Mist Net Interaction, Sampling Effort, and Species of Bats Captured on Montserrat, British West Indies

BY

Roxanne J. Larsen

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This thesis is approved as a creditable and independent investigation by a candidate for the Master of Science degree and is acceptable for meeting the thesis requirements for this degree. Acceptance of this thesis does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

Dr. Scott Pedersen
Thesis Advisor   Date

Dr. Thomas Cheesbrough
Head, Biology/Microbiology   Date

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Abstract

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Mist nets are commonly used to survey bat populations and to estimate bat biodiversity, but several studies have found that mist net capture data and methods are biased due to a number of factors, including size and placement of nets, and the frequency at which investigators check their nets (Francis 1989; Jenni and Leuenberger 1996; Kunz and Anthony 1977; Simmons and Voss 1998). Despite the wealth of literature and anecdotal reports, few investigators have quantified the interactions of bats with mist nets directly (Berry et al. 2004; Francis 1989; Kunz and Anthony 1977; Lang et al. 2004; MacCarthy et al. 2006).

I employed night vision camcorders to monitor bat behavior when bats encountered a mist net and then utilized these data to re-evaluate years of survey data collected on Montserrat, Lesser Antilles. Observations were conducted on four successive nights at four different sites that provided evidence of avoidance-learning behavior. I recorded 2523 bat passes on 43.3 hours of videotape during work in July 2005 and June 2006. When a mist net was present, 5.4% of bats captured on film came into contact with the net giving an overall capture rate of 3.2% (range 0–10.3%).

After observing the low capture rates, I decided to take a closer look at surveys conducted on Montserrat from 1994, 1997-98, and 2000-2006. The amount of effort expended in the 10 years of survey was important in determining numbers of bats being captured. Several species were not being caught on a regular basis on Montserrat; therefore a careful analysis of the previous surveys was conducted to find more species specific information. Using the Jamaican fruit-eating bat (*Artibeus jamaicensis*) as a reference species, I reassessed some assumptions about capture biases.

Mist nets did not accurately sample bats utilizing flyways on Montserrat and such fieldwork thereby generated potentially misleading data. Mist nets are valuable tools used to survey bats, but the limitations of mist nets must be considered when choosing appropriate capture devices to study the bat fauna of a particular area. Biodiversity assessments and conservation guidelines based on short-term mist net surveys alone are not sufficient or reliable. The pragmatic solution is to repeatedly sample a target region in different seasons and years, utilize various netting sites and net sets, carefully analyze species over time, and quantify and account for biases in sampling methods.

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Chapter 1

INTRODUCTION

Of the approximately 4600 species of extant mammals, bats make up one fourth of the total species, a number that is increasing as more careful analyses are conducted (Wilson and Reeder 2005). Bats are distributed globally within numerous complex ecosystems, but are not found in the polar regions due to a lack of food year round. Bats occupy several feeding guilds including fruigivores, insectivores, nectivores, carnivores, piscivores, and sanguivores. Seventy percent of all bats are insectivorous, and each bat can eat several hundred insects in one night (Adams 2003), reducing pests and other vectors of disease. Bats are also vital in pollination and seed dispersal for much of the flora found in tropical forests (Neuweiler 2000). As well as being important in the overall flow of ecosystems, bats also serve as biological indicators of disturbance and can be used to follow recovery phases in disturbed environments via tracking their overall health and reproductive conditions (Fenton 1997; Fenton et al. 1992).

In order to study bats, they must first be caught and examined. There are several methods that have been used to capture bats, but few are effective or efficient. Methods include mist nets, hoop nets, hand capture, funnel or bag traps, canopy nets, harp traps, net flicking, throwing objects, and shotguns as described by Kunz et al. (1996). However, mist nets have been the most commonly used live capture devices for several decades and are also the most cost effective (Kunz et al. 1996).

Nets made of silk were first implemented by Japanese hunters more than 300 years ago to capture birds for food. Ornithologists brought the technique to North America and biologists began using mist nets to capture birds and bats for study (Keyes and Grue 1982; Gardner et al. 1989). One of the first recorded uses of mist nets by investigators was in a cave survey for bats by Poole (1932), as cited by Barbour and Davis (1969).

Mist Net Interaction

Mist net capture data can be biased by many factors. One of which, is the mechanism of the net itself. The match between animal/head size, mesh size, and construction of the deployed net directly affects the efficiency of the net (Jenni and Leuenberger 1996), however, as mist net design and protocols become more standardized, we frequently encounter issues relating to the amount of play in each shelf, the tension of the net, and the frequency of clearing the net of debris and captured animals. Detection and perception of the net by a bat are greatly affected by the heights at which the trapping/netting devices are placed, dimensions of the device, opportunities to avoid the device, structure of the habitat, proximity to food or water, and ambient weather and light conditions (Francis 1989; Remsen and Good 1996).

Studies in Malaysia, Borneo, French Guiana, and Panama have commented on the method of capture for various species (Kingston et al. 2003), the need for the placement of mist nets at different heights (Francis 1989; Simmons and Voss 1998), surveys over several years (Kalko et al. 1996), or estimating species abundance via captures in the net

(Simmons and Voss 1998). These issues concerning capture devices require careful consideration. Investigators have also documented decreased capture success on nights of repeated mist netting at a single site (Gram and Faaborg 1997; Simmons and Voss 1998), which is credited to a learned avoidance response by bats to the net. Bats may also respond adversely to handling once caught in the net, hence their responses are not conducive to successful mark and recapture methods (Gannon and Willig 1998; Kuenzi and Morrison 1998; Kunz and Brock 1975; Kunz and Kurta 1988; Kunz et al. 1996; LaVal 1970).

The height at which mist nets are set and timing of the survey are variables that we have better control over, but evidence suggests mist nets at ground level may provide questionable data. Bats from various feeding guilds use different portions of the ecosystem to decrease competition (Kalko and Handley 2001; Kalko et al. 1996; Simmons and Voss 1998). Nets set in varying levels of the forest have documented this “vertical stratification” in bat communities (Kalko et al. 1996). Species compositions were similar, but capture frequencies of species were different at various heights. These observations indicate the data collected may be biased and that surveys conducted at only one level of the forest need to be carefully analyzed.

Francis (1989, 1994) observed a difference in abundance and species diversity between ground level and subcanopy mist netting in peninsular Malaysia and northern Borneo. Frugivores and nectivores were less likely to be caught in mist nets set at ground level (Francis 1994). LaVal and Fitch (1977) observed evidence of differential vulnerability to capture among various species of bats in Costa Rica. Larger frugivorous phyllostomids were often caught in ground level mist nets and rarely were trapped, whereas small vespertilionids were more likely to be caught in harp traps. In Panama, capture rates of species differed significantly between nets set at ground level and nets set 3 to12m above the ground (Bonaccorso 1979). The behavioral and morphological differences between neotropical and paleotropical bats influence their interaction with and use of changing habitats within their home ranges and respective communities (Francis 1989 1994; LaVal and Fitch 1977).

These studies suggest the trophic structures of bat communities at ground level are not representative of the community as a whole. This is partly due to a lack of information regarding the vertical stratification of tropical bats, because capture is generally required for identification (Francis 1994). Therefore, a 2.6 m high net at ground level cannot possibly catch all bats flying through an area, especially those that forage in the canopy or sub-canopy. Species will be missed unless the methods of capture and the amount of effort are changed. Mist nets have been used for several years, yet bats are able to detect and avoid the net, therefore mist nets cannot be the lone sampling method for all bat species (Gannon and Willig 1998; Gram and Faaborg 1997; Kuenzi and Morrison 1998; Kunz and Brock 1975; Kunz and Kurta 1988; Kunz et al. 1996;

The most common alternative to mist nets is harp traps. As suggested by its name, the harp trap is similar to a harp, with vertically strung fishing line within a rectangular frame and a catch bag attached below (Francis 1989; Kunz et al. 1996). Constantine

(1958) first documented the use of harp traps to capture Mexican free-tailed bats (*Tadarida brasiliensis*). Traps eliminate some monotonous aspects of watching a mist net (i.e. extracting several bats at once versus one at a time). Since Constantine's first version of the harp trap, others have modified the basic design by including one to two additional banks of fishing line, which increased the number of bats caught per trap-night or simply by making the trap smaller, collapsible, and more portable (Francis 1989, Tuttle 1974).

Shooting bats with firearms as they flew or as they roosted was also a common method employed by many early field biologists (Barbour and Davis 1969; Borell 1937; LaVal and LaVal 1979; Miller 1897), yet has declined in recent years due to a new conservative ethic regarding non-lethal study and collection, and the need for museum quality specimens. Acoustic sampling, video analysis, and thermal imaging are additional high-tech alternatives to mist netting, and are being used more frequently in combination with mist netting to provide more accurate and unbiased surveys (Fenton 1997).

On Montserrat, mist nets were the method of choice for sampling, although other methods could have been used to survey the bats. However, harp traps were somewhat difficult to transport into a site and did not cover the flyway as well as mist nets. Acoustic sampling was also attempted but background noise from insects and tree frogs did not allow us to use our detectors and record a clear signal despite considerable effort to do so. Also, the majority of bats on Montserrat are of the family Phyllostomidae, which do not emit very loud echolocation signals (Fenton et al. 1992) and the structure of their signals is also less discernable among species (Kalko et al. 1996).

Another important variable observed in several studies was a decrease in capture rate under a full moon or bright moonlight (Kunz et al. 1996; Lang et al. 2004; LaVal 1970; Morrison 1978; Simmons and Voss, 1998). Such lunar phobia is common among insect gleaners and bats that cruise forest canopies for fruit. Lunar phobia has been linked to increased predation when light levels are high – bats are more visible to predators like owls and hawks (Erkert 1988; Morrison 1978).

Very few investigators document bat/net interactions directly. Despite extensive survey efforts throughout the Caribbean (Genoways et al. 1998, 2001, 2005, 2006, 2007; Larsen and Pedersen 2002; Larsen, P.A. et al. 2006; Pedersen 2001; Pedersen et al. 1996, 2003, 2005, 2006, 2007), this critical aspect of bat survey work has been neglected. However, two studies in the last few years used infrared lights and video cameras to specifically record bat interactions with the net (Lang et al. 2004; MacCarthy et al. 2006). The efforts of Lang et al. (2004) provided the incentive for employing a similar technique in an attempt to re-evaluate the last ten years of our own mist net data collected on Montserrat.

Sampling Effort

The previous section suggests a need for a new metric or at least that another perspective on the interpretation of surveys is warranted, specifically in the number of bats caught and effort applied each year. Past investigators on Montserrat decided to quantify bat abundance and animal activity via the simple metric of bats captured per net per night (Pedersen et al. 1996). Others have used a unit of bats per square meter of mist net or bats per hour to estimate numbers (Gannon and Willig 1998; Thomas and LaVal 1988). Each new quantification of numbers or activity helps to indicate the amount of effort used to capture bats, but without consistent units, comparisons of effort amongst investigators are difficult to achieve.

Since mist netting is a simple and low-tech method used to capture bats (Gardner et al. 1989; Kunz and Kurta 1988; Kunz et al. 1996; Lang et al. 2004), some have utilized bat capture rates as a proxy for fluctuations in bat populations (Pedersen et al. 1996). However, such efforts may be misleading as several studies have found that mist net capture data are biased due to a myriad of issues including survey effort, factors affecting detection of the net, type of net, the surrounding habitat, weather, and the avoidance and echolocation capabilities of bats (Francis 1989; Kuenzi and Morrison 1998; Kunz and Anthony 1977; Kunz et al. 1996; Lang et al. 2004; Remsen and Good 1996; Simmons and Voss 1998). Others may use mist net capture data to establish species inventories but may miss elusive, highly agile, or rare species due to lack of thoroughness, consistency of techniques, (Morton and Courts 1999; Pedersen et al. 2003) or simply the fact that bats readily avoid mist nets (Lang et al. 2004).

The surveys of Caribbean islands performed over the last few decades have mostly obtained general information on reproduction, age, or sex of bats, and did not look at the adequacy of the techniques used to collect these data (Genoways et al.1998; Jones and Baker 1979; Morton and Fawcett 1996; Pedersen et al. 1996, 2003, 2005, 2006, 2007; Pierson et al 1986). Organized surveys on Montserrat began in 1978 with Jones and Baker (1979). In 1984, Pierson et al. (1986) undertook another short survey and Morton and Fawcett (1996) surveyed in 1995. All other surveys were conducted by Pedersen (or some member of the Pedersen group) over the last 13 years. I will examine the years of 1994, 1997-98, and 2000-2006, to investigate how natural disasters influence the island's bat fauna, how the number of captures fluctuates over time, and to what extent mist net bias may affect such observations.

The surveys on Montserrat by Pedersen were conducted in June or July for different amounts of time each year since 1994, although not every year has been surveyed. The number of netting sites in each survey period varied from year to year in addition to the amount of time spent on the island (range from 2 to 4 weeks). Sites were sometimes chosen due to proximity to established roads and other conveniences, while the difficulty of the terrain, and distance to the site were also considered. Specific sites were not always sampled each year and the number of nets set at each locality varied from 4 to 6 depending on the amount of time before sunset, the number of individuals watching the nets, or the space available in the habitat to set up nets (Pedersen et al. 1996). Morton and Fawcett (1996) had a set number of nets, a specific radius in which the nets could be set, and a randomly generated grid of sites. However, the latter approach did not provide a more complete inventory of the bats species on Montserrat than any previous method used.

While examining the previous mist netting data on Montserrat, shorter surveys and reduced effort appeared to affect the total number of bats and bat species captured.

Short-term surveys only give an idea of the species inventory at a small period of time and were biased due to the numerous factors regarding mist nets and effort already mentioned, but also large-scale phenomenon (e.g., hurricanes, volcanoes). Long-term surveys collect several years of data, over various seasons, and can be analyzed more completely and accurately than data collected sporadically over smaller amounts of time.

Species of Bats Captured

Capture rates also are confounded by variation among species of bats: differential size, speed, agility, wing loading, mode and power of echolocation calls, age and experience of bats, characteristic foraging pattern/altitude, and the facultative use of their other senses–-vision and olfaction (Berry et al. 2004; Francis 1989; Kunz and Anthony 1977). Mist nets are biased towards bats that are larger in size, have higher wing loading, and have reduced maneuverability and agility (Francis 1989; Norberg 1987; Simmons and Voss 1998). These findings showed a tendency towards overestimation of the number of frugivorous bats as compared to other feeding guilds. Simmons and Voss (1998) stated, “frugivores blunder into mist nets more frequently than do members of other feeding guilds,” and the biases they encountered were compensated by “sustained inventory effort” and use of additional capture methods.

The abilities of some bats to escape or avoid mist nets are other aspects we must consider as factors of bias, namely the dentition of different feeding guilds. Frugivores and nectarivores with rounded teeth cannot chew through the net as well as the sharp and pointed molar and premolar teeth of insectivores or carnivores. Due to differential dependence on echolocation, net detection varies among bats. Species with loud, long distance, and high-frequency calls seem to be captured less frequently by mist nets because high frequency calls can better resolve smaller targets much earlier than quiet, short distance, low frequency calls (Phyllostomidae). Species that use high frequencies are often adapted for short-distance maneuvering in addition to their net detection capabilities. Wing morphology of the various feeding guilds also plays a key role in their ability to maneuver around clutter, control flight speed, capture prey in air, or carry prey (Norberg 1987). Additionally, different visual capabilities also affect how bats see and consequently detect the net (Galambos and Griffin 2005). As long as the effects of these factors vary among species, the proportion of species in the sample will be biased (Francis 1989), but can be taken into consideration and used to better understand bias in mist net survey results.

Montserrat was chosen for my project because of its relatively simple chiropteran fauna of ten species of bats in addition to access to a large database from its 13 documented surveys spanning 29 years. Four teams have conducted surveys on the island throughout these years, but all parties have pooled their information on the descriptions of census methods and species encountered. These surveys have resulted in an understanding that Montserrat has one piscivore (*Noctilio leporinus*), one omnivore (*Brachyphylla cavernarum*), one nectivore (*Monophyllus plethodon*), four frugivores (*Ardops nichollsi, Artibeus jamaicensis, Chiroderma improvisum, Sturnira thomasi*), and three insectivorous species (*Natalus stramineus, Tadarida brasiliensis, Molossus molossus*), representing four families—Noctilionidae, Phyllostomidae, Natalidae, and

Molossidae. Of these species, *C. improvisum and S. thomasi* are rarely encountered. For my study purposes, *N. stramineus* was excluded from capture counts and any other summarized data due to the fact that it was only hand captured in caves on the island. All records herein will be from net captures or mist netting observations.

One of the most common bats in the region is the Jamaican fruit-eating bat, *Artibeus jamaicensis*, has a distribution that spans from central Mexico across to the Florida Keys and south to Brazil and Argentina. *A. jamaicensis* is abundant throughout its range and can live up to nine years in the wild (Gardner et al. 1991). They have a bimodal polyestrous breeding pattern, with peaks of production around February to April and then again from June to August when fruit production is most likely highest. These months of parturition vary regionally and latitudinally (Fleming et al. 1972); *A. jamaicensis* breeds year-round in Mexico, Central America and the Caribbean Islands (Ortega and Castro-Arellano 2001). Each female normally gives birth to two young each year, but is capable of having 3 to 4 (Fleming et al. 1972; Ortega and Castro-Arellano 2001). As such, this species can proliferate rapidly in any area that can support its dietary needs. Roost sites are less of a concern for *A. jamaicensis* than for other Phyllostomids, which may be more selective in roost choice. With a higher rate of reproduction than most species on Montserrat and a reasonably long lifespan, *A. jamaicensis* can readily increase its numbers within a few years and has a reproductive advantage over other bat species on this island (Ortega and Castro-Arellano 2001).

Major natural disasters have caused great fluctuations in the number of bats caught in mist nets as well as the number of species caught throughout the years. On Montserrat, *A. jamaicensis* composed almost 50% of all captures in both the 1978 and 1984 surveys. Hugo destroyed vegetation in 1989 and volcanic activity disrupted the faunal composition dramatically leaving the *A. jamaicensis* population greatly reduced to just 17% of total captures by 1994 (Pedersen et al. 1996). All species of bats had declined at this time, but *A. jamaicensis* was no longer dominant during this period. The decline in *A. jamaicensis*, and an increase in other species could be due to many factors including roost destruction and interruption of reproduction.

Examining studies from other regions in which surveys of the neotropical bat fauna were conducted. The genus *Artibeus* appears in most if not all netting sites as the numerically dominant genus, even though they may not be the highest percentage of known species. Simmons and Voss (1998) found similarly high percentages of frugivores in Paracou, French Guiana wherein frugivores accounted for a total of 63% of overall captures, yet were only 22% of the known species in Paracou. On Montserrat, the fruigivores made up 60% of the known species (Pedersen et al. 1996). Kalko et al. (1996) also saw dominance of frugivores (81.1%; specifically *Artibeus* species) in the nets on Barro Colorado Island (BCI), Panama. Since 2000, *A. jamaicensis* had been the numerically dominant species on Montserrat (67%), had high capture numbers, and were easily captured at all of my sites in 2005 and 2006. Therefore, I used *A. jamaicensis* as a reference species in my evaluation of the previous 10 years of data.

Objectives

This study consisted of three sections, each investigating the bats of Montserrat. The first of which describes results of a bat-net interaction survey conducted during the summers of 2005-2006. The primary objectives were to: observe behaviors of bats approaching the mist net and determine if there were any changes in interactions (via increase or decrease in activity around the net) with the net on successive nights at the same site; and to determine if there was any evidence of a learning curve regarding the position of a novel obstacle, such as a mist net, in the flyway.

The second section puts the observed interaction data into context, framing it against all of the previous mist net survey data collected. The primary objectives were to: determine the number of bats caught in mist nets and the amount of effort each year; and to look at general trends in captures throughout the 10 years of previous survey including the last two years of my own study.

The last section will contain information on the individual species captured during mist netting of the island from all survey years. One species (*A. jamaicensis*) was used as an index through time to look for trends, identify sources of bias due to age or sex, and suggest methods to correct biased data. The primary objectives were: to identify specific patterns in captures over time for the bat species on Montserrat, and track categories of bats according to age, sex, and reproductive status across time.

MATERIALS AND METHODS

Location

Montserrat (16° 45' N, 62° 12' W; Fig. 1) is one of several volcanic islands that comprise the Northern Lesser Antilles. This archipelago is bordered by the Caribbean Sea to the west and the Atlantic Ocean to the east. Montserrat is a Crown colony of the United Kingdom and is 102 square kilometers (16 km long, 11km wide). It has coastal lowlands, but is mostly mountainous, with three volcanic centers – the Silver Hills in the north, the Centre Hills, and the Soufrière Hills in the south, which is the youngest and most active. The lowest elevation is at the Caribbean Sea (0m), while the highest is the ever changing lava dome in English's Crater in the Soufrière Hills volcanic complex (currently over 930m). Its climate is tropical and shows little variation throughout the year. It is often affected by hurricanes and tropical depressions that enter the region and has also experienced earthquakes as well as volcanic activity (CIA: Montserrat 2007).

Recently, comparable mist net surveys have been conducted on Montserrat (1994, 1997-98, 2000-06; Pedersen 2001; Pedersen et al. 1996, 2003, 2005, 2006, 2007; Larsen, R. J. et al. 2005, 2006). Of the 40 plus sites surveyed during these years, the sites selected for the net interaction study in 2005 and 2006 were representative of the island's biotic diversity and had previous baseline netting data. Typically, mist nets were deployed in a variety of habitats. A diversity of possible netting sites were used and were not difficult to find because the island was covered with bamboo thickets, fruit plantations, open meadows, vegetated ravines, and small streams. These streams provided pools of drinking water for both bats and small pockets of cultivated and wild fruit trees (Pedersen 2001; Pedersen et al. 1996; Larsen and Pedersen 2002; Larsen, R. J. et al. 2005, 2006). Qualifications for being a location for the net interaction study were accessibility and level of bat activity in previous years. Even though the island is not necessarily homogeneous, most factors (e.g., site composition, fruit and water availability, elevation, temperature, humidity, and light levels after sundown) were relatively similar and comparable among all possible sites.

From all the sites previously used on Montserrat, data from 16 sites were chosen as the core group used in subsequent estimation of bat activity at these sites over the years. These 16 representative sites had at least three years of mist net data and several had over five years. Six of these sites were videotaped and only four sites (Hope Springs, Sappit River, Mango Hill, and Cassava Ghaut; Fig. 2) were chosen for net-interaction analysis. Two minor eruptions of the Soufriere Hills volcano interrupted fieldwork in 2005, and the volcano erupted again two weeks prior to my arrival on Montserrat in 2006. This 2006 eruption sent boulders, mud, volcanic ash, and toxic gases down into my field sites at Hope Springs and Sappit River, effectively sterilizing both watercourses and defoliating most of the vegetation at both sites. Because these sites could not be observed in 2006, alternative sites were chosen and videotaped. Similar disturbances in the past two decades have also rendered several other mist net sites incapable of survey temporarily or permanently (Hurricane Hugo – 1989, Soufriere Hills volcano – 1997).

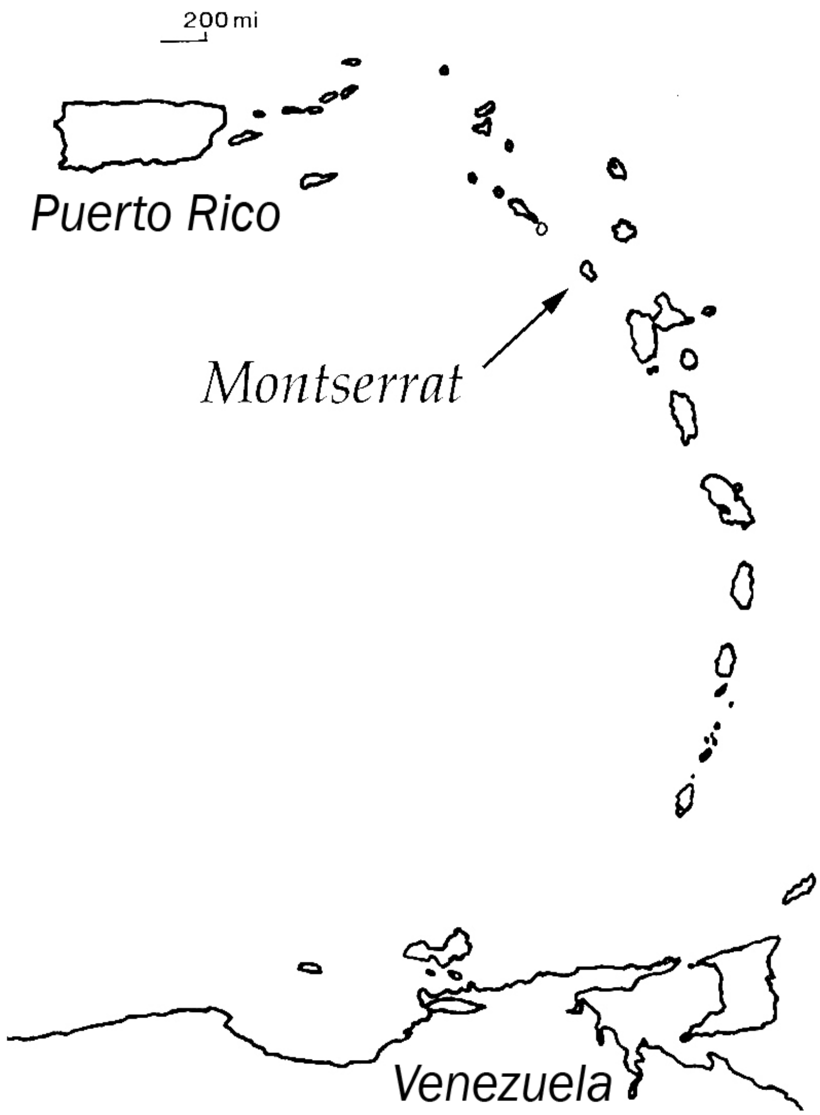

Figure 1: Map of the Lesser Antilles.

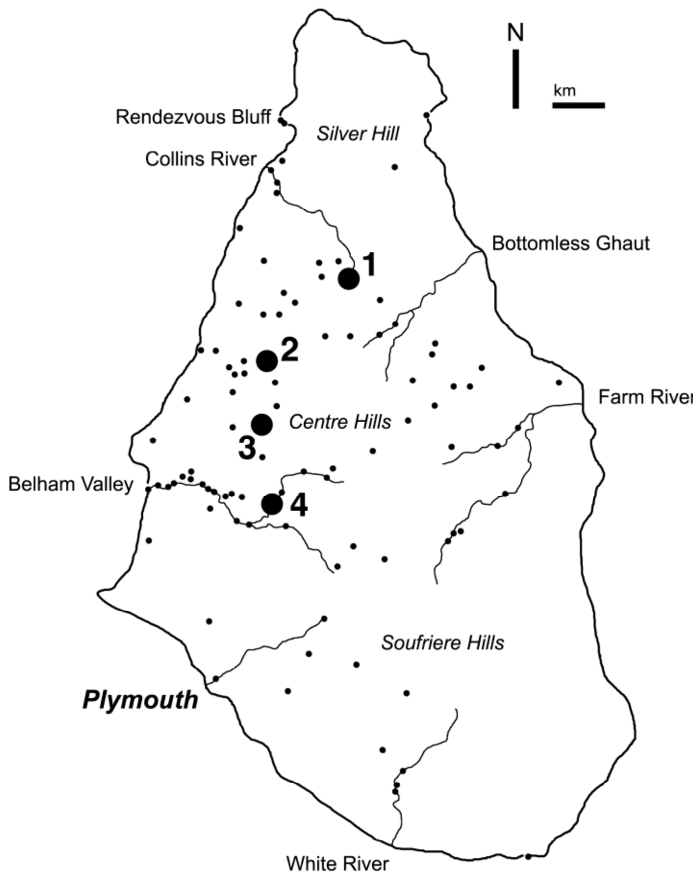

Figure 2: A map of Montserrat, West Indies; mist netted sites are indicated by small black dots; large black dots indicate four videotaped sites: **1** = Mango Hill (16° 46’ 40.0” N, 62° 11’ 43.0” W), **2** = Cassava Ghaut (16° 45’ 48.0” N, 62° 13’ 12.0” W), **3** = Hope Springs (16° 45’ 06.0” N, 62° 12’ 43.5” W), **4** = Sappit River (16° 44’ 24.5” N, 62º 12’ 27.9” W)

Equipment

The lengths of the mist nets used for the interaction study were dictated by the width of the chosen flyways (AVINET, Inc., black nylon, 4-shelf, 6-9 m wide, 2.6 m high, 38mm mesh, 50/2 denier). The single net at each location during the interaction study was set up at approximately 1800-1830 each night and came down between 2000-2030. This period of time has been shown to be the most active time frame for bats on this island (Larsen and Pedersen 2002).

The netting effort at all other localities concurrent with my 2005 – 2006 work consisted of five to eight mist nets of varying lengths that were erected at 20 to 100 meter intervals along a geographical feature (trail, body of water), and were monitored for four to six hours depending on activity and weather. The nets used throughout all survey years were the same, except the lengths varied from 3 to 30 meters wide and could reach up to 6 meters high. The nets were set and opened at approximately 1800 - 1830 each night, and taken down at 2200 – 2300 (approximately four hours each night).

Ambient temperatures and humidity were recorded during standard field observations with a Kestrel® 3000 Pocket Weather Station. Other recorded information included weather conditions (e.g. rain, wind), changes in weather conditions, a description of the area with key features (e.g. trees, rocks, streams), where and how many nets were set, when bats first appeared, and when all equipment was taken down.

Flyways were illuminated using two infrared lights (Wildlife Engineering Model IRlamp6 40-degree beam) powered by 12-volt car batteries (Fig 3). I used Sony Night-

Shot camcorders (Models #CCDTRV87 and #CCD-TRV138) and Hi-8 videotape to record bat activity. A single video camera was placed approximately 5m perpendicular to the mist net (Camera 1: Fig. 3). In 2006, we added an additional Night-Shot video camera that was placed parallel to the net to better discern bat activity at the net surface (Camera 2: Fig. 3). This camera was no more than 1m away from the net pole so that all the net was in the filming plane.

The infrared lights were positioned on either side of the mist net to illuminate bats approaching from either side of the net. The second Night shot video camera gave another perspective from which to view the net and to make sure the numbers of bats seen on the perpendicular camera were being counted accurately.

In 2006, I deployed the "*Batcam*" to facilitate the visual tracking of individual bats as they circled about the net (*Batcam*: Fig. 3). The *Batcam* consisted of a *Watec* camera (WAT-902H2), a *Rainbow* S16mm lens, a Wildlife Engineering Model IRlamp6 20 degree beam angle infrared light, and an *Accelevision* 7-inch wide TFT-LCD color monitor (LCDP7W) all mounted coaxially on a bracket that could be hand-held or mounted on a tripod. A 12-volt car battery powered all of this equipment. The *Batcam* was basically a large-screen, night-vision video camera that greatly reduced eyestrain and allowed for continual observation of the mist net. It also provided a wider visual field in which to track various activities of individual bats beyond the range of the stationary video cameras.

Sony TCM-200DV tape recorders were used to dictate comments concerning bat behavior, activity, and specific time checks. This was done while observing the interactions from the *Batcam* and allowed us to check for errors in counting or behaviors that may not have been seen with the stationary cameras. The integral clocks in each camcorder and a digital watch used by the observer were synchronized to facilitate record keeping and data analysis when the various tapes were played back the following day.

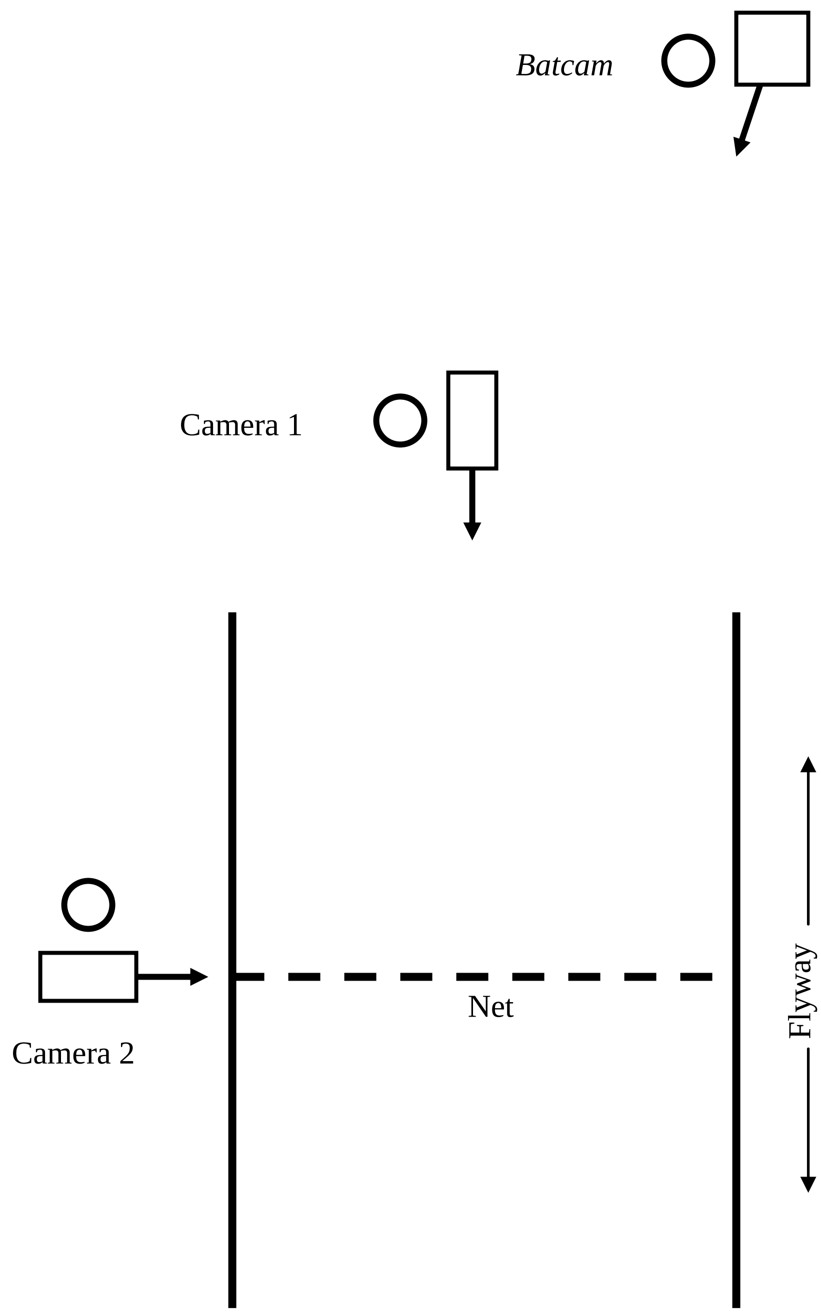

Figure 3: An aerial view of the setup to demonstrate locations of the: night-shot video cameras with arrows indicating direction of filming, *Batcam*, infrared lights (indicated by circles), the mist net, and flyway.

Data Collection

The four primary sites analyzed were Hope Springs and Sappit River in 2005, while Mango Hill and Cassava Ghaut were added in 2006. Four consecutive nights were spent at each site with each night being filmed via video recording equipment (unless inclement weather or ash fall interrupted our filming). The first night was used as a control to quantify how many bats fly through an empty airspace on a given night – only the video cameras were in place on the first night. On subsequent nights, the video equipment and a single mist net were erected at the site.

The flyway was videotaped for 2 or 3 hours depending on conditions on each of the four nights and the interaction between bats and the mist net were analyzed during playback of the videotape footage the next day. The videotapes were watched, bat passes counted, behaviors described, and the times recorded when bats were active. The same persons viewed the videotapes the first year (RJL and KAB) and initial control counts were performed by each to determine percent error (~1%), while the next year only RJL counted bat passes. This information was compiled and entered into a computer for later statistical analysis.

Bats were removed from the net every 10 – 15 minutes and placed according to species in separate cloth bags (made with a breathable material) in an attempt to reduce the stress of recapture that same night. At the end of the night, bat bags were sorted and each bat was measured to the nearest metric unit for weight (g) with a digital scale and forearm length (mm) with a small metal ruler. The reproductive status (pregnant, lactating, post-lactating, scrotal, non-scrotal, or non-reproductive), tooth-wear, and presence of scars/injuries or external parasites were noted for each individual bat.

If bats were captured and marked, most would have an aversion to the netting site and may not appear in the flyway for several days after the initial capture (Gannon and Willig, 1998; Kuenzi and Morrison, 1998; Kunz and Brock, 1975; Kunz and Kurta, 1988; Kunz *et al*., 1996; LaVal, 1970). Yet one species (*Artibeus jamaicensis*) was frequently banded with flange-lipped incoloy 2.8mm bands (*Lambournes Ltd.)* at the end of each evening and then released. Due to the high number of *A. jamaicensis* captured and their prevalence on the island, the effects of marking them was not considered harmful to their health or to their reoccurrence at various netting sites.

Impromptu filming events were performed at three of my six sites to determine if equipment was working properly. These data were not included in final analysis, but were noted for future study. In 2006, we wrapped two cotton bed sheets tightly around 5 vertical meters of a tree trunk adjacent to the net to test if flying bats could be more easily observed against the white sheet (*sensu* Hirsh et al. 2003). There was nothing visually aberrant about the tree – no cavities, abundant insects, leaking sap, vines, etc. However, at least one bat exhibited a great deal of interest in these cotton sheets and flew up and down the trunk (20+ cycles) and landed on the sheets numerous times. Because my objective was to obtain data on mist net bias, and the lighter background offered only minor improvement during filming, we did not use sheets at other locations, as they seemed to impose a bias of their own.

Data Organization

For the interaction study, the numbers of bats approaching the net or using the flyway in the absence of the net were tallied and the behavioral responses of each bat to the net were recorded and classified into 5 main categories: (1) circled or reversed their direction of flight; (2) flew over the net; (3) flew under or to either side of the net; (4) were caught and manually removed from the net; or (5) bounced off the net or quickly escaped and flew away. In order to see if there were any changes in activity over consecutive nights of mist netting in an airspace and to observe the potential differences, the amount of activity (i.e. bat passes or bats per hour) for each interaction site was plotted against the net nights and then the net nights from each site were summed in order to identify any decrease in bat activity on successive net nights.

The pool consisted of 16 sites (from the 10 years of previous survey work), from which I had records of more than three years of data at each of the individual sites. From these 16 representative sites, four experimental sites were chosen for statistical analysis. In order to examine bat activity, a simple count of bat passes (BP) taken each night. Then a standardization of bat passes per hour (BPPH) was introduced in order to compare among sites. To analyze effort over the years of survey, I standardized the bats captured each year by using net hours from each year. I divided the total number of bats captured in each year, by the total net hours from each respective year. This allowed for a comparison between years over the ten years of survey. Statistically, alpha values were set at 0.1 and linear regression and a Kruskal-Wallis One-Way ANOVA were performed using SYSTAT version 11 (SYSTAT 2004).

RESULTS

Mist Net Interaction

In 2005, I recorded 1,970 bat passes (BP) on 25.3 hours of videotape. In 2006, 553 BP were recorded on 18 hours of videotape, giving a total of 2,523 BP captured on 43.3 hours of videotape on all nights during the project. These raw numbers include the additional filming events for equipment testing previously mentioned. The numbers at the four experimental sites were 1,847 total BP observed on 20.3 hours of video in 2005, and 535 BP observed on 16 hours of video in 2006. A total of 2,382 BP were observed at all four sites on all nights (Table 1).

During control evenings at our experimental sites I recorded an average of 28.6 BPPH (2.6–83.7; Table 1) on nights without a net. In the presence of a mist net, I recorded 70.0 BPPH (13.0 – 338.7; Table 1). However, bat activity and bat captures decreased on consecutive nights. Fewer bats were observed flying through the target area on control nights than on nights when a net was blocking the flyway.

When a mist net was present, 112 of the 2,069 bats observed on film came into contact with the net (5.4%) and 66 of these were captured (3.2%), giving us a range of capture rates from all nights of 0–10.3%. The different behavior categories were tallied and the percent of bats that approached the net and were not captured would either circle/reverse direction (47.5%), fly over the top of the net (38.9%), fly under and around the net (8.2%), became entangled in the net and captured (3.2%), or 2.2% bounced off the net (Table 1).

Table 1: Summary of bat activity at four mist net locations on Montserrat.

Location	Date	Over	Under & Around	Circle/ Reverse	Bounce	Caught	Total	Bats/Hour	% Caught
Mango Hill	6/10/06						35	17.5 (no net)	no net
	6/11/06	19	29	31	6	2	87	43.5	2.3
	6/12/06	55	21	41	4	4	125	63.5	3.1
	6/13/06	8	8	8	2	3	29	14.5	10.3
Cassava Ghaut	6/14/06						21	10.5 (no net)	no net
	6/16/06	90	49	33	4	5	181	90.5	2.8
	6/17/06	11	5	7	7	1	31	15.5	3.2
	6/18/06	9	9	8	0	0	26	13.0	0.0
Hope Springs	7/9/05						6	2.6 (no net)	no net
	7/10/05	64	7	121	0	3	195	65.0	1.5
	7/11/05	24	4	64	0	8	100	33.3	8.0
	7/12/05	15	0	40	0	4	59	19.7	6.8
Sappit	7/16/05						251	83.7 (no net)	no net
	7/17/05	412	16	555	12	22	1017	338.7	2.2
	7/18/05	98	22	74	11	14	219	73.0	6.4
Totals:		805	170	982	46	66	2382		
Percent of Total:		**38.9%**	**8.2%**	**47.5%**	**2.2%**	**3.2%**			
Averages:								70.0	4.2

Net interaction data from the 2005 and 2006 sites were analyzed via linear regression (Fig. 4). The control nights (0) were not included in the analysis since they were not comparable to nights with a net. Each of the net nights (1, 2, 3), at each site (Mango, Cassava, Hope, Sappit), were plotted as BPPH and three of the four sites exhibited a similar trend (Note: curves joining each point do not represent linear regression; Fig. 4). The third night at Sappit was not videotaped due to ash that had fallen and the affect it had on the flyway. A sum of ranks test was completed (Kruskal-Wallis One-Way ANOVA; SYSTAT 2004) on the dependent variable BPPH and localities were grouped by time (nights 1, 2, 3) to confirm the difference between combined data from sequential netting nights.

However, the Sappit River site has been a highly productive site throughout the years and exhibited higher bat activity than the other three sites (Larsen and Pedersen 2002; Larsen, P.A. et al. 2006; Pedersen 2001; Pedersen et al. 1996, 2003, 2005, 2006, 2007). The initial net night at the Sappit showed a high capture rate and high biodiversity. Capture rates on the second net night at Sappit were more comparable with BP numbers from the three other sites. Simple linear regression revealed a significant decline in the number of BPPH on successive nights ($\alpha = 0.1$, $p = 0.08$, $r^2 = 0.30$); Fig. 4). The slope was certainly affected by the first night from Sappit, but the general trend is the same (Fig. 4). The sum of ranks for each of the combined net nights were 35.00 (first net night), 24.00 (second), and 7.00 (third). The overall decrease in ranked sums from the three nights does show a significant difference ($p = 0.04$) between BPPH on successive net nights.

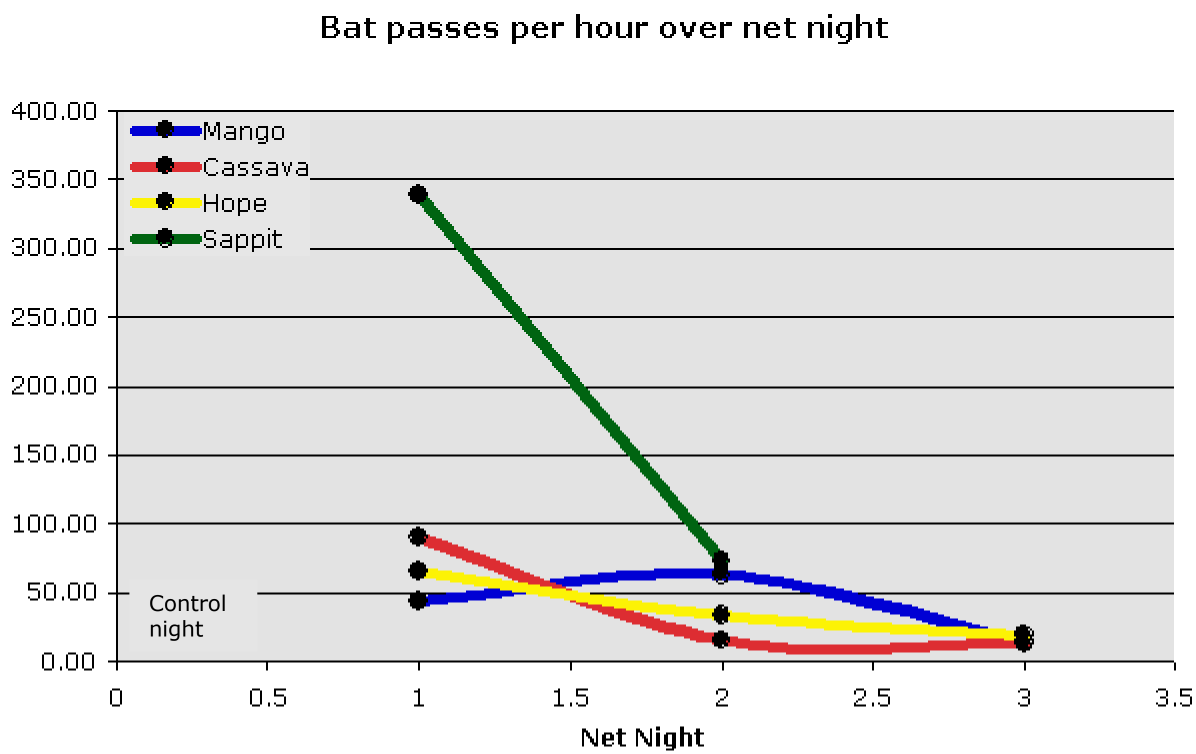

Figure 4: The number of bat passes at each net night by site. (Curves joining points are for aesthetic purposes only, they do not depict the linear regression; $p = 0.08$, $r^2 = 0.30$; Kruskal-Wallis: $p = 0.04$; SYSTAT 2004)

Sampling Effort

The only data we could use from the previous survey work on the island were the number of nets set and the number of species caught in each survey year. During the first formal survey of Montserrat in 1978, Jones and Baker's (1979) mist netting consisted of only two nights at the end of July, yet they were able to capture 432 bats of six different species in five mist nets set along a golf course. In January of 1984, another short survey was undertaken by Pierson et al. (1986), which consisted of four consecutive nights at four different sites (across a river, across an estate road, Hope Springs, and a cave) and netted 195 bats of seven different species in 17 nets. In 1995, Morton and Fawcett (1996) initially chose 18 random sites, but later chose sites where greater bat activity was expected. The initial approach was not pragmatic and he shifted his emphasis to netting at sites with open bodies of fresh water, potential flyways, fruiting trees, and easy access (Morton and Fawcett 1996). The resulting captures of 204 bats included seven species in 18 nets. The first surveys by Pedersen were in 1993 and 1994 and have continued to the present date. Those surveys generally last two to four weeks. Nets were set at several different locations and five to eight nets were set each night, totaling around 2800 captures throughout the years.

Discerning what species are found or obtaining counts of individuals in any study area is a daunting task. There is no way to count every bat. With this limiting factor, past investigators on Montserrat quantified bat abundance and animal activity via a simple metric, BNN, or bats captured per net per night (Pedersen et al. 1996). A simple accumulation curve was derived, wherein sampling effort and yearly inventory numbers demonstrate the inadequacy of mist nets to consistently capture all species reported from this island in most surveys years (Fig 5). The number of net nights per survey is also plotted and indicates that increases in effort coincide with spikes in the number of species captured per survey. Fleming et al. (1972) and Kalko et al. (1996) also used this method to evaluate bat survey data.

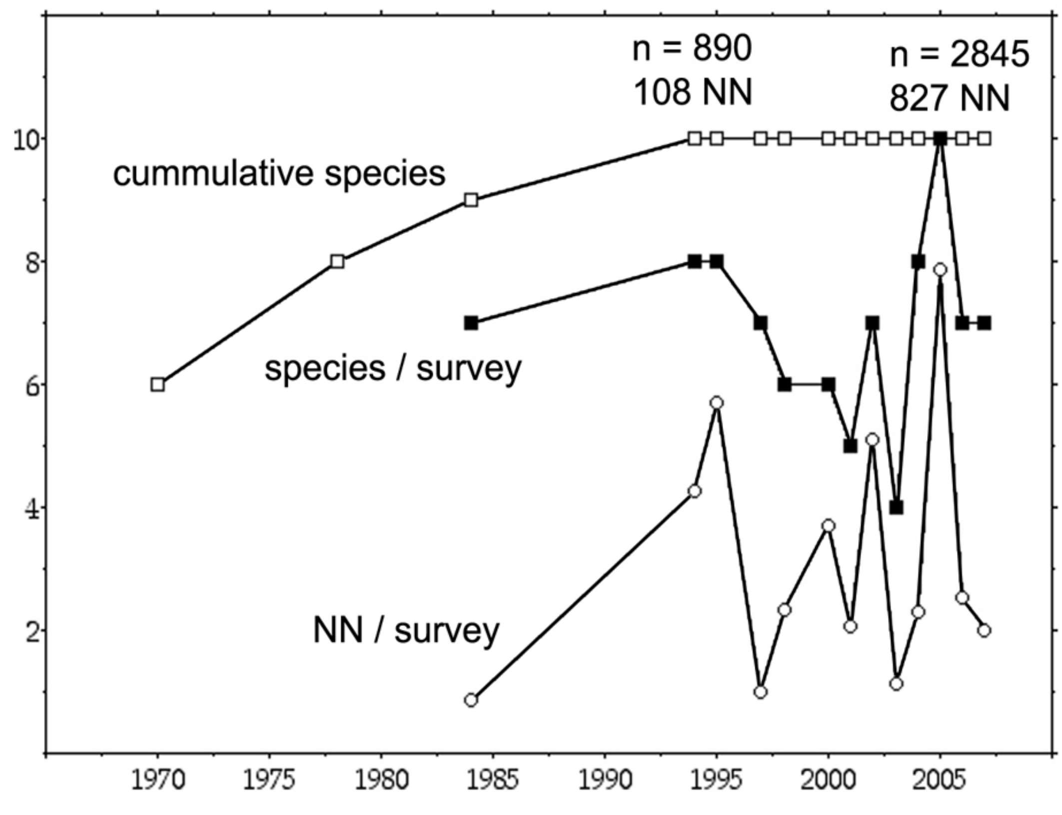

Figure 5: Accumulation curve for Montserrat from 1978 to 2006.
NN/20 surveys: Net-Nights = effort expended per survey; n = bats captured.

Despite net bias issues, consistent survey efforts were made to analyze population fluctuations across 10 sample years. Initially, looking at the bats per hour over the years, a definite low point is apparent in 1997 (Fig. 6) and coincides with a large eruption of the Soufrière Hills volcano and a very short-term survey under difficult conditions. This was one of the first eruptions to cause severe damage to the lower third of the island and it dropped ash on vegetation and water sources across most of the island. The ecosystem was greatly disturbed and bat captures decreased for many reasons including habitat destruction, lower reproductive rates, and higher mortality rates. These influences could have affected the number of bats in the population, meaning less bats were flying and hitting the net, and total capture rates decreased accordingly.

Three different teams of scientists the conducted surveys in 1978, 1984 and 1995 (Jones and Baker 1979; Morton and Fawcett 1996; Pierson et al. 1986). These data were not included in the statistical analysis because they are not directly comparable to the studies by Pedersen. The trend after the nadir of 1997 could be considered a period of rebound for the population of bats on Montserrat after extreme disturbance. Increasing bat captures may have been due to several factors including the amount of effort put forth, the types of sites chosen (closeness to water sources and fruit trees), weather conditions, and time of netting. From 1998 on, there was a slight increase in the number of bats being captured in the net per hour (Note: curves joining points do not represent a linear regression; Fig. 6). A linear regression ($p = 0.11$; $r^2 = 0.29$) was run, but did not provide evidence of a significant trend. The unpredictable fluctuations and amount of variation in this dataset over the 10-year time span seem to coincide with environmental change and effort expended, but the data does not lend itself to a simple analysis.

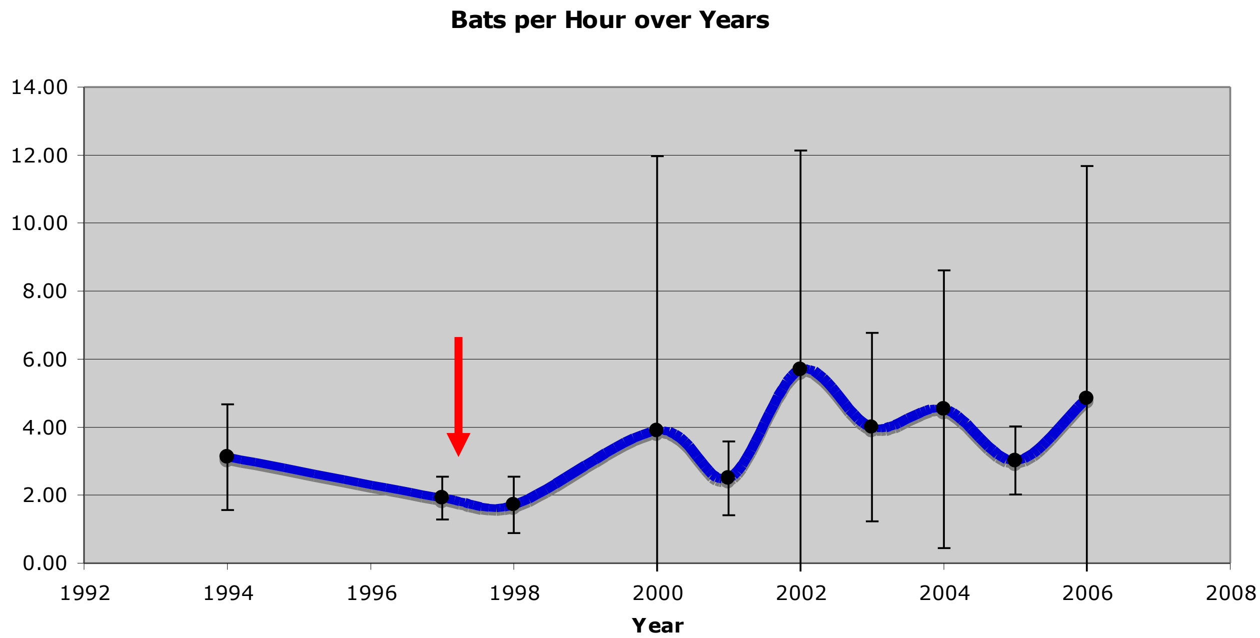

Figure 6: Bats per hour over the 10 years of survey (Curve fitted to these points does not represent a linear regression; $p = 0.11$; $r^2 = 0.29$; SYSTAT, 2004). Note the low point in 1997-8 (red arrow) and the variation (+/- 1 SE) from 2000 to 2006.

Species inventories were recorded each year of study (Table 2). Species are listed top to bottom, from most to least common, and are marked with an “x” to indicate their capture on Montserrat in the specified year. *A. jamaicensis* was caught every year, whereas *Chiroderma improvisum* and *Sturnira thomasi* were only caught randomly. In this part of the analysis, I included the surveys from 1978, 1984, and 1995, to obtain a better sense of the species captured in each year pre- and post-disturbance. Before the major volcanic eruption in 1997, up to seven species were caught in any one survey. From 1998 to 2003 there was a decrease to five commonly netted species throughout survey years. Nine species were netted in 2005, but all 10 species known from Montserrat were captured (Table 2; Note: the tenth species (*Natalus stramineus*) was not included in Table 2 because it had never been netted and was only hand captured in cave roosts as of the end of my field season in 2006.

The majority of captures made by Jones and Baker (1979) were of *Artibeus jamaicensis* (46.3%) and *Molossus molossus* (46.3%). The most numerous species captured in 1984 by Pierson et al. (1986) were *A. jamaicensis* (50.7%) and *Monophyllus plethodon* (40.0%). In the end of July and the beginning of September of 1995, Morton and Fawcett (1996) found 36.7% of the captures were *M. molossus* while 25.0% were *A. jamaicensis*. Additional information on individual species captured by Pedersen will be presented in the next section.

Table 2: Species of mist netted bats on Montserrat: listed in order from top to bottom from most common to least common. Years of survey are listed across the top, left to right, and an "x" indicates year of capture.

Species:	1978	1984	1994	1995	1997	1998	2000	2001	2002	2003	2004	2005	2006
Artibeus jamaicensis	x	x	x	x	x	x	x	x	x	x	x	x	x
Ardops nichollsi	x	x	x	x	x	x	x	x	x	x	x	x	x
Brachyphylla cavernarum	x	x	x	x	x	x	x	x	x	x	x	x	x
Molossus molossus	x	x	x	x	x	x	x	x	x		x	x	x
Monophyllus plethodon		x	x	x	x	x	x	x	x	x	x	x	x
Noctilio leporinus	x	x	x	x	x						x	x	
Tadarida brasiliensis				x					x		x	x	
Chiroderma improvisum	x	x										x	
Sturnira thomasi			x									x	x

Species of Bats Captured

Once the overall bat activity was analyzed, I looked for patterns of variation among species across time. Initially *A. jamaicensis* were being caught at less than one per hour for the first few years (Fig. 7). We can see that the general trend after 1994 shows that capture rates for *A. jamaicensis* and for all bats combined increased. The period in each month when surveys were conducted varied and are as follows: throughout July in 2000, the end of July in 2001 and 2002, the middle of June in 2003, the beginning of June in 2004, the beginning of July in 2005, and the middle of June in 2006 (Fig. 7). These monthly differences in surveys can have an important impact on the sample and bias the numbers and types of bats that are netted. From 2002 to 2006, the number of *A. jamaicensis* per hour increases but fluctuates from around 1.5 to just below 4.0 per hour (Fig. 7).

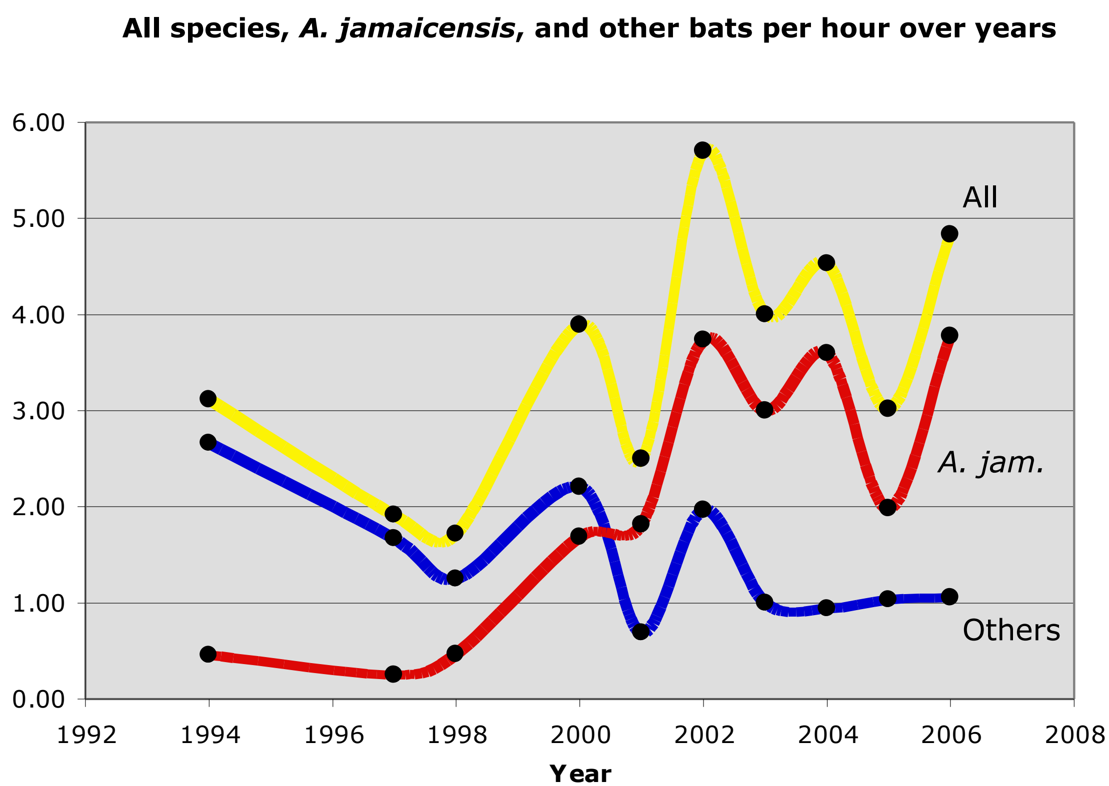

Figure 7: All species plotted as bats per hour in each of the 10 years of mist net survey. The yellow line indicates all species of bats, *A. jamaicensis* (*A. jam.*) are indicated by red and all other species are indicated by blue. There is a significant increase in *A. jamaicensis* from 1994-2006 ($p = 0.007$, $r^2 = 0.62$), but no significant trend in other species combined ($p = 0.12$, $r^2 = 0.28$; SYSTAT 2004).

Before 1997, the dynamics of which bats were being caught were quite different. *M. molossus* was captured most frequently, while *A. jamaicensis* captures were below 1.0 per hour, as were capture rates of other species during this time period (Fig. 8). From 2002 to 2006, *A. jamaicensis* populations increased significantly ($p = 0.007$, $r^2 = 0.62$; Fig. 8). While *A. jamaicensis* populations increased, the capture rates of other species of bats either remained constant or decreased in captures per hour ($p = 0.12$, $r^2 = 0.28$; Fig. 8). I looked at the other species more closely and looked for patterns. Capture rates of other species of bats combined had declined slightly (slope = -0.09). Most other commonly captured species (*A. nichollsi*, *B. cavernarum*, *M. molossus*, *M. plethodon*) had capture rates of less than 1.0 per hour, since 2001. The capture rates of these bats did not seem to fluctuate as erratically from year to year, as did those of *A. jamaicensis*.

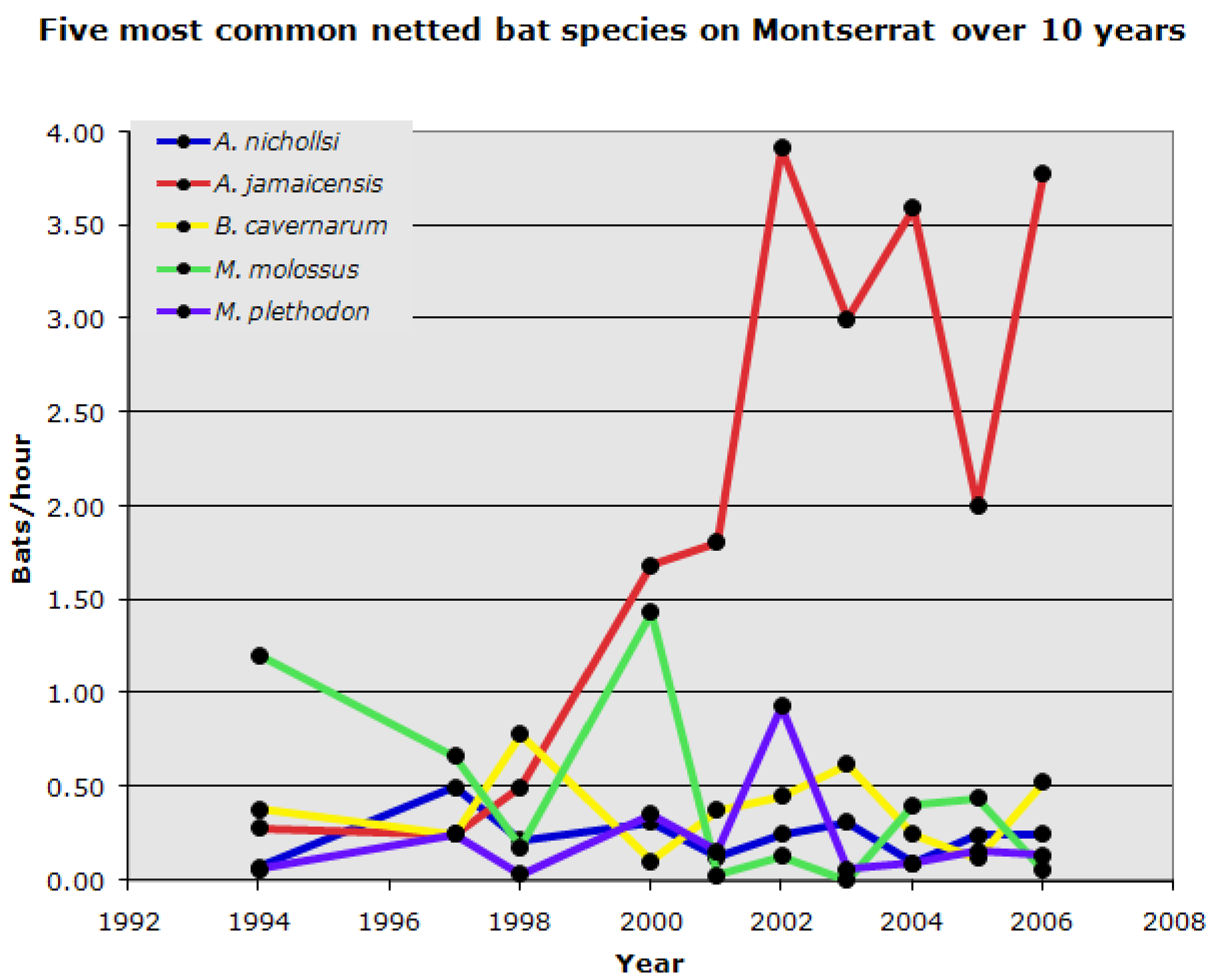

Figure 8: Top five most commonly netted species from 10 years of mist net surveys on Montserrat. Species not included in this figure are: *N. leporinus*, *N. stramineus*, *S. thomasi*, and *T. brasiliensis* due to low or no captures.

I evaluated *A. jamaicensis* further, by dividing the data into male and female categories and running linear regression analyses on each (Fig. 9). Both female and male *A. jamaicensis* captures per hour showed a highly significant increase in captures per hour from 1998 to 2006 (females: $p = 0.009$, $r^2 = 0.59$; males: $p = 0.007$, $r^2 = 0.61$; Fig. 9). Males and females both increased at comparable rates throughout the years and the proportions of males to females did not change drastically, together indicating a general increase in the population of *A. jamaicensis*. The male to female capture ratio data during the 2005 - 2006 interaction study was 36:64 and 41:59 for the 16 representative survey sites on Montserrat from 1994 to 2006 (824 captures).

To investigate the influence of reproductive status and age on net bias, female *A. jamaicensis* were broken into finer categories based on reproductive status (pregnant or non-pregnant) and all *A. jamaicensis* were divided into age groups (juvenile or adult) for statistical analysis. A Pearson correlation matrix was run on each, but no significant differences were found in numbers of pregnant versus non-pregnant females that were netted ($p = 0.93$), or in the numbers of juveniles versus adults captured in mist nets ($p = 0.29$).

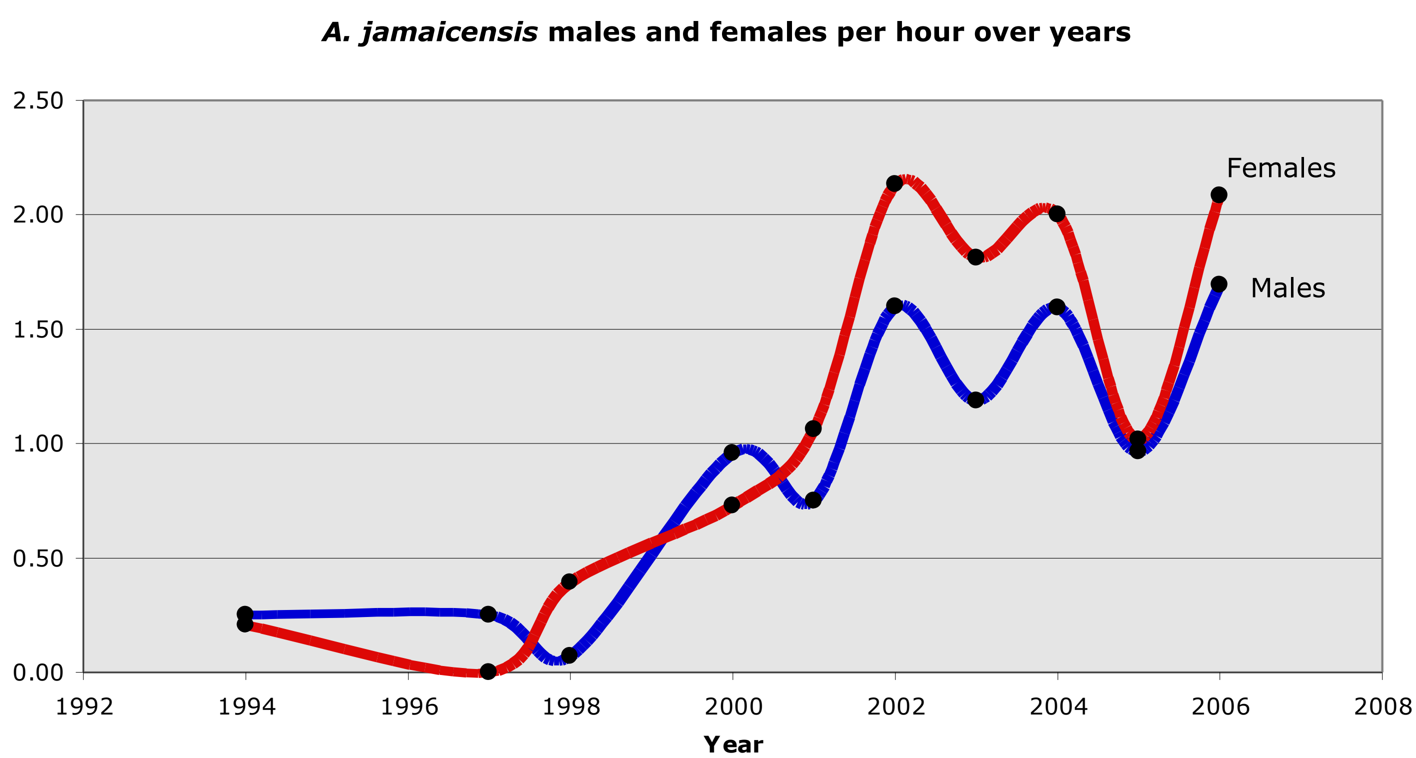

Figure 9: Captures of male and female *A. jamaicensis* during the 10 years of mist net survey on Montserrat. Both females ($p = 0.009$, $r^2 = 0.59$) and males ($p = 0.007$, $r^2 = 0.61$; SYSTAT, 2004) significantly increased throughout this time period.

Given these results, the only way to reduce these data so as to eliminate the bias imposed by parturition, lactation, and volancy was to restrict the time scale. Therefore, I decided to look at only the months of June and July, and redefine the categories of *A. jamaicensis*. Figure 10 shows captures for pregnant, lactating, and non-reproductive females, in addition to scrotal and non-reproductive males, and all juveniles in June and July only. This figure shows each of these categories as a proportion of total bats caught in each week across all years. Captures of pregnant females drop dramatically after the first week of July (week 5) and the number of captured lactating females rises at that point in time. Lactating females and scrotal males comprise most of the captures after the first week of July. Other categories remain relatively consistent through the time period with only small fluctuations (Fig. 10).

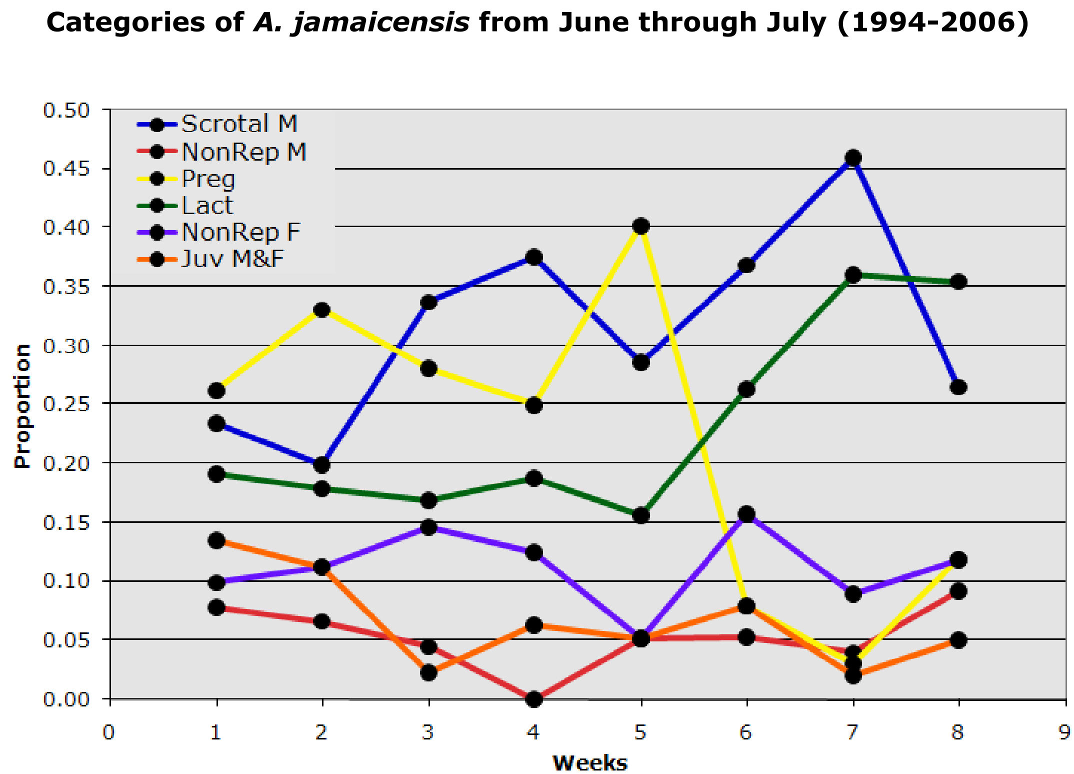

Figure 10: Proportions of the defined age and reproductive categories of *A. jamaicensis* from June to July: Scrotal Male (Scrotal M), Non-reproductive Male (NonRep M), Pregnant (Preg), Lactating (Lact), Non-reproductive Female (NonRep F), and Juvenile Males and Females (Juv M&F). Note decline in pregnant *A. jamaicensis* after week 5.

DISCUSSION

Mist Net Interaction

Mist netting along trails, paths, or pools of water remains a standard protocol for many investigators despite observations that show that a fair number of species are missed or under-represented because they simply do not fly near to or are able to avoid ground-level mist nets – this stratification has been well documented (Francis 1994; Kunz et al. 1996; O'Farrell and Gannon 1999; Simmons and Voss 1998). Our data shows that the total numbers of bats and species of bats on Montserrat are not well represented by the number and diversity of bats caught in a mist net. Those that hit the net, bounced off, or were snared by the net (5.4%) were a very small percentage of the total bat activity near, over, or around the nets. These data compare well with those reported by others (2.6%: Dobson et al. 2001; 4%: Berry et al. 2004; ~4%: Lang et al. 2004; 3.1%: Larsen, R.J. et al. 2005, 2006). Due to these low capture rates, mist nets are not accurately sampling bats that utilize flyways and are generating inaccurate or misleading data due to the level at which the net is set in the flyway or differential abilities in detection and flight of bats.

My observations show that bat activity and capture success decrease over consecutive nights of mist netting at the same location match data collected by others in similar situations (Gram and Faaborg 1997; Simmons and Voss 1998). More bat activity was observed on the first net night than during the night without a net and during subsequent net nights in the sequence. The increased activity in the airspace on the first net night suggests curiosity and investigation of a new obstacle. Hinde (1966) indicates that when animals are exposed to a new object or situation, the sensitivity and response to the object increases and then gradually wanes. I believe this decreased activity on successive nights is a learned response by the bats, in that bats react to a new obstacle in the pathway, then decide to either use the pathway again the next night or not. When they do use the flyway, they can circle the net investigating the new obstacle, or fly over and ignore the obstacle (Gannon and Willig 1998; Kuenzi and Morrison 1998; Kunz and Brock 1975; Kunz and Kurta 1988; Kunz et al. 1996; LaVal 1970). Closer evaluations of bat-net interactions and laboratory trials, would allow us to better understand net bias and learning behavior. Ultimately, we would like to be able to reduce bias and the detectability of a net by bats, for a more accurate survey. This however, may not be possible given the limitations of net construction and field conditions.

Some bats are better at detecting the net and maneuvering around the net, while some blindly fly into the net (Galambos and Griffin 2005; Francis 1989; Simmons and Voss 1998). With so many different types of bats and abilities, how can surveys of sites be conducted accurately? To compensate for mist net bias, a combination of methods (acoustic devices, mist nets, harp traps, and visual observation) may provide the best outcome along with long-term, thorough surveys that account for the respective biases of each additional technique. This formula should eventually give an adequate amount of observations and the ability to make inferences over time. The more times that sites are sampled and different habitats are chosen, the more likely that I can document better representations of the relative number of individuals and species abundance.

Sampling Effort

Known limitations of mist net surveys can be compensated for, in part, by repetitive sampling efforts over several years, with careful analyses of species accumulation curves. These species accumulation curves allow for analysis of completeness and amount of effort for each survey year (Ke and Bales 2007; Simmons and Voss 1998). The need to re-evaluate previous mist net surveys in various regions has been established.

The first two surveys (1978, 1984) were conducted before extreme disturbances occurred on the island (Hugo – 1989, Soufrière Hills volcano – 1995). These minimal effort surveys only netted two to four sites, therefore limiting their results to the six or seven species caught in these short surveys (Baker and Jones 1978; Pierson et al. 1986).

In 2002, there was a peak in the number of bats per hour. This year may have been very productive for capturing bats because of a low incidence of disturbance (e.g., hurricanes, volcanoes) and/or high fruit abundance (i.e., wet year). Additionally, 2002 had increased mist netting effort, which could lead to the increased, capture rates. In 2005, all 10 species were captured after a substantial increase in netting nights, net sets, locations, and workers.

Overall, Pedersen's surveys (1993-2007) found five to eight species per survey but these were interspersed with disturbance periods, and varied in terms of numbers of nets, netting nights, and workers. These data were limited by the amount of disturbance and consistency of survey time and effort, but were biased by site selection as well. Sites found near water, fruiting trees, and those that are more easily accessed are biased due to the types of bats that would frequent these areas, namely *A. jamaicensis*. Each bat species has a different preference for foraging and roosting. The sites chosen may not sample every area that each species may prefer and therefore, bias the data collected.

The slightly positive trend in the number of bats captured since 2000 could be explained by many factors. The amount of effort put into capture, whether it be hours of netting, number of individuals handling nets, number of nets set, or number of surveys in a time period (month, season, year, etc.), greatly affects the numbers of bats being caught and the ability to compare capture rates among years. The same group of people have been involved in surveying Montserrat recently on a consistent basis (June through July), therefore I was able to distinguish signs of response by the overall and species-specific bat populations to habitat destruction and other factors, due to the fluctuations and variation between years.

Short-term studies can only provide underestimations of the true faunal diversity of an island, as shown by the early studies of Montserrat. Each time period is going to provide a very different view of what species are on the island. The overall decrease in population size noted in 1994 was most likely related to fatalities that occurred during the hurricane itself, but also to starvation resulting from defoliation and the susceptibility of juveniles to habitat destruction caused by the hurricane (Pedersen et al. 1996). Reproductive capacity and the ability to survive extreme disturbances allow some species to recover quickly for example, *A. jamaicensis* and *M. molossus* can reproduce twice a year, while most other bats only reproduce once annually (Nowak 1999). Some species may not be as resilient to disturbance to habitat or food sources (Fenton et al. 1992) as the more common generalist bats.

Species of Bats Captured

Timing is everything. Natural disasters have interrupted several surveys and differentially impacted the bat fauna on the island. Destruction of the habitat can decrease the number of available roost sites for some tree dwelling bats (e.g. *A. jamaicensis*; Fenton et al. 1992) but have little affect the cave dwelling bats (e.g. *Brachyphylla cavernarum*). Roosts (trees or caves), foraging sites (valleys, pathways, streams), and fruit availability (flowering plants, trees) all of which are important in supporting the bat fauna are in an area, are also affected by disturbance (Fenton et al. 1992; Fleming et al. 1972). The bats captured in these years may be in a population boom after a wet season (e.g., 2002), when reproduction is high and mortality is low, or a survey may have been conducted just after a destructive period of volcanic activity or hurricanes (1997,1998), when overall numbers are low due to disrupted reproduction and high mortality.

Not all species are being caught on a regular basis, but by surveying for several years and accounting for the low capture rates indicated by my interaction study, we eventually can obtain a better overall picture of species diversity and variability in relative bat activity on this island. If we had simply relied on a few short term surveys performed during any year on this island, we may have only reported a few species and assumed that this island did not have the diversity of some of the other Caribbean islands in the region. Whereas Montserrat is actually above the norm for numbers of species compared to total area of the island (Fig. 11). The picture of biodiversity could be painted quite differently at various periods of time on this island when the habitat and populations were dramatically affected by a series of natural disasters. Thus the need for multiple surveys, conducted over many years, seasons, and with consideration of capture biases.

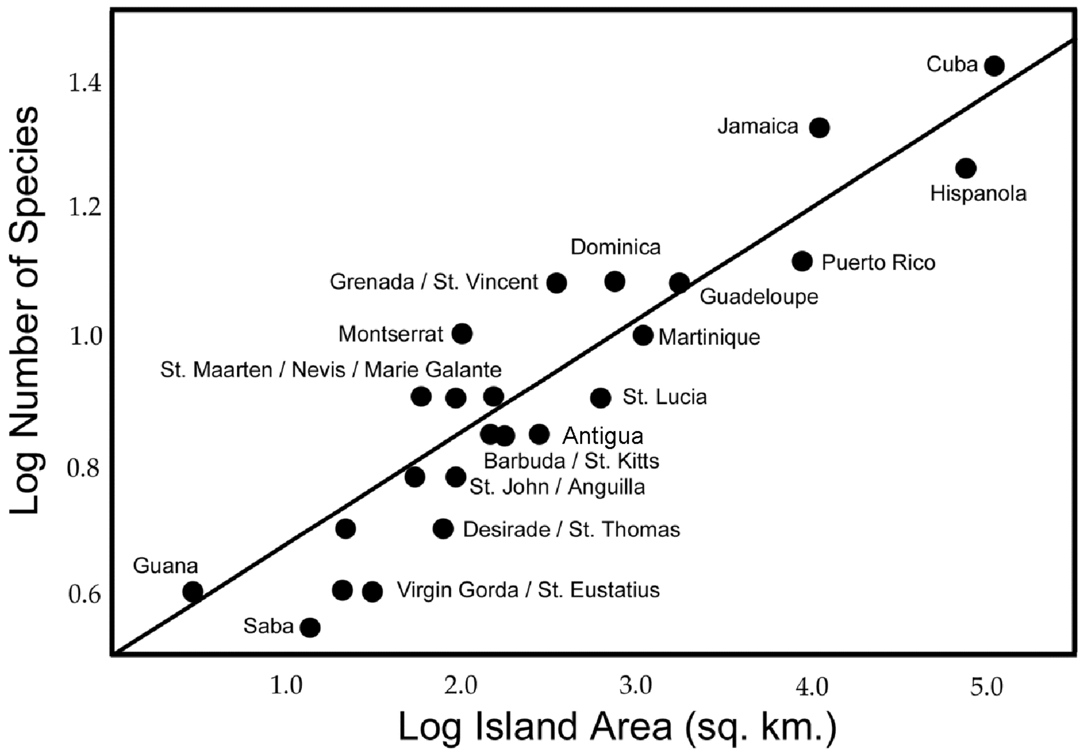

Figure 11: Species area curve (Pedersen et al. 2005).
Linear regression of log-transformed data: $y = 0.17x + 0.49$ ($r^2 = 0.81$).

A. jamaicensis has once again come to dominate Montserrat's bat fauna and most likely will continue until another driving force disrupts the pattern. Other species of bats were seemingly a larger portion of the captures during the 10-year period between 1989 and 2000. Reasons for the increase in *A. jamaicensis* populations may be because they are considered food and roost generalists or due to their ability to survive disturbances, but is most likely due to their relatively high reproductive rate (Ortega and Castro-Arellano 2001). Roost specialist species are though to be more sensitive to changes in the ecosystem and could not adapt or recover as quickly as *A. jamaicensis*.

If sex ratios in a captive colony (1995-1998; G. Kwiecinski, pers. comm.) and the National Zoological Park (NZP) captive colony (Keast Taft and Handley 1991) are representative of ratios in the wild, the expected male to female ratio would be nearly 50:50. Field data collected on Montserrat during my 2005 and 2006 seasons suggested a net capture ratio of 40:60. Gardner et al. (1991) found sex ratios of captured *A. jamaicensis* were 47:53 from July to December (1976 to 1980: 11,000 captures) on BCI, Panama. On Montserrat, it appears that females are more easily captured and comprise a larger portion of captures in both the interaction study and in the general surveys over the last 10 surveys. Female *A. jamaicensis* were not necessarily a larger portion of the total population, but the sex ratio netting bias noted in my study was skewed to females when compared to expected ratios.

Surveying only two months in each year could also impose some seasonal bias in the data. Due to previous field observations, I expected more captures of heavily loaded pregnant female and newly volant juvenile *A. jamaicensis*. The captive colony at the NZP was used to study reproduction and development of *A. jamaicensis* and found that pregnant females weighed on average, 35% more than non-pregnant females and that maneuverability and speed decreased as wing loading increased. Juveniles were shown to have distinct flight styles and were captured more easily in mist nets in the laboratory (Keast Taft and Handley 1991). The assumptions of more pregnant females and juveniles were warranted in my study, but due to low sample numbers, the grouping of bats in such general categories, and the variation in status of the bats in different survey months, no concrete conclusions can be made with the data on hand. However, I was able to see that around the first week of July, most *A. jamaicensis* had given birth and the proportions of scrotal males and lactating females increased, whereas pregnant females declined. This was an obvious sequence of events, given that once parturition had occurred, lactation would ensue. Reproductively active males were also more prevalent after the fifth week, most likely as mates prepared for breeding the available females during their postpartum estrus cycle (Wilson et al. 1991).

If *A. jamaicensis* is dominant, then who is rare? What do we mean by the term ‘rare’ with respect to what we now understand about mist net bias? Do rarely encountered species naturally occur in low numbers? Are they really rare, or are the choices of netting site biasing the data towards *A. jamaicensis*, or are no other species being detected because we do not survey all possible habitats? Species can be rare because of insufficient sampling efforts, their status in the food chain as top predators or food specialists, or their reliance on scarce local resources (Kalko et al. 1996). Is rarity a factor that merely reflects the constant movements of a vagile organism in response to the destruction of key habitat and foraging areas? Does rarity imply the decline of a species, or simply reflect the animals' abilities to avoid mist nets and humans? To really answer these questions, repetitive sampling and careful analysis of species accumulation curves must be conducted to compensate for the limitations of mist netting. These curves allow for analysis of completeness and amount of effort for each survey year.

We must reassess some assumptions about mist nets surveys. Mist nets are valuable tools used to survey bats, but the limitations of mist nets must be considered when choosing capture devices to study the bat fauna of a particular area. Data can only be suggestive of the entire species inventory and relative population size of bats, not an absolute estimate of those in the entire population. From these data, the importance of studying populations over time, obtaining bias estimates to correct data collection, sampling and obtaining a large number of observations, and observing the reactions of species to different capture situations is evident. Eventually, consideration of the effects of long and short-term disturbance, recovery periods after a natural disaster, and individual species reactions to these events can be combined to make suggestions on improvement of survey methods, protocol, and length of survey.

A multivariate analysis is needed to answer many of the questions raised by my study on mist net bias and capture rates. A formula that incorporates the many variables affecting mist net capture (i.e., effort, habitat, net construction, and the diversity of bat species) can then be used to adjust the data collected. From this, we can reassess and recalibrate our data, effort, and methods; suggest better capture techniques and approaches to survey; as well as emphasize the need for unbiased data from which better conservation guidelines and management efforts can be implemented.

Beyond this present study, we need to conserve the available habitat, identify species in need, and manage the populations to maintain biodiversity. Understanding the differential habitat requirements of each species, the fluctuations in populations over time, and the affects disturbances have on an ecosystem, allows us to obtain a firmer grasp of the potential biases and limits of our own efforts.

Obtaining a completely unbiased sample is unlikely when using only one method of capture or detection. Due to this fact, simple capture rates with any capture method should not be used as an index of relative abundance, but should be framed with a consideration of the many other factors involved in the capture of bats. The methods and techniques used to capture and identify bats are essential in obtaining consistent and comparable results. Long term inventories and increased effort will help to overcome the limitations of mist nets and allow for a better understanding of the true biodiversity within a survey area.

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