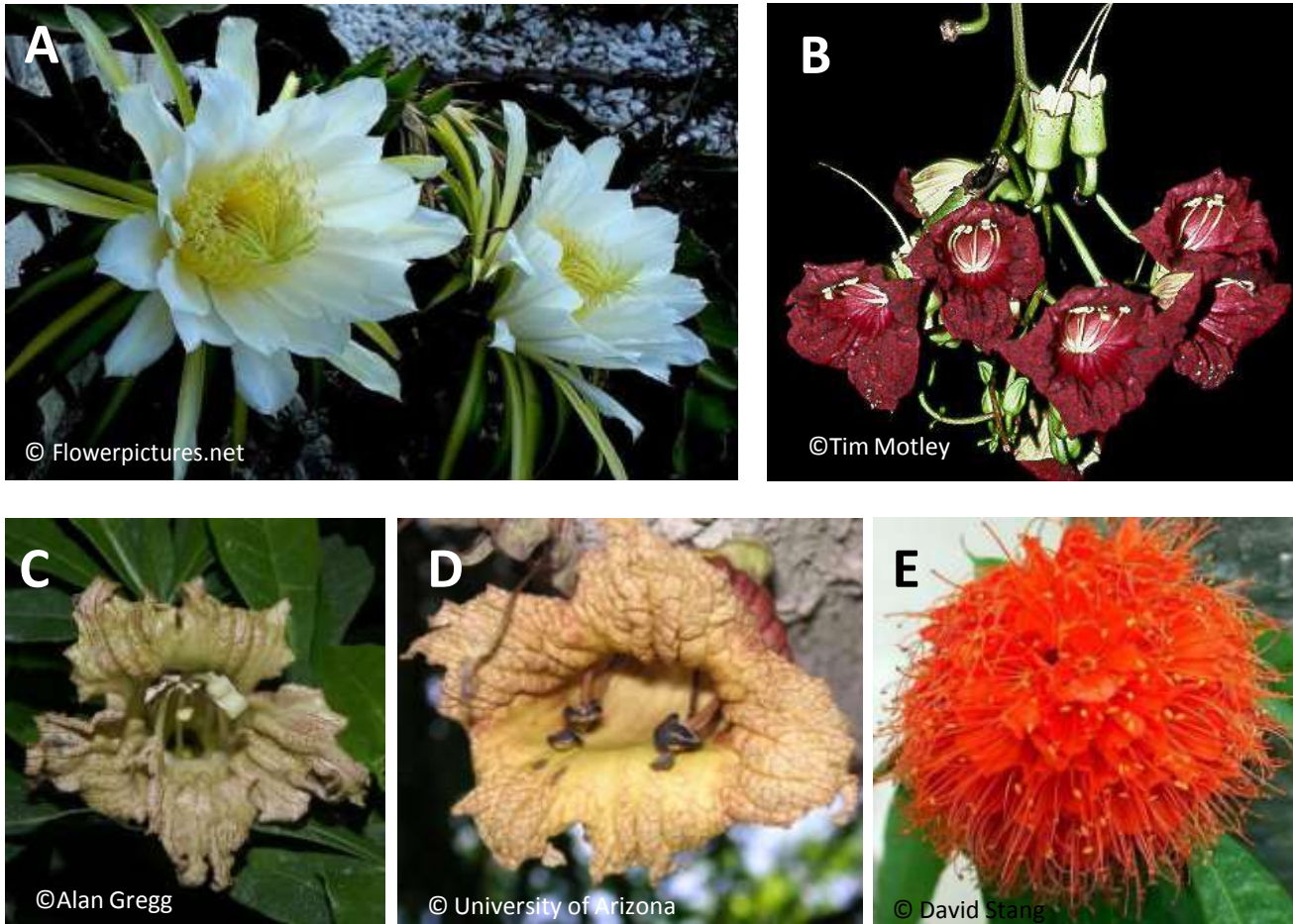
a different flower on a different tree each night. I also placed another microphone in a non-flowering tree every night that recordings were made, and chose a random subset of 7 nights as a control to determine if recorded flower-visiting bats visited the flowers in question as opposed to being active in the area.

I analyzed recorded bat calls using CallViewer18, a MatLab (The MathWorks, Natick, MA, USA)-based program for analyzing echolocation recordings (Skowronski and Fenton 2008). I went through each recorded file individually to look for calls and then identified them to species based on echolocation call characteristics including minimum frequency, maximum frequency, frequency with maximum energy (FME) and call duration which are specific to each species. The values for the call characteristics that I used were obtained from the literature on echolocation in each species (Appendix C). For each recorded file I determined the bat species and the number of individuals of each species on the recording. The presence of calls from one individual of a given species on a given recorded file was considered a single pass.

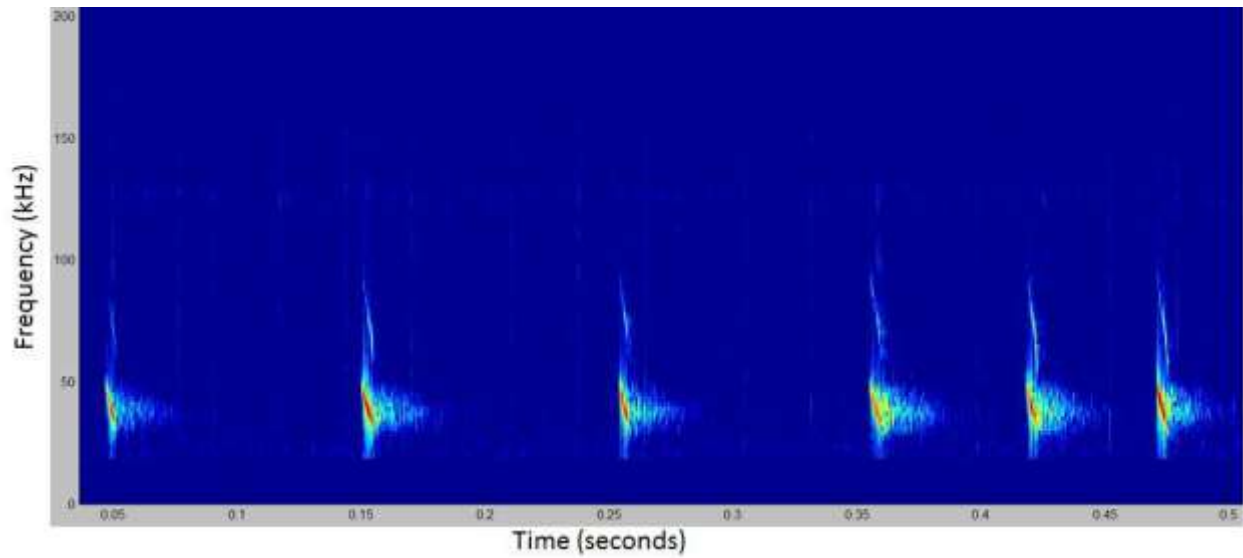
I used an acoustic activity index (AI) to measure bats' visits to flowers (Miller 2001). I calculated AI for each species on each night by the number of passes by that species excluding any calls recorded within a minute of each other. I compared the AI's of each bat species at the different plant species by using a Kruskal-Wallis test with a Bonferroni correction and a Conover-Inman multiple pair-wise comparison using xLSTAT.

**Table 2: Plant morphology and flowering characteristics for five species of plants studied.**

<b>Plant Species</b>	<b>Growth Habit</b>	<b>Corolla Color</b>	<b>Flower Shape</b>	<b>Blooming Period</b>	<b>Nectar Production</b>	<b>Pollination Syndrome</b>
<b>Bignoniaceae</b>						
<i>Crescentia alata</i>	Tree	White	Bell	Nocturnal	Nocturnal	Chiropterophilic
<i>Crescentia cujete</i>	Tree	White	Bell	Nocturnal	Nocturnal	Chiropterophilic
<i>Kigelia Pinnata</i>	Tree	Deep Red	Bell	Nocturnal	Nocturnal	Chiropterophilic
<b>Cactaceae</b>						
<i>Hylocereus undatus</i>	Epiphyte	White	Large Bell	Nocturnal	Nocturnal	Chiropterophilic
<b>Fabaceae</b>						
<i>Brownea grandiceps</i>	Tree	Red	Tubular	Diurnal	Diurnal	Ornithophilic



**Figure 2: Images of flowers for five species of plants studied.** A) *Hylocereus undatus*, B) *Kigelia pinnata*, C) *Crescentia kujete*, D) *Crescentia alata* and E) *Brownea grandiceps*.



**Figure 3: Spectrogram of a pass in the program CallViewer18 made by *Erophylla sezekorni*, recorded at a *Crescentia cujete* flower at the National Botanic Garden (Havana, Cuba).**

## Chapter 3 - Results

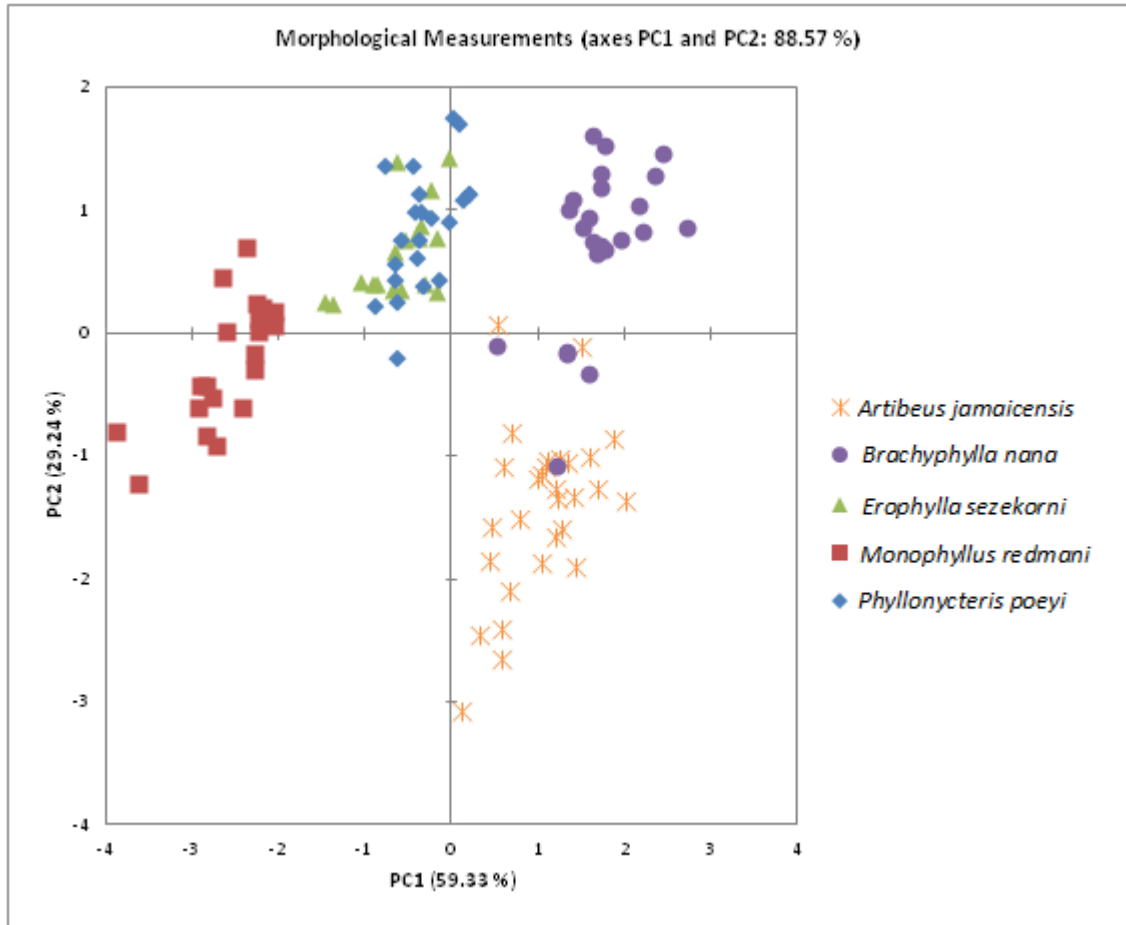
### 3.1 Morphological Results

#### 3.1.1 Field Specimens

Only in *A. jamaicensis* did I find significant differences in morphology between males and females (Appendix D Table 12). Because most of my study species did not show sexual dimorphism in the characters I measured, I pooled data from both sexes for all species. I found interspecific differences in most morphological measurements. The exception to this is *E. sezekorni* and *P. poeyi* which did not differ in any of the measurements taken.

Principal components analysis (PCA) identified two components that together accounted for 89% of the variation in field measurements within and among species. The first principal component (PC1) accounted for 59.3 % of the variation in the data set and was positively associated with forearm length, head length and snout width (Table 3). Principal component 2 (PC2) accounted for an additional 29.2% of the variation and was positively associated with snout length (Table 3). Plotting PC1 versus PC2 revealed four distinct groupings corresponding to the species *B. nana*, *A. jamaicensis*, *P. poeyi*/*E. sezekorni* and *M. redmani* (Figure 4).





**Figure 4: Plot of morphological PC1 versus PC2 scores of five species of flower-visiting Cuban bats from field measurements.** PC1 represents forearm length, skull length and rostrum width and PC2 represents rostrum length. High positive values of PC1 are associated with greater forearm length, skull length and snout width. Numbers in parentheses indicate the proportion of variation explained by each component. Sample sizes are 29 (*A. jamaicensis*), 23 (*B. nana*), 17 (*E. sezekorni*), 20 (*M. redmani*) and 22 (*P. poeyi*).

**Table 3: Factor loadings and eigenvalues for the first two principal components of the morphological characteristics PCA of field-caught bats (N=112 field-caught bats of 5 species).**

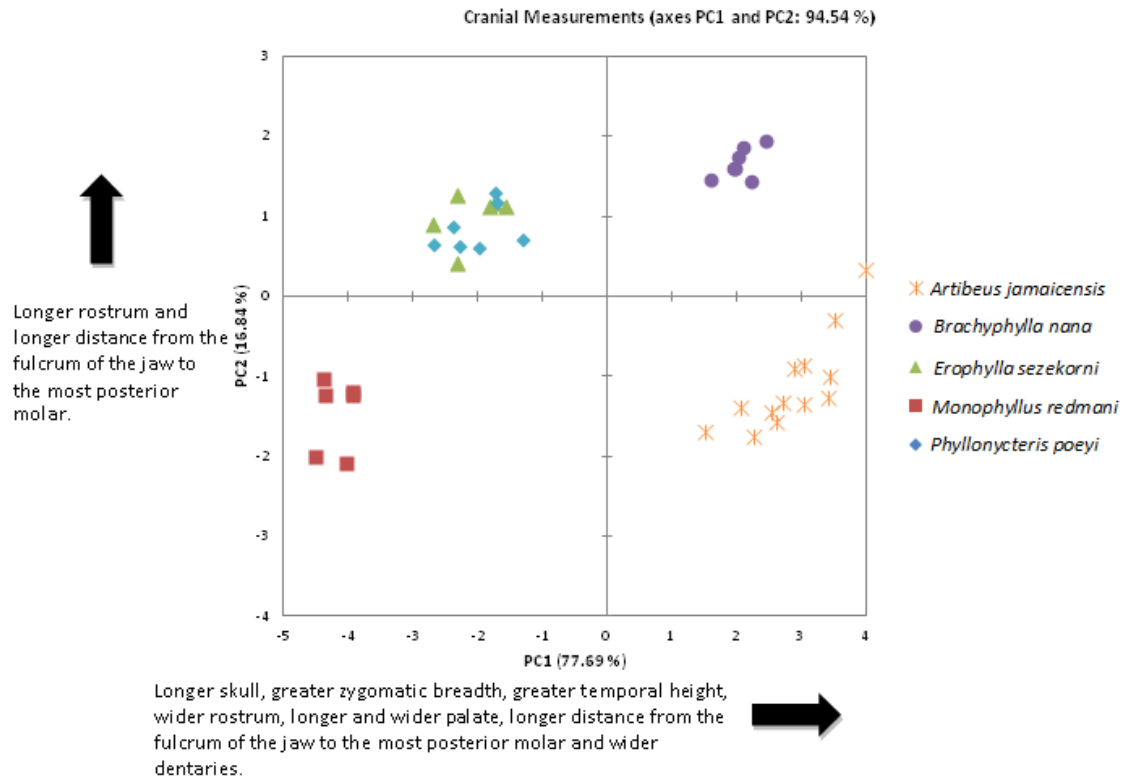
	PC1	PC2
Forearm Length	0.964	-0.163
Head Length	0.817	0.332
Snout Width	0.815	-0.504
Snout Length	0.336	0.883
Eigenvalue	2.373	1.170

### 3.1.2 Museum Specimens

Raw measurements and size-adjusted measurements of cranial museum-measured features differed among species for some measurements but not others (Appendix D Table 13 and Table 14). The PCA of raw cranial morphology, to assess the degree of overall differentiation among the species, showed the same general pattern as the PCA of field measurements in that the same four distinct groupings were identified: *A. jamaicensis*, *B. nana*, *E.sezekorni/P.poeyi* and *M. redmani*. The first two principal components accounted for 94.84% of the variation in the data (Figure 5). PC1 accounted for 77.69 % of the variation and was positively associated with skull length, zygomatic breadth, temporal height, width across the canines, palate length, palate width and dentary width (Table 4). PC2 accounted for 16.84% of the variation and was positively associated with rostrum length (Table 4). The length from the dentary condyle to the most posterior molar shows a weak positive association with both principal components. *M. redmani* and *E. sezekorni/P. poeyi* are largely segregated from *B. nana* and *A. jamaicensis* along PC1 while *M. redmani* and *A. jamaicensis* are segregated from *E.sezekorni/P. poeyi* and *B. nana* along PC2.

The PCA of size-adjusted measurements associated with feeding specialization and the space index indicated the degree of morphological specialization for nectarivory among the species. The first two principal components accounted for 92.79% of the variation in the data (Figure 6). PC1 accounted for 70.54% of the variation and was positively associated with dentary width, width across the canines and palate width and was negatively associated with the space index and rostrum length (Table 5). Thinner dentaries (Freeman 1995), narrowing and elongation of the rostrum and palate (Winter and Von Helversen 2003; Gonzalez-Terrazas 2012) and greater space index values (Freeman 1995) are all features associated with phyllostomid nectarivores so morphological specialization increases with decreasing values of PC1. PC2 accounted for only 22.24% of the variation and was positively associated with palate length (Table 5) thus morphological specialization increases with increasing values of PC2. Increased lengths from the fulcrum of the jaw joint (dentary condyle) to the most posterior molar is a characteristic associated with nectarivory (Freeman 1995) and the length from the

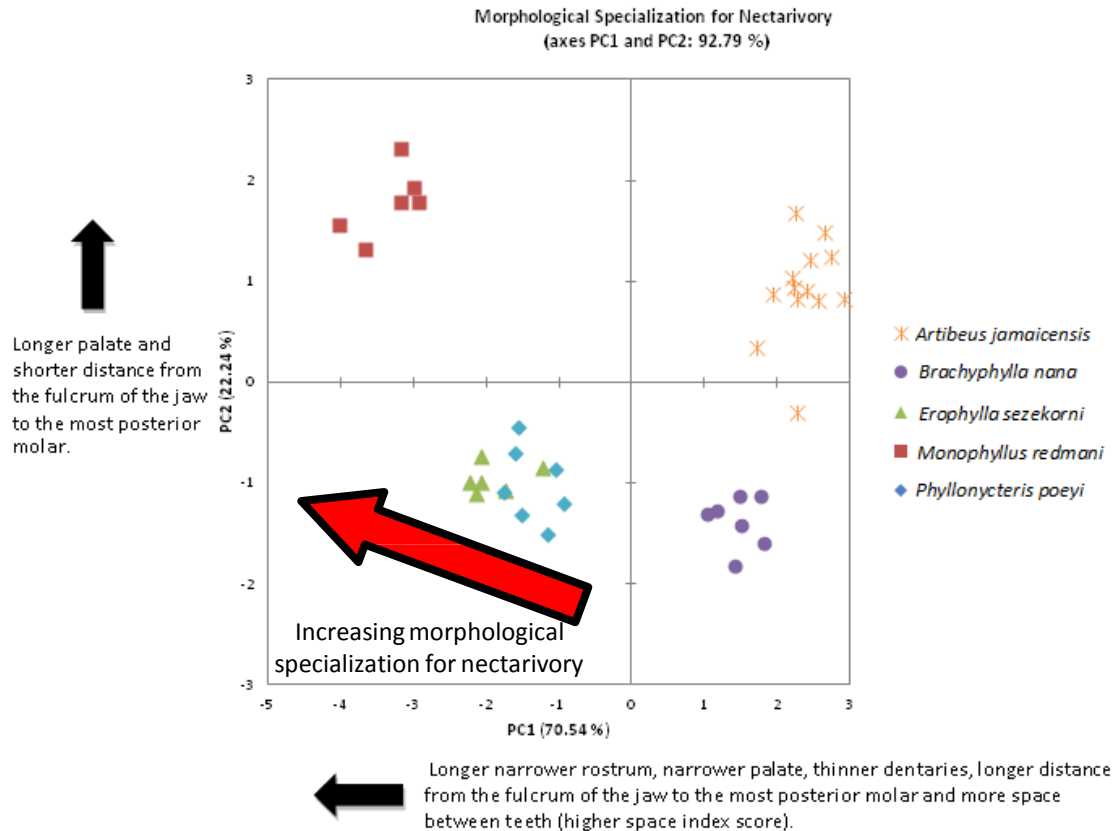
dentary condyle to the most posterior molar showed weak negative associations with both principal components. Overall specialization increases primarily along PC1 which is associated with more factors and accounts for more of the variability in the dataset than PC2. From the PCA we can see that once again there are four distinct groupings associated with the different species and from most-specialized to least these groupings are *M. redmani*, *P. poeyi*/*E. sezekorni*, *B. nana* and *A. jamaicensis*. Based on the morphological measures included in this PCA *M. redmani*, *P. poeyi* and *E. sezekorni* appear to be relatively specialist species and *B. nana* and *A. jamaicensis* appear to be generalists.



**Figure 5: Plot of Morphological PC1 versus PC2 scores of five species of flower-visiting Cuban bats from museum measurements.** PC1 represents skull length, zygomatic breadth, temporal height, width across the canines, palate length, palate width, the length from the dentary condyle to M3 and dentary width and PC2 represents rostrum length and the length from the dentary condyle to M3. Increasing values of PC1 reflect greater skull length, zygomatic breadth, temporal height, width across the canines, palate length, palate width and dentary width, and lower rostrum lengths. Numbers in parentheses indicate the proportion of variation explained by each component. Sample sizes are 13 (*A. jamaicensis*), 7 (*B. nana*), 6 (*E. sezekorni*), 6 (*M. redmani*) and 7 (*P. poeyi*).

**Table 4: Factor loadings and eigenvalues for the first two principal components of the cranial morphology PCA from museum specimens (N= 39 museum skull specimens from 5 bat species).**

	PC1	PC2
Skull Length	0.869	0.425
Zygomatic Breadth	0.992	-0.047
Temporal Height	0.975	0.041
Rostrum length	-0.473	0.852
Width across Canines	0.946	0.242
Palate Length	0.813	-0.482
Palate Width	0.983	-0.113
Length from Dentary Condyle to M3	0.691	0.658
Dentary Width	0.978	-0.143
<b>Eigenvalue</b>	<b>8.492</b>	<b>1.692</b>



**Figure 6: Plot of morphological PC1 versus PC2 scores of five species of flower-visiting Cuban bats from size-adjusted cranial measurements reflecting morphological specialization for nectarivory.** PC1 represents rostrum length, width across the canines, palate width, dentary thickness and the space index (tooth space) and the length from the dentary condyle to the most posterior molar and PC2 represents palate length and the length from the dentary condyle to the most posterior molar. Increasing values of PC1 are associated with lower values for rostrum length, length from the dentary condyle to the most posterior molar and the space index, and higher values for width across the canines and dentary thickness. Increasing values of PC2 are associated with higher values of palate length and lower length from the dentary condyle to the most posterior molar. Morphological specialization for nectarivory is associated with decreasing values of PC1 and, to a lesser extent, increasing values of PC2 (red arrow). Numbers in parentheses indicate the proportion of variation explained by each component. Sample sizes are 13 (*A. jamaicensis*), 7 (*B. nana*), 6 (*E. sezekorni*), 6 (*M. redmani*) and 7 (*P. poeyi*).

**Table 5: Factor loadings and eigenvalues for the first two principal components of the morphological specialization for nectarivory PCA from museum specimens (N= 39 museum skull specimens from 5 bat species).**

	PC1	PC2
Rostrum Length	-0.903	-0.353
Width across Canines	0.787	-0.527
Palate Length	-0.521	0.824
Palate Width	0.979	0.104
Dentary Condyle to M3	-0.633	-0.676
Dentary Thickness	0.967	0.061
Space Index	-0.968	0.066
Eigenvalues	4.938	1.557

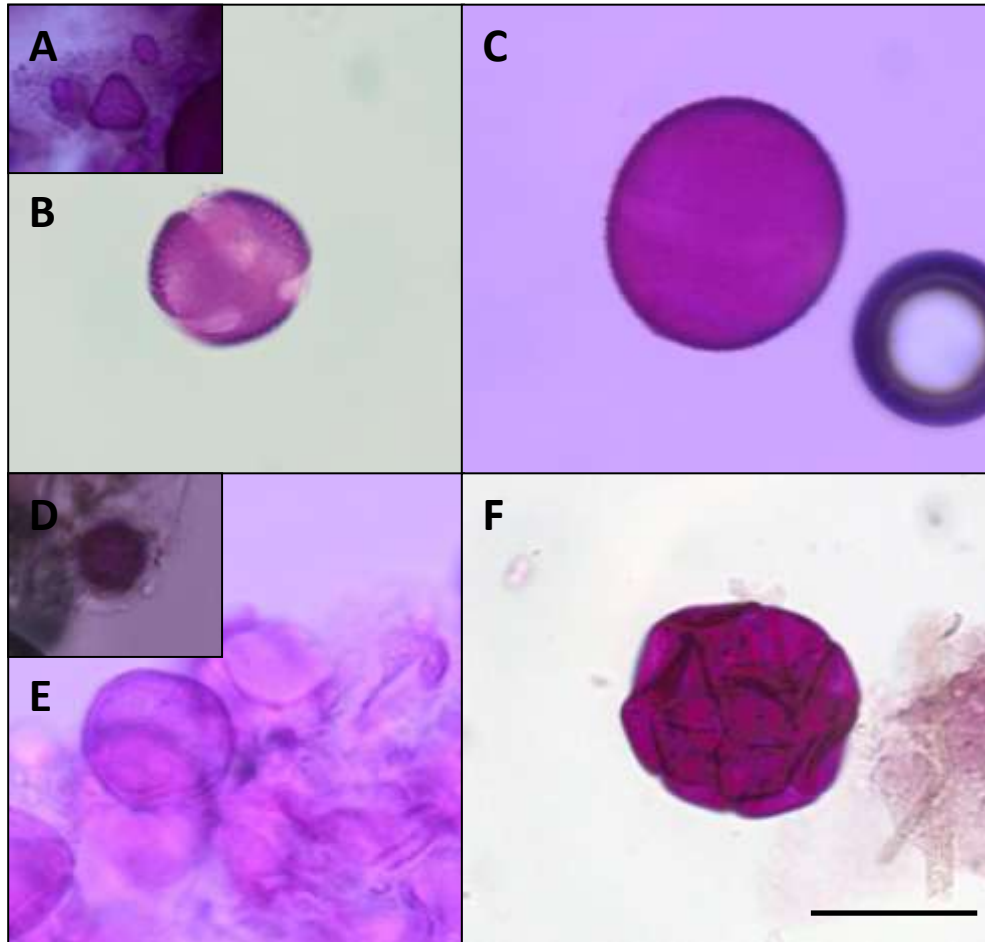


## 3.2 Diet Preferences, Breadth and Evenness

I found pollen from a total of 34 plant species in the guano of the five bat species. I identified 10 different species of pollen to either the genus or species level using a reference collection or published literature on pollen morphology. These species included *Talipariti elatum* (Malvaceae), *Coccothrinax* spp (Arecaceae), *Colpothrinax* spp (Arecaceae), two *Crescentia* spp (including *C. cujete*) (Bignoniaceae), *Kigelia pinnata* (Bignoniaceae), *Hylocereus undatus* (Cactaceae), *Albizia* spp (Fabaceae), *Dichrostachys cinerea* (Fabaceae) and *Syzygium jambos* (Myrtaceae) (Figure 7). Two other species of pollen were only identifiable to family (Cactaceae and Arecaceae). All of these species (or genus groups) have been previously reported as being pollinated or visited by bats except *Colpothrinax* (Fleming *et al.* 2009). The remaining 22 pollen species could not be identified to family, genus or species level but were visually distinct from one another and from those listed above.

The five bat species differed in the total number of different plant species they visited during the study period. The species identified in Figure 5 as morphological specialists for nectivory (*M. redmani*, *P. poeyi* and *E. sezekorni*) visited fewer plant species than the generalists (*A. jamaicensis* and *B. nana*) (Table 6).

My sample included 111 guano samples from the five bat species. The percentage of samples from each bat species containing either pollen, insects or fruit remnants differed among species (Table 6). *M. redmani* had the highest percentage of samples which contained pollen (95%), followed by *B. nana* (92 %), *P. poeyi* (87%), *E. sezekorni* (81 %), and *A. jamaicensis* (48%). In general, the morphological specialists for nectivory had high occurrences of pollen but *B. nana*, a generalist species, did as well. The morphological specialists for nectivory also had the higher percentages of samples containing insect remains than the generalists. Conversely the highest percentage of samples containing fruit remnants including seeds and pulp were those of the generalist species.



**Figure 7: Micrographs of pollen from the guano of the flower-visiting bats of Cuba.**

A) *Syzygium jambos* pollen found in the guano of *Artibeus jamaicensis*, B) *Kigelia pinnata* pollen found in the guano of *Monophyllus redmani*, C) *Hylocereus undatus* pollen found in the guano of *Monophyllus redmani*, D) *Tilapariti elatum* pollen found in the guano of *Artibeus jamaicensis*, E) *Crescentia cujete* pollen found in the guano of *Phyllonycteris poeyi* and F) *Albizia* spp (Fabaceae) pollen found in the guano of *Phyllonycteris poeyi*. All photographs were taken using a Nikon D800 with a DD20ZNT – 2.0 X digital SLR large format camera coupler on a Zeiss Axio Imager A1 AX10 microscope. Scale bar is equal to 50  $\mu$ m.

**Table 6: Dietary characteristics of the five species of Cuban flower-visiting bats.** The nightly pollen species, Simpson's diversity and Pielou's evenness values are mean values  $\pm$  standard error. Significant differences in the number of pollen species per night between species were determined by a Kruskal-Wallis analysis with a Bonferroni correction and Conover-Iman pairwise comparisons. Significant differences in the values for Simpson's diversity and Pielou's evenness between species were determined by an ANOVA and Tukey's range test pair-wise comparisons (significance level = 5%). Values with the same letters are not statistically different.

	<i>Artibeus jamaicensis</i>	<i>Brachyphylla nana</i>	<i>Erophylla sezekorni</i>	<i>Monophyllus redmani</i>	<i>Phyllonycteris poeyi</i>
N	23	24	21	20	23
Samples with pollen (%)	48	92	81	95	87
Samples with insect remains (%)	22	38	52	70	44
Samples with seeds/fruit pulp (%)	100	88	62	20	48
Total number of different pollen species present	17	21	14	11	12
Nightly pollen species	$3.55 \pm 1.57^{AB}$	$5.26 \pm 2.05^C$	$3.88 \pm 1.50^{BC}$	$2.37 \pm 1.12^A$	$3.45 \pm 1.36^{AB}$
Simpson's diversity (D)	$0.35 \pm 0.27^A$	$0.33 \pm 0.16^A$	$0.29 \pm 0.24^A$	$0.43 \pm 0.33^A$	$0.38 \pm 0.19^A$
Pielou's Evenness (J')	$0.89 \pm 0.14^A$	$0.86 \pm 0.09^A$	$0.89 \pm 0.09^A$	$0.87 \pm 0.18^A$	$0.89 \pm 0.10^A$

The number of different pollen species present in individual guano samples differed significantly among some species but not others and did not show clear trends associated with morphological specialization (Table 6;  $K=25.683$ ,  $df=4$ ,  $p= <0.0001$ ). Values for Simpson's diversity index ( $F=0.957$ ,  $df=4$ ,  $p=0.435$ ) and Pielou's evenness index ( $F=0.236$ ,  $df=4$ ,  $p=0.917$ ) did not differ significantly among the species (Table 6).

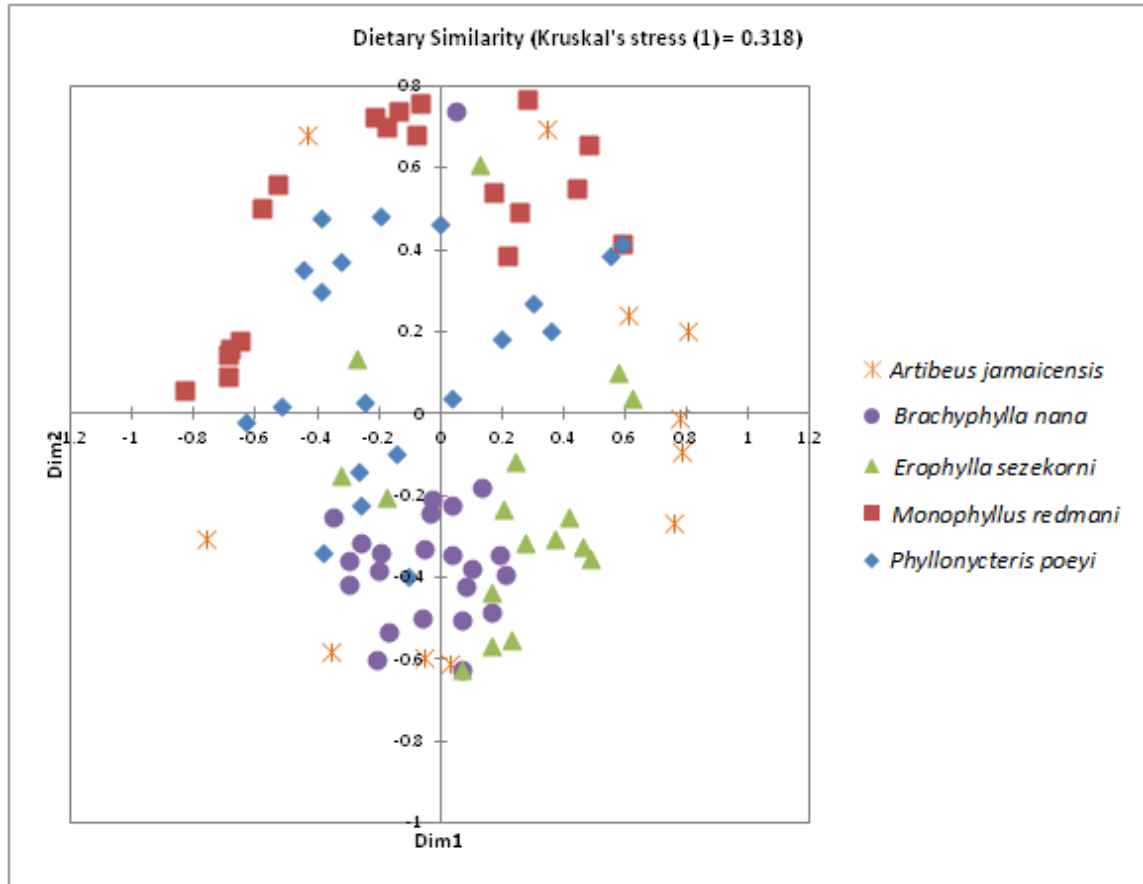
### 3.3 Dietary Overlap

The dietary similarity index calculated (degree of overlap) within and among bat species indicated consistently lower interspecific than intraspecific overlap providing evidence of species' specializations (Table 7). These results were reiterated in the non-metric multidimensional scaling of dietary similarities, where the diets of each bat species occupy relatively unique space in the 2-dimensional plot (Figure 8). *A. jamaicensis* is the only species that did not show this trend and it had the most highly variable diet of any species in my sample. *A. jamaicensis* is said to be primarily frugivorous, opportunistically visiting flowers for pollen and nectar (Heithaus *et al.* 1975). Variability within the diets of each species was highest for *A. jamaicensis* and lowest for *B. nana*. *M. remdani*, *E. sezekorni* and *P. poeyi* all had intermediate dietary variability (Figure 7). Dietary overlap was highest between *B. nana* and *E. sezekorni* (35%) (Table 9, Figure 7). *B. nana* and *P. poeyi* also had relatively high dietary overlap (22%) as did *P. poeyi* and *E. sezekorni* (19%) (Table 7, Figure 8).

The Mantel test to determine the correlation between dietary similarity and morphological differences among bat species did not detect a significant correlation ( $r=0.577$ ,  $df=8$ ,  $p= 0.909$ ).

**Table 7: Dietary similarity index for mean dietary overlap (%) within and between Cuban flower-visiting bat species.** Values were obtained by determining proportional dietary dissimilarities using Manhattan distance and then converting these to proportional similarities between 0 and 100, where 100 represents complete similarity.

	<i>Artibeus jamaicensis</i>	<i>Brachyphylla nana</i>	<i>Erophylla sezekorni</i>	<i>Monophyllus redmani</i>	<i>Phyllonycteris poeyi</i>
<i>Artibeus jamaicensis</i>	19				
<i>Brachyphylla nana</i>	15	51			
<i>Erophylla sezekorni</i>	10	35	37		
<i>Monophyllus redmani</i>	2	5	4	19	
<i>Phyllonycteris poeyi</i>	6	22	19	11	31



**Figure 8: Non- metric multidimensional scaling for proportional dietary similarities between flower-visiting Cuban bat species.** The dimensions represent the coordinates of points calculated to fit as closely as possible to measured similarities between the diets of the flower-visiting bat species. Sample sizes are 11 (*A. jamaicensis*), 22 (*B. nana*), 17 (*E. sezekorni*), 19 (*M. redmani*) and 20 (*P. poeyi*).

### 3.4 Flower Preference

I recorded all five species of bats at the flowers of each of the five species of plants investigated except for *B. nana* at the flowers of *B. grandiceps*. Overall bat acoustic activity index values were highest at the four species of chiropterophilous plants and lowest at the control sites, which would be expected if the bats being recorded were only visiting flowers (Table 8). Activity index values at the flowers of the ornithophilous plant (*B. grandiceps*) were intermediate. Flower-feeding bats are known to be extremely curious and frequently feed from artificial bird feeders so it is not surprising that bats visited a plant adapted to bird pollination (Hinman 2000; Tschapka and Dressler 2002). Visits by *E. sezekorni*, *M. redmani* and *P. poeyi*, the morphological flower-feeding specialist species, were recorded more often than visits from either generalist species. Activity levels differed significantly among the bat species at all plant species except *C. alata* (Table 8). *E. sezekorni*, *A. jamaicensis* and *B. nana* showed no significant differences in their preference for use of the different study plants. Conversely, *M. redmani* had significantly higher activity at *C. alata*, *K. pinnata* and *H. undatus* flowers than at either *C. cujete* or *B. grandiceps*. Similarly *P. poeyi* had significantly higher activity at *C. cujete*, *K. pinnata* and *H. undatus* and lower activity at *C. alata* and *B. grandiceps* (Table 8). No social calls of any kind were recorded at any of the flowers where recordings were made.

**Table 8: Total acoustic activity index for each species of Cuban flower-visiting bat at five different flower species.** The acoustic activity index is the number of recorded bat passes per night during one minute time intervals. Numbers represent the total acoustic activity index over seven nights at each site for each species. Significant differences in a bat species' activity at each different plant species (plant preference) is indicated by uppercase letters (read across rows) while significant differences in the activity of different bat species within a given plant species is indicated by lowercase letters (read down columns). Significant differences in the activity of each species at different plants were determined by using a Kruskal-Wallis analysis with a Bonferroni correction and Conover-Iman pairwise comparisons. Values with the same letter are not significantly different (significance level = 5%).

Species	<i>Crescentia alata</i>	<i>Crescentia cujete</i>	<i>Kigelia pinnata</i>	<i>Hylocereus Undatus</i>	<i>Brownea grandiceps</i>	Control
<i>Artibeus jamaicensis</i>	7 <sup>A/a</sup>	4 <sup>A/a</sup>	6 <sup>A/a</sup>	8 <sup>A/ab</sup>	1 <sup>A/ab</sup>	0 <sup>A/a</sup>
<i>Brachyphylla nana</i>	8 <sup>A/a</sup>	3 <sup>A/a</sup>	3 <sup>A/a</sup>	4 <sup>A/a</sup>	0 <sup>A/a</sup>	0 <sup>A/a</sup>
<i>Erophylla sezekorni</i>	15 <sup>AB/a</sup>	28 <sup>B/bc</sup>	51 <sup>B/b</sup>	58 <sup>B/bc</sup>	37 <sup>B/c</sup>	1 <sup>A/a</sup>
<i>Monophyllus redmani</i>	24 <sup>BCD/a</sup>	9 <sup>ABC/ab</sup>	29 <sup>CD/b</sup>	68 <sup>D/c</sup>	9 <sup>AB/ab</sup>	0 <sup>A/a</sup>
<i>Phyllonycteris poeyi</i>	14 <sup>AB/a</sup>	60 <sup>C/c</sup>	54 <sup>C/b</sup>	47 <sup>BC/abc</sup>	10 <sup>AB/bc</sup>	3 <sup>A/a</sup>



## Chapter 4 –Discussion

### 4.1 Summary of Results

My first prediction that species with similar morphologies would have more similar diets was not supported by my data as I found that although *E. sezekorni* and *P. poeyi* had the highest degree of overlap morphologically, *E. sezekorni* and *B. nana* (35%) showed the highest degree of dietary overlap, followed by *B. nana* and *P. poeyi* (22%).

My second prediction, that species with morphological specialization for nectarivory would use plant resources differently than species with more generalist morphologies was supported by my data. The generalist species had a higher occurrence of fruit and a lower occurrence of insects in their diets than the nectivory-specialist species. Moreover, the nectivory-specialists all had high frequencies of pollen in their diets (above 80% of individuals); however this was also true of the generalist *B. nana*. Specialist species visited fewer different plant species overall than the generalists. Specialists also showed higher activity levels at all bat-pollinated plants than generalists. *M. redmani* and *P. poeyi* were the only bat species that exhibited a significant difference in their usage of the flowers of the different plant species where recordings were made.

I hypothesized that morphological differences among sympatric flower-visiting bat species would translate into different plant-based diets. I found that all of the species of bats studied were morphologically divergent except *E. sezekorni* and *P. poeyi* and there was minimal dietary overlap among species. However, evidence from acoustic monitoring at flowers suggested that within a given area, all bat species present were visiting all available flowers, but at different frequencies.

### 4.2 Morphological Differences and Overlap

My findings from morphological measurements made on live field-caught bats and from measurements taken from the skulls of museum specimens showed that the five species of flower-feeding bats in Cuba cluster into 4 very distinct groupings. All of the species

sharing flower-based food resources are morphologically distinct with the exception of *P. poeyi* and *E. sezekorni* which are notably indistinguishable in nearly every measure of morphology obtained during this study (Figure 4, 5; Appendix D). As previously discussed in chapter 1.4 on food resource partitioning, morphological differences may be associated with reduced interspecific competition so based on these morphological differences I would predict that *P. poeyi* and *E. sezekorni* are likely experiencing the greatest amount of interspecific competition. I would also predict that the high level of morphological divergence among the other study species likely points to limited interspecific competition among individuals of these species.

### 4.3 Food Resource Partitioning

I found that all species of flower-visiting bats fed at each species of chiropterophilic flower available (Table 8). This supports the idea that most chiropterophilic flowers are accessible to all flower-visiting bats within a given community (von Helversen and Winter 2003; Tschapka 2004; Fleming *et al.* 2005). However, this appears to contrast with the generally low degree of dietary overlap detected among bat species (Table 7; Figure 8). This apparent discrepancy may be explained by the different frequencies with which the bat species used the flowers where recordings were made. Similarly, Muchhala and Jarrín-V. (2002) demonstrated that within a cloud forest in Ecuador, flower-visiting bats fed from many of the same flower species but at different frequencies. Despite the use of flowers by all five bat species, no social calls were recorded from any species, suggesting that flowers are not being defended as occurs in some other species of pollinators including bats (e.g. Gould 1978; Lemke 1984), honeyeaters (e.g. Ford and Paton 1982; McFarland 1986), hummingbirds (e.g. Stiles and Wolf 1970; Feinsinger 1976; Arizmendi and Ornelas 1990) and bees (e.g. Roubik 1982; Johnson and Hubbell 1974; Nagamitsu and Inoue 1997).

The fact that I detected no social calls at the flowers where recordings were made, may suggest that floral resources are not actually limiting in this community. Several studies of floral resource availability in guilds of flower-visiting bats have also found that these resources were not limiting (e.g. Heithaus *et al.* 1975, Horner *et al.* 1998). Similarly, a study of hawkmoth pollination in the tropics also demonstrated an

overabundance of nectar at hawkmoth-visited flowers (Haber and Frankie 1989). Evidence of low dietary overlap among species in the face of seemingly abundant food sources has also been found in some species of hummingbirds (Abrahamczyk and Kressler 2010) and insectivorous bats (Fenton and Thomas 1980; Emrich *et al.* 2013). Non-limiting food resources may help explain the co-existence of *E. sezekorni* and *P. poeyi* in Cuba despite their being very morphologically similar (Figure 4, 5). It should also be noted that *P. poeyi* roosts almost exclusively in the innermost chambers of caves which have temperatures between 29° and 38°C with relative humidity between 80 and 99% (Silva and Pine 1969). This roosting behavior is unique to *P. poeyi* whereas *E. sezekorni* only uses these hot cave environments occasionally (Silva and Pine 1969). This may be another element that helps to explain the co-existence of these similar species as differences in roost requirements can be an important factor contributing to niche differentiation between morphologically similar bat species (Jacobs and Barclay 2009).

#### 4.4 Morphology as a Predictor of Diet

Morphology has been repeatedly shown to affect the types of flowers that a flower-visiting animal may visit or have access to (e.g. Heinrich 1976; Haber and Frankie 1989; Brown and Hopkins 1995). Thus it should be expected that morphologically similar species would use similar flowers as food resources as in some species of bumblebees (*Bombus*) (Harder 1985). However, my results indicate that phylogenetic relationships may also play a role in food plant choice among some species of flower-visiting bats. The highest dietary overlap occurred between *B. nana* and *E. sezekorni*, *B. nana* and *P. poeyi* and *E. sezekorni* and *P. poeyi*, in decreasing order. As previously mentioned in section 1.7 *Brachyphylla*, *Erophylla* and *Phyllonycteris* are related on the basis of molecular and morphological data forming a monophyletic clade (e.g. Carstens *et al.* 2002; Jones *et al.* 2002; Dávalos 2004; Dávalos *et al.* 2012) in which *Brachyphylla* represents the more basal taxon. *Brachyphylla* shares many morphological similarities (e.g. Silva and Pine 1969) with *Phyllonycteris* and *Erophylla*, but is also fairly distinct in terms of morphological adaptations affecting feeding such as size, dentition and snout length (e.g. Freeman 2000). Additionally the tongue of *Brachyphylla* is unspecialized for nectar feeding as it lacks the hair-like papillae found on the tongues of both *Erophylla* and

*Phyllonycteris* and other glossophagine species (Griffiths 1982). As such it could be expected that these bats would feed on different species of plants, because morphological specialization can affect the extraction efficiency of nectar and thus make different flowers profitable for differentially specialized bats (Gonzalez-Terrazas *et al* 2012). However, as noted previously, it is possible that in this system flowers are accessible to all bat species. Indeed, Gonzalez-Terrazas *et al.* (2012) noted larger differences in nectar extraction efficiencies among the study species *Glossophaga soricina*, *Leptonycteris yerbabuenae* and *Musonycteris harrisoni*, primarily when nectar was only present at deeper levels, mimicking longer corolla tube lengths.

#### 4.5 What Makes a Generalist or a Specialist?

Minckley and Roulston (2006) define a specialized pollinator on the basis of the number and relatedness of the host plants it uses; this definition was formulated in the context of bee pollination. Alternatively, Fleming and Muchhala (2008) define a specialist based on two criteria: 1) morphological adaptation for flower-feeding and 2) the degree to which the diet of the animal relies solely on nectar/pollen. This definition applies to the context of pollination by bats and birds.

Although insects and vertebrates are both important pollinators of many plant species, in most cases, insects are the more specialized group of pollinators. Flower-visiting bees obtain all of their food resources from the flowers they pollinate, including nectar, pollen and in some cases oil (Vogel 1974; Kevan and Baker 1983; Minckley and Roulston 2006). Notably Apoidea, the superfamily including sphecid wasps and bees are considered to be the most specialized pollinators within the insect class (Kevan and Baker 1983). Most adult Lepidoptera also rely almost exclusively on nectar from the flowers they pollinate for their food resources (e.g. Kevan and Baker 1983; Wäckers *et al.* 2007). Within the order Coleoptera predominant flower-visiting species belong to the families Elateridae, Scarabeidae, Cleridae, Nitidulidae, Chrysomelidae, Staphylinidae, Meloidae and Cerambycidae (Kevan and Baker 1983). Some of these beetles are thought to rely wholly on flowers for their food resources as adults including all beetle species belonging to the families Mordellidae, Oedemeridae and many species within the family Melyridae as well (Müller 1883). In contrast, vertebrate pollinators (birds and bats) are

more likely to be generalists in their diets. For example, honeyeaters (Meliphagidae), a family of avian pollinators, have comparatively diverse diets consisting largely of flower nectar, fruit and insects. All honeyeater diets contain nectar to some degree, however no species is exclusively nectarivorous and all diets include some insects (Pyke 1980). Hummingbirds, widely considered the most ‘specialized’ avian pollinators (Fleming and Muchhala 2008) also do not rely entirely on nectar and need to also consume insects to meet their metabolic needs for protein and fat (Pyke 1980; Calder and Hiebert 1983). For the most part, bats appear to be similar to birds in this respect; however there are a few reports of bat species which consume nectar/pollen almost exclusively (Table 9). These observations are based solely on the diets of phyllostomid flower-visiting bats as there is very limited information available on pteropodid flower-visiting bat diets. The majority of flower-visiting bats seem to consume primarily nectar/pollen and fruit, nectar/pollen and insects or all three dietary items to meet their nutritional needs. The flower-visiting bats from this study fall into the third category of omnivory, consuming all three food sources. As such, according to Fleming and Muchhala’s (2008) definition of a specialist, as a group, bat pollinators would be generalists, compared to bees, moths, butterflies and even beetles.

This apparent difference in feeding specialization between insect and vertebrate pollinators is almost certainly due to differences in physiology and life history. Adult insects retain energy and nutrients obtained during their larval development and different insects may rely on these resources to different extents (Romeis *et al.* 2005). Lepidoptera and Diptera may rely almost exclusively on energy reserves from larval development throughout their adult life (Drew and Yuval 2000; Jervis *et al.* 2005; Miller 1996). Additionally, many insect pollinators are short lived and only seasonally active. By contrast, vertebrate pollinators have longer life spans and most are active year round. Thus, vertebrate pollinators are likely to encounter fluctuating flower resource availability, as floral resources available to pollinators can vary dramatically among seasons (Tschapka 2004) and even among years (Gentry 1974; Zimmerman and Aide 1989). Additionally, vertebrate pollinators have a higher energy demand than their invertebrate counterparts due to homeothermy (Heinrick 1975) and generally larger body size (Calder and King 1947; King and Farner 1961; Lasiewski 1963; McNab 1970). As

**Table 9. The frequency of fruit, insects and pollen in the diets of neotropical flower-visiting bats.** Values of pollen/nectar, fruit and insects are the % of individuals of each species which were found to have consumed each food source. Such values with an “ $\chi$ ” refer to each dietary item in terms of a percent of the total volume of stomach contents. Values obtained by me are reported in bold type and parentheses, following values previously reported in the literature. Fruit values with an “S” included only seeds in the measurement while “S/P” used both seeds and fruit pulp to calculate values. Masses marked with an asterisk are mean values while others are ranges.

Species	Feeding Guild	Body Mass (g)	Pollen/Nectar	Fruit	Insects	Reference
<i>Anoura caudifera</i>	Nectarivore	11.5*	25	25 (S/P)	50	von Helversen and Reyer 1984; Zortéa 2003
<i>Anoura geoffroyi</i>	Nectarivore	14*	12.7	10 (S/P)	40	Lim and Engstrom 2001; Zortéa 2003
<i>Artibeus jamaicensis</i>	Frugivore	36-48	54.1 <b>(48)</b>	8.6 (S) <b>(100)</b>	25.0 <b>(22)</b>	Heithaus <i>et al.</i> 1975; Ortega and Castro-Arellano 2001
<i>Artibeus lituratus</i>	Frugivore	67*	47.5	2.7 (S)	25	Lim and Engstrom 2001; Heithaus <i>et al.</i> 1975
<i>Artibeus phaeotis</i>	Frugivore	8-15.6	40	8 (S)	0	Timm 1985; Heithaus <i>et al.</i> 1975
<i>Brachyphylla nana</i>	Frugivore	27-41	68 <b>(92)</b>	1.2 (S) <b>(88)</b>	52 <b>(38)</b>	Silva 1979
<i>Carollia perspicillata</i>	Frugivore	21*	38.2	44.9 (S)	13	Winter and von Helversen 2003; Heithaus <i>et al.</i> 1975

<i>Choeronycteris mexicana</i>	Nectarivore	17*	100%	0	0.5%	Winter and von Helversen 2003; Howell 1974b
<i>Erophylla sezekorni</i>	Nectarivore	16-21	75 (81)	85 (S)(62)	76 (52)	Gannon <i>et al.</i> 2005; Soto-Centeno and Kurta 2006
<i>Glossophaga longirostris</i>	Nectarivore	14-15	44	55 (S)	1	Petit 1997; Sosa and Soriano 1996
<i>Glossophaga soricina</i>	Nectarivore	10.9*	59.6	14.8 (S)	66	Winter <i>et al.</i> 1993; Heithaus <i>et al.</i> 1975
<i>Hylonycteris underwoodi</i>	Nectarivore	7.5*	100	2.8 (S)	0	Winter and von Helversen 2003; Tschapka 2004
<i>Leptonycteris curasoae</i>	Nectarivore	23.4*	100%	0	0.5%	Howell 1974b; Horner <i>et al.</i> 1998
<i>Monophyllus redmani</i>	Nectarivore	6-10	91 (95)	22 (S) (20)	73 (70)	Gannon <i>et al.</i> 2005; Soto-Centeno and Kurta 2006
<i>Musonycteris harrisoni</i>	Nectarivore	11-12	100	0	33.3	Tschapka <i>et al.</i> 2008
<i>Phyllonycteris poeyi</i>	Nectarivore	15-29	87 (87)	71 (S)(48)	31 (44)	Mancina 2010
<i>Phyllostomus discolor</i>	Omnivore	39-45	82.1	29.6 (S/P)	99	Heithaus <i>et al.</i> 1975; Kwiecinski 2006
<i>Phyllostomus hastatus</i>	Omnivore	85*	46.9	40.6 (S/P)	9.4	Lim and Engstrom 2001; Giannini and Kalko 2004
<i>Sturnira lilium</i>	Frugivore	18*	41.8	29.6 (S)	0	Lim and Engstrom 2001; Heithaus <i>et al.</i> 1975

such vertebrate pollinators have higher energy demands to satisfy in the face of often uncertain food resources. Not surprisingly, then, the majority of bat species may generalize in their sources of nutrition.

Despite the many differences between vertebrate and insect pollinators, it is important to have a definition of specialization that encompasses all groups of pollinators, for the purpose of intergroup comparisons. Combining the two definitions reviewed above (Minckley and Roulston 2006, Fleming and Muchhala 2008) results in a definition of specialization that is applicable to all groups of pollinators. This more inclusive definition of specialization encompasses the number and relatedness of a pollinator's host plants (Minckley and Roulston 2006), the degree of morphological specialization for feeding on nectar/pollen from flowers (Fleming and Muchhala 2008) and the degree to which the species or group of species' depends on pollen/nectar as their primary food source (Fleming and Muchhala 2008). I will refer to each of these aspects of pollinator specialization as host plant, morphological and dietary specialization respectively. Importantly, the terms 'specialist' and 'generalist' are not categorical. Instead they can be viewed as endpoints of a continuum, and the designations of 'specialist' and 'generalist' will always depend on what we are comparing. For example, I found that *E. sezekorni*, *M. redmani* and *P. poeyi* were more morphologically specialized for pollination/flower-visiting than *A. jamaicensis* and *B. nana* (Figure 6). However, these three species would be relative generalists compared to bat species such as *Musonycteris harrisoni* or *Choeronycteris mexicana* (Freeman 1995, Table 9).

## 4.6 Host-Plant Specialization

The number of plant species visited nightly by *M. redmani* were very similar to the values obtained by Geiselman (2010) for *Anoura geoffroyi* (2.7 in the dry season and 2.6 in the wet season) and *Lionycteris spurrelli* (2.3 in the dry season and 1.9 in the wet season), two other primarily nectarivorous bats, in French Guiana. *A. jamaicensis*, *B. nana* and *E. sezekorni*, *P. poeyi* all have relatively larger numbers of nightly pollen species ranging from an average of 3.5 – 5.3 (individuals carried anywhere from 1-9 pollen species each). This range of nightly pollen species appears to be similar to that



reported for a community of hawkmoths in Costa Rica, where captured moths carried anywhere from 1-8 species of pollen (Haber and Frankie 1989). Heithaus *et al.* (1975) reports on this subject for seven species of flower-visiting bats in a Costa Rican tropical dry forest (*Carollia perspicillata*, *Sturnira lillum*, *Artibeus jamaicensis*, *Artibeus lituratus*, *Artibeus phaeotis*, *Glossophaga soricina* and *Phyllostomus discolor*). Individual bats often carried more than one pollen species and as many as six at a time. Heithaus *et al.* (1975) also determined the proportion of bats carrying pollen from more than one plant species (i.e. mixed pollen loads) and found that between 16% (*Artibeus lituratus*) and 79% (*Phyllostomus discolor*) of individuals were carrying mixed pollen loads.

In the study reviewed above (Heithaus *et al.* 1975), pollen was collected from the fur of the animals rather than from guano. In contrast, my pollen data collected through guano analysis of Cuban bats shows a higher percentage of mixed pollen loads ranging from 75% (*M. redmani*) to 95% (*P. poeyi*; data not shown). However, calculating mixed pollen loading from guano as opposed to fur may overestimate the number of pollen species that would be present on the animal's fur at any one point in time because as the bat forages, pollen will likely be lost from the fur at a faster rate than the ingested pollen moving through the digestive tract which is retained for an average of approximately 2 hours (Herrera and Martínez Del Río 1998). Determining the percent of mixed pollen loads or the number of nightly pollen species may be a good determinant of host-plant specialization because multiple species of pollen present on the fur of a pollinator during foraging reduces the likelihood of successful pollination by increasing the probability of pollen from one plant species being lost on the floral parts of another species. By having a higher number of nightly pollen species or a higher percentage of mixed loads within a flower-visiting species this species becomes a less effective pollinator. As such determining these measures from fur-collected pollen as opposed to guano-collected pollen will likely be a more accurate measure of host-plant specialization.

The total number of plants visited by each species during my study period was higher than values reported in the literature for these and other bat species. In my study, the number of flower species visited ranged from 11 (*M. redmani*) to 21 (*B. nana*). By

contrast, a study in a karst region of Puerto Rico over a similar time period as this study found that *E. sezekorni* and *M. redmani* only visited 7 and 9 species of plants, respectively (Soto-Centeno and Kurta 2006). Geiselman (2010) reports only 12 species visited in total by both *L. spurrelli* and *A. geoffroyi* over two years and values between 4.6 and 6.4 for the average number of species visited per month. Hevly (1979) found that *Leptonycteris sanborni* only visited from 1-5 species per season and 6 species in a year and *Choeronycteris Mexicana* visited 3 or more species in a month and 15 species throughout the year. Similarly, *Musonycteris harrisoni* was reported to only visit 14 pollen-producing plant species annually in western Mexico, and 2.03 and 0.83 species per month during the dry and wet seasons, respectively (Tschapka *et al.* 2008). These differences may not necessarily reflect a difference in host-plant specialization among these species as my study included bats from four different locations, as opposed to just one location in the studies cited above. This difference in spatial scale may explain why the bats I captured visited a wider variety of different plant resources. However, for *B. nana* and *A. jamaicensis*, which had larger numbers of nightly pollen species and the largest values for total plant species visited, another explanation may be likely. These species are much larger than all those previously mentioned as seen in their greater mass, skull size and forearm length (Appendix D). Larger animals are more mobile due to more cost-efficient flight (Brown *et al.* 1978) and thus tend to travel greater distances in a night (Horner *et al.* 1998). For example in bees, foraging range increases with increasing body size (Greenleaf *et al.*, 2007). This may provide larger plant-visitors with access to more species of plants to feed from and thus increase their host-plant diet breadth. In general, the morphologically specialized nectarivore species tend to be smaller than the opportunistic less morphologically specialized bats (Table 9). This is likely due to the fact that most flower-visiting phyllostomids hover at flowers, allowing them to move quickly between plants and access a wider variety of flowers (Winter and von Helversen 2003). Hovering flight is extremely energetically expensive and becomes more costly with increasing body size (Voigt and Winter 1999). However, another consequence of smaller body size may be greater host-plant specialization for these smaller bat species.

## 4.7 Morphological Specialization

My classification of *E. sezekonri*, *M. redmani* and *P. poeyi* as less morphologically specialized for flower-visiting than *B. nana* and *A. jamaicensis* is consistent with other literature on cranial morphology in phyllostomid bats (Freeman 1995; Freeman 2000). Genus *Monophyllus* is often considered to be a more morphologically specialized nectarivore than either *Erophylla* or *Phyllonycteris* (Freeman 1995; Monteiro and Nogueira 2011). Genus *Brachyphylla* is considered to be intermediate between these groups and more morphologically specialized frugivores (e.g. *Artibeus*) in terms of cranial morphology (Freeman 1995; Freeman 1998; Monteiro and Nogueira 2011). *Brachyphylla* is similar to phyllostomid frugivores in several characteristics including zygomatic breadth over length of toothrow, total tooth area of palate, molariform area of total tooth area, and the lack of space between the teeth (Freeman 1995). However, *Brachyphylla* are also similar to nectarivores in several other cranial characteristics such as area for non-molariform premolars and length from the most posterior molar to the dentary condyle (Freeman 1995). Similarities in cranial morphology between *Brachyphylla* and other frugivores has also been noted by Freeman (2000) and Griffin (1985). Additionally, Monteiro and Nogueira (2011) found that *Brachyphylla* was phenotypically similar to genera *Phylloderma* (primarily insectivorous) and *Sturnia* (primarily frugivorous), placing *Brachyphylla* between frugivore and insectivore species in principal component space.

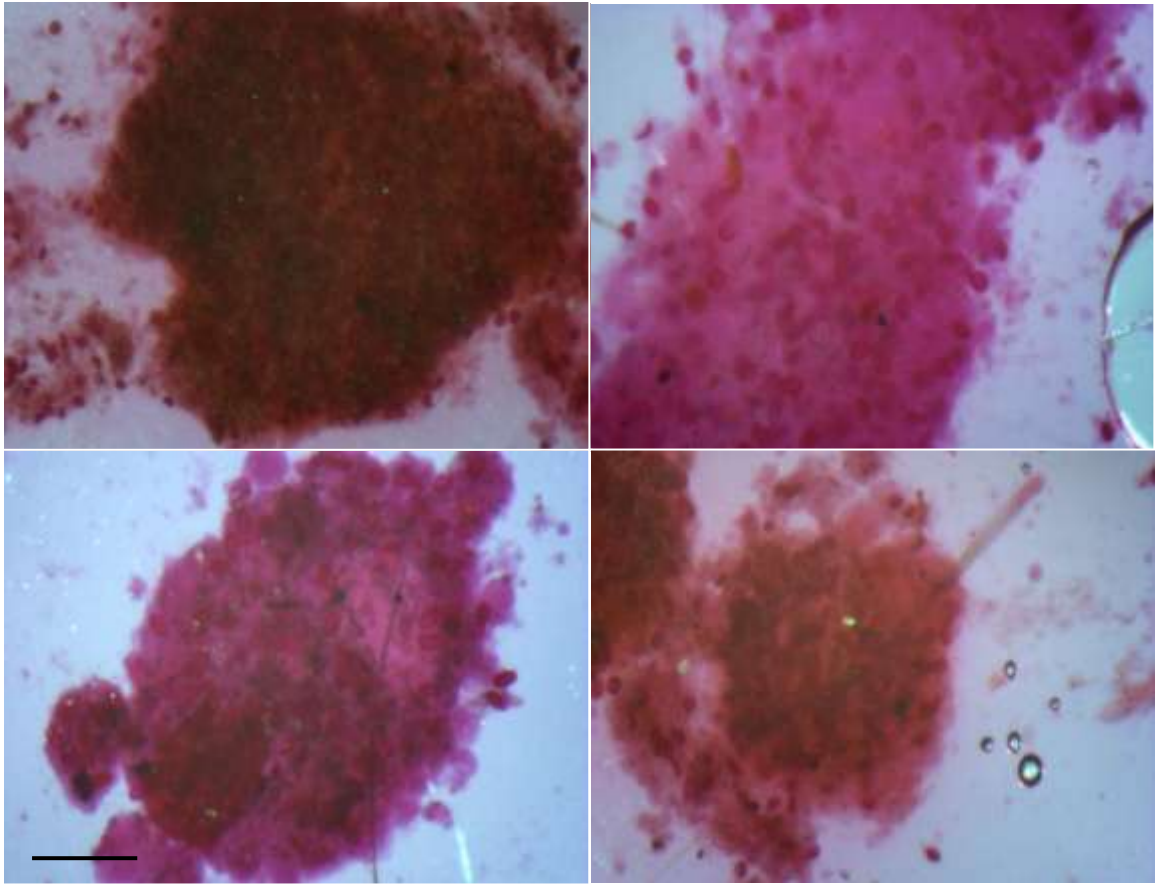
## 4.8 Dietary Specialization

Dietary specialization, for the most part, reflected morphological specialization in the five species of bats I studied. However, *B. nana* is a notable exception. Despite the more generalist morphology of this species, the frequency with which pollen was found in its guano was second only to *M. redmani*. This may seem unexpected. However, a review of the literature suggests that it is not uncommon for morphologically unspecialized flower-visitors to use nectar and pollen as an important food source (Table 9). For example, *Phyllostomus discolor* has been classified as an insectivore based on morphology (Freeman 2000) but has an omnivorous diet. This species has been found on multiple occasions to carry pollen at least as often than more morphologically specialized

nectarivorous bats (Heithaus *et al.* 1974; Heithaus *et al.*, 1975; Gribel *et al.* 1999) Additionally, I found pollen to be present in large quantities and clumps in the guano of *B. nana* (Figure 8), in contrast to *A. jamaicensis* which had fewer more isolated pollen grains in its guano. The presence of large aggregates of a single species of pollen in the guano of *B. nana* could be evidence of feeding on pollen directly from anthers or anther/flower eating. Flower-eating was suggested by Freeman (1995) as a possible explanation for the puzzling cranial morphology within the genus. This type of flower-visiting behavior has also been noted in *Glossophaga soricina* (Lemke 1985) and *Leptonycteris sanborni* (Baker *et al.* 1971).

## 4.9 Future Research Directions

This study was undertaken to help elucidate the role of morphology in diet and plant resource use for flower-visiting bat species. Although the study answered some important questions about how this guild of flower-visiting bats uses their resources, it also raised several new questions. For example I found that morphology was not a good predictor of dietary overlap among species which seemed to be more correlated with phylogenetic relationships in *B. nana*, *E. sezekorni* and *P. poeyi*. This finding raises the question, what aspect of this evolutionary relationship is responsible for the use of such similar food plants by these species? The first step in answering this question is to determine the identity of the food plants shared among these species and how they may be unique. In my study I used microscopic identification of pollen to determine unique pollen species from guano however this method is extremely time consuming and only yields the number of different pollen species present and not the identities of these species unless a thorough reference collection of pollen from all possible plant species in each study area has already been assembled. DNA barcoding is a method that has been successfully used to study food resource partitioning among groups of insectivorous



**Figure 9: Micrographs of pollen aggregates found in the guano of *Brachyphylla nana*.** Images were obtained using a Zeiss SteReo Lumar V12 Microscope courtesy of the Biotron Institute (University of Western Ontario, 1151 Richmond St. N, London, Ontario, Canada). Scale bar is equal to 250  $\mu\text{m}$ .

animals on numerous occasions (e.g. Bohmann *et al.* 2011, Emrich *et al.* 2013, Krüger *et al.* 2013) and shows great promise for use in the study of plant-pollinator interactions (Clare *et al.* 2013). A combination of genomic regions for use as the barcode for land plants has already been identified (CBOL Plant Working Group 2009) and one study has been published using this methodology to identify plants pollinated by Hawaiian solitary bees (*Hylaeus* spp.) (Wilson *et al.* 2010). Some drawbacks in the methodology used by Wilson *et al.* 2010 was that when multiple pollen species were detected on a specimen, sequencing only identified the dominant pollen species. This will clearly be problematic if this technique is to be applied to other studies, as I discussed section 4.6 on host-plant specialization, between 75% to 95% of captured bats had mixed pollen loads and individuals had anywhere from 1 to 9 species of pollen present in their guano. Future research should focus on refining the methodology used in Wilson *et al.* 2010 for use with mixed pollen loads so that this promising new technique may be used among wider applications in the field of plant-pollinator interactions.

My study examined the role of morphology in food resource partitioning, however, this is only one aspect of partitioning, merely a single piece of the bigger picture. Partitioning resources to limit interspecific competition can occur on many scales and through many different means. My study was limited to investigating food plant use in terms of the frequencies of different plant species consumed. However, individuals may also be using resources at different times and in different places, partitioning resources both in time and space (e.g. Emrich *et al.* 2013). Additionally roost sites and roosting behavior may also be an important aspect of species co-existence as was shown to be true for two bat species, *Scotophilus dinganii* and *S. mhlanganii*, living in sympatry (Jacobs and Barclay 2009). Future studies should focus on the role of multi-dimensional aspects of partitioning in guilds of flower-visiting bats to better understand the co-existence of similar sympatric species and the role of morphology in this partitioning and co-existence.

## 4.10 Significance

Although the role of morphology in plant resource use has been thoroughly investigated in many species and guilds of pollinating insects, very little work has been done to

investigate this relationship in bats. This is the first study to look at plant-pollinator interactions from a morphological perspective in a guild of bats in nature. Studies in this area have largely been limited to lab experiments on the significance of bat species' morphological adaptations for flower feeding (e.g. Gonzalez-Terrazas *et al.* 2012). However, field studies of bats in nature are needed in order to put the findings of these lab experiments into perspective. For example, as I have discussed previously Gonzalez-Terrazas *et al.* (2012) found that greater morphological specialization for flower-feeding increased nectar extraction efficiency at greater corolla tube depths, indicating that for reasons of energetic efficiency, morphologically specialized bats will likely prefer different flowers than less specialized bats. However, my study with acoustic monitoring at flowers found that in nature flower-visiting bats likely visit all available flowers in a given area, but at different frequencies, with morphological specialists showing stronger preferences for particular flower species than generalists.

My study found that morphological specialist species visit fewer species of food plants than generalists, visit food plants more often than generalists and also rely more heavily on flower-based food resources. This information indicates that morphological specialists may be better pollinators than morphological generalists and this can be valuable information for conservation efforts. For example, when conserving endangered species of plants one must also consider the conservation of its pollinators. My study suggests that when conserving the pollinators of bat-pollinated plants, conservation efforts should be focused on the more morphologically specialized bat pollinators as they may be more reliable and effective in pollination.

Finally my study also contributes to our understanding of how very morphologically similar species can co-exist in nature, as is the case for *P. poeyi* and *E. sezekorni* in Cuba. My findings with acoustic monitoring at flowers suggest that individuals do not compete for flowers, indicating that floral resources are not actually limiting. Future studies may consider this finding and test it, as a hypothesis to help explain the co-existence of other very similar sympatric species.

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## Appendix A: Museum Specimens

All cranial morphological measurements were collected from specimens housed at the Royal Ontario Museum (100 Queens Park Toronto, Ontario, Canada). All specimens originated from Cuba and are adults. The sex of specimens is indicated in parentheses following the specimen number.

Family Phyllostomidae: *Aritbeus jamaicensis* 38830 (♂), 38831(♂), 38832 (♂), 38833 (♀), 38834 (♀), 41828 (♀), 63152 (♂), 63153 (♂), 63154 (♂), 63155 (♀), 63156 (♀), 63157 (♀), 78590 (♀); *Brachyphylla nana* 63158 (♂), 63159 (♂), 63160 (♂), 63161 (♀), 63162 (♀), 63163 (♀), 78442 (♀); *Erophylla sezekorni* 63164 (♂), 63165 (♂), 63166 (♂), 63167 (♀), 63168 (♀), 63169 (♀); *Monophyllus redmani* 63146 (♂), 63147 (♂), 63148 (♂), 63149 (♀), 63150 (♀), 63151 (♀); *Phyllonycteris poeyi* 63170 (♂), 63171 (♂), 63172 (♂), 63173 (♀), 63174 (♀), 63175 (♀), 78764 (♀)

## Appendix B: Measurements

**Table 10: Cranial measurements, their definitions and references from the literature.** Measurements in bold are those used to differentiate between phyllostomid nectarivorous and frugivorous bats.

Measurement	Definition	Reference
Skull length	Greatest distance from the back of the skull to the tip of the rostrum	Dumont 2004
Zygomatic breadth (ZB)	Greatest width across zygomata	Freeman 1988
Temporal height (TH)	Distance from basicranium to the top of the sagittal crest	Freeman 1988
<b>Rostrum length</b>	Length from preorbital foramina to the alveolus of the inner incisor	Kruskop 2004
<b>Width across canines</b>	Greatest width across the canines at the cingula	Freeman 1988
<b>Palatal breadth (PW)</b>	Greatest width across molars	Freeman 1988
<b>Palatal length (PL)</b>	Distance from posterior nasal spine to anterior edge of incisor	Dumont 2004
<b>Length from dentary condyle to most postetrior tooth in lower toothrow</b>	Length from midpoint of dentary condyle to posterior most edge of most posterior tooth in toothrow	Freeman 1995
<b>Dentary thickness</b>	Lateral width of the dentary at the first root of M1, to the ventral border of the dentary	Freeman 1988
<b>Space Index</b>	The distance between the upper postcanine teeth and the medial gap between canines at the frontal end of the toothrows when the teeth are occluded divided by the length of the maxillary toothrow	Freeman 1995

## Appendix C: Echolocation

**Table 11: Echolocation call parameters of Cuban flower-visiting bats.**

Bat Species	Harmonic	Call Duration (ms)	Max Freq. (kHz)	Min Freq. (kHz)	FME (kHz)	Reference
<i>Artibeus jamaicensis</i>	1 <sup>st</sup>	4.28 ± 0.63	77.11 ± 5.69	25.42 ± 3.62	57.25 ± 6.06	Mora <i>et al.</i> 2007
<i>Brachyphylla nana</i>	1 <sup>st</sup>	2.38 ± 0.38	88.52 ± 2.56	34.12 ± 6.07	58.99 ± 3.88	Macías <i>et al.</i> 2006
<i>Erophylla sezekorni</i>	1 <sup>st</sup>	2.3 ± 0.2	59.6 ± 1.3	32.5 ± 1.3	45.1 ± 1.7	Murray <i>et al.</i> 2009
	2 <sup>nd</sup>	2.3 ± 0.2	90 ± 4.9	51.6 ± 2.5	65.3 ± 3.4	
<i>Monophyllus redmani</i>	1 <sup>st</sup>	1.8 ± 0.6	79.5 ± 6.4	40.7 ± 5.9	70.9 ± 7.1	Amanda Adams, personal communication, June 12, 2012
	2 <sup>nd</sup>	1.7 ± 0.5	133.7 ± 12.6	72.2 ± 7.3	97.4 ± 11.2	
<i>Phyllonycteris poeyi</i>	1 <sup>st</sup>	4.69 ± 1.04	45.92 ± 2.25	34.44 ± 1.77	38.74 ± 1.92	Mora <i>et al.</i> 2007

## Appendix D: Morphological Measurements

**Table 12: Measurements of morphological characteristics for five species of Cuban flower-visiting bats taken in the field.** Given values represent the mean measurement in millimetres  $\pm$  standard error. Sexually dimorphic characters within a species and significant differences between species for a given characteristic were determined by using a Kruskal-Wallis analysis with a Bonferroni correction and Conover-Iman pairwise comparisons and are either bolded or indicated by different letters, respectively (significance level = 5%).

	<i>Artibeus jamaicensis</i>	<i>Brachyphylla nana</i>	<i>Erophylla sezekorni</i>	<i>Monophyllus redmani</i>	<i>Phyllonycteris poeyi</i>
N	29	23	17	20	22
Forearm Length	55.84 $\pm$ 1.75 <sup>C</sup>	58.14 $\pm$ 2.13 <sup>D</sup>	46.59 $\pm$ 1.41 <sup>B</sup>	38.39 $\pm$ 1.62 <sup>A</sup>	46.94 $\pm$ 1.01 <sup>B</sup>
Head Length	25.59 $\pm$ 1.88 <sup>B</sup>	28.11 $\pm$ 1.36 <sup>C</sup>	25.11 $\pm$ 1.10 <sup>B</sup>	22.12 $\pm$ 1.54 <sup>A</sup>	26.01 $\pm$ 1.00 <sup>B</sup>
Snout Length	9.99 $\pm$ 0.90 <sup>A</sup>	8.20 $\pm$ 0.50 <sup>B</sup>	6.10 $\pm$ 0.45 <sup>B</sup>	4.71 $\pm$ 0.31 <sup>A</sup>	6.11 $\pm$ 0.54 <sup>B</sup>
Snout Width	<b>5.93 <math>\pm</math> 0.93<sup>D</sup></b>	7.97 $\pm$ 0.85 <sup>C</sup>	7.40 $\pm$ 0.60 <sup>B</sup>	6.01 $\pm$ 0.65 <sup>A</sup>	7.51 $\pm$ 0.69 <sup>B</sup>



**Table 13: Raw cranial morphological measurements for five species of Cuban flower-visiting bats obtained from museum specimens.** Given values represent the mean measurement in millimetres  $\pm$  standard error. Sexually dimorphic characters within a species and significant differences between species for a given characteristic were determined by using a Kruskal-Wallis analysis with a Bonferroni correction and Conover-Iman pairwise comparisons and are either bolded or indicated by different letters, respectively (significance level = 5%).

	<i>Artibeus jamaicensis</i>	<i>Brachyphylla nana</i>	<i>Erophylla sezekorni</i>	<i>Monophyllus redmani</i>	<i>Phyllonycteris poeyi</i>
N	13	7	6	6	7
Skull length	26.26 $\pm$ 0.86 <sup>C</sup>	28.38 $\pm$ 0.31 <sup>D</sup>	24.44 $\pm$ 0.40 <sup>B</sup>	21.96 $\pm$ 0.30 <sup>A</sup>	24.53 $\pm$ 0.94 <sup>B</sup>
Zygomatic Breadth	16.00 $\pm$ 0.62 <sup>C</sup>	15.30 $\pm$ 0.50 <sup>C</sup>	11.22 $\pm$ 0.25 <sup>B</sup>	9.30 $\pm$ 0.22 <sup>A</sup>	11.13 $\pm$ 0.30 <sup>B</sup>
Temporal Height	11.92 $\pm$ 0.51 <sup>C</sup>	11.47 $\pm$ 0.33 <sup>C</sup>	<b>9.41 <math>\pm</math> 0.53<sup>B</sup></b>	7.47 $\pm$ 0.26 <sup>A</sup>	9.20 $\pm$ 0.28 <sup>B</sup>
Rostrum Length	7.02 $\pm$ 0.60 <sup>A</sup>	9.18 $\pm$ 0.31 <sup>C</sup>	9.72 $\pm$ 0.39 <sup>C</sup>	8.18 $\pm$ 0.68 <sup>B</sup>	9.44 $\pm$ 0.36 <sup>B</sup>
Width across Canines	6.55 $\pm$ 0.33 <sup>C</sup>	6.91 $\pm$ 0.11 <sup>D</sup>	5.21 $\pm$ 0.14 <sup>B</sup>	3.90 $\pm$ 0.08 <sup>A</sup>	5.37 $\pm$ 0.30 <sup>B</sup>
Palate Length	13.15 $\pm$ 0.51 <sup>C</sup>	11.69 $\pm$ 0.34 <sup>B</sup>	10.85 $\pm$ 0.32 <sup>A</sup>	11.19 $\pm$ 0.09 <sup>B</sup>	10.65 $\pm$ 0.21 <sup>A</sup>

Palate Width	$11.29 \pm 0.31^E$	$10.33 \pm 0.21^D$	$6.38 \pm 0.14^B$	$5.27 \pm 0.39^A$	$6.95 \pm 0.12^C$
Length from Dentary Condyle to M3	$7.25 \pm 0.59^B$	$8.13 \pm 0.41^C$	$7.23 \pm 0.40^B$	<b><math>5.71 \pm 0.21^A</math></b>	$7.10 \pm 0.27^B$
Dentary Width	$1.59 \pm 0.11^D$	$1.34 \pm 0.07^C$	$0.80 \pm 0.05^B$	$0.60 \pm 0.05^A$	$0.85 \pm 0.10^B$
Space Index (%)	0	0	$1.1 \pm 0.01^A$	$5.0 \pm 0.02^B$	$1.2 \pm 0.02^A$

**Table 14: Size-adjusted cranial morphological measurements contributing to feeding specialization for five species of Cuban flower-visiting bats obtained from museum specimens.** Given values represent the mean log-transformed size-adjusted values  $\pm$  standard error. Significant differences between species for a given characteristic were determined by using a Kruskal-Wallis analysis with a Bonferroni correction and Conover-Iman pairwise comparisons and are indicated by different letters, respectively (significance level = 5%).

	<i>Artibeus jamaicensis</i>	<i>Brachyphylla nana</i>	<i>Erophylla sezekorni</i>	<i>Monophyllus redmani</i>	<i>Phyllonycteris poeyi</i>
N	13	7	6	6	7
Rostrum Length	$-0.39 \pm 0.07^A$	$-0.132 \pm 0.03^B$	$0.12 \pm 0.05^C$	$0.08 \pm 0.07^C$	$0.09 \pm 0.05^C$
Width across Canines	$-0.45 \pm 0.04^{CD}$	$-0.42 \pm 0.02^D$	$-0.51 \pm 0.02^{AB}$	$-0.66 \pm 0.02^A$	$-0.47 \pm 0.04^{BC}$
Palate Length	$0.24 \pm 0.02^C$	$0.11 \pm 0.03^A$	$0.23 \pm 0.02^{BC}$	$0.40 \pm 0.02^D$	$0.21 \pm 0.02^B$
Palate Width	$0.09 \pm 0.02^D$	$-0.01 \pm 0.02^C$	$-0.31 \pm 0.02^A$	$-0.36 \pm 0.06^A$	$-0.21 \pm 0.02^B$
Length from Dentary Condyle to M3	$-0.35 \pm 0.06^A$	$-0.26 \pm 0.05^{BC}$	$-0.18 \pm 0.04^D$	$-0.28 \pm 0.04^B$	$-0.20 \pm 0.03^{CD}$
Dentary Width	$-1.87 \pm 0.05^D$	$-2.06 \pm 0.05^C$	$-2.38 \pm 0.06^B$	$-2.54 \pm 0.08^A$	$-2.32 \pm 0.12^B$

## Appendix E: Permits

**MINISTERIO DE CIENCIA TECNOLOGIA Y MEDIO AMBIENTE  
OFICINA DE REGULACION AMBIENTAL Y DE SEGURIDAD NUCLEAR  
CENTRO DE INSPECCION Y CONTROL AMBIENTAL**

La Habana, 5 de julio de 2012  
Año 54 de la Revolución


**Dra. Alicia Gíaz**  
Decana Facultad de Biología  
Universidad de la Habana

Señada compañera:

La presente es para comunicarle que ha sido otorgado el Permiso Especial de Acceso a Áreas Naturales 2012/63 y DA 21/2012, a favor de la **Facultad de Biología de la Universidad de la Habana**, con el Código: LH 40 AN (63) 2012

Pueden pasar a recoger el documento oficial en la Ventanilla Única de la ORASEN, previo pago de los gastos incurridos durante el trámite de evaluación, de lunes a jueves en el horario de 9:00 pm a 12:00 pm y de 2:00 pm a 4:00 pm.

Atentamente,

Ingeniero  Álvarez

SELV

428
9/2/12
CTCA

643  
5/2/12

**MINISTERIO DE CIENCIA, TECNOLOGÍA Y MEDIO AMBIENTE  
PERMISO DE ACCESO ÁREAS NATURALES Y MONTAÑOSAS**

**ESPECIAL**

El Ministerio de Ciencia, Tecnología y Medio Ambiente en virtud de la Ley 81 de 1996 de Medio Ambiente y de la Resolución 24 de 1996 de este Ministerio y luego de un proceso de consulta previa con otros Organismos de la Administración Central de Estado, ha decidido conceder el permiso **No. PE 2012/63**, a favor de la **FACULTAD DE BIOLOGÍA DE LA UNIVERSIDAD DE LA HABANA**, (Responsable: Lic. Ariadna Cobe Cuan), con el objetivo de realizar grabaciones de las emisiones acústicas de murciélagos polívoros cubanos en el Jardín Botánico Nacional, provincia La Habana, quedando sujeto a los siguientes requisitos:

Las medidas que a continuación se relacionan, son de estricto cumplimiento por el Responsable y demás participantes de la actividad antes descrita. Cualquier violación de las mismas constituye una contravención prevista y sancionada en el Decreto-Ley 200.

1. El Permiso es un instrumento de trabajo por lo que será portado por el responsable de la expedición durante la realización de la misma.
2. Se autoriza a visitar las áreas que aparecen en el Anexo I.
3. Se autoriza la visita del personal nacional y extranjero que aparece descrito en el Anexo II.
4. No se permite el empleo de GPS ni toma de video sin la autorización correspondiente.
5. El Responsable de la expedición le comunicará por teléfono a la Delegación Territorial del CITMA correspondiente, 72 horas antes, el comienzo de la realización de la misma.
6. Antes de comenzar con la ejecución del permiso, el responsable con 72 hrs de antelación, debe presentarse en la Región Militar de la Habana, con la civil Florencia teléfono 06457178, para puntualizar cronograma de ejecución, las actividades previstas, los medios a emplear y la presencia del personal en el área. Además el responsable por la parte cubana deberá confirmar la autorización con la Jefatura Provincial del MININT.
7. Coordinar las visitas con la Unidad de Medio Ambiente (UMA) de la Delegación del CITMA de la provincia antes mencionada.
8. Se deberán cumplir los términos establecidos en el Permiso de Captura No 21/2012.
9. Después de finalizado el trabajo se dejara constancia, de los resultados de cada visita, a través de un informe que se entregará a la UMA antes señalada.
10. Se enviará al Centro de Inspección y Control Ambiental en un término de 30 días hábiles a partir de finalizada la expedición o visita, un informe con los resultados de la actividad, incluir declaración de las coordinaciones previas orientadas en el permiso (Organismos y Personal), el cual estará firmado por el responsable de la expedición.



11. En el caso que la expedición no se realice deberá explicar de forma breve las causas por las cuáles no se efectuó la misma. Esta información será presentada en un término de 15 días hábiles a partir de la fecha de inicio de la expedición que aparece en este documento.
12. Cumplir todos los trámites y leyes vigentes en el País para la realización de este Permiso.

Esta autorización es válida desde el 10 de julio hasta el 30 de septiembre de 2012.

A los 04 del mes de julio de 2012.



Esta autorización es válida con boletines o fechadores y consta de 4 páginas debidamente firmadas y acopiadas. Esta licencia se expide sin perjuicio de otras licencias, permisos o autorizaciones que se emitan por los organismos competentes. El incumplimiento de los requisitos podrá ser sancionado con las contravenciones previstas en el Decreto-Ley 200/99 "De las Contravenciones en Materia de Medio Ambiente".

#### ANEXO I

##### AREAS A VISITAR:

Nombre del Área o localidad	Coordenadas planas o rectangulares		Municipio	Provincia
	X (Lat)	Y (Lon)		
Jardín Botánico Nacional			Arroyo Naranjo	La Habana



## ANEXO II

Nombre de los participantes cubanos y extranjeros en la expedición:

Nombre de los Especialistas Cubanos	Número de Identidad	Centro de trabajo	Especialidad	Esfera de Trabajo
1. Ariadna Cobo Cuan	73072709370	Universidad de La Habana	Biología	Investigación en ecofisiología de murciélagos
2. Emiliad Mora Macías	73002673184	Universidad de La Habana	Biología	Investigación en ecofisiología de murciélagos
3. Yohani Fernández Delgado	86043004813	Universidad de La Habana	Biología	Investigación en ecofisiología de murciélagos
4. Silvio Macías Herrera	76110902329	Universidad de La Habana	Biología	Investigación en ecofisiología de murciélagos
Nombre de los especialistas extranjeros	Número del pasaporte y Estado o país emisor	Fecha y país de nacimiento	Especialidad	Esfera de trabajo
1. Lindsey Kathryn Clairmont	QA55985, Canadá	8 Agosto de 1988, Canadá	Biología	Investigación en ecofisiología de murciélagos
2. Leslie Erdman	QC571323	10 de noviembre de 1985, Canadá	Biología	Investigación en ecofisiología de murciélagos



**MINISTERIO DE CIENCIA TECNOLOGIA Y MEDIO AMBIENTE  
CENTRO DE INSPECCION Y CONTROL AMBIENTAL**

**PERMISO DE CAPTURA-COLECTA No. 21/2012**

El Centro de Inspección y Control Ambiental, en uso de las facultades conferidas en la Resolución 111/1996 del Ministerio de Ciencia, Tecnología y Medio Ambiente, otorga el presente **Facultad de Biología -Universidad de la Habana**, con propósitos científicos, de la especie de murciélagos polívoros cubanos.


**CONDICIONES ESPECIALES:**

Las condiciones que establece el presente permiso son de obligatorio cumplimiento y su violación constituye una contravención prevista y sancionada en el Decreto-Ley 200.

1. El permiso es un instrumento de trabajo por lo que será portado por el responsable durante la captura y mostrarlo a las autoridades competentes.
2. Este permiso de captura-colección con fines investigativos, está amparado bajo el Permiso de Acceso a Áreas Naturales y Montañas **PE No. 2012/63**, otorgado por el Centro de Inspección y Control Ambiental.
3. Se prohíbe la colecta plantas, animales (que no sean los autorizados), de objetos de valor arqueológico, paleontológico y geológico de las áreas que serán visitadas.
4. Una vez realizado los estudios correspondientes con las especies capturadas, serán devueltos inmediatamente a su medio natural.
5. Se prohíbe la exportación del país de cualquier espécimen, parte o derivado de los especímenes capturados sin la autorización del CICA.
6. Se entregará al CICA en un término de 30 días hábiles a partir de finalizada la expedición, un informe resultante de las actividades anexo al informe solicitado en el Permiso de Acceso a Áreas Naturales y Montañas que incluirá la siguiente información:
  - Cantidad de ejemplares capturados
  - Personal que participó en la expedición.

Esta autorización es válida desde el 10 de julio hasta el 30 de septiembre de 2012.

Así lo Resuelvo y Firmo a los 5 del mes de julio de 2012.

Ing.  ez Alvarez

*Este documento no es válido con borrones o tachaduras y consta de 1 página debidamente firmada y acullada. Esta licencia se expide sin perjuicio de otras licencias, permisos o autorizaciones que se emitan por los organismos competentes. El incumplimiento de los requisitos podrá ser sancionado con las contravenciones previstas en el Decreto-Ley 200/99 "De las Contravenciones en Materia de Medio Ambiente"*



**AUSPC**

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**From:** eSiriusWebServer [esiriusadmin@uwo.ca]  
**Sent:** Monday, May 02, 2011 8:44 AM  
**To:** [REDACTED]  
**Cc:** [REDACTED]  
**Subject:** eSirius Notification - Annual Protocol Renewal APPROVED by the AUS 2008-003-04::3



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.

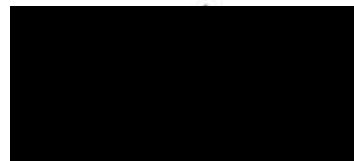
1. This AUP number must be indicated when ordering animals for this project.
2. Animals for other projects may not be ordered under this AUP number.
3. Purchases of animals other than through this system must be cleared through the ACVS office. Health certificates will be required.

**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



*The University of Western Ontario*  
Animal Use Subcommittee / University Council on Animal Care  
Health Sciences Centre, • London, Ontario • CANADA – N6A 5C1  
PH: 519-661-2111 ext. 86768 • FL 519-361-2028  
Email: [aupam@uwo.ca](mailto:aupam@uwo.ca) • <http://www.uwo.ca/animal/website/>

## Curriculum Vitae

**Name:** Lindsey Clairmont

**Post-secondary Education and Degrees:** Wilfrid Laurier University  
Waterloo, Ontario, Canada  
2006-2011 B.Sc.

The University of Western Ontario  
London, Ontario, Canada  
2012-2013 M.Sc.

**Honours and Awards:** National Science and Engineering Research Council (NSERC)  
Undergraduate Student Research Award  
2010

Wilfrid Laurier President's Scholarship  
2010-2011

NSERC Undergraduate Student Research Award  
2011

Wilfrid Laurier Alumni Gold Medal  
2012

Province of Ontario Graduate Scholarship  
2011-2012

NSERC Canadian Graduate Scholarship  
2012-2013

North American Symposium on Bat Research's (NASBR) Organization  
for Bat Conservation Award  
2013

**Related Work Experience:** Instructional Assistant  
Wilfrid Laurier University  
2009-2011

Teaching Assistant  
University of Western Ontario  
2012-2013

**Publications:**

Clemow, S.R., Clairmont, L., Madsen, L.H. and F.C. Guinel. (2011) Reproducible hairy root transformation and spot-inoculation methods to study root symbioses of pea. *Plant Methods*, 7, 46.

**Presentations:**

Clairmont, L. (2011) Investigating the regulation of root symbioses using the pea mutant E151 (*sym15*). Canadian Society of Plant Physiologists Eastern Regional Meeting, Ottawa, Canada.

Clairmont, L. (2012) The pollination of two endemic Cuban cacti exhibiting chiropterophilic pollination syndromes. Cuba-Canada Bat Research Meeting, Havana, Cuba.

Clairmont, L. (2012) Pollinator specialization in flower-visiting bats. Conference on Bat-Moth Interactions, Havana, Cuba.

Clairmont, L and M.B. Fenton. (2013). Morphology and food resource partitioning among five species of Cuban flower visiting bats. 43<sup>rd</sup> Annual NASBR and 16<sup>th</sup> International Bat Research Conference, San José, Costa Rica.