ORNITOLOGIA NEOTROPICAL 16: 337–346, 2005

PATTERNS OF DAILY TEMPORAL VARIATION IN DETECTABILITY OF FOREST BIRDS IN BOLIVIA

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Resumen. – Patrones temporales diarios de variación en la detectabilidad de aves de bosques en Bolivia. – Existen pocas publicaciones que incluyen descripciones cuantitativas de la variación de la actividad vocal de aves de bosques tropicales en función de las horas de un día. Sin embargo, esta información es crítica para el diseño adecuado de los métodos de muestreo. Examiné la variación en la detectabilidad de aves en las distintas horas del día, durante la época seca en una concesión forestal de Bolivia. Tanto en el análisis por familia como en distintos grupos por dieta y vulnerabilidad hacia la perturbación de hábitats, la actividad vocal cambió considerablemente en cinco censos de una hora. El mayor número de aves (~70%) fue detectado en muestreos de las primeras dos horas después del amanecer. Los censos conducidos antes del amanecer, así como antes y después del atardecer, fueron importantes para detectar varias familias incluyendo: Tinamidae, Cracidae, Odontophoridae, Falconidae, Strigidae, Caprimulgidae, Momotidae, Furnariidae y Dendrocolaptidae. De los grupos estudiados, la mayoría de los con distinta dieta contenían al menos un grupo que era proporcionalmente más audible durante tiempos en los que no se hacen conteos de aves típicamente. Aves muy vulnerables a la fragmentación de hábitat fueron detectadas con más frecuencia en conteos antes del amanecer y antes del atardecer que las aves de mediana o baja sensibilidad. Los conteos nocturnos y antes del atardecer pueden contribuir considerablemente a las estimaciones de densidad y abundancia relativa de aves, y deberían ser considerados en estudios de comunidades de aves en bosques tropicales.

Abstract. – Published quantitative descriptions of daily variation in detectability or vocal activity of tropical forest birds are few, but such information is critical to designing effective survey protocols. I examined daily temporal variation in detectability of a bird community during the dry season in a lowland Bolivian forestry concession. Whether analyzed by family, foraging guild or by sensitivity to habitat disturbance, the detectability of birds varied considerably across five one-hour census periods. The greatest number of birds (~70%) was detected in surveys during the first two hours following sunrise. Pre-sunrise and pre- and post-dusk surveys were important for detecting several families, including Tinamidae, Cracidae, Odontophoridae, Falconidae, Strigidae, Caprimulgidae, Momotidae, Furnariidae, and Dendrocolaptidae. Among ecological guilds identified by diet and forest stratum, most diet groups contained at least one guild that was proportionately more detectable during times not typically surveyed in other studies. Birds considered highly sensitive to habitat fragmentation were detected proportionately more frequently in pre-sunrise surveys than birds with medium or low sensitivity. Nocturnal and pre-dusk surveys can contribute considerably to estimates of bird density and relative abundance, and should at least be explored in all tropical forest bird community studies. *Accepted 5 April 2005.*

Key words: Census methods, survey design, tropical forest bird communities, Bolivia, detectability, forestry concession.

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INTRODUCTION

Conducting censuses of tropical forest avifaunas is notoriously difficult for many reasons, including thick vegetation, difficult terrain, lack of time, lack of money, and the challenge of efficiently identifying a large number of species by sight and sound under often suboptimal conditions (Karr 1981). When conducting forest bird surveys using point-count or transect-based methods, a common approach is to begin surveys at dawn, and to continue for several hours thereafter. This approach makes sense in light of the fact that many tropical forest birds are most easily detected by sound, and that the vocal activity of many tropical birds is greatest in early morning hours. Indeed, in tropical forest bird surveys, the majority of detections are of birds heard only, thus the terms "detectability" and "vocal activity" may often be considered largely synonymous (Karr 1981, Blake 1992).

In temperate systems, much attention has been directed at the evaluation of survey methodologies (Ralph & Scott 1981, Verner 1985). Progress continues to be made in our understanding of methods and assumptions of observer-based survey methods, including questions about song rate, movements of individuals, and how these factors influence detection probability (e.g., Nichols *et al.* 2000, Buckland *et al.* 2001, Farnsworth *et al.* 2002, Rosenstock *et al.* 2002, Pollock *et al.* in press). Due partially to vastly more diverse communities and to a paucity of methodology-based studies in tropical regions, our understanding of how well assumptions of different survey methods are met in tropical forests is relatively poor (Remsen & Good 1996). Whitman *et al.* (1997) compared point count and mist-net data from Belize and described relatively poor comparability. Conversely, Casagrande & Beissinger (1997) report comparisons of several survey techniques in Venezuela that are encouraging, at least for one species. In Puerto Rico, the height of the observer in the forest (canopy vs ground) was found to influence abundance estimates of canopy and ground species (Waide & Narins 1988). Few studies have quantitatively examined variation in temporal detectability of birds in a tropical forest; Blake (1992) and Lynch (1995) describe patterns of declining vocal activity following sunrise in Costa Rica and Mexico, respectively.

Understanding when different species or guilds of birds are most detectable is crucial to designing effective survey methods, but documenting these times has received little attention. When the goal is to document avian diversity (most often meaning species richness) of tropical forests, researchers typically make an effort to survey for nocturnal and crepuscular species (e.g., Bates *et al.* 1998, Poulsen & Krabbe 1998). In community-level comparisons within- and between-sites in fragmented habitats, within-day temporal variation in detectability can have profound impacts on impressions of community composition, and especially on the apparent abundances of individual species. Although many forest fragmentation studies tacitly imply complete avian inventories, investigators frequently either do not sample all appropriate time periods, or do not adequately document their efforts to do so. This potentially creates problems when comparing avifaunal characteristics of areas surveyed using different methodologies. In a survey of over 160 published studies of effects of fragmentation on tropical forest birds, gathered from a wide variety of journals and edited volumes, I found that few (~ 30%) included quantitative surveys outside of the 2–5 h post-sunrise time period.

In this paper, I describe daily temporal variation in the vocal activity of birds during the dry season in a lowland Neotropical forest. Specifically, I ask: How do times of peak vocal activity differ between birds grouped by family, foraging stratum, diet, and sensitivity to habitat disturbance?

STUDY SITE AND METHODS

The study site, "La Chonta" (15º45'S, 62º45'W, c. 300 m a.s.l.), in Depto. Santa Cruz, Bolivia, is classified as subhumid tropical forest (Pinard *et al.* 1999), receives 1562 mm of rain per year, and has a mean annual temperature of 25º C that varies little seasonally. A pronounced dry season occurs from May to October. Twelve bird survey transects were located in three areas that differed only in their history of disturbance (undisturbed, selectively harvested, burned + selectively harvested). The site and habitats surveyed are described in greater detail elsewhere (Pinard *et al.* 1999, Woltmann 2003).

Birds were surveyed along 650-m transects established along old skidder trails in disturbed forest and along timber survey paths in undisturbed forest. The minimum perpendicular distance between transects was 350 m; transects along a single trail were separated by a minimum of 100 m. Transect width for most species was 50 m on either side of the transect, but was 100 m for the families Tinamidae, Cracidae, Odontophoridae, Accipitridae, Falconidae, Columbidae, Psittacidae, Strigidae, Caprimulgidae and Nyctibiidae. All surveys were conducted between 8 July–15 October 1999.

I sampled transects for 45 min during five 1-h daily time periods: (1) Pre-sunrise, ending just before sunrise; (2) Dawn, beginning at sunrise; (3) Post-dawn, beginning 1 h after sunrise; (4) Pre-sunset, ending at sunset; (5) Post-sunset, beginning at sunset. Periods 1 and 5 were mostly dark. Survey times were adjusted to account for changes in sunrise and sunset times throughout the study period. Surveys were only conducted during fair weather (little wind and no precipitation). During each survey, I walked slowly (c. 0.9 km h^{-1}), stopping frequently to look and listen. I include here all detections made within the transect boundaries, including birds flying over or through the forest. I was conservative when recording birds that may have moved between successive detections, and used countercalling individuals whenever possible to avoid double-counting. Detectability, strictly speaking, is a relative measure in the current analyses; estimated densities are presented elsewhere (Woltmann 2003). Most transects were sampled three times within each daily time period throughout the study period. The number of replicate surveys along each transect during each time period varied somewhat due to logistical reasons, but the proportion of surveys conducted during each time period was identical among areas. Excessive noise from cicadas (Insecta: Cicadidae) made evening surveys ineffective towards the end of the study period. Variation in temporal patterns of detectability between the three different areas (with different disturbance histories) was not apparent, therefore I pooled all data presented here.

I analyzed detectability of birds within several classification schemes. For taxonomic analysis, I follow familial nomenclature of AOU (1998) and supplements (through 2003). For guild analysis, I follow the diet and stratum classifications of Karr *et al.* (1990) where possible, with few modifications based on Cohn-Haft *et al.* (1997), and my own observations at the site. I use the sensitivity assessments of Parker *et al.* (1996). Some detections could not be identified beyond the family or generic level (e.g., trochilids, *Patagioenas*, *Monasa*, *Ara*, *Turdus* spp.). This meant I could not always assign the detection to a precise guild; I assigned such detections to the most precise guild possible, but sometimes this was only to a diet class. Birds detected, but unidentified and not assignable to guilds, were few (< 5% of all detections) and were omitted

TABLE 1. Percentage of detections by time periods for bird families at La Chonta. Rows may not add to 100 due to rounding. Families with inadequate sample sizes (< 10 detections) not included here are Cathartidae, Accipitridae, Nyctibiidae, and Galbulidae. Time periods are defined in the text.

Families	Time periods						
	1	2	3	4	5	*N*	CV[1]
Tinamidae	35	13	7	36	9	232	0.710
Cracidae	60	14	7	11	8	169	1.137
Odontophoridae	19	23	0	19	38	26	0.685
Falconidae	47	26	23	4	0	57	0.958
Columbidae	0	46	47	6	0	315	1.224
Psittacidae	12	39	33	16	<1	951	0.791
Cuculidae	10	41	31	17	0	29	0.821
Strigidae	41	2	4	6	47	110	1.108
Caprimulgidae	63	0	0	6	30	142	1.363
Apodidae	0	43	32	26	0	47	0.962
Trochilidae	6	53	37	4	0	317	1.176
Trogonidae	9	37	47	7	0	135	1.044
Momotidae	69	13	6	12	<1	207	1.380
Bucconidae	1	31	44	24	1	85	0.931
Ramphastidae	4	42	38	15	1	184	0.947
Picidae	2	50	38	10	0	58	1.132
Furnariidae	41	23	18	18	0	39	0.733
Dendrocolaptidae	25	30	23	20	2	321	0.539
Thamnophilidae	14	41	36	9	0	931	0.889
Formicariidae	9	44	22	25	0	32	0.831
Tyrannidae	14	42	37	8	0	635	0.921
Genera *incertae sedis*[2]	3	42	39	16	0	198	0.989
Cotingidae	0	57	17	27	0	30	1.173
Pipridae	2	43	43	13	0	54	1.061
Vireonidae	1	56	43	0	0	89	1.365
Troglodytidae	2	52	40	6	0	50	1.210
Sylviidae	0	42	48	9	0	33	1.181
Turdidae	7	35	38	16	3	214	0.790
Parulidae	8	42	48	3	0	183	1.133
Coerebidae	7	64	29	0	0	28	1.369
Thraupidae	8	42	34	15	<1	579	0.879
Emberizidae	7	27	60	7	0	15	1.225
Cardinalidae	2	41	48	9	0	64	1.142
Icteridae	2	29	41	28	0	58	0.914
Fringillidae	0	54	35	11	0	37	1.192
All birds (mean CV)	16	37	32	12	2	6671	1.026

[1] Coefficient of variation, derived from raw count data.

[2] Includes the genera *Lipaugus, Laniocera, Pachyramphus* and *Tityra.*

from analyses. All data were converted to percentages to facilitate comparison between families or guilds. Coefficients of Variation (CVs; as an index of evenness of detectability

TABLE 2. Similarity indices of samples collected at different times of day at La Chonta. Values above the diagonal are Morista-Horn indices (quantitative data), those below the diagonal are Jaccard indices (qualitative data). For both indices, 1.0 indicates complete congruence. Time periods are defined in the text.

Time periods	Time periods				
	1	2	3	4	5
1	-	0.354	0.305	0.616	0.315
2	0.477	-	0.627	0.636	0.040
3	0.455	0.810	-	0.614	0.046
4	0.475	0.602	0.575	-	0.097
5	0.182	0.085	0.079	0.145	-

across time periods) were calculated for groups containing at least 10 detections, and were calculated using raw data. I present few statistical analyses of these data, focusing on documenting patterns of detectability. These data as analyzed here were not collected with specific hypotheses of detectability in mind, thus any tests would be applied in a *post hoc* fashion. Even if applied *post hoc*, the number of potential comparisons to make is large, and the corresponding statistical corrections for multiple tests would result in a large Type II error rate for single comparisons. I statistically compared the proportions of detections by time according to sensitivity to disturbance because I wanted to assess the probability of this pattern arising more rigorously.

RESULTS

The data analyzed here are the result of 150 surveys (112.5 survey-h), during which I identified 6671 individuals comprising 187 species or species groups (full species list available from the author upon request). Approximately 70% of all detections were made in the first 2 h following sunrise (Table 1). Detections were predominantly of birds heard only (69%), followed by birds both seen and heard (21%) and seen only (10%), hence I use the terms "detectability" and "vocal activity" interchangeably. Both quantitative (Morista-Horn) and qualitative (Jaccard) similarity indices between samples taken at different time periods were quite low (mostly < 0.70) indicating that time of day had a significant effect on apparent species composition and abundance (Table 2). Similarity was greatest between periods 2 and 3, and generally lowest between period 5 and all other periods.

Detectability of bird families during the five time periods varied greatly (Table 1). During pre-sunrise surveys (period 1), relatively high detectability of some families – notably Cracidae, Falconidae, Momotidae, and Furnariidae – suggests that the abundance of these families may be frequently underestimated. The nocturnal nature of strigids and caprimulgids is not surprising, and these families are typically undersampled in many studies. Most tinamid detections were from periods 1 and 4. Within families, variation was sometimes large, and several species were disproportionately detected outside time periods typical for their families e.g., Grayish Mourner (*Rhytipterna simplex*), Dusky-capped Flycatcher (*Myiarchus tuberculifer*), Plain-winged Antshrike (*Thamnophilus schistaceus*), Hauxwell's Thrush (*Turdus hauxwelli*). In other cases, common species sometimes heavily influenced the perceived family-wide pattern of detectability. For example, Buff-throated Woodcreeper (*Xiphorhynchus guttatus*) was by far the most abundant dendrocolaptid, and was more or less equally detectable in periods 1–4, but other less abundant species in this family were more commonly detected during period 1. CVs of detectability for bird families across the five time periods ranged from 0.54 in Dendrocolaptidae to 1.38 in Momotidae (Table 1).

Considerable variation in detectability, both between and within dietary groups was

TABLE 3. Percentage of detections by foraging guild at La Chonta. Rows may not add to 100 due to rounding. Only guilds with at least 10 detections are included. Time periods are defined in the text.

Guilds[1]	Time periods						
	1	2	3	4	5	*N*[2]	CV
Frugivores	14	39	32	13	2	1801	0.754
Ground	17	21	17	20	24	75	0.141
Understory	5	33	40	23	0	124	0.606
Canopy	8	45	36	11	< 1	1317	0.977
Multiple	45	15	15	20	5	285	0.760
Large invertebrates and small vertebrates	32	21	19	15	13	729	0.356
Ground	9	44	22	25	0	32	0.568
Near-Ground	29	18	24	29	0	17	0.225
Understory	33	15	16	13	22	313	0.409
Bark	27	27	24	20	2	262	0.516
Multiple	46	14	9	7	23	97	0.796
Large invertebrates, fruit, and small vertebrates	23	33	31	13	< 1	737	0.677
Understory	33	29	27	11	< 1	488	0.685
Bark	5	60	15	20	0	20	0.966
Canopy	0	36	49	16	0	45	0.503
Multiple	4	42	38	15	1	184	0.947
Small invertebrates	13	43	36	8	< 1	1899	0.913
Ground	14	43	36	7	0	14	0.680
Near-Ground	10	51	30	9	0	456	0.791
Understory	14	38	39	9	0	960	0.633
Bark	22	37	25	16	0	89	0.356
Canopy	8	55	36	<1	0	215	1.018
Above Canopy	26	25	19	23	8	80	0.378
Multiple	1	43	53	2	0	81	1.081
Small invertebrates, fruit	5	38	41	14	1	814	0.918
Ground	19	23	0	19	38	26	0.366
Near-Ground	13	37	25	25	1	174	0.684
Understory	4	39	43	13	< 1	327	1.004
Canopy	1	34	55	10	0	170	0.968
Multiple	2	44	48	6	0	109	0.969
Omnivore	30	18	16	35	1	247	0.664
Ground	40	14	7	38	1	183	0.899
Canopy	3	43	54	0	0	37	0.812
Multiple	0	15	26	59	0	27	0.694
Nectar, small invertebrates	6	56	35	4	0	325	1.000
Understory	5	55	36	4	0	297	0.988
Canopy	7	64	29	0	0	28	0.866

TABLE 3. Continued.

Guilds[1]	Time periods						
	1	2	3	4	5	N^2	CV
Vertebrates							
Multiple	45	26	21	8	0	53	0.676

[1] Guild designations mainly from Karr *et al.* (1990) and Cohn-Haft *et al.* (1997), with some modifications based on my observations at La Chonta.

[2] Total sample size for diet-only groups may be greater than the sum of samples for guild + stratum groups because of detections not identified to species (see Methods).

also apparent (Table 3). For example, within frugivores from pre-sunrise surveys, the percent of detections of species that forage in different strata varied from 5–45%. Periods 1 and 5 were important survey times (containing ≥ 20% of all detections) for some guilds in nearly every diet class. CVs of detectability by guild varied from 0.14 for ground frugivores to 1.08 for multiple-strata small insectivores (Table 3).

The percentages of birds detected during each time period grouped by sensitivity to disturbance were generally similar to those of all birds pooled. Highly sensitive species were detected proportionately more frequently during period 1 than other species; the difference is small (6–7%) but statistically significant (Table 4; Tukey-type multiple comparison of arcsine-transformed proportions: low vs medium $q = 2.537$, $P > 0.05$; low vs high $q = 8.132$, $P < 0.001$; medium vs. high $q = 6.805$, $P < 0.001$; see Zar 1999: p. 564). During period 4, highly sensitive species were also detected more frequently than moderately sensitive ones, but not more frequently than species with low sensitivity to disturbance (low vs medium $q = -5.570$, $P < 0.001$; low vs high $q = 1.169$, $P > 0.05$; medium vs high $q = 7.182$, $P < 0.001$). Conversely, highly sensitive species were least likely to be detected during period 3 (low vs medium $q = -0.618$, $P > 0.05$; low vs high $q = -8.184$, $P < 0.001$; medium vs high $q = -8.679$, $P < 0.001$). No tests within period 2 were significant (all $P > 0.05$). Period 5 was not tested due to low sample size.

DISCUSSION

Variation in temporal detectability of birds documented here has several implications for studies of bird communities in tropical forests. When estimating species richness of an area or the abundance of a particular population, it is obviously desirable to sample at times when individuals are most easily detected (see Terborgh *et al.* 1990). The results of my analyses show that detectability of birds, whether grouped by family, foraging guild or sensitivity to disturbance varied substantially by time of day at La Chonta. That the majority of birds were detected within the first 2 h following sunrise should surprise no one, although even differences between the first and second hour after sunrise were pronounced for some foraging guilds (Table 3). Most importantly, a number of families, foraging guilds and species were disproportionately detected during times that are not frequently sampled, at least in studies of forest fragmentation.

Complete and well-documented inventories of tropical forest bird communities, using all appropriate sampling methods (e.g., surveys, mist-nets, audio recordings and collections) are critical to our understanding of bird distributions and abundances. Precise density estimates of birds in tropical forests are crucial to conservation monitoring efforts and to better document responses of bird communities to habitat degradation and fragmentation. At La Chonta, few species were detected on pre-sunrise or evening surveys that were never detected at other times during the study, yet the contribution of these surveys to the derivation of density estimates for several species was considerable. Elsewhere, I analyzed a subset of the data presented here (Woltmann 2003), but was only able to generate moderately precise density estimates for 29 out of 174 species due to low sample sizes for most species. Density estimation for 9 of those 29 species (~30%) would not have been possible without the data from pre-sunrise and evening surveys.

Analyses from other regions and from studies designed to test specific hypotheses regarding detectability are needed to help clarify whether my results can be generalized to other tropical forests and other seasons. For studies designed to investigate temporal variation in detectability explicitly, a finer resolution of time periods may be desirable (Blake 1992). In my study, census periods of one hour potentially hid a greater amount of variation than I was able to present. For example, detections of some species during pre-sunrise surveys did not occur in total darkness, but rather in the 15–20 min before dawn, when there was at least a hint of light in the forest. For tropical forests, the relationships between relative abundances or density estimates and actual densities remain unclear. Elsewhere, estimated densities of birds on 100-ha plots were made from massive efforts using multiple methods (Terborgh *et al.* 1990, Thiollay 1994, Robinson *et al.* 2000) but such efforts are rare, and most studies are conducted over short times using few observers. Our understanding of tropical bird communities will benefit greatly from additional inventories from other areas, and new or continuing studies should incorporate quantitative evaluations of various survey methods, especially compared to more complete inventories.

Although my pre-sunrise and post-dusk surveys were invaluable for estimating densities of several species, there is, of course, an added cost of time required to complete such surveys. Moreover, some tropical forests may contain few species not active during typical survey times (pers. observ.). Birds considered more sensitive to habitat disturbance were slightly more detectable during atypical survey times in this study, and this aspect requires further investigation. I recommend that investigators conduct (and present results of) at least some quantitative pre-sunrise and post-dusk surveys at all sites in order to assess the potential benefits. Where possible to conduct safely, I suggest that a greater number of nocturnal surveys will add considerably to our understanding of the behavior, abundances and distribution of tropical forest birds.

ACKNOWLEDGMENTS

This work was supported by BOLFOR, a USAID-funded project designed to study and implement sustainable forestry practices in Bolivia. I thank Frank Moore for supporting my work, both directly and indirectly. Todd and Nell Fredericksen provided advice and logistical support that made this work possible. Sarah Mabey, Ted Simons, Raymond McNeil, and two anonymous reviewers offered very useful suggestions that improved this manuscript. I thank Genoveva Rodriguez for providing the Spanish abstract.

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