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MURCIÉLAGOS INSECTÍVOROS AÉREOS EN AGROECOSISTEMAS: EL CASO DE PIÑERAS Y BANANERAS EN SARAPIQUÍ, COSTA RICA

Tesis sometida a la consideración de la Comisión del Programa de Estudios de Posgrado en Biología para optar al grado y título de Maestría Académica en Biología

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RESUMEN

Los murciélagos se encuentran entre los mamíferos que proveen más variedad de servicios ambientales, por ejemplo dispersión de semillas, polinización de plantas y control de poblaciones de insectos. Durante los últimos años se ha sugerido que los murciélagos insectívoros aéreos podrían funcionar como agentes de control biológico de plagas. En Costa Rica, entre los años 2008 y 2012, las áreas dedicadas a la agricultura mostraron un incremento de 59 230 ha. Los cultivos de piña y banano son dos de las frutas frescas con mayor área sembrada en el país (45 000 y 42 016 ha respectivamente). Esto recalca la importancia de conocer el valor que tienen los cultivos agrícolas en la conservación de especies tan diversas y ecológicamente importantes como lo son los murciélagos.

En el primer capítulo analizo el impacto que tienen las plantaciones de piña y banano en la zona de Sarapiquí sobre el ensamble de murciélagos insectívoros aéreos y la forma en la que estos mamíferos utilizan el paisaje. Encontré que ambos tipos de agro-ecosistemas funcionan como sitios de vuelo y de forrajeo para los murciélagos. Sin embargo, en los bosques muestreados, se encontraron solamente el 55% de las especies esperadas. Planteo que los microhábitats del bosque permiten la presencia de todos los grupos funcionales de murciélagos y que proveen más recursos, por ejemplo refugios, que las plantaciones. Por lo tanto, la conservación de los parches de bosque circundantes a las piñeras y bananeras son vitales para mantener las poblaciones de murciélagos insectívoros aéreos. Se deberían realizar estudios futuros y planes de manejo en conjunto con las compañías agrícolas de la zona para preservar los parches de bosque y las especies de murciélagos.

En el segundo capítulo reviso los estudios que se han realizado en el mundo sobre la dieta de los murciélagos insectívoros aéreos, con el fin de determinar qué tanto se conoce de murciélagos como agentes de control biológico. Encontré que la mayoría de los estudios de dieta se han concentrado en pocas especies que están ampliamente distribuidas y que la mayor parte de la investigación se ha realizado en zonas templadas. Por estas razones se conoce poco del tema para Costa Rica. Sólo tres estudios han estimado el aporte monetario de murciélagos como agentes de control biológico. Este tópico constituye un área relevante de investigación en Costa Rica y los trópicos, en donde la extensión dedicada a la agricultura es considerable y se cuenta con una gran diversidad de murciélagos insectívoros aéreos.

ABSTRACT

Bats are among the mammals that provide the widest variety of ecosystem services, such as seed dispersal, pollination, and insect population control. In recent years, it has been suggested that aerial insectivorous bats could function as agents of biological pest control. In Costa Rica, between the years 2008 and 2012, agricultural areas increased by 59,230 ha. Pineapple and banana are two of the fresh fruit crops with the largest planted areas in the country (45,000 and 42,016 ha respectively). This highlights the importance of knowing the value that agricultural areas have in the conservation of species as diverse and environmentally important as bats.

In the first chapter, I analyze the impact that pineapple and banana plantations in Sarapiquí have on the aerial insectivorous bat ensemble, and how these mammals are using this landscape. I found that both agro-ecosystems are working as flight and feeding areas for bats. However, in the sampled forests, only 55% of the expected species were found. I propose that the forest's microhabitats can support all of the bat functional groups and that they provide more diverse resources, such as roosts, than plantations. Considering this, I suggest that the conservation of surrounding forest patches in the area is vital to maintain the populations of aerial insectivorous bats. Finally, I recommend that further studies should be done and that joint management programs (researchers-companies) should start in order to preserve forest fragments immersed in farmland and the bat species living within them.

In the second chapter, I review the research done around the world on the diet of aerial insectivores, with the aim to determine how much is known about bats acting as biological control agents. I found that most of the studies have focused on a few widely-distributed species, and that most of them have been done in temperate zones. This means that very little or nothing is known for most of the species found in Costa Rica. Only three studies have quantified the actual economic value of an aerial insectivorous bat species functioning as a biological control agent. This is an open area of research in Costa Rica and the tropics, where the crop-growing area is considerable and where there is a large richness of aerial insectivorous bats.

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LISTA DE ABREVIATURAS

B	Banana Plantation / Bananera
F	Forest / Bosque
P	Pineapple Plantation / Piñera
NMDS	Non Metric Multidimensional Scaling / Escalamiento Multidimensional No Métrico
χ^2	Chi square / Chi cuadrado
p	Probability / Probabilidad
df	Degrees of freedom / Grados de libertad

INTRODUCCIÓN GENERAL

La reducción, fragmentación y transformación de los hábitats naturales representan las principales causas de pérdida de biodiversidad en el planeta (Cosson *et al.* 1999, Primack 2000, Fahrig 2003, Gorresen *et al.* 2005). Estos tres fenómenos son los principales causantes de las elevadas tasas de extinción de especies y de la pérdida de la biodiversidad (Wilcox y Murphy 1985). Dentro de los principales factores que causan estos fenómenos de alteración de hábitat se encuentran múltiples factores antropogénicos como la urbanización, la agricultura, la ganadería y la silvicultura (Daily *et al.* 2003, Avila-Flores y Fenton 2005).

Esta expansión e intensificación del uso de la tierra por parte de los humanos es la principal causa de la fragmentación del hábitat, la cual incluye tres aspectos claves: la pérdida del hábitat original, la reducción del tamaño del parche y el aumento del aislamiento de los parches (Andrén 1994). A pesar de que se conoce que estos factores contribuyen con la pérdida de la biodiversidad (Andrén 1994, Meffe y Carroll 1994, Pardini 2004, Pardini *et al.* 2005, Ewers y Didham 2006), se debe considerar la capacidad que tienen los organismos para sobrevivir y utilizar la matriz en la que los parches se encuentran inmersos (Laurance 1991, Saunders *et al.* 1991, Fahrig 2001, Ricketts 2001, Bali *et al.* 2007). No todas las especies tienen la misma capacidad de utilizar la matriz, por lo que medir esta capacidad representa un parámetro útil para predecir la vulnerabilidad que tienen las especies a la fragmentación (Laurance 1991, Fahrig 2001).

El Neotrópico es un claro ejemplo de cómo la conversión rápida y extensiva de bosques a zonas de pastoreo y agricultura (las cuales representan matrices hostiles para muchos vertebrados) han llevado a la desaparición y al aislamiento de muchas poblaciones (Estrada et al. 1994). En el caso específico de Costa Rica, en el año 2011, existían 500 927 ha dedicadas a la agricultura (SEPSA 2012). En el mismo año, la piña y el banano se encontraban entre los cultivos con mayor área en el país (45 000 ha y 42 016 ha, respectivamente) (SEPSA 2012).

A pesar de que Costa Rica cuenta con un sólido sistema de parques nacionales y áreas protegidas (1 861 715 ha, 26,8% del territorio nacional) (SINAC 2012) y este tipo de zonas son herramientas vitales para prevenir la pérdida de la biodiversidad (Rodrigues *et al.* 2004), todavía falta mucha investigación para cuantificar la respuesta de los organismos dentro de hábitats antropogénicos. El campo en las zonas rurales es la fracción de la tierra no urbana cuyas características de ecosistema son determinadas por los humanos, tales como las áreas dedicadas a agricultura (agroecosistemas), zonas agroforestales y jardines (Daily *et al.* 2003). Es claro que, en dichas zonas, los servicios del ecosistema (tales como polinización, control biológico, renovación de suelos y purificación del agua) requieren para su funcionamiento de las especies que perduran en ellas (Daily *et al.* 2003). Varios estudios han probado que el campo tiene un rol en la conservación (Moguel y Toledo 1999, Rice y Greenberg 2000, Daily et al. 2003, Schroth *et al.* 2004).

Murciélagos en agroecosistemas: Las respuestas de los mamíferos terrestres ante los cambios en el uso de la tierra y los impactos humanos asociados a esto son variables. En general, se ha observado que la intensificación de la agricultura tiende a favorecer a especies abundantes y generalistas y no a las que son escasas y con necesidades especializadas de hábitat y recursos (Millán de la Pena *et al.* 2003).

Se han reportado resultados variables en relación a cómo se ven afectados los murciélagos por la alteración de hábitat. Se ha observado que las especies voladoras de vertebrados son más resistentes a los cambios de uso de tierra porque presentan mayor movilidad que las especies no voladoras (Gilbert 1989). Sin embargo, otros estudios han demostrado que hay más riqueza de murciélagos de la familia Phyllostomidae en remanentes de bosque (Numa *et al.* 2005). Finalmente, estudios más recientes en áreas urbanas han demostrado que la persistencia de los murciélagos en una zona urbana estaba relacionada con rasgos morfológicos concernientes a la movilidad de las especies (Jung y Kalko 2011), por lo que el efecto podría considerarse como específico para la especie.

En Europa e Inglaterra se ha observado que los ensambles de murciélagos están en declive debido a la pérdida de hábitat y la intensificación de la agricultura (Hutson *et al.* 2001). A pesar de esto, se sabe que todas las especies de murciélagos de Gran Bretaña, las cuales son insectívoras, forrajean en zonas de campo, principalmente en agroecosistemas (Wickramasinghe *et al.* 2003). También se conoce que algunos grupos de insectos se ven afectados por la intensificación de la agricultura (Feber *et al.* 1997, di Giulio *et al.* 2001), lo cual influye indirectamente en los murciélagos.

Murciélagos insectívoros aéreos como agentes de control biológico de plagas: Las áreas dedicadas a la agricultura, que generalmente tienen un espacio aéreo completamente abierto, representan el hábitat ideal para el forrajeo de algunos murciélagos insectívoros

(Wickramasinghe *et al.* 2003), los cuales son los principales depredadores de insectos nocturnos (Warner 1984, Rydell 1986, Rakotoavirelo *et al.* 2007). Los murciélagos insectívoros consumen, aproximadamente, entre un cuarto y la mitad de su masa corporal por noche(Leelapaibul *et al.* 2005, Kunz *et al.* 2011). Existen muchos estudios relacionados con la dieta de los murciélagos insectívoros, pero la mayoría se centra en especies de distribución amplia o zonas templadas y han sido realizados en Estados Unidos (e.g. Brigham y Saunders 1990, Lee y McCracken 2005).

Varios autores han planteado que estos murciélagos podrían actuar potencialmente como controladores biológicos de plagas (Leelapaibul *et al.* 2005, Kunz *et al.* 2011). Si bien la mayoría de estudios simplemente determinan si los murciélagos se alimentan de algún insecto plaga, otros estudios han calculado el aporte económico brindado por el murciélago al mantener a las plagas bajo el nivel de daño económico. Según Cleveland *et al.* (2006) el valor real del servicio de control de pestes proveído por *Tadarida brasiliensis* en plantaciones de algodón en Texas y Nuevo México es de $741000 anuales. Generar información sobre consumo de insectos plaga podría llegar a funcionar como una forma de acercarse a los dueños de plantaciones masivas y explicarles la importancia que tienen los murciélagos para el ecosistema y, específicamente, sus cultivos. Esta información podría ser un incentivo para motivar a los dueños de agroecosistemas a implementar técnicas de manejo que favorezcan la sobrevivencia de una parte significativa de la biodiversidad local.

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CAPÍTULO 1. Aerial Insectivorous Bats' Vulnerability and Habitat Use in Industrialized Agroecosystems in Sarapiquí, Costa Rica

(Con formato para Conservation Biology)

Aerial Insectivorous Bats' Vulnerability and Habitat Use in Industrialized Agroecosystems in Sarapiquí, Costa Rica

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Abstract: The banana and pineapple industry occupy more than 1% of Costa Rica's total area, having significant impacts on the conservation of local organisms. Considering that bats have a wide range of ecosystem services, such as controlling insect populations, aerial insectivores could potentially function as biological pest control agents in agroecosystems. During 2012 and 2013, we sampled bats via acoustic surveys and insects (potential preys) with flight interception traps in banana, pineapple plantations and control forests in Sarapiquí, Costa Rica. We identified 20 species of aerial insectivorous bats in the sampled sites; 11 in forests, 15 in pineapple, and 16 in banana plantations. Rarefied species richness was highest in the forest in comparison to both agroecosystems. General bat (passes min^{-1}) and feeding (feeding buzzes min^{-1}) activities were higher in banana plantations. Only 12 species were recorded feeding during the study, most of them in plantations. The most common species in both plantations was the *Molossus currentium / sinaloae* complex, and in forests, *Centronycteris centralis*. For insects, rarefied richness was highest in pineapple, and dominance was highest in plantations. Insect dry mass was not correlated with general bat or feeding activities. Even if bats use the agroecosystems as flight and feeding areas, the forest patches immersed in them probably play a vital role in maintaining a significant sample from the original ensemble and their populations since they provide roosts and other resources. Also, the microhabitat diversity in forests can support all of the bat functional groups, which allows more species to fly nearby agricultural areas. Given the intense use of these agroecosystems by aerial insectivorous bats, biologists, pineapple, and banana producers should work on joint conservation management and educational programs focused on the forest fragments that remain immersed in agricultural areas.

Key Words: pineapple, banana, functional groups, landscape ecology, Chiroptera

Vulnerabilidad y uso de hábitat de murciélagos insectívoros aéreos en agro-ecosistemas industrializados en Sarapiquí, Costa Rica

Resumen: Las industrias bananera y piñera ocupan más del 1% del territorio costarricense, lo que causa que tengan impactos significativos en la conservación de organismos locales. Como los murciélagos proveen un amplio rango de servicios ambientales, tal como controlar poblaciones de insectos, los insectívoros aéreos podrían funcionar como controles biológicos de plagas en los agro-ecosistemas. Durante el 2012 y 2013, realizamos un muestreo acústico de murciélagos y utilizamos trampas de intercepción de vuelo para capturar insectos (presas potenciales) en plantaciones de banano y piña y bosques en Sarapiquí, Costa Rica. Identificamos 20 especies de murciélagos insectívoros aéreos en las zonas muestreadas; 11 en bosques, 15 en piñeras y 16 en bananeras. La actividad general (pases min^{-1}) y de forrajeo (fases terminales min^{-1}) fue mayor en las plantaciones de banano. Sólo encontramos 12 especies forrajeando durante el estudio y la mayoría en plantaciones. La especie más común en las plantaciones fue el complejo *Molossus currentium / sinaloae*; y en bosques, *Centronycteris centralis*. Para los insectos, el índice de rarefacción fue mayor en piñeras y la dominancia en plantaciones. La masa seca de los insectos no se correlacionó significativamente con la actividad general ni la de forrajeo de los murciélagos. Aunque los murciélagos utilizan los agro-ecosistemas como áreas de vuelo y de alimentación, los parches de bosque circundantes probablemente tienen un papel vital para mantener una muestra significativa del ensamble original y sus poblaciones, ya que proveen recursos como refugios. Además, la diversidad de microhábitats en los bosques puede mantener todos los grupos funcionales; lo cual permite que más especies vuelen en dichas áreas. Como los murciélagos insectívoros aéreos están utilizando los agro-ecosistemas, los biólogos y los productores de banano y piña deberían crear programas conjuntos de manejo y educación en las zonas aledañas a los parches de bosque que están inmersos en zonas de cultivos.

Palabras clave: piñeras, bananeras, grupos funcionales, ecología del paisaje, Chiroptera

Introduction

Amongst all possible causes for biodiversity loss, there are three main ones that are closely related to human activities. Habitat reduction, fragmentation, and transformation are directly linked to high extinction rates (Wilcox & Murphy 1985; Cosson et al. 1999; Primack 2000; Fahrig 2003; Gorresen et al. 2005), and anthropogenic factors like urbanization and agriculture are a direct cause of these three phenomena (Daily et al. 2003; Avila-Flores & Fenton 2005). The Neotropics are a good example of how rapid change in land use, mainly from forest to pasture and agricultural areas, has led to the disappearance and isolation of wildlife populations (Estrada et al. 1994).

Although Costa Rica has one of the best systems of protected areas in Latin America (1,861,715 ha; 26% of the country's territory) (SINAC 2002), with these areas being vital tools for preventing biodiversity loss (Rodrigues et al. 2004), it is still experiencing a significant transformation in agricultural land cover. In 2011, 10% of the land was used for crop cultivation, an increase of 59,230 ha since 2008 (from 441,697 to 500,927 ha) (SEPSA 2012). Pineapple and banana are the two fresh fruit crops with the most extensive areas in the country, 45,000 ha and 42,016 ha respectively (SEPSA 2012). These are also two of the crops with the largest gross value (over 694,000 US dollars each, more than 15% of agricultural production each), as well as those with most exports (over 715,000 thousands US dollars per year, more than 17% of agricultural exports each) (SEPSA 2012).

In tropical countries with extensive agricultural areas it is vital to determine the impact these areas have on wildlife, and to consider the ecosystem services (e.g. pollination, pest control, water purification) that depend directly on species that can withstand loss of their original habitat (Daily et al. 2003). Bats provide a wider range of ecosystem services than any other group of mammals, including pollination, seed dispersal, and control of insect populations (Kunz et al. 2011). It has been observed that bat ensembles in Europe are decreasing, and that there is a direct relationship with agricultural intensification (Hutson et al. 2001; Wickramasinghe et al. 2003). In spite of this, European bats have been observed to forage in agroecosystems (Wickramasinghe et al. 2003), and recent studies suggest that aerial insectivorous bats can act as biological pest control agents (Leelapaibul et al. 2005; Cleveland et al. 2006; Kunz et al. 2011).

Our aim in this study was to determine the impact that two of the most important industrialized agroecosystems in Costa Rica (pineapple and banana) have on the aerial insectivorous bat ensemble. We wanted to verify how species richness, composition, flight and foraging activity vary between pineapple and banana plantations and forests, and if they were related to prey availability. We hypothesized that, due to original habitat loss, low levels of vegetation cover, and habitat homogeneity, agroecosystems have an effect on the aerial insectivorous bat ensemble of the area. We predicted that aerial insectivorous bats would still be present in the agroecosystems, but in smaller numbers than in control forests, and that foraging activity would also decrease in pineapple and banana plantations.

Methods

Study site

Our research was done in Sarapiquí, Heredia, Costa Rica during the years 2012 and 2013. The area has tropical weather, with a dry season from March to May and a rainy season from May to February. The mean annual temperature is 26ºC and the mean annual precipitation around 3710 mm (Solano 1996). We conducted acoustic and insect surveys in four sites: two forests (Tirimbina Biological Reserve and La Selva Biological Station) and two plantation types (pineapple and banana) (Fig. 1). The four study sites were located between 40 and 200 meters elevation and possess similar climatic conditions. TBR is located in the community named Tirimbina, in La Virgen, Sarapiquí and has an area of 412 ha. The forest includes two different life zones (tropical pre-montane forest with transition to basal and very humid tropical forest) and is mainly composed by primary forest, but also has patches of secondary forest, cacao plantation, and secondary forest in early regeneration. LSBS is close to Puerto Viejo, Sarapiquí and has an area of 1,600 ha of wet tropical forest. It contains several habitats, ranging from primary forest to cleared pastures, secondary forest, and abandoned plantations. The banana plantation fields we used were located in the Nogal project of Chiquita Banana, in Puerto Viejo, Sarapiquí, and the pineapple plantations belonged to Collin Street Bakery and were part of an organic farming project called Finca Corsicana, in La Virgen.

Bat ensemble and habitat use

We conducted acoustic surveys in five points in La Selva and the banana plantations and in four points in Tirimbina and the pineapple plantations to determine bat species richness, composition, activity, and occurrence counts (Jung & Kalko 2011) as well as feeding activity. We recorded from March to August 2012 using two Song Meter SM2 Bat recorders (Alana Ecology, United Kingdom) with a sampling frequency of 192 kHz and 16 bits resolution. Each recording site within the same category was at least 200 meters apart from the others and 50 m away from edges, roads or water bodies. Sampling points in the forests included secondary and primary forests inside the selected continuous sites. We simultaneously surveyed the points in La Selva and banana, as well as Tirimbina and pineapple, during three consecutive nights. Each acoustic monitoring session consisted of recordings done from 15:30 until 0:00.

Due to the large number of recordings (21,060 minutes), we only analyzed those that were done between 17:30 and 21:00 hours (11,340 minutes), when the major activity occurs (Jung, pers.com). We identified the sound sequences to species level by comparing their structure and frequency with the ones found in the call library prepared by E. Kalko and K. Jung in Ulm University, Germany, and by consulting existing articles on echolocation (Obrist 1995; O'Farrell et al. 1999; Rydell et al. 2002; Jung et al. 2007; Jung & Kalko 2011; Jung et al. 2014). We analyzed the recordings using Avisoft Saslab Pro 5.1.20 (Raimund Specht, Avisoft Bioacustics, Berlin, Germany). To determine the species that were foraging in each site, we found feeding buzzes preceded by search phases, and identified the species emitting them. Feeding buzzes, also known as terminal phases, are call sequences emitted at a high repetition rate before prey capture attempts (Schnitzler & Kalko 2001).

The use of acoustic recordings for species monitoring has several identification issues. First, due to the sampling rate of the recorder, the Proboscis Bat (*Rhynchonycteris naso*, Emballonuridae) could not be recorded, but it is expected to be in the study area. Since *Eumops* species cannot be identified acoustically, and, according to Timm et al. (1999), the only species in the study area is the Dwarf Bonneted Bat (*Eumops bonariensis*), all *Eumops* sequences were classified as this species. Also, we worked with two species complexes (*Eptesicus furinalis/brasiliensis* and *Molossus currentium/sinaloae*) because their call frequencies overlap and their distinction is complicated.

Potential prey

We sampled insects during the same nights and in the same spots where we did the acoustic surveys. We used flight interception traps, like the ones used by Jung & Kalko (2010) and Estrada-Villegas (2010). In each spot, we used one trap, in the same place where we put the recorder, at three meters height. We conserved the samples obtained from the flight interception traps in 70% alcohol and identified the insects to family or the lowest taxonomic level possible. After the identifications were done we dried the specimens in an oven at 70ºC for 24 hours and we then calculated their dry weight using an electronic balance (in mg, precision 0.001 mg).

Data analysis

When using acoustic monitoring, bat abundance cannot be related to bat passes because individual identification is not possible (Jung & Kalko 2011). We therefore used the same method used by Jung and Kalko (2011) who estimated species occurrence and used it for inventory completeness, richness, and species composition analyses. We excluded members from the families Noctilionidae and Phyllostomidae, as well as non-identified calls, from all analyses.

We created species accumulation curves for each site category using a randomized (1,000 times) null model analysis based on samples (Gotelli & Enstminger 2006). To calculate inventory completeness we used the Coleman species richness estimator (S_{est}) and calculated a percentage of completeness by dividing the number of observed species in each site (S_{obs}) between the estimator (S_{est}) and multiplying it by 100. Both of these analyses were done using EstimateS 9.1.0 (Colwell 2013). To determine species richness, we did a rarefaction analysis using 1,000 iterations and independent sampling. We also calculated the Berger-Parker index to determine single species dominance in the site categories. Both of these analyses were done with PAST (Hammer et al. 2001).

We standardized bat activity by calculating the number of bat passes (Estrada-Villegas et al. 2010, Jung & Kalko 2010) per minute for each species during each night in each site (mean bat activity). To determine if there were differences between mean bat activity (general or flight activity) and feeding activity between site categories, we used a Kruskal-Wallis test. We also ran Kruskal-Wallis tests for all species with more than 20 bat passes during the study to determine if there were differences between their general activities in the site categories. To explore the differences between site categories in species composition and activity we did a Non Metric Multidimensional Scaling (NMDS) based on Bray-Curtis dissimilarities where the dependent variable used were the mean passes per minute per night in each site category. These analyses were done using R 2.15.3 (R Development Core Team 2013).

To explore the insect composition in each site category, we calculated a sample-based rarefied model using 1,000 iterations and independent sampling and a Berger-Parker index of dominance using PAST (Hammer et al. 2001). To determine the relationship between general (passes min^{-1}) and foraging activity (feeding buzzes min^{-1}) with insect dry mass and with insect abundance, we used a Spearman rank order correlation test. These analyses were done using R 2.15.3 (R Development Core Team 2013).

Results

Ensemble structure and habitat use

We identified 20 species of aerial insectivorous bats in the sampled sites (Table 1). We recorded 4,696 bat passes which corresponded to 247 occurrence counts. We found the lowest number of species in forest sites (S_{obs}=11) and the highest in banana plantations (S_{obs}=16). In the forest we only found 55% of all potential species (Table 2). At both plantations, the Coleman estimate of predicted species was close to the number of observed species, but in the forest this did not occur (Fig. 2). Rarefied species richness differed between site categories with highest species richness in the forest compared with the plantations (Fig. 3a). The forest sites also had higher single species dominance than the plantations (Fig. 3a).

Both general bat activities and feeding activities differed between the site categories (bat activity: χ^2=13.0168, df=2, p=0.0015; feeding activity: χ^2=17.3259, df=2, p=0.0002). General bat activity was higher in banana plantations than in pineapple plantations and forests, while feeding activity was lower in forests than in both plantations (Fig. 4). Only 12 out of the 20 species were recorded feeding during this study (Table 1). General bat activity differed in all insectivorous bat species analyzed except in the Chestnut Sac-winged Bat (*Cormura brevirostris*) (Table 1). Aerial insectivorous bats were separated between plantations and forest using NMDS (Fig. 5, final stress=0.11, linear fit of ordination distance and observed dissimilarity

R^2=0.94). The forest category was properly clustered and separated from both plantations. Banana and pineapple plantations were grouped closer together due to similar occurrence patterns of aerial insectivorous bat species.

Potential prey

We captured a total of 383 insects that belonged to 60 families distributed in 11 orders (Appendix 1). Rarefied family richness differed between site categories with highest species richness in pineapple plantations (Fig. 3). Single family dominance was higher in plantations than in the forest (Fig. 3). Insect dry mass was not significantly correlated with general bat activity (R_s=1230, p=0.28) nor with feeding activity (R_s=1011.26, p=0.86).

Discussion

Forests, with their diversity of microhabitats and succession levels, seem like the ideal landscape category to find a larger richness of aerial insectivorous bats (Entwistle et al. 1996; Patriquin & Barclay 2003). Aerial insectivorous bats have been divided in three categories according to the proximity of their prey items to clutter (vegetation or ground): those that hunt in uncluttered space, in background-cluttered space, and in highly-cluttered space (Schnitzler & Kalko 2001). The presence of edges, cluttered and uncluttered areas, and water bodies, as well as different succession levels, allow all kinds of aerial insectivores to be present in forests compared to areas as homogeneous as plantations. The heterogeneous forest conditions, as well as the larger amount of obstacles, could have affected the recorder and had an influence on the recorded number of bat species, which was not as high as the estimated number. Further sampling in sites with different vegetation conditions and water bodies could provide a better estimator of the number of aerial insectivorous bats present in forests.

The natural forest coverage and the diversity also represent wider resource availability for bats, especially roosts. In plantations, aerial insectivorous bats should either adapt quickly and use man-made structures, or depend on surrounding forest patches. Man-made structures have been observed to foster large populations of several insectivorous bat species, but mainly those from the Molossidae family (Nowak 1994; LaVal & Rodríguez-H. 2002), which made up almost 50% of the bat activity in both plantations in this study. Using surrounding forest patches means that the bats should eventually fly across the plantations, which exposes them more to predators and represents a high energy cost (Norberg 1994; Verboom & Spoelstra 1999; Russo et al. 2007), either to feed in them or to reach other forest patches to feed or roost.

Since flying across plantations could represent both an exposure to predators as well as an energy expense, it is possible that not all bat species could afford these consequences. The effect that plantations have on the aerial insectivorous bat ensemble seems to be related to the functional groups described by Schnitzler and Kalko (2001). Larger bats with higher wing loading/aspect ratio and faster flight are expected to cover long distances more easily than small, low wing loading/aspect ratio, slow flying species (Norberg & Rayner 1987; Schnitzler & Kalko 2001), which could explain why molossids were more active in plantations than in the forest sites. As mentioned above, low molossid activity in forest sites could also be related to the reach of the recorder because they are expected to fly over the canopy.

Inherent species characteristics (like the ones mentioned above) can also help explain the patterns observed in Thomas's Shaggy Bat (*Centronycteris centralis*, Emballonuridae) and the *Molossus currentium/sinaloae* (Molossidae) complex. *C. centralis*, which was never recorded during this study in either plantation but made up for most of the bat activity in the forest sites, has a strong association with forest cover (Estrada-Villegas et al. 2010). It is a small emballonurid that usually roosts in hollow trees or foliage (Simmons & Handley 1998; LaVal & Rodriguez-H. 2002). The *M. currentium/sinaloae* complex, and imolossids in general, fly in in open spaces (Norberg & Rayner 1987; Schnitzler & Kalko 2001), so the lack of forest canopy in plantations should not affect them, but should rather support the increased activity of these species. Also, personal observations showed that several of the houses found around the plantations were functioning as roosts for these bats.

The results of this study (only one out of 20 species was never recorded in either plantation) highlight the role that the ecological characteristics of the landscape have on the occurrence of insectivorous bats in banana and pineapple plantations. Forest patches (especially large ones) are responsible for maintaining populations over the long-term (Harrison & Bruna 1999; Vandermeer & Perfecto 2006). The occurrence of species that are slightly tolerant to changes in land use in the studied plantations could be influenced by the distance between forest patches, the hostility of the matrix and how these factors interact with the species' inherent echolocation and flight characteristics (Estrada et al. 1994; Fahrig 2001; Ricketts 2001; Passamani & Ribeiro 2009).

The plantations showed similarities with respect to species composition, but differed in terms of bat activity. When contrasting banana and pineapple plantations, the main difference is the height of the vegetation (banana can grow up to 7.5 m and pineapple does not grow over 1 m). Higher vegetation could mean more coverage and protection against predators, which can translate into more bat activity (as seen in this study). Another possible explanation is that the variation between prey items in each plantation could be related to the difference in bat activity. However, the similarities in species composition could be further explained by the landscape present around both agroecosystem categories, in which forest patches (both small and large ones) surround them, and provide bats with roosts and food.

Considering the mentioned consequences that flying across plantations might have, bats that manage to do so should obtain some benefit from this action. The insectivorous bats' feeding activity was higher in plantations (mainly in banana) in comparison to forests, which seems to be supported by the presence of insect swarms in these sites. It has been observed that aerial insectivorous bats search for large insect swarms on which to feed because they spend less energy, and obtain food more easily and faster (Bell 1980). For this study, the dominance index for insects was higher in plantations than in the forest, which suggests that aggregations of one insect species are present. We did not find a correlation between insect dry mass or insect abundance and general bat activity or feeding activity. The small number of insects caught in the interception traps, as well as the underrepresentation of key insect orders (e.g. Lepidoptera) in insectivorous bats' diets (Feldman et al. 2000; Brack & LaVal 2006; Lacki et al. 2009), might influence these results.

Banana and pineapple are two of the crops generating the greatest debate regarding agrochemicals, both in Costa Rica and the world, which could lead one to assume that insects are not very abundant in these crops. In the studied banana plantations, where agrochemicals were sprayed frequently using a small airplane, the sampling sessions never coincided with the spraying due to a ban on people entering the field during these days. The pineapple fields used in this study were part of an organic pineapple project in the area, so no agrochemicals were used in them. Both of these factors probably have an influence on the high insect richness and abundance in these plantations, and it would be worth looking into differences in these aspects during periods of agrochemical application and in non-organic plantations.

Despite aerial insectivorous bats using agroecosystems such as banana and pineapple plantations as flight and feeding areas, no landscape can substitute for forests in maintaining the original species richness. Forests can provide bats with more resources, and their microhabitat diversity can support all of the functional groups. Because bats are using agroecosystems, we should begin to ask what effects agroecosystems have on bats and on humans. The interaction between these organisms could lead to positive (e.g. biological pest control in plantations) and negative effects (e.g. diseases, bats feeding on insects filled with agrochemicals, favoring a range of species over another). Finally, this interaction should be handled carefully, preferably with conservation, management, and education programs in order to preserve the wildlife's integrity.

Management implications

The interaction of aerial insectivorous bats flying and feeding in agroecosystems could lead to important joint management programs between plantation owners and biologists. Since these bats are feeding here, and could potentially act as biological control agents, it might be of interest for agricultural companies to aid in the conservation of local bats and help create and maintain artificial roosts close to the plantations. After studies like the one by Cleveland et al. (2006) have been carried out for specific crops, the money saved by the bats acting as biological control agents, could become an incentive for the companies to decrease the amount of pesticides used and increase organic plantations, which would not only have a positive influence on the bats, but also on other organisms, soils, and water bodies around the agroecosystems. Finally, considering that the small and large forest patches around the plantations probably are working as roosting and feeding sites for some of the species, it is vital to conserve them and, if possible, start reforestation/regeneration programs where possible to increase forested lands in the area.

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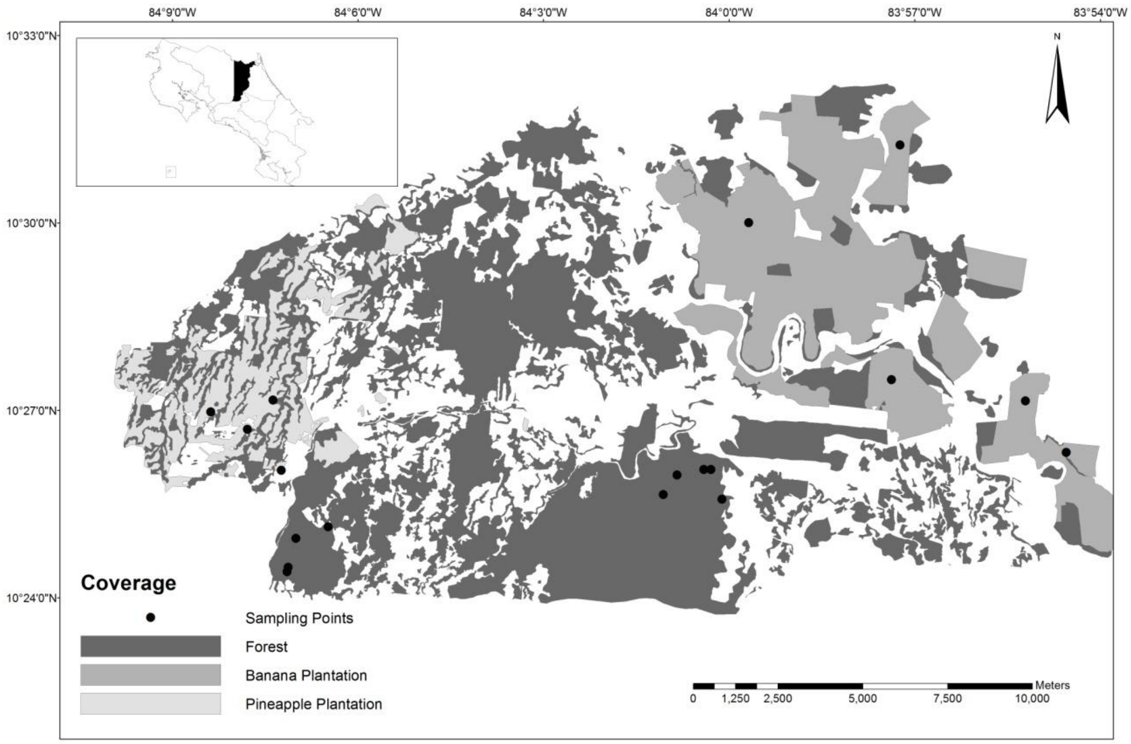


Fig. 1. Map of the study area in Sarapiquí, Costa Rica.

[a] Elaborated by M. Runnebaum

[b] Image sources: Mosaic generated in SIG OTS from aerial photographies issued by the Costa Rica Airborne Research and Technology Applications (CARTA 2005), Centro Nacional de Alta Tecnología (CENAT) and Nasa Johnson Space Center (2014).

Table 1. Mean bat activity (passes min^{-1} per night) and total count of feeding buzzes of aerial insectivorous bats in each site category by species.

Species	Abbr.	Family	Passes min^{-1} per night			Difference among categories		Total count of feeding buzzes	N
			Banana	Pineapple	Forest	χ^2	p		
Centronycteris centralis	C.cen	EMB	0	0	2.122	23.24	<0.05	18	1203
Cormura brevirostris	C.bre	EMB	0.051	0.012	0.034	3.99	0.14	1	38
Diclidurus albus	D.alb	EMB	0.003	0	0			0	1
Eptesicus brasiliensis/furinalis	E.bf	VES	0.898	0.302	0.092	26.44	<0.05	15	411
Eumops sp.	Eum	MOL	0.311	0.325	0.009	22.73	<0.05	0	185
Lasiurus ega	L.ega	VES	0.029	0.004	0			0	10
Molossus currentium/sinaloae	M.cs	MOL	3.156	1.032	0.141	34.48	<0.05	94	1334
Molossus molossus	M.mol	MOL	0.016	0.028	0			0	12
Myotis albescens	M.alb	VES	0.133	0.040	0	23.61	<0.05	1	52
Myotis elegans	M.ele	VES	0.022	0	0			1	7
Myotis nigricans	M.nig	VES	1.003	0.607	0.055	21.13	<0.05	26	500
Myotis riparius	M.rip	VES	0.003	0	0.016			0	10
Noctilio spp.	Noct	NOC	0.048	0.004	0			0	16
Peropteryx kappleri	P.kap	EMB	0.140	0.012	0.002	15.81	<0.05	2	48
Peropteryx macrotis	P.mac	EMB	0.014	0.008	0			1	6
Pteronotus davyi	P.dav	MOR	0	0.004	0			0	1
Pteronotus gymnonotus	P.gym	MOR	0.003	0	0			0	1
Pteronotus parnellii	P.par	MOR	0	0.008	0.042	10.52	<0.05	1	26
Rhogeessa io	R.io	VES	0	0.004	0			0	1
Saccopteryx bilineata	S.bil	EMB	1.254	0.048	0.169	12.88	<0.05	20	503
Saccopteryx leptura	S.lep	EMB	0.432	0.052	0.048	10.52	<0.05	21	176
Various species		PHY	0.276	0	0.007			0	102
Not identified			0.105	0	0.035			1	53

[a] Bat families recorded in this study were: Emballonuridae (EMB), Molossidae (MOL), Mormoopidae (MOR), Noctilionidae (NOC), Phyllostomidae (PHY), and Vespertilionidae (VES).
[b] Difference between categories were only calculated for aerial insectivorous bat species with more than 20 bat passes during the entire study using Kruskal-Wallis test with df=2.
[c] Mean bat activity has been multiplied by 10 in this table to obtain numbers with less decimals.
[d] Total count of bat passes min^{-1} for all study sites is also given (N).

Table 2. Inventory completeness in the three site categories.

Site category	Observed species	Coleman estimate	Inventory completeness (%)
Banana	16	16.37	98
Pineapple	15	18.53	81
Forest	11	20	55

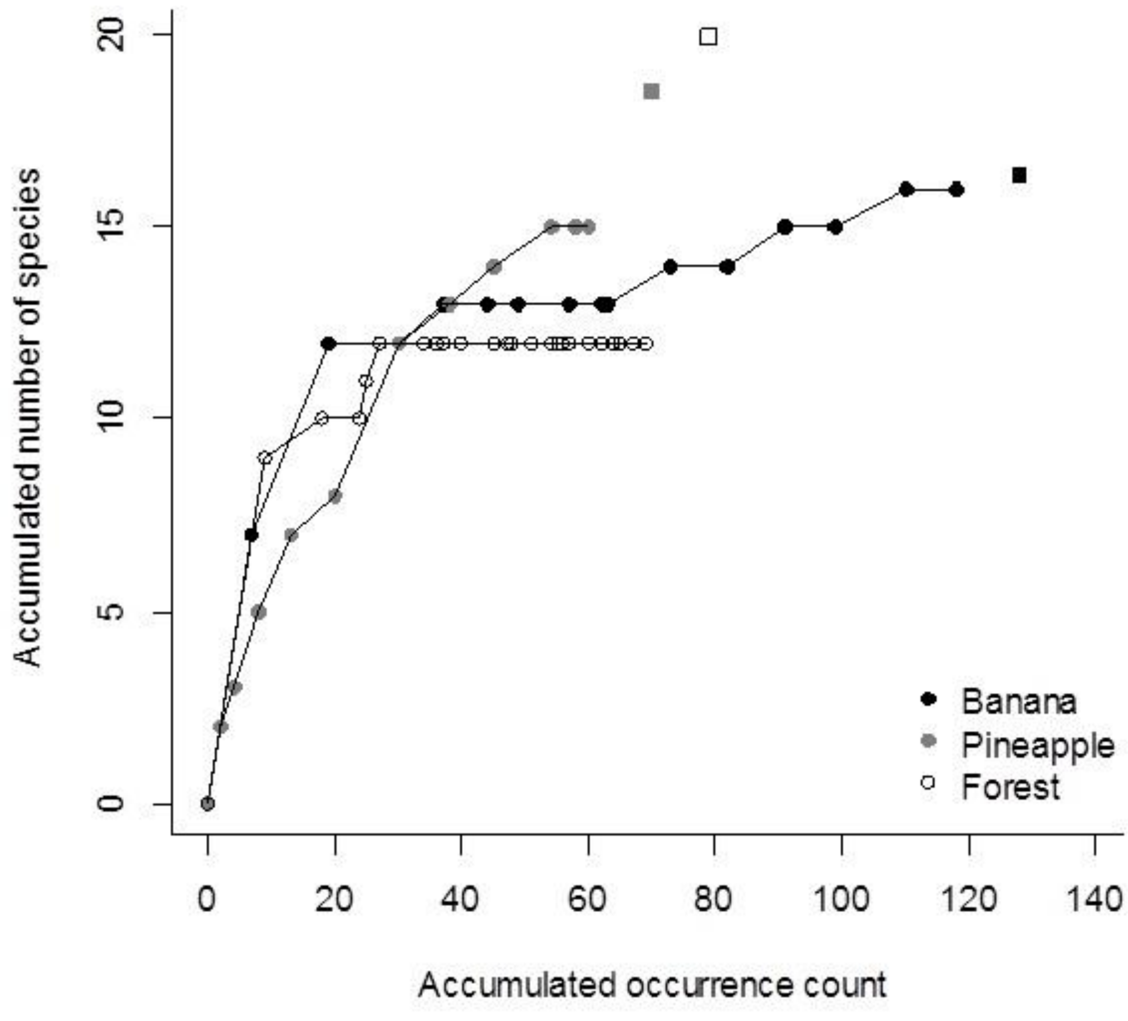


Fig. 2. Species accumulation curves using occurrence counts at the three site categories.
[a] Squares indicate the Coleman species richness estimator: banana (16.37), pineapple (18.53), and forest (20).

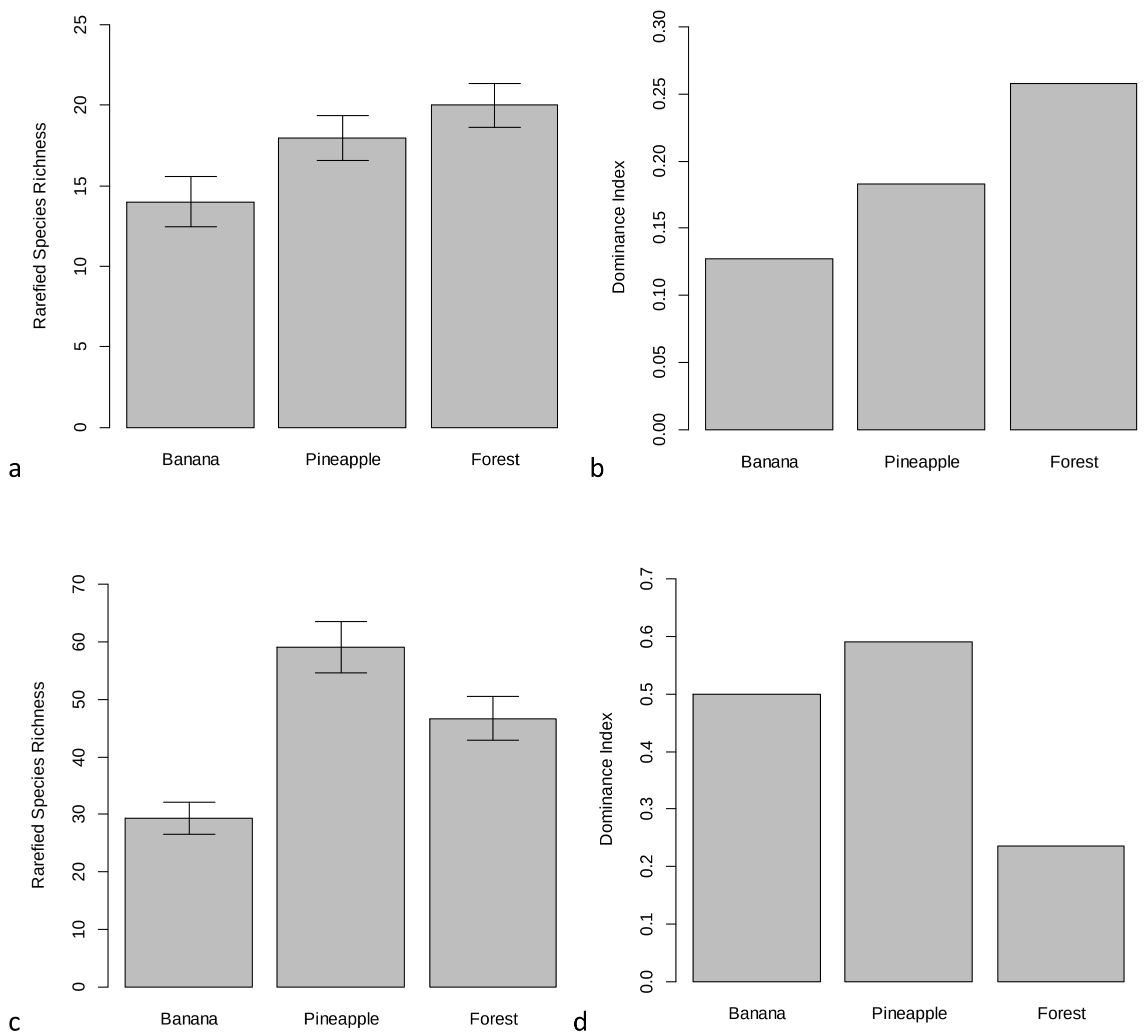
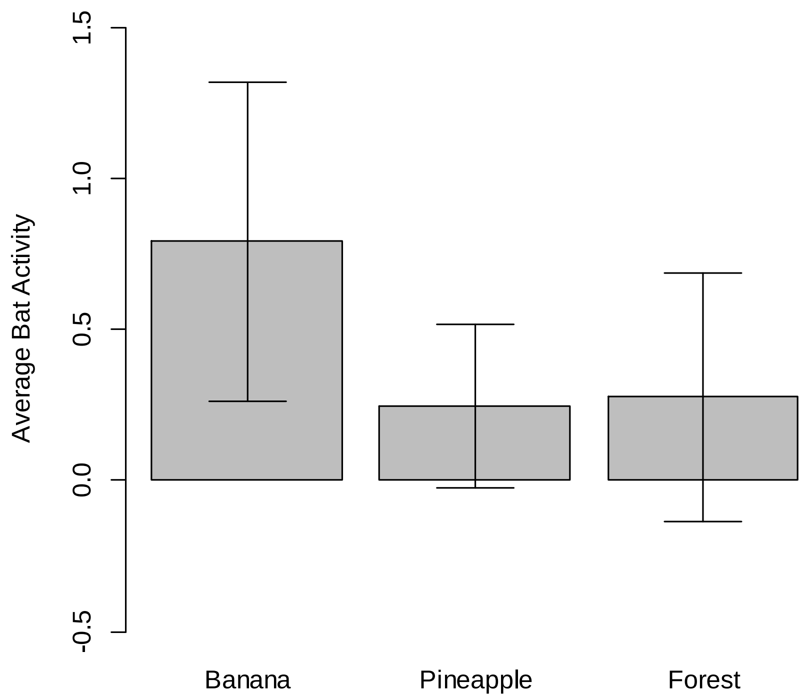
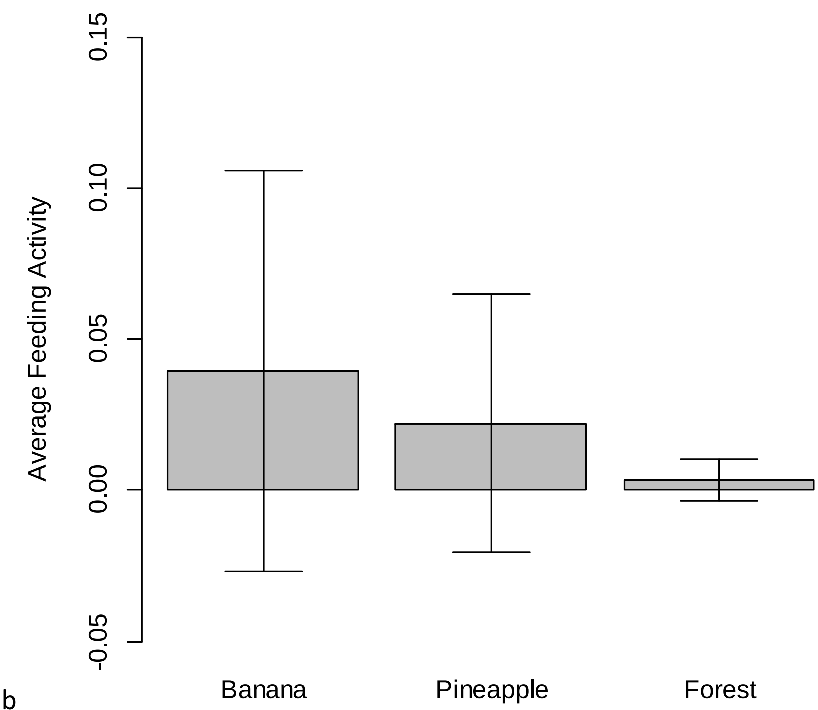


Fig. 3. Rarefied species richness and dominance index for bats (a-b) and insects (c-d) ensembles in the study area.

[a] Bars represent standard deviation for the rarefied species richness analysis.



a



b

Fig. 4. Average of (a) general bat activity (passes min^{-1}) and (b) feeding activity (feeding buzzes min^{-1}) in the three site categories.

[a] Bars represent standard deviation.

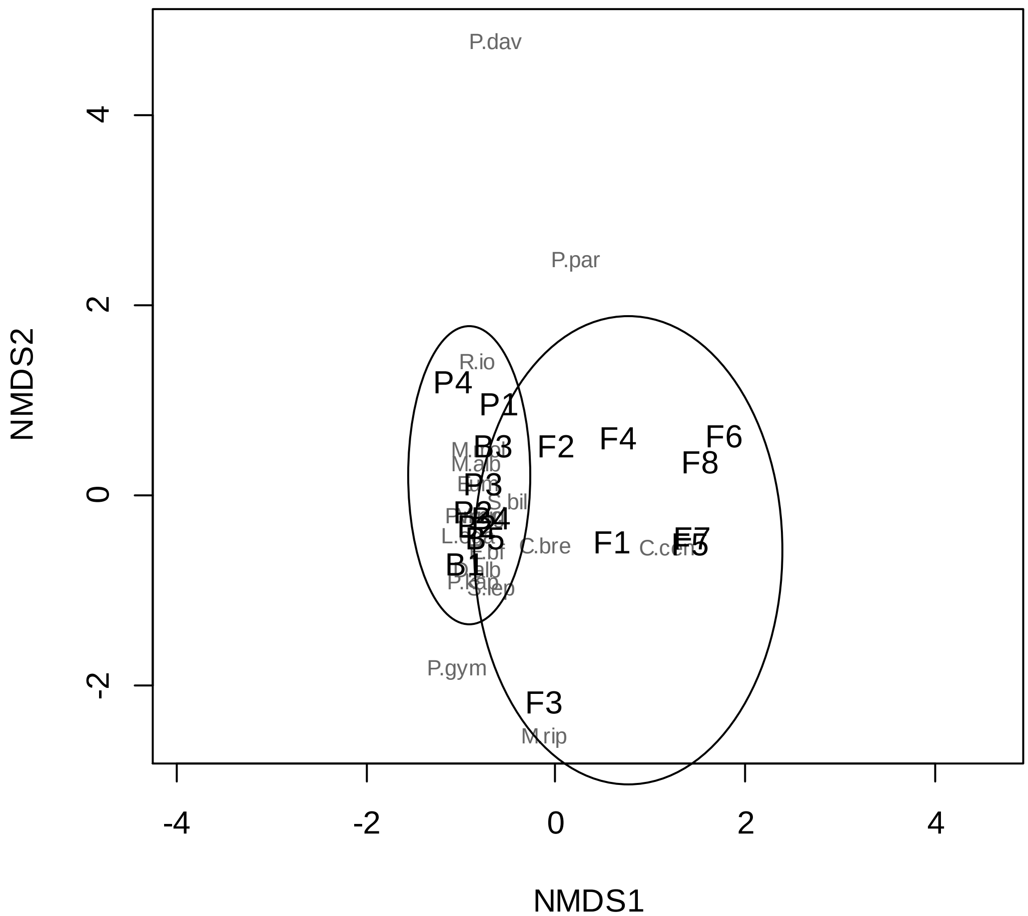


Fig. 5. Ordination of recording sites based on Bray-Curtis dissimilarity of occurrence and activity of aerial insectivorous bats.

[a] Study sites represented are: banana plantations (B), pineapple plantations (P), and forests (F).

CAPÍTULO 2. Diet of Aerial Insectivorous Bats: Study Techniques and the Use of Bats as Potential Biological Control Agents

(Con formato para Acta Chiropterologica)

Diet of Aerial Insectivorous Bats: Study Techniques and the Use of Bats as Potential Biological Control Agents

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Abstract: We prepared a bibliographic review of the research done concerning the diet of insectivorous bats. We analyzed which families, species, and places have received more attention. We also evaluated the different techniques used to obtain information about a bat's diet and the insects present in the study site. Finally we studied how many articles have information about insectivorous bats acting as biological control agents. The family with most mentiones in studies is Vespertilionidae (188), while the most researched species is *Eptesicus fuscus*, which is easily captured and found in their roosts in comparison to other insectivorous bats, as well as the worldwide distribution of the family. Most studies have been done in temperate areas, such as the United States whereas research in the Tropics is still insufficient. The information about diet is obtained using stomach or fecal contents and the data expressed as a volume percentage. Most recent studies are using molecular techniques to identify diet components. There are numerous kinds of traps used to sample insects, but most researchers suggest combining several types because each technique possesses different biases. There were only three studies that calculated the economic value provided by bat species as biological control agents. Diet studies can be taken a step further when calculating the environmental services provided by insectivorous bats as biological control agents, and, due to the high diversity and abundance of bats and insects and to the agricultural intensification problem in the area, they could become an important tool for bat conservation in the Neotropics.

Key words: Vespertilionidae, stomach contents, fecal contents, volume percentage, insect census, United States

In the Neotropics, bats are the most abundant and diverse group of mammals (they represent more than 50% of the local mammal species) (Medellín *et al.* 2000). Bats are the group of mammals with the greatest diversity of feeding habits, ranging from frugivores to those that feed on blood. Most species of Microchiroptera (currently Yangochiroptera and the families Rhinopomatidae, Rhinolophidae and Megadermatidae) have an insectivorous diet (Kunz and Pierson 1994). Even though insectivorous bats comprise an important percentage of bat communities in the Neotropics, they have not been as intensively studied as other feeding guilds and are usually underrepresented in surveys due to the typical use of mist nets as sampling methods (Rydell *et al*. 2002, MacSwiney *et al*. 2008).

Insectivorous bats have an important role in maintaining the size of insect populations. They feed on insects and other arthropods, such as spiders and scorpions (Warner 1984, Rydell 1986, Kunz *et al.* 1995). Insectivores represent the main predators of nocturnal insects (Rakotoarivelo *et al.* 2007) and over their cosmopolitan distribution they feed on a variety of species of insects and other arthropods (Kunz and Pierson 1994, Kunz *et al.* 2011). These bats eat approximately one fourth to half of their body mass per night, making the amount of food they ingest extremely high (Leelapaibul *et al.* 2005, Kunz *et al.* 2011).

Due to the large amount of insects eaten per night by each individual, it has been proposed that insectivorous bats might work, potentially, as biological pest control agents (Leelapaibul *et al.* 2005, Kunz *et al.* 2011). Organisms that are considered as pests in agriculture are those that feed on plant parts and lead to a decline in the plant's production (Brown *et al.* 2001). Despite the environmental services that bats might provide as biological control agents, what is known about their diet seems to be restricted to a few species.

The main objective of this research was to review the scientific literature on the diet of insectivorous bats, especially in the Neotropics. The specific objectives of this review were (1) to identify the bat species and the places where the majority of investigations have taken place, (2) to assess the research status of this topic in the Neotropics, (3) to determine the main techniques used to obtain information about the diet of insectivorous bats, and (4) to analyze the existent knowledge of bats as biological control agents in agriculture.

Methods

We prepared a bibliographic review of all the research that has been done concerning the description of insectivorous bats' diet from the 1970's to March 2014. We searched for studies about this subject using the ISI Web of Science, Science Direct and Google Scholar databases. We extracted the following information from each article: bat species studied, study site, and methods used. In addition, we quantified the number of investigations that have analyzed the role of bats as biological control agents.

For the analysis of bat species and study sites, we used the articles where researchers carried out a direct study of the diet of one or more bat species. We determined the number of times that each species was incorporated in a study of its diet. We also established which family of insectivorous bats was the subject of the largest number of investigations. Finally, we calculated which country had the most studies.

We divided the sampling techniques in three categories: obtaining the contents of a bat's diet (stomach or fecal contents, droppings or culled parts, molecular techniques), analyzing the diet results, and determining the insects present in the study site. For each one of these categories, we reviewed the different techniques and their positive and negative aspects.

Results

The information concerning bat species and study sites was extracted from 135 scientific articles. In these papers, 140 aerial insectivorous bat species were studied; nine species were included in more than five studies, while 131 were included in fewer than five (Fig. 1, Appendix 1). The species that has been mentioned most frequently in diet studies is *Eptesicus fuscus* (Vespertilionidae), followed by *Myotis lucifugus* (Vespertilionidae) and *Tadarida brasiliensis* (Molossidae) (Fig. 1). The insectivorous bats that were included in the greatest number of articles are those that belong to Vespertilionidae (Fig. 2). Out of the 132 scientific papers analyzed, 31 % of them have been done in the United States (Fig. 3). Only seven studies were conducted in Neotropical countries (Rautenbach *et al.* 1998, Whitaker and Rodríguez-Durán 1999, Whitaker *et al.* 1999, Bernard 2002, Aguirre *et al.* 2003, Dechmann *et al.* 2006, Aguiar and Antonini 2008).

We found that the typical methods used to determine diet components were to visually analyze fecal or stomach contents or dropped insect parts from roosts. 94% of the reviewed studies used fecal contents, and some of these studies combined this technique with others. However, very few studies (2.9%) used just stomach contents to characterize the bats' diets. Two papers were bibliographic diet studies (2.2%) and one combined both fecal and stomach analyses (0.7%). This information is usually obtained either by capturing bats using mist nets or by extracting them directly from their roost. Also, in most of the studies, fecal or stomach contents were analyzed under a dissecting scope or microscope, moistening the contents with water or alcohol. Nine of the most recent studies analyzed fecal contents using molecular techniques. In most articles, the data obtained were expressed as a volume percentage (calculated as the sum of individual volumes of each prey divided by the total volume and multiplied by 100) (Whitaker *et al.* 1981, Whitaker and Rodríguez-Durán 1999, Whitaker *et al.* 1999, Agosta *et al.* 2003, McWilliams 2005, Whitaker and Barnard 2005, Wei *et al.* 2008).

There were a variety of ways used to capture insects (Table 1). However, more than half of the analyzed studies did not provide an insect list of the area during the investigation of the bat's diet (Whitaker *et al.* 1981, Kunz and Whitaker 1983, Whitaker *et al.* 1993, Whitaker *et al.* 1996, Whitaker *et al.* 1999, Whitaker and Rodríguez-Duran 1999, Pavey and Burwell 2000, Seamark and Bogdanowicz 2002, Whitaker and Yom-Tov 2002, Agosta and Morton 2003, Sparks and Valdez 2003, Lee and McCracken 2005, McWilliams 2005, Whitaker and Barnard 2005, Zhang *et al.* 2005, Debelica *et al.* 2006, Ma *et al.* 2006, Lacki *et al.* 2007, Li *et al.* 2007, Thabah *et al.* 2007, Zahn *et al.* 2007,Ma *et al.* 2008, Storm and Whitaker 2008, Feldhamer *et al.* 2009, Painter *et al.* 2009, Valdez and Bogan 2009). In the research that did provide such a list, it was generally suggested that insects be captured during the same nights used to obtain samples to determine the bat's diet. In addition, some researchers emulated the way bats hunt in order to prepare the list (Kunz and Whitaker 1983, Almenar *et al.* 2008).

Several studies suggested that bats can function in biological pest control. However, we only found three articles that calculated the economic value of the service provided by bats (e.g. Cleveland *et al.* 2006, Boyles *et al.* 2011, Wanger *et al.* 2014).

Discussion

There seems to be a relationship between the large number of studies on the diet of *Eptesicus fuscus, Myotis lucifugus,* and *Tadarida brasiliensis,* the ease of capturing these species and the accessibility of their roosts compared to other insectivorous bats (Brigham and Saunders 1990, Whitaker *et al.* 1996, Whitaker and Rodríguez-Durán 1999, Whitaker *et al.* 1999, Agosta and Morton 2003, Agosta *et al.* 2003, McWilliams 2005, Whitaker and Barnard 2005, Feldhamer *et al.* 2009). Two out of these three species have a widespread distribution in the Americas; however most of the studies that have used these species were done in United States or Canada. *M. lucifugus* is restricted to North America (Arroyo-Cabrales and Ticul Álvarez Castaneda 2008), so the existing studies cover most of its range except Mexico. The range of *E. fuscus*' extends from Alaska and southern Canada to Colombia, northern Brazil, the Greater Antilles, Bahamas, and Barbados (Miller *et al.* 2008), but it has not been studied in Latin American countries. *T. brasiliensis* is found from southern Brazil, Bolivia, Argentina, and Chile to Oregon, southern Nebraska, and Ohio and in the Greater and Lesser Antilles (Bárquez *et al.* 2008), with two out of eight studies done in Puerto Rico (e.g. Whitaker *et al.* 1999, Whitaker and Weeks 2001).

The examples given for these three species are representative of a trend in articles about the diet of insectivorous bats. Most of the published articles are concentrated in temperate regions, such as the United States. The large proportion of studies done in temperate regions could be explained by several factors. First, developed countries are usually located in these regions, so funding might be easier to obtain than in other places. Also, temperate regions usually have fewer bat species and they are either all insectivorous and dominate the bat ensemble of the area, so bat research has to be focused on what is available.

The large amount of research about the diet of insectivorous bats in temperate regions is congruent with the high number of studies done with vespertilionids. This family, unlike other insectivorous bat families, has a cosmopolitan distribution (Nowak 1994) and a high number of species (Simmons 2005), which should allow studies to be conducted around the world and with many different species. For example, the genus *Myotis* has around 109 species in the world (Simmons 2005), and 31 of them have had their diet studied at least once. However, the study sites used do not represent their cosmopolitan distribution but are constrained to temperate regions. The few exceptions are species that are endemic or have small distributions, so the studies must be done in a specific region (e.g. Jones *et al.* 2006, Ma *et al.* 2008).

In the reviewed articles, researchers obtained data about a bat's diet in three different ways: sampling stomach or fecal contents, or from droppings or culled parts in roosts. When using stomach contents, the analysis becomes easier because the insects are partially intact; however, the animal must be sacrificed to carry out such a study (Kunz and Whitaker 1983). When analyzing feces, insects are more concentrated and the bat is not killed (Kunz and Whitaker 1983). Nevertheless, fecal analyses present a bias because some insects survive digestion better than others, for example hard-bodied species survive better than those with soft bodies (Whitaker *et al.* 1981, Kunz and Whitaker 1983, Whitaker and Barnard 2005). Since chitin is almost indigestible by insectivorous bats, fecal analyses can provide a rather good evaluation of their diet (Whitaker and Barnard 2005). These analyses can also become more complicated because some individuals cull parts of their prey before ingesting them (Kunz and Whitaker 1983), which helps explain why some researches also collected insect parts directly from the roost (Jacobs 1999, Aspetsberger *et al.* 2003). However, only collecting culled parts or droppings can underestimate the richness of insect species eaten by the bats because it focuses on larger prey, which need culling before consumption (Vaughan 1997). Moreover, this only works with bat species with known feeding roosts (Alberdi *et al.* 2012). If the diet study is not using molecular techniques, we believe that the best way to obtain a more complete survey of the eaten prey is to combine techniques (like fecal contents and collecting parts from the roost).

Visually analyzing stomach or fecal contents in order to study bats' diets can be complicated, and, due to the damage of the morphological features during digestion, identification to lower taxonomic levels is difficult to achieve (Alberdi *et al.* 2012). In order to solve these kinds of issues and thanks to current developments, recent studies have started using molecular techniques, such as DNA barcodes to identify fecal components to lower taxonomic levels (e.g. Clare *et al.* 2009, Zeale *et al.* 2011, Bohmann *et al.* 2011, Clare *et al.* 2011, Alberdi *et al.* 2012). This identification of diet components to lower taxonomic levels has several benefits, such as providing an insight into determined predator-prey relationships (Dodd and Lacki 2007) and studying other habitat parameters (Clare *et al.* 2011).

A bat's feeding habits can also be expressed using a frequency percentage or a total enumeration. The frequency percentage is based on the number of animals in which one prey was found, and the total enumeration counts the minimal number of prey using a reconstruction of the parts found. However, the data interpretation changes if these two methods are used instead of volume percentage (Anthony and Kunz 1977, Kunz and Whitaker 1983, Ramos *et al.* 2002, Lee and McCracken 2004, Johnson *et al.* 2007). Since most articles use volume percentage, it is preferable to utilize it to explain a bat's diet, so that comparisons can be more readily made with other studies (Kunz and Whitaker 1983, Matthews *et al.* 2010).

Due to the different biases, i.e. the advantages and disadvantages present in the different kinds of traps used to capture insects, it is recommended to use several types in order to reduce the potential errors (Brigham and Saunders 1990, Feldman *et al.* 2000, Brack and LaVal 2006, Ober and Hayes 2008, Lacki *et al.* 2009). Evaluating insect abundance and potential prey for bats is complicated because not all the insects of a census are detected equally by bats (Kunz 1988, Whitaker *et al.* 1994, Whitaker *et al.* 1996, Wickramasinghe *et al.* 2004, Burles *et al.* 2008). Also, since bat activity is influenced by time, climate, habitat variables, and capture technique, it is important to capture insects at the same time and place when bats are feeding (Kunz 1988, McWilliams 2005, Debelica *et al.* 2006). Even though researchers can take precautions to reduce errors, obtaining non biased information about available prey for bats is impossible (Kunz 1988, Whitaker 1994). Emulating how bats hunt may help reduce potential errors when obtaining information about available insects. Finally, it is important to determine if bats are feeding in a certain place and how often they do so in one site per night (Wickramasinghe *et al.* 2003).

It has often been observed that, due to the contents of some insectivorous bats' diet, these species might serve in biological pest control (Agosta 2002, Leelapaibul *et al.* 2005, Aguiar and Antonini 2008, Kunz *et al.* 2011). One of the analyzed studies managed to calculate the real economic value provided by *Tadarida brasiliensis* (Molossidae) working as a pest control agent in cotton plantations in Texas and New Mexico. This service was valued at 741 000 USD per year (Cleveland *et al.* 2006). Using this study, Boyles *et al.* (2011) managed to estimate that losing bats in North America could lead to a loss ranging from $3.7 billion/year to $53 billion/year. Another study calculated that the interaction of *Tadarida plicata* (Molossidae) in rice plantations in Thailand could possess a value of more than 1.2 million USD per year (Wanger *et al.* 2014). Scientific papers like these three strongly suggest that carrying out more studies on this topic may provide a real value to the environmental services provided by insectivorous bats, which might translate into better farmer-bat relationships and play an important role in bat conservation.

The Neotropics seem like an adequate area to start researching this topic. The forests in these areas are facing constant deforestation threats due to change in land use (García-Barrios *et al.* 2009), and, as a result of the use of agrochemicals and loss of natural habitats, agricultural intensification is one of the major threats to biodiversity (Fischer *et al.* 2011). Also, bats are the most abundant and diverse group of mammals in the Neotropics (Medellín *et al.* 2000), and it has been observed in Costa Rica that several aerial insectivorous species are feeding over banana and pineapple plantations (pers. obs.). Even if researching this topic in the Neotropics seems like a challenge (due to the high amount of bat and insects species available), it could lead to positive results that might aid in bat conservation.

In conclusion, evaluating the diet of insectivorous bats can become a complicated matter due to the diversity of available techniques and the bias present in each one of them. However, it seems best to combine the largest possible number of techniques to minimize the errors. Also, elaborating an insect census in the study site is important due to the diversity of places used by insectivorous bats to feed and the differences between them. These studies can become of great interest if they are taken a step further when calculating the environmental services provided by insectivorous bats as biological control agents, and they could become vital conservation tools in the Neotropics due to the high diversity and abundance of bats and insects and to the agricultural intensification problem in the area.

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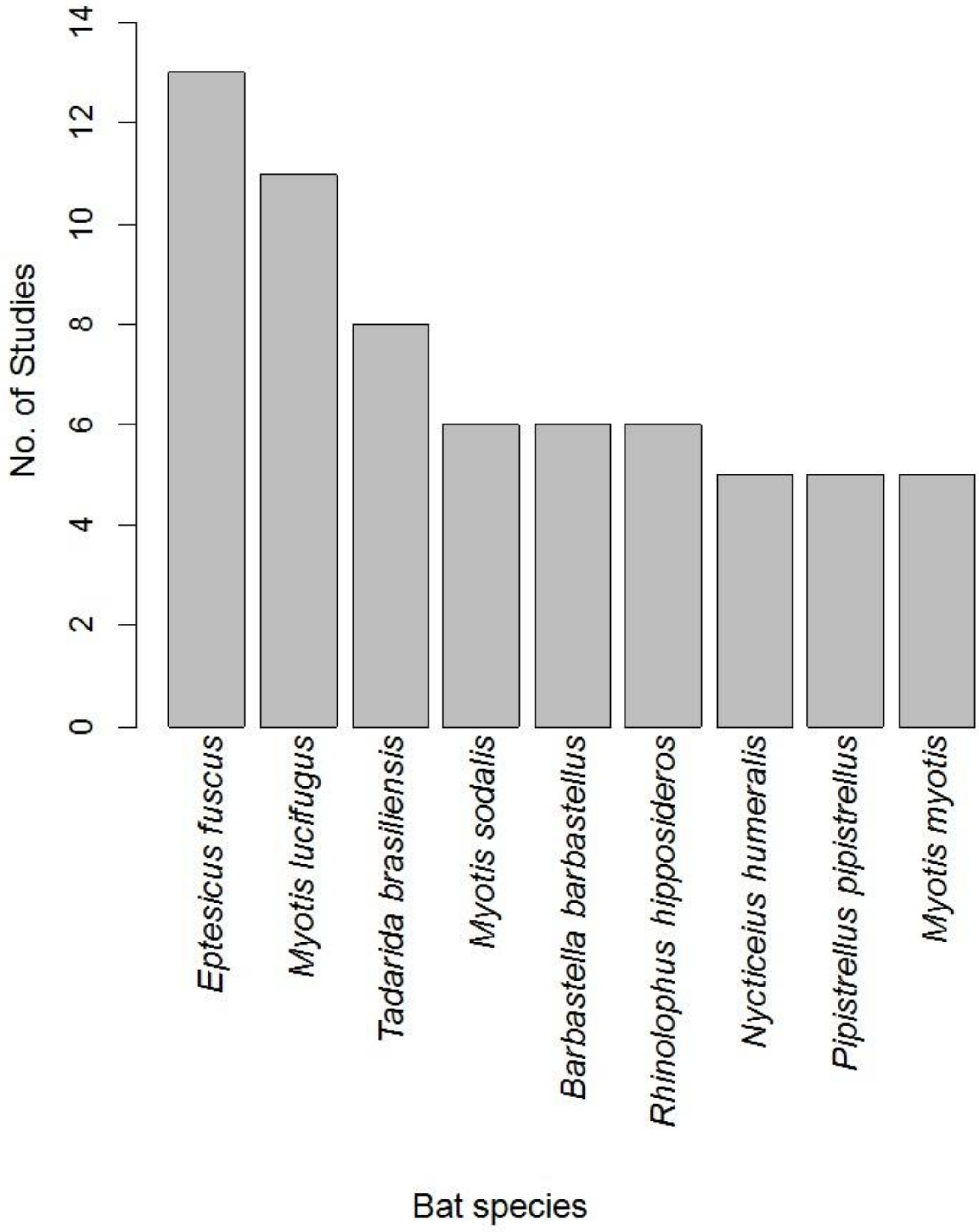

Fig 1. Top nine aerial insectivorous bat species for which diet studies have been done and number of articles published on the subject.

Note. The species with fewer than five studies are shown in the appendix.

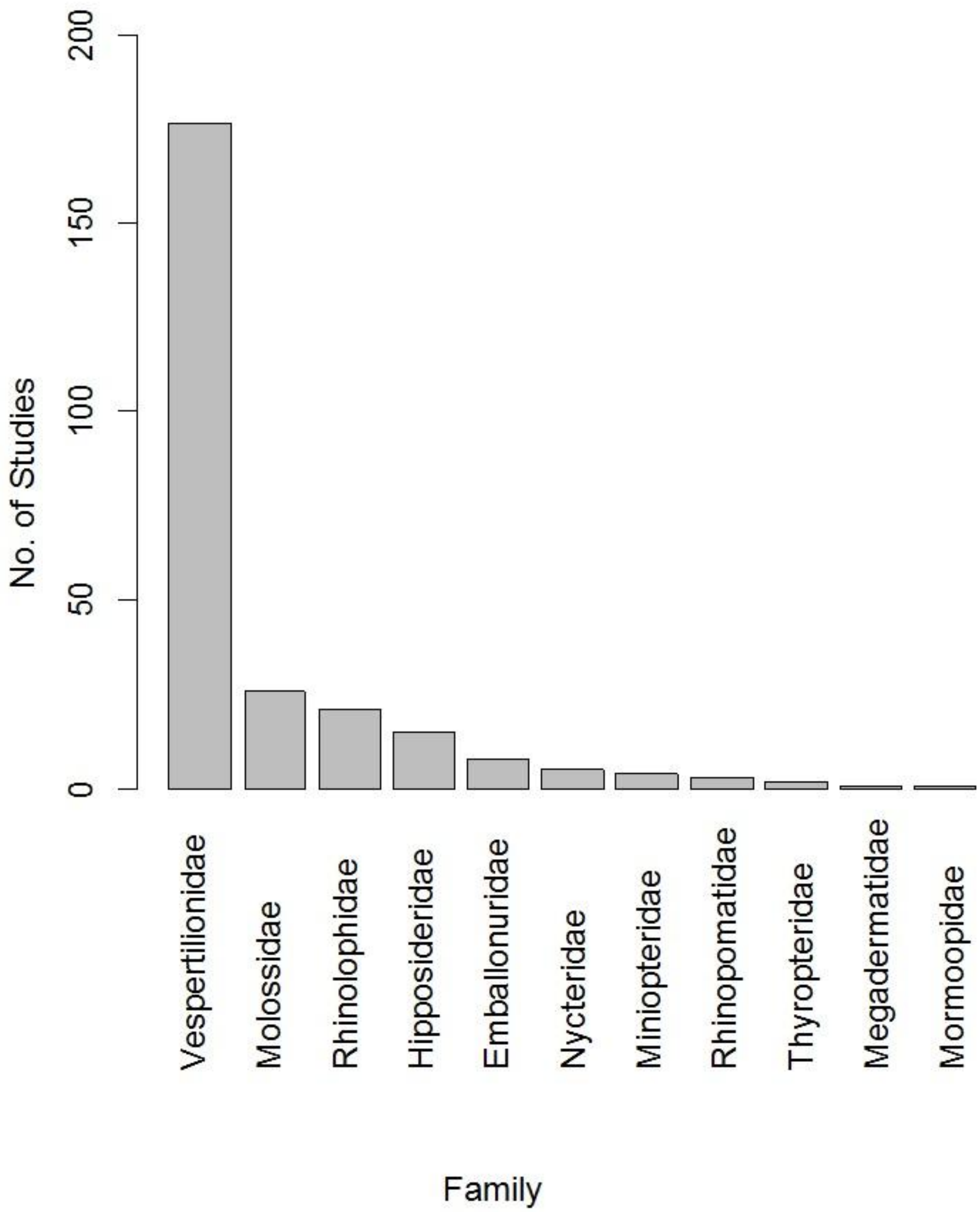

Fig 2. Number of times bat families have been included in studies done regarding aerial insectivorous bats' diets.

Note. The sum of the number of articles per family is higher than 135 because some articles studied several species.

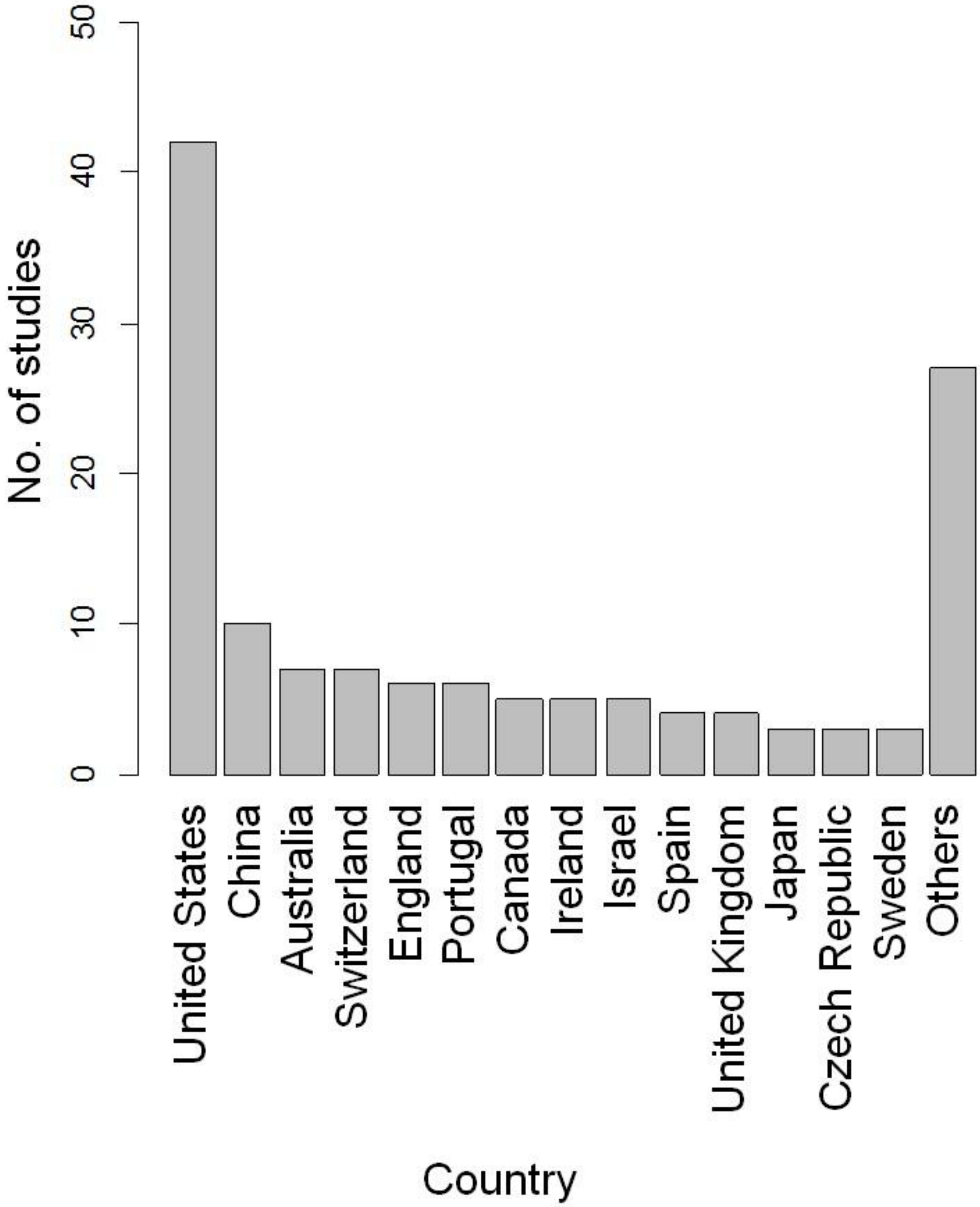

Fig. 3. Number of studies done on aerial insectivorous bats' diets by country in which the field work was done.

Note. The countries with only one study are: Afghanistan, Belgium, Bolivia, Costa Rica, Italy, Kazakhstan, Latvia, Mexico, Pakistan, Poland, Seychelles, Slovenia, Sri Lanka, Swaziland, South Africa, Tajikistan, Tanzania, Tasmania, Uzbekistan, Zambia, Zimbabwe.

Note. The countries with two studies are: Brazil, India, Iran, Germany, Kirghizstan, Madagascar, Puerto Rico, Slovakia, Thailand.

Table 1. Techniques used to capture insects during studies of the diet of aerial insectivorous bats.

Type of trap	Trap	Important aspects
Non attractive	Suction	Useful in heights close to the ground. Efficiency varies with wind speed, insect size, and how well the fan works.
	Rotator traps	Efficiency is somewhat independent of wind speed until it exceeds the trap's speed.
	Tow nets	The reachable height is limited and subject to the type of terrain and the vehicle used. Turbulence caused by the vehicle should be avoided.
	Malaise traps	Advantages: simple design, versatility. Disadvantages: if it is placed at ground level, it can be biased toward capturing insects that are not available to aerial insectivorous bats; biased toward capturing Diptera and Hemiptera; does not work well for temporary sampling.
	Interception traps	Advantages: easy to carry and to assemble in the field. Disadvantages: extremely directional.
	Sticky traps	Advantages: highly versatile and portable, low assembling cost, easy to use. Disadvantages: commercial adhesives are not very soluble, so it is hard to separate the specimens.
	Emergence traps	Advantages: cheap, work for temporary studies, portable.
	Pitfall traps	Effectiveness is influenced by its shape, amount, material, and position in wind and vegetation. Used for diet studies of ground-feeding insectivorous bats.
Attractive	Chemical	They use chemicals, like pheromones, to attract insects.
	Light	They use light to attract insects. Broadly used in insect census.

Apéndices

Apéndice 1.1

Table 1. Total insect individuals captured in the flight interception trap by family in each site category.

Order	Family	Number of individuals captured Banana	Forest	Pineapple
Coleoptera	Anthicidae		1	
	Bostrichidae			1
	Carabidae		2	1
	Chrysomelidae		2	2
	Ciidae			1
	Coccinelidae	1	3	2
	Curculionidae	2	9	8
	Elateridae		1	
	Erotylidae	1	1	2
	Eucnemidae		2	
	Leiodidae		1	
	Nitidulidae		1	2
	Not identified	1	1	
	Ptiliidae		2	
	Ptilodactylidae	1		
	Scarabaeidae		2	5
	Staphylinidae	4	4	104
	Tenebrionidae		1	2
Collembola	Not identified	1	1	
Dermaptera	Anisolabididae		2	
	Labiidae		1	
Diptera	Acroceridae			2
	Cecidomyiidae		3	
	Ceratopogonidae	5		3
	Chironomidae	1		
	Chloropidae	1		2
	Culicidae		1	2
	Drosophilidae	6	1	3
	Not identified	1		1
	Psychodidae	55		
	Sarcophagidae	1		
	Scatopsidae			2
	Simuliidae	10	1	1
	Tephritidae			2
	Ulidiidae	1		
	Xylomyidae			1
Hemiptera	Achilidae		2	
	Alydidae		1	1

Table 1. Continued

Order	Family	Number of individuals captured		
		Banana	Forest	Pineapple
Hemiptera	Aphididae	6		
	Cercopidae	1	1	
	Cicadellidae		1	2
	Coreidae		1	1
	Cydnidae		5	1
	Miridae	2		
	Pentatomidae		1	
	Pyrrhocoridae	1		
Hymenoptera	Apidae		1	
	Bethylidae		1	
	Formicidae	8	20	5
	Not identified		1	
	Pergidae		1	
	Scelionidae	1		
	Trigonalidae		2	
	Vespidae		1	
Lepidoptera	Arctiidae			1
	Gealeachioidea (superfamily)			1
	Not identified (Microlepidoptera)	1	1	
	Not identified		2	1
Psocoptera	Not identified			15
Unidentified apterygote	Not identified		2	

Apéndice 2.1

Table 1. Number and reference of diet studies, listed by aerial insectivorous bat family, genus, and species.

Family	Genus	Species	Number of studies	References
Emballonuridae	*Centronycteris*	*C. maximiliani*	1	Bernard 2002
	Coleura	*C. seychellensis*	1	Gerlach and Taylor 2006
	Cormura	*C. brevirostris*	1	Bernard 2002
	Rhynchonycteris	*R. naso*	1	Aguirre *et al.* 2003
	Saccopteryx	*S. bilineata*	1	Bernard 2002
		S. canescens	1	Bernard 2002
		S. leptura	1	Bernard 2002
	Taphozous	*T. melanopogon*	1	Wei *et al.* 2008
Hipposideridae	*Asellia*	*A. tridens*	3	Whitaker *et al.* 1993, Feldman *et al.* 2000, Whitaker and Yom-Tov 2002
	Aselliscus	*A. stoliczkanus*	1	Li *et al.* 2007
	Cloeotis	*C. percivali*	1	Findley and Black 1983
	Hipposideros	*H. ater*	1	Pavey and Burwell 2000
		H. caffer	1	Findley and Black 1983
		H. cervinus	1	Pavey and Burwell 2000
		H. commersoni	1	Rakotoavirelo *et al.* 2007
		H. diadema	2	Pavey and Burwell 1997, Pavey and Burwell 2000
		H. turpis	1	Fukui *et al.* 2009
	Rhinonicteris	*R. aurantia*	1	Churchill 1994
	Triaenops	*T. furculus*	1	Rakotoavirelo *et al.* 2007
		T. rufus	1	Rakotoavirelo *et al.* 2007
Megadermatidae	*Megaderma*	*M. lyra*	1	Goonatilake *et al.* 2005
Miniopteridae	*Miniopterus*	*M. fuscus*	1	Fukui *et al.* 2009
		M. manavi	1	Rakotoavirelo *et al.* 2007
		M. shreibersii	2	Findley and Black 1983, Presetnik and Aulagnier 2013
Molossidae	*Cynomops*	*C. abrasus*	1	Bernard 2002
		C. greenhalli	1	Bernard 2002
	Eumops	*E. glaucinus*	1	Aguirre *et al.* 2003
		E. hansae	1	Aguirre *et al.* 2003
	Molossops	*M. temminckii*	1	Aguirre *et al.* 2003
	Molossus	*M. molossus*	1	Aguirre *et al.* 2003
		M. rufus	2	Aguirre *et al.* 2003, Fenton *et al.* 1998

Table 1. Continued

Family	Genus	Species	No. of studies	References
Molossidae	*Nyctinomops*	*N. femorosaccus*	1	Matthews *et al.* 2010
		N. macrotis	2	Sparks and Valdez 2003, Debelica *et al.* 2006
	Otomops	*O. madagascariensis*	1	Andriafidison *et al.* 2007
	Tadarida	*T. brasiliensis*	8	Kunz *et al.* 1995, Whitaker *et al.* 1996, Whitaker and Rodríguez-Durán 1999, Whitaker *et al.* 1999, Lee and McCracken 2005, McWilliams 2005, Cleveland *et al.* 2006, Matthews *et al.* 2010
		T. condylura	1	Bohmann *et al.* 2010
		T. plicata	2	Leelapaibul *et al.* 2005, Wanger *et al.* 2014
		T. pumila	2	Aspetsberger *et al.* 2003, Bohmann *et al.* 2011
		T. teniotis	1	Whitaker *et al.* 1993
Mormoopidae	*Pteronotus*	*P. parnellii*	1	Bernard 2002
Nycteridae	*Nycteris*	*N. macrotis*	1	Findley and Black 1983
		N. thebaica	3	Findley and Black 1983, Feldman *et al.* 2000, Seamark and Bogdanowicz 2002
		N. woodi	1	Findley and Black 1983
Rhinolophidae	*Rhinolophus*	*R. blasii*	1	Findley and Black 1983
		R. clivosus	2	Whitaker *et al.* 1993, Feldman *et al.* 2000,
		R. euryale	2	Goiti *et al.* 2004, Andreas *et al.* 2013
		R. ferremequinum	4	Jones 1990, Wickramasinghe *et al.* 2004, Ma *et al.* 2008, Andreas *et al.* 2013
		R. hipposideros	6	Mcaney and Fairley 1989, Feldman *et al.* 2000, Wickramasinghe *et al.* 2004, Bontadina *et al.* 2008, Williams *et al.* 2010, Andreas *et al.* 2013

Table 1. Continued

Family	Genus	Species	Number of studies	References
Rhinolophidae	*Rhinolophus*	*R. megaphyllus*	1	Pavey and Burwell 2004
		R. mehelyi	2	Sharifi and Hemmati 2004, Salsamendi *et al.* 2008
		R. perditus	1	Fukui *et al.* 2009
		R. simulator	1	Findley and Black 1983
		R. swinnyi	1	Findley and Black 1983
Rhinopomatidae	*Rhinopoma*	*R. hardwickii*	1	Whitaker and Yom-Tov 2002
		R. microphyllum	2	Sharifi and Hemmati 2002, Whitaker and Yom-Tov 2002
Thyropteridae	*Thyroptera*	*T. tricolor*	2	Bernard 2002, Dechmann *et al.* 2006
Vespertilionidae	*Antrozous*	*A. pallidus*	1	Whitaker *et al.* 1981
	Barbastella	*B. barbastellus*	6	Rydell *et al.* 1996, Sierro and Arlettaz 1997, Wickramasinghe *et al.* 2003, Wickramasingue *et al.* 2004, Zeale *et al.* 2011, Andreas *et al.* 2012
		B. leucomelas	1	Sierro and Arlettaz 1997
	Chalinolobus	*C. gouldii*	1	O'Neill and Taylor 1989
		C. morio	1	O'Neill and Taylor 1989
	Corynorhinus	*C. rafinesquii*	1	Hurst and Lacki 1997
		C. townsendii	4	Whitaker *et al.* 1981, Sample and Whitmore 1993, Leslie and Clark 2002, Ober and Hayes 2008
	Eptesicus	*E. bottae*	1	Feldman *et al.* 2000,
		E. brasiliensis	1	Bernard 2000
		E. chiriquinus	1	Bernard 2000
		E. furinalis	2	Aguirre *et al.* 2003, Aguiar and Antonini 2008

Table 1. Continued

Family	Genus	Species	Number of studies	References
	Eptesicus	*E. fuscus*	13	Whitaker *et al.* 1981, Brigham and Saunders 1990, Whitaker and Weeks 2001, Agosta 2002, Agosta *et al.* 2003, Agosta and Morton 2003, Whitaker 2004, Whitaker and Barnard 2005, Lacki *et al.* 2007, Ober and Hayes 2008, Storm and Whitaker 2008, Feldhamer *et al.* 2009, Moosman *et al.* 2012
		E. nilssonii	3	Rydell 1986, Rydell 1989, Gajdosik and Gaisler 2004
		E. sagittula	1	O'Neill and Taylor 1989
		E. serotinus	2	Wickramasinghe *et al.* 2003, Gajdosik and Gaisler 2004
	Euderma	*E. maculatum*	1	Painter *et al.* 2009
Vespertilionidae	*Falsistrellus*	*F. tasmaniensis*	1	O'Neill and Taylor 1989
	Ia	*I. io*	1	Thabah *et al.* 2007
	Lasionycteris	*L. noctivagans*	3	Whitaker *et al.* 1981, Lacki *et al.* 2007, Ober and Hayes 2008
	Lasiurus	*L. borealis*	4	Feldhamer *et al.* 1995, Whitaker 2004, Clare *et al.* 2009, Feldhamer *et al.* 2009
		L. cinereus	4	Belwood and Fullard 1984, Jacobs 1999, Ober and Hayes 2008, Perlik *et al.* 2012
	Murina	*M. florium*	1	Schulz and Hannah 1998
		M. leucogaster	1	Ma *et al.* 2008
	Myotis	*M. albescens*	1	Aguirre *et al.* 2003
		M. austroriparius	1	Feldhamer *et al.* 2009
		M. bechsteinii	2	Wickramasinghe *et al.* 2003, Wickramasinghe *et al.* 2004

Table 1. Continued

Family	Genus	Species	Number of studies	References
	Myotis	*M. blythii*	1	Arlettaz *et al.* 1998
	Myotis	*M. brandtii*	1	Wickramasinghe *et al.* 2003
		M. californicus	3	Whitaker *et al.* 1981, Lacki *et al.* 2007, Ober and Hayes 2008
		M. capaccinii	1	Almenar *et al.* 2008
		M. chinensis	1	Ma *et al.* 2008
		M. dasycneme	1	Ciechanowski and Zapart 2012
		M. daubentonii	2	Flavin *et al.* 2001, Wickramasinghe *et al.* 2003
		M. emarginatus	1	Steck and Brinkmann 2006
		M. evotis	3	Whitaker *et al.* 1981, Lacki *et al.* 2007, Ober and Hayes 2008
		M. goudoti	1	Rakotoavirelo *et al.* 2007
Vespertilionidae		*M. grisescens*	1	Brack and LaVal 2006
		M. keenii	1	Burles *et al.* 2008
		M. leibii	1	Whitaker *et al.* 1981
		M. lucifugus	11	Belwood and Fenton 1976, Anthony and Kunz 1977, Whitaker *et al.* 1981, Kunz and Whitaker 1983, Lee and McCracken 2004, Whitaker 2004, Burles *et al.* 2008, Ober and Hayes 2008, Feldhamer *et al.* 2009, Clare *et al.* 2011, Moosman *et al.* 2012
		M. myotis	5	Kervyin 1996, Arlettaz *et al.* 1997, Pereira *et al.* 2002, Ramos *et al.* 2002, Zahn *et al.* 2007
		M. mystacinus	1	Wickramasinghe *et al.* 2003

Table 1. Continued

Family	Genus	Species	Number of studies	References
	Myotis	*M. nattereti*	4	Shiel *et al.* 1991, Whitaker *et al.* 1993, Arlettaz 1996, Zeale *et al.* 2011
		M. nigricans	2	Aguirre *et al.* 2003, Aguiar and Antonini 2008
		M. occultus	1	Valdez and Bogan 2009
		M. pequinius	1	Jones *et al.* 2006
		M. pilosus	3	Ma *et al.* 2003, Ma *et al.* 2005, Ma *et al.* 2006
		M. riparius	1	Bernard 2002
		M. septentrionalis	4	Lee and McCracken 2004, Whitaker 2004, Feldhamer *et al.* 2009, Lacki *et al.* 2009
		M. simus	1	Aguirre *et al.* 2003
Vespertilionidae		*M. sodalis*	6	Brack and LaVal 1985, Kurta and Whitaker 1998, Lee and McCracken 2004, Whitaker 2004, Tuttle *et al.* 2006, Feldhamer *et al.* 2009
		M. thysanodes	1	Ober and Hayes 2008
		M. velifer	1	Kunz 1974
		M. volans	4	Whitaker *et al.* 1981, Johnson *et al.* 2007, Lacki *et al.* 2007, Ober and Hayes 2008
		M. yumanensis	2	Whitaker *et al.* 1981, Ober and Hayes 2008
	Nyctalus	*N. lasiopterus*	1	Dondini and Vergari 2000
		N. leisleri	4	Shiel *et al.* 1998, Waters *et al.* 1999, Wickramasinghe *et al.* 2003, Kanuch *et al.* 2005a
		N. noctula	4	Gloor *et al.* 1995, Mackenzie and Oxford 1995, Wickramasinghe *et al.* 2003, Kanuch *et al.* 2005b

Table 1. Continued

Family	Genus	Species	Number of studies	References
	Nycticeius	*N. humeralis*	5	Whitaker and Clem 1992, Feldhamer *et al.* 1995, Whitaker 2004, Geluso *et al.* 2008, Feldhamer *et al.* 2009
	Nyctophilus	*N. geoffroyi*	1	O'Neill and Taylor 1989
		N. timoriensis	1	O'Neill and Taylor 1989
	Otonycteris	*O. hemprichii*	3	Whitaker *et al.* 1993, Arlettaz *et al.* 1995, Fenton *et al.* 1999
	Perimyotis	*P. subflavus*	1	Feldhamer *et al.* 2009
	Phoniscus	*P. papuensis*	2	Schulz and Wainer 1997, Schulz 2000
	Pipistrellus	*P. abramus*	1	Hiray and Kimura 2004
		P. ariel	2	Whitaker *et al.* 1993, Feldman *et al.* 2000,
		P. hesperus	1	Whitaker *et al.* 1981
		P. kuhlii	2	Whitaker *et al.* 1993, Feldman *et al.* 2000,
Vespertilionidae		*P. nathusii*	1	Krüger *et al. In press*,
		P. pipistrellus	5	Swift *et al.* 1985, Barlow 1997, Wickramasinghe *et al.* 2003, Wickramasinghe *et al.* 2004, Zeale *et al.* 2011
		P. pygmaeus	2	Wickramasinghe *et al.* 2003, Wickramasinghe *et al.* 2004
		P. rueppellii	2	Whitaker *et al.* 1993, Feldman *et al.* 2000
		P. subflavus	1	Whitaker 2004
		P. tenuis	1	Whitaker *et al.* 1999
	Plecotus	*P. auritus*	3	Rydell 1989, Shiel *et al.* 1991,
		P. austriacus	2	Whitaker *et al.* 1993, Feldman *et al.* 2000
		P. macrobullaris	1	Alberdi *et al.* 2012
	Scotophilus	*S. leucogaster*	1	Barclay 1985
	Tylonycteris	*T. pachypus*	1	Zhang *et al.* 2005
		T. robustula	1	Zhang *et al.* 2005

Table 1. Continued

Family	**Genus**	**Species**	**Number of studies**	**References**
Vespertilionidae	*Vespadelus*	*V. regulus*	1	O'Neill and Taylor 1989
		V. vulturnus	1	O'Neill and Taylor 1989
	Vespertilio	*V. murinus*	1	Rydell 1992
		V. sinensis	1	Fukui and Agetsuma 2010