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Do Bats Forage at Different Heights When in the Presence of Other Species?

Benjamin L. Wagenberg
CUNY Hunter College

Do Bats Forage at Different Heights When in the Presence of Other Species?

by

Benjamin Littman Wagenberg

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May 15th, 2020	Ofer Tchernichovski
Date	Thesis Sponsor
May 15th, 2020	Colleen McCann
Date	Second Reader

Abstract

Physical capture is the best way to reliably identify and examine insectivorous bats, but current techniques are likely to capture non-target species and negatively impact welfare of the animals captured. Acoustic monitoring is typically used for sampling bat populations, but the results of physical capture have been shown to provide different snapshots of the same area. The aim of this study was to examine whether bats forage at different heights in the presence of other species using acoustic monitoring, information that could be used to compliment physical identification techniques. Two ultrasonic recorders placed at different heights were used to collect acoustic data from native bats at the Bronx Zoo, NY over 84 recording days. Of the nine species of bats in New York State, six species were identified using SonoBat analysis software: little brown bats (*Myotis lucifugus*), tricolored bats (*Perimyotis subflavus*), big brown bats (*Eptesicus fuscus*), eastern red bats (*Lasiurus borealis*), hoary bats (*Lasiurus cinereus*), and silver-haired bats (*Lasionycteris noctivagans*), although likelihood of presence estimates suggested that little brown bats and tricolored bats had negligible presences. The results showed that silver-haired bats, big brown bats, and hoary bats did forage at different heights in the presence of other species, while eastern red bats did not. These findings suggest that further studies on height preferences and prey species can provide greater insights into the foraging strategies of native bat species.

Keywords: SonoBat, bats, acoustic monitoring, foraging, animal behavior, mist nets, flight, species identification

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Chapter I: Introduction

Physical capture is the most reliable and accurate way to identify bat species in the wild. However, this places a great deal of stress on the bat while entangled in the net, extracted from the net, and subsequently handled by an investigator - for examination or care. In order to reduce the risk to bats caused by capture and handling, other techniques could be employed in conjunction with mist nets to maximize both the efficiency of the study as well as the welfare of the wild animals involved. This study explores the potential use of acoustic monitoring as a technique for distinguishing foraging behaviors in the presence of multiple species. With greater confidence about which species are likely to be found at a particular height, mist net placement effectiveness can be optimized for a given study, while minimizing the capture and handling of any species not being targeted.

Physical Capture

Mist netting is a capture technique used for studying birds and bats, in which a large net is stretched between two poles. When a bat strikes the net, it becomes entangled in the pockets formed by additional horizontal strands toward the bottom of the net (Dalquest, 1954). The width is traditionally 5-18 m and is often 2-3 m in height. The placement height of mist nets can vary greatly, with some set as high as 8-10 m from the ground. While larger nets are technically possible to use, the practical difficulties of using very large net systems impedes more widespread usage. In addition, bats have been shown to learn to avoid established mist nets, so that moving the nets regularly is necessary to increase effectiveness (Marques et al., 2013). A potential alternative to mist nets are harp traps, created by Constantine (1958), which are formed by two aluminum posts in a frame suspending wires or fishing line in the style of a harp, that guides caught bats to a funnel leading to a collecting pocket. As a result, captured bats are less likely to escape by damaging the net, and less likely to be injured trying to escape. However, they cover a significantly smaller area than mist nets, generally 1.5-2 m wide and 5-7 m tall, and are generally used in specific locations, such as portals and discrete flyways (Constantine, 1958; Duffy, Lumsden, Caddle, Chick, & Newell, 2000).

Berry, O'Connor, Holderied, and Jones (2004) found that bats with higher frequency calls are particularly skilled at avoiding harp traps because higher frequencies reflect traps more conspicuously. They further concluded that mist nets, being more structurally complex than harp nets, would produce more acoustic echoes and that frequency-dependent echo reflectivity should be considered in any experiment design. Despite the effectiveness of harp nets, particularly for smaller species of bats, the width of coverage provided by mist nets still makes them a valuable tool (Francis, 1989).

In any study involving the capture of wild animals the welfare of the individuals should be a main consideration, with a research design that includes the fewest number of animals as possible. Serra-Gonçalves, López-Baucells, and Rocha (2017) searched existing literature beginning in 1990 for reports of opportunistic predation of entangled bats and found 12 publications covering at least 15 bat species and 11 species of predators, including owls and other opportunistic birds, snakes, other bats, mammalian carnivores, and invertebrates such as centipedes and spiders. They also published their own report of the predation of a silky short-tailed bat (*Carollia brevicauda*) caught in a mist net by a tawny bellied screech owl (*Megascops watsonii*). As a result, they recommended that researchers check the mist nets every 15-20 minutes to ensure that mist nets do not reach ground level when an animal is entangled to minimize opportunistic predation. Furthermore, bats that remain entangled for long periods have been known to chew themselves free, leaving the net damaged (Constantine, 1958), as well as injuring themselves while trying to escape.

Reducing the number of wild animals handled can also increase the safety of researchers. Recent studies have shown that handling stress does not inhibit the immune response in bats (Becker, Czirjak, Rynda-Apple, & Plowright, 2019; Strobel, Becker, & Encarnação, 2015). Due to the natural metabolism of a flighted mammal, bats have a higher body temperature than other mammals, which allows them to act as asymptomatic vectors for diseases that would normally kill other terrestrial mammals. This characteristic of bats to act as a reservoir host to function with little or no apparent symptoms also poses a potential threat to any person handling a captured bat, even when using proper safety precautions (Shountz, 2014).

Acoustic Monitoring

Using acoustic monitoring for bats is a relatively recent tool for researchers. Acoustic monitoring can be used to sample bat populations by recording the echolocation calls of foraging insectivorous bats from dusk to dawn. These calls are analyzed for distinctive characteristics, which can be attributed to different species. Duffy, Lumsden, Caddle, Chick, and Newell (2000), using Anabat software, found that acoustic monitoring is most effective in areas where there are fewer potential species to be identified, and had compiled a reference library of 250 calls from Southeast Australia in preparation for their study. Even with the compiled reference library, the inter-specific overlap of call characteristics necessitated a conservative approach to identification. In comparison, the SonoBat reference library used for this study contains 257 calls from the six species detected out of a total regional sub-library of 459 calls derived from 14 different species. As technology has improved, so has the ability and accuracy of detecting, recording, and resolving the vocalizations of bats.

Despite this, relying too heavily on acoustic monitoring can have limitations. Misidentification due to call characteristic overlap is often the primary problem (Kuenzi & Morrison, 1998; Caddle, Chick, & Newell, 2000), as is recording the same individuals multiple times, resulting in a skewed image of relative abundance of species (Hayes, 2000; Miller, 2001; Parkins, Michelle, McCann, & Clark, 2017). Clement, Rodhouse, Ormsbee, Szewczak, and Nichols (2014) found that false positives from acoustic data can be sufficient to significantly impact the accuracy of occupancy models. Their study emphasizes the importance of considering of a site's detection history, as well as using mist nets in conjunction with acoustic recording, when considering the data obtained. Miller (2001) introduced a new acoustic activity index for bat data in an effort to reduce falsely inflated call numbers garnered from acoustic activity. By using a presence/absence model for the data over a particular time period, the possibility of incorrectly inflating the presence of any given species from a single bat being recorded multiple times in succession could be significantly reduced.

Many studies have found that using acoustic monitoring in conjunction with physical capture techniques, whether harp trap or mist net, are significantly more effective at surveying bat populations than physical capture on its own (Kuenzi & Morrison, 1998; O'Farrell & Gannon, 1999; MacSwiney G., Clarke, & Racey, 2008). MacSwiney G., Clarke, & Racey (2008) used multiple physical capture techniques (ground mist nets, canopy nets, and harp traps) and found that using only physical capture failed to sample 30% of the bat fauna in the area and that aerial insectivores were only sampled by ultrasonic detectors. This study aims to investigate whether ultrasonic acoustic recording can be used to identify species-specific flight or foraging behaviors to allow for more accurate net placement, as well as support the concept that using acoustic monitoring in conjunction with physical capture techniques is more effective than either technique alone.

Natural Histories of Detected Species

There are nine species of bats known to live in New York state: northern bats (*Myotis septentrionalis*), little brown bats (*Myotis lucifugus*), Indiana bats (*Myotis sodalis*), tricolored bats (*Perimyotis subflavus*), big brown bats (*Eptesicus fuscus*), small-footed bats (*Myotis leibii*), eastern red bats (*Lasiurus borealis*), hoary bats (*Lasiurus cinereus*), and silver-haired bats (*Lasionycteris noctivagans*). Of these, six species were detected in this study.

Eastern Red Bat (Lasiurus borealis)

Eastern red bat males tend to be a bright rusty red and have white tipped guard hairs, which creates a frosted appearance. Females are often a more muted chestnut color, and have an even more vivid frosted aspect. The wing membranes and furless area of the tail are dark brown, and the ears are short and rounded (Saunders, 1988). Females have four mammary glands, as opposed to most chiropterans, who have two. Both males and females have four sets of facial glands thought to be used in intra-specific communication (Saunders, 1988). Adult eastern red bats are approximately 95-126 mm long and have a wingspan of approximately 330 mm, as well as a 36-46 mm forearm and an 8-10 mm hind foot. The tail typically measures 38-63 mm, and the ear reaches 8-13 mm. Mature adults generally weigh 6-14 g (Shump & Shump, 1982). Eastern red bats have an average echolocation frequency range of approximately 40-70 kHz (Murray, Britzke, & Robbins, 2001).

The range of the migratory eastern red bat extends from the central US to the east coast, as far north as southern Canada and as far south as northern South America (Cryan, 2003) as they search for warmer climes. They typically roost in dense trees and large, elevated shrubs, but are also commonly found in human developed areas, particularly if there are still large trees, such as in city parks (Elmore, Miller, & Vilella, 2004). Eastern red bats are tree roosting migratory bats, and roosting sites have been observed at heights ranging from 0.6-13 m above the ground (Constantine, 1966).

Except during migration and mating, eastern red bats are solitary animals, although the females are promiscuous (Saunders, 1988). They do not undergo a pre-hibernation fattening period, unlike some other migratory bats (Milam-Dunbar, 2005). Mating usually occurs during August and September, particularly around cave entrances (Shump & Shump, 1982), after which females store the collected sperm and delay implantation until spring. Migration begins in mid-October, and the return is usually complete by the middle of April (Fenton, 1985).

Gestation is 80-90 days, and birth occurs in late June to mid-July, usually resulting in a litter of 1-5 pups, averaging two. Newborn eastern red bats weigh approximately 1.5 g, and by four weeks they will have reached half the mother's weight. They are ready to fly at 3-6 weeks and ready to be weaned at 4-6 weeks. They have been observed to reach 12 years old in the wild. (Shump & Shump, 1982).

Eastern red bats generally begin foraging at dusk, primarily feeding on lepidoptera, coleoptera, hemiptera, and diptera. Moths and beetles have been seen to comprise about half of an eastern red bat's diet (Carter et al., 2003). Most often, they will feed until full in one foraging session, but they have been observed foraging throughout the night. They often prefer to hunt near light sources (within 500 m of a source), if available, although their activity when hunting near lights reflects their foraging patterns when away from lights (Hickey, Acharya, & Pennington, 1996). Their predators are typically great horned owls, kestrels, and hawks, and blue jays have been known to eat young bats (Saunders, 1988).

Silver-Haired Bat (Lasionycteris noctivagans)

Although the fur which covers almost every part of their body is black, silver-haired bats get their name from the silver tips of the fur. The only furless areas are the wings and posterior uropatagium membrane, which are both dark brown or black, and the snout, which is slightly upturned (Kunz, 1982). Adults measure 92-115 mm long with a 35-45 mm tail, and have a wingspan of 270-310 mm (Barbour & Davis, 1968; Saunders, 1988). The ear, which is rounded at the top, measures 5-9 mm and the hindfoot is 6-12 mm. The forearm typically measures from 37-44 mm and adult bats usually weigh 8-11 g (Kunz, 1982). The average echolocation range of silver-haired bats is approximately 25-40 kHz (Barclay, 1986).

Silver-haired bats can be found across the entire United States, as well as Bermuda (Cryan, 2003). Their range stretches into Canada, as well as some parts of Alaska during the summer, and south into Mexico during the winter (Simmons, 2005). In the summer, they typically roost under loose bark in trees, particularly willow, maple, and ash trees (Kunz, 1982a). Cavities of dead trees can sometimes host maternity or summer bachelor male colonies, although silver-haired bats are generally solitary. Maternity colonies tend to be small, usually less than 20 individuals (Parsons, Smith, & Whittam, 1986), although colonies as large as 55 have been observed (Mattson, Buskirk, & Stanton, 1996). Silver-haired bats also occasionally use human structures such as garages and sheds, but do not do so in large numbers (Patriquin & Barclay, 2003).

During the summer, males and females are geographically separated and generally only unite in the fall, during migration. Swarming is a behavior exhibited by many old and new world bats, and is best described as the intense circular flight activity of a large gathering of bats, typically around underground roosting sites (van Schaik, et al., 2015). In silver-haired bats, however, it occurs during migration, rather than before. Like the eastern red bat, sperm is stored and fertilization is delayed until spring (van Schaik et al., 2015). Gestation is 50-60 days, and the average litter size is two pups, which tend to be born in June and July (Kunz, 1982). Silver-haired bats have been reported living 5-10 years in the wild, although dental records have been discovered for bats as old as 12 years (Kunz, 1982).

Typical foraging times for silver-haired bats are early evening, either just before or after dark, as well as just before dawn. Cryan (2003) has suggested that this gap is to prevent conflict from flying at the same times as eastern red, hoary, and big brown bats, although they have been observed foraging at these times even when these species are not present. Silver-haired bats typically have a foraging range of approximately 30 km^2, ranging from 14-37 km^2. They generally eat diptera, coleoptera, and lepidoptera. Additionally, they will forage opportunistically on most insects they come across if encountered in large concentrations. They do not always eat in mid-flight, having been seen feeding on larvae on trees, and have been found caught in mouse traps, suggesting ground foraging (Lacki, Johnson, Dodd, & Baker, 2007). Cats, skunks, and raccoons have been known to prey on silver-haired bats, although their primary predator is owls.

Big Brown Bat (Eptesicus fuscus)

The dorsal hair of big brown bats varies in coloration depending on location and subspecies, ranging from pink to chocolate, with lighter ventral hair (Barbour & Davis, 1969). The ears, wing membranes, and exposed face are all black (Kurta & Baker, 1990). Adults measure 110-130 mm long, including a 38-50 mm tail, and have a wingspan of approximately 330 mm (Baker, 1983). The forearm is 41-50 mm and the hindfoot is 10-14 mm long. The ears are comparatively long, 16-20 mm (Kurta, 1995). Adult weights range from 14-29 g, although males are slightly smaller (Kurta & Baker, 1990). The average echolocation range of big brown bats is approximately 25-50 kHz (Murray, Britzke, & Robbins, 2001).

Big brown bats can be found almost everywhere in North America, including urban environments (Kurta, 1995), and range from southern Canada through Central America to northern South America, and the West Indies (Nowak & Walker, 1999). They are hibernating bats, and have been observed putting on an additional third of their body weight before hibernation (Baker, 1983). They can be found roosting in almost any man-made structure, and have even been found in storm sewers. Males and non-reproductive females generally roost alone or with a few other individuals in buildings, trees, and rock crevices. Caves and man-made structures are preferred hibernacula (Baker, 1983). Forest-dwelling reproductive females switch roosts often during the summer (approximately every two days) to stay cool (Willis, Voss, & Brigham, 2006). Big brown bats are relatively sedentary, generally remaining within 50 km of their birthplace. Even when moving between summer and winter roosts, they rarely move more than 80 km (Barbour & Davis, 1969). They also typically forage 1-2 km from their roost sites (Brigham, 1991). Reproductive females will tend to roost in buildings in maternity colonies, which can reach up to 200 individuals (Brigham, 1991).

Swarming, and subsequent mating, typically occurs near hibernacula in the fall, at the end of August and early September (Barbour & Davis, 1969). Gestation is approximately 60 days, and a single pup is born in June. The pup is left alone at night to roost while the mother forages (Davis, Barbour, & Hassell, 1968). Big brown bats have been estimated to have the potential to live up to 20 years, but tend to die after 6-8 years (Reid, 2006).

Big brown bats tend to begin foraging approximately 20 minutes after sunset. After eating their fill, they will rest at a night roost while digesting, and return to their day roost before dawn (Kurta, 1995). They forage with other bat species, but there is no evidence of direct competition. Big brown bats prey primarily on coleoptera using their powerful jaws (Carter et al., 2003; Whitaker, 2004). They also eat other flying insects, lepidoptera, diptera, hymenoptera, neuroptera, and anisoptera. There are estimates that big brown bats can catch at least 1.4 g of insects per hour (Baker, 1983). Raccoons and cats opportunistically prey on young bats that have fallen from their roosts, but the primary predators of big brown bats are owls and falcons.

Hoary Bat (Lasiurus cinereus)

The body fur of the hoary bat is brown-gray, long, dense, and soft, with white tips, which creates the intense ‘hoary’ appearance, similar to the effect of the eastern red bat, although the belly has less of a frosted appearance. They have rounded noses and short, thick, and broad ears (Shump & Shump, 1982). The wings membranes, tail, and face are exposed, and dark brown in color. There is also a distinct yellow patch on the throat, and whiter patches on the wrists and shoulders. Hoary bats generally reach 130-150 mm long, including an approximately 50-63 mm tail, with a wingspan of 430 mm. The hindfoot generally measures 6-14 mm, with a 46-55 mm forearm and approximately 18 mm ears. Adults tend to weigh 20-35 g, with females being slightly larger. Like eastern red bats, hoary bats have four mammary glands (Shump & Shump, 1982). The hoary bat echolocates at a lower frequency than many other North American bats, averaging approximately 15-25 kHz (Barclay, 1999).

The hoary bat is one of the most wide-ranging bats in the Americas, ranging from Argentina and Chile to as far north as Canada (Shump & Shump, 1982). There are also hoary bat populations in the Galapagos Islands and in Hawaii (*Lasiurus cinereus semotus*) (Bonaccorso & McGuire, 2013). Their habitat is primarily coniferous and deciduous forests, but they also live in human inhabited areas. Hoary bats are solitary and tend to roost individually rather than in colonies. They roost anywhere from 3-19 m above the ground, but usually under dense foliage with an open area below. They rarely roost in caves, but will occasionally roost in rock crevices. They exhibit low roost fidelity and change roosts willingly and frequently (Perry & Thill, 2007).

Although hoary bats are migratory, cases have been observed where some hoary bats further north will hibernate instead of migrating (Whitaker, 1980). Usually solitary, hoary bats form large groups of individuals, often numbering in the hundreds, during migration, which takes place in waves. Generally, females will precede males during migration (Valdez & Cryan, 2009). Individual hoary bats are capable of migrating more than 2000 km (Cryan, Bogan, Rye, Landis, & Kester, 2004), although there does not seem to be evidence of significant migrations between North and South America (Cryan, 2003).

Breeding begins in September and has been observed through early winter. Like other migratory bats, fertilization is delayed, and birth usually occurs from May to July. Gestation is approximately 57 days, and average litter size is two, but litters ranging from one to four have been observed. Pups weigh approximately 4.5 g at birth (Barclay, 1989). Hoary bats have been recorded living as long as 14 years in the wild, though they often only reach 6-7 years of age (Wilkinson & South, 2002).

Hoary bats have two foraging bouts each night. The first peak is about five hours after sunset, and the second is a few hours before dawn. They forage in the tree tops and along streams and lake shores. In non-urban settings, hoary bats sometimes forage around light sources (Furlonger et al., 1987). They often take breaks between foraging sessions to rest. Despite being solitary, hoary bats will often form groups when hunting (Tuttle, 1995), and have been recorded using especially low frequency social calls (~9.8 kHz) which are thought to be used to warn off other species of bats (Tuttle, 1995). Their diet is almost exclusively lepidoptera, but includes coleoptera, hymenoptera (including ants), and hemiptera (Carter et al., 2003; Valdez & Cryan, 2009). Hoary bats are preyed on by owls, hawks, and rarely, snakes.

Tricolored Bat (Perimyotis subflavus)

Previously called eastern pipistrelles, tricolored bats are small with yellow-brown fur. They get their name from their tri-colored hairs which have a dark base, yellow-brown middle, and dark tip. The ear ranges 12.4-14.1 mm, and has a long, straight, and rounded tragus. The wing membrane is dark, and although it is hairless, the dorsal base has fur (Schmidly, 1991). Adults range from 77-89 mm with a 34-41 mm tail and 7-10 mm hind foot. Wingspan ranges from 220-250 mm with a 31-34 mm forearm (Farney & Fleharty, 1969). Adults weigh from 4-8 g, with females being slightly larger. Tricolored bats echolocate at an average range of approximately 40-60 kHz (Murray, Britzke, & Robbins, 2001).

Tricolored bats are found throughout the eastern United States, reaching as far west as Texas, and the eastern edge of Mexico and Central America. They are found as far north as Quebec and the southern edge of their range ends in Honduras (Fujita & Kunz, 1984). While tricolored bats are not typically found in deep forests or open fields (Nowak & Walker, 1999), they are generally found in open woods near, and sometimes over, water. They roost in rock crevices, caves, buildings, and tree foliage. Maternity colonies sometimes use human-made structures, such as the underside of bridges or large buildings (Ferrara & Leberg, 2005; Barbour & Davis, 1969).

Tricolored bats are obligate hibernators, and will hibernate in warmer climates even when food is available (Briggler & Prather, 2003). Hibernacula are most often caves, but can also include mines, tunnels, and under elevated highways. During hibernation, they roost separately or in small groups (Briggler & Prather, 2003). During summer, however, females roost in colonies of 15 individuals on average, while males roost alone (Whitaker, 1998). Young tricolored bats are able to call to their mothers using social calls which allow mutual recognition (Pfalzer & Kusch, 2003).

Swarming occurs from August to October in front of caves. This is the only time both sexes are together, and females will copulate with multiple males (Whitaker & Hamilton, 1998). Fertilization is delayed, and birth usually results in a litter of two, most often twins (Wimsatt, 1945) which weigh up to half the mother's weight. Gestation is approximately 44 days, and birth typically occurs from late May to early June, but varies by the population's latitude (Whitaker, 1998). The lifespan of the tricolored bat is 4-8 years, with the oldest ever recorded living 14.8 years (Nowak & Walker, 1999).

The diet of tricolored bats is extremely varied, consisting of coleoptera, diptera, hymenoptera, lepidoptera, neuroptera, ephemeroptera, hemiptera, psocoptera, and trichoptera. Their actual diet varies by location and opportunity (Griffith & Gates, 1985; Carter et al., 2003). Despite their fluttering and sporadic flight, often likened to that of a moth (Patterson & Hardin, 1969), their effective use of harmonics during echolocation makes them particularly effective hunters, and they are able to consume 25% of their body weight within 30 minutes (Gould, 1955; MacDonald, Matsui, Stevens, & Fenton, 1994). Birds of prey are the primary predators of tricolored bats, although other predators include racoons, skunks, prairie voles, and cats.

Little Brown Bat (Myotis lucifugus)

Little brown bats are small and covered in brown fur, and are slightly darker on the dorsal side. The wings are dark brown and the membranes are hairless. Adults generally measure from 40-55 mm, not including the long 30-65 mm tail, and have a forearm ranging 33-41 mm with an 8-10 mm hindfoot. The tragus is blunt and long, approximately half the height of the ear, which is typically 11-15 mm (Hall, 1981). Adults have a wingspan of approximately 220-225 mm, and the adults tend to weigh 5-14 g, with females being larger. The little brown bat can be distinguished from the Indiana bat (*M. sodalis*), which has a range that overlaps with the little brown bat, by the absence of a keel on the calcar and long hairs on the hindfoot that stretch longer than the toes (Barbour & Davis, 1969). They do not exhibit eye shine due to lack of folded retinas (Kurta, 1995). Little brown bat echolocation frequency ranges from 35-70 kHz (Murray, Britzke, & Robbins, 2001).

The little brown bat range stretches from Alaska through southern Canada to the east coast, and south to the Midwest United States (Barbour & Davis, 1969). While little brown bats usually inhabit forested lands near water, some subspecies can be found in dry areas where water is not readily available. In such areas, little brown bats stay hydrated by licking moisture from cave walls or drinking the condensation that forms on their fur. Little brown bats are able to live over a wide elevational range (Havens & Myers, 2006). They will also often roost in buildings, particularly for maternity sites (Fenton & Barclay, 1980). To avoid attracting predators, little brown bats have separate day and night roosts in different locations to prevent accumulation of feces. Little brown bats will travel several kilometers between day roosts and feeding sites at night (Nowak & Walker, 1999). Hibernation usually starts between September and November and ends from March to May. During hibernation, little brown bats undergo repeated periods of torpor lasting 12 to 19 days, but may remain torpid for as long as 83 days. Arousal of neighboring bats can signal the end of torpor. Younger bats remain active longer in the fall to build up fat deposits for winter. Little brown bats do not migrate long distances for hibernation roosts, with individuals traveling only up to 160 km (Davis & Hitchcock, 1965). Being social, little brown bats spend a large amount of time each day grooming in groups (Fenton, 1980).

They do not exhibit territoriality at roosts, and large colonies up to 300,000 bats have been seen in a single roost. Little brown bats have been seen flying outside hibernation sites during the winter periodically, particularly in mild weather (Whitaker & Rissler, 1992).

Mating generally occurs while swarming in September and October, although ovulation and fertilization are delayed until spring, after hibernation. The gestation period is 50-60 days, and a single pup is born in late June or early July, and weighs on average 1.5-2 g. The pups cling to the mother for the first few days (Davis & Hitchcock, 1965). Females produce first young usually in their first or second year (Herd & Fenton 1983). There have been reports of little brown bats living as long as 30 years in the wild (Kurta, 1995).

Little brown bats begin foraging about two or three hours after dusk, with secondary activity occurring before dawn. They generally return to their roost by four or five in the morning, and enter daily torpor. Little brown bats eat a variety of insects, including coleoptera, lepidoptera, homoptera, diptera, hymenoptera, and trichopteran (Anthony & Kunz, 1977; Carter et al., 2003). Adult bats will begin foraging in more cluttered areas once juveniles begin foraging on their own to reduce competition (Adams, 1997). Little brown bats are preyed upon by owls and hawks, but are also particularly vulnerable to terrestrial roost predators due to their small size. Weasels, raccoons, cats, snakes, and even mice and rats, have been reported preying on little brown bats.

Materials and Methods

Location

Data were collected by omni-directional microphones fitted with directional attachments to recorders placed near and on the roof of the World of Birds exhibit building at the Bronx Zoo in New York City. One recorder (LOSPOT) was chained to a tree out of sight of the public, and the microphone, attached by cable, was anchored approximately 3 m off the ground. The other recorder (HISPOT) was placed on the roof of the World of Birds building, approximately 10 m tall, and the connected microphone was anchored to the top of a 2.13 m pole on the roof. The two microphones were anchored approximately 8 m apart horizontally. Taking into account the grade of the area, the central axis of the LOSPOT microphone's effective recording area was approximately 4.6 m off the ground, and the central axis of the HISPOT microphone's effective recording area was approximately 13.7 m from the ground. Both microphones were anchored facing the same direction, down a paved walkway used by zoo visitors. This path was chosen for its distance from any path illumination (more than 12 m in any direction), which could unnaturally attract insects and impact activity levels, as well as the relatively light leaf cover to minimize echolocation bouncing off hard surfaces. Trees and heavy leaf litter flanked the entirety of the targeted path for the duration of the study. At the end of the path, approximately 30 m from the LOSPOT recorder is a brook, approximately 2 m wide, that runs perpendicular to the path.

Recording Period

Recording began the evening of 13 August 2019 and ended the morning of 15 November 2019. Both recorders had been set to automatically record calls continuously through the night, which had been defined for this study as civil twilight to civil twilight. Starting 31 August 2019, batteries and memory cards were replaced for both recorders every two weeks until 15 November 2019.

Equipment

Recording equipment employed were two Song Meter SM4BAT Full-Spectrum (SM4BAT-FS) Ultrasonic Recorders, two Song Meter SMM-U1 Ultrasonic Microphones, and two Song Meter SM-X Horn attachments (Wildlife Acoustics, Concord, MA). Data were recorded using 4 SanDisk Extreme 150 MB/s 64 GB SDXC SD memory cards. Both recorders used the same settings: 12 dB gain, 256 kHz sample rate, with a trigger level of 12 dB, minimum trigger frequency of 16 kHz, trigger window of 3.0 seconds, and a maximum length of 15.0 seconds. To prevent obtaining duplicate data from the omni-directional microphones, a directional horn attachment was attached to each microphone, and both microphones were directed along the path while keeping a parallel horizontal axis.

Analysis

The methodology used by Parkins, Mathios, McCann, & Clark (2017) was the basis for the acoustic analysis used in this study, and the Miller acoustic activity index (Miller, 2001) was used to reduce the possibility of incorrectly inflating the presence of any given species from a single bat being recorded multiple times in succession. In this study, the acoustic index was modified to quantify the presence or absence of any given species in 1-minute time blocks.

Recorded data were analyzed and classified using SonoBat software v4.3.0 base software with Regional Classifier nE[c20180819] and subregion North-northeastern US and Southern Ontario. All data were first run through the SonoBat Batch File Scrubber (part of the SonoBat Data Wizard v4.4.1), designed to filter out files that do not contain tonal features, set to Medium noise tolerance. Once the data were scrubbed, all files, including those which had been filtered by the scrubber, were viewed manually through the SonoBat software both to ensure that no noise files were missed by the scrubber and that no valid files were scrubbed by mistake. For files to be considered acceptable for this study, the sonogram had to contain at least two complete and unbroken pulses, regardless of whether or not the software was able to attribute the pulses to a particular species.

Files containing identifiable vocalizations from multiple species were quantified in the data as positive presence for each of the species identified, provided at least four consecutive passes were identified. Files deemed to be either noise or of insufficient quality were separated from the rest of the data and not included in the classification process. Software settings were set to: 32 maximum calls to consider per file, 0.80 acceptable call quality, 0.90 sequence decision threshold, 30.000 second maximum segment to process, 256 kHz detector sampling frequency, a time expansion factor of 10, and a filter frequency of 25 kHz (with added anti-katydid filter).

Results

Of the nine species of bats that are present in New York state, six were detected during the recording period, based on the acoustic data processed by SonoBat (Figure 1).

Figure 1. Sample Sonograms of All Detected Species

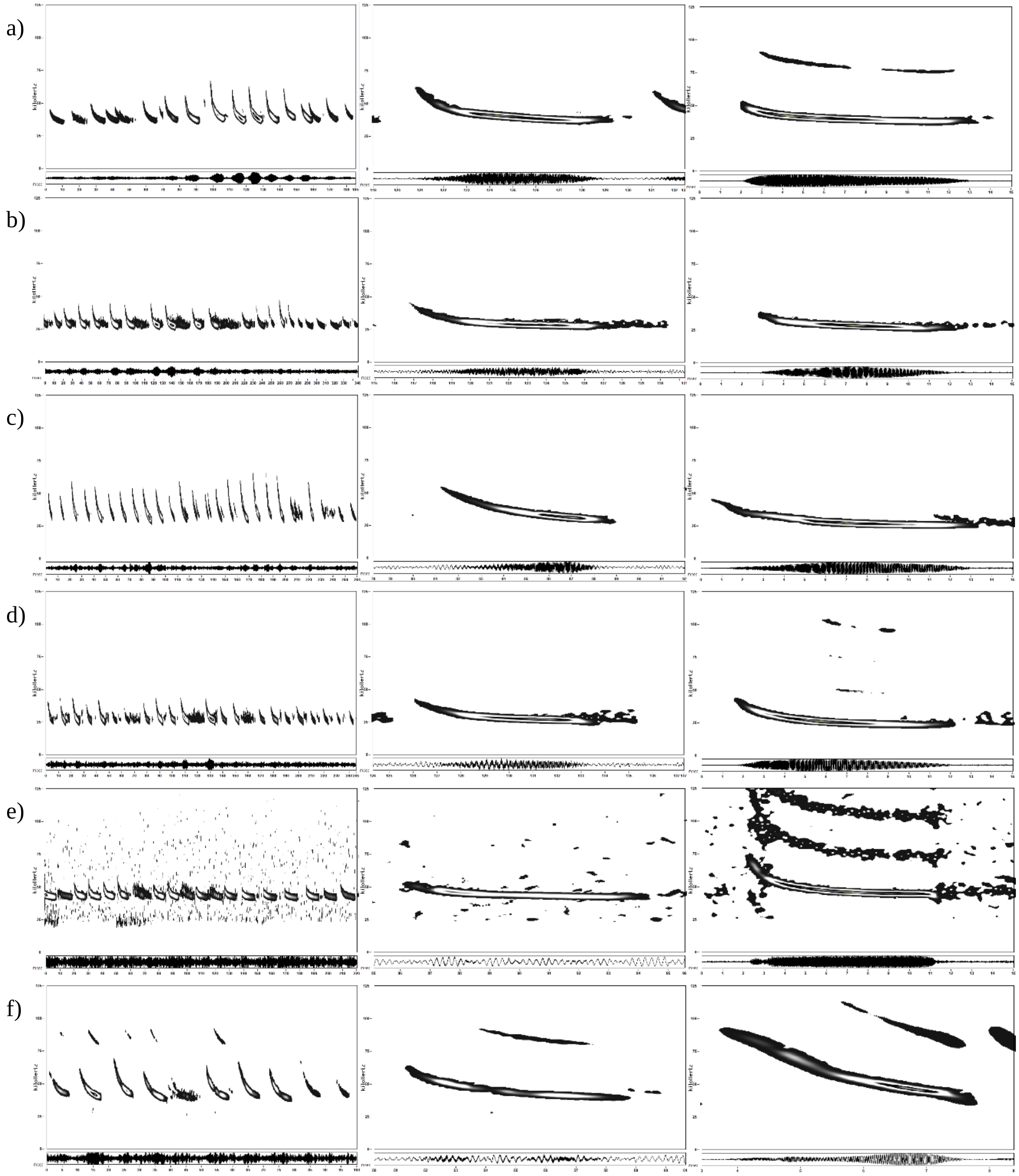


Figure 1. Sonograms, presented left to right, for each row are a sample sonogram from the collected data, a single characteristic pulse from the sonogram on the left, and a reference call from the SonoBat reference call library (Szewczak, 2018).

Note. a) *L. borealis*, b) *L. noctivagans*, c) *E. fuscus*, d) *L. cinereus*, e) *P. subflavus*, f) *M. lucifugus.*

The data summarized in Table 1 were derived from a total of 4,858 files recorded over 84 nights across both recorders. Of those passes, 2,658 were evaluated as fit for analysis by SonoBat, which successfully identified 1,502 passes by consensus. Of the remaining 1,156 passes, 837 passes were classified as likely to be a high frequency species and 319 were classified as likely to be a low frequency species. SM4BAT-FS recorders also record temperature, and during the recording period, temperature ranged from 32.00ºC to -2.50ºC at the HISPOT recorder over the course of the entire recording period, and 30.25ºC to -3.25ºC at the LOSPOT recorder. It must be noted that the recording days used for analysis were not all continuous. There were short periods during which only one recorder was functioning due to low battery power in the other. To allow for paired data testing, only data that were collected while both recorders were functioning was used. The calls designated by the SonoBat software program as uncertain high frequency or uncertain low frequency were not included in the analysis.

Table 1. Summary of Collected Data
Consensus Report of Identified Calls by Species at Two Recording Locations Adjusted Using the Miller Acoustic Index

	HISPOT			LOSPOT		
Species	Sum	M	SD	Sum	M	SD
L. borealis	262	3.12	6.055	267	3.18	7.451
L. noctivagans	207	2.46	6.291	31	.37	.941
E. fuscus	190	2.26	4.820	31	.37	1.180
L. cinereus	33	.39	1.513	7	.08	.278
P. subflavus	7	.08	.318	0	.00	.000
M. lucifugus	1	.01	.109	3	.04	.243

The likelihood of presence of each of the species is determined by the maximum likelihood estimate (MLE) seen in Table 2, where a value of 1.00 likelihood of presence indicates a certainty of presence and a value of 0.00 MLE indicates the opposite. Given the MLE for each of the species present, it would be reasonable to assume that the vast majority of uncertain high frequency passes could be attributed to eastern red bats. However, the same supposition cannot be made about the uncertain low frequency species, due to there being multiple possible and likely attributable species. Additionally, although tricolored bat and little brown bat calls were identified by consensus, the likelihood of presence estimates for both species signify that while the calls remain as designated by SonoBat, the software returned a corrected estimate of 0 passes for both species. As a result, these two species will be considered to have no presence for the analysis.

Table 2. Likelihood of Presence and Maximum Likelihood Estimate (MLE)
Likelihood of presence estimate and MLE at both HISPOT and LOSPOT recorders

HISPOT	*L. borealis*	*L. noctivagans*	*E. fuscus*	*L. cinereus*	*P. subflavus*	*M. lucifugus*
Likelihood	1.00	1.00	1.00	1.00	0.07	0.02
MLE	0.00	0.00	0.00	0.00	0.93	0.98
LOSPOT						
Likelihood	1.00	1.00	1.00	0.63	0.00	0.01
MLE	0.00	0.00	0.00	0.37	1.00	0.99

Note. MLE and likelihood of presence estimates were calculated using all valid collected data, including data not used for analysis.

Because the data collected were not normally distributed, to evaluate the statistical significance of the differences in the presence of each species' different heights, the Wilcoxon signed ranks test was used to test the mean ranks of each species of bat against itself by recorder location. The results, in Table 3, indicated that the foraging heights of eastern red bats (p = .495, z = -.683) were not significantly influenced by the presence of other species. Conversely, the detected presences of big brown bats (p < .001, z = -4.931), silver-haired bats (p < .001, z = -4.879), and hoary bats (p = .010, z = -2.559) differed significantly across recorder heights.

Table 3. Wilcoxon Signed Ranks Test Results
Wilcoxon Signed Ranks Test Statistics[a] for the Same Species at Different Heights

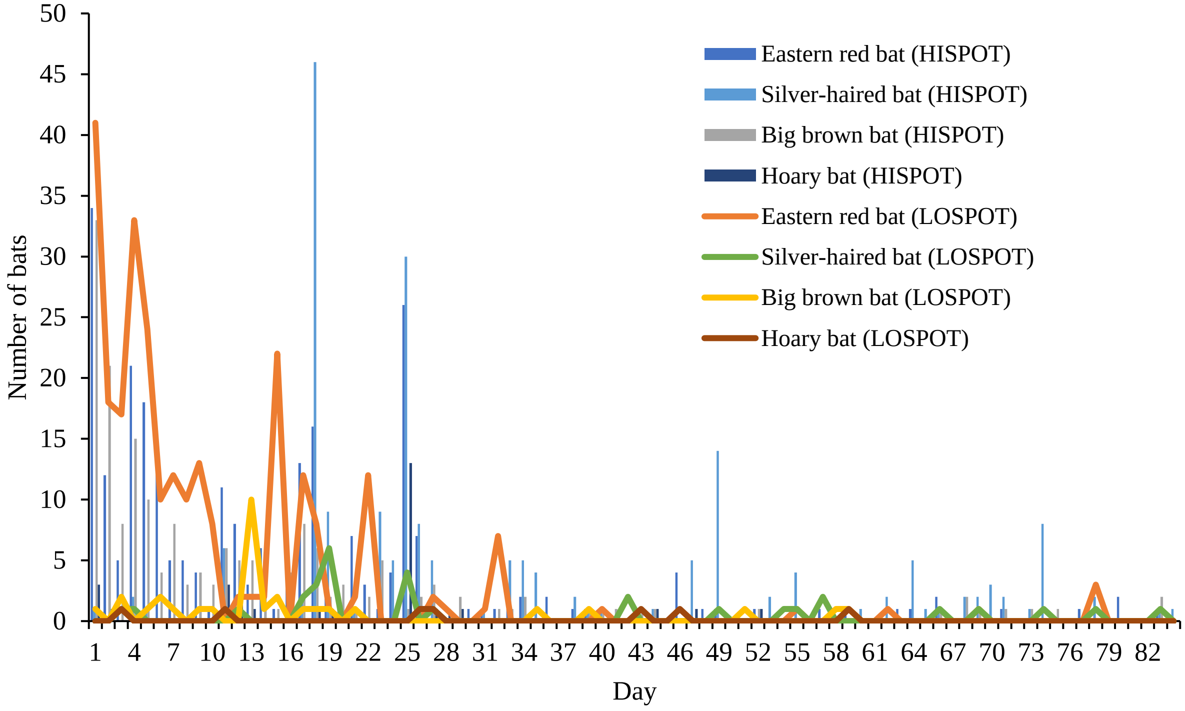
	L. borealis (low) – *L. borealis* (high)	*L. noctivagans* (low) – *L. noctivagans* (high)	*E. fuscus* (low) – *E. fuscus* (high)	*L. cinereus* (low) – *L. cinereus* (high)
Z	-.683[b]	-4.879[b]	-4.931[b]	-2.559[b]
Asymp. Sig. (2-tailed)	.495	.000	.000	.010

a. Wilcoxon Signed Ranks Test

b. Based on positive ranks.

The data reflected an anticipated decrease in activity as temperature decreased (Figure 2), with the majority of the activity detected during the first 30 days of recording (Figure 3). This negative correlation of each species with day is best explained by bat activity decreasing as temperature decreases (Parkins, Mathios, McCann, & Clark, 2017), and species begin to migrate or hibernate as the winter months approach.

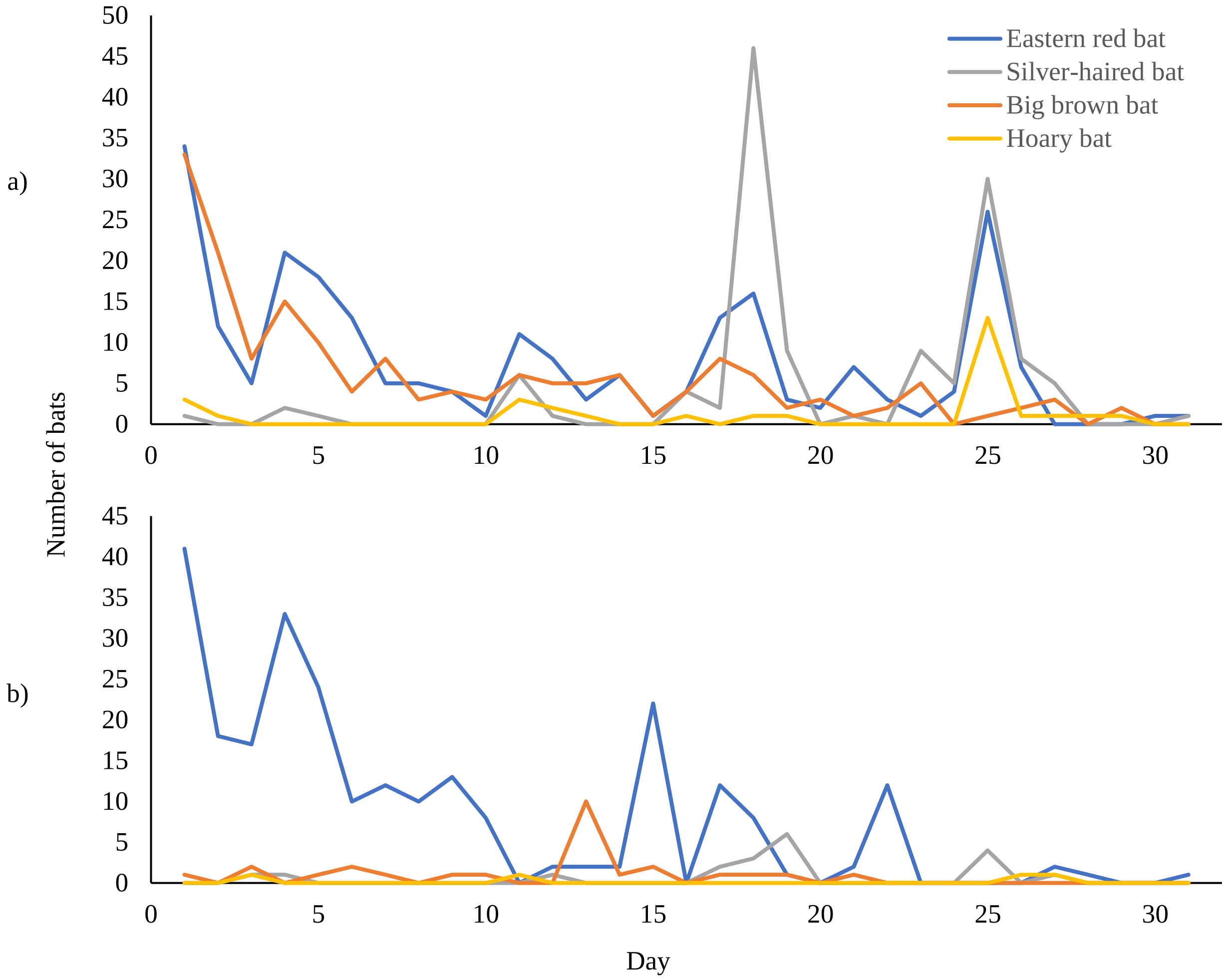
Figure 2. Number of Bats of Each Species Identified at Both Recorders



Note. Dates of recording day 1, 30, and 60 are 13 August 2019, 11 September 2019, and 12 October 2019 respectively.

To prevent loss of statistical power from autocorrelation, a random sample of the data were tested for autocorrelation with minimal results. Furthermore, the Wilcoxon Signed Ranks test run on the random sample had similar trends (*L. borealis* (p = .528, Z = -.632), *L. noctivagans* (p = .003, Z = -2.962), *E. fuscus* (p = .002, Z = -3.058), and *L. cinereus* (p = .034, Z = -2.121)).

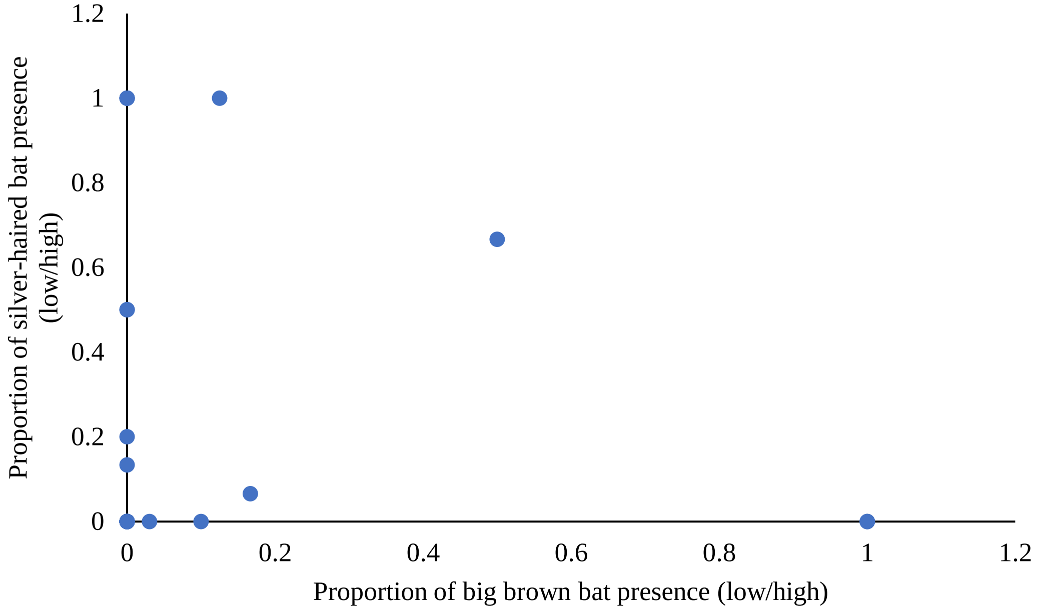
Figure 3. Number of Bats of Each Species Identified at Both Recorders During the First 30 Days



Note. a) HISPOT recorder data b) LOSPOT recorder data; dates of recording day 1 and 30 are 13 August 2019 and 11 September 2019 respectively.

To evaluate the possible correlation of the presence of a species with another species, the proportion of each species of bat across heights was plotted compared to that of each other species. Of the resulting tests, only the relationship between the presence of silver-haired bats and big brown bats appeared to be correlated (Figure 4). Despite the limited data, there is a trend of silver-haired bat presence being negatively correlated with big brown bat presence.

Figure 4. Correlation of Proportion of Presence of Big Brown Bats to Proportion of Presence of Silver-Haired Bats Across Height



Note. Proportion of presences by height used for both species is LOSPOT/HISPOT.

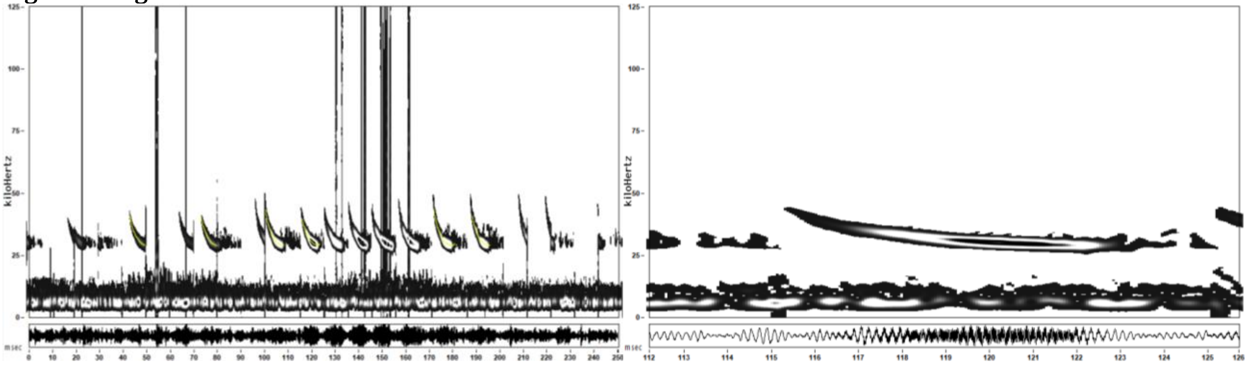
Quality Control

All data were manually reviewed for quality control. The automatic scrubbing software removed 660 files from the HISPOT recorder data and 1098 files from the LOSPOT recorder data. 34.1% of the total HISPOT scrubbed files and 31.2% of the total LOSPOT scrubbed files were recorded during the first recording period, which fell into the period of greatest bat activity. Upon manual evaluation of the scrubbed files, 310 of the scrubbed HISPOT files and 390 of the scrubbed LOSPOT files were deemed to have tonal features and returned to the data to be analyzed. For both groups, more of the files returned for analysis were obtained during the first recording period than during any other.

Upon review, some of the data not filtered by the automatic scrubber were removed manually, either because they did not satisfy the requirements set for this study, or because they did not contain bat vocalizations. 825 files were manually removed from the HISPOT recorder data over the course of the recording period, but it should be noted that 558 of those files were removed from the final recording period of the study, and the majority of these files were vocalizations from other wildlife. 354 files were manually removed from the LOSPOT recorder data.

To test the effectiveness of SonoBat against that of a human, I performed my own identification of 43 files, 22 from the HISPOT data and 21 from the LOSPOT data. From each recorder, the random sample data set was comprised of: five eastern red bat files, four silver-haired bat files, four big brown bat files, and one file that was deemed inadequate. Additionally, two files identified as hoary bats were taken from the HISPOT data, and one was taken from the LOSPOT data. The files were stripped of any previous identification from SonoBat and randomized, and I attempted to identify them myself, ignoring the sample composition. The result was 35 out of 43 files being identified correctly. Six of the eight files that were incorrect were misidentifying silver-haired bats as big brown bats, or vice versa. Figure 5 shows a big brown bat call I mistakenly identified as a silver-haired bat.

Figure 5. Big Brown Bat Call Misidentified as Silver-Haired Bat



This misidentification is common, and the calls often require increased scrutiny in areas where both bats are present (Betts, 1998). One file was incorrectly identified as a tricolored bat, and one file had the tonal features I had identified, but also features of two other species, and SonoBat identified the file as primarily different from my identification.

Discussion

The data in this study support the hypothesis that some bat species will forage at different heights in the presence of other species. As a result, there are multiple follow-up questions that bear consideration. Most important to ask is whether it is, in fact, the presence of other species of bats that results in any particular species foraging at a different height. The collected data suggest that such a trend may exist in this study, in the case of silver-haired bats and big brown bats, but more data would be required to be more conclusive. Furlonger, Dewar, and Fenton (1987) found that bats of different species forage differently in varied habitats, although their research also supported the idea that there are no unique associations between individual species of insectivorous foraging bats and specific habitats. They also observed cases of some species of bats, including the big brown bat, foraging in the presence of other species, without clear evidence of direct competition. However, even in cases of non-competition, it cannot be assumed that abundance of preferred resources is the cause, which invites further studies into factors such as interspecific communication. For example, the facial glands of the eastern red bat have been seen to attract other eastern red bats. This could explain the relatively stable presence of eastern red bats across height, as they continue to follow scent marks along the same pathways. Furthermore, future studies could examine whether the presence of a variety of individual species has consistent effects on the behavior of a target species, such as the warning vocalization of hoary bats, as well as the possibility that different permutations of species presences could have unique outcomes.

Due to the nature of this study as an observational one with some limitations, and not an experimental design where contributing factors can be controlled, it is possible that factors other than the presence of other species have influenced the results. The environment covered by the detection field in this study had varying levels of leaf cover and tree density. The HISPOT location, with its areas of relatively high leaf cover and tree density, could be ideal for the silver-haired bat, with its shorter wingspan and willingness to find prey that sits on branches and tree trunks, and the tricolored and little brown bats, which have both short forearms and wingspans, and tend to have lower flight speeds (Hayward & Davis, 1964). The wingspans of the detected species might suggest that bats with larger wingspans could favor areas of the LOSPOT recording field, with its lower leaf cover and tree density, to allow more direct foraging. Larger, slower insects in particular could be reached faster by those bats than bats with shorter forearms and wingspans, such as the tricolored or little brown bat. However, bats that have a larger wingspan do not necessarily rely upon speed to hunt, and instead have unusual flight patterns which can result in low speed (Hayward & Davis, 1964), but effective flight in complex environments. Because hoary bats use a near-constant low frequency echolocation that can only detect smaller insects at close range, they tend to feed on larger insects (Barclay, 1986). Despite this, they use their large, powerful wings to make sharp and erratic turns that allow them to even catch insects that they have just discovered.

There are many factors that act as sources of error and variability. First and foremost is the simple fact that the microphones used, with the added directional attachment, have a very limited scope with which to record the presence of bats. The Bronx Zoo, where the recorders are placed, is approximately 1.07 km^2, with many sources of water and artificial light, although the microphone coverage area is closer to 200 m^2 over a height of approximately 1.5-17 m. It is important to keep in mind when considering this study that any bats of a particular species may simply have not encountered the recording fields of the directional microphones. This could account for the periods during which the recorders were functioning within normal parameters but no passes were recorded, particularly in September, a period which often sees a swell of activity as some bats begin to swarm and mate (Barbour & Davis, 1969; Cryan, 2003).

This study, or variations thereof, would benefit from multiple iterations, particularly in warmer months of the year and in a variety of locations in the zoo. Additional studies should include an investigation of the insect population of the testing area and that of any subsequent studies to see if there is a correlation between the relative presence of any particular prey insect species and the presence of any particular bat species. While most of the species of insects consumed are shared by the detected species, this does not preclude preference or high value target hunting by each species of bat. Future data of this type could aid in insect population modeling by finding times and areas that bats partial to a particular species are especially active.

While this study on its own does not provide enough evidence to make definitive statements about species and condition-specific foraging heights, it does suggest that further studies may give insight into foraging behavior preferences of particular species. Armed with such information, future studies of wild bats could be much more efficient and, as a result, easier to replicate and substantiate. Acoustic data collection is especially effective as a foundational tool, because acoustic monitoring is non-invasive and takes relatively little time to assess whether a potential site is effectively viable to study a target species. In addition, using multiple acoustic recorders in a study site could allow investigators to choose areas of relatively higher activity of a target species for relocation sites for the capture equipment for successive recording days. For example, using the data from this study, future studies of hoary bats, which are of interest for their exceptionally low vocalization frequencies among North American bats and the role these vocalizations may play in interspecific communications, could be pre-empted by acoustic monitoring to judge relative activity levels across heights and establish multiple height optimized mist net locations prior to erecting any nets. Acoustic data can also provide a temporal snapshot of an area, offering insight into times of relative abundance of activity for a species in different seasons, as well as map trends of concurrent movement of multiple species.

Still, Barclay (1999) raised a very important point – relying exclusively on acoustic data to identify bat species should be guarded, even with the technological advances made since his comments were published. While different species of bats do have distinct vocalization characteristics, these characteristics are not always present, unlike bird songs which can be used to identify species with a high success rate. To rely on the presence of particular aural factors as the sole means for bat species identification is insufficient, as seen in my own attempts at species identification, as an individual who is not trained in bat call analysis. While acoustic monitoring is a valuable tool with many potential uses, it is best used as a tool to support other methods to identify the presence of bat species.

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