TROPICAL FOREST BIRD COUNTS AND THE EFFECT OF SOUND ATTENUATION

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ABSTRACT.—Simultaneous variable circular-plot censuses were conducted by two observers at five heights above ground in lower montane rain forest in Puerto Rico. One observer began the censuses at the top of a 22-m walk-up tower, and the other observer began at the bottom. Tests for interobserver variability indicated that the observers were not significantly different in their ability to detect birds. Sufficient numbers of 6 species (*Columba squamosa, Spindalis zena, Vireo altiloquus, Coereba flaveola, Nesospingus speculiferus,* and *Todus mexicanus*) were observed to compare differences in the efficiency of canopy and ground observers. More birds that sing from the canopy were detected by the canopy observer than by the ground observer. The reverse was true for birds that sing near the ground. Species were most often detected at the station closest to their mean singing height. Population densities of canopy-singing species were underestimated by 33–46% by the ground observer. Measurements of the attenuation of pure tones of different frequency indicate that low-frequency sound attenuates less rapidly than high-frequency sound. Species with low-frequency songs are heard equally well by ground and canopy observers. *Received 24 June 1987, accepted 12 December 1987.*

THE effectiveness of auditory signals in communication is greatly affected by physical characteristics of the environment, including the absorptive effect of vegetation and background noise (Wiley and Richards 1978, Richards and Wiley 1980, Michelsen and Larsen 1983, Narins and Zelick 1987). These physical characteristics vary in time and space, as do the constraints they impose on acoustical signals. In addition, signals have been subjected to selection pressures to distinguish them from those of heterospecifics and to confuse predators. As a result, auditory signals of different species have an effective range that depends on physical characteristics of the signal related to function, vegetative absorption, background noise, and local microclimatic conditions.

Ornithologists have often made use of avian auditory signals in censuses of bird populations (Cyr 1981, Emlen and DeJong 1981, Richards 1981). In tall or structurally complex habitats, many more birds are heard than are seen, and the use of auditory cues is often mandatory for accurate counts. When using avian vocalizations in estimating populations, the effective range of each species song or call is usually taken into account. For example, both variable strip-transect (Emlen 1971) and variable circular-plot (Reynolds et al. 1980) counts use estimates of the horizontal distance to aurally detected birds in calculating population densities. In structurally simple habitats these horizontal distances result in a good estimate of effective range (or detection distance) and thus abundance for most species. In taller, more complex forests, canopy-dwelling birds may be beyond the effective range for the species even if they sing directly above the observer, resulting in an underestimate of the true density (Reynolds et al. 1980).

Because the effective range of bird song varies with species, habitat, and weather conditions, it would be difficult to generalize about the magnitude of the aforementioned underestimate even if other confounding factors such as observer variability were ignored. However, a rough idea of the importance of the underestimate under given conditions can be obtained by empirical means. With the empirical estimate derived in this study as a guide, observers conducting counts in forest can predict the general magnitude of underestimates of canopy-singing birds. Observers with access to the forest canopy can also develop empirical estimates for their own sites using our methodology.

We used an established observation tower to conduct counts in and above the canopy, and compared population estimates made by observers stationed at, above, and below the mean singing height of several species.

Study Area and Methods

The El Verde Field Station of the Center for Energy and Environment Research is located in the Luquillo Experimental Forest in northeastern Puerto Rico. The area was declared a forest reserve in 1903 and has been managed by the U.S. Forest Service as the Caribbean National Forest since 1917. The region has a long history of ecological research (summarized by Odum and Pigeon 1970 and Brown et al. 1983).

The study area lies in the lower montane wet forest life zone (Ewel and Whitmore 1973) at an elevation of 425 m. The dominant tree species is the tabonuco (*Dacryodes excelsa*), with *Prestoea montana* (sierra palm) and *Sloanea berteriana* also abundant. The tower is an enclosed ladder with 13 platforms spaced at 1.8-m intervals. The tower has become completely enclosed and interwoven with canopy foliage in the 21 yr since it was erected.

Mean annual rainfall at the El Verde Field Station is 346 cm, based on 15 yr of records (Brown et al. 1983). The driest months (January–April) average more than 20 cm of rain, and well-dispersed rains during this period prevent the ground from drying completely. Daily mean relative humidity rarely falls below 80% either at ground level or above the canopy and usually is above 95%. Although the prevailing trade winds for eastern Puerto Rico are from the east and northeast, the light and variable winds at the tower are predominantly from the southeast. Wind velocity is greater at 27.6 m above the ground (range = 0–5 mph, $\bar{x}$ = 2.55 mph) than in the canopy at 16.5 m (range = 0–4 mph, $\bar{x}$ = 0.74 mph). Wind speeds are greater at 1 m above the ground than in the canopy, providing evidence of a local wind system within the more open lower forest (Odum et al. 1970).

Wadsworth (1951) listed 168 tree species from tabonuco forest, which is best developed on protected, well-drained ridges below 600 m in elevation. The forest type has three tree strata, a closed canopy at about 20 m, and an understory layer. The sparse vegetation of the forest floor and the lack of branches on the lower half of trunks gives the tabonuco forest an open appearance. Epiphytes are common, in the form of bromeliads, lianas, vines, and arborescent ferns and as a covering on shade leaves (Brown et al. 1983). Forest structure and foliage distribution have been examined by several investigators (Odum et al. 1963, Briscoe and Wadsworth 1970, Holdridge 1970, Rushing 1970, Wadsworth 1970).

Two observers performed simultaneous 8-min variable circular-plot counts at each of 5 heights above ground (0, 5.5, 11.0, 16.5, 22.0 m). Observer A began at 22 m and finished at 0 m, while observer B did the reverse. Both observers occupied the intermediate station at the same time, providing a check on inter-observer variability. Counts were performed on 8 days between 6 April and 8 May 1981, and all counts began between 0800 and 0930.

Observers underwent a short training period to promote uniformity in species identification and distance estimation. During counts both visual and aural detections were recorded. In calculating densities, only detections from species-specific song were used for the Scaly-naped Pigeon (*Columba squamosa*), Black-whiskered Vireo (*Vireo altiloquus*), and Bananaquit (*Coereba flaveola*) (Fig. 1). Detections from call notes were used for the Stripe-headed Tanager (*Spindalis zena*; "seep" call) and Puerto Rican Tanager (*Nesospingus speculiferus*; "chewp" and "tsweep" calls; Bond 1971). All vocalizations of the Puerto Rican Tody (*Todus mexicanus*) were used to calculate densities. Detections were grouped in 10-m intervals from 0 to 100 m, 50-m intervals from 100 to 200 m, and beyond 200 m. Determination of inflection points and calculation of densities followed Reynolds et al. (1980).

Sound attenuation was measured by playing tones from a speaker 18.3 m above the ground in the tower and measuring sound levels at 0, 25, 50, 75, and 100 m from the base of the tower. Tones at 500, 1,000, 2,000, 4,000, and 8,000 Hz were produced with a Heathkit Sine Square Audio Generator (1G-18) and recorded on a Uher 4200 tape recorder. Tones were played through a portable 15-W speaker/amplifier (Calrad 20-257), and sound level was measured with an impulse precise sound level meter (GENRAD 1982) using the octave filter, fast detector, and capture facility to obtain peak readings. Five consecutive sound pressure level readings were made for each octave filter center frequency at each distance from the tower. The mean of the five readings was calculated by first converting each decibel reading to sound pressure, averaging, and reconverting the mean sound pressure back to decibels. Distance from the sound source to ground recording point was calculated using the Pythagorean theorem.

The tape and speaker were calibrated at 1 m, and the expected loss in decibels at each distance was calculated by the inverse square law. All calibrations were made between 0900 and 1600, the period of minimum ambient noise. Background noise was taken into account in calculating expected sound levels at each frequency and distance using a standard decibel subtraction chart (Peterson and Gross 1972) for signals within 6 dB of the background. Attenuation was calculated as the difference between the expected and the measured levels.

The distribution of foliage was estimated by counting the number of leaves within 1 m of the tower at 1-m intervals from the ground. At each sampling height, a 1-m stick was passed around the periphery of the tower, and the leaves touching the stick were counted.

The mean height of singing birds was determined during transect counts (Emlen 1971) in 4 1-ha plots

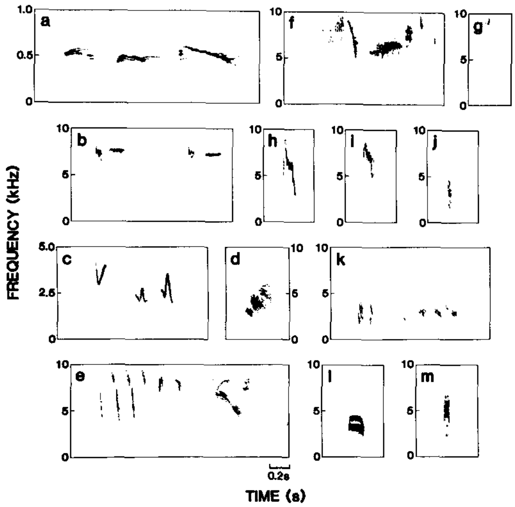

Fig. 1. Sound spectrograms of representative vocalizations of six species near El Verde, Puerto Rico. (a) Scaly-naped Pigeon (*Columba squamosa*); (b) Stripe-headed Tanager (*Spindalis zena*); (c and d) Black-whiskered Vireo (*Vireo altiloquus*); (e–g) Bananaquit (*Coereba flaveola*); (h–j) call notes of the Puerto Rican Tanager (*Nesospingus speculiferus*); (k) whisper song of *N. speculiferus*; (l and m) Puerto Rican Tody (*Todus mexicanus*). Spectrograms were made from the record "Caribbean Bird Songs" (produced by P. P. Kellogg, 1969, Ithaca, New York) using a Uniscan II FFT real-time spectrogram spectral display (Multigon 4600). The output of the analyzer was band-pass filtered (0.5–20 kHz) to reduce the low-frequency rumble and extraneous high-frequency noise from the record.

within 0.5 km of the tower. Transect counts were performed throughout the course of a year (Waide and Hernández Prieto 1981). The heights of singing birds seen during transect counts were estimated with a range-finder (Reagan et al. 1982).

RESULTS

We analyzed six abundant and vocal species (*C. squamosa*, *S. zena*, *V. altiloquus*, *C. flaveola*, *N. speculiferus*, and *T. mexicanus*; Fig. 1). Foliage distribution varies over the height at which five of these species vocalized (Fig. 2). Although not shown, *S. zena* sang from perches just within or above the canopy (Waide pers. obs.).

Differences between observers were tested in two ways. During each series of counts on a given morning, the observers took simultaneous counts at the intermediate platform (11.0 m). There were no significant differences between observers in the number of birds of each species detected in these counts. Only for *S. zena* was there a suggestion that the observers were unequal in their detection abilities, but the difference was not significant ($P > 0.10$, paired t-test, df = 7). The more experienced (and older) observer detected fewer *S. zena*, which might be expected because this species sings at about 8 kHz, and the sensitivity of the human ear to high frequencies decreases with age.

When data from all heights and censuses were pooled, there were significant differences between observers in the estimation of the distance to singing *C. squamosa* and *V. altiloquus*. These differences will affect the selection of the inflection point in calculating densities. Hence, data were pooled and a single inflection point chosen for each species at each height. This reduced the possibility of systematic bias due to differences in distance estimation between observers. In addition, comparisons between heights were made on the basis of the raw observational data rather than calculated densities.

The canopy observer detected significantly more singing *V. altiloquus* and *S. zena* and significantly fewer *T. mexicanus* and *C. squamosa*. This result was obtained both in comparisons of simultaneous counts by the two observers (between observers) and comparisons of canopy and ground counts for each observer on the same day (within observer; Table 1). There was no difference in the number of *C. flaveola* and *N. speculiferus* observed between canopy and ground observers.

All species except *C. squamosa* showed a close correspondence between singing height and the height where maximum numbers of individuals were recorded (Fig. 3). *Todus mexicanus* was recorded equally at the lower three heights that span the range at which this species commonly sings. *Nesospingus speculiferus* was heard more often at the lower end of its range of singing heights. The number of observations of *C. flaveola* was highest at 11 m, which corresponds to the species' mean singing height. *Vireo altiloquus* and *S. zena* are both canopy singers and were most often recorded at the top of the tower. *Columba squamosa* was recorded less frequently near its mean singing height at the top of the canopy than at the lower stations.

Two canopy singers (*V. altiloquus* and *S. zena*) had higher population densities in canopy (22.0-m station) counts than in ground (0-m station) counts, while one understory singer (*T.

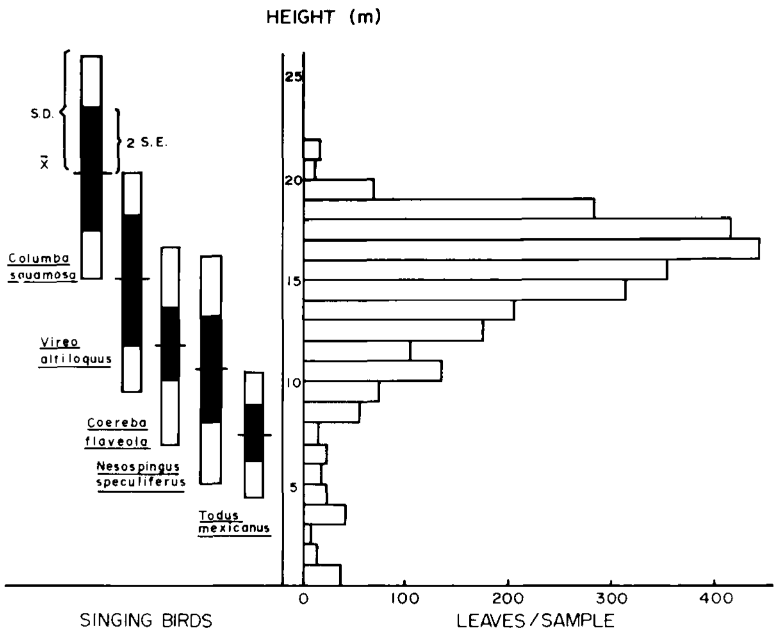

Fig. 2. Heights of singing birds and foliage around the tower at El Verde. Methods are described in the text.

mexicanus) had a higher population density in ground counts than in canopy counts (Table 2). One canopy species (*C. squamosa*) had lower population densities in canopy than in ground-level counts.

Sound attenuation of different frequencies differed around the tower. For each doubling of distance from the source, intensity should decline by 6 dB. Declines in intensity greater than the predicted 6 dB (excess attenuation) result from absorption, reflection, and scattering. Declines less than the predicted 6 dB (negative excess attenuation) are due principally to reinforcement. All sound frequencies (Fig. 4) showed excess attenuation, but the lower frequencies showed relatively less.

No direct measurements of song intensity are available for the species under consideration. We estimated the distance to each singing bird, however, and the distance at which bird song can be heard is partly a reflection of song intensity. Ten percent of the detections of *C. squamosa* and *V. altiloquus* occurred at greater than 200 m. Ninety percent of the detections of *C.*

Table 1. Mean difference in number of individuals heard singing between canopy and ground counts. A positive value means more birds were detected at the canopy station. The total number of paired observations (counts by observers at canopy and ground stations) is 16 for each species. "Between observers" refers to simultaneous counts taken by the two observers. "Within observer" refers to canopy and ground counts taken on the same day by the same observer. The mean difference is the same whether data pairs are organized between or within observers.

Species	Mean difference between ground and canopy counts	Between observers		Within observer	
		Paired *t*-test	One-tailed significance level	Paired *t*-test	One-tailed significance level
C. squamosa	−0.81	1.98	$P < 0.05$	2.21	$P < 0.025$
S. zena	+0.50	1.83	$P < 0.05$	2.07	$P < 0.05$
V. altiloquus	+4.50	3.60	$P < 0.005$	3.25	$P < 0.005$
C. flaveola	−0.13	0.24	$P > 0.40$	0.24	$P > 0.25$
N. speculiferus	−0.50	1.10	$P > 0.10$	1.04	$P > 0.10$
T. mexicanus	−0.63	2.61	$P < 0.01$	2.82	$P < 0.01$

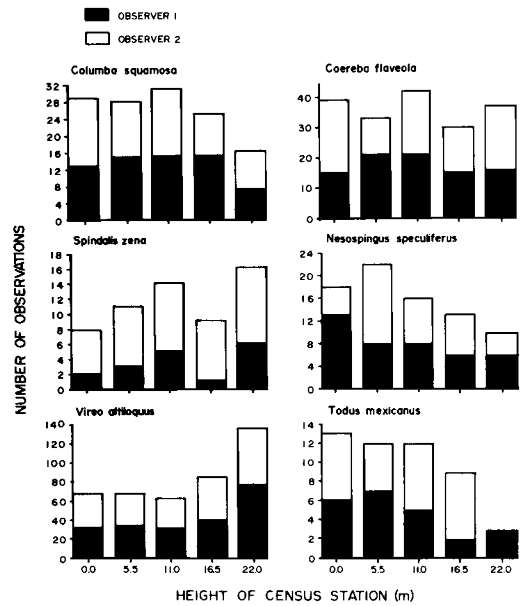

Fig. 3. Number of observations of 6 bird species in 16 censuses conducted at each of 5 heights (0, 5.5, 11.0, 16.5, 22.0 m).

flaveola and *T. mexicanus* were within 40 m, and 90% of the detections of *N. speculiferus* and *S. zena* were within 50 m of the observers. Only one individual of any of the latter four species was detected at a distance greater than 100 m, suggesting that the intensity of their songs is less than those of *C. squamosa* and *V. altiloquus.*

DISCUSSION

Census techniques that estimate the number of birds in an area are more useful for a variety of purposes than counts of relative abundance (Reynolds et al. 1980). Variable strip-transect and variable circular-plot counts provide estimates of population density, but both methods tend to underestimate species that sing from the canopy in tall forest. Because 80–90% of the birds in dense coniferous or rain forest are detected by their vocalizations, an appreciable bias against canopy-dwelling species occurs in data from such habitats. In this relatively low-canopied (22 m height) study area in Puerto Rico, 2 of 3 canopy-singing species were underestimated by 33–46% in ground counts.

The third canopy species, *C. squamosa,* is extremely wary of humans as a result of being hunted. The behavior of this species apparently was affected by the presence of the canopy observer, and a disproportionately small number of observations near the tower and low density estimates (22–33/km^2) resulted. The density of *C. squamosa* was estimated independently at over 200/km^2 in 166 transect counts taken in 1980–1981 (Waide unpubl. data). Although this species sings from bare branches at canopy level or above, it was heard more often below canopy level. Canopy observers rarely recorded *C. squamosa* within 50 m of the tower, suggesting that the presence of the observer frightened all but the lowest birds into silence.

High-frequency sound attenuates more rapidly in this forest than low-frequency sound. Observations of *S. zena* dropped rapidly with vertical distance of the observer from calling birds. Within the canopy (10–20 m height), there was an inverse relationship between foliage density and the number of *S. zena* recorded calling, further demonstrating the attenuating effect of vegetation on this species' vocalizations. The lowest-frequency song (*C. squamosa*) was heard well at ground level, below the mean singing height (20 m). *Vireo altiloquus* has a song of intermediate frequency that was strongly attenuated by the high leaf density near its mean singing height (15 m). We conclude that maximum range in this forest can be obtained by low-frequency songs delivered from above or below the canopy foliage. Other constraints are important in the evolution of bird song, particularly the necessity to prevent predators from localizing the singer and the vertical distribution of the potential receivers, which may be affected by any number of nonacoustic selection

TABLE 2. Comparison of population densities calculated from canopy (22.0-m station) and ground (0-m station) counts. The sample size is 16 counts for each species at each level.

	Population density (birds/km^2)		Absolute difference (%)	Sign
	Ground counts	Canopy counts		
C. squamosa	33	22	50	−
S. zena	56	103	84	+
V. altiloquus	282	422	50	+
C. flaveola	1,365	597	129	−
N. speculiferus	221	112	97	−
T. mexicanus	221	66	235	−

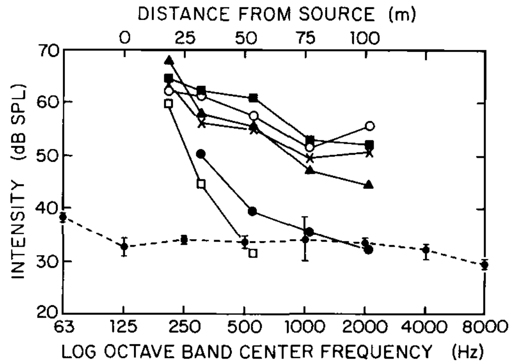

Fig. 4. Intensity of a continuous pure tone as a function of source frequency and distance from the source measured in the tabonuco forest near El Verde, Puerto Rico. Source height was fixed at 18.3 m. Symbols indicate tone frequency: × = 250 Hz, ○ = 500 Hz, ■ = 1,000 Hz, ▲ = 2,000 Hz, ● = 4,000 Hz, and □ = 8,000 Hz. The dashed line indicates background noise level in the absence of singing birds, measured with a sound-level meter and an octave filter centered at the frequencies indicated.

pressures. Hence, the singing height and frequency of a species may be a compromise among conflicting necessities.

Canopy foliage density seems to be effective in attenuating sound from the canopy to the ground, as well as from the ground to the canopy. The former is important for ground-based observers because it results in the bias against canopy-singing species. The magnitude of the underestimate of canopy populations depends on the characteristics of the signal, the attenuating effect of the vegetation, and the choice of census method. For species that sing loudly (*V. altiloquus*, *C. squamosa*), there was little difference between ground and canopy counts in the number of detections within 50 m of the observer. The relatively large mean difference between canopy and ground counts for these species (Table 1) was due largely to differences in the number of birds detected more than 100 m from the observer. For birds that sing softly (*T. mexicanus*) or at frequencies barely audible to some observers (*S. zena*), considerable differences between high and low counts occurred within 50 m of the observer but not within 20 m. Hence, a fixed, small-radius circular-plot census or a narrow, fixed-width transect will minimize the bias against canopy-singing species and may eliminate it completely for species that sing loudly.

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