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TEMPORAL VARIATION IN POINT COUNTS OF BIRDS IN A LOWLAND WET FOREST IN COSTA RICA[1]

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Abstract. Hourly variation in bird activity can influence census results but has not been well studied in tropical habitats. I examined hourly variation in numbers of birds detected during 10 min point counts in a tropical wet forest site in Costa Rica. Counts started one-half hour before and continued for 4.5 hr after sunrise. Counts were conducted along three routes (20 points each on two routes; 11 points on one route) in primary forest during early (January), middle (March), and late (April) dry season of 1991, prior to the main breeding season (May–June) for most species. Total numbers of individuals and species detected per point declined significantly from early to late morning. Birds of forest understory declined markedly during the first hour; detections of canopy birds, by contrast, tended to increase from the first to second or third hour, before declining. Hourly variation was more pronounced, overall, later in the dry season. Individual species differed in patterns of detection during the morning. Results indicate that point counts in this forest should be restricted to the first three hours of the morning.

Key words: Abundance, census technique; hourly variation; point count; seasonal variation; tropical forest.

INTRODUCTION

Methods for censusing birds in temperate habitats have been well studied (e.g., Ralph and Scott 1981, Verner 1985, Verner and Milne 1989). With some exceptions (Scott et al. 1986, Waide and Narins 1988, Terborgh et al. 1990), much less effort has been expended on methods for sampling tropical birds; only two of 82 papers in Ralph and Scott (1981) dealt primarily or substantially with tropical birds. Many factors affect abilities of observers to detect birds (papers in Ralph and Scott 1981, Järvinen et al. 1977, Verner 1985) and must be evaluated when designing sampling procedures for a particular study.

Hourly variation in bird activity (e.g., singing rates) has been recognized as an important consideration when sampling birds (Dawson 1981, Verner 1985). Various studies conducted during the breeding season in temperate habitats have demonstrated significant diurnal variation in numbers of birds detected, with detections typically greatest early in the morning (Järvinen et al. 1977, Shields 1977, Skirvin 1981). Not all studies have reported similar results (Dawson 1981, Verner and Ritter 1986) and species often differ in diurnal patterns of activity (Dawson 1981, Robbins 1981, Scott et al. 1986, Blake et al. 1991). Diurnal variation in bird activity also occurs in tropical habitats (Karr 1981, Parker 1991). Many species of tropical birds have characteristic dawn choruses or songs (Skutch 1954, 1960, 1967; Stiles et al. 1989; Parker 1991, pers. observ.); singing activity often declines later in the day. Consequently, the ability of an observer to detect and count birds in tropical forests likely changes during the morning as well.

Monitoring studies of tropical birds are increasing in importance as habitats are lost (see Lynch 1989). Community studies of birds in tropical areas also deserve much greater work. Thus, it is important to recognize and evaluate factors that influence bird sampling in tropical areas. To this end, I examined how detections of birds varied during morning point counts in lowland wet forest in Costa Rica. More specifically, I asked the following questions: (1) Is there significant variation in number of birds detected during the first five hours of the morning? (2) Do hourly patterns of detection vary among species and between canopy and understory birds? (3) For how many hours in the morning should birds be counted in this tropical forest?

STUDY AREA AND METHODS

STUDY AREA

I conducted this research at Estación Biológica La Selva, located in the lowlands of northeastern Costa Rica, near Puerto Viejo de Sarapiqui,

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Provincia Heredia (10°25′N, 84°01′W). La Selva encompasses approximately 1,510 ha, of which about 64% is primary forest (Clark 1990); the station also supports successional habitats in various stages of regrowth. La Selva lies across a transition between tropical premontane and tropical wet forest life zones (Holdridge 1967, Hartshorn 1983). The current checklist of plants includes approximately 1,740 species of vascular plants; 1,450 of these are considered native "forest species" (Hammel 1990). Height of primary forest canopy reaches 30 m–40 m (Hartshorn and Peralta 1988). La Selva ranges in elevation from approximately 40 m–200 m. The southern boundary adjoins Parque Nacional Braulio Carrillo (approximately 44,900 ha) so that continuous forest exists from approximately 40 m–2,900 m above sea level (Pringle et al. 1984). Rainfall at La Selva averages 3,900–4,000 mm/year (Organization for Tropical Studies, unpubl. data). The dry season typically lasts from January or February to April or May, with a second, less pronounced dry season in September and October.

A total of 412 species of birds have been recorded at La Selva (Blake et al. 1990, pers. observ.), with approximately 360 occurring on a more or less regular basis. Breeding occurs throughout the year, with a peak in May and June (Levey and Stiles, in press). The breeding avifauna is seasonally enriched by additions of latitudinal (long-distance) and altitudinal migrants (Blake et al. 1990; Blake and Loiselle 1991, in press; Loiselle and Blake 1991).

BIRD COUNTS

I established three sample routes within forest at La Selva; routes covered an elevational range of about 40–150 m. Two routes were entirely within primary forest: Camino Circular Cercano–Camino Central–Lindero Sur (CCC route hereafter); and Camino Circular Lejano–Sendero Suroeste–Lindero Occidental–Sendero Jaguar (CCL route hereafter). The third route (Camino Experimental Sur–Camino Experimental Norte–Sendero Occidental—CES hereafter) was mostly in primary forest but also included a few areas of mature secondary forest.

I used point counts located 200 m apart along 1–2 m wide trails to sample bird abundance. Two sample routes (CCC and CCL) were 3.8 km and included 20 points each; only 2 km (11 points) could be accommodated along the CES route. I counted birds during three sample periods: 11–13 January, 3–6 March, and 1–3 April 1991 (early, middle, and late dry season). All points along each route were sampled once during each sample period. The same direction of travel was followed on each route during each sample period. All counts were started approximately 0.5 hr before sunrise and took 4 hr 55 min (CCC, CCL routes) or 2 hr 40 min (CES route) to complete. Counts were conducted on days with no rain and little or no wind (<5 km/hr).

I counted birds for 10 min at each point, allowing 5 min between points (4 points/hour). All birds seen or heard were recorded and the distance from the point was estimated; I did not include birds that were observed flying by over the canopy. The great majority (>80–90%) of all detections were aural rather than visual; throughout the text, I use "detections" to refer to birds observed or heard. I classified birds as understory or canopy birds following Stiles et al. (1989): understory birds included species described as found primarily on the ground, in the understory, or in low canopy; canopy species included those using the middle and upper canopies.

ANALYSES

I used the CCC and CCL routes (20 points/route) for most analyses of hourly variation in number of birds recorded; data from the shorter route were used for comparison when appropriate. I examined variation in abundance at two temporal scales: 10 min intervals (by single point); and hourly intervals (means of 4 points). Variation was examined: (1) for each route separately, by sample (early, middle, late dry season); (2) by sample, pooling data from the different routes; and (3) with data from both routes and all samples pooled. Data from CCC and CCL routes were used to calculate mean number of birds seen per point. I examined variation in the following: total individuals; total species; canopy birds; understory birds; and individual species. I analyzed canopy and understory birds separately to determine if activity patterns differed between these two groups.

I used Spearman rank correlations (Sokal and Rohlf 1981) to examine general trends in detections during the morning (10 min intervals). I used parametric one-way ANOVA (or nonparametric Kruskal-Wallis test) followed by a Tukey

TABLE 1. Correlations (Spearman's *r*) between time of day (based on 10 min point counts) and number of birds detected. Results are presented separately for the three samples (early, middle, and late dry season) and with results combined. For description of routes, see text.

Route	Early	Middle	Late	Combined
CCC (20 points)				
Total birds	−0.73***	−0.82***	−0.92***	−0.84***
Understory birds	−0.79***	−0.93***	−0.73***	−0.82***
Canopy birds	−0.40 ns	−0.54*	−0.68***	−0.56***
Total species	−0.67**	−0.79***	−0.86***	−0.77***
CCL (20 points)				
Total birds	−0.71***	−0.85***	−0.92***	−0.82***
Understory birds	−0.57**	−0.84***	−0.92***	−0.80***
Canopy birds	−0.36 ns	−0.55*	−0.87***	−0.53***
Total species	−0.65**	−0.76***	−0.92***	−0.78***
CES (11 points)				
Total birds	−0.22 ns	−0.62*	−0.93***	−0.52**
Understory birds	−0.79**	−0.84**	−0.86***	−0.82***
Canopy birds	0.04 ns	−0.09 ns	−0.20 ns	−0.07 ns
Total species	−0.18 ns	−0.24 ns	−0.74**	−0.39*

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; ns = not significant.

multiple comparison among means test to compare mean number of birds counted per point during different hours of the morning. Kruskal-Wallis tests were used for all tests of individual species. Variables were tested for normality (Wilk-Shapiro test) and equality of variances (Bartlett's test) before statistical analyses and were log-transformed (ln) when assumptions were violated. Nonparametric tests were used when necessary.

RESULTS

TOTAL INDIVIDUALS

Total numbers of individuals and species recorded during point counts declined significantly from early to late morning when analyses were based on individual point counts (Table 1, Fig. 1). Declines occurred during each sample (early, middle, late dry season) but were more pronounced overall late in the dry season (Fig. 2).

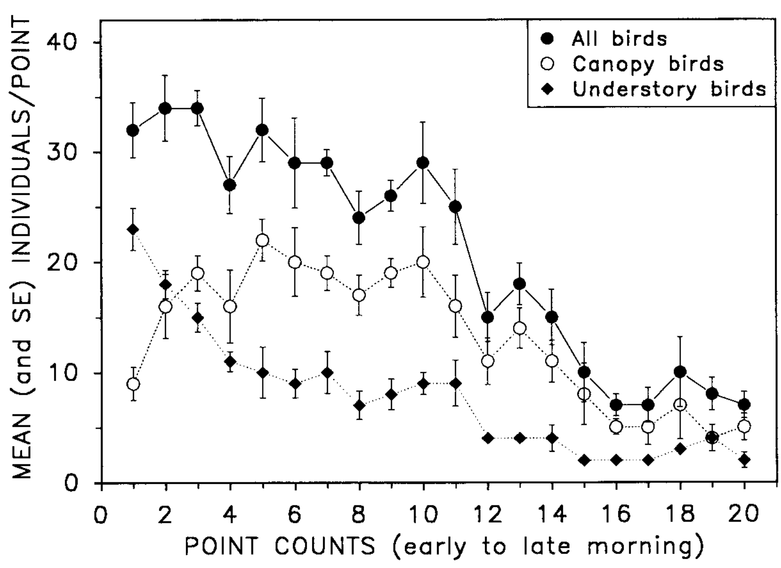

FIGURE 1. Numbers of birds detected during 10 min point counts that started one-half hour before sunrise. Results are pooled from two routes over three samples (early, middle, late dry season).

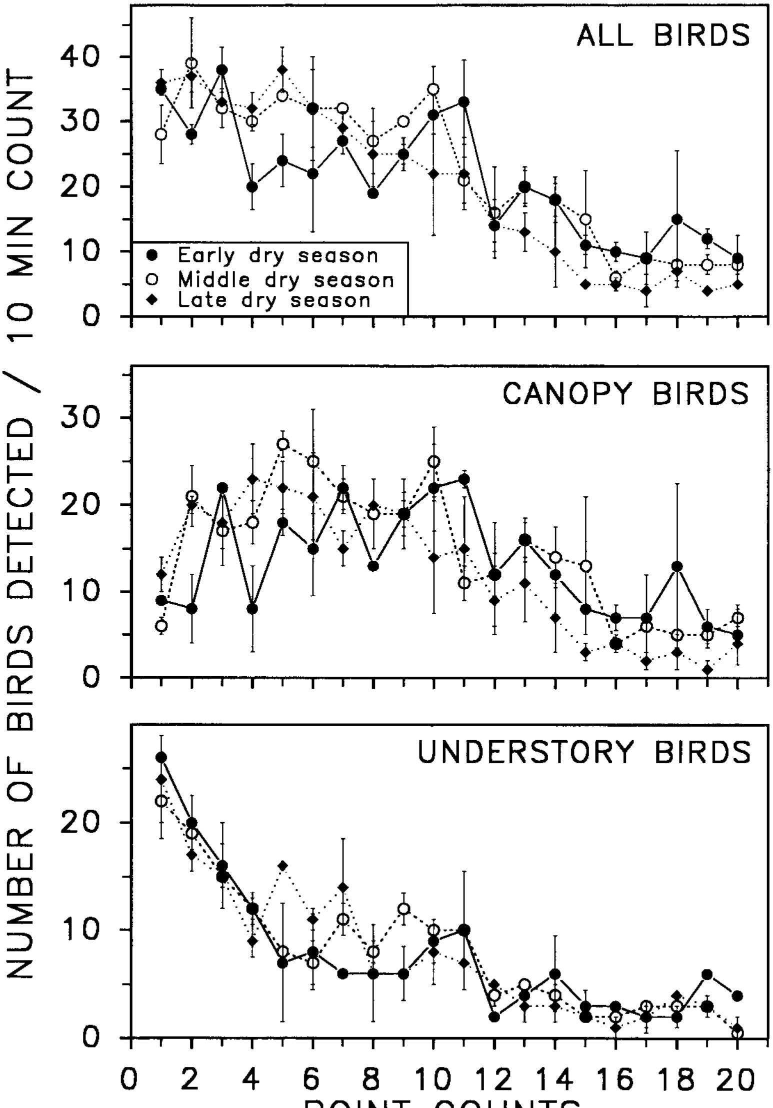

FIGURE 2. Seasonal variation in numbers of birds detected during 10 min point counts. Results are pooled from two routes.

Detections of understory birds declined dramatically during the first hour, tended to level off during the next two hours, and were consistently low during the last two hours (Figs. 1, 2). Detections of canopy birds, by contrast, tended to increase from the first to second hour but, as with understory birds, declined substantially during the last two hours. Variation in number of birds detected per point was somewhat greater among canopy birds than among understory birds (Fig. 2).

Differences between understory and canopy birds were reflected in results from the shorter (CES) route as well; detections of understory birds showed a significant negative correlation with time during the first three hours (11 point counts) but canopy birds did not (Table 1). Results were not simply a function of the smaller sample size for the CES route. When data from the first 11 points on the CCC and CCL routes were analyzed, results were similar to those obtained from the CES route.

TABLE 2. Means and SDs for number of birds observed per point during the first through fifth hours of the morning during point counts (4 points/hr). Results from two routes (CCC, CCL) are combined within each sample. Samples are from early, middle, and late dry seasons. Results of ANOVA (F) or Kruskal-Wallis (KW) tests and multiple comparison among means tests are shown.

Sample	First hr		Second hr		Third hr		Fourth hr		Fifth hr		F or KW	$P <$
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD		
Early dry season												
Total birds	29^{a}	±8.4	23^{ab}	±6.3	25^{a}	±9.1	14^{bc}	±5.3	11^{c}	±6.8	F = 7.7	0.001
Understory birds	17^{a}	±5.8	6^{b}	±3.6	7^{b}	±4.5	4^{b}	±2.4	3^{b}	±1.8	F = 13.2	0.001
Canopy birds	12^{ab}	±7.5	17^{a}	±4.9	19^{a}	±5.9	11^{ab}	±4.2	8^{b}	±6.9	F = 4.5	0.01
Middle dry season												
Total birds	32^{a}	±6.7	31^{a}	±5.8	25^{a}	±9.1	15^{b}	±7.3	8^{b}	±1.3	KW = 27.1	0.001
Understory birds	17^{a}	±4.7	8^{b}	±2.1	9^{b}	±4.3	3^{c}	±1.5	2^{c}	±1.3	F = 27.1	0.001
Canopy birds	15^{ab}	±6.7	23^{a}	±5.2	17^{ab}	±7.3	12^{bc}	±6.8	5^{c}	±1.5	KW = 20.1	0.001
Late dry season												
Total birds	34^{a}	±3.1	31^{a}	±6.9	20^{b}	±7.5	8^{c}	±5.0	5^{c}	±2.0	F = 50.4	0.001
Understory birds	16^{a}	±6.6	11^{ab}	±5.3	6^{b}	±2.4	2^{c}	±1.5	2^{c}	±1.6	F = 18.6	0.001
Canopy birds	18^{a}	±5.2	19^{a}	±4.4	14^{a}	±6.8	6^{b}	±4.5	2^{c}	±1.7	F = 24.2	0.001
Combined samples												
Total birds	32^{a}	±6.4	28^{ab}	±7.2	24^{b}	±8.6	12^{c}	±6.5	8^{c}	±4.8	F = 55.4	0.001
Understory birds	17^{a}	±5.5	9^{b}	±4.3	7^{b}	±3.8	3^{c}	±1.9	3^{c}	±1.6	F = 51.8	0.001
Canopy birds	15^{a}	±6.7	20^{a}	±5.3	17^{a}	±6.7	9^{b}	±5.6	5^{c}	±4.6	F = 24.1	0.001

^{abc} Means not sharing the same letter are significantly different, $P < 0.05$; Tukey multiple comparison among means tests.

TABLE 3. Correlations (Spearman's *r*) between time of day (based on 10 min point counts) and number of birds detected. Only species with a minimum of 50 total observations are included. Results from two routes (CCC, CCL) are combined within each sample. Results are presented separately for the three samples (early, middle, and late dry season) and with results combined.

Species	Early	Middle	Late	Combined
Understory species				
Tinamus major	−0.58***	−0.77***	−0.57***	−0.64***
Trogon rufus	−0.30	−0.32*	0.00	−0.20*
Henicorhina leucosticta	−0.10	−0.09	−0.46*	−0.21*
Canopy species				
Columba nigrirostris	−0.18	−0.56***	−0.22	−0.32***
Amazona farinosa	−0.62***	−0.31*	−0.72***	−0.54***
Trogon massena	−0.01	−0.41**	−0.58***	−0.36***
Ramphastos sulphuratus	−0.10	−0.24	−0.38*	−0.23*
Ramphastos swainsoni	0.03	0.42**	−0.29	0.06
Lipaugus unirufus	0.02	−0.00	−0.17	−0.04
Hylophilus decurtatus	0.15	0.05	−0.18	0.01
Euphonia gouldi	−0.16	−0.04	−0.32*	−0.13
Cacicus uropygialis	0.06	−0.33*	−0.26	−0.18
Psaracolius montezumae	−0.24	−0.19	−0.26	−0.18

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

Hourly variation in number of birds detected (i.e., mean of 4 point counts/hr) reflected results based on individual point counts (Table 2). Mean total counts were highest in the first hour during each sample. Significantly fewer birds were detected in the fourth and fifth hours than in earlier periods.

INDIVIDUAL SPECIES

Patterns in the number of birds detected per point during the morning varied among species. Significant declines in number of birds detected were noted for some species (Table 3); many species did not show significant declines. Detections of only two species (*Tinamus major, Amazona farinosa*) declined significantly over time during all samples. Detections of *Ramphastos swainsoni* increased significantly during the morning during the middle dry season sample. Declines in number of birds detected per point were somewhat more pronounced during the middle and late dry season samples (Table 3).

When analyses were based on comparisons among hours, mean number of birds detected per point varied significantly for 21 of 28 species tested (Figs. 3, 4). Of these 21, 11 were most frequently detected during the first hour, 6 during the second, and 4 during the third hour. No species was observed most often during the fourth or fifth hours. Detections of most understory species were highest during the first hour (Fig. 3), whereas detections of most canopy species tended to peak during the second or third hour (Fig. 4). Hourly variation in abundance was particularly pronounced (i.e., one hour with significantly more detections than all other hours) for two understory (*Tinamus major, Baryphthengus ruficapillus*) and two canopy species (*Amazona farinosa, Xiphorhynchus lachrymosus*).

DISCUSSION

Substantial diurnal variation in activity is known to occur among tropical forest birds (Karr 1981, Scott et al. 1986). Effects of such variation on bird sampling procedures are not, however, well known. Results of this study demonstrate that the number of birds detected during 10 min point counts can vary substantially during the first five hours of the morning. Substantially more birds and species were detected during the first three hours of the morning than in the subsequent two hours. Declines in bird detections from early to late morning have been reported from several studies in temperate habitats (e.g., Skirvin 1981, Blake et al. 1991) but overall declines typically are not as pronounced as they were in the current study (see Dawson 1981, Verner and Ritter 1986).

Although patterns in total numbers of birds detected in forest at La Selva were relatively clear and consistent, overall trends obscured substantial differences among groups and species. Such differences probably accounted for the fact that

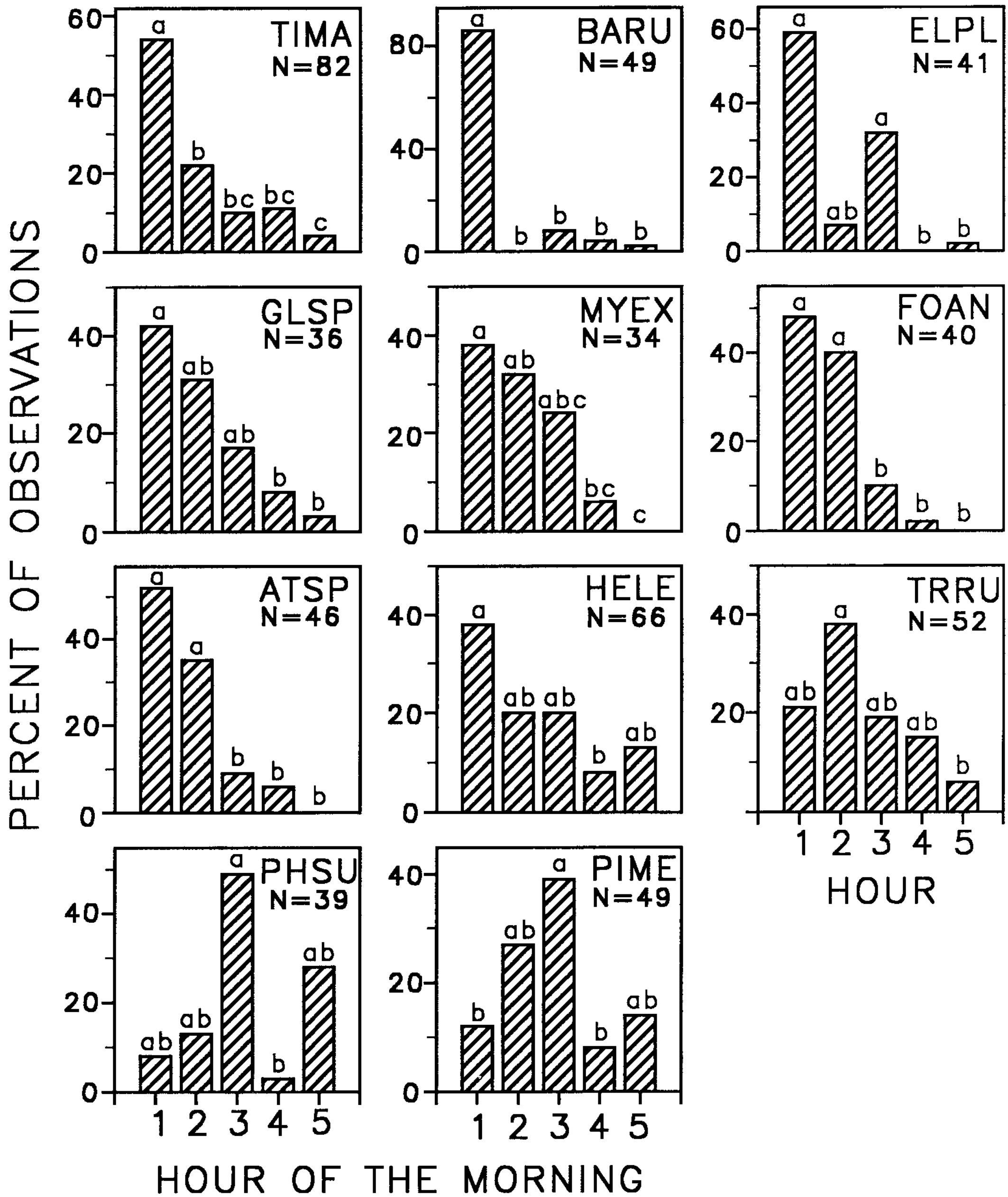

FIGURE 3. Percentage of total individuals (N) of understory birds detected during the first through fifth hours of the morning. Results from two routes were pooled across three samples (early, middle, late dry season). Comparisons among hours were based on Kruskal-Wallis tests. Significant differences among hours are indicated by lower-case letters: hours not sharing the same letter were significantly different ($P < 0.05$). Species codes are: TIMA = *Tinamus major*; BARU = *Baryphthengus ruficapillus*; ELPL = *Electron platyrhynchum*; GLSP = *Glyphorynchus spirurus*; MYEX = *Myrmeciza exsul*; FOAN = *Formicarius analis*; ATSP = *Attila spadiceus*; HELE = *Henicorhina leucosticta*; TRRU = *Trogon rufus*; PHSU = *Phaethornis superciliosus*; PIME = *Pipra mentalis*.

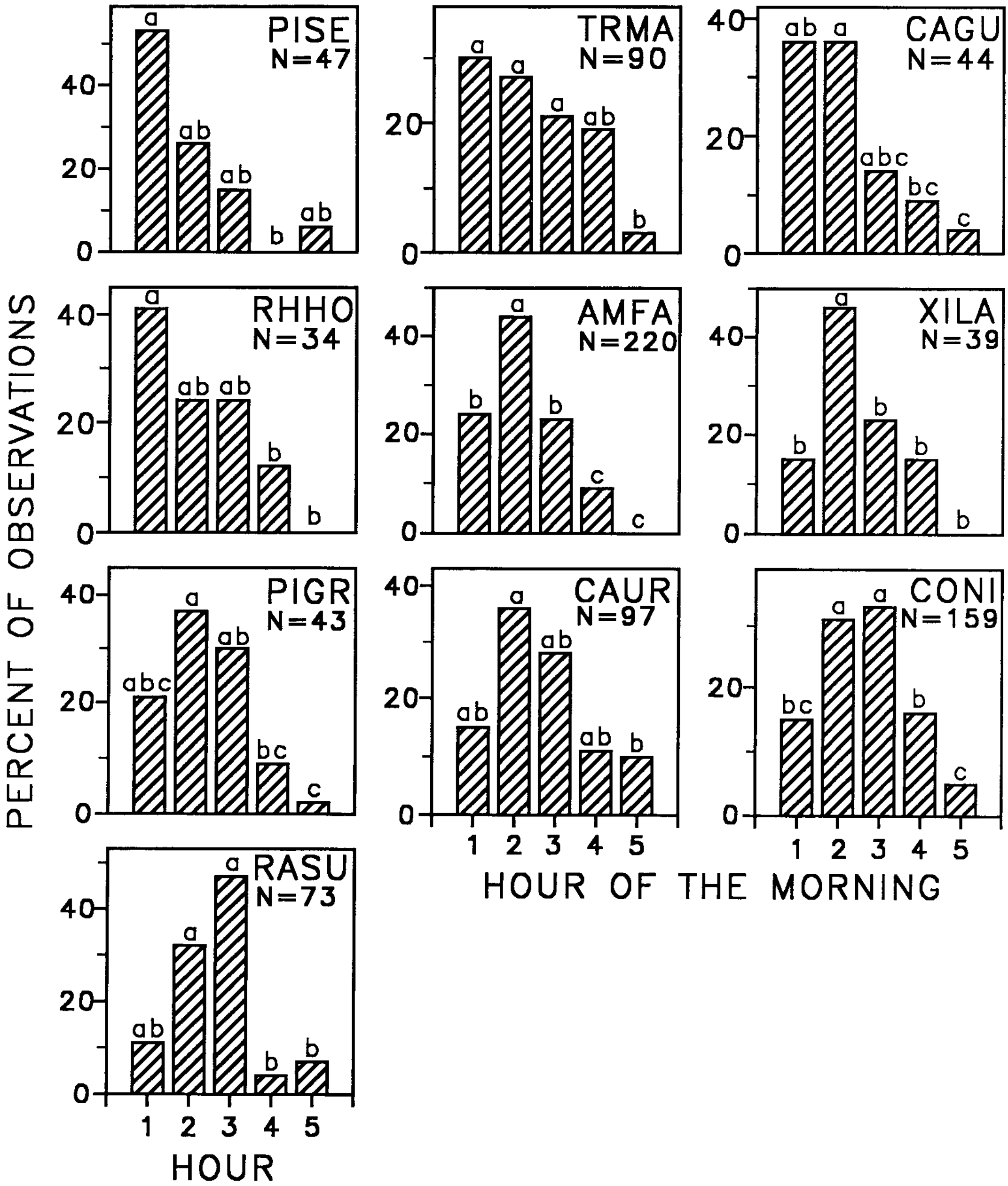

FIGURE 4. Percentage of total individuals (N) of canopy birds detected during the first through fifth hours of the morning. Results from two routes were pooled across three samples (early, middle, late dry season). Comparisons among hours were based on Kruskal-Wallis tests. Significant differences among hours are indicated by lower-case letters: hours not sharing the same letter were significantly different ($P < 0.05$). Species codes are: PISE = *Pionus senilis*; TRMA = *Trogon massena*; CAGU = *Campephilus guatemalensis*; RHHO = *Rhytipterna holerythra*; AMFA = *Amazona farinosa*; XILA = *Xiphorhynchus lachrymosus*; PIGR = *Pitylus grossus*; CAUR = *Cacicus uropygialis*; CONI = *Columba nigrirostris*; RASU = *Ramphastos sulphuratus*.

total numbers of birds detected during the first two or three hours did not consistently vary (e.g., see Figs. 1, 2). Verner and Ritter (1986) suggested that species differences contributed to their failure to detect significant hourly trends in total counts. In this study, detections of understory birds declined strongly from the first to second hours of the morning but detections of canopy birds increased during this same period. Consequently, the total numbers of birds detected did not change as dramatically during the first few hours. Detections of almost all birds declined substantially during the last hours, so that general trends accurately reflected group trends.

Species differed in diurnal patterns of activity, even within understory or canopy groups. Detections of some species fell off very rapidly during the morning, with some species singing only briefly at dawn (e.g., *Jacamerops aurea*, pers. observ.; see also Parker 1991). Much of the abrupt decline in understory birds observed during this study was attributed to rapid declines in numbers of vocalizing tinamous (e.g., *Tinamus major*) and motmots (e.g., *Baryphthengus ruficapillus*). Other understory species, in contrast, became more vocal later in the morning (e.g., *Pipra mentalis*; see Fig. 3). A similar pattern occurred among canopy birds. *Pionus senilis* was detected most often during the first hour whereas *Columba nigrirostris* increased in abundance from the first to second and third hours (see Fig. 4).

Differences in behavior among understory and canopy birds affected patterns of hourly variation. Most understory birds observed did not occur in flocks, so that often there was less variation in abundance from point to point, particularly after the first hour. In contrast, several species of canopy birds (*Amazona farinosa, Ramphastos swainsoni, R. sulphuratus, Pteroglossus torquatus, Psaracolius montezumae, Cacicus uropygialis*) occurred in wide-ranging flocks. Presence of such species contributed to the often high variance in birds detected per point.

In areas where a few species are very abundant but many are rare or uncommon, the presence of those common species may mask the presence of the more uncommon species (van Riper 1981). Although many species at La Selva are relatively rare (Blake et al. 1990), few species were so abundant that their calls made it difficult to detect others, except in certain circumstances. Presence of flocks also may contribute to variation in count data by making it difficult to detect other species. When flocks of *Amazona farinosa* landed overhead, for example, their loud vocalizations made it difficult to detect quieter species. Although presence of loud flocks may increase the variance in count data, their presence will not be likely to affect temporal trends unless such occurrences are correlated with hour of the morning.

Seasonal changes in bird behavior may influence singing rates and thereby affect patterns of hourly variation in detectability (Skutch 1960, Shields 1979, Best 1981). Changes in singing rates can be particularly influential in habitats where the majority of birds are detected by sound rather than sight, as was true in this study (see also Blake et al. 1991). The more pronounced hourly variation seen later in the dry season at La Selva may have been related to effects of weather and breeding. The drier and hotter conditions that typically prevail later in the dry season likely contributed to the more rapid declines during the morning in numbers of birds detected. Although breeding can occur throughout the year at La Selva, there is a major breeding period during May and June, at the beginning of the rainy season (Levey and Stiles, in press). The somewhat higher numbers of birds detected during the first hour or two of the morning during the late dry season sample may have been associated with increasing breeding activity of some species.

Seasonal variation in abundance of altitudinal (species that breed at higher elevations and seasonally descend to lower elevations) and latitudinal migrants in primary forest at La Selva (Blake et al. 1990, Loiselle and Blake 1991) influences composition of the bird community and might be expected to affect count data. Few migrants were detected during point counts, relative to the number of nonmigratory species, and migrants likely exerted little influence on hourly or seasonal trends reported here. Two latitudinal migrants (*Hylocichla mustelina, Dendroica pensylvanica*) were recorded on a regular basis, but showed no pronounced temporal variation in numbers detected per point.

Latitudinal migrants at La Selva are particularly common in second-growth habitats (Blake et al. 1990; Blake and Loiselle 1991; Blake and Loiselle, in press) and seasonal variation in abundance might be more likely to influence census results in such habitats than in primary forest. Altitudinal migrants, by contrast, are more common in primary forest (e.g., *Corapipo leucorrhoa*) but, with some exceptions (e.g., *Procnias trica-*

runculata) are not particularly vocal during their residence in lower elevation forests (pers. observ.). Their presence or absence at La Selva likely did not influence hourly variation in counts.

Hourly variation in bird activity can affect results of bird counts and should be taken into account when designing a sampling procedure (Scott et al. 1986, Verner 1985). In tropical forests, many birds sing only or primarily at or just before dawn (Skutch 1954, 1960, 1967; Stiles et al. 1989; Parker 1991, pers. observ.), so counts must include that period. Some birds, however, become more vocal somewhat later in the morning (e.g., Scott et al. 1986, this study), indicating that counts should continue for some time after the dawn chorus. Significant declines in bird activity during the morning indicate that counts should not be continued for many hours past dawn.

Results of this study suggest that bird counts in this tropical wet forest should be concentrated in the first 2–3 hr of the morning, starting approximately 20–30 min before dawn. Relatively abrupt declines in numbers of birds detected during the fourth hour and continued low counts during the fifth hour argue against counting for more than three hours. These results differ somewhat from studies conducted in temperate habitats (e.g., Verner and Ritter 1986, Blake et al. 1991), where declines from the first to fourth hours of the morning often are not pronounced (see also Dawson 1981). In those habitats, it might be possible to extend count periods for more than three hours or even to count during the middle of the day (Dawson 1981). Counts conducted late in the morning at La Selva, by contrast, yield relatively few birds and are not comparable to those conducted earlier. Further, if both early and late morning counts are pooled, the increased variance in counts will make it more difficult to detect differences (e.g., from one sample to the next). If, however, the aim is to gather complete species lists from a particular site, as opposed to obtaining statistically comparable samples for habitat or temporal comparisons, then sampling periods could and probably should include both early and later periods during the day.

Results presented here apply to one site in tropical wet forest of Costa Rica during the dry season. The extent to which these results apply during the wet season at La Selva or at any season elsewhere in the tropics is not known. Complementary studies in dry deciduous tropical forests (e.g., Guanacaste Province in Costa Rica), in more seasonal evergreen forests (e.g., Barro Colorado Island, Panama), and in higher elevation (montane) forests are needed. Work at higher elevations (e.g., 2,000 m) in Parque Nacional Braulio Carrillo, Costa Rica, for example, indicates that birds are more vocal later in the morning than at lower elevations (Blake and Loiselle, unpubl. data). Importance of second-growth habitats for many resident and migratory species (Blake and Loiselle 1991) argues for studies in those habitats as well. There is an increasing need for studies that monitor bird populations in tropical (and temperate) habitats (Lynch 1989). To ensure that results from different studies and regions are comparable, attention must be placed on proper design of counting techniques. Additional information on the extent to which census results in tropical habitats are affected by various factors (e.g., weather, time of day, season, habitat) is necessary.

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