EVALUATING THE USE OF ACOUSTIC MONITORING FOR SURVEYING TROPICAL BIRDS

BY

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THESIS

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ABSTRACT

In this study I evaluated the effectiveness of an acoustic recording system (SRS) for surveying tropical bird communities and species relative to traditional point count surveys. To address this goal, I compared species richness, composition and detection probability of 20 species between SRS and point counts across six tropical habitats in the northeastern Yucatan Peninsula. SRS performed in a similar fashion to point counts for estimating species richness and composition, two main features of community structure. Estimates of species richness were not significantly different between methods in any of the habitats. Although similarity in species composition between SRS and point counts was lower in coastal dunes than secondary and mature semi-evergreen forests, at least 92% of the species were shared between the two methods in all habitats. Similarly, the multi-method occupancy models demonstrated that SRS yielded detection probabilities similar to or greater than those of point counts for nearly all species across all habitats, although a few important exceptions occur for species in which SRS performed better than point counts in some habitats. Collectively my results on richness and similarity suggest that, although there are a small number of species detected exclusively by one method or the other, SRS and point counts perform equally well at detecting and identifying the majority of species in the communities I studied. Thus, the choice of a survey technique for characterizing bird communities is more of a logistic question than a monitoring technique question. Because SRS offers a logistically easier method given the lack of experienced point count technicians, SRS stands to help characterize bird communities in tropical habitats.

To my family –

Jill, Sofia, my Mom, Liza, Javier and Francisco

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CHAPTER 1: INTRODUCTION

Tropical habitats are being lost and altered at a high rate (Bradshaw et al. 2008), presumably with substantial effects on birds. Bird communities in the tropics are generally characterized by high species diversity (Terborgh et al. 1990, Karr 1990), and relative to temperate regions, especially in North America or Europe, very little is known about the basic ecology of tropical birds and even less about their responses to habitat alteration. Knowledge of basic population and community parameters is urgently needed to estimate trends for monitoring the health of tropical ecosystems; however, reliable estimates of bird species distributions and abundances in the tropics are difficult to obtain because of biases inherent to common survey methods (Whitman et al. 1997).

Mist-netting has long been the preferred technique for surveying birds in the tropics because of researchers' unfamiliarity with species vocalizations (e.g., Karr 1971, Robinson et al. 2000, Whitman et al. 1997); however, this approach has been widely criticized because it generally samples only a subset of the community (2-3 m above the ground) and the proportion of the community sampled generally varies among habitats (increasing as vegetation height decreases) (Karr 1981). Point counts, a standard avian survey method used widely in the North American temperate region whereby an observer records all birds seen and/or heard at a given location during a specified time period (Ralph et al. 1995, Bibby et al. 2000), has been used with increasing frequency in the tropics over the past two decades (Blake 1992, Lynch 1992, 1995). Point counts allow birds to be sampled from all substrates in tropical habitats. Point counts also increase the number of sites that can sample over mist netting, which require extensive sampling effort for each survey location. Although both visual and auditory cues are used to detect birds during point counts, the majority of detections in tropical habitats, like temperate habitats, are auditory (Scott et al. 1981, Dejong and Emlen 1985, Sauer et al. 1994, Brewster and Simons 2009, Celis-Murillo et al. 2009) and consequently, some researchers have begun to use acoustic recording survey methods (i.e., acoustic recordings of the entire soundscape of a particular location at any given time) for collecting data on bird populations and communities (Hobson et al. 2002, Haselmayer and Quinn 2000, Celis-Murillo et al. 2009, Hutto and Stutzman 2009).

Acoustic recording surveys have several advantages over point counts for sampling species that are detected primarily via vocalizations. During transcription, recordings can be replayed to resolve ambiguities. In addition multiple observers can interpret recordings, analyze spectrograms, allowing regional experts to verify identifications. Recordings also provide a permanent record that can be re-analyzed with song identification programs (Hobson 2002, Rempel et al 2005, Brandes 2008, Celis-Murillo et al. 2009). Additionally, from a logistical perspective, acoustic recordings are advantageous because they do not require skilled observers often rare in the tropical areas. Rather technicians without experience with bird vocalizations can collect recordings in the field, which can then be interpreted by an expert in the laboratory. Point counts, on the other hand, do perform better for sampling species that are primarily detected visually (e.g., hummingbirds and raptors; Haselmayer and Quinn 2000).

Acoustic recording surveys are expected to perform better than point counts in the tropics, where bird communities have high diversity and a large number of rare species (MacArthur et al. 1966, Ricklefs 1990), and where most species' vocal repertoires have not been fully described (Herzog et al. 2002). High species diversity makes detecting and identifying birds in the field challenging even for the expert (Terborgh et al. 1990, Haselmayer and Quinn 2000) because it becomes more difficult to isolate and identify birds as the total number of individuals and species increases (Bart and Schoultz 1984). Acoustic recordings can be replayed multiple times increasing the probability of detecting each individual and species. Rare species are also problematic for observers conducting point counts because they tend to be less familiar with these vocalizations and hence are more likely to misidentify them or report them as “unknown species”. The ability to view sonograms and cross reference identifications with regional experts increases the likelihood of properly identifying rare species. All of these factors can lead to biases in species detections and counts that impact conclusions about species diversity and ultimately the health of ecosystems (Karr 1981a, 1990).

Although the use of acoustic recordings for surveying birds has recently gained popularity, and studies in temperate regions suggest that they perform as well or possibly better than observers in the field (Hobson et al. 2002, Celis-Murillo et al. 2009), little is known about the relative effectiveness of acoustic recording systems compared to point counts for tropical bird surveys (Haselmayer and Quinn 2000). Furthermore, very little is known about how the effectiveness of acoustic recording surveys varies across different habitat types in either tropical or temperate areas (Hutto and Stutzman 2009). The issue of habitat–specific differences in auditory detectablity is critical for the accuracy and confidence of estimates of community parameters (e.g. species richness, species composition).

The objective of this study is to evaluate the effectiveness of a Soundscape Recording System (SRS, Celis et al. 2009) for estimating species distributions, species richness and the composition of tropical communities. I assess the performance of acoustic recordings relative to the standard expert ‘point counts’ by comparing the two methods in multiple habitats in the Yucatan Peninsula of Mexico. Here I focus solely in distributional data (detection/non-detection). I compared population and community parameters estimated from both SRS recordings and expert point counts in six habitats in the Yucatan Peninsula, and specifically addressed the following questions: 1) How similar are species richness and composition estimates generated by the two survey methods in the different habitats? 2) How does detection probability differ between the two survey methods across habitats? 3) Do the two survey methods perform differently when monitoring common vs. rare species?

CHAPTER 2: METHODS

Study area

This study was conducted in the northeastern region of the Yucatan Peninsula, at the Ria Lagartos Biosphere Reserve and Ejidos Santa Isabel and Santa Pilar in Yucatan and the El Eden Ecological Reserve in Quintana Roo (Figure 1a-b). The study sites included six natural and human-modified habitat types: coastal dune scrub, mangrove, mature low-stature deciduous thorn forest, mature medium-stature semi-evergreen forest, secondary semi-evergreen forest, and grazed pastures. With the exception of low-stature deciduous thorn forest, which has a restricted distribution in the peninsula, all habitat types were sampled at multiple sites.

Coastal dune scrub vegetation is comprised primarily of woody shrubs, cacti, herbaceous vegetation and scattered palm trees, including introduced coconut palms (*Cocos nucifera*) in some areas. Plant density in coastal scrub is very high, and vegetation reaches an average height of around 2.1 m. The areas of mangrove sampled in my study are best described as mangrove scrub rather than mangrove forest. At some survey locations the vegetation was very open, consisting of scattered patches of short red (*Rhizophora mangle*) and black (*Avicennia germinans*) mangroves, whereas at other survey locations secondary mangroves (*Conocarpus erectus*) dominated the plant community and the vegetation was less patchy, although still relatively open. Mangroves reach an average height of 3.0 m in the areas where I surveyed birds. Mature and secondary semi-evergreen forests have relatively similar plant species composition, although they differ from one another in structure. Mature forests reach an average height of 8.5 m, whereas secondary forests have a height of 6.2 m. Mature forests have also have more open shrub and ground layers than secondary-forests. Thorn forests are the shortest of the three forest types I studied, reaching an average height of 1.7 m. Vegetation density is substantially lower in thorn forests than both mature and secondary semi-evergreen forests, and vegetation in thorn forests is more patchy in its distribution. Thorn forests are distributed in the western portion of my study region and are drier than semi-evergreen forests, reflecting a natural east-west precipitation gradient in the Yucatan Peninsula; consequently, thorn forests are dominated by *Fabacea* and cacti species. Pastures ranged in size from approximately 2 to 200 hectares, and many fields were surrounded by living fences (i.e., linear forests) and had scattered trees or small forest patches in their interior. Grazing activity was light at the survey locations during the time of sampling. Deppe and Rotenberry (2008) and Carabias Lillo et al (1999) provide a detailed description of the vegetation types surveyed in my study.

I established 53 survey locations (hereafter referred to as locations) distributed as evenly as possible among the six vegetation types. Point counts were placed along paths and dirt roads available in the study site. Each point was placed 500 m apart from adjacent points and 250 m away from nearest habitat edge. Because of the distribution of habitats along paths and roads some points were separated by more than 500 m to satisfy these criteria. At each location I simultaneously surveyed birds using acoustic recordings and point counts on three consecutive days in June and July 2008. Sampling on consecutive days avoided the potential problems of seasonal variation in singing activity and/or movement into or out of the population (see closed population assumption below).

After arriving at each survey location, I recorded environmental data (temperature, relative humidity, and wind speed). After five minutes I started the recording system and began a standard point count. Data were collected for 10 minutes at each location. Based on a previous study using the same recorder and microphone sensitivities as I used in the current study, demonstrated that SRS and point counts sampled comparable areas (Celis-Murillo et al. 2009). All surveys were conducted within four hours after sunrise.

Recording System

I used a Soundscape Recording System (SRS), which consists of a four-microphone/four-channel discrete recording system combined with a quadraphonic playback system (Celis-Murillo et al. 2009). SRS is a portable system that records all environmental sounds (i.e., the entire soundscape) with each microphone pointing in one the four cardinal directions. In the field microphone one was always directed towards the north, and microphones were numbered in clockwise order. The audio was recorded onto a 4-channel digital recorder (Edirol R4- Roland©). I used *AUDACITY* to convert the four channel recordings to stereo and transcribed the data using a pair of noise-cancelling headphones (Sennheiser HD-280©). SRS recordings are designed to be played back in a quadraphonic playback room for estimating bird abundances (Celis-Murillo et al. 2009); however, for this analysis I was interested only in species detection/non-detection, and stereo headphones were adequate for this purpose. Four-channel recordings provided better acoustic information than stereo recordings even when converted after the fact to stereo and ensured that the recordings included information from the entire 360-degree range.

Transcription of acoustic recordings

To avoid confounding observer and survey method I conducted all the point counts and interpreted the recordings. To ensure that my prior knowledge, from point counts, did not influence my transcriptions of the recordings, a second person copied the master set of recordings and removed all of the identifying information (e.g., location, date) prior to transcription. Additionally, recordings were not interpreted until April and May 2009, almost one year after the surveys were conducted. This further guarded against experience biasing the transcriptions. During the 2008 field season I conducted 240 point counts and SRS recordings, further reducing the likelihood that interpretations would be affected by experience during point counts. Once identifying information was deleted from the acoustic recordings, I listened to each recording and created a list all of the species detected during each acoustic survey.

Data analysis

Species richness. – I used *SPADE* (Species Prediction And Diversity Estimation, Chao et al. 2003) to estimate species richness. The Chao2 non-parametric estimator (Coldwell and Coddington 1994) is preferred over raw species counts because it accounts for the relationship between sampling effort and species richness as well as imperfect species detection (i.e., total species richness is usually unknown because not all species are detected). Chao2 has also been shown to be one of the most precise species richness estimation methods (Walther and Martin 2001) and is robust even when estimates are made from relatively small sample sizes (Coldwell and Coddington 1994). I compared species richness between survey methods in the six habitat types by examining the overlap of standard errors for the estimates.

Species composition. – I used Chao-Jaccard multiple incidence-based (Chao-Jaccard MIB; Chao et al. 200) similarity index to estimate the overlap in species composition between the two survey methods in each of the six habitats. Chao-Jaccard MIB similarity index was selected because is less sensitive to rare species and small sample sizes (Chao et al. 2005). Additionally, the Chao-Jaccard MIB index uses information about the frequencies and identities of rare species to adjust the index to account for undetected species, therefore, assessing the probability that individuals belong to shared vs. unshared species (Chao et al 2005). I used data from the repeated visits to the 53 survey locations to calculate Chao-Jaccard MIB similarity index. I used *SPADE* to calculate Chao-Jaccard MIB similarity indices, and I compared overlap of standard errors to assess differences in species similarity between the two techniques among the six habitat types.

Common vs rare bird species. – An occupancy modeling framework was used to estimate detection probabilities for 20 common and rare species for the two survey methods and six habitat types. Occupancy modeling uses a likelihood method based on capture-recapture theory; it uses species detection/non-detection data collected over a series of visits to each survey location to estimate species detection probabilities, which are then incorporated into estimates of species occupancy rates and predict local distributions (Mackenzie et al. 2002, 2003). Occupancy models assume that: 1) the population is closed, with no emigration or immigration occurring during the sampling period, 2) species are correctly identified, and 3) the probability of detecting a species at one survey location is independent of the probability of detecting it at another location (Mackenzie et al. 2002). Covariates, such as habitat attributes or meteorological variables, are included in the models to reduce variance in parameter estimates (Mackenzie et al. 2006) and to assess relationships between detection probability or occupancy and environmental variables (Ball et al. 2005, Bailey et al. 2004, Watson et al. 2008). Nichols and his colleagues (2008) developed a multi-method occupancy approach, an extension of the single-season, single species occupancy model, to incorporate data from multiple methods, in this case SRS and point counts, into a single model. The multi-method occupancy model accounts for the lack of independence of detections between the two survey methods within sampling occasions and makes inferences about method-specific detection probabilities (Nichols et al. 2008). I used the multi-method occupancy modeling approach described by Nichols et al. (2008) to directly compare the detection probability of SRS and point counts.

I created detection histories for the 20 species using data from the three visits to the 53 survey locations; I produced detection histories for SRS and point count surveys, which were incorporated into a single data set. For each method, I assigned a "1" if the species was detected during a visit and "0" if it was not detected. I selected 10 endemic/quasi-endemic species of the Yucatan Peninsula, which are regionally and/or locally rare, and the 10 species that are common in the area. Habitat type was included as a categorical covariate, and I only included data for habitats in which a species was detected on at least one visit. Including habitats where the species is not known to occur or is detected very infrequently leads to inflated error estimates. Because the goal of my study was to compare detection probabilities between the two survey methods within and among vegetation types, rather than examine habitat occupancy patterns, removing habitats where the species was not detected does not influence the results. I ran the multi-methods models using the program *PRESENCE* (Hines 2006).

For each species, SRS and point count data were evaluated using four models testing different hypotheses regarding the factors affecting detection probability of birds, and Akaike's Information Criterion (AIC) was used to select the models that best fit the data (Burnham and Anderson 2002). I considered four models: 1. A *constant model* estimated a single detection probability for both methods and all habitat types and represented the null hypothesis of no effect of method or habitat, 2. A *method model* estimated separate detection probabilities for each survey method and tested the hypothesis that detection probability was different between methods only, 3. A *habitat model* estimated separate detection probabilities for each habitat and represented the hypothesis that habitat alone influences detection probability, and 4. The *interaction model* estimated detection probabilities for each method by habitat combination, evaluating the hypothesis that method and habitat interact to influence detection probability. I calculated second order Akaike's Information Criterion (AIC_c) values, ΔAIC_c values and model weights for each model in the candidate set; all models with ΔAIC_c values ≤ 2.0 were considered to have substantial support, such that when multiple models had ΔAIC_c values ≤ 2.0 there was uncertainty in selecting a single best model (Burnham and Anderson 2002). We used model averaging to calculate average estimates of p for each method and habitat, (equation 4.9, Burnham and Anderson 2002). Model averaging allowed me to compute unconditional estimates of variances and standard errors for each parameter. I repeated this for all 20 species. To compare the two survey methods, I compared average parameter estimates of detection probability and standard errors across the different habitats separately for each species.

CHAPTER 3: RESULTS

Species richness

A total of 132 different species, belonging to 22 families, were detected during SRS and/or point count surveys; 120 species were detected by SRS and 123 species by point counts. Based on Chao2, there was no significant difference in the estimated species richness between SRS and point counts when all habitats were combined or considered separately (Figure 2).

Species composition

Chao-Jaccard MIB similarity index ranges from 0 to 1, where 0 indicates no overlap in species composition and 1 denotes complete overlap or 100% similarity in species composition between the two survey methods. When all habitats were considered, the similarity index between the two methods indicated a non-significant difference in species composition (98% similarity ± 1). However, when habitats were considered separately, estimates of species overlap between the two survey methods varied significantly across habitat types, ranging from 92-100% (Figure 3); species composition was most similar between survey methods in habitats with dense vegetation (secondary semi-evergreen forest and mature medium-stature semi-evergreen forest) and least similar in coastal dune scrubs.

Common vs rare species

Based on the multi-method occupancy models and AIC model selection for the 20 species, the *method model* was the best-supported model for five species (Table 2). Detection probability was higher for SRS than point counts for all five species (Figures 4-5). For two (Yellow-lored Parrot and Black-headed Trogon) species, however, there was considerable uncertainty in selecting the best model (i.e., multiple models had ΔAIC_c values ≤ 2.0; Table 2).The *habitat model* was the best model for six species with detection probabilities varied among habitats where the species were found but not between methods (Table 2). For three species, Caribbean Doves (*Leptotila jamaicensis*), Mangrove Vireos (*Vireo pallens*) and Yucatan Jays (*Cyanocorax yucatanicus*), this was the only model with substantial empirical support. The *interaction model* had a ΔAIC_c value ≤ 2.0 and a high model weight for Black-throated Bobwhites (*Colinus nigrogularis*), Spot-breasted Wrens (*Thryothorus maculipectus*), and Mexican Sheartails (*Doricha eliza*) showing that the possibility of a method by habitat interaction could not be ruled out for these species. For Mexican Sheartail, the ΔAIC_c value for the *interaction model* was 0.02, indicating essentially no difference between it and the *habitat model* (Table 2). Detection probability of sheartails was higher using SRS than point counts for both habitats where the species was found, although the magnitude of the difference was larger in thorn forest than coastal dune (Figure 4). For bobwhites and wrens, SRS had a higher detection probability than point counts in all habitats except pastures, where the pattern was reversed and point counts had slightly higher detection probabilities (Figures 4-5).

The *interaction model* was the top-ranked model for four other species, indicating that method and habitat influenced detection probability (Table 2). The detection probability of Tropical Kingbirds (*Tyrannus melancholicus*), Rufous-browed Peppershrike (*Cyclarhis gujanensis*), and Thicket Tinamous (*Crypturellus cinnamomeus*) was higher for SRS than point counts in all habitats (Figure 5), but the magnitude of the difference between survey methods was not constant. Black Catbirds (*Melanoptila glabrirostris*), on the other hand, had higher detection probabilities using SRS in all habitats except pastures, where point counts performed better at detecting the species (Figure 4). There was some uncertainty regarding the best model for catbirds, as the *constant* and *method models* both had ΔAIC_c values ≤ 2.0 (Table 2).

Finally, the *constant model* was the top-ranked model for five species, suggesting no influence of method or habitat on detection probability (Table 2). For all five species, however, the *method model* also had low ΔAIC_c values and high model weights, demonstrating some uncertainty in selecting the best model. Yucatan Flycatcher showed extremely strong support for the *habitat model* ($\Delta AIC_c = 0.01$), indicating that there was essentially no difference between *constant model* and *habitat model*.

CHAPTER 4: DISCUSSION

SRS performed in a similar fashion to point counts for estimating species richness and composition, two main features of community structure. Estimates of species richness were not significantly different between methods in any of the habitats. Although similarity in species composition between SRS and point counts was lower in coastal dunes than secondary and mature semi-evergreen forests, at least 92% of the species were shared between the two methods in all habitats. Similarly, the multi-method occupancy models demonstrated that SRS yielded detection probabilities similar to or greater than those of point counts for nearly all species across all habitats, although a few important exceptions occur for species in which SRS performed better than point counts in some habitats.

Effectiveness of acoustic recordings for surveying bird communities

Haselmayer and Quinn (2000) and Celis-Murillo et al (2009) compared acoustic recording systems to point counts in Peru and California, respectively, and found no difference in the number of species detected by the two survey methods. The similarity in species richness between the two methods may be attributable to tradeoffs between the two techniques; acoustic methods may perform better than point counts for detecting and identifying vocal species, particularly rare ones, whereas point counts have the advantage of detecting quiet but visually detectable species. If this is the case then differences between the survey methods should be reflected in their species composition, as each method should detect a unique subset of species; however, my results on community similarity demonstrate that the two methods differed little in terms of species composition; estimated similarity was 92-100%. There were only a handful of species that were exclusively detected by one method or the other, likely due to behavioral differences of the species (Table 1). Point counts detected species that rarely vocalize, move frequently, and/or perch in conspicuous locations, such as pelicans, frigatebirds, egrets, and vultures. SRS, on the other hand, exclusively detected species known to be highly vocal and rare, such as Piratic Flycatcher (*Legatus leucophaius*), and hence likely to go undetected on point counts.

Although similarity in species composition between SRS and point counts was high in all habitats, similarity was significantly higher in secondary and mature semi-evergreen forests than coastal dune scrub; mangroves, thorn forests and pastures had intermediate levels of species similarity. Although I did not annotate the type of detection for each species (visual or acoustic) during point counts, it is likely that the variation in similarity across habitats is mainly due to the fact that a greater proportion of birds are detected visually in habitats where vegetation is shorter (coastal dune scrub) and/or more open (mangroves, thorn forests, and pastures), resulting in less similarity between the two survey methods. On the other hand, in tall, dense habitats, like forests, the majority of detections (up to 97%) are based on auditory cues (Brewester and Simons 2009). Like other forests, most birds in semi-evergreen forests in the Yucatan Peninsula are detected by sounds and, hence, are available for detection by both survey methods, resulting in greater overlap in species composition. Nevertheless, despite spatial variation in the proportion of species that are detected visually, the proportion of such species is small. This may be due to the fact that many species, although visually detected, often vocalize as well and are available to both techniques.

Effectiveness of acoustic recordings for surveying target species

The multi-method occupancy modeling approach provides a way to directly compare detection probabilities of multiple survey methods conducted simultaneously (Nichols et al. 2008). Using multi-method occupancy models I found clear evidence that method influenced species detection probabilities, either independently or interactively with habitat, for six species (Golden-fronted Woodpecker, Orange Oriole, Rose-throated Tanager, Tropical Kingbird, Rufous-browed Peppershrike, and Thicket Tinamou); in all species SRS yielded higher detection probabilities than point counts, although the magnitude of the advantage of SRS varied among habitats for some species (indicated by the strong support for the *interaction model*). Thus, if a researcher needs to select a single method for surveying these species, SRS would be the preferred choice. Several other species showed some support for an effect of method, but the strength of support was reduced, and given the set of four candidate models, there was considerable uncertainty in selecting the best model to fit the data. For most species (those in which the *habitat* or *constant models* were the top-ranked models) SRS and point counts performed equally well, suggesting either survey method would be appropriate for those species.

Several researchers have documented significant effects of habitat on the detection probability of vocalizing species. Schieck (1997) broadcasted vocalizations at different distances and heights in different habitat types demonstrated significant influence of habitat type in the detection probability of species. Gonzalo-Turpin et al (2008) suggested that bird behavior was affected by habitat and consequently, affected species detectability and occupancy estimations. Furthermore, Pacifici et al. (2008) found similar results using an experimental bird-simulation system to firmly demonstrate that habitat has a significant effect on detection probability of bird species that are detected via vocalizations. Many species I examined also showed differences in detection probability among habitats, both for SRS and point counts. These differences are not surprising. Furthermore, variation in detection probability among habitats is not problematic when using approaches such as occupancy modeling, which account for imperfect detection probability, to estimate species occupancy or relative abundances.

For Black Catbird and, to a lesser extent, Black-throated Bobwhite and Spot-breasted Wren, there was evidence that SRS and point counts performed differently across the habitats where the species were found, suggesting that the use of a single survey method may not be appropriate for sampling these species. All three species demonstrated higher detection probabilities using point counts in pastures, whereas SRS had higher detection probabilities in the remaining habitats. These three species vocalize frequently in all three habitats, although in pastures, the most open habitat type sampled, they are sighted almost as often as they are heard. It may be that the availability of visual cues in addition to acoustic cues in pastures enhances their detection in pastures when using point counts. The advantage of point counts over SRS in pastures was greatest for Black Catbirds. A combination of both SRS and point counts would be the best approach for surveying these species. Using the multi-method model data from both techniques can be combined into a single analysis to estimate more accurate occupancy rates than a single method models (Nichols et al. 2008).

As expected SRS performed better than point counts for rare species (e.g. endemic species), that are detected primarily by vocalizations, because field observers are less likely to be familiar with their vocalizations. There was no clear advantage of SRS over point counts for rare species, however, some rare species had higher detection probabilities using SRS (e.g., Orange Oriole, Rose-throated Tanager, Yellow-lored Parrot), but many other rare species were sampled equally well using both techniques (e.g., Yucatan Flycatcher and Yucatan Wren). Additionally, many common species were detected better using SRS than point counts. With possibly the exceptions of Black Catbird and Black-throated Bobwhite, SRS performs as well or better than point counts, and SRS is an appropriate choice for surveying these species.

Collectively my results on richness and similarity suggest that, although there are a small number of species detected exclusively by one method or the other, SRS and point counts perform equally well at detecting and identifying the majority of species in six tropical habitats in the northeastern Yucatan Peninsula. Thus, the choice of a survey technique for characterizing bird communities is more of a logistic question than a monitoring technique question. Because SRS offers a logistically easier method given the lack of experienced point count technicians, SRS stands to help characterize the bird communities in tropical habitats. However, in some cases, a combination of techniques, each with different advantages, should be used, and data should be combined into a single analysis (Nichols et al. 2008).

In addition to biological considerations, the choice of one survey technique over another or a combination of methods will be dependent to a large extent on financial considerations. Celis-Murillo et al. (2009) discussed the financial costs and benefits of using SRS and similar portable acoustic recording surveys. It is worth noting that such systems will be most cost-effective when many locations are being sampled so that the cost of the unit is spread out across all the points and years of the study and when volunteers or inexperienced technicians are hired to collect recordings in the field. Although experts are currently required to interpret recordings, costs will be further reduced once automated sound recognition software has been thoroughly developed and tested.

The use of acoustic recordings for monitoring bird communities and populations in temperate and tropical regions is in its infancy. Researchers need to be careful in selecting survey methods that most accurately estimate the parameters of interest.

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FIGURES AND TABLES

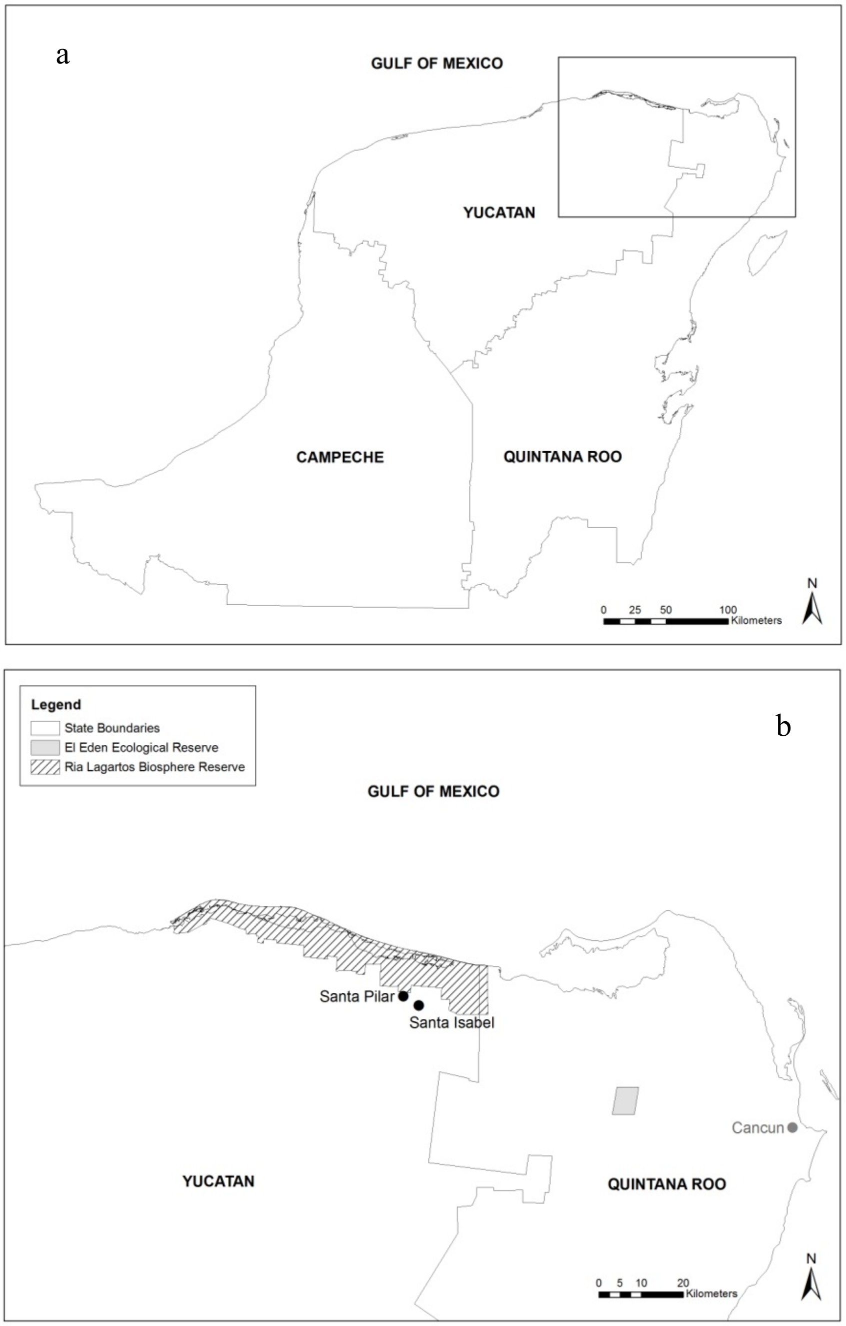

Figure 1. – Yucatan Peninsula (a) and northeastern region of the peninsula (b) illustrating the four study sites. Survey locations were distributed throughout the Ria Lagartos Biosphere Reserve and El Eden Ecological Reserve.

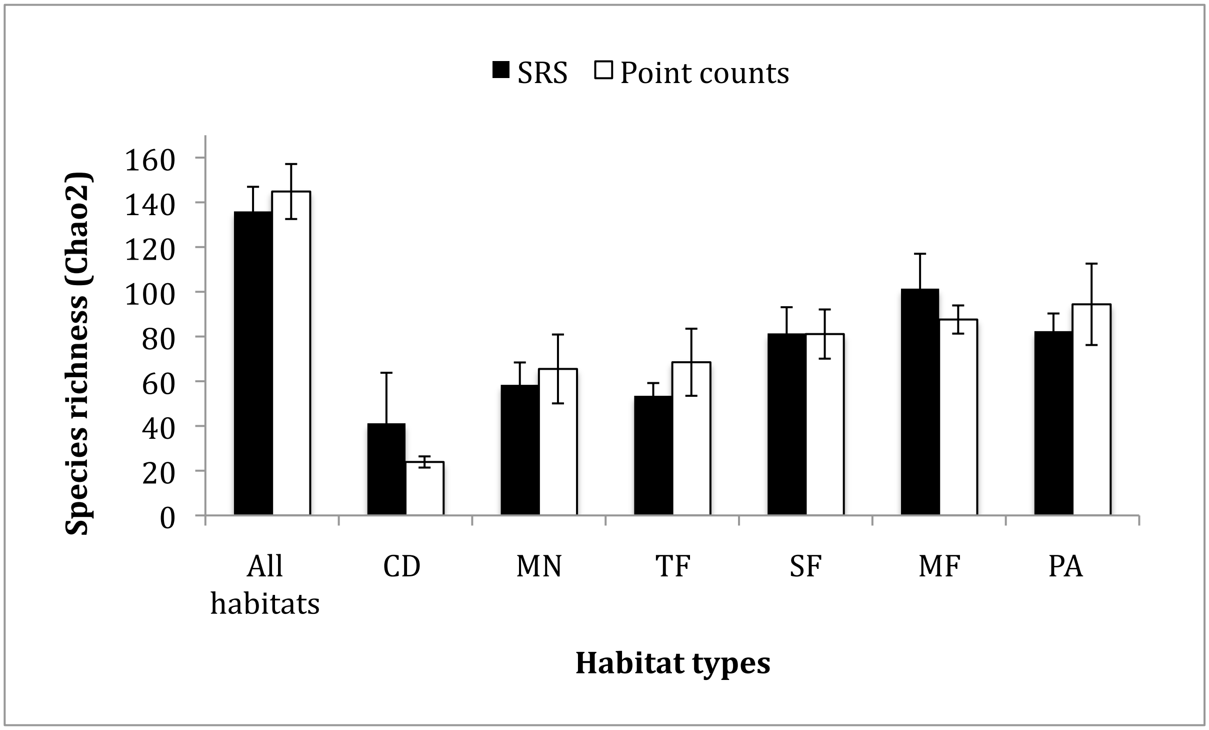

Figure 2. Estimates of species richness ± standard error based on Chao2 estimator for six tropical habitats combined and separately for SRS and point counts.

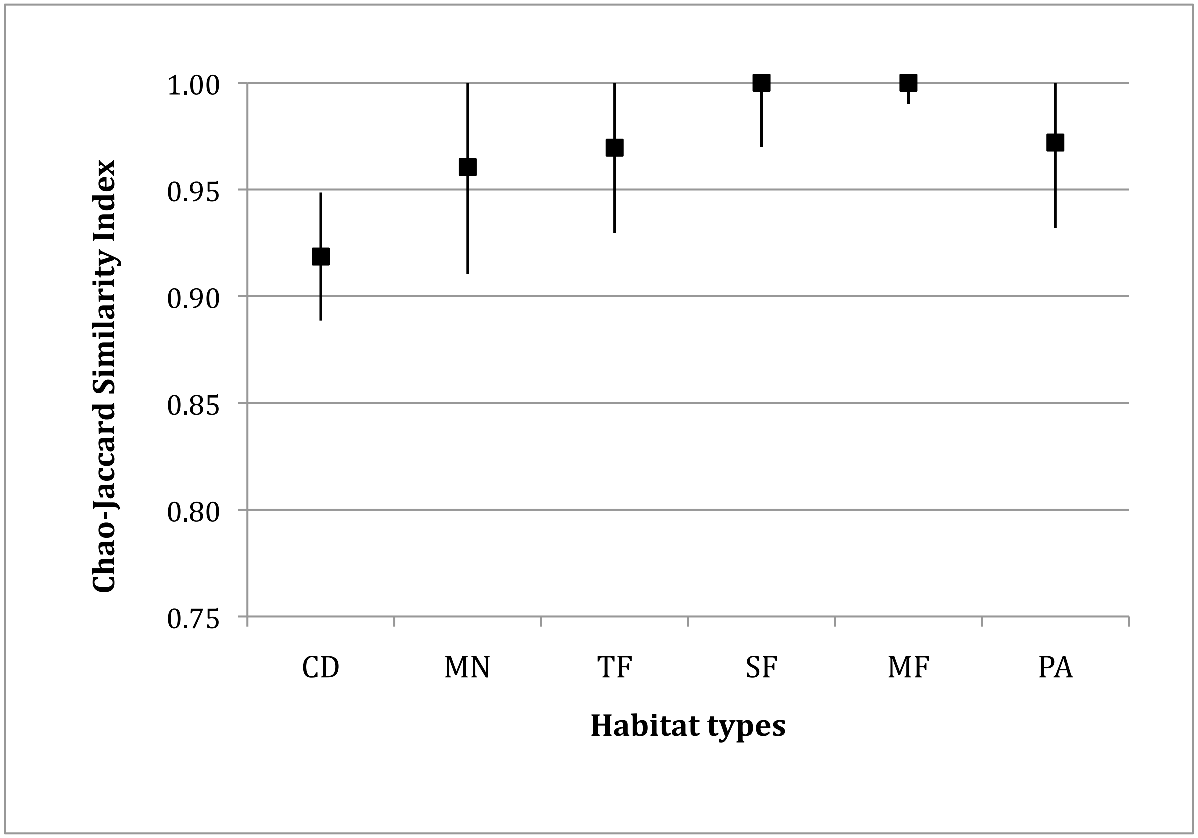

Figure 3. Estimate ± standard error of similarity in species composition between SRS and point counts surveys in six habitat types. CD = coastal dune scrub, MN = mangrove, TF = mature low-stature deciduous thorn forest, SF = secondary semi-evergreen forest, MF = mature medium-stature semi-evergreen forest, and PA = grazed pastures.

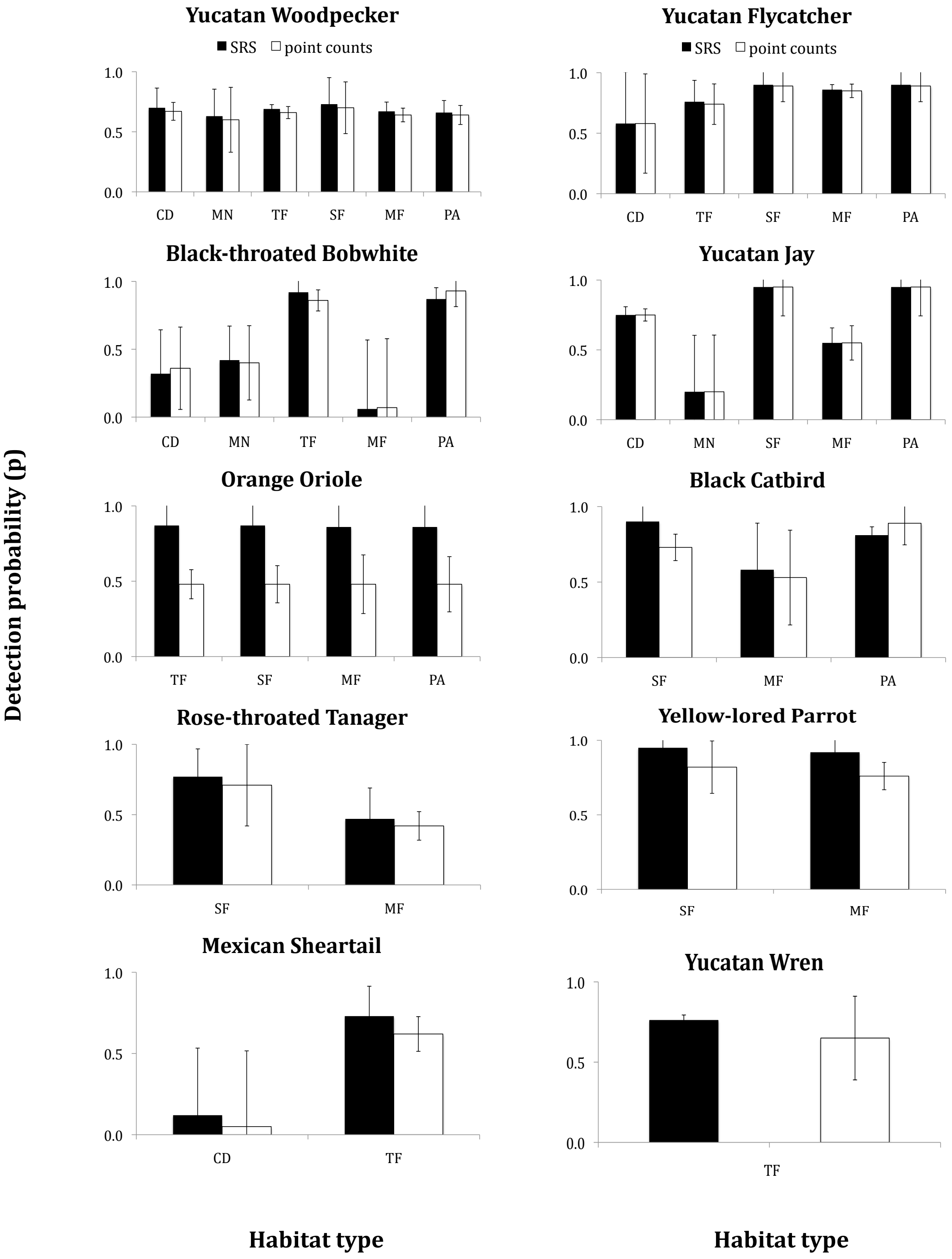

Figure 4. Model-averaged detection probability estimates (± SE) for SRS and point counts for 10 endemic/quasi-endemic species in the study area and the habitats where they detected on at least one visit. CD = coastal dune scrub, MN = mangrove, TF = mature low-stature deciduous thorn forest, SF = secondary semi-evergreen forest, MF = mature medium-stature semi-evergreen forest, and PA = grazed pastures.

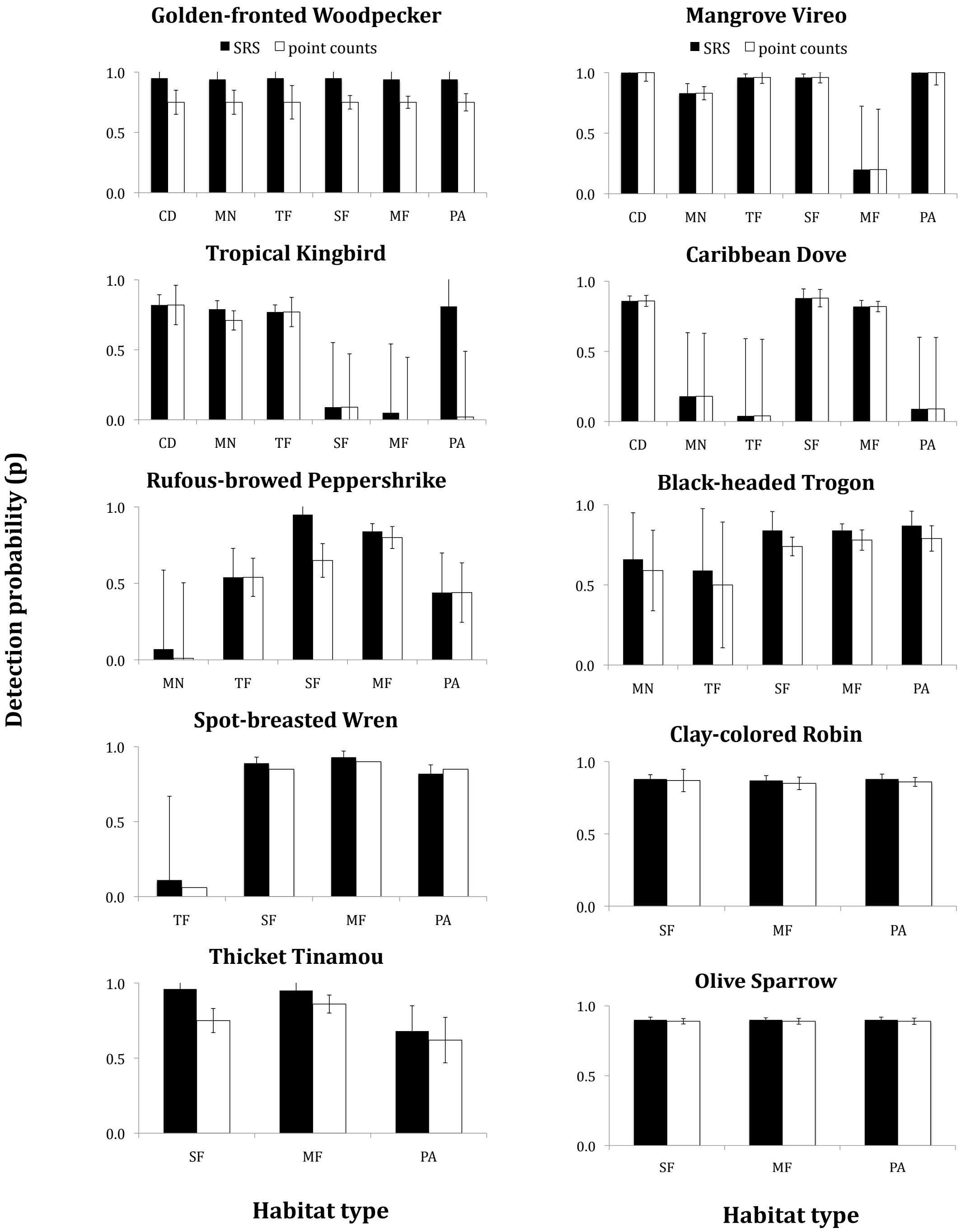

Figure 5. Model-averaged detection probability estimates (± SE) for SRS and point counts for the 10 most common bird species in the study area and the habitats where they detected on at least one visit. CD = coastal dune scrub, MN = mangrove, TF = mature low-stature deciduous thorn forest, SF = secondary semi-evergreen forest, MF = mature medium-stature semi-evergreen forest, and PA = grazed pasture.

Table 1. Total number of visits during which each species was detected in the six habitat types and by the two survey methods (SRS or Point Counts). CD = coastal dune scrub, MN = mangrove, TF = mature medium-stature semi-evergreen forest, SF = mature low-stature deciduous thorn forest, SF = secondary semi-evergreen forest and PA = grazed pastures. SRS = Soundscape Recording System, PC= Point Counts. Raw counts of species richness and similarity (unadjusted for imperfect detection and sampling effort) for each habitat.

Species	**CD**		**MN**		**TF**		**SF**		**MF**		**PA**	
	SRS	**PC**	**SRS**	**PC**	**SRS**	**PC**	**SRS**	**PC**	**SRS**	**PC**	**SRS**	**PC**
Thicket Tinamou (*Crypturellus cinnamomeus*)	0	0	0	0	0	0	18	13	30	27	10	9
American White Pelican (*Pelecanus erythrorhynchos*)**	0	0	0	1	0	0	0	0	0	0	0	0
Brown Pelican (*Pelecanus occidentalis*)**	0	2	0	0	0	0	0	0	0	0	0	0
Magnificent Frigatebird (*Fregata magnificens*)**	0	3	0	4	0	3	0	0	0	0	0	0
Bare-throated Tiger-Heron (*Tigrisoma mexicanum*)	0	0	2	1	1	1	0	0	0	0	0	0
Cattle Egret (Bubulcus ibis)**	0	0	0	0	0	1	0	0	0	0	0	0
White Ibis (*Eudocimus albus*)	0	0	1	1	0	0	0	0	0	0	0	0
Black-bellied Whistling-Duck (*Dendrocygna autumnalis*)	0	0	11	8	5	4	0	0	0	0	0	0
Black Vulture *(Coragyps atratus*)**	0	0	0	0	0	0	0	0	0	0	0	3
Turkey Vulture (*Cathartes aura*)**	0	0	0	0	0	1	0	0	0	0	0	3
Snail Kite (*Rostrhamus sociabilis*)**	0	1	0	0	0	0	0	0	0	0	0	0
Common Black-Hawk (*Buteogallus anthracinus*)	0	0	3	1	0	0	0	0	0	0	0	0
Great Black-Hawk (*Buteogallus urubitinga*)	0	0	1	0	0	0	0	0	0	0	0	0
Roadside Hawk (*Buteo magnirostris*)	0	0	0	0	0	0	4	1	2	2	2	1
Laughing Falcon (*Herpetotheres cachinnans*)	0	0	5	4	0	0	1	1	1	2	0	0
Plain Chachalaca (*Ortalis vetula*)	7	9	0	0	1	1	9	9	11	12	4	3
Ocellated Turkey (*Meleagris ocellata*)	0	0	0	0	0	0	0	0	1	1	0	0
Black-throated Bobwhite (*Colinus nigrogularis*)	4	6	6	6	14	11	0	0	1	2	9	11
Ruddy Crake (*Laterallus ruber*)	0	0	5	2	0	0	0	0	0	0	0	0
Gray-necked Wood-Rail (*Aramides cajanea*)	0	0	0	0	2	2	0	1	0	0	0	0
Limpkin (*Aramus guarauna*)	0	0	0	0	1	1	0	0	0	0	1	0
Black-necked Stilt *(Hymantopus mexicanus*)	0	0	1	1	1	1	0	0	0	0	0	0
Northern Jacana (*Jacana spinosa*)	0	0	0	0	2	1	0	0	0	0	0	0
Greater Yellowlegs (*Tringa melanoleuca*)	3	0	0	0	1	0	0	0	0	0	0	0
Semipalmated Sandpiper (*Calidris pusilla*)*	0	0	3	0	0	0	0	0	0	0	0	0
Least Sandpiper (*Calidris minutilla*)**	0	0	0	1	0	0	0	0	0	0	0	0
Laughing Gull (*Leucophaeus atricilla*)	1	0	4	4	0	1	0	0	0	0	0	0
Royal Tern (*Thalasseus maximus*)*	1	0	0	0	0	0	0	0	0	0	0	0

Table 1. Continued.

Species	CD		MN		TF		SF		MF		PA	
	SRS	PC	SRS	PC	SRS	PC	SRS	PC	SRS	PC	SRS	PC
Red-billed Pigeon (*Patagioenas flavirostris*)	0	0	0	0	0	0	12	9	8	5	0	1
White-winged Dove (*Zenaida asiatica*)	3	2	18	18	12	10	10	12	5	8	4	4
Zenaida Dove (*Zenaida aurita*)	0	0	7	4	0	0	0	0	0	0	0	0
Common Ground-Dove (*Columbina passerina*)	4	6	8	7	6	5	1	1	0	0	5	4
Ruddy Ground-Dove (*Columbina talpacoti*)	0	0	0	0	0	0	0	0	0	0	3	5
Blue-ground Dove (*Columbina pretiosa*)	0	0	0	0	0	0	0	1	9	12	2	3
White-tipped Dove (*Leptotila verreauxi*)	0	1	6	5	12	11	3	1	8	6	10	10
Caribbean Dove (*Leptotila jamaicensis*)	18	18	2	6	0	1	18	17	30	25	1	3
Olive-throated Parakeet (*Aratinga nana*)	0	0	0	0	2	2	4	4	5	4	0	1
White-fronted Parrot (*Amazona albifrons*)	0	0	0	0	2	2	4	2	19	21	3	1
Yellow-lored Parrot (*Amazona xantholora*)	0	0	0	0	0	0	1	1	6	4	0	0
Yellow-billed Cuckoo (*Coccyzus americanus*)	0	0	0	0	0	0	0	0	1	1	0	0
Mangrove Cuckoo (*Coccyzus minor*)	4	2	2	2	5	4	0	0	0	0	0	0
Squirrel Cuckoo (*Piaya cayana*)	0	0	0	0	0	0	4	3	7	5	0	0
Groove-billed Ani (*Crotophaga sulcirostris*)	11	7	8	7	10	9	1	1	0	0	1	2
Ferruginous Pygmy-Owl (*Glaucidium brasilianum*)	0	0	4	4	2	2	2	2	6	7	1	2
Lesser Nighthawk (*Chordeiles acutipennis*)	0	0	0	1	1	1	0	0	0	0	0	0
Common Pauraque (*Nyctidromus albicollis*)**	0	0	0	0	0	0	0	0	0	1	0	0
Vaux's Swift (*Chaetura vauxi*)	0	0	2	2	0	0	0	0	2	2	0	0
Wedge-tailed Sabrewing (*Campylopterus curvipennis*)**	0	0	0	0	0	0	0	1	0	0	0	0
Cinnamon Hummingbird (*Amazilia rutila*)	1	1	0	1	0	0	0	0	1	1	0	1
Mexican Sheartail (*Doricha eliza*)	2	0	0	0	7	5	0	0	0	0	0	0
Black-headed Trogon (*Trogon melanocephalus*)	0	0	5	4	3	1	9	6	22	20	9	7
Violaceous Trogon (*Trogon violaceus*)	0	0	0	0	0	0	1	1	6	4	6	5
Blue-crowned Motmot (*Momotus momota*)	0	0	0	0	0	0	8	4	20	13	4	1
Turquoise-browed Motmot (*Eumomota superciliosa*)	0	0	0	0	0	1	0	1	1	2	5	2
Yucatan Woodpecker (*Melanerpes pygmaeus*)	3	2	2	1	3	4	3	3	3	3	2	2
Golden-fronted Woodpecker (*Melanerpes aurifrons*)	18	15	16	10	12	11	13	9	19	17	14	12
Ladder-backed Woodpecker (*Picoides scalaris*)*	0	0	0	0	1	0	0	0	0	0	0	0
Lineated Woodpecker (*Dryocopus lineatus*)	0	0	0	0	0	0	0	0	1	1	1	0
Pale-billed Woodpecker (*Campephilus guatemalensis*)	0	0	0	0	0	0	0	0	1	1	0	0

Table 1. Continued.

Species	**CD**		**MN**		**TF**		**SF**		**MF**		**PA**	
	SRS	**PC**	**SRS**	**PC**	**SRS**	**PC**	**SRS**	**PC**	**SRS**	**PC**	**SRS**	**PC**
Tawny-winged Woodcreeper (*Dendrocincla anabatina*)	0	0	0	0	0	0	0	0	2	2	0	0
Ruddy Woodcreeper (*Dendrocincla homochroa*)	0	0	0	0	0	0	1	1	0	0	0	0
Ivory-billed Woodcreeper (*Xiphorhynchus flavigaster*)	0	0	1	0	0	0	6	3	10	9	1	0
Barred Antshrike (*Thamnophilus doliatus*)	0	0	0	0	0	0	4	3	2	2	4	4
Northern Beardless-Tyrannulet (*Camptostoma imberbe*)	0	0	0	0	1	0	5	3	8	6	0	0
Greenish Elaenia (*Myiopagis viridicata*)	0	0	0	0	0	0	3	1	4	4	0	0
Yellow-bellied Elaenia (*Elaenia flavogaster*)	0	0	0	0	0	0	1	0	0	0	2	1
Northern Bentbill (*Oncostoma cinereigulare*)	0	0	0	0	0	0	2	3	16	13	2	0
Yellow-olive Flycatcher (*Tolmomyias sulphurescens*)	0	0	0	0	0	0	4	0	3	2	6	3
Tropical Pewee (*Contopus cinereus*)	0	0	0	1	1	1	0	0	1	1	5	1
Vermilion Flycatcher (*Pyrocephalus rubinus*)**	0	0	0	0	0	0	0	0	0	0	0	1
Bright-rumped Attila (*Attila spadiceus*)	0	0	7	5	2	0	4	2	10	12	2	1
Yucatan Flycatcher (*Myiarchus yucatanensis*)	1	0	0	0	2	1	2	2	9	9	1	1
Dusky-capped Flycatcher (*Myiarchus tuberculifer*)	0	0	3	1	0	0	5	2	10	12	5	4
Brown-crested Flycatcher (*Myiarchus tyrannulus*)	1	1	9	7	4	2	2	2	0	0	6	7
Geat Kiskadee (*Pitangus sulphuratus*)	0	0	12	4	3	3	1	0	1	2	6	4
Boat-billed Flycatcher (*Megarynchus pitangua*)*	0	0	0	0	0	0	0	0	0	0	1	0
Social Flycatcher (*Myiozetetes similis*)	0	0	4	2	5	2	3	1	5	1	10	8
Sulphur-bellied Flycatcher (*Myiodynastes luteiventris*)	0	0	0	0	0	0	1	0	0	1	2	1
Piratic Flycatcher (*Legatus leucophaius*)*	0	0	0	0	0	0	0	0	1	0	3	0
Tropical Kingbird (*Tyrannus melancholicus*)	11	11	10	10	5	5	1	1	1	0	10	5
Couchi's Kingbird (*Tyrannus couchii*)	4	3	4	3	1	0	2	1	4	5	7	5
Stub-tailed Spadebill (*Platyrinchus cancrominus*)	0	0	0	0	0	0	4	1	10	4	0	0
Rose-throated Becard (*Pachyramphus aglaiae*)	0	0	0	0	0	0	0	0	0	0	3	3
Masked Tityra (*Tityra semifasciata*)**	0	0	0	0	0	0	0	0	0	1	0	0
Black-crowned Tityra (*Tityra inquisitor*)	0	0	2	0	0	0	0	0	0	0	1	1
Green Jay (*Cyanocorax yncas*)	0	0	1	0	0	0	1	2	3	2	0	0
Brown Jay (*Cyanocorax morio*)	0	0	0	0	0	0	8	7	12	7	4	4
Yucatan Jay (*Cyanocorax yucatanicus*)	4	4	0	1	0	0	3	3	5	5	2	2
Yucatan Wren (*Campylorhynchus yucatanicus*)	0	0	0	0	9	9	0	0	0	0	0	0
Spot-breasted Wren (*Thryothorus maculipectus*)	0	0	0	0	2	0	17	14	29	26	10	11

Table 1. Continued.

Species	CD		MN		TF		SF		MF		PA	
	SRS	**PC**	**SRS**	**PC**	**SRS**	**PC**	**SRS**	**PC**	**SRS**	**PC**	**SRS**	**PC**
Carolina Wren (*Thryothorus ludovicianus*)	0	0	0	0	0	0	4	4	17	12	0	0
White-bellied Wren (*Uropsila leucogastra*)	0	0	0	0	3	5	5	3	8	5	0	0
House Wren (*Troglodytes aedon*)	0	0	0	0	0	0	0	0	0	0	4	3
Long-billed Gnatwren (*Ramphocaenus melanurus*)	0	0	0	0	0	0	0	0	3	3	1	0
Blue-gray Gnatcatcher (*Polioptila caerulea*)	1	0	0	0	5	4	1	1	0	0	3	2
Tropical Gnatcatcher (*Polioptila plumbea*)	0	0	0	0	0	0	0	0	3	2	0	0
Clay-colored Robin (*Turdus grayi*)	0	0	0	0	0	0	6	7	10	9	15	13
Black Catbird (*Melanoptila glabrirostris*)	0	0	0	0	0	0	12	8	5	4	7	9
Tropical Mockingbird (*Mimus gilvus*)	17	15	6	4	11	9	0	0	0	0	0	4
Mangrove Vireo (*Vireo pallens*)	22	22	17	15	14	13	13	12	6	3	6	6
Yellow-green Vireo (*Vireo flavoviridis*)	0	0	0	0	0	0	9	9	19	18	11	10
Rufous-browed Peppershrike (*Cyclarhis gujanensis*)	0	0	1	0	4	4	18	11	15	14	4	4
Northern Waterthrush (*Seiurus noveboracensis*)*	0	0	0	0	0	0	0	0	1	0	0	0
Grey-crowned Yellowthroat (*Geothlypis poliocephala*)	0	0	1	2	2	0	0	0	0	0	5	3
Gray-throated Chat (*Granatellus sallaei*)	0	0	0	0	0	0	0	0	1	1	0	0
Red-legged Honeycreeper (*Cyanerpes cyaneus*)	0	0	0	0	0	0	0	0	2	1	1	1
Scrub Euphonia (*Euphonia affinis*)	0	0	1	0	0	0	0	0	1	1	1	0
Yellow-throated Euphonia (*Euphonia hirundinacea*)	0	0	0	0	0	0	0	0	3	2	0	0
Red-crowned Ant-Tanager (*Habia rubica*)	0	0	0	0	0	0	4	0	7	4	0	0
Red-throated Ant-tanager (*Habia fuscicauda*)	0	0	0	0	0	0	4	8	10	8	1	0
Rose-throated Tanager (*Piranga roseogularis*)	0	0	0	0	0	0	9	4	18	9	0	0
Grayish Saltator (*Saltator coerulescens*)	0	0	0	0	0	0	2	2	7	6	13	8
Black-headed Saltator (*Saltator atriceps*)	0	0	1	1	0	0	0	0	5	4	1	0
Northern Cardinal (Cardinalis cardinalis)	17	10	1	1	12	11	0	0	4	5	2	4
Blue Bunting (*Cyanocompsa parellina*)	0	0	0	0	0	0	1	2	12	6	1	1
Olive Sparrow (*Arremonops rufivirgatus*)	0	0	0	0	0	0	13	13	12	12	13	12
Green-backed Sparrow (*Arremonops chloronotus*)	0	0	0	0	0	0	1	0	5	3	2	0
Blue-black Grasquit (*Volatinia jacarina*)	0	0	0	0	0	0	0	1	0	0	7	9
White-collared Seedeater (*Sporophila torqueola*)	0	0	0	0	0	0	1	0	0	0	11	8
Yellow-faced Grassquit (*Tiaris olivaceus*)	0	0	0	0	0	0	2	1	0	0	7	4
Botteri's Sparrow (*Aimophila botterii*)	0	0	0	0	0	0	0	0	0	0	1	1
Red-winged Blackbird (*Agelaius phoeniceus*)	0	0	3	3	10	9	0	0	0	0	0	0

Table 1. Continued.

Species	**CD**		**MN**		**TF**		**SF**		**MF**		**PA**	
	SRS	**PC**	**SRS**	**PC**	**SRS**	**PC**	**SRS**	**PC**	**SRS**	**PC**	**SRS**	**PC**
Melodious Blackbird (*Dives dives*)	0	0	4	3	1	1	4	2	10	9	14	9
Great-tailed Grackle (*Quiscalus mexicanus*)	0	0	1	0	15	12	0	1	0	0	4	1
Shiny cowbird (*Molothrus bonariensis*)	0	0	0	1	1	1	0	0	0	0	0	0
Black-cowled Oriole (*Icterus prosthemelas*)*	0	0	0	0	0	0	1	0	0	0	0	0
Hooded Oriole (*Icterus cucullatus*)	9	6	1	0	0	1	0	0	3	3	0	0
Yellow-backed Oriole (*Icterus chrysater*)	0	0	0	0	0	0	3	2	1	1	0	0
Yellow-tailed Oriole (*Icterus mesomelas*)	0	0	1	3	0	0	0	0	1	1	2	1
Orange Oriole (*Icterus auratus*)	0	0	0	0	6	3	6	3	4	2	1	1
Altamira Oriole (*Icterus gularis*)	0	0	0	0	0	0	0	0	2	1	4	4
Yellow-billed Cacique (*Amblycercus holosericeus*)	0	0	0	0	0	0	9	6	8	5	0	0
Total number of visits in each habitat	22	22	22	22	15	15	21	21	36	36	18	18
Raw count of total number of species detected	24	22	45	44	46	46	64	62	78	78	70	66
Raw count of total number of shared species	18		36		39		56		75		59	

* = Species detected only by SRS

** = Species detected only by Field Observer

Table 2. AICc differences and model weights for the four candidate models for the 20 species analyzed. For each species, we fit SRS and point count data to four models testing different hypothesis regarding factors affecting detection probability of birds: *constant model,* no effects of habitat or method, *method model,* differences in detection probability between methods, *habitat model,* different detection probabilities among habitats, and *interaction method-habitat model,* method and habitat interaction influencing detection probability. Only models with $\Delta AIC_c \leq 2$ are shown in the table. Models with the lowest ΔAIC_c value and highest Akaike weight are shown in bold. When the ΔAIC_c value of the second best model was less than 0.03 both it and the top model are in bold text. Common names follow the AOU - Checklist of North American birds, 7th edition, and Table 5 provides scientific names for all 20 species.

Species (common name)	Status	p(*method*)		p(*habitat*)		p(*interaction method-habitat*)		p(*constant model*)	
		ΔAIC	W	ΔAIC	W	ΔAIC	W	ΔAIC	W
Golden-fronted Woodpecker	Common	**0.00**	**0.98**						
Orange Oriole	Endemic	**0.00**	**0.92**						
Rose-throated Tanager	Endemic	**0.00**	**0.83**						
Yellow-lored Parrot	Endemic	**0.00**	**0.45**					0.77	0.31
Black-headed Trogon	Common	**0.00**	**0.38**	0.28	0.33			1.69	0.16
Caribbean Dove	Common			**0.00**	**1.00**				
Mangrove Vireo	Common			**0.00**	**0.98**				
Yucatan Jay	Endemic			**0.00**	**0.84**				
Black-throated Bobwhite	Endemic			**0.00**	**0.70**	1.74	0.30		
Spot-breasted Wren	Common			**0.00**	**0.70**	1.72	0.30		
Mexican Sheartail	Endemic			**0.00**	**0.50**	**0.02**	**0.49**		
Tropical Kingbird	Common					**0.00**	**0.95**		
Rufous-browed Peppershrike	Common					**0.00**	**0.75**		
Thicket Tinamou	Common					**0.00**	**0.71**		
Black Catbird	Endemic	1.98	0.17			**0.00**	**0.45**	1.00	0.27
Yucatan Wren	Endemic	2.00	0.27					**0.00**	**0.73**
Olive Sparrow	Common	1.49	0.29					**0.00**	**0.62**
Clay-colored Robin	Common	1.50	0.28					**0.00**	**0.60**
Yucatan Woodpecker	Endemic	1.60	0.26					**0.00**	**0.59**
Yucatan Flycatcher	Endemic	1.80	0.17	**0.01**	**0.41**			**0.00**	**0.41**