Spring 5-2012

# Host Specificity of Ecuadorian Bat Flies (Diptera: Streblidae)

Eric Stamper
*Western Kentucky University*, eric.stamper829@topper.wku.edu

## Recommended Citation

Stamper, Eric, "Host Specificity of Ecuadorian Bat Flies (Diptera: Streblidae)" (2012). *Honors College Capstone Experience/Thesis Projects.* Paper 358.
http://digitalcommons.wku.edu/stu_hon_theses/358

# HOST SPECIFICITY OF ECUADORIAN BAT FLIES (DIPTERA: STREBLIDAE)

A Capstone Experience/Thesis Project

Presented in Partial Fulfillment of the Requirements for

the Degree Bachelor of Sciences with

Honors College Graduate Distinction at Western Kentucky University

By

Eric Austin Stamper

*****

Western Kentucky University

2012

CE/T Committee:

Dr. Carl Dick, Advisor

Dr. Cheryl Davis

Dr. Courte Voorhees

Approved by

______________________________

Advisor

Department of Biology

# ABSTRACT

Diptera: Streblidae are ectoparasites of bat populations found in many locations throughout the world. These ectoparasites are generally known as bat flies. They attach themselves to the wing membranes and bodies of bats to bite and feed on their blood. Using a large sample consisting of over 2,000 bats and 6,000 bat flies, I have conducted a study of the degree of host specificity of these ectoparasites. Host specificity is a measurement of the degree to which a particular parasite is restricted to its host or hosts. Here I find evidence to support more recent findings that bat flies are highly host specific. Not a single bat fly species was found to have more than four species as primary hosts or a specificity index value greater than 3.3012, and most fly species were restricted to one or two closely related host species. This is certainly considered highly host specific by parasitological standards. Research on parasite-host associations promises to increase our knowledge of both parasite and host groups, but also the myriad of ecological, evolutionary, and epidemiological properties that emerge from the intimate parasite-host relationships.

Key Words: Bat Fly, Host Specificity, Parasitic Relationships, Specificity Index

Dedicated to my Mother and Father, who I know have not had the easiest time with me, but their continued support has been essential to my success.

# ACKNOWLEDGMENTS

I would first like to acknowledge my advisor, Dr. Carl Dick. Without him this project would have been impossible from collecting and processing data to showing me the standards of successful scientific writing. I cannot thank him enough for providing me with numerous opportunities and making my final year at Western one full of academic triumphs.

Secondly, I would also like to thank the many teachers and professors who have inspired me to enjoy science as much as I do to this day.

Finally, I would acknowledge the WKU honors college, which is also responsible for pushing me towards this project and helping to make college a truly rewarding experience.

# VITA

September 6, 1989 ...................................................................... Born – Lexington, KY

2008.............................................................................................. North Oldham High School,
Goshen, Kentucky

2011.............................................................................................. Student Researcher, Biology
Department, Western Kentucky University

# FIELDS OF STUDY

Major Field: Biology

Second Major Field: Chemistry

# TABLE OF CONTENTS

Chapters:

# LIST OF FIGURES

# CHAPTER 1

# INTRODUCTION

Parasitism is the most common form of lifestyle in the animal kingdom. It is so successful that it has evolved individually in nearly every phylum of animals (Roberts et al. 2009). Because parasites are always associated with another species, they are categorized into “endoparasites” (those living inside the host’s body) and “ectoparasites” (those living on the outside of the host’s body) (Roberts et al. 2009). Research into blood-feeding ectoparasites, such as bat flies, is important due to the fact that many have the ability to infect humans, infect our livestock and food, or to serve as vectors for zoonotic diseases (Roberts et al. 2009). Investigation of ectoparasites also provides insight into the areas of ecology and evolution. The intimate relationship between parasite and host often leads to interesting evolutionary outcomes, including morphological and behavioral adaptation, host specificity, and perhaps even commensalism. By studying parasitic relationships, ecologists and parasitologists can reevaluate previously understood host-parasite relationships and shed new light on ancient biological associations (Brooks and McLennan 1993).

Host specificity is one of the more intriguing emergent properties of the host-parasite association. It is a measurement of the degree to which a particular parasite is restricted to its host or hosts (Poulin 1998; Dick and Patterson 2007). A highly host specific parasite will only be able to survive and reproduce on one particular (specific) host species, whereas a non-host specific parasite infests multiple, unrelated host species. These are the extremes of host specificity, and many host-parasite associations show some intermediate degree of specificity. Understanding a parasitic species' host specificity can reveal various facts about the relationship with its host. These include its level of intimacy with the host, the likelihood for evolutionary patterns and connections with its host, and even its ability to transfer pathogens among hosts. Non- or low-host specific parasites are more likely to distribute pathogens among groups of different organisms because of their ability to infect multiple host species.

Bat flies exhibit a degree of habitat specificity, living on the wing and tail membranes or in the fur of the bats that they infest (Dick and Patterson 2006). There, they feed on the blood of bats by biting them and drinking. Bat flies reproduce sexually with the eggs being fertilized in the female and larval development also occurring in the female. After molting twice the third-instar larva is deposited onto the roost substrate where it immediately forms a puparium. After about three to four weeks of pupal development, the adult fly emerges and begins to search for a host (Dick and Patterson 2006). Originally, based off of this behavior it was thought that male bat flies would never have to leave a host unless it choose to switch hosts, whereas female bat flies must necessarily leave the host each time she deposits a larva for development. However, we are becoming increasingly aware that male flies leave their hosts as well (Dick and Patterson 2006; Dittmar et al. 2011).

Bat flies exhibit multiple morphological and behavioral adaptations to finding hosts, attaching to hosts, and to evading their attempts at removal. Most bat flies are capable of moving rather quickly on and around their host. Many species even possess the ability to fly short distances. Many bat flies (e.g. Nycteribiids and the Streblidae) possess ctenidia or comb-like structures. As in fleas, these are used by the insect to catch and attach to the fur of bats and prevent them from being stroked back off of the host's body. Moreover, the setae of most bat flies is strong and stout, almost spine like, which is assumed to aid the insect in holding fast to the host bat. The most important mode of attachment for the bat fly is the tarsal claws. When flexed these claws have the ability to grasp both hair and body membrane with surprising strength. In fact grasping by the tarsal claws causes many live bat flies to be rather difficult to remove from the host (Dick and Patterson 2006).

The degree of host specificity among bat flies has been a topic of debate for several decades (Jobling 1949; Wenzel et al. 1966; Wenzel 1976; ter Hofstede et al. 2004; Dick 2007; Dick and Patterson 2007). Originally, bat flies were thought to be relatively non-host specific parasites due to the motility of bats and the fact that it is very common for several species of bat to inhabit the same space while roosting (e.g. large caves housing multiple species of bats; Jobling 1949). However, the historical treatments of host specificity among bat flies relied on poorly or haphazardly collected data, collected by people not interested in specificity. Such lackadaisical sampling increased the potential for sample-to-sample contamination and other sources of human error. Poor sampling dynamics contributed to early conclusions of a lack of host specificity in bat flies. This has been attributed mainly to a lack of awareness about the necessity to keep samples isolated and the use of other means to tightly control the collection of host and parasite (Dick and Patterson 2007; Dick 2007). More recent surveys and experiments have recognized this issue, and precautions have been taken to minimize contamination of parasites to non-primary hosts (Gettinger 1992; Presley 2004; Dick and Gettinger 2005).

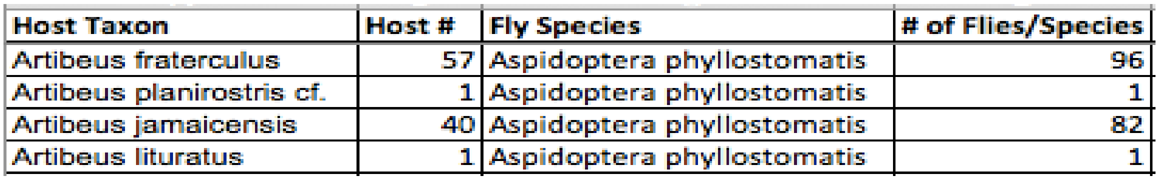
One concern for humans when studying bat flies is their potential ability to transfer human pathogens among bats. As shown by Dr. Hume Field with the Hendra virus in Australia, bats have the potential to be reservoir species, meaning they can house pathogens that have the potential to infect humans (Leroy et al. 2005; Roberts et al. 2009; Field 2004). This concern is especially acute for bat species that are likely to come in contact with humans (e.g. house-inhabiting freetail bats, old world fruit bats) or livestock (e.g. vampire bats). In this study, the parasite-host specificity of bat flies from Ecuador was examined and evaluated shedding light into the host and parasite relationship, and giving implications for the field of epidemiology by gauging the potential risks for the transfer of zoonotic diseases by bat flies.

# CHAPTER 2

## MATERIALS, METHODS, AND RESULTS

The most direct way to study the host specificity of a parasitic population is to numerically evaluate the values of the number of individuals of a parasite species living on particular host species. For this study, bats from the country of Ecuador were used as the host species and the bat flies sampled from them were used as the parasitic species. More than 2,000 bats and over 6,000 bat flies were collected from numerous localities and across Ecuador (Table 3, Figure 5) for a total of 77 bat species and 97 bat fly species. The first step for analyzing the collected data was establishing a set of acceptable parameters for the samples to ensure they could be numerically analyzed. Using data from host or parasite species that were sampled in very small numbers could lead to spurious results. Therefore, it was determined that only bat fly samples with greater than five bat individuals of any species and 20 bat flies of the same species would meet the required sample size in order to yield valid results.

**Figure 1. Example of single fly species (*Aspidoptera phyllostomatis*) to illustrate sampling parameters**

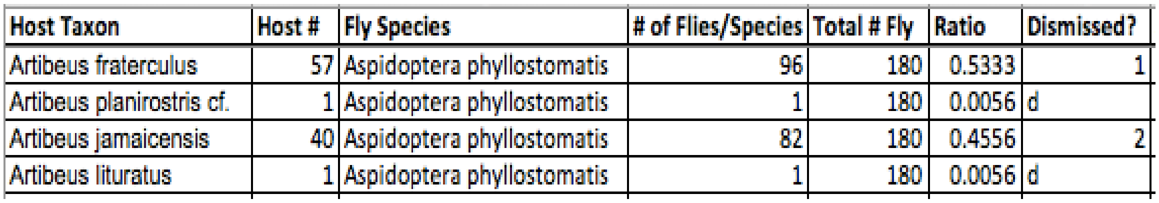


| Host Taxon | Host # | Fly Species | # of Flies/Species |
|---|---|---|---|
| Artibeus fraterculus | 57 | Aspidoptera phyllostomatis | 96 |
| Artibeus planirostris cf. | 1 | Aspidoptera phyllostomatis | 1 |
| Artibeus jamaicensis | 40 | Aspidoptera phyllostomatis | 82 |
| Artibeus lituratus | 1 | Aspidoptera phyllostomatis | 1 |

For example, Figure 1 depicts the fly species *Aspidoptera phyllostomatis*, which had four potential host associations. However, only two host species meet the established sample size parameters Accordingly, fly records from both *Artibeus planirostris cf.* and *Artibeus lituratus* were dismissed because each represented fewer than five host individuals for this fly species. These parameters were chosen in order to reduce spurious effects of small sample size. After filtering through these parameters, I was left with informative data to conduct a numerical evaluation of the host specificity using proportions of individuals of bat fly species found on particular bat species (Table 1).

Table 1 shows all of the bat and bat fly sample information collected from Ecuador that met the sample size criteria. It includes fifty-seven bat species (out of an original total of 77) and forty-two bat fly species (out of an original total of 97). In regard to host specificity, an important number is the final ratio of bat fly species abundance across host species. This ratio represents the proportion of individuals of a particular bat fly species on any given host species.

**Figure 2. Example of *Aspidoptera phyllostomatis* illustrating primary host ratio**



| Host Taxon | Host # | Fly Species | # of Flies/Species | Total # Fly | Ratio | Dismissed? |
|---|---|---|---|---|---|---|
| Artibeus fraterculus | 57 | Aspidoptera phyllostomatis | 96 | 180 | 0.5333 | 1 |
| Artibeus planirostris cf. | 1 | Aspidoptera phyllostomatis | 1 | 180 | 0.0056 | d |
| Artibeus jamaicensis | 40 | Aspidoptera phyllostomatis | 82 | 180 | 0.4556 | 2 |
| Artibeus lituratus | 1 | Aspidoptera phyllostomatis | 1 | 180 | 0.0056 | d |

For example, figure 2 illustrates primary host ratio data for the fly species *Aspidoptera phyllostomatis*. The ratio is calculated by dividing the number of individual flies per host species by the total number of fly individuals collected. The resulting ratio is then used to determine primary host associations, and distinguish them from non-primary associations, which were likely caused by human error or chance (Dick 2007). Fly species that are absolutely host specific have a value of one because all individuals of that particular bat fly species were collected from a single host species. However, as is always true when sampling from nature, there are bound to be errors or discrepancies that need to be accounted for and either dismissed due to numerical irrelevance or explained using some forms of logic and reasoning.

In order to account for sampling errors or discrepancies caused by sampling contamination, a set of parameters was employed to determine what qualified as being a “valid” or “true” association between bat flies and their hosts. For this criterion I decided that a cut off of 0.05 of the ratio previously described was reasonable. Indeed, 0.05 is the typical cutoff for significance in statistical tests. It is also a reasonable cut off for this ratio-based assessment of primary host association, because it reinforces my chosen parameters for sample size. While exclusion of rare taxa decreases the likelihood of spurious results due to small sample size, the 0.05 cutoff for primary host associations greatly decreases the possibility that random human error will bias an assessment of host specificity. Moreover, this level has been used by other workers assessing specificity in host-parasite associations (Presley 2011), making results of my project comparable to other such projects. Based on this cutoff level, when the number of any given fly species on any given host species is less than 5% of the total number of individuals collected, I will dismiss the record, as it has a high probability of having been caused by sampling contamination events (Dick 2007). Thus, any bat species hosting fewer than 5% of the total number of bat flies for a particular species are not considered a true host, rather just an accidental or temporary host. Those bat species that hosted greater than 5% of the total number of fly individuals of a given species are deemed a "primary" host. After applying this guideline it was found that out of 42 bat fly species, 17 bat fly species were host specific to one host species (monoxenous), 15 bat flies were host specific to two host species (stenoxenous), seven bat flies were host specific to three host species (oligoxenous), and three bat fly species were host specific to four host species (polyxenous) (Table 2). This means that 76% of the bat fly species sampled were host specific to one or two hosts while 24% were specific to three or four hosts. Not a single species was so non-specific that they parasitized a number of host species greater than four.

Because standardization of collection protocol has been shown to influence the outcomes of parasite-host specificity studies (Dick 2007), I evaluated the Ecuadorian data in two sets. One set, the total data (as described above), included all samples from multiple collection events over multiple years in Ecuador, some of which are old and employed little if any control over sampling. These data were collected by numerous individuals, who lacked parasitological training, and who were less likely to be aware of the necessity for sampling protocols to ensure true primary host associations were determined. The second set is a subset of the total data that included only samples from one large but recent collection (Sowell Expedition) where all of the sampling protocols were known, several appropriate measures were taken to avoid sampling error, and all samples were collected by only two people (Dr. Carl Dick, and a student under his direct supervision). The

Sowell data was collected by a trained parasitologist with a keen awareness of the necessity of proper sampling protocols to ensure true primary host associations were determined. The collecting methods involved for the Sowell data were at all times geared toward keeping host bat individuals and their associated parasites separate at all points of collection, greatly decreasing the likelihood of host-host contamination of ectoparasite individuals. Evaluating these data in two sets that differed in degree of sampling control should aid in understanding the degree of host specificity of these bat flies, and allow me to assess whether sampling conditions influence the degree of host specificity observed for these bat flies. A finding demonstrating increased specificity among the more controlled Sowell Expedition samples would support the idea that many of the early findings on bat fly host specificity need to be scrutinized and reevaluated.

Using the same parameters for determining primary host associations, the analysis was applied to samples collected during a single expedition in Ecuador (Sowell Expedition). This expedition was conducted in 2004 and great care was taken to prevent sampling contamination of flies to non-primary hosts. This single collection includes more than half the data from the entire Ecuadorian dataset including 32 bat species and 30 bat fly species, but is considered less likely to have errors due to contamination or misidentification. When using only the data from this expedition, a picture of even greater host specificity emerges. It was found that out of 30 bat fly species, 17 were monoxenous, 10 were stenoxenous, and three were oligoxenous. Using only the data from the controlled survey, no fly species showed polyxenous host associations. This means that 57% were completely host specific, 33% were specific to only two hosts, and 10% were specific to three hosts.

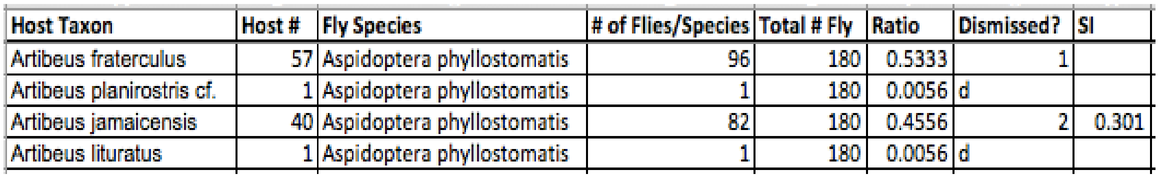
Clearly, these results suggest that Ecuadorian bat fly species are quite specific to individual species of bats, and are consistent with emerging consensus of specificity evaluations from elsewhere in the Neotropical region (Wenzel et al. 1966; Wenzel 1976; Dick and Gettinger 2005; Dick 2007). However, given this specificity and the likelihood that bat flies have speciated in concert with their hosts (Patterson et al. 1998), the degree of host relatedness must be accounted for. Many patterns in ecology and evolution are the result of phylogenetic history (Felsenstein 1985) and this is certainly true in obligate host-parasite relationships such with the bat fly that is dependent on the bat for survival.

A parasite infesting multiple host species of the same genus must be considered more host specific than a parasite infesting multiple host species belonging to different genera (Brooks and McLennan 1993). The reasoning would apply to a parasite infesting two different genera versus a parasite infesting two different families of hosts. Although methods exist to account for phylogenetic relatedness (Phylogenetic Independent Contrasts; Felsenstein 1985), we currently lack phylogenies for streblid bat flies, making such analyses impossible at this point in time. However, when faced with such shortcomings, numerous authors have employed Linnean taxonomy as a surrogate for phylogeny (Krasnov et al. 2009). This allows for a reasonably thorough assessment of how phylogeny interacts with interpretations of host specificity. One popular method that employs taxonomy as a surrogate for phylogeny is called the Specificity Index (SI).

The specificity index is calculated using software that incorporates the hosts' species, genera, families, orders, and classes, generating a numerical value for host specificity (Caira et al. 2003). A parasite that infects a single host species will have a specificity index value of zero and a rank of one. An example of this from Ecuadorian bat flies is the nycteribiid species *Basilia tiptoni*. Notice how a sample with a ratio to the number of bat flies on a host species of one will always give a value of zero for the specificity index. Also and in general, bat fly species with ratios closer to one will have lower scores on the specificity index. A parasite that infects two host species belonging to the same host genus will have a specificity index value of 0.301 and a rank of two. This can be seen in the data for the bat fly species *Aspidoptera falcata*. A parasite that infects two host species belonging to two host genera will have a specificity index value of 3.0004 and a rank of 1001. An example of this in the data is the bat fly species *Exastinion clovisi*. Notice how an increase in number of host species has relatively little effect on specificity index value and rank as compared to an increase in the number of host genera. Increases in number at higher levels of classification have a much greater effect. In Ecuador, there was not a single bat fly species that infected two different families of bat.

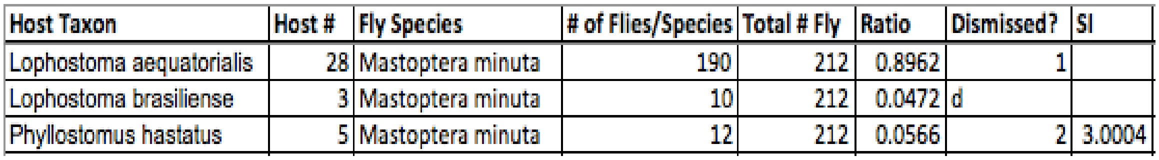
The host specificity index for each Ecuadorian bat fly species was calculated (Table 2). Overall, it was found that 33 out of 42 (79%) of the bat fly species had a specificity index of less than one. This indicates that the majority of bat fly species did not infect any bats belonging to different genera. Nine of 42 (21%) of the bat fly species had an SI value greater than three, indicating that they infect at least two different genera of bats.

Figure 3. Example of *Aspidoptera phyllostomatis* with specificity index value.



| Host Taxon | Host # | Fly Species | # of Flies/Species | Total # Fly | Ratio | Dismissed? | SI |
|---|---|---|---|---|---|---|---|
| Artibeus fraterculus | 57 | Aspidoptera phyllostomatis | 96 | 180 | 0.5333 | 1 | |
| Artibeus planirostris cf. | 1 | Aspidoptera phyllostomatis | 1 | 180 | 0.0056 | d | |
| Artibeus jamaicensis | 40 | Aspidoptera phyllostomatis | 82 | 180 | 0.4556 | 2 | 0.301 |
| Artibeus lituratus | 1 | Aspidoptera phyllostomatis | 1 | 180 | 0.0056 | d | |

Figure 4. Example of *Mastoptera minuta* with specificity index value.



| Host Taxon | Host # | Fly Species | # of Flies/Species | Total # Fly | Ratio | Dismissed? | SI |
|---|---|---|---|---|---|---|---|
| Lophostoma aequatorialis | 28 | Mastoptera minuta | 190 | 212 | 0.8962 | 1 | |
| Lophostoma brasiliense | 3 | Mastoptera minuta | 10 | 212 | 0.0472 | d | |
| Phyllostomus hastatus | 5 | Mastoptera minuta | 12 | 212 | 0.0566 | 2 | 3.0004 |

For an example of calculating the SI, figures 3 and 4 illustrate two different fly species, each of which has two primary host associations. However, *Aspidoptera phyllostomatis*' hosts (Figure 3) are congeneric, making it a more host specific parasite than *Mastoptera minuta* whose hosts belong to two different genera. The idea behind this is that because genera are more widely separated phylogenetically than are species, so too should be the species of parasites harbored by each. This explains why the specificity index software gives a value of 0.301 (less than one) for *Aspidoptera phyllostomatis* and a value of 3.0004 (greater than one) for *Mastoptera minuta.* When focused only on the Sowell Expedition dataset, these analyses reveal an even greater degree of host specificity than was observed for the total dataset. For the Sowell data, fully 28 out of 30 (93.3%) of the bat fly species had specificity indices less than one, and only 2 out of 30 (6.7%) of the bat fly species showed specificity indices greater than three.

These data indicate that Ecuadorian bat flies are highly host specific parasites. Moreover, they indicate that our assessment of host specificity is increased when we focus on a single, carefully controlled set of data. Because being limited to only one host species is considered absolute host specificity, a parasite that has four host species, particularly when they all belong to the same genus, is still considered to be highly host specific from an ecological, taxonomical, and parasitological viewpoint. This becomes increasingly obvious when one compares this to other parasites (e.g. ticks and chiggers) that have the ability to infect nearly any species of mammal (or even most vertebrate animals) that they might encounter (Roberts et al. 2009). Results of the specificity index calculations support the notion of specificity above the species level, and provide a numerical value for the level of host specificity. Therefore, even the least host specific Ecuadorian bat fly species analyzed in these data would have to be considered highly host specific, relative to many other parasite groups. These results have interesting implications for humans residing near these bat fly populations and even more interesting implications for the bats infested with these parasite populations.

# CHAPTER 3

# DISCUSSION

The results of this study demonstrate unequivocally that bat flies are highly host specific. These results are in support of previous recent studies for other bat fly populations (ter Hofstede et al. 2004; Dick and Patterson 2007; Dick 2007), and upholds the trend that increasing levels of control on collections of mammals and ectoparasites is concomitant to an increased assessment of host specificity in certain parasite groups (Jobling 1949; Wenzel et al. 1966; Wenzel 1976).

These results are even more compelling when considered within the paradigm of host specificity for obligate versus facultative parasites. Facultative parasites are parasites that may be parasitic on another organism but can exist in free-living form as well (Roberts et al. 2009). Bat flies are obligate parasites, meaning they are dependent on their host for survival (Dick and Patterson 2006). Parasites that are obligate are generally more specific than facultative parasites. However, many obligate parasites easily break down their primary host associations in the absence of dispersal barriers (e.g. bat bugs; Dick et al. 2009). Considering how bats roost in colonies often consisting of multiple bat species in close proximity, there are few dispersal barriers present for bat flies preventing them from infesting multiple species. Bat flies are also highly mobile. They are capable of moving rapidly on and off the host. Many Streblidae (97% possess wings and only 10.9%, 24 species, of those are considered to be vestigial) possess wings that have the ability to fly at least short distances such as those inside of a cave between two species of bat (Dick and Patterson 2006). Despite these factors, bat flies have remained through evolutionary time intimately and fully obligated to their host species with a high degree of specificity. The mechanisms behind this degree of specificity present many interesting findings and questions for parasitologists, mammalogists, and ecologists.

Given few ecological barriers to bat fly dispersal, high host specificity in bat flies is likely due to evolutionary adaptations made over generations that increase survival and reproduction of flies on one or a limited number of host species (Dick and Patterson 2007). This is evident from the fact that many bat flies cannot survive on a bat species that is their unnatural host (Fritz 1983). It is probable that there are physiological and biochemical factors that limit a bat fly species to a narrow number of host species. It has been noted that generalist parasites such as mosquitoes and fleas prefer to attack individual hosts with a weakened immune system (Moller et al. 2004). Since bat flies are highly specific they appear to be able infest bat individuals of all immunological strengths. This makes it increasingly likely that they have developed at least some degree of immunocompatibility with their host species (Dick and Patterson 2007). This would allow bat flies to decrease the level of host immune response by using the same or similar immunological signaling molecules (Salzet et al. 2000). More specifically, this immunocompatibility is hypothesized to be a result of the development of many different shared antigenic epitopes (Dick and Patterson 2007). These shared immunological factors would be in the host's blood and perhaps also in the parasite's saliva allowing for the bat flies to reduce immunological and physiological responses to repeated feeding. They would allow for the bat fly to feed from the bat and not be recognized as immunologically foreign. Given individual bat flies are known to feed up to 7.5 times per hour (Fritz 1983), feeding bouts and their consequences represent strong and steady selective pressure.  Factors working to reduce the bat's response to the feeding would cause less irritation and decrease the amount of effort used by the bats for mechanical removal of the bat flies, which is believed to be the leading cause of adult fly mortality (Marshall 1981). This led me to predict that a bat fly inhabiting and feeding from a non-primary host would stimulate a greater response from that bat than one of its primary host (due to lack of coevolved immunocompatibility). This would in turn cause the non-primary bat to spend more energy and time attempting to mechanically remove the fly, increasing its likelihood for morbidity on a non-primary host

Bat flies may be subject to reproductive isolation pressure via a reproductive filter, which may isolate them to certain bat species (Dick and Patterson 2007). For example, if a bat fly ends up on a non-primary host species, it would be highly unlikely that this fly would encounter an opposite-sex member of its species. This would eliminate the chance that the bat fly will reproduce, if it remains on the non-primary host.  Since it will not reproduce, this colonization of a non-primary host would lead to local extinction of the bat fly species on that new (potential) host species. In this sense, the bat fly's choice to infest a non-primary host has removed it genetically from the population.

The reproductive filter may operate in conjunction with the encounter and compatibility filters first outlined by Combes (1991) in his treatment on the evolution of parasitism. The encounter filter excludes potential hosts the parasite cannot encounter and colonize for behavioral or ecological reasons, while the compatibility filter excludes all host individuals that the parasite cannot survive on for morphological, physiological, or immunological reasons (Timms and Read 1999). These filters combined serve to isolate individual parasites that choose to infest non-primary hosts, and remove them from the gene pools of effective, viable parasite populations.

Host specificity as an emergent property of parasitism has numerous and profound implications not only for the parasites themselves, but also for the host populations and human populations that often live in proximity to wildlife. For the bats, host specificity may mean that one particular species of bat typically must defend itself from only one or a limited number of bat fly species. At least for bat flies (bats are infested with other parasitic arthropods as well), their host can limit the amplitude of potential immunological responses, lessening the cost of parasitism. Moreover, host specificity would translate into a lower likelihood that the host bat would be infected by bacterial and viral transfers from other bat species, since bat fly species often do not infect multiple species. For humans this is relevant information when considering the following scenario: Assume a wild bat, that would not normally have contact with domestic cattle, is carrying a viral pathogen that is potentially infective to cows. This bat is then fed on by a blood-feeding bat fly, which ingests the pathogen. Assuming viral viability is maintained, the bat fly then proceeds to move to a new bat and take a blood meal from this bat. Although the feeding mechanisms of bat flies are not entirely understood, it is likely that during feeding episodes, bat flies are able to infect a new host with blood-borne pathogens present in the previous host. This second bat, however, may be of a species that is likely to come in contact with domestic cattle (e.g. *Desmodus rotundus*, the common vampire bat). Therefore, eventually this bat comes in contact with cows and infects them with the pathogen, potentially diminishing the cow's health and ability to be used as food or produce milk. However, the high host specificity of bat flies strongly precludes such a scenario from actually developing.

There are other non-host specific or less host specific parasites that may be taking on the role of pathogen vector for bat populations and many other animals. For example, ticks and mosquitoes are well-understood generalist parasites (Roberts et al. 2009) that have the ability to feed from bats. Being generalists, both are known to target the immunologically weaker individuals of the populations from which they feed (Roberts et al. 2009). This would include animals with weak or weakened immune systems or ones that have been damaged by physical or pathological injury. Another parasite of certain bats is the bat bug (Hemiptera: Polyctenidae). These parasites also feed from the blood of bats. However, in the absence of dispersal barriers they are known to readily take to secondary hosts (Dick et al. 2009) making them much less operationally host specific and therefore possibly more likely to transfer pathogen among different species of bat. These parasites may have a greater potential than bat flies for fulfilling the scenario of direct transfer of pathogen between multiple species. However, the bat flies have an equally interesting and probable scenario of their own.

By way of example, a scenario that currently may be playing out with bat flies feeding on multiple host individuals of the same species is the transfer of pathogens from bat to bat within a host species reservoir. Bats have been shown to harbor many dangerous pathogens such as SARS, Hendra virus, Ebola, and others (Leroy et al. 2005). If blood-feeding bat flies are capable of transferring the pathogen from bat to bat, it is highly probable that the virulence of the pathogen is increased. This is natural and expected among pathogens that are exposed to multiple immune systems. It is logical to postulate that before the Hendra virus broke out and killed several humans and many horses, it was possibly passed from bat to bat among the flying fox population in Australia by bat flies feeding on multiple bats. This potential increased virulence mediated by bat flies needs to be studied for its probability and effectiveness. This could become a dangerous situation even in places where bat to human or bat to livestock contact is low because a highly virulent pathogen wouldn’t need to be introduced into a population multiple times in order to have a large impact.

It is information such as this that is valuable to epidemiologists. A large aspect of epidemiologic science is applied toward preventative measures against potential pathogenic threats that could strike human populations either directly or indirectly through a food source or other necessary natural resource. Ecological and evolutionary studies of parasites, including host specificity, are necessary in order to realistically assess threats and take action when suitable and effective. This is especially important considering the fact that preventative measures are in general considered to be less expensive and intensive than dealing with the aftermath of an epidemic.

Researchers in the fields of mammalogy, parasitology, and host-parasite ecology and evolution can potentially benefit from the findings presented herein. Studies into the relationship of intimate parasites and hosts reveal just how connected these species truly are in space and time. This allows for studies into the evolutionary history of how they became so intimate, ecological studies of how they maintain their intimacy, and parasitological studies into the requirements for both host and parasite.

The result that Ecuadorian bat flies are highly host specific poses more questions than it does answers. In the pursuit of scientific knowledge there are many experiments for these animals that still need to be conducted. For example, an experimental approach to testing bat flies' ability to uptake and transfer specific pathogens is necessary. This is essential to determine if blood-feeding bat ectoparasites are capable of serving as potential vectors of emerging infectious disease. A statistical comparison that would be an appropriate next step for my research would be the comparison of specificity assessments from the Sowell data to the assessments from the total data. This would allow me to conclude in a probabilistic sense whether increased rigor of collection protocols produce statistically significant higher assessments of host specificity among bat flies. Statistical comparisons could also be done with other ectoparasites of bats, if they happened to be sampled in comparable ways. This could yield results that demonstrate which of the parasites truly warrant concern as potential vectors and which seem unlikely to cause harm by inter-host species vectoring. Furthermore, the immunocompatibility aspects of the bat-bat fly associations could be tested to determine if shared antigenic epitopes allow bat flies to feed as a seemingly unnoticed extension of the bat. This approach could yield further knowledge into how parasite and host can become so intimately related and how an ectoparasite can immunologically disguise itself to avoid harm from the host. Finally, investigation into the proximate cues bat flies use to find their appropriate (specific) host after eclosion from the pupa stage needs to be tested. There are potentially a myriad of interesting and highly specialized biochemical interactions occurring between the host and parasite allowing for proper host identification, colonization, and maintenance. The potential for gain of theoretical and applicable scientific knowledge regarding these relationships is vast. It is to answer these questions and others that the bat-bat fly system should continue to be studied.

# REFERENCES

Brooks, D.R. and McLennan, D.A. 1993. Parascript: Parasites and the Language of Evolution. Smithsonian Institution Press, Washington, DC.

Caira, J.N. Jensen, K. Holsinger, K.E. 2003. On a new index of host specificity. Pp 161-201 in Combes, C. and Jourdane J. (eds.) *Taxonomy, ecology and evolution of metazoan parasites*. Perpignan Press.

Combes, C. 1991. Evolution of parasite life cycles. In: Toft, C.A. Aeschlimann, A. Bolis, L. (Eds.), Parasite–Host Associations: Coexistence or Conflict?. Oxford University Press Oxford, pp. 62–82.

Dick, C.W. Esbérard, C.E.L. Graciolli, G. Bergallo, H.G. Gettinger, D. 2009. Assessing host specificity of obligate ectoparasites in the absence of dispersal barriers. Springer-Verlag. Parasitology Research 105: 1345-1349

Dick, C.W. and Gettinger, D. 2005. A faunal survey of streblid bat flies (Diptera: Streblidae) associated with bats in Paraguay. Journal of Parasitology 91: 1015-1024.

Dick, C.W. and Patterson, B.D. 2006. Bat flies – obligate ectoparasites of bats. in Morand, S. Krasnov, B. and Poulin, R. (eds.). Micromammals and macroparasites: from evolutionary ecology to management. Springer-Verlag, Tokyo. Pp. 179–194

Dick, C.W. and Patterson, B.D. 2007. Against all odds: explaining high host specificity in dispersal-prone parasites. International Journal for Parasitology 37: 871-876.

Dick, C.W. 2007. High host specificity of obligate ectoparasites. Ecological Entomology 32: 446-450.

Dittmar, K. Morse, S. Gruwell, M. Mayberry, J. DiBlasi, E. 2011. Spatial and Temporal Complexities of Reproductive Behavior and Sex Ratios: A Case from Parasitic Insects. PLoS ONE 6: 1-9.

Gettinger, D. 1992. Host specificity of Laelaps (Acari: Laelapidae) in central Brazil. Journal of Medical Entomology, 29**:** 71–77.

Felsenstein, J. 1985. Phylogenies and the Comparative Method. American Naturalist 125: 1-15.

Field, H. 2004. The ecology of the hendra virus and Australian bat lyssavirus. (Doctoral dissertation, University of Queensland, Brisbane, Australia) Retrieved from http://espace.library.uq.edu.au/eserv/UQ:13859/field_thesis_05.pdf (last accessed 2 April 2012)

Fritz, G.N. 1983. Biology and ecology of bat flies (Diptera: Streblidae) on bats of the genus Carollia. Journal of Medical Entomology 20: 1–10

Jobling, B. 1949. Host-parasite relationship between the American Streblidae and the bats, with a new key to the American genera and a record of the Streblidae from Trinidad, British West Indies (Diptera). Parasitology 39: 315-329.

Krasnov, B.R. Mouillot, D. Shenbrot, G.I. Khokhlova, I.S. Vinarski, M.V. Korallo-Vinarskaya, N. P. Poulin, R. 2009. Similarity in ectoparasite faunas of Palaearctic rodents as a function of host phylogenetic, geographic or environmental distances: which matters the most?. International Journal of Parasitology. 40: 807-17.

Leroy, E.M. Kumulungui, B. Pourrut, X. Rouquet, P. Hassanin, A. Yaba, P. Delicat, A. Paweska, J.T. Gonzalez, J-P. Swanepoel, R. 2005. Fruit bats as reservoirs of Ebola virus. Nature 438: 575–576.

Marshall, A.G. 1981. The Ecology of Ectoparasitic Insects. Academic Press, London.

Moller, A.P. Christe, P. Garamszegi, L.Z. 2004. Coevolutionary arms races: increased host immune defense promotes specialization by avian fleas. Journal of Evolutionary Biology 18: 46–59.

Patterson, B.D. Ballard, J.W.O. Wenzel, R.L. 1998. Distributional evidence for cospeciation between Neotropical bats and their bat fly ectoparasites. Studies on Neotropical Fauna and Environment 33: 76–84.

Poulin, R. 1998. Evolutionary Ecology of Parasites: From Individuals to Communities. Chapman and Hall, London.

Presley, S.J. 2004. Ectoparasitic Assemblages of Paraguayan Bats: Ecological and Evolutionary Perspectives. PhD Dissertation, Texas Tech University, Lubbock, Texas.

Presley, S.J. 2011. Interspecific aggregation of ectoparasites on bats: importance of hosts as habitats supersedes interspecific interactions. Oikos 120: 832-841.

Roberts, L. Janvoy, J. Schmidt, G. 2009. Foundations of parasitology (8th ed.). McGraw-Hill, New York.

Salzet, M. Capron, A. Stefano, G.B. 2000. Molecular crosstalk in host–parasite relationships: schistosome– and leech–host interactions. Parasitology Today 16: 536–540.

ter Hofstede, H.M. Fenton, M.B. Whitaker, J.O.Jr. 2004. Host and host-site specificity of bat flies (Diptera: Streblidae and Nycteribiidae) on Neotropical bats (Chiroptera). Canadian Journal of Zoology 82: 616–626.

Timms, R. Read, A.F. 1999. What makes a specialist special? Trends in Ecology and Evolution 14: 333–334.

Wenzel, R. L. 1976. The streblid batflies of Venezuela (Diptera: Streblidae). Brigham Young University Science Bulletin 20: 1–177.

Wenzel, R.L. Tipton, V.J. Kiewlicz, A. 1966. The streblid batflies of Panama (Diptera: Calypterae: Streblidae). Pp. 405-675 in Ectoparasites of Panama (R .L . Wenzel and V.J. Tipton, eds.). Field Museum of Natural History, Chicago, Illinois.

# APPENDIX

Table 1. List of bat (host) species, the number of hosts, the bat fly species, the number of bat flies on a particular host species, the total number of bat flies for that species, and finally the ratio of the number of bat flies on a particular host species per total number of bat flies for that species. The asterisks indicate that this data was also in the Sowell Expedition and the numbers in brackets are from the Sowell Expedition.

| Host Taxon | Total Host # | Fly Species | # of Flies/Species | Total # Fly by Species | Ratio Fly Species on Host |
|---|---|---|---|---|---|
| Platyrrhinus brachycephalus | 1 | Aspidoptera falcata | 1 | 98 | 0.0102 |
| Sturnira lilium* | 35 [19] | Aspidoptera falcata* | 60 [34] | 98 [51] | 0.6122 [0.6667] |
| Sturnira ludovici* | 2 [1] | Aspidoptera falcata* | 2 [1] | 98 [51] | 0.0204 [0.0196] |
| Sturnira luisi* | 13 [6] | Aspidoptera falcata* | 31 [16] | 98 [51] | 0.3163 [0.3137] |
| Sturnira magna | 3 | Aspidoptera falcata | 3 | 98 | 0.0306 |
| Sturnira tildae | 1 | Aspidoptera falcata | 1 | 98 | 0.0102 |
| Artibeus fraterculus* | 58 [57] | Aspidoptera phyllostomatis* | 97 [96] | 199 [180] | 0.4874 [0.5333] |
| Artibeus jamaicensis* | 42 [40] | Aspidoptera phyllostomatis* | 86 [82] | 199 [180] | 0.4322 [0.4556] |
| Artibeus lituratus* | 3 [1] | Aspidoptera phyllostomatis* | 4 [1] | 199 [180] | 0.0201 [0.0056] |
| Artibeus obscurus | 1 | Aspidoptera phyllostomatis | 5 | 199 | 0.0251 |
| Artibeus planirostris* | 5[1] | Aspidoptera phyllostomatis* | 7 [1] | 199 [180] | 0.0352 [0.0056] |
| Myotis albescens cf. | 1 | Basilia anceps | 1 | 24 | 0.0417 |
| Myotis nigricans | 3 | Basilia anceps | 15 | 24 | 0.6250 |
| Myotis oxyotus | 1 | Basilia anceps | 1 | 24 | 0.0417 |
| Myotis riparius | 3 | Basilia anceps | 7 | 24 | 0.2917 |
| Myotis albescens cf.* | 2 [2] | Basilia ferrisi* | 6 [6] | 59 [57] | 0.1017 [0.1053] |
| Myotis nigricans* | 19 [19] | Basilia ferrisi* | 51 [49] | 59 [57] | 0.8644 [0.8596] |
| Myotis riparius* | 1 [1] | Basilia ferrisi* | 1 [1] | 59 [57] | 0.0169 [0.0175] |
| Platyrrhinus matapalensis* | 1 [1] | Basilia ferrisi* | 1 [1] | 59 [57] | 0.0169 [0.0175] |
| Mimon crenulatum* | 10 [8] | Basilia tiptoni* | 36 [21] | 36 [21] | 1.0000 [1.0000] |
| Lonchophylla chocoana cf.* | 5 [5] | Eldunnia breviceps* | 56 [56] | 60 [56] | 0.9333 [1.0000] |
| Anoura geoffroyi | 11 | Exastinion clovisi | 29 | 31 | 0.9355 |
| Glossophaga soricina | 1 | Exastinion clovisi | 2 | 31 | 0.0645 |
| Phyllostomus hastatus* | 14 [13] | Mastoptera guimaraesi* | 72 [71] | 72 [71] | 1.0000 [1.0000] |
| Lophostoma aequatorialis* | 29 [28] | Mastoptera minuta* | 194 [190] | 308 | 0.6299 [0.8962] |
| Lophostoma brasiliense* | 3 [3] | Mastoptera minuta* | 10 [10[ | 308 | 0.0325 [0.0472] |

| | | | | | |
|---|---|---|---|---|---|
| Lophostoma silvicolum | 9 | Mastoptera minuta | 45 | 308 | 0.1461 |
| Phyllostomus elongatus | 4 | Mastoptera minuta | 7 | 308 | 0.0227 |
| Phyllostomus hastatus* | 8 [5] | Mastoptera minuta* | 52 [12] | 308 | 0.1688 [0.0566] |
| Artibeus fraterculus* | 57 [57] | Megistopoda aranea complex* | 85 [85] | 217 [189] | 0.3917 [0.4497] |
| Artibeus jamaicensis* | 55 [54] | Megistopoda aranea complex* | 90 [90] | 217 [189] | 0.4147 [0.4762] |
| Artibeus lituratus* | 7 [1] | Megistopoda aranea complex* | 10 [1] | 217 [189] | 0.0461 [0.0053] |
| Artibeus obscurus | 2 | Megistopoda aranea complex | 2 | 217 | 0.0092 |
| Artibeus planirostris | 11 | Megistopoda aranea complex | 14 | 217 | 0.0645 |
| Platyrrhinus dorsalis* | 8 [8] | Megistopoda aranea complex* | 13 [13] | 217 [189] | 0.0599 [0.0688] |
| Sturnira bidens | 1 | Megistopoda aranea complex | 1 | 217 | 0.0046 |
| Uroderma bilobatum | 2 | Megistopoda aranea complex | 2 | 217 | 0.0092 |
| Artibeus jamaicensis* | 2 [1] | Megistopoda proxima complex* | 3 [2] | 211 [115] | 0.0142 [0.0174] |
| Sturnira erythromos | 1 | Megistopoda proxima complex | 3 | 211 | 0.0142 |
| Sturnira lilium* | 62 [46] | Megistopoda proxima complex* | 98 [74] | 211 [115] | 0.4645 [0.6435] |
| Sturnira ludovici | 15 | Megistopoda proxima complex | 27 | 211 | 0.1280 |
| Sturnira luisi* | 38 [22] | Megistopoda proxima complex* | 69 [39] | 211 [115] | 0.3270 [0.3391] |
| Sturnira magna | 4 | Megistopoda proxima complex | 10 | 211 | 0.0474 |
| Sturnira tildae | 1 | Megistopoda proxima complex | 1 | 211 | 0.0047 |
| Artibeus fraterculus* | 96 [12] | Metelasmus pseudopterus* | 13 [13] | 33 [25] | 0.3939 [0.5200] |
| Artibeus jamaicensis* | 12 [9] | Metelasmus pseudopterus* | 11 [12] | 33 [25] | 0.3333 [0.4800] |
| Artibeus lituratus | 2 | Metelasmus pseudopterus | 2 | 33 | 0.0606 |
| Artibeus planirostris | 4 | Metelasmus pseudopterus | 5 | 33 | 0.1515 |
| Artibeus obscurus | 18 | Neotrichobius bisetosus | 30 | 32 | 0.9375 |
| Phylloderma stenops | 1 | Neotrichobius bisetosus | 2 | 32 | 0.0625 |
| Dermanura cinereus | 1 | Neotrichobius delicatus complex | 2 | 22 | 0.0909 |
| Dermanura gnomus | 1 | Neotrichobius delicatus complex | 2 | 22 | 0.0909 |
| Lasiurus blossevillii | 1 | Neotrichobius delicatus complex | 1 | 22 | 0.0455 |
| Micoureus demerarae | 1 | Neotrichobius delicatus complex | 1 | 22 | 0.0455 |
| Rhinophylla fischerae | 1 | Neotrichobius delicatus complex | 1 | 22 | 0.0455 |
| Rhinophylla pumilio | 3 | Neotrichobius delicatus complex | 4 | 22 | 0.1818 |
| Vampyressa thyone | 10 | Neotrichobius delicatus complex | 11 | 22 | 0.5000 |
| Noctilio albiventris | 10 | Noctiliostrebla maai | 119 | 119 | 1.0000 |
| Noctilio leporinus* | 5 [5] | Noctiliostrebla traubi* | 81 [81] | 81 [81] | 1.0000 [1.0000] |
| Noctilio albiventris | 3 | Paradyschiria fusca | 12 | 26 | 0.4615 |
| Noctilio leporinus | 2 | Paradyschiria fusca | 14 | 26 | 0.5385 |
| Noctilio leporinus* | 5 [5] | Paradyschiria lineata* | 142 [142] | 142 [142] | 1.0000 [1.0000] |
| Noctilio albiventris | 14 | Paradyschiria parvula | 309 | 309 | 1.0000 |

| | | | | | |
|---|---|---|---|---|---|
| Artibeus lituratus* | 27 [14] | Paratrichobius longicrus* | 50 [21] | 50 [21] | 1.0000 [1.0000] |
| Artibeus fraterculus* | 1 [1] | Speiseria ambigua* | 2 [2] | 154 [74] | 0.0130 [0.0270] |
| Artibeus obscurus | 1 | Speiseria ambigua | 1 | 154 | 0.0065 |
| Carollia brevicauda* | 31 [19] | Speiseria ambigua* | 49 [32] | 154 [74] | 0.3182 [0.4324] |
| Carollia castanea | 5 | Speiseria ambigua | 6 | 154 | 0.0390 |
| Carollia perspicillata* | 58 [23] | Speiseria ambigua* | 96 [39] | 154 [74] | 0.6234 [0.5270] |
| Lonchorrhina aurita | 1 | Speiseria ambigua | 11 | 154 | 0.0714 |
| Phyllostomus elongatus* | 1 [1] | Speiseria ambigua* | 1 [1] | 154 [74] | 0.0065 [0.0135] |
| Carollia brevicauda | 10 | Speiseria peytonae | 12 | 33 | 0.3636 |
| Carollia castanea | 14 | Speiseria peytonae | 17 | 33 | 0.5152 |
| Carollia perspicillata | 3 | Speiseria peytonae | 4 | 33 | 0.1212 |
| Phylloderma stenops | 7 | Strebla christinae | 66 | 67 | 0.9851 |
| Phyllostomus hastatus | 1 | Strebla christinae | 1 | 67 | 0.0149 |
| Chrotopterus auritus | 5 | Strebla chrotopteri | 34 | 34 | 1.0000 |
| Artibeus lituratus | 1 | Strebla consocia | 1 | 69 | 0.0145 |
| Phyllostomus discolor | 1 | Strebla consocia | 5 | 69 | 0.0725 |
| Phyllostomus elongatus | 17 | Strebla consocia | 63 | 69 | 0.9130 |
| Phyllostomus hastatus | 1 | Strebla galindoi | 3 | 147 | 0.0204 |
| Tonatia bidens | 1 | Strebla galindoi | 8 | 147 | 0.0544 |
| Tonatia saurophila* | 16 [13] | Strebla galindoi* | 136 [115] | 147 [115] | 0.9252 [1.0000] |
| Artibeus fraterculus* | 1 [1] | Strebla guajiro* | 3 [3] | 247 [80] | 0.0121 [0.0375] |
| Carollia brevicauda* | 49 [22] | Strebla guajiro* | 75 [41] | 247 [80] | 0.3036 [0.5125] |
| Carollia castanea* | 28 [14] | Strebla guajiro* | 39 [18] | 247 [80] | 0.1579 [0.2250] |
| Carollia perspicillata* | 74 [13] | Strebla guajiro* | 127 [16] | 247 [80] | 0.5142 [0.2000] |
| Lonchophylla thomasi | 1 | Strebla guajiro | 1 | 247 | 0.0040 |
| Micronycteris giovanniae* | 1 [1] | Strebla guajiro* | 1 [1] | 247 [80] | 0.0040 [0.0303] |
| Rhinophylla alethina* | 1 [1] | Strebla guajiro* | 1 [1] | 247 [80] | 0.0040 [0.0303] |
| Phyllostomus discolor* | 39 [38] | Strebla hertigi* | 159 [158] | 221 [220] | 0.7195 [0.7182] |
| Phyllostomus hastatus* | 15 [15] | Strebla hertigi* | 62 [62] | 221 [220] | 0.2805 [0.2818] |
| Phyllostomus elongatus* | 9 [9] | Strebla mirabilis* | 31 [31] | 64 [33] | 0.4844 [0.9394] |
| Phyllostomus hastatus* | 4 [1] | Strebla mirabilis* | 17 [1] | 64 [33] | 0.2656 [0.0303] |
| Tonatia saurophila | 1 | Strebla mirabilis | 1 | 64 | 0.0156 |
| Trachops cirrhosus* | 8 [1] | Strebla mirabilis* | 15 [1] | 64 [33] | 0.2344 [0.0303] |
| Desmodus rotundus* | 42 [33] | Strebla wiedemanni* | 144 [110] | 144 [110] | 1.0000 [1.0000] |
| Phyllostomus discolor* | 39 [37] | Trichobioides perspicillatus* | 191 [177] | 191 [177] | 1.0000 [1.0000] |
| Carollia brevicauda* | 10 [5] | Trichobius anducei* | 13 [7] | 140 [31] | 0.0929 [0.2258] |
| Carollia perspicillata* | 62 [13] | Trichobius anducei* | 127 [24] | 140 [31] | 0.9071 [0.7742] |
| Phyllostomus discolor* | 51 [48] | Trichobius costalimai* | 244 [225] | 244 [225] | 1.0000 [1.0000] |
| Artibeus lituratus* | 1 [1] | Trichobius dugesii* | 1 | 51 | 0.0196 |
| Carollia brevicauda | 1 | Trichobius dugesii | 3 [1] | 51 [40] | 0.0588 [0.0250] |
| Glossophaga soricina* | 29 [27] | Trichobius dugesii* | 47 [39] | 51 [40] | 0.9216 [0.9750] |

| | | | | | |
|---|---|---|---|---|---|
| Phyllostomus elongatus* | 11 [11] | Trichobius dugesioides* | 98 [98] | 124 [103] | 0.7903 [0.9515] |
| Trachops cirrhosus* | 9 [1] | Trichobius dugesioides* | 26 [5] | 124 [103] | 0.2097 [0.0485] |
| Lophostoma aequatorialis* | 30 [30] | Trichobius dybasi* | 36 [36] | 36 [36] | 1.0000 [1.0000] |
| Artibeus fraterculus* | 1 [1] | Trichobius joblingi* | 18 [18] | 1107 [569] | 0.0163 [0.0316] |
| Artibeus jamaicensis* | 1 [1] | Trichobius joblingi* | 3 [3] | 1107 [569] | 0.0027 [0.0053] |
| Carollia brevicauda* | 124 [68] | Trichobius joblingi* | 483 [330] | 1107 [569] | 0.4363 [0.5800] |
| Carollia castanea* | 41 [18] | Trichobius joblingi* | 73 [34] | 1107 [569] | 0.0659 [0.0598] |
| Carollia perspicillata* | 151 [41] | Trichobius joblingi* | 477 [166] | 1107 [569] | 0.4309 [0.2917] |
| Myotis nigricans* | 1 [1] | Trichobius joblingi* | 1 [1] | 1107 [569] | 0.0009 [0.0018] |
| Phyllostomus discolor | 1 | Trichobius joblingi | 7 | 1107 | 0.0063 |
| Phyllostomus elongatus* | 18 [6] | Trichobius joblingi* | 41 [14] | 1107 [569] | 0.0370 [0.0246] |
| Sturnira tildae | 1 | Trichobius joblingi | 1 | 1107 | 0.0009 |
| Trinycteris nicefori* | 1[1] | Trichobius joblingi* | 3 [3] | 1107 [569] | 0.0027 [0.0053] |
| Lonchophylla concava* | 2 [2] | Trichobius lonchophyllae* | 4 [4] | 27 [26] | 0.1538 [0.1538] |
| Lonchophylla robusta* | 6 [5] | Trichobius lonchophyllae* | 22 [22] | 27 [26] | 0.8462 [0.8462] |
| Nephelomys albigularis | 1 | Trichobius longipes | 3 | 183 | 0.0164 |
| Phyllostomus discolor | 1 | Trichobius longipes | 1 | 183 | 0.0055 |
| Phyllostomus elongatus | 8 | Trichobius longipes | 15 | 183 | 0.0820 |
| Phyllostomus hastatus* | 33 [26] | Trichobius longipes* | 163 [144] | 183 [145] | 0.8907 [0.9931] |
| Platyrrhinus dorsalis * | 1 [1] | Trichobius longipes* | 1 [1] | 183 [145] | 0.0055 [0.0069] |
| Macrophyllum macrophyllum | 3 | Trichobius macrophyllae | 75 | 76 | 0.9868 |
| Platyrrhinus dorsalis | 1 | Trichobius macrophyllae | 1 | 76 | 0.0132 |
| Desmodus rotundus* | 56 [48] | Trichobius parasiticus* | 598 [550] | 599 [550] | 0.9983 [1.0000] |
| Glossophaga soricina | 1 | Trichobius parasiticus | 1 | 599 | 0.0017 |
| Glossophaga soricina* | 11 [11] | Trichobius uniformis* | 23 [23] | 23 [23] | 1.0000 [1.0000] |

Table 2. List of fly species, total number of flies for the fly species, and number of primary hosts associations for the fly species. The asterisks indicate that the fly species are also in the Sowell Expedition data and the numbers in brackets represent the numbers for the Sowell Expedition.

| Fly Species | # of Flies | # of Primary Associations | Specificity Index |
|---|---:|---:|---:|
| Aspidoptera falcata* | 98 [51] | 2 [2] | 0.301 [0.301] |
| Aspidoptera phyllostomatis* | 199 [180] | 2 [2] | 0.301 [0.301] |
| Basilia anceps | 24 | 2 | 0.3010 |
| Basilia ferrisi* | 59 [57] | 2 [2] | 0.301 [0.301] |
| Basilia tiptoni* | 36 [21] | 1 [1] | 0 [0] |
| Eldunnia breviceps* | 60 [56] | 1 [1] | 0 [0] |
| Exastinion clovisi | 31 | 2 | 3.0004 |
| Mastoptera guimaraesi* | 72 [71] | 1 [1] | 0 [0] |
| Mastoptera minuta* | 308 [212] | 3 [2] | 3.0008 [3.0004] |
| Megistopoda aranea complex* | 220 [189] | 4 [3] | 3.0013 [3.0009] |
| Megistopoda proxima complex* | 211 [115] | 3 [2] | 0.477 [0.301] |
| Metelasmus pseudopterus* | 33 [25] | 4 [2] | 0.602 [0.301] |
| Neotrichobius bisetosus | 32 | 2 | 3.0004 |
| Neotrichobius delicatus complex | 22 | 4 | 3.3012 |
| Noctiliostrebla maai | 119 | 1 | 0.0000 |
| Noctiliostrebla traubi* | 81 [81] | 1 [1] | 0 [0] |
| Paradyschiria fusca | 26 | 2 | 0.3010 |
| Paradyschiria lineata* | 142 [142] | 1 [1] | 0 [0] |
| Paradyschiria parvula | 309 | 1 | 0.0000 |
| Paratrichobius longicrus* | 50 [21] | 1 [1] | 0 [0] |
| Speiseria ambigua* | 154 [74] | 3 [2] | 3.0009 [0.301] |
| Speiseria peytonae | 33 | 3 | 0.4770 |
| Strebla christinae | 67 | 1 | 0.0000 |
| Strebla chrotopteri | 34 | 1 | 0.0000 |
| Strebla consocia | 69 | 2 | 0.3010 |
| Strebla galindoi* | 147 [115] | 2 [1] | 0.301 [0] |
| Strebla guajiro* | 247 [80] | 3 [3] | 0.477 [0.477] |
| Strebla hertigi* | 221 [220] | 2 [2] | 0.301 [0.301] |
| Strebla mirabilis* | 64 [33] | 3 [1] | 3.0009 [0] |
| Strebla wiedemanni* | 144 [110] | 1 [1] | 0 [0] |
| Trichobioides perspicillatus* | 191 [177] | 1 [1] | 0 [0] |
| Trichobius anducei* | 140 [31] | 2 [2] | 0.301 [0.301] |

|  |  |  |  |
|---|---|---|---|
| Trichobius costalimai* | 244 [225] | 1 [1] | 0 [0] |
| Trichobius dugesii* | 51 [40] | 2 [1] | 3.0004 [0] |
| Trichobius dugesioides* | 124 [103] | 2 [1] | 3.0004 [0] |
| Trichobius dybasi* | 36 [33] | 1 [1] | 0 [0] |
| Trichobius joblingi* | 1107 [569] | 3 [3] | 0.477 [0.477] |
| Trichobius lonchophyllae* | 27 [26] | 2 [2] | 0.301 [0.301] |
| Trichobius longipes* | 183 [145] | 2 [1] | 0.301 [0] |
| Trichobius macrophyllae | 76 | 1 | 0.0000 |
| Trichobius parasiticus* | 599 [550] | 1 [1] | 0 [0] |
| Trichobius uniformis* | 23 [23] | 1 [1] | 0 [0] |

Table 3. Ecuador Gazetteer. Lists the provinces and full localities of where all of the bats and bat flies were collected in Ecuador.

| Province | Full Locality | Lat | Long | Elevation |
|---|---|---|---|---|
| Azuay | A1. Cuenca | -2.8962 | -79.0050 | 2550m |
| Azuay | A2. Río Jubones | -3.3200 | -79.2954 | 1007m |
| Azuay | A3. Santa Isabel. Trincay | -3.2646 | -79.3271 | 1708m |
| Carchi | B1. El Pailón | 1.0000 | -78.2333 | 970m |
| Cotopaxi | C1. Santa Rosa | -0.3501 | -78.9178 | 1217m |
| El Oro | D1a. Arenillas, military reserve. El Cubo | -3.6469 | -80.1613 | 93m |
| El Oro | D1b. Arenillas, military reserve. Quebrada Seca. 7.1 km west and 12.5 km south of the Militar Base | -3.6567 | -80.1823 | 45m |
| El Oro | D2. Arenillas, military reserve. Palmales | -3.6743 | -80.1056 | 67m |
| El Oro | D3. Arenillas, military reserve. Punta Brava | -3.4666 | -80.1283 | 4m |
| El Oro | D4. Puyango petrified forest. Los Sabalos creek | -3.8795 | -80.0929 | 325m |
| El Oro | D5a. Portovelo. El Tablón. Farm Palomares | -3.7365 | -79.5948 | 671m |
| El Oro | D5b. Zaruma. Amarillo river | -3.6809 | -79.5819 | 839m |
| El Oro | D5c. Zaruma. Cerro Urcu | -3.6841 | -79.6224 | 1101m |
| El Oro | D5d. Zaruma. El Faique | -3.7020 | -79.6218 | 885m |
| El Oro | D5e. Zaruma. La Colón Neighborhood. Mines | -3.6900 | -79.5958 | 939m |
| El Oro | D6. Moromoro High School Botanical Garden. Border with Jocotoco private reserve | -3.6626 | -79.7448 | 1036m |
| El Oro | D7. Cerro Chiche. Cantonal limit between Portovelo and Piñas | -3.7666 | -79.6475 | 557m |
| Esmeraldas | E1a. Farm east of San Lorenzo on highway between Lita and San Lorenzo | 1.2587 | -78.7810 | 57m |
| Esmeraldas | E1b. La Chiquita, experimental station | 1.2320 | -78.7660 | 65m |
| Esmeraldas | E2. Mataje | 1.3559 | -78.7243 | 69m |
| Esmeraldas | E3a. San Francisco de Bogota | 1.0877 | -78.6915 | 74m |
| Esmeraldas | E3b. Surroundings of San Francisco de Bogota | 1.0726 | -78.7115 | 86m |
| Esmeraldas | E4. Río Piedras | 0.5333 | -78.6333 | 1576m |
| Esmeraldas | E5. Palestina. Marco Galarza's farm | 0.9811 | -79.4584 | 169m |
| Esmeraldas | E6. Quinindé. Jesús Quiñones's farm | 0.3266 | -79.4732 | 85m |
| Esmeraldas | E7. Quingue | 0.7112 | -80.0939 | 28m |
| Guayas | F1. Cerro Blanco, protected forest | -2.1799 | -80.0216 | 43m |
| Guayas | F2. Isla Puná | -2.7595 | -79.9171 | 10m |
| Guayas | F3a. Manglares Churute. Cerro Cimalón | -2.4268 | -79.5613 | 34m |
| Guayas | F3b. Manglares Churute. Cerro Pancho Diablo | -2.4315 | -79.6363 | 9m |
| Guayas | F3c. Manglares Churute. La Laguna | -2.4273 | -79.5880 | 46m |
| Loja | G1. Puyango petrified forest. Las Pailas. Chirimoyos creek | -3.8968 | -80.0764 | 394m |
| Los Rios | H1. Vinces | -1.5556 | -79.7473 | 15m |
| Los Rios | H2. Río Palenque | -1.4360 | -79.7513 | 29m |
| Manabi | I1. Matapalo | -1.5267 | -80.3693 | 127m |
| Morona Santiago | J1a. Macas | -2.2950 | -78.1274 | 1103m |

| | | | | |
|---|---|---|---|---|
| Morona Santiago | J1b. Macas. Bosque Domono | -2.2206 | -78.1239 | 1170m |
| Morona Santiago | J1c. San Luis | -2.3751 | -78.1117 | 862m |
| Morona Santiago | J1d. Sucua | -2.4526 | -78.1606 | 832m |
| Morona Santiago | J1e. Road Macas to Sta. Rosa de Naranjales. Quichua community | -2.2959 | -78.0771 | 996m |
| Morona Santiago | J2. Pastaza river bridge | -1.9111 | -77.8330 | 644m |
| Napo | K1a. Cotundo parroquia. Huamaní | -0.7183 | -77.6117 | 1180m |
| Napo | K1b. WildSumaco Lodge [Lodge Loop] | -0.6759 | -77.6008 | 1471m |
| Napo | K2. El Salado. Alto Coca | -0.1917 | -77.7000 | 1700m |
| Napo | K3. Puerto Misahuallí | -1.0317 | -77.6645 | 432m |
| Orellana | L1. 4.5 km north and 2 km west of Puerto Francisco de Orellana | -0.4267 | -77.0083 | 226m |
| Orellana | L2. San José de Payamino | -0.5000 | -77.3000 | 333m |
| Orellana | L3. Alto Coca | -0.0833 | -77.2500 | 457m |
| Orellana | L4a. Estación Cientifica Yasuní | -0.6769 | -76.3965 | 246m |
| Orellana | L4b. Yasuní National Park, close to the Yasuní field station (PUCE) | -0.6772 | -76.4096 | 238m |
| Orellana | L5. Tiputini Biodiversity Station | -0.7162 | -76.0245 | 213m |
| Orellana | L6. Cabeceras' of Rumiyacu river | -0.8697 | -75.9069 | 217m |
| Orellana | L7. Zancudo | -0.5722 | -75.4722 | 207m |
| Pastaza | M1a. K4 camp. AGIP | -1.4756 | -77.4846 | 393m |
| Pastaza | M1b. Villano B camp. AGIP. Lliquino river | -1.4528 | -77.4423 | 367m |
| Pastaza | M2. La Mariscal, near Rivadeneira river | -1.3507 | -77.8589 | 939m |
| Pastaza | M3a. Alvarez-Miño camp | -1.4344 | -78.1228 | 1229m |
| Pastaza | M3b. Cuevas de Mera | -1.4177 | -78.0380 | 1264m |
| Pastaza | M3c. Puyo | -1.5038 | -78.0301 | 933m |
| Pastaza | M3d. Puyo. Parque etnobotánico Omaere | -1.4711 | -77.9939 | 944m |
| Pastaza | M3e. Shell. Fuerte Militar Amazonas | -1.5065 | -78.0607 | 1044m |
| Pichincha | N1a. El Paraíso. Km 20th. road Quito to Santo Domigo de los Colorados | -0.3146 | -79.0207 | 712m |
| Pichincha | N1b. Road between Unión del Toachi and Alluriquín | -0.3142 | -78.9696 | 816m |
| Pichincha | N1c. Unión del Toachi. Otongachi | -0.3291 | -78.9418 | 1024m |
| Pichincha | N2. El Colorado. Toll gate to Santo Domingo | -0.2744 | -79.0791 | 617m |
| Pichincha | N3. Yanacocha reserve | -0.1116 | -78.5849 | 3507m |
| Pichincha | N4. El Pahuma, orchid reserve | 0.0622 | -78.6820 | 2400m |
| Pichincha | N5. Mindo. Mariposario | -0.0659 | -78.7648 | 1331m |
| Pichincha | N6. Puerto Quito | 0.1048 | -79.2110 | 160m |
| Sucumbios | O1a. San Rafael waterfalls | -0.0967 | -77.5783 | 1213m |
| Sucumbios | O1b. San Rafael waterfalls (2) | -0.0817 | -77.5783 | 1600m |
| Sucumbios | O2a. 1 km east of Lago Agrio | 0.0861 | -76.8742 | 298m |
| Sucumbios | O2b. 1.5 km north and 1.5 km west of Lago Agrio | 0.0833 | -76.9083 | 305m |
| Sucumbios | O3. 12 km northeast of Lago Agrio | 0.1917 | -76.7833 | 286m |
| Sucumbios | O4. 5 km southwest of Marián | -0.0833 | -76.3500 | 257m |
| Sucumbios | O5. Laguna Grande. Cuyabeno river | 0.0000 | -76.1833 | 215m |

| | | | | |
|---|---|---|---|---|
| Sucumbios | O6a. Cuyabeno river bridge. Monte Tour Hostal. Km 18 road Tarapoa-Puerto El Carmen | -0.0322 | -76.3205 | 238m |
| Sucumbios | O6b. Marián | -0.0533 | -76.3222 | 283m |
| Sucumbios | O7. Aguarico river. 200 m southwest of mouth of Cuyabeno river | -0.2606 | -75.8983 | 205m |
| Sucumbios | O8. Zabalo. Criollo family's property | -0.3181 | -75.7662 | 211m |
| Sucumbios | O9. Destacamento Patria. Milestone 63 of Ecuador-Perú frontier | -0.4650 | -75.3451 | 188m |
| Sucumbios | O10. Destacamento Lagarto Cocha, at confluence of Lagarto and Aguarico rivers | -0.6333 | -75.2667 | 196m |
| Tungurahua | P1a. Comunidad Azuay. Farm over Topo river | -1.3695 | -78.1839 | 1877m |
| Tungurahua | P1b. Los Angeles, near Río Negro | -1.4195 | -78.1704 | 1334m |
| Tungurahua | P1c. Río Negro | -1.4147 | -78.2008 | 1219m |
| Tungurahua | P1d. Río Negro. Banana plantation north of the Pastaza river | -1.4000 | -78.2167 | 1558m |
| Tungurahua | P1e. Río Verde. Cabañas Indillama | -1.4044 | -78.2968 | 1462m |
| Tungurahua | P1f. Río Verde. Pailón del Diablo. Al otro lado hostal | -1.4038 | -78.2911 | 1453m |
| Zamora-Chinchipe | Q1. Podocarpus National Park. San Francisco | -3.9884 | -79.0929 | 2219m |
| Zamora-Chinchipe | Q2. Podocarpus National Park. Bombascaro | -4.1146 | -78.9650 | 1128m |

FIGURES

Figure 5. Map of Ecuador. Depicts all bat and bat fly collecting localities listed in the gazetteer (Table 3).