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CO-OCCURRENCE PATTERNS OF BAT FLIES ON NEOTROPICAL CHIROPTERA

A Thesis
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Western Kentucky University
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Master of Biology

By
Mitchell Schooler

May 2017

CO-OCCURRENCE PATTERNS OF BAT FLIES ON NEOTROPICAL CHIROPTERA

Date Recommended 20 April 2017

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Dean, Graduate School Date 4/24/17

I dedicate this thesis to my loving family, who even through difficult times have been very supportive. I also dedicate this to the friends who have consistently been by my side even through the difficulties of reality. Finally, I dedicate this to my fellow graduate students who have helped with their knowledge and their humor.

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CONTENTS

LIST OF FIGURES

LIST OF TABLES

CO-OCCURRENCE PATTERNS OF BAT FLIES ON NEOTROPICAL CHIROPTERA

Mitchell Schooler May 2017 156 Pages

Directed by: Carl W. Dick, Jarrett Johnson, and Keith Philips

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Parasite-host systems provide excellent opportunities to explore ecological dynamics such as competition, competitive exclusion, and co-occurrence. The distribution of streblid bat flies on their host bats were examined for patterns of species co-occurrence and to understand mechanisms driving these patterns. The purpose of this study was to determine patterns of co-occurrence among individuals of different Neotropical bat fly species. After establishing patterns of co-occurrence, tests on whether variation in fly morphology was linked to observed patterns of co-occurrence were performed. Co-occurrence patterns were determined using null model analyses, and a predominant pattern of aggregation was detected. To examine the relationship between co-occurrence and morphology, geometric morphometric analyses were performed to compare morphologies of co-occurring individuals of different species. Examination of ratios of species-pairs with significant differences in their morphology relative to species-pairs without significant differences resulted in both insight and more questions. Species segregation may result from morphological similarity between co-occurring streblid species, potentially reflecting historical niche overlap leading to competitive exclusion of one species from infesting the host individual. Aggregation of multiple streblid species however, does not appear to be due to differences in morphology. Results also indicate that explanations of co-occurrence patterns are not straightforward, and that multiple mechanisms may underlie patterns of co-occurrence. These results underscore important

potential connections between morphology and patterns of co-occurrence, but future research is needed to verify these conclusions and examine other possible contributing mechanisms to patterns of co-occurrence in this biological system.

Introduction to Thesis

Properties emerging from the intimate relationships between parasites and their hosts offer unique opportunities to examine aspects of evolutionary ecology such as competition and co-occurrence. The parasite-host system possesses several properties that render it a model system for examining patterns of population and community ecology. One such property is that individual hosts represent well-defined and independent units of habitat space. This property is relevant because hosts-as-habitats are limited by the full extent of their body and therefore at some level act as a closed system. Second is that each host provides a sample of a parasite population or community for the purposes of study (Presley, 2011). Moreover, diverse host species serve as replicate samples in order to examine ecological patterns. Additionally, with species-rich host taxa, researchers are given the opportunity to inspect whether patterns apply to the general group of hosts or specifically to certain species of hosts. Lastly, host species vary widely in their ecology, morphology, and behavior. This can allow researchers quantitative approaches to analyzing how this variation affects assemblages of parasites.

The bat – bat fly system has been explored by myself and others to uncover biological patterns and to probe general concepts of population and community ecology. The Streblidae comprise a group of insects that are highly specialized ectoparasites that feed only on the blood of bats. They are most diverse in the tropics of the Western Hemisphere, much like their bat hosts (Dick and Patterson, 2006). The bat flies (Streblidae and Nycteribiidae) are recognized as a monophyletic group within the hippoboscoid Diptera (Dittmar et al., 2015). This clade of bat flies is sister to the Hippoboscidae (bird flies, ked flies) and Glossinidae (tsetse flies). Although bat flies are

monophyletic, the family Streblidae itself is not monophyletic but is currently understood to comprise three different clades; one is composed of the subfamily Nycteriboscinae, the second is composed of the streblid subfamily Ascodipterinae and the family Nycteribiidae, and the third clade is composed of the subfamilies Trichobiinae and Streblinae. This current vision of bat fly relationships based on phylogenetic analyses (Bayesian approach) is still debated, and the current division of bat flies into two families has little support given that the family Streblidae is not monophyletic (Dittmar et al., 2015). Earliest evidence of bat flies comes from a single male Nycterophiliinae specimen found in Dominican amber dating to the Early or Middle Miocene (15-20 mya). However, based on the derived nature of the preserved specimen, it is hypothesized that the Streblidae (and bat flies as a whole) are evolutionarily older than the Miocene (Dittmar et al., 2015).

Streblid bat flies vary widely in their morphology including body shape (from laterally compressed, to dorsal-ventrally compressed, to an uncompressed body shape), leg shape, overall body size, presence or absence of ctenidia, size and complexity of eyes, and the presence or absence of wings (Dick et al., 2016). Within the New World Streblidae, there are three different morphotypes categorized on the basis of microhabitat preference and evasive behavior on their bat hosts (ter Hofstede et al., 2004). Streblids specialize on either the fur or naked skin of the tail or wing membrane of the bat and possess morphological and behavioral characteristics to allow for this specialization. Streblid bat flies that specialize to the wing or tail membrane possess short hind legs, no ctenidia, and exhibit avoidance behavior by hiding in the folds of the membranes to avoid grooming pressures of their bat host. Streblids that specialize to the fur fall into one of

two different categories; fur runners and fur swimmers. Fur runners possess long hind legs, no ctenidia, and use their hind legs to push off the surface of the fur and run over the fur in order to avoid host grooming behavior. Fur swimmers possess short hind legs, ctenidia, and push through the fur to avoid host grooming behavior in a way that has been described as similar to rapid swimming (ter Hofstede et al., 2004). Host grooming appears to be the primary pressure that has selected for host-site specificity in streblids and for the characteristics associated with this specialization (Marshall, 1981; ter Hofstede et al., 2004).

This group of parasites reproduces through the use of viviparous puparity in which fertilization and all three larval stages occur within the female, where larvae are nourished via intrauterine glands (Meier et al., 1999). The use of an intrauterine gland is shared within the superfamily Hippoboscoidea. The third instar larvae is then deposited by the female onto or near the host's roost where the larvae immediately pupates and continues the rest of its development into an adult (Dittmar et al., 2009). It is hypothesized that the female deposits the larvae on or near the roost instead of directly on the host where it would easily be removed by grooming. After approximately three to four weeks of development the adult bat fly emerges from the pupae and must locate and colonize a bat host within a small time span to prevent starvation (Dick et al., 2016). Despite the host separation created by this reproductive system, streblids are highly host specific (Dick and Gettinger, 2005). It is hypothesized that this high degree of host specificity may in part be due to a Reproductive Filter or an immunocompatibility. The Reproductive Filter Concept states that streblids will only infest hosts where they can expect to find mates of the same species. Alternatively, the immunocompatibility

hypothesis states that streblids will infest hosts with a similar immunocomposition to their host. This would be because if parasites share a similar immunocomposition to their host they don't elicit a painful response in their host, which would reduce the rates of grooming performed (Dick and Patterson, 2007).

Although bat flies feed on bats, they do not appear to inflict pain or sores/lesions on their bat hosts (Dick and Patterson, 2006). The parasitic relationship exhibited between streblid species and the bat hosts are not as detrimental to their hosts as with other types of parasitic relationships. Streblids benefit from both being able to use their bat hosts as habitat and as a constant food source. The parasitic relationship exhibited by streblid species and their bat hosts possess all five of the primary components described by Presley (2011). These host-parasite system characteristics found in this system allowed for examination of the concept of co-occurrence and the mechanisms facilitating co-occurrence within this system.

Literature Cited

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

Dick, C. W., and B. D. Patterson. 2006. Bat flies - obligate ectoparasites of bats. : *In* Micromammals and macroparasites: From ecology to management. R. Poulin and B. R. Krasnov (eds.). Springer-Verlag, Tokyo, Japan, p. 179–194.

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

Dick, C. W., G. Garciolli, and R. Guerrero. 2016. Family Streblidae. Zootaxa **4122**: 784–802.

Dittmar, K., C. W. Dick, B. D. Patterson, M. F. Whiting, and M. E. Gruwell. 2009. Pupal deposition and ecology of bat flies (Diptera: Streblidae): Trichobius sp. (caecus group) in a Mexican cave habitat. The Journal of Parasitology **95**: 308–314.

Dittmar, K., S. F. Morse, C. W. Dick, and B. D. Patterson. 2015. Bat fly evolution from the Eocene to the Present (Hippoboscoidea, Streblidae and Nycteribiidae). *In* Parasite diversity and diversification: Evolutionary ecology meets phylogenetics. S. Morand, B. R. Kasnov, and D. T. J. Littlewood (eds.). Cambridge University Press, Cambridge, U.K., p. 246–264.

Marshall A. G. 1981. The ecology of ectoparasitic insects. Academic Press, London.

Meier, R., M. Kotrba, and P. Ferrar. 1999. Ovoviviparity and viviparity in the Diptera. Biological Reviews **74**: 199–258.

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

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

Chapter 1: Patterns of Co- occurrence Among Streblid Species

Introduction

Studying parasite communities can lead to a better overall understanding of important ecological concepts such as competition, competitive exclusion, and co-occurrence. Interspecific competition occurs when there is niche overlap between two or more species with the degree of differences in niche use from each species and the competitive ability of each species determining the outcome of the interaction (Mayfield and Levine, 2010). Niche-based competition theory predicts that niche partitioning is the key to species co-occurrence (Colwell and Fuentes, 1975). Within this theoretical framework, competitive ability is described as the difference in fitness between two species based on multiple factors including but not limited to their differences in utilizing limited resources, reproductive output, susceptibility to predation, and obtaining habitat space. When the differences in competitive ability between two species within a competitive interaction are greater than the differences in niche space used by the two species, competitive exclusion is predicted to follow. Conversely, when the differences in niche usage are greater than the competitive differences between two species, then co-occurrence will occur (Mayfield and Levine, 2010). Crucial to this theory is the assumption that resources in some form are limiting to both species and that if resources are fairly abundant, competition will not be as strong. In many host-parasite system, the host acts as a food resource and arguably is not a strong limiting resource. However, as host grooming is a major contributor to parasite mortality, the amount of habitat space

available to avoid the selective pressure of host grooming is likely a strongly limiting resource for parasite species (Reiczigel and Rózsa, 1998; ter Hofstede et al., 2004).

A major aspect of this research was the consideration of parasite co-occurrence and its possible relationship to competition. There is voluminous literature on the community dynamics of parasite species, specifically regarding concepts related to competition and co-occurrence (Reed et al., 2000; Gotelli & Rohde, 2002; Friggens & Brown, 2005; Tello et al., 2008). Currently, there is little consensus on whether competition is an important factor in structuring parasite communities (Friggens and Brown, 2005). The lack of consensus may be due in part to the great variety of parasite and host life histories. For example, ectoparasite assemblages on marine fish have been regarded as unstructured, with little to no resource limitation or competitive influence (Gotelli and Rohde, 2002). However, some studies suggest that a lack of competitive influence between parasite species could be due to differences in microhabitat partitioning among the different species (Tello et al., 2008). Reed et al. (2000) looked at spatial partitioning among two genera of chewing lice (*Geomydoecus* and *Thomomydoecus*) on geomyid pocket gophers. The two genera of lice were not evenly distributed over the host, but instead showed a tendency to partition the habitat. Differences in the hair diameter, temperature and humidity gradients, and the location and density of sebaceous glands on the host were all posited as explanatory mechanisms allowing for microhabitat partitioning (Reed et al., 2000). Friggens and Brown (2005) examined niche partitioning in cestode communities of two closely related host species, the round stingray (*Urobatis halleri*) and the skate (*Leucoraja naevus*). Using null model methods, they concluded that cestode communities in both host species were highly

structured, and cestodes were found to be distributed non-randomly in regard to niche dynamics. Species were clumped more than expected in a randomly structured community, and communities were structured in a way that is consistent with a community based on competition theory. As such, the null model method based on randomization (along with other appropriate quantitative tests) was deemed an effective way to characterize patterns of parasite communities and useful in examining possible factors that create and maintain these patterns in community structure (Gotelli, 2000; Friggens and Brown, 2005). This method for examining co-occurrence has been used to evaluate co-occurrence in streblid bat flies. Null model analyses have suggested that there are positive patterns of co-occurrence between different species of streblidae species on the same host (Tello et al., 2008; Presley, 2011).

The purpose of this study was to determine whether individuals of different species of bat flies show patterns of co-occurrence on the same bat host individuals. The prediction for this study was that streblid species would show patterns of co-occurrence that could be described as either aggregation or segregation. In the context of this study, aggregation will be defined as when individuals of two or more batfly species are more likely to occur on the same host individual than by chance, while segregation will be defined as when individuals of two or more batfly species are less likely to occur on the same host than by chance. Similar to previous research on batflies, this prediction was tested using a null model analysis to search for any patterns of co-occurrence. Unlike previous research, this study has made use of the largest survey data ever collected on streblid bat flies, providing high resolving power for determining patterns of co-occurrence of parasite species on host species.

Materials and Methods

Streblid Collection

The streblid parasites studied in this project were part of the collections of Neotropical (Venezuelan) bat flies collected during the Smithsonian Venezuelan Project (SVP). The SVP was conducted from 1965 to 1968 with the intent of broadly surveying mammals and their ectoparasites. It is the largest collection of its kind, which sampled 38,213 mammals representing 270 species, including 24,797 sexed bats of 133 species, which harbored 116 different streblid species (Handley, 1976; Wenzel, 1976). During the survey, bats were collected using mist nets and held in individual paper bags, fumigated with ether, and the parasites were collected and preserved in 70% ethanol (Patterson et al., 2008a). Host names were reviewed using computerized records from the National Museum of Natural History (USNM), which confirmed that the host identification was accurate, consistent, and could be reevaluated. Parasite samples were collected and then organized based on individual host with a total of 36,663 streblids, representing 22 genera and 116 species identified and enumerated at the Field Museum of Natural History.

The parasite and host species used in this project were chosen based on several important criteria. One such criterion was the need for a large enough sample size for each bat species (at least 10 individuals per host species) and for each individual parasite species (at least 20 individuals per parasite species). This minimizes spurious results by excluding non-representative samples. The second criterion was that the bat host harbored two to the maximum of four co-occurring species of streblids. This aspect was

necessary in order to examine the interaction between different parasite species on the same individuals of the same host species. Based on these criteria, streblid species from 31 different species of bats were examined to discern patterns of co-occurrence among parasite species.

Three different families are represented by the bat species used in this study. The majority (28 species) belonged to the Phyllostomidae, but also included two species of noctilionids, and one species of natalid (Table 1.1). This collection of bat hosts represents a diverse array of functional feeding guilds, including frugivores, insectivores, nectarivores, piscivores, carnivores, and sanguinivores. This assortment also represents species that utilize a diversity of roosting structures, including isolated cave dwellings, super-colony cave dwellings, tree cavities, anthropogenic structures, and palm leaf tents.

From the 31 species of bats examined, 38 species of Streblidae were examined. The 38 fly species are representative of all three Neotropical subfamilies of Streblidae: Nycterophiliinae (represented by one genus containing two species), Streblinae (representing three genera containing 17 species), and Trichobinae (representing ten genera containing 19 species). Most of these species occur on a single host species or genus (Presley, 2005; Table 1.2).

Null Model Analysis

A null model approach was used to evaluate patterns of streblid species co-occurrence using presence/absence and abundance matrices. The matrices were established so that each column represented a host individual and each row represented a streblid species. Values in each cell represented the number of individuals of a particular

parasite species on a specific host individual. Each matrix was used to examine what is referred to as a co-occurring relationship, or a relationship between individuals of two or more different streblid species that occur on the same host species. A total of 79 of co-occurring relationships were examined using a null model analysis. A null model analysis compares the observed distributions of individual fly species against numerous simulated or null matrices. Simulated matrices were created by redistributing the values within the cells at random to compare them to the observed matrix. This comparison allows determination of whether there is pattern of co-occurrence within the relationship and if the pattern can be described as aggregation or segregation.

The null model analyses were conducted in R (ver. 3.2.2) using the package EcoSim 7.0 (Gotelli and Entsminger, 2001; Appendix C). The "RA3" algorithm, which fixes row totals while allowing column totals to be equiprobable, was used to randomize the matrix. Null models that use a pure randomization algorithm are biologically unrealistic and are prone to type I errors (Presley, 2011). Fixing the row totals limits the occurrence of type I errors while at the same time being more biologically realistic, as they reflect the concept that abundance and intensity are species level characteristics that should not be changed dramatically. Keeping columns equiprobable is also biologically realistic because it treats each individual host as being just as likely to be infested by a parasite species as any other host individual of the same species.

For this study, 'empty' sites, or hosts without parasites, were included in the evaluation of patterns of co-occurrence. This is based on the assumption that any lack of parasites present on a host individual are due to chance rather than another factor, and assumes each individual within a host species is as likely to be infested by parasites as

any other host (Presley, 2011). The hosts without parasites were included in null model analyses to reflect our current knowledge of the streblid-bat system as we do not possess a testable assumption that would exclude 'empty' sites.

In each null model analysis, the observed C-score, which quantifies "checkerboardness" within a distribution (Stone and Roberts, 1990), was compared to 10,000 simulated C-scores to determine if any pattern of co-occurrence was present and if so, whether it was a pattern of aggregation or segregation. A C-score (checkerboard score) measures distributions for non-randomness in the form of measuring checkeboard units. A basic checkerboard unit for example would be if you have two parasite species that inhabit a different host individual (Stone and Roberts, 1990). Due to the lack of normality in these null distributions, each tail in the two-tailed distribution required separate p-values with one being associated with aggregation and the other with segregation (Gotelli and Enstminger, 2001). C-score values were made comparable using standardized effect size (SES) that was calculated using the mean and standard deviation of the C-score values from all 10,000 null models. Results were considered significant if SES values either fell below -2 or exceeded 2. Some host species possessed three or four co-occurring species of parasites and in these cases ectoparasite analyses were conducted for the entire assemblage as well as for each pair of parasite species.

Co-occurrence was rated as either a pattern of aggregation or segregation based on if the SES was greater than 2.0 or less than -2.0 and if the p-value was less than or equal to 0.05 (Figure 1.1 and 1.2). Each relationship examined through EcoSim produced a visualization of the data matrix and a randomly selected simulated matrix (Fig. A.1). The null distribution figures (see Appendix A Fig. A.2 for an example) provide a

visualization of where the observed data are located relative to the 10,000 simulated matrices. Scatterplots of density between all species pairs that exhibited aggregation were created with Poisson regressions used in order to examine any possible pattern of facilitation. A Bonferroni correction was used for the results of the multiple Poisson regressions used.

Results

In this study, 67 co-occurring relationships between individuals of two different parasite species occurring on the same host species (species-pairs), eight relationships between individuals of three different parasite species on the same host species, and four relationships between individuals of four different parasite species on the same host species were examined (species-assemblages). Results from the null model analyses of the presence/absence matrices determined that of the 67 relationships between two species, 35 showed a pattern of aggregation, nine showed a pattern of segregation, and the remaining 23 showed neither patterns of aggregation nor segregation. Of the eight relationships among three species, seven showed a pattern of aggregation and one showed no significant pattern of co-occurrence. Of the four relationships among four species, two showed a pattern of aggregation and two showed no significant pattern of co-occurrence (Table 1.3).

Results from the null model analyses of the abundance matrices determined that of the 67 relationships between two species, 29 showed patterns of aggregation, one showed a pattern of segregation, and the remaining 37 show no significant pattern of aggregation or segregation. Of the eight relationships among three species, five showed

patterns of aggregation and three showed no significant patterns of aggregation or segregation. Of the four relationships among four species, two showed patterns of aggregation and two showed no significant patterns of aggregation or segregation (Table 1.4; Appendix A). Few cases of significant correlations of parasite abundances in species pairs were found. In cases where there were statistically significant correlations, the correlations were weak, with only two examples of moderately strong correlation (see Appendix B).

Discussion

Multiple species of streblid bat fly parasites are known to infest individual species of Neotropical bats (Wenzel, 1976). These relationships are conducive to examining patterns of species co-occurrence using numerous bat and fly species, and large sample sizes of each. Null model analyses of such data provided clear results, determining that patterns of co-occurrence exist among bat fly species on different host species. In the majority of cases, the pattern of co-occurrence detected was aggregation, with only one case of segregation being present between parasite species. In other words, most often, host individuals with one species of bat fly are likely to host at least one more species of bat fly. These findings are consistent with previous studies, which also found patterns of aggregation among streblid species pairs and assemblages when there were significant patterns of co-occurrence (Tello et al., 2008; Presley, 2011). Tello et al. (2008) examined patterns of co-occurrence of streblids on short-tailed fruit bats (*Carollia perspicillata*) from Ecuador using null model analyses. The results from this study found clear patterns of aggregation between the parasites found on *C. perspicillata,* which is consistent with the patterns of aggregation observed with parasites of several bat species (including *C.*

perspicillata) in this study. Presley (2011) examined patterns of co-occurrence among the streblid species of 11 bat species using null model analyses. The results of this study found similar patterns of co-occurrence among bat species analyzed in both studies. However, there was one contradiction where Presley (2011) found no pattern of co-occurrence for *C. perspicillata* at the assemblage level, while the results of this study and the Tello et al. (2008) study found patterns of aggregation for *C. perspicillata*. This could be a result of differing parasite species among the three studies.

The patterns found here clearly comport with initial predictions and are consistent with previous studies (Tello et al., 2008; Presley, 2011). The establishment of clear patterns of co-occurrence necessarily leads to questions regarding the biological mechanisms that may form the observed patterns. Strong competitive interactions among streblid species that share similar niche spaces on the same host species may ultimately lead to competitive exclusion, in turn creating patterns of segregation between streblid species (Mayfield and Levine, 2010). That many of the sampled bat species possessed only one species of streblid may be indicative of past competitive exclusion. Based on the strong patterns of aggregation at both the assemblage and species-pair levels and lack of segregation patterns at either of those levels, neither interspecific nor intraspecific competition seem to be crucial driving mechanisms to explain the observed patterns of co-occurrence. If interspecific competition was a critical component contributing to the patterns of co-occurrence exhibited between streblid species, we would have expected more cases of segregation, far fewer cases of aggregation, and/or more cases of hosts with only one type of parasite (exclusion). Previous studies examining this same collection have found that the majority of bat species with primary host-parasite

associations (measured as the case when a host species has 5% or more of the total individuals of a given parasite species found on all host species) had two or more primary associations (Patterson et al., 2007). Of the 67 bat species that were considered to have primary associations in this study, 42 bat species had two or more primary associations. The idea that competitive interactions does not act as a mechanism in this system is further supported by the lack of statistically significant and strong negative correlations between the abundances of co-occurring parasite speices in this study (Appendix B).

The observed patterns of aggregation could be a result of one or more possible mechanisms, including positive fly species interactions, host species characteristics, and/or lack of strong competitive pressures. For example, the presence and high abundance of one parasite species can facilitate the presence of one or more parasite species (Krasnov et al., 2005). The presence of an abundant species of parasite on a host could allow for redirection of grooming pressure from a facilitated second parasite species. This type of facilitation mechanism among parasite species would be similar to proposed explanations for co-occurrence among prey species in a free-roaming environment, whereas the presence of multiple prey species reduces the pressure exhibited by predators on any single species (Holt and Lawton, 1994), similar to models examining persistence of two species on a single host over time (Reiczigel and Rózsa, 1998). Further, the presence of one parasite species could negatively affect the immunocompetence of the host, where the threshold of the energetic constraints for grooming/immunological response of the host limits the host's ability to groom effectivley (Tello et al., 2008). Yet, evidence of such a mechanism in explaining patterns of aggregation is currently lacking (Presley, 2011). These results are further

supplemented by the Possion regressions, which also indicated that there was very little evidence for facilitation based on non-significant p-values and weak correlation values (low r^2 values) when p-values were significant (see Appendix B). If facilitation was a mechanism driving these patterns, then these linear regressions would predominantly have significant p-values with strong correlation values. Because our results and the results of previous studies do not reflect the prediction associated with facilitation, we have failed to indicate that facilitation is a mechanism for patterns of co-occurrence between streblids (Presley, 2011).

Another possible mechanism driving aggregation of streblid species are host and/or environmental conditions that affect how parasites can survive on their host. First, the size of the host affects both parasite abundance and diversity, provided larger body size allows for more niche space subdivision (Presley, 2011). This has been tested in bat species but does not provide a convincing explanation for aggregation patterns (Patterson et al., 2008b). Second, the mobility and home range of the host could allow for greater chance of parasite encounter for the host. However, this explanation does not seem likely, as bats are not exposed to ectoparasites while in flight (Presley, 2011). Third, the host social system could help explain parasite abundances and hosts forming social harems harboring positively co-occurring species (Presley, 2011). This could be seen as similar to an encounter filter explanation as part of the Filter Concept for under what circumstances certain parasite species can be found on what host species (Combes, 1991; Presley, 2007; Patterson et al., 2008b; Tello et al., 2008).

Characteristics that minimize niche similarities between two or more co-occurring streblid species will reduce competition and prevent competitive exclusion of a parasite

species (Mayfield and Levine, 2010). For example, microhabitat specialization has been previously noted to affect the spatial partitioning of parasite species (Reed et al., 2000; Friggens and Brown, 2005). Microhabitat specialization has also been noted among streblid species with unique morphological characteristics segregating between fur and wing membrane regions of hosts (ter Hofstede et al., 2004). Microhabitat partitioning has been hypothesized to result from the selective pressure of host grooming behavior (Reiczigel and Rózsa, 1998; ter Hofstede et al., 2004), and this is supported by a simulation model developed by Reiczigel and Rózsa (1998). Streblid bat flies have one of three different morphotypes on the basis of body shape, hind leg, and ctendia characteristics that are associated with specific behaviors that allow for avoiding grooming behavior in particular regions of their host. Streblids of the "wing crawler" morphotype possess small uncompressed body shape and short legs in order to crawl on the wing membrane of their hosts and to hide in the folds of the wing membrane (ter Hofstede et al., 2004). Streblids of the "fur runner" morphotype have a laterally compressed bodies and long hind legs that allow them to step on top of the fur and run alongside the host's body to avoid grooming (Dick and Patterson, 2006). Streblids of the "fur swimmer" morphotype have a dorsoventrally compressed body, short hind legs, and ctendium; these characteristics allow these bat flies to maneuver through the host's fur like a how flea moves through its host. The ctendium is used to grasp on the fur to prevent being dislodged from the host during grooming. Along these general lines, streblids appear able to partition microhabitats and thereby reduce negative, competitive interactions among species that exist on the same host.

There is evidence of this microhabitat partitioning hypothesis acting as a contributing mechanism towards species-pairs that showed patterns of aggregation exhibiting different morphotypes. The single case of segregation was comprised of two species with the same morphotype (wing crawlers). These observed patterns in aggregating and segregating species-pairs is consistent with predictions that species with different morphotypes should be able to aggregate while those with the same morphotypes would segregate. There were also no species-pairs where both species were fur runners or both fur swimmers, which is in line with the idea that two species that have a high degree of niche overlap would lead to exclusion, which is why no such species-pairs were observed (Mayfield and Levine, 2010). However, there were seven aggregating species-pairs where both species were wing crawlers, which contradicts earlier made predictions. This suggests that despite sharing the same microhabitat space, the differences in fitness capability is not greater than the niche difference or that habitat usage was not limited enough to create strong competitive pressure. Another inconsistency is that the majority of species-pairs that exhibited no patterns of co-occurrence were comprised of species with different morphotypes. This indicates that while microhabitat partitioning may explain some cases of aggregation, it is not the sole factor in determining such patterns. Microhabitat partitioning appears to act as a contributing mechanism towards patterns of co-occurrence, so further research into other mechanisms will be necessary.

Another characteristic that would reduce niche overlap is differences in morphology, which has been demonstrated to affect the niche utilized by a species (Dayan and Simberloff, 2005). Such morphological displacement is a viable mechanism

in co-occurring streblid species as the morphology exhibited is widely diverse, which could reduce competition. This would allow for research into the discrepencies shown within the microhabitat partitioning hypothesis by comparing the morphology between co-occurring species. The predictions of this hypothesis would be that co-occurring species with significantly differing morphologies would aggregate while those that do not have significantly differing morphologies would segregate. Further research will allow for the prominent patterns of co-occurrence to be examined for the underlying mechanisms.

The results of this study have provided the largest examination at patterns of co-occurrence among streblid species, and the results have demonstrated that the majority of patterns were that of aggregation. Future research should examine the possible mechanisms behind patterns of co-occurrence including host characteristics (Combes, 1991; Presley, 2007; Patterson et al., 2008b; Tello et al., 2008; Presley, 2011), microhabitat partitioning (ter Hofstede et al, 2004), and differences in parasite morphology ((Dayan and Simberloff, 2005).

Literature Cited

Colwell, R. K., and E. R. Fuentes. 1975. Experimental studies of the niche. Annual Review of Ecology and Systematics **6**: 281–310.

Combes, C. 1991. Aspects of parasite transmission. The American Naturalist **138**: 866–880.

Dayan, T., and D. Simberloff. 2005. Ecological and community-wide character displacement: The next generation. Ecology Letters **8**: 875–894.

Dick, C. W., and B. D. Patterson. 2006. Bat flies - obligate ectoparasites of bats. *In* Micromammals and macroparasites: From ecology to management. R. Poulin and B. R. Krasnov (eds.). Springer-Verlag, Tokyo, Japan, p. 179–194.

Friggens, M. M., and J. H. Brown. 2005. Niche partitioning in the cestode communities of two elasmobranchs. Oikos **108**: 76–84.

Gotelli, N. J. 2000. Null model analysis of species co-occurrence patterns. Ecology **81**: 2606–2621.

Gotelli, N. J. and G. L. Entsminger. 2001. R (ver. 3.2.2) package EcoSim 7.0.

Gotelli, N. J., and K. Rohde. 2002. Co-occurrence of ectoparasites of marine fishes: A null model analysis. Ecology Letters **5**: 86–94.

Handley, C. O. J. 1976. Mammals of the Smithsonian Venezuelan Project. Brigham Young University Science Bulletin, Biological Series **20**: 1–91.

Holt, R. D., and J. H. Lawton. 1994. The ecological consequences of shared natural enemies. Annual Review of Ecology and Systematics **25**: 495–520.

Krasnov, B. R., D. Mouillot, I. S. Khokhlova, G. I. Shenbrot, and R. Poulin. 2005. Covariance in species diversity and facilitation among non-interactive parasite taxa: All against the host. Parasitology **131**: 557–568.

Mayfield, M. M., and J. M. Levine. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. Ecology Letters **13**: 1085–1093.

Patterson, B. D., C. W. Dick, and K. Dittmar. 2007. Roosting habits of bats affect their parasitism by bat flies (Diptera: Streblidae). Journal of Tropical Ecology **23**: 177–189.

Patterson, B. D., C. W. Dick, and K. Dittmar. 2008a. Parasitism by bat flies (Diptera: Streblidae) on Neotropical bats: Effects of host body size, distribution, and abundance. Parasitology Research **103**: 1091–1100.

Patterson, B. D., C. W. Dick, and K. Dittmar. 2008b. Sex biases in parasitism of Neotropical bats by bat flies (Diptera: Streblidae). Journal of Tropical Ecology **24**: 387–396.

Presley, S. J. 2005. Ectoparasitic assemblages of Paraquayan bats: Ecological and evolutionary perspectives. PhD Dissertation. Texas Tech University, Lubbock,

Texas, 326 p.

Presley, S. J. 2007. Streblid bat fly assemblage structure on Paraguayan *Noctilio leporinus* (Chiroptera: Noctilionidae): nestedness and species co-occurrence. Journal of Tropical Ecology **23**: 409–417.

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

Reed, D. L., M. S. Hafner, S. K. Allen, and M. B. Smith. 2000. Spatial partitioning of host habitat by chewing lice of the genera Geomydoecus and Thomomydoecus (Phthiraptera: Trichodectidae). The Journal of Parasitology **86**: 951–5.

Reiczigel, J., and L. Rózsa. 1998. Host-mediated site segregation of ectoparasites: an individual-based simulation study. The Journal of Parasitology **84**: 491–498.

Stone, L., and A. Roberts. 1990. The checkerboard score and species distributions. International Association for Ecology **85**: 74–79.

Tello, S. J., R. D. Stevens, and C. W. Dick. 2008. Patterns of species co-occurrence and density compensation: A test for interspecific competition in bat ectoparasite infracommunities. Oikos **117**: 693–702.

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

Wenzel, R. L. 1976. The streblid batflies of Venezuela (Diptera: Streblidae). Brigham Young University Science Bulletin **20**: 1–77.

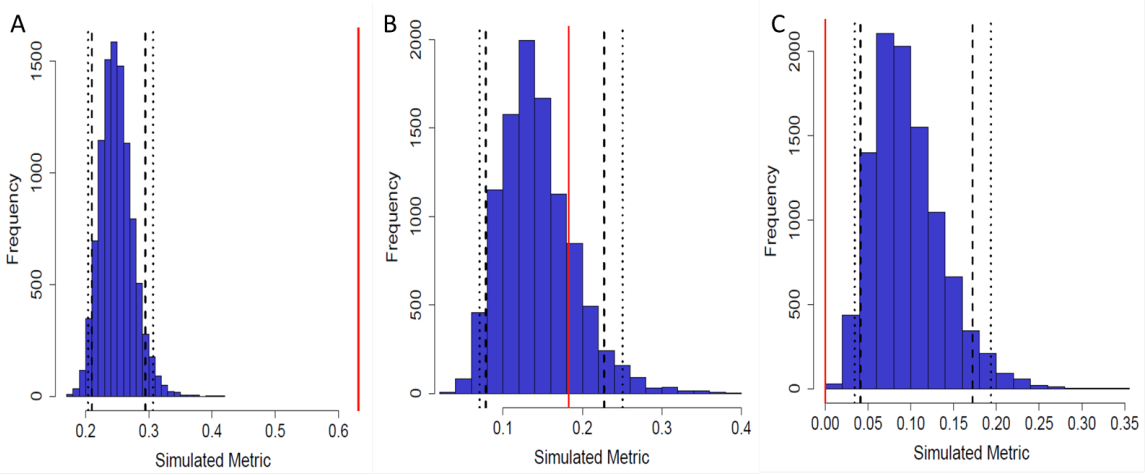

Figure 1.1: Three figures that describe the comparison between the C-score for the observed matrix (represented by the red line) and C-scores for the 10,000 simulated matrices (represented by the blue histograms). The dotted black lines represent the points at the end of the confidence intervals. These three graphs provide a visualization of what the three different types of results look like: (A) aggregation, (B) neither patterns of aggregation nor segregation, and (C) segregation.

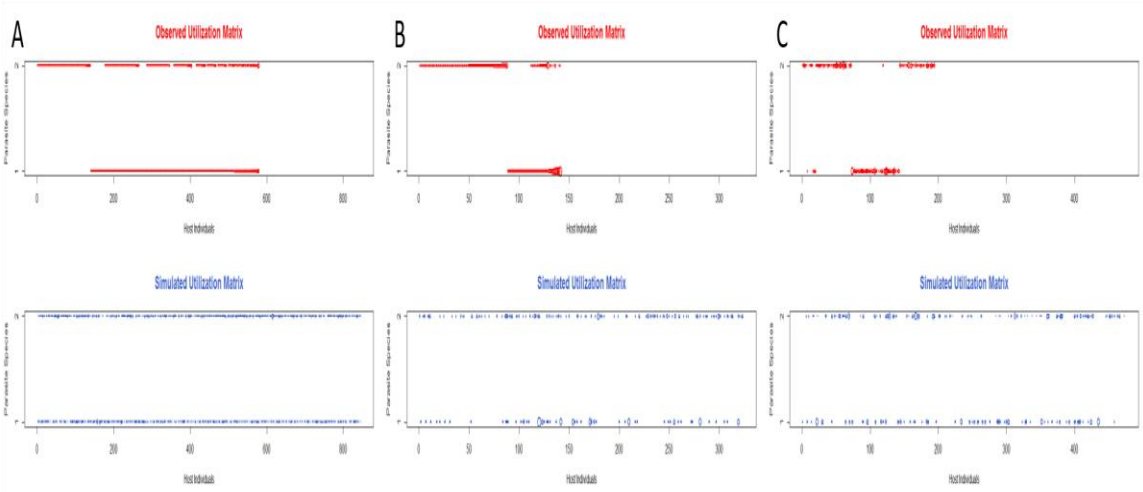

Figure 1.2: These graphs provide a visualized comparison between the parasite distributions of the observed matrix (colored in red) and a randomly selected simulated matrix (colored in blue). The x-axis represents each host individual with the y-axis representing a parasite species with only two parasite species being represented in these examples. Each circle represents the presence of a particular parasite species on an individual host with the size of the circle describing the abundance of that parasite species on an individual host (the larger the circle, the more of that parasite species on that particular host). These three examples are for the three different types of patterns of co-occurrence: (A) aggregation, (B) no pattern of co-occurrence, and (C) segregation.

Table 1.1: List of bat species, by family, examined in this study.

Bat Family	**Species**
Natalidae	*Natalus tumidirostris*
Noctilionidae	*Noctilio albiventris*
Noctilionidae	*Noctilio leporinus*
Phyllostomidae	*Anoura caudifer*
Phyllostomidae	*Anoura geoffroyi*
Phyllostomidae	*Anoura latidens*
Phyllostomidae	*Artibeus amplus*
Phyllostomidae	*Artibeus planirostris*
Phyllostomidae	*Carollia brevicauda*
Phyllostomidae	*Carollia perspicillata*
Phyllostomidae	*Chrotopterus auritus*
Phyllostomidae	*Desmodus rotundus*
Phyllostomidae	*Diaemus youngi*
Phyllostomidae	*Glossophaga longirostris*
Phyllostomidae	*Glossophaga soricina*
Phyllostomidae	*Leptonycteris curasoae*
Phyllostomidae	*Lionycteris spurrelli*
Phyllostomidae	*Lonchophylla robusta*
Phyllostomidae	*Lonchorhina aurita*
Phyllostomidae	*Lonchorhina orinocensis*
Phyllostomidae	*Macrophyllum macrophyllum*
Phyllostomidae	*Micronycteris minuta*
Phyllostomidae	*Phyllostomus discolor*
Phyllostomidae	*Phyllostomus elongatus*
Phyllostomidae	*Phyllostomus hastatus*
Phyllostomidae	*Sturnira lilum*
Phyllostomidae	*Sturnira ludovici*
Phyllostomidae	*Sturnira tildae*
Phyllostomidae	*Tonatia sylvicola*
Phyllostomidae	*Trachops cirrhosus*
Phyllostomidae	*Uroderma bilobatum*

Table 1.2: List of streblid genera and species by subfamily, and their respective host taxa.

Subfamily	**Bat Fly Species**	**Host Species**
Nycterophiliinae	*Nycterophilia coxata*	*Leptonycteris curasoae*
Nycterophiliinae	*Nycterophilia natali*	*Natalus tumidirostris*
Streblinae	*Anastrebla caudiferae*	*Anoura caudifer*
Streblinae	*Anastrebla modestini*	*Anoura geoffroyi*
Streblinae	*Anastrebla nycteridis*	*Lonchophylla robusta*
Streblinae	*Anastrebla spurrelli*	*Lionycteris spurrelli*
Streblinae	*Paraeuctenodes longipes*	*Glossophaga soricina*
Streblinae	*Strebla altmani*	*Lonchorhina aurita* and *Lonchorhina orinocensis*
Streblinae	*Strebla chrotopteri*	*Chrotopterus auritus*
Streblinae	*Strebla consocia*	*Phyllostomus elongatus* and *Phyllostomus hastatus*
Streblinae	*Strebla curvata*	*Glossophaga longirostris* and *Glossophaga soricina*
Streblinae	*Strebla diaemi*	*Diaemus youngi*
Streblinae	*Strebla guajiro*	*Carollia brevicauda* and *Carollia perspicillata*
Streblinae	*Strebla hertigi*	*Phyllostomus discolor*
Streblinae	*Strebla machadoi*	*Micronycteris minuta*
Streblinae	*Strebla matsoni*	*Macrophyllum macrophyllum*
Streblinae	*Strebla mirabilis*	*Trachops cirrhosus*
Streblinae	*Strebla paramirabilis*	*Artibeus amplus*
Streblinae	*Strebla wiedemanni*	*Desmodus rotundus*
Trichobinae	*Aspidoptera falcata*	*Sturnira lilum, Sturnira ludovici,* and *Sturnira tildae*
Trichobinae	*Aspidoptera phyllostomatis*	*Artibeus planirostris*
Trichobinae	*Exastinion clovesi*	*Anoura geoffroyi*
Trichobinae	*Mastoptera guimaraesi*	*Phyllostomus hastatus*
Trichobinae	*Mastoptera minuta*	*Phyllostomus hastatus* and *Tonatia sylvicola*
Trichobinae	*Megistopoda aranea*	*Artibeus planirostris*
Trichobinae	*Noctiliostrebla aitkeni*	*Noctilio leporinus*
Trichobinae	*Noctiliostrebla maai*	*Noctilio albiventris*
Trichobinae	*Noctiliostrebla traubi*	*Noctilio leporinus*
Trichobinae	*Paradyschiria curvata*	*Noctilio albiventris*
Trichobinae	*Paradyschiria fusca*	*Noctilio leporinus*
Trichobinae	*Paratrichobius dunni*	*Uroderma bilobatum*
Trichobinae	*Speiseria ambigua*	*Carollia perspicillata*
Trichobinae	*Speiseria magnioculus*	*Trachops cirrhosus*
Trichobinae	*Speiseria peytonae*	*Carollia brevicauda*
Trichobinae	*Trichobioides perspicillatus*	*Phyllostomus discolor*

Trichobinae	*Trichobius dugesii*	*Glossophaga longirostris* and *Glossophaga soricina*
Trichobinae	*Trichobius dugesioides*	*Carollia perspicillata*
Trichobinae	*Trichobius joblingi*	*Phyllostomus elongatus*

Table 1.3: Lists all 79 relationships examined in this study and states the host species in each relationship, the parasite species associated in this relationship, describes the type of relationship exhibited between the different parasite species in each relationship, and standardized effect size (SES) value for that analysis. Full comparison analyses refer to null model analyses where all potential parasite species for a host species were examined. Relationship data described in this table are based off of null model analyses that made use of presence/absence matrices.

Bat Host Sp.	**Parasite Sp. 1**	**Parasite Sp. 2**	**Pattern**	**SES**
Artibeus amplus	*Strebla paramirabilis*	*Trichobius assimilis*	No Pattern	1.98
Anoura caudifer	*Anastrebla caudiferae*	*Trichobius tiptoni*	No Pattern	1.87
Anoura geoffroyi	*Full comparison*		No Pattern	0.66
Anoura geoffroyi	*Anastrebla modestini*	*Exastinion clovesi*	Aggregation	2.97
Anoura geoffroyi	*Anastrebla modestini*	*Trichobius propinquus*	No Pattern	1.03
Anoura geoffroyi	*Exastinion clovesi*	*Trichobius propinquus*	Segregation	-2.76
Anoura latidens	*Anastrebla modestini*	*Exastinion clovisi*	Aggregation	2.77
Artibeus planirostris	*Full comparison*		Aggregation	9.93
Artibeus planirostris	*Aspidoptera phyllostomatis*	*Megistopoda aranea*	Aggregation	4.51
Artibeus planirostris	*Aspidoptera phyllostomatis*	*Metelasmus pseudopterus*	Aggregation	9.14
Artibeus planirostris	*Megistopoda aranea*	*Metelasmus pseudopterus*	Aggregation	3.55
Carollia brevicauda	*Full comparison*		Aggregation	3.93
Carollia brevicauda	*Speiseria peytonae*	*Strebla guajiro*	Aggregation	3.00
Carollia brevicauda	*Speiseria peytonae*	*Trichobius persimilis*	No Pattern	0.81
Carollia brevicauda	*Strebla guajiro*	*Trichobius persimilis*	Aggregation	2.90
Carollia perspicillata	*Full comparison*		Aggregation	25.8
Carollia perspicillata	*Speiseria ambigua*	*Strebla guajiro*	Aggregation	10.2

Carollia perspicillata	*Speiseria ambigua*	*Trichobius dugesioides*	Aggregation	4.17
Carollia perspicillata	*Speiseria ambigua*	*Trichobius joblingi*	Aggregation	16.4
Carollia perspicillata	*Strebla guajiro*	*Trichobius dugesioides*	Aggregation	7.81
Carollia perspicillata	*Strebla guajiro*	*Trichobius joblingi*	Aggregation	18.8
Carollia perspicillata	*Trichobius dugesioides*	*Trichobius joblingi*	Aggregation	6.79
Chrotopterus auritus	*Strebla chrotopteri*	*Trichobius dugesioides*	No Pattern	1.92
Desmodus rotundus	*Strebla wiedemanni*	*Trichobius parasiticus*	Aggregation	13.0
Diaemus youngi	*Strebla diaemi*	*Trichobius diaimi*	Aggregation	2.16
Glossophaga longirostris	*Full comparison*		Aggregation	3.81
Glossophaga longirostris	*Strebla curvata*	*Trichobius dugesii*	Aggregation	3.26
Glossophaga longirostris	*Strebla curvata*	*Trichobius uniformis*	No Pattern	2.36
Glossophaga longirostris	*Trichobius dugesii*	*Trichobius uniformis*	No Pattern	0.96
Glossophaga soricina	*Full comparison*		No Pattern	-0.49
Glossophaga soricina	*Paraeuctenodes longipes*	*Strebla curvata*	Aggregation	2.19
Glossophaga soricina	*Paraeuctenodes longipes*	*Trichobius dugesii*	No Pattern	-0.72
Glossophaga soricina	*Paraeuctenodes longipes*	*Trichobius uniformis*	No Pattern	0.89
Glossophaga soricina	*Strebla curvata*	*Trichobius dugesii*	Segregation	-2.14
Glossophaga soricina	*Strebla curvata*	*Trichobius uniformis*	No Pattern	0.41
Glossophaga soricina	*Trichobius dugesii*	*Trichobius uniformis*	Segregation	-2.93
Lonchorhina aurita	*Strebla altmani*	*Trichobius flagellatus*	Aggregation	5.66
Leptonycteris curasoae	*Nycterophilia coxata*	*Trichobius sphaeronotus*	Aggregation	18.8
Lonchorhina orinocensis	*Strebla altmani*	*Trichobius ethophallus*	No Pattern	1.84
Lonchophylla robusta	*Anastrebla nycteridis*	*Trichobius lonchophyllae*	No Pattern	-0.90

Lionycteris spurrelli	*Anastrebla spurrelli*	*Trichobius lionycteridis*	No Pattern	1.76
Macrophyllum macrophyllum	*Strebla matsoni*	*Trichobius macrophylli*	Aggregation	3.74
Micronycteris minuta	*Strebla machadoi*	*Trichobius handleyi*	No Pattern	1.72
Natalus tumidirostris	*Nycterophilia natali*	*Trichobius galei*	No Pattern	1.89
Noctilio albiventris	*Full comparison*		Aggregation	3.29
Noctilio albiventris	*Noctiliostrebla maai*	*Paradyschiria curvata*	No Pattern	1.66
Noctilio albiventris	*Noctiliostrebla maai*	*Paradyschiria parvula*	Aggregation	9.28
Noctilio albiventris	*Paradyschiria curvata*	*Paradyschiria parvula*	Segregation	-4.95
Noctilio leporinus	*Full comparison*		Aggregation	4.69
Noctilio leporinus	*Noctiliostrebla aitkeni*	*Noctiliostrebl a traubi*	Segregation	-2.30
Noctilio leporinus	*Noctiliostrebla aitkeni*	*Paradyschiria fusca*	Aggregation	10.1
Noctilio leporinus	*Noctiliostrebla aitkeni*	*Paradyschiria lineata*	Segregation	-2.54
Noctilio leporinus	*Noctiliostrebla traubi*	*Paradyschiria fusca*	Segregation	-2.02
Noctilio leporinus	*Noctiliostrebla traubi*	*Paradyschiria lineata*	Aggregation	10.7
Noctilio leporinus	*Paradyschiria fusca*	*Paradyschiria lineata*	Segregation	-2.28
Phyllostomus discolor	*Full comparison*		Aggregation	5.72
Phyllostomus discolor	*Strebla hertigi*	*Trichobioides perspicillatus*	Aggregation	4.29
Phyllostomus discolor	*Strebla hertigi*	*Trichobius costalimai*	No Pattern	1.17
Phyllostomus discolor	*Trichobioides perspicillatus*	*Trichobius costalimai*	Aggregation	4.75
Phyllostomus elongatus	*Full comparison*		Aggregation	2.98
Phyllostomus elongatus	*Strebla consocia*	*Trichobius joblingi*	Aggregation	3.08
Phyllostomus elongatus	*Strebla consocia*	*Trichobius longipes*	No Pattern	0.14
Phyllostomus elongatus	*Trichobius joblingi*	*Trichobius longipes*	Aggregation	2.19
Phyllostomus hastatus	*Full comparison*		No Pattern	-0.30
Phyllostomus hastatus	*Mastoptera guimaraesi*	*Mastoptera minuta*	Segregation	-2.35

Phyllostomus hastatus	*Mastoptera guimaraesi*	*Strebla consocia*	No Pattern	0.14
Phyllostomus hastatus	*Mastoptera guimaraesi*	*Trichobius longipes*	Aggregation	2.33
Phyllostomus hastatus	*Mastoptera minuta*	*Strebla consocia*	No Pattern	-1.33
Phyllostomus hastatus	*Mastoptera minuta*	*Trichobius longipes*	No Pattern	-0.54
Phyllostomus hastatus	*Strebla consocia*	*Trichobius longipes*	Aggregation	2.64
Sturnira lilum	*Aspidoptera falcata*	*Megistopoda proxima*	Aggregation	7.40
Sturnira ludovici	*Aspidoptera falcata*	*Megistopoda theodori*	No Pattern	1.82
Sturnira tildae	*Aspidoptera falcata*	*Megistopoda sp.*	Aggregation	4.85
Tonatia sylvicola	*Mastoptera minuta*	*Trichobius silvicolae*	Aggregation	2.16
Trachops cirrhosus	*Full comparison*		Aggregation	12.3
Trachops cirrhosus	*Speiseria magnioculus*	*Strebla mirabilis*	Aggregation	3.89
Trachops cirrhosus	*Speiseria magnioculus*	*Trichobius dugesioides*	Aggregation	5.47
Trachops cirrhosus	*Strebla mirabilis*	*Trichobius dugesioides*	Aggregation	12.4
Uroderma bilobatum	*Paratrichobius dunni*	*Trichobius urodermae*	No Pattern	0.63

Table 1.4: Lists all 79 relationships examined in this study and states the host species in each relationship, the parasite species associated in this relationship, describes the type of relationship exhibited between the different parasite species in each relationship and the standardized effect size (SES) value for that analysis. Relationship data described in this table are based off of null model analyses that made use of abundance matrices. Full comparison analyses refer to null model analyses where all potential parasite species for a host species were examined. All figures describing the null model distributions and visualization of the matrices for each assemblage and individual-pair comparison can be found in Appendix A.

Bat Host Sp.	**Parasite Sp. 1**	**Parasite Sp. 2**	**Pattern**	**SES**
Artibeus amplus	*Strebla paramirabilis*	*Trichobius assimilis*	No Pattern	1.36
Anoura caudifer	*Anastrebla caudiferae*	*Trichobius tiptoni*	No Pattern	1.58
Anoura geoffroyi	*Full comparison*		No Pattern	0.59
Anoura geoffroyi	*Anastrebla modestini*	*Exastinion clovesi*	Aggregation	2.32
Anoura geoffroyi	*Anastrebla modestini*	*Trichobius propinquus*	No Pattern	0.85
Anoura geoffroyi	*Exastinion clovesi*	*Trichobius propinquus*	No Pattern	-1.92
Anoura latidens	*Anastrebla modestini*	*Exastinion clovisi*	Aggregation	4.06
Artibeus planirostris	*Full comparison*		Aggregation	7.27
Artibeus planirostris	*Aspidoptera phyllostomatis*	*Megistopoda aranea*	Aggregation	4.06
Artibeus planirostris	*Aspidoptera phyllostomatis*	*Metelasmus pseudopterus*	Aggregation	7.54
Artibeus planirostris	*Megistopoda aranea*	*Metelasmus pseudopterus*	No Pattern	1.17
Carollia brevicauda	*Full comparison*		Aggregation	3.87
Carollia brevicauda	*Speiseria peytonae*	*Strebla guajiro*	Aggregation	2.26
Carollia brevicauda	*Speiseria peytonae*	*Trichobius persimilis*	No Pattern	0.93
Carollia brevicauda	*Strebla guajiro*	*Trichobius persimilis*	Aggregation	3.59
Carollia perspicillata	*Full comparison*		Aggregation	22.72

Carollia perspicillata	*Speiseria ambigua*	*Strebla guajiro*	Aggregation	8.76
Carollia perspicillata	*Speiseria ambigua*	*Trichobius dugesioides*	Aggregation	3.20
Carollia perspicillata	*Speiseria ambigua*	*Trichobius joblingi*	Aggregation	15.34
Carollia perspicillata	*Strebla guajiro*	*Trichobius dugesioides*	Aggregation	9.41
Carollia perspicillata	*Strebla guajiro*	*Trichobius joblingi*	Aggregation	17.51
Carollia perspicillata	*Trichobius dugesioides*	*Trichobius joblingi*	Aggregation	2.83
Chrotopterus auritus	*Strebla chrotopteri*	*Trichobius dugesioides*	Aggregation	3.66
Desmodus rotundus	*Strebla wiedemanni*	*Trichobius parasiticus*	Aggregation	14.63
Diaemus youngi	*Strebla diaemi*	*Trichobius diaimi*	No Pattern	0.41
Glossophaga longirostris	*Full comparison*		Aggregation	3.48
Glossophaga longirostris	*Strebla curvata*	*Trichobius dugesii*	Aggregation	3.11
Glossophaga longirostris	*Strebla curvata*	*Trichobius uniformis*	No Pattern	2.30
Glossophaga longirostris	*Trichobius dugesii*	*Trichobius uniformis*	No Pattern	0.57
Glossophaga soricina	*Full comparison*		No Pattern	0.56
Glossophaga soricina	*Paraeuctenodes longipes*	*Strebla curvata*	No Pattern	1.10
Glossophaga soricina	*Paraeuctenodes longipes*	*Trichobius dugesii*	No Pattern	-0.73
Glossophaga soricina	*Paraeuctenodes longipes*	*Trichobius uniformis*	No Pattern	1.21
Glossophaga soricina	*Strebla curvata*	*Trichobius dugesii*	No Pattern	-1.46
Glossophaga soricina	*Strebla curvata*	*Trichobius uniformis*	No Pattern	1.07
Glossophaga soricina	*Trichobius dugesii*	*Trichobius uniformis*	No Pattern	-1.29
Lonchorhina aurita	*Strebla altmani*	*Trichobius flagellatus*	No Pattern	2.01
Leptonycteris curasoae	*Nycterophilia coxata*	*Trichobius sphaeronotus*	Aggregation	8.73
Lonchorhina orinocensis	*Strebla altmani*	*Trichobius ethophallus*	Aggregation	4.01

Lonchophylla robusta	*Anastrebla nycteridis*	*Trichobius lonchophyllae*	No Pattern	-1.30
Lionycteris spurrelli	*Anastrebla spurrelli*	*Trichobius lionycteridis*	Aggregation	3.49
Macrophyllum macrophyllum	*Strebla matsoni*	*Trichobius macrophylli*	No Pattern	1.64
Micronycteris minuta	*Strebla machadoi*	*Trichobius handleyi*	No Pattern	1.61
Natalus tumidirostris	*Nycterophilia natali*	*Trichobius galei*	No Pattern	-0.38
Noctilio albiventris	*Full comparison*		No Pattern	1.34
Noctilio albiventris	*Noctiliostrebla maai*	*Paradyschiria curvata*	No Pattern	0.51
Noctilio albiventris	*Noctiliostrebla maai*	*Paradyschiria parvula*	Aggregation	4.23
Noctilio albiventris	*Paradyschiria curvata*	*Paradyschiria parvula*	Segregation	-2.34
Noctilio leporinus	*Full comparison*		Aggregation	3.20
Noctilio leporinus	*Noctiliostrebla aitkeni*	*Noctiliostrebla traubi*	No Pattern	-1.13
Noctilio leporinus	*Noctiliostrebla aitkeni*	*Paradyschiria fusca*	Aggregation	4.90
Noctilio leporinus	*Noctiliostrebla aitkeni*	*Paradyschiria lineata*	No Pattern	-1.24
Noctilio leporinus	*Noctiliostrebla traubi*	*Paradyschiria fusca*	No Pattern	-0.88
Noctilio leporinus	*Noctiliostrebla traubi*	*Paradyschiria lineata*	Aggregation	7.25
Noctilio leporinus	*Paradyschiria fusca*	*Paradyschiria lineata*	No Pattern	-1.00
Phyllostomus discolor	*Full comparison*		Aggregation	4.94
Phyllostomus discolor	*Strebla hertigi*	*Trichobioides perspicillatus*	No Pattern	0.73
Phyllostomus discolor	*Strebla hertigi*	*Trichobius costalimai*	No Pattern	1.60
Phyllostomus discolor	*Trichobioides perspicillatus*	*Trichobius costalimai*	Aggregation	7.01
Phyllostomus elongatus	*Full comparison*		No Pattern	0.71
Phyllostomus elongatus	*Strebla consocia*	*Trichobius joblingi*	Aggregation	2.36
Phyllostomus elongatus	*Strebla consocia*	*Trichobius longipes*	No Pattern	-0.54
Phyllostomus elongatus	*Trichobius joblingi*	*Trichobius longipes*	No Pattern	-0.30
Phyllostomus hastatus	*Full comparison*		No Pattern	0.57

Phyllostomus hastatus	*Mastoptera guimaraesi*	*Mastoptera minuta*	No Pattern	-1.09
Phyllostomus hastatus	*Mastoptera guimaraesi*	*Strebla consocia*	No Pattern	-0.74
Phyllostomus hastatus	*Mastoptera guimaraesi*	*Trichobius longipes*	Aggregation	4.71
Phyllostomus hastatus	*Mastoptera minuta*	*Strebla consocia*	No Pattern	-0.81
Phyllostomus hastatus	*Mastoptera minuta*	*Trichobius longipes*	No Pattern	-0.58
Phyllostomus hastatus	*Strebla consocia*	*Trichobius longipes*	No Pattern	0.49
Sturnira lilum	*Aspidoptera falcata*	*Megistopoda proxima*	Aggregation	5.02
Sturnira ludovici	*Aspidoptera falcata*	*Megistopoda theodori*	No Pattern	0.86
Sturnira tildae	*Aspidoptera falcata*	*Megistopoda sp.*	Aggregation	2.81
Tonatia sylvicola	*Mastoptera minuta*	*Trichobius silvicolae*	Aggregation	4.65
Trachops cirrhosus	*Full comparison*		Aggregation	7.46
Trachops cirrhosus	*Speiseria magnioculus*	*Strebla mirabilis*	No Pattern	0.77
Trachops cirrhosus	*Speiseria magnioculus*	*Trichobius dugesioides*	Aggregation	3.18
Trachops cirrhosus	*Strebla mirabilis*	*Trichobius dugesioides*	Aggregation	9.17
Uroderma bilobatum	*Paratrichobius dunni*	*Trichobius urodermae*	No Pattern	0.92

Chapter 2: Morphology in Relation to Co-occurrence

Introduction

Under niche-based competition theory, species co-occurrence is driven by differences in niche usage. If the differences in niche utilization is greater than the competitive differences between two species, then they are predicted to coexist within the same space (Mayfield and Levine, 2010). Competitive differences in this context refers to the difference in fitness between two individuals in regard to reproductive output, obtaining habitat space, susceptibility to predation, ability to gain limited resources, and other factors. Species co-occurrence has been well researched within various parasite communities to examine patterns of co-occurrence and the possible underlying mechanisms (Reed et al., 2000; Gotelli & Rohde, 2002; Friggens & Brown, 2005; Tello et al., 2008). While there is a lack of consensus in regards to the effects of competition on the structuring of parasite communities, it has been shown in cestodes and streblids that there is evidence for community structure based on competition (Friggens and Brown, 2005; Tello et al., 2008; Presley, 2011; Schooler, 2017a). These results have provided the opportunity for examining possible mechanisms for patterns of co-occurrence, such as strong negative interactions between co-occurring parasite species or facilitation. The purpose of this project is to explore possible mechanisms for patterns of co- occurrence by using previously studied assemblages of streblid parasites on Neotropical bat hosts.

Research on streblid bat flies have provided useful baseline information in regard to several important host-parasite characteristics including parasite abundance, species diversity, and patterns of co-occurrence. Generally, when patterns of co-occurrence are

detected on the species-pair and assemblage levels, they are predominantly found to be patterns of aggregation (Tello et al., 2008; Presley, 2011; Schooler, 2017a). Several mechanisms have been proposed to explain species aggregation, including positive interactions between streblid species, various host characteristics, and reduced negative interaction between streblid species. Positive interactions, or facilitation, may occur when a large number of individual bat flies of one species occupy a host individual in a way that facilitates the occurrence of second species. Facilitation may be indicative of a mutualistic relationship between co-occurring bat flies (Dick and Patterson, 2006), in which the first parasite species might lessen the grooming pressure on the second parasite species. This mechanism has been explored in models developed by Reicizigel and Rosza (1998) when examining the presence of two parasite species on a host individual. However, positive interactions as a mechanism for aggregation among streblid species has failed to acquire the needed evidence to be considered a major contributing factor to aggregation (Presley, 2011; Schooler, 2017a).

Host characteristics such as body size, mobility, range, and social behavior have been offered as plausible explanations for aggregation (Tello et al., 2008; Presley, 2011). For example, it has been proposed that host sex-related traits may explain aggregation among co-occurring parasites. Sexual dimorphism, in which males with larger bodies represent larger targets for host-seeking parasites and more habitat for established ectoparasites, may help to create aggregation. Moreover, the larger home ranges and dispersal distances of males is known to explain why males typically harbor more parasites than females (Krasnov et al. 2005). However, when separated from host sex, size does not appear to be a reason for parasite aggregation on certain bat species from

Venezuela and Paraguay (Patterson et al. 2008; Presley and Willig, 2008), and because bats are not exposed to streblids while in flight, range and dispersal distance are likely unimportant to parasite loads (Presley, 2011). More plausibly, host species that form social harems allow for greater opportunities for parasite encounters and transfers (Presley, 2011), and host-specific attributes such as roost selection or other variables may affect host transfer opportunities for parasites (Dick, 2007; Dick and Patterson, 2007; Presley, 2011).

Finally, microhabitat partitioning and/or differences in morphology may reduce antagonistic interactions between streblid species and facilitate their aggregation (Tello et al., 2008). An interesting concept is that differences in morphology reduce negative interactions by segregating flies into different niches that would allow for aggregation rather than competitive exclusion. This differs from facilitation in that mutualism is not required. Microhabitat partitioning has been demonstrated to occur in multiple co-occurring parasite species including chewing lice on geomyid pocket gophers (Reed et al., 2000), cestode species of round stingrays and skates (Friggens and Brown, 2005), and streblid species of bats (ter Hofstede et al, 2004). A notable aspect of microhabitat partitioning is that parasite species possess specific morphological adaptations that increase their fitness in particular locations on the host individual. Streblids possess a number of morphological and behavioral traits that allow for partitioning among the two primary habitat types available to them—body fur or patagia of bat hosts (ter Hofstede et al., 2004). In line with this prediction, it is expected that co-occurring streblid species with similar morphology have a greater amount of competitive interaction compared to

morphologically divergrent species, and the resulting niche overlap would lead to segregation.

The theory of niche-based competition assumes a strong relationship between ecology and morphology, where physical form enables or necessitates ecological function (Juliano and Lawton, 1990a). In many cases, species with similar morphological characteristics make use of similar resources or obtain resources in a comparable way (Juliano and Lawton, 1990b). This concept is supported by numerous empirical studies involving birds (Ricklefs et al., 1980), lizards (Ricklefs et al., 2008), fish (Gatz-Jr., 1979), and bats (Findley and Black, 1983). However, it should be noted that in some cases, morphological traits are poor niche indicators and instead may arise from other factors such as sexual selection (Wiens and Rotenberry, 1980). Assuming that morphology parallels ecology, we expect an increase in interspecific morphological similarity within a community will increase the intensity of competition for resources (Juliano and Lawton, 1990a). In terms of affecting co-occurrence, there may be a threshold in morphological dissimilarity facilitating co-occurrence of two or more species (Juliano &and Lawton, 1990a). In other words, there may be a certain amount of measurable morphological difference among co-occurring parasite species that is necessary for aggregation.

The overall body shape and the shape of the hind legs have been linked to micro-habitat selection and niche usage in bat flies (ter Hofstede et al., 2004). Streblids have three different morphotypes with two specifically adapted to survival in the furred regions of the bat and the third adapted to survival within the membranes. Host grooming is hypothesized to explain host-site specificity and corresponding morphology in streblid species that is supported by a simulation model performed by ter Hofstede et al. (2004).

In this simulation, two different generalist ectoparasite species were introduced to bats and the grooming behavior was noted to be different between the wing membrane, where they used licking, and the fur where they used scratching to remove parasites (ter Hofstede et al, 2004). The simulation was run for 300 generations and replicated 200 times and reuslted in one of two outcomes. The first outcome was that one parasite species would go extinct and the second outcome was that the two parasite species specialized to specific regions on the bat host (Reiczigel and Rozsa, 1998). This provides strong evidence that host-site specificity in streblid species could be a result of host grooming behavior.

Bat flies in segregated host microhabitats demonstrate differing behaviors and morphology in order to avoid the unique grooming behavior associated with these host-sites. The "fur runner" morphotype possess extremely elongated legs and body with a broad, flat ventral thorax. "Fur runners" use their long legs to push up to the surface of the host's fur to run or "skim" along the body to avoid host grooming pressure (ter Hofstede et al., 2004). The "fur swimmer" morphotype possesses a compressed body, with shorter legs, and ctenidium (combs located around the head). The "fur swimmers" overall morphology allows them to maneuver through the host's fur to avoid host grooming in a similar fashion to fleas (Dick and Patterson, 2006). The "wing crawler" morphotype is more general, having a smaller uncompressed body with relatively short legs. Membrane-specific "wing crawlers" may use their short legs to help cling to the smooth surfaces and small size to hide in the folds of the membrane to avoid host grooming (ter Hofstede et al., 2004). Previous research found evidence that microhabitat partitioning plays a role in patterns of co-occurrence, but notable discrepancies suggest

that this is not the sole mechanism behind patterns of co-occurrence (Schooler, 2017a). These discrepancies include cases of aggregation between species of the same morphotype and a high frequency of no patterns of co-occurrence when the species were of different morphotypes. Examining and comparing overall body shape and hind leg shape between co-occurring species will allow for the continued examination of the hypothesis of microhabitat partitioning as a mechanism for patterns of co-occurrence. Species that share the same morphotype should segregate while those with different morphotypes should aggregate.

The purpose of this study was to explain the patterns of co-occurrence seen in streblid species. I would predict that species of significantly differing morphology would be more likely to demonstrate patterns of aggregation, while species with more similar morphologies would more likely demonstrate patterns of segregation. To examine this prediction, the relationship between morphology and patterns of co-occurrence was examined using geometric morphometric analyses.

Materials and Methods

Streblid Collection

The streblid parasites studied in this project were part of the collections of Neotropical (Venezuelan) bat flies collected as part of the Smithsonian Venezuelan Project (SVP). The SVP was conducted from 1965 to 1968 with the intent of surveying mammals and their ectoparasites. It is the largest collection of its kind that sampled 38,213 mammals representing 270 species, which included 24,797 sexed bats of 133 species that harbored in total 116 different streblid species (Handley, 1976). During the

survey, bats were collected using mist nets and held in individual paper bags, fumigated with ether, and then the parasites were collected and preserved in 70% ethanol (Patterson et al., 2008). Host names were reviewed using computerized records from the National Museum of Natural History (USNM) that confirmed that the host identification could be considered accurate, consistent, and can be reexamined. Parasite samples were collected and then organized based on individual host with a total of 36,663 streblids, representing 22 genera and 116 species were sorted, identified, and enumerated at the Field Museum of Natural History.

The data used for this project were limited based on several criteria of importance. One such criterion was the need for a high enough sample size for each individual bat species (at least 10 individuals per host species) and parasite species (at least 20 individuals per host species) in order minimize spurious results based on not having a representative sample. The second criterion was that the bat host harbored potentially two to at maximum four co-occurring species of streblids. This was necessary in order to decipher the mechanism behind the patterns of co-occurrence exhibited in these parasites. The third criterion was that there was at least one species-pair for each type of pattern of co-occurrence based on previous work on abundance data of these parasites (Schooler, 2017a). The fourth criterion was that there was at least one bat species included that had two potential co-occurring parasites, one that had three potential co-occurring parasites, and one that had four potential co-occurring parasites. A fifth criterion was that there were both parasite species-pairs that showed pattern of co-occurrence reflective of predictions on microhabitat partitioning and those that did not follow this prediction

(Schooler, 2017a). Based on these criteria, six bat species hosting a total of 15 parasite species were selected for examination (Table 2.1).

Morphology Measurements

Bat flies were photographed using a Canon Rebel XTi/400 D camera that was mounted on a Leica MZ16 microscope, with each specimen being placed on a wet mount. The focus was kept consistent between each photograph. At each magnification used, linear measurements were made for the length of the visual field, which allowed for metric units to be applied in the measurements. Landmark-based geometric morphometrics (GM) were used to quantify the shape of the bat flies based on anatomical landmarks (Adams et al., 2013). Generalized Procrustes analysis (GPA) was used to render size, orientation, and position invariant by using generalized least squares superimposition in order to describe organismal shape (Rohlf and Slice, 1990).

Photos of 300 individuals were digitized from 15 different streblid species where 20 individuals were photographed per species. Three separate images were captured per individual specimen; two captured the overall body shape from a ventral and lateral perspective and one focused on a lateral view of the hind leg. The three images used to capture overall body shape and the hind leg were selected due to the association that both the overall body shape and hind leg have with habitat partitioning. Each image was compartmentalized into three individual attributes with the ventral and lateral overall body images broken down by body segment (head, thorax, and abdomen) and the hind leg broken down by leg segment (femur, tibia, and tarsus). Due to the inconsistency of

the abdomen between individual specimen based on their reproductive cycle the abdomen shape was excluded from analysis.

The body shape images were digitized through the use of the tpsDig2 software (Rohlf, 2014) that allowed for quantification of body shape by placing landmarks on images. For the ventral view of the full body, eight fixed landmarks were placed along with 43 semi-landmarks (sliding landmarks) on each image (Figure 2.1). The lateral view of the full body had five fixed landmarks and 51 semi-landmarks placed on each image (Figure 2.2). Six fixed landmarks and 34 semi-landmarks were placed on each hind leg image (Figure 2.3). Fixed landmarks were placed on consistent anatomical features on the specimen, while semi-landmarks were used to estimate curves and are able to freely "slide" along tangency vectors during GPA. This allowed homologous curves or surfaces to be quantified through the use of resulting Cartesian points (Gunz and Mitteroecker, 2013). The method of minimizing Procrustes distances among specimens was used, with Procrustes distances measured as the square root of summed square distances between corresponding landmarks (Figures 2.4, 2.5, & 2.6). The morphological variation in the abdomen is reflective of reproductive status rather than of constant characteristics associated with habitat partitioning, which is why the abdomen was removed in order to prevent shape data that would conflict with the objective of this study. The resulting Procrustes residuals were used as shape variables for later statistical analyses. A strong relationship between shape and size was detected, so the variables were adjusted so that allometry-free Procrustes residuals were used (Figure 2.7, 2.8, & 2.9). GPA was performed using the package geomorph (Adam et al., 2015), version 3.0.2 within R (R Core Team 2015; Appendix D).

The three adjusted shape components and their individual components were compared between individual flies within a co-occurring relationship to see if the species were significantly different from one another using Procrustes ANOVA and pairwise analyses. A frequency table was created where each row represented an individual body section being compared between individuals of two different species in a co-occurring relationship and each column described both the type of relationship and whether there was a significant difference in a particular shape component (Table 2.2). To determine if there was a significant difference between the three different patterns of co-occurrence in regard to the ratio of species-pairs with and with out significant differences in morphology, a Fisher's exact test for each body part was used. This test was also performed on species-pairs that showed either patterns of aggregation or no pattern of co-occurrence, with segregation being excluded from these tests due to having only a single observartion of segregation.

Results

No significant differences were uncovered between the three different co-occurrence patterns when examining any of the morphological aspects (Table 2.3) or between the two patterns of co-occurrence when excluding segregation (Table 2.4). To determine if there was a larger number of aggregating species-pairs that had significant morphological differences than expected, a chi-squared test was used for each morphological aspect. The chi-squared tests were performed under an assumption where the expected values were the ratios expressed by the no pattern of co-occurrence species-pairs. This is under the assumption that demonstrating neither pattern of co-occurrence

would be the biological default. Due to the use of multiple tests Bonferroni correction was used that required a test result to have a $p<0.007$ to be significant. The results of these chi-square tests found no significant differences from the expected values (Table 2.5).

Discussion

The results of this study are not straightforward, but do provide evidence that differences in morphology among streblid species may act as a contributing mechanism driving patterns of co-occurrence among streblid species. When species co-occurrence patterns were detected, they were overwhelmingly cases of aggregation rather than segregation (Schooler, 2017a). This means that species tend to occur together on host individuals much more often than expected by chance. Due to the lack of segregation-based relationships observed, there is no way to provide an accurate and quantifiable method as to how morphological differences affect patterns of segregation. However, this trend can be explained based on the comparisons of morphological aspects between the species-pairs exhibiting segregation. No significant differences in any morphological aspect follows the prediction that parasite species that occur on the same host species that exhibit patterns of segregation will have significantly similar morphology. Still, more cases of species-pair relationships showing patterns of segregation and examination of their morphological similarities would need to occur to confirm this speculation.

Results from the chi-square test examining the ratio of aggregated species-pairs, comparing pairs with significantly differing morphology and not significantly differing morphology, found no significant results under the assumption being used. The results from this test found no significant differences between the aggregation and no pattern of

co-occurrence ratios in any region of the body. Taken together, these results seem to indicate that morphology does not play a significant role in determining aggregation between co-occurring species. Based on these results it would indicate that the morphological difference while serving the primary purpose of lessening host gromming pressure in different host microhabitats, it does not play a role in determining patterns of aggregation based on niche-based competition theory. These results also seem to indicate that morphology may play some role in determining patterns of co-occurrence; but to what degree is unclear based on the conflicting results from the patterns of aggregation and segregation.

Fisher's exact tests and chi-squared tests comparing ratios between species-pairs exhibiting patterns of aggregation and species-pairs exhibiting neither patterns of aggregation nor segregation were run to determine if there were significant differences in the ratio of relationships with significant differences between co-occurring species' morphology and relationships with no significant differences in co-occurring species' morphology. This seems to further indicate that while morphology may contribute to patterns of segregation, it does not appear to be the sole mechanism for patterns of co-occurrence.

Because the morphological traits we examined do not explain patterns of co-occurrence, future studies should examine other contributing mechanisms, such as social harems (Presley, 2011). Research into the frequency of aggregating streblid pairs in relation to the degree of socializing in their bat hosts would be one avenue of research. Additionally roost selection, which has been noted to affect ectoparasite abundance (ter Hofstede and Fenton, 2005), would be another avenue of study.

Future studies should also attempt to identify different morphological characteristics and make comparisons among more streblid species pairs to see whether our lack of significant effects is a common conclusion. While this study does not provide strong evidence that leg morphology or overall body shape is a primary mechanism driving patterns of co-occurrence, it furthers our understanding to the complex mechanisms underpinning of the ecological structure exhibited among streblid species in regards to co-occurrence.

Literature Cited

Adams, D.C., M.L. Collyer and E. Sherratt. 2015. Geomorph: Geometric morphometric analyses of 2d/3D landmark data, version 2.1.3.

Adams, D. C., F. J. Rohlf, and D. E. Slice. 2013. A field comes of age: Geometric morphometrics in the 21st century. Hystrix **24**: 7–14.

Combes, C. 1991. Aspects of parasite transmission. The American Naturalist **138**: 866–880.

Dick, C. W., and B. D. Patterson. 2006. Bat flies - obligate ectoparasites of bats. *In* Micromammals and macroparasites: From ecology to management. R. Poulin and B. R. Krasnov (eds.). Springer-Verlag, Tokyo, Japan, p. 179–194.

Dick, C. 2007. High host specificity of obligate ectoparasites. Ecological Entemology **32**: 446–450.

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

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

Friggens, M. M., and J. H. Brown. 2005. Niche partitioning in the cestode communities of two elasmobranchs. Oikos **108**: 76–84.

Gatz-Jr., A. J. 1979. Community organization in fishes as indicated by morphological features. Ecology **60**: 711–718.

Gotelli, N. J., and K. Rohde. 2002. Co-occurrence of ectoparasites of marine fishes: A null model analysis. Ecology Letters **5**: 86–94.

Gunz, P., and P. Mitteroecker. 2013. Semilandmarks: A method for quantifying curves and surfaces. Hystrix **24**.

Handley, C. O. J. 1976. Mammals of the Smithsonian Venezuelan Project. Brigham Young University Science Bulletin, Biological Series **20**: 1–91.

Juliano, S. A., and J. H. Lawton. 1990a. The relationship between competition and morphology. I. Morphological patterns among co-occurring Dysticid beetles. The Journal of Animal Ecology **59**: 403–419.

Juliano, S. A, and J. H. Lawton. 1990b. The relationship between competition and morphology. II. Experiments on co-occurring. Journal of Animal Ecology **59**: 831–848.

Krasnov, B. R., D. Mouillot, I. S. Khokhlova, G. I. Shenbrot, and R. Poulin. 2005. Covariance in species diversity and facilitation among non-interactive parasite taxa: All against the host. Parasitology **131**: 557–568.

Mayfield, M. M., and J. M. Levine. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. Ecology Letters **13**: 1085–1093.

Patterson, B. D., C. W. Dick, and K. Dittmar. 2008. Sex biases in parasitism of neotropical bats by bat flies (Diptera: Streblidae). Journal of Tropical Ecology **24**: 387–396.

Presley, S. J. 2007. Streblid bat fly assemblage structure on Paraguayan *Noctilio leporinus* (Chiroptera: Noctilionidae): nestedness and species co-occurrence. Journal of Tropical Ecology **23**: 409–417.

Presley, S. J. and M. R. Willig. 2008. Intraspecific patterns of ectoparasite abundances on Paraguayan bats: Effects of host sex and body size. Journal of Tropical Ecology **24**: 75–83.

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

R Core Team (2015) R: A language and environment for statistical computing, version 3.1.3. R Foundation for Statistical Computing, Vienna, Austria.

Reed, D. L., M. S. Hafner, S. K. Allen, and M. B. Smith. 2000. Spatial partitioning of host habitat by chewing lice of the genera Geomydoecus and Thomomydoecus (Phthiraptera: Trichodectidae). The Journal of Parasitology **86**: 951–5.

Ricklefs, R. E., and J. Travis. 1980. A morphological approach to the study of avian community organization. The Auk **97**: 321–338.

Ricklefs, R. E., D. Cochran, and E. R. Planka. 2008. A morphological analysis of the structure of communities of lizards in desert habitats. Ecology **62**: 1474–1483.

Reiczigel, J., and L. Rózsa. 1998. Host-mediated site segregation of ectoparasites: An individual-based simulation study. The Journal of Parasitology **84**: 491–498.

Rohlf, F.J. and D. Slice. 1990. Extensions of the procrustes method for the optimal superimposition of landmarks. Systematic Zoology **39**: 40–59.

Rohlf, F.J. (2014) tpsDIG2, version 2.17. http://life.bio.sunysb.edu/morph/

Schooler, M. 2017a. Patterns of Co- occurrence Among Streblid Species. M.S. Thesis. Western Kentucky University, Bowling Green, Kentucky.

Tello, S. J. et al. 2008. Patterns of species co-occurrence and density compensation: A test for interspecific competition in bat ectoparasite infracommunities. Oikos **117**: 693–702.

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

ter Hofstede, H. M. and M. B. Fenton. 2005. Relationships between roost preferences, ectoparasite density, and grooming behaviour of neotropical bats. Journal of Zoology **266**: 333–340.

Wiens, J. A., and J. T. Rotenberry. 1980. Patterns of morphology and ecology in grassland and shrubsteppe bird populations. Ecological Monographs **50**: 287–308.

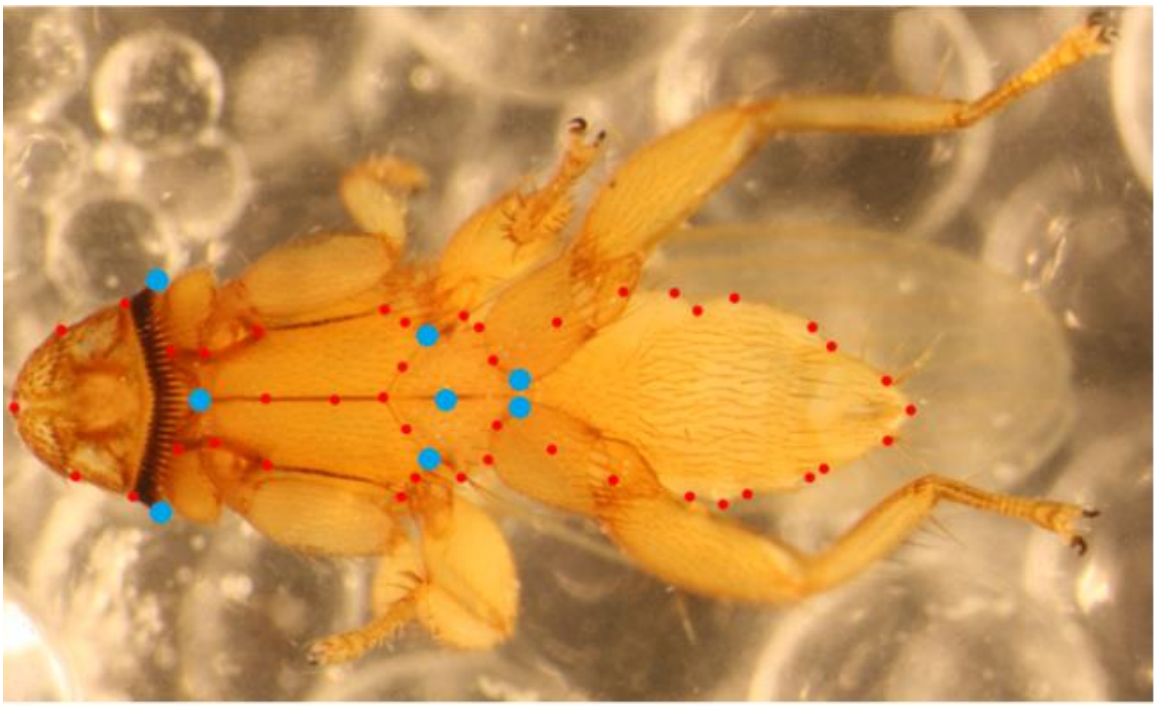

Figure 2.1: Example of anatomical landmarks used for the ventral view of overall body shape. Blue points are fixed landmarks; red points are semi-landmarks.

Figure 2.2: Example of anatomical landmarks used for the lateral view of overall body shape. Blue points are fixed landmarks; red points are semi-landmarks.

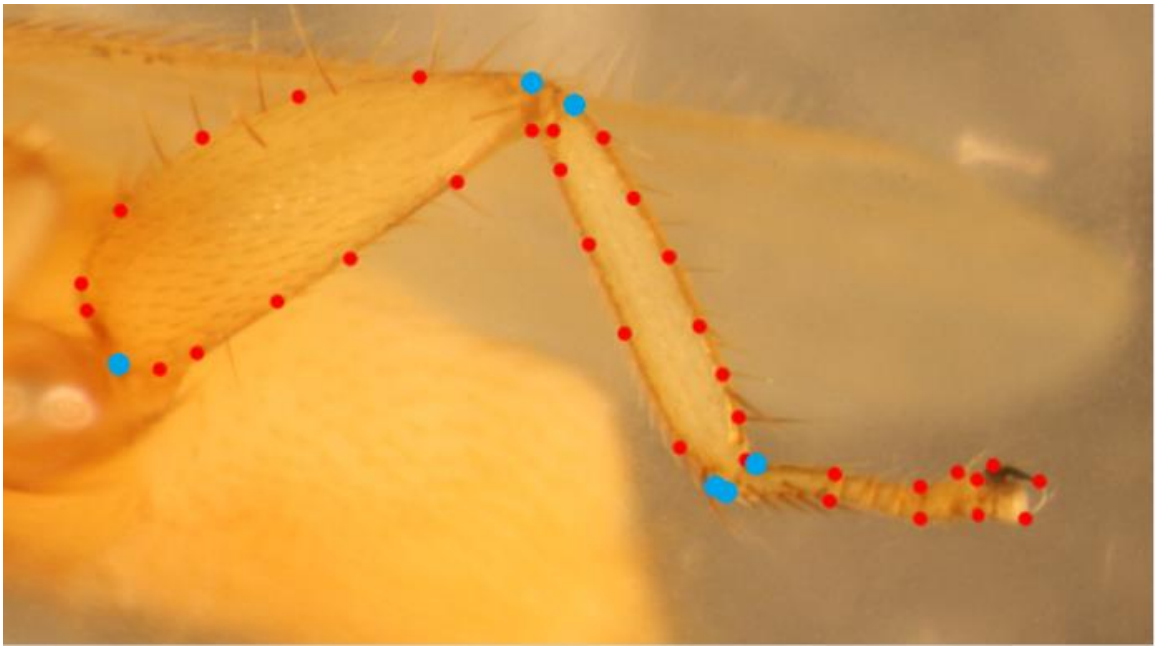

Figure 2.3: Example of anatomical landmarks used for the hind leg shape. Blue points are fixed landmarks; red points are semi-landmarks.

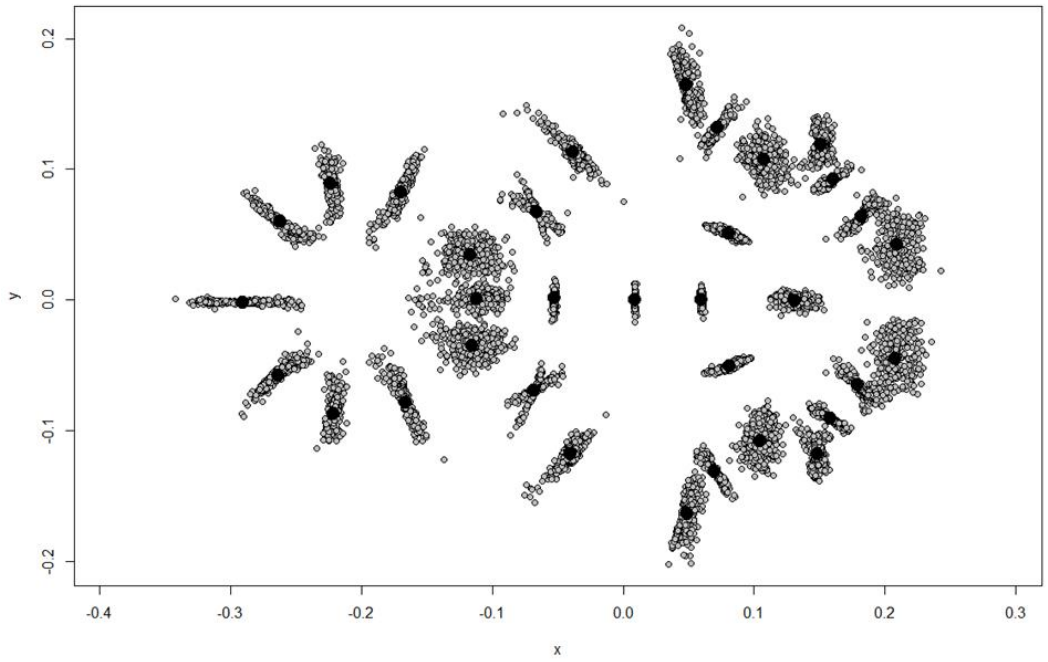

Figure 2.4: Visualization of the Cartesian coordinates of landmarks of the overall body from a ventral perspective (excluding the abdomen) after undergoing GPA.

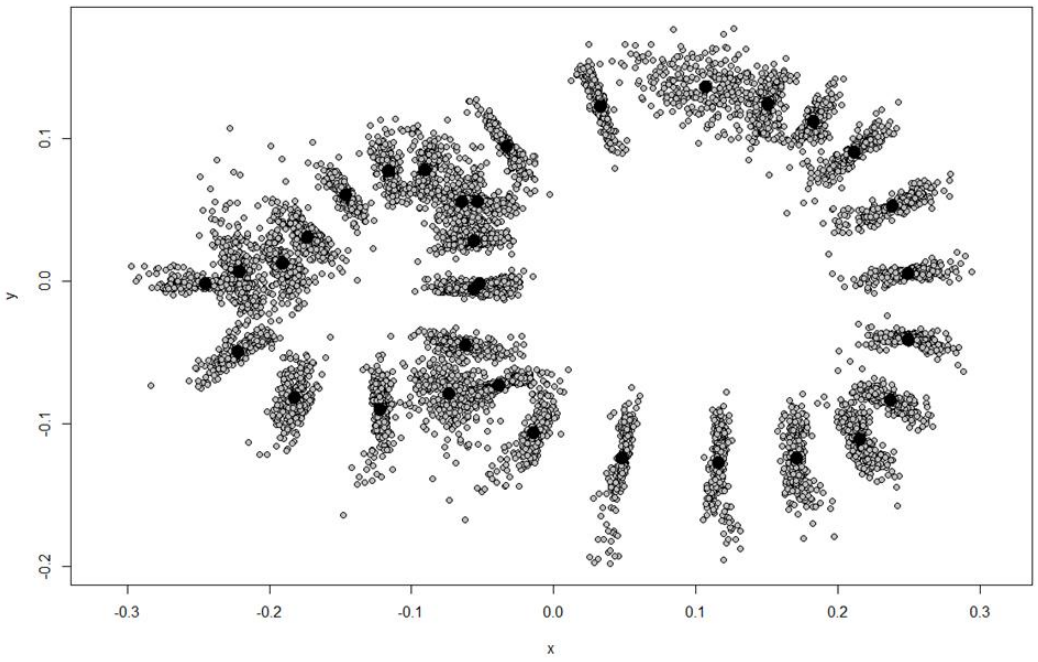

Figure 2.5: Visualization of the Cartesian coordinates of landmarks of the overall body from a lateral perspective (excluding the abdomen) after undergoing GPA.

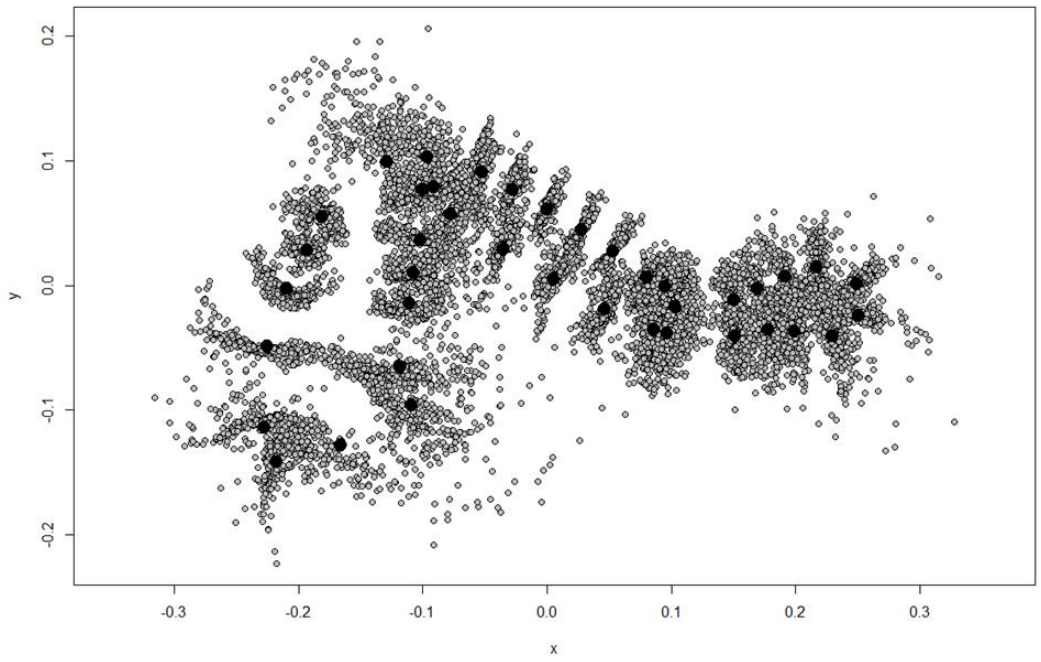

Figure 2.6: Visualization of the Cartesian coordinates of landmarks of the hind leg after undergoing GPA.

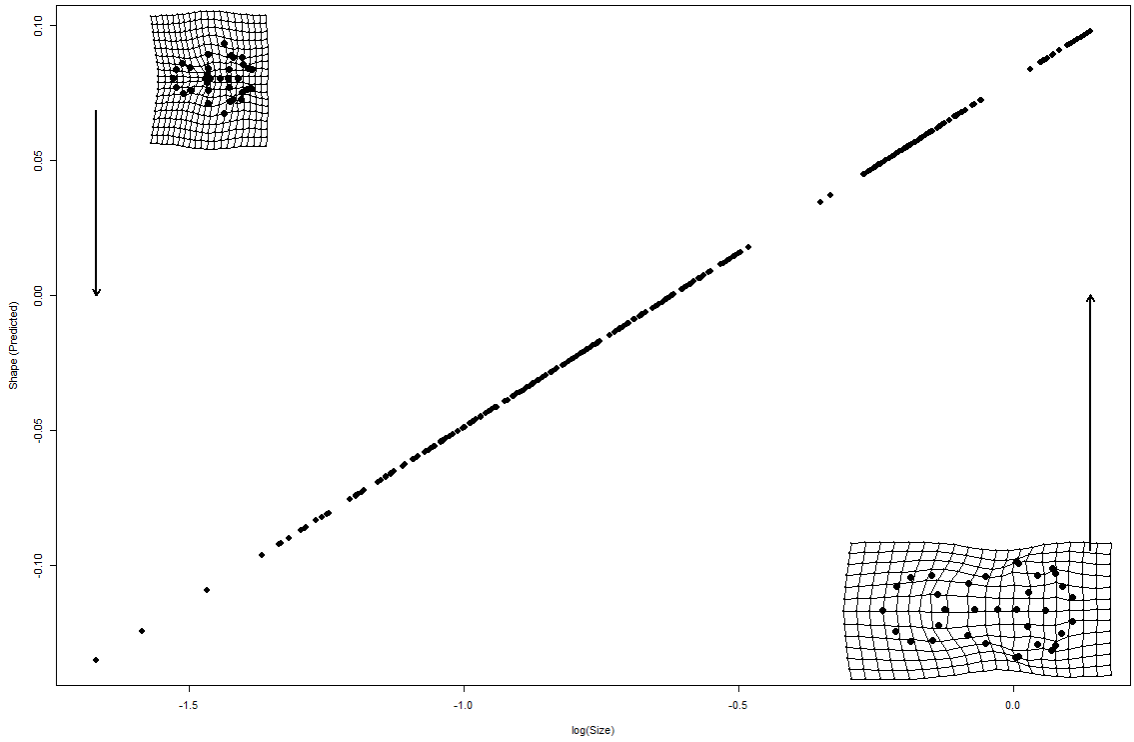

Figure 2.7: Size to shape comparison of the head and abdomen from a ventral perspective.

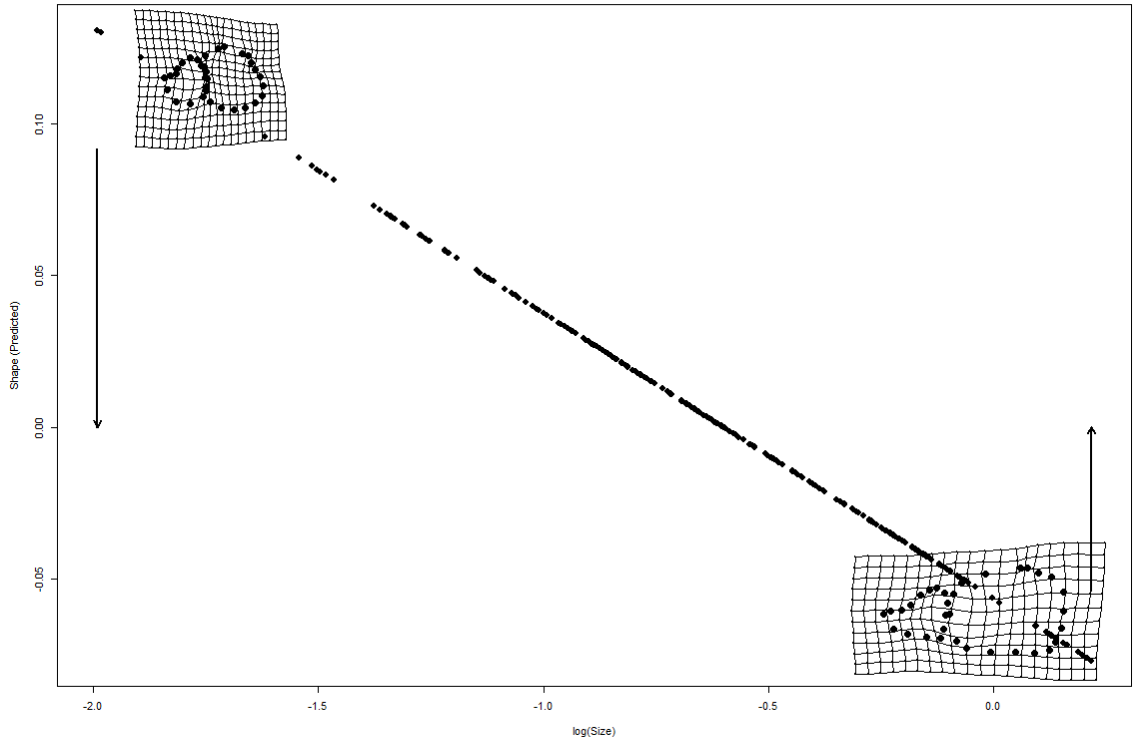

Figure 2.8: Size to shape comparison of the head and abdomen from a lateral perspective.

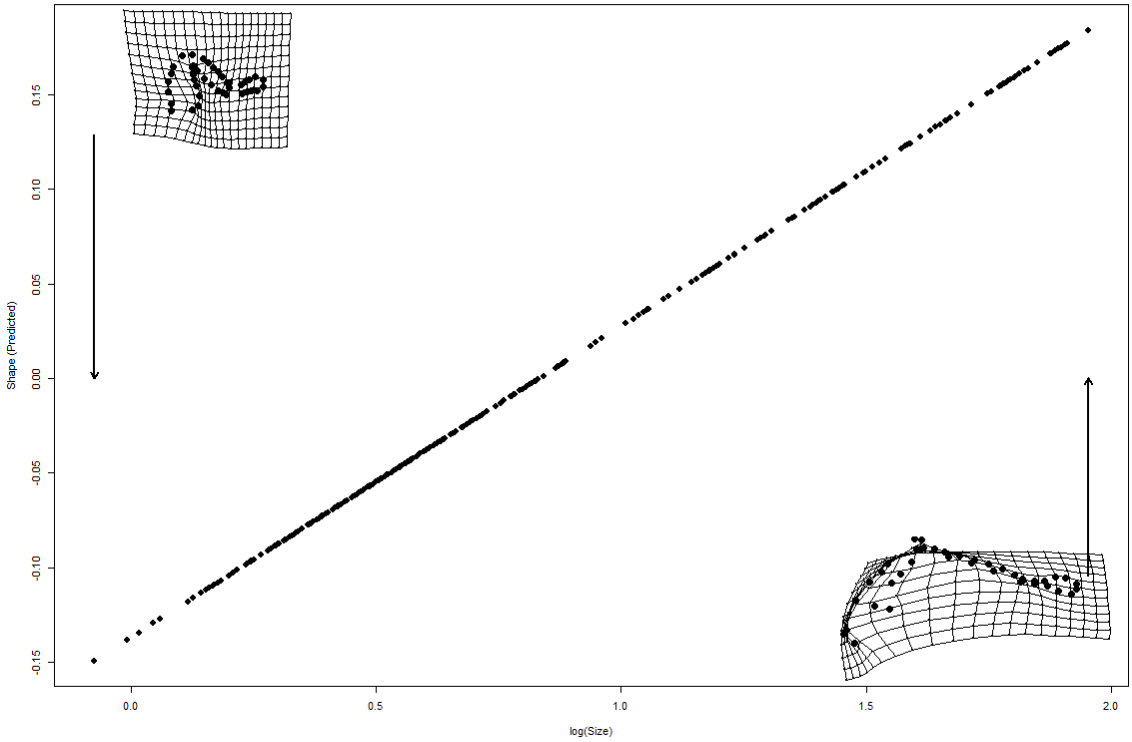

Figure 2.9: Size to shape comparison of the hind leg.

Table 2.1: The list of streblid species whose morphology was examined and their respective host taxa.

Bat Host	Streblid Species
Carollia brevicauda	*Speiseria peytonae*, *Strebla guajiro*, and *Trichobius persimilis*
Carollia perspicillata	*Speiseria ambigua*, *Strebla guajiro*, *Trichobius dugesioides*, and *Trichobius joblingi*
Desmodus rotundus	*Strebla wiedemanni* and *Trichobius parasiticus*
Noctilio albiventris	*Noctiliostrebla maai*, *Paradyschiria curvata*, and *Paradyschiria parvula*
Noctilio leporinus	*Noctiliostrebla aitkeni*, *Noctiliostrebla traubi*, *Paradyschiria fusca*, and *Paradyschiria lineata*
Sturnira lilum	*Aspidoptera falcata* and *Megistopoda proxima*

Table 2.2: Each row represents a different morphological feature that was compared between individuals from two different species in each co-occurring relationship. Each column represents the type of relationship (aggregation, segregation, or no pattern of co-occurrence) and whether there was a significant difference in the morphology of individuals between two different species within a relationship.

	Aggregation with Significant Difference	**Aggregation with No Significant Difference**	**No Pattern with Significant Difference**	**No Pattern with No Significant Difference**	**Segregation with Significant Difference**	**Segregation with No Significant Difference**
Ventral Shape 1 ~ CS	9	1	3	1	0	1
Ventral Shape 2 ~ CS	10	0	4	0	0	1
Lateral Shape 1 ~ CS	9	1	3	1	0	1
Lateral Shape 2 ~ CS	9	1	4	0	0	1
Leg Shape 1 ~ CS	7	3	3	1	0	1
Leg Shape 2 ~ CS	8	2	2	2	0	1
Leg Shape 3 ~ CS	3	7	1	3	0	1

Table 2.3: Examination of the Fisher's exact test results including segregation. This table displays the p-value for each Fisher's exact test (Column 2), the p-value between pair-wise relationships (Columns 3, 5, and 7), and the adjacent p-value for each pair-wise relationship (Columns 4, 6, and 8). Pair-wise relationships between aggregation and no pattern relationships p-values were shown in columns 3 and 4, the p-values for the pair-wise relationship between aggregation and segregation relationships were shown in columns 5 and 6, and the p-values for the pair-wise relationship between no pattern and segregation relationships were shown in columns 7 and 8.

Fisher w/Seg	**p-value**	**Agg:NoP p.Fisher**	**Agg:Nop p.adj Fisher**	**Agg:Seg p.Fisher**	**Agg:Seg p.adj Fisher**	**NoP:Seg p.Fisher**	**NoP:Seg p.adj Fisher**
Ventral 1	0.1099	0.505	0.505	0.182	0.505	0.400	0.505
Ventral 2	0.06667	1.0000	1.000	0.0909	0.273	0.2000	0.300
Lateral 1	0.1099	0.505	0.505	0.182	0.505	0.400	0.505
Lateral 2	0.1905	1.000	1.0	0.182	0.3	0.200	0.3
Leg 1	0.4805	1.000	1.0	0.364	0.6	0.400	0.6
Leg 2	0.3207	0.520	0.78	0.273	0.78	1.000	1.00
Leg 3	1	1	1	1	1	1	1

Table 2.4: Results table examining the Fisher exact test results excluding segregation. Each column represents the test results for each morphological component.

Fisher Without Segregation	**P-value**
Ventral 1	0.5055
Ventral 2	1
Lateral 1	0.5055
Lateral 2	1
Leg 1	1
Leg 2	0.5205
Leg 3	1

Table 2.6: Table of the results of the chi-squared test with no pattern assumptions. Each column represents the test results for each morphological component. The no pattern assumption was that the expected values were reflective of the no pattern results.

No Pattern Assumptions	**Chi-squared**	**df**	**p-value**
Ventral 1	1.2	1	0.2733
Ventral 2	NaN	1	NA
Lateral 1	1.2	1	0.2733
Lateral 2	Inf	1	**< 2.2e-16**
Leg 1	0.13333	1	0.715
Leg 2	3.6	1	0.05778
Leg 3	0.13333	1	0.715

APPENDIX A: DATA VISUALIZATIONS AND NULL DISTRIBUTION FOR FULL AND PAIR-WISE COMPARISONS

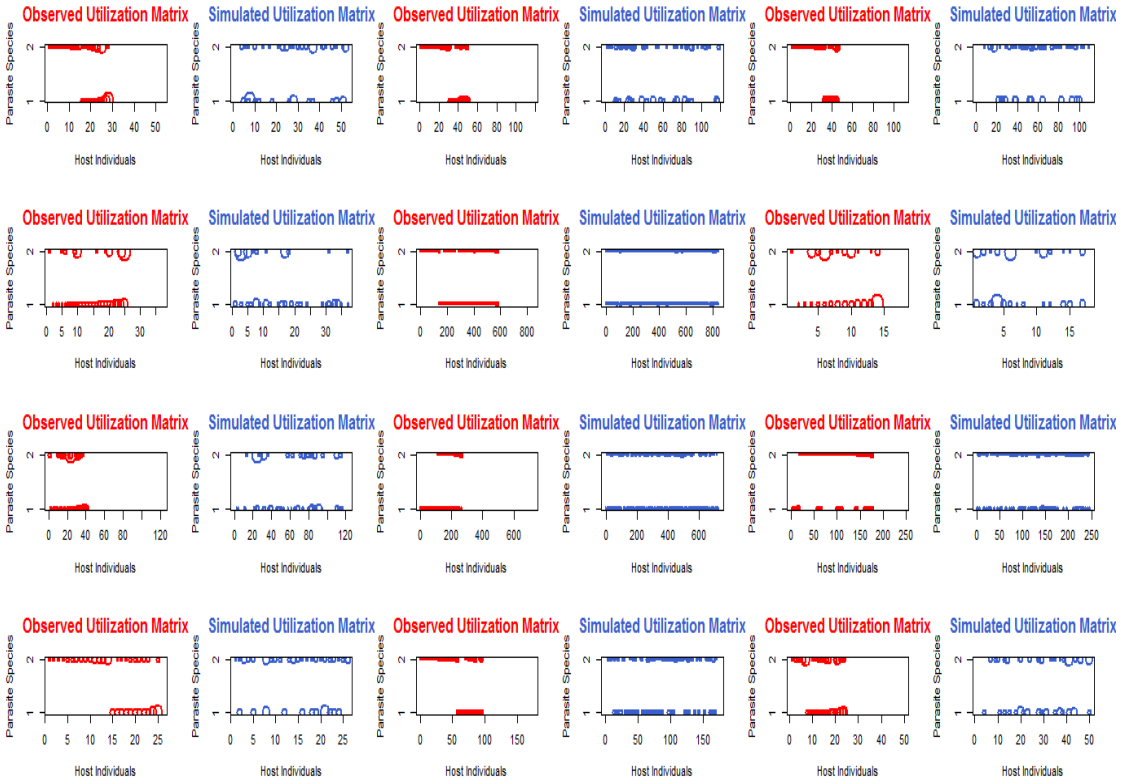

Figure A.1: Data visualization comparing the observed distribution (in red) versus a randomly generated simulated distribution (in blue). Each observed distribution and simulated distribution found to the right of that observed distribution is associated with one host species. These visualizations are representative of the relationships between twelve different host species and their respective two streblid species. The host species represented in this image are as followed from the top left to the bottom right: *Artibeus amplus, Anoura caudifer, Anoura latidens, Chrotopterus auritus, Desmodus rotundus, Diaemus youngi, Lonchorhina aurita, Leptonycteris curasoae, Lonchorhina orinocensis, Lonchophylla robusta, Lionycteris spurrelli,* and *Macrophyllum macrophyllum*.

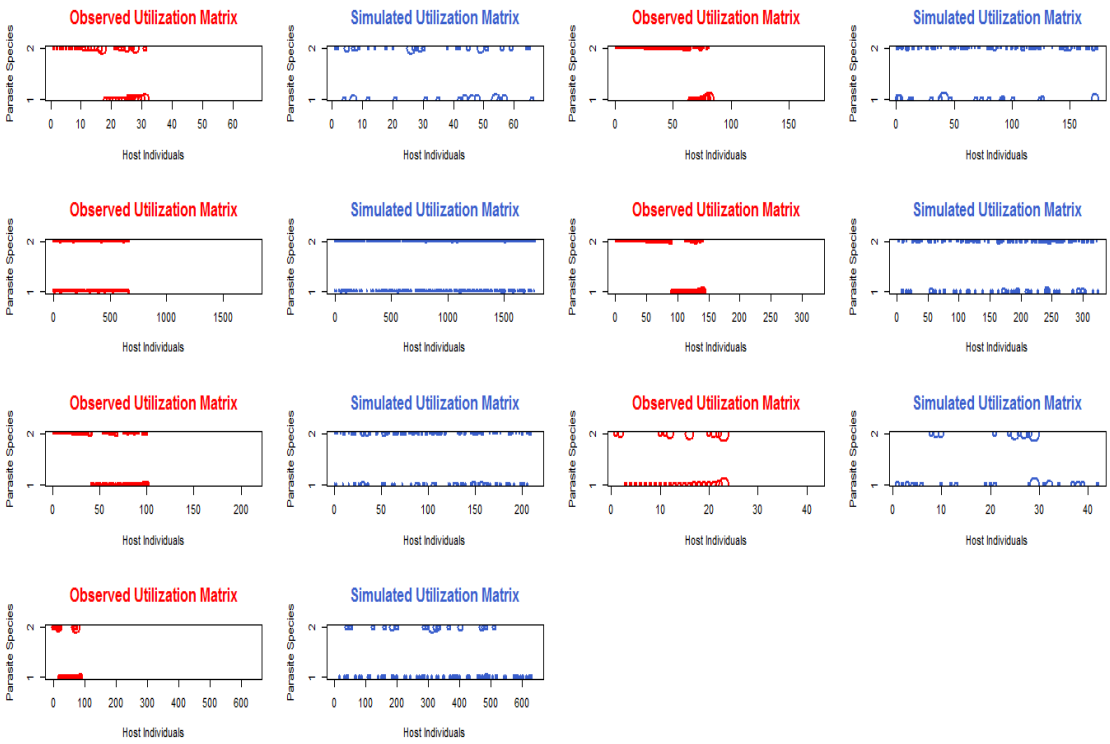

Figure A.2: Data visualization comparing the observed distribution (in red) versus a randomly generated simulated distribution (in blue). Each observed distribution and simulated distribution found to the right of that observed distribution is associated with one host species. These visualizations are representative of the relationships between seven different host species and their respective two streblid species. The host species represented in this image are as followed from the top left to the bottom right: *Micronycteris minuta, Natalus tumidirostris, Sturnira lilum, Sturnira Ludovici, Sturnira tildae, Tonatia sylvicola,* and *Uroderma bilobatum*.

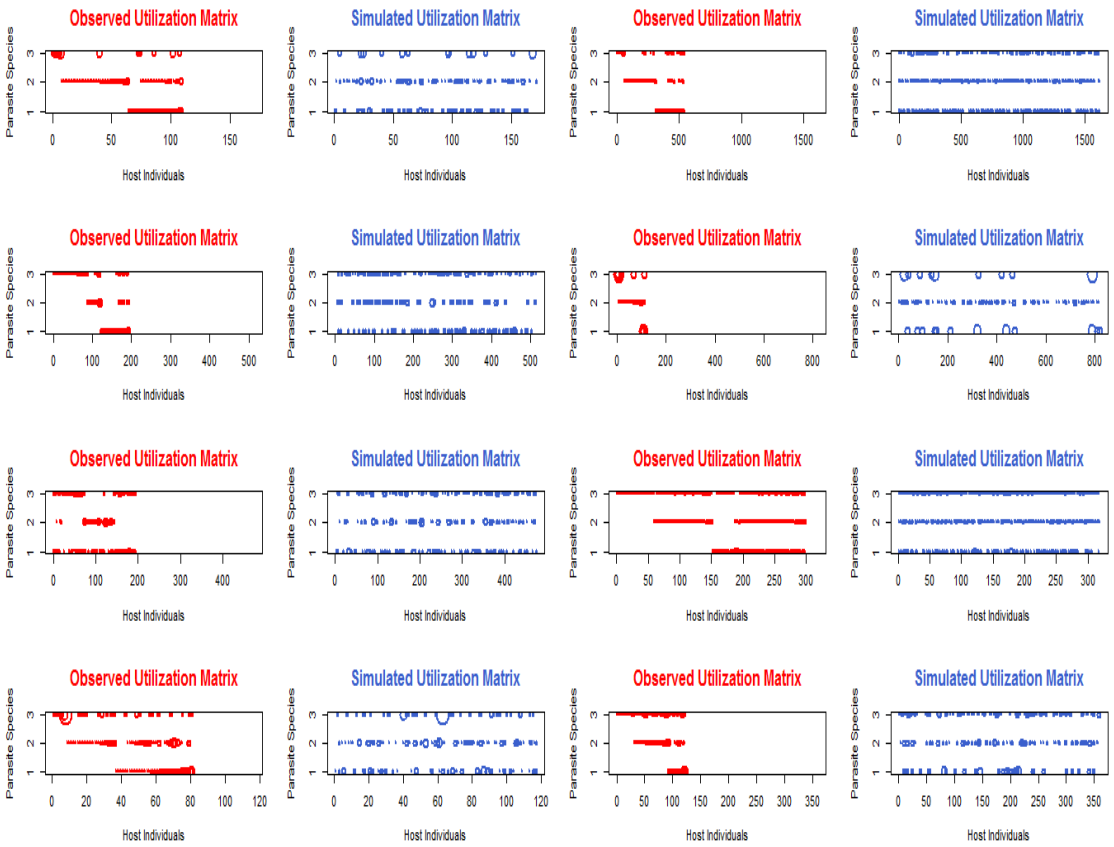

Figure A.3: Data visualization comparing the observed distribution (in red) versus a randomly generated simulated distribution (in blue). Each observed distribution and simulated distribution found to the right of that observed distribution is associated with one host species. These visualizations are representative of the relationships between eight different host species and their respective three streblid species. The host species represented in this image are as followed from the top left to the bottom right: *Anoura geoffroyi*, *Artibeus planirostris*, *Carollia brevicauda*, *Glossophaga longirostris*, *Noctilio albiventris*, *Phyllostomus discolor*, *Phyllostomus elongates*, and *Trachops cirrhosis*.

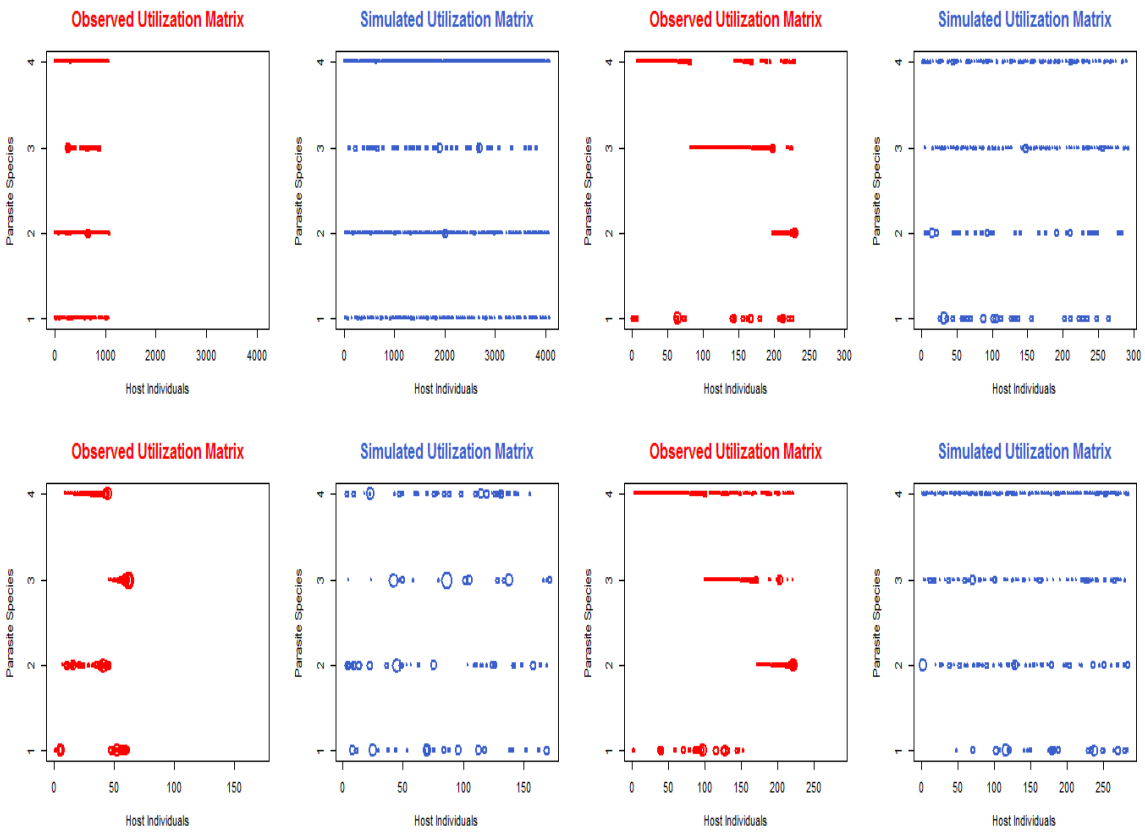

Figure A.4: Data visualization comparing the observed distribution (in red) versus a randomly generated simulated distribution (in blue). Each observed distribution and simulated distribution found to the right of that observed distribution is associated with one host species. These visualizations are representative of the relationships between four different host species and their respective four streblid species. The host species represented in this image are as followed from the top left to the bottom right: *Carollia perspicillata, Glossophaga soricina, Noctilio leporinus,* and *Phyllostomus hastatus.*

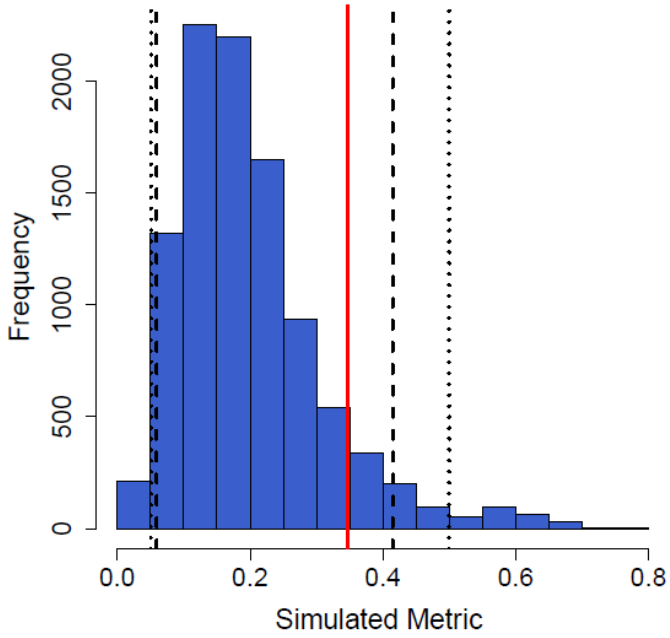

Figure A.5: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *A. amplus*.

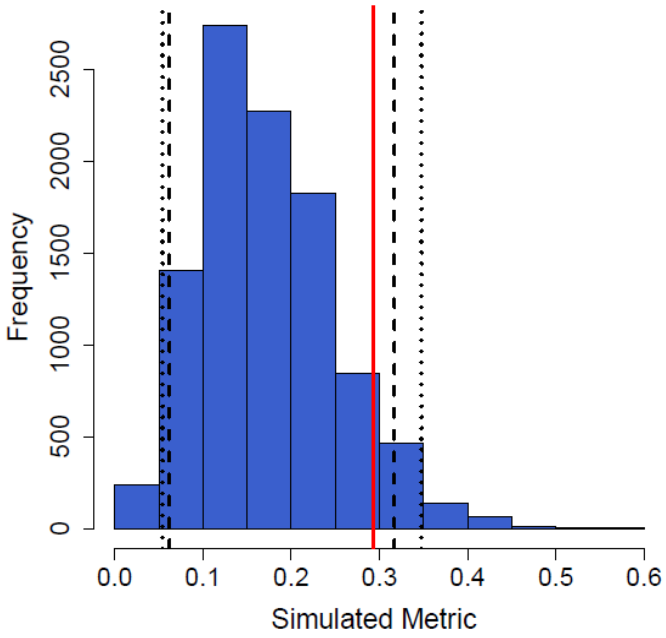

Figure A.6: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *A. caudifer*.

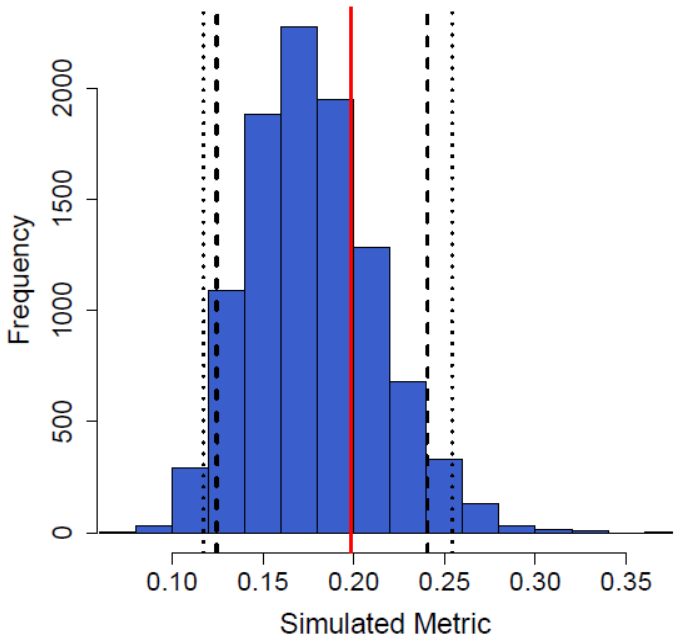

Figure A.7: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *A. geoffroyi*.

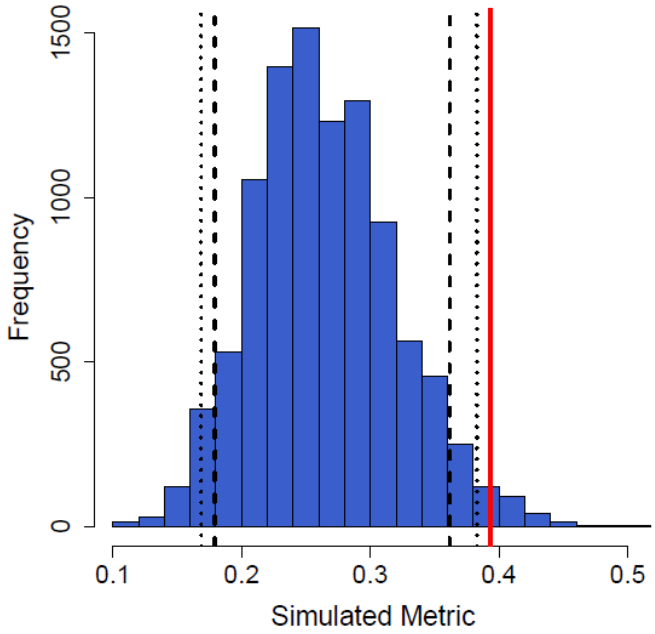

Figure A.8: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Anastrebla modestini* and *Exastinion clovesi* found on *A. geoffroyi*.

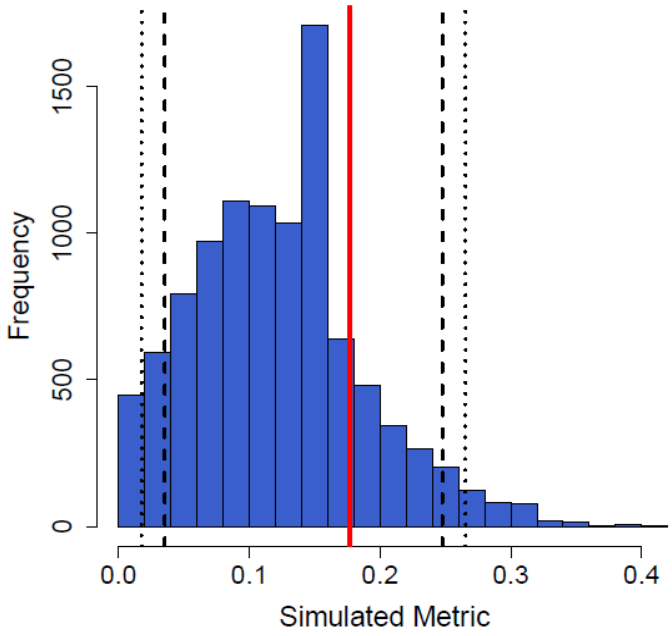

Figure A.9: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Anastrebla modestini* and *Trichobius propinguus* found on *A. geoffroyi*.

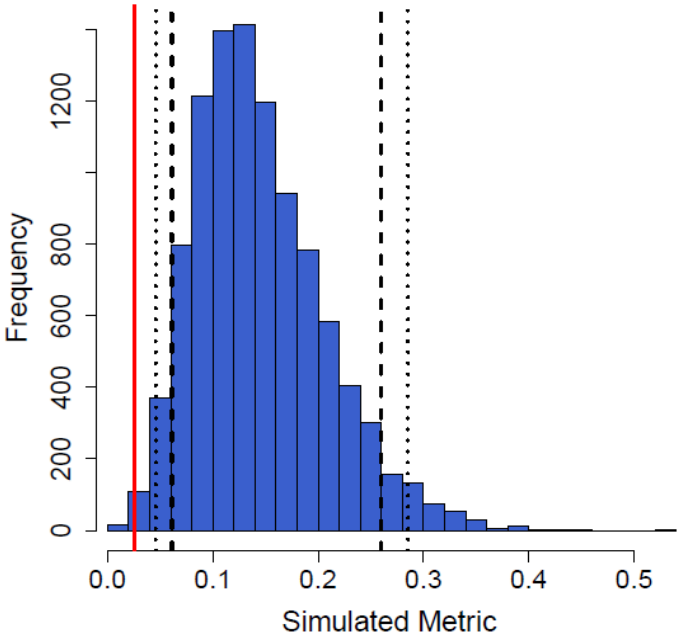

Figure A.10: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Exastinion clovesi* and *Trichobius propinguus* found on *A. geoffroyi*.

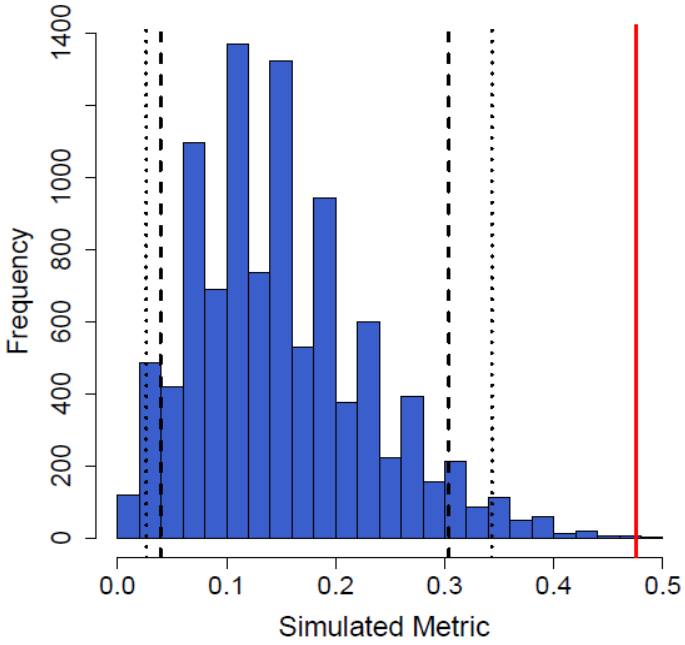

Figure A.11: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *A. latidens*.

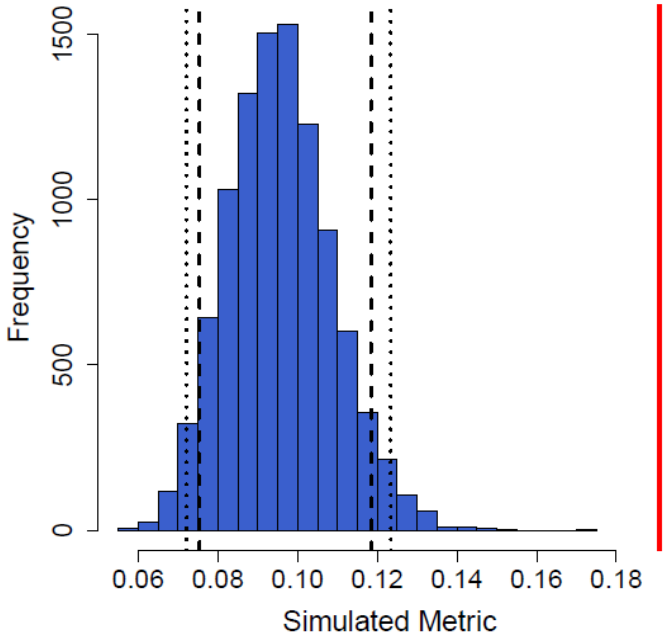

Figure A.12: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *A. planirostris*.

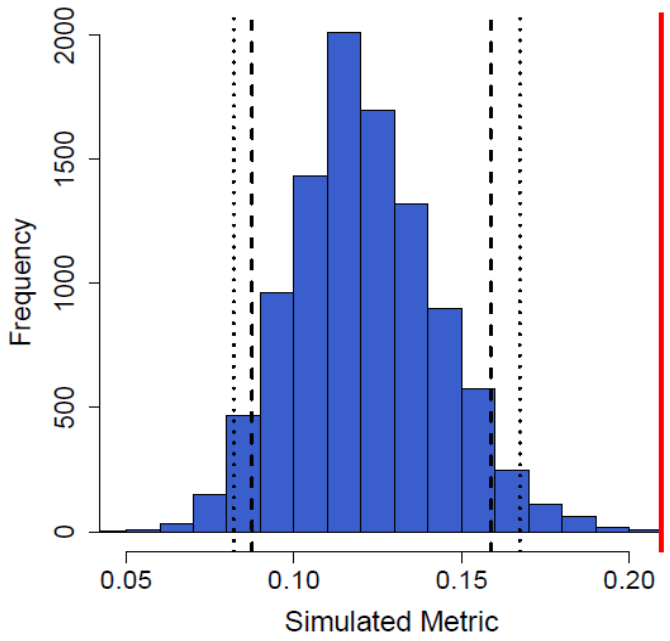

Figure A.13: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Aspidoptera phyllostomatis* and *Megistopoda aranea* found on *A. planirostris*.

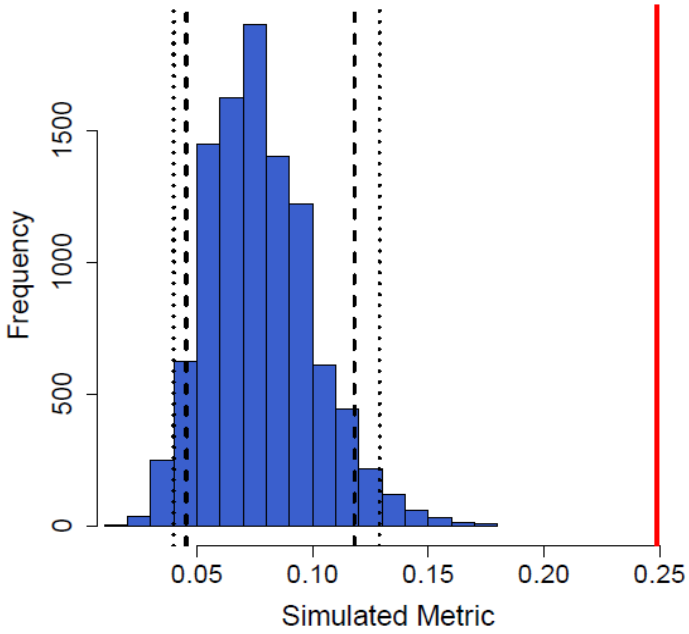

Figure A.14: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Aspidoptera phyllostomatis* and *Metelasmus pseudopterus* found on *A. planirostris*.

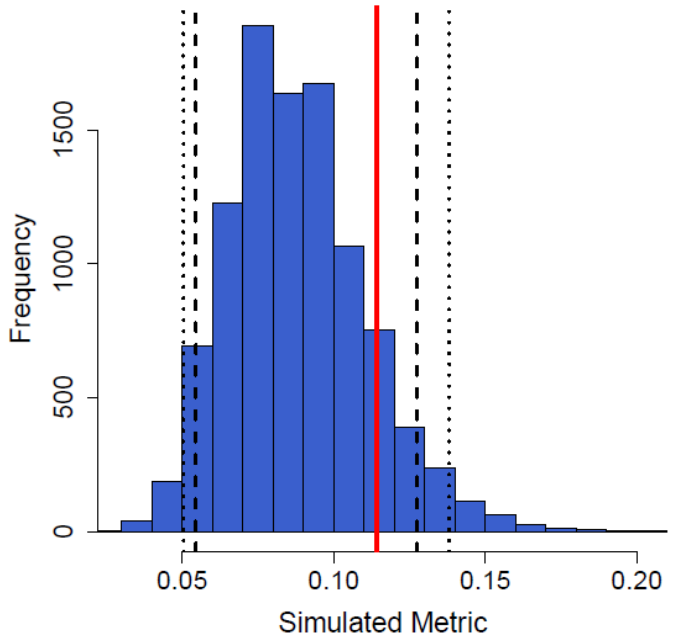

Figure A.15: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Megistopoda aranea* and *Metelasmus pseudopterus* found on *A. planirostris*.

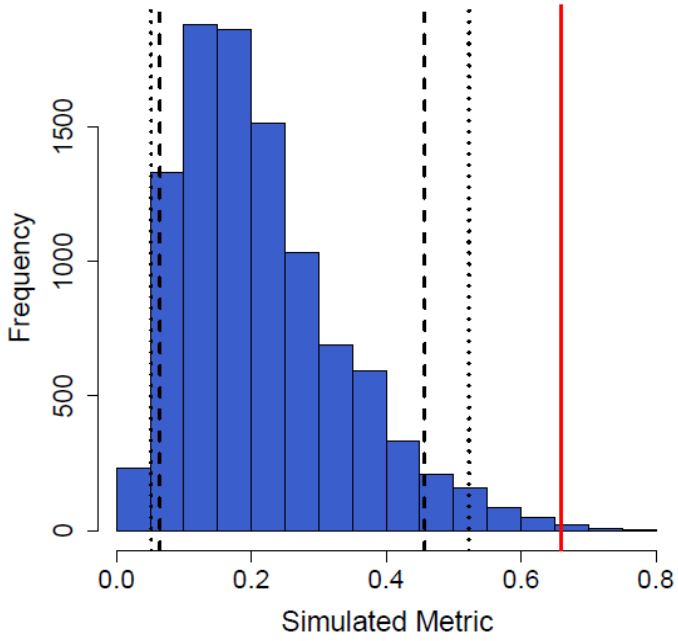

Figure A.16: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *C. auritus*.

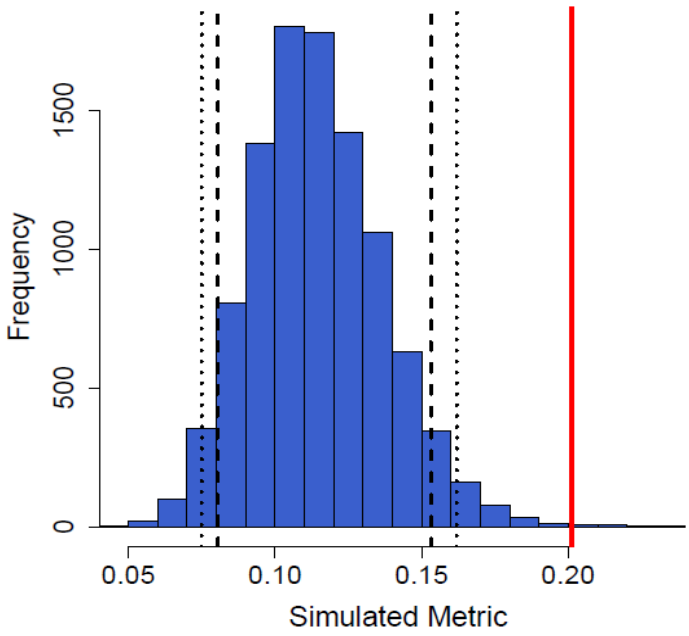

Figure A.17: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *C. brevicauda*.

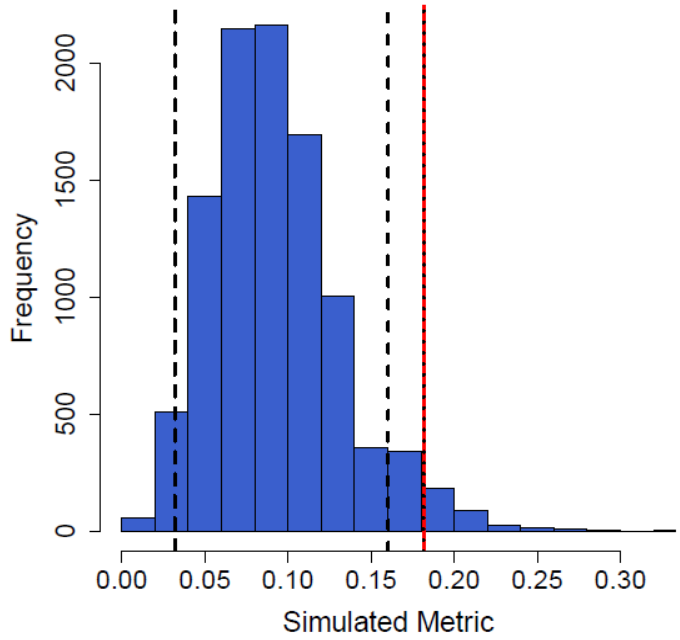

Figure A.18: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Speiseria peytonae* and *Strebla guajiro* found on *C. brevicauda*.

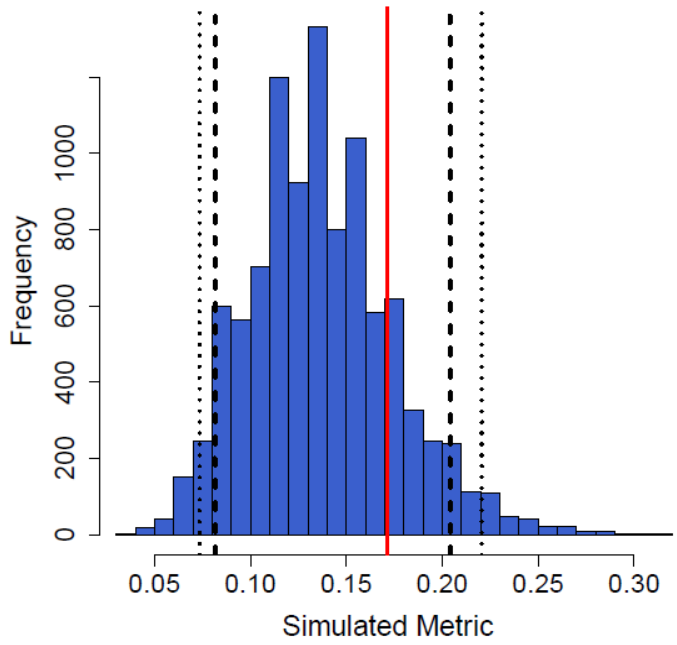

Figure A.19: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Speiseria peytonae* and *Trichobius persimilis* found on *C. brevicauda*.

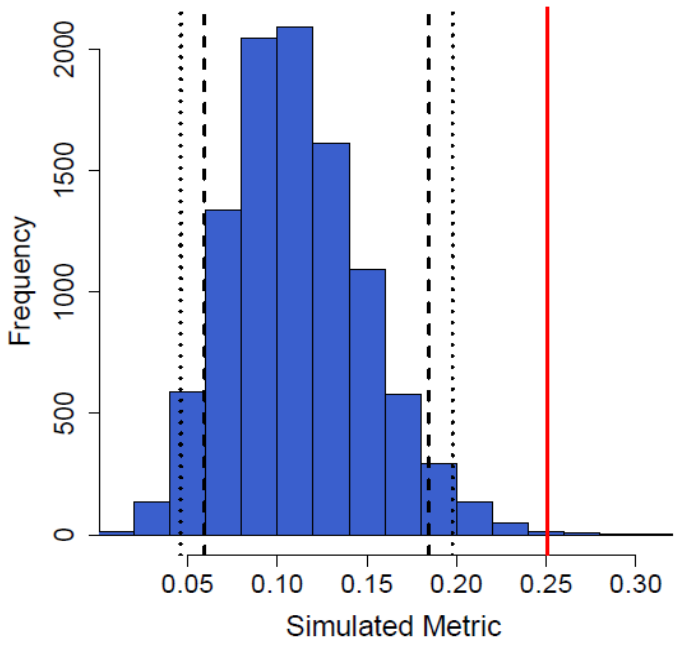

Figure A.20: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Strebla guajiro* and *Trichobius persimilis* found on *C. brevicauda*.

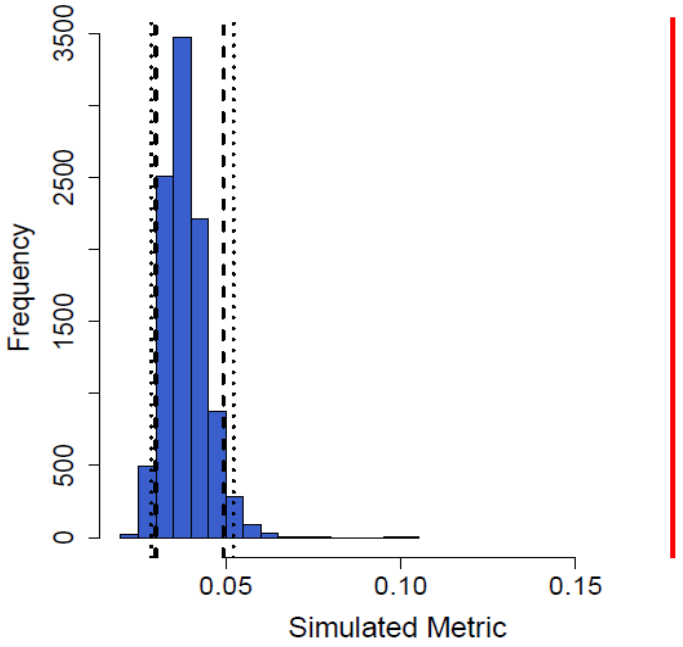

Figure A.21: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *C. perspicillata*.

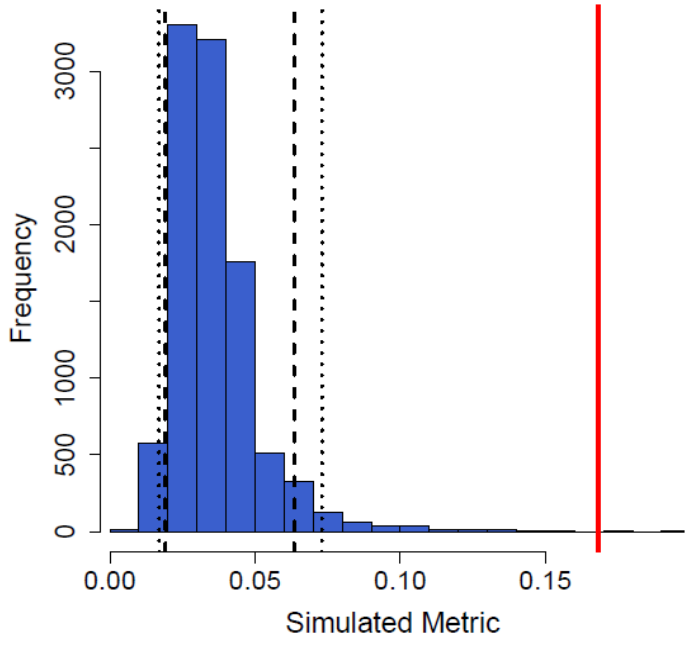

Figure A.22: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Speiseria ambigua* and *Strebla guajiro* found on *C. perspicillata*.

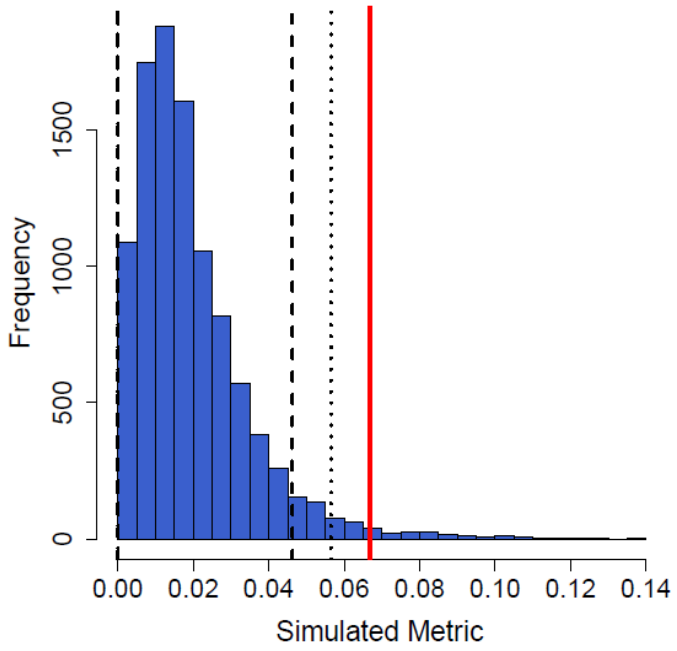

Figure A.23: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Speiseria ambigua* and *Trichobius dugesioides* found on *C. perspicillata*.

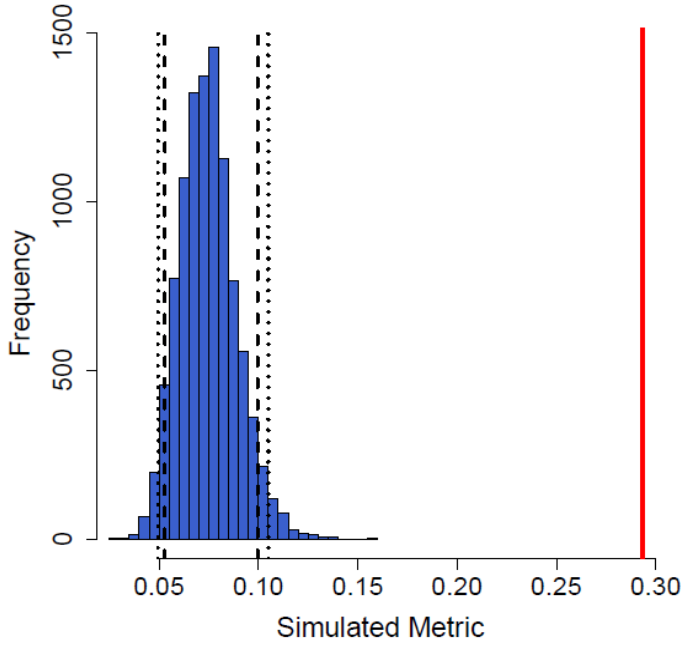

Figure A.24: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Speiseria ambigua* and *Trichobius joblingi* found on *C. perspicillata*.

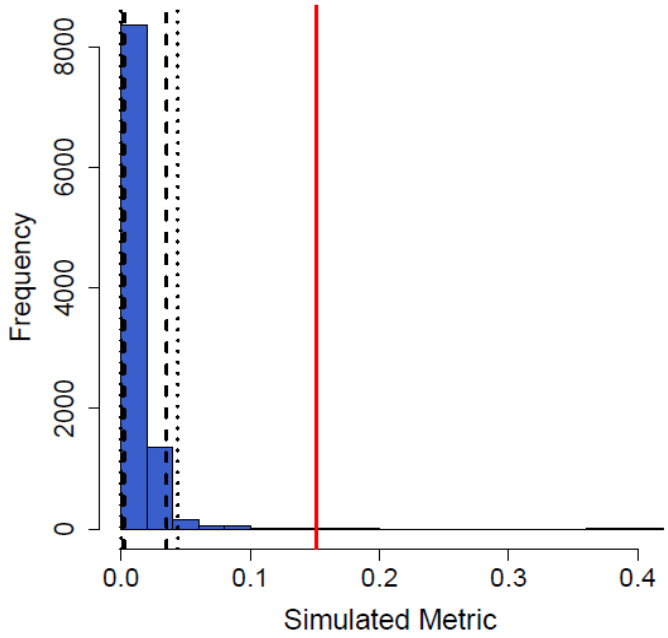

Figure A.25: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Strebla guajiro* and *Trichobius dugesioides* found on *C. perspicillata*.

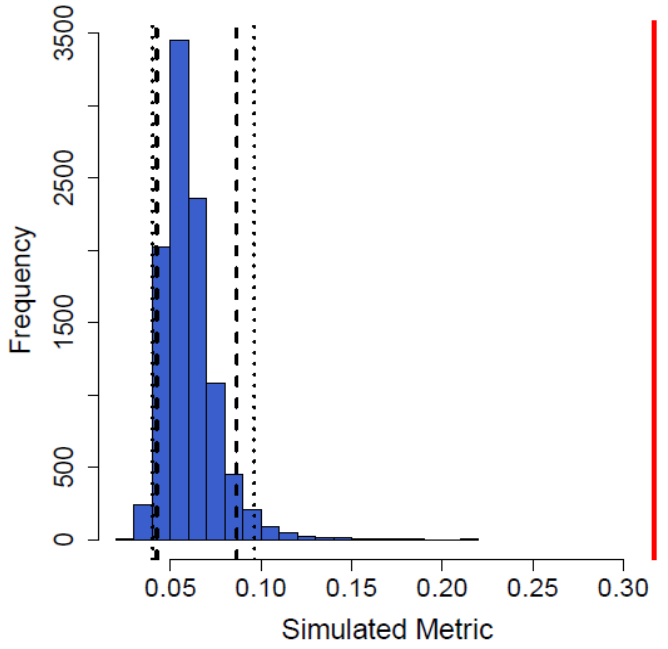

Figure A.26: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Strebla guajiro* and *Trichobius joblingi* found on *C. perspicillata*.

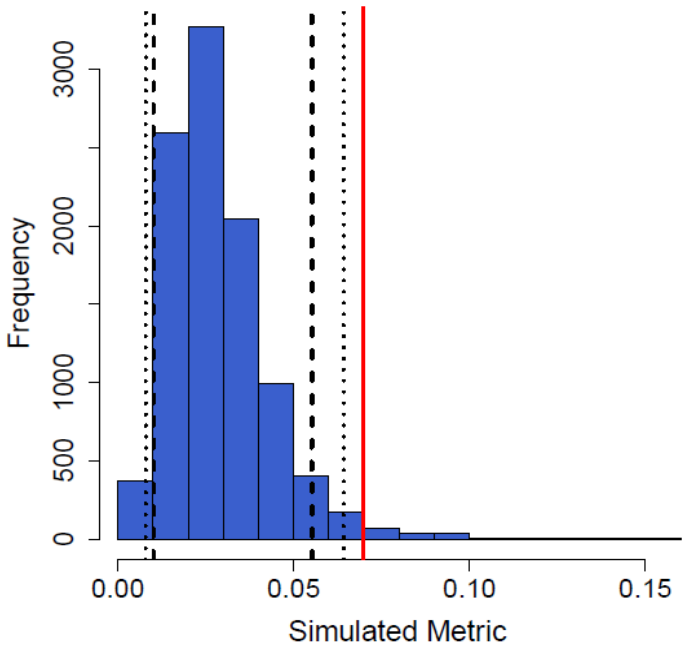

Figure A.27: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Trichobius dugesioides* and *Trichobius joblingi* found on *C. perspicillata*.

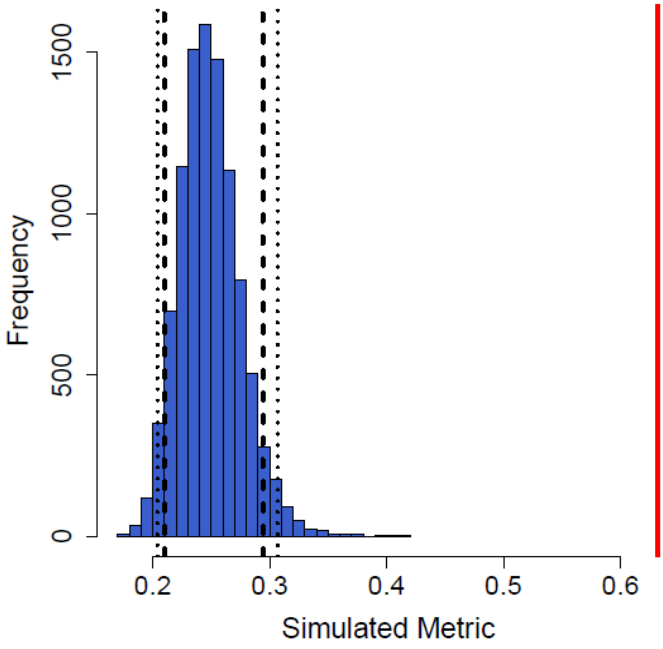

Figure A.28: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *D. rotundus*.

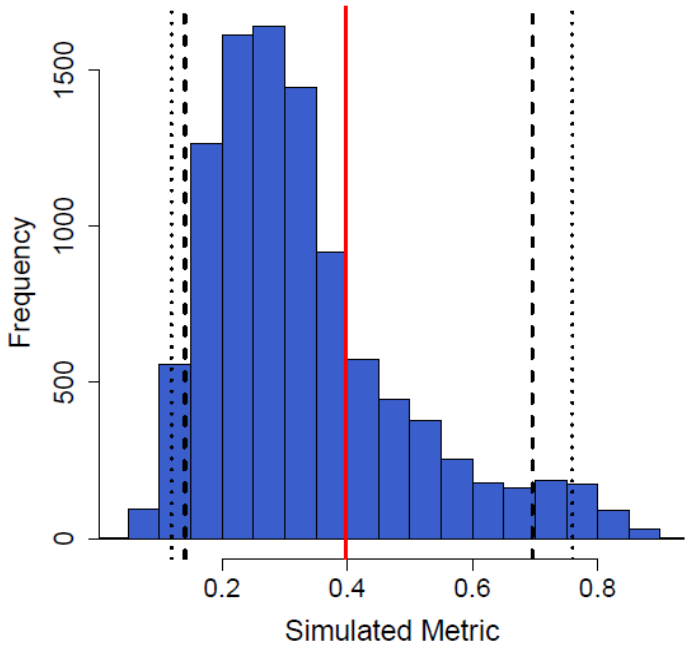

Figure A.29: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *D. youngi*.

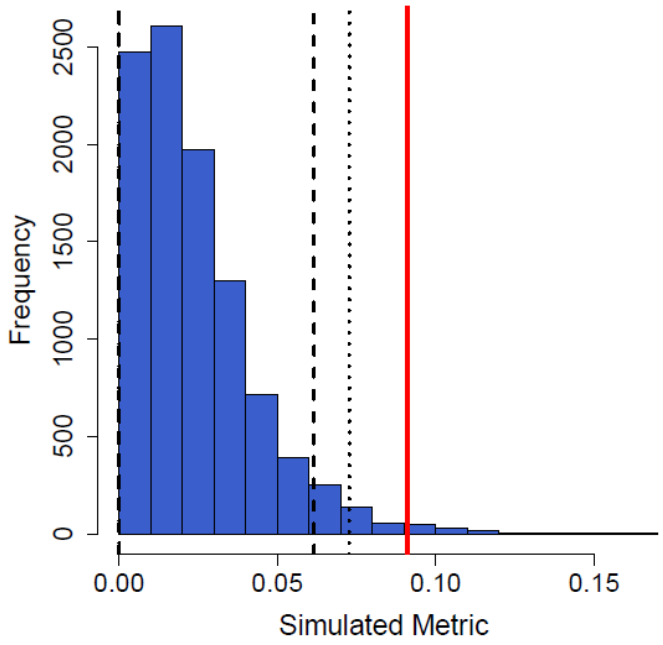

Figure A.30: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *G. longirostris*.

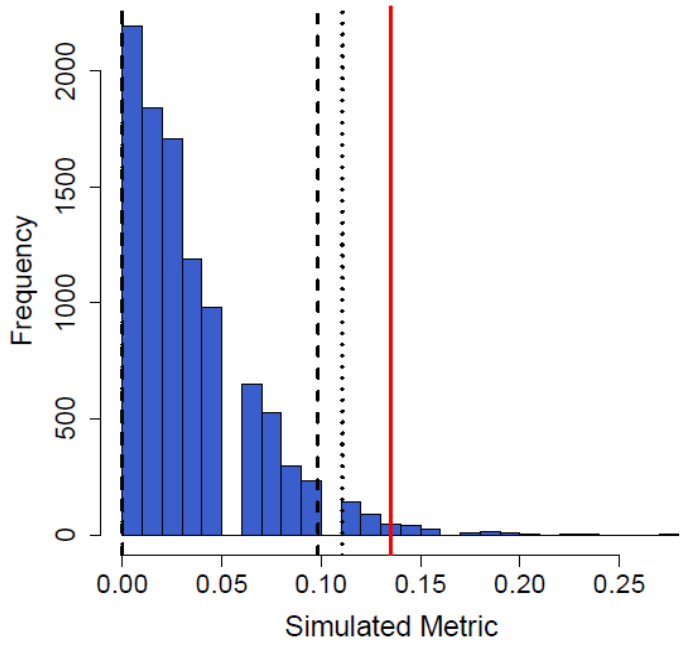

Figure A.31: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Strebla curvata* and *Trichobius dugesii* found on *G. longirostris*.

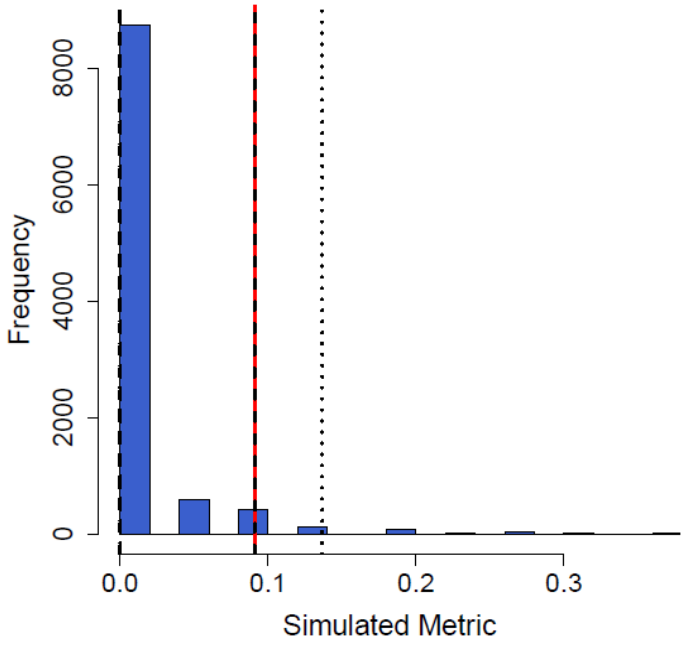

Figure A.32: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Strebla curvata* and *Trichobius uniformis* found on *G. longirostris*.

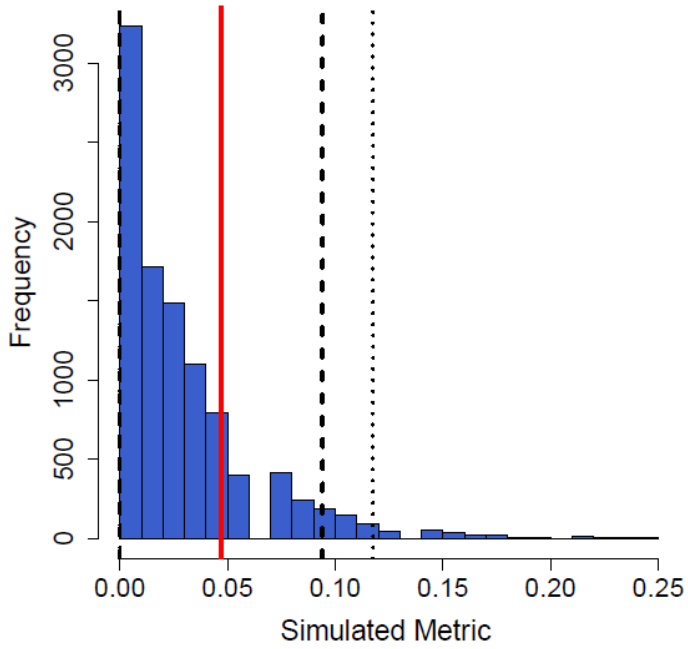

Figure A.33: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Trichobius dugesii* and *Trichobius uniformis* found on *G. longirostris*.

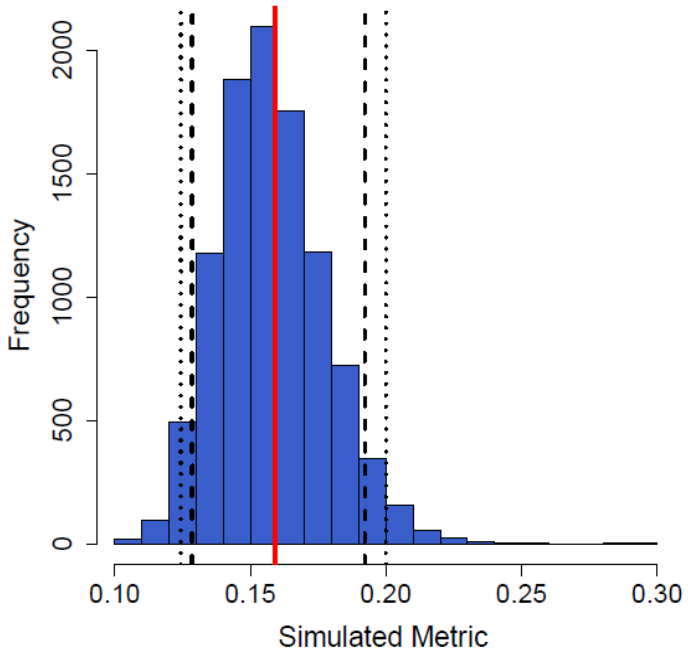

Figure A.34: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *G. soricina*.

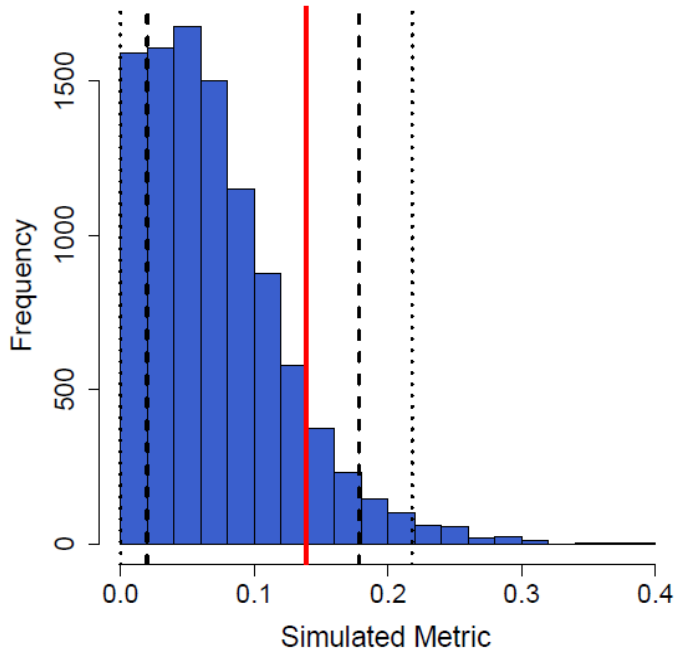

Figure A.35: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Paraeuctenodes longipes* and *Strebla curvata* found on *G. soricina*.

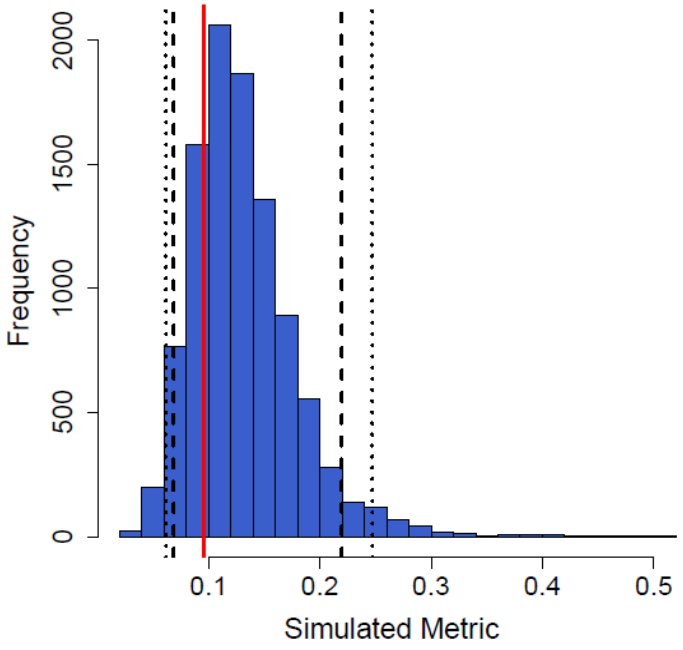

Figure A.36: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Paraeuctenodes longipes* and *Trichobius dugesii* found on *G. soricina*.

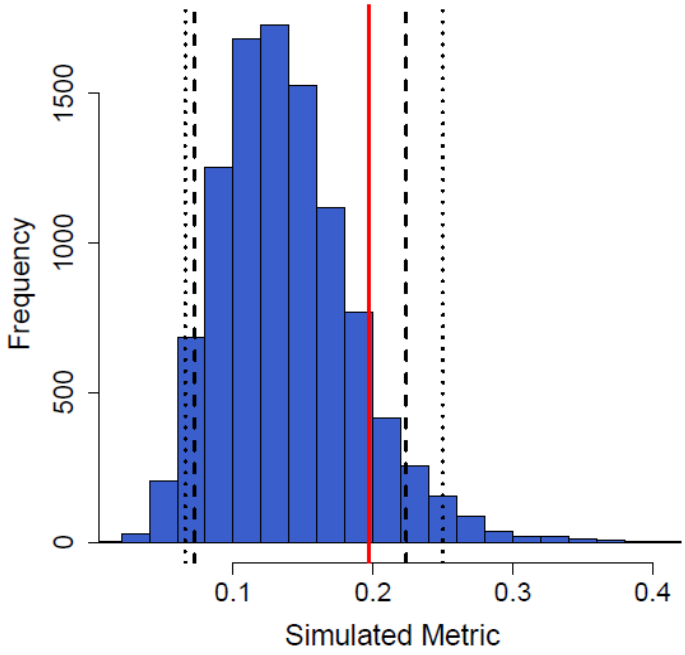

Figure A.37: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Paraeuctenodes longipes* and *Trichobius uniformis* found on *G. soricina*.

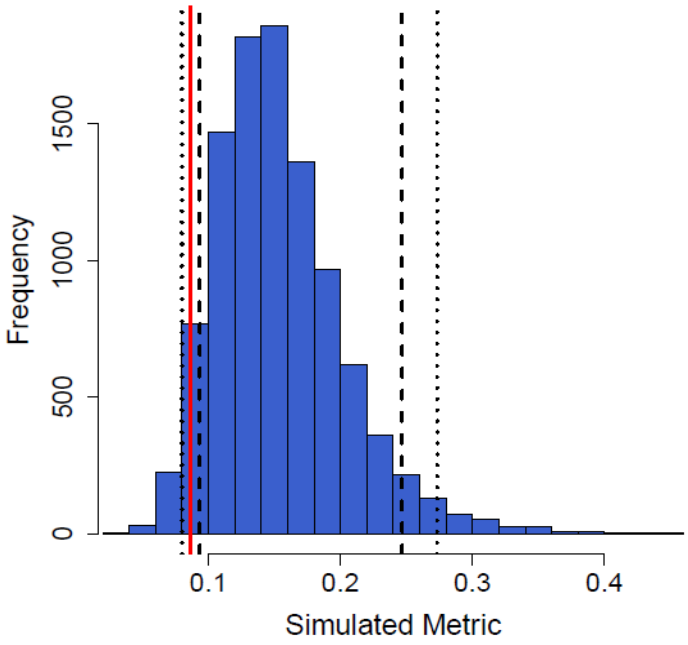

Figure A.38: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Strebla curvata* and *Trichobius dugesii* found on *G. soricina*.

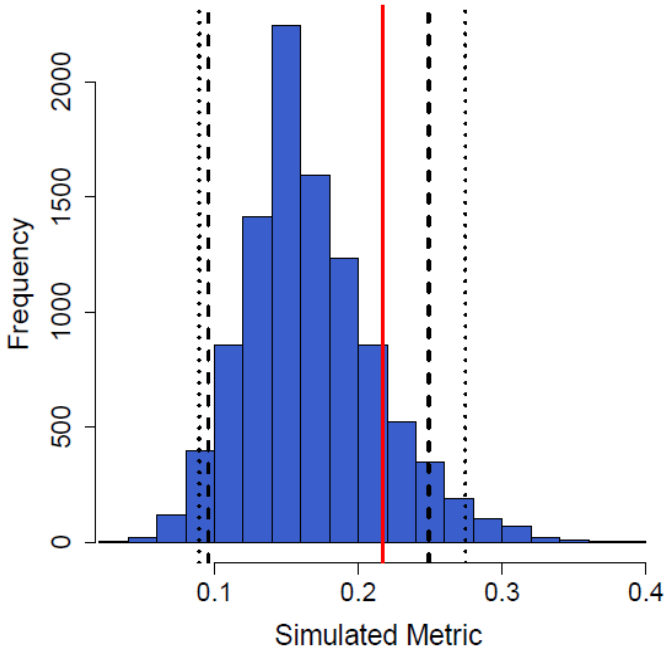

Figure A.39: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Strebla curvata* and *Trichobius uniformis* found on *G. soricina*.

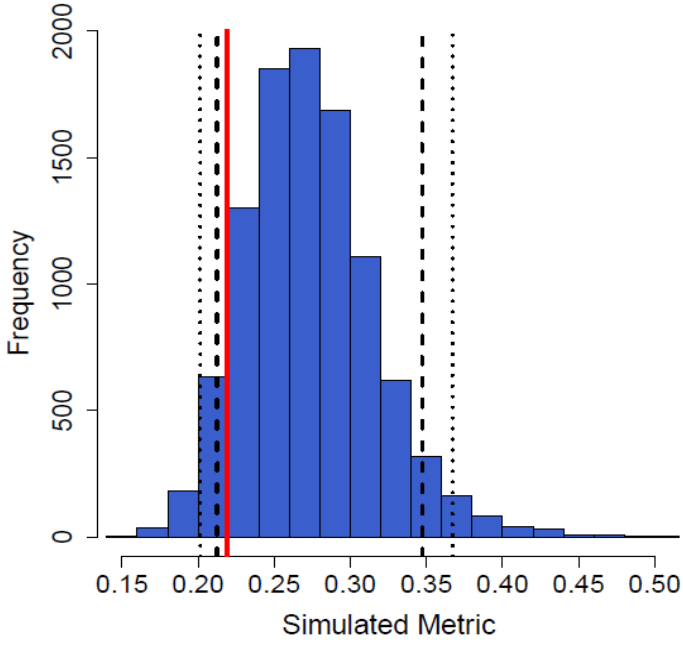

Figure A.40: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Trichobius dugesii* and *Trichobius uniformis* found on *G. soricina*.

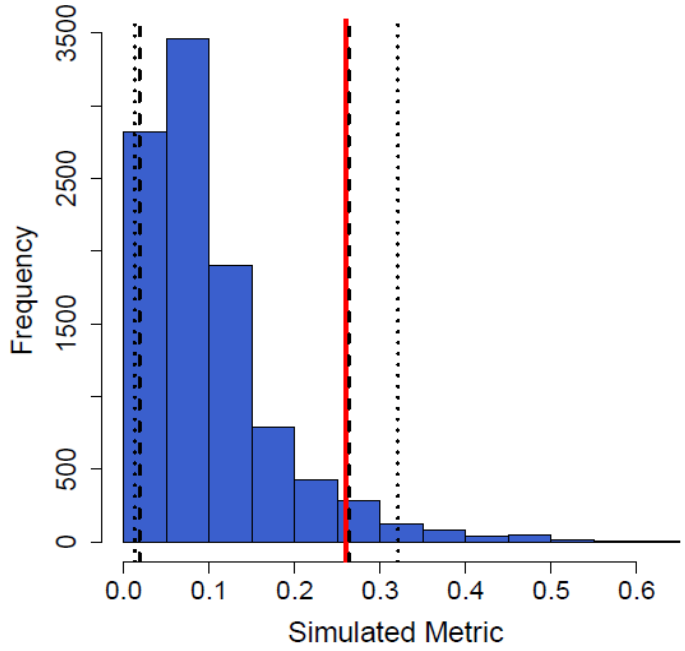

Figure A.41: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *L. aurita*.

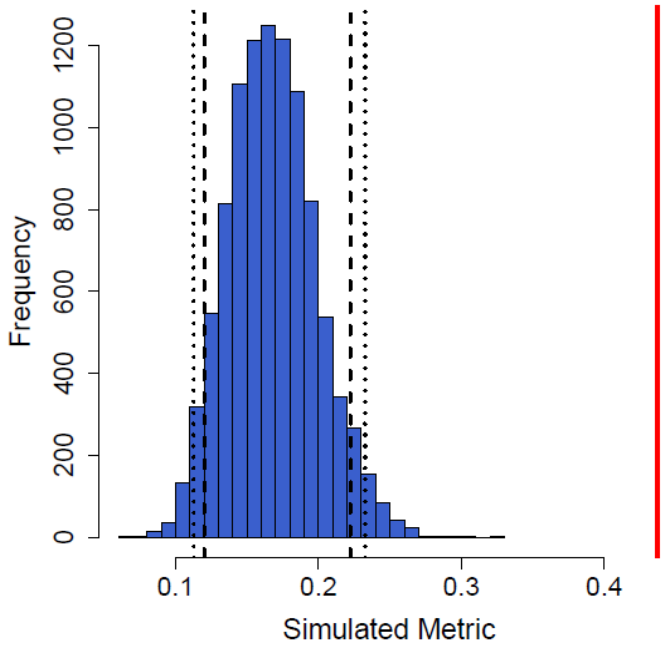

Figure A.42: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *L. curasoae*.

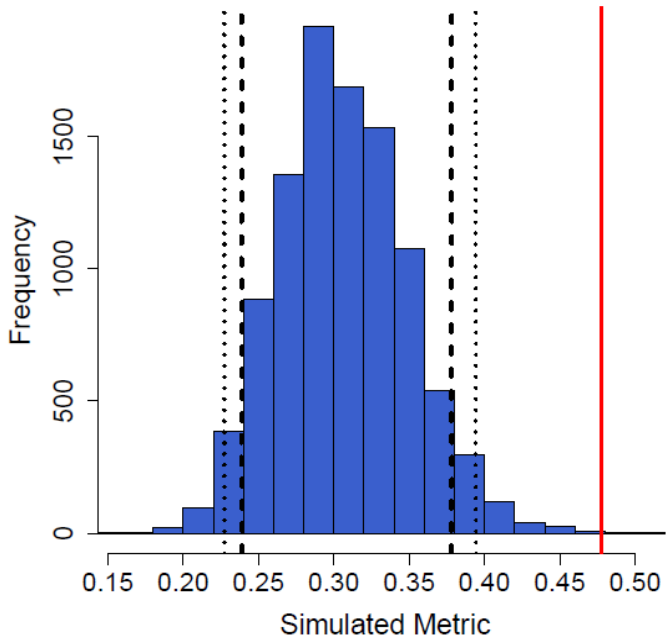

Figure A.43: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *L. orinocensis*.

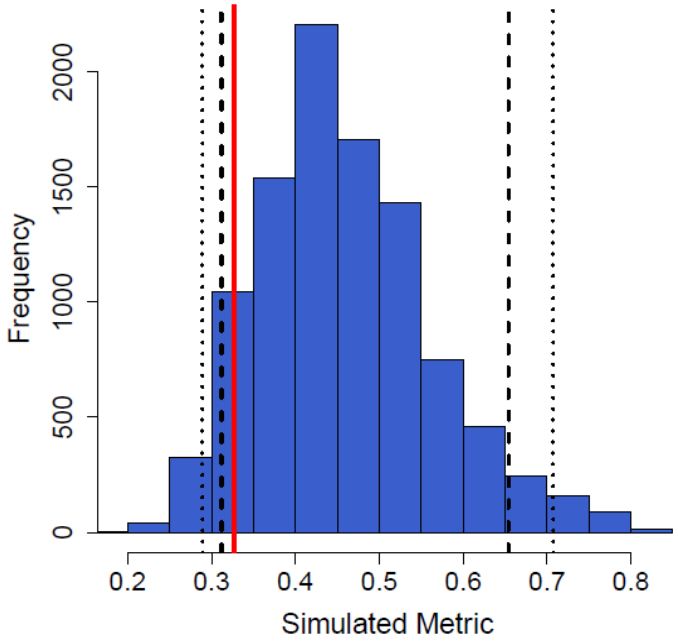

Figure A.44: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *L. robusta*.

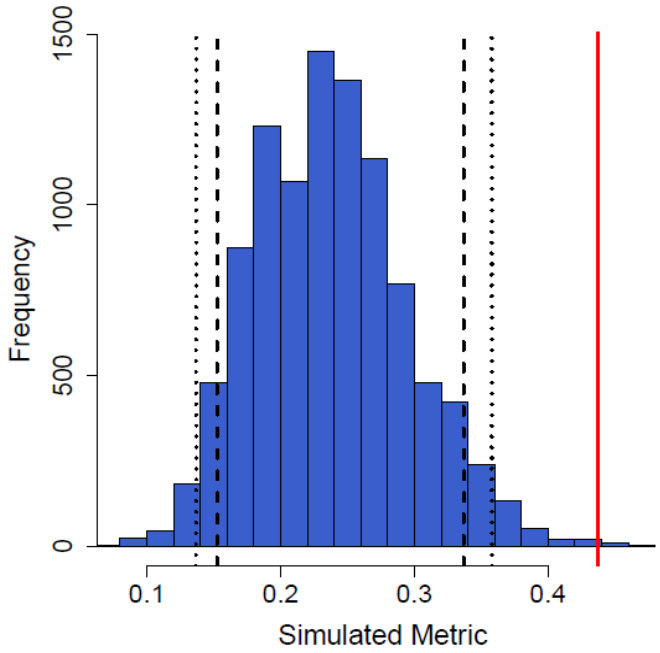

Figure A.45: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *L. spurrelli*.

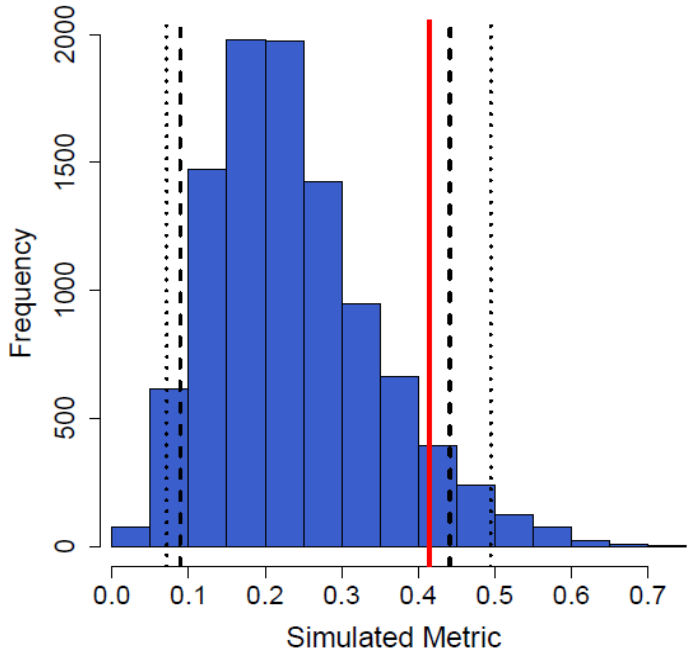

Figure A.46: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *M. macrophyllum*.

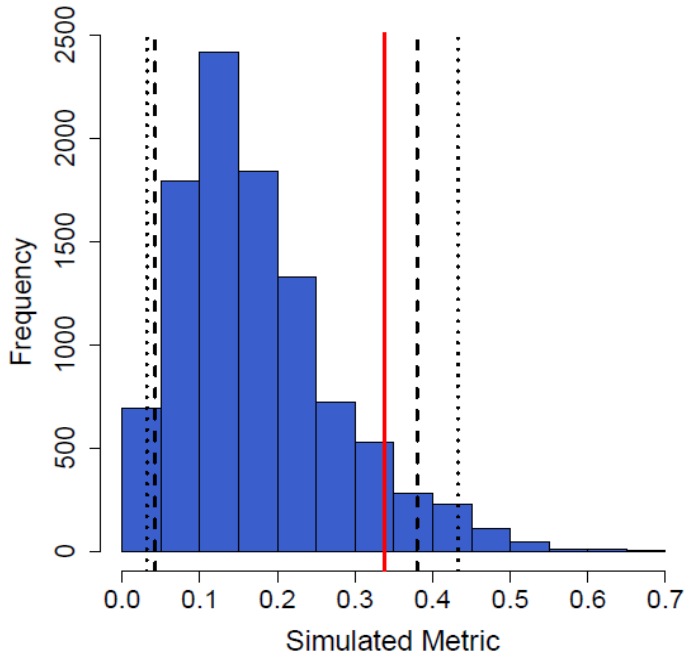

Figure A.47: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *M. minuta*.

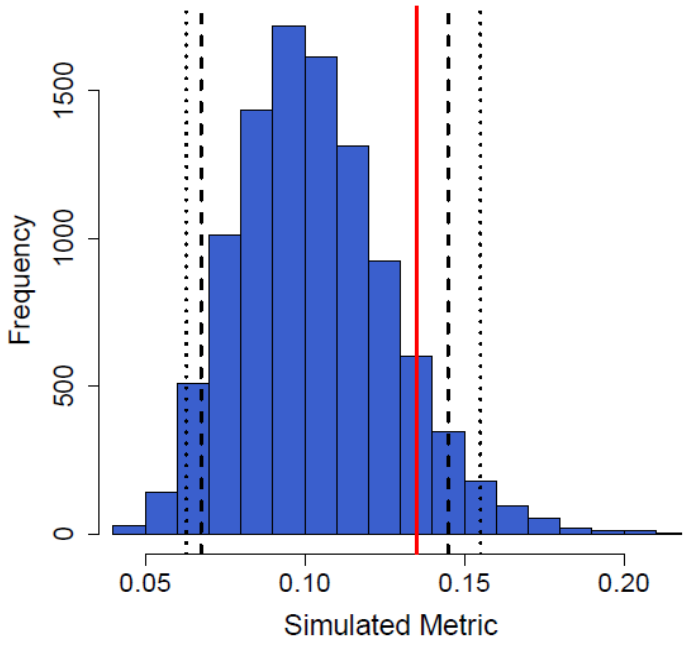

Figure A.48: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *N. albiventris*.

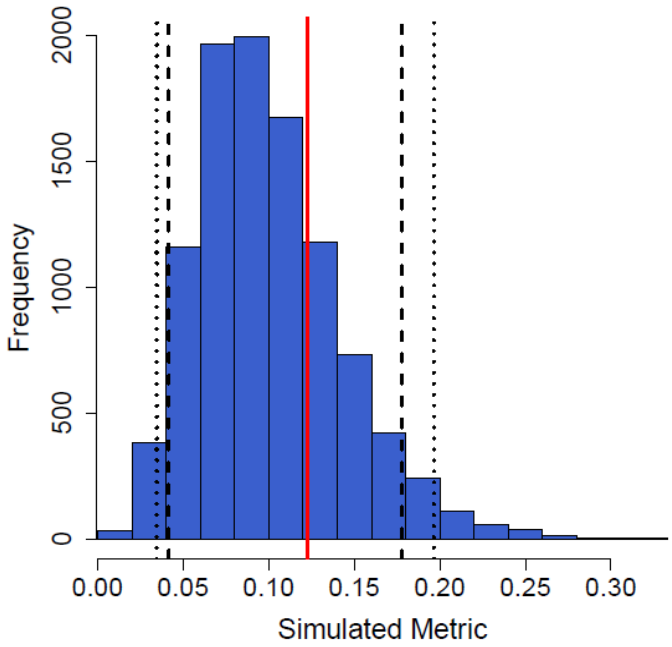

Figure A.49: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Noctiliostrebla maai* and *Paradyschiria curvata* found on *N. albiventris*.

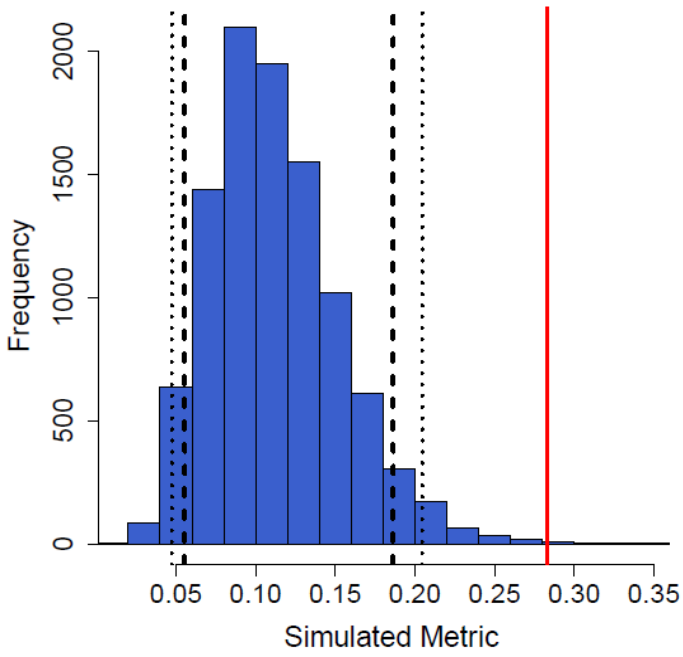

Figure A.50: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Noctiliostrebla maai* and *Paradyschiria parvula* found on *N. albiventris*.

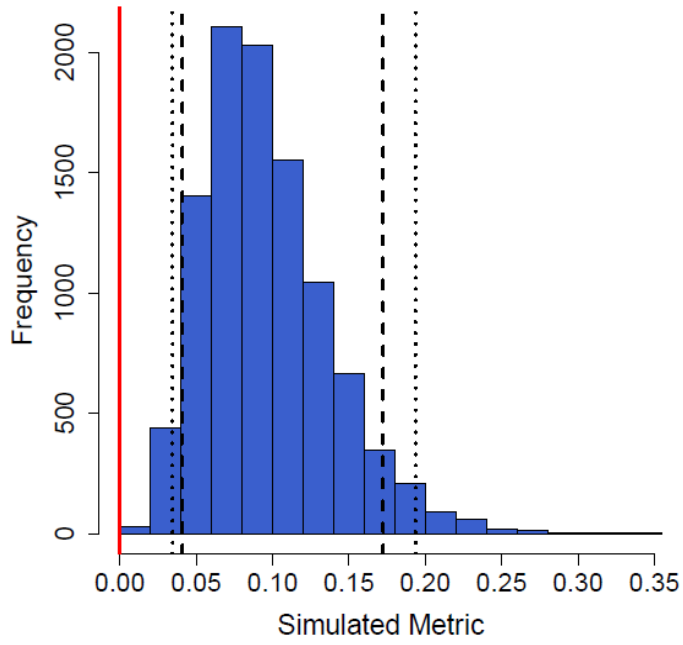

Figure A.51: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Paradyschiria curvata* and *Paradyschiria parvula* found on *N. albiventris*.

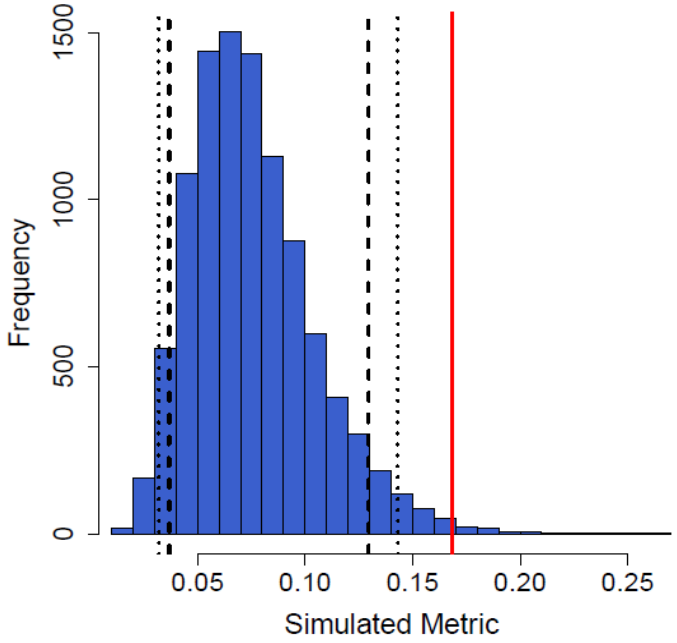

Figure A.52: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *N. leporinus*.

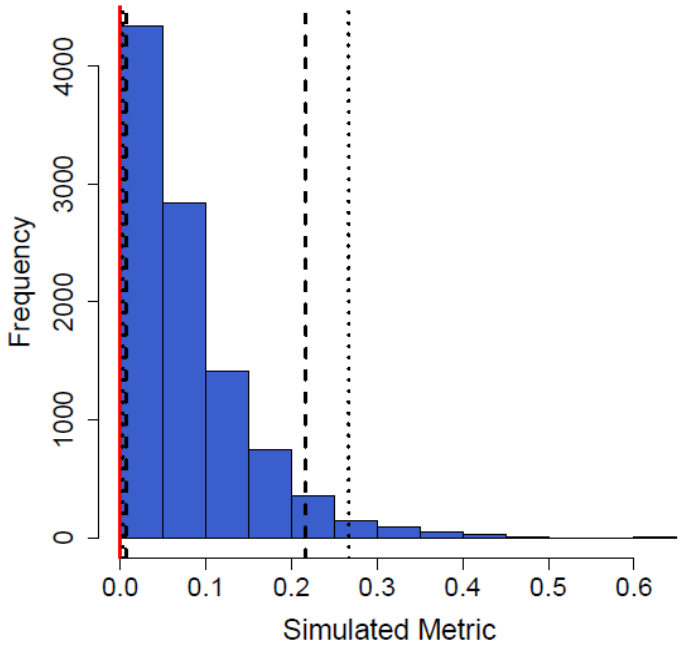

Figure A.53: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Noctiliostrebla aitkeni* and *Noctiliostrebla traubi* found on *N. leporinus*.

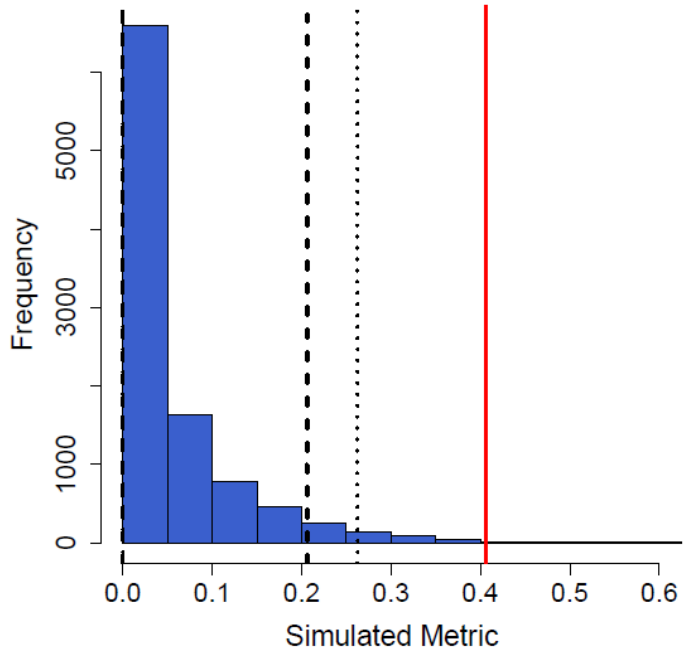

Figure A.54: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Noctiliostrebla aitkeni* and *Paradyschiria fusca* found on *N. leporinus*.

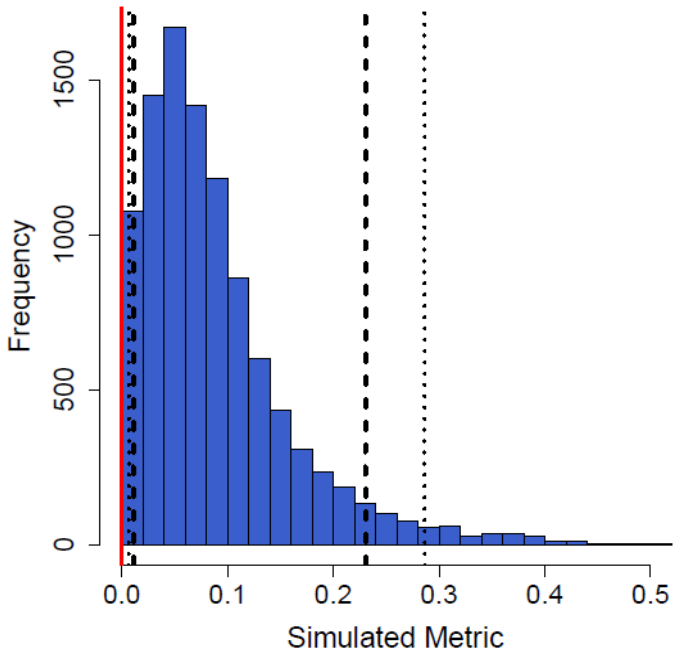

Figure A.55: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Noctiliostrebla aitkeni* and *Paradyschiria lineata* found on *N. leporinus*.

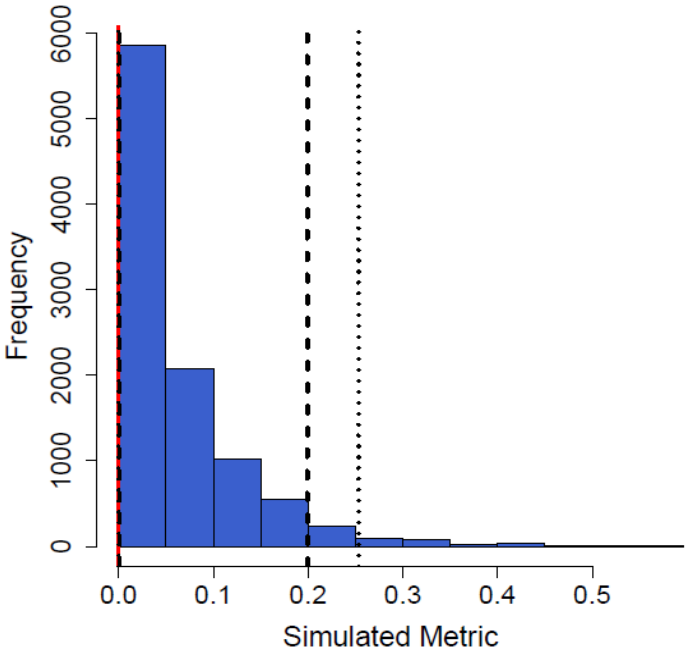

Figure A.56: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Noctiliostrebla traubi* and *Paradyschiria fusca* found on *N. leporinus*.

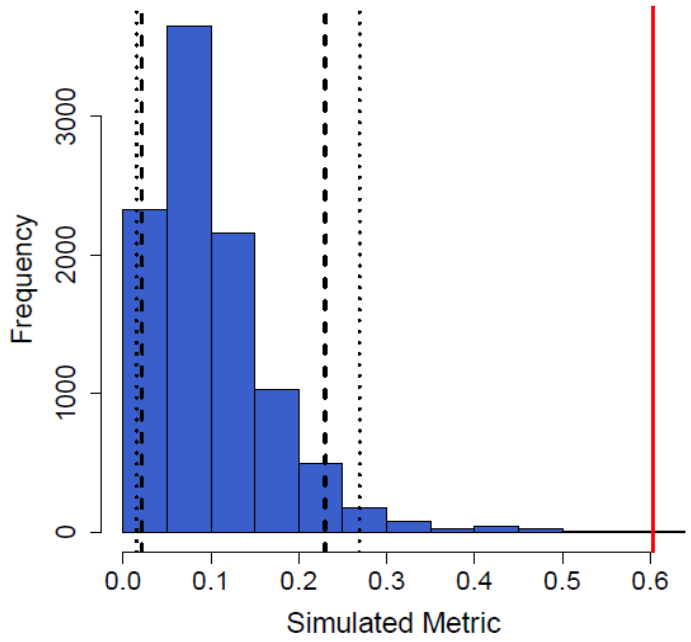

Figure A.57: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Noctiliostrebla traubi* and *Paradyschiria lineata* found on *N. leporinus*.

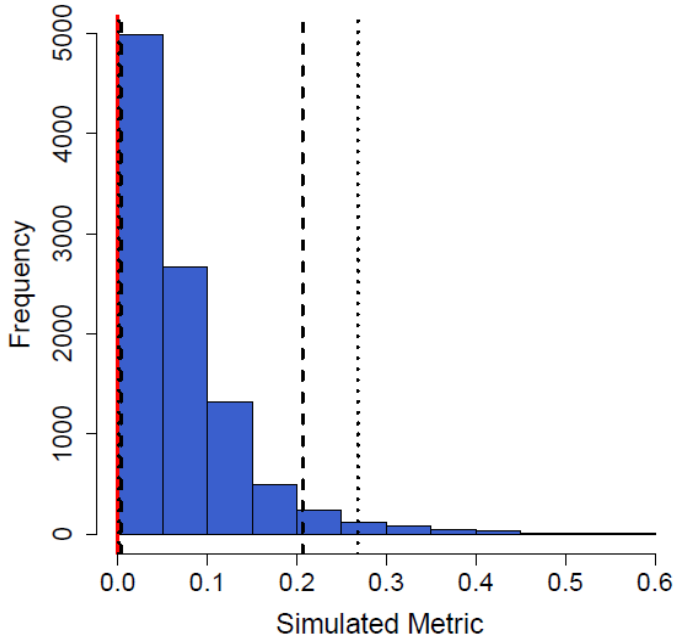

Figure A.59: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Paradyschiria fusca* and *Paradyschiria lineata* found on *N. leporinus*.

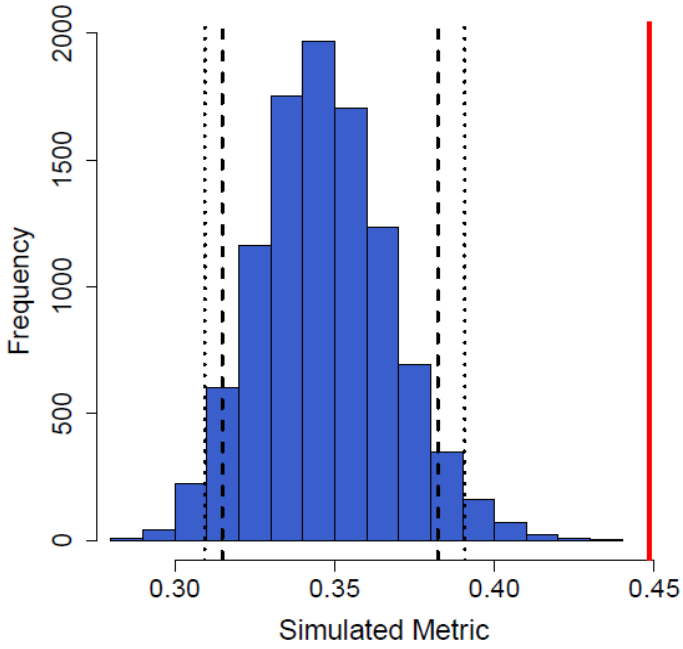

Figure A.60: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *P. discolor*.

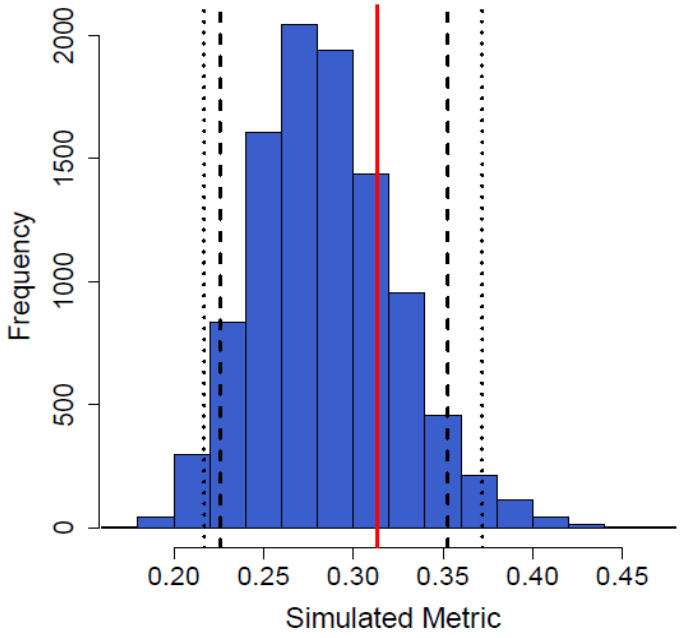

Figure A.61: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Strebla hertigi* and *Trichobioides perspicillatus* found on *P. discolor*.

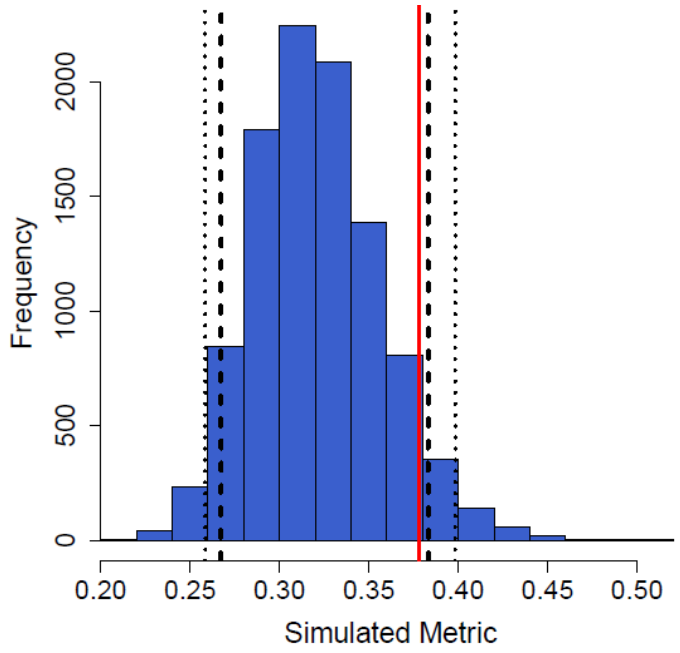

Figure A.62: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Strebla hertigi* and *Trichobius costalimai* found on *P. discolor*.

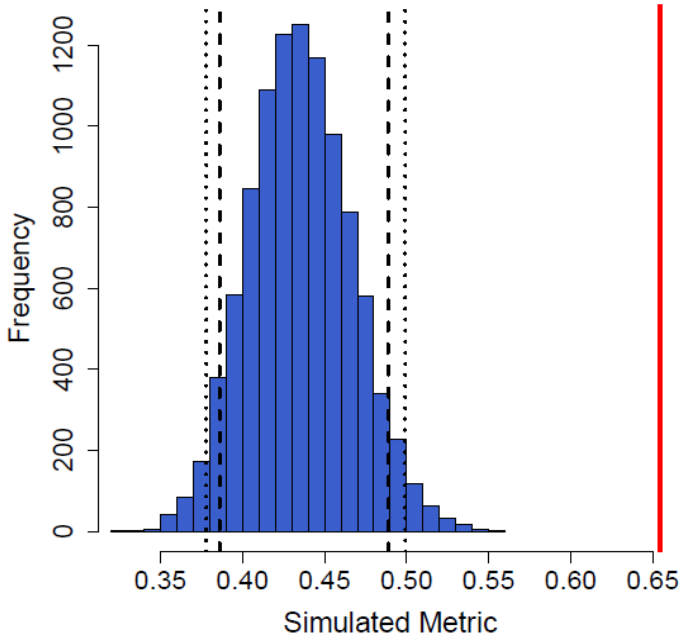

Figure A.63: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Trichobioides perspicillatus* and *Trichobius costalimai* found on *P. discolor*.

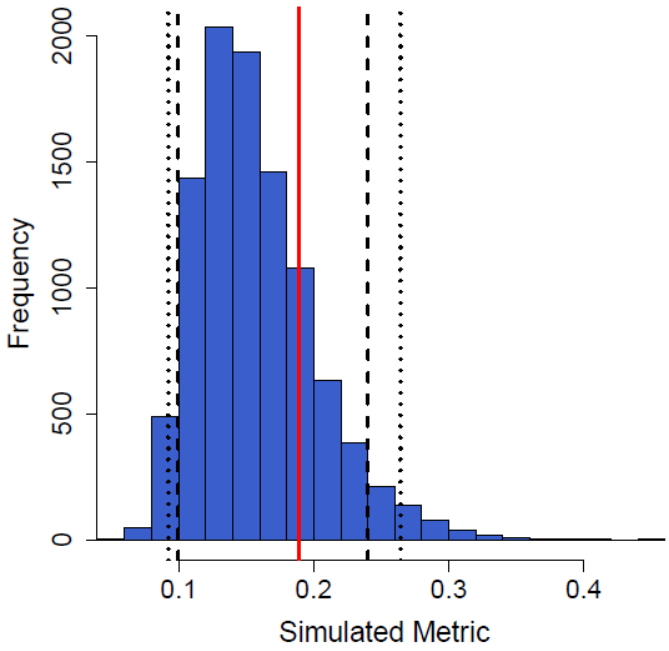

Figure A.64: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *P. elongatus*.

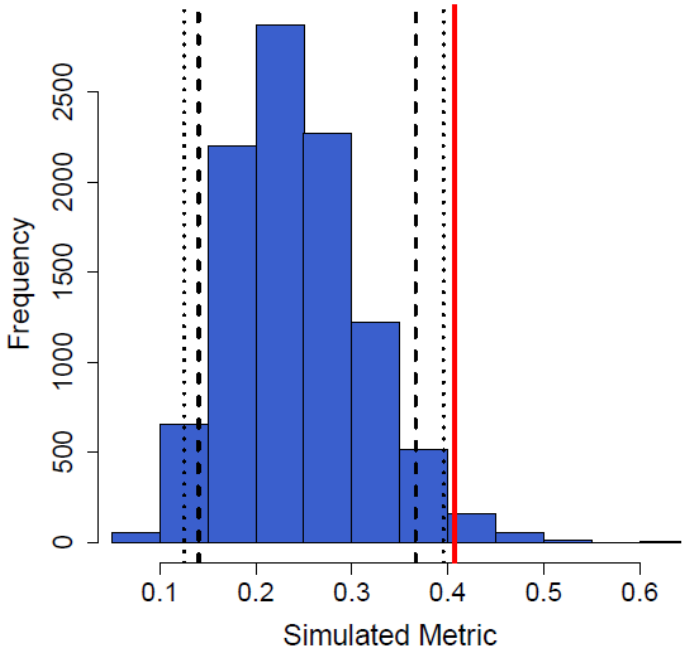

Figure A.65: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Strebla consocia* and *Trichobius joblingi* found on *P. elongatus*.

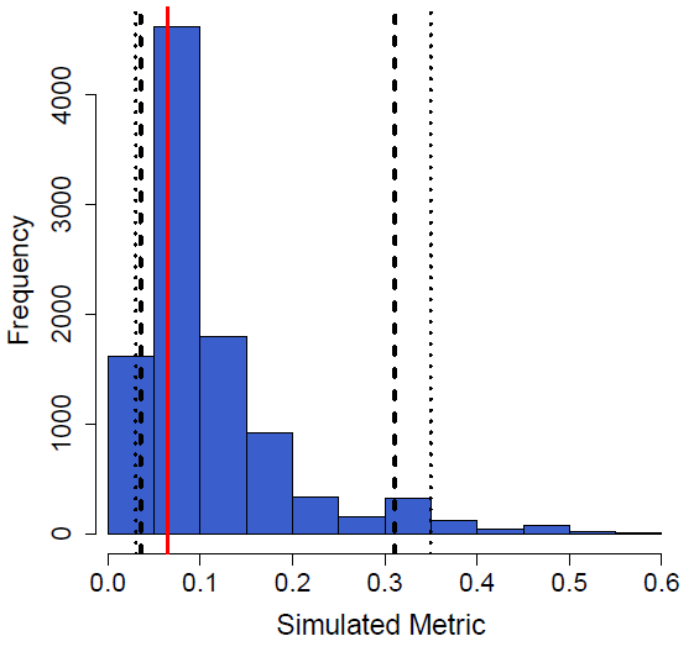

Figure A.66: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Strebla consocia* and *Trichobius longipes* found on *P. elongatus*.

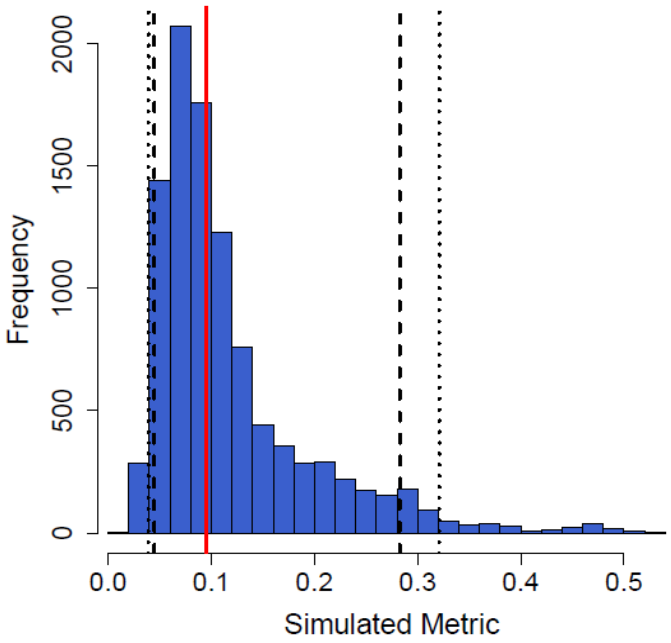

Figure A.67: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Trichobius joblingi* and *Trichobius longipes* found on *P. elongatus*.

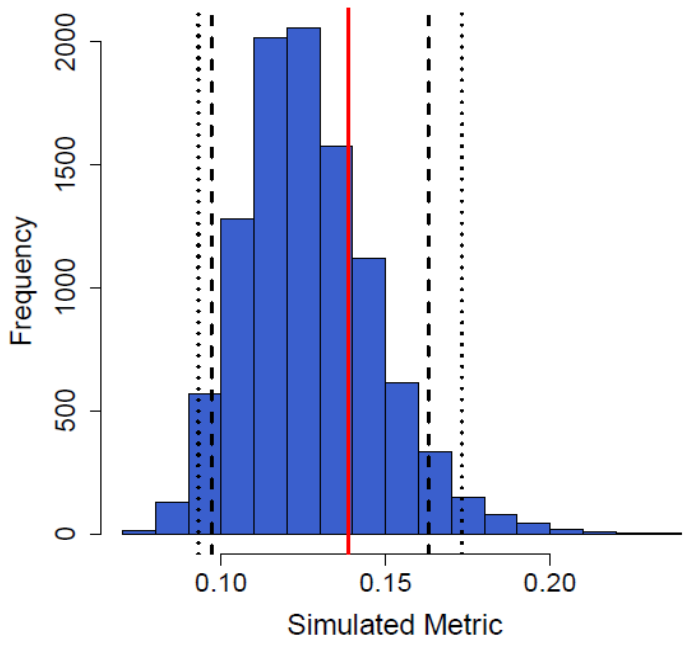

Figure A.68: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *P. hastatus*.

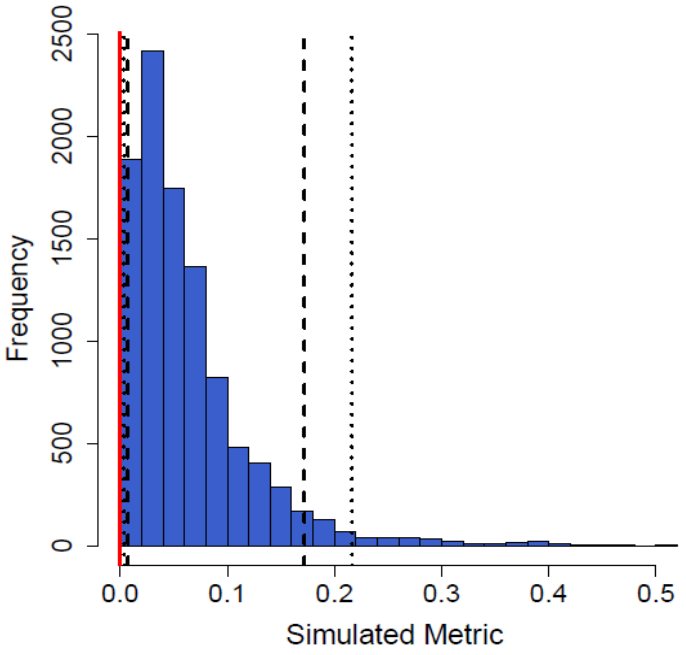

Figure A.69: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Mastoptera guimaraesi* and *Mastoptera minuta* found on *P. hastatus*.

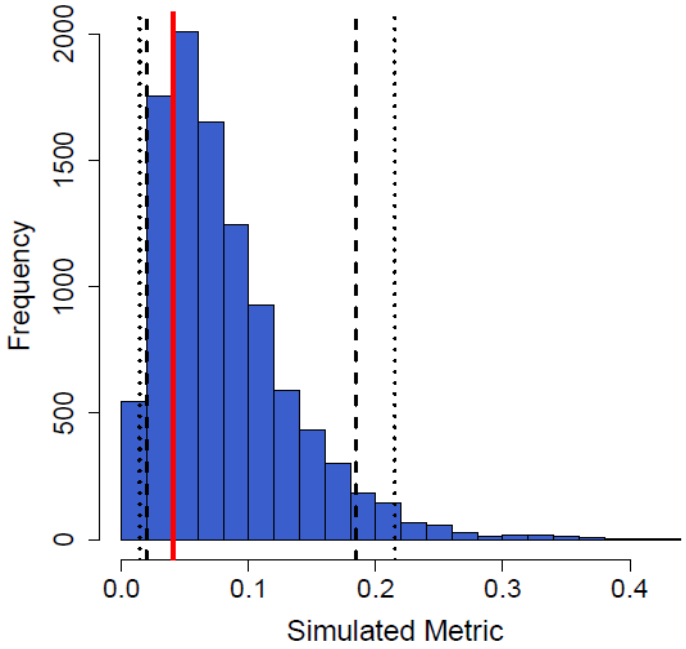

Figure A.70: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Mastoptera guimaraesi* and *Strebla consocia* found on *P. hastatus*.

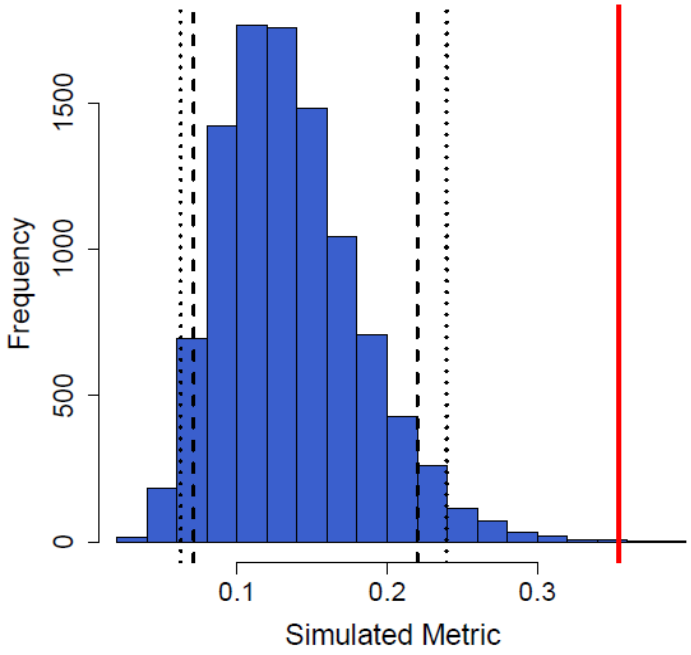

Figure A.71: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Mastoptera guimaraesi* and *Trichobius longipes* found on *P. hastatus*.

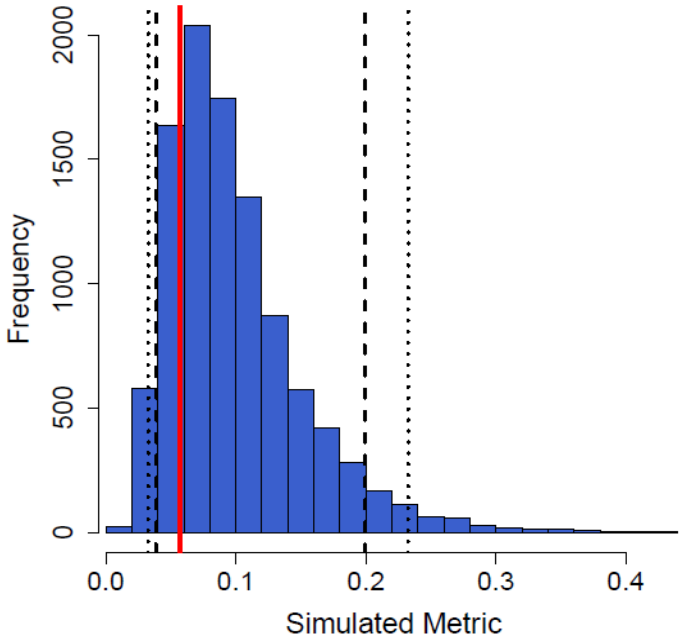

Figure A.72: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Mastoptera minuta* and *Strebla consocia* found on *P. hastatus*.

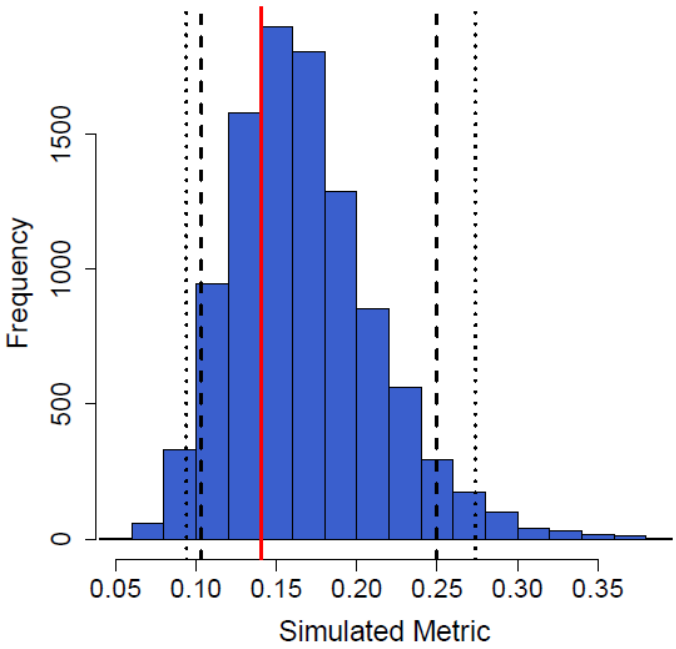

Figure A.73: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Mastoptera minuta* and *Trichobius longipes* found on *P. hastatus*.

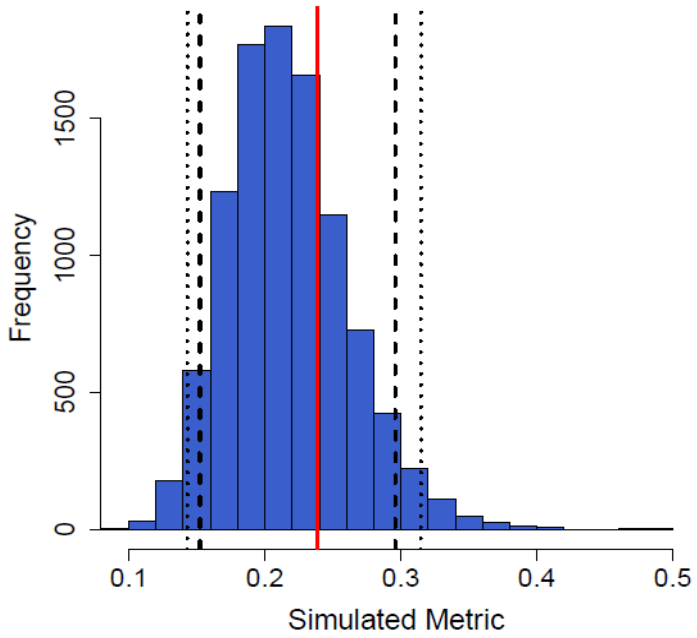

Figure A.74: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Strebla consocia* and *Trichobius longipes* found on *P. hastatus*.

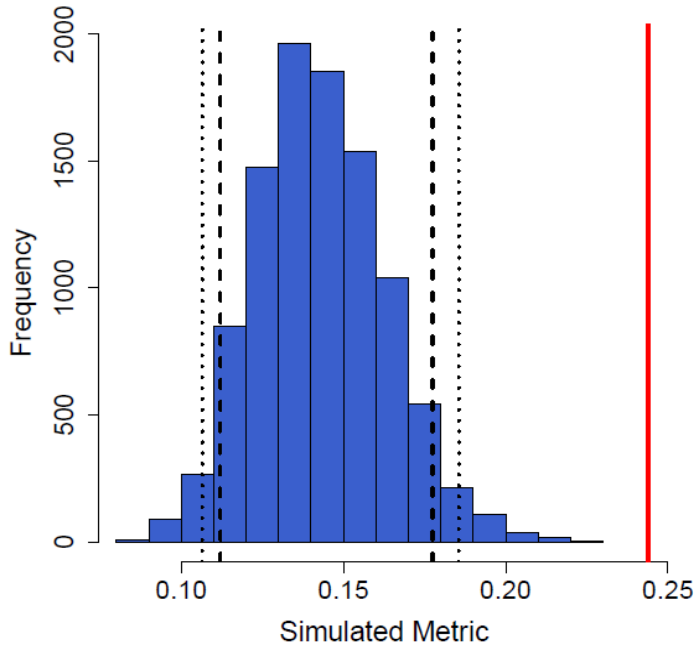

Figure A.75: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *S. lilium*.

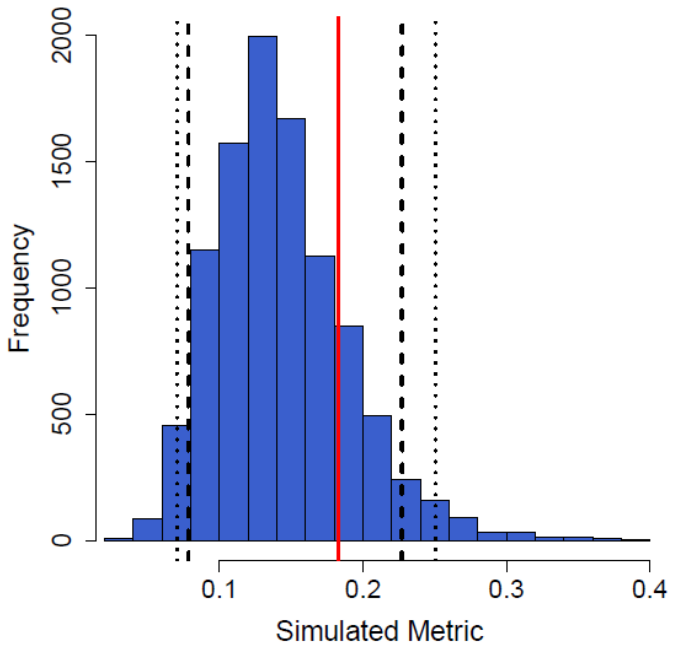

Figure A.76: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *S. ludovici*.

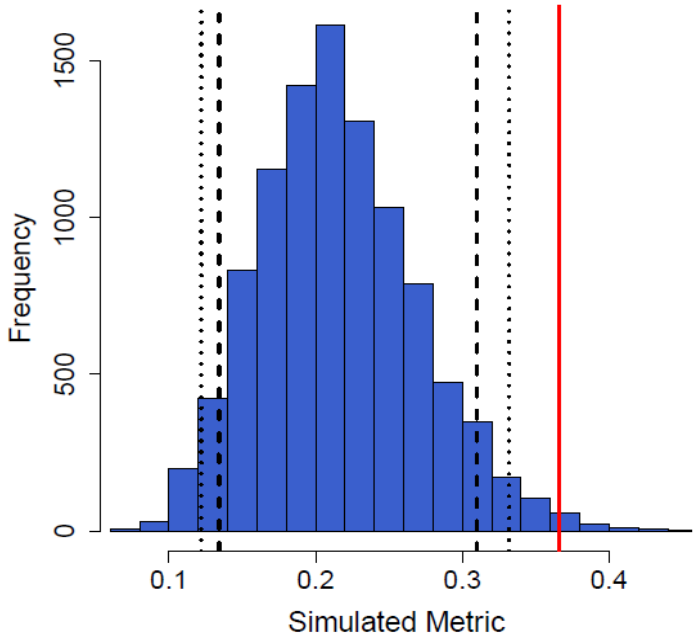

Figure A.77: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *S. tildae*.

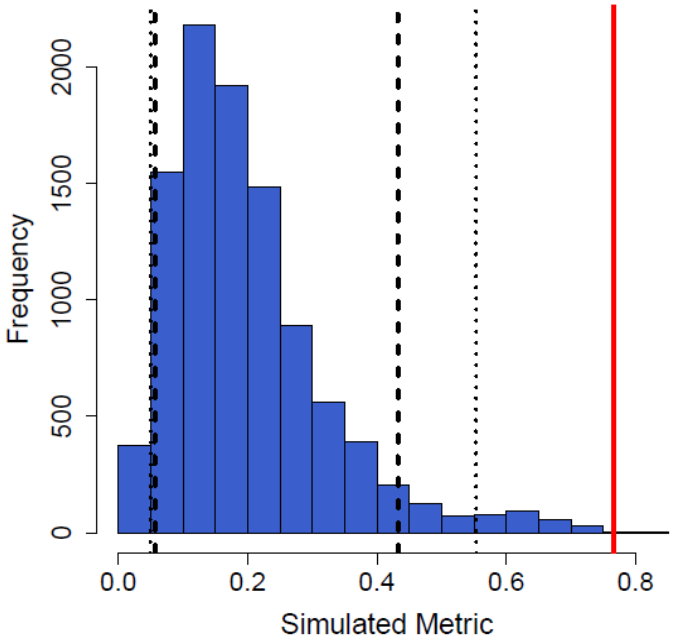

Figure A.78: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *T. sylvicola*.

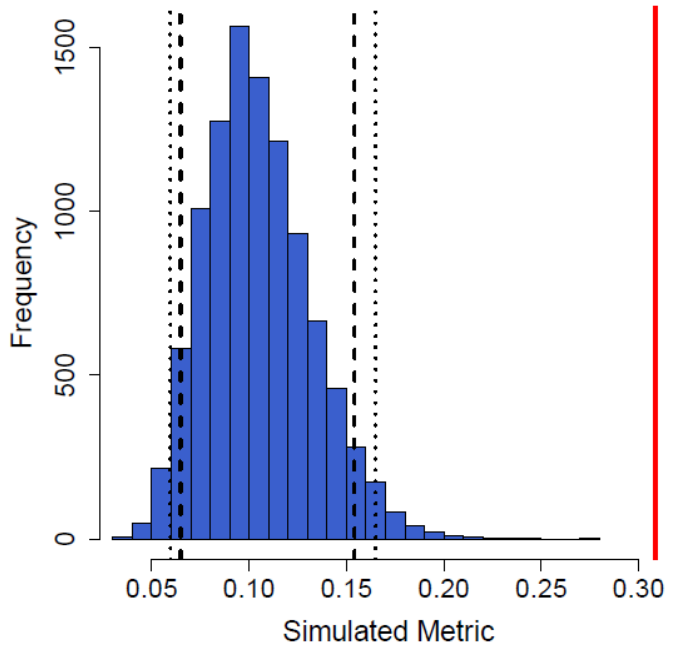

Figure A.79: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *T. cirrhosus*.

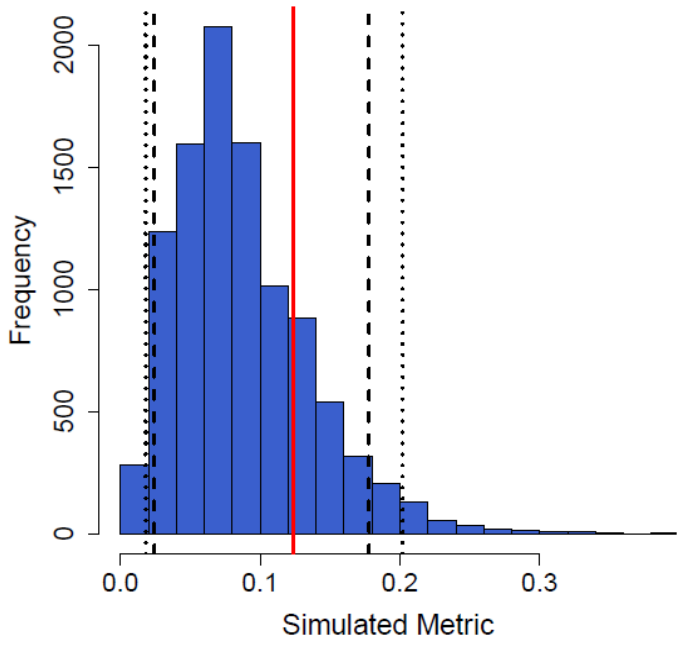

Figure A.80: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Speiseria magnioculus* and *Strebla mirabilis* found on *T. cirrhosus*.

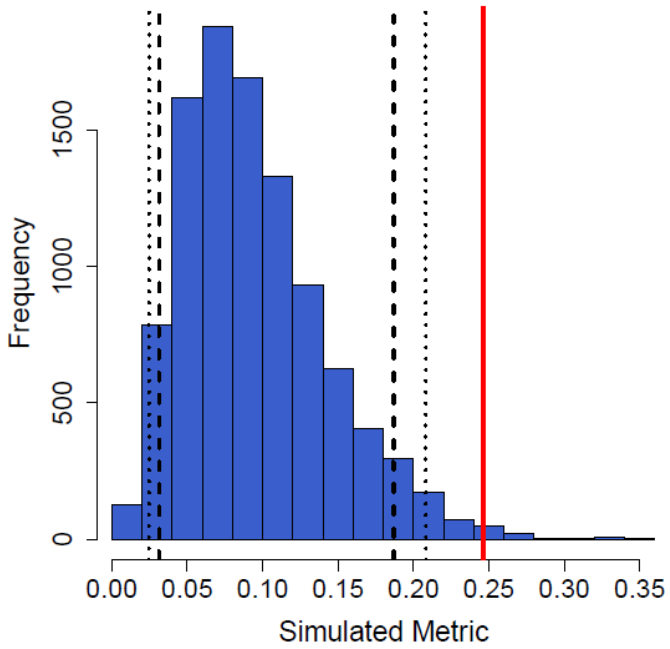

Figure A.81: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Speiseria magnioculus* and *Trichobius dugesioides* found on *T. cirrhosus*.

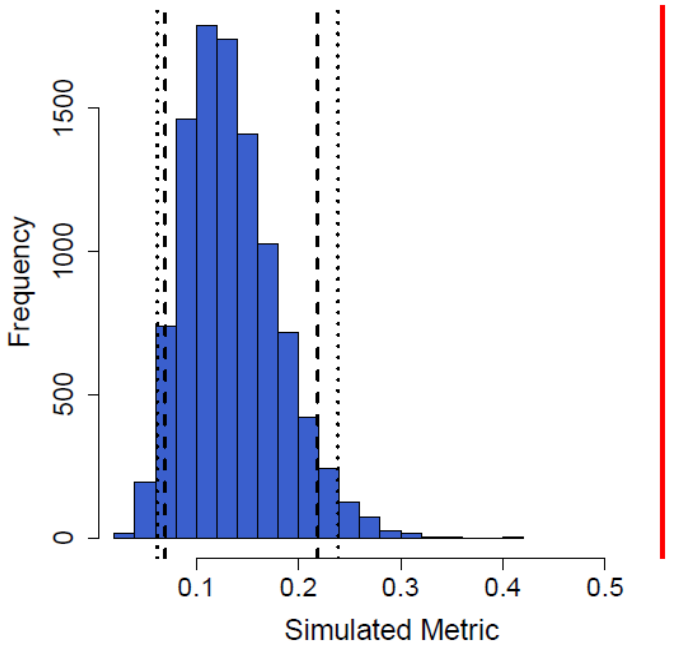

Figure A.82: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species *Strebla mirabilis* and *Trichobius dugesioides* found on *T. cirrhosus*.

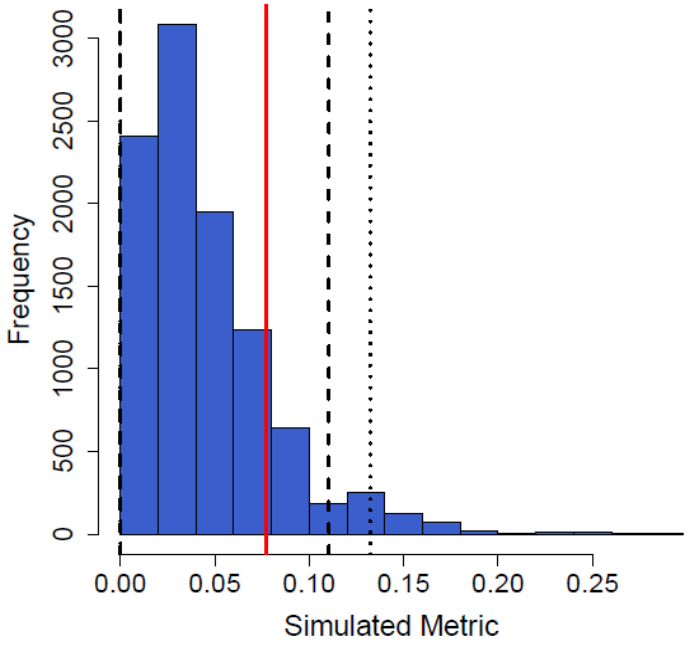

Figure A.83: Null distribution comparing the 10,000 simulated matrices (blue histogram) to the observed value (red line) for the streblid species found on *U. biliobatum*.

APPENDIX B: POISSON REGRESSION GRAPHS

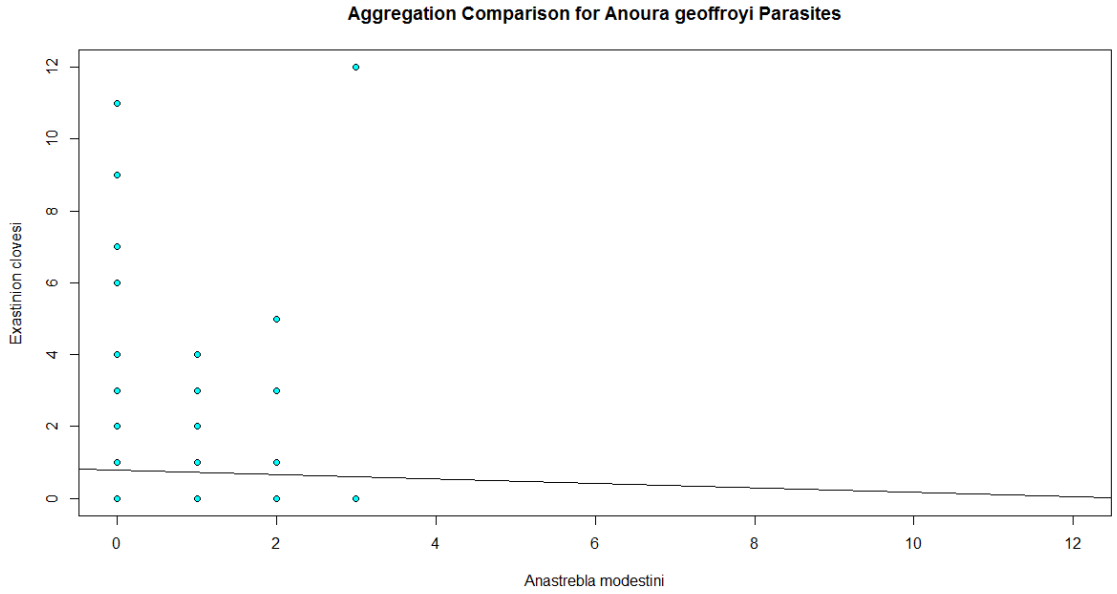

Figure B.1: A linear regression examining the relationship between the presence of *Anastrebla modestini* and *Exastinion clovesi* on the species *Anoura geoffroyi*. The correlation between these two parasite species is r = -0.040962, the F-value is 0.1798, and the p-value for this correlation is 0.668.

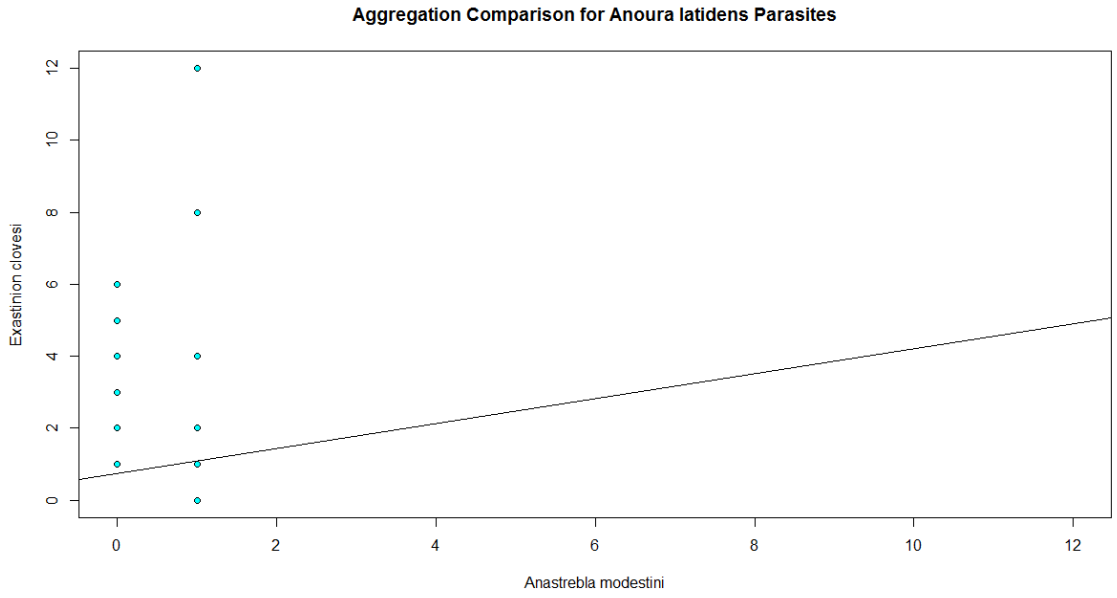

Figure B.2: A linear regression examining the relationship between the presence of *Anastrebla modestini* and *Exastinion clovisi* on the species *Anoura latidens*. The correlation between these two parasite species is r = 0.1725283, the F-value is 1.3192, and the p-value for this correlation is 0.262.

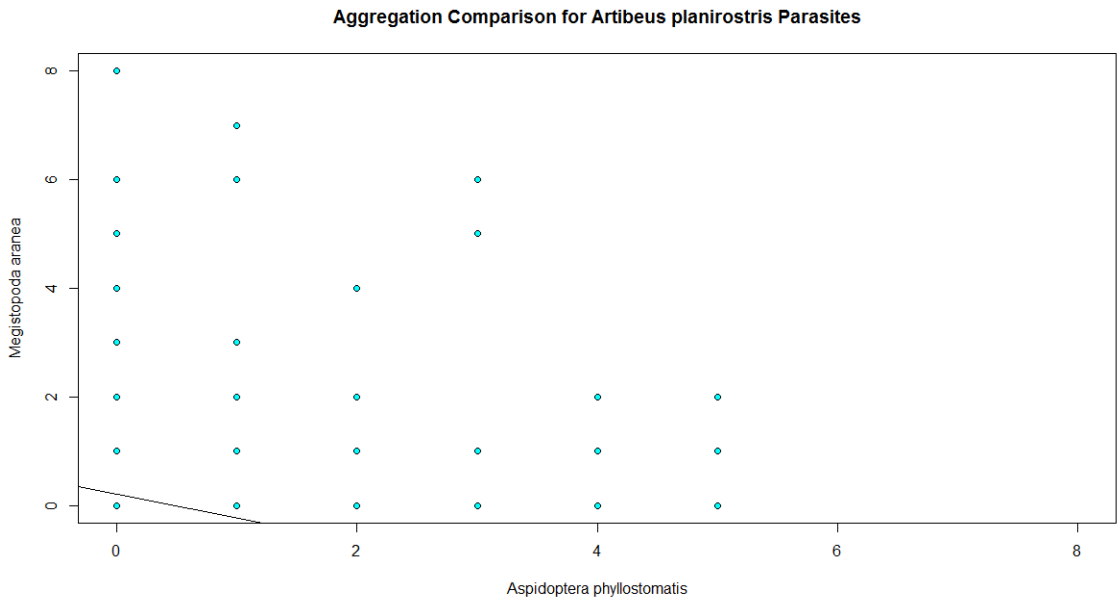

Figure B.3: A linear regression examining the relationship between the presence of *Aspidoptera phyllostomatis* and *Megistopoda aranea* on the species *Artibeus planirostris*. The correlation between these two parasite species is r = -0.2462092, the F-value is 34.524, and the p-value for this correlation is 0.001.

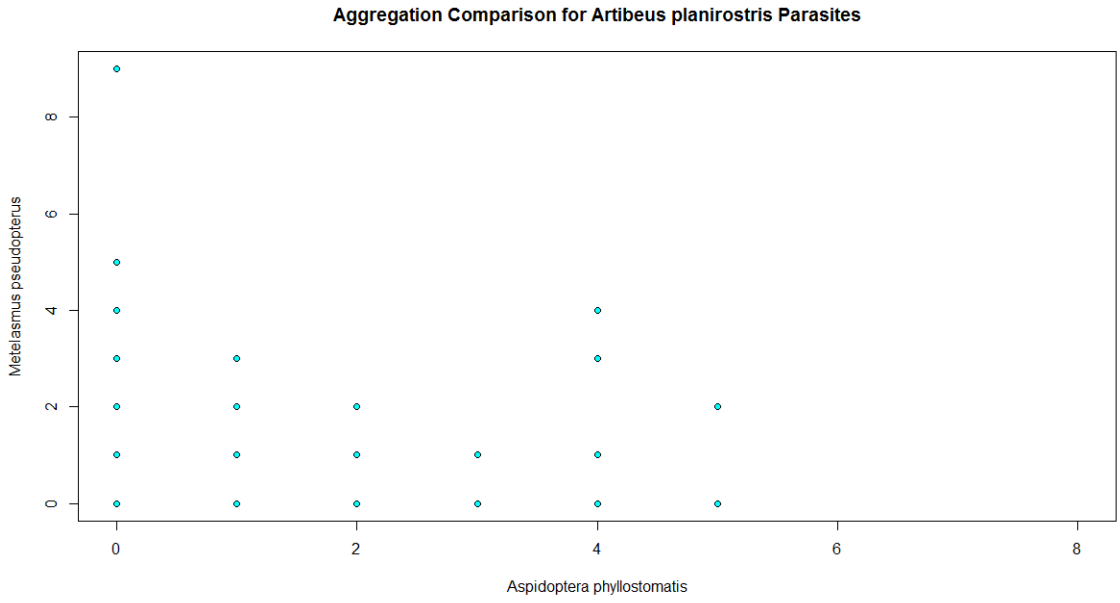

Figure B.4: A linear regression examining the relationship between the presence of *Aspidoptera phyllostomatis* and *Metelasmus pseudopterus* on the species *Artibeus planirostris*. The correlation between these two parasite species is r = 0.0193241, the F-value is 0.1999, and the p-value for this correlation is 0.655.

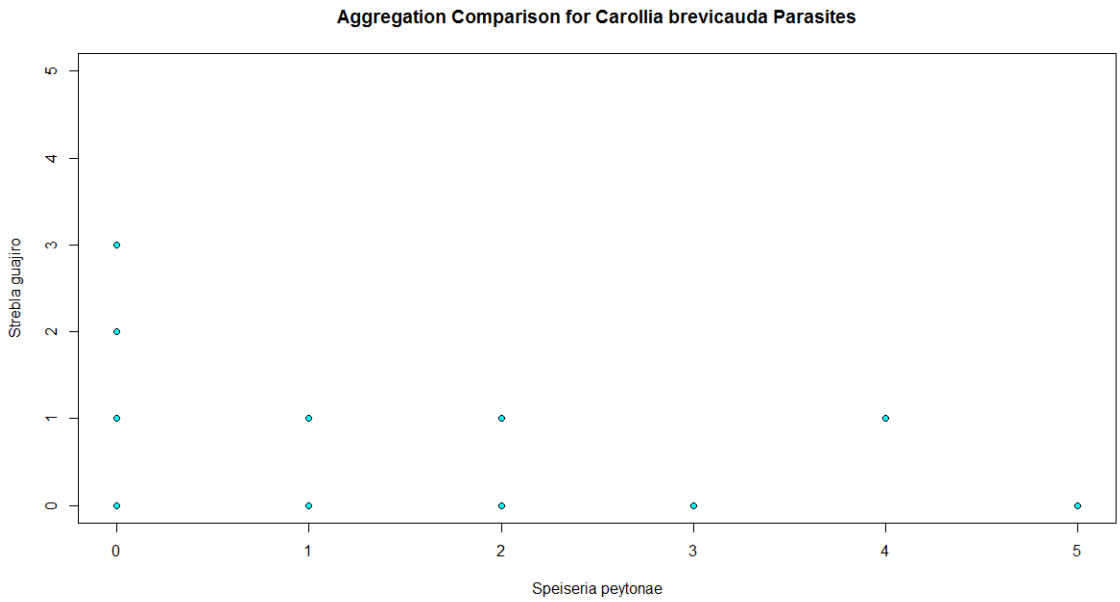

Figure B.5: A linear regression examining the relationship between the presence of *Speiseria peytonae* and *Strebla guajiro* on the species *Carollia brevicauda*. The correlation between these two parasite species *Aspidoptera phyllostomatis* is r = -0.0876436, the F-value is 1.4785, and the p-value for this correlation is 0.227.

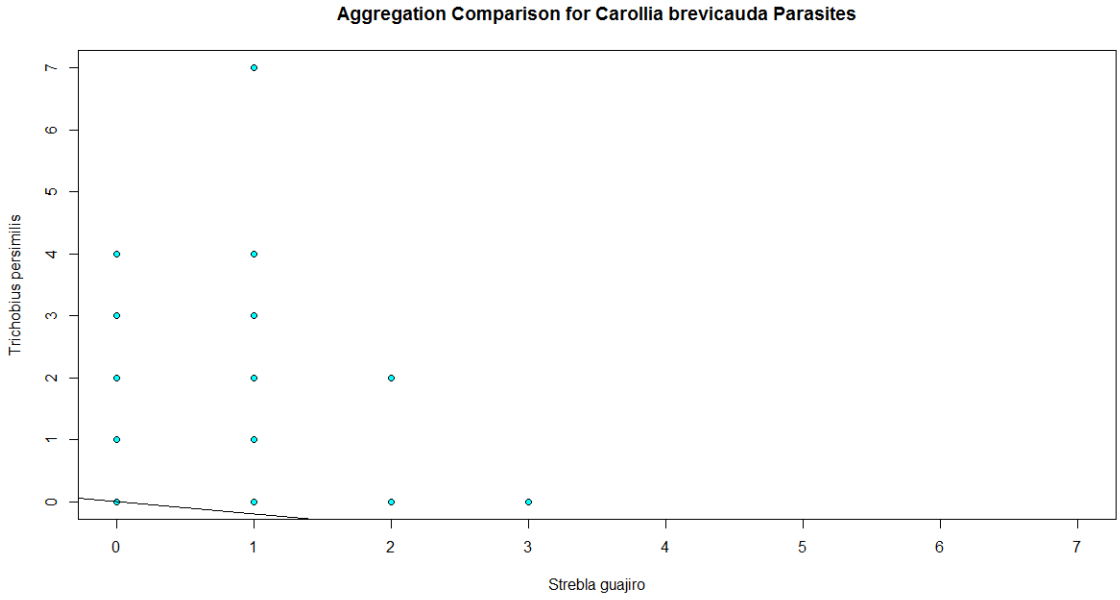

Figure B.6: A linear regression examining the relationship between the presence of *Strebla guajiro* and *Trichobius persimilis* on the species *Carollia brevicauda*. The correlation between these two parasite species *Aspidoptera phyllostomatis* is r = -0.0796335, the F-value is 1.219, and the p-value for this correlation is 0.2515.

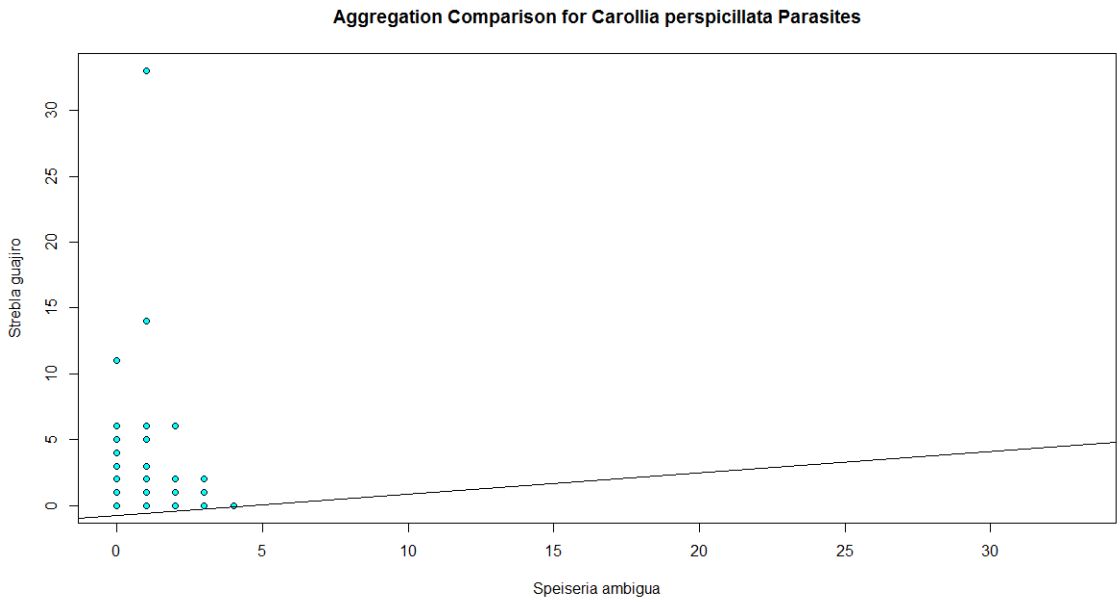

Figure B.7: A linear regression examining the relationship between the presence of *Speiseria ambigua* and *Strebla guajiro* on the species *Carollia perspicillata*. The correlation between these two parasite species *Aspidoptera phyllostomatis* is r = 0.0362422, the F-value is 1.4086, and the p-value for this correlation is 0.191.

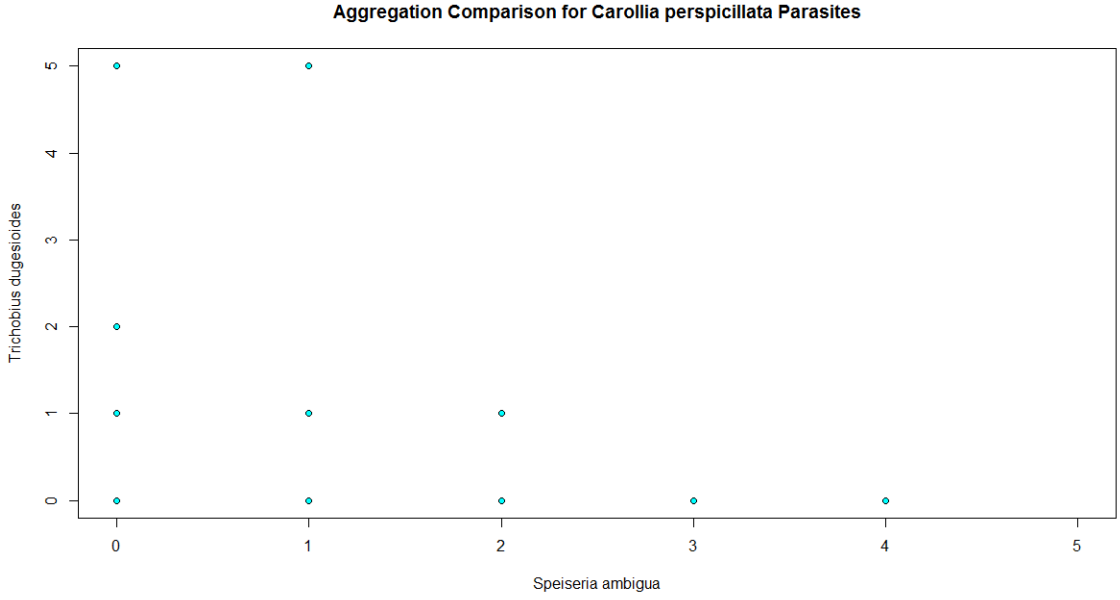

Figure B.8: A linear regression examining the relationship between the presence of *Speiseria ambigua* and *Trichobius dugesioides* on the species *Carollia perspicillata*. The correlation between these two parasite species *Aspidoptera phyllostomatis* is r = 0.00212337, the 0.0048, and the p-value for this correlation is 0.9665.

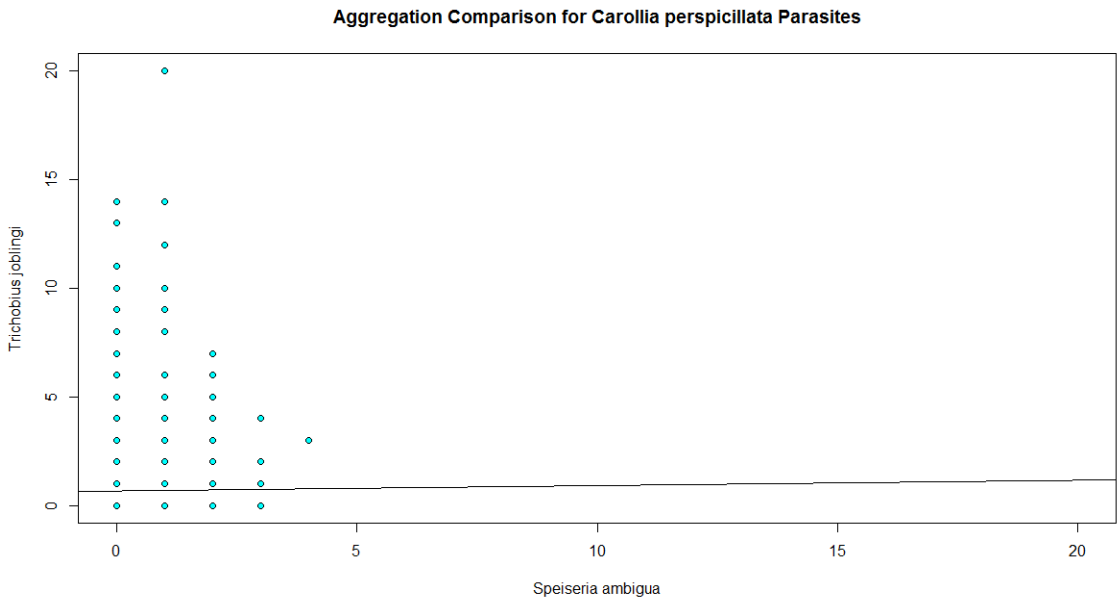

Figure B.9: A linear regression examining the relationship between the presence of *Speiseria ambigua* and *Trichobius joblingi* on the species *Carollia perspicillata*. The correlation between these two parasite species *Aspidoptera phyllostomatis* is r = 0.01417427, the F-value is 0.2152, and the p-value for this correlation is 0.629.

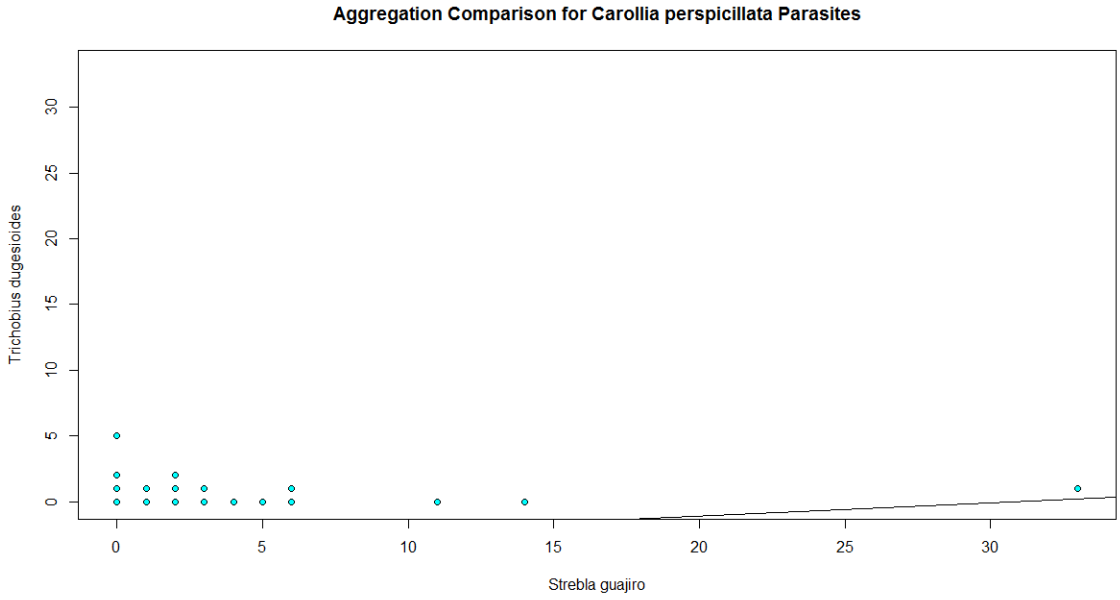

Figure B.10: A linear regression examining the relationship between the presence of *Strebla guajiro* and *Trichobius dugesioides* on the species *Carollia perspicillata*. The correlation between these two parasite species *Aspidoptera phyllostomatis* is r = 0.1060707, the F-value is 12.187, and the p-value for this correlation is 0.011.

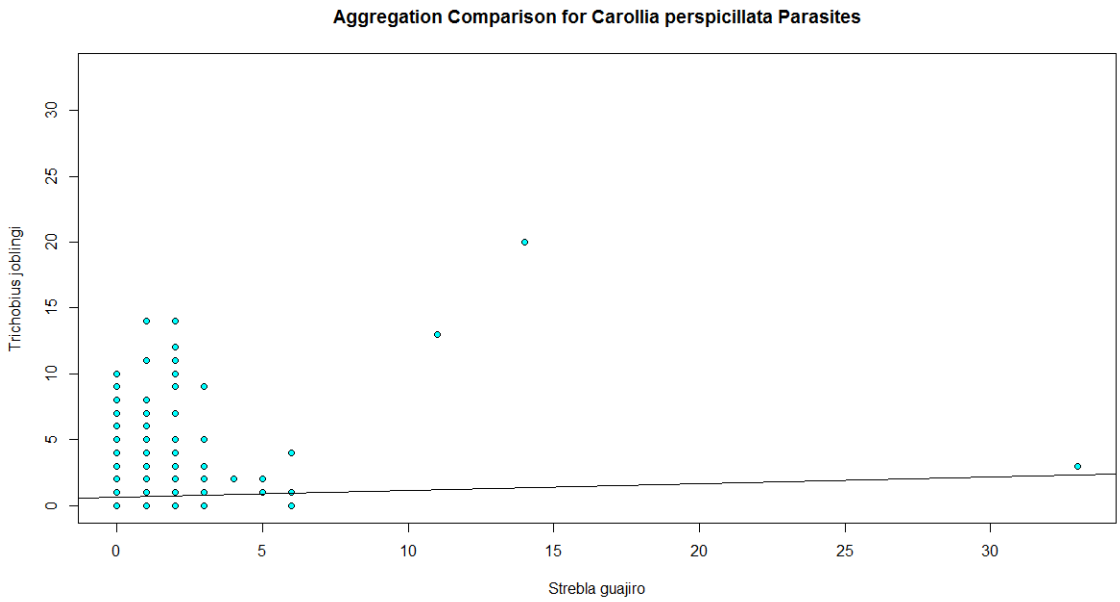

Figure B.11: A linear regression examining the relationship between the presence of *Strebla guajiro* and *Trichobius joblingi* on the species *Carollia perspicillata*. The correlation between these two parasite species *Aspidoptera phyllostomatis* is r = 0.1283589, the F-value is 17.942, and the p-value for this correlation is 0.005.

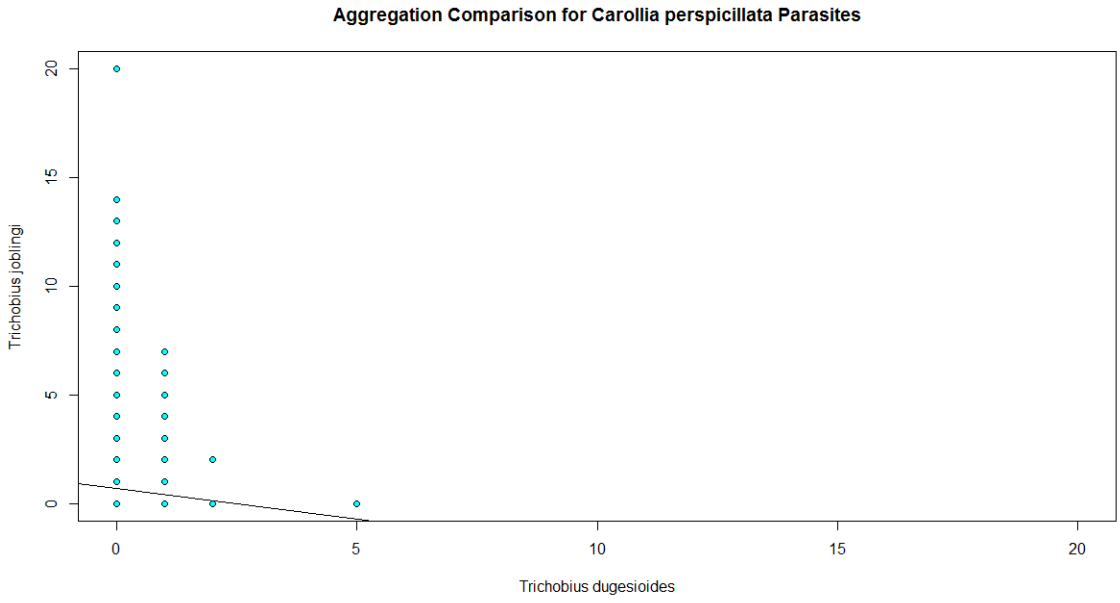

Figure B.12: A linear regression examining the relationship between the presence of *Trichobius dugesioides* and *Trichobius joblingi* on the species *Carollia perspicillata*. The correlation between these two parasite species *Aspidoptera phyllostomatis* is r = -0.05393886, the F-value is 3.1251, and the p-value for this correlation is 0.09.

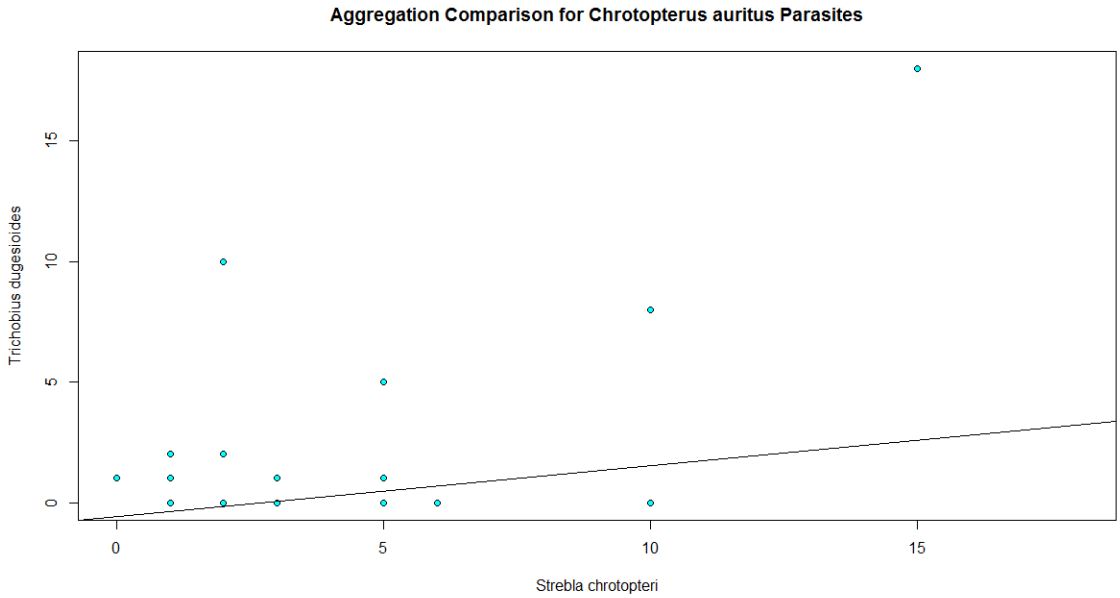

Figure B.13: A linear regression examining the relationship between the presence of *Strebla chrotopteri* and *Trichobius dugesioides* on the species *Chrotopterus auritus*. The correlation between these two parasite species *Aspidoptera phyllostomatis* is r = 0.5671684, the F-value is 10.907, and the p-value for this correlation is 0.014.

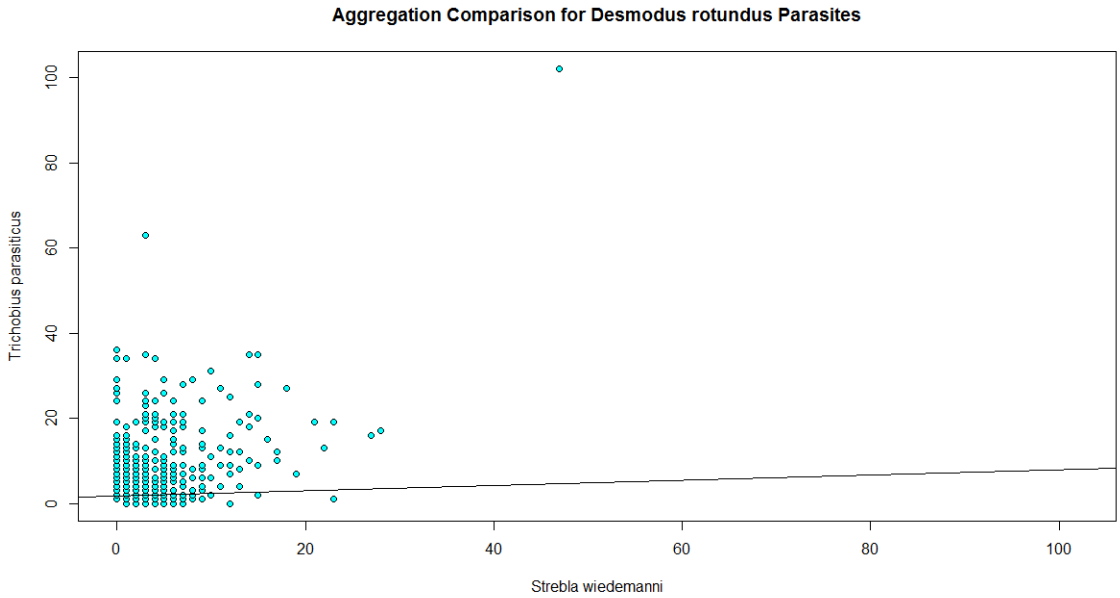

Figure B.14: A linear regression examining the relationship between the presence of *Strebla wiedemanni* and *Trichobius parasiticus* on the species *Desmodus rotundus*. The correlation between these two parasite species *Aspidoptera phyllostomatis* is r = 0.4215448, the F-value is 124.48, and the p-value for this correlation is 0.001.

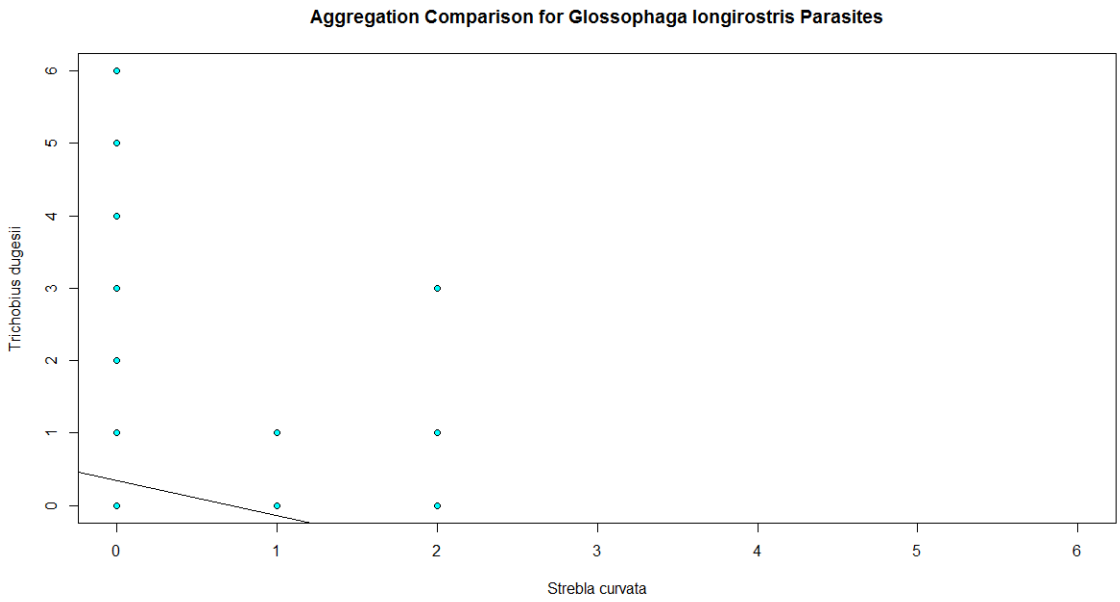

Figure B.15: A linear regression examining the relationship between the presence of *Strebla curvata* and *Trichobius dugesii* on the species *Glossophaga longirostris*. The correlation between these two parasite species *Aspidoptera phyllostomatis* is r = -0.195576, the F-value is 4.3351, and the p-value for this correlation is 0.042.

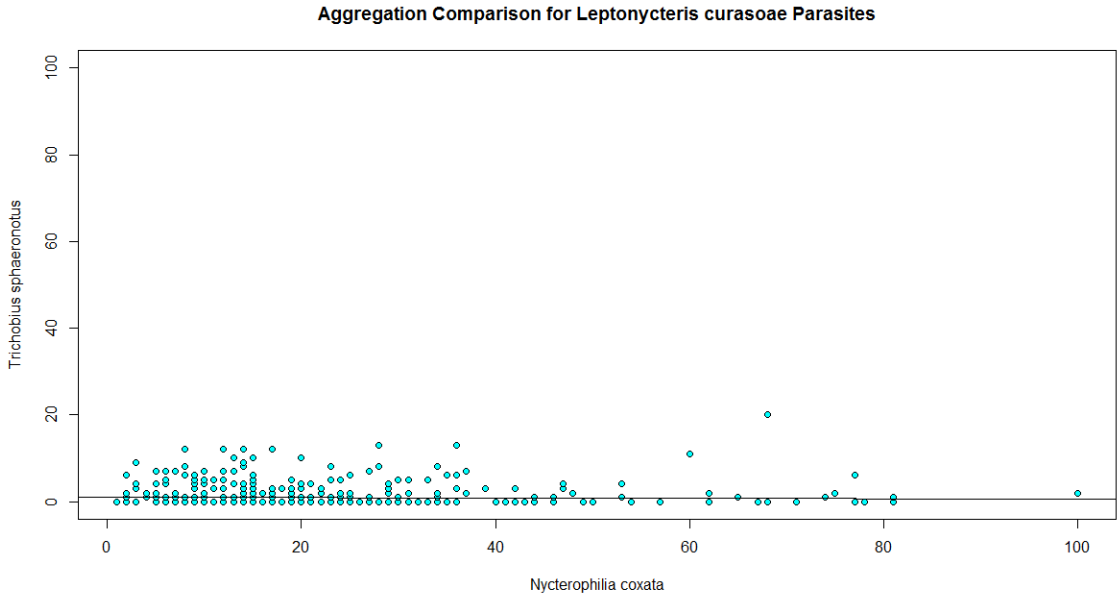

Figure B.16: A linear regression examining the relationship between the presence of *Nycterophilia coxata* and *Trichobius sphaeronotus* on the species *Leptonycteris curasoae*. The correlation between these two parasite species *Aspidoptera phyllostomatis* is r = -0.06631741, the F-value is 1.1353, and the p-value for this correlation is 0.293.

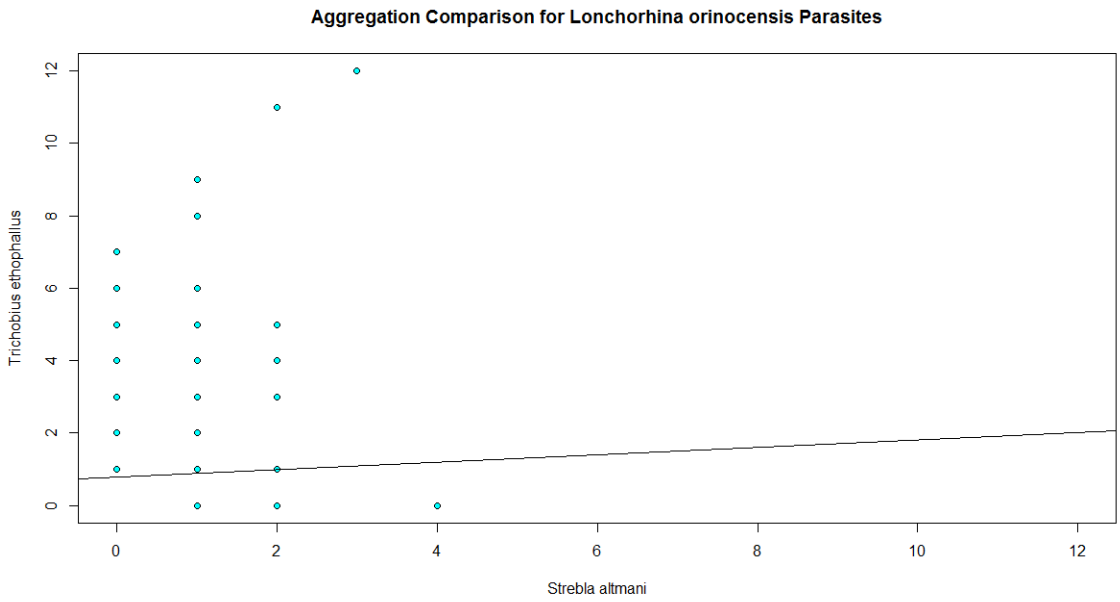

Figure B.17: A linear regression examining the relationship between the presence of *Strebla altmani* and *Trichobius ethophallus* on the species *Lonchorhina orinocensis*. The correlation between these two parasite species *Aspidoptera phyllostomatis* is r = 0.09565563, the F-value is 1.6068, and the p-value for this correlation is 0.1905.

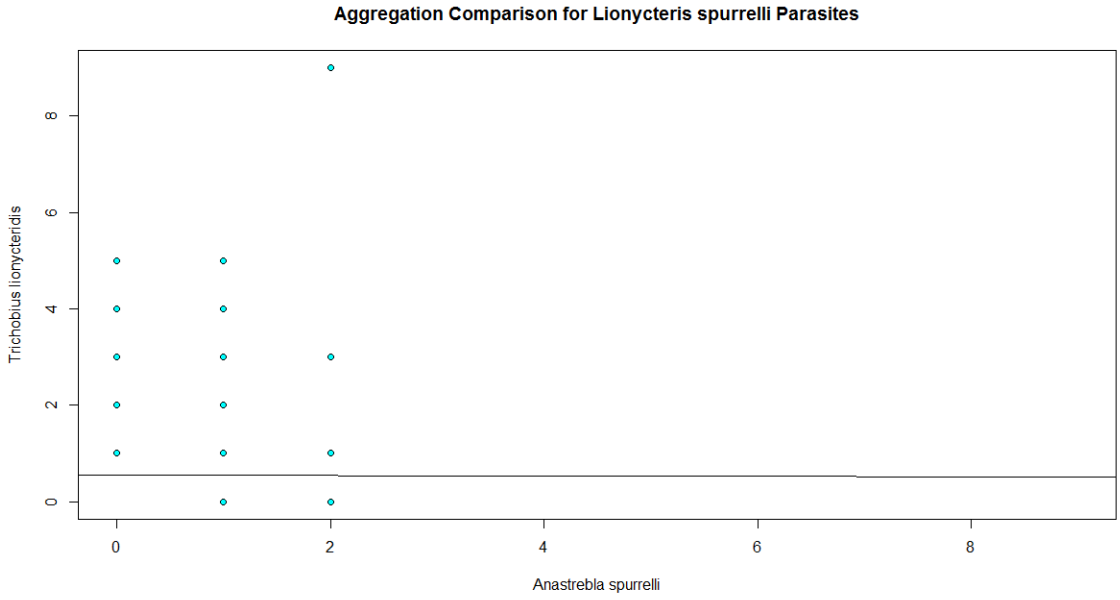

Figure B.18: A linear regression examining the relationship between the presence of *Anastrebla spurrelli* and *Trichobius lionycteridis* on the species *Lionycteris spurrelli*. The correlation between these two parasite species *Aspidoptera phyllostomatis* is r = -0.003562864, the F-value is 0.0012, and the p-value for this correlation is 0.98.

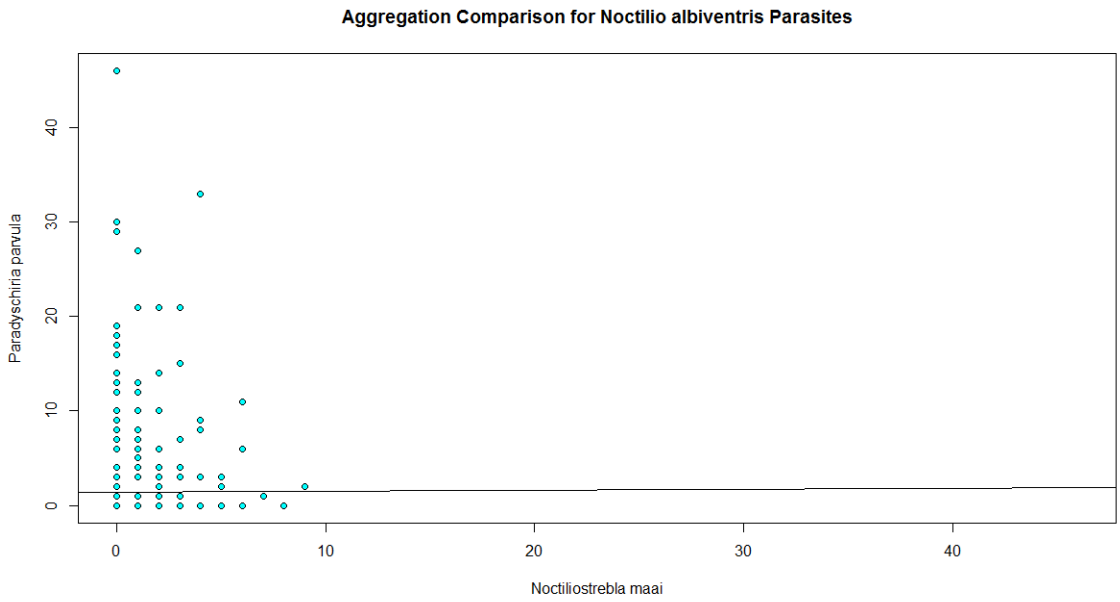

Figure B.19: A linear regression examining the relationship between the presence of *Noctiliostrebla maai* and *Paradyschiria parvula* on the species *Noctilio albiventris*. The correlation between these two parasite species *Aspidoptera phyllostomatis* is r = 0.009953592, the F-value is 0.019, and the p-value for this correlation is 0.8965.

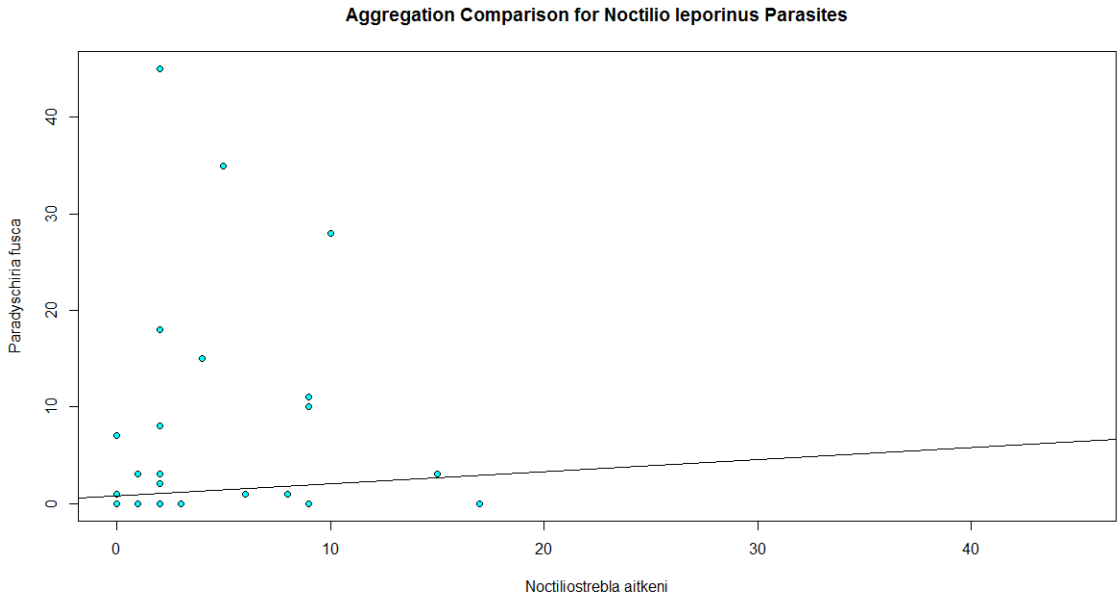

Figure B.20: A linear regression examining the relationship between the presence of *Noctiliostrebla aitkeni* and *Paradyschiria fusca* on the species *Noctilio leporinus*. The correlation between these two parasite species *Aspidoptera phyllostomatis* is r = 0.3005728, the F-value is 5.959, and the p-value for this correlation is 0.031.

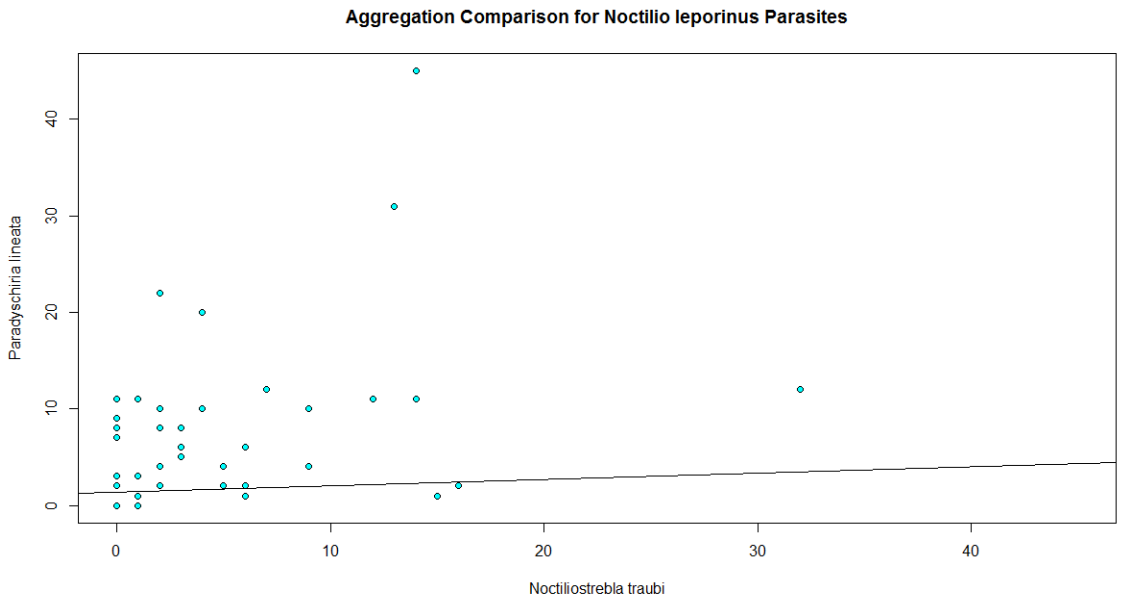

Figure B.21: A linear regression examining the relationship between the presence of *Noctiliostrebla traubi* and *Paradyschiria lineata* on the species *Noctilio leporinus*. The correlation between these two parasite species *Aspidoptera phyllostomatis* is r = 0.4522168, the F-value is 15.424, and the p-value for this correlation is 0.007.

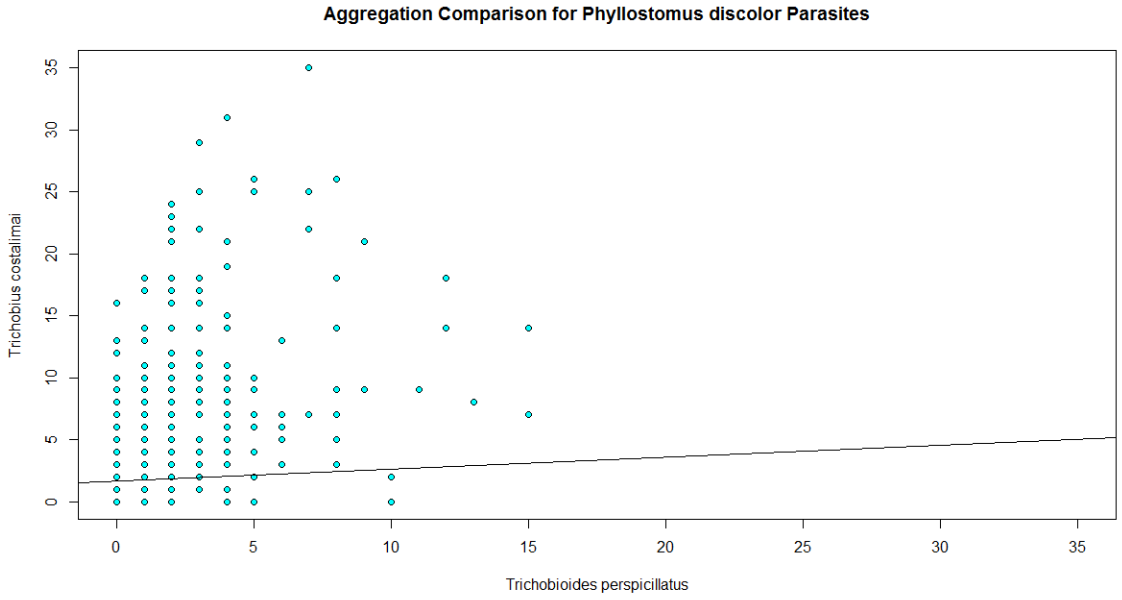

Figure B.22: A linear regression examining the relationship between the presence of *Trichobioides perspicillatus* and *Trichobius costalimai* on the species *Phyllostomus discolor*. The correlation between these two parasite species *Aspidoptera phyllostomatis* is r = 0.3570854, the F-value is 43.26, and the p-value for this correlation is 0.001.

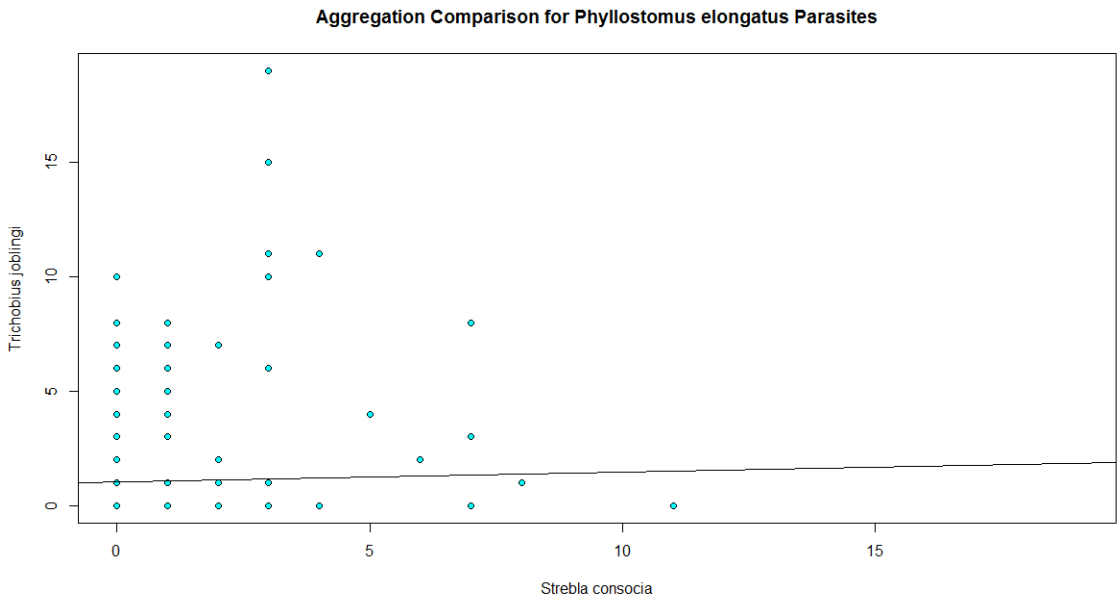

Figure B.23: A linear regression examining the relationship between the presence of *Strebla consocia* and *Trichobius joblingi* on the species *Phyllostomus elongatus*. The correlation between these two parasite species *Aspidoptera phyllostomatis* is r = 0.08533404, the F-value is 0.5795, and the p-value for this correlation is 0.461.

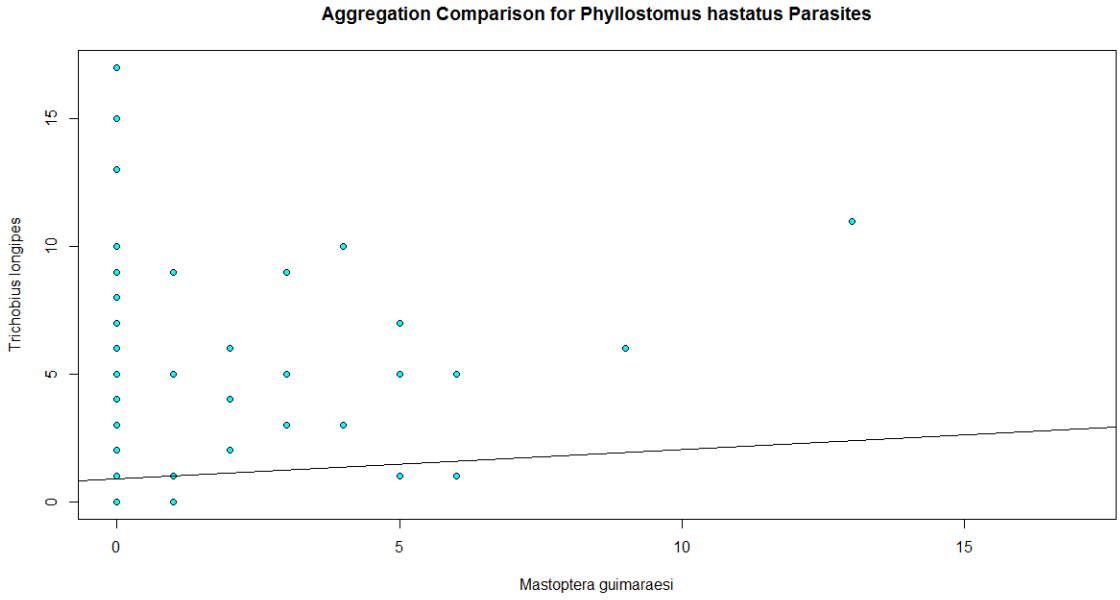

Figure B.24: A linear regression examining the relationship between the presence of *Mastoptera guimaraesi* and *Trichobius longipes* on the species *Phyllostomus hastatus*. The correlation between these two parasite species *Aspidoptera phyllostomatis* is r = 0.2553899, the F-value is 15.351, and the p-value for this correlation is 0.002.

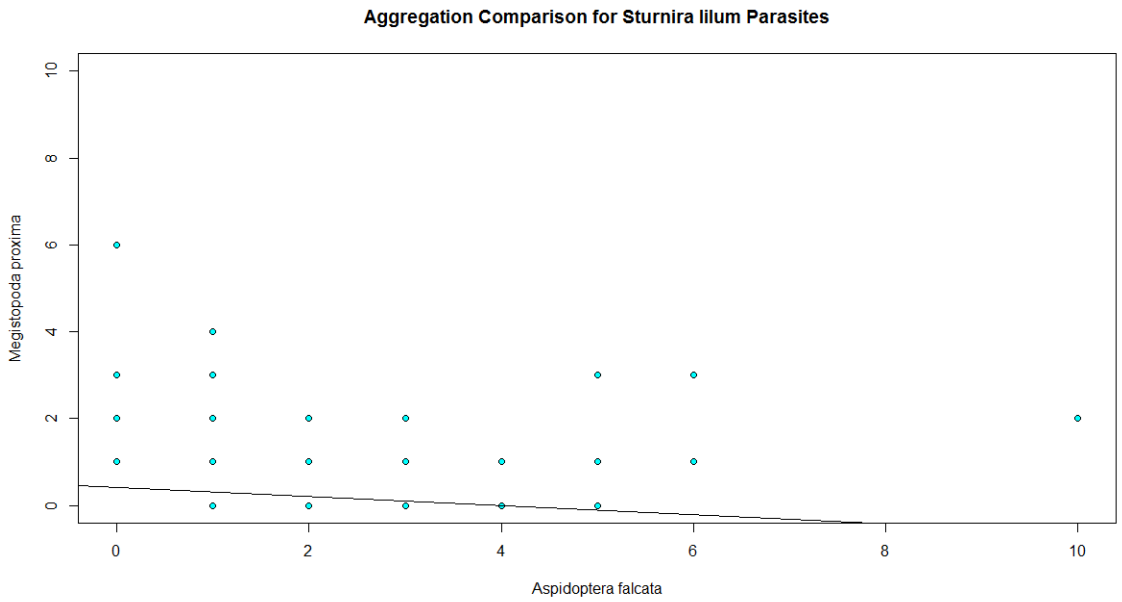

Figure B.25: A linear regression examining the relationship between the presence of *Aspidoptera falcata* and *Megistopoda proxima* on the species *Sturnira lilum*. The correlation between these two parasite species *Aspidoptera phyllostomatis* is r = -0.1811739, the F-value is 3.3259, and the p-value for this correlation is 0.066.

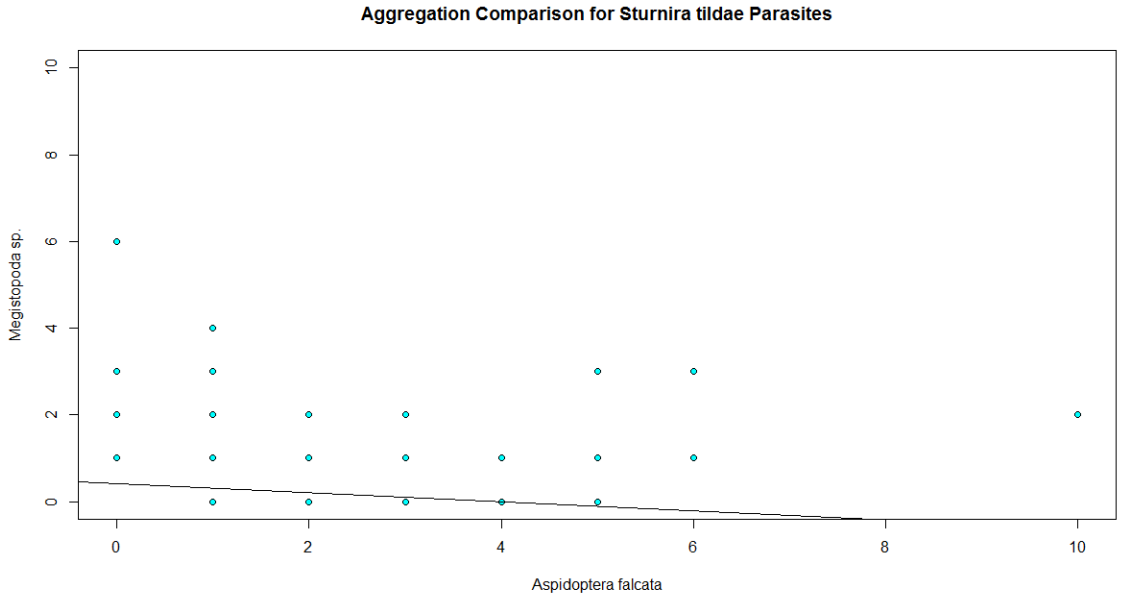

Figure B.26: A linear regression examining the relationship between the presence of *Aspidoptera falcata* and *Megistopoda sp.* on the species *Sturnira tildae*. The correlation between these two parasite species *Aspidoptera phyllostomatis* is r = -0.1811739, the F-value is 3.3259, and the p-value for this correlation is 0.074.

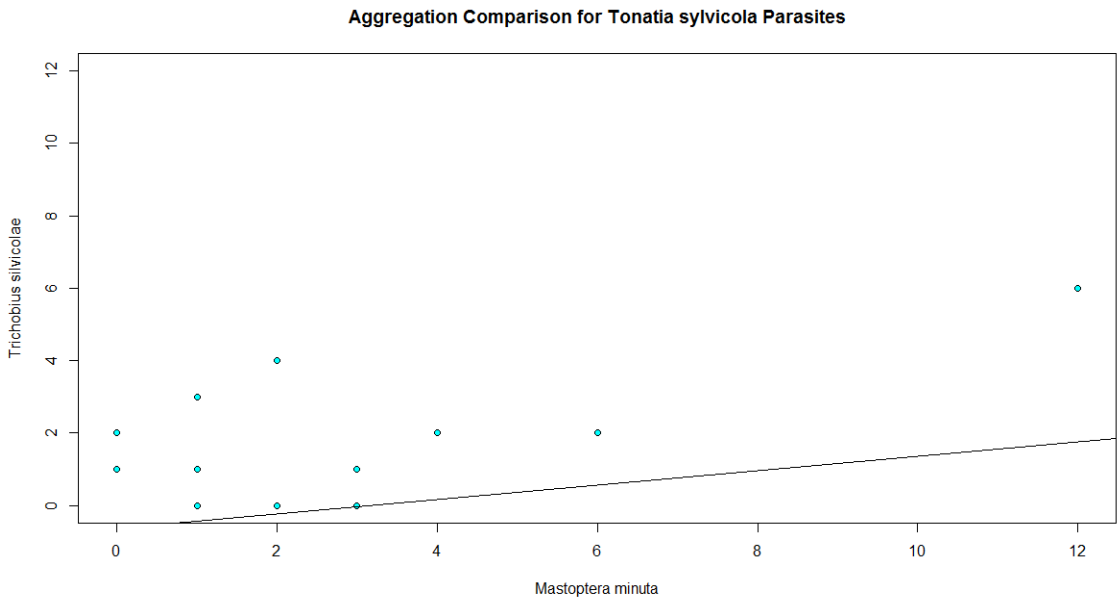

Figure B.27: A linear regression examining the relationship between the presence of *Mastoptera minuta* and *Trichobius silvicolae* on the species *Tonatia sylvicola*. The correlation between these two parasite species *Aspidoptera phyllostomatis* is r = 0.643063, the F-value is 14.807, and the p-value for this correlation is 0.0075.

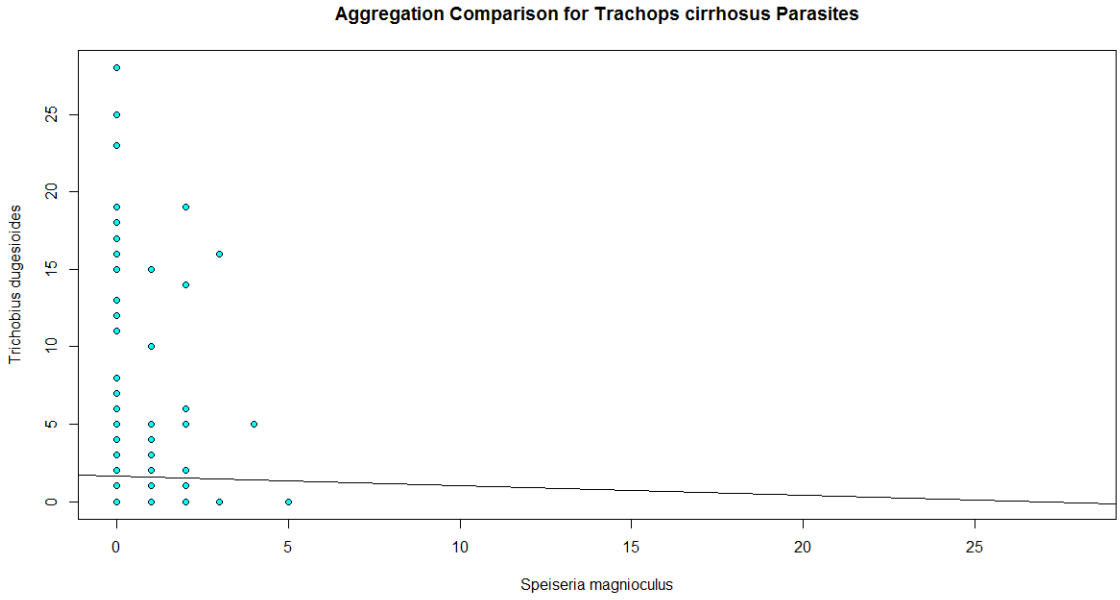

Figure B.28: A linear regression examining the relationship between the presence of *Speiseria magnioculus* and *Trichobius dugesioides* on the species *Trachops cirrhosus*. The correlation between these two parasite species *Aspidoptera phyllostomatis* is r = -0.04221492, the F-value is 0.216, and the p-value for this correlation is 0.6485.

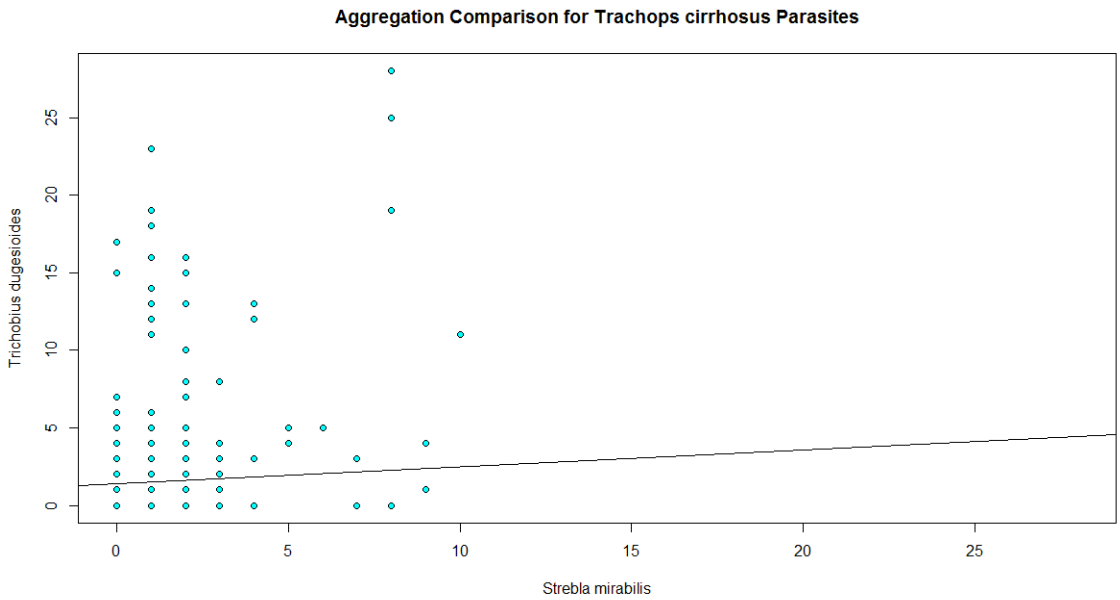

Figure B.29: A linear regression examining the relationship between the presence of *Strebla mirabilis* and *Trichobius dugesioides* on the species *Trachops cirrhosus*. The correlation between these two parasite species *Aspidoptera phyllostomatis* is r = 0.2688215, the F-value is 9.4252, and the p-value for this correlation is 0.005.

APPENDIX C: CHAPTER 1 R SCRIPT

```
#############################################
## EcoSimR: R code for Null Model Analysis
##
##
##
#############################################
## EcoSimR Niche Overlap Shell
## Nicholas J. Gotelli & Aaron M. Ellison
##
##
#############################################
## Version 1.00
## 15 June 2013
#############################################
## Modified on 18 May 2013 by NJG to pass a single Param.List to all functions
#############################################
####For beginners - start here####

## clean the slate ##

rm(list=ls())   # remove all objects in memory


## load EcoSimR

source("EcoSimR - Main Source.R")

#############################################
## Model input parameters
## USER CAN MODIFY PARAMETERS IN THIS SECTION
Data.File <- "2spp.AamplusPA.csv"
Output.File <-"Niche Overlap Output.txt"
Algorithm <- "RA3"   #choices are "RA1", "RA2", "RA3", "RA4"; default is "RA3"
Metric <- "Pianka"      #choices are "Pianka", "Czekanowski",
                        #"Pianka.var", "Czekanowski.var",
                        # "Pianka.skew", "Czekanowski.skew"; default is Pianka
N.Reps <- 10000        # 1000 is the typical number of replicates, but any number > 2 will
run
Random.Seed <- 625 ## If 0, uses random integer. User can replace 0 with your integer
of choice e.g. 107
Plot.Output <- "file"   #choices are "file", "screen", "none"; default is "screen"
Print.Output <- "screen"         #choices are "file", "screen", "none"; default is "screen"
Display.About <- "none" # choices are "screen", "none"; default is "none"
Graphic <- "Niche.Overlap.Plot" # other choices will be added with other modules
```

```
##############################################


##############################################
## Execute analyses
## Beginning users should NOT modify this section
##
## First command initialized the parameter list from the user inputs
## Second command runs niche overlap analysis using Data.File, Algorithm, and Metric
from user inputs
## Third command outputs graphics and statistics to devices specified from user inputs

Param.List <- Get.Params(Data.File,Output.File,Algorithm,Metric,
                  N.Reps,Random.Seed,Plot.Output,Print.Output,Display.About,Graphic)
RandomInteger <- Set.The.Seed(Param.List)


Null.Result <- Null.Model.Engine(Param.List)

Output.Results(Param.List,Null.Result)

#########################################################################
##Poisson Regression in cases of Aggregation
rm(list=ls())   # remove all objects in memory

Batdata=read.csv(file.choose())

A = as.integer(Batdata$A)
B = as.integer(Batdata$B)

glmtry = glm(B ~ A, family = poisson())
glmtry

source("biol.582.rscript.ANOVA.source.code.for.R")#Non-parametric method
np.anova(glmtry)

# best fit line is y = a + bx
plot(A,B,pch=21,bg='cyan', xlim = c(0,28), xlab="Strebla mirabilis",ylab="Trichobius
dugesioides",main="Aggregation Comparison for Trachops cirrhosus Parasites")
abline(glmtry)
```

APPENDIX D: CHAPTER 2 R SCRIPT

```
#Prelimaries

rm(list=ls())
batflies = read.csv(file.choose())
Morph = as.factor(batflies$Morphotype)
Genus = as.factor(batflies$Genus)
Sp = as.factor(batflies$Species)
CP = as.factor(batflies$Cntedium.Presence)
WF = as.factor(batflies$Wing.Formation)

library(geomorph)
library(gplots)

#####Issues Examining the Ventral & Lateral with Abdomen - So exclude it!
#Start with the basics
venX.coords = as.matrix(batflies[,(8:75)]) #X as in saperated from abdomen like an ex
latX.coords = as.matrix(batflies[,(111:176)])

# sliders
venX.sliders = rbind(c(1,2,3),
                     c(2,3,4),
                     c(3,4,5),
                     c(4,5,6),
                     c(6,7,8),
                     c(7,8,9),
                     c(8,9,10),
                     c(9,10,11),
                     c(10,11,12),
                     c(11,12,13),
                     c(12,13,14),
                     c(14,15,16),
                     c(15,16,17),
                     c(16,17,18),
                     c(17,18,19),
                     c(19,20,21),
                     c(20,21,22),
                     c(21,22,23),
                     c(24,25,26),
                     c(25,26,27),
                     c(1,27,26),
                     c(28,29,30),
                     c(29,30,31),
                     c(19,34,31),
                     c(1,33,31),
                     c(30,31,32))
```

```
latX.sliders = rbind(c(1,2,3),
                     c(2,3,4),
                     c(3,4,5),
                     c(5,6,7),
                     c(6,7,8),
                     c(7,8,9),
                     c(8,9,10),
                     c(9,10,11),
                     c(10,11,12),
                     c(11,12,13),
                     c(12,13,14),
                     c(13,14,15),
                     c(1,15,14),
                     c(16,17,18),
                     c(17,18,19),
                     c(18,19,20),
                     c(19,20,21),
                     c(20,21,22),
                     c(21,22,23),
                     c(22,23,24),
                     c(23,24,25),
                     c(24,25,26),
                     c(25,26,27),
                     c(26,27,28),
                     c(27,28,29),
                     c(28,29,30),
                     c(29,30,31),
                     c(30,31,32),
                     c(31,32,33),
                     c(16,33,32))

#GPA
venX.gpa = gpagen(arrayspecs(venX.coords, 34,2), curves=venX.sliders)
latX.gpa = gpagen(arrayspecs(latX.coords, 33,2), curves=latX.sliders)

venXshape = venX.gpa$coords
venXcs = venX.gpa$Csize
latXshape = latX.gpa$coords
latXcs = latX.gpa$Csize

#GPA plots
plotAllSpecimens(venXshape)
plotAllSpecimens(latXshape)

##Now to check on Allometry
```

```
#First the Ventral (labeled Fire, cause why not)
Fire = procD.allometry(venXshape ~ log(venXcs))
summary(Fire)
plot(Fire, method = "PredLine")
plot(Fire, method = "RegScore") #Clearly strong effect of allometry here
#Now for the Lateral (labeled Ice, also why not)
Ice = procD.allometry(latXshape ~ log(latXcs))
summary(Ice)
plot(Ice, method = "PredLine")
plot(Ice, method = "RegScore") #Also clear strong effect of allometry

##Now to adjust these values to get rid of allometry problem
#First Fire
FireAnova = procD.lm(venXshape ~ log(venXcs))
summary(FireAnova)
shape.resid = arrayspecs (FireAnova$residuals, p=dim(venXshape)[1],
k=dim(venXshape)[2])
adj.venshape = shape.resid + array(venX.gpa$consensus, dim(shape.resid))
plotTangentSpace(adj.venshape) #Ventral body shape has now been adjuisted
#Now for Ice
IceAnova = procD.lm(latXshape ~ log(latXcs))
summary(IceAnova)
shape.resid = arrayspecs (IceAnova$residuals, p=dim(latXshape)[1],
k=dim(latXshape)[2])
adj.latXshape = shape.resid + array(latX.gpa$consensus, dim(shape.resid))
plotTangentSpace(adj.latXshape) #Also now adjusted

###GPA plots
plotAllSpecimens(adj.venshape) #Ventral
plotAllSpecimens(adj.latXshape) #Lateral

####PCA plots examining Morph and Spp.#####
###Morph

plotTangentSpace(adj.venshape, groups= Morph) #Ventral
plotTangentSpace(adj.latXshape, groups= Morph) #Lateral

###Spp.
#Set up
col.Sp <- rainbow(length(levels(Sp)))
names(col.Sp) <- levels(Sp)
col.Sp <- col.Sp[match(Sp, names(col.Sp))] # col.Sp must NOT be a factor

#Actual Plots
plotTangentSpace(adj.venshape, groups = col.Sp) #Ventral
plotTangentSpace(adj.latXshape, groups = col.Sp) #Lateral
```

```
##Now to run 2bpls analyses to compare the two adjusted body shapes
VenXAdj.LatXAdj.cor = two.b.pls(adj.venshape,adj.latXshape) #Compare Ventral Ex shape and Lateral Ex shape
VenXAdj.LatXAdj.cor #Significant
plot(VenXAdj.LatXAdj.cor)

###Examining relationships and groups
##First grouped by Morphotypes
VenXAdj.M.Test = advanced.procD.lm(adj.venshape ~ log(venXcs), ~log(venXcs) + Morph, groups = ~Morph, iter= 9999) #Significant
LatXAdj.M.Test = advanced.procD.lm(adj.latXshape ~ log(latXcs), ~log(latXcs) + Morph, groups = ~Morph, iter= 9999) #Significant
##Second grouped by Genus
VenXAdj.G.Test = advanced.procD.lm(adj.venshape ~ log(venXcs), ~log(venXcs) + Genus, groups = ~Genus, iter= 9999) #Significant
LatXAdj.G.Test = advanced.procD.lm(adj.latXshape ~ log(latXcs), ~log(latXcs) + Genus, groups = ~Genus, iter= 9999) #Significant
##Third grouped by Species
VenXAdj.S.Test = advanced.procD.lm(adj.venshape ~ log(venXcs), ~log(venXcs) + Sp, groups = ~Sp, iter= 9999) #Significant
LatXAdj.S.Test = advanced.procD.lm(adj.latXshape ~ log(latXcs), ~log(latXcs) + Sp, groups = ~Sp, iter= 9999) #Significant


######Separated Ventral and Lateral Shapes######
##Separating the different aspects of the different shapes
#Ventral: 1= Head 2= Thorax
ven1coords = as.matrix(vencoords[,(11:28)])
ven2coords = as.matrix(vencoords[,-(13:26)]) #Part 1
ven2coords = as.matrix(ven2coords[,-(55:88)]) #Part 2
#Lateral: 1= Head 2= Thorax
lat1coords = as.matrix(latcoords[,(1:30)])
lat2coords = as.matrix(latcoords[,(31:66)])

##Separated Sliders
#Ven
ven1.sliders = rbind(c(1,2,3),
                     c(2,3,4),
                     c(3,4,5),
                     c(4,5,6),
                     c(5,6,7),
                     c(6,7,8),
                     c(7,8,9))

ven2.sliders = rbind(c(1,2,3),
```

```
                c(2,3,4),
                c(3,4,5),
                c(4,5,6),
                c(7,8,9),
                c(8,9,10),
                c(9,10,11),
                c(10,11,12),
                c(12,13,14),
                c(13,14,15),
                c(14,15,16),
                c(17,18,19),
                c(18,19,20),
                c(1,20,19),
                c(21,22,23),
                c(22,23,24),
                c(12,27,24),
                c(1,26,24),
                c(23,24,25))

#Lat
lat1.sliders = rbind(c(1,2,3),
                c(2,3,4),
                c(3,4,5),
                c(5,6,7),
                c(6,7,8),
                c(7,8,9),
                c(8,9,10),
                c(9,10,11),
                c(10,11,12),
                c(11,12,13),
                c(12,13,14),
                c(13,14,15),
                c(1,15,14))

lat2.sliders = rbind(c(1,2,3),
                c(2,3,4),
                c(3,4,5),
                c(4,5,6),
                c(5,6,7),
                c(6,7,8),
                c(7,8,9),
                c(8,9,10),
                c(9,10,11),
                c(11,12,13),
                c(12,13,14),
                c(13,14,15),
```

```
            c(14,15,16),
            c(15,16,17),
            c(16,17,18),
            c(1,18,17))

##Separate GPA
#ven
ven1.gpa = gpagen(arrayspecs(ven1coords, 9,2), curves=ven1.sliders)
ven2.gpa = gpagen(arrayspecs(ven2coords, 27,2), curves=ven2.sliders)
ven1shape = ven1.gpa$coords
ven1cs = ven1.gpa$Csize
ven2shape = ven2.gpa$coords
ven2cs = ven2.gpa$Csize

#Lat
lat1.gpa = gpagen(arrayspecs(lat1coords, 15,2), curves=lat1.sliders)
lat2.gpa = gpagen(arrayspecs(lat2coords, 18,2), curves=lat2.sliders)
lat1shape = lat1.gpa$coords
lat1cs = lat1.gpa$Csize
lat2shape = lat2.gpa$coords
lat2cs = lat2.gpa$Csize

##GPA plots
#ven
plotAllSpecimens(ven1shape)
plotAllSpecimens(ven2shape)

#lat
plotAllSpecimens(lat1shape)
plotAllSpecimens(lat2shape)


###Now to adjust on Allometry
##Ventral 1
SmokeAnova = procD.lm(ven1shape ~ log(ven1cs))
summary(SmokeAnova)
shape.resid = arrayspecs (SmokeAnova$residuals, p=dim(ven1shape)[1],
k=dim(ven1shape)[2])
adj.ven1shape = shape.resid + array(ven1.gpa$consensus, dim(shape.resid))
plotTangentSpace(adj.ven1shape) #Ventral body shape 1 has now been adjuisted

##Ventral 2
EmberAnova = procD.lm(ven2shape ~ log(ven2cs))
summary(EmberAnova)
shape.resid = arrayspecs (EmberAnova$residuals, p=dim(ven2shape)[1],
k=dim(ven2shape)[2])
```

```
adj.ven2shape = shape.resid + array(ven2.gpa$consensus, dim(shape.resid))
plotTangentSpace(adj.ven2shape) #Ventral body shape 2 has now been adjuisted

##Lateral 1
FrostAnova = procD.lm(lat1shape ~ log(lat1cs))
summary(FrostAnova)
shape.resid = arrayspecs (FrostAnova$residuals, p=dim(lat1shape)[1],
k=dim(lat1shape)[2])
adj.lat1shape = shape.resid + array(lat1.gpa$consensus, dim(shape.resid))
plotTangentSpace(adj.lat1shape) #Lateral body shape 1 has now been adjuisted

##Lateral 2
SnowAnova = procD.lm(lat2shape ~ log(lat2cs))
summary(SnowAnova)
shape.resid = arrayspecs (SnowAnova$residuals, p=dim(lat2shape)[1],
k=dim(lat2shape)[2])
adj.lat2shape = shape.resid + array(lat2.gpa$consensus, dim(shape.resid))
plotTangentSpace(adj.lat2shape) #Lateral body shape 2 has now been adjuisted


####PCA plots examining Morph and Spp.#####
###Morph
#Ven
plotTangentSpace(adj.ven1shape, groups= Morph) #Ventral 1
plotTangentSpace(adj.ven2shape, groups= Morph) #Ventral 2
#Lat
plotTangentSpace(adj.lat1shape, groups= Morph) #Lateral 1
plotTangentSpace(adj.lat2shape, groups= Morph) #Lateral 2

###Spp.
#Set up
col.Sp <- rainbow(length(levels(Sp)))
names(col.Sp) <- levels(Sp)
col.Sp <- col.Sp[match(Sp, names(col.Sp))] # col.Sp must NOT be a factor

#Actual Plots
#Ven
plotTangentSpace(adj.ven1shape, groups = col.Sp) #Ventral 1
plotTangentSpace(adj.ven2shape, groups = col.Sp) #Ventral 2
#Lat
plotTangentSpace(adj.lat1shape, groups = col.Sp) #Lateral 1
plotTangentSpace(adj.lat2shape, groups = col.Sp) #Lateral 2

##Now to run 2bpls analyses to compare the adjusted body shapes
Ven1Adj.Ven2Adj.cor = two.b.pls(adj.ven1shape,adj.ven2shape) #Compare Ventral 1
shape and Ventral 2 shape
```

```
Ven1Adj.Ven2Adj.cor #Significant
plot(Ven1Adj.Ven2Adj.cor)

Lat1Adj.Lat2Adj.cor = two.b.pls(adj.lat1shape,adj.lat2shape) #Compare Lateral 1 shape and Lateral 2 shape
Lat1Adj.Lat2Adj.cor #Significant
plot(Lat1Adj.Lat2Adj.cor)

###Examining relationships and groups
#Ventral 1 & 2 First
##First grouped by Morphotypes
Ven1Adj.M.Test = advanced.procD.lm(adj.ven1shape ~ log(ven1cs), ~log(ven1cs) + Morph, groups = ~Morph, iter= 9999) #Significant
Ven2Adj.M.Test = advanced.procD.lm(adj.ven2shape ~ log(ven2cs), ~log(ven2cs) + Morph, groups = ~Morph, iter= 9999) #Significant
##Second grouped by Genus
Ven1Adj.G.Test = advanced.procD.lm(adj.ven1shape ~ log(ven1cs), ~log(ven1cs) + Genus, groups = ~Genus, iter= 9999) #Significant
Ven2Adj.G.Test = advanced.procD.lm(adj.ven2shape ~ log(ven2cs), ~log(ven2cs) + Genus, groups = ~Genus, iter= 9999) #Significant
##Third grouped by Species
Ven1Adj.S.Test = advanced.procD.lm(adj.ven1shape ~ log(ven1cs), ~log(ven1cs) + Sp, groups = ~Sp, iter= 9999) #Significant
Ven2Adj.S.Test = advanced.procD.lm(adj.ven2shape ~ log(ven2cs), ~log(ven2cs) + Sp, groups = ~Sp, iter= 9999) #Significant

#Lateral 1 & 2 Now
##First grouped by Morphotypes
Lat1Adj.M.Test = advanced.procD.lm(adj.lat1shape ~ log(lat1cs), ~log(lat1cs) + Morph, groups = ~Morph, iter= 9999) #Significant
Lat2Adj.M.Test = advanced.procD.lm(adj.lat2shape ~ log(lat2cs), ~log(lat2cs) + Morph, groups = ~Morph, iter= 9999) #Significant
##Second grouped by Genus
Lat1Adj.G.Test = advanced.procD.lm(adj.lat1shape ~ log(lat1cs), ~log(lat1cs) + Genus, groups = ~Genus, iter= 9999) #Significant
Lat2Adj.G.Test = advanced.procD.lm(adj.lat2shape ~ log(lat2cs), ~log(lat2cs) + Genus, groups = ~Genus, iter= 9999) #Significant
##Third grouped by Species
Lat1Adj.S.Test = advanced.procD.lm(adj.lat1shape ~ log(lat1cs), ~log(lat1cs) + Sp, groups = ~Sp, iter= 9999) #Significant
Lat2Adj.S.Test = advanced.procD.lm(adj.lat2shape ~ log(lat2cs), ~log(lat2cs) + Sp, groups = ~Sp, iter= 9999) #Significant


###Now to examine the Leg
legcoords = as.matrix(batflies[,(224:303)])
```

```
# sliders
leg.sliders = rbind(c(1,2,3),
                    c(2,3,4),
                    c(3,4,5),
                    c(4,5,6),
                    c(5,6,7),
                    c(6,7,8),
                    c(8,9,10),
                    c(9,10,11),
                    c(10,11,12),
                    c(11,12,13),
                    c(12,13,14),
                    c(1,14,13),
                    c(15,16,17),
                    c(16,17,18),
                    c(17,18,19),
                    c(18,19,20),
                    c(19,20,21),
                    c(20,21,22),
                    c(21,22,23),
                    c(23,24,25),
                    c(24,25,26),
                    c(25,26,27),
                    c(26,27,28),
                    c(15,28,27),
                    c(29,30,31),
                    c(30,31,32),
                    c(31,32,33),
                    c(32,33,34),
                    c(33,34,35),
                    c(34,35,36),
                    c(35,36,37),
                    c(36,37,38),
                    c(37,38,39),
                    c(38,39,40))

#GPA
leg.gpa = gpagen(arrayspecs(legcoords, 40,2), curves=leg.sliders)
legshape = leg.gpa$coords
legcs = leg.gpa$Csize

#GPA plots
plotAllSpecimens(legshape)


##Now to check on Allometry
```

```
#Leg (labeled Water)
Water = procD.allometry(legshape ~ legcs)
summary(Water)
plot(Water, method = "PredLine")
plot(Water, method = "RegScore") #Clearly strong effect of allometry here

##Now to adjust these values to get rid of allometry problem
#Now Water
WaterAnova = procD.lm(legshape ~ log(legcs))
summary(WaterAnova)
shape.resid = arrayspecs (WaterAnova$residuals, p=dim(legshape)[1],
k=dim(legshape)[2])
adj.legshape = shape.resid + array(leg.gpa$consensus, dim(shape.resid))
plotTangentSpace(adj.legshape) #hind leg shape has now been adjuisted

###GPA plot
plotAllSpecimens(adj.legshape)


####PCA plots examining Morph and Spp.#####
###Morph

plotTangentSpace(adj.legshape, groups= Morph)

###Spp.

plotTangentSpace(adj.legshape, groups = col.Sp)

##Now to run 2bpls analyses to compare adjusted body shapes
VenXAdj.LegAdj.cor = two.b.pls(adj.venshape,adj.legshape) #Compare Ventral Ex
shape and Leg shape
VenXAdj.LegAdj.cor #Significant
plot(VenXAdj.LegAdj.cor)

LatXAdj.LegAdj.cor = two.b.pls(adj.latXshape,adj.legshape) #Compare Ventral Ex
shape and Leg shape
LatXAdj.LegAdj.cor #Significant
plot(LatXAdj.LegAdj.cor)

###Examining relationships and groups
##First grouped by Morphotypes
LegAdj.M.Test = advanced.procD.lm(adj.legshape ~ log(legcs), ~log(legcs) + Morph,
groups = ~Morph, iter= 9999) #Significant
##Second grouped by Genus
LegAdj.G.Test = advanced.procD.lm(adj.legshape ~ log(legcs), ~log(legcs) + Genus,
groups = ~Genus, iter= 9999) #Significant
```

```
##Third grouped by Species
LegAdj.S.Test = advanced.procD.lm(adj.legshape ~ log(legcs), ~log(legcs) + Sp, groups
= ~Sp, iter= 9999) #Significant


######Separated Leg Shapes######
##Seperating the different aspects of the different shapes
#Leg: 1= Femora 2= Tibia 3= Tarsus
leg1coords = as.matrix(legcoords[,(1:28)])
leg2coords = as.matrix(legcoords[,(29:56)])
leg3coords = as.matrix(legcoords[,-(1:56)])

#Sliders
leg1.sliders = rbind(c(1,2,3),
                     c(2,3,4),
                     c(3,4,5),
                     c(4,5,6),
                     c(5,6,7),
                     c(6,7,8),
                     c(8,9,10),
                     c(9,10,11),
                     c(10,11,12),
                     c(11,12,13),
                     c(12,13,14),
                     c(1,14,13))

leg2.sliders = rbind(c(1,2,3),
                     c(2,3,4),
                     c(3,4,5),
                     c(4,5,6),
                     c(5,6,7),
                     c(6,7,8),
                     c(7,8,9),
                     c(9,10,11),
                     c(10,11,12),
                     c(11,12,13),
                     c(12,13,14),
                     c(1,14,13))

leg3.sliders = rbind(c(1,2,3),
                     c(2,3,4),
                     c(3,4,5),
                     c(4,5,6),
                     c(5,6,7),
                     c(6,7,8),
                     c(7,8,9),
```

```
            c(8,9,10),
            c(9,10,11),
            c(10,11,12))

##Separate GPA
leg1.gpa = gpagen(arrayspecs(leg1coords, 14,2), curves=leg1.sliders)
leg2.gpa = gpagen(arrayspecs(leg2coords, 14,2), curves=leg2.sliders)
leg3.gpa = gpagen(arrayspecs(leg3coords, 12,2), curves=leg3.sliders)

leg1shape = leg1.gpa$coords
leg1cs = leg1.gpa$Csize
leg2shape = leg2.gpa$coords
leg2cs = leg2.gpa$Csize
leg3shape = leg3.gpa$coords
leg3cs = leg3.gpa$Csize

##GPA plots
plotAllSpecimens(leg1shape)
plotAllSpecimens(leg2shape)
plotAllSpecimens(leg3shape)


##Now to adjust these values to get rid of allometry problem
#Now named for water theme
RainAnova = procD.lm(leg1shape ~ log(leg1cs)) #Leg 1
summary(RainAnova)
shape.resid = arrayspecs (RainAnova$residuals, p=dim(leg1shape)[1],
k=dim(leg1shape)[2])
adj.leg1shape = shape.resid + array(leg1.gpa$consensus, dim(shape.resid))
plotTangentSpace(adj.leg1shape) #hind leg 1 shape has now been adjuisted

DropAnova = procD.lm(leg2shape ~ log(leg2cs)) #Leg 2
summary(DropAnova)
shape.resid = arrayspecs (DropAnova$residuals, p=dim(leg2shape)[1],
k=dim(leg2shape)[2])
adj.leg2shape = shape.resid + array(leg2.gpa$consensus, dim(shape.resid))
plotTangentSpace(adj.leg2shape) #hind leg 2 shape has now been adjuisted

AquaAnova = procD.lm(leg3shape ~ log(leg3cs)) #Leg 3
summary(AquaAnova)
shape.resid = arrayspecs (AquaAnova$residuals, p=dim(leg3shape)[1],
k=dim(leg3shape)[2])
adj.leg3shape = shape.resid + array(leg3.gpa$consensus, dim(shape.resid))
plotTangentSpace(adj.leg3shape) #hind leg 3 shape has now been adjuisted
```

```
###GPA plots
plotAllSpecimens(adj.leg1shape) #Leg 1
plotAllSpecimens(adj.leg2shape) #Leg 2
plotAllSpecimens(adj.leg3shape) #Leg 3


####PCA plots examining Morph and Spp.#####
###Morph

plotTangentSpace(adj.leg1shape, groups= Morph)
plotTangentSpace(adj.leg2shape, groups= Morph)
plotTangentSpace(adj.leg3shape, groups= Morph)

###Spp.

plotTangentSpace(adj.leg1shape, groups = col.Sp)
plotTangentSpace(adj.leg2shape, groups = col.Sp)
plotTangentSpace(adj.leg3shape, groups = col.Sp)


##Now to run 2bpls analyses to compare adjusted body shapes
Leg1Adj.Leg2Adj.cor = two.b.pls(adj.leg1shape,adj.leg2shape) #Compare Leg 1 shape
and Leg 2 shape
Leg1Adj.Leg2Adj.cor #Significant
plot(Leg1Adj.Leg2Adj.cor)

Leg1Adj.Leg3Adj.cor = two.b.pls(adj.leg1shape,adj.leg3shape) #Compare Leg 1 shape
and Leg 3 shape
Leg1Adj.Leg3Adj.cor #Significant
plot(Leg1Adj.Leg3Adj.cor)

Leg2Adj.Leg3Adj.cor = two.b.pls(adj.leg2shape,adj.leg3shape) #Compare Leg 2 shape
and Leg 3 shape
Leg2Adj.Leg3Adj.cor #Significant
plot(Leg2Adj.Leg3Adj.cor)


###Examining relationships and groups
##First grouped by Morphotypes
Leg1Adj.M.Test = advanced.procD.lm(adj.leg1shape ~ log(leg1cs), ~log(leg1cs) +
Morph, groups = ~Morph, iter= 9999) #Significant
Leg2Adj.M.Test = advanced.procD.lm(adj.leg2shape ~ log(leg2cs), ~log(leg2cs) +
Morph, groups = ~Morph, iter= 9999) #Significantish
Leg3Adj.M.Test = advanced.procD.lm(adj.leg3shape ~ log(leg3cs), ~log(leg3cs) +
Morph, groups = ~Morph, iter= 9999) #Significantish
##Second grouped by Genus
```

```
Leg1Adj.G.Test = advanced.procD.lm(adj.leg1shape ~ log(leg1cs), ~log(leg1cs) +
Genus, groups = ~Genus, iter= 9999) #Significant
Leg2Adj.G.Test = advanced.procD.lm(adj.leg2shape ~ log(leg2cs), ~log(leg2cs) +
Genus, groups = ~Genus, iter= 9999) #Significant
Leg3Adj.G.Test = advanced.procD.lm(adj.leg3shape ~ log(leg3cs), ~log(leg3cs) +
Genus, groups = ~Genus, iter= 9999) #Significant
##Third grouped by Species
Leg1Adj.S.Test = advanced.procD.lm(adj.leg1shape ~ log(leg1cs), ~log(leg1cs) + Sp,
groups = ~Sp, iter= 9999) #Significant
Leg2Adj.S.Test = advanced.procD.lm(adj.leg2shape ~ log(leg2cs), ~log(leg2cs) + Sp,
groups = ~Sp, iter= 9999) #Significant
Leg3Adj.S.Test = advanced.procD.lm(adj.leg3shape ~ log(leg3cs), ~log(leg3cs) + Sp,
groups = ~Sp, iter= 9999) #Significant
#Running Chi-squared tests with naive and more informed assumptions
#about the morphology and co-occurrence patterns between 2 species pairs

###chi-squared tests examining agg vs naive expected
#Ventral Shape 1
Ven1 = c(9,1)
p = c(0.5,0.5)

chisq.test(Ven1, p=p)

#Ventral Shape 2
Ven2 = c(10,0)
p = c(0.5,0.5)

chisq.test(Ven2, p=p)

#Lateral Shape 1
Lat1 = c(9,1)
p = c(0.5,0.5)

chisq.test(Lat1, p=p)

#Lateral Shape 2
Lat2 = c(9,1)
p = c(0.5,0.5)

chisq.test(Lat2, p=p)

#Leg Shape 1
Leg1 = c(7,3)
p = c(0.5,0.5)

chisq.test(Leg1, p=p)
```

```
#Leg Shape 2
Leg2 = c(8,2)
p = c(0.5,0.5)

chisq.test(Leg2, p=p)

#Leg Shape 3
Leg3 = c(3,7)
p = c(0.5,0.5)

chisq.test(Leg3, p=p)

###chi-squared tests examining agg vs No Pattern Assumption
#Ventral Shape 1
Ven1 = c(9,1)
p = c(3,1)

chisq.test(Ven1, p=p, rescale.p= T)

#Ventral Shape 2
Ven2 = c(10,0)
p = c(4,0)

chisq.test(Ven2, p=p, rescale.p= T)

#Lateral Shape 1
Lat1 = c(9,1)
p = c(3,1)

chisq.test(Lat1, p=p, rescale.p= T)

#Lateral Shape 2
Lat2 = c(9,1)
p = c(4,0)

chisq.test(Lat2, p=p, rescale.p= T)

#Leg Shape 1
Leg1 = c(7,3)
p = c(3,1)

chisq.test(Leg1, p=p, rescale.p= T)

#Leg Shape 2
Leg2 = c(8,2)
```

```
p = c(2,2)

chisq.test(Leg2, p=p, rescale.p= T)

#Leg Shape 3
Leg3 = c(3,7)
p = c(1,3)

chisq.test(Leg3, p=p, rescale.p= T)

#####Fisher's test include and exclude seg. and chisq tests
##Fisher's test include Seg.
#Ven 1

Input =("
Co-occur   Sig   No.Sig
Agg        9     1
Nop        3     1
Seg        0     1
")

FisherVen1 = as.matrix(read.table(textConnection(Input),
                      header=TRUE,
                      row.names=1))

fisher.test(FisherVen1, alternative = "two.sided")

pairwiseNominalIndependence(FisherVen1,

                      fisher = TRUE,

                      gtest  = FALSE,

                      chisq  = FALSE,
                      digits = 3)

#Ven 2

Input =("
Co-occur   Sig   No.Sig
Agg        10    0
Nop        4     0
Seg        0     1
")

FisherVen2 = as.matrix(read.table(textConnection(Input),
```

```
                        header=TRUE,
                        row.names=1))

fisher.test(FisherVen2, alternative = "two.sided")

pairwiseNominalIndependence(FisherVen2,

                        fisher = TRUE,

                        gtest  = FALSE,

                        chisq  = FALSE,
                        digits = 3)

#Lat 1

Input =("
      Co-occur   Sig   No.Sig
      Agg        9     1
      Nop        3     1
      Seg        0     1
      ")

FisherLat1 = as.matrix(read.table(textConnection(Input),
                        header=TRUE,
                        row.names=1))

fisher.test(FisherLat1, alternative = "two.sided")

pairwiseNominalIndependence(FisherLat1,

                        fisher = TRUE,

                        gtest  = FALSE,

                        chisq  = FALSE,
                        digits = 3)

#Lat 2

Input =("
      Co-occur   Sig   No.Sig
      Agg        9     1
      Nop        4     0
      Seg        0     1
      ")
```

```
FisherLat2 = as.matrix(read.table(textConnection(Input),
                        header=TRUE,
                        row.names=1))

fisher.test(FisherLat2, alternative = "two.sided")

pairwiseNominalIndependence(FisherLat2,

                    fisher = TRUE,

                    gtest  = FALSE,

                    chisq  = FALSE,
                    digits = 3)

#Leg 1

Input =("
      Co-occur   Sig   No.Sig
      Agg        7     3
      Nop        3     1
      Seg        0     1
      ")

FisherLeg1 = as.matrix(read.table(textConnection(Input),
                        header=TRUE,
                        row.names=1))

fisher.test(FisherLeg1, alternative = "two.sided")

pairwiseNominalIndependence(FisherLeg1,

                    fisher = TRUE,

                    gtest  = FALSE,

                    chisq  = FALSE,
                    digits = 3)

#Leg 2

Input =("
      Co-occur   Sig   No.Sig
      Agg        8     2
      Nop        2     2
```

```
      Seg       0     1
      ")

FisherLeg2 = as.matrix(read.table(textConnection(Input),
                        header=TRUE,
                        row.names=1))

fisher.test(FisherLeg2, alternative = "two.sided")

pairwiseNominalIndependence(FisherLeg2,

                        fisher = TRUE,

                        gtest  = FALSE,

                        chisq  = FALSE,
                        digits = 3)

#Leg 3

Input =("
      Co-occur   Sig   No.Sig
      Agg        3     7
      Nop        1     3
      Seg        0     1
      ")

FisherLeg3 = as.matrix(read.table(textConnection(Input),
                        header=TRUE,
                        row.names=1))

fisher.test(FisherLeg3, alternative = "two.sided")

pairwiseNominalIndependence(FisherLeg3,

                        fisher = TRUE,

                        gtest  = FALSE,

                        chisq  = FALSE,
                        digits = 3)


##Fisher's test excluding Seg.
#Ven 1
```

```
Input =("
      Co-occur   Sig   No.Sig
      Agg        9     1
      Nop        3     1
      ")

FisherVen1E = as.matrix(read.table(textConnection(Input),
                        header=TRUE,
                        row.names=1))

fisher.test(FisherVen1E, alternative = "two.sided")

#Ven 2

Input =("
      Co-occur   Sig   No.Sig
      Agg        10    0
      Nop        4     0
      ")

FisherVen2E = as.matrix(read.table(textConnection(Input),
                        header=TRUE,
                        row.names=1))

fisher.test(FisherVen2E, alternative = "two.sided")

#Lat 1

Input =("
      Co-occur   Sig   No.Sig
      Agg        9     1
      Nop        3     1
      ")

FisherLat1E = as.matrix(read.table(textConnection(Input),
                        header=TRUE,
                        row.names=1))

fisher.test(FisherLat1E, alternative = "two.sided")

#Lat 2

Input =("
      Co-occur   Sig   No.Sig
      Agg        9     1
      Nop        4     0
```

```
      ")

FisherLat2E = as.matrix(read.table(textConnection(Input),
                        header=TRUE,
                        row.names=1))

fisher.test(FisherLat2E, alternative = "two.sided")

#Leg 1

Input =("
      Co-occur   Sig   No.Sig
      Agg        7     3
      Nop        3     1
      ")

FisherLeg1E = as.matrix(read.table(textConnection(Input),
                        header=TRUE,
                        row.names=1))

fisher.test(FisherLeg1E, alternative = "two.sided")

#Leg 2

Input =("
      Co-occur   Sig   No.Sig
      Agg        8     2
      Nop        2     2
      ")

FisherLeg2E = as.matrix(read.table(textConnection(Input),
                        header=TRUE,
                        row.names=1))

fisher.test(FisherLeg2E, alternative = "two.sided")

#Leg 3

Input =("
      Co-occur   Sig   No.Sig
      Agg        3     7
      Nop        1     3
      ")

FisherLeg3E = as.matrix(read.table(textConnection(Input),
                        header=TRUE,
```

```
                        row.names=1))

fisher.test(FisherLeg3E, alternative = "two.sided")

####Chi-sq tests
##Including Seg
#Ven 1

chisq.test(FisherVen1)
pairwiseNominalIndependence(FisherVen1,

                        fisher = FALSE,

                        gtest  = FALSE,

                        chisq  = TRUE,
                        digits = 3)

#Ven 2

chisq.test(FisherVen2)
pairwiseNominalIndependence(FisherVen2,

                        fisher = FALSE,

                        gtest  = FALSE,

                        chisq  = TRUE,
                        digits = 3)

#Lat 1

chisq.test(FisherLat1)
pairwiseNominalIndependence(FisherLat1,

                        fisher = FALSE,

                        gtest  = FALSE,

                        chisq  = TRUE,
                        digits = 3)

#Lat 2

chisq.test(FisherLat2)
pairwiseNominalIndependence(FisherLat2,
```

```
                    fisher = FALSE,

                    gtest  = FALSE,

                    chisq  = TRUE,
                    digits = 3)

#Leg 1

chisq.test(FisherLeg1)
pairwiseNominalIndependence(FisherLeg1,

                    fisher = FALSE,

                    gtest  = FALSE,

                    chisq  = TRUE,
                    digits = 3)

#Leg 2

chisq.test(FisherLeg2)
pairwiseNominalIndependence(FisherLeg2,

                    fisher = FALSE,

                    gtest  = FALSE,

                    chisq  = TRUE,
                    digits = 3)

#Leg 3

chisq.test(FisherLeg3)
pairwiseNominalIndependence(FisherLeg3,

                    fisher = FALSE,

                    gtest  = FALSE,

                    chisq  = TRUE,
                    digits = 3)

##Excluding Seg
#Ven 1
```

```
chisq.test(FisherVen1E)

#Ven 2

chisq.test(FisherVen2E)

#Lat 1

chisq.test(FisherLat1E)

#Lat 2

chisq.test(FisherLat2E)

#Leg 1

chisq.test(FisherLeg1E)

#Leg 2

chisq.test(FisherLeg2E)

#Leg 3

chisq.test(FisherLeg3E)

#####Fisher's test reverse include and exclude seg. and chisq tests
##Fisher's test reverse include Seg.
#Ven 1

Input =("
      Co-occur   Agg   Nop  Seg
      Sig        9     3    0
      Not        1     1    1
      ")

FisherRVen1 = as.matrix(read.table(textConnection(Input),
                        header=TRUE,
                        row.names=1))

fisher.test(FisherRVen1, alternative = "two.sided")

pairwiseNominalIndependence(FisherRVen1,

                        fisher = TRUE,
```

```
                    gtest  = FALSE,

                    chisq  = FALSE,
                    digits = 3)

#Ven 2

Input =("
      Co-occur   Agg   Nop  Seg
      Sig        10    4    0
      Not        1     1    1
      ")

FisherRVen2 = as.matrix(read.table(textConnection(Input),
                        header=TRUE,
                        row.names=1))

fisher.test(FisherRVen2, alternative = "two.sided")

pairwiseNominalIndependence(FisherRVen2,

                    fisher = TRUE,

                    gtest  = FALSE,

                    chisq  = FALSE,
                    digits = 3)

#Lat 1

Input =("
      Co-occur   Agg   Nop  Seg
      Sig        9     3    0
      Not        1     1    1
      ")

FisherRLat1 = as.matrix(read.table(textConnection(Input),
                        header=TRUE,
                        row.names=1))

fisher.test(FisherRLat1, alternative = "two.sided")

pairwiseNominalIndependence(FisherRLat1,

                    fisher = TRUE,
```

```
                    gtest  = FALSE,

                    chisq  = FALSE,
                    digits = 3)

#Lat 2

Input =("
      Co-occur   Agg   Nop  Seg
      Sig        9     4    0
      Not        1     0    1
      ")

FisherRLat2 = as.matrix(read.table(textConnection(Input),
                        header=TRUE,
                        row.names=1))

fisher.test(FisherRLat2, alternative = "two.sided")

pairwiseNominalIndependence(FisherRLat2,

                    fisher = TRUE,

                    gtest  = FALSE,

                    chisq  = FALSE,
                    digits = 3)

#Leg 1

Input =("
      Co-occur   Agg   Nop  Seg
      Sig        7     3    0
      Not        3     1    1
      ")

FisherRLeg1 = as.matrix(read.table(textConnection(Input),
                        header=TRUE,
                        row.names=1))

fisher.test(FisherRLeg1, alternative = "two.sided")

pairwiseNominalIndependence(FisherRLeg1,

                    fisher = TRUE,
```

```
                    gtest  = FALSE,

                    chisq  = FALSE,
                    digits = 3)

#Leg 2

Input =("
      Co-occur   Agg   Nop  Seg
      Sig        8     2    0
      Not        2     2    1
      ")

FisherRLeg2 = as.matrix(read.table(textConnection(Input),
                          header=TRUE,
                          row.names=1))

fisher.test(FisherRLeg2, alternative = "two.sided")

pairwiseNominalIndependence(FisherRLeg2,

                    fisher = TRUE,

                    gtest  = FALSE,

                    chisq  = FALSE,
                    digits = 3)

#Leg 3

Input =("
      Co-occur   Agg   Nop  Seg
      Sig        3     1    0
      Not        7     3    1
      ")

FisherRLeg3 = as.matrix(read.table(textConnection(Input),
                          header=TRUE,
                          row.names=1))

fisher.test(FisherRLeg3, alternative = "two.sided")

pairwiseNominalIndependence(FisherRLeg3,

                    fisher = TRUE,
```

```
                gtest  = FALSE,

                chisq  = FALSE,
                digits = 3)


##Fisher's test excluding Seg.
#Ven 1

Input =("
      Co-occur   Agg   Nop
      Sig        9     3
      Not        1     1
      ")

FisherRVen1E = as.matrix(read.table(textConnection(Input),
                        header=TRUE,
                        row.names=1))

fisher.test(FisherRVen1E, alternative = "two.sided")

#Ven 2

Input =("
      Co-occur   Agg   Nop
      Sig        10    4
      Not        0     0
      ")

FisherRVen2E = as.matrix(read.table(textConnection(Input),
                        header=TRUE,
                        row.names=1))

fisher.test(FisherRVen2E, alternative = "two.sided")

#Lat 1

Input =("
      Co-occur   Agg   Nop
      Sig        9     3
      Not        1     1
      ")

FisherRLat1E = as.matrix(read.table(textConnection(Input),
                        header=TRUE,
```

```
                        row.names=1))

fisher.test(FisherRLat1E, alternative = "two.sided")

#Lat 2

Input =("
      Co-occur   Agg   Nop
      Sig        9     4
      Not        1     0
      ")

FisherRLat2E = as.matrix(read.table(textConnection(Input),
                        header=TRUE,
                        row.names=1))

fisher.test(FisherRLat2E, alternative = "two.sided")

#Leg 1

Input =("
      Co-occur   Agg   Nop
      Sig        7     3
      Not        3     1
      ")

FisherRLeg1E = as.matrix(read.table(textConnection(Input),
                        header=TRUE,
                        row.names=1))

fisher.test(FisherRLeg1E, alternative = "two.sided")

#Leg 2

Input =("
      Co-occur   Agg   Nop
      Sig        8     2
      Not        2     2
      ")

FisherRLeg2E = as.matrix(read.table(textConnection(Input),
                        header=TRUE,
                        row.names=1))

fisher.test(FisherRLeg2E, alternative = "two.sided")
```

```
#Leg 3

Input =("
      Co-occur   Agg   Nop
      Sig        3     1
      Not        7     3
      ")

FisherRLeg3E = as.matrix(read.table(textConnection(Input),
                         header=TRUE,
                         row.names=1))

fisher.test(FisherRLeg3E, alternative = "two.sided")


####Chi-sq tests
##Including Seg
#Ven 1

chisq.test(FisherRVen1)

#Ven 2

chisq.test(FisherRVen2)

#Lat 1

chisq.test(FisherRLat1)

#Lat 2

chisq.test(FisherRLat2)

#Leg 1

chisq.test(FisherRLeg1)

#Leg 2

chisq.test(FisherRLeg2)

#Leg 3

chisq.test(FisherRLeg3)

##Excluding Seg
```

```
#Ven 1

chisq.test(FisherRVen1E)

#Ven 2

chisq.test(FisherRVen2E)

#Lat 1

chisq.test(FisherRLat1E)

#Lat 2

chisq.test(FisherRLat2E)

#Leg 1

chisq.test(FisherRLeg1E)

#Leg 2

chisq.test(FisherRLeg2E)

#Leg 3

chisq.test(FisherRLeg3E)
```