Stable Isotope Ecology of Tropical Bats

by

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AUTHOR'S DECLARATION

This thesis consists of material all of which I authored or co-authored: see Statement of Contributions included in the thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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STATEMENT OF CONTRIBUTIONS

Co-authorship statements

Chapter 2 – *Community structure of a Neotropical bat fauna as revealed by stable isotope analysis* was co-authored by Dr. Nancy B. Simmons, Dr. M. Brock Fenton and Dr. Hugh G. Broders. It is in publication in the journal *Biotropica*.

Chapter 3 – *Frugivorous bats in Brazil's fragmented Atlantic Forest: Effects of habitat fragmentation and fragment composition on diet* was co-authored by Dr. Elizabeth L. Clare and Tiago S. M. Teixeira and Dr. Hugh G. Broders

Chapter 4 – *Multi-tissue stable isotope analysis reveals seasonality in the diets of tropical bats* was co-authored by Dr. Burton K. Lim and Dr. Hugh G. Broders

List of Contributions

1) Dr. Hugh G. Broders (Professor and Department Chair, Department of Biology, University of Waterloo) – Acted as supervisor, provided all funding and support in project design, revision and execution.
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3) Dr. Brock Fenton (Professor emeritus, Department of Biology, Western University) – Served on the supervisory committee, provided support for Chapter 2 data collection and revisions for Chapter 2.

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6) Dr. Burton Lim (Assistant Curator of Mammalogy, Royal Ontario Museum) – Provided support for sample collection and revisions for Chapter 4, assisted in data collection for Chapter 2.

ABSTRACT

Stable isotopes have been used to characterize differences in animal diet and behaviour since experimental studies by DeNiro and Epstein (1979; 1981). Examining isotopic ratios enables researchers to track how animals interact with their environment as these ratios are derived from intake of nutrients and are fractionated into tissue at a calculable factor; in short, 'you are what you eat' (Tykot 2004). Studying bats, I use carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes to: (1) characterize community structure of a diverse fauna in Belize, (2) examine dietary differences between populations in a fragmented forest in Brazil, and (3) tested multiple tissues from the same individual to discern seasonal difference in diet in species from both the Neotropics and Paleotropics. In Belize, I found significant amounts of niche overlap between species which I predicted would belong to different guilds, and several cases of overlap which would suggest that species may compete for resources. In Brazil, I found that habitat composition (i.e., vegetation density) was more important than landscape metrics (*sic* fragment area, fragment nearest neighbour distance, etc.) in predicting the diets of frugivorous bats. I also found that multi-tissue stable isotope analysis is valuable in determining both individual variation in diet throughout the year and tracking seasonal changes as a result of resource availability or local-scale migration. Stable isotope analysis is a valuable tool in understanding the dietary ecology of animals.

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DEDICATION

In loving memory of Dr. Emmanuel S. Lilker (z”l)

I love you Zaida

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF ABBREVIATONS

1) SIA – Stable Isotope Analysis
2) AIC – Akaike's Information Criterion
3) EIL – Environmental Isotope Lab
4) SINLab – Stable Isotopes in Nature Lab
5) SIAR – Stable Isotope Analysis in R
6) SIBER – Stable Isotope Bayesian Ellipses in R
7) SHM – SIBER Hull Metrics
8) dNr - Nitrogen range
9) dCr - Carbon range
10) CD - Centroid Distance
11) MNND - Mean Nearest Neighbour Distance
12) SDNND - Standard Deviation of the Nearest Neighbour Distance
13) SEA – Stable Ellipse Area
14) SEAc – Stable Ellipse Area corrected for sample size
15) SEA.b – Bayesian corrected Stable Ellipse Area
16) N_R – Niche Range
17) KS – Kolmogorov Smirnov
18) PC – Principle component
19) PROX – Proximity Index
20) REGUA – Reserva Ecológia de Guapiaçu

LIST OF SYMBOLS

1) $\delta^{13}C$ – Carbon isotopic ratio
2) $\delta^{15}N$ – Nitrogen isotopic ratio
3) ‰ – Parts per thousand
4) $\delta^{34}S$ – Sulfur isotopic ratio
5) $\delta^{2}H$ – Hydrogen isotopic ratio
6) Δi – Difference between the top-ranked model and the i^{th} model
7) W_i – Akaike (AIC) Weight
8) NW_i – Normalized AIC Weight
9) β – Parameter estimates

CHAPTER 1 – Introduction to Stable Isotope Ecology of Tropical Bats

CHAPTER 1 – Introduction to Stable Isotope Ecology of Tropical Bats

Understanding how animals interact with one another and their physical surroundings is fundamental for our understanding of nature. Examining individuals, populations and communities of animals, particularly in the tropics where they are much more diverse than their temperate counterparts, ecologists can ask broad questions about how so many different species can coexist, and indeed thrive. Establishing baseline knowledge of what animals eat, where they live, and how changes in their physical environment can impact them is critical to protecting threatened or endangered species and making relevant management decisions. In essence, we strive to understand the 'role' within a community that a species occupies, defined as the ecological niche (Hutchinson 1957). Conceptualized as an n-dimensional hypervolume, all elements of an animal's behaviour and environment impact the space that the niche occupies within an ecosystem (Blonder *et al.* 2014). Habitat loss, pesticide use, decreases in prey availability, and competition with other individuals (be that inter- or intraspecific) are a few of many factors which may act to limit a species' niche. These factors can act together to transform the fundamental niche (i.e., the space a species should occupy given no limitations) into the realized niche (i.e., the space a species actually does occupy) (Vandermeer 1972).

In recent years, the previously nebulous concept of the ecological niche has become more of a mathematically defined concept. When environmental data is compiled, we are able to measure and better define the role of a species as niche breadth, or the space within a larger community structure that a species occupies (Feinsinger *et al.* 1981). Often, however, niche breadth is presented as unidimensional and only accounts for some variation in the environment which affects a species realized niche dimensions.

Dietary, feeding and trophic structure data are frequent measures of niche breadth (i.e., trophic niche) as an animal's ability to eat and quality of diet is a direct measure of its ability to survive (Bearhop *et al.* 2004). For species that are larger and whose feeding and behaviour are readily observable, observational studies are often used to quantify contents of their diet. Studying trophic niche in cryptic species, or species which are not readily observable, most traditional studies have relied on fecal or stomach contents analyses to asses niche breadth (Cummings *et al.* 2012, Perkins *et al.* 2014). Unfortunately, these methods only offer a snapshot of diet often reflecting the last meal an animal ate prior to capture (Perkins *et al.* 2014). Additionally, fecal collection is not always possible and examining stomach contents often involves sacrificing the animal which is far from ideal in most cases (Bearhop *et al.* 2004). For these reasons, stable isotope analysis (SIA) has become an important method in characterizing the trophic niche breadth of many cryptic species.

Stable isotope analysis was established as a beneficial method for assessing diet through experimental studies by DeNiro and Epstein (1978, 1981). Naturally occurring isotopes of carbon, nitrogen, sulfur, oxygen and hydrogen found in animal tissues exist at different ratios and can be used to map how, where, and on what an animal is feeding (Peterson & Fry 1987). While studies in aquatic and marine systems often use sulfur, oxygen and hydrogen isotopic ratios (Vander Zanden *et al.* 2016), in terrestrial studies variation in carbon and nitrogen ratios are most frequently used to characterize diet (Ben-David & Flaherty 2012). The ratios observed in tissues are understood to be a result of the natural input of the element (i.e., food), changed by a known and calculable factor (fractionation), and maintained through the element's half life, termed isotopic turn-over (Peterson & Fry 1987, Crawford *et al.* 2008). While fractionation and turn-over rates are determined experimentally and are assumed to be constant, they may be

sensitive to extrinsic factors such as species, sex, diet quality, reproductive status, season, etc. (Dalerum & Angerbjörn 2005).

The carbon isotopic ratio ($\delta^{13}C$ = ratio of stable isotopes ^{13}C : ^{12}C) is conserved in tissues and reflects the ultimate source of carbon from the environment, be that organic (C_3 or C_4 photosynthesis) or inorganic; each source has a unique and identifiable isotopic signature (Crayn *et al.* 2001, Sanseverino *et al.* 2012). For example, C_3 photosynthetic plants have a net fractionation rate of approximately 21‰ between atmosphere and biomass, such that atmospheric carbon dioxide has a $\delta^{13}C$-value of approximately -7 ‰ while C_3 plant tissue would have a $\delta^{13}C$ of approximately -28 ‰ (Peterson & Fry 1987). In contrast, C_4 plants are more efficient and have a net fractionation rate of only 6 ‰ resulting in higher values of $\delta^{13}C$ (≈ -13 ‰). While carbon fractionation factors vary between different animal tissue types (Dalerum & Angerbjörn 2005) they are relatively stable and do not vary significantly between individuals such that the original source of carbon can be determined through sampling the environment (Phillips 2012).

The nitrogen isotopic ratio ($\delta^{15}N$ = ratio of stable isotopes ^{15}N : ^{14}N) is determined initially by the rate of nitrogen gas fixation by plants, and fractionates approximately 3 – 5 ‰ between food and consumer tissues (Peterson & Fry 1987). With this known enrichment factor, trophic level can be easily established such that a secondary or tertiary consumer would have higher $\delta^{15}N$ than a primary consumer in the same community (Layman, Arrington, Montaña & Post 2007). Using $\delta^{13}C$ and $\delta^{15}N$ values together we are able to accurately represent the two-dimensional niche space of an individual (Anderson *et al.* 2009), population (Bearhop *et al.* 2004), or community (Layman *et al.* 2007).

Bats (Chiroptera) represent the second largest order of mammals with approximately 1,400 species accounting for 20% of global mammalian diversity (Simmons 2005). Tropical bat communities may be extremely diverse, from ten to over 100 species found sympatrically (Allen 1939, Findley 1993). Additionally several thousand to 20-million individuals can be found roosting at the same sites, making up the largest mammalian assemblages in the world (Tuttle & Moreno 2005). With this staggering amount of diversity and abundance, the question of how so many species can co-exist comes to the forefront. The competitive exclusion principle states that no two species can occupy the same niche indefinitely, such that one species will gain a competitive edge and eventually exclude the other (Gause 1934). With this ecological principle in mind, we therefore assume that bats are partitioning resources to avoid costly competition and that niche spaces should not overlap completely.

We traditionally associate bats with 1 of 6 trophic guilds (e.g., insectivore, frugivore, carnivore, nectarivore, piscivore, or sanguivore; Allen 1939) though a large amount of omnivory exists within many of these broad groupings (Rex *et al.* 2010). For example, Pallas' long-tongued bat, *Glossophaga soricina*, is a highly adapted nectar feeder however is also known to eat insects (Clare *et al.* 2014). The use of trophic guilds though is important in simplifying many of the relationships between species however as community structure would be further complicated if all species are viewed equally as omnivores (Simberloff & Dayan 1991). Bats may also partition resources spatially, by foraging in different areas, or temporally, by emerging at different times of night to avoid competition with conspecifics (Howell & Burch 1974). In this study, I use carbon and nitrogen stable isotope analysis to characterize the diets and niche breadths of tropical bats to discern community structure (Chapter 2), differences in foraging

behaviour between populations of the same species in a fragmented landscape (Chapter 3), and variation in diet of individuals and populations throughout the year (Chapter 4).

There is an extensive body of literature which has used SIA to characterize trophic niche dynamics in bats (Fleming *et al.* 1993, Herrera *et al.* 1998, Mirón M *et al.* 2006, Voigt & Kelm 2006, York & Billings 2009, Rex *et al.* 2010, Lam *et al.* 2013, Dammhahn & Goodman 2014). This study seeks to build on this growing field and to use SIA to answer questions related to niche theory, the competitive exclusion principle and elucidate how animals cope in different environments or seasons, particularly when resources are scarce. In Chapter 2, I examine the community structure of a diverse Neotropical bat fauna in northern Belize and examine niche overlap between populations both with and between trophic guilds. In Chapter 3, I examined the niche breadth and isotope ratios of different populations of fruit bats found in Brazil's Atlantic Forest and used Akaike's Information Criterion (AIC) to determine the effect of landscape and local scale variables on diet. In Chapter 4, I analyzed nitrogen isotope ratios of individuals in multiple tissues to assess seasonal variability in the diets of individuals. These chapters are all written in the format of individual manuscripts for publication. Chapter 5 is a summary and discussion of the manuscript chapters.

CHAPTER 2 - Community structure of a Neotropical bat fauna as revealed by stable isotope analysis

OVERVIEW

Neotropical bat communities are among the most diverse mammal communities in the world, and a better understanding of these assemblages may permit inferences about how so many species can coexist. While bat species can be grouped into broad trophic guilds (e.g., frugivore, insectivore), details of diet and similarities among species remain largely unknown. We used stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) to characterize the community structure of a diverse Neotropical bat fauna from Belize to test predictions of niche theory and the competitive exclusion principle. We predicted that (1) interspecific isotopic overlap would be greater within guilds than between guilds, and (2) no two sympatric populations would have isotopic niches that overlap completely, unless there is variation along some other axis (e.g., temporal, spatial). We additionally tested body size as an explanatory metric of potential overlap and predicted that larger-bodied animals would have greater niche breadths. Results suggest that while guild-level characterizations of communities are at least somewhat informative, there are multiple examples of intra- and inter-guild species pairs with significantly overlapping isotopic niches, suggesting that, counter to predictions, they may compete for resources. Understanding the trophic structure of animal communities is fundamental to conservation and management of endangered species and ecosystems and important for evolutionary studies, and stable isotope analyses can provide key insights as well as informing hypotheses of the diet of species that are not well known.

INTRODUCTION

HUTCHINSON (1957) defined the ecological niche as a fundamental unit of community structure describing the 'role' of a population in a community, conceptualized as an *n*-dimensional hyper-volume. Niche theory now has a more quantitative definition, allowing measurement of previously nebulous dimensions (defined as niche breadth) which can be compared to characterize the role of species within a community (Vandermeer 1972, Whittaker *et al.* 1973, Bearhop *et al.* 2004). Theoretical models may predict the potential niche breadth of a species, while the realized niche breadth is the actual niche after accounting for competition and resource availability (e.g., light, food, water, roosting sites). These extrinsic factors can affect how effectively individuals access resources (Colwell & Futuyma 1971). When niches overlap, the competitive exclusion principle states that no two species competing for the same resource can coexist indefinitely at constant population sizes. This predicts that one species will inevitably exclude the other if they have sufficient niche overlap (Gause 1934).

Trophic niche describes the diet of an animal – what it eats over time for both nutrition and necessary vitamins and minerals. Traditional means to characterize trophic niche breadth (e.g., observational studies or fecal analysis) can be ineffective or inappropriate when sampling some cryptic or elusive species whose feeding behavior may not be observable and where fecal collection is not possible. These methods also only offer a snapshot of what an animal ate immediately before capture (Bearhop *et al.* 2004). In contrast, stable isotope analysis (SIA) permits quantitative characterization of at least some components of the trophic niche of a population over time while avoiding many of the limitations of more traditional means (Bearhop *et al.* 2004, Layman *et al.* 2007).

Studies using SIA to determine trophic niches infer dietary niche breadth from profiles of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) in animal tissues (Bearhop *et al.* 2004; Layman *et al.* 2007). The effectiveness of this method has been supported by experimental studies (DeNiro and Epstein 1978, 1981). Studies in marine or aquatic systems have used sulphur ($\delta^{34}S$) or hydrogen ($\delta^{2}H$) isotopic ratios to characterize niche dynamics; however these elements appear less effective as indicators of trophic interactions in terrestrial systems (Peterson & Fry 1987, McCutchan *et al.* 2003, Dalerum & Angerbjörn 2005). Stable isotope ratios are the product of diet and net fractionation between what is consumed and what is incorporated into tissue (Peterson & Fry 1987). Diet-tissue fractionation factors are calculated as the amount isotopic ratios change between the environment and tissue and are assumed to be constant though may vary by age, sex, species, body condition, or various other factors (Tieszen & Boutton 1989).

Values of $\delta^{13}C$ differ greatly between photosynthetic pathways (C_3 or C_4 plants) and the ultimate source of biological carbon may be identified in the tissues of a consumer using SIA (Peterson & Fry 1987). C_3 plants have an expected net fractionation of $\delta^{13}C$ of approximately 21‰ from carbon uptake between the atmosphere (-7 ‰) and biomass (-28 ‰), while C_4 plants have much lower fractionation approximately 6 ‰. As a result, plants using the C_3 photosynthetic pathway have a lower $\delta^{13}C$ ratio than C_4 plants (Peterson & Fry 1987). Other inputs of carbon into natural systems may also be incorporated into tissues, and aquatic or marine sources can be identified through SIA (Tyler 1986, Whiticar *et al.* 1986, Jones & Grey 2004, Broders *et al.* 2014). There is negligible carbon isotope fractioning between consumer levels making $\delta^{13}C$ a reliable basis of estimating the original source of organic carbon in an animal's tissue when the fractionation factor is known (DeNiro and Epstein 1978). Nitrogen isotopic ratio ($\delta^{15}N$) reflects rate of nitrogen gas fixation in plants and $\delta^{15}N$ values increase with trophic levels

(DeNiro & Epstein 1981, Peterson & Fry 1987). Unlike $\delta^{13}C$, $\delta^{15}N$ values of consumer tissues are, on average, 3-5 ‰ higher than their diet (Peterson & Fry 1987). This enrichment factor makes $\delta^{15}N$ a reliable indicator of the consumer trophic level of populations within communities, such that animals at higher trophic levels will have higher $\delta^{15}N$ (Layman *et al.* 2007). Stable isotope analysis allows researchers to quantify tropic niche breath more precisely than traditional measures and better define community structure (Lesage *et al.* 2001, Herrera *et al.* 2003, Hyodo *et al.* 2011, Rex *et al.* 2011a, Dammhahn & Kappeler 2014, Dammhahn *et al.* 2015, Brewster *et al.* 2016).

Bat communities can be very diverse, ranging from tens to well over 100 sympatric species (Findley 1993). Stable isotope analysis has been used to characterize the niche dynamics of some bat populations in different areas (Fleming *et al.* 1993, Herrera *et al.* 1998, Mirón *et al.* 2006, Voigt & Kelm 2006, Rex *et al.* 2010, Lam *et al.* 2013, Dammhahn & Goodman 2014). There is a significant body of literature linking SIA to trophic niche in bats although details of niche breadth and overlap in many cases remains unclear. Classification of bats into feeding guilds can simplify the situation, but does not reveal how so many species can be sympatric (Webb *et al.* 2002, Losos 2008, Razgour *et al.* 2011). Tropical bat communities are more diverse and complex than their temperate counterparts, reflecting the greater diversity, abundance, and reliability of resources (Fleming *et al.* 1972, Findley 1993, Fenton *et al.* 2001, Brown 2014).

In general, the dietary diversity of bats is well known and our understanding has changed little since Allen's (1939) characterization, but we still have relatively few details of what bats actually eat. Traditionally recognized feeding guilds of bats include insectivores, carnivores, piscivores, frugivores, nectarivores, and sanguivores (Allen 1939, Arata *et al.* 1967, Gardner 1977, Humphrey *et al.* 1983). Unfortunately, we often lack details of variation in diet among

closely related or similar species, and many species do not neatly belong to one guild or another. For example, *Glossophaga soricina* is typically considered a nectarivore, but has been shown to regularly eat insects and fruit during different seasons in various habitats (Simberloff & Dayan 1991, Clare *et al.* 2014). Some broad dietary guilds are inherently flawed no matter what definition is used (*e.g.* carnivores) because different bats take very different prey; while all may eat vertebrates, there are varying degrees of carnivory, diets of the same species may vary considerably across space and time depending on prey availability (Norberg & Fenton 1988). To further complicate the situation, studies of bat diet provide little data about variation in prey within the population or feeding on more than one tropic level. A more fine-grained approach to understanding trophic guilds is necessary to effectively use guild categorizations as a tool in elucidating community structure (Rex *et al.* 2010). We used SIA to look at these idealized bat trophic guilds from a different perspective. Examining a community as an ensemble (*sensu* Fauth *et al.* 1996), as bats share both geography and resources, allows us to better holistically characterize species interactions. We predicted that (1) interspecific variation in isotopic overlap would be greater within guilds than between guilds, and (2) no two sympatric populations would have isotopic niches that overlap completely, unless there is variation along some other axis (e.g., temporal, spatial). Additionally, we examined body size as a potential explanatory metric of niche partitioning. We predicted that larger species would have larger niche breadths than smaller bodied species.

We examined species in a diverse community of Neotropical bats in Orange Walk District, Belize (≈ 40 species). The bats represent 7 families (Phyllostomidae [22 species]; Mormoopidae [4 spp.]; Vespertilionidae [5 spp.]; Emballonuridae [4 spp.]; Molossidae [3 spp.]; Noctilionidae [1 sp.]; Natalidae [1 sp.]). Arguably, these bats fall into one of six traditionally-

recognized trophic guilds (frugivores [13 spp.]; nectarivores [2 spp.]; insectivores [19 spp.]; carnivores [3 spp.]; piscivores [1 sp.] and sanguivores [1 sp.]) (Allen 1939; Fenton et al. 2001; Herrera *et al.* 2018). We used SIA to characterize community structure of this tropical bat community and make inferences based on predictions of niche theory (Vandermeer 1972). While there is some information on the food items taken by many species in the community (Fleming *et al.* 1972, Baker & Clark 1987, Adams 1989, Fenton *et al.* 1991, Baker *et al.* 2002), the diets of many species remain unstudied, and dietary habits of populations in our study area have not been characterized. We assessed the literature on the diet and feeding habits of the sampled bat species and made predictions about expected isotopic niche patterns based on these data (Fig. 2.1).

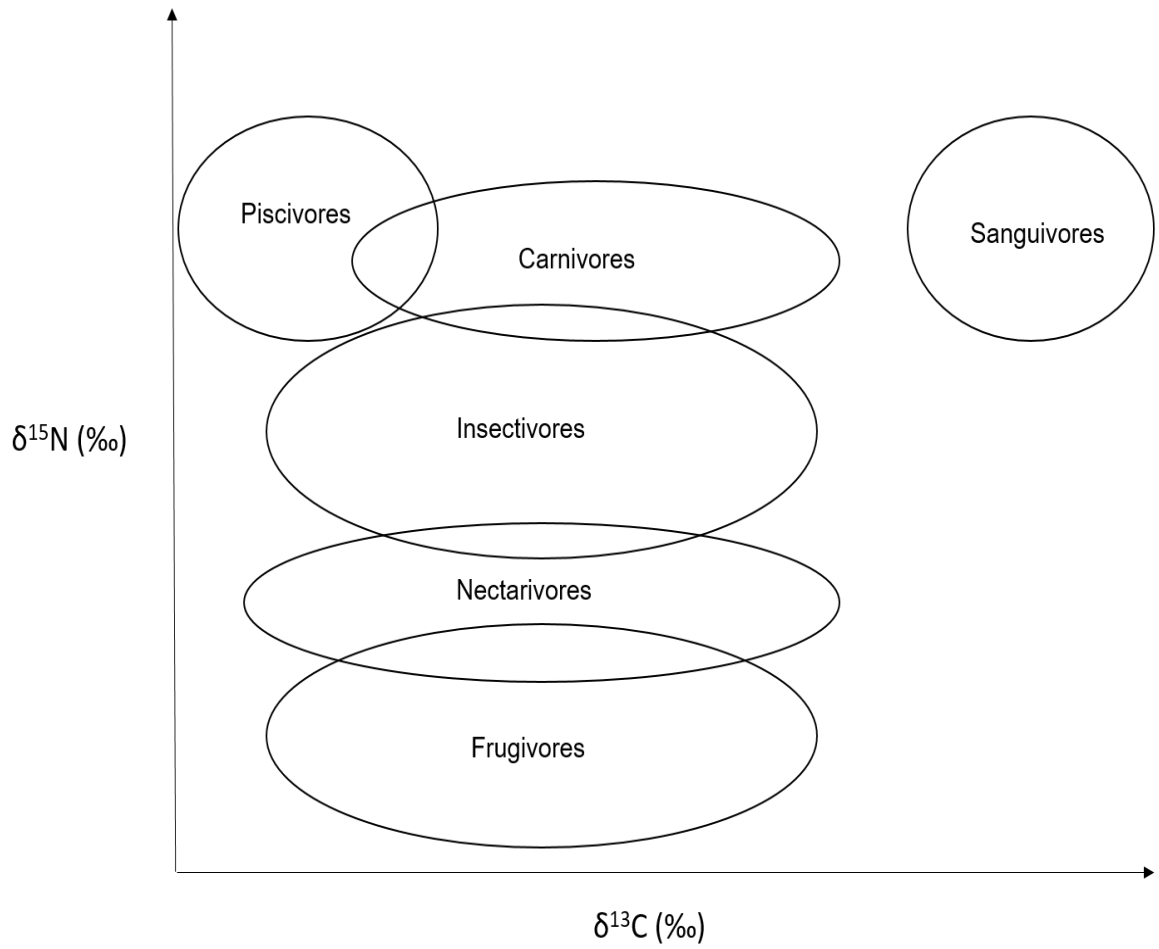

Figure 2.1 – Prediction of positions of dietary guilds in isotope space. Predictions were based on findings of previous SIA studies and experimental studies by DeNiro and Epstein (1978, 1981). Sanguivore prediction is based on published data from the same study area (Becker *et al.* 2017).

METHODS

SAMPLE SIZE AND TISSUE SELECTION — Bats were captured in Orange Walk District, Belize, in the Lamanai Archaeological Reserve and adjacent secondary forest and gardens near the Lamanai Outpost Lodge (17.75117 N, -88.65446 W) and the Ka'kabish Archaeological Project (17.8147 N, -88.73052 W) in two-week periods during late April through early May, 2014, 2016, and 2018 at the end of the dry season. The Lamanai locality consists of approximately 450-ha of

contiguous semi-deciduous tropical dry forest including habitats ranging from closed-canopy forest to clearings and secondary growth. Ka'kabish is a 45-ha forest fragment located approximately 10 km from Lamanai. Two previous surveys of the bat fauna have been published from these sites, the second examining differences in species richness between the two sites (Fenton *et al.* 2001; Herrera *et al.* 2018).

Animals were captured using mist nets, harp traps and hand nets. Bats were identified to species and grouped into trophic guilds based on previous dietary studies (Table 2.1). Guilds are inherently artificial as many of these species (particularly among frugivores and carnivores) are largely omnivorous, and species were placed according to 'best fit'(Allen 1939; Humphrey *et al.* 1983; Simberloff & Dayan 1991). Here, we define carnivores as species which specialized feeding strategies and/or anatomical or physiological adaptations to feed on vertebrates (as opposed to species which may opportunistically feed on vertebrates *e.g. Phyllostomus discolor* and *Micronycteris microtis*) (Norberg & Fenton 1988; Fenton *et al.* 1992, Cramer *et al.* 2001). Therefore, we predict their $\delta^{15}N$ to be higher than other animalivores (i.e., obligate insectivores).

We clipped a small (≈ 2 mg) sample of hair from between the scapulae of each individual. For bats with little to no hair on their back (e.g., *Noctilio leporinus* and *Pteronotus fulvus)*, the sample was taken from the abdomen. Hair samples were stored dry until analysis. All research was conducted in accordance with accepted standards for humane capture and handling of bats published by the American Society of Mammalogists (Sikes *et al.* 2016) and approved by the Saint Mary's University Animal Care Committee (Protocol # 14-10), University of Waterloo Animal Care Committee (AUPP: 18-04) and U.S. Institutional Animal Care and Use Committee protocols (American Museum of Natural History AMNHIACUC-20180123, Brown University IACUC 1205016 and 1504000134, University of Georgia IACUC AUP A2009-

10003-0 and A2014 04-016-Y3-A5). All fieldwork was conducted under permits from the Forestry Department of Belize (Permit numbers CD/60/3/14(17), WL/1/1/16(26), and WL/2/1/18(16)).

STABLE ISOTOPE ANALYSIS — Tissue analysis was performed at the Stable Isotopes in Nature Laboratory (SINLab) at the University of New Brunswick, Fredericton in 2015 (2014 samples) and at the Environmental Isotope Lab (EIL) at the University of Waterloo in 2017-2018 (2016 and 2018 samples), following procedures outlined in Segers and Broders (2015). Hair samples were washed three times in a 2:1 (v/v) chloroform:methanol for 10-15 minutes and then removed from the vial. Once washed, samples were left to air dry overnight. At SINLab, dry samples were combusted in ThermoQuest CE Instruments NC2500 Element Analyzer (ThermoQuest Italia, Rodano, Italy) and then placed into a Thermoquest Finnigan-Mat Delta Plus Continuous Flow Mass Spectrometer (ThermoFinnigan, Bremen, Germany). Stable isotope ratio measurements were recorded as δ-values in parts per thousand (‰). δ-values were anchored in VPBD ($\delta^{13}C$) and AIR ($\delta^{15}N$) scales respectively using international calibrated standards [International Atomic Energy Agency].

At EIL dry samples were weighed whole to the nearest 0.001 mg and then combusted in a 4010 Elemental Analyzer (Costech Instruments) attached to a Delta Plus XL (Thermo) continuous flow isotope ratio mass spectrometer (CFIRMS). Standards used include international standards and in-house (corrected to internationational) standard materials. Stable isotope data was then recorded as δX values using the formula:

$$\delta X = [\ (R_{sample}/R_{standard})\ -1\ ]\ x\ 10^3$$

where $R_{standard}$ is equal to the isotopic ratio of VPDB or AIR (Segers & Broders 2015). We tested a duplicate of seven samples at SINLab and EIT Lab and noted no significant difference between

results. Additionally, we tested 10 unwashed hair samples and found no significant difference in isotope ratios between treated and untreated samples (single-factor ANOVAs).

STATISTICAL ANALYSIS — The Stable Isotope Analysis in R (SIAR) package and the Stable Isotope Bayesian Ellipses in R (SIBER) package were used to calculate isotopic metrics for the two stable isotope ratios for each species (Jackson *et al.* 2011). R version x64 3.2.3 (R Core Team 2015) was used for this analysis and package "devtools" (Wickham & Chang 2016). SIBER Hull Metrics (SHM) (Layman *et al.* 2007) were calculated to test for variation between sample sites and years. These metrics include nitrogen range (dNr), carbon range (dCr), centeroid distance (CD), mean nearest neighbour distance (MNND) and standard deviation of the nearest neighbour distance (SDNND).

To test our prediction that larger animals will have larger niche breadth, average species size (forearm, mass) were calculated from field notes collected in Belize from 2010-2017. We used the median Bayesian corrected stable ellipse area (SEA.b) and both mean weight (g) and average forearm length (mm) for each species. We compared body size and median SEA.b both within trophic guilds, and among all species using a linear regression model. We repeated this analysis excluding species which were the only representatives of their trophic guilds (*Desmodus rotundus* and *Noctilio leporinus*) and species with sample sizes ≤ 4 (*Lophostoma evotis*). Stable ellipse area corrected for sample size (SEAc) was also tested, however was more relevant for shape and relative position of ellipses (Fig. 2.3) and was less suitable for further analysis than SEA.b (Jackson *et al.* 2011).

To test the prediction that (1) populations would have more overlap between species within a guild than between guilds, and (2) that no two ellipses would overlap completely, we used the package nicheROVER (Swanson *et al.* 2015) to calculate niche range (N_R) and overlap.

Overlap was calculated as the probability that an individual from Species A would be found within the N_R of Species B in isotope space, bootstrapped to n = 10,000. Only species for which we had ≥ 3 samples were included in species-level analysis using SEAc as ellipses cannot be drawn for smaller samples; species with sample size ≥ 4 were further analyzed using SEA.b and N_R (Jackson *et al.* 2011, Swanson *et al.* 2015). Species with smaller sample sizes were included in community-wide isotope metrics (Layman *et al.* 2007).

Results

We sampled 470 bats from 35 species and 6 *a priori* determined trophic guilds. As noted previously, these guilds represent broad groupings, and many species arranged to a guild may eat other items (e.g., many frugivores also consume insects; Table 2.1).

TABLE 2.1 – Number of individuals captured by species and sex from Lamanai and Ka'kabish, Orange Walk, Belize (April-May 2014, 2016, 2018) with description of diet. Primary diet reflects trophic guild while secondary diet includes any other prey material found in fecal or stomach contents analyses or notable feeding behaviours. Colours (descending order) denote guild: Yellow – frugivores, Blue – insectivores, Maroon – carnivores, Purple – nectarivores, Orange – piscivores, Green – sanguivores.

Species	n (male, female)[1]	Primary diet	Secondary diet	Information Source(s)
Artibeus intermedius	11(7, 4)	Fruit	Insects	(García-Estrada *et al.* 2012)
Artibeus jamaicensis	23(11, 11)	Fruit	Insects, nectar	(Heithaus *et al.* 1975)
Artibeus lituratus	27(13, 13)	Fruit	Insects, pollen	(Humphrey *et al.* 1983a, Fleming *et al.* 1972)
Carollia perspicillata	6(4, 1)	Fruit	Insects	(Herbst 1986a, Mello *et al.* 2004c)
Carollia sowelli	21(10, 10)	Fruit	Insects	(Miller *et al.* 2015a)
Dermanura phaeotis	35(18, 29)	Fruit	Insects	(Herrera *et al.* 2002)
Platyrrhinus helleri	2(0, 2)	Fruit	Insects	(Ferrell & Wilson 1991)
Sturnira parvidens	32(16, 16)	Fruit	Insects	(Fleming *et al.* 1972; Mello *et al.* 2008)
Uroderma convexum	18(8, 10)	Fruit	Insects	(Fleming *et al.* 1972; Herrera *et al.* 2002)
Bauerus dubiaquercus	7(4, 3)	Insects		(Engstrom *et al.* 1987, Miller & Medina 2008)
Eptesicus furinalis	17(7, 10)	Insects		(Aguiar & Antonini 2008)
Lasiurus ega	2(0, 2)	Insects		(Kutra & Lehr 1995)
Lophostoma evotis	4(4, 0)	Insects		(Cajas & Miller 2008)
Gardnernycteris keenani	2(0, 2)	Insects	Plants, vertebrates	(Humphrey *et al.* 1983, Giannini & Kalko 2005)
Micronycteris microtis	3(1, 2)	Insects	Fruit, vertebrates	(LaVal & LaVal 1980)
Micronycteris schmidtorum	2(1, 1)	Insects	Fruit	(Howell & Burch 1974)
Molossus rufus	19(9, 10)	Insects		(Aguirre *et al.* 2003)
Mormoops megalophylla	3(2, 1)	Insects		(Dávalos & Mantilla 2008)
Myotis elegans	24(13, 11)	Insects		(Whitaker & Findley 1980)
Natalus mexicanus	3(3, 0)	Insects		(Reid 1997)
Pteronotus fulvus	26(13, 13)	Insects		(Howell & Burch 1974, Adams 1989)
Pteronotus mesoamericanus	28(14, 14)	Insects		(Howell & Burch 1973, Herrera *et al.* 2001)
Pteronotus personatus	1(0, 1)	Insects		(Davalos 2006)
Rhogeesa anaeus	16(6, 10)	Insects		(Barclay & Brigham 1991)
Rhynchonycteris naso	15(8, 7)	Insects		(Bradbury & Vehrencamp 1976)
Saccopteryx bilineata	22(11, 10)	Insects		(Bradbury & Vehrencamp 1976)
Chrotopterus auritus	6(3, 2)	Vertebrates	Insects, fruit, plants	(Medellín 1989a, Barquez *et al.* 2015)
Mimon cozumelae	7(4, 3)	Insects	Vertebrates, fruit	(Gardner 1977, Whitaker & Findley 1980)
Trachops cirrhosus	10(7, 3)	Insects	Vertebrates, plants	(Kalko *et al.* 1999,)
Glossophaga soricina	32(16, 16)	Nectar	Insects, fruit	(Fleming *et al.* 1972; Clare *et al.* 2014)
Phyllostomus discolor	1(1, 0)	Nectar	Insects, vertebrates, plants	(Willig *et al.* 1993, Kwiecinski 2006)
Noctilio leporinus	6(3, 3)	Fish	Insects	(Brooke 1994)
Desmodus rotundus	27(21, 6)	Blood	Insects	(Arata *et al.* 1967)

[1]Individuals for which sex was not recorded are included in the total (n)

Community-wide niche metrics (Layman *et al.* 2007) suggested that samples from Lamanai and Ka'kabish, and those collected in 2014, 2016 and 2018 were representative of the same community (Fig. 2.2), and therefore combined for further analysis.

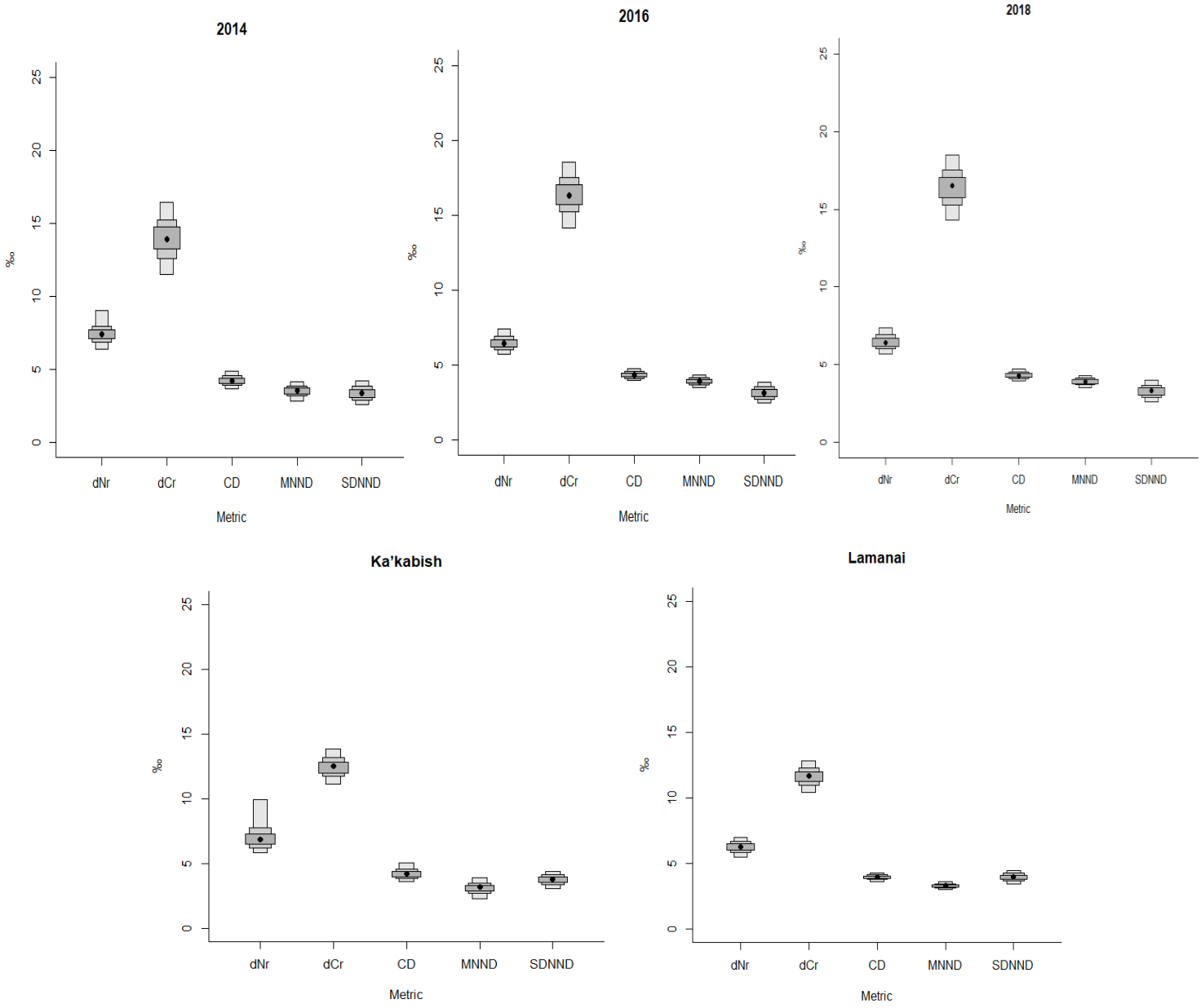

Figure 2.2 – SIBER density plot of Layman/SIBER-Hull metrics (Layman *et al.* 2007, Jackson *et al.* 2011) for bat hair samples collected in 2014, 2016 and 2018 at Ka'kabish and Lamanai, Orange Walk District, Belize. X-axis values are: range of nitrogen values, range of carbon values, centeroid distance, mean nearest neighbour distance, and standard deviation of nearest neighbour distance. Dots represent the median value for each metric, boxes are the distribution of values.

Among all species the relationship between niche breadth and body size metrics were not statistically significant ($R^2_W = 0.002$, $p = 0.873$; $R^2_{FA} = 0.013$, $p = 0.595$; Table 2.2), even when *Desmodus rotundus* and *Noctilio leporinus* were not included in the dataset ($R^2_W = 0.054$, $p = 0.300$; $R^2_{FA} = 0.006$, $p = 0.724$). Within guilds there was no statistically significant effect of body size, however among insectivores there was positive relationship ($R^2_W = 0.299$, $p = 0.102$, $\beta = 5.548 \pm 3.007$; $R^2_{FA} = 0.212$, $p = 0.180$, $\beta = 4.442 \pm 3.072$) and among frugivores the relationship was negative ($R^2_W = 0.309$, $p = 0.153$, $\beta = -14.951 \pm 9.135$; $R^2_{FA} = 0.212$, $p = 0.086$, $\beta = -12.360 \pm 6.019$). When insectivores were analyzed without *L. evotis* the results were not statistically significant though still trending to a positive effect ($R^2_W = 0.279$, $p = 0.144$, $\beta = 6.309 \pm 3.838$; $R^2_{FA} = 0.165$, $p = 0.279$, $\beta = 4.574 \pm 3.897$).

TABLE 2.2 – Species-level niche breadths (SEAc and SEA.b) with body size and sample size. Ellipse data is reported in squared parts per thousand ($‰^2$). Mean forearm length and body mass are from unpublished field notes from captures at the Lamanai and Ka'kabish study sites made between 2010 and 2017. Mean forearm and weight for *Noctilio leporinus* and *Mimon cozumelae* are from Reid (1997). Species are grouped into guilds (Colours correspond to Table 2.1) and sorted by median SEA.b.

Guild	Species	SEA.b	SEAc	Forearm (mm)	Mass (g)	Sample (n)
Frugivores						
	Carollia sowelli	3.241	3.150	38.18	15.23	21
	Dermanura phaeotis	2.825	2.786	39.04	13.19	35
	Sturnira parvidens	2.377	2.233	38.20	14.44	32
	Artibeus intermedius	2.070	1.833	61.84	47.30	11
	Uroderma convexum	1.930	1.718	42.70	15.07	18
	Artibeus lituratus	1.644	1.479	68.95	57.70	27
	Carollia perspicillata	1.586	0.800	43.50	20.17	6
	Artibeus jamaicensis	1.324	1.135	60.80	38.63	23
Insectivores						
	Lophostoma evotis	4.757	2.566	50.50	18.50	4
	Saccopteryx bilineata	4.165	4.344	44.00	6.61	22
	Molossus rufus	4.138	4.154	52.25	36.16	19
	Pteronotus mesoamericanus	3.606	3.625	57.21	18.99	28
	Eptesicus furinalis	3.482	3.315	38.88	8.83	17
	Pteronotus fulvus	2.849	2.864	44.19	7.45	26
	Rhogeesa anaeus	2.367	2.278	27.73	4.20	16
	Rhynchonycteris naso	2.178	1.852	37.64	3.89	15
	Myotis elegans	2.176	2.088	32.43	3.61	24
	Bauerus dubiaquercus	1.880	1.335	53.90	15.07	7
Carnivores						
	Mimon cozumelae	5.362	4.438	57.00	20.00	7
	Chrotopterus auritus	1.463	2.106	83.64	80.40	6
	Trachops cirrhosus	1.422	1.992	59.64	27.56	10
Nectarivores						
	Glossophaga soricina	1.655	1.794	35.39	9.20	32
Piscivores						
	Noctilio leporinus	4.009	4.244	85.50	63.50	6
Sanguivores						
	Desmodus rotundus	8.004	8.531	56.75	27.46	27

There was little overlap in niche areas between most guilds, and the community was largely structured as per predictions in Fig. 2.1 (Fig. 2.3). However, there was substantial overlap between insectivores and carnivores, probably as a result of how the carnivore guild was defined (see Discussion). In many cases there was substantial (though not complete) overlap between populations of species within guilds. Surprisingly however there were several cases where the niche area of one species was fully overlapped by that of another species. For example, among frugivores the SEAc of *Carollia perspicillata* is shown to be fully within the ellipse area of *C. sowelli*. There appears to be two distinct groupings of frugivores separated along $\delta^{13}C$, with *Sturnira parvidens, Carollia perspicillata* and *C. sowelli* constituting one group and *Artibeus intermedius, A. jamaicensis, A. lituratus,* and *Uroderma convexum* making up the other. *Dermanura phaeotis* overlaps with both groups. Among insectivores, there was large amount of overlap with all species within the guild except for *Rhynchonycteris naso*, an insectivorous species that appears as highly disjunct in isotopic niche space, having the lowest $\delta^{13}C$ among all species sampled. More detailed figures of within-guild overlap can be found in Appendix 1.

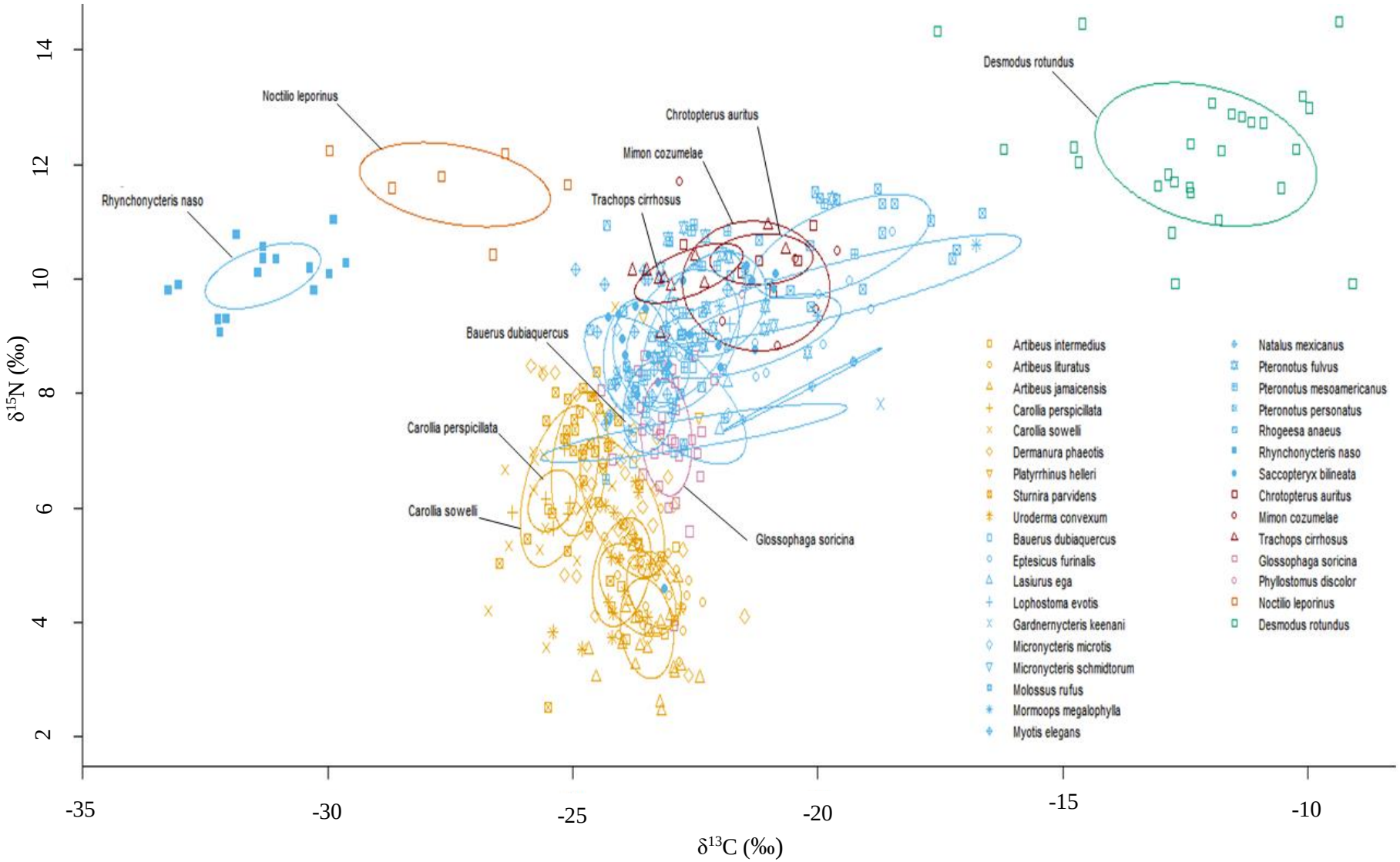

Figure 2.3 – Species-level community structure of all individuals sampled in the bat fauna of Lamanai and Ka'kabish, Orange Walk District, Belize April-May 2014, 2016 and 2018 using stable isotope analysis of nitrogen and carbon ratios. Ellipses represent the niche breadth as sample size corrected ellipse area (SEAc) of each species with a sample size ≥3; points mark one individual. Colours denote groupings by guild: Yellow – frugivores, Blue – insectivores, Maroon – carnivores, Purple – nectarivores, Orange – piscivores, Green – sanguivores. Ellipses with labels are species featured in discussion.

While most pairwise comparisons of species both within and between dietary guilds had little overlap (Table 2.3), there are cases which seemingly violate our predictions. Between guilds (black) there were no cases of > 95 % overlap, however there were 4 cases involving carnivores overlapping with insectivores with > 90 % [*Chrotopterus auritus – Molossus rufus* (93.3 %), *Trachops cirrhosus – Saccopteryx bilineata* (93.7 %), *T. cirrhosus – Pteronotus mesoamericanus* (90.6 %), *T.cirrhosus – P. fulvus* (90.0 %)], and even more cases by >75 %. Within guilds we noted 4 cases where > 95 % overlap occurred [*Carollia perspicillata – C.sowelli* (99.1 %), *Bauerus dubiaquercus – S. bilineata* (95.7 %), *Rhogeesa anaeus – S. bilineata* (95.0 %), *C. auritus – Mimon cozumelae* (95.9 %)] violating our second prediction that guilds would not overlap completely (Table 2.3).

TABLE 2.3 – Mean probability values (%) that an individual from Species A (row labels) will be found within the Niche Region of Species B (column labels), sorted alphabetically by guild. All individuals were captured at Lamanai and Ka'kabish, Orange Walk, Belize in April-May 2014, 2016 and 2018. Values were calculated in nicheROVER (Swanson *et al.* 2015) and bootstrapped to *n* = 10,000. All values over 90% overlap are underlined. Colours (descending order) denote guild: Yellow – frugivores, Blue – insectivores, Maroon – carnivores, Purple – nectarivores, Orange – piscivores, Green – sanguivores and Black - inter-guild overlap.

Species	*Ai*	*Aj*	*Al*	*Cp*	*Cs*	*Dp*	*Sp*	*Ub*	*Gs*	*Bd*	*Ef*	*Le*	*Mr*	*Me*	*Pf*	*Pm*	*Ra*	*Rn*	*Sb*	*Ca*	*Mc*	*Tc*	*Nl*	*Dr*
A. intermedius	NA	76.6	79.0	4.6	24.0	87.4	27.8	77.3	12.2	2.5	0.1	0.7	>0.1	1.9	>0.1	3.6	0.7	>0.1	4.5	>0.1	0.3	>0.1	>0.1	>0.1
A. jamaicensis	91.4	NA	88.2	0.8	9.3	94.4	11.5	76.8	20.7	2.3	>0.1	0.2	>0.1	1.6	>0.1	2.5	0.7	>0.1	4.0	>0.1	0.3	>0.1	>0.1	>0.1
A. lituratus	80.1	72.0	NA	0.5	6.5	71.7	8.0	66.1	7.5	1.1	>0.1	0.1	>0.1	0.8	>0.1	1.2	0.4	>0.1	1.8	>0.1	0.1	>0.1	>0.1	>0.1
C. perspicillata	23.5	1.4	0.9	NA	**99.1**	72.2	93.5	12.7	1.1	3.2	2.4	15.7	>0.1	5.1	0.2	12.6	1.8	>0.1	16.1	>0.1	0.7	>0.1	>0.1	>0.1
C. sowelli	17.6	3.3	3.0	36.4	NA	61.2	78.5	16.5	8.3	11.1	15.9	17.8	1.4	24.4	4.8	24.6	15.7	>0.1	31.6	0.2	3.7	2.2	0.4	>0.1
D. phaeotis	49.2	40.5	35.1	13.7	55.3	NA	58.1	58.4	36.5	21.1	10.3	15.7	0.5	28.7	2.6	33.0	15.8	>0.1	37.0	>0.1	2.4	0.4	0.1	>0.1
S. parvidens	23.3	6.0	5.4	33.6	92.5	82.0	NA	25.1	12.5	17.6	23.0	21.9	1.8	38.8	6.4	38.4	24.4	>0.1	47.2	0.1	4.8	2.9	0.5	>0.1
U. bilobatum	78.7	64.9	68.7	3.9	34.2	83.9	40.3	NA	22.8	7.9	0.8	2.3	0.1	7.3	0.5	10.5	3.5	>0.1	11.8	>0.1	0.7	>0.1	>0.1	>0.1
G. soricina	8.6	8.9	5.8	0.7	21.9	55.7	18.7	26.3	NA	62.6	41.7	30.8	8.0	70.6	35.8	77.5	67.7	>0.1	82.2	0.6	20.6	3.6	0.4	>0.1
B. dubiaquercus	2.9	1.7	1.1	1.7	44.8	54.7	41.1	14.7	89.7	NA	66.7	30.9	11.6	92.0	50.7	94.7	87.0	>0.1	**95.7**	0.8	26.0	4.5	0.5	>0.1
E. furinalis	0.1	>0.1	>0.1	0.4	10.9	7.5	9.1	0.4	23.1	18.7	NA	3.4	62.6	29.8	69.4	64.7	38.4	>0.1	71.4	13.8	75.0	8.5	0.9	0.3
L. evotis	1.5	0.1	0.1	7.8	29.1	34.3	26.1	7.5	37.2	28.8	17.9	NA	0.6	34.6	13.1	47.0	34.6	>0.1	57.3	>0.1	16.9	>0.1	0.1	0.1
M. rufus	>0.1	>0,1	>0.1	>0.1	1.0	0.4	0.8	>0.1	2.4	1.9	45.0	0.2	NA	5.3	39.2	34.2	7.3	>0.1	32.8	33.5	62.3	18.1	1.4	6.6
M. elegans	1.2	0.7	0.5	1.2	45.8	30.7	44.4	4.7	53.6	47.5	59.2	9.9	20.7	NA	58.6	80.7	84.9	>0.1	91.0	4.1	38.6	29.4	5.4	>0.1
P. fulvus	>0.1	>0.1	>0.1	0.1	5.6	2.2	4.1	0.3	20.7	15.3	68.4	2.3	71.3	37.4	NA	91.0	48.8	>0.1	92.1	36.4	86.7	45.4	3.8	>0.1
P. mesoamerican	1.3	0.7	0.5	1.2	16.1	14.1	14.0	3.8	39.3	31.2	63.6	8.4	52.9	52.9	79.1	NA	60.3	>0.1	91.3	24.8	69.4	35.4	3.0	>0.1
R.anaeus	0.5	0.3	0.2	0.6	33.1	20.0	29.8	2.9	62.5	51.4	70.0	9.6	29.0	88.1	72.2	88.6	NA	>0.1	**95.0**	5.2	49.0	28.7	3.6	>0.1
R.naso	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	NA	>0.1	>0.1	0.1	>0.1	7.4	>0.1
S.bilineata	1.3	0.7	0.5	1.3	20.5	16.5	18.3	3.8	41.5	32.4	63.9	10.1	43.4	58.7	73.4	85.8	64.6	>0.1	NA	17.3	62.3	30.6	3.5	>0.1
C.auritus	>0.1	>0.1	>0.1	>0.1	0.4	>0.1	0.2	>0.1	0.8	1.0	46.7	>0.1	**93.3**	7.3	87.7	83.3	10.6	>0.1	78.8	NA	**95.9**	63.5	4.8	0.1
M.cozumelae	0.1	>0.1	>0.1	0.1	2.3	1.0	1.7	1.8	0.2	5.0	58.1	2.5	71.6	16.2	71.5	67.4	21.7	>0.1	68.8	39.1	NA	33.9	4.2	0.2
T.cirrhosus	>0.1	>0.1	>0.1	>0.1	8.2	0.8	6.7	>0.1	9.4	6.8	30.2	>0.1	68.3	51.6	**90.0**	**90.6**	55.4	>0.1	**93.7**	52.3	85.8	NA	7.5	>0.1
N.leporinius	>0,1	>0.1	>0.1	>0.1	0.3	>0.1	0.3	>0.1	>0.1	0.1	0.4	>0.1	0.9	0.9	3.5	1.7	2.0	4.5	3.0	0.8	4.1	1.4	NA	>0.1
D.rotundus	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	0.1	>0.1	3.4	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	0.2	>0.1	>0.1	NA

DISCUSSION

COMMUNITY STRUCTURE — The isotopic profiles of the bat fauna at Lamanai and Ka'kabish largely supports our *a priori* characterization of guild structure, though there are some exceptions. Our empirical description of community structure shows that: (1) while most populations overlap primarily with other species within their trophic guilds, there are some cases with substantial overlap between species of different guilds, and (2) there were some cases with > 95 % overlap suggesting similar food selection and potentially significant competition. We found no relationship between niche breadth and body size among all species. Our results suggest that while trophic guilds may be informative for grouping species for many purposes, caution should be used in making assumptions about diet and niche breadth, particularly for species which are less well known or those which may utilize diverse resources including food items outside their core dietary niche.

Comparing the organization of trophic groups in our results to our predictions of community structure at the guild level (Fig. 2.1), we can note few deviations. Our predictions for both the piscivorous species *Noctilio leporinus* and sanguivorous *Desmodus rotundus* match the results obtained; both species have feeding strategies that are unique in the fauna and appeared clearly distinct in our stable isotope plots. We predicted that nectarivorous *Glossophaga soricina* would have higher $\delta^{15}N$ than frugivorous species due to the proportion of insects in their diet as noted in the literature (Fleming *et al.* 1972, Clare *et al.* 2014), and we found more overlap of *Glossophaga* with insectivores than with frugivorous species in our analyses. This suggests that at least during the period of hair growth, nectarivorous bats in the fauna have a significant insect contribution to their diet (Voigt & Matt 2004, Clare *et al.* 2014). We found that, in general, insectivorous species had a wide range of $\delta^{15}N$ and $\delta^{13}C$ as was predicted, likely because obligate

insectivores consume insects that are themselves secondary, tertiary or higher trophic level consumers from various environments (e.g., aquatic, terrestrial). *Rhynchonycteris naso* had the lowest $\delta^{13}C$ recorded and was isolated from all other insectivores in our sample, probably due to feeding on aquatic insects as does its nearest neighbour in our isotope plot, *Noctilio leporinus* (Broders *et al.* 2014, Becker *et al.* 2018). Notably, carnivores were expected to have the highest $\delta^{15}N$ because they represent a higher trophic level however the carnivores in our sample overlapped considerably with several insectivorous species. This is likely because most of the 'carnivores' in our study may in fact be eating predominantly non-vertebrate prey. Two species in our carnivore guild, *Mimon cozumelae* and *Trachops cirrhosus*, may consume more insects and other arthropods than vertebrate prey (Medellín 1989, Cramer *et al.* 2001, Arroyo-Cabrales *et al.* 2015). These gleaning animalivores probably represent an intermediate between species that rely almost entirely on vertebrate prey (e.g., *Chrotopterus auritus*) and aerial insectivores which never consume vertebrates (e.g. species of *Pteronotus*, *Myotis*, *Eptesicus*).

NICHE BREADTH AND BODY SIZE — Across all species there is no statistically significant relationship between niche breadth and body size. There was however a trend towards a positive relationship for insectivorous species and a negative trend for frugivores between median niche breadth (SEA.b) with both forearm length and weight. Community-wide metrics of body size are likely less relevant to resource availability as many bats within the fauna vary significantly in feeding strategy. From an energetics perspective, larger bats may require more time to forage to harvest more resources, though this may not reflect a larger niche breadth; some species may be specialists searching for ideal food sources (Peters 1983, Esbérard & Bergallo 2008). Barclay and Brigham (1991) argued that body size does not limit prey type as much as does detection method, noting the high abundance of small generalist aerial insectivores that detect prey via

echolocation, whereas bats that listen for prey-generated sounds and glean their prey off the ground or vegetation tend to be larger and less common.

Insectivorous bats at Lamanai and Ka'kabish exhibited a large range of sizes (Mass = 3.6 – 36.2 g; FA = 27.2 – 57.2 mm) though notably none of the species at the extremes of these ranges had either the largest or smallest niche breadth. *Bauerus dubiaquercus,* a larger gleaning insectivore (White 1969) had the smallest niche breadth, while *Saccopteryx bilineata,* a small mid-sized aerial feeder, had the largest niche. Because smaller prey are likely to be more abundant and diverse, smaller aerial insectivores will likely have larger niche breadths than larger, specialized, gleaning species like *Bauerus dubiaquercus*. Despite these outliers at the extremes of the SEA.b distribution, the positive relationship between niche breadth and body size seen in insectivores in our sample is likely driven by the large niche of *Molossus rufus,* the largest insectivorous bat sampled, and the comparativley small niches of *Myotis elegans, Rhynchonycteris naso,* and *Rhogeesa anaeus* which are the three smallest species captured (NB: all are aerial insectivores; Carter *et al.* 1966, Whitaker & Findley 1980). The only species which seemingly contradicts Barclay and Brigham's (1991) hypothesis and supports our prediction that larger bats should have larger niche breadths is *Molossus rufus* (formerly known as *M. ater*), whose niche breadth may be explained by its wing form, flight habits, and robust skull and dentition (Fenton *et al.* 1998). Molossids are unusual among aerial insectivores in having high aspect-ratio wings that make them fast fliers with low maneuverability, and accordingly they preferentially forage in open areas unlike other species in the same guild (Aldridge & Rautenbach 1987, Norberg & Rayner 1987, Fenton *et al.* 1998). Foraging over larger areas and with access to diverse insect prey of many different sizes and hardness, *Molossus rufus* may be something of a generalist in terms of prey choice. With strong jaws and teeth, it shows

anatomical specializations for consuming large, hard-shelled, fast-flying beetles that may not be accessible to other bats, but also eats a wide variety of other insects (Freeman 1981).

Despite predicting that larger bats should have larger niche breadths, among frugivores in our sample there was a negative relationship between body and niche size. This is largely driven by the small niche breadth of *Artibeus jamaicensis* and *A. lituratus*. *Artibeus lituratus* is thought to occupy a similar trophic role as *A. jamaicensis* with temporal partitioning of the foraging environment (different nocturnal peaks in activity); both are among the largest bats sampled, and both are known to specialize on *Ficus* spp. fruits (Humphrey and Bonaccorso 1979, Ortega & Castro-Arellano 2001). Frugivores in our sample with larger niche breadth tended to be smaller in size and their diets are less well known. Similar to predatory bats, larger frugivorous bats may be able to specialize more on a particular resource, perhaps because they are able to forage over a greater area than smaller bats in the guild (Laska 1990). Additional drivers of dietary specialization (as a function of niche breadth) appear to relate to dietary preference and the size, mass and hardness of preferred sources of fruits (Saldana-Vazquez 2014).

OVERLAP BETWEEN GUILDS — While in most cases there was more overlap between species within trophic guilds than between guilds, there are several instances where this is not the case, violating our first prediction. Ellipses of *Trachops cirrhosus* and *Chrotopterus auritus* (carnivores) were lower in $\delta^{15}N$ than what was predicted in Figure 1, overlapping extensively with some insectivorous species. We found that while these two carnivorous species did not overlap significantly with one another, *Chrotopterus auritus* overlapped significantly with insectivorous *Molossus rufus*, *Pteronotus fulvus*, *P. mesoamericanus*, and *Saccopteryx bilineata*; *Trachops cirrhosus* also overlapped with *Pteronotus fulvus*, *P. mesoamericanus* and with

Saccopteryx bilineata. None of this particularly surprising because, as noted above, both *Chrotopterus* and *Trachops* are known to have diets that include large numbers of insects.

Chrotopterus auritus, the largest bat sampled in our study, has been described as a both generalist omnivore and generalist animalivore (Medellín 1988, 1989, Munin *et al.* 2012, Barquez *et al.* 2015). It is therefore possible the small ellipse area noted here is due to isotope averaging from a generalist diet (Bearhop *et al.* 2004), where all individuals in the fauna are equally diverse in their dietary habits. However, without sampling available prey species there is no way to confirm this without further investigation. It is notable that of the six *C. auritus* sampled, five were captured at Ka'kabish where a study of its foraging behaviour was recently completed (Brigham *et al.* 2018). They found that these bats did not forage far from their roost, and most observations were within one forested block of Ka'kabish. As *C. auritus* seem to forage nearly exclusively in a small and isolated forest fragment, these bats are likely limited to abundant prey which may consist mostly of large insects or other arthropods given the $\delta^{15}N$ range which was smaller than predicted.

Trachops cirrhosus is traditionally viewed as gleaning carnivore or insectivore; this species eats large quantities of insects, but it exhibits highly specialized behaviour in which it eavesdrops on anuran mating calls and uses them to pick out prey, hence its common name of "frog-eating bat" (Cramer *et al.* 2001, Giannini & Kalko 2005, Page 2008, Miller *et al.* 2015). Given this behaviour, we grouped *T. cirrhosus* as a carnivore, but our data suggests that, similar to *Chrotopterus auritus*, it is primarily insectivorous for at least the period of hair growth sampled in our study.

Another possible explanation for the overlap observed between carnivores and insectivores seen in our data is that insectivores have higher $\delta^{15}N$ than predicted because their

prey have higher $\delta^{15}N$. Some insects and arachnids are known to have higher $\delta^{15}N$ due to their diets, especially ground beetles, spiders (Girard *et al.* 2011), and wasps (Hyodo *et al.* 2011). Particularly for larger insectivores like *Pteronotus mesoamericanus* and *Molossus rufus*, feeding on larger, higher trophic level insects may contribute to the significant overlap in $\delta^{15}N$ values with the carnivorous bat species.

Glossophaga soricina was the only abundant nectarivorous species that we sampled, and this species overlapped in isotope profiles most with *Pteronotus mesoamericanus* and *Saccopteryx bilineata*, both insectivorous species with large niche breadths. While *Glossopaga soricina* are adapted to nectar feeding, even feeding opportunistically at hummingbird feeders (Murphy *et al.* 2016), our results show that most individuals in our sample fed at a higher trophic level and likely had a large insect contribution to their diet. This conforms with previous dietary studies that found that insects are a regular part of the diet of this species (Fleming *et al.* 1973, Clare *et al.* 2014). Notably at the time of capture for our study, the faeces of *Glossophaga soricina* (collected for different projects) were mostly liquid and did not contain insect parts. However, at least during the period of hair growth, our isotope results suggest that these bats may be largely or primarily insectivorous, behavior that may correspond to periods of low nectar availability (Howell 1974, Clare *et al.* 2014). Further dietary and/or stable isotope studies sampling different tissues from *Glossophaga soricina* at Lamanai might reveal if there is an observable trophic shift during different times of the year corresponding to temporal changes in nectar availability (Bond *et al.* 2016).

OVERLAP WITHIN GUILDS — We predicted that species would comply with the competitive exclusion principle such that no two ellipses (representing niche space) should overlap completely (> 95%). However, several cases within frugivores, insectivores and carnivores in

our data set seemingly violate this ecological principle (at least in the two niche-dimensions measured), which may imply competition between species. In all cases with significant overlap, a species with a small perceived niche breadth was completely covered by the broader isotopic ellipse of another species. This is most prominent in the case of *Carollia perspicillata* and *C. sowelli*, where the former species is found within the niche region of the latter 99.1% of cases. *Carollia perspicillata* had among the smallest niche breadths in the fauna, which may imply specialization on a particular set of resources, while *C. sowelli* had a much larger niche breadth, suggesting a more generalist strategy. *Carollia perspicillata* has been studied extensively and is well known to be a *Piper* spp. specialist (Herbst 1986a, Bizerril & Raw 1998, Thies & Kalko 2004a, Bonaccorso *et al.* 2007, Saldaña-Vázquez 2014, Montoya-Bustamante *et al.* 2016). Da Silva *et al.* (2008) found that while both *Carollia* species sampled had a strong preference for fruits of the genus *Piper* spp., *C. sowelli* had a more variable diet overall with some representation from all plant groups sampled in their study area. York and Billings (2009), using stable isotope analysis, found that *Carollia* spp. in general tend to partition resources by consuming varying quantities of insects, with *C. perspicillata* having the lowest insect contribution and *C. sowelli* having intermediate insect consumption. While there are other potential niche axes which may be affecting the populations at Lamanai and Ka'kabish, it is also notable that *C. perspicillata* are rare in the fauna (though they are extremely common elsewhere in the Neotropics; Herrera *et al*. 2018), which may indicate that abundances are being limited by competition.

Significant overlap in stable isotope space was also noted between *Bauerus dubiaquercus* and *Saccopteryx bilineata*. As noted, *Bauerus dubiaquercus* had the smallest insectivorous ellipse area, while *Saccopteryx bilineata* had the largest. *Bauerus dubaquercus* also overlapped

extensively with *Pteronotus mesoamericanus,* which similarly had among the largest ellipse areas among insectivores. Contrary to what was described for *Carollia* species, there is no evidence that this overlap would indicate competitive exclusion. *Bauerus dubiaquercus* is likely a specialist feeder gleaning prey close to the forest floor (White 1969, Engstrom *et al.* 1987), while *Saccopteryx bilineata* and *Pteronotus mesoamericanus* catch their prey on the wing and are known to exhibit more of a generalist feeding strategy (Bradbury & Vehrencamp 1976, Yancey *et al.* 1998). *Rhogeesa anaeus* also had significant overlap with *Saccopteryx bilineata,* but the diet of *Rhogeesa anaeus* is largely unknown. It is unlikely that insect abundance is limiting these species, though there are seasonal peaks in insect abundance and seasonal diet switching may be occurring as was proposed by Bradbury and Vehrencamp (1976).

Among carnivorous bats, the isotope ellipse of *Chrotopterus auritus* overlapped significantly with that of *Mimon cozumelae*. The diet and foraging behaviours of *Mimon cozumelae* are poorly known, though Whitaker and Findley (1980) in a fecal analysis study found remains of insects, birds, and plant material. Body size and morphology of this species suggest that it is able to regularly include small vertebrates in its diet, and for that reason, *M. cozumelae* was grouped with the carnivores although these bats may functionally be generalist omnivores (Fenton *et al.* 1992). *Mimon cozumelae* had a much larger ellipse area than other carnivores and also had a greater δ^{15}N range. Similar to *Chrotopterus auritus,* the majority of *M. cozumelae* in our sample were captured at Ka'kabish, however it is possible that they are ranging further from their roosts, foraging individually, or simply eating more diverse foods than *Chrotopterus*, any one of which might have contributed to the larger ellipse area. While both species are omnivorous to varying degrees, it is unlikely that the overlap observed here is

significant in an ecological sense because both species seemingly forage opportunistically and are likely separating resources spatially or along some other niche axis.

CONCLUSIONS — As the niche of a species in a community is *n*-dimensional, niche dynamics are incredibly complex, and animals are able to separate and partition resources along many different axes to coexist. We face several limitations in our analysis since we only sampled one tissue from each individual (hair) for which moulting time is not known and did not sample potential prey items which would be significant in our analyses. Additionally, we did not attempt to age the bats we sampled, and diet quality was not assessed; both factors which might influence stable isotope ratios. We believe that with larger sample size (a metanalysis of niche breadth as relative to body size) or re-defined guilds (*sensu* Segura-Trujillo *et al.* 2016) the positive relationship between body size and niche breadth in insectivores and negative relationship in frugivores may be biologically relevant.

This study presents a comprehensive and complex representation of the community structure of a Neotropical bat fauna in the two niche dimensions we measured using stable isotope analysis. We have shown that there is no statistically significant relationship between dietary niche breadth and body size in bats and therefore body size should not be a factor in accounting for apparent violations of the competitive exclusion principle. We found that in most cases there was more overlap between species within trophic guilds than between guilds as was predicted. There were several cases where there was significant overlap between species which may indicate competition, though further studies along other niche dimensions, along with abundance of prey, to further elucidate the species-species interactions in this fauna are needed.

CHAPTER 3 - Interspecific variation in diet of frugivorous bats in fragments of Brazil's Atlantic Forest explained by vegetation density

OVERVIEW

The effects of landscape structure on species persistence has long been an area of research but questions on how species biology changes with landscape fragmentation remain. Using stable isotope analysis, we examined interspecific variation in the diet of frugivorous bats among remnant forest habitat patches of Brazil's Atlantic Forest. We hypothesized that individuals captured in habitat patches would have a different foraging strategy than those captured in contiguous habitats, altering their niche breadth and taking different prey, and we also hypothesized that species which are more mobile will be less impacted by small scale landscape changes. We predicted that (1) wide ranging species (*Artibeus lituratus*), which move through open areas, should be less affected by landscape and patch composition and (2) narrow ranging species (*Carollia perspicillata* and *Sturnira lilium*) will have more variation between populations in niche breadth and isotopic ratio ranges dependant on their environment (i.e., size, composition and degree of isolation of habitat patches). Using Akaike's Information Criterion (AIC) to rank models explaining this variation, we found that fragment composition, largely involving vegetation density, and subsequently fruit availability, rather than spatial aspects of landscape structure best explained diet variation in fruit bats. This finding supports the contention that bats resident to in fragments and do alter their feeding behaviour in response to environmental perturbation.

INTRODUCTION

Habitat fragmentation occurs when a once contiguous environment is divided into remnant fragments, or patches, of various sizes and composition in a disturbed matrix (Franklin *et al.* 2002, Leitão *et al.* 2006). Its impacts on local animals may be wide-ranging, positive or negative, and can be broadly grouped as barrier, edge and disturbance effects (Goosem 2007, Fahrig 2017). Remnant patch size, number, edge density, composition, and degree of isolation from contiguous habitat have all been shown to significantly affect species biology and persistence potential (Fahrig 2017). While habitat loss may result in lower population sizes or decreasing diversity of the community, in many instances' species can persist in fragmented landscapes but their biology and behaviour may change. Changes in patterns of consumer abundance and distribution have been shown to be impacted by habitat fragmentation (Fahrig & Jonsen 1998, Crooks 2002, Gehring & Swihart 2003, Swihart *et al.* 2003, Stratford & Stouffer 2015).

The question of how landscape fragmentation impacts species biology poses additional challenge for the study of cryptic species, whose natural behaviours are not readily observable, and niche is not easily characterized based on direct observations. To understand niche dynamics of such species, the niche concept must first be simplified and defined within quantifiable dimensions rather than the conceptual 'role' as proposed by Hutchinson (1957). When niche parameters are measured, the most widely used metric in quantifying the niche is niche breadth, referring to the 'distance through' a larger trophic structure that a species occupies (Feinsinger *et al.* 1981). When niche breadth is calculated, it may permit characterization of community

structure, population dynamics, allows for comparison of how these niches may change over time, or enables a comparison of populations of the same species (Bearhop *et al.* 2004).

While traditional measures of trophic niche breadth are invasive or relied on observational data, Stable Isotope Analysis (SIA) may allow for a quantitative characterization of the niches of populations and is particularly useful for cryptic species (Bearhop *et al.* 2004, Boecklen *et al.* 2011, Owen *et al.* 2011). Based on experimental studies by DeNiro and Epstein (1979; 1981) naturally occurring carbon and nitrogen isotopic ratios ($\delta^{13}C$ and $\delta^{15}N$) have become the most widely used measures of niche breadth in terrestrial systems (Gannes *et al.* 1997, 1998, Herrera *et al.* 2002, Crawford *et al.* 2008, Jackson *et al.* 2011, Syväranta *et al.* 2013). The ratio of isotopes ^{15}N and ^{14}N increases with trophic level, therefore species which, for example, consume more insects should have a higher $\delta^{15}N$ than species which exclusively consume fruit (DeNiro & Epstein 1981, Herrera *et al.* 1998, Kelly 2000). The ratio of carbon isotopes ^{12}C and ^{13}C are conserved between trophic levels in animal tissues, and are dependant on the original source of organic carbon as aquatic, marine and terrestrial systems have predictable variation in $\delta^{13}C$ ratios (DeNiro & Epstein 1978, Voigt *et al.* 2003, Kelly 2000). For many systems the ultimate source of organic carbon is from plants where the photosynthetic pathway largely determines the $\delta^{13}C$ ratio; C_3 photosynthetic plants have a $\delta^{13}C$ ratio of approximately -28‰, while C_4 plants better conserve the atmospheric isotopic ratio of carbon with an approximate $\delta^{13}C$ of -13‰ (Peterson & Fry 1987).

Habitat fragmentation in the Atlantic Forest is not a new phenomenon as there has been extensive human settlement in the area and land use since approximately 1500 CE (Ribeiro *et al.* 2009, Tabarelli *et al.* 2010). Despite this, Brazil's Atlantic Forest remains one of the most diverse and largest rainforests. The once contiguous forest covering approximately 150 million

hectares, is now fragmented into over 200,000 remnant patches representing 11-16% of original forest cover (Ribeiro et al 2009; Haddad et al 2015). Additionally, 32-40% of the remnant forest patches are comprised of either young successional forests or fragments smaller than 100 hectares (Ribeiro *et al.* 2009). The Atlantic Forest is home to the richest mammal fauna in Brazil at 246 species, of which 98 are bats (Bergallo *et al.* 2003, Muylaert *et al.* 2017). This biodiversity 'hotspot' is under continuing and increasing threat and further habitat loss could lead to staggering loss to global biodiversity (Myers *et al.* 2000, Galindo-Leal & Câmara 2003, Ribeiro *et al.* 2009). Contemporary threats include expanding urban and agricultural areas, illegal logging (on small scales), hunting, forest fires, climate change and shifting government policies which may lead to further destruction (Galindo-Leal & Câmara 2003, Ribeiro *et al.* 2009, Joly *et al.* 2014). Due to its long and well-recorded history of exploitation, and its conservation significance, Brazil's Atlantic Forest represents a unique study region where habitat patches of various ages, size, isolation and successional states can be compared, and the long-term effects of fragmentation quantified.

In tropical forests, a main driver of reforestation is seed dispersal by frugivorous bats, birds and insects (Voigt *et al.* 2009, Muscarella & Fleming 2007, Saldaña-Vázquez *et al.* 2010). The feeding behaviour of bats plays a key role, as many fruit-eating bats carry food away from the fruiting tree distributing seeds (Voigt *et al.* 2009, Carvalho-Ricardo *et al.* 2014). Regardless of fruiting strategy, be that high or low investment, annual or seasonal, plants that depend on animal dispersal for reproduction are more at risk in fragmented landscapes if these populations of animals are vulnerable to fragmentation (Quesada *et al.* 2003, Bernard & Fenton 2007, Muscarella & Fleming 2007).

Studies that have examined how animal diets change in response to habitat fragmentation (de Souza & Brown 1994, Nour *et al.* 1998, Layman, *et al.* 2007b, Bommarco *et al.* 2010, Dunn *et al.* 2010, Clare *et al.* 2011, Hu 2011, Boyle *et al.* 2012, Chaves *et al.* 2012, Nowak & Lee 2013, Araújo *et al.* 2014, Streicker & Allgeier 2016) are spread across taxa and aquatic and terrestrial systems, and have conflicting results. Studies have generally noted patterns involving shifting trophic levels and changes in niche breadth. Many species that persist in fragmented areas switch from being specialist consumers to generalists such that their niche breadth increases (de Souza & Brown 1994, Nour *et al.* 1998, Dunn *et al.* 2010, Hu 2011, Chaves *et al.* 2012, Araújo *et al.* 2014, Streicker & Allgeier 2016). Others might specialize when previously diverse and abundant resources are limited and their niche breadth decreases (Layman *et al.* 2007a, Bommarco *et al.* 2010, Boyle *et al.* 2010). In most cases specialist and generalist consumers might entirely switch to abundant resources such that niche breadth remains the same though position might change; diet switching may also occur under natural seasonal or temporal conditions due to fruiting phenology or otherwise trophic flexibility (Clare *et al.* 2011, 2014, Nowak & Lee 2013). Typically animals, particularly frugivores, will switch from previously abundant resources to resources which may have been present before but were passed over in contiguous forests (Dunn *et al.* 2010, Hu 2011, Boyle *et al.* 2012, Chaves *et al.* 2012). The purpose of this study is to assess how the diets of three species of Neotropical fruit bats are affected by landscape composition.

The bat fauna of the Atlantic Forest is diverse with 5 families and approximately 98 species (Muylaert *et al*. 2017). Belonging to different trophic guilds (*sic* insectivores, sanguivores, nectarivores, carnivores, frugivores), resource partitioning extends within groups with many species adapted to specialize on particular resources, and many are generalists and

forage indiscriminately (Fleming *et al.* 1972, Bonaccorso & Gush 1987, Willig *et al.* 1993, Streicker & Allgeier 2016). Many phyllostomid bats, which are the most abundant family in the Atlantic Forest (Muylaert *et al*. 2017), exhibit a specialized feeding strategy that is flexible and this may explain their diversity (Rex *et al.* 2010). Many of the findings of bat responses to habitat fragmentation are contradictory, with some studies pointing to a significant change in abundance, species richness and diversity, while others found little or no change (Bernard & Fenton 2007, Klingbeil & Willig 2009).

Metrics such as abundance and diversity are informative, but we expect there may be changes in diet of species as a result of fragmentation and this may have fitness consequences. Therefore, using stable isotope analysis, we hope to characterize the relationship between habitat fragmentation and diet of three species of Neotropical frugivorous bats which vary in movement potential. We hypothesize bat populations (bother inter- and intraspecific comparisons) in habitat fragments would have a different foraging strategy than those captured in contiguous forest; species which are more mobile and able to move through open areas will be less impacted by small scale habitat fragmentation. We predict that (1) wide ranging species (*Artibeus lituratus*) should be less affected by landscape and patch composition, such that there are minimal changes in niche breadth and position in isotope space and (2) narrow ranging species (*Carollia perspicillata* and *Sturnira lilium*) will have alter their diet dependant on the landscape, as in smaller patches, fewer preferred resources should be available. Therefore, in habitat fragments, *Carollia* and *Sturnira* will likely be more generalised in their diet (larger niche breadth) than those in contiguous forest.

METHODS

SAMPLE AND DATA COLLECTION - Sampling took place in two fragmented landscapes in Brazil's Atlantic Forest in and near to Reserva Ecologica de Guapiacu (REGUA) between December 18, 2015 and January 18, 2017. There was no sampling during the rainy season period between December 2015 and May 19, 2016. REGUA is connected to Serra dos Orgaos National Park and Tres Picos State Park, making up 7000 hectares of contiguous old growth and secondary forest; this is the third largest contiguous portion of Atlantic Forest remaining in Brazil (REGUA 2002). Twelve areas were sampled and allocated as REGUA, REGUA2, REGUA3 for those sampled in the reserve (considered repeated efforts sampling in the same fragment), and fragments T02, T10, T11, T12, T13, T19, T21, T23, T25 and T26 named to comply with the labelling of earlier studies of the same forest fragments (Vieira *et al.* 2009, Forero-Medina & Vieira 2009, Prevedello *et al.* 2010). Sampled fragments were characterized using ArcGIS 10.1 and the following landscape metrics were recorded: area (ha), isolation (nearest neighbour distance, m), perimeter (m), PARA (perimeter area ratio), forest cover (percentage of forested area within 500 m and 1000 m buffers), PROX (proximity index of like-fragments within 500 m and 1000 m buffers), and distance from source (distance from contiguous forest, m). Additionally two principal component variables calculated by Delciellos *et al.* (2016) were recorded for each fragment; PC1 corresponds to the abundance of grasses, *Cecropia* sp. and water course, and PC2 is correlated with overstory and understory vegetation density and the presence of fallen logs, where negative values indicate less of these features present in the fragment than positive values (Table 3.1).

Table 3.1 - Principal components of variables from Atlantic Forest habitat fragments. Bolded values are the highest correlated variable within each principal component. Adapted from Delciellos et al. (2016).

Habitat Variable	**PC1**	**PC2**
Overstory vertical vegetation density	0.354	**0.750**
Understory horizontal vegetation density	0.036	**0.717**
Tree size	0.012	0.275
Fallen logs	-0.236	**0.813**
Lianas	**-0.831**	0.085
Palm	0.599	0.336
Grass	0.189	-0.065
Cecropia sp.	**0.819**	-0.165
Water course	**0.781**	-0.110
Eigenvalue	2.548	1.978
% variance explained	28.31	21.97

Bats of at least 34 species were captured using mist nets over 6-day periods in each fragment and three small discs of flight membrane (patagia) were taken using a punch biopsy of the dactylopatagium major or medius of the wings of wild-captured bats (Faure *et al.* 2009). Tissue was then stored in sample vials with silica gel beads for desiccation. Benefits of using patagium include a low isotopic turnover rates which is unaffected by the quality of diet, (Voigt *et al.* 2003, Mirón M *et al.* 2006); punch biopsies can be taken in the field, are minimally invasive, heal rapidly and the tissue has a known isotopic turnover rate of approximately 100-130 days (Voigt *et al*. 2003; Herrera *et al.* 2008; Pollock *et al*. 2015). As accuracy in statistical analysis depends on sample size, only tissues from species with $n > 5$ for most fragments are analyzed (Jackson *et al.* 2011). For this study we analyzed tissue samples from 354 individuals [*Artibeus lituratus* (n = 111), *Carollia perspicillata* (n = 213), and *Sturnira lilium* (n = 30)].

TISSUE PROCESSING AND STABLE ISOTOPE ANALYSIS - Dried samples were weighed into tin capsules which were then crushed and submitted to the Environmental Isotope Laboratory (EIL) at the University of Waterloo for analysis. As samples were below an ideal

target weight of 0.350 mg (patagium ranged in mass from 0.050 – 0.150 mg), non-diluted CO_2 protocol was used as is standard for low-mass samples. The samples were combusted to gas at 1030 ºC and put through a 4010 Elemental Analyzer (Costech Instruments) coupled to a Delta Plus XL (Thermo) continuous flow isotope ratio mass spectrometer (CFIRMS). The output is reported in δ-notation in parts per thousand (‰) anchored against standardized scales (VPDB for $\delta^{13}C$ and AIR for $\delta^{15}N$).

STATISTICAL ANALYSIS - All data was processed using R-Studio version 1.1.453 using packages Stable Isotope Analysis in R (SIAR; Jackson *et al.* 2011), Stable Isotope Bayesian Ellipses in R (SIBER; Jackson *et al.* 2011) and Caret (Kuhn *et al.* 2018) and ggplot2 (Wickham *et al.* 2018). To control for natural variation in diet as caused by seasonal changes, separated samples from bats captured within 100 days of the end of the superhumid season and analyzed these separately (seasonal groupings 'superhumid' and 'humid'). For each population we calculated the median Bayesian corrected standard ellipse area (SEA.b) in squared parts per thousand ($‰^2$) to estimate niche breadth and examined the range of carbon and nitrogen values. We used an omnibus ANOVA (single factor) with a post-hoc Tukey-Kramer test to compare if mean $\delta^{13}C$ and $\delta^{15}N$ differed significantly between fragments and two-tailed Kolmogorov-Smirnov tests (KS) to compare the range of carbon and nitrogen values. For SEA.b we used SIBER to test the probability that the niche breadth of Population 1 is less than the niche of Population 2 bootstrapped to n = 10,000.

To evaluate the impact that landscape variables have on diet, we constructed 9 *a priori* selected linear regression models in the caret package and used Akaike's Information Criterion (AIC) for model ranking and selection (Burnham & Anderson 2002, Garroway & Broders 2007). Due to high correlation between various landscape metrics and small sample size, we limited

models to univariate and bivariate parameters to avoid overfitting (Burnham & Anderson 2002). For bivariate models we used a correlation cut-off of 40% to be able to include AREA + ISOLATION model which was used in other studies. Candidate models are presented in Table 3.2:

TABLE 3.2 – *A priori* selected candidate models for linear regression analysis of the effect of landscape-scale metrics on the diet of fruit bats. Each model was run for species-season pairs with $n \geq 5$ in 3 or more fragments and for 3 response variables (median SEA.b, mean $\delta^{13}C$ and mean $\delta^{15}N$). Description of each variable is in Sample and Data Collection section of Methods.

Model statement
AREA + ISOLATION
AREA + PC2
ISOLATION + PC1
ISOLATION + PC2
PC1 + PC2
AREA
PC1
PC2
PROX1000

We calculated the AICc (corrected for small sample size; Burnham and Anderson 2002) value for each season-species pair with samples from ≥ 3 fragments for each of the three response variables (median SEA.b, mean $\delta^{13}C$, mean $\delta^{15}N$). For REGUA replicates (REGUA, REGUA2, REGUA3) when comparing between fragments, we selected the replicate with the largest sample size. Though these samples were taken from different parts of the reserve in different habitats, by selecting the largest sample, we feel it would best represent the overall forest though we did still statistically test all REGUA replicates. We then calculated the difference between the best model in each set (lowest AICc value) and all other models, recorded as Δi values. We then calculated Akaike weights (W_i) which are the probability that the ith model is the best model of the proposed set. For each model with $\Delta i < 2$, for which have a 95% chance

of containing the top model, we normalized the Akaike weights (N_{Wi}) to better represent the top set of candidate models (Burnham & Anderson 2002). Each landscape variable within the normalized model set we present the weighted means of the coefficient ($\beta \pm SE$). We then used multi-model inference to determine the strength and direction of each relationship.

RESULTS

Sampled fragments were heterogenous in forest composition and degree of isolation and ranged in area from 21 to > 60,000 hectares (Table 3.3).

Table 3.3 – Landscape metrics for lowland forested fragments sampled in Rio de Janeiro State, Brazil. Fragments are sorted by area in hectares from largest to smallest. Principal component variables are explained in Table 3.1 and were calculated in Delciellos *et al.* (2016). Proximity index (PROX) is described in Carrié *et al.* (2017).

Fragment	Area (ha)	Isolation (m)	Perimeter (m)	PARA	Forest cover (500m)	Forest cover (1000 m)	PROX (500 m)	PROX (1000 m)	Distance to REGUA (m)	PC1	PC2
REGUA	62378.64	60.00	1186620	19.02	100.00	98.70	112485	112494	0	-2.5795	0.7472
T25	228.78	480.00	12480	54.55	98.74	59.02	2707.00	2707	889	-0.4701	0.0193
T12	184.77	174.92	11700	63.32	76.28	51.54	27.55	38.52	5276	0.7110	-2.4449
T19	117.27	134.16	10980	93.63	76.78	37.89	4266.10	4266	529	-1.1985	0.6717
T21	99.99	349.85	7260	72.60	71.01	32.26	40.72	41.35	6629	0.2637	-2.6653
T02	92.34	210.00	8940	96.82	68.63	20.97	2.32	3.35	4405	1.4415	2.7211
T13	84.33	150.00	9560	89.65	53.70	33.58	83.577	83.75	6274	2.2378	-0.4858
T23	52.11	362.49	6300	120.90	45.29	17.43	0.45	1.04	9873	1.7715	1.1704
T11	41.04	84.85	4020	99.41	52.82	33.38	114.52	114.68	3163	-0.5559	-0.8731
T10	34.11	234.00	3540	103.78	44.92	18.86	101.71	115.13	580	2.9793	1.5869
T26	21.15	600.00	2940	139.01	29.48	6.89	0	0.16	3667	0.5584	-1.9418

In several cases, there were significant differences $\delta^{13}C$ and $\delta^{15}N$ between populations (Appendix 2). Cases where statistical tests yielded a significant result between contiguous forest replicates (REGUA, REGUA2, REGUA3) we assume this is a result of natural variation in the environment, sampling period, or inter-individual or inter-sex ratio in the sample. There were no significant differences in niche breadths (SEA.b) between populations within each season-species pairing.

Mean $\delta^{13}C$ and $\delta^{15}N$ varied among fragments for each season-species pair (Fig. 3.1). There appears to be more variation in $\delta^{15}N$ both between and within fragments than variability in $\delta^{13}C$ in all test cases. Additionally, there appears to be more variability in both mean carbon and mean nitrogen values between populations of narrow-ranging species than for wide-ranging *Artibeus lituratus*.

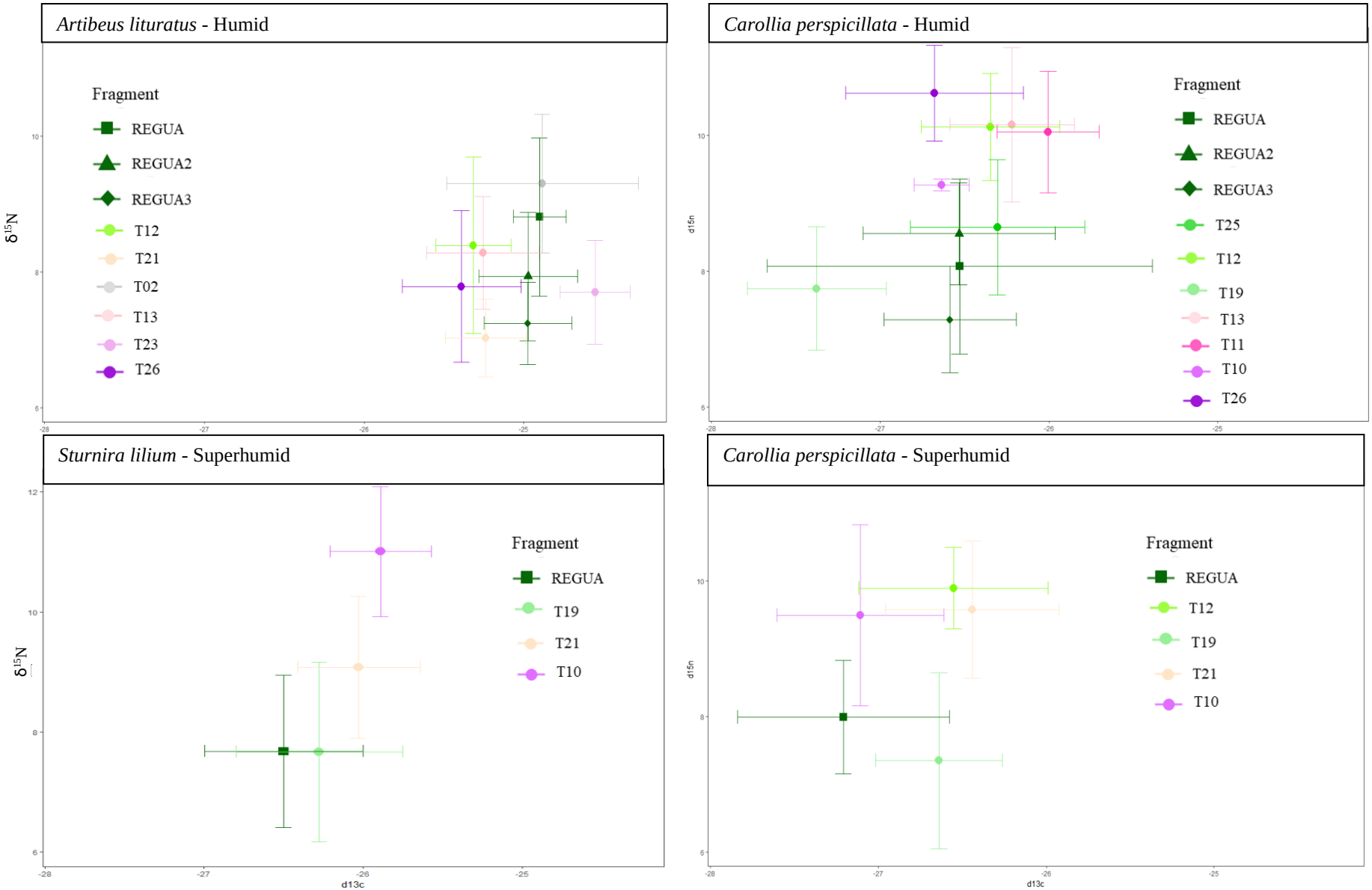

Figure 3.1– Carbon and nitrogen isotopic ratios for each fragment presented as mean and standard deviation. Each panel represents one species-season pairing. Colours correspond to fragment where the sample was collected ordered by area. Darker greens are largest fragments; darkest purple are smallest fragments.

Normalized AICc weights revealed the top candidate models (Table 3.4a-d). This process was repeated for each season-species pair and each response variable. In most cases PC2 had some, if not the largest weight indicating the overall importance of horizontal and vertical vegetation density in explaining variation in the diet of fruit bats.

Table 3.4a – Difference between the top-ranked model and the i^{th} model (Δi) with AICc weight (W_i) and normalized weights (NW_i) for models of *Artibeus lituratus* in the humid season. Models with Δi value < 2 were used for multi-model inference and are presented here. Weight (W_i) is reported for the full set of 9 candidate models.

Model	Δi	W_i	NW_i
SEA.b			
PC2	**0**	**0.2948**	**0.4052**
PC1	1.0183	0.1771	0.2435
PROX1000	1.5617	0.1350	0.1856
AREA	1.7880	0.1206	0.1657
$\delta^{15}N$			
PC2	**0**	**0.3621**	**0.7264**
PC1	1.9525	0.1364	0.2736
$\delta^{13}C$			
PC2	**0**	**0.6699**	**1.0000**

Table 3.4b - Difference between the top-ranked model and the i^{th} model (Δi) with AIC weight (W_i) and normalized weights (NW_i) for models of *Carollia perspicillata* in the humid season. Models with Δi value < 2 were used for inference and are presented here.

Model	Δi	W_i	NW_i
SEA.b			
PC2	**0**	**0.2227**	**0.2764**
PC2+PC1	0.3806	0.1841	0.2285
PROX1000	0.9199	0.1406	0.1745
PC1	1.0379	0.1325	0.1645
AREA	1.1408	0.1259	0.1562
$\delta^{15}N$			
PC2	**0**	**0.5680**	**1.0000**
$\delta^{13}C$			
PROX1000	**0**	**0.2476**	**0.2890**
PC1	0.1302	0.2320	0.2707
PC2	0.1753	0.2268	0.2647
AREA	0.9962	0.1505	0.1756

Table 3.4c - Difference between the top-ranked model and the i^{th} model (Δi) with AIC weight (W_i) and normalized weights (NW_i) for models of *Carollia perspicillata* in the superhumid season. Models with Δi value < 2 were used for inference and are presented here.

Model	Δi	W_i	NW_i
SEA.b			
AREA + ISOLATION	**0**	**0.9362**	**1.0000**
$\delta^{15}N$			
PC1	**0**	**0.6122**	**1.0000**
$\delta^{13}C$			
PC2	**0**	**0.4919**	**0.5377**
AREA	1.6648	0.2140	0.2339
PROX1000	1.7125	0.2090	0.2284

Table 3.4d - Difference between the top-ranked model and the i^{th} model (Δi) with AIC weight (W_i) and normalized weights (NW_i) for models of *Sturnira lilium* in the superhumid season. Models with Δi value < 2 were used for inference and are presented here.

Model		Δi	W_i	NW_i
SEA.b				
	PC2	**0**	**0.5545**	**1.0000**
$\delta^{15}N$				
	PC1	**0**	**0.94505**	**1.0000**
$\delta^{13}C$				
	ISOLATION+PC2	**0**	**0.4862**	**0.6543**
	PC1	1.2762	0.2569	0.3457

The variable with the greatest weight (the sum of the NW_i for each model the variable occurs in) in 8 of 12 possible cases was PC2 which is most associated with fragment-scale variation in vertical and horizontal vegetation density. Landscape level metrics (Area, Isolation, PROX1000) were rarely the most significant in the top set of candidate models, except for species captured in the superhumid season.

Table 3.5 – Akaike weights and multi-model parameter estimates (coefficients) for the variables selected from the normalized set of candidate models. Bolded values indicate the case where standard error overlaps zero.

Species-Season		Variable	ΣNW_i	Coefficient (β±SE)	R^2
A.lituratus - Humid					
	SEA.b	PC2	0.405	0.125 ± 0.087	0.2885
	$\delta^{15}N$	PC2	0.726	0.217 ± 0.123	0.3398
	$\delta^{13}C$	PC2	1.000	0.188 ± 0.117	0.6577
C.perspicillata - Humid					
	SEA.b	PC2	0.505	0.212 ± 0.142	0.1755
	$\delta^{15}N$	PC2	1.000	-0.735 ± 0.216	0.6989
	$\delta^{13}C$	PROX1000	**0.289**	**$-6.82^{-8} \pm 4.65^{-7}$**	**0.0043**
C.perspicillata - Superhumid					
	SEA.b	AREA	1.000	$-2.45^{-5} \pm 1.70^{-7}$	0.9953
		ISOLATION	1.000	-0.005 ± 0.001	
	$\delta^{15}N$	PC1	1.000	0.372 ± 0.208	0.6142
	$\delta^{13}C$	PC2	0.538	-0.154 ± 0.086	0.6154
S. lilium - Superhumid					
	SEA.b	PC2	1.000	-0.166 ± 0.093	0.6127
	$\delta^{15}N$	PC1	1.000	0.640 ± 0.160	0.8886
	$\delta^{13}C$	ISOLATION	0.654	0.003 ± 2.20^{-4}	0.9945
		PC2	0.654	0.090 ± 0.014	

In most cases, PC2 is the most significant variable across all species; this component corresponds with vertical and horizontal vegetation density within the fragment. There is also substantial evidence indicating the importance of PC1 which corresponds to water courses and presence of *Cecropia* spp. plants. There is little evidence that other landscape variables impact diet in frugivorous bats.

DISCUSSION

Our data demonstrates that fragment composition, primarily related to vegetation density (PC2), rather than landscape scale metrics has the most significant impact on the diet of fruit bats. For nearly every species-season pairing and across all response variables PC2 was the most significant metric in 8 of our 12 sets of models. Of our top models, after normalization, only 5 of the 12 contained some metric related directly to what would be defined as habitat fragmentation *per se* (Fahrig 2017). This implies that while fragment size and isolation may have some impact on the diet of frugivorous bats, the results suggest that these animals' diets are most influenced by habitat structure (i.e., forest quality, successional state, etc.) than by the overall landscape. PC2 is most positively associated with the presence and abundance of fallen logs, overstory vertical vegetation density, and understory horizontal vegetation density, such that negative values of PC2 reflect less brush density and a more open habitat (Delciellos *et al.* 2016). Generally, landscape scale metrics were more predictive of variation for narrow ranging species (*Carollia perspicillata* and *Sturnira lilium*) than wide ranging species (*Artibeus lituratus*) as we predicted. Additionally, there was more variation in nitrogen than in carbon between populations within the same species-season pair (Fig. 3.1); increasing $\delta^{15}N$ implies a higher trophic level diet, which would mean populations with high $\delta^{15}N$ are likely consuming more insects. Differences in diet however were driven almost entirely by fragment composition, rather than landscape scale variation.

Wide-Ranging Fruit Bats

Bats of the genus *Artibeus,* are noted to have low habitat specificity and are highly adaptive to novel environments (Ortega & Castro-Arellano 2001) with *A. lituratus* being the most common frugivorous bat in many urban areas of Brazil (Zortéa & Mendes 1993, Sazima *et*

al. 1994, Kunz & Diaz 1995, Oprea *et al.* 2007). *Artibeus* spp. exhibit flexible feeding strategies, sometimes engaging in folivory or nectarivory when fruit supply in a region is low, and also eat insects (Fleming *et al.* 1972, Heithaus *et al.* 1975, Zortéa & Mendes 1993, Sazima *et al.* 1994, Kunz & Diaz 1995, Passos & Graciolli 2004, Oprea *et al.* 2007). It is likely that as *Artibeus lituratus* prefer the fruit of *Ficus* spp. which are canopy fruits, they must cover a larger overall area, flying between patches to find fruit (Bianconi *et al*. 2006, Trevelin *et al.* 2013).

For wide ranging *Artibeus lituratus*, PC2 was a metric in the top three models for every response variable. For variation in SEA.b the top model only had approximately 40% chance of being the best model while for mean $\delta^{15}N$, the top model had a 72% chance of being the best model and mean $\delta^{13}C$, PC2 was the only model remaining after normalization (i.e. the only model that had Δi value < 2; Burnham and Anderson 2002). In all cases the relationship with PC2 was positive, as such median niche breadth, and mean carbon and nitrogen ratios all increased with increasing vegetation density. In denser fragments therefore, *A. lituratus* likely have a larger insect component in their diet than in open areas, irrespective of fragment size or distance between fragments. In REGUA, which is a forested heterogenous environment (PC2 is close to the median among all sampled fragments), SEA.b, $\delta^{13}C$, and $\delta^{15}N$ are all similarly intermediate, while denser fragments had higher values of these three response variables.

Differences in $\delta^{13}C$ between fragments correlated with PC2 notably follow a pattern consistent with the 'canopy effect' whereby plants closer to the forest floor have lower $\delta^{13}C$ than plants which grow in the canopy (van der Merwe & Medina 1991, Voigt 2010). Fragments with less vertical vegetation density are likely earlier successional forest, while denser fragments are likely to be old growth; fragments with positive values of PC2 are likely to have more fruiting plants in the canopy (Delciellos *et al.* 2016). Of the populations from fragments which

significantly differed from REGUA in $\delta^{13}C$, most are sparse, likely primary forests while T23 is denser, likely a remnant fragment of old growth forest. With a denser canopy, *Artibeus* are feeding on fruits higher up, contributing to the higher $\delta^{13}C$ values (Voigt 2010). This may also suggest that during the period prior to capture, these bats are resident to these fragments, or seek out a preferred forest type which would preserve this pattern.

Most notable is the model prediction that increased $\delta^{15}N$ should be associated with denser forests, suggesting that in fragments with denser foliage, *Artibeus lituratus* have a larger insect component in their diet than in sparse fragments. While it is unlikely that these wide-ranging bats are residents in these fragments, it is more likely they are only foraging in certain fragments for short periods, as *Artibeus lituratus* have a low recapture rate when banded (Heithaus *et al.* 1975, Bianconi *et al.* 2006, Bernard & Fenton 2007) and are known to make long-range movements of over 100-kilometers (Arnone *et al.* 2016, Esbérard *et al.* 2017). It is possible that *Artibeus* that seek out denser fragments and spend more commuting between them, eating insects on the wing. Flight and large body size necessitates high energy expenditure (Peters 1983) and as *A. lituratus* are known to be dietary specialists, they may require more time to seek out preferred food sources, requiring an insect 'snack' while searching for, or in transit to known ideal foraging locations (Herrera *et al.* 2001; Clare *et al.* 2014). With these behaviours accounted for, it is unlikely insect consumption is related to in-fragment vegetation density, and seemingly supports our prediction that long-ranging *Artibeus lituratus* population diets are less affected by local landscape scale metrics and their immediate environment.

Narrow-Ranging Fruit Bats

Carollia perspicillata and *Sturnira lilium* are both narrow-ranging, similar in size and feed primarily on early successional, understory fruits (Gannon *et al.* 1989, Bernard 2001,

Evelyn & Stiles 2003, Mello *et al.* 2008). *Carollia* have a preference for *Piper* spp. (Herbst 1986b, Mikich 2002, Mello *et al.* 2004c) while *Sturnira* have a preference for Solanaceae (Gannon *et al.* 1989, Evelyn & Stiles 2003, Mello *et al.* 2008a). Both species have been noted to have a significant insect contribution in their diets (Fleming *et al.* 1972, Herbst 1986b, Herrera *et al.* 2002, Mello *et al.* 2004c). Additionally, both have relatively low habitat requirements (Estrada & Coates-Estrada 2002, Bonaccorso *et al.* 2006) and can be found in fragmented landscapes, though *S. lilium* are less frequently captured than *C. perspicillata* (Bernard & Fenton 2003, 2007).

As both species are (at least superficially) ecologically similar, landscape metrics affected these species diets and niche breadths in similar ways. Similar to *Artibeus*, PC2 was the most significant variable in the majority of cases, however, PC1, isolation and area are also included as key contributors in some of the top weighted models. Through examining the coefficients however, there is one case where the standard error overlaps zero (*C. perspicillata* – humid, $\delta^{13}C$) which indicates that this result is likely not significant. As we predicted however, landscape scale metrics appear to be more significant for these species than for *Artibeus lituratus* as they occur more frequently in the top sets of models.

There were no significant differences between any populations niche breadth however our models suggest that under enough environmental stress, niche breadth would be affected by landscape. For *Carollia*, PC2 was included in the top two models in humid season. As *Carollia perspicillata* prefer early successional 'pioneer' fruit species this trend likely reflects the availability of *Piper* spp. as sparse fragments are likely to have more of this preferred resource (Thies & Kalko 2004a, Mello *et al.* 2004a, Pereira *et al.* 2010, Montoya-Bustamante *et al.* 2016). Similar to the studies of primates in a fragmented landscape, when preferred resources are

abundant animals exploit them, and when resources are rare, animals are able to exhibit a more flexible generalist foraging strategy (Cristobal-Azkarate & Arroyo-Rodríguez 2007, Boyle *et al.* 2012, Nowak & Lee 2013). In the superhumid season, AREA+ISOLATION had a 93.6% chance of being the best model to predict variation in SEA.b before normalization. The relationships are negative, though the parameter estimates are small and may not be biologically relevant. At constant isolation, our model shows little variation in niche breadth between a 10-ha fragment and 10,000-ha fragment (3.1415 - 2.9568 ‰^{2}) while above 100,000-ha niche breadth is considerably smaller (0.6918 ‰^{2}). There is likely little difference in the niche breadth of a population in a 10,000 ha forest and 100,000 ha forest, particularly as *C. perspicillata* have a foraging range of approximately 1.5 km and have high site fidelity (Heithaus & Fleming 1978a, Bianconi *et al.* 2006, Bernard & Fenton 2007). Notably at constant area, between 1-100 m in isolation, there is little variation in SEA.b (3.6324 – 3.1394 ‰^{2}), however at approximately 500 m isolation, niche breadth is considerably smaller (1.1474 ‰^{2}). Bernard and Fenton (2003) found *Carollia perspicillata* were able to utilize a network of habitat fragments at a local scale and would cross over open areas, though given their limited foraging range and high energy costs associated with flight, its likely that if a fragment is more isolated, commutes between neighbouring fragments would be increasingly taxing, forcing bats in isolated fragments to specialize and narrow their niche breadth.

For *Sturnira lilium*, the best model for median niche breadth was PC2 and differs from *Carollia perspicillata* in the humid season, as the relationship is negative. Our model shows that populations in fragments with dense vegetation have a smaller niche breadth than those in sparse fragments. Across all fragments *Sturnira* have on average a broader niche than *Carollia* (2.802‰^{2} versus 1.885‰^{2}) and generally have been noted to have a more variable diet (Herrera

et al. 2002, Aguiar & Marinho-Filho 2007, Mello *et al.* 2008b). While *Carollia* and *Sturnira* respond to landscape composition in different ways, there are many species of bats which do not respond in the same way to changes in forest type and landscape composition, even if they are superficially biologically similar (Arroyo-Rodríguez *et al.* 2016, Willcox *et al.* 2017).

For predicting $\delta^{13}C$, the reverse pattern of *Artibeus* was observed for *Carollia* in the superhumid season and is also likely a result of the canopy effect as *C. perspicillata* prefer to feed on low-growing fruits. While fragments with greater vertical vegetation density would likely have a denser canopy, and therefore fewer shade-intolerant *Piper* spp., there are some species which are shade tolerant and they are likely to be abundant particularly on or near the fragment edge (Thies & Kalko 2004). Additionally shade tolerant variants of the same species may have different carbon isotopic composition (Krishnaprasad *et al.* 2017). Changes in mean $\delta^{13}C$ between fragments might therefore be related to consuming different species of *Piper* or having a different quality of diet which might change the fractionation of carbon between the environment and the animal's tissue. In the humid season, the best model for $\delta^{13}C$ (PROX1000, 28.9% probability of being the best model) was considered spurious as the standard error overlapped 0 when examining the parameter estimates (Table 7).

In the superhumid season, mean $\delta^{13}C$ in *Sturnira* was best explained by PC1, where higher $\delta^{13}C$-values were in areas with more abundant *Cecropia* spp., more water courses and fewer liana vines (Delciellos *et al.* 2016). As in the superhumid season it is unlikely that water is a limiting resource, fruit from *Cecropia* spp. are likely the influencing factor as it has been recorded in the diet *S. lilium* (Lobova *et al.* 2003). The significance of *Cecropia* fruits in the diets of both *Carollia* and *Sturnira* has not been explored and it is possible that an abundance of these fruits in times when preferred food items are less abundant would drive this difference in $\delta^{13}C$.

Examining differences in the nitrogen isotopic ratio between populations, for *Carollia* in the humid season, PC2 was once again the best (and only) model after normalization. The relationship is negative, suggesting that in sparser fragments *Carollia* take more insects. Significant differences in δ^{15}N-range and mean between fragments and REGUA indicate that different populations likely vary in insect consumption, and perhaps insect abundance is a major contributing factor (Appendix 2).

In the superhumid season the relationship between landscape variables and mean δ^{15}N was clear for both *Carollia* and *Sturnira* however differences in biology between these species makes these trends difficult to interpret. The best model for mean δ^{15}N in *Carollia perspicillata* populations was PC1 with fragments with more *Cecropia* sp. seeming to have higher insect consumption. In *Sturnira lilium*, the best model (ISOLATION + PC2) would predict populations in denser and more isolated fragments to have higher mean δ^{15}N. Seasonal fluctuations in insect abundance as relative to fruit availability may explain these different responses (Wolda 1978, 1988, Levey 1988). Both *Carollia* and *Sturnira* switch resources at different points in the year (Heithaus & Fleming 1978b, Mello *et al.* 2008b). Previously we have noted that *Carollia* seem to have a more specialized diet than *Sturnira* and are therefore more sensitive to periods of preferred resource scarcity. When *Piper* fruits are less available as they would likely be in the superhumid season in denser fragments, we would predict that insect consumption should increase, as in *Sturnira*, however this is not what our model predicts. Foraging behaviour is also noted to change between the superhumid and humid season, however changes in insect consumption have not been noted (Fleming & Heithaus 1986).

We faced several limitations in the methodology of this study, precipitated by the highly correlated nature of the landscape variables, and not sampling of potential prey items. As a

result, we were only able to compare populations isotopic data to one another and not directly to isotopic inputs (i.e., plants and insects) from their environment. Our models were limited in their use of the landscape data to avoid overfitting and thus some of the complexities may have been overlooked. Additionally, while splitting the sample into seasonal groups is a necessary control for the SIA component given fruiting peaks and shifting isotopic baselines in the environment, fragments were only sampled once and grouped in either humid or superhumid seasons. Some of the patterns observed may be as a result of this sample distribution.

Conclusions

While habitat composition had a clear effect on stable isotope ratios in most cases, landscape scale metrics only had significant impacts in one third of cases. Our models predicted in most cases that forest vegetation density (likely as related to successional state and fruit availability) was the best indicator of differences in diet between populations for most of our season-species pairs and response variables, regardless of species range, which does not support our predictions. There were more significant effects of landscape metrics in narrow-ranging species however and more testing is required in more fragments with other, less correlated landscape variables to determine the true drivers of dietary differences. It is unlikely that insect consumption in frugivorous bats is driven by landscape composition however is may be linked to habitat type. Similarly, niche breadth is not significantly affected by landscape, however differences between populations is best explained by habitat type in most cases. Nearest neighbour distance between fragments was the most important landscape scale variable for narrow-ranging species and had more weight in determining diet than fragment area. The effects of seasonality in diet of these animals should be further explored.

Chapter 4 - Stable isotope analysis of multiple tissue types reveals seasonal changes in diet of tropical bats

OVERVIEW

Seasonal changes in temperature and precipitation in the tropics are known to drive many biological processes. When food resources become scarce, animals may move to areas with greater resource abundance, reduce metabolic activity (i.e., use torpor) or switch to other available (though perhaps less efficient) resources. Stable isotope analysis is a technique that may be used to track temporal variation in diet of individuals and/or populations by repetitive sampling of a single tissue type. However, because different tissues have different isotopic turnover rates (i.e., metabolically latent tissues such as bone, hair and skin have longer turnover times than metabolically active tissues such as muscle and organs), by sampling multiple tissues from the same individual, variation in diet might be better elucidated. In this study we sampled multiple tissues from individuals of Neotropical and Paleotropical bat species representing different trophic guilds and foraging ranges. Examining variation in nitrogen isotopic ratio ($\delta^{15}N$) and niche breadth among tissue types we found more variance in diet between individuals with larger assumed foraging ranges than those of smaller foraging ranges. Additionally, we found a significant effect of time of capture on the pattern of $\delta^{15}N$ in different tissues across several species. Primary diet also had a substantial effect as frugivorous bats had a similar pattern of shifts in $\delta^{15}N$ throughout the year, whereas insectivores were more variable. There were no significant differences in niche breadth for any species when comparing tissues. Using multi-tissue stable isotope analysis is a beneficial way to assess individual and population level variation in diet and may be a valuable technique as it requires fewer sampling periods than other techniques to assess year-round diet.

INTRODUCTION

Seasonal changes in temperature and precipitation influence many biological and physical processes on scales ranging from individuals to populations and from localities to continents. Organismal growth, reproduction, and primary productivity, are often correlated with seasonality (Karr 1976, Battey 2000). Each season has its own unique challenges for native animal species due to availability of water, prey abundance and plant fruiting phenology (Wolda 1978, 1988, Valtonen *et al.* 2013, Grimbacher & Stork 2009). In terrestrial tropical systems, precipitation defines the rainy and dry seasons whereas in temperate areas temperatures fluctuate more widely and results in four distinct seasons (Wright & Cornejo 1990). Seasonality drives changes in behaviour as well, as many animals migrate to areas with more resources, enter torpor or hibernation to conserve energy, or use stored or previously non-exploited resources (Karr, 1976; Fleming et al., 1993). Additionally, many animals and plants may time reproduction to correspond with seasonal resource availability (Bendix et al., 2006; Bronson, 1985; Brown & Shine, 2006; Wikelski et al., 2000; Wright & Cornejo, 1990; Zimmerman et al., 2007). Frugivorous and nectarivorous animals may synchronize lactation and weaning of young with peaks in fruit and nectar, and insectivores with peaks in insect abundance (Bronson, 1985; Di Bitetti & Janson, 2000; Dinerstein, 1986; Goldizen et al., 1988; Julien-Laferriere & Atramentowicz, 1990; Pereira et al., 2010; Zortéa, 2003). It has been posited that omnivory evolved as a response to seasonal abundance of resources, and has contributed to the diversity of many groups (Burin et al., 2016; Chubaty et al., 2014; Rex et al., 2010a). Seasonal diet switching is one way to persist in a changing environment without resorting to more energetically costly tactics such as migration.

Understanding the ecological niche, or 'role', of a species and how that might change throughout the year is important in understanding how species interact with one another and their environment (Hutchinson 1957). Originally conceptualized as an n-dimensional hypervolume, this nebulous concept has become more defined in recent years, particularly by assessing trophic niche breadth as an animal's quality of diet (as opposed to only the composition of diet), which may be a more direct measure of its ability to survive (Vandermeer 1972). For many animals, diet may be characterized by observation, but for cryptic species such as small nocturnal species, faecal and/or stomach content analysis have commonly been used. However, these methods reflect only the most recent meal and is often unreliable as soft prey items might not be identifiable because of partial digestion (Bearhop et al., 2004). Based on experimental studies by DeNiro and Epstein (1978; 1981) researchers have shown that quantification of naturally occurring ratios of stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes in tissues, may permit inference on diet of individuals (Anderson *et al.* 2009), populations (Bearhop *et al.* 2004) and communities (Layman, Arrington, Montaña, Post, *et al.* 2007). Using these isotope ratios together, dietary niche breadth of populations can be assessed, and overlap with other populations can be used to examine species interactions (Bearhop et al., 2004; Jackson et al., 2011; Swanson et al., 2015). Other isotopic ratios have also been used to characterize aspects of diet, such as hydrogen ($\delta^{2}H$), oxygen ($\delta^{18}O$), and sulfur ($\delta^{34}S$) however these isotopes are less useful for assessing dietary variation in terrestrial systems (Bearhop et al., 2004; Jackson et al., 2011).

When isotopes are incorporated into tissues, a predictable fractionation, or change, in the ratios of heavy and light isotopes of elements occurs between the environment and the animal (Dalerum & Angerbjörn 2005, Hobson & Clark 1992a, Ben-David & Flaherty 2012).

Fractionation factors and the period of the isotopic turnover differ for different species and tissues (Caut et al., 2009; 2010). For some metabolically active tissues (e.g., blood, muscle), isotope turnover rates are dependant on metabolic rate (MacAvoy et al., 2006), whereas for inert tissues (hair, bone*)* the rate of tissue renewal (e.g., moulting) is responsible for the changes in isotope record over time (Ben-David & Flaherty 2012). Isotopic fractionation may also be affected by other factors including age, quality of diet, body condition, and reproductive status (Ben-David & Flaherty 2012). Through captive experimental studies, average fractionation for many tissues and species has been calculated (Dalerum & Angerbjörn 2005). Latent tissues also store isotope records for longer times than more metabolically active tissues which can be used to make inference on recent diet (Cabanellas-Reboredo et al., 2009; Hobson & Clark, 1992; Voigt et al., 2003). Additionally, faeces and exhaled breath have been used to characterize diet immediately prior to capture (Aliperti et al., 2017; Lam et al., 2013; Voigt et al., 2008). Mixing models may improve the accuracy of diet estimates, however, this approach may be used only in systems where range of diet options in the system are known (Phillips *et al.* 2014). Testing various tissues from a single animal may elucidate different elements of an animal's diet over an extended period of time and perhaps detect seasonal diet switching which was not previously known (Dalerum & Angerbjörn, 2005; Kurle, 2009; MacAvoy et al., 2006; Tieszen et al., 1983).

The carbon isotopic ratio, $\delta^{13}C$, in tissue reflects the original source of carbon in an animal's diet (DeNiro & Epstein 1978). Different organic and inorganic diet sources have different carbon ratios and are incorporated with little fractionation, though these fractionation rates may be different depending on the tissue (Post 2002, Ben-David & Flaherty 2012). Organic carbon may originate from C_3 (most tropical trees and flowering plants) or C_4 (grasses) photosynthesis, each of which produce unique and identifiable isotopic ratios ($C_3 \approx$ -28‰ and C_4

≈ -13‰) (Peterson & Fry 1987). Additionally, within a vertically stratified terrestrial system (*e.g.,* forest), it may be possible to infer vertical feeding zone because $\delta^{13}C$ of plants increases from ground level into the canopy (Rex et al., 2011; Voigt, 2010). For these reasons, $\delta^{13}C$ has been used to indicate where an animal is feeding, but differential fractionation among different tissues complicates inference from these studies (MacNeil et al., 2005).

Nitrogen isotopic ratio, $\delta^{15}N$, may be used to characterize trophic level (Bearhop et al., 2004; DeNiro & Epstein, 1981). While naturally occurring in plants and animals, heavy nitrogen isotope ^{15}N bioaccumulates in trophic systems such that $\delta^{15}N$ increases from primary producers to apex predators. Therefore, by comparing $\delta^{15}N$ of two or more species we can infer relative trophic positions (Peterson & Fry 1987). The $\delta^{15}N$ may fluctuate for an individual as it switches among prey of different trophic levels to sustain itself during different times of year, and this would be preserved in tissue (DeNiro & Epstein, 1981). Additionally, different from $\delta^{13}C$, there is little difference in fractionation between tissue types making $\delta^{15}N$ ideal for examining seasonal changes in diet (MacNeil *et al.* 2005). Using carbon and nitrogen isotopic ratios in combination, researchers have reliably measured niche breadth, which is the two-dimensional overall space within a larger community structure that a species occupies (Bearhop et al., 2004; Feinsinger et al., 1981).

There are different approaches for examining seasonal changes in diet including re-sampling tissues with either rapid-turnover (e.g., blood) (Fleming et al., 1993; Dietz et al., 2013; Ogden et al., 2004; Salvarina et al., 2013; Trudel et al., 2010) or those with longer, known turnover times such as bone, hair, or skin (Aliperti et al., 2017; Miron et al., 2006; Popa-Lisseanu et al., 2015) from individuals over time. Additional limitations to using low-turnover tissues, particularly hair, is that in many cases the period of hair growth is not known (Fraser et al.,

2013). However, in studies where sampling time or sample size is limiting because of the need to recapture or sacrifice large numbers of animals, it may be possible to sample from multiple tissues of a single animal specimen to measure temporal variation in diet (Dalerum & Angerbjörn, 2005; MacNeil et al., 2005). This method is also especially useful in cases where animals are rare or elusive, and only limited sampling can be done for conservation or logistical reasons, and can also account for degree of individual specialization within a larger population (Bond et al., 2016). Additionally, using multiple tissues may account for underlying seasonal isotopic baselines (Popa-Lisseanu *et al.* 2015) which may impact the interpretation of C/N isotopic analysis. Using multiple tissues from a single specimen might allow for an entire natural dietary history to be compiled (Tykot 2004).

Tropical bat faunas are among the most diverse mammalian assemblages, with up to 100 species existing sympatrically. Several species of these animals in many cases roost together, forage in the same flightpaths and may interact with one another on a nightly basis (Findley, 1993; Howell & Burch, 1974; Humphrey et al., 1983). Many bat species are known to adapt their diet in response to seasonal environmental changes and competition (Arnone et al., 2016; Cisneros et al., 2015; Ferreira et al., 2017; Fleming & Heithaus, 1986; Klingbeil & Willig, 2010; McNab, 1969; Mello et al., 2004; Zortéa, 2003). While these animals may be grouped into broad trophic guilds, most are omnivorous, and likely driven by seasonal availability of fruits, insects, nectar and other food sources (Frick et al., 2014; Rex et al., 2010). Additionally, many bats are known to traverse large distances in response to seasonal changes in resource abundance, though this is not typically defined as 'migration' (Arnone et al., 2016; Fraser, 2011). We predict that (1) there will be little change in the diets (δ^{15}N-range and niche breadth) of wide-ranging bats, and (2) species or individuals which alter their diets throughout the year should have more variation

in δ^{15}N-range and niche breadth between tissue types. We also intend to compare nitrogen ratios between tissues to estimate the period of moulting and hair growth in the species sampled. Understanding seasonal changes in animals' diets is fundamental to understanding how these animals interact with their environments. Seasonality in diet is also important with the encroaching impacts of climate change altering animal behaviour and reproduction (Bronson, 2009; Walther et al., 2002).

METHODS

Sample Collection

Tissue samples from 54 bats of 7 species from the Royal Ontario Museum, Department of Natural History – Mammalogy were collected. Species sampled were selected with the target sample size of 10 individuals (5 male, 5 female) captured at the same location during the same sampling period. Species were also selected to represent both typical frugivorous and insectivorous species from both the Neotropics and Paleotropics, and both narrow and wide-ranging species. For each specimen, a small (≈ 1mg) sample of bone, hair, patagium, spleen, heart, liver and kidney was subsampled. In museum collections, bone, patagium, and hair were stored dry and at room temperature. Organ tissues (heart, liver, spleen and kidney) were frozen in the field using liquid nitrogen (-196 ^{o}C) and stored at -80 ^{o}C in ultracold freezers at the museum. For subsampling, organ tissues were stored in 70% ethanol and at -20^{o}C until analysis. Only two individuals of *Nanonycteris veldkampi* and *Pipistrellus tenuis* were sampled as these species diet is less well known; these samples are to be treated a pilot project (Table 4.1).

Table 4.1 – Overview of tropical bat species sampled with country of origin, primary diet and range. Primary diet is based on literature references for each species, but omnivory likely exists. Range extent is broadly defined as the size of the nightly foraging area and knowledge of long-distance movements.

Species	Sample size n (f, m)	Range Extent	Primary Diet	Country of Sample	Season of Capture	Reference
Artibeus lituratus	10 (5, 5)	Wide	Fruit	Guyana	Dry	(Arnone et al., 2016)
Carollia perspicillata	10 (5, 5)	Narrow	Fruit	Guyana	Dry	(Cloutier & Thomas, 1992)
Pteronotus parnelli	10 (5, 5)	Narrow	Insects	Guyana	Wet	(Herd, 1983)
Hipposideros larvatus	10 (5, 5)	Narrow	Insects	China	Wet	(Bates & Harrison, 1997)
Cynopterus sphinx	10 (5, 5)	Wide	Fruit	China	Dry	(Storz & Kunz, 1999)
*Nanonycteris veldkampi**	2 (1, 1)	Wide	Fruit	Ivory Coast	Dry	(Fahr 2013)
*Pipistrellus tenius**	2 (1, 1)	Narrow	Insects	Vietnam	Wet	(Bates & Harrison, 1997)

*Species sampled as a part of a pilot project. Only 2 individuals (1 female, 1 male) were sampled.

Tissue Analysis

Tissues were processed at the Environmental Isotope Lab at the University of Waterloo. Organ samples were air dried overnight in a fume hood and then placed in a sample oven at 50ºC overnight to remove the ethanol. Dry tissue samples were not pre-treated before stable isotope analysis (Tomaszewicz, et al., 2015, Voigt et al., 2003). Samples were ground or cut to homogenize and weighed into tin capsules. Samples of organs, hair and patagium of between 0.300-0.400 mg and bone samples of 0.500-1.00 mg were placed in a 4010 Elemental Analyzer (Costech Instruments) and combusted; this was coupled to a Delta Plus XL (Thermo) continuous flow isotope ratio mass spectrometer (CFIRMS). Stable isotope ratios were reported in δ-notation in parts per thousand (‰) using the formula:

$$\delta X = [\ (R_{sample}/R_{standard})\ -1\ ] \times 10^3$$

where $R_{standard}$ is the isotopic ratio anchored in VPBD ($\delta^{13}C$) and AIR ($\delta^{15}N$) scales using international and in-house calibrated standards [International Atomic Energy Agency]. Low mass samples (4 patagium samples: P34378, P43720, P47801, P47827) were analyzed using a non-diluted CO_2 protocol.

Statistical Analysis

Fractionation factors and isotopic turnover rates were assessed using Dalerum and Angerbjörn (2005; Table 4.2). To qualitatively characterize variation within populations, and general trends of dietary change, we examined differences in $\delta^{15}N$ among tissues as the differences between values. To assess individual variability within the population we took the mean and standard deviation of these differences. We did not use $\delta^{13}C$ as this ratio is more

sensitive to differences in fractionation and metabolic rates among tissues and would therefore be less reliable for assessing temporal variation in diet (see MacNeil et al., 2005). We also used non-parametric bootstrapping (R = 1000) for each tissue type both for each species and each species-sex pairing. From these distributions we calculated 95% confidence intervals; we defined statistically significant differences between tissues as cases where these intervals do not overlap (Figure 4.1). Additionally, to minimize any effects differential fractionation would have on organ tissues, we grouped tissues that had similar isotopic turnover rates (i.e., liver, spleen and kidney are grouped as 'organs'; Vander Zanden et al. 2015).

We considered male and female samples as different treatment groups and only sampled specimens which were collected in the same sampling period (within several days). We used the smallest differences between averages of differences in $\delta^{15}N$ within the population to estimate the period of hair growth (Fraser et al., 2013). Though isotope data is difficult to compare between tissue type as different species metabolize or process proteins differently, we assume that the averages presented are conservative estimates for the species.

Table 4.2 – Mean isotopic half lives and coefficients of fractionation adapted from Dalerum and Angerbjörn (2005) for ^{13}C and ^{15}N. Data reported are those that represent the closest in body size and/or phylogenetically to our sampled species of tropical bats. Data in italics are model-calculated means for a 50 g mammal from Vander Zanden, et al., (2015). Tissues are listed in order of duration of isotopic record prior to capture; time of isotopic record is unknown in hair as moulting period is not known. Blank cells identify gaps in the scientific literature such that an accurate estimate is not known.

Tissue	Half Life (days)		Fractionation (‰)	
	^{13}C	^{15}N	$\Delta^{13}C$	$\Delta^{15}N$
Bone (Collagen)[1]			3.8	
Patagium	118			
Heart (Muscle)	27.6	*29.4*	> 1.0	3.6
Liver	6.4	*11.3*	> 1.0	3.6
Spleen	*11.3*	*11.3*		
Kidney	*11.3*	*11.3*		
Hair[1]	537			

[1]Hair and bone preserve the isotopic record from the time they were produced as they are metabolically latent tissues. Hair isotopic ratios therefore reflect the period of hair growth and are dependant on moulting.

To assess niche breadth we used the package Stable Isotope Analysis Bayesian Ellipses in R (SIBER – Jackson et al., 2011) in R (version 3.4.1). Niche breadth is reported as median Bayesian corrected Stable Ellipse Area (SEA.b) bootstrapped to R = 10,000. To test for significant differences in niche breadth for species between tissue types we assessed the probability that median SEA.b of Tissue A is less than the SEA.b of Tissue B.

RESULTS

Bone, patagium and heart had consistently higher mean $\delta^{15}N$ than hair and organ tissues (Table 4.3). Bone and patagium were most notably considerably higher in $\delta^{15}N$ than all other tissues in *Pteronotus parnelli*; in most cases with significant differences, heart tissue was the most ^{15}N enriched. There were no significant differences in $\delta^{15}N$ between tissues in *Artibeus lituratus* (both males and females) and *Hipposideros larvatus* females (Figure 4.1).

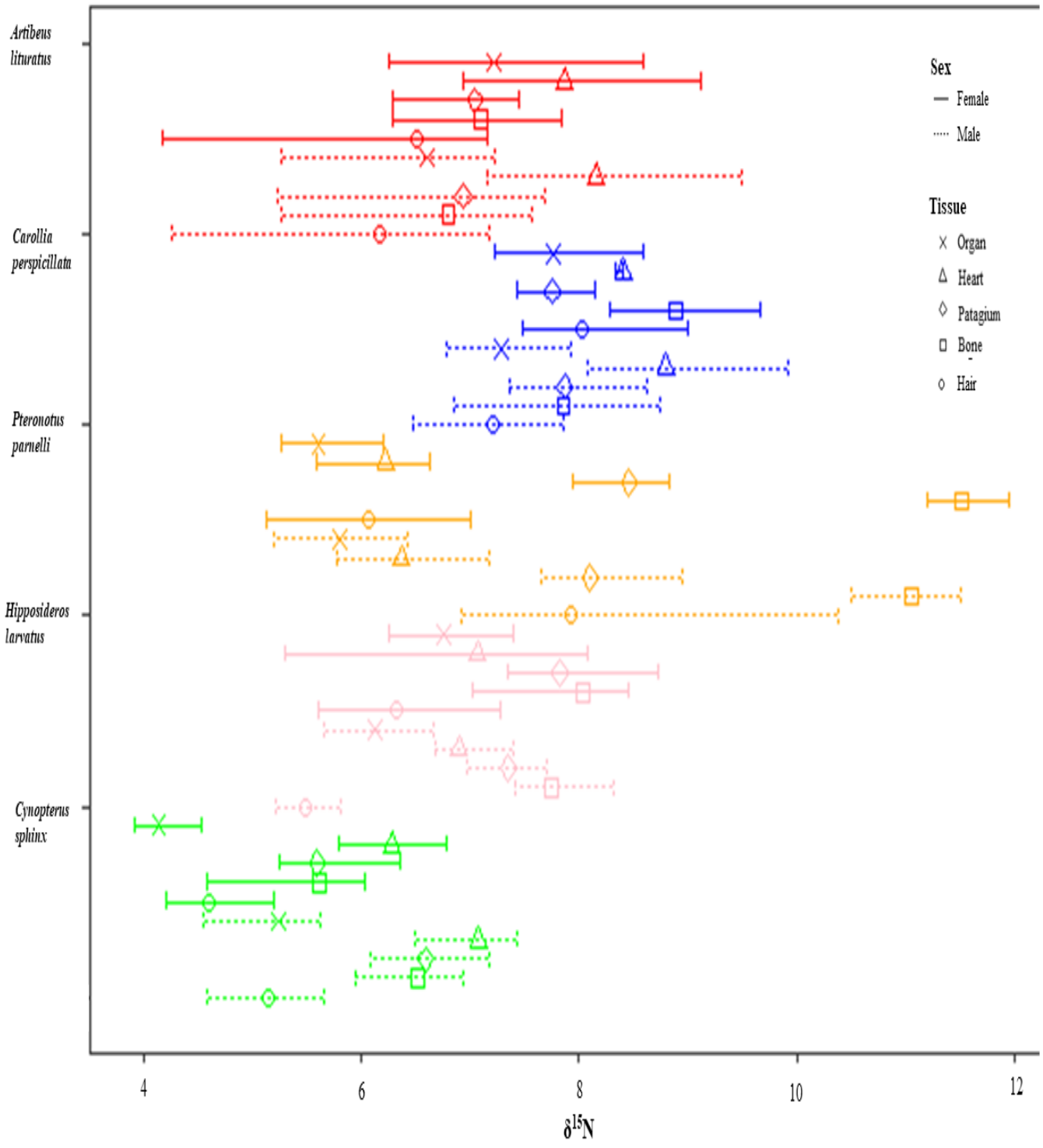

Figure 4.1 – Non-parametric bootstrap distribution estimates (F; R = 1000) sampled with replacement, and 95% confidence intervals of $\delta^{15}N$ (‰) for each species-sex pairing for each tissue type. Sample means are reported as points.

There was little variation when comparing narrow- and wide-ranging species in the differences between tissue types (Table 4.3). Species which were captured in the same region during the same season had similar patterns of variation in $\delta^{15}N$ (Figure 4.1). Males and females of the same species follow similar patterns across all tissue types and there were no significant differences in the bootstrap distributions (with the exception of organ tissues in *Cynopterus sphinx*). All individuals followed similar patterns though distribution of $\delta^{15}N$ varied, except for *Hipposieros larvatus* where one individual had higher $\delta^{15}N$ than any other sampled in hair, patagium and heart, and a second individual had the lowest heart $\delta^{15}N$. Additionally, *Carollia perspicillata* and *Cynopterus sphinx* have significant individual variation though individuals follow the same trends (Appendix 3).

Although there were no significant differences in niche breadth in any species among tissues, there was significant variation in mean $\delta^{15}N$ among tissues in *Carollia perspicillata*, *Pteronotus parnelli*, *Cynopterus sphinx* and male *Hipposideros larvatus*. We did not have sufficient sample size to assess variation in the diet of *Pipistrellus tenius*, however we did find indication of variation in $\delta^{15}N$ for *Nanonycteris veldkampi*. While $\delta^{13}C$ varied significantly among tissues for each species-sex pair, fractionation factors are not known for the species sampled; in the absence of experimental studies this data is not considered to be biologically significant.

Table 4.3 – Mean differences with standard deviations between $\delta^{15}N$-values for each tissue type within the tropical bat species-sex group. Differences are calculated from tissue in column to tissue in row. Bolded hair values correspond with the difference closest to zero indicating the tissue with the closest mean $\delta^{15}N$; period of hair growth.

Species-Sex		Bone	Patagium	Heart	Organs	Hair
A. lituratus	Bone	0	-0.05 ± 0.85	0.41 ± 1.25	0.12 ± 1.98	-0.58 ± 1.48
Female	Patagium		0	0.78 ± 0.65	0.17 ± 1.23	**-0.53 ± 0.83**
	Heart			0	-1.20 ± 0.50	-1.58 ± 1.05
	Organs				0	-0.71 ± 1.18
	Hair					0
A. lituratus	Bone	0	0.13 ± 0.25	0.99 ± 1.55	-0.20 ± 0.29	-0.63 ± 0.53
Male	Patagium		0	0.86 ± 1.42	-0.33 ± 0.23	-0.77 ± 0.49
	Heart			0	-1.19 ± 1.27	-1.62 ± 1.79
	Organs				0	**-0.44 ± 0.67**
	Hair					0
C. perspicillata	Bone	0	-1.13 ± 0.55	-0.09 ± 0.12	-1.12 ± 0.51	-0.86 ± 0.34
Female	Patagium		0	0.68 ± 0.28	0.01 ± 0.74	**0.27 ± 0.48**
	Heart			0	-1.32 ± 0.01	-0.80 ± 0.09
	Organs				0	**0.26 ± 0.72**
	Hair					0
C. perspicillata	Bone	0	0.01 ± 0.69	1.09 ± 1.20	-0.57 ± 1.19	-0.64 ± 0.60
Male	Patagium		0	0.96 ± 0.63	-0.59 ± 0.60	-0.65 ± 0.42
	Heart			0	-1.38 ± 0.42	-1.76 ± 0.94
	Organs				0	**-0.07 ± 0.94**
	Hair					0
P. parnelli	Bone	0	-3.03 ± 0.65	-5.29 ± 0.48	-6.02 ± 0.27	-5.44 ± 0.97
Female	Patagium		0	-2.26 ± 0.35	-2.35 ± 0.14	-2.10 ± 0.56
	Heart			0	-0.48 ± 0.49	-0.15 ± 0.62
	Organs				0	**0.07 ± 0.39**
	Hair					0
P. parnelli	Bone	0	-2.96 ± 0.80	-4.69 ± 1.15	-5.29 ± 1.19	-3.05 ± 1.88
Male	Patagium		0	-1.95 ± 0.53	-2.33 ± 0.56	**-0.24 ± 1.11**
	Heart			0	-0.60 ± 0.32	1.45 ± 1.10
	Organs				0	1.98 ± 1.16
	Hair					0
H. larvatus	Bone	0	-0.21 ± 1.33	-0.22 ± 1.13	-1.21 ± 1.21	-1.41 ± 1.48
Female	Patagium		0	-0.01 ± 0.39	-1.00 ± 0.26	-1.20 ± 0.20
	Heart			0	-0.30 ± 1.41	-0.75 ± 0.97
	Organs				0	**-0.45 ± 0.60**
	Hair					0

Species-Sex		Bone	Patagium	Heart	Organs	Hair
H. larvatus	Bone	0	-0.46 ± 0.35	-0.83 ± 0.60	-1.78 ± 0.12	-2.31 ± 0.13
Male	Patagium		0	-0.60 ± 0.58	-1.22 ± 0.38	-1.87 ± 0.22
	Heart			0	-0.66 ± 0.80	-1.34 ± 0.49
	Organs				0	**-0.65 ± 0.32**
	Hair					0
C. sphinx	Bone	0	-0.28 ± 0.52	0.59 ± 0.29	-1.68 ± 0.81	-1.23 ± 0.47
Female	Patagium		0	0.63 ± 0.27	-1.58 ± 0.31	-0.99 ± 0.32
	Heart			0	-2.14 ± 0.44	-1.66 ± 0.29
	Organs				0	**0.46 ± 0.39**
	Hair					0
C. sphinx	Bone	0	0.07 ± 0.73	0.70 ± 0.91	-1.29 ± 0.90	-1.38 ± 1.11
Male	Patagium		0	0.58 ± 0.68	-1.36 ± 0.79	-1.45 ± 0.90
	Heart			0	-1.98 ± 0.23	-1.76 ± 0.12
	Organs				0	**-0.10 ± 0.65**
	Hair					0

In general, standard deviations are higher between tissues in wide-ranging species than in narrow-ranging species, reflecting more individual variability in diet (Table 4.3). There is little variation between males and females of the same species across all tissue types. In 8 of 10 cases, the difference between organs and hair was closest to zero, and in 2 cases the smallest difference was between patagium and hair. For both insectivorous species (*Hipposideros larvatus* and *Pteronotus parnelli*) bone had on average the highest nitrogen isotopic ratio and all other tissues progressively (from longest turnover rate to shortest) were lower, reflected by negative mean differences between tissues.

DISCUSSION

Among tissues of *Carollia perspicillata*, *Pteronotus parnelli*, *Cynopterus sphinx* and male *Hipposideros larvatus* there were significant differences in $\delta^{15}N$ between tissues representing seasonal dietary shifts. However, there were no significant differences in niche breadth observed, indicating that these species do not specialize or generalize in seasons when resources are limited. Males and females of the same species appear to respond the same way to changes in their environments. Trophic guild (i.e., frugivores, insectivores, etc.) also seems to explain some variation as *Artibeus lituratus*, *Carollia perspicillata* and *Cynopterus sphinx* all follow a similar pattern across tissue types. Notably, wide- and narrow-ranging bats had similar patterns with more inter-individual variation in populations of wide-ranging bats. Metabolically latent tissues had higher mean $\delta^{15}N$ than active tissues; this may be as a result of diet quality at different points of the year or differential fractionation between tissues (Hobson & Clark 1992b).

We were able to identify the probable period of hair growth as the smallest average difference between hair and tissue of known turnover rate. Based on this, the data indicates that in most species hair grew in the same season as capture (organs) however in some cases (*Artibeus lituratus* and *Pteronotus parnelli*), hair grew 3-4 months prior to capture (patagium). There were several species where estimates of timing of hair growth differed between males and females, perhaps because moulting has a high associated energy cost and females may time the growth of new fur so that it does not overlap with reproduction (Fraser *et al.*, 2013). The only species in our study which moulting has been documented is *Pteronotus parnelli* (Smith 1972). This study noted reproductive females had new hair growth later in the year than males or females that did not reproduce; moulting took place between May and July which corresponds to the wet season in Guyana (Smith, 1972; Fraser *et al.* 2013). We also noted several instances

where repeated SIA of different hair samples for the same individual produced significantly different values of $\delta^{15}N$. In most cases, this is likely the result of asynchronous moulting as hairs are lost and re-grown at different times throughout the year (Fraser *et al.* 2013). Understanding the moulting patterns of species should be further studied as hair is an ideal tissue for SIA in most cases; collection is non-invasive and minimally disruptive.

Range and Diet

Comparing narrow- and wide-ranging species, there appears to be little difference in seasonal dietary patterns and differences in diet. The most direct comparisons we can make are the two Neotropical frugivorous species, *Artibeus lituratus* and *Carollia perspicillata*. *Artibeus lituratus* is a widespread and wide-ranging species found throughout Central and South America that is typically viewed as a *Ficus* spp. specialist feeder (Arnone *et al.*, 2016; Herrera *et al.*, 1998; Sazima *et al.*, 1994). *Carollia perspicillata* are similarly widespread and abundant throughout the continental Neotropics, however, have a narrower foraging range. Additionally, *Carollia* are viewed as *Piper* spp. specialists (Heithaus & Fleming, 1978; Herbst, 1986; Mello *et al*., 2004). Iwokrama Forest in central Guyana where *Artibeus lituratus* and *Carollia perspicillata* were collected has two rainy seasons (December to February and April to August) and fruiting phenology of many *Piper* and *Ficus* species are dependent on seasonal rainfalls (Gautier-Hion & Michaloud 1989, Persaud & Persaud 1995, Thies & Kalko 2004a, Zimmerman *et al.* 2007). Fruiting peaks often also correspond with reproductive peaks in bats, which results in seasonal dietary differences (Mello *et al.*, 2004; Saldaña-Vázquez, 2014).

For both *Artibeus* and *Carollia*, heart tissue samples had the highest or second highest average $\delta^{15}N$, which reflects diet roughly from the beginning of the dry season when these specimens were collected. Differences between the averages for all other tissue-type pairs had

little variation (differences ≈ 0 - 0.5) indicating consistent trophic level throughout the remainder of wet and dry seasons. A fecal analysis study in the wet season at Iwokrama Forest, Guyana (the site where our specimens were captured) showed that *Artibeus* primarily took *Ficus* and *Cecropia* fruits, whereas *Carollia* were mostly feeding on *Piper* (Horsley et al., 2015). This study did not assess insect content of diet, however, for *Carollia perspicillata* insects are often underreported in this type of study as this species has been noted to discard most of the exoskeleton of insects after capture (Arata *et al.*, 1967; Fleming *et al.*, 1972). The spike in $\delta^{15}N$ at the beginning in the dry season may indicate an increase in the number of insects both *Artibeus* and *Carollia* take, perhaps in response to seasonal shortages in other resources (Herrera et al., 2001a, b; Herrera et al., 2002). Increased $\delta^{15}N$ at the beginning of the dry season may also correspond to an increase in fruit production (Milton 1991) and though seemingly counterintuitive, nitrogen stress has been shown to increase $\delta^{15}N$ in tissues of bats (Voigt & Matt 2004). Additionally, there was more variance in $\delta^{15}N$ among individuals of *Artibeus lituratus* (assessed by standard deviation), which may reflect the larger range, though niche breadth of the population was not significantly different between the two species. While *A. lituratus* roost in small groups, they may forage alone, congregating at times, and alter their behaviour dependant on the season and phase of the moon (Morrison 1980).

In the Paleotropics, comparisons between species are more tenuous as species were captured in different regions and have different foraging strategies (e.g., *Hipposideros larvatus*, an insectivore, and *Cynopterus sphinx*, a frugivore, were captured in different but adjacent provinces in China during different times of the year). Regardless, wide-ranging species appear to have a greater variation in $\delta^{15}N$ than narrow-ranging species, contrary to our prediction that wide-ranging species would have a less variable diet throughout the year. However, individual

variability in nitrogen isotopic ratio was greater in *Hipposideros larvatus*. Both species, organ isotopic ratios (reflecting diet prior to period of capture) had significantly lower average $\delta^{15}N$ than any other tissue. This suggests that *C. sphinx* forages over a larger range but may specialize more at different times during the year. *Hipposideros larvatus* is presumed to have a smaller range, however, individuals vary substantially in what they eat (Bond *et al.* 2016). Further study of these and similar species, and analysis of potential food items would further help to clarify these seasonal dietary patterns.

Effect of Capture Season

As we only sampled individuals of a species that were captured within days of each other assessing the effect of season of capture on isotopic ratios must be done across species captured at the same locality. *Pteronotus parnelli* in this study were captured in Kaieteur National Park, approximately 100 km from Iwokrama Forest in Guyana; differences in geography and microclimate may also drive seasonal patterns as Kaieteur is a mountainous region while Iwokrama is situated in lowlands. Visually comparing the patterns of mean $\delta^{15}N$, it is evident that there is significant difference between *P. parnelli* and its sympatric species, and this is likely a result of being sampled during a different time of the year or geographic differences. Due to isotopic turnover rates, all tissue types except for bone and patagium likely reflect diet during one of the two wet seasons. While bone has the highest $\delta^{15}N$, the exact period of growth is not known (Keegan & DeNiro, 1988). Patagium is intermediate between bone and other tissues, and likely reflects the dry period between February and April in which *Pteronotus* are likely taking larger, higher trophic level prey than during the wet season. Changes in insect abundance and distributions have been shown to influence foraging habits of *Pteronotus* (de Oliveira *et al.* 2015) and such changes may be related to seasonal climate (Wolda 1978, 1988). Herrera *et al*.

(2001a) found comparable $\delta^{15}N$ values throughout the year to our study, however mean $\delta^{15}N$ is lower in *Pteronotus* than what would be expected of an obligate insectivore, and for most tissues is lower than sympatric frugivores. This may be a result of the consumption of insect-derived chitin which has lower $\delta^{15}N$ than soft tissues; *Pteronotus parnelli* may only eat the exoskeleton of larger insects, discarding soft tissues while frugivorous bats such as *Carollia perspicillata* will only eat the soft tissues of insects (Herrera et al., 2001a). It is possible that the high $\delta^{15}N$ in bone is related to a different feeding behaviour in young *Pteronotus*, such that younger bats consume insects whole while older bats only eat the chitinous exoskeletons resulting in the lower $\delta^{15}N$ (Webb, 1997; Herrera et al., 2001a).

In the Paleotropics, capture season appears to have a significant effect on differences in $\delta^{15}N$; the same patterns appear among Neotropical bats. *Cynopterus sphinx* (and *Nanonycteris veldkampi* though sample size is a limitation for this species), captured in the dry season, followed the same pattern, with enriched nitrogen in heart, and a decrease of mean nitrogen in organ tissues as in the Neotropical frugivores. Species captured in the wet season (*Hipposideros larvatus*) had highest nitrogen values in metabolically latent tissues and progressively lower as turnover rates approach the period of capture. This pattern was also evident in the Neotropic species *Pteronotus parnelli* that was caught in the wet season. We would predict that if these species were re-sampled in different seasons isotopic patterns would change across tissues; this is evidence of seasonal diet switching within populations.

Conclusions

Understanding seasonal variations in diet is valuable to understand how these animals interact with their environment year-round. Using multi-tissue stable isotope analysis to examine seasonal dietary changes, we found that this technique is valuable to assess individual and population-level variation. There were significant differences in the nitrogen isotopic ratios of different tissues when we compared them within each species; niche breadth was also assessed and was not statistically different when compared across tissue type. We were able to identify the probable period of hair growth for the species we sampled by comparing average $\delta^{15}N$ from other tissue types with known isotopic turnover rates. Distinct patterns differed for species with wide- and narrow-ranges of foraging behaviour suggesting different coping strategies in seasons with fewer available resources. Wide-ranging species had more individual variance than narrow ranging, but both groups had similar patterns in $\delta^{15}N$ responding to changes in seasonal resource availability. Future studies should focus on experimentally determining isotopic turnover and fractionation in different tissues to further advance this technique. Sampling of potential prey items would also allow direct comparisons between the isotopic signatures in tissue and actual diet. Testing multiple tissues of the same individuals and species of bats is invaluable in understanding the seasonal variation in diet in the highly diverse tropical environment.

Chapter 5 - Discussion

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Using carbon and nitrogen stable isotope analysis, I examined the trophic niche dynamics of multiple tropical bat populations. In chapter 2, I characterized niche partitioning and overlap between 35 sympatric species in northern Belize and observed several cases of complete niche overlap, seemingly violating the competitive exclusion principle (Gause 1934). I also noted several cases where species overlapped significantly between different trophic guilds (e.g., carnivores overlapping insectivores) calling into question the use of these blunt measures to characterize community structure. In chapter 3, I found little impact of habitat fragmentation on the diets of frugivorous bats in Brazil's Atlantic Forest, but significant effects of habitat patch composition. While there were significant differences in $\delta^{13}C$ and $\delta^{15}N$ between populations of all three species sampled, patch area and isolation were only predictive of variation for narrow-ranging species (*Carollia perspicillata* and *Sturnira lilium*). In chapter 4, I used multi-tissue SIA to assess seasonal temporal variation in diet and found this to be an effective method of assessing the natural history of these animals. I noted significant differences in the diets of sympatric species that differ in range, primary diet, and differed in capture season. While single tissue SIA only offers a snapshot of diet (albeit averaged over an extended period) using multiple tissues allowed us to develop a complete picture of variation in $\delta^{15}N$ throughout the year, examine differences in diet between juveniles (or subadults) and adults of the same species by examining bone tissue, and identify the period of hair growth based on these seasonal fluctuations. Below, I summarize the key findings of these studies and outline the implications and future directions for examining trophic niche dynamics of bat populations.

Community Structure of Neotropical Bat Fauna

In northern Belize, niches of sympatric species, both within and between trophic guilds, overlapped significantly in isotope space. Contrary to predictions, (1) guilds were not as informative as dietary studies would suggest as there were several cases of > 90 % overlap between members of different guilds and (2) seemingly in violation of the competitive exclusion principle, there were several cases of > 95 % overlap between populations (NB: overlap was measured as the probability of finding an individual of Species A in the niche region of Species B; Swanson *et al.* 2015). Additionally, I examined body size (measured as mass and forearm length) as an explanatory metric of niche partitioning and found no relationship between body size and niche breadth among all bats. Unique feeding strategies in the fauna by the greater bulldog bat, *Noctilio leporinus* (piscivorous), and the common vampire bat, *Desmodus rotundus* (sanguivorous), are clearly separated from the rest of the community in isotope space. The proboscis bat, *Rhynchonycteris naso* (insectivore), which had the lowest mean $\delta^{13}C$ of any species in the fauna and was similarly isolated. This species is known to feed on insects close to the water which are likely a part of the aquatic system; the low $\delta^{13}C$ is likely consistent with pelagic aquatic primary production or inorganic carbon (i.e., methane from local wetlands) being incorporated into the animal's tissue (Broders *et al.* 2014, Becker *et al.* 2018).

Overlap between guilds was most often between carnivorous and insectivorous species, likely as a result of the artificial nature of the carnivore guild (Norberg & Fenton 1988). For this study, I defined carnivores as species which are adapted to capturing vertebrates (either physiologically or behaviourally) rather species which are known to eat vertebrates opportunistically (e.g., *Phyllostomus discolor* or *Micronycteris microtis*) as I would expect these species to have higher $\delta^{15}N$ than other species in the fauna. However, even species which are

known to specialize on vertebrates like the woolly false-vampire bat, *Chrotopterus auritus*, are also known to consume insects and plant material, and would perhaps be better described as opportunistic animalivores (Medellín 1989b, Barquez *et al.* 2015). While the carnivores in this study did have among the highest δ^{15}N-values, there were several insectivores which had equivalent nitrogen values including *Molossus rufus* and *Pteronotus mesoamericanus* which may be a result of feeding on larger, higher trophic level insects (Girard *et al.* 2011, Hyodo *et al.* 2011). There was also significant overlap between nectarivorous *Glossophaga soricina* and insectivores, suggesting that during the period of hair growth *G. soricina* are primarily insectivorous (Howell 1974, Clare *et al.* 2014).

Within guilds there were four cases where niche breadth overlapped significantly suggesting a violation of the competitive exclusion principle, at least in the two niche dimensions measured. While for insectivores and carnivores resources are not likely to be limiting (3 of 4 cases), among frugivores *Carollia perspicillata* was overlapped 99.1% by *C. sowelli*, suggesting that these species may compete. Competition between conspecifics has been documented among *Carollia* spp. before; species may partition resources by incorporating insects into their diet (da Silva *et al.* 2008, York & Billings 2009). Notably, *Carollia perspicillata* are rare in the fauna while elsewhere in the Neotropics they are among the most common species captured, suggesting that *C. sowelli* may be out-competing (and excluding) *C. perspicillata* in some way (Gause 1934).

By examining community structure in this way, I was able to characterize species interactions which otherwise would not be observable. Understanding how so many similar species can coexist and how they partition resources is vital to our understanding of the evolution of these species and ecosystem functioning.

Variation in the Diet of Fruit Bats in a Fragmented Landscape

Examining different populations of three species of frugivorous bats in Brazil's Atlantic Forest, I found habitat patch composition, rather than landscape-wide spatial metrics of fragmentation, were better predictors of variation in diet and niche breadth. Using Akaike's Information Criterion (AIC) and general linear models, I found that a principle component (established in Delciellos *et al.* 2016) which accounted for variation in vertical and horizontal vegetation density (PC2) was the best variable for predicting variation in niche breadth, carbon and nitrogen isotopic ratios in 8 of 12 possible cases. As I predicted, narrow-ranging species (*Carollia perspicillata* and *Sturnira lilium*) were more affected by landscape metrics (e.g., fragment area or isolation) than wide-ranging species (*Artibeus lituratus*).

For the great fruit-eating bat, *Artibeus lituratus*, PC2 was involved in the top set of models for niche breadth (SEA.b), $\delta^{13}C$ and $\delta^{15}N$ explaining 23, 25 and 45 % of variation for each response variable respectively. As *A. lituratus* are rarely recaptured and are known to make long-distance movements (Arnone *et al.* 2016, Esbérard *et al.* 2017) it is unlikely that local fragment composition is impacting diet significantly. It is possible however that bats which are found in densely forested fragments (positive values of PC2) are more likely to seek out denser forests, while those that are found in sparse forest (negative PC2) may prefer similar habitats. Individual preference or other underlying environmental baselines (Popa-Lisseanu *et al.* 2015) may account for the observed variation in diet.

Narrow-ranging Seba's short-tailed bat, *Carollia perspicillata,* and little yellow-shouldered bat, *Sturnira lilium*, were similarly impacted by vegetation density, however both species were impacted by landscape scale metrics particularly in the superhumid season. When fruit is abundant in the humid season, PC2 was the best metric to explain variation in niche

breadth and $\delta^{13}C$, however prediction variation in $\delta^{15}N$ (which may be influenced by insect consumption) was inconclusive. There is likely some metric not accounted for in the models which influences insect consumption in *Carollia* spp. in the humid season. In the superhumid season when preferred fruit resources are limited (Mello *et al.* 2004c, Thies & Kalko 2004b), one of habitat area and isolation (measured as shortest distance to a neighbouring fragment) were involved in half of the top predicted models. Notably however these relationships differed (isolation had a negative effect on *C. perspicillata* and a positive effect on *S. lilium*) as despite being superficially similar (similar size, diet, foraging range, roost selection) these species are biologically different.

It is evident that landscape and habitat composition have significant effects on the diet of narrow- and wide-ranging species of frugivorous bats. Surprisingly, species which are wide-ranging are more likely to be impacted by habitat successional state (i.e., vegetation density) than any other landscape scale metric, while narrow-ranging species are more impacted by landscape in the superhumid season than the humid season when resources are scarce.

Multi-tissue SIA reveals seasonal dietary variability

Assessing the year-round diet of 5 species of bats from both the Neotropics and Paleotropics I found significant variation in $\delta^{15}N$ between tissue types while there were no significant differences in niche breadth. This suggests that while species do not alter their niche breadth (i.e., specialize or generalize) to cope with seasonal resource shortages, some species (particularly frugivores) may shift their trophic niche to include more/fewer insects in their diet depending on the season. Sympatric species appeared to follow the same pattern with an enrichment in $\delta^{15}N$ corresponding to periods with lower fruit availability. Insectivorous Horsfield's leaf-nosed bat, *Hipposideros larvatus*, similarly had differences in $\delta^{15}N$ between

tissue types as diet appeared to remain more-or-less constant throughout the year. Similarly Parnell's mustached bat, *Pteronotous parnelli,* also did not differ significantly in $\delta^{15}N$ except between bone and all other tissues; this suggests that while younger bats may eat whole insects, adults may discard many of the soft-parts of insects in favour of the chitinous exoskeleton which has significantly lower $\delta^{15}N$ than the rest of many insects (DeNiro & Epstein 1981, Herrera, Hobson, Manzo A., *et al.* 2001).

Using this technique, animals do not have to be recaptured to assess temporal variation in diet. With a limited sampling period, and small sample size I was able to elucidate a comprehensive image of diet throughout the year; I was able to assess both individual variability in diet and population level variability utilizing no more than 10 individuals. With known carbon fractionation factors, and/or fractionation factors for other isotopic ratios, this technique can be used to understand more about the way that animals interact with their environment.

Conclusion

Stable isotope analysis is a valuable technique in understanding the diets of tropical bats. Future studies should focus on sampling tissues with known turnover rates (i.e., patagium) and may also use multiple tissues to examine individual variation within a larger population (Bond *et al.* 2016). Experimental studies should be undertaken to assess fractionation rates between tissues for different stable isotope ratios. Additionally, other measures of trophic niche breadth, including the emerging field of microbiome analysis (Ingala *et al.* 2018) are valuable in conjunction with SIA in adding more dimensions to the trophic niche, and further studying niche partitioning between species. The taxonomic and trophic diversity within Chiroptera makes bats an ideal study system for understanding niche theory and particularly how so many similar

species can coexist sympatrically, especially as omnivory is common (Rex *et al.* 2010, Brown 2014).

Other future avenues of research include re-analyzing the community structure data from Belize in the context of phylogenetic niche conservatism. With this guiding ecological principle, I would predict that closer related species should have more niche overlap than those that are less related (Webb *et al.* 2002, Losos 2008). Additionally, examining differences in niche breadth and isotopic ranges between males and females of the same species may point to other ways that these animals are partitioning resources. In cases where my data suggested that there may be competition occurring, further study of these species foraging habits, abundance, and other potential areas of niche overlap (e.g., roosts, foraging area) should be examined in the system.

In Brazil, frugivorous bats are important for seed dispersal of many pioneer fruiting plant species (Howe & Smallwood 1982). While our data suggests that habitat fragmentation does impact the diets of narrow-ranging fruit bats and has less of an effect on wide-ranging species, the much of the details of these differences remain unknown. Seasonality appears to play a major role in the diet of *Carollia perspicillata* (Fleming & Heithaus 1986) however small sample size made these comparisons impossible for *Sturnira lilium* (only abundant in the superhumid season) and *Artibeus lituratus* (only abundant in the humid season). Additionally these three species, while the most abundant, only make up a small fraction of the Chiropteran diversity of the Atlantic Forest (Bergallo *et al.* 2003, Muylaert *et al.* 2017) and many other species may be more dramatically affected by landscape or local scale changes. Future studies should examine the impacts of landscape on diet in other areas and on other species as I have shown that landscape composition does influence biological processes.

Multi-tissue SIA is a valuable technique which has been thus far underutilized. The benefits of exploring both population and individual level variation in diet are evident particularly when compared with 'snapshot' studies sampling only a single tissue. Particularly for species that persist in a seasonal environment, SIA studies in the future should strive to sample tissues with known turnover rates that represent diet in all seasons. In the tropics, this can be achieved without lethal sampling by examining blood (from period of capture; 1-2 day isotopic turnover) and patagium (3-4 month turnover; Dalerum & Angerbjörn 2005). Sampling of potential prey items in the environment can also be done and diet can be determined through SIA mixing models, however in tropical systems this is typically not practical as there is a massive diversity of potential inputs (Phillips 2012).

Understanding trophic niche dynamics as they relate to population and community structure is vital to the understanding of natural systems. The role that bat species play in their ecosystem, while likely far more complex than the two-dimensions presented would suggest, is largely dictated by what they eat and how they might compete for resources. In habitats or seasons when resources are scarce, bats may adapt to survive by shifting their niche (or trophic level) in order to feed on more abundant resources. Stable isotope analysis is a valuable tool in estimating the niche breadths and species interactions of cryptic or elusive species.

Letter of Copyright Permission for Chapter 2

To whom it may concern,

I hereby grant Phillip Oelbaum permission to include the text of his manuscript submitted to the journal Biotropica (BITR-18-346 -"Community structure of a Neotropical bat fauna revealed using stable isotope analysis") in his thesis to be published online in the Univ. Of Waterloo's thesis database. Doing so will not violate copyright - indeed, it is consistent with our policy of encouraging authors to post preprints of manuscripts submitted to our journal.

Respectfully,

Emilio M. Bruna

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Appendix 1 – Supplementary figures of species-level Neotropical bat community structure

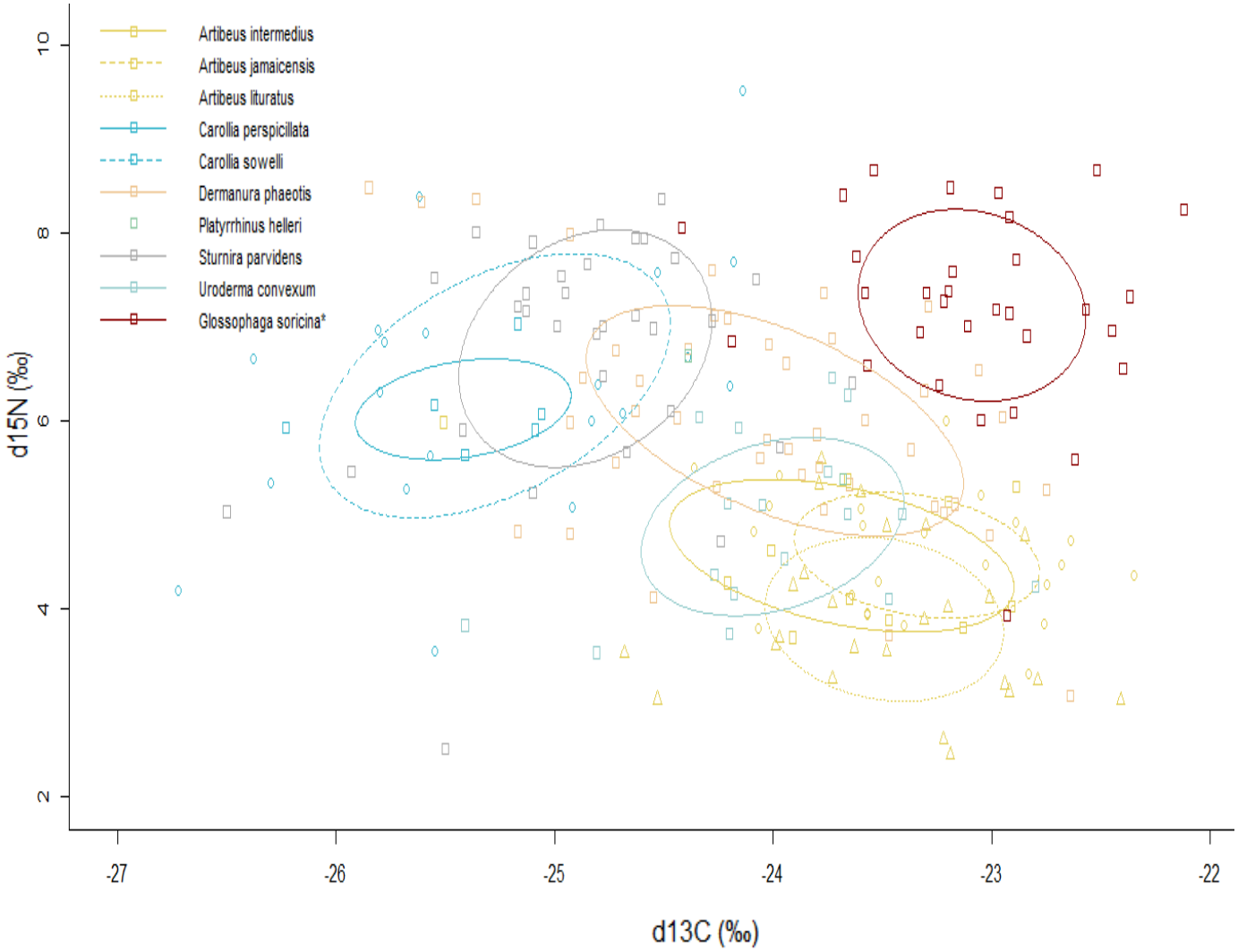

Figure 1 - Species-level community structure of frugivorous (* and nectarivorous) bats sampled in the bat fauna of Lamanai and Ka'kabish, Orange Walk District, Belize April-May 2014, 2016 and 2018 using stable isotope analysis of nitrogen and carbon ratios. Ellipses represent the niche breadth as sample size corrected ellipse area (SEAc) of each species with a sample size ≥3; points mark one individual. Colours denote groupings by genus.

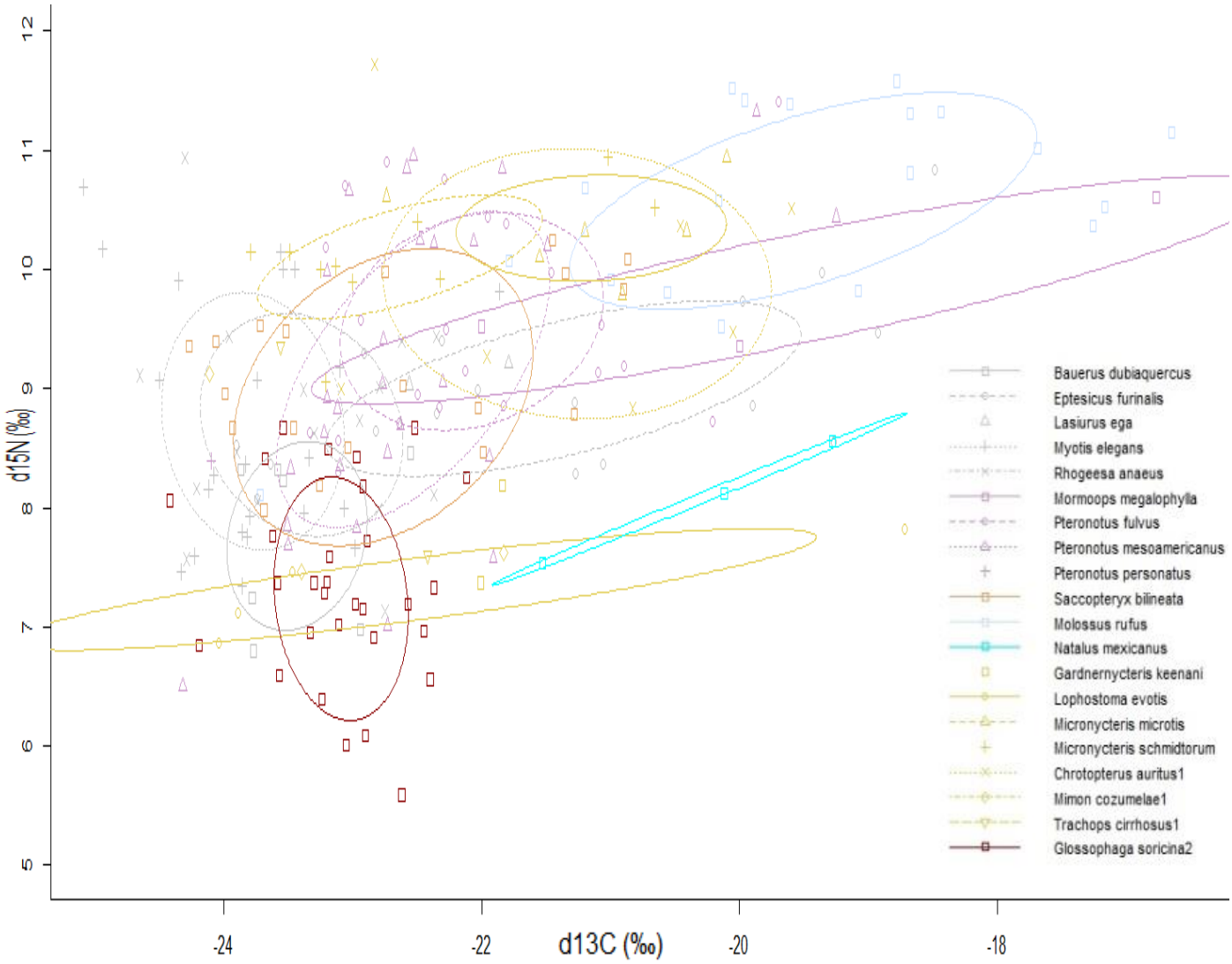

Figure 2 - Species-level community structure of insectivores, carnivores[1] and nectarivorous[2] bats sampled in the bat fauna of Lamanai and Ka'kabish, Orange Walk District, Belize April-May 2014, 2016 and 2018 using stable isotope analysis of nitrogen and carbon ratios. Ellipses represent the niche breadth as sample size corrected ellipse area (SEAc) of each species with a sample size ≥3; points mark one individual. Colours denote groupings by family: Grey – Vespertilionidae, Purple – Mormoopidae, Orange – Emballonuridae, Light Blue – Molossidae, Cyan – Natalidae, Yellow – Phyllostomidae. Maroon is *Glossophaga soricina* (Phyllostomidae) to be consistent with Figure 1.

Appendix 2 – Statistical significance testing (Tukey-Kramer and Kolmogorov-Smirnov test) of isotopic ratios between habitat fragments.

Table 1 – Significance testing of isotopic means and distributions between Reserva Ecológica de Guapiaçu and surrounding habitat fragments in Rio de Janeiro State, Brazil. Q- and P-values are reported for each pairwise comparison. Bolded values are considered statistically significant at $\alpha = 95\%$.

Genus - Season	Frag1	Frag2	Q-values for Tukey-Kramer test		p-values for KS-tests (distribution)	
			$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
Artibeus - Humid						
Q-Critical = 4.13	REGUA	REGUA2	0.50	**4.65**	0.59	0.08
	REGUA	REGUA3	0.44	**7.01**	0.30	> **0.01**
	REGUA	T12	6.33	1.35	> **0.01**	0.87
	REGUA	T13	3.05	1.80	**0.01**	**0.97**
	REGUA	T02	0.57	1.42	0.70	0.12
	REGUA	T21	3.59	**6.20**	**0.02**	> **0.01**
	REGUA	T23	3.96	3.18	**0.01**	0.17
	REGUA	T26	**5.98**	**4.63**	> **0.01**	> **0.01**
	REGUA2	REGUA3	0.03	2.65	0.71	**0.02**
	REGUA2	T12	**5.95**	2.81	> **0.01**	0.16
	REGUA2	T13	2.73	1.39	**0.03**	0.63
	REGUA2	T02	0.91	**4.63**	**0.95**	0.06
	REGUA2	T21	3.21	2.41	0.16	**0.02**
	REGUA2	T23	**4.35**	0.19	**0.02**	**0.98**
	REGUA2	T26	**5.58**	0.24	> **0.01**	0.46
	REGUA3	T12	**5.70**	**5.07**	> **0.01**	**0.01**
	REGUA3	T13	2.67	3.21	0.10	0.08
	REGUA3	T02	0.87	**6.36**	0.72	> **0.01**
	REGUA3	T21	3.11	0.11	0.12	0.60
	REGUA3	T23	**4.19**	2.15	**0.03**	0.07
	REGUA3	T26	**5.32**	2.29	> **0.01**	0.42
	T12	T13	1.72	0.72	0.42	0.93
	T12	T02	**5.16**	2.33	0.05	0.21
	T12	T21	2.08	**4.60**	0.41	**0.01**
	T12	T23	**8.60**	1.96	> **0.01**	0.26
	T12	T26	0.67	2.90	**0.96**	0.14
	T13	T02	2.93	2.61	0.44	0.14
	T13	T21	0.05	3.05	0.78	0.06
	T13	T23	**5.71**	1.01	**0.02**	0.33
	T13	T26	1.26	1.52	0.79	0.50
	T02	T21	3.23	**5.98**	0.82	**0.01**
	T02	T23	2.67	3.72	0.11	**0.02**

	T02	T26	**4.80**	**4.67**	0.23	0.13
	T21	T23	**6.40**	2.06	**0.01**	**0.04**
	T21	T26	1.56	2.11	0.31	0.31
	T23	T26	**8.34**	0.37	> **0.01**	0.50
Carollia – Humid						
Q-Critical = 4.01	REGUA	REGUA2	0.02	1.63	0.54	0.63
	REGUA	REGUA3	0.31	2.58	0.33	0.10
	REGUA	T10	2.26	**5.26**	0.57	0.29
	REGUA	T11	0.59	**6.82**	0.08	0.08
	REGUA	T12	1.45	**5.98**	0.24	**0.01**
	REGUA	T13	**4.42**	1.04	0.24	**0.03**
	REGUA	T19	1.22	1.92	0.09	0.44
	REGUA	T25	0.83	**8.61**	0.12	0.69
	REGUA	T26	0.45	**6.51**	0.56	> **0.01**
	REGUA2	REGUA3	2.90	**5.05**	0.92	> **0.01**
	REGUA2	T10	1.03	**8.69**	0.68	0.14
	REGUA2	T11	1.96	**6.16**	0.06	**0.02**
	REGUA2	T12	**6.56**	3.85	0.47	> **0.01**
	REGUA2	T13	1.96	0.49	0.29	**0.01**
	REGUA2	T19	1.30	**11.26**	> **0.01**	0.06
	REGUA2	T25	3.13	**9.11**	0.22	0.94
	REGUA2	T26	1.45	**15.11**	0.59	> **0.01**
	REGUA3	T10	2.24	**10.72**	**0.98**	0.06
	REGUA3	T11	**5.88**	2.08	**0.02**	> **0.01**
	REGUA3	T12	2.31	**6.82**	0.28	> **0.01**
	REGUA3	T13	0.78	**17.16**	0.09	> **0.01**
	REGUA3	T19	2.37	0.05	> **0.01**	0.43
	REGUA3	T25	1.00	0.30	0.42	> **0.01**
	REGUA3	T26	0.02	**7.36**	0.59	> **0.01**
	T10	T11	0.31	**4.69**	0.10	0.29
	T10	T12	2.26	1.93	0.47	0.12
	T10	T13	0.59	0.47	0.20	0.33
	T10	T19	1.45	**11.53**	0.06	0.06
	T10	T25	**4.42**	**7.91**	0.70	0.14
	T10	T26	1.22	3.43	0.68	**0.01**
	T11	T12	0.83	**8.63**	**0.02**	0.94
	T11	T13	0.45	**5.73**	0.66	0.91
	T11	T19	2.90	1.80	> **0.01**	> **0.01**
	T11	T25	1.03	**4.20**	0.08	**0.04**
	T11	T26	1.96	**13.69**	> **0.01**	0.48
	T12	T13	**6.56**	**10.48**	0.71	0.87
	T12	T19	1.96	1.63	> **0.01**	> **0.01**
	T12	T25	1.30	2.58	0.89	> **0.01**
	T12	T26	3.13	**5.26**	0.12	0.05

	T13	T19	1.45	**6.82**	> **0.01**	> **0.01**
	T13	T25	2.24	**5.98**	0.22	0.05
	T13	T26	**5.88**	1.04	0.11	0.60
	T19	T25	2.31	1.92	> **0.01**	0.18
	T19	T26	0.78	**8.61**	> **0.01**	> **0.01**
	T25	T26	2.37	**6.51**	0.05	> **0.01**
Carollia - Superhumid						
Q-Critical = 3.33	REGUA	T10	0.77	**5.57**	0.80	> **0.01**
	REGUA	T19	2.94	1.62	0.05	0.25
	REGUA	T21	**6.23**	**6.26**	> **0.01**	> **0.01**
	T10	T19	2.43	**5.45**	0.17	**0.01**
	T10	T21	**5.50**	0.31	> **0.01**	0.77
	T19	T21	1.06	**5.82**	0.45	**0.02**
Sturnira - Superhumid						
Q-Critical = 3.41	REGUA	T10	3.21	**6.70**	0.05	> **0.01**
	REGUA	T19	1.31	0.16	0.89	0.91
	REGUA	T21	2.01	2.27	0.42	0.17
	T10	T19	2.09	**6.63**	0.08	**0.02**
	T10	T21	0.56	2.87	0.86	0.29
	T19	T21	1.12	2.33	0.70	0.07

Appendix 3 – Individual isotope data for multiple tissues assessed including repeats

Table 2 – Raw isotopic data for Chapter 4 demonstrating individual level variability in isotopic ratios. Samples with replicates are noted as repeat = "y".

Individual	Genus	Sex	Tissue	$\delta^{13}C$	$\delta^{15}N$	repeat
43735	*Artibeus*	f	hair	-23.61	6.91	n
43735	*Artibeus*	f	patagium	-23.67	7.73	n
43735	*Artibeus*	f	bone	-21.81	8.49	n
43735	*Artibeus*	f	liver	-24.70	7.75	n
43735	*Artibeus*	f	spleen	-24.75	7.11	n
43735	*Artibeus*	f	heart	-24.85	8.18	n
43735	*Artibeus*	f	kidney	-24.84	6.91	n
43741	*Artibeus*	f	hair	-23.14	4.18	n
43741	*Artibeus*	f	patagium	-24.05	5.98	n
43741	*Artibeus*	f	bone	-22.21	6.83	n
43741	*Artibeus*	f	liver	-25.37	6.47	y
43741	*Artibeus*	f	liver	-25.15	5.94	y
43741	*Artibeus*	f	spleen	-25.15	5.26	n
43741	*Artibeus*	f	heart	-25.39	6.49	y
43741	*Artibeus*	f	heart	-25.50	6.49	y
43757	*Artibeus*	m	hair	-23.57	7.16	n
43757	*Artibeus*	m	patagium	-24.23	7.20	n
43757	*Artibeus*	m	bone	-22.84	7.38	n
43757	*Artibeus*	m	liver	-25.49	8.84	n
43757	*Artibeus*	m	spleen	-25.15	6.40	y
43757	*Artibeus*	m	spleen	-25.26	6.05	y
43757	*Artibeus*	m	heart	-25.03	6.43	y
43757	*Artibeus*	m	heart	-25.32	5.82	y
43757	*Artibeus*	m	kidney	-25.38	5.91	n
43760	*Artibeus*	f	hair	-23.90	7.39	n
43760	*Artibeus*	f	patagium	-24.57	7.12	n
43760	*Artibeus*	f	bone	-23.32	7.68	n
43760	*Artibeus*	f	liver	-25.36	6.46	n
43760	*Artibeus*	f	spleen	-25.46	5.61	n
43760	*Artibeus*	f	heart	-25.40	7.39	n
43760	*Artibeus*	f	kidney	-25.67	6.12	n
43775	*Artibeus*	m	hair	-23.83	6.98	n
43775	*Artibeus*	m	patagium	-24.26	7.75	n
43775	*Artibeus*	m	bone	-23.74	7.67	n
43775	*Artibeus*	m	liver	-25.00	7.60	n
43775	*Artibeus*	m	spleen	-25.28	7.17	n

43775	*Artibeus*	m	heart	-25.08	6.82	n
43775	*Artibeus*	m	kidney	-25.49	6.74	n
43779	*Artibeus*	m	heart	-26.33	9.99	n
43816	*Artibeus*	m	hair	-23.27	7.55	n
43816	*Artibeus*	m	patagium	-23.85	8.16	n
43816	*Artibeus*	m	bone	-21.66	7.74	n
43816	*Artibeus*	m	liver	-25.29	8.07	n
43816	*Artibeus*	m	spleen	-25.37	8.07	n
43816	*Artibeus*	m	heart	-25.55	10.01	n
43816	*Artibeus*	m	kidney	-25.35	7.11	n
43816	*Artibeus*	m	kidney	-25.19	7.53	n
43832	*Artibeus*	m	hair	-24.09	3.01	n
43832	*Artibeus*	m	patagium	-24.55	4.57	n
43832	*Artibeus*	m	bone	-22.44	4.64	n
43832	*Artibeus*	m	liver	-25.87	5.48	n
43832	*Artibeus*	m	heart	-25.00	7.01	y
43832	*Artibeus*	m	heart	-25.42	4.62	y
43832	*Artibeus*	m	kidney	-25.27	4.47	y
43832	*Artibeus*	m	kidney	-25.17	4.25	y
43832	*Artibeus*	m	kidney	-25.51	4.40	y
43836	*Artibeus*	m	hair	-23.99	6.13	y
43836	*Artibeus*	m	hair	-24.04	6.02	y
43836	*Artibeus*	m	patagium	-24.24	6.98	n
43836	*Artibeus*	m	bone	-22.76	6.57	n
43836	*Artibeus*	m	liver	-25.40	6.83	n
43836	*Artibeus*	m	heart	-25.16	8.70	n
43836	*Artibeus*	m	kidney	-25.26	6.57	n
43856	*Artibeus*	f	hair	-23.63	7.38	n
43856	*Artibeus*	f	patagium	-24.34	6.88	n
43856	*Artibeus*	f	bone	-23.27	5.63	n
43856	*Artibeus*	f	spleen	-24.99	9.40	n
43868	*Artibeus*	f	hair	-23.52	6.70	n
43868	*Artibeus*	f	patagium	-24.30	7.52	n
43868	*Artibeus*	f	bone	-23.26	6.85	n
43868	*Artibeus*	f	liver	-25.64	8.12	n
43868	*Artibeus*	f	spleen	-25.87	7.94	y
43868	*Artibeus*	f	spleen	-25.48	6.95	y
43868	*Artibeus*	f	heart	-25.27	9.42	n
43868	*Artibeus*	f	kidney	-25.37	6.95	n
43717	*Carollia*	m	hair	-25.68	5.94	n
43717	*Carollia*	m	patagium	-25.31	7.04	n
43717	*Carollia*	m	bone	-24.29	6.83	n
43717	*Carollia*	m	liver	-26.39	6.71	n

43717	*Carollia*	m	spleen	-26.18	7.68	n
43717	*Carollia*	m	heart	-26.36	8.69	n
43717	*Carollia*	m	kidney	-26.08	7.95	y
43717	*Carollia*	m	kidney	-25.92	7.09	y
43719	*Carollia*	f	hair	-26.14	7.23	n
43719	*Carollia*	f	patagium	-25.64	7.18	n
43719	*Carollia*	f	bone	-24.73	7.88	n
43719	*Carollia*	f	liver	-26.29	9.12	n
43719	*Carollia*	f	spleen	-26.08	6.31	n
43719	*Carollia*	f	kidney	-25.86	6.77	n
43720	*Carollia*	f	hair	-25.67	8.10	n
43720	*Carollia*	f	patagium	-25.32	7.65	n
43720	*Carollia*	f	bone	-23.67	9.51	n
43720	*Carollia*	f	liver	-26.09	9.19	y
43720	*Carollia*	f	liver	-25.77	8.84	y
43720	*Carollia*	f	spleen	-25.82	8.82	n
43721	*Carollia*	f	hair	-26.58	7.61	n
43721	*Carollia*	f	patagium	-25.91	7.54	n
43721	*Carollia*	f	bone	-26.20	8.69	n
43721	*Carollia*	f	liver	-26.29	7.61	n
43721	*Carollia*	f	spleen	-25.96	7.39	n
43721	*Carollia*	f	heart	-26.30	8.49	n
43721	*Carollia*	f	kidney	-25.94	6.55	n
43754	*Carollia*	f	hair	-25.43	7.62	n
43754	*Carollia*	f	patagium	-25.20	7.93	n
43754	*Carollia*	f	bone	-24.58	8.30	n
43754	*Carollia*	f	liver	-26.44	7.02	n
43754	*Carollia*	f	heart	-25.32	8.33	n
43754	*Carollia*	f	kidney	-25.36	6.98	n
43765	*Carollia*	m	hair	-26.02	7.94	n
43765	*Carollia*	m	patagium	-25.78	7.98	n
43765	*Carollia*	m	bone	-25.09	8.45	n
43765	*Carollia*	m	spleen	-26.02	6.70	n
43765	*Carollia*	m	kidney	-26.16	6.81	n
43791	*Carollia*	m	hair	-25.32	8.11	n
43791	*Carollia*	m	patagium	-25.04	9.19	n
43791	*Carollia*	m	bone	-23.68	9.32	n
43791	*Carollia*	m	spleen	-26.31	8.20	n
43791	*Carollia*	m	heart	-26.29	10.34	y
43791	*Carollia*	m	heart	-26.40	9.99	y
43791	*Carollia*	m	kidney	-25.58	8.34	n
43792	*Carollia*	m	hair	-25.98	7.25	n
43792	*Carollia*	m	patagium	-25.60	7.54	n

43792	*Carollia*	m	bone	-25.14	8.31	n
43792	*Carollia*	m	heart	-26.29	7.48	n
43792	*Carollia*	m	kidney	-25.91	6.52	n
43793	*Carollia*	m	hair	-26.14	6.84	n
43793	*Carollia*	m	patagium	-25.52	7.59	n
43793	*Carollia*	m	bone	-24.20	6.37	n
43793	*Carollia*	m	liver	-26.25	7.99	
43793	*Carollia*	m	spleen	-26.10	7.04	n
43793	*Carollia*	m	heart	-26.27	8.68	n
43793	*Carollia*	m	kidney	-26.04	7.48	n
43807	*Carollia*	f	hair	-24.89	9.57	y
43807	*Carollia*	f	hair	-24.93	9.41	y
43807	*Carollia*	f	patagium	-24.86	8.47	n
43807	*Carollia*	f	bone	-23.91	10.05	n
43807	*Carollia*	f	liver	-25.00	8.34	y
43807	*Carollia*	f	liver	-25.43	8.28	y
43807	*Carollia*	f	heart	-25.57	8.85	
43807	*Carollia*	f	kidney	-25.31	8.25	
47358	*Cynopterus*	f	hair	-25.73	4.63	n
47358	*Cynopterus*	f	patagium	-25.79	5.10	n
47358	*Cynopterus*	f	bone	-24.02	5.56	n
47358	*Cynopterus*	f	liver	na	na	y
47358	*Cynopterus*	f	liver	-26.22	4.37	y
47358	*Cynopterus*	f	liver	-26.01	4.62	y
47358	*Cynopterus*	f	spleen	-26.24	4.21	n
47358	*Cynopterus*	f	heart	-26.19	6.02	n
47358	*Cynopterus*	f	kidney	-26.07	3.95	n
47371	*Cynopterus*	f	hair	-25.41	4.54	n
47371	*Cynopterus*	f	patagium	-25.50	5.36	n
47371	*Cynopterus*	f	bone	-22.89	6.14	n
47371	*Cynopterus*	f	liver	-26.60	4.26	n
47371	*Cynopterus*	f	spleen	-26.39	3.48	n
47371	*Cynopterus*	f	kidney	-26.63	3.82	n
47372	*Cynopterus*	f	hair	-25.93	5.59	n
47372	*Cynopterus*	f	patagium	-25.19	6.64	n
47372	*Cynopterus*	f	spleen	-26.08	4.19	n
47372	*Cynopterus*	f	spleen	-26.17	5.33	y
47372	*Cynopterus*	f	spleen	-26.02	4.89	y
47372	*Cynopterus*	f	spleen	-26.31	5.28	y
47372	*Cynopterus*	f	heart	-26.10	7.04	n
47372	*Cynopterus*	f	kidney	-26.36	3.73	n
47373	*Cynopterus*	m	hair	-26.75	5.93	n
47373	*Cynopterus*	m	patagium	-25.10	7.58	n

47373	*Cynopterus*	m	bone	-22.84	6.16	n
47373	*Cynopterus*	m	spleen	-25.73	5.76	n
47373	*Cynopterus*	m	heart	-25.42	7.71	n
47373	*Cynopterus*	m	kidney	-25.98	5.22	y
47373	*Cynopterus*	m	kidney	-26.22	5.49	y
47377	*Cynopterus*	m	hair	-25.64	5.57	n
47377	*Cynopterus*	m	patagium	-24.85	5.77	n
47377	*Cynopterus*	m	bone	-25.92	5.64	n
47377	*Cynopterus*	m	liver	-25.37	6.71	n
47377	*Cynopterus*	m	spleen	-25.12	5.29	y
47377	*Cynopterus*	m	spleen	-25.21	5.29	y
47377	*Cynopterus*	m	heart	-25.62	7.20	n
47377	*Cynopterus*	m	kidney	-24.99	5.04	n
47379	*Cynopterus*	f	hair	-25.58	4.36	n
47379	*Cynopterus*	f	patagium	-25.01	5.71	n
47379	*Cynopterus*	f	bone	-22.26	6.18	n
47379	*Cynopterus*	f	liver	-26.30	3.86	n
47379	*Cynopterus*	f	heart	-26.34	6.49	n
47379	*Cynopterus*	f	kidney	-26.11	4.12	y
47379	*Cynopterus*	f	kidney	-26.04	3.89	y
47380	*Cynopterus*	f	hair	-25.60	3.91	n
47380	*Cynopterus*	f	patagium	-25.01	5.17	n
47380	*Cynopterus*	f	bone	-24.21	4.58	n
47380	*Cynopterus*	f	spleen	-25.85	4.06	n
47380	*Cynopterus*	f	heart	-25.71	5.57	n
47380	*Cynopterus*	f	heart	-25.91	5.67	n
47380	*Cynopterus*	f	kidney	-25.75	4.04	n
47383	*Cynopterus*	m	hair	-26.51	4.33	n
47383	*Cynopterus*	m	patagium	-25.22	6.55	n
47383	*Cynopterus*	m	bone	-22.69	6.88	y
47383	*Cynopterus*	m	bone	-22.64	7.25	y
47383	*Cynopterus*	m	liver	-25.94	4.70	n
47383	*Cynopterus*	m	spleen	-25.96	4.12	n
47383	*Cynopterus*	m	heart	-26.44	6.28	n
47383	*Cynopterus*	m	kidney	-25.59	3.70	n
47384	*Cynopterus*	m	hair	-27.38	4.43	n
47384	*Cynopterus*	m	patagium	-25.00	6.97	n
47384	*Cynopterus*	m	bone	-22.38	7.12	n
47384	*Cynopterus*	m	spleen	-26.12	6.12	y
47384	*Cynopterus*	m	spleen	-25.93	6.23	y
47384	*Cynopterus*	m	kidney	-26.07	5.06	n
47389	*Cynopterus*	m	hair	-24.71	5.43	n
47389	*Cynopterus*	m	patagium	-25.06	6.08	n

47389	*Cynopterus*	m	bone	-24.28	6.80	n
47389	*Cynopterus*	m	heart	-25.91	7.10	y
47389	*Cynopterus*	m	heart	-26.67	6.02	y
47389	*Cynopterus*	m	kidney	-26.48	5.78	y
47389	*Cynopterus*	m	kidney	-26.46	4.46	y
47742	*Hipposideros*	m	hair	-21.47	6.07	n
47742	*Hipposideros*	m	patagium	-22.33	7.93	n
47742	*Hipposideros*	m	bone	-21.38	8.54	n
47742	*Hipposideros*	m	liver	-23.24	7.72	n
47742	*Hipposideros*	m	spleen	-23.18	6.35	n
47742	*Hipposideros*	m	heart	-23.75	6.90	n
47742	*Hipposideros*	m	kidney	-23.01	6.76	n
47750	*Hipposideros*	f	hair	-21.98	5.93	n
47750	*Hipposideros*	f	patagium	-23.98	7.22	n
47750	*Hipposideros*	f	bone	-23.06	8.03	n
47750	*Hipposideros*	f	liver	-24.25	6.31	n
47750	*Hipposideros*	f	spleen	-24.91	5.55	n
47750	*Hipposideros*	f	heart	-24.82	7.04	n
47750	*Hipposideros*	f	kidney	-24.72	5.94	n
47756	*Hipposideros*	m	hair	-22.16	5.14	n
47756	*Hipposideros*	m	patagium	-23.75	6.75	n
47756	*Hipposideros*	m	bone	-23.14	7.50	n
47756	*Hipposideros*	m	liver	-24.64	5.87	n
47756	*Hipposideros*	m	kidney	-24.54	5.47	n
47771	*Hipposideros*	m	heart	-26.45	5.31	n
47801	*Hipposideros*	f	hair	-21.83	6.44	n
47801	*Hipposideros*	f	patagium	-22.83	7.55	n
47801	*Hipposideros*	f	bone	-21.06	8.71	n
47801	*Hipposideros*	f	spleen	-23.90	6.55	n
47801	*Hipposideros*	f	heart	-24.23	8.19	n
47801	*Hipposideros*	f	kidney	-24.25	7.05	y
47801	*Hipposideros*	f	kidney	-24.24	6.75	y
47808	*Hipposideros*	f	hair	-21.79	5.93	n
47808	*Hipposideros*	f	patagium	-23.62	7.40	n
47808	*Hipposideros*	f	bone	-21.63	8.36	n
47808	*Hipposideros*	f	heart	-24.82	7.30	n
47808	*Hipposideros*	f	kidney	-24.42	6.67	n
47818	*Hipposideros*	m	hair	-21.51	5.23	n
47818	*Hipposideros*	m	patagium	-23.21	7.47	n
47818	*Hipposideros*	m	bone	-21.07	7.34	n
47818	*Hipposideros*	m	liver	-23.92	6.53	n
47818	*Hipposideros*	m	spleen	-24.36	4.94	y
47818	*Hipposideros*	m	spleen	-24.60	4.95	y

47818	*Hipposideros*	m	heart	-24.53	6.70	n
47818	*Hipposideros*	m	kidney	-24.42	5.81	n
47827	*Hipposideros*	f	hair	-20.36	8.17	n
47827	*Hipposideros*	f	patagium	-22.67	9.11	n
47827	*Hipposideros*	f	bone	-23.27	7.02	n
47827	*Hipposideros*	f	spleen	-23.96	7.88	n
47827	*Hipposideros*	f	heart	-24.43	8.72	n
47835	*Hipposideros*	m	hair	-21.63	5.32	n
47835	*Hipposideros*	m	patagium	-22.75	7.00	n
47835	*Hipposideros*	m	bone	-21.30	7.62	n
47835	*Hipposideros*	m	spleen	-23.53	5.69	n
47835	*Hipposideros*	m	heart	-24.46	7.40	n
47843	*Hipposideros*	f	hair	-20.90	5.10	y
47843	*Hipposideros*	f	hair	-21.16	5.04	y
47843	*Hipposideros*	f	liver	-23.89	6.54	n
47843	*Hipposideros*	f	heart	-25.15	4.07	n
47850	*Hipposideros*	m	hair	-21.26	5.62	n
47850	*Hipposideros*	m	patagium	-23.24	7.58	n
47850	*Hipposideros*	m	liver	-24.99	6.78	n
47890	*Hipposideros*	m	heart	-25.45	6.60	n
48540	*Hipposideros*	m	kidney	-22.89	8.83	n
34377	*Nanonycteris*	m	hair	-22.91	12.56	y
34377	*Nanonycteris*	m	hair	-22.88	9.13	y
34377	*Nanonycteris*	m	hair	-22.81	9.15	y
34377	*Nanonycteris*	m	patagium	-23.20	10.35	y
34377	*Nanonycteris*	m	patagium	-23.13	12.14	y
34377	*Nanonycteris*	m	bone	-22.96	4.29	n
34377	*Nanonycteris*	m	liver	-23.01	10.88	n
34377	*Nanonycteris*	m	heart	-23.18	11.97	y
34377	*Nanonycteris*	m	heart	-23.40	11.62	y
34377	*Nanonycteris*	m	kidney	-22.57	9.64	n
34378	*Nanonycteris*	f	hair	-22.27	8.25	y
34378	*Nanonycteris*	f	hair	-23.70	9.28	y
34378	*Nanonycteris*	f	patagium	-22.84	10.47	y
34378	*Nanonycteris*	f	patagium	-23.13	8.76	y
34378	*Nanonycteris*	f	bone	-21.40	9.50	n
34378	*Nanonycteris*	f	liver	-23.45	9.10	n
34378	*Nanonycteris*	f	heart	-23.40	9.99	n
34378	*Nanonycteris*	f	kidney	-22.70	8.23	n
42540	*Pipistrellus*	f	heart	-22.94	9.23	n
42542	*Pipistrellus*	m	liver	na	na	y
42542	*Pipistrellus*	m	liver	-23.72	10.62	y
42542	*Pipistrellus*	m	kidney	-24.20	10.26	n

51120	*Pteronotus*	f	hair	-23.47	7.26	n
51120	*Pteronotus*	f	patagium	-24.00	9.03	n
51120	*Pteronotus*	f	bone	-23.07	11.17	n
51120	*Pteronotus*	f	liver	-25.05	7.20	n
51120	*Pteronotus*	f	heart	-25.53	6.63	n
51120	*Pteronotus*	f	kidney	na	na	y
51120	*Pteronotus*	f	kidney	-25.07	6.36	y
51121	*Pteronotus*	m	hair	-23.37	6.67	n
51121	*Pteronotus*	m	patagium	-26.18	7.53	n
51121	*Pteronotus*	m	bone	-24.58	11.33	n
51121	*Pteronotus*	m	liver	-25.27	5.39	n
51121	*Pteronotus*	m	spleen	-24.80	4.11	y
51121	*Pteronotus*	m	spleen	-25.02	4.06	y
51121	*Pteronotus*	m	heart	-25.71	5.31	n
51121	*Pteronotus*	m	kidney	-25.03	4.68	n
51164	*Pteronotus*	m	patagium	-24.74	7.78	n
51164	*Pteronotus*	m	bone	-25.54	11.49	n
51164	*Pteronotus*	m	spleen	-25.16	4.48	n
51164	*Pteronotus*	m	heart	-25.75	5.82	n
51164	*Pteronotus*	m	kidney	-25.41	5.28	n
51194	*Pteronotus*	m	liver	-24.70	5.95	n
51198	*Pteronotus*	f	hair	-23.63	5.21	n
51198	*Pteronotus*	f	bone	-24.36	11.57	n
51198	*Pteronotus*	f	liver	-25.01	5.57	n
51198	*Pteronotus*	f	spleen	-25.54	5.35	y
51198	*Pteronotus*	f	spleen	-25.18	4.60	y
51198	*Pteronotus*	f	heart	-25.42	6.28	n
51206	*Pteronotus*	m	hair	-23.18	7.84	n
51206	*Pteronotus*	m	patagium	-24.44	7.91	n
51206	*Pteronotus*	m	bone	-23.64	10.52	n
51206	*Pteronotus*	m	liver	-25.07	5.93	n
51206	*Pteronotus*	m	heart	-25.37	5.75	n
51206	*Pteronotus*	m	kidney	-25.46	5.65	n
51208	*Pteronotus*	f	hair	-23.73	6.76	n
51208	*Pteronotus*	f	patagium	-24.54	8.41	n
51208	*Pteronotus*	f	bone	-23.76	12.08	n
51208	*Pteronotus*	f	liver	-24.92	6.60	n
51208	*Pteronotus*	f	spleen	-23.56	5.54	n
51208	*Pteronotus*	f	heart	-25.81	6.63	y
51208	*Pteronotus*	f	heart	-25.89	6.08	y
51208	*Pteronotus*	f	kidney	-25.37	6.47	n
51211	*Pteronotus*	m	hair	-23.18	11.19	n
51211	*Pteronotus*	m	patagium	-24.41	9.52	n

51211	*Pteronotus*	m	bone	-25.41	11.03	n
51211	*Pteronotus*	m	liver	-24.74	7.81	n
51211	*Pteronotus*	m	spleen	-25.00	6.50	n
51211	*Pteronotus*	m	heart	-25.33	8.00	n
51211	*Pteronotus*	m	kidney	-24.39	7.21	n
51246	*Pteronotus*	f	hair	-24.39	5.05	n
51246	*Pteronotus*	f	patagium	-24.97	7.94	n
51246	*Pteronotus*	f	bone	-25.56	11.22	n
51246	*Pteronotus*	f	liver	-25.23	5.65	y
51246	*Pteronotus*	f	liver	-25.29	5.52	y
51246	*Pteronotus*	f	spleen	-25.23	5.88	n
51246	*Pteronotus*	f	heart	-26.18	5.35	n
51246	*Pteronotus*	f	kidney	-25.69	4.74	n
51249	*Pteronotus*	m	hair	-23.30	6.80	n
51249	*Pteronotus*	m	patagium	-24.41	8.49	n
51249	*Pteronotus*	m	bone	-24.02	11.98	n
51249	*Pteronotus*	m	heart	-25.21	6.62	n
51249	*Pteronotus*	m	kidney	-25.18	6.13	n
51263	*Pteronotus*	m	hair	-23.40	7.13	n
51263	*Pteronotus*	m	patagium	-24.59	7.36	n
51263	*Pteronotus*	m	bone	-22.95	10.00	n
51263	*Pteronotus*	m	liver	-24.58	6.31	n
51263	*Pteronotus*	m	spleen	-24.66	6.16	n
51263	*Pteronotus*	m	heart	-25.59	6.70	n
51263	*Pteronotus*	m	kidney	-24.86	5.80	n