AN ABSTRACT OF THE DISSERTATION OF

Winifred F. Frick for the degree of Doctor of Philosophy in Forest Science presented on February 16, 2007.

Title: Influences of Island Characteristics on Community Structure and Species Incidence of Desert Bats in a Near-shore Archipelago, Baja California, Mexico.

Abstract approved:

John P. Hayes

Island biogeography has strongly influenced the study of biodiversity because archipelagos provide natural model systems for investigating patterns of diversity and the processes that shape ecological communities. I investigated the influence of area and isolation of islands (n = 32) in the Gulf of California, Mexico on patterns of richness, nestedness, and incidence of desert bats to determine factors important in shaping community structure and patterns of occurrence of bats in a naturally insular landscape.

Species richness of bats was positively influenced by island size and declined with isolation from the Baja peninsula in two distinct subarchipelagos. Southern islands, which are associated with greater density of vegetation from summer rainfall, supported more species than dry, barren islands in the northern subarchipelago, suggesting that both area and habitat characteristics contribute to species richness of bats.

Community composition of bats was nested by area and isolation, such that species found on smaller and more isolated islands were subsets of communities found on large, less isolated islands that harbored higher richness. The influences of area and isolation on community nestedness suggest species differ in immigration and persistence rates on islands. Bat communities were also nested at 27 sites in coastal habitat on the Baja peninsula, indicating that nestedness may occur in contiguous habitats that lack immigration and extinction filters.

Probability of species occurrence on islands was influenced by area for five species of insectivorous bat (*Pipistrellus hesperus, Myotis californicus*, *Macrotus californicus*, *Antrozous pallidus*, and *Mormoops megalophylla*), suggesting occupancy of islands by these species is limited by resource requirements. The threshold of island size for occupancy of most species was ca. 100 ha, which is similar to area thresholds of incidence for many landbirds in the same archipelago. Isolation also influenced incidence of insectivorous bat species.

My research shows that area and isolation influence both community structure and occupancy of bat species in a near-shore archipelago. My results raise important questions about connectivity and persistence of populations of bats in isolated habitats, especially when patch size is small.

Influences of Island Characteristics on Community Structure and Species Incidence of Desert Bats in a Near-shore Archipelago, Baja California, Mexico

by
Winifred F. Frick

A DISSERTATION

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APPROVED:

Major Professor, representing Forest Science

Head of the Department of Forest Science

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Winifred F. Frick, Author

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CONTRIBUTION OF AUTHORS

Dr. John P. Hayes contributed to study design, interpretation of data, and writing of Chapters 2-4. Paul A. Heady III contributed to study design, data collection, and interpretation of data of Chapters 2-4.

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Influences of Island Characteristics on Community Structure and Species Incidence of Desert Bats in a Near-shore Archipelago, Baja California, Mexico

by
Winifred F. Frick

CHAPTER 1: INTRODUCTION

Understanding factors that influence diversity of species is one of the cornerstones of ecology. Island biogeography has been pivotal in the study of species diversity because archipelagoes provide natural model systems for investigating patterns of diversity and processes that shape ecological communities (Rosenzweig 1995). The equilibrium theory of island biogeography (MacArthur and Wilson 1963, 1967), which explains species richness on islands as being a dynamic equilibrium between opposing forces of immigration and extinction, has strongly influenced the study of diversity in real and habitat-fragment archipelagos (Doak and Mills 1994). MacArthur and Wilson's equilibrium model has been the foundation of island biogeography theory and of early conservation biology, in part because of its simplicity, but also because its predictions can be tested empirically by measuring species richness on islands in different types of archipelagoes (Lomolino 2000a).

One of the short-comings of the equilibrium model, however, is its focus on species-neutral counts of richness rather than explicitly accounting for differences in immigration and extinction rates among species (Brown and Lomolino 2000). Research on how area and isolation influence composition of communities provides a species-specific extension of the equilibrium model that demonstrates how species may differ in their vagility and persistence capacities (Lomolino 2000b). Analyses of community nestedness, a pattern of composition where species at sites that contain fewer species form subsets of species found at richer sites, aim to determine whether deterministic or stochastic processes shape community structure (Atmar and Patterson 1993, Patterson and Atmar 2000). Analyzing patterns of nestedness may offer potential insights for conservation by identifying species at risk of extinction across fragmented landscapes (Patterson 1987), but these inferences are dependent on understanding the underlying mechanisms (Donlan et al. 2005).

Species richness and nestedness are properties of ecological communities. In comparison, metapopulation research focuses population dynamics by investigating the role of persistence and dispersal of populations across isolated habitats. Metapopulation theory has emerged as a distinct discipline (Hanski 1999), but its origins are rooted in both equilibrium theory (MacArthur and Wilson 1963, 1967) and Diamond's (1975) pioneering concept of incidence functions (Hanski 1991). Investigating the influence of area and isolation of islands on incidence of species provides potential insight into how persistence and vagility of species may vary (Diamond 1975, Adler and Wilson 1985, Taylor 1991). By addressing community and species-level questions, I hope to better understand factors important in shaping patterns of species diversity.

My dissertation research investigated the influence of area and isolation of islands on the richness, nestedness and occurrence patterns of a desert bat assemblage in the Gulf of California, Baja California, Mexico. Bats comprise a quarter of all mammal species, but are distinct from other mammals in their ability to fly. Bats are generally assumed to have high immigration and dispersal rates among isolated habitats (Lomolino 1984, Lawlor 1986, Lomolino 1986, Carvajal and Adler 2005), but our understanding of factors influencing community structure in isolated and fragmented habitats remains deficient (Racey and Entwistle 2003). Fifty-one percent of Microchiropteran bats are considered either critically endangered, endangered, data deficient, vulnerable or near threatened (Hutson et al. 2001) presumably due to low population densities of many species and degradation and loss of habitat (Racey and Entwistle 2003). Understanding the roles of persistence and vagility on community structure and incidence in a naturally insular system may provide some insight for bat conservation.

In Chapter 2 of this dissertation, we explore how area and isolation influence species richness of bats on two subarchipelagos in the Gulf of California, Mexico. The positive species-area relationship is one of the best supported patterns in ecology, but multiple causal mechanisms may generate such patterns (Rosenzweig 1995, Gotelli 2001). We compare richness of bats on two subarchipelagos that share a similar source fauna, but differ in vegetation density, in an attempt to tease apart the independent influences of area *per se* and habitat diversity on species richness. In addition, we ask whether isolation from source populations negatively influences richness of this vagile group of mammals.

In the third chapter, we examine the influence of area and isolation of islands on the nested subset structure of community composition in the southern subarchipelago in Baja California, Mexico. To explore how differential vagility may influence community composition, we compared an ecomorphological trait, representing cost of transport, to nestedness of species. We compared nested composition patterns on the archipelago to composition patterns at sites in coastal habitats on the Baja peninsula to investigate how nestedness may manifest in different landscape types and at different spatial scales. In addition, we assessed the impact of imperfect detection probabilities on accuracy of presence-absence matrices by estimating the probability a site was used by a species given it was never detected (MacKenzie et al. 2006).

In the fourth chapter, we focus our research questions at the level of species and compare patterns of insular incidence for six species to better understand the role of persistence and vagility on probability of occurrence on islands for bats. We examined whether incidence is influenced by minimum area thresholds, maximum isolation effects, or combinations of both and discuss the potential mechanisms that produce different patterns of island occupancy.

Each of the three manuscripts attempts to provide potential insights about the ecological theory from which it draws as well as better our understanding of the ecology of bats. The study of species richness, community nestedness, and species incidence are linked by the fundamental goal of seeking to understand patterns of species diversity and the underlying processes that shape such patterns. Ecology has long been a science of pattern, but recent emphasis has been placed on focusing ecological research on causal mechanisms (Gaston and Blackburn 2000). Although the research presented here is pattern-oriented, I have tried throughout to connect the mechanistic dots and hope our work will represent an initial step in a continuing research program aimed at studying community and population ecology of desert bats.

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CHAPTER 2: ISLAND BIOGEOGRAPHY OF BATS IN BAJA: PATTERNS OF BAT SPECIES RICHNESS IN A DESERT ARCHIPELAGO

ABSTRACT

MacArthur and Wilson's (1963, 1967) influential equilibrium theory of island biogeography has inspired four decades of research on species richness patterns of various taxa in different archipelago settings. However, biogeography research on insular bat faunas remains scant, particularly in near-shore archipelagos. We investigated the influence of size and isolation of islands on patterns of species richness of bats in a near-shore archipelago in Baja California, Mexico to evaluate forces important in determining community structure of bats in isolated habitats. Presence/absence surveys for bat species were conducted on 32 islands in the Gulf of California using acoustic and mist-net surveys. Using an information-theoretic approach, we compared a priori biological hypotheses about the influence of area, isolation, and island group (two subarchipelagos) on species richness of bats. Species richness was influenced by both area and isolation of islands and was higher in the southern subarchipelago, which has denser vegetation. Log_{10} area was positively related to bat species richness, which increased by one species for every 5.4-fold increase in island area. Richness declined by one species per 6.25 km increase in isolation from the Baja peninsula. Our results demonstrate that even highly vagile organisms like bats can be affected by moderate isolation distances in some contexts. Furthermore, regional differences in habitat may also influence bat richness.

INTRODUCTION

The study of insular populations has received prolonged interest in ecology, in part because islands provide simplified model systems for understanding how ecological communities are structured. MacArthur and Wilson's (1963, 1967) equilibrium theory of island biogeography provided a theoretical foundation for understanding patterns of species richness in island systems by proposing richness is at a balance between the opposing forces of extinction and colonization. Four decades of research have been inspired by MacArthur and Wilson's influential theory and numerous studies have field-tested the predictions of the theory by estimating the influence of size and isolation of island on richness of various taxa in different archipelagos (Brown 1986, Rosenzweig 1995, Lomolino 2000a).

The species-area relationship is one of the most widely-documented phenomena in ecology (Arrhenius 1921, Preston 1962, MacArthur and Wilson 1967, Rosenzweig 1995). There are several competing hypotheses about mechanisms driving species-area relationships, including 1) direct effects of area *per se* resulting from a fundamental link between area and population size, affecting extinction probability (Preston 1962, MacArthur and Wilson 1967); 2) indirect effects of area resulting from a strong correlation between area and habitat diversity (Williams 1943, Ricklefs and Lovette 1999); and 3) the passive sampling hypothesis, which results from larger areas being larger targets for colonizing individuals (Connor and McCoy 1979, Coleman et al. 1982). Discriminating among these hypotheses has proved difficult, as measures of area and habitat diversity are often confounded, making their contributions to richness difficult to disentangle (Ricklefs and Lovette 1999).

The species-isolation relationship has historically received less attention than the species-area relationship (Lomolino 1986), but has equally important implications for the influences of dispersal and vagility of species on distribution patterns. Ecologically, isolation is a combination of both physical distance from a source population and the relative vagility, or dispersal capability, of the organism under study (Moilanen and Nieminen 2002, Taylor et al. 2006). Negative species-isolation relationships may occur when colonization rates decline as isolation from a source population increases (MacArthur and Wilson 1967). Isolation can also influence population persistence via a "rescue effect", if populations are "rescued" from extinction by high immigration rates (Brown and Kodric-Brown 1977).

This study focuses on the influences of area and isolation of islands on bats. Although bats comprise a quarter of all mammal species, our understanding of factors influencing community structure in isolated or fragmented habitats is minimal (Racey and Entwistle 2003). The only volant mammals, bats are highly mobile and therefore generally assumed to have high immigration and dispersal rates among isolated habitats (Lomolino 1984, Lawlor 1986, Lomolino 1986, Carvajal and Adler 2005). A few biogeographic studies have analyzed insular bat faunas in oceanic archipelagos and report species-area relationships similar to birds, the other volant homeotherms (Wright 1981, Lomolino 1984, Lawlor 1986, Ricklefs and Lovette 1999, Carvajal and Adler 2005).

Our first research objective was to determine whether bat communities on a near-shore archipelago conform to predictions of island biogeography theory. By investigating the influence of area and isolation of islands on species richness of bats, we aimed to describe species-area and species-isolation relationships for vagile mammals

(Brown and Kodric-Brown 1977, Lomolino 1984). Our second goal was to explore how area *per se* and habitat diversity may independently influence bat richness. Earlier studies have shown that richness of bats may be less affected by habitat diversity than other taxa because they are habitat generalists (Ricklefs and Lovette 1999). But habitat characteristics may influence occurrence of bats in some isolated habitats (Carvajal and Adler 2005). Finding relevant metrics of habitat diversity that are not significantly correlated with island area is challenging (Gotelli and Graves 1996, Ricklefs and Lovette 1999). Instead, we compared bat richness among two natural subdivisions of the greater archipelago of islands off the gulf coast of Baja California.

The southern subarchipelago tends to have brushier, denser vegetation than islands in the northern Midriff and Bahía de Los Ángeles groups (Cody et al. 2002). Vegetative differences influence bird richness, with higher numbers of bird species on southern islands (Cody and Velarde 2002). The links to vegetation complexity are less well-established for bat species than for birds (MacArthur and MacArthur 1961, Tomoff 1977, Cody 1989, Gill 1995), but we hypothesized that patterns of bat richness would mirror those observed for birds and be higher on southern islands due to differences in habitat between the two subarchipelagos.

A common problem with comparing archipelago faunas is determining the appropriate source fauna (Gotelli and Graves 1996). All islands in this study are situated off the gulf coast of the Baja California peninsula, the likely source pool for insular populations. Because distribution of bats in Baja California is poorly known, we sampled for presence of bats in coastal habitats in four regions of the peninsula to determine the potential pool of colonizing species. Determining source pools of species provides a context for understanding how characteristics of islands influence community structure of bats that is not confounded by potential differences in regional source faunas.

METHODS

Study Region

The Gulf of California (Figure 2.1) in northwest Mexico contains more than 100 islands and islets that range in size from a few hectares to 1,123 km^2 (Carreño and Helenes 2002). There are two subarchipelagos off the gulf coast of Baja California (Cody et al. 2002, Cody and Velarde 2002): the northern subarchipelago, which includes the Bahía de Los Ángeles and Midriff island groups, and the southern subarchipelago, which extends from Loreto to La Paz, Baja California Sur. Islands and adjacent gulf coast habitats of the Baja California peninsula conform to a Sonoran Desert "sarcocaulescent" vegetation type (Shreve 1951, Wiggins 1980), dominated by columnar cacti (*Pachycereus pringlei* and *Stenocereus thurberias*) and desert trees (*Cercidium*, *Bursera*, and *Jatropha*).

The climate in the region is hot and dry with unpredictable rainfall averaging between 100 and 150 mm per year (Cody et al. 2002). The northern islands receive most of their rainfall in winter and are considerably more arid and barren than islands in the southern part of the Gulf, where approximately 40% of the rainfall occurs in the summer, resulting in denser vegetation (Cody et al. 2002).

Very few of the islands have permanent sources of freshwater, but some of the larger islands that have well-developed drainage courses (i.e., *arroyos*) have ephemeral freshwater in remnant pools known as *tinajas* (Cody and Velarde 2002). Smaller islands (< 200 ha) do not have the surface area nor soil type to develop drainages and typically have no freshwater except for ephemeral puddles after rainstorms (Cody et al. 2002, Cody and Velarde 2002). The peninsular coastal region is used extensively for grazing livestock and has a network of maintained spring-boxes that provide permanent or semi-permanent water.

Five of the islands included in this study are oceanic (Partida Norte, Rasa, Salsipuedes, San Lorenzo, San Ildefonso, and Santa Catalina); the remainder are land-bridge islands that were once connected to the Baja peninsula (Carreño and Helenes 2002). Most islands are composed of granitic or volcanic rocks and have steep terrain (Carreño and Helenes 2002). Crevices and small caves are abundant on all islands, but large caves probably only occur on larger islands. Interior areas of large islands are only accessible by foot via arroyos and narrow canyons. Apart from temporary fishing camps on beaches, almost all islands are uninhabited by humans (Bahre and Bourillón 2002).

Data Collection

We conducted presence-absence surveys for bats on 32 islands across the northern (n = 12) and southern (n = 20) subarchipelagos in the Gulf of California from 1 April to 1 June 2004-2006. We sampled for presence of bat species on each island for a five-day period using passive Anabat acoustic stations (Titley Electronics, Australia). On 10 islands, active hand-held Anapocket acoustic monitoring (Corben 2004) and mist-net surveys were conducted to verify species detected with passive acoustic stations.

A species was considered present if it was detected at least once, without determination of breeding or residency status. Generally one island was sampled at a time, but occasionally multiple small islands were sampled simultaneously. Historical records of bat observations exist for some islands in the study region (see Lawlor et al.

2002 for a review). In the few cases where a historical record existed for a species that we did not detect during our sampling, we did not include it in the analysis.

Repeat sampling across years on 10 islands (Table 2.1) determined that patterns of species detection were typically consistent across years, allowing islands sampled in different years to be pooled in a single analysis. However, two species (*Nyctinomops femorosaccus* and *Tadarida brasiliensis*) were not re-detected on islands re-sampled in 2006 on islands in both the northern and southern subarchipelagos. Our sampling was limited to spring and we make no inferences regarding seasonality of presence of bats on islands.

Four regions of the Baja gulf coast (Figure 2.1) were sampled to determine the regional source pool for islands; sample sites ranged from 6 to 13 per region (Table 2.2). Regions were selected for sampling based on accessibility and proximity to study islands. Sampling on the peninsula was conducted in a similar manner to that on islands with five-day sampling periods.

Acoustic sampling

We recorded bat echolocations using broadband ultrasonic bat detectors (Anabat II; Titley Electronics) to determine presence of species (Hayes 1997, O'Farrell et al. 1999, Gehrt and Chelsvig 2004). Passive monitoring stations contained an Anabat II detector attached to a high-frequency microphone housed in a waterproof shroud with a 45° reflector (Messina 2004) mounted on a 1m tall pole. The detector was connected to an Anabat Compact Flash Zero-Crossings Interface Module (Titley Electonics) recording device.

The number of passive acoustic stations placed on an island increased with island size (range: 1-13 detectors per island). We placed detectors at randomly determined distances between 100 and 1,000m from safe boat landings. Given a lack of adequate a priori information about accessible landings, safe landings were assessed on arrival. We randomly selected landings after circumnavigating an island to determine beach landings with terrain accessible on foot. When adverse field conditions prohibited random selection, landings were selected haphazardly according to accessibility and safe deployment. Number of landings ranged from 1-8 per island and 18 islands (all less than 105 ha) were sampled with only one detector. We sampled 113 sites with passive acoustic stations on 32 islands (Table 2.1) and 40 sites on four areas of the Baja peninsula (Table 2.2).

On 10 islands, active monitoring of bat activity was conducted at mist-net survey locations using a spotlight and Anapocket software (Corben 2004) on a handheld PDA, which displays bat calls as time versus frequency graphs in real time. Species identified with visual confirmation in the spotlight were used to verify presence of species detected with passive acoustic detectors and to build a reference call library of echolocation signatures of free-flying bats.

Mist-net sampling

Mist-net surveys were conducted to verify identification of species detected with acoustic sampling, to build an echolocation call reference library from hand-release recordings, and to train observers to recognize flight patterns and body shapes in the spotlight for identifying free-flying bats with active monitoring. Hand-release recordings were conducted using Anapocket (Corben 2004) and a bright spotlight. Bats were released and recorded as long as they remained in constant view in the spotlight.

Mist-net sites on islands were selected in attempt to maximize captures and were typically placed in dry arroyos (flyways) and desert scrub habitats or over freshwater pools (*tinajas* or spring-boxes) when available. Typically, five different locations were sampled on each island, except in two cases where access was limited. We opened mist-nets at sunset and monitored them at least every 15 minutes for 4 hours. Captured bats were identified to species, age, sex, and reproductive status (Anthony 1988, Racey 1988).

Echolocation analysis for species identification

We developed a graphical and descriptive key of Anabat echolocation calls (Appendix A). Anabat uses a zero-crossings analysis (ZCA) (Parsons et al. 2000) which produces files displaying echolocation calls on time-frequency graphs. Sequences were identified to species if they had greater than two diagnostic pulses that met defined criteria based on reference calls (see Appendix A). A total of 286,994 Anabat files were randomly assigned by detector night to three observers trained to identify calls using the key. Observers labeled 123,505 bat echolocation files with a species, phonic group, or bat fragment label (see Appendix A). The remainder of unlabeled files represente files created by wind, insects, mice and birds. Sequences identified to species were proofed by the senior author.

Identifying echolocation calls can produce false negative and false positive errors. False negative errors (species is present and not detected) occur when a species is present and is recorded by the detector, but the call is insufficiently diagnostic to be labeled as produced by that species. False positive errors (species is absent and is falsely detected) occur when an echolocation call is misclassified as a species that was in fact not present. Our approach to classifying echolocation calls was designed to minimize both false negative and false positive errors, but greater emphasis was placed on avoiding false positive errors. In general, the species in the assemblage were easily identifiable to the species level using the key.

Because of our efforts to minimize false positive errors, our approach was not sensitive to detecting rare taxa with echolocation call morphologies similar to common taxa. For example, some calls from the regionally rare species *Lasiurus cinereus* may be confused with the common *Nyctinomops femorosaccus*. This bias was uniform across islands and peninsular sites and although it may have negatively biased overall species richness, our identification of recorded species should be a reasonable index of community composition.

Data Analysis

Species Richness Estimation

The count of observed species, which is a reliable estimate of species richness when a species accumulation asymptote has been reached (Gotelli and Colwell 2001), was used to estimate species richness. Inspection of species accumulation curves indicated species richness was asymptotic by the fourth night (n = 28) of sampling and on nine islands no new species were detected after the initial night of sampling (Appendix B).

To determine whether five nights of sampling resulted in an exhaustive sample, we sampled 10 islands for up to eight nights. In only one case was there an additional species detected after night five (*Leptonycteris curasoae* on Isla San Francisco on the sixth night).

Island Characteristics

Island characteristics were measured using a "heads-up" digitized GIS layer created in Arcview 3.2 from Landsat 7 satellite images (Table 2.1). We measured the shortest over-water path (km) to the Baja peninsula (the source population) using Nearest Features and Path extension tools (Jenness 2004, 2005) in ArcView 3.2 as an index for isolation. This metric allowed for stepping-stone type movements by summing over-water legs if stepping-stone paths were the shortest route to the peninsula. This approach accounts for the presence of neighboring islands if they function as stepping stones, but emphasizes the role of the Baja peninsula as the source pool. More complex measures of isolation, including area-based metrics, are often advocated (Moilanen and Nieminen 2002, Bender et al. 2003, Matter et al. 2005), but these approaches are more applicable to fragmented systems where there is no clear source population (Moilanen and Nieminen 2002). These metrics may also be less appropriate for community questions as they are highly sensitive to variation in scales of movement among species (Bender et al. 2003, Bélisle 2005, Taylor et al. 2006).

Species richness regression analysis

We used the semi-log model of the species-area relationship (number of species vs. $\log_{10}$ area) because it better met the assumptions of constant variance and fit than did the log-log form of the linearized Arrhenius (1921) power function (Rosenzweig 1995) based on inspection of residual plots. Explanatory variables included $\log_{10}$ area (ha), isolation (km), and a grouping variable for subarchipelago for the comparison of regression lines among the northern and southern island groups. We developed 13 a priori candidate models (Table 2.3) representing biological hypotheses that incorporate combinations of main effects, additive effects, and selected interactions among area and isolation and subarchipelago. We did not model an interaction between isolation and subarchipelago because we saw no a priori reason to suspect that the species-isolation relationship would differ between the two subarchipelagos.

Assumptions of constant variance and normality of residuals were assessed by inspection of residual plots and summaries prior to consideration of model results. Collinearity among explanatory variables was assessed by inspection of scatterplots and estimation of Pearson correlation coefficients. All models presented met assumptions of linear regression models and all analyses were conducted using Program R v.2.4.1.

Model Selection

We used AIC model selection methods to compare the set of 13 a priori candidate models (Table 2.3), using the small sample size correction form (AIC_c) (Burnham and Anderson 2002). All models had the same sample size (n = 32 islands). Models were ranked by AIC_c value (lowest AIC_c has the most support from the data) and were compared using ΔAIC_c and AIC_c model weights. We considered models with $\Delta AIC_c \leq 2$ to be strongly competing models (Burnham and Anderson 2002). Model weights give the relative support of evidence in favor of a given model for the set of a priori candidate models (Burnham and Anderson 2002).

RESULTS

Regional source fauna

Fifteen species of bat were detected in coastal habitats across four regions of the Baja peninsula (Table 2.4). Four species detected on the peninsula were never detected on islands (*Eptesicus fuscus*, *Lasiurus blossevilli*, *Myotis volans,* and *Myotis yumanensis*). Community composition was similar among three areas sampled in the south and the northern region, with a few exceptions. *Mormoops megalophylla* and *Nyctinomops macrotis* were detected in the southern region but not in the northern region. *E. fuscus*, *M. volans*, and *Lasiurus xanthinus* were detected in at least one of the three southern areas and were not detected at northern sampling sites. However, three of these species were captured at Mision San Borjas in the mountains above Bahía de Los Ángeles, indicating they occur in the north, but may not be common in coastal habitats. The fish-eating bat, *Myotis vivesi,* was not detected at sites in the north, but was detected on southern peninsular sites and both northern and southern islands.

Species richness patterns

The model best explaining variation in species richness on islands incorporated parallel slopes for the influences of $\log_{10}$ area and isolation on bat richness in the two subarchipelagos (Table 2.3). This suggests area and isolation influence species richness of bats in both subarchipelagos, but overall richness differs between the island groups after accounting for area and isolation. The parallel slopes model had $w_i = 0.76$. The next best model ($\Delta AIC_c = 2.85$, $w = 0.18$) included all the same terms plus an interaction term for $\log_{10}$ area and isolation. These two models combined accounted for 94% of model weights. The null model had no support ($\Delta AIC_c = 41.76$, $w = 0.00$).

The best-fit model estimated the intercept for bat richness in the northern subarchipelago at 1.79 species (SE = 0.49; 95% C.L.: 0.78, 2.81) and at 4.35 species (SE = 0.48; 95% C.L.: 3.36, 5.34) in the south, indicating that northern islands had 2.55 fewer species than southern islands after accounting for size and isolation of islands (Figure 2.2). The regression coefficient for $\log_{10}$ area was 1.38 (SE = 0.18; 95% C.L.: 1.01, 1.75), indicating richness increases by about one species for every 5.37-fold increase in island area across the study region. The coefficient estimate for isolation was -0.16 (SE = 0.03; 95% C.L.: -0.22, -0.10), indicating richness decreases by one species for every 6.25 km further away from the Baja peninsula in the study region. Across the range of isolation values in the region, this results in a decrease of about two bat species at the more isolated islands (ca. 25 km from the peninsula) for islands of the same size.

DISCUSSION

Our results demonstrate that species richness of bat communities on islands in the Gulf of California is affected by area and isolation in ways consisted with and predicted by island biogeography theory (MacArthur and Wilson 1963, 1967). Previous studies of island biogeography of bats have focused on comparative studies of different taxonomic groups on oceanic archipelagos to investigate how vagility may affect slopes (*z*-values) of species-area curves when comparing taxonomic communities, such as birds, butterflies, or non-volant mammals (Wright 1981, Lomolino 1984, Lawlor 1986, Ricklefs and Lovette 1999). Comparing *z*-values among taxonomic groups may be misleading and may have no biological meaning (Connor and McCoy 1979, Gotelli and Graves 1996). In general bat faunas demonstrate patterns more similar to birds than to non-volant mammals, presumably because of similar dispersal capabilities.

Influence of isolation on species richness

Although vagility of bats and birds may be similar, species richness of bats was reduced by moderate distances of isolation, whereas isolation does not appear to reduce species richness of birds or reptiles on islands in the Gulf of California (Case 2002, Cody and Velarde 2002). Richness of bats is generally expected to be influenced by isolation only in very distant archipelagos (Lomolino 1984, Lawlor 1986, Carvajal and Adler 2005). However, two studies of bat communities on near-shore archipelagos in Scandinavia report similar results that bat faunas are richer on larger islands and that isolation reduces the number of insular species (Ahlén 1983, Johansson and de Jong 1996). Similarity of patterns in Baja and Scandinavia suggests bat communities in insular habitats may be negatively influenced by relatively modest distances of isolation in different habitat settings.

Two possible mechanisms could underlie observed influences of isolation on bat richness: reduced rates of immigration as isolation increases (island biogeography hypothesis) or habitat use decisions by individuals (foraging use hypothesis). Patterns of richness on near-shore archipelagos may offer a different perspective than traditional island biogeography hypotheses by focusing at a scale where presence of species results from habitat selection choices of individuals rather than from communities being shaped by the passive forces of immigration and extinction (Russell et al. 2006). The species-isolation relationship observed for bats in this study could occur from foraging use of islands near the Baja peninsula, as our presence/absence data did not distinguish between foraging and breeding use of islands.

The traditional explanation for a species-isolation relationship is diminished rates of immigration as isolation from a source population increases is (MacArthur and Wilson 1967). Although many bat species have large home ranges and the ability to travel large distances in a single foraging bout (Kunz and Lumsden 2003), the ability or willingness to cross open water is unknown for most species (Ahlén 1983). Experimental research on orientation and navigation suggests acoustic cues and landmarks are important for some bat species (Jensen et al. 2005), but these studies are focused on close-range orientation rather than large-scale navigation. At least one species (*E. fuscus*) may use magnetic fields to navigate over large distances (ca. 20 km) (Holland et al. 2006). Some species appear to have no problems traveling over water. For example, previous studies on *L. curasoae* revealed this species regularly commutes ca. 30 km from a maternity cave on Isla Tiburon on the Sonoran side of the gulf to forage near Bahia Kino, Sonora (Sahley et al. 1993, Horner et al. 1998a). More research on navigation and dispersal of bats is necessary to determine how landscape conditions influence movements of bats. Regardless of whether presence of species represents foraging activity related to habitat selection decisions or equilibrium of immigration and extinction rates, isolated habitats in this archipelago appear to support fewer species of bats even at distances that do not affect richness of other vertebrates, such as birds and reptiles (Case 2002, Cody and Velarde 2002).

Influences of area and habitat on species richness

Increased richness of bats with island size is consistent with island biogeography theory, but does not distinguish among competing hypotheses about causal factors responsible for observed species-area relationships (Gotelli and Graves 1996). Species-area relationships may result from direct influences of area *per se* on population persistence or from indirect influences from the correlation of habitat diversity with area (Rosenzweig 1995). Ricklefs and Lovette (1999) reported that bats in the Lesser Antilles displayed strong species-area relationships, but habitat diversity did not significantly contribution to richness. Many species of bats occur in a wide variety of habitats and may be less susceptible to direct effects of habitat diversity on species richness (Ricklefs and Lovette 1999).

Both area and habitat diversity may influence bat richness in our study. Larger islands support greater topographical diversity, which creates greater habitat diversity and produces formations, such as rocky canyons, that may contain semi-permanent pools of freshwater (*tinajas*) (Cody et al. 2002, Cody and Velarde 2002). In Sonoran desert ecosystems, topographical diversity is strongly related to habitat diversity (Búrquez et al. 1999).

Although habitat diversity was not measured directly on islands and surrogates such as elevation were too strongly correlated with area to be included in our models, there are substantial differences in vegetation structure between islands in the southern subarchipelago, which is more exposed to summer monsoons, and islands in the northern subarchipelago tend to be drier (Cody et al. 2002). Southern islands, which have denser vegetation, supported higher numbers of bat species than more xeric northern islands. Reduced richness in the northern subarchipelago in our study is consistent with patterns of bat richness in tropical Pacific islands, where frugivorous bats are absent from islands with low plant and topographical diversity (Carvajal and Adler 2005).

Vegetation structure and xericity could affect persistence of bat populations by affecting food resources (i.e., insect availability) and access to semi-permanent freshwater in *tinajas* that persist for long periods after infrequent rainstorms. Although some desert bat species may be completely water independent or only need infrequent access to freshwater (Geluso 1978, Bell et al. 1986), many species require regular drinking to maintain positive water balance (Carpenter 1969, Geluso 1978, Kurta et al. 1990, Webb et al. 1995). During our surveys, we only found freshwater on Isla Carmen and Isla Espiritu Santo/Partida Sur. The influence of xericity on community structure is also evident for bird populations, where species that prefer brushier, denser vegetation are more commonly distributed in the southern islands and species that prefer more open, drier habitats frequent northern islands (Cody and Velarde 2002).

Historical factors could also influence present-day patterns of species richness (Ricklefs and Schluter 1993). Northern and southern parts of the gulf have distinct geologic histories, and the Baja peninsula was separated by a mid-peninsular seaway during the middle Pleistocene (Riddle et al. 2000, Lindell et al. 2006). This historical separation may lead to differences in the source faunas on the peninsula, thus affecting patterns of insular richness. The source faunas were similar among sampled regions in the northern and southern peninsula, indicating both subarchipelagos were subject to a similar pool of potential colonizing species. Similarity of source faunas suggest historical factors are probably not responsible for observed differences in bat richness on islands.

Future phylogeographic studies comparing genetic separation of insular and peninsular populations could provide valuable insights into the dispersal and vicariance histories of bat species, as has been shown for other vertebrates in the region (Riddle et al. 2000). Phylogeographic patterns could help distinguish between ecological and historical mechanisms behind community patterns and may also provide an indirect means of understanding dispersal of bats and connectivity of populations among islands and the Baja peninsula (Ricklefs and Schluter 1993, Avise 2000).

Our results present an important step in understanding how bat communities are structured in isolated habitats. The patterns we observed in this desert ecosystem suggest bat communities may be more sensitive to isolation than previously expected (Lomolino 1984, Lawlor 1986, Carvajal and Adler 2005). More research is needed, however, to understand the mechanistic relationships between species richness and isolation of islands. In addition, larger islands that had greater topographical and vegetative diversity tended to support greater numbers of bat species as is predicted by island biogeography theory and the species-area relationship (Rosenzweig 1995). Additional studies on the direct linkages between species richness and habitat requirements of individual species will increase our understanding of the functional relationships between area, habitat diversity, and structure of bat communities.

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Table 2.1. Sampling effort and characteristics of islands (n = 32) in the Gulf of California, Mexico sampled for presence of bat species. Number of detectors equals the number of passive acoustic detectors that ran for ≥ 3 nights. Espiritu Santo is combined with Partida Sur as a single island.

Island	**Archi-pelago**	**No. of Species**	**Area (ha)**	**Isolation (km)**	**No. of Detectors**	**Mistnet Surveys**	**Year**
San José	South	12	18,494.5	4.75	11	yes	2005
Carmen	South	9	14,801.4	5.50	13	yes	2004, 2006
Danzante	South	8	423.7	2.67	6	yes	2004
Espiritu Santo	South	8	10,367.1	6.21	10	yes	2005
San Francisco	South	8	419.0	7.16	2		2005, 2006
Coronados	South	7	715.8	2.60	7	yes	2004
Gallina	South	6	2.0	7.18	1		2005
Monserrat	South	6	1,902.8	13.66	8	yes	2004-2006
San Lorenzo	North	6	3,632.3	16.31	9	yes	2006
Cabezo Caballo	North	5	71.0	1.89	1		2004, 2006
Gemelitos East	North	5	3.9	0.82	1		2004
Pardo	South	5	4.3	0.36	1		2004
Santa Catalina	South	5	3,995.6	25.06	13	yes	2005
Santa Cruz	South	5	1,315.1	19.81	3	yes	2005
Ventana	North	5	128.2	3.09	2		2004, 2006
Blanco	South	4	1.3	0.84	1		2004
Cayo	South	4	6.7	6.22	1		2005
Coronados Smith	North	4	852.1	2.22	2		2006
Galeras East	South	4	5.4	16.40	1		2004-2006
Islitas	South	4	3.3	0.41	1		2004
San Ildefonso	South	4	104.2	10.01	7	yes	2004, 2006
Tijeras	South	4	4.0	1.90	1		2004
Galeras West	South	3	3.2	16.77	1		2004-2006
Las Animas Sur	South	3	9.1	16.49	1		2005
San Diego	South	3	62.9	19.06	2		2005
Bota	North	2	9.6	2.64	1		2004
Gemelitos West	North	2	2.4	0.86	1		2004, 2006
Pata	North	2	14.5	2.57	1		2004, 2006
Piojo	North	2	67.6	4.57	1		2006
Salsipuedes	North	2	102.6	17.70	1		2006
Partida Norte	North	1	94.0	17.84	1		2006
Rasa	North	1	59.2	20.75	1		2006

Table 2.2. Sampling effort and number of species detected at four areas sampled on the Baja peninsula, Mexico.

Name	Region	No. of Species	No. of Detectors	Mistnet Surveys	Year
San Evaristo	South	13	11	yes	2005
Agua Verde	South	12	10	yes	2005
Tecolote	South	9	13	yes	2005
Bahía de Los Ángeles	North	7	6	yes	2006

Table 2.3. Model selection results for 13 candidate models of insular richness of bat species. Isol = isolation variable representing shortest route to the Baja peninsula; Arch = grouping variable for subarchipelago. K = number of model parameters; + indicates additive effects; * indicates interaction effects.

Model Name	**K**	**Δ_i**	**w_i**
S = logArea + Isol + Arch	**5**	**0.00**	**0.76**
S = logArea + Isol + Arch + logArea*Isol	6	2.85	0.18
S = logArea + Isol + Arch + logArea*Isol + logArea*Isol*Arch	7	5.46	0.05
S = logArea + Isol + Arch + logArea*Arch + logArea*Isol +logArea*Isol*Arch	8	8.73	0.01
S = logArea + Arch	4	19.62	0.00
S = logArea + Isol	4	21.54	0.00
S = logArea + Arch + logArea*Arch	5	21.90	0.00
S = logArea + Isol + logArea*Isol	5	24.00	0.00
S = logArea	3	29.64	0.00
S = Isol + Arch	4	32.99	0.00
S = Arch *(group means)*	3	34.83	0.00
S = null *(overall mean)*	2	41.76	0.00
S = Isol	3	41.98	0.00

Table 2.4. Bat species detected in northern and southern regions of the Baja peninsula and subarchipelagos with acoustic sampling methods. * indicates species captured in mist-nets, but not detected with acoustic sampling.

	Detected on Peninsula		Detected on Islands	
Species	Northern Region	Southern Region	Northern Archipelago	Southern Archipelago
Family: Mormoopidae				
Mormoops megalophylla		✓		✓
Family: Phyllostomidae				
Macrotus californicus	✓	✓	✓	✓
Leptonycteris curasoae	✓	✓	✓	✓
Family Vespertilionidae				
Antrozous pallidus	✓	✓		✓
Eptesicus fuscus	✓*	✓		
Lasiurus blossevilli		✓		
Lasiurus xanthinus	✓*	✓		✓
Myotis californicus	✓	✓	✓	✓
Myotis volans	✓*	✓		
Myotis yumanensis		✓		
Myotis vivesi		✓	✓	✓
Pipistrellus hesperus	✓	✓	✓	✓
Family Molossidae				
Tadarida brasiliensis	✓	✓	✓	✓
Nyctinomops femorosaccus	✓	✓	✓	✓
Nyctinomops macrotis		✓	✓	✓
Eumops sp.				✓

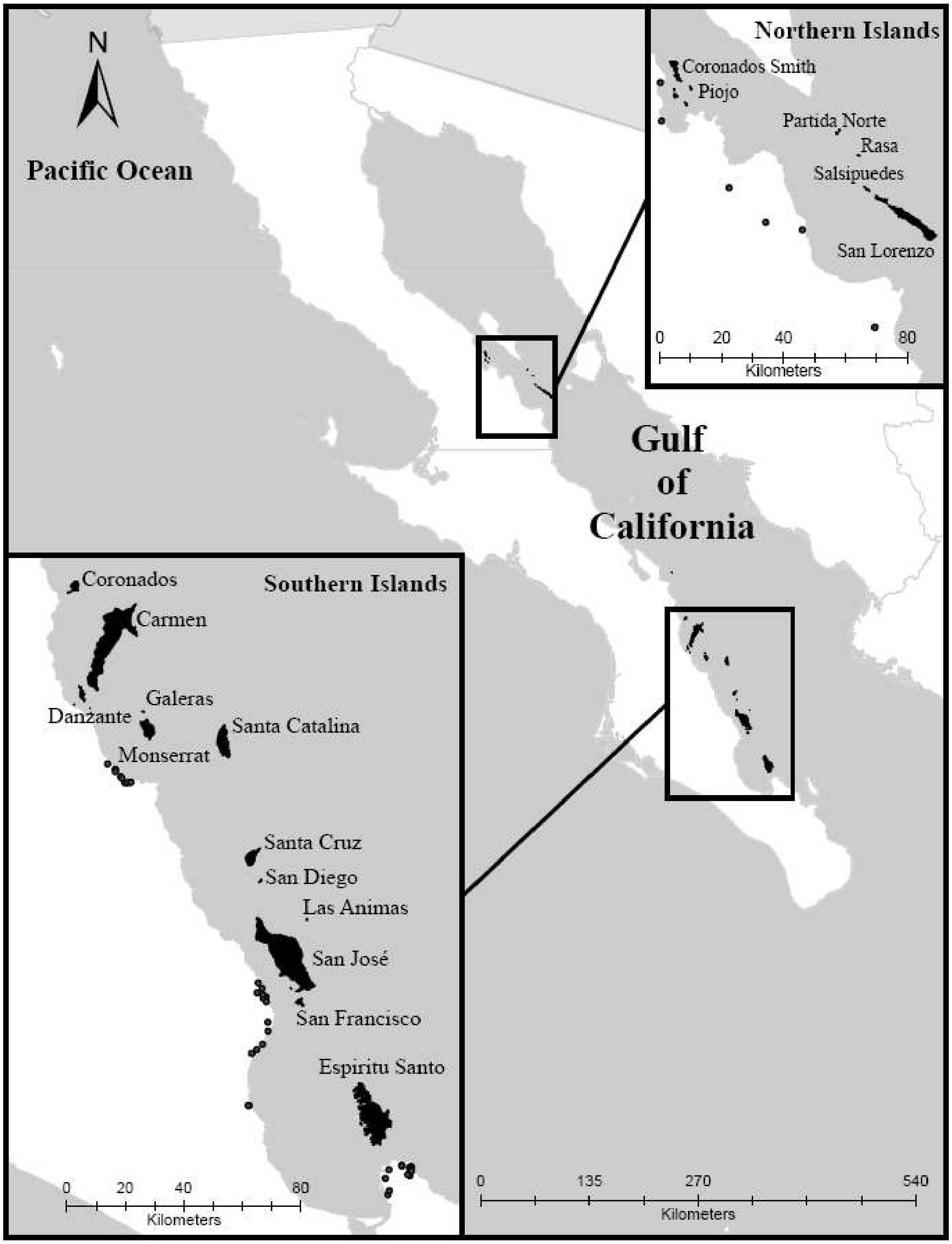

Figure 2.1. Map of study islands (in black) in the southern and northern subarchipelagos in the Gulf of California, Baja California, Mexico. Points on the Baja peninsula represent acoustic sites used to sample regional source faunas, grouped into four regions. Sampled regions on the peninsula from north to south are here referred to as: Bahía de Los Ángeles, Agua Verde, San Evaristo, Tecolote.

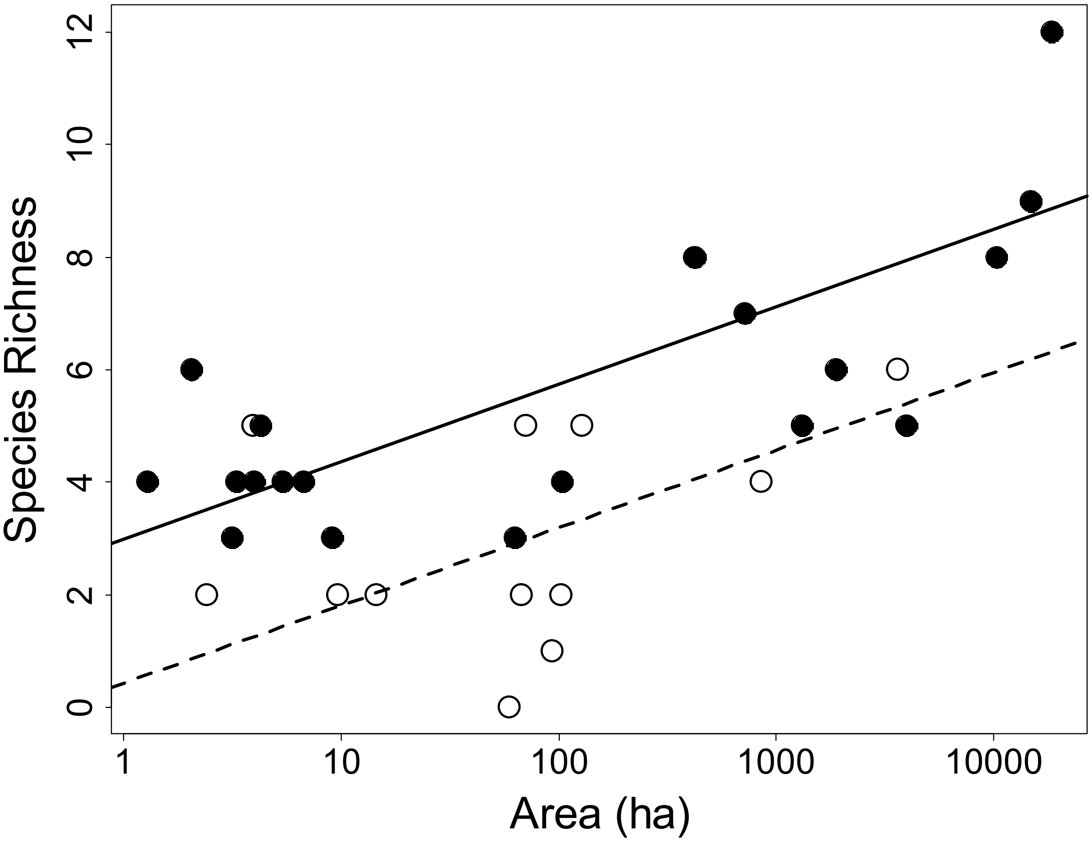

Figure 2.2. Species-area relationship of bat richness for southern islands (solid line) and northern islands (dashed line) in the Gulf of California, Mexico. Regression lines are drawn using average isolation, because of the parallel negative influence of isolation on species richness.

CHAPTER 3: NESTEDNESS OF A DESERT BAT ASSEMBLAGE: COMPOSITION PATTERNS IN INSULAR AND CONTIGUOUS LANDSCAPES

ABSTRACT

Community composition is nested when species at more depauperate sites are subsets of the suite of species occurring at more species-rich sites. Nested patterns can result from several different mechanisms, which may depend on landscape type and spatial scale. We investigated patterns and processes of nested composition for desert bat assemblages in two different landscape types in Baja California, Mexico. Community composition for bats was significantly nested across an island archipelago in the Gulf of California. Nestedness on the archipelago was associated with island characteristics, suggesting selective immigrations and extinctions are important drivers of nestedness for insular bat faunas. However, nestedness also occurred across sites in coastal peninsular habitat, despite an absence of regional influences such as extinction and immigration dynamics. Nestedness can be a useful step in describing patterns of composition and identifying species at conservation risk, but autecological details will be necessary for robust conservation decision-making and additional analyses are needed to understand mechanisms behind composition patterns.

INTRODUCTION

Understanding factors important in structuring diversity and community composition is an elusive, yet important, goal for conservation. Identifying how communities are structured across landscape types and spatial scales has particular relevance to conservation aimed at preserving species diversity in fragmented landscapes (Patterson 1987, Patterson and Atmar 2000). Nested subset theory provides a useful framework for analyzing community composition patterns and has potential to identify mechanisms that influence local diversity (Patterson and Atmar 2000), yet its applicability to conservation decision-making remains debatable (Boecklen 1997, Donlan et al. 2005).

A nested subset occurs when species at species-poor sites are subsets of the suite of species that occur at more species-rich sites (Patterson and Atmar 1986). Numerous studies have investigated nestedness patterns for a variety of taxa over the past 15 years (Patterson and Atmar 1986, Bolger et al. 1991, Wright and Reeves 1992, Cook and Quinn 1995, Kadmon 1995, Wright et al. 1998, Conroy et al. 1999, Davidar et al. 2002, Bascompte et al. 2003, Hausdor and Hennig 2003, Cook et al. 2004, Sfenthourakis et al. 2004, Fischer and Lindenmayer 2005, Greve et al. 2005, Martínez-Morales 2005, McAbendroth et al. 2005, Wethered and Lawes 2005). These studies and others have shown that nestedness is a pervasive pattern in faunal assemblages. Indeed, absence of nestedness may be more interesting than its presence (Simberloff and Martin 1991, Kadmon 1995).

Although patterns of nestedness have been well-documented, the underlying mechanisms are more difficult to determine. Nestedness may be caused by several mechanisms, including: 1) selective extinction vulnerabilities (Patterson and Atmar 1986, Wright and Reeves 1992); 2) selective immigration abilities (Darlington 1957, Cook and Quinn 1995, Kadmon 1995, Loo et al. 2002); 3) gradients in species tolerance for habitat variables (Cook et al. 2004); 4) a nested structure of habitat diversity (Cutler 1994, Calmé and Desrochers 1999); and 5) sampling artifacts (Cutler 1994, Higgins et al. 2006). These mechanisms can all produce nested composition patterns across sites that share common evolutionary and recent histories and similar environmental conditions (Cutler 1994).

Nestedness analyses traditionally focus on patterns in insular and fragmented landscapes, applying a species-specific extension of the MacArthur and Wilson paradigm (Kadmon 1995, Lomolino 1996). In this context, nestedness is a metric that characterizes community composition across a set of sites, where each site represents an island or habitat patch (Wright and Reeves 1992). Generally, inferences about mechanisms are made about the influence of characteristics of islands (or patches) on community assembly with emphasis on the differential responses of species to those characteristics. Nestedness analysis builds on island biogeography theory by providing information about how area and isolation influence community composition (Lomolino 1996).

In insular and fragmented landscapes, differential immigration and persistence abilities among species are likely drivers of nestedness patterns (Patterson and Atmar 1986, Cutler 1994, Cook and Quinn 1995, Lomolino 1996, 2000b). While some systems may be dominantly extinction-driven (i.e., landbridge islands) and others colonization-driven (i.e., oceanic islands), these forces reinforce each other to produce nestedness when species immigration and persistence abilities are correlated (Cutler 1994, Lomolino 2000b). Both immigration and persistence are expected to contribute to nestedness patterns in systems where the gradients of area and isolation are sufficient to influence the persistence and immigration of some, but not all, species (Lomolino 2000b). Understanding the role of selective immigrations and extinctions in shaping composition patterns across insular landscapes helps identify the scale at which isolation and area influence incidence of species (Wright and Reeves 1992).

Area and isolation values are often used to test hypotheses about selective immigrations and extinctions (Lomolino 1996), but species traits could also be useful for assessing the contribution of differential abilities of species to nestedness. For example, if immigration ability is a strong determinant of nested patterns (Kadmon 1995, Lomolino 1996, Loo et al. 2002), then ecomorphological characters representing relative mobility of species may indicate the role of immigration in structuring composition patterns.

Factors influencing species composition may operate at different spatial scales, such that species that are widespread across one scale (e.g., local sites within habitats) could be rare across another scale (e.g., a suite of discrete habitat patches or islands) (Wiens 1989, Cook et al. 2004, Sfenthourakis et al. 2004). If nestedness patterns are created by scale-dependent processes, such as selective immigrations and extinctions operating across a landscape, we hypothesize that composition will not be nested in contiguous habitats where those mechanisms are weaker or lacking. However, if passive sampling or stochastic processes associated with species-abundance distributions strongly influence nested composition patterns (Cutler 1994, Higgins et al. 2006), nestedness may also appear at sites within contiguous habitats. Investigating nestedness patterns across insular and contiguous habitats may provide insight about the influence of landscape type and spatial scale on community composition.

We investigated nested subset structure for insular bat assemblages on a near-shore archipelago in the Gulf of California to determine whether island characteristics such as size and isolation influence community composition of bats. We assessed the potential role of selective immigrations and extinctions on shaping nested subset patterns by analyzing the association of size and isolation of islands and traits of species on nested structure. In addition, we examined whether bat composition was nested across sites on the adjacent Baja California peninsula to determine whether composition patterns would be similar to those found on the archipelago. We hypothesized that community composition patterns would not be nested across local sites along the peninsula if island biogeographical dynamics are the primary drivers of nestedness.

Comparing community composition patterns may be misleading if sites where species were never detected were in fact occupied (or used) by the species (Cam et al. 2000). This false negative bias in detection/non-detection data has received considerable attention in the last few years, particularly since development of approaches for simultaneously estimating probabilities of site occupancy and detection (MacKenzie et al. 2002, Tyre et al. 2003). We estimated probability of use of sites in coastal habitat on the Baja peninsula using the MacKenzie et al. (2002) approach to establish whether probabilities of detection at sites were sufficient for determining species composition patterns. We also compared estimates for probability of use to insular incidence to determine whether species that were widespread in coastal peninsular habitats were also widespread across the archipelago. If composition patterns are scale-dependent, then the scale of investigation could strongly influence which species are identified as conservation priorities (Hartley and Kunin 2003).

METHODS

Study Region

The Gulf of California (Figure 3.1) in northwest Mexico contains more than 100 islands and islets that range in size from a few hectares to 1,223 km^2 (Carreño and Helenes 2002). The southern subarchipelago and adjacent gulf coast of the Baja California peninsula, extending from Loreto to La Paz, conform to a Sonoran Desert sarcocaulescent vegetation type (Shreve 1951, Wiggins 1980), dominated by columnar cacti (*Pachycereus pringlei* and *Stenocereus thurberias*) and desert trees (*Cercidium*, *Bursera*, and *Jatropha*).

The climate of the region is hot and dry with unpredictable rainfall averaging between 100 and 150 mm per year (Cody et al. 2002). The southern part of the gulf receives approximately 40% of its rainfall in the summer (Cody et al. 2002).

Very few of the islands have permanent sources of freshwater, but some of the larger islands that have well-developed drainage courses (i.e., *arroyos*) have ephemeral freshwater in remnant pools known as *tinajas* (Cody and Velarde 2002). Smaller islands (< 200 ha) do not have the surface area nor soil type to develop drainages and typically have no freshwater except for ephemeral puddles after rainstorms (Cody et al. 2002, Cody and Velarde 2002). We found freshwater on Isla Carmen (maintained spring-boxes for *Ovis canadensis*) and Isla Espiritu Santo/Partida Sur (natural *tinajas*). The peninsular coastal region is used extensively for grazing livestock and has a network of maintained spring-boxes that provide permanent or semi-permanent water.

Most islands are composed of granitic or volcanic rocks and have steep terrain (Carreño and Helenes 2002). Crevices and small caves are abundant on all islands, but large caves probably only occur on larger islands. Interior areas of large islands are only accessible by foot via arroyo and narrow canyons. Apart from temporary fishing camps on beaches, almost all islands are uninhabited by humans (Bahre and Bourillón 2002).

Data Collection

Sampling on islands

We conducted presence-absence surveys for bats on 20 islands in the southern subarchipelago in the Gulf of California from 1 April to 1 June 2004-2005 (Figure 3.1). We sampled for presence of bat species on each island for a five-day period using passive Anabat acoustic stations (Titley Electronics, Australia). On seven islands, active hand-held Anapocket acoustic monitoring (Corben 2004) and mist-net surveys were conducted to verify species detected with passive acoustic stations. A species was considered present if it was detected at least once, without determination of breeding or residency status. Generally one island was sampled at a time, but occasionally multiple small islands were sampled simultaneously.

Sampling on the peninsula

We conducted presence-absence surveys in three coastal regions of the Baja peninsula from April 1 to June 1 in 2005 (Figure 3.1). Regions were selected for sampling based on accessibility and proximity to study islands. Sampling on the peninsula was conducted in a similar manner to that on islands with five-day sampling periods. Passive acoustic stations were placed in randomly selected road-accessible arroyos within 3 km of the shore. Passive acoustic stations that ran for five consecutive nights (n = 27) were used in analyses of probability of site use (Ψ) and peninsular nestedness.

Acoustic sampling

We recorded echolocations of bats using broadband ultrasonic bat detectors (Anabat II; Titley Electronics) to determine presence of species (Hayes 1997, O'Farrell et al. 1999, Gehrt and Chelsvig 2004). Passive monitoring stations contained an Anabat II detector attached to a high-frequency microphone housed in a waterproof shroud with a 45° reflector (Messina 2004) mounted on a 1m tall pole. The detector was connected to an Anabat Compact Flash Zero-Crossings Interface Module (Titley Electonics) recording device.

The number of passive acoustic stations placed on an island increased with island size (range: 1-13 detectors per island). We placed detectors at randomly determined distances between 100 and 1,000 m from safe boat landings. Given a lack of adequate a priori information about accessible landings, safe landings were assessed on arrival. We randomly selected landings after circumnavigating an island to determine beach landings with terrain accessible on foot. When adverse field conditions prohibited random selection, landings were selected haphazardly according to accessibility and safe deployment. Number of landings ranged from 1-8 per island and nine islands (all less than 100 ha) were sampled with only one detector.

On seven islands and three peninsular regions, active monitoring of bat activity was conducted at mist-net survey locations using a spotlight and Anapocket software (Corben 2004) on a handheld PDA, which displays bat calls as time versus frequency graphs in real time. Species identified with visual confirmation in the spotlight were used to verify presence of species detected with passive acoustic detectors and to build a reference call library of echolocation signatures of free-flying bats.

Mist-net sampling

Mist-net surveys were conducted on nine of the 20 islands and in each of the peninsular areas to verify identification of species detected with acoustic sampling, to build an echolocation call reference library from hand-release recordings, and to train observers to recognize flight patterns and body shapes in the spotlight for identifying free-flying bats with active monitoring. Hand-release recordings were conducted using Anapocket (Corben 2004) and a bright spotlight. Bats were released and recorded as long as they remained in constant view in the spotlight.

Mist-net sites on islands were selected in attempt to maximize captures and were typically placed in dry arroyos (flyways) and desert scrub habitats or over freshwater pools (*tinajas* or spring-boxes) when available. Typically, five different locations were sampled on each island, except in two cases where access was limited. Mist-net surveys were limited to four visits at the Agua Verde and Tecolote peninsular regions. We opened mist-nets at sunset and monitored them at least every 15 minutes for 4 hours. Captured bats were identified to species, age, sex, and reproductive status (Anthony 1988, Racey 1988).

Echolocation analysis for species identification

We developed a graphical and descriptive key of Anabat echolocation calls (Appendix A). Anabat uses a zero-crossings analysis (ZCA) (Parsons et al. 2000) which produces files displaying echolocation calls on time-frequency graphs. Sequences were identified to species if they had greater than two diagnostic pulses that met defined criteria based on reference calls (see Appendix A for detail). Anabat files were randomly assigned by detector night to three observers trained to identify calls using the key. Sequences identified to species were proofed by the senior author.

Identifying echolocation calls can produce false negative and false positive errors. False negative errors (species is present and not detected) occur when a species is present and is recorded by the detector but the call is insufficiently diagnostic to be labeled as being produced by that species. False positive errors (species is absent and is falsely detected) occur when an echolocation call is misclassified as a species that was in fact not present. Our approach to classifying echolocation calls was designed to minimize both false negative and false positive errors, but greater emphasis was placed on avoiding false positive errors. In general, the species in the assemblage were easily identifiable to the species level using the key.

Because of our efforts to minimize false positive errors, our approach was not sensitive to detecting rare taxa with echolocation call morphologies similar to common taxa. For example, some calls from the regionally rare species *Lasiurus cinereus* may be confused with the common *Nyctinomops femorosaccus*. This bias was uniform across islands and peninsular sites and although may have negatively biased overall species richness, our identification of recorded species should be a reasonable index of community composition.

Data Analysis

Probability of peninsular site use

We used Program PRESENCE (MacKenzie et al. 2006) to estimate probabilities of detector site occupancy (Ψ) and detection (p) for species using 27 detector sites sampled for five consecutive nights in coastal peninsular habitats (Figure 3.1). Key assumptions of the site occupancy model are 1) closure to changes in occupancy during repeat sample visits and 2) no misclassification of species. The assumption of closure may be relaxed if a species moves in and out of the sample site randomly with respect to sample visits (MacKenzie et al. 2006). When closure is violated, apparent occupancy should be interpreted as use rather than true occupancy (MacKenzie et al. 2006).

Given the high mobility of bats and our sampling methodology, we interpret our data to be indicative of use rather than occupancy as the area sampled by an acoustic detector is not constantly occupied by a species. Under this interpretation, probability of detection (p) is a function of the probabilities that the species is available to be detected and that the species is detected and identified correctly. These two components are not separately estimable, but jointly account for both sources of imperfect detectability to allow an unbiased estimate of site use.

Violation of the misclassification assumption could lead to positively biased estimates of site use if a species that is not present is recorded as present (Royle and Link 2006). For the majority of the species investigated, distinct echolocation calls make misclassification unlikely. However, echolocation calls from *Macrotus californicus* and *Myotis californicus* are similar and estimates of site use for these two species may be confounded.

To determine if sampling at the detector-site scale was exhaustive, we used MacKenzie et al.'s (2006) approach for calculating Ψ_{condl}, the probability a site was used by a species, given it was never detected during the five night sampling period, using the following equation:

$$\Psi_{condl} = \frac{\Psi \sum_{j=1}^{5} (1 - p_j)}{(1 - \Psi) + \Psi \sum_{j=1}^{5} (1 - p_j)}$$

where p_j is the probability of detection and Ψ is the probability of site use. The associated standard error estimates were calculated using the approximate asymptotic variance from the delta method (MacKenzie et al. 2006; pg. 98). This allowed us to determine the probability that non-detections in the presence-absence matrix used in the nestedness analysis represented true absences of species.

We relied on examination of species accumulation curves to determine that sampling on islands was exhaustive (Appendix B).

Nested subset structure analysis

We estimated nestedness using the program BinMatNest (Rodríguez-Gironés and Santamaría 2006), which uses a genetic algorithm to maximally pack the binary presence-absence matrix and calculates a uniquely defined isocline that minimizes nestedness temperature. Temperatures of 0° represent perfectly ordered or nested matrices and temperatures of 100° represent perfectly disordered matrices (Atmar and Patterson 1993, Rodríguez-Gironés and Santamaría 2006). In the archipelago analysis, rows represent islands and presence-absence data from detector sites within islands are aggregated. For the peninsular analysis, rows represent individual detector sampling sites.

We compared estimated nestedness temperature of our matrix to 1,000 Monte Carlo simulations generated with a constrained null model (null model 3) that accounts for the incidences of species (column totals) and richnesses of islands (row totals) while sampling the null space uniformly (Bascompte et al. 2003, Rodríguez-Gironés and Santamaría 2006). There is little agreement on which null model is most appropriate for estimating significance of nested subset patterns (Gotelli and Graves 1996, Wright et al. 1998, Brualdi and Sanderson 1999, Jonsson 2001, Fischer and Lindenmayer 2002, Rodríguez-Gironés and Santamaría 2006). We chose a constrained null model because we believe building more biological realism into the null model provides a more meaningful test of the significance of nestedness by minimizing Type I errors (Brualdi and Sanderson 1999, Rodríguez-Gironés and Santamaría 2006, but see Jonsson 2001). In addition, null model 3 is less prone to Type I and II errors than null model 1 (unconstrained row and column totals) (Atmar and Patterson 1993) and null model 2 (constrained species column totals) (Fischer and Lindenmayer 2002), even when the generating constraints correspond to a different null algorithm (i.e., null 1 and 2) (Rodríguez-Gironés and Santamaría 2006). However, null model 3 is prone to Type II errors if the generating constraints of the system under investigation correspond to null algorithm 1, making it a conservative test of nestedness if there is no biological expectation of constrained incidence and richness totals (Rodríguez-Gironés and Santamaría 2006).

Nested temperature is dependent on size and fill of the matrix, but the probability of observing the calculated nestedness metric from chance is not (Rodríguez-Gironés and Santamaría 2006). Therefore, we restrict our comparison of matrices to interpretation of the *p*-values from the Monte Carlo simulations and do not directly compare nestedness temperatures (Rodríguez-Gironés and Santamaría 2006).

Selective immigration and extinction on islands

To determine correlates of nestedness, we used Spearman rank and partial Spearman rank correlation tests of the order of island rows in the maximally packed matrix to island area and isolation ranks. Partial Spearman rank correlation tests were used to assess the correlation of area on isolation after accounting for the effect of the other variable (Shipley 2000). Islands with shared compositions were given tied ranks.

Island characteristics were measured using a “heads-up” digitized GIS layer created in Arcview 3.2 from Landsat 7 satellite images (Table 3.1). We measured the shortest over-water path (km) to the Baja peninsula using Nearest Features and Path extension tools (Jenness 2004, 2005) in ArcView 3.2 as an index for isolation. This metric allowed for stepping-stone type movements by summing over-water legs if stepping-stone paths were the shortest route to the peninsula. This approach accounts for the presence of neighboring islands if they function as stepping stones, but emphasizes the role of the Baja peninsula as the source pool. More complex measures of isolation, including area-based metrics, are often advocated (Moilanen and Nieminen 2002, Bender et al. 2003, Matter et al. 2005), but these approaches are more applicable to fragmented systems where there is no clear source population (Moilanen and Nieminen 2002). These complex metrics may also be less appropriate for community questions as they are highly sensitive to movement scales that vary among species (Bender et al. 2003, Bélisle 2005, Taylor et al. 2006).

To evaluate the contribution of vagility of bats to nestedness, we performed a Spearman rank correlation of the rank of species order in the maximally packed matrix to wing aspect ratio of species, an ecomorphological trait that strongly relates to cost of transport during flight (Norberg and Rayner 1987). Wing aspect ratio values were taken from published sources (Norberg and Rayner 1987, Milner et al. 1990, Sahley et al. 1993). Average values for Lasiurines in Norberg and Rayner (1987) were used in lieu of available estimates for *Lasiurus xanthinus*. Aspect ratio of the ecomorphologically similar *Tadarida brasiliensis* was used for *Nyctinomops femorosaccus*.

Comparison of peninsular and archipelago species composition

To determine whether species detected frequently across peninsular sites are also detected frequently across the archipelago, we compared the rank order of species in nested matrices for the peninsula and archipelago with a Spearman rank correlation test. Species that were detected on the peninsula and never detected on islands were given a tied rank of last place on the archipelago. Spearman Rank and Partial Rank correlation analyses were conducted with PROC CORR in SAS v.9.1.

Sampling artifacts on the archipelago

Because the nestedness analysis for archipelago aggregates presence-absence data across multiple detector sites for larger islands (n = 9), we tested whether nestedness of the archipelago could arise as a sampling artifact. We randomly sampled single detectors that ran for five nights from islands with multiple detectors and re-ran the nestedness analysis on 20 randomly compiled matrices using only the presence-absence information from single detectors for each island. Each matrix consisted of 20 rows representing the same islands as in the archipelago analysis, but each row represented a randomly selected detector from that island rather than the aggregate of presence-absence information from all detector sites within an island. Rows representing small islands that only had one detector site (n = 11) were repeated in each run. This approach does not rule out passive sampling as a mechanism of nestedness, but does provide some insight into the potential bias from greater sampling effort on larger islands to produce nested patterns.

RESULTS

Twelve species of bat were detected on islands, including 10 insectivorous species, 1 nectarivorous species, and 1 piscivorous species (Table 3.2). Fifteen species were detected in coastal habitats on the Baja peninsula, including 11 of the species detected on islands and 4 additional species of insectivorous bat (Table 3.2).

Archipelago Nestedness

The maximally packed incidence matrix (Table 3.3) for the archipelago had an estimated nestedness temperature of T = 10.04, which was significantly lower ($p < 0.001$) than the mean temperature of 1,000 randomly generated matrices (T = 35.3; SE = 0.17) using null model 3.

Nestedness does not appear to be a sampling artifact from greater sampling effort on larger islands as 20 runs of matrices compiled from randomly-selected single detectors from each island were still significantly nested (Mean T = 15.68, SE = 0.57; Mean *p*-value < 0.03, SE = 0.001) (Table 3.4).

Selective Immigration and Extinction

Area and order of islands in the maximally packed matrix were correlated (Spearman rank correlation $\rho = 0.72$, $p < 0.0003$). When the effect of isolation was accounted for, area and order of islands was even more strongly correlated (partial Spearman rank correlation $\rho = 0.82$, $p < 0.0001$). Nested island order was also significantly and inversely correlated with isolation rank when the effects of area were accounted for (partial Spearman rank correlation $\rho = - 0.61$, $p < 0.006$), but not significant otherwise (Spearman rank correlation $\rho = - 0.26$, $p < 0.27$). Species order in the maximally packed matrix was not significantly correlated with wing aspect ratios of bats (Spearman rank correlation $\rho = 0.13$, $p < 0.69$) (Table 3.5).

Peninsular Site Use

Of the fifteen species detected in coastal peninsular habitat, we detected six species (*Myotis californicus*, *Pipistrellus hesperus*, *Macrotus. californicus*, *Nyctinomops femorosaccus*, *Antrozous pallidus*, *Mormoops megalophylla*) at greater than 50% of sites (Table 3.6, Figure 3.2). For seven species (*Myotis californicus*, *Pipistrellus hesperus*, *Macrotus californicus*, *Nyctinomops femorosaccus*, *Antrozous pallidus*, *Eptesicus fuscus, Nyctinomops macrotis*), the probability that a species was present at a site where it was never detected was extremely low (Table 3.6), providing confidence in the interpretation that failure to detect these species at a site represents a true absence. For these species, the estimated probability of use of detector sites (Ψ) was the same as the naive estimate (Table 3.6), which is the proportion of sites surveyed where a species was detected (Mackenzie 2006). For four species (*Myotis vivesi, Mormoops megalophylla, Tadarida* *brasiliensis*, and *Leptonycteris curasoae*), detection probabilities were sufficiently low to negatively bias naive estimates of use (Table 3.6). At the scale of the detector site, occurrences may be more common than represented in our analysis for those species. Estimation for four species (*Lasiurus blossevillii, Lasiurus xanthinus, Myotis volans, and Myotis yumanensis*) was not possible due to sparse data.

Peninsular Nestedness

Use of peninsular coastal sites by bats was significantly nested, as the maximally packed matrix of detections at peninsular sites (Table 3.7) had an estimated nestedness temperature of $T = 16.64$, significantly lower ($p < 0.001$) than the mean temperature of 1,000 randomly generated matrices ($T = 38.47$; $SE = 0.14$) using null model 3.

Comparison of Peninsular and Archipelago Species Composition

The rank order of the species occurring across peninsular sites and the archipelago were significantly correlated (Spearman rank correlation $\rho = 0.61$, $p < 0.01$), indicating species that contributed to nestedness on the peninsula also contributed to nestedness across the archipelago. However, substantial correspondence between insular and peninsular incidence only occurred for species that were rarely detected (occur at < 20% sites or islands) and two ubiquitous species (*P. hesperus* and *N. femorosaccus*) (Figure 3.2). Four species on the peninsula (*E. fuscus, L. blossevillii, M. volans, M. yumanensis*) were never detected on islands and one rare insular species (*Eumops sp.*) was never detected on the peninsula.

DISCUSSION

Assemblages of bats were significantly nested across the archipelago and across sites on the peninsula, indicating nestedness of bat faunas can occur in both insular and contiguous landscapes. The presence of nestedness in both the archipelago and peninsular landscapes suggests that different mechanisms may create nestedness patterns at multiple spatial scales (Hartley and Kunin 2003). For the archipelago, nestedness suggests community composition is structured across islands in a predictable manner that can be related to island characteristics (Patterson and Atmar 1986, Lomolino 1996). Across peninsular sites, inference is limited to local influences on diversity rather than associated with regional influences like colonization and extinction (Cook et al. 2004). Other studies have also found that nestedness occurs at multiple spatial scales (Cook et al. 2004, Sfenthourakis et al. 2004).

We did not expect to observe nestedness at peninsular sites, because unlike the archipelago scale where mechanisms that structure community composition may be associated with island characteristics, sites on the peninsula occurred in similar habitats that lacked a distinct gradient in conditions. Across local sites, nestedness should be associated with a gradient in species tolerances for habitat variables or environmental conditions (Cook et al. 2004). In this study, peninsular sites were chosen without such a habitat filter in mind.

Nestedness patterns at peninsular sites may have been associated with an unidentified environmental gradient or habitat heterogeneity that affected use of sites or simply from a lack of other types of composition-structuring mechanisms, like competition, that lead to highly disordered matrices (e.g., checkerboards). Species turnover (beta diversity) is typically low in bat assemblages because vagility associated with flight allows for overlapping home ranges (Patterson et al. 2002). Six species were detected at greater than 50% of peninsular sites (Figure 3.2) and the similarity in site use among these species had a strong influence on nestedness. Consistent with the passive sampling hypothesis, nested patterns may arise from random placement of individuals from species with different abundance distributions (Cutler 1994, Higgins et al. 2006). Our results provide some evidence that nestedness may occur in ecological communities even without apparent underlying factors (Simberloff and Martin 1991). Nestedness analysis may be useful for examining patterns of community composition, but we caution against making inferences to deterministic mechanisms based solely on presence of nestedness.

For the archipelago, we examined potential processes affecting nestedness by analyzing the relationship of island characteristics to nestedness (Lomolino 1996). Selective immigration and extinction likely play important roles in shaping this insular bat assemblage as demonstrated by the strong correlation between area and isolation with the order of islands in the nested matrix (Table 3.3). The strong nestedness pattern and correlation with both area and isolation to nestedness suggests bat vagility and persistence ability are positively correlated (Wright and Reeves 1992, Lomolino 2000b). Our results highlight that immigration and extinction may both contribute to nested patterns rather than assuming faunal systems must be driven by one or the other (Lomolino 1986, 1996).

The fact that immigration and extinction are both important mechanisms behind nestedness may help explain why we failed to detect a relationship between wing aspect ratio and species rank in the nested matrix. Area had the strongest association with nested rank, indicating that persistence may have a stronger influence than vagility on composition patterns. Nested order of species appears to be a combination of vagility and persistence and not easily summarized by a simple ecomorphological trait relating to cost of flight.

Other mechanisms suggested to create nestedness include habitat nestedness and sampling artifacts. The habitat nestedness hypothesis is similar to the habitat diversity – area hypothesis that states that higher richness on larger islands is due to greater habitat diversity, not area *per se* (Cutler 1994). Habitat nestedness associated with stepwise changes in drainage morphology as island area increases has been suggested as a likely mechanism driving nested bird distributions on Baja islands (Cody 1983, Cody and Velarde 2002). Increasing topographical and habitat diversity with island size could contribute to the association between island size and nestedness of bat communities, if some species require greater topographical diversity for roosting habitat and greater vegetation diversity for foraging habitat.

We determined nestedness was not likely due to sampling artifacts by showing that nested patterns occurred even when we randomly sampled single detectors from larger islands (Table 3.4). This does not eliminate the possibility that passive sampling may contribute to nested patterns if widespread species also have much higher abundances and thereby have higher detection probabilities (Higgins et al. 2006). But if passive sampling were responsible for nestedness, we would not expect strong associations between area and isolation and the nested order of islands. These associations suggest selective immigration and extinction are important forces in structuring composition patterns in this system (Lomolino 1996).

The nestedness patterns suggest area and isolation influence species composition as well as total richness on islands (MacArthur and Wilson 1967). This may have important conservation implications if composition and focal species have predictable distributions based on island or patch characteristics (Wright and Reeves 1992). Nestedness may prove useful as a starting point for identifying potential conservation concerns, but given that nestedness may occur from multiple mechanistic explanations and that species traits may not be easily correlated with ranking in a nested matrix, we agree that autecological details should be considered for robust conservation decision-making (Boecklen 1997, Donlan et al. 2005).

Comparison of Peninsular and Insular Composition

Results from the test of Spearman rank correlation on nested order of species in the insular and peninsular matrices suggest that the same species contribute to nestedness in both landscapes. This correlation seems to be dominated by four species that were rarely detected on the peninsula and on the archipelago (Figure 3.2). Only two species were commonly detected on both the peninsula and archipelago (Figure 3.2). The remaining species were either commonly detected on the peninsula and uncommonly detected on the archipelago or vice versa. For our purposes, we define common as occurring at greater than 50% of sites or islands and uncommon as occurring at less than 50%. Although four species detected on the peninsula were never detected on islands, there was not a strong tendency to be more widespread on the peninsula as nearly half the species had higher incidences on islands than across peninsular sites (Figure 3.2).

The absence of *E. fuscus* from islands is surprising considering it is capable of dispersing long distances (Holland et al. 2006, Neubaum et al. 2006) in some landscapes. Access to permanent freshwater may be an important factor in restricting the distribution of this species in desert landscapes (Carpenter 1969, Kurta et al. 1990). Peninsular habitats were structurally similar to island habitats, with the exception that they tended to support regular access to freshwater in the form of spring-boxes for livestock and natural *tinajas*.

Of the seven species that were more frequently detected on the archipelago, four belong to the Molossidae, a family characterized by high-flying species adapted for long-distance foraging (Norberg and Rayner 1987). The migratory *L. curasoae* was also detected on more islands (85%) than estimated to occur on sites on the peninsula (53% after accounting for imperfect detectability). This species is known to commute long distances between roosts and foraging grounds (Sahley et al. 1993, Horner et al. 1998b). *M. vivesi*, the endemic fish-eating bat, occurred on all 20 islands, but was only detected at 26% of peninsular sites. Accounting for imperfect detection probabilities at peninsular sites, the estimated proportion of sites used by *M. vivesi* was still only 53% (Table 3.6). It appears that species that were more frequently detected on the archipelago than the peninsula have high vagility or unique natural histories (i.e., piscivory).

Using presence-absence matrices to analyze community composition patterns has a long history in community ecology, but little attention has been paid to the impact of imperfect detectability on observed incidence patterns. Imperfect detectability could lead to false absences in the presence-absence matrix if species were present but not detected at sites. We found for most bat species in our assemblage that five nights of acoustic sampling was sufficient to adequately determine presence of species at local sites.

Our research raises interesting questions about the underlying mechanisms behind the assembly of desert bat communities. A gradient in species immigration abilities and extinction vulnerabilities appears to contribute to composition patterns in the insular landscape we studied. The nestedness of communities at sites in contiguous coastal habitats indicates the prevalence of nested patterns at different spatial scales and in different landscapes.

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Table 3.1. Characteristics of 20 islands sampled for presence of bat species in the southern Gulf of California, Baja California Sur, Mexico. Islands are presented in order of descending size.

Island	**Area (ha)**	**Isolation (km)**	**Species Richness**	**Nested Matrix Rank**
San José	18,494.5	4.75	12	1
Carmen	14,801.4	5.50	9	2
Espiritu Santo/Partida Sur	10,367.1	6.21	8	4
Santa Catalina	3,995.6	25.06	5	11
Monserrat	1,902.8	13.66	6	8
Santa Cruz	1,315.1	19.81	5	7
Coronados	715.8	2.60	7	6
Danzante	423.7	2.67	8	5
San Francisco	419.0	7.16	8	3
San Ildefonso	104.2	10.01	4	12
San Diego	62.9	19.06	3	18
Las Animas Sur	9.1	16.49	3	19
Cayo	6.7	6.22	4	13
Galeras East	5.4	16.40	4	16
Pardo	4.3	0.36	5	10
Tijeras	4.0	1.90	4	14
Islitas	3.3	0.41	4	15
Galeras West	3.2	16.77	3	20
Gallina	2.0	7.18	6	9
Blanco	1.3	0.84	4	17

Table 3.2. Bat species detected during sampling on southern islands in the Gulf of California and coastal habitats of the Baja peninsula. Foraging guild classifications follow Schnitzler and Kalko (2001).

Species	**Species Code**	**No. Islands Occupied**	**No. Peninsular Sites Used**	**Foraging Guild**	**Roosting Guild**
Family: Mormoopidae					
Mormoops megalophylla	MOME	3	16	edge & gap insectivore	cave obligate
Family: Phyllostomidae					
Macrotus californicus	MACA	6	23	narrow-space insectivore	cave obligate
Leptonycteris curasoae	LECU	17	13	nectarivore	cave obligate
Family: Vespertilionidae					
Antrozous pallidus	ANPA	5	19	narrow-space insectivore	cave & crevice
Eptesicus fuscus	EPFU	0	11	edge & gap insectivore	crevice
Lasiurus blossevillii	LABL	0	4	edge & gap insectivore	foliage
Lasiurus xanthinus	LAXA	2	1	edge & gap insectivore	foliage
Myotis californicus	MYCA	7	26	edge & gap insectivore	crevice
Myotis volans	MYVO	0	1	edge & gap insectivore	crevice
Myotis yumanensis	MYYU	0	1	edge & gap insectivore	crevice
Myotis vivesi	MYVI	20	7	piscivore	crevice
Pipistrellus hesperus	PIHE	14	25	edge & gap insectivore	crevice
Family: Molossidae					
Eumops sp.	EUSP	1	0	open-space insectivore	crevice
Nyctinomops femorosaccus	NYFE	19	23	open-space insectivore	crevice
Nyctinomops macrotis	NYMA	7	4	open-space insectivore	crevice
Tadarida brasiliensis	TABR	11	6	open-space insectivore	cave & crevice

Table 3.3. Maximally packed nested matrix of insular bat species on 20 islands in the Gulf of California, Baja California Sur, Mexico. Espiritu Santo includes Partida Sur. Species codes are provided in Table 3.2.

	MYVI	NYFE	LECU	PIHE	TABR	MYCA	NYMA	MACA	ANPA	MOME	LAXA	EUSP
San José	1	1	1	1	1	1	1	1	1	1	1	1
Carmen	1	1	1	1	0	1	1	1	1	1	0	0
San Francisco	1	1	1	1	1	1	1	1	0	0	0	0
Espiritu Santo	1	1	1	1	1	1	1	1	0	0	0	0
Danzante	1	1	1	1	0	1	1	1	0	1	0	0
Coronados	1	1	1	1	1	1	0	1	0	0	0	0
Santa Cruz	1	1	0	1	0	0	0	0	1	0	1	0
Monserrat	1	1	1	1	0	0	1	0	1	0	0	0
Gallina	1	1	1	1	1	1	0	0	0	0	0	0
Pardo	1	1	1	1	1	0	0	0	0	0	0	0
Santa Catalina	1	0	1	1	0	0	1	0	1	0	0	0
San Ildefonso	1	1	1	0	1	0	0	0	0	0	0	0
Cayo	1	1	1	0	1	0	0	0	0	0	0	0
Tijeras	1	1	1	0	1	0	0	0	0	0	0	0
Las Islitas	1	1	0	1	1	0	0	0	0	0	0	0
Galeras East	1	1	1	0	1	0	0	0	0	0	0	0
Blanco	1	1	1	1	0	0	0	0	0	0	0	0
San Diego	1	1	0	1	0	0	0	0	0	0	0	0
Las Animas Sur	1	1	1	0	0	0	0	0	0	0	0	0
Galeras West	1	1	1	0	0	0	0	0	0	0	0	0

Table 3.4. Nested temperatures and associated *p*-values for 20 matrices compiled using randomly selected detectors from each island. *P*-values generated from 1,000 Monte Carlo simulations using null algorithm 3.

Run	Nested Temp.	*p*-value
1	17.93	0.002
2	10.74	0.000
3	14.21	0.001
4	15.89	0.001
5	16.65	0.002
6	12.53	0.000
7	12.71	0.000
8	16.97	0.002
9	15.47	0.003
10	19.63	0.011
11	13.53	0.002
12	16.63	0.002
13	20.12	0.007
14	19.74	0.019
15	17.12	0.002
16	15.16	0.002
17	14.01	0.000
18	16.92	0.001
19	14.43	0.001
20	13.23	0.000

Table 3.5. Wing aspect ratios and species rank in the nested matrix.

Species	**Nested Matrix Rank**	**Wing Aspect Ratio**
Myotis vivesi	1	7.4
Nyctinomops femorosaccus	2	8.2
Leptonycteris curasoae	3	6.6
Pipistrellus hesperus	4	5.7
Tadarida brasiliensis	5	8.2
Myotis californicus	6	5.6
Nyctinomops macrotis	7	9.7
Macrotus californicus	8	6.4
Antrozous pallidus	9	6.1
Mormoops megalophylla	10	7.1
Lasiurus xanthinus	11	7.5
Eumops sp	12	9.5

Table 3.6. Estimates of proportion of site use at 27 coastal sites on the peninsula, Baja California Sur, Mexico. NaiveΨ is the proportion of sites where a species was detected. Estimation of Ψ and Ψ_{condl} for *L. blossevillii, L. xanthinus, M. volans,* and *M. yumanensis* was not possible due to sparse data.

		Probability of Site Use		Probability of Detection		Probability of Use, Given Not Detected	
Species	**Naive Ψ**	**Ψ**	**SE**	***p***	**SE**	**Ψ_{condl}**	**SE**
My. californicus	0.96	0.96	0.04	0.83	0.03	0.00	0.005
P. hesperus	0.93	0.93	0.05	0.90	0.03	0.00	0.000
Ma. californicus	0.85	0.85	0.06	0.71	0.04	0.01	0.011
N. femorosaccus	0.85	0.85	0.07	0.72	0.03	0.01	0.008
A. pallidus	0.70	0.70	0.09	0.67	0.05	0.01	0.008
M. megalophylla	0.59	0.66	0.11	0.37	0.06	0.17	0.106
L. curasoae	0.48	0.53	0.11	0.38	0.07	0.10	0.070
E. fuscus	0.41	0.42	0.10	0.53	0.07	0.02	0.014
M. vivesi	0.26	0.53	0.29	0.13	0.08	0.28	0.356
T. brasiliensis	0.22	0.33	0.15	0.20	0.10	0.11	0.132
N. macrotis	0.15	0.16	0.07	0.42	0.12	0.01	0.015
N. blossevillii	0.15	--	--	--	--	--	--
L. xanthinus	0.04	--	--	--	--	--	--
M. volans	0.04	--	--	--	--	--	--
M. yumanensis	0.04	--	--	--	--	--	--

Table 3.7. Maximally packed matrix of 15 bat species on 27 sites in coastal peninsula habitat, Baja California Sur, Mexico.

	MYCA	PIHE	NYFE	MACA	ANPA	LECU	MOME	EPFU	MYVI	TABR	NYMA	LABL	LAXA	MYVO	MYYU
SE1_AC06	1	1	1	1	1	1	1	1	0	1	1	0	0	0	0
SE9_AC08	1	1	1	1	1	1	1	1	0	1	1	0	0	0	0
AV4A_AC11	1	1	1	1	1	1	1	1	1	0	0	1	0	0	0
AV3_AC09	1	1	1	1	1	1	1	1	1	0	0	1	0	0	0
TE11_AC11	1	1	1	1	1	1	1	0	0	0	0	0	0	1	0
AV2B_AC10	1	1	1	1	1	0	1	1	1	0	1	1	0	0	0
SE3_AC01	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
AV2A_AC04	1	1	1	1	0	0	1	1	1	0	0	0	1	0	0
SE2_AC05	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
SE5_AC10	1	1	1	1	1	0	1	1	0	1	0	0	0	0	0
SE10_AC07	1	1	1	1	1	0	0	0	1	1	1	0	0	0	0
AV2R_AC02	1	1	1	1	0	0	1	0	1	0	0	1	0	0	0
SE1_ACH9	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0
AV6_AC06	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0
AV8_ACH9	1	1	1	1	1	0	1	0	0	0	0	0	0	0	1
SE6_AC09	1	1	1	1	0	0	1	0	0	1	0	0	0	0	0
TE8_AC07	1	1	1	0	1	1	0	0	1	0	0	0	0	0	0
SE4_AC11	1	1	0	0	1	0	1	1	0	0	0	0	0	0	0
TE5_AC12	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0
TE1_AC09	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
TE3_AC08	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0
AV1_AC01	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
TE9_AC05	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
TE2_AC04	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0
AV8_ACH7	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
TE4_AC02	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0
TE6_AC01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

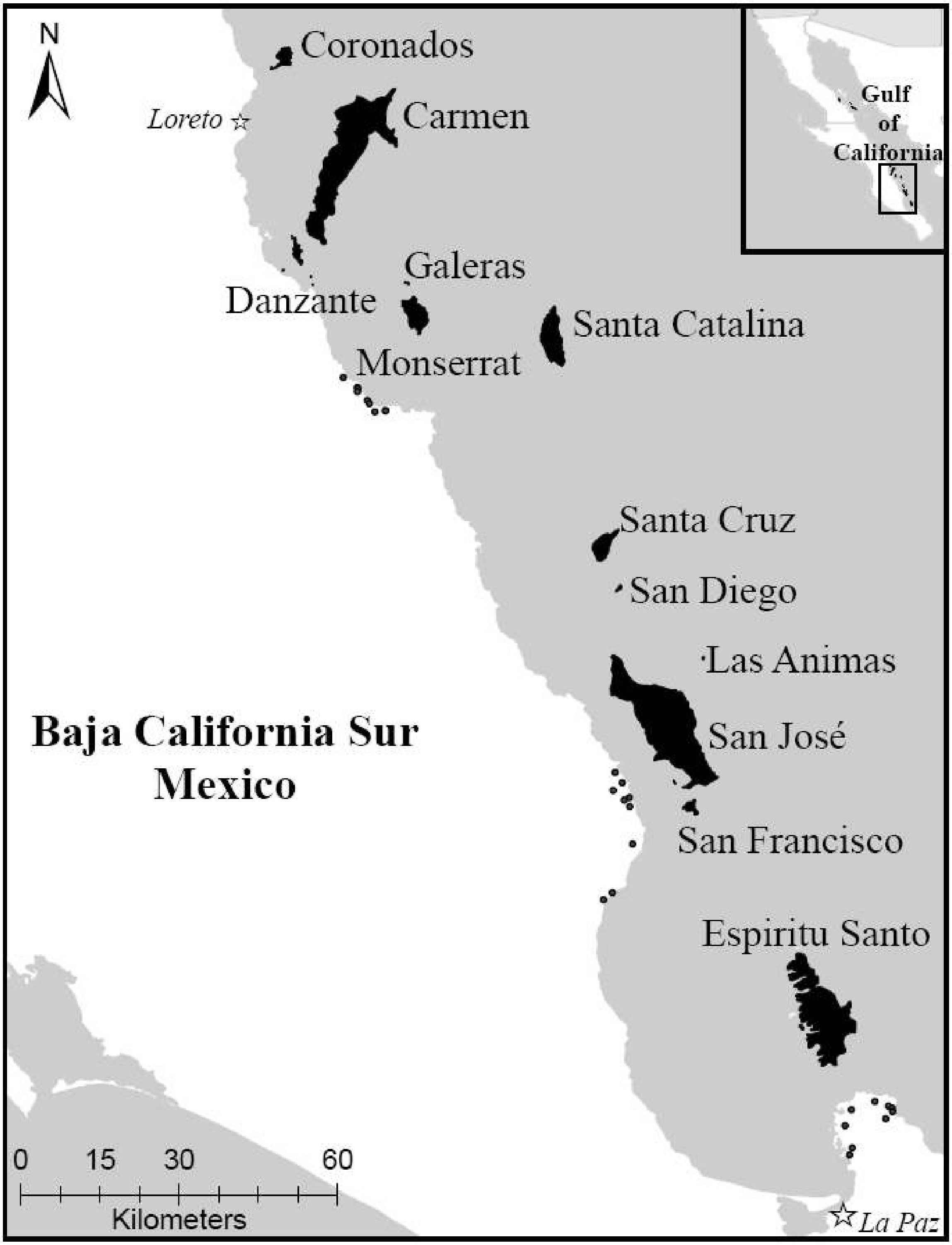

Figure 3.1. Map of study islands (in black) in the Gulf of California, Mexico and acoustic sample sites (points) on the Baja peninsula. Names of peninsular regions from north to south are: Agua Verde, San Evaristo, and Tecolote.

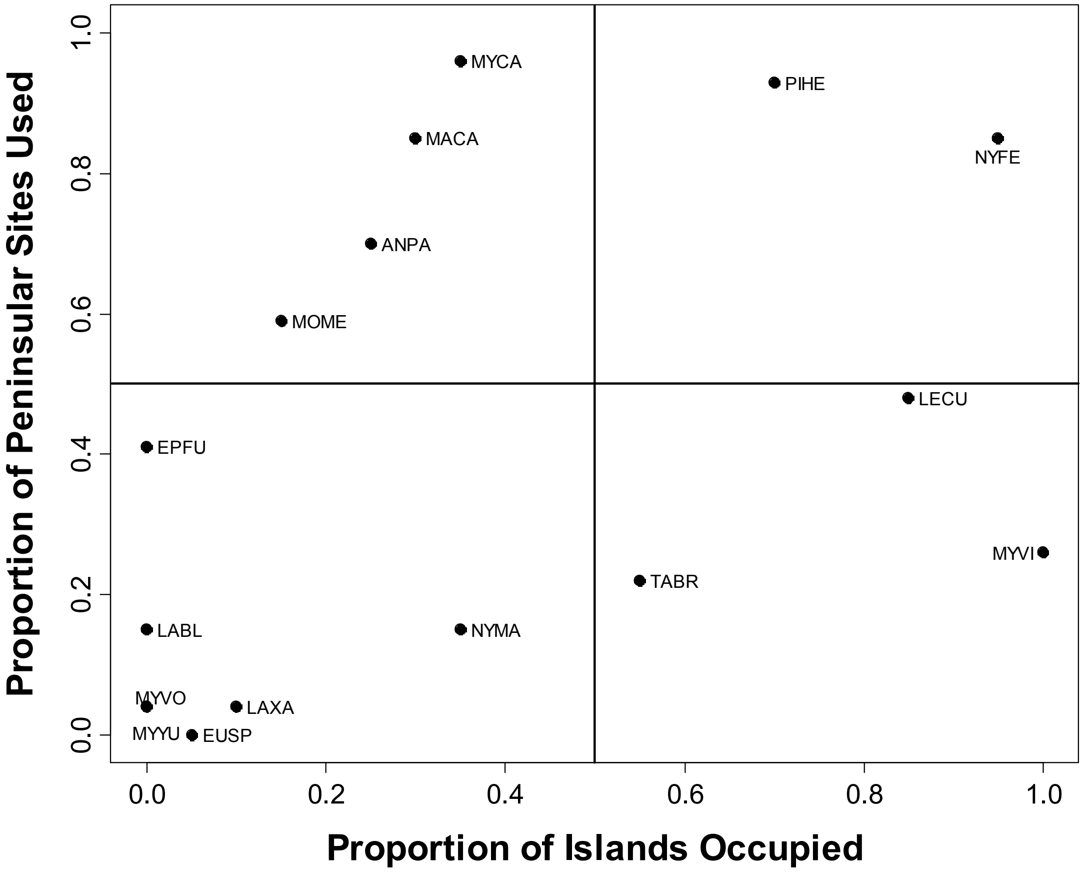

Figure 3.2. Frequency of occurrences across peninsular sites and islands. Top left quadrant contains species that were frequently found at sites on the peninsula, but detected on few islands. Top right quadrant contains species frequently detected on both the peninsula and islands. Bottom right quadrant contains species found at few sites on the peninsula, but frequently detected on islands. Bottom left quadrant contains species detected at few sites on the peninsula and on few islands.

CHAPTER 4: PATTERNS OF ISLAND OCCUPANCY IN BATS: INFLUENCES OF AREA AND ISOLATION ON INSULAR INCIDENCE OF VOLANT MAMMALS

ABSTRACT

We investigated the influence of area and isolation of islands on probability of occurrence of six bat species on 32 islands in a desert island archipelago in Baja California, Mexico. We extended Lomolino's (1986) hypotheses about patterns of insular incidence to volant mammals (bats) using an information theoretic (AIC) model selection approach. We compared five a priori models to explain patterns of island occupancy, including random patterns, minimum area effects, maximum isolation effects, additive area and isolation effects, and compensatory area and isolation effects. Five species of insectivorous bat (*Pipistrellus hesperus, Myotis californicus*, *Macrotus californicus*, *Antrozous pallidus*, and *Mormoops megalophylla*) displayed minimum area thresholds on incidence, suggesting island occupancy by these species is limited by resource requirements. Islands smaller than 100 ha typically did not support occupancy or use by most insectivorous species of bats, except at minimal isolation distances. Minimum area thresholds on occupancy by bats mirror patterns found for occupancy by birds in the same archipelago. Probability of occurrence on islands tended to be lower at greater isolations for some species. Two species of bats (*Leptonycteris curasoae* and *Myotis vivesi*) had high levels of incidence across islands of all size and isolations, indicating no effect of area or isolation on these species for the range of values available in this archipelago.

INTRODUCTION

The equilibrium theory of island biogeography (MacArthur and Wilson 1963, 1967) explains patterns of species richness in insular habitats in terms of recurring colonization and extinction events in ecological time scales (Rosenzweig 1995). The concepts of the equilibrium theory can be extended to species-level patterns to investigate inter-specific differences in how distributions of species are influenced by immigration and persistence abilities (Lomolino 1986, Peltonen and Hanski 1991, Lomolino 2000b). By focusing on species-level patterns, research questions shift from community-level dynamics to population dynamics of individual species in a metapopulation context (Hanski and Gaggiotti 2004).

Investigation of patterns of insular distributions may provide insight into how species vary in persistence and immigration abilities by determining the influence of area and isolation of islands on the probability of occurrence of species (Diamond 1975, Gilpin and Diamond 1981, Adler and Wilson 1985, Peltonen and Hanski 1991, Taylor 1991). Five potential patterns of insular distributions were proposed by Lomolino (1986), including random patterns, minimum area effects, maximum isolation effects, non-compensatory (or additive) area and isolation effects, and compensatory (or interactive) area and isolation effects (Figure 4.1). Each of these patterns corresponds to a biological hypothesis about the influence of vagility and persistence abilities of species on probability of occurrence on islands. With the exception of random patterns, these hypothesized distributional patterns correspond to deterministic factors associated with characteristics of species that shape patterns of incidence in predictable ways (Lomolino 2000b).

Minimum area effects (Figure 4.1b) occur when incidence of species becomes negligible on islands below a threshold of island size (Robbins et al. 1989, Peltonen and Hanski 1991, Hinsley et al. 1996, Watson et al. 2005). Minimum area thresholds suggest extinction dynamics are important determinants of incidence of species, as populations can not be sustained below a critical minimum area either due to demographic stochasticity or limited habitat availability (Lomolino 1986, Hanski 1991, Taylor 1991, Gaggiotti and Hanski 2004). Maximum isolation patterns (Figure 4.1c) suggest incidence of species is influenced by immigration rates via a threshold response such that beyond some isolation value immigration rates become sufficiently low as to prevent colonization or rescue effects (Lomolino 2000b). Depending on the range of area and isolation values in the landscape and capacities of the species being studied, these two mechanisms (extinction or immigration) may independently explain incidence of species.

If the range of area and isolation values encompasses the extent of persistence and immigration abilities, then area and isolation may both influence probability of occurrence on islands (Adler and Wilson 1985, Lomolino 1986). The additive (non-compensatory) hypothesis (Figure 4.1d) incorporates the influences of area and isolation on incidence when immigration and extinction events are not inter-dependent (Lomolino 1986). Compensatory effects (Figure 4.1e) occur either when low immigration rates are compensated by low extinction rates or when high extinction rates are compensated by high immigration rates, such that presence on small islands is dependent on island isolation and presence on far islands is dependent on island size (Lomolino 1986, Lomolino et al. 1989). Compensatory patterns suggest species-level manifestations of the equilibrium model of island biogeography where probability of occurrence results from recurrent immigration and extinction dynamics (Lomolino 1986, Hanski and Gaggiotti 2004).

Studies of non-volant mammals have demonstrated that vagility increases compensatory effects by increasing immigration rates relative to extinction rates (Adler and Wilson 1985, Lomolino 1986, Peltonen and Hanski 1991). In this study, we extend Lomolino's (1986) hypotheses about patterns of insular distribution to volant mammals (bats) to determine factors important in shaping patterns of insular incidence of highly vagile mammals. Previous analyses on the insular bat fauna in the Gulf of California (Chapters 2 and 3), demonstrate that size and isolation of islands influence both species richness and community composition patterns. The goal of this study was to determine whether insular incidence of bat species is influenced by immigration and persistence abilities by exploring how area and isolation of islands influence incidence and comparing patterns among species.

METHODS

Study Region

The Gulf of California in northwest Mexico contains more than 100 islands and islets that range in size from a few hectares to 1,123 km^2 (Carreño and Helenes 2002). Island vegetation conforms to the Sonoran Desert "sarcocaulescent" type (Shreve 1951, Wiggins 1980), dominated by columnar cacti (*Pachycereus pringlei* and *Stenocereus thurberias*) and desert trees (*Cercidium*, *Bursera*, and *Jatropha*).

The climate of the region is hot and dry with unpredictable rainfall averaging between 100 and 150 mm per year (Cody et al. 2002). Very few of the islands have permanent sources of freshwater, but some of the larger islands that have well-developed drainage courses (i.e., *arroyos*) have ephemeral freshwater in remnant pools (Cody and Velarde 2002). Smaller islands (< 200 ha) do not have the surface area nor soil type to develop drainages and typically have no freshwater except for ephemeral puddles after rainstorms (Cody et al. 2002, Cody and Velarde 2002).

Most islands are composed of granitic or volcanic rocks and have steep terrain (Carreño and Helenes 2002). Crevices and small caves are abundant on all islands, but large caves probably only occur on larger islands. Interior areas of large islands are only accessible by foot via arroyos and narrow canyons. Apart from temporary fishing camps on beaches, almost all islands are uninhabited by humans (Bahre and Bourillón 2002).

Data Collection

Sampling on islands

We conducted presence-absence surveys for bats on 32 islands in the Gulf of California from 1 April to 1 June, 2004-2006. We sampled for presence of bat species on each island for a five-day period using passive Anabat acoustic stations (Titley Electronics, Australia). On 10 islands, active hand-held Anapocket acoustic monitoring (Corben 2004) and mist-net surveys were conducted to verify species detected with passive acoustic stations. A species was considered present if it was detected at least once, without determination of breeding or residency status. Generally one island was sampled at a time, but occasionally multiple small islands were sampled simultaneously. Repeat sampling across years on 10 islands determined that patterns of species detection were consistent across years, allowing islands sampled in different years to be pooled in a single analysis. Species accumulation curves (Appendix B) demonstrate sampling effort was sufficient to accurately determine presence of species on islands.

Acoustic sampling

We recorded echolocations of bats using broadband ultrasonic bat detectors (Anabat II; Titley Electronics) to determine presence of species (Hayes 1997, O'Farrell et al. 1999, Gehrt and Chelsvig 2004). Passive monitoring stations contained an Anabat II detector attached to a high-frequency microphone housed in a waterproof shroud with a 45° reflector (Messina 2004) mounted on a 1m tall pole. The detector was connected to an Anabat Compact Flash Zero-Crossings Interface Module (Titley Electonics) recording device.

The number of passive acoustic stations placed on an island increased with island size (range: 1-13 detectors per island). We placed detectors at randomly determined distances between 100 and 1,000 m from safe boat landings. Given a lack of adequate a priori information about accessible landings, safe landings were assessed on arrival. We randomly selected landings after circumnavigating an island to determine beach landings with terrain accessible on foot. When adverse field conditions prohibited random selection, landings were selected haphazardly according to accessibility and safe deployment. Number of landings ranged from 1-8 per island and eighteen islands (all less than 105 ha) were sampled with only one detector.

On 10 islands, active monitoring of bat activity was conducted at mist-net survey locations using a spotlight and Anapocket software (Corben 2004) on a handheld PDA, which displays bat calls as time versus frequency graphs in real time. Species identified with visual confirmation in the spotlight were used to build a reference call library of echolocation signatures of free-flying bats and verify presence of species detected with passive acoustic detectors.

Mist-net sampling

Mist-net surveys were conducted to verify identification of species detected with acoustic sampling, to build an echolocation call reference library from hand-release recordings, and to train observers to recognize flight patterns and body shapes in the spotlight for identifying free-flying bats with active monitoring. Hand-release recordings were conducted using Anapocket (Corben 2004) and a bright spotlight. Bats were released and recorded as long as they remained in constant view in the spotlight.

Mist-net sites on islands were selected in attempt to maximize captures and were typically placed in dry arroyos (flyways) and desert scrub habitats or over freshwater pools (*tinajas* or spring-boxes) when available. Typically, five different locations were sampled on each island, except in two cases where access was limited. We opened mist-nets at sunset and monitored them at least every 15 minutes for 4 hours. Captured bats were identified to species, age, sex, and reproductive status (Anthony 1988, Racey 1988).

Echolocation analysis for species identification

We developed a graphical and descriptive key of Anabat echolocation calls (Appendix A). Anabat uses a zero-crossings analysis (ZCA) (Parsons et al. 2000) which produces files displaying echolocation calls on time-frequency graphs. Sequences were identified to species if they had greater than two diagnostic pulses that met defined criteria based on reference calls (see Appendix A). Anabat files were randomly assigned by detector night to three observers trained to identify calls using the key. Sequences identified to species were proofed by the senior author.

Identifying echolocation calls can produce false negative and false positive errors. False negative errors (species is present and not detected) occur when a species is present and is recorded by the detector but the call is insufficiently diagnostic to be labeled as being produced by that species. False positive errors (species is absent and is falsely detected) occur when an echolocation call is misclassified as a species that was not present. Our approach to classifying echolocation calls was designed to minimize both false negative and false positive errors, but greater emphasis was placed on avoiding false positive errors. In general, the species in the assemblage were easily identifiable to the species level using the key.

Data Analysis

Species Incidence

Species incidence was estimated using logistic regression with binomial errors (Taylor 1991, Rita and Ranta 1993, Crawley 2005). Probability of occurrence (p) is the binomial response (0 = unoccupied, 1 = occupied) and the logit link transformation is fit to the response variable in the form:

$$\text{logit}(p) = \beta_0 + \beta_1(X_1) + \beta_2(X_2) + \ldots \beta_k(X_k)$$

where β's represent parameter coefficients on the logit scale associated with $X_1 \ldots X_k$ explanatory variables. Parameter coefficients were estimated using maximum likelihood methods (Hosmer and Lemeshow 1989).

Five models of incidence were fit for each species to investigate factors influencing species-specific occurrence patterns, including null, area-only, isolation-only, additive area and isolation, and interactive area and isolation (compensatory) models (Table 4.1).

Island characteristics were measured using a “heads-up” digitized GIS layer created in Arcview 3.2 from Landsat 7 satellite images (Table 4.2). We measured the shortest over-water path (km) to the Baja peninsula using Nearest Features and Path extension tools (Jenness 2004, 2005) in ArcView 3.2 as an index for isolation. This metric allowed for stepping-stone type movements by summing over-water legs if stepping-stone paths were the shortest route to the peninsula. This approach accounts for the presence of neighboring islands if they function as stepping stones, but emphasizes the likely role of the Baja peninsula as a predominant source pool.

Model Selection and Model Averaging

To compare our five a priori models on species incidence, we used Akaike Information Criteria (AIC) model selection criteria (Burnham and Anderson 2002). Models were ranked by $\mathrm{AIC_c}$ value (small sample-size correction form of AIC) and compared using $\Delta\mathrm{AIC_c}$ and $\mathrm{AIC_c}$ model weights. The $\Delta\mathrm{AIC_c}$ values represent the relative support between the best approximating model ($\mathrm{AIC_{min}}$) and each competing model (AIC_i). We considered models with $\Delta\mathrm{AIC_c} \leq 2$ to be strongly competing models (Burnham and Anderson 2002). $\mathrm{AIC_c}$ model weights were used to assess the relative support of individual models, using the formula:

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta\mathrm{AIC}_{\mathrm{c}_i}\right)}{\sum_{i=1}^{R}\exp\left(-\frac{1}{2}\Delta\mathrm{AIC}_{\mathrm{c}_i}\right)}$$

To account for model uncertainty, we used model averaging (Burnham and Anderson 2002) of parameter coefficient estimates to determine a final model of species incidence. Model-averaged parameter estimates were computed as:

$$\left(\hat{\bar{\beta}}_j\right) = \sum_{r=1}^{5} w_i\left(\hat{\beta}_j\right)$$

where w_i is the Akaike weight and $\left(\hat{\beta}_j\right)$ is the parameter coefficient estimate for explanatory variable *j* in model *i*. The unconditional sampling variance for the model-averaged parameter estimates was estimated as (Burnham and Anderson 2002):

$$\operatorname{var}\left(\hat{\bar{\beta}}\right)=\left[\sum_{i=1}^{5}\hat{w}_i\sqrt{\operatorname{var}\left(\hat{\beta}_j \middle| Model_i\right)+\left(\hat{\beta}_j-\hat{\bar{\beta}}_j\right)^2}\,\right]^2$$

When a given model did not include a given parameter, the coefficient value was assumed to be 0 (Burnham and Anderson 2002). All statistical analyses were conducted in Program R v.2.4.1.

RESULTS

Logistic regression models were fit for six species (Table 4.1) whose occurrences ranged from three to 25 islands in the archipelago. Estimation was not possible for *Myotis vivesi*, as this species occurred on all islands except one, nor for *Lasiurus xanthinus*, which occurred on only two islands (Figure 4.2).

Model Selection Results

Area, independently or in combination with isolation, was a variable in strongly competing models for each of five species of insectivorous bat (Table 4.1). However, for *Leptonycteris curasoae* the null model had the lowest AIC$_c$ value; the null model was not a strongly competing model for any other species. The sum of the AIC$_c$ weights for models which included area indicate strong support for the relative importance of area as an explanatory variable on incidence of five species (Table 4.3). The model selection results also suggest that isolation influences occurrences of some species.

The additive area and isolation model was the best-fit model for *Myotis californicus*, *Macrotus californicus, Antrozous pallidus,* and *Mormoops megalophylla* (Table 4.1). Probability of occurrence of *Myotis californicus* and *Macrotus californicus* was strongly influenced by area and isolation and the relationship between incidence and area may depend on the level of isolation as the compensatory model (interactive area and isolation) was the second best model ranked by AIC_c weights for these species (Table 4.1). For *A. pallidus* and *M. megalophylla*, the area-only model had competing support from the data (i.e., $\Delta AIC_c < 2.0$) (Table 4.1). These species occurred on only a few islands (*A. pallidus*: n = 5; *M. megalophylla*: n = 3) (Figure 4.2), affecting the precision of our estimates and limiting the strength of our inferences about patterns of occupancy of these species.

For *Pipistrellus hesperus*, all three models that included area (area-only, area*isolation, and area + isolation) were strongly competing models ($\Delta AIC_c < 2.0$) with w_i values similar for the three models (Table 4.1). Area appears to have the strongest influence on incidence of this species, but this may be dependent on the level of isolation (Figure 4.3).

No species had overwhelming support ($w_i > 0.90$) for a single approximating model on incidence of species. Therefore, we present model results using model-averaged parameter estimates, which account for the uncertainty in model selection (Table 4.4) (Burnham and Anderson 2002).

Model-Averaged Parameter Estimates

Model-averaged estimates for coefficients were positive for area for all species and were negative for isolation for all species except *A. pallidus* (Table 4.4). This suggests that probability of occurrence of most bat species tended to increase with island size (Figure 4.3) and decrease with island isolation (Figure 4.4). The positive effect of isolation on incidence for *A. pallidus* (Figure 4.4) may be due to a combination of a steep threshold of minimum area on occupancy for this species and statistical leverage caused by islands in the smallest size classes also being the least isolated. Confidence intervals on most model-averaged parameter estimates were wide due to small sample sizes and from using the unconditional sampling variance to account for model selection uncertainty (Burnham and Anderson 2002).

DISCUSSION

Our analysis extends Lomolino's (1986) hypotheses about insular distributions to another group of mammals and demonstrates that volant mammals display similar patterns of occupancy to non-volant mammals in real archipelagoes. Insular distributions of insectivorous bats in this archipelago (Table 4.5) appear to be characterized by minimum area thresholds with some evidence that isolation may also influence incidence (Figure 4.5). Patterns of island occupancy by insectivorous bats are consistent with the results from analyses of richness and composition of bat communities in the study region, which demonstrated that both area and isolation influence richness and composition, with area representing the strongest influence.

The influence of island size on the species we examined suggests extinction dynamics could be important in determining insular distributions of bats in this system. Most of these species display a minimum area threshold effect on occupancy (Figure 4.2), suggesting that below a certain size, species do not use islands or are unable to sustain populations due to lack of habitat or small population dynamics (Hanski 1991).

The observed thresholds for occupancy of roughly 100 ha is similar to patterns of occupancy by breeding landbirds in the same archipelago (Cody and Velarde 2002). Reduced plant and bird richness on islands below 200 ha in Baja California has been attributed to the lack of geologic structure permitting formation of canyons and arroyos that increase both topographical and habitat diversity (Cody et al. 2002, Cody and Velarde 2002).

Of the five insectivorous species that appear sensitive to area thresholds on occupancy (Figure 4.3), two species (*Macrotus californicus* and *Antrozous pallidus*) are medium- to large-bodied gleaners of large arthropods; two species (*Myotis californicus* and *Pipistrellus hesperus*) are small-bodied aerial insectivores, and one species (*Mormoops megalophylla*) is a large-bodied aerial insectivore. Although precision was poor for detecting significant parameter coefficients for *A. pallidus* and *M. megalophylla* due to small numbers of islands occupied (n = 5 and 3, respectively), distributions of these species appear to be limited by higher minimum area thresholds (ca. 1,000 ha) than those estimated for other species.

In addition to the influence of area on occupancy, isolation may also influence insular distributions for some species, but isolation appears to be less important than area in shaping incidence patterns (Table 4.3). Inference about the influence of isolation on insular incidence is hampered by wide confidence intervals of model-averaged estimates of the isolation coefficient. Equivocal results may be due to the range of values of isolation being fairly moderate in comparison to vagility of many bat species. A general trend toward negative influence of isolation on occupancy of bats for the moderate values of isolation that occur in this archipelago suggest some bats may be sensitive to modest distances between spatially separated habitat patches, especially if patch size is small (Figure 4.3).

For small islands (< 100 ha) the influence of isolation could be masked by very low levels of occupancy for most species (except *M. vivesi*, *L. curasoae*, and *P. hesperus*) due to the threshold response of area on incidence. Presence of species such as *P. hesperus* on islands smaller than 100 ha within 5 km of the Baja peninsula may represent occasional foraging activity from populations resident on the peninsula. Based on predictions from model-averaged estimates, compensatory effects are suggested by how the relationship between incidence and isolation changes at different levels of island size for several species (Figure 4.4). In particular, an interaction between area and isolation for *P. hesperus* is evident, as the relationship between incidence and isolation is negative for islands smaller than 100 ha, but no relationship exists between isolation and incidence for islands greater than 100 ha (Figure 4.4). This pattern supports the compensatory hypothesis that immigration rates can compensate for high extinction rates for close, small islands and that high persistence on large islands can compensate for low immigration rates at greater isolations (Lomolino 1986).

Isolation appears to approach a threshold-type effect at distances of 10-15 km from the Baja peninsula for two species, *Myotis californicus* and *Macrotus californicus* (Figure 4.4). For *M. megalophylla*, a strong threshold appears at 5 km, but data for this species are based on only 3 island occurrences and are suggestive at best. *A. pallidus* has an anomalous pattern of a positive relationship between isolation and probability of occupancy due to low occurrences and statistical leverage.

Use of islands smaller than 100 ha was largely limited to two non-insectivorous species: *Myotis vivesi*, a fish-eating bat, and *L. curasoae*, a nectar-feeding species. A regional endemic, *M. vivesi* forages over the ocean for small bait fish (Blood and Clark 1998). Small rocky islands provide habitat for roosting in close proximity to foraging areas (Blood and Clark 1998), explaining the prevalence of this species across the range of island size and isolation values in the archipelago.

L. curasoae is highly vagile and capable of commuting long distances in a night (Sahley et al. 1993, Horner et al. 1998a). The isolation distances in this archipelago do not appear to pose a significant immigration filter for this species. In addition, lack of a relationship between area and use of islands for *L. curasoae* demonstrates that this species is capable of using small islands as foraging patches. Almost all small islands in Baja have at least a few cardon cacti (*P. pringleii*), a major source of food for this nectarivorous bat. The stationary and temporally predictable nature of a floral food source may permit greater use of small, spatially isolated resource patches.

Habitat quality or complexity can have a positive influence on incidence for some species (Adler and Wilson 1985, Thomas et al. 2001). To better understand the fundamental relationships between occurrences of bats and resource availability, future studies should focus on specific habitat relationships among species and how habitat differences on islands influence patterns of use and occupancy. Due to small sample sizes, we were unable to assess whether habitat differences associated with the northern and southern subarchipelagos (see Chapter 2) influenced patterns of occupancy by bats. Insular distributions are generally assumed to be determined by immigration and extinction dynamics at both the community and population level in ecological time scales, but other mechanisms may also play important roles in shaping incidence of species, including inter-specific competition and functional relationships relating to prey or food availability.

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Table 4.1. Model selection results for five a priori models on incidence for six species of bat. Models are ranked by ΔAIC_c. K = number of model parameters.

Species	**Model**	Δ_i	w_i	**K**
Leptonycteris curasoae	null	0.000	0.368	1
	isolation	0.585	0.275	2
	area + isolation	1.809	0.149	3
	area	1.813	0.149	2
	area*isolation	3.672	0.059	4
Pipistrellus hesperus	area	0.000	0.340	2
	area*isolation	0.027	0.335	4
	area + isolation	0.164	0.313	3
	null	7.363	0.009	1
	isolation	9.467	0.003	2
Myotis californicus	area + isolation	0.000	0.685	3
	area*isolation	2.093	0.241	4
	area	4.583	0.069	2
	null	11.231	0.002	1
	isolation	11.236	0.002	2
Macrotus californicus	area + isolation	0.000	0.724	3
	area*isolation	2.437	0.214	4
	area	4.931	0.062	2
	null	17.028	0.000	1
	isolation	17.810	0.000	2
Antrozous pallidus	area + isolation	0.000	0.507	3
	area	0.802	0.339	2
	area*isolation	2.406	0.152	4
	isolation	13.297	0.001	2
	null	13.759	0.001	1
Mormoops megalophylla	area + isolation	0.000	0.583	3
	area	1.820	0.235	2
	area*isolation	2.601	0.159	4
	null	7.422	0.014	1
	isolation	8.399	0.009	2

Table 4.2. Island characteristics of 32 islands in the Gulf of California, Mexico used for analyzing patterns of species incidence.

Island	**Area (ha)**	**Isolation (km)**
Blanco	1.3	0.84
Bota	9.6	2.64
Cabezo Caballo	71.0	1.89
Carmen	14,801.4	5.50
Cayo	6.7	6.22
Coronados	715.8	2.60
Coronados Smith	852.1	2.22
Danzante	423.7	2.67
Espiritu Santo/Partida Sur	10,367.1	6.21
Galeras East	5.4	16.40
Galeras West	3.2	16.77
Gallina	2.0	7.18
Gemelitos East	3.9	0.82
Gemelitos West	2.4	0.86
Islitas	3.3	0.41
Las Animas Sur	9.1	16.49
Monserrat	1,902.8	13.66
Pardo	4.3	0.36
Partida Norte	94.0	17.84
Pata	14.5	2.57
Piojo	67.6	4.57
Rasa	59.2	20.75
Salsipuedes	102.6	17.70
San Diego	62.9	19.06
San Francisco	419.0	7.16
San Ildefonso	104.2	10.01
San José	18,494.5	4.75
San Lorenzo	3,632.3	16.31
Santa Catalina	3,995.6	25.06
Santa Cruz	1,315.1	19.81
Tijeras	4.0	1.90
Ventana	128.2	3.09

Table 4.3. Relative variable importance for estimated parameter coefficients (area and isolation) based on the sum of w_i values of models that contain a given parameter.

Species	**Area**	**Isolation**
Leptonycteris curasaoe	0.357	0.483
Pipistrellus hesperus	0.988	0.652
Myotis californicus	0.995	0.928
Macrotus californicus	0.999	0.938
Antrozous pallidus	0.999	0.660
Mormoops megalophylla	0.977	0.751

Table 4.4. Model-averaged parameter estimates and associated 95% confidence intervals in parentheses for the effects of area, isolation, and an interaction term on incidence of bat species on islands in Baja California, Mexico. Parameter estimates are reported in logits.

Species	**β_0(Intercept)**	**β_1(logArea)**	**β_2(Isolation)**	**β_3(logArea*Isolation)**
Leptonycteris curasoae	1.39 (-0.13, 2.91)	0.16 (-0.43, 0.75)	-0.04 (-0.15, 0.08)	0.00 (-0.02, 0.01)
Pipistrellus hesperus	-1.16 (-3.29, 0.98)	0.95 (-0.24, 2.14)	-0.14 (-0.49, 0.20)	0.04 (-0.11, 0.20)
Myotis californicus	-2.77 (-5.28, -0.26)	1.63 (0.32, 2.94)	-0.15 (-0.43, 0.13)	-0.01 (-0.08, 0.05)
Macrotus californicus	-5.28 (-10.34, -0.23)	2.62 (0.33, 4.92)	-0.32 (-0.93, 0.29)	0.02 (-0.12, 0.12)
Antrozous pallidus	-13.90 (-33.41, 5.61)	3.41 (-1.09, 7.92)	0.23 (-0.50, 0.96)	-0.02 (-0.15, 0.11)
Mormoops megalophylla	-7.87 (-21.16, 5.42)	2.98 (-2.46, 8.43)	-0.59 (-3.79, 2.62)	-0.03 (-0.54, 0.47)

Table 4.5. Traits of bat species, including foraging and roosting guild classifications. Foraging guild classifications follow Schnitzler and Kalko (2001).

Species	No. Islands Occupied	Foraging Guild	Roosting Guild
Myotis vivesi	31	piscivore	crevice
Leptonycteris curasoae	25	nectarivore	cave obligate
Pipistrellus hesperus	17	edge & gap insectivore	crevice
Myotis californicus	10	edge & gap insectivore	crevice
Macrotus californicus	8	narrow-space insectivore	cave obligate
Antrozous pallidus	5	narrow-space insectivore	cave & crevice
Mormoops megalophylla	3	edge & gap insectivore	cave obligate
Lasiurus xanthinus	2	edge & gap insectivore	foliage

Figure 4.1. Hypothetical distributions of species corresponding to five biological hypotheses about patterns of species incidence (after Lomolino 1986). Filled circles represent islands occupied by a species and open circles represent unoccupied islands. Values of area and isolation are from our data, but occupancy is hypothetical. (a) Random distribution pattern where the probability of occurrence is not affected by area or isolation; (b) Minimum area pattern where occurrence is only on islands greater than a minimum size threshold; (c) Maximum isolation pattern where occurrence is only on islands within some distance threshold; (d) Non-compensatory (or additive) patterns where incidence is affected by both area and isolation by only occurring on big, close islands; (e) Compensatory (or interactive) patterns where the relationship between probability of occurrence and area depends on the isolation value and the relationship between probability of occurrence and isolation depends on the size of an island.

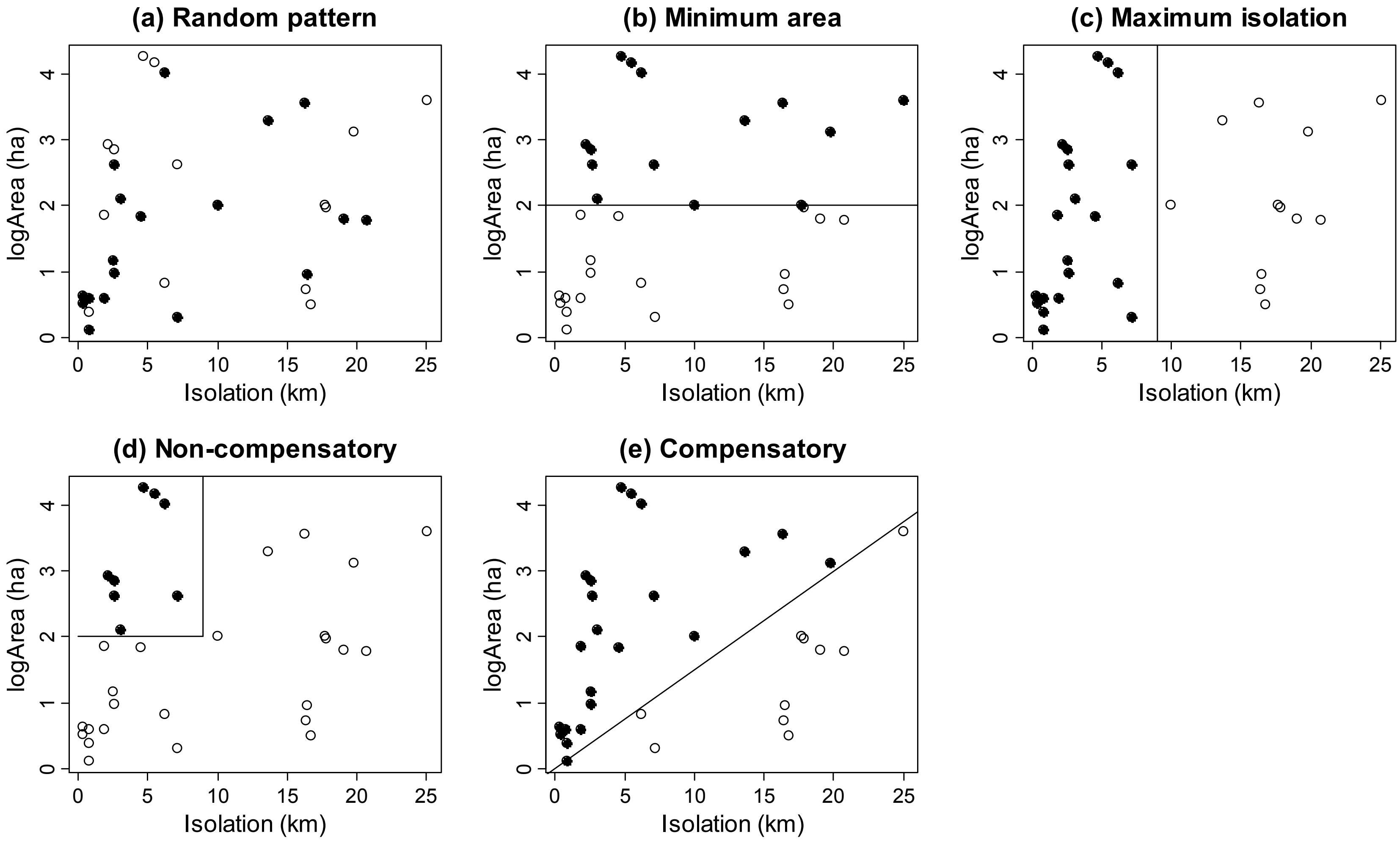
(a) Random pattern
(b) Minimum area
(c) Maximum isolation
(d) Non-compensatory
(e) Compensatory
logArea (ha)
Isolation (km)
0
1
2
3
4
0
5
10
15
20
25

Figure 4.1.

Figure 4.2. Insular distributions of eight species of bat on 32 islands in the Gulf of California, Baja California, Mexico. Filled circles represent occupied islands, open circles represent unoccupied islands. Lines represent the predicted threshold above which probability of occurrence is > 50% based on model-averaged parameter coefficients from logistic regression models. (a) *Myotis vivesi*, a fish-eating species, shows no relationship between occurrence and area and isolation as it occurs on 31 islands; (b) *Leptonycteris curasoae*; a nectar-feeding species, occurs on 25 islands and has a random pattern of distribution with no relationship to size and isolation; (c) *Pipistrellus hesperus*, a small-bodied insectivore, displays a compensatory pattern of distribution with the relationship between probability of occurrence and isolation dependent on island size; (d) *Myotis californicus*, a small-bodied insectivore, displays a pattern intermediate between an additive and compensatory pattern demonstrating that both area and isolation are associated with the probability of occurrence; (e) *Macrotus californicus*, a medium-bodied insectivore, displays a pattern very similar to *My. californicus*, intermediate between non-compensatory and compensatory patterns; (f) *Antrozous pallidus*, a large-bodied insectivore, shows a minimum area effect on probability of occurrence; (g) *Mormoops megalophylla*, a large-bodied insectivore, was only detected on three islands that were large and close to the peninsula; (h) *Lasiurus xanthinus*, a medium-bodied insectivore, was only detected on two islands. Logistic regression models were not fit for either *M. vivesi* or *L. xanthinus*.

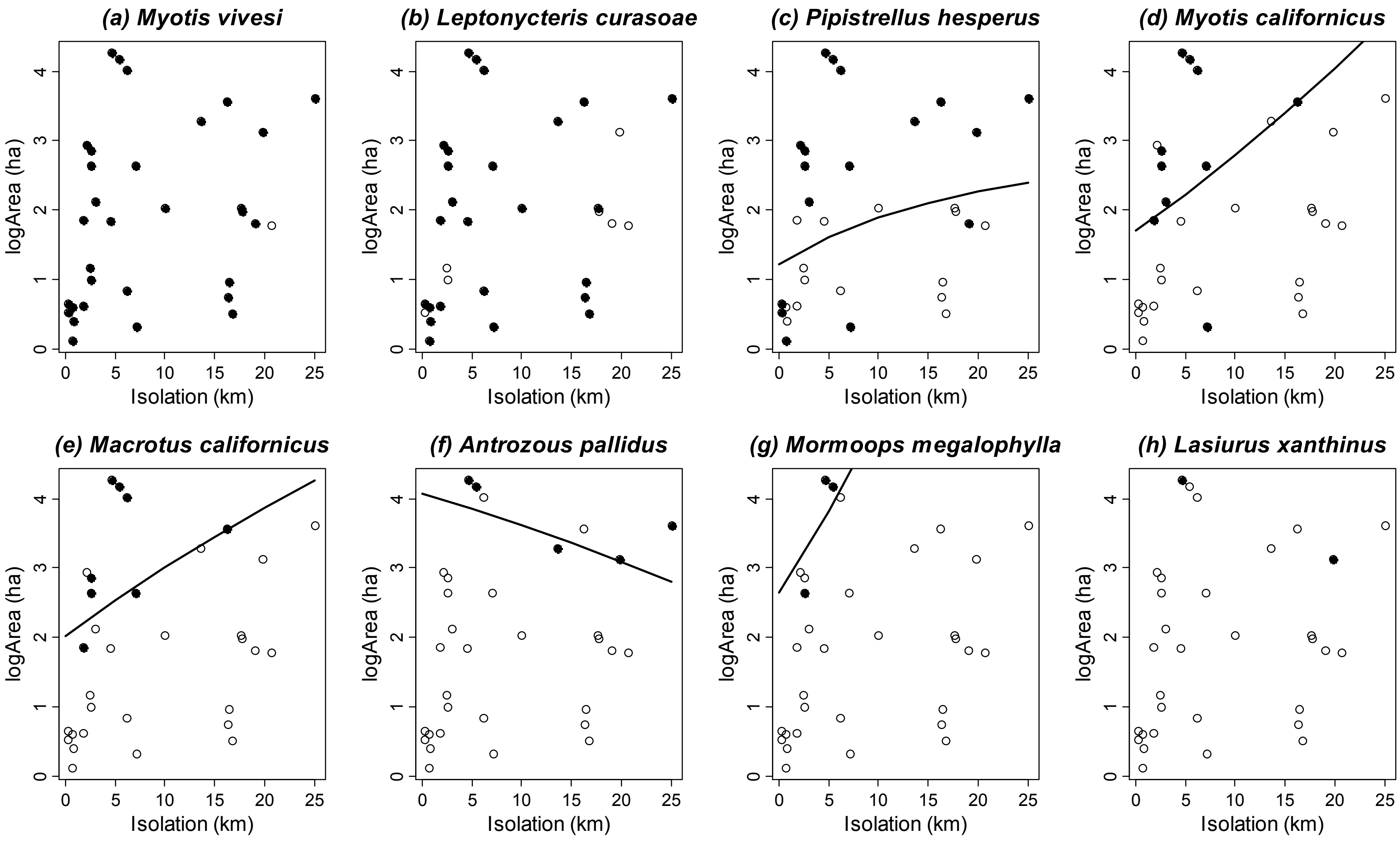
(a) Myotis vivesi
(b) Leptonycteris curasoae
(c) Pipistrellus hesperus
(d) Myotis californicus
(e) Macrotus californicus
(f) Antrozous pallidus
(g) Mormoops megalophylla
(h) Lasiurus xanthinus
logArea (ha)
Isolation (km)
0
1
2
3
4
0
5
10
15
20
25

Figure 4.2.

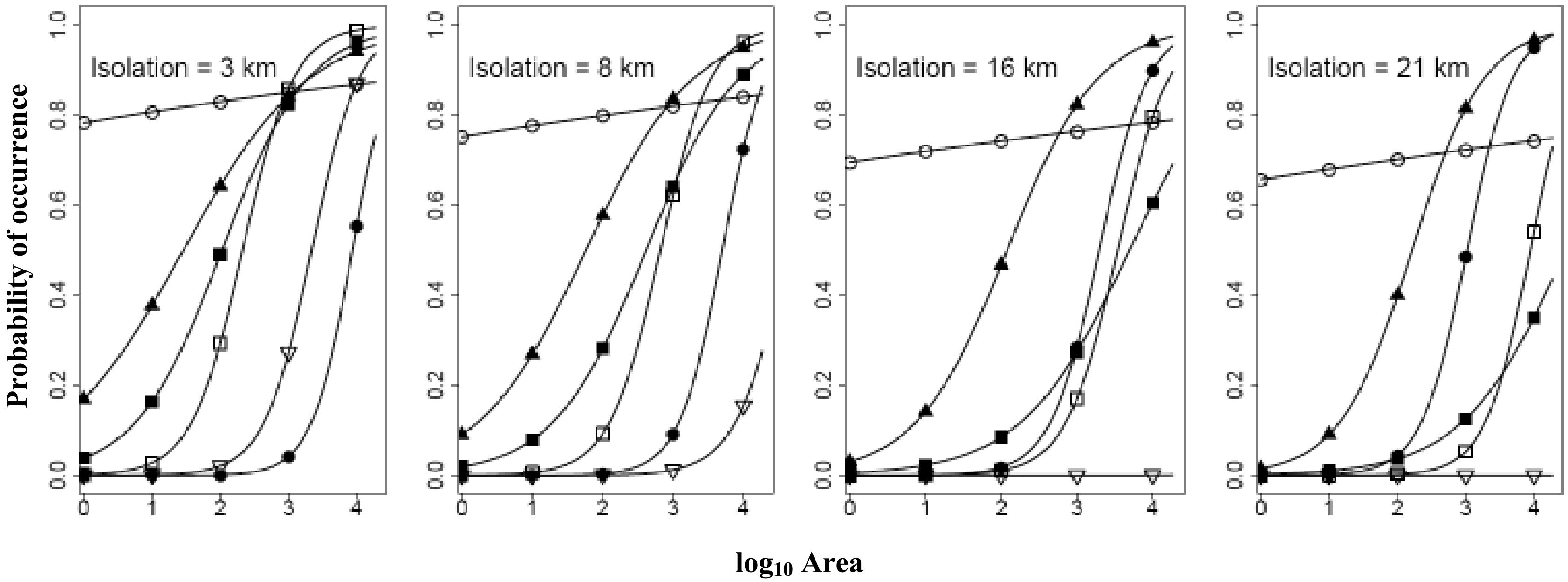

Figure 4.3. Incidence functions based on model-averaged parameter estimates showing the relationship between probability of occurrence on islands and island size at four values of isolation for six species: ─○─ = *L. curasoae*; ─▲─ = *P. hesperus*; ─■─ = *My. californicus*; ─□─ = *Ma. californicus*; ─●─ = *A. pallidus*; and ─▽─ = *M. mormoops*. Points along lines are used to distinguish species and do not represent observed data values.

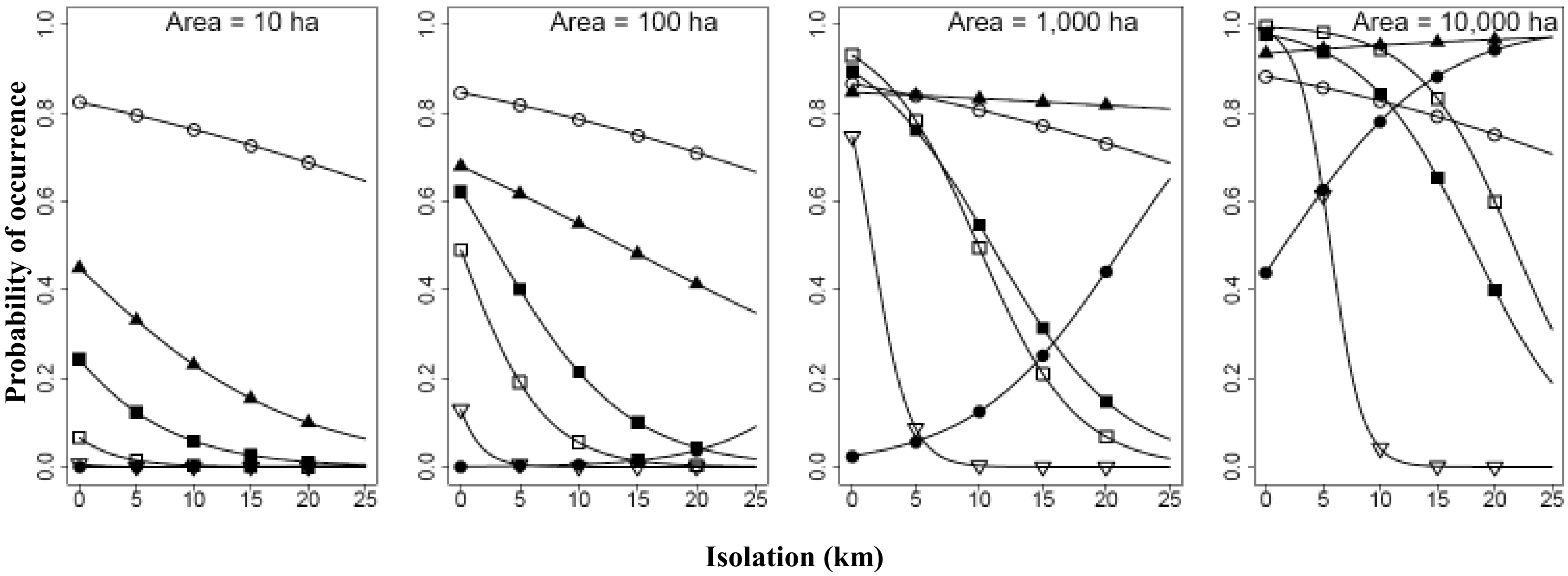

Figure 4.4. Incidence functions based on model-averaged parameter estimates showing the relationship between probability of occurrence and island isolation at four values of area for six species: —○— = *L. curasoae*; —▲— = *P. hesperus*; —■— = *My. californicus*; —□— = *Ma. californicus*; —●— = *A. pallidus*; and —▽— = *M. mormoops*. Points along lines are used to distinguish species and do not represent observed data values.

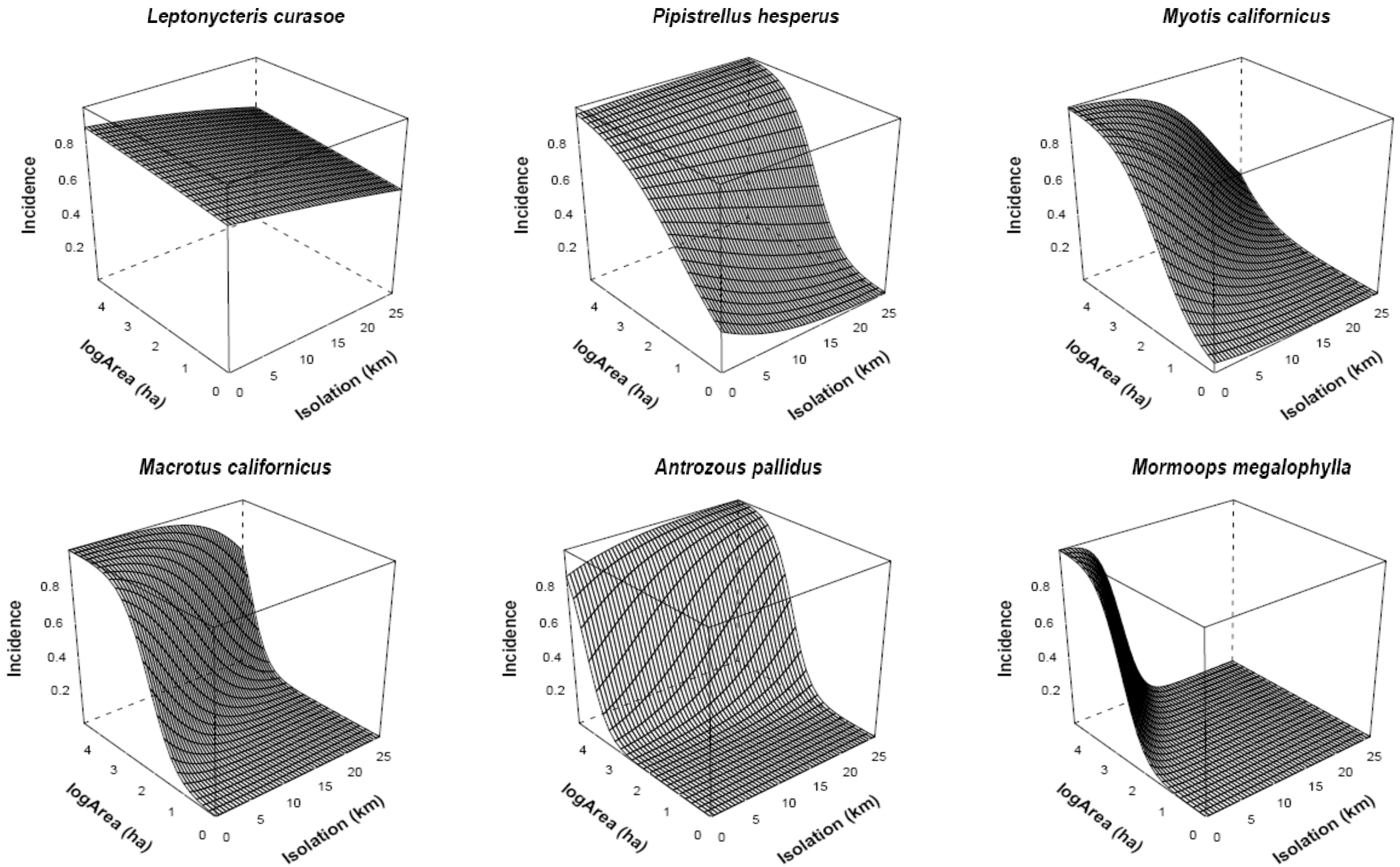

Figure 4.5. Incidence graphs for each species showing the relationship between probability of occurrence and area and isolation of islands. Model predictions are based on model-averaged parameter estimates.

CHAPTER 5: CONCLUSIONS

In this dissertation, I investigated the influence of area and isolation of islands on community structure and insular distributions of desert bats in Baja California, Mexico. My research represents one of the more extensive studies of island biogeography of bats and contributes to our knowledge of bat ecology by demonstrating that area and isolation influence composition and richness of bat communities. In addition, area and isolation appear to influence the probability of occurrence on islands for insectivorous species.

Area had a strong influence on richness, nestedness, and incidence of bat species, indicating that desert bats likely have a minimum area needed for populations to persist. In the second chapter, I showed that habitat differences between two subarchipelagos also influenced the number of species occurring on islands, demonstrating that both area *per se* and differences in habitat diversity may contribute to species-area relationships for bats. The influence of area on nested subset structure of composition of bat communities suggests there is a gradient in extinction vulnerabilities among species. In particular, insectivorous bats appear more sensitive to minimum area thresholds on persistence of populations than either a wide-ranging nectarivorous bat (*Leptonycteris curasoae*) or an endemic fish-eating bat (*Myotis vivesi*).

Despite their vagility, bats appear sensitive to modest distances of isolation in insular landscapes as evidenced by the negative influence of isolation from the Baja peninsula on species richness, community nestedness, and incidence of some species. Potential mechanisms for this species-isolation relationship include processes of selection of foraging habitat by individuals and declining immigration rates of species as isolation from a source population increases. My research revealed this surprising pattern of negative influences of isolation on community structure and occurrence of a vagile group of mammals, but more research is needed on the dispersal and movements of individuals to fully understand why fewer bats occur on isolated islands.

Although I am cautious about making direct inferences for conservation based on our research, my results raise interesting questions about the potential connectivity and persistence of populations in isolated habitats, especially if patch size is small. Nestedness analyses should only be used as initial steps in robust conservation strategies, as patterns of nestedness may be detected for bat assemblages even when clear mechanisms relating to selective immigration and extinction probabilities are lacking. Overall, my research demonstrates that bats may be more sensitive to area and isolation than previously expected based on their vagility and therefore may be more sensitive to fragmentation. My research provides a valuable baseline for understanding factors important in shaping communities of bats that will hopefully aid in future efforts and studies of bat conservation.

At the start of my research, very little was known about the distribution of bats on islands in Baja. Northwest Mexico is considered a conservation priority area (Arita and Ortega 1998), but a recent volume on conservation of biodiversity of the region (Cartron et al. 2005) only briefly mentions one species of bat (the endemic fishing bat). The archipelago in the Gulf of California has served as a natural laboratory for a plethora of studies on a variety of taxa, including most land vertebrates (Case 2002, Cody and Velarde 2002, Lawlor et al. 2002), several arthropods (Boulton and Ward 2002, Piñero and Aalbu 2002), and plants (Cody et al. 2002). In contrast, only accidental and casual records of bats existed on these otherwise well-studied islands (Lawlor et al. 2002). In addition to the ecological questions explored in this dissertation, my research added 138 new distributional records on 33 islands for 12 species (Appendix C), providing valuable information for potential meta-analyses and for future conservation efforts in this ecologically diverse and fragile system.

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APPENDICES

APPENDIX A: ANABAT ECHOLOCATION CALL IDENTIFICATION KEY

Introduction:

Characteristics of echolocation calls are based on recordings from active monitoring of free-flying bats and recordings of hand-released individuals made with a hand-held PDA running Anapocket (Corben 2004) in Baja California, Mexico as well as call sequences available on the University of New Mexico bat database (http://www.msb.unm.edu/mammals/batcall/html/calllibrary.html) and calls recorded from hand-released individuals by Chris Corben or Paul Heady in the western U.S. All files were analyzed in AnalookW v.3.2 (www.hoarybat.com). The species call characterization discussions and figures are based on plotting call traces as $\log_{10}$ frequency versus time and call slopes as $\log_{10}$ rate of change (in octaves/second) versus time. Figures of species call sequences are compressed by removing time intervals between calls.

Call parameters such as characteristic frequency (flattest part of the call), minimum and maximum frequency, characteristic slope (slope of the flattest part of the call), call duration, interpulse interval, and shape of the body of the call were measured from known reference calls and used to characterize call sequences of species (O’Farrell et al. 1999, Gannon et al. 2004).

General Approach: Call sequences were placed into 5 categories.

Species ID category. Only sequences that met diagnostic standards with measurable parameters were identified to species (see Species ID key below). Sequences consisted of 2 or more calls that met criteria for species identification. A conservative approach aimed at limiting false identification was used such that criteria are defined to ensure positive identification of species. Call descriptions for species provided in this key do not necessarily represent their entire echolocation repertoires.

Phonic group category. Call sequences with considerable overlap in parameter values among species and little basis for identifying to species were grouped into defined phonic groups. Phonic groups were based on measurable call parameters.

Frag--frequency category (fragmentary calls). Sequences with at least 2 distinct calls, but no diagnostic calls because of poor quality were classified as Frag-frequency. There were 2 pre-defined Frag-frequency categories (Frag45, Frag<20), but observers could create additional categories, using minimum frequencies, if needed. Poor call quality is recognized as sufficient noise (scattered dots) to obscure determination of call characteristics.

Q-frequency category (unknown calls). Q-frequency labels were based on minimum frequencies and used to label unusual sequences that did not fit in defined categories.

Other. File sequences generated by wind, insects, birds or mice were not labeled.

Definitions:

Call: Single echolocation pulse separated from other pulses by silence.

CF: Constant frequency. Calls described as CF use a constant frequency for the duration of the call (or a portion of it) and appear as flat or nearly flat.

Distinct call: A distinct call is defined as a line or curve that is made of more than 6 smoothly connected dots and is separated by regularly spaced intervals (silence). A call can be *distinct* without being *diagnostic*, but it cannot be *diagnostic* without being *distinct*.

Diagnostic call: A diagnostic call has characteristics that correspond to those in the sample files or key description. Call characteristics include, shape, minimum frequency, maximum frequency, characteristic frequency, frequency of the knee (the start of the body of the call), pulse duration, and slope.

File Sequence: A related string of calls recorded in a single Anabat file. File sequences received labels based on identification of the calls contained in the sequence. If calls generated by multiple species were identified within a file sequence, multiple labels were applied to that file sequence.

FM: Frequency modulated. FM calls are those that modulate frequency over time, appearing as steep or vertical sweeps.

Species Identification and Label Criteria:

Species Labels:

ANPA: *Antrozous pallidus* sequences are identifiable to species if 2 or more consecutive calls display short-duration, steep FM sweeps with minimum frequencies between 30-35 kHz. Slopes are straight or slightly modulated and between 120- 80 octaves/second. ANPA social calls are typically steep, often irregular FM sweeps starting between 25-30 kHz and ending at 10-12 kHz or below (see Figure A.1). Social calls are usually in groups of several pulses at very short interpulse intervals. Description and reference files are based on hand-release and active monitoring recordings made by W. Frick in Baja California Sur, Mexico.

EPFU: *Eptesicus fuscus* sequences are identifiable to species if 2 or more consecutive calls display minimum frequencies near 30 kHz and are steep to shallow FM sweeps of long duration (6-11 ms). A slope change plot is mostly linear with some variation, descending from 200 to 20 octaves/second. The body of the call is more curved than the steep FM sweep of an ANPA call. EPFU calls can have minimum frequencies near 25 kHz but can be distinguished from TABR by differences in shape of call body and characteristic frequencies above 25 kHz. Description and reference files are based on active monitoring recordings made by W. Frick in Baja California Sur, Mexico.

EUSP: *Eumops spp.* sequences are identifiable to species if 2 or more consecutive calls are very shallow FM sweep to CF calls at very low frequencies: maximum frequencies near 13-14 kHz and minimum frequencies near 9-10 kHz. These calls may be either

Eumops perotis (see Figure A.3) or possibly *Eumops underwoodi* (not shown). Call description based on Adams (2003) and reference file provided by the UNM database (http://www.msb.unm.edu /mammals/batcall/).

LABL: *Lasiurus blossevilli* sequences are identifiable to species when 2 or more consecutive calls in a sequence have undulating minimum frequencies between 50 and 40 kHz and calls display moderately sloping, FM sweeps that end with a CF component, producing a "scooped" shape. LABL calls are typically distinguished from PIHE by longer pulse durations (longer than 8 ms) and minimum frequencies varying substantially from pulse to pulse. PIHE sequences usually maintain fairly consistent minimum frequencies near 45 kHz. Description and reference files are based on hand-release recordings by Paul Heady in California, USA.

LACI: *Lasiurus cinereus* sequences are identifiable to species when 2 or more consecutive calls display shallow FM sweeps ending in a CF component, creating a lazy backwards J "scoop". Calls are long duration (8 ms) and minimum frequencies undulate near 20 kHz. The "undulating" minimum frequency and the J-shape distinguish LACI calls from NYFE. Some open-air LACI calls can be a flat CF call near 18-16 kHz, but due to confirmation of NYFE being abundantly common in the area (from visual confirmation and netting) and no capture records or visual confirmation records of LACI, only if a call seems distinctly Lasiurine by the "undulating" minimum frequency and J-shape will it be identified as LACI. We recognize that some LACI calls may not be positively identified, because of the prevalence of and similarity to NYFE calls.

Description and reference files are based on hand-release recordings by Paul Heady in California, USA.

LAXA: *Lasiurus xanthinus* sequences are identifiable to species when 2 or more consecutive calls display typical Lasiurine undulating minimum frequency (see LACI or LABL) near 30 kHz and FM sweeps that end in a CF component and an upward frequency sweep at the end of the call (creating an upward hook shape). A slope change plot is mostly linear, descending from 300 to 10 or -20 octaves/second. Description and reference files are based on hand-release recordings taken in the Southwestern USA by Chris Corben.

LECU: *Leptonycteris curasoae* sequences are identified to species if 2 or more consecutive calls display a short CF component at the maximum frequency (near 70 kHz, but variable) followed by a steep FM sweep that flattens slightly in the middle of the call and is followed by another steep FM sweep to a minimum frequency near 45-30 kHz, creating a “hooked top” and “elbowed” FM sweep shape (see Figure A.7). Minimum frequencies are variable and range from 30-45 kHz. The pulse slope change plot is sinusoidal, with increasing slope (sometimes dramatically, starting from close to 0) cresting between 150-300 octaves/second (commonly above 200 octaves/second) and then descending toward 100 octaves/second and ascending again at the end. Not all LECU calls have the “hooked top” shape described above, but are identifiable as an FM sweep that flattens slightly in the middle to lower third of the call followed by another steep FM sweep at the end. In contrast, ANPA calls are steeper FM sweeps with sometimes flattened portions at the very end (reverse J). Description and reference files are based on hand-release and active monitoring recordings made by W. Frick in Baja California Sur, Mexico.

MACA: *Macrotus californicus* sequences are identifiable to species when 2 or more consecutive calls display short duration (2 ms), steep FM sweeps that are shaped like a forward slash (e.g. \ ) with little or no curvature in the body of the call. Minimum frequency is near 50kHz (may terminate as low as 48kHz). To be identified to species, slopes of calls should be split between being negative (less than -1 octaves/second) and being positive (greater than 150 octaves/second). Some calls have an additional harmonic visible, around 40-35 kHz, with a gap between the main sequence and the harmonic. MACA calls are distinguished from MYCA calls by lack of any curvature during the steep FM sweep (MACA calls are more vertical) and by lack of a flattening/curving at the terminus. Reference files are based on hand-release recordings and active monitoring in Baja California Sur, Mexico by W. Frick.

MOME: *Mormoops megalophylla* sequences are identified to species if 2 or more consecutive calls display a long-duration, CF component at 55-50 kHz followed by a gradual FM sweep to 50-45 kHz. No other species in the region produces a CF to FM call structure similar to MOME. Description and reference files are based on active monitoring recordings made by W. Frick in Baja California Sur, Mexico.

MYCA: *Myotis californicus* sequences are identifiable to species if 2 or more consecutive calls that are high FM calls that sweep steeply to minimum frequencies of 50 to 43 kHz. The steep FM sweep often has a slight rightward curve, sometimes with small J-hook at the end. Slopes are generally greater than 150 octaves/second. MYCA calls are typically longer duration than MACA (approx. 4ms) and generally have a higher maximum frequency (100-70 kHz), but can be confused with many MACA calls. MYCA calls typically have slightly more curvature to the FM sweep than the straight "forward slash" shape of MACA calls. Description and reference files are based on hand-release and active monitoring recordings made by W. Frick in Baja California Sur, Mexico.

MYEV: *Myotis evotis* sequences are identifiable to species if 2 or more consecutive calls display short-duration (ca. 4 ms), steep FM sweeps with maximum frequencies between 100-60 kHz and minimum frequencies near 35-30 kHz. Slopes are very high (greater than 200 octaves/second and can be greater than 300 octaves/second). MYEV calls are distinguishable from ANPA calls by the steepness of the FM sweep and uniformly high slope. Description and reference files are based on hand-release recordings made by Paul Heady in California, USA.

MYVI: *Myotis vivesi* sequences are identifiable to species if 2 or more consecutive calls display short-duration (ca. 5 ms), steep FM sweeps that terminate at a minimum frequency near 18-20 kHz. Slopes are steep, typically greater than 100 octaves/second.

Description and reference files are based on hand-release and active monitoring recordings made by W. Frick in Baja California Sur, Mexico.

MYVO: *Myotis volans* sequences are identifiable to species if 2 or more consecutive calls display FM sweeps from maximum frequencies near 70 kHz and terminating at minimum frequencies near 40 kHz. Slopes are typically greater than 80 octaves/second, descending from 300 octaves/second. Several other Myotis species (including, *M. ciliolabrum*, *M. lucifugus*, and *M. velifer*) produce similar “40 kHz” calls, but none of these other species are known to occur on the Baja peninsula (Medellín et al. 1997), whereas distributional range maps for *Myotis volans* extend the length of the Baja peninsula and mist-net surveys in coastal peninsular habitats confirmed presence of *M. volans* in the study region. Description and reference files are based on hand-release recordings by Paul Heady in California, USA.

NYFE: *Nyctinomops femorosaccus* sequences are identifiable to species if 2 or more consecutive calls are shallow FM to CF calls, starting at maximum frequencies near 23 kHz and terminating at minimum frequencies between 18 and 16 kHz. NYFE will occasionally do a “signature” pulse that has a slightly higher minimum frequency than the main trend of the sequence. NYFE also produces flat CF calls near 15-16 kHz. Some NYFE calls can be confused with LACI calls (see LACI description for details) and TABR calls. For species identification purposes, NYFE can be separated from TABR by having a consistently lower minimum frequency (below 20 kHz) (see MOL phonic group and TABR descriptions for more details). Description and reference files are based on hand-release and active monitoring recordings made by W. Frick in Baja California Sur, Mexico.

NYMA: *Nyctinomops macrotis* sequences are identifiable to species if 2 or more consecutive calls display shallow FM to CF sweeps with maximum frequencies at 18-16 kHz and terminating at minimum frequencies near 14-12 kHz. Call description based on Adams (2003) and reference file provided by the UNM database (http://www.msb.unm.edu /mammals/batcall/).

PIHE: *Pipistrellus hesperus* sequences are identifiable to species if 2 or more consecutive calls that have a short FM sweep followed by CF component at 45 kHz, creating a “backwards comma” shape. Pulse duration is usually short (ca. 4 ms) and calls are easily distinguishable by their regularity of shape and minimum frequency. Description and reference files are based on hand-release and active monitoring recordings made by W. Frick in Baja California Sur, Mexico.

TABR: *Tadarida brasiliensis* sequences are identifiable to species if 2 or more consecutive calls display steep to shallow FM sweeps with CF components that terminate at minimum frequencies near 25 kHz. TABR can produce CF calls at 25 kHz. For species identification, TABR and NYFE calls are distinguishable by minimum frequency, such that calls identified as TABR have minimum frequencies near 25 kHz and calls identified as NYFE have minimum frequencies near 18-16 kHz. There is morphological overlap between TABR and NYFE calls that display minimum frequencies in the 23-19 kHz range; these sequences are labeled with a MOL phonic group classification. Call description based on Adams (2003) and reference file provided by the UNM database (http://www.msb.unm.edu /mammals/batcall/).

MYYU: *Myotis yumanensis* sequences are identifiable to species if 2 or more consecutive pulses display high frequency FM sweeps that terminate at minimum frequencies near 50 kHz. Calls are not as steep MYCA calls and may have a flattening in the middle of the call creating reverse sigmoid shape. Slopes descend from 300 octaves/second to as low as 60 or 40 octaves/second. Description and reference files are based on hand-release recordings by Paul Heady in California, USA.

Phonic Groups:

MOL: The Molossid phonic group consists of any call that has at least 2 distinct calls that are shallow, sloped FM sweeps with minimum frequencies below 25 kHz.

G30: Short-duration, steep FM calls that terminate <35 and >25.

G40: Short-duration, steep FM calls that terminate <45 and >35

G50: Short-duration, steep FM calls that terminate <55 and >45

G60: FM calls that terminate <65 and >55

Frag-Freq:

Frag45: Sequences with at least 2 distinct calls near 45 kHz, but call quality is too poor (due to noise or echoes obscuring the pulses) to determine species identification.

Frag<20: Sequences with at least 2 distinct calls, but call quality is too poor to determine species identification.

Other:

Rodent: Ultrasonic communications in rodents (likely *Peromyscus spp.*) appear as long-duration pulses that appear like wavy lines near 20 kHz.

Bird: Bird calls are long-duration calls that look like highly patterned "songs" that occur below 15 kHz and can usually be identified by looking at the time stamp of the call (usually appear after 6:30 am).

Insects: Insects produce fuzzy "noise" filled screens that usually fill up the entire 15s recording window.

Sample Files of Species:

A sample reference file from each species described in the key is provided. Observers were provided a booklet with multiple samples of each species.

LITERATURE CITED

Corben, C. 2004. Anapocket -- Anabat on a PDA, v.2.34. Available at: http://www.hoarybat.com.

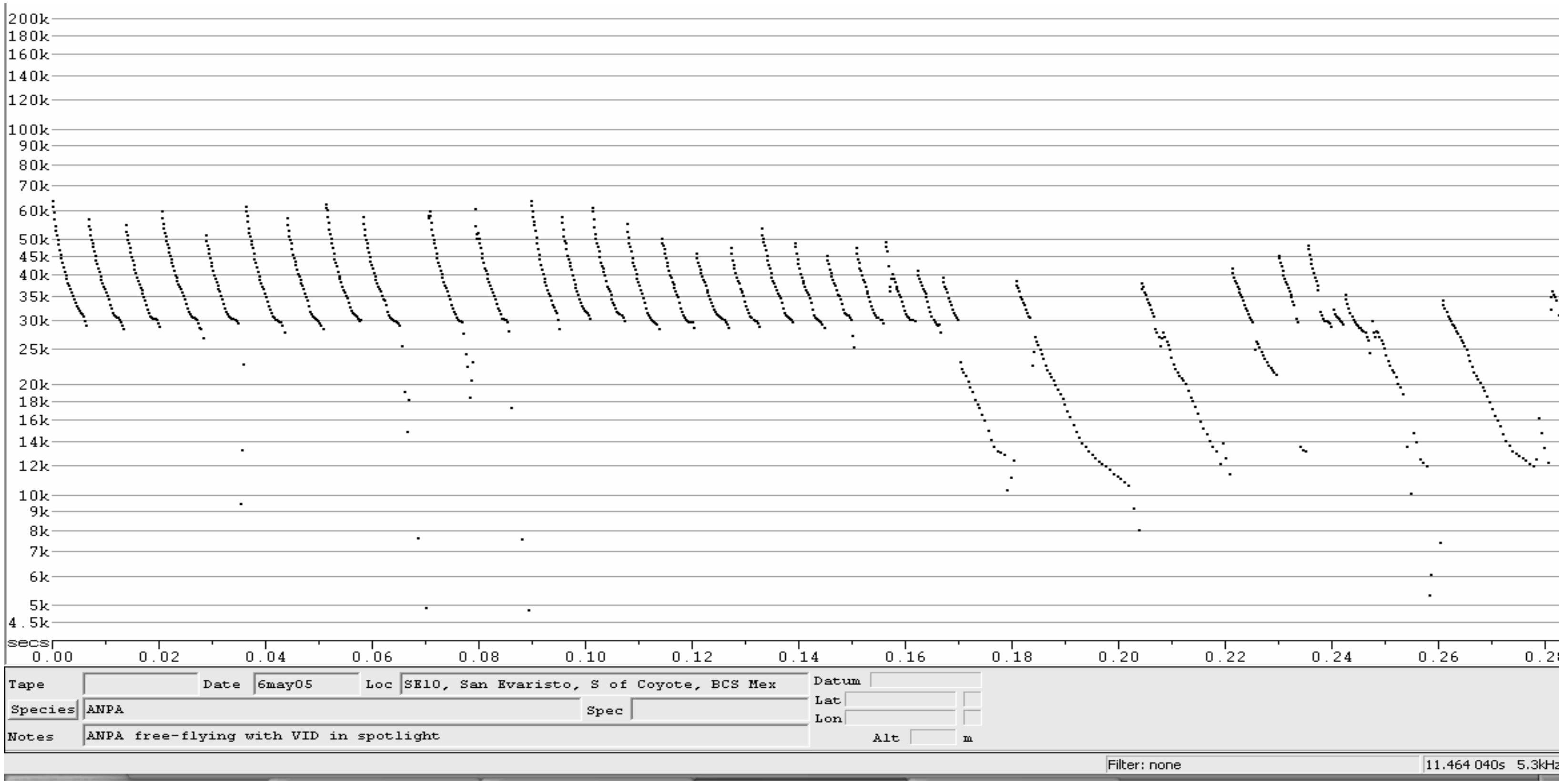
Gannon, W. L., M. J. O'Farrell, C. Corben, and E. Bedrick. 2004. Call character lexicon and analysis of field recorded bat echolocation calls. Pages 478-483 *in* J. A. Thomas, C. F. Moss, and M. V. Vater, editors. Echolocation in Bats and Dolphins. University of Chicago, Chicago, Illinois, USA.

Medellín, R. A., H. T. Arita, and Ó. H. Sánchez. 1997. Identificación de los murciélagos de México: Clave de campo. Asociación Mexicana de Mastozoología, A.C., Ciudad Universitaria, México.

O'Farrell, M. J., B. W. Miller, and W. L. Gannon. 1999. Qualitative identification of free-flying bats using the Anabat detector. Journal of Mammalogy 80:11-23.
.

Pallid bat (*Antrozous pallidus*)

ANPA



Date 6may05

Loc SE10, San Evaristo, S of Coyote, BCS Mex

Species ANPA

Notes ANPA free-flying with VID in spotlight

Filter: none

11.464 040s 5.3kHz

Figure A.1. Echolocation call sequence by *A. pallidus*, displaying characteristic call with diagnostic social chirp at the end of the sequence. Recorded by W. Frick in Baja California Sur, Mexico by active monitoring.

Big brown bat (*Eptesicus fuscus*)
EPFU

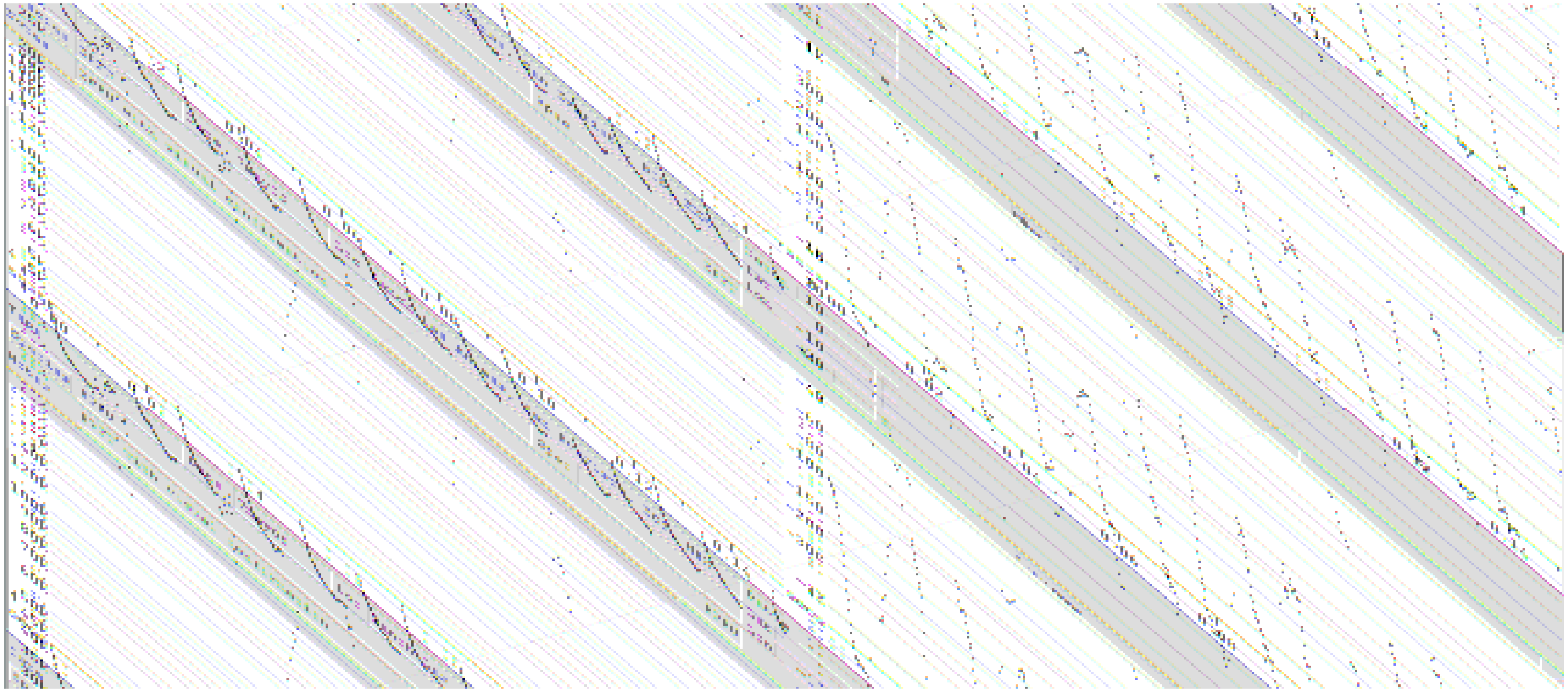
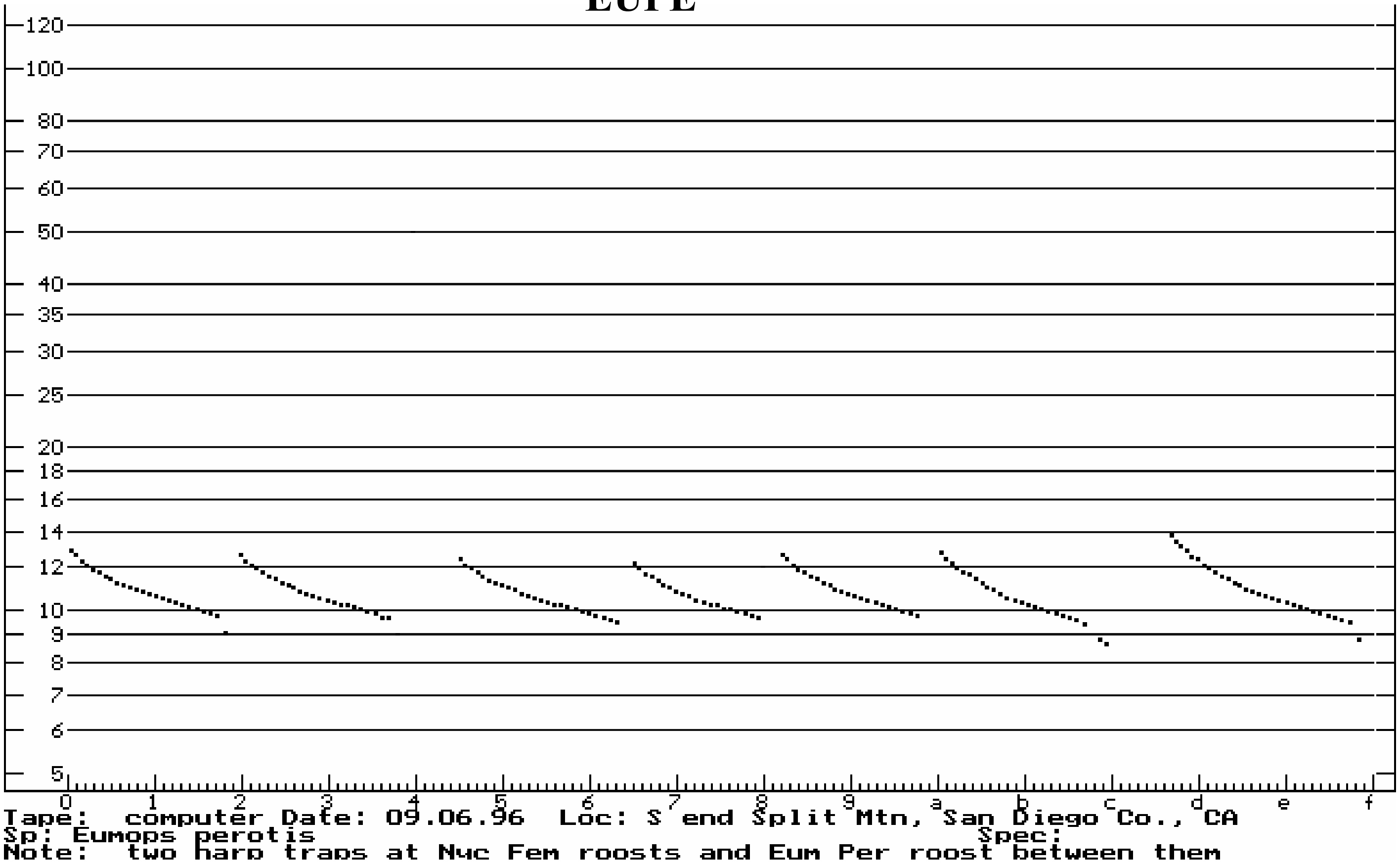


Figure A.2. Echolocation call sequence by *E. fuscus*. Left-hand screen displays echolocation pulses; right-hand screen displays associated slopes of pulses. Recorded by W. Frick in Baja California Sur, Mexico by active monitoring.

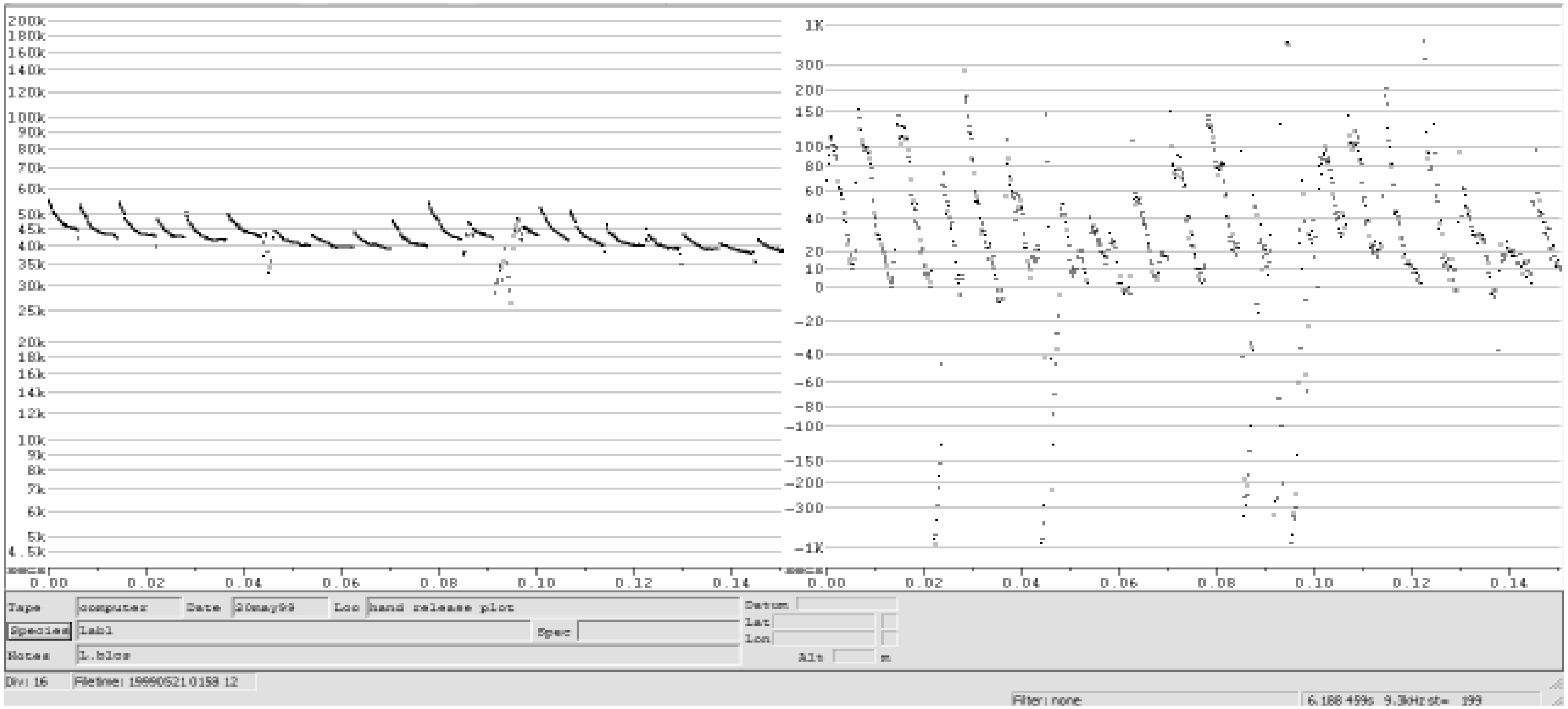
Western mastiff bat (*Eumops perotis*)
EUPE



```
Tape:  computer Date: 09.06.96  Loc: S end Split Mtn, San Diego Co., CA
Sp: Eumops perotis                                       Spec:
Note:  two harp traps at Nyc Fem roosts and Eum Per roost between them
```

Figure A.3. Echolocation call sequence by *E. perotis*. Reference call available from the University of New Mexico Bat Call Library (http://www.msb.unm.edu/mammals/batcall/html/calllibrary.html).

Western red bat (*Lasiurus blossevillii*)
LABL



Tape computer Date 20may99 Loc hand release plot

Species labl

Notes L.blos

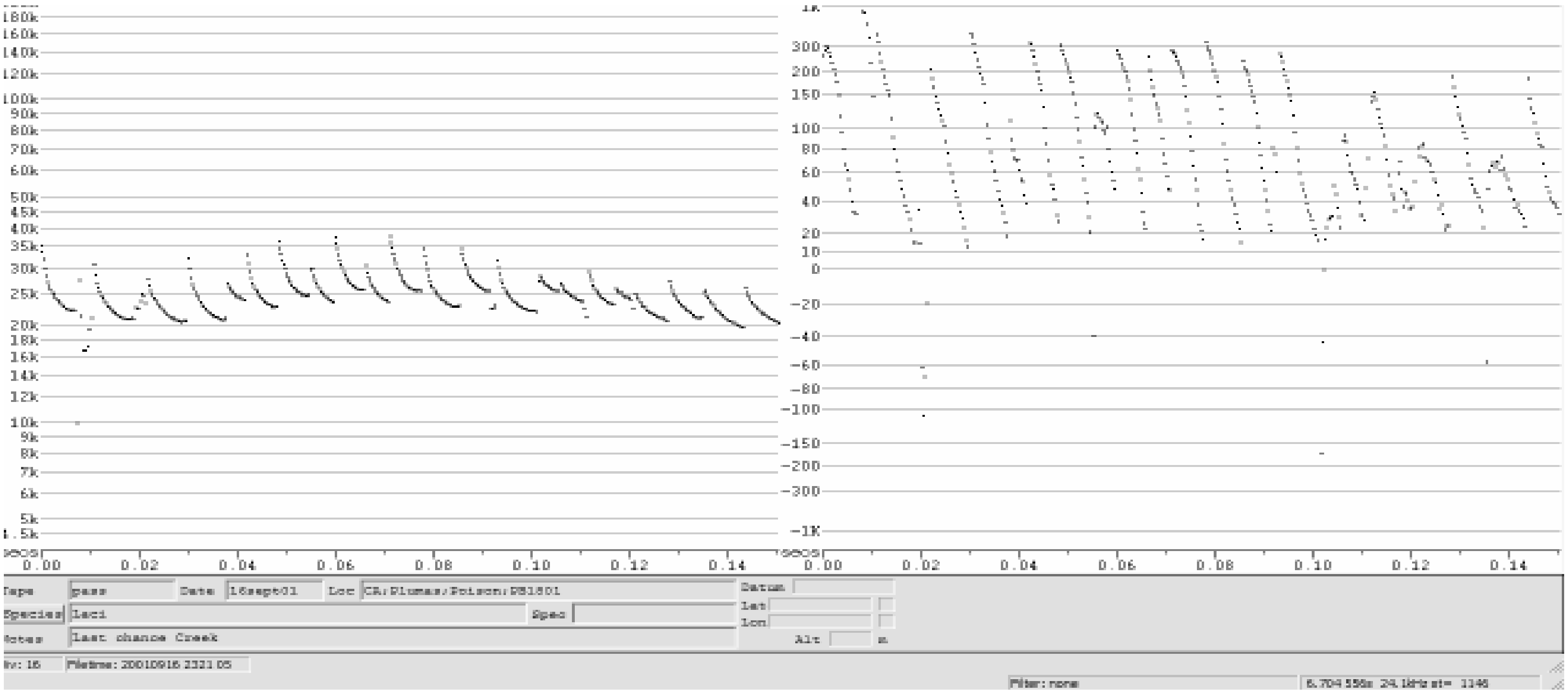
Div: 16 Filetime: 19990521 0158 12

Filter: none

6.188 459s 9.3kHz st= 199

Figure A.4. Echolocation call sequence by *L. blossevillii*. Left-hand screen displays echolocation pulses; right-hand screen displays associated slopes of pulses. Recorded by P. Heady in California by hand release.

Hoary bat (*Lasiurus cinereus*)
LACI



Tape: pass
Date: 16sept01
Loc: CA;Plumas;Poison;PS1501
Species: Laci
Notes: last chance Creek
Div: 16
Filetime: 20010916 2321 05
Filter: none
6.704 556s 24.1kHz st= 1146

Figure A.5. Echolocation call sequence by *L. cinereus*. Left-hand screen displays echolocation pulses; right-hand screen displays associated slopes of pulses. Recorded by P. Heady in California by hand release.

Western yellow bat (*Lasiurus xanthinus*)
LAXA

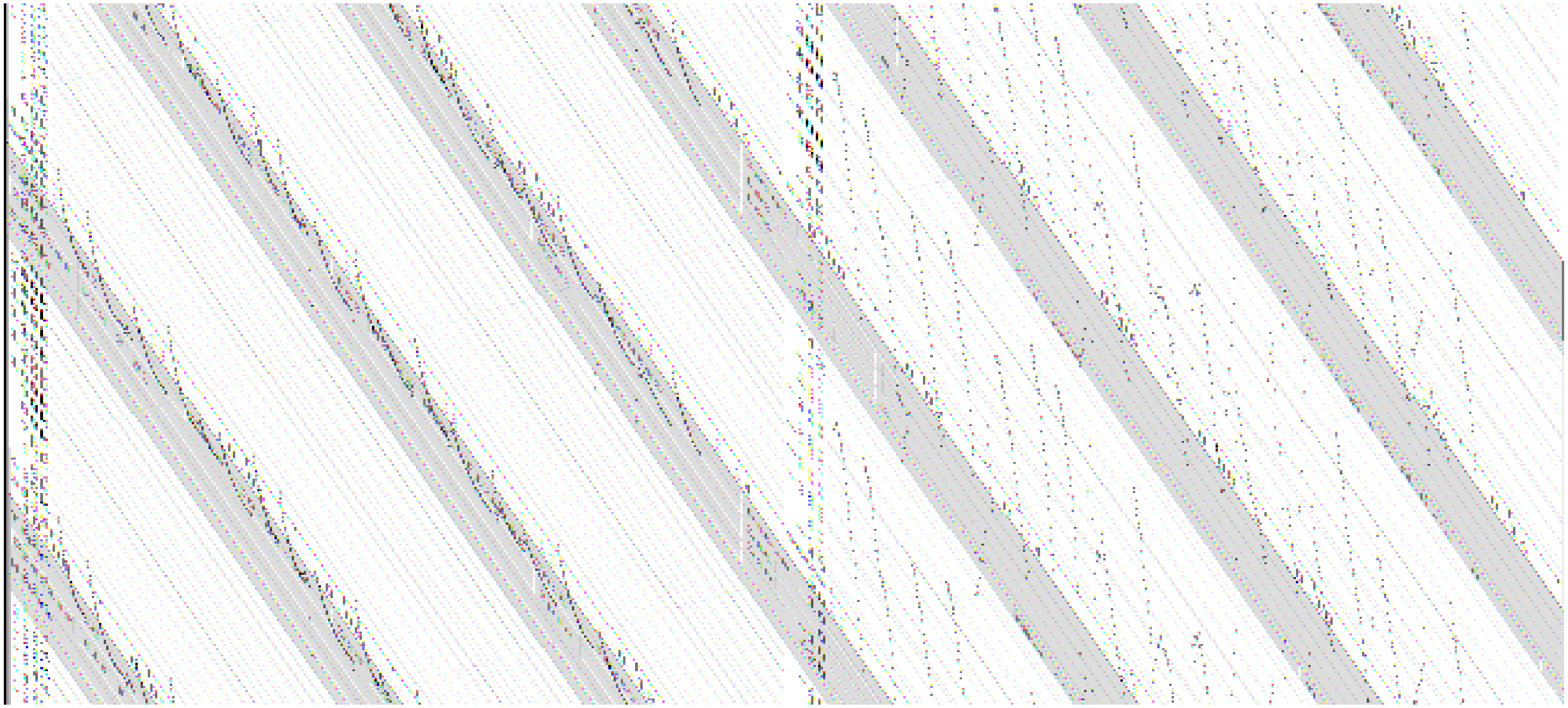


Figure A.6. Echolocation call sequence by *L. xanthinus*. Left-hand screen displays echolocation pulses; right-hand screen displays associated slopes of pulses. Reference call provided by Chris Corben; recorded in Nevada by hand release.

Lesser long-nosed bat (*Leptonycteris curasoae*)
LECU

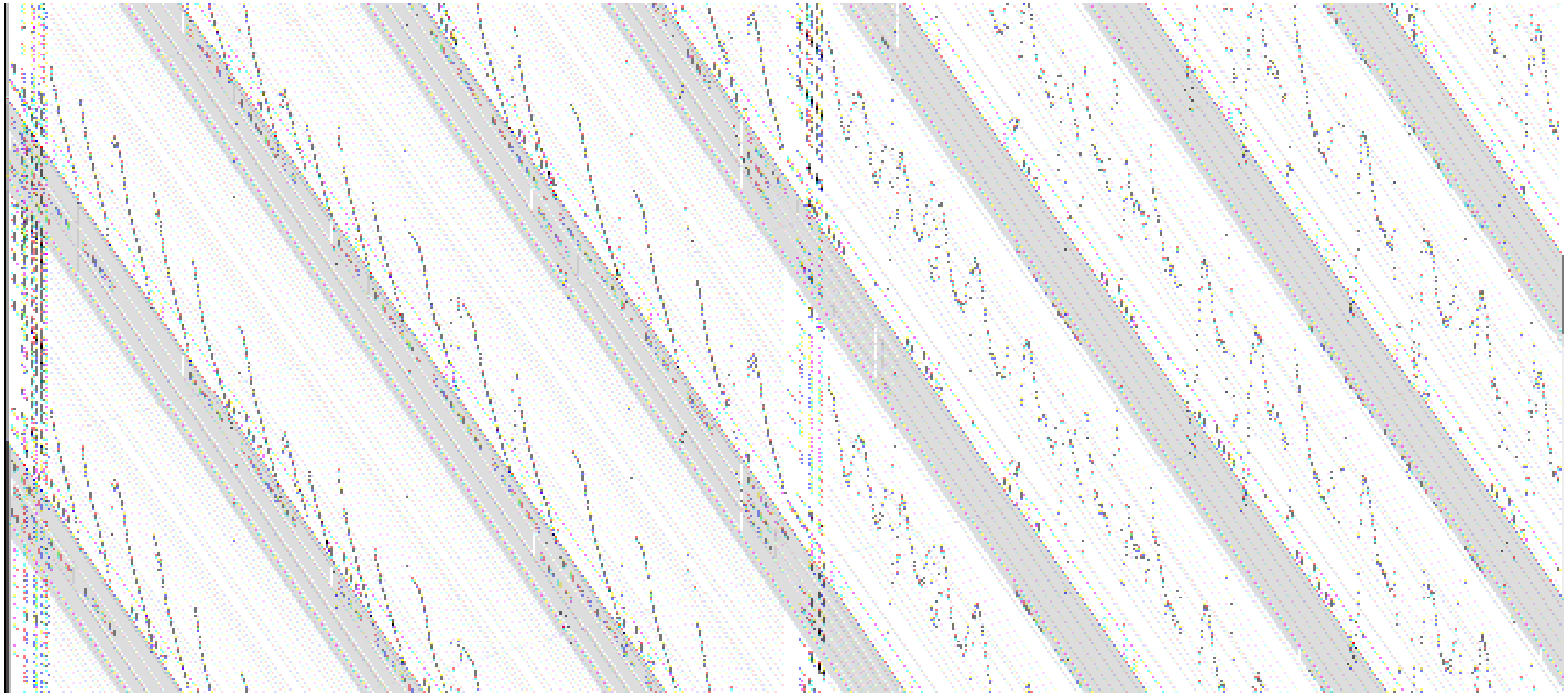


Figure A.7. Echolocation call sequence by *L. curasoae*. Left-hand screen displays echolocation pulses; right-hand screen displays associated slopes of pulses. Recorded by W. Frick in Baja California Sur, Mexico by active monitoring.

California leaf-nosed bat (*Macrotus californicus*)
MACA

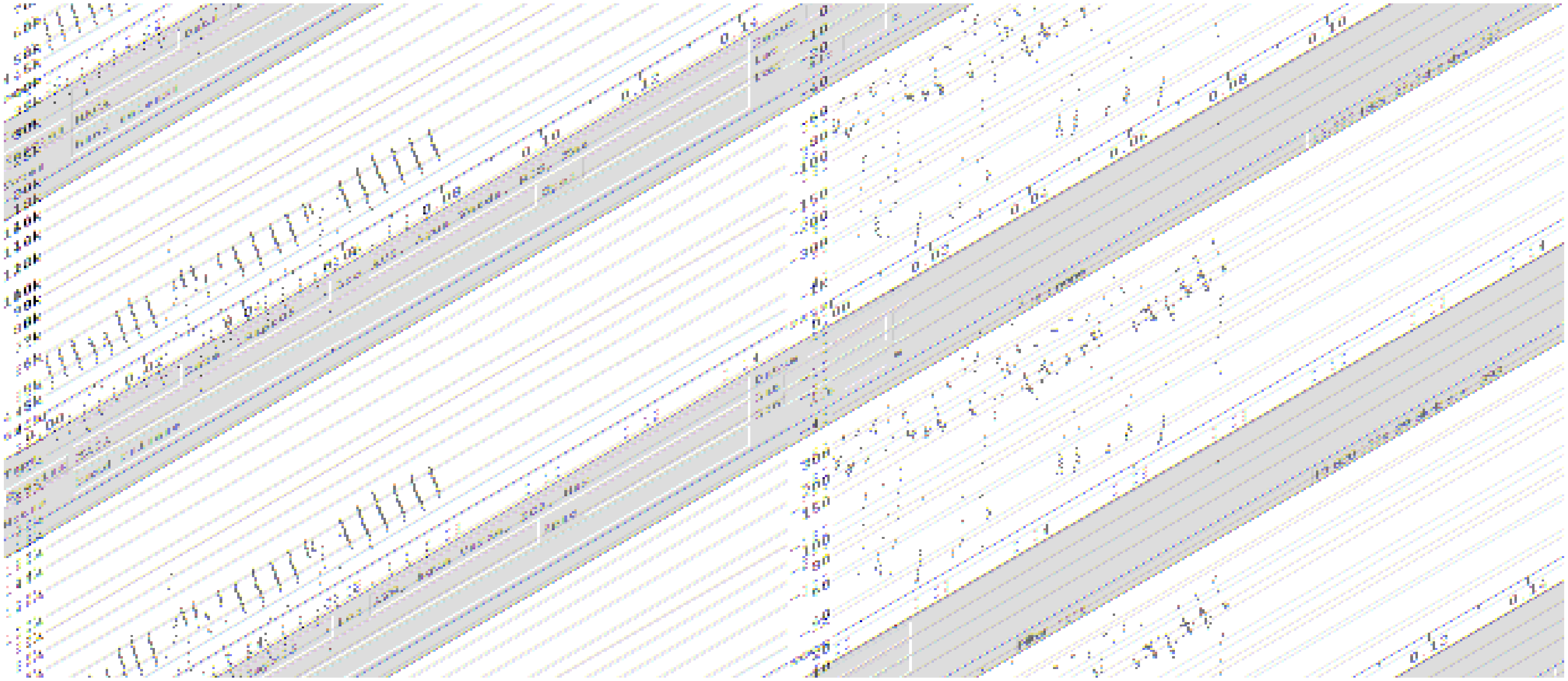


Figure A.8. Echolocation call sequence by *M. californicus*. Left-hand screen displays echolocation pulses; right-hand screen displays associated slopes of pulses. Recorded by W. Frick in Baja California Sur, Mexico by hand release.

Ghost-faced bat (*Mormoops megalophylla*)
MOME

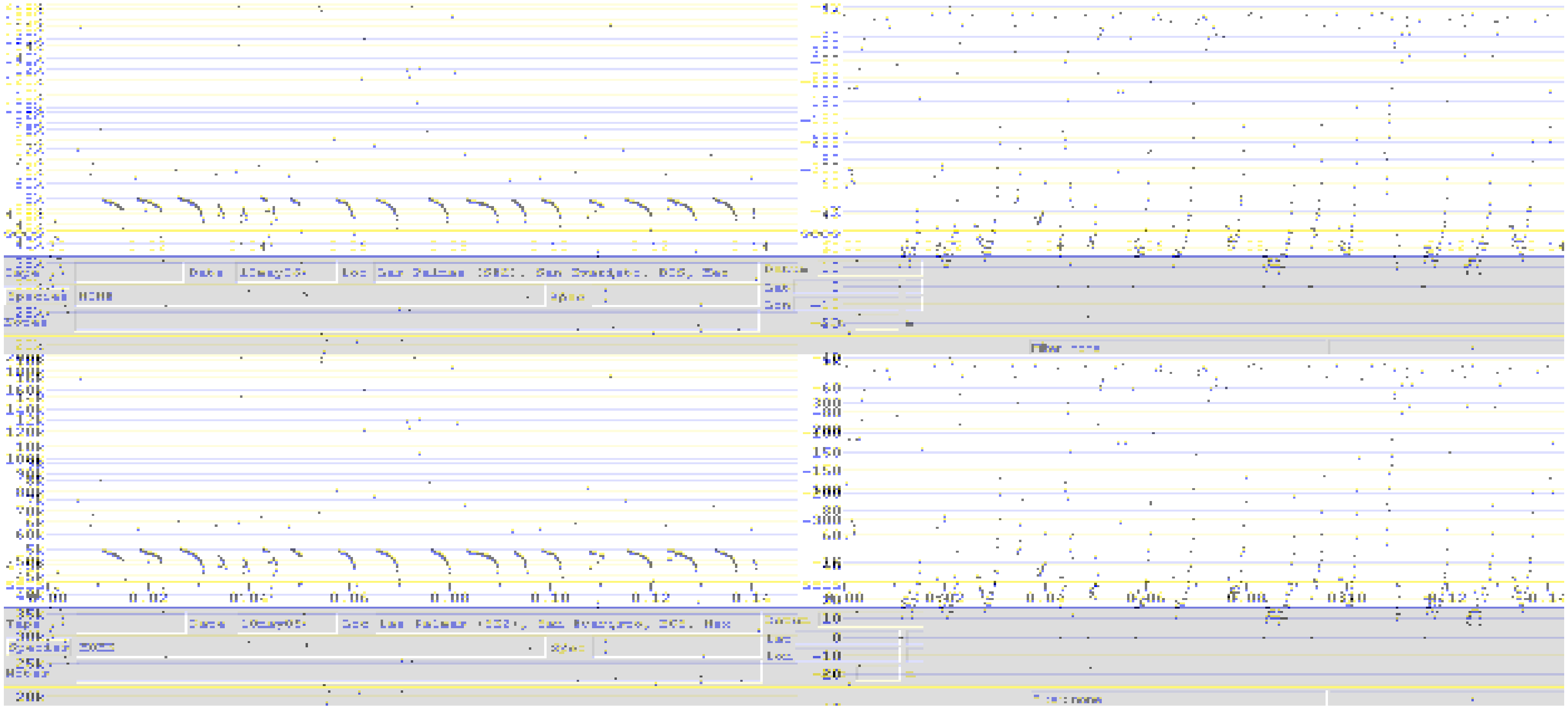


Figure A.9. Echolocation call sequence by *M. mormoops*. Left-hand screen displays echolocation pulses; right-hand screen displays associated slopes of pulses. Recorded by W. Frick in Baja California Sur, Mexico by active monitoring.

California myotis (*Myotis californicus*)

MYCA

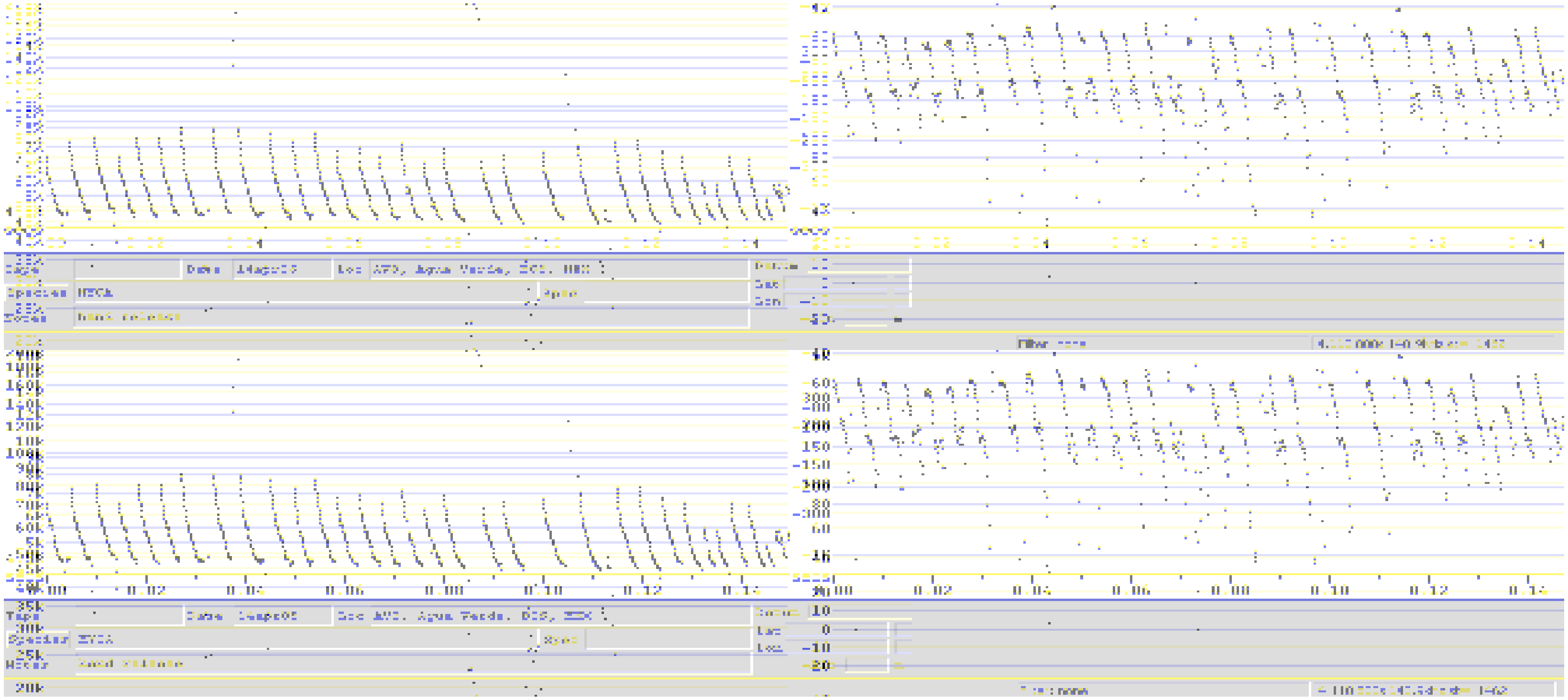
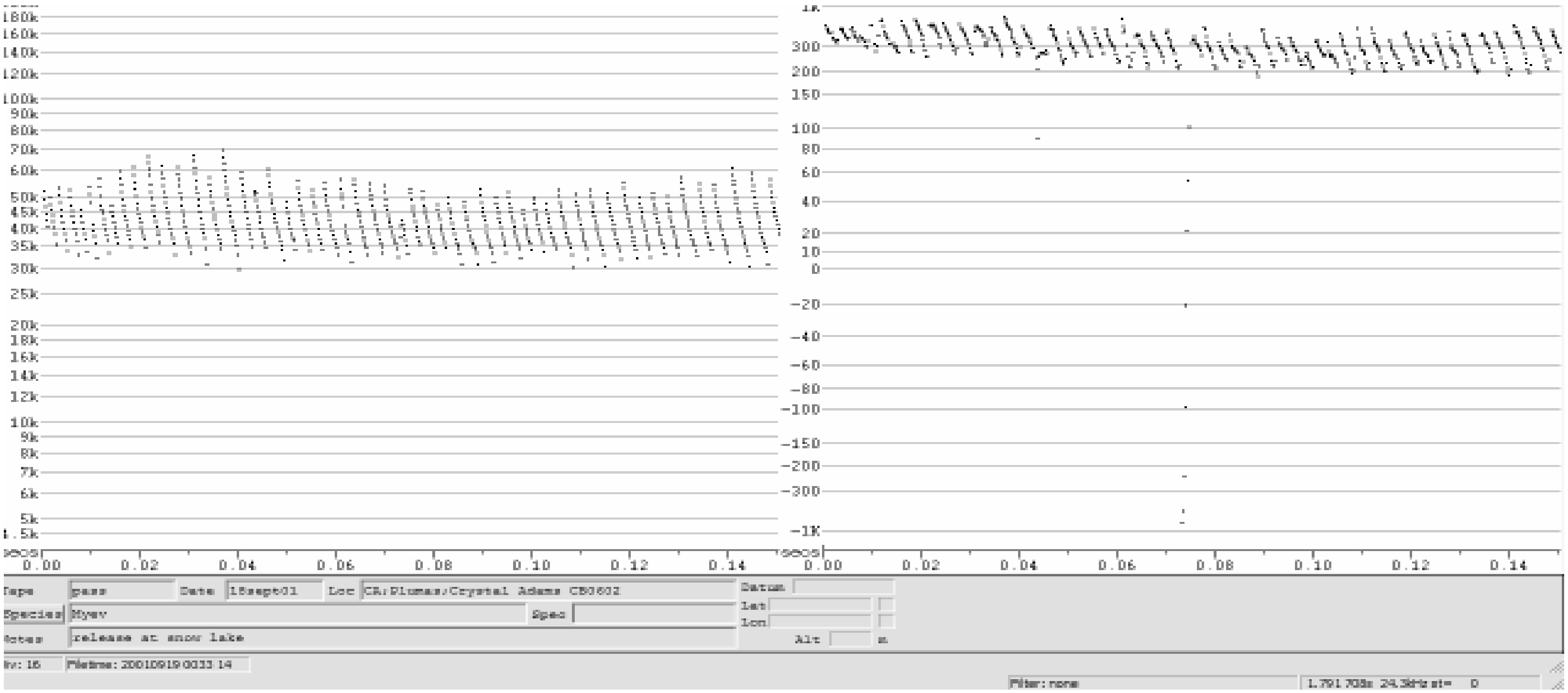


Figure A.10. Echolocation call sequence by *M. californicus*. Left-hand screen displays echolocation pulses; right-hand screen displays associated slopes of pulses. Recorded by W. Frick in Baja California Sur, Mexico by hand release.

Western long-eared myotis (*Myotis evotis*)
MYEV



Tape pass Date 15sept01 Loc CA:Plumas/Crystal Adams CB0602

Species Myev Spec

Notes release at snow lake

Datum

lat

lon

Alt m

iv: 16 Filetime: 20010919 0033 14

Filter: none 1.791 708s 24.3kHz st= 0

Figure A.11. Echolocation call sequence by *M. evotis*. Left-hand screen displays echolocation pulses; right-hand screen displays associated slopes of pulses. Recorded by P. Heady in California by hand release.

Fish-eating bat (*Myotis vivesi*)

MYVI

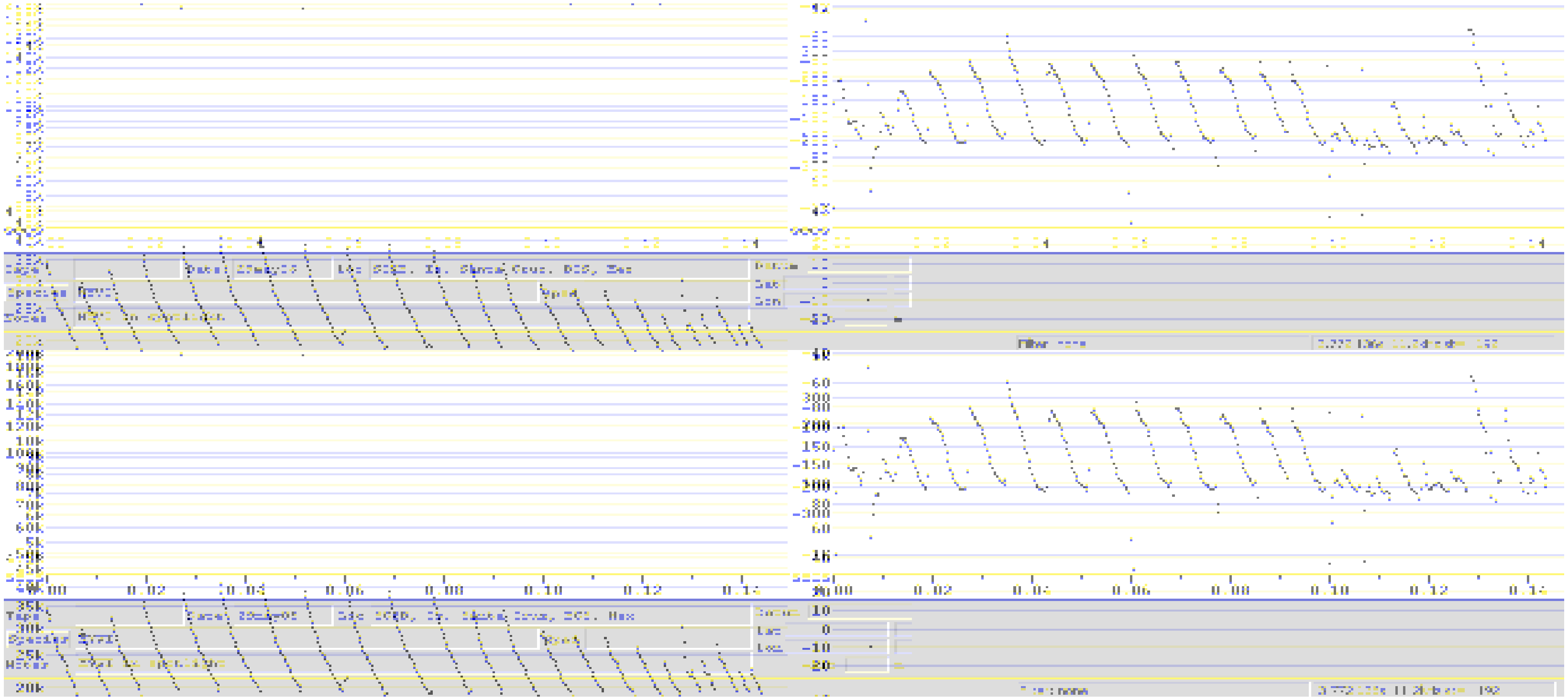
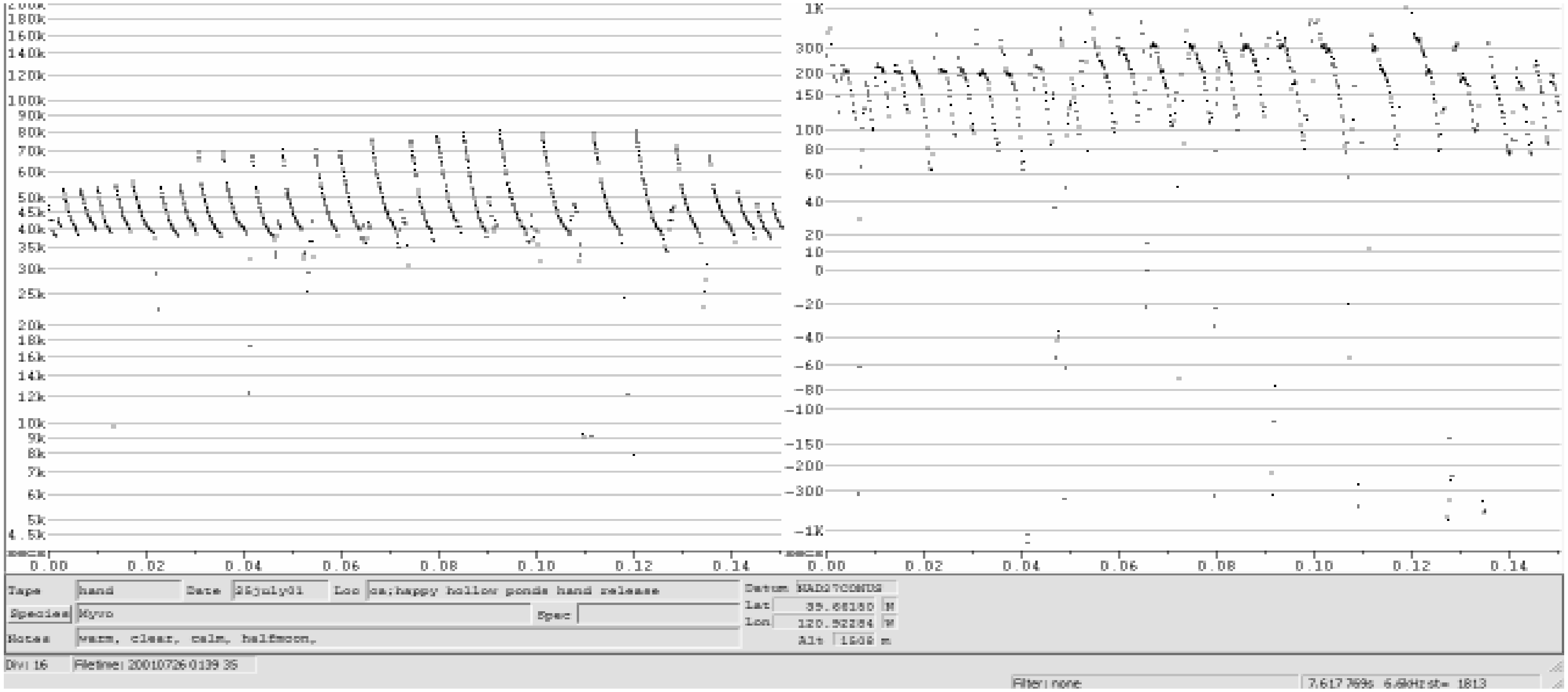


Figure A.12. Echolocation call sequence by *M. vivesi*. Left-hand screen displays echolocation pulses; right-hand screen displays associated slopes of pulses. Recorded by W. Frick in Baja California Sur, Mexico by active monitoring.

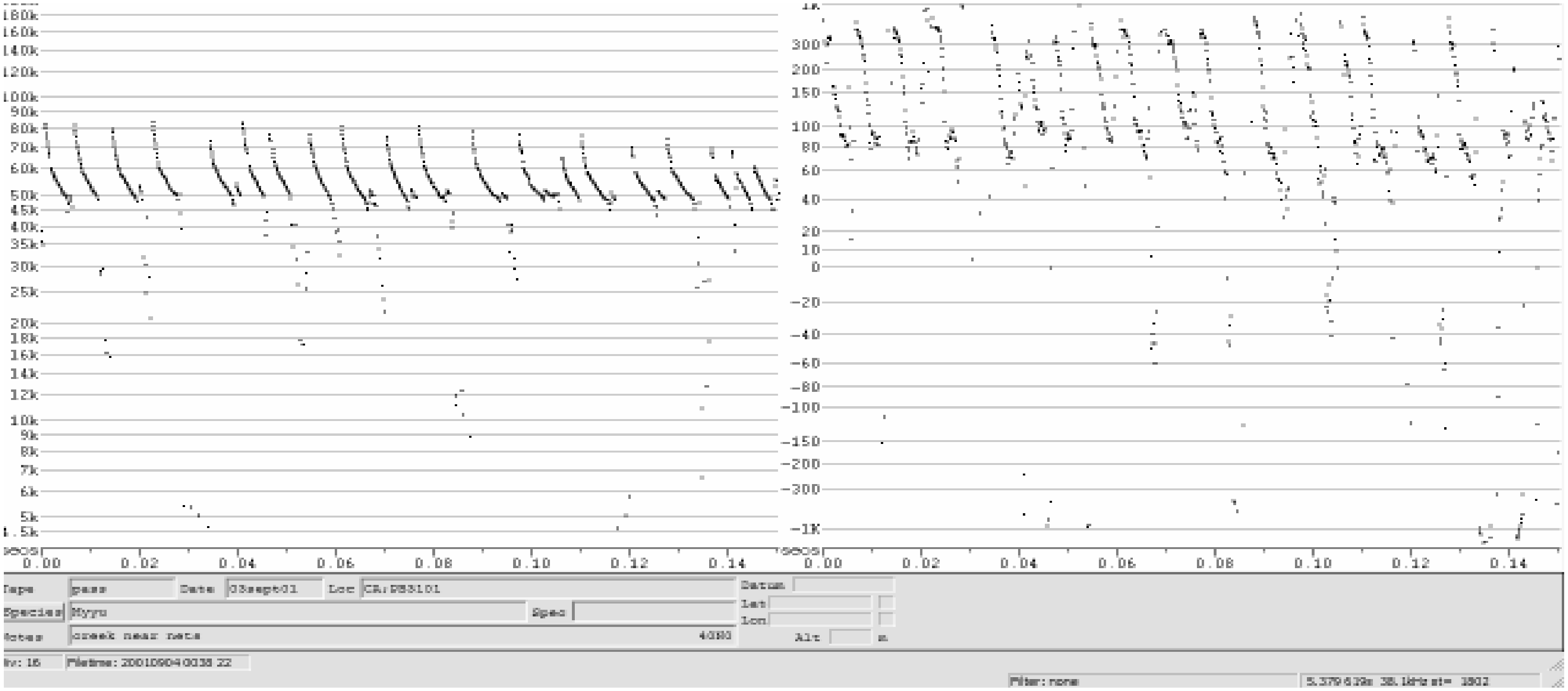
Long-legged myotis (*Myotis volans*)
MYVO



Tape: hand
Date: 25july01
Loc: ca;happy hollow ponds hand release
Species: Myvo
Spec:
Notes: warm, clear, calm, halfmoon,
Datum: NAD27CONUS
Lat: 35.68180 N
Lon: 120.52284 W
Alt: 1608 m
Div: 16
Filetime: 20010726 0139 35
Filter: none
7.617 769s 6.6kHz st= 1813

Figure A.13. Echolocation call sequence by *M. volans*. Left-hand screen displays echolocation pulses; right-hand screen displays associated slopes of pulses. Recorded by P. Heady in California by hand release.

Yuma myotis (*Myotis yumanensis*)
MYYU



Tape pass Date 03sept01 Loc CA:PS3101
Species Myyu Spec
Notes creek near nets 40H0
Datum
Lat
Lon
Alt m
Div: 16 Filetime: 20010904 0038 22
Filter: none
5.379 639s 38.1kHz st= 1802

Figure A.14. Echolocation call sequence by *M. yumanensis*. Left-hand screen displays echolocation pulses; right-hand screen displays associated slopes of pulses. Recorded by P. Heady in California by hand release.

Pocketed free-tail bat (*Nyctinomops femorosaccus*)
NYFE

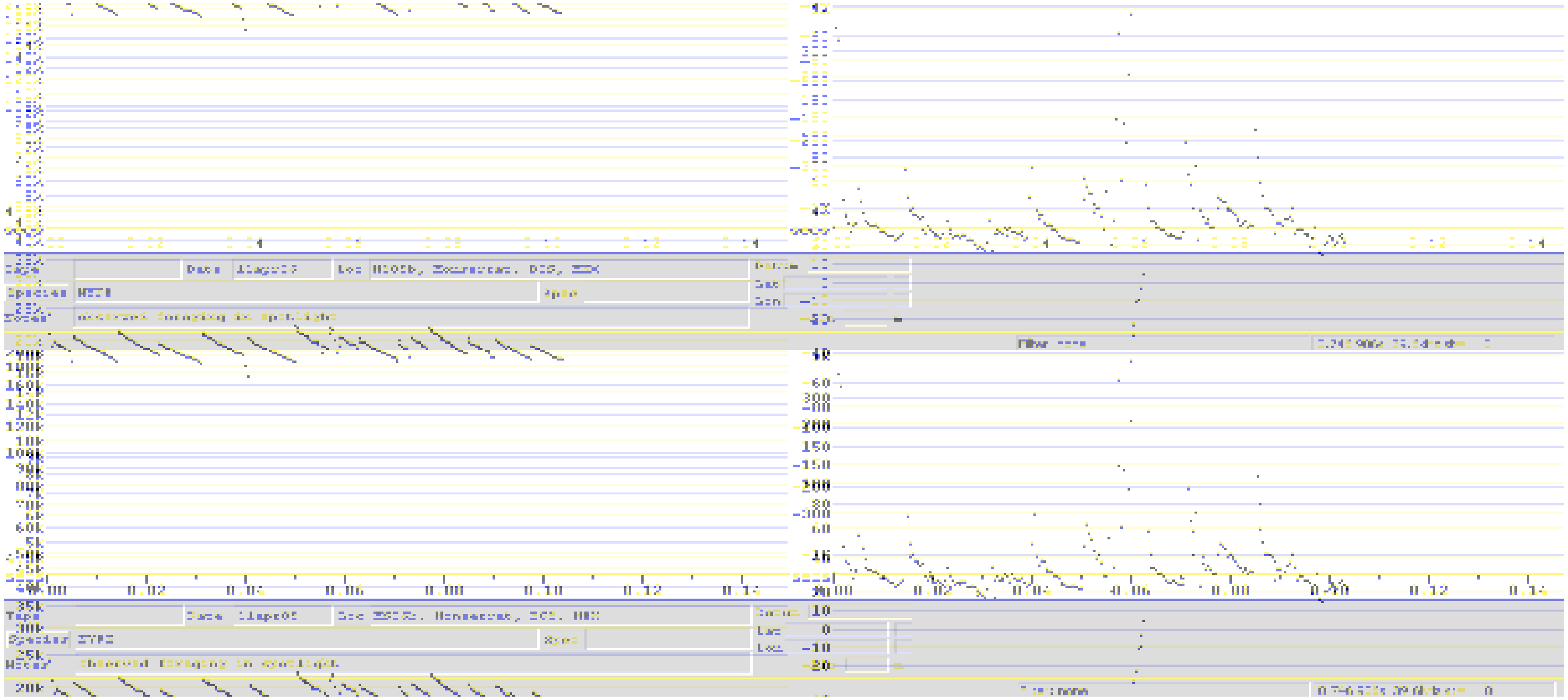
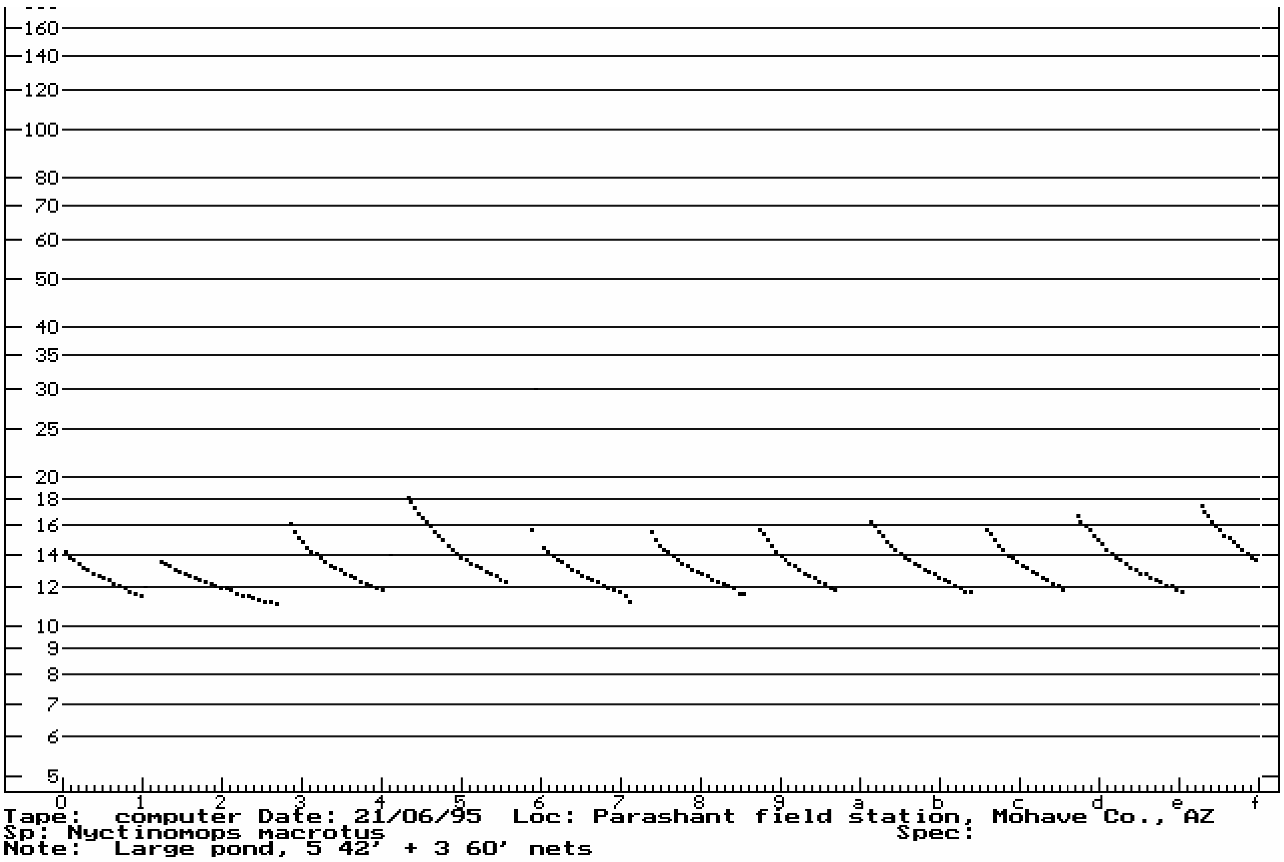


Figure A.15. Echolocation call sequence by *N. femorosaccus.* Left-hand screen displays echolocation pulses; right-hand screen displays associated slopes of pulses. Recorded by W. Frick in Baja California Sur, Mexico by active monitoring.

Big free-tailed bat (*Nyctinomops macrotis*)

NYMA



```
Tape:  computer Date: 21/06/95  Loc: Parashant field station, Mohave Co., AZ
Sp: Nyctinomops macrotus                                Spec:
Note:  Large pond, 5 42' + 3 60' nets
```

Figure A.16. Echolocation call sequence by *N. macrotis*. Reference call available from the University of New Mexico Bat Call Library (http://www.msb.unm.edu/mammals/batcall/html/calllibrary.html).

Western pipistrelle (*Pipistrellus hesperus*)
PIHE

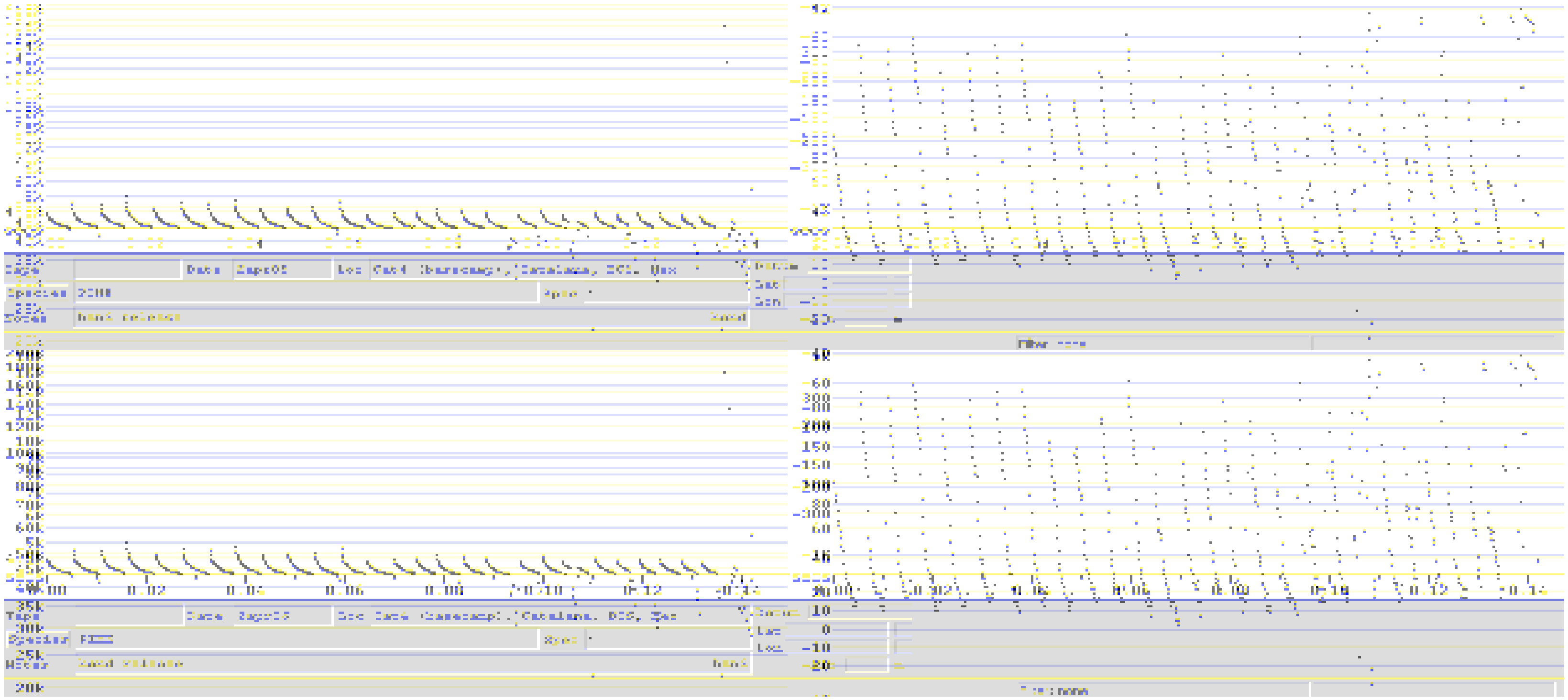
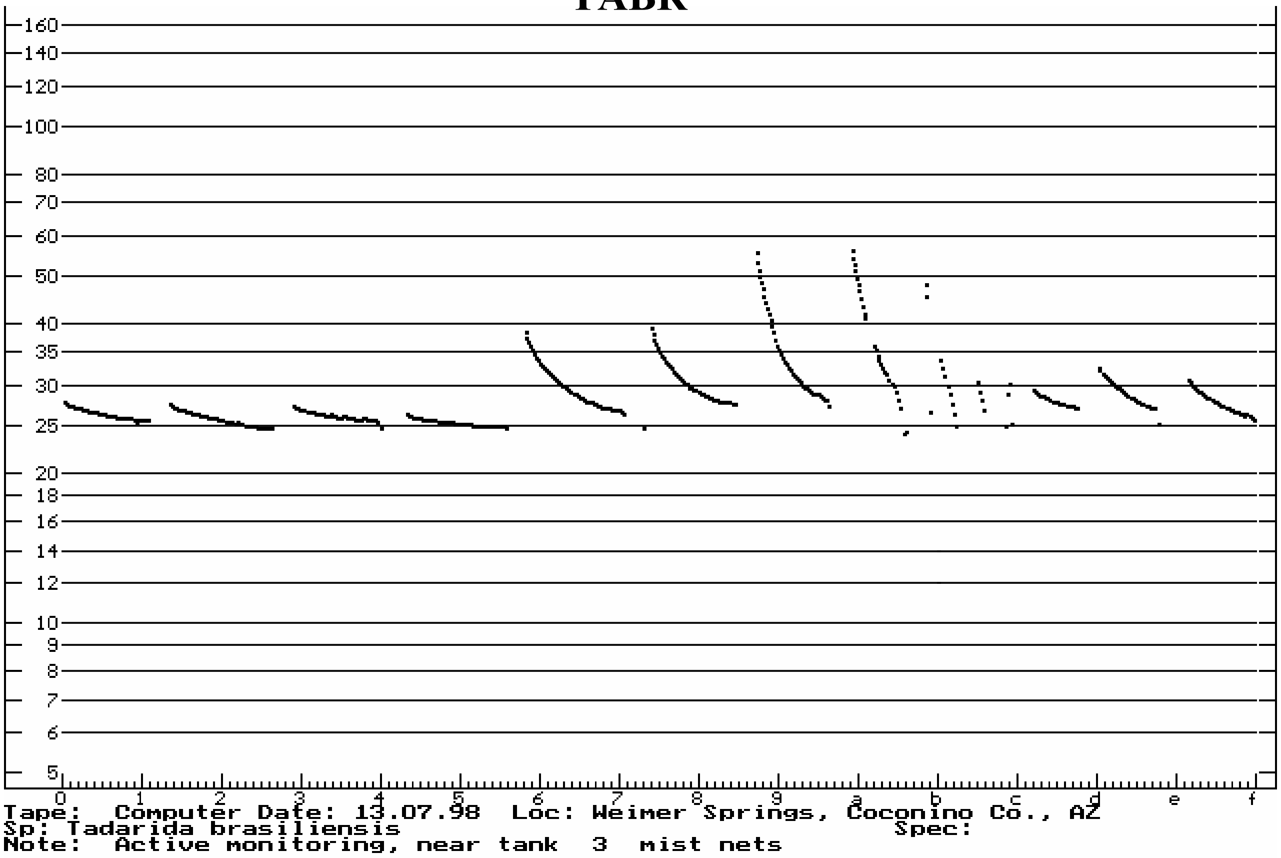


Figure A.17. Echolocation call sequence by *P. hesperus*. Left-hand screen displays echolocation pulses; right-hand screen displays associated slopes of pulses. Recorded by W. Frick in Baja California Sur, Mexico by hand release.

Mexican free-tailed bat (*Tadarida brasiliensis*)
TABR

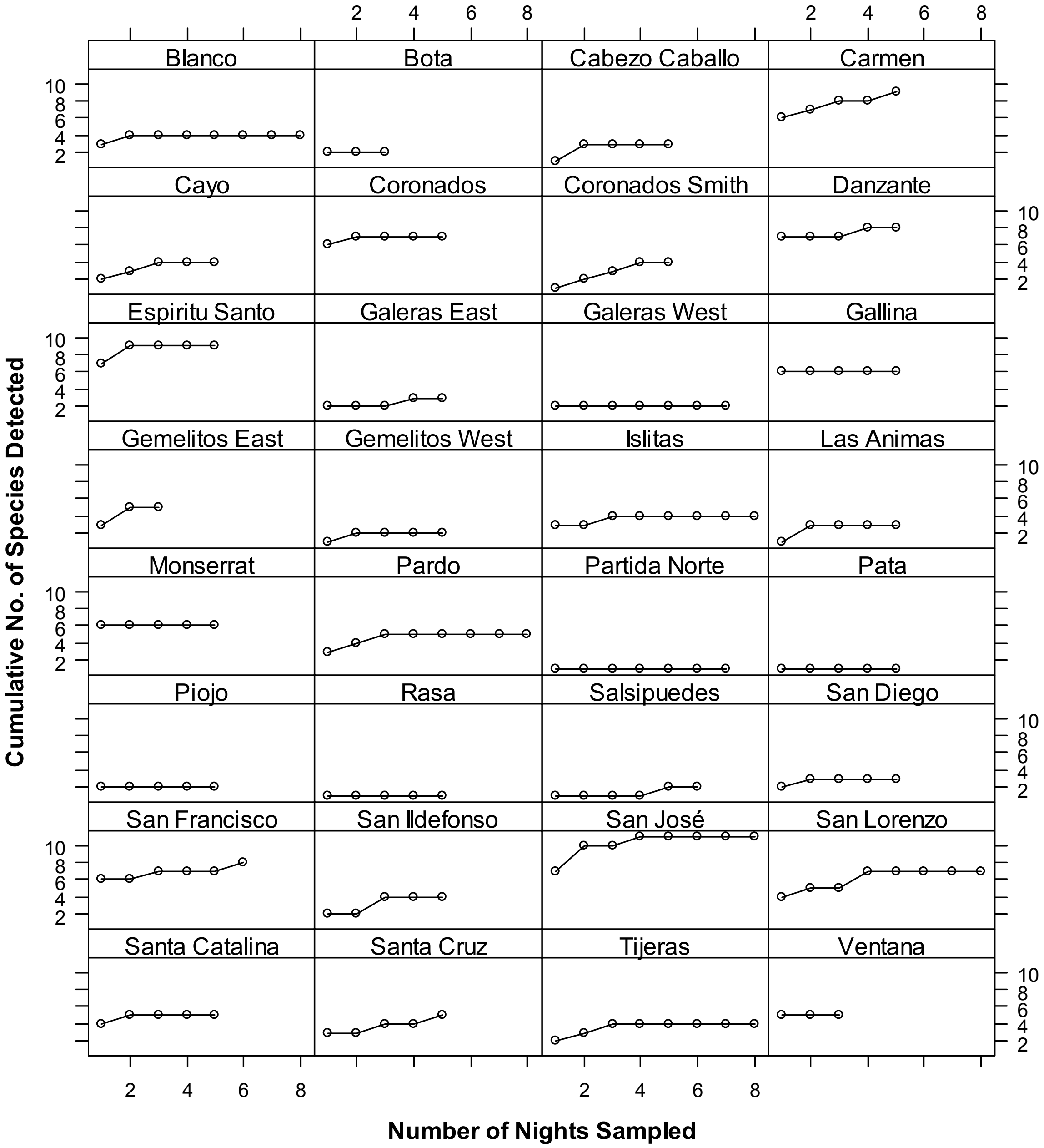


Tape: Computer Date: 13.07.98 Loc: Weimer Springs, Coconino Co., AZ
Sp: Tadarida brasiliensis Spec:
Note: Active monitoring, near tank 3 mist nets

Figure A.18. Echolocation call sequence by *T. brasiliensis.* Reference call available from the University of New Mexico Bat Call Library (http://www.msb.unm.edu/mammals/batcall/html/calllibrary.html).

APPENDIX B: SPECIES ACCUMULATION CURVES

Figure B.1. Species accumulation curves generated from acoustic sampling for bats from April 1 to June 1, 2004-2006 on 32 islands in the Gulf of California, Mexico. Most islands (n = 21) were sampled for five consecutive nights. Ten islands were sampled for greater than five nights (6-8 nights) and two islands were sampled for three nights.



APPENDIX C: PRESENCE OF BATS ON ISLANDS IN THE GULF OF CALIFORNIA, MEXICO

Table C.1. Distribution of 12 bats on 34 islands in the Gulf of California, Mexico. Two islands (in italics) were sampled for bats but were excluded from final analyses as they were outliers due to extreme values of isolation and geographic locations.

Island	Area (ha)	Isolation (km)	*Antrozous pallidus*	*Eumops perotis*	*Lasiurus xanthinus*	*Leptonycteris curasoae*	*Macrotus californicus*	*Mormoops megalophylla*	*Myotis californicus*	*Myotis vivesi*	*Nyctinomops femorosaccus*	*Nyctinomops macrotis*	*Pipistrellus hesperus*	*Tadarida brasiliensis*	Total Richness
Blanco	1.3	0.84	0	0	0	1	0	0	0	1	1	0	1	0	**4**
Bota	9.6	2.64	0	0	0	0	0	0	0	1	1	0	0	0	**2**
Cabezo Caballo	71.0	1.89	0	0	0	1	1	0	1	1	1	0	0	0	**5**
Carmen	14,801.4	5.50	1	0	0	1	1	1	1	1	1	1	1	0	**9**
Cayo	6.7	6.22	0	0	0	1	0	0	0	1	1	0	0	1	**4**
Coronados	715.8	2.60	0	0	0	1	1	0	1	1	1	0	1	1	**7**
Coronados Smith	852.1	2.22	0	0	0	1	0	0	0	1	1	0	1	0	**4**
Danzante	423.7	2.67	0	0	0	1	1	1	1	1	1	1	1	0	**8**
Espiritu Santo	10,367.1	6.21	0	0	0	1	1	0	1	1	1	1	1	1	**8**
Galeras East	5.4	16.40	0	0	0	1	0	0	0	1	1	0	0	1	**4**
Galeras West	3.2	16.77	0	0	0	1	0	0	0	1	1	0	0	0	**3**
Gallina	2.0	7.18	0	0	0	1	0	0	1	1	1	0	1	1	**6**
Gemelitos East	3.9	0.82	0	0	0	1	0	0	0	1	1	1	0	1	**5**
Gemelitos West	2.4	0.86	0	0	0	1	0	0	0	1	0	0	0	0	**2**

Table C.1. Continued.

Island	Area (ha)	Isolation (km)	*Antrozous pallidus*	*Eumops perotis*	*Lasiurus xanthinus*	*Leptonycteris curasoae*	*Macrotus californicus*	*Mormoops megalophylla*	*Myotis californicus*	*Myotis vivesi*	*Nyctinomops femorosaccus*	*Nyctinomops macrotis*	*Pipistrellus hesperus*	*Tadarida brasiliensis*	Total Richness
Islitas	3.3	0.41	0	0	0	0	0	0	0	1	1	0	1	1	**4**
Las Animas Sur	9.1	16.49	0	0	0	1	0	0	0	1	1	0	0	0	**3**
Monserrat	1,902.8	13.66	1	0	0	1	0	0	0	1	1	1	1	0	**6**
Pardo	4.3	0.36	0	0	0	1	0	0	0	1	1	0	1	1	**5**
Partida Norte	94.0	17.84	0	0	0	0	0	0	0	1	0	0	0	0	**1**
Pata	14.5	2.57	0	0	0	0	0	0	0	1	1	0	0	0	**2**
Piojo	67.6	4.57	0	0	0	1	0	0	0	1	0	0	0	0	**2**
Rasa	59.2	20.75	0	1	0	0	0	0	0	0	0	0	0	0	**1**
Salsipuedes	102.6	17.70	0	0	0	1	0	0	0	1	0	0	0	0	**2**
San Diego	62.9	19.06	0	0	0	0	0	0	0	1	1	0	1	0	**3**
San Francisco	419.0	7.16	0	0	0	1	1	0	1	1	1	1	1	1	**8**
San Ildefonso	104.2	10.01	0	0	0	1	0	0	0	1	1	0	0	1	**4**
San José	18,494.5	4.75	1	1	1	1	1	1	1	1	1	1	1	1	**12**
San Lorenzo	3,632.3	16.31	0	0	0	1	1	0	1	1	0	0	1	1	**6**

Table C.1. Continued.

Island	Area (ha)	Isolation (km)	*Antrozous pallidus*	*Eumops perotis*	*Lasiurus xanthinus*	*Leptonycteris curasoae*	*Macrotus californicus*	*Mormoops megalophylla*	*Myotis californicus*	*Myotis vivesi*	*Nyctinomops femorosaccus*	*Nyctinomops macrotis*	*Pipistrellus hesperus*	*Tadarida brasiliensis*	Total Richness
San Pedro Mártir	259.3	50.13	0	0	0	1	0	0	0	1	0	0	0	1	**3**
Santa Catalina	3,995.6	25.06	1	0	0	1	0	0	0	1	0	1	1	0	**5**
Santa Cruz	1,315.1	19.81	1	0	1	0	0	0	0	1	1	0	1	0	**5**
Tijeras	4.0	1.90	0	0	0	1	0	0	0	1	1	0	0	1	**4**
Tortuga	1,141.2	35.64	0	0	0	1	1	0	0	1	0	0	0	1	**4**
Ventana	128.2	3.09	0	0	0	1	0	0	1	1	1	0	1	0	**5**
Total Number of Occurrences:			**5**	**2**	**2**	**27**	**9**	**3**	**10**	**33**	**25**	**8**	**17**	**15**	