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Effectiveness and utility of acoustic recordings for surveying tropical birds

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ABSTRACT. Although acoustic recordings have recently gained popularity as an alternative to point counts for surveying birds, little is known about the relative performance of the two methods for detecting tropical bird species across multiple vegetation types. During June and July 2008, we collected species detection/nondetection data to compare the performance of a quadraphonic acoustic recording system and point counts for estimating species richness and composition and detection probabilities of 15 rare, moderately common, and common tropical bird species across six structurally distinct vegetation types (coastal dune scrub, mangrove, low-stature deciduous thorn forest, early and late successional medium-stature semievergreen forest, and grazed pastures) in the northern Yucatan Peninsula. We selected five rare species endemic to the Yucatan Peninsula and 10 moderately common and common species that also occur in other tropical regions. Species richness and composition did not differ between survey methods in any of the vegetation types. At the population level, however, we found support for an effect of method on detection probability for most species. For 13 species, regardless of their abundance, acoustic recordings yielded detection probabilities as high as or higher than those for point counts across all vegetation types. The remaining two species were better detected by point counts in pastures and coastal scrub, where greater visibility likely improved sightings of these species. However, these species were detected as well as or better by acoustic recordings in forests and mangroves where detections were primarily auditory. In tropical regions where experienced field observers may not be available and funding for field surveys may be limited, acoustic recordings offer a practical solution for determining species richness and composition and the occupancy patterns of most species. However, for some species, a combination of methods will provide the most reliable data. Regardless of the method selected, analyses that account for variation in detection probability among vegetation types will be necessary because most species in our study demonstrated vegetation-dependent detection probabilities.

RESUMEN. **Eficacia y utilidad de las grabaciones acústicas para el muestreo de aves tropicales**
El uso de grabaciones acústicas recientemente ha ganado popularidad como una alternativa a los conteos por punto para el muestreo de aves. Sin embargo, poco se sabe sobre el desempeño de ambos métodos en la detección de especies de aves tropicales en múltiples tipos de vegetación. En Junio y Julio del 2008, se colectaron datos de detección/no-detección para comparar el desempeño de un sistema portátil de grabación cuadrafónico y los conteos por punto en la estimación de riqueza de especies, composición y probabilidades de detección de 15 especies tropicales raras, moderadamente comunes y comunes a través de seis diferentes tipos de vegetación tropicales (duna costera, manglar, selva baja caducifolia espinosa, selva mediana subcaducifolia primaria y secundaria y pastizales) en el norte de la Península de Yucatán, México. De las 15 especies seleccionadas para estimar probabilidades de detección, las 5 especies raras son endémicas de la Península de Yucatán y las 10 especies moderadamente comunes y comunes, se distribuyen en otras regiones tropicales. Las estimaciones de la riqueza de especies no fueron significativamente diferentes entre ambos métodos y entre cualquiera de los tipos de vegetación. A nivel poblacional, encontramos efectos de metodología en la probabilidad de detección para la mayoría de las especies. Para 13 especies, independientemente de su estatus de abundancia, el método de grabaciones acústicas resultó en altas o mayores probabilidades de detección que los puntos de conteo en todos los tipos de vegetación. Las otras dos especies fueron mejor detectadas en conteos por puntos en pastizales y en dunas costeras, donde la visibilidad posiblemente mejoró su detección. Sin embargo, estas especies, se detectaron tan bien o mejor por las grabaciones acústicas en selvas y manglares, donde las detecciones fueron primeramente auditivas. En regiones tropicales donde existe limitación de observadores de campo bien capacitados y financiamiento para estudios de campo, las grabaciones acústicas ofrecen una solución practica para describir la riqueza de especies, composición y patrones de ocupación para la mayoría de las especies. Sin embargo, paras algunas especies, la combinación de métodos ofrecerá datos más confiables.

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Independientemente del método seleccionado, serán necesarios análisis que tomen en cuenta la variación en la probabilidad de detección entre tipos de vegetación ya que la mayoría de las especies demostraron probabilidades de detección dependientes de la vegetación.

Key words: acoustic monitoring, acoustic recording systems, detection probability, multimethod model, point counts, tropical birds, Yucatan Peninsula

Point counts have long been used to survey tropical birds (Blake 1992, Lynch 1995) because they are easy to implement, require minimal equipment, and allow sampling of birds across multiple vegetation types during all seasons (Lynch 1995). More recently, researchers have used acoustic recordings to collect data on bird populations and communities (Hobson et al. 2002, Celis-Murillo et al. 2009, Hutto and Stutzman 2009, Dawson and Efford 2009). Acoustic recordings have several potential advantages, e.g., recordings create a permanent record of surveys that can be replayed to resolve ambiguities, can be listened to by multiple observers to verify species identifications (Rempel et al 2005), and can be re-analyzed using song identification programs (Brandes 2008, Goyette et al. 2011).

Point counts and acoustic recordings also have limitations, with neither method performing equally well at sampling all species in all environments at all times (Gregory et al. 2004). Thus, when sampling birds to produce a species inventory (composition) or estimate species richness, occupancy, or abundance, determining which survey method is most effective is critical. In some cases, such as when an entire community is of interest, a combination of methods may be required. Because many, if not most, studies examining population trends and responses to habitat alteration involve sampling birds across vegetation types, the method used must either perform similarly across vegetation types or investigators must know and account for biases associated with the method used in the various vegetation types.

Several investigators have examined the capabilities and biases of acoustic recording surveys by comparing data collected with recordings (and subsequently reviewed in the lab) to data collected by observers performing point counts (Haselmayer and Quinn 2000, Hobson et al. 2002, Celis-Murillo et al. 2009, Hutto and Stutzman 2009). Acoustic recordings have generally produced similar or higher estimates of species richness than point counts (Haselmayer and Quinn 2000, Hobson et al. 2002, Acevedo and Villanueva-Rivera 2006, Celis-Murillo et al. 2009). However, Hutto and Stutzman (2009) found that significantly more bird species were detected using point counts than acoustic recordings, a pattern they suggested was due to the inability of their recording system to record distant sounds or sounds embedded in other noise.

Haselmayer and Quinn (2000) and Acevedo and Villanueva-Rivera (2006) compared species richness estimates determined using acoustic recordings and point counts in tropical forests, where recordings may be advantageous because of the high species diversity and low visibility. Haselmayer and Quinn (2000) found that more species were detected using acoustic recordings than point counts at locations with a greater number of species, but reported no difference when data were averaged over all survey locations. Additionally, rare species were detected more frequently with point counts than recordings, possibly due to the limited detection range of the highly directional recording system. Haselmayer and Quinn (2000) hypothesized that use of an omni-directional system could improve detection rates of rare species. Acevedo and Villanueva-Rivera (2006) used an omni-directional microphone to estimate species richness and documented significantly higher richness using an acoustic recording system, but they did not evaluate the relative effectiveness of the two methods for surveying rare species. Furthermore, their acoustic recording data included birds sampled over 24 h, whereas point count data were restricted to mornings, therefore biasing their evaluation of the acoustic recording system.

The results of studies comparing the effectiveness of point counts and acoustic surveys in detecting rare species in temperate regions have also been inconclusive. For example, Hutto and Stutzman (2009) found that point counts were better for detecting rare species than recordings made using a stereo microphone system. In contrast, Celis-Murillo et al. (2009) detected

more rare species using a quadraphonic recording system than when conducting point counts. The ability of acoustic recordings to effectively sample rare species is a key issue in the tropics because bird communities are comprised mostly of rare species (Ricklefs and Schulter 1994), and underdetection of such species can bias estimates of species occurrence and richness.

Tropical habitats vary widely in vegetation structure, ranging from open pastures to tall dense evergreen forests. Although such differences may affect the performance of acoustic recordings relative to point counts (Haselmayer and Quinn 2000, Acevedo and Villanueva-Rivera 2006), the effectiveness of these two methods in different tropical vegetation types has not been compared. Thus, our objective was to compare the relative effectiveness of a portable quadraphonic acoustic recording system and point counts for estimating bird species richness, composition, and detection probabilities of rare, moderately common, and common species across six structurally distinct tropical vegetation types in the Yucatan Peninsula. We compared bird community and population parameters based on species detection/nondetection data, accounting for imperfect detection probability through use of repeated visits to survey locations. Our specific objectives were to determine (1) if the two survey methods generated similar estimates of species richness and composition across vegetation types, and (2) how detection probabilities of rare and common resident bird species differed between the two methods across a range of vegetation types.

METHODS

Our study was conducted at three locations in the northeastern region of the Yucatan Peninsula of Mexico, including the Ria Lagartos Biosphere Reserve and the Santa Isabel Ejidos in Yucatan, and the El Eden Ecological Reserve in Quintana Roo. Study sites included natural and human-modified vegetation types, including coastal dune scrub, mangrove scrub, mature low-stature deciduous thorn forest, early and late successional medium-stature semievergreen forest, and grazed pastures. These six vegetation types represent the dominant vegetation types in the northeastern Yucatan Peninsula, and span the spectrum of variation in vegetation structure in the region, ranging from short, open, simply structured vegetation to tall, dense, structurally diverse vegetation (Miranda 1958, Rzedowski 1978). Most of these vegetation types occur in other tropical regions, e.g., mangroves, coastal scrub, and grazed pastures (Moreno-Cassasola and Espejel 1986, Britton and Morton 1989, J. L. Deppe and A. Celis-Murillo, pers. obs.)

During the same months as the surveys (June and July 2008), we characterized the structure of vegetation at each survey location using a modified circular plot technique (5-m radius; James and Shugart 1970, Deppe and Rotenberry 2008). For each survey plot, we visually estimated the percent cover of the tree canopy, shrubs and saplings, and herbaceous vegetation in the 5-m radius circular plots. In each plot, we also counted the number of trees with a dbh (diameter at breast height) ≥ 5 cm, measured vegetation height along the circumference of the plot at each of the four cardinal directions, and measured maximum vegetation height using a meter tape or clinometer. We calculated the average vegetation height by averaging over the four height measurements taken at the four cardinal directions.

Coastal dune scrub was comprised of dense woody shrubs, cacti, herbaceous plants, scattered introduced coconut palms (*Cocos nucifera*), and high local abundances of several native palm species. Coastal scrub was relatively short, with a mean height of 2.2 m. Dominant species included *Pseudophoenix sargentii*, *Thrinax radiata*, *Pithecellobium keyense*, *Bravaisia tubiflora*, and *Caesalpinia vesicaria* (see Table 1 for summary of all vegetation measurements). Areas of mangrove sampled in our study were characterized by halophytic, wetland species, including red (*Rhizophora mangle*) and black (*Avicennia germinans*) mangroves, buttonwoods (*Conocarpus erectus*), *Batis maritima*, and *Salicornia bigelovii*. They were relatively short (mean height = 3.0 m) and best described as mangrove scrub. Low-stature thorn forests were also primarily shrubby in nature with few trees with a dbh > 5.0 cm and a dense herbaceous layer. Thorn forests were dominated by *Fabaceae* spp. and cactus species. With the exception of the open grassy areas of grazed pastures (see below), low-stature thorn forests were the shortest vegetation type. Early- and late successional semievergreen forests had similar plant species composition, and the dominant tree species included *Manilkara zapota*, *Sideroxylong foetidissium, Metopium brownii*,

Table 1. Mean (± SD) vegetation measurements for each of the six vegetation types where bird surveys were conducted in the northeastern Yucatan Peninsula.

Vegetation type	Percent tree cover	Percent shrub/sapling cover	Percent herbaceous cover	Maximum vegetation height (m)	Average vegetation height (m)	Number of trees
Coastal dune scrub	41.9 ± 17.9	89 ± 9.5	33.3 ± 16.3	4.4 ± 1.1	2.2 ± 0.3	8.9 ± 7.4
Mangrove	42.4 ± 37.3	52.3 ± 31.9	67.2 ± 36.6	7.1 ± 3.0	3 ± 2.3	13.7 ± 17.5
Thorn forest	23.6 ± 25.3	58.6 ± 20.4	76.4 ± 14.1	4.3 ± 1.8	1.7 ± 1.1	3.7 ± 5.4
Early successional semievergreen forest	78.7 ± 11.8	80 ± 4.7	46.8 ± 15.9	10 ± 2.2	6.3 ± 1.7	14.1 ± 9.1
Late successional semievergreen forest	89.1 ± 5.9	75.4 ± 17.7	59.4 ± 26.4	14.7 ± 5.8	8.4 ± 2.0	42.8 ± 19.3
Pasture[a]	42.1 ± 26.6	36.3 ± 18.7	68.5 ± 23.7	8.6 ± 2.4	3 ± 1.2	14.7 ± 9.7

[a]Vegetation measurements in pasture included living fences. Average vegetation height in the grassy areas of the pasture was 1.2 m at the time of our surveys and overhead canopy cover was absent.

Ceiba aesculifolia, and *Bursera simaruba*. Early successional forests (<15 yr old) at our sites were shorter than late successional forests (> 40 yr old) and had less tree and herbaceous cover, greater shrub/sapling cover, and fewer trees with a dbh > 5.0 cm. Pastures ranged in size from ~5 to 200 ha, and were surrounded by living fences (i.e., narrow fence rows consist of remnant trees or established plantings of cuttings harvested from nearby trees; Zahawi 2005) and some had scattered remnant trees in their interior. Pastures were dominated by *Panicum* spp., and remnant trees were those found in semievergreen forests. Livestock grazing at survey locations occurred at a low intensity during the time of sampling; the herbaceous strata was the best developed strata in pastures, and vegetation height in the open grassy areas of the pasture averaged 1.2 m. Overhead canopy cover was absent in the grassy portion of the pastures. Deppe and Rotenberry (2008) and Carabias Lillo et al. (1999) provided detailed descriptions and photographs of the vegetation types in our study.

Point counts and acoustic recordings. We established 53 survey points distributed among the six vegetation types, including eight in coastal dune scrub, eight in mangrove, seven in thorn forest, 10 in early successional semievergreen forest, 12 in late successional semievergreen forest, and eight in pasture. Points were placed along available paths and dirt roads. Each point was 250 to 500 m from adjacent points and at least 250 m from the nearest edge of contiguous vegetation. Living fences were an integral component of the pasture vegetation type for birds in the northeastern Yucatan Peninsula; grassland birds observed in our study frequently flew between open grassy areas of the pasture where they foraged and trees where they sought cover (A. Celis-Murillo and J. L. Deppe, pers. observ.).

At each survey location, we simultaneously surveyed birds using acoustic recordings and point counts on either two (25 locations) or three (28 locations) consecutive days in June and July 2008. Sampling on consecutive days reduced issues caused by possible temporal variation in weather and vocalization rates and by birds entering or leaving the population (Sutherland et al. 2004). Upon arriving at each point, the observer (ACM) waited for 5 min then began a 10-min point count and acoustic recording. Only the presence of species was recorded at each location, not numbers of individuals. During point counts, we included both aural and visual detections because visual detection represents the main advantage of field surveys over recordings, and are included in most analyses of count data (Celis-Murillo et al. 2009). All surveys were conducted within 4 h after local sunrise, with the earliest surveys conducted at 06:00.

We used a portable quadraphonic acoustic recording system to record the soundscape in 360° by having each of the four microphones pointed in one of the four cardinal directions. This microphone array was originally designed

to record audio in four channels and to be able to listen to the recordings using a quadraphonic playback system to interpret acoustic recordings and estimate the abundance of bird species (Soundscape Recording System, SRS; Celis-Murillo et al. 2009). However, for this study, we were only interested in species detections so we converted the four-channel recordings to stereo recordings and, in the lab, listened to them using headphones (Sennheiser HD-280). To produce a two-channel (stereo) recording, we merged the north and east channels into one channel and the south and west channels into a second channel; each of the resulting two channels provided the listener with information from 180° of the soundscape. Four-channel microphone recording arrays were used instead of stereo arrays because they sample 360° more evenly.

Analysis of acoustic recordings. The same person (ACM) conducted all point counts and reviewed all recordings, listing all species detected during each 10-min survey. To ensure that prior knowledge from point counts did not influence data collected from recordings, a second person copied the master set of recordings and removed all identifying information (e.g., location and date). Each recording was then assigned a random number and reviewed randomly in the lab. ACM reviewed 8 to 11 recordings each day. Recordings were reviewed multiple times in full or in part until ACM felt confident that all species in the recordings were detected, taking on average ~20 min to listen to each recording. Additionally, ACM compared vocalizations to an independent reference collection (Celis-Murillo et al. 2008), evaluated spectrograms, and, in a few instances, requested verification from regional experts. Recordings were not reviewed until almost 1 yr after surveys were conducted to avoid confounding experience and method (Celis-Murillo et al. 2009).

Statistical analyses. We used the program Species Prediction And Diversity Estimation (SPADE, Chao and Shen 2003) to estimate species richness using the Chao2 estimator. Chao2 is a nonparametric estimator (Colwell and Coddington 1994) that accounts for the relationship between sampling effort and species richness indices as well as imperfect species detection (i.e., total species richness is usually unknown because not all species, particularly rare ones, are detected).

Evaluation of alternative methods for estimating richness demonstrated that Chao2 provides a robust estimate (Walther and Martin 2001) even with relatively small sample sizes (Colwell and Coddington 1994). We compared species richness between the two survey methods for each of the six vegetation types and for all vegetation types combined by examining the overlap of 95% log-linear confidence intervals (CI) for the estimates.

We used the Chao-Jaccard multiple incidence-based similarity index (Chao-Jaccard MIB) to estimate overlap in species composition between the acoustic recordings and point counts in each of the six vegetation types (Chao et al. 2005). This index ranges from 0 to 1, where 0 indicates no overlap in species composition and 1 denotes complete overlap. The Chao-Jaccard MIB similarity index is slightly sensitive to rare species and small sample sizes (Chao et al. 2005). Additionally, it uses information about the frequencies and identities of rare species to adjust for the probability of undetected species. We used SPADE to calculate Chao-Jaccard MIB similarity indices using data from repeated visits to the 53 survey locations as the replicated incidence data. We compared the overlap of 95% CI to assess differences in species similarity between the two survey methods in each of the six vegetation types and for all vegetation types combined.

We used an occupancy modeling approach to estimate detection probabilities for 15 year-round resident bird species for the two survey methods and six vegetation types using data from repeat visits to survey locations. This set of 15 species included widespread and common species, species with restricted distributions, but common in the vegetation types where they are found, and rarer species that have restricted distributions or are uncommon where they are found. We ranked species based on the proportion of visits during which they were detected by at least one survey method. Only five species were detected on >20% of visits (the most common species was detected on 34% of visits); we analyzed all five species. Most species (87 of 132, 65.9%) were rare (detected on <5% of visits). We selected five rare species based on their endemic status; six endemic species fell into the rare category, but one species was not included because it was detected in only one vegetation

type. We also selected five moderately common species (10–15% of visits).

Occupancy modeling uses species detection/nondetection data collected over a series of visits to each survey location (detection histories) to estimate species detection probabilities and occupancy rates (MacKenzie et al. 2002). 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 detecting it at another location (MacKenzie et al. 2002). Covariates, such as vegetation attributes or meteorological variables, may be included in the models to reduce variance in parameter estimates (Mackenzie et al. 2006) and to assess relationships between detection probability or occupancy rates and covariates (Bailey et al. 2004, Ball et al. 2005, Watson et al. 2008). Nichols et al. (2008) developed an extension of the single-season, single-species occupancy model to deal with data from multiple survey methods conducted at the same survey locations. This "multimethod" approach accounts for the lack of independence of detections inherent with simultaneous survey methods while allowing one to make inferences about method-specific detection probabilities (Nichols et al. 2008). We used the multimethod occupancy modeling approach to compare species' detection probabilities between acoustic recordings and point counts in the six vegetation types.

We created detection histories for each of the 15 species using data from consecutive visits to the 53 survey locations; detection histories for the acoustic recordings and point count surveys were incorporated into a single data set. Vegetation type was included as a categorical covariate in our models. We only included data for vegetation types where a species was detected during at least one visit. Because the goal of our study was to compare detection probabilities between the two survey methods in each vegetation type rather than to examine vegetation occupancy patterns, removing the vegetation types where the species was not detected does not influence the results. We ran multimethod occupancy models using the program PRESENCE (Hines 2006).

For each species, we used acoustic recording and point count data to evaluate four hypotheses regarding the factors affecting bird species detection probabilities. We considered the following: (1) a constant model estimated a single detection probability for both methods and all vegetation types and represented the hypothesis of no effect of method or vegetation, (2) a method model estimated separate detection probabilities for each survey method and tested the hypothesis that detection probability was different between acoustic recordings and point counts, (3) a vegetation model estimated separate detection probabilities for each vegetation type and represented the hypothesis that vegetation alone influences detection probability, and (4) the interaction model estimated detection probabilities for each method by vegetation type combination, evaluating the hypothesis that method and vegetation interact to influence a species detection probability. We used Akaike's Information Criterion (AIC) to compare models and estimate relative model fit (Burnham and Anderson 2002). We 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 (Burnham and Anderson 2002). We used multimodel averaging to estimate model parameters.

RESULTS

Species richness. During acoustic recording and point count surveys, 132 species belonging to 22 families were detected; 120 species were detected in the acoustic recordings and 123 during point counts (Table S1). Based on Chao2, we found no significant differences between acoustic recordings and point counts in estimated species richness when vegetation types were combined or considered separately (Fig. 1).

Species composition. Seven species were detected only by acoustic recordings, 12 only by point counts, and the remaining 113 species by both methods (Table S1). When we accounted for imperfect species detection and considered all six vegetation types collectively, overlap in species composition estimates was very high (0.98 similarity). When vegetation types were considered separately, estimates of species overlap between the two survey methods varied
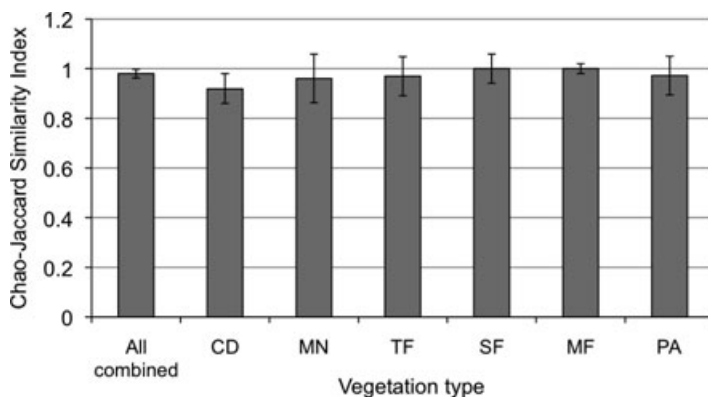
Fig. 1. Estimates of species richness based on the Chao2 estimator and 95% confidence intervals for six tropical vegetation types analyzed collectively and separately for acoustic recordings and point counts. Confidence intervals are log-linear and asymmetrical. CD = coastal dune scrub, MN = mangrove, TF = mature low-stature deciduous thorn forest, SF = early-successional or secondary semievergreen forest, MF = late-successional or mature medium-stature semievergreen forest, and PA = grazed pastures.
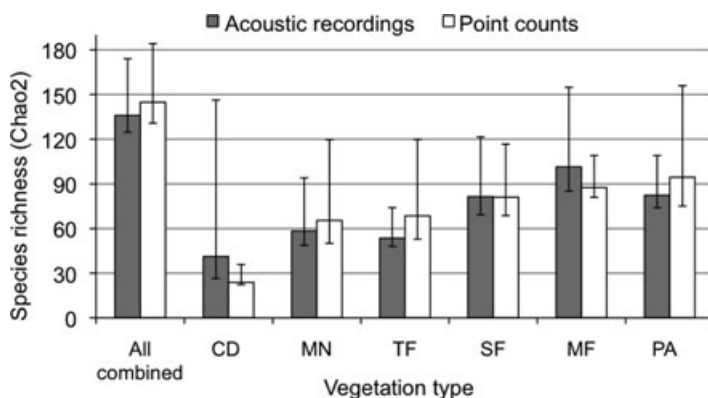

Fig. 2. Estimate of similarity in species composition based on Chao-Jaccard multiple incidence-based (MIB) and 95% confidence intervals between acoustic recording surveys and point counts surveys in six vegetation types. CD = coastal dune scrub, MN = mangrove, TF = mature low-stature deciduous thorn forest, SF = early-successional or secondary semievergreen forest, MF = late-successional or mature medium-stature semievergreen forest, and PA = grazed pastures.

nonsignificantly from 0.92 to 1.00 (Fig. 2); species composition was most similar between survey methods in areas with tall, dense vegetation (semievergreen forests) and least similar in coastal dune scrub.

Species detection probabilities. Based on the multimethod occupancy models and AIC$_c$ model selection criteria for the 15 bird species, the method model was the best-supported model for four species (Golden-fronted Woodpecker, *Melanerpes aurifrons*; Orange Oriole, *Icterus auratus*; Yellow-lored Parrot, *Amazona* *xantholora*; and Black-headed Trogon, *Trogon melanocephalus*). Based on detection probabilities averaged across all models, detection probabilities were higher for acoustic recordings than point counts (Fig. 3). However, there was considerable uncertainty in selecting the best model for two species (i.e., multiple models had ΔAIC$_c$ values $\leq$ 2.0; Table 2); the vegetation model had strong empirical support for Black-headed Trogons, and the constant model had substantial support for both Yellow-lored Parrots and Black-headed Trogons.

Table 2. Akaike's Information Criterion (AIC_c), AIC_c relative differences (ΔAIC_c), model weights (w_i) and number of parameters (K) for models examining detection probability of birds, including a constant model (no effects of vegetation or method), method model (differences in detection probability between methods), vegetation model (different detection probabilities among vegetation types), and interaction method-vegetation model (method and vegetation interaction influencing detection probability). Occupancy was kept constant in all models because it was not a focus of our study. Models with the lowest ΔAIC_c value and highest model weight (w_i) are shown in bold. Common names and scientific names follow the American Ornithologists' Union Checklist of North American birds, 7th edition (2010). Species are arranged in order of increasing model weight for the top-ranked model.

Species[a]	p(method)				p(vegetation)				p(interaction method-vegetation)				p(constant model)			
	AIC_c	ΔAIC_c	w_i	K	AIC_c	ΔAIC_c	w_i	K	AIC_c	ΔAIC_c	w_i	K	AIC_c	ΔAIC_c	w_i	K
Golden-fronted Woodpecker (*Melanerpes aurifrons*)[C]	304.53	**0.00**	**0.98**	4	317.31	12.78	0.00	4	312.84	8.31	0.02	14	319.17	14.64	0.00	8
Orange Oriole (*Icterus auratus*)[R]	124.40	**0.00**	**0.92**	4	133.59	9.19	0.01	4	133.90	9.50	0.01	6	129.76	5.36	0.06	3
Yellow-lored Parrot (*Amazona xantholora*)[R]	57.08	**0.00**	**0.45**	4	59.24	2.16	0.15	4	60.34	3.26	0.08	4	57.85	0.77	0.30	3
Black-headed Trogon (*Trogon melanocephalus*)[M]	249.82	**0.00**	**0.38**	4	250.10	0.08	0.33	4	252.17	2.35	0.12	7	251.51	1.69	0.16	3
Caribbean Dove (*Leptotila jamaicensis*)[C]	302.19	58.32	0.00	4	243.87	**0.00**	**1.00**	3	256.56	12.69	0.00	8	304.15	60.28	0.00	4
Mangrove Vireo (*Vireo pallens*)[C]	234.15	24.19	0.00	4	209.96	**0.00**	**0.98**	4	217.77	7.81	0.02	8	235.29	25.33	0.00	3
Yucatan Jay (*Cyanocorax yucatanicus*)[R]	151.16	5.96	0.04	4	145.20	**0.00**	**0.84**	4	153.68	8.48	0.01	7	149.27	4.07	0.11	3
Black-throated Bobwhite (*Colinus nigrogularis*)[M]	211.51	18.75	0.00	4	192.76	**0.00**	**0.70**	4	194.50	1.74	0.30	7	209.58	16.82	0.00	12
Spot-breasted Wren (*Thryothorus maculipectus*)[C]	199.08	19.14	0.00	4	179.94	**0.00**	**0.70**	4	181.66	1.72	0.30	6	199.74	19.80	0.00	10
Tropical Kingbird (*Tyrannus melancholicus*)[M]	241.17	28.36	0.00	4	218.56	5.75	0.05	4	212.81	**0.00**	**0.95**	8	244.40	31.59	0.00	14
Rufous-browed Peppershrike (*Cyclarhis gujanensis*)[M]	228.19	10.49	0.00	4	219.99	2.29	0.24	4	217.70	**0.00**	**0.75**	7	230.63	12.93	0.00	12
Thicket Tinamou (*Crypturellus cinnamomeus*)[C]	168.56	3.84	0.10	4	167.74	3.02	0.16	4	164.72	**0.00**	**0.71**	5	171.57	6.85	0.02	8
Clay-colored Robin (*Turdus grayi*)[M]	148.48	1.50	0.28	4	150.52	3.54	0.10	4	153.75	6.77	0.02	5	146.98	**0.00**	**0.60**	3
Yucatan Woodpecker (*Melanerpes pygmaeus*)[R]	161.79	1.60	0.27	4	163.00	2.81	0.14	4	175.36	15.17	0.00	8	160.19	**0.00**	**0.59**	3
Yucatan Flycatcher (*Myiarchus yucatanensis*)[R]	130.37	1.80	0.17	4	128.58	0.01	0.41	4	137.31	8.74	0.01	7	128.57	**0.00**	**0.41**	3

[a] Superscripts after species names indicate relative abundance: [C] = Common, [M] = Moderately common, and [R] = Rare
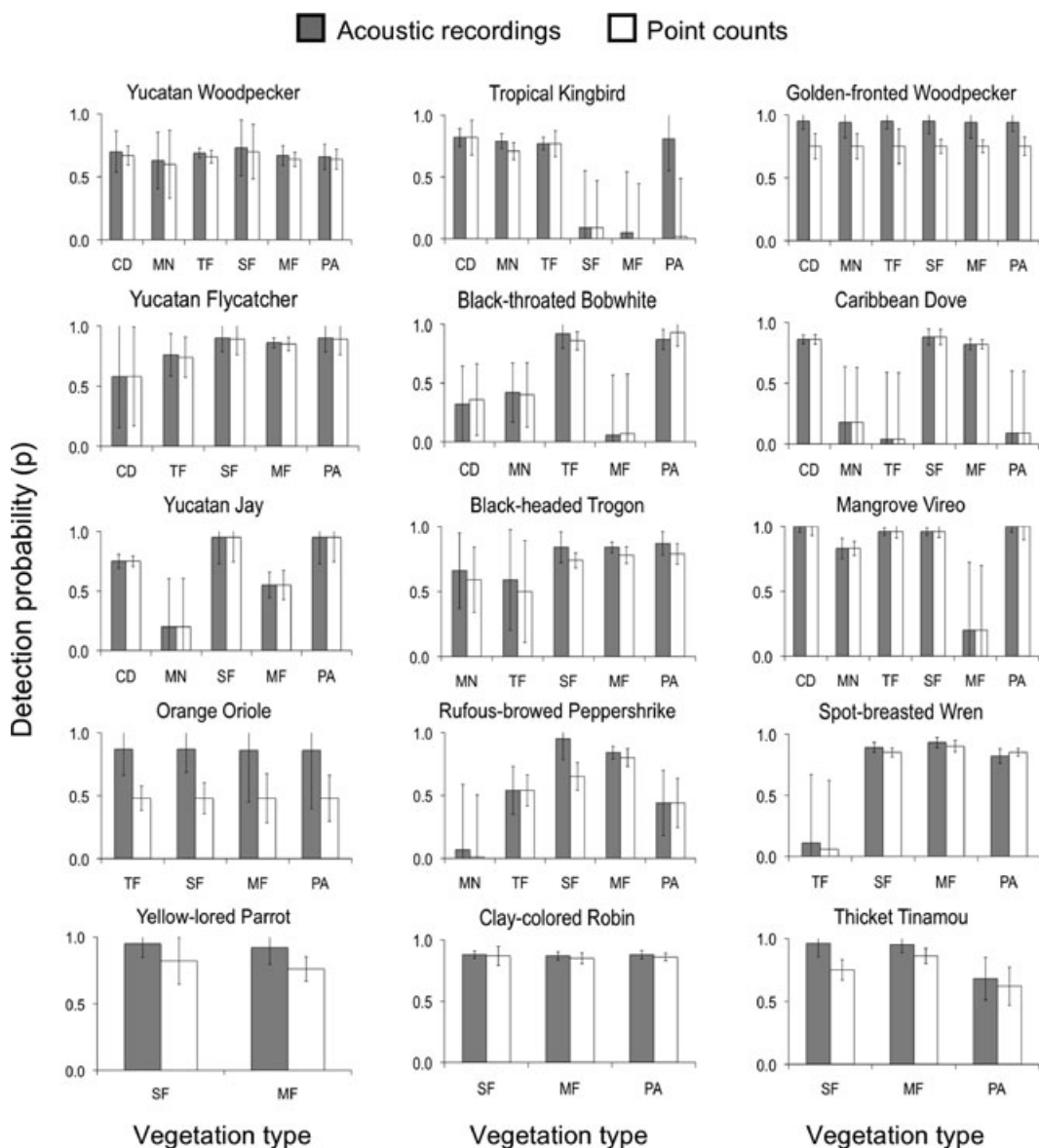
Fig. 3. Model-averaged detection probability estimates and standard error for acoustic recordings and point counts for 15 species in the study area and the vegetation types where they were detected on at least one visit. Species in the left column were considered rare, species in the central column were considered moderately common, and species in the right column were considered common. CD = coastal dune scrub, MN = mangrove, TF = mature low-stature deciduous thorn forest, SF = secondary semievergreen forest, MF = mature medium-stature semievergreen forest, and PA = grazed pastures.

The vegetation model was the best model for five species whose detection probabilities varied among the vegetation types where they were found (Table 2). For three species (Caribbean Dove, *Leptotila jamaicensis*; Mangrove Vireo,

Vireo pallens; and Yucatan Jay, *Cyanocorax yucatanicus*), the vegetation model was the only model with substantial support. Detection probability was lowest in vegetation types with the highest vegetation density for some species, but,

for other species, was lowest in structurally open vegetation types (e.g., pastures and thorn forest; Fig. 3). For two species (Black-throated Bobwhite, *Colinus nigrogularis*; and Spot-breasted Wren, *Thryothorus maculipectus*), the interaction model had a ΔAIC_c value ≤ 2.0 and a high model weight, indicating that a method by vegetation interaction could not be ruled out. Support for the interaction model in these species was due to higher detection probabilities for acoustic recordings in some vegetation types (forests) and for point counts in others (pastures and coastal dunes; Fig. 3).

The interaction model was the top-ranked model for three species (Tropical Kingbird, *Tyrannus melancholicus*; Rufous-browed Peppershrike, *Cyclarhis gujanensis*; and Thicket Tinamou, *Crypturellus cinnamomeus*), indicating that both method and vegetation type influenced detection probability (Table 2). In all vegetation types, detection probabilities for acoustic recordings were the same as or higher than those for point counts, although the magnitude of the advantage of acoustic recordings varied among vegetation types (Fig. 3).

Finally, the constant model was the top-ranked model for three species (Clay-colored Robin, *Turdus grayi*; Yucatan Woodpecker, *Melanerpes pygmaeus*; and Yucatan Flycatcher, *Myiarchus yucatanensis*), suggesting little or no influence of method or vegetation on detection probability (Table 2). For all species, however, the method model also had low ΔAIC_c values and high model weights, suggesting that the type of survey method may influence the probability of detecting these species, and detection probabilities were slightly higher for acoustic recordings.

Based on ΔAIC_c values, model weights, and detection probability estimates for the two methods in each of the six vegetation types, the relative performance of the two methods generally was not influenced by the status of a species as rare, common, or moderately common (Table 2, Fig. 3). No rare species showed evidence of an interaction and, for the four rare species where the method model had substantial empirical support (ΔAIC_c value ≤ 2.0), detection probability estimates were higher for acoustic recordings than point counts (Fig. 3). Similarly, for most common and moderately common species, detection probabilities for acoustic recordings were as high or higher than

detection probabilities for point counts. However, only common and moderately common species demonstrated interactions among vegetation type and method, and only two species exhibited interactions showing patterns of higher detection rates for acoustic recordings in some vegetation types and for point counts in others.

DISCUSSION

We found no difference in the performance of acoustic recordings and point counts at the community level in the northern Yucatan Peninsula. The two methods provided comparable estimates of richness and composition, and vegetation type did not affect the relative performance of the methods. However, at the population level, we found support for a method effect on the detection probability of 12 species (i.e., the method or interaction method*vegetation models had ΔAIC_c values ≤ 2) and for no method effect for three species (i.e., those where only the vegetation model had a ΔAIC_c value ≤ 2). Only two species showed an interaction where detection probabilities for point counts were higher in some vegetation types and those for acoustic recordings were higher in others, indicating that selecting a single method for those species may not be wise. For the remaining 13 species, regardless of whether they were rare, moderately common, or common, detection probabilities were either similar for the two methods or higher for acoustic recordings in the vegetation types where they occurred.

Estimates of species richness did not differ significantly between acoustic recordings and point counts in any vegetation type. Similar results have been reported in previous studies (Haselmayer and Quinn 2000, Celis-Murillo et al. 2009). Hobson et al. (2002) documented higher species richness using acoustic recordings, but differences between methods were small (≤ 5 species). In contrast, Hutto and Stutzman (2009) reported lower species richness using acoustic recordings. A larger detection radius for point counts and the inclusion of flyovers in their point count data may have contributed to the differences between survey methods in their study. However, like Hutto and Stutzman (2009), we found that the performance of acoustic recordings and point counts for estimating richness was unaffected by vegetation

type. Although few investigators have compared acoustic recordings and point counts, the results of most studies suggest that acoustic recordings can perform as well as or better than point counts for enumerating species richness in landbird-dominated systems. Furthermore, we found that acoustic recordings performed well in vegetation ranging from forests to pastures.

The similarity between methods in determining species composition in our study (92–100% across vegetation types) was comparable to that in temperate mixed coniferous-deciduous forests in Canada (83–97%, Hobson et al. 2002). In contrast, Acevedo and Villanueva-Rivera (2006) detected 74% of species using both acoustic recordings and point counts in Puerto Rico (based on data presented in Table 1 of their paper), whereas Celis-Murillo et al. (2009; 59%) and Hutto and Stutzman (2009; 54%) reported lower similarity estimates in temperate vegetation types. Differences among studies may be due to variation in specific vegetative features (e.g., vertical and horizontal distribution of vegetation), bird behavior (e.g., proportion of individuals present that vocalize), characteristics of species' vocalizations (e.g., frequency or intensity), species richness, sample size, study design, or the type of recording/playback system (e.g., number and arrangement of microphones, number of channels recorded and played back during review of recordings, and use of headphones vs. speakers during review). This last factor may influence key aspects of the detection process, such as relative differences in detection range or area between the two methods. In our study, similarity in composition was high even in open vegetation types where, despite the greater potential to visually detect species, most are detected by their vocalizations (A. Celis-Murillo and J. L. Deppe, pers. observ.).

If the goal of a study is to perform a species inventory, investigators should consider the effectiveness and utility of acoustic recordings and point counts in their study area prior to selecting a method and perform a preliminary comparison, especially if surveys are limited to a single method. An important part of the evaluation process will be to identify the cause of any discrepancies in composition (Hutto and Stutzman 2009) and determine which method yields the most reliable data, keeping in mind that no single method works equally well for all species.

We found that detection probabilities for some species were influenced by survey method, either independently of or interactively with vegetation type. Detection probabilities were higher using acoustic recordings for seven species in all six vegetation types (Golden-fronted Woodpecker, Orange Oriole, Yellow-lored Parrot, Black-headed Trogon, Yucatan Flycatcher, Yucatan Woodpecker, and Clay-colored Robin). For three additional species (Rufous-browed Peppershrike, Thicket Tinamou, and Tropical Kingbird), there was an interaction between method and vegetation; detection probabilities for acoustic recordings were the same as those for point counts in some vegetation types, slightly higher in others, and higher still in others. Some species detected more often using acoustic recordings sang infrequently during the 10-min surveys, including the two species of woodpeckers, Orange Orioles, Yellow-lored Parrots, and Thicket Tinamous. These species were detected better using recordings because recordings could be replayed multiple times; in the field, especially in tropical regions characterized by high species diversity, they may go undetected or recorded. Furthermore, some of these species are difficult to see (e.g., Thicket Tinamou) and, thus, do not provide field observers with any visual advantage. On the other hand, other species, such as Mangrove Vireos, Caribbean Doves, and Yucatan Jays, sang frequently during surveys and were detected equally well by both survey methods, although the overall probability of detection varied among vegetation types. Variation in detection probability among the vegetation types was likely due to a low number of detections in some vegetation types, reflected as very high CI, and often resulting in very low detection probabilities.

Of particular interest were Black-throated Bobwhites and Spot-breasted Wrens that were detected better by point counts in pastures and coastal dunes, but as well as or better by acoustic recordings in forests and mangrove. These species vocalize frequently, although in coastal dune and pasture they are seen almost as often as they are heard (A. Celis-Murillo and J. L. Deppe, per. observ.), likely because vegetation density is generally low in the shrub/sampling or herbaceous strata where these birds are most active, thereby enhancing detection during point counts. For example, in combination with the low shrub/sapling cover

of pastures, the characteristic display behavior of Spot-breasted Wrens in the open grassy areas of the pasture makes them especially obvious to an observer in the field (A. Celis-Murillo and J. L. Deppe, per. observ.). For these two bird species, a combination of methods would likely provide the most reliable data. The multimethod occupancy modeling approach provides a way to incorporate data from both techniques into a single analysis to estimate occupancy rates more accurately than using data from a single method (Nichols et al. 2008). From a practical standpoint, acoustic recordings were effective for surveying 13 of 15 tropical species in our study, and provide a practical method for surveying birds in the tropics where experienced field observers and funding for field surveys may be limited. Regardless of the method selected, however, analyses that account for variation in detection probability among vegetation types are needed.

Our results indicate that acoustic recordings were equally effective at detecting rare, common, and moderately common species. However, Celis-Murillo et al. (2009) suggested that acoustic recordings were better than point counts for surveying rare species in riparian vegetation in southern California. In contrast, Hutto and Stutzman (2009) noted that rare species were detected more frequently using point counts because of visual cues and the smaller apparent detection radius of their microphone relative to point counts. Haselmayer and Quinn (2000) also detected rare species more frequently using point counts than recordings in Peru, but attributed this to the limited detection area of their single, directional microphone system that was rotated during their surveys. They hypothesized that an omni-directional microphone system would enhance detection of rare species. Our results, obtained using a quadraphonic recording system that provided an omni-directional pattern, support Haselmayer and Quinn's (2000) hypothesis. Our recording system may have detected rare species better than the system used by Hutto and Stutzman (2009) because the technical specifications of our microphone array allowed us to sample in all directions with an average detection range comparable to that of a field observer. We did not calibrate our recording system to detect birds to a distance comparable to the effective hearing distance of a human observer, a challenging exercise because

detection distances vary among species, among human observers, among particular survey locations within each vegetation type, and with environmental conditions. However, previous assessments of the recording system used in our study have demonstrated that its average detection range across species is comparable to that of a human observer in the field (Celis-Murillo et al. 2009). Thus, although the choice of recording system specifications may be less important for estimating species richness at the community level, the technical specifications of the recording array likely impact its performance at detecting a given bird species at the population level.

In sum, we found that acoustic recordings performed as well or better than point counts for detecting most species across all vegetation types. Furthermore, the two methods produced similar estimates of species richness and composition in all vegetation types, demonstrating that acoustic recordings can be used effectively for surveying both rare and common species across a variety of tropical vegetation types. One advantage of using acoustic recordings in the tropics is that they can be used to survey remote areas without the need for trained field surveyors; acoustic recordings can be made by personnel on-site and later reviewed in the lab by a skilled surveyor (Celis-Murillo et al. 2009, Hutto and Stutzman 2009). Because of the cost and effort associated with finding skilled observers and the time needed to review recordings and examine spectrograms, conducting acoustic recording surveys may not be cost effective (Hutto and Stutzman 2009). However, automated sound recognition software could reduce the cost and time needed to review recordings (Brandes 2008, Blumstein et al. 2011). Software designed to detect and recognize species vocalizations autonomously have been used successfully in other studies (Figueroa and Robbins 2008, Trifa et al. 2008, Kasten et al. 2010, Goyette et al. 2011), and such results suggest that, in the near future, acoustic survey methods could potentially be as or even more effective than traditional point counts for surveys of species richness, composition, or occupancy in tropical regions.

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Supporting Information

The following supporting information is available for this article online:

Table S1. Proportion of visits during which each species was detected and raw count of total number of species detected and shared in the six vegetation types and by the two survey methods (acoustic recordings or point counts). CD = coastal dune scrub, MN = mangrove, TF = mature low-stature deciduous thorn forest, SF = early-successional semievergreen forest, MF = late successional medium-stature semievergreen forest, and PA = grazed pastures. AR = acoustic recordings, and PC = Point Counts.

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