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SURVEYING BIRDS IN THE TROPICS

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ABSTRACT.—Numerous difficulties plague the researcher as he/she sets out to determine the species composition and abundances of birds frequenting a specific area. Many of these difficulties have been minimized for temperate environments as censusing procedures have been improved in the past two decades. But procedures developed in temperate situations are often inadequate in tropical regions where avifaunas are composed of many rare species and, in addition, many "peculiarities" of species biology diverge from the "norm" of temperate avifaunas. Examples of these peculiarities include permanent occupation of territories, decreased levels of singing, secretive habits, extensive overlap in home ranges, and numerous species which wander over relatively large areas in search of mobile (e.g., army ants) or otherwise spatially patchy (e.g., fruits) food resources. The significance of these problems for censusing and procedures to improve the reliability of bird census data are described.

Many factors affect the degree to which census results reflect real densities of birds in a census area. These include both physical (weather, topography) and biotic (vegetation type, biology of birds) factors. For most terrestrial habitats in temperate regions acceptable census procedures have been developed and are in widespread use. However, even in temperate regions, selected species may be very difficult to census. The unusual pairing pattern and use of "territory" in Brown-headed Cowbirds (*Molothrus ater*) results in considerable difficulty in applying conventional census procedures. In grassland and marsh habitats, polygamous species may be abundant and make accurate censuses difficult. Because most birds are territorial and monogamous, however, the proportion of temperate birds for which peculiarities of natural history affect census results is low.

In sharp contrast, many tropical species exhibit "unusual" behavior and natural history attributes that significantly affect census accuracy. Consequently, researchers in tropical regions must use caution in selection of census methodology. It is too early to present a detailed and precise guide to censusing tropical birds. Rather, it is my intent here to discuss briefly many of the special circumstances obtaining in tropical habitats and their effects on accuracy of censuses. Since the greatest concentration of these peculiarities is in forest habitats, my discussion emphasizes forest birds.

THE ROLE OF PHYSICAL FACTORS

Weather and topography are the two most important physical factors affecting census accuracy. Primary weather factors that reduce census reliability are wind and rainfall. Wind is significant because it directly affects bird activity and because it reduces the ability of observers to hear vocalizations and detect movements of birds. Dry season winds are a problem in some areas. Occasionally these winds persist for extended periods, forcing one to avoid censusing or to census with results of less than optimum quality. Obviously, little else can be done to reduce the importance of this factor.

The other physical factor of major concern is rainfall. Lowland forest in the humid tropics often receives large quantities of rain. During late wet season several days of continuous rain may limit census opportunities. However, the effect of rain is usually less than expected from rainfall quantity because rains typically are concentrated in late afternoon due to their convectional origin. In contrast to the short, heavy rains of lowland areas, persistent light rain and fog in mountainous areas may limit census accuracy.

These problems are essentially the same as those in many temperate environments. To census or not must be determined by the field worker following guidelines formulated to minimize census activity during periods when census results are likely to be unreliable. However, strict adherence to such guidelines may result in periods without data.

THE ROLE OF VEGETATION

Type of vegetation on a study area is important in determining census accuracy. Vegetation density may inhibit one's ability to traverse the study plot and may make it difficult or impossible to observe birds. Both problems are common in early successional habitats and in grasslands. Grassland habitats in relatively wet areas present serious difficulties when grass heights exceed 5 m. Often this vegetation is impenetrable because of the sharp edges of grass blades. Late successional areas become impenetrable thickets in which movement results in noise levels sufficient to cause a reduction in bird activity. In habitats with very dense ground-level vegetation, trails can be cut to minimize distur-

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TABLE 1
TOTAL NUMBER OF BIRD SPECIES KNOWN FROM AREAS OF SEVERAL SIZES IN PANAMA AND ILLINOIS

Region	Area (km²)	Number of bird species
Panama	75,600	905
Illinois	144,700	390
Canal Zone	1424	560
East-central Illinois[a]	6050	292
Limbo Hunt Club study plot	0.02	205
Bottomland forest, Kickapoo State Park	0.02	70

[a] Three-county area of Champaign, Piatt, and Vermilion Counties.

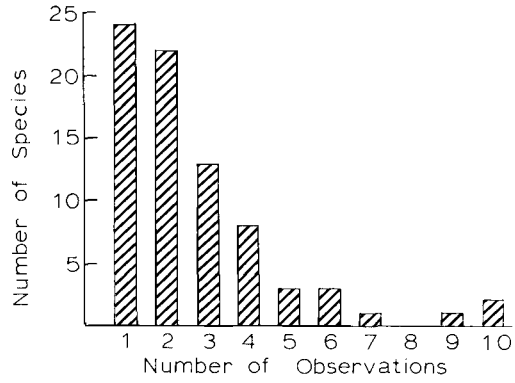

FIGURE 1. Number of observations for each of 77 rarely observed bird species at Limbo Hunt Club, Pipeline Road, Republic of Panama.

bance to vegetation while allowing the observer to pass throughout the area with relative ease and a minimum of disturbance. However, trails may require considerable work to keep them clear. I try to vary origin, direction of travel, and termination point for censusing along trails. This prevents secretive species from escaping the observer by the same behavior during each census. In my experience, density of undergrowth in forested areas is not sufficient to deter reliable censusing.

Major problems of censusing in forest are darkness in the undergrowth and extreme height of vegetation. When these factors are compounded with some topographic irregularity, censusing can be especially challenging. Tree heights above 30 m are not uncommon, and identification of small canopy species (e.g., hummingbirds and flycatchers) may thus be difficult or impossible. Consequently, the observer depends on vocalizations as a cue to bird presence to a greater extent than in many temperate habitats.

An abundance of "peculiar" plant life forms can also make censusing difficult. Dense epiphytes and lianas can limit unobstructed views of foraging birds. Flowering and fruiting plants (sites of major bird activity) in the forest canopy may be out of view from the ground.

The final difficulty that originates as a consequence of the nature of tropical vegetation is an extraordinary species richness. Barro Colorado Island, Panama, an area of 1450 ha, supports more than 1350 species of higher plants, including 652 woody species (Croat 1978). This wide array of species makes vegetation sampling and classification exceptionally difficult, especially in view of the many recent studies that show the importance of specific plant species in tropical (Howe 1977) and temperate environments (Holmes et al. 1979).

THE ROLE OF AVIAN NATURAL HISTORY

The most vexing problems in censusing tropical birds result from the birds themselves. Limitations of time and space prevent a detailed analysis of all relevant factors. At best, I can highlight a few of the more significant difficulties.

The most commonly cited characteristic of tropical forest avifaunas is their high species richness (Table 1). The number of species seen in a relatively small forest area in central Panama (Limbo Hunt Club) continues to increase after over a decade of intensive research. In two weeks of field work, I commonly record 100 to 110 species on that 2-ha study plot, and I have observed over 200 species on the study plot. South American forests are often richer.

This extraordinary species richness is combined with striking rarity for many species (Fig. 1). Rare species may be encountered only once or twice per year; rarest species are only encountered every few years. When mist nets are used to census forest undergrowth avifaunas, rare species (<2% of sample) constitute 75–85% of the species included in samples from Brazil (Novaes 1969) and Panama (Karr et al., In press).

Presence of species with very similar plumage compounds the problem of identification, especially when birds are seen as shadowy forms in dark undergrowth. In some cases males may be well-marked, but females are difficult to distinguish. Males of different species may be similar in nonbreeding plumages. Even voices may be similar, compounding the problem of distinguishing species.

One of the most popular census procedures used in temperate environments (spot-map or

singing-male) is based on the assumption that most resident birds form monogamous pairs that defend clearly delineated territories (type A territories of Nice 1943). But in many tropical habitats many species do not defend type A territories (Karr 1971). My rather rough compilation suggested that most species (98%) in structurally simple habitats, such as grassland, defend exclusive territories. In more complex forest habitats, relatively fewer species (32%) defend exclusive territories. Even species that defend territories may do so in ways that are unusual. Plain-brown Woodcreepers (*Dendrocincla fuliginosa*) do not form permanent pair bonds; males and females establish territories that overlap extensively, but with little or no congruence in boundaries (Willis 1972).

Many unusual breeding systems exist that differ from conventional spacing and habitat-use patterns. The lekking behavior of the manakins (Foster 1977), hummingbirds (Stiles and Wolf 1979), and others are excellent examples. Intraspecific and interspecific flocking are common also. A tremendous diversity of spatial patterns is used by many flocking species. In some cases several species may co-defend territory boundaries, while other species joining the same mixed flock may not be territorial or may have entirely different territory boundaries (Munn and Terborgh 1979, Gradwohl and Greenberg 1980). The nature of flocks varies significantly and is often associated with type of food resource exploited and its spatial distribution (Karr 1971, Moriarty 1976).

Aggregations of individuals may involve single species (undergrowth tanager such as *Tachyphonus delatrii*) or mixed species (tanager-honeycreeper) flocks. Many types of interactions occur with varying spatial and temporal stability due to local variations in resource density and presumably other factors. Finally, even species that occupy type A territories may exhibit behavior different from that of ecologically similar species in North Temperate areas (e.g., Plain-brown Woodcreeper mentioned above).

Many species are more or less permanently mated and occupy territories all year. In this circumstance, it is not unusual for singing activity to be reduced throughout the year with obvious consequences for the probability of the observer recording the species.

To add further complicating factors, occupation of space may vary seasonally. This has been well documented for many migrant species that initially set up winter territories (Morton 1980) and later abandon territories to feed in mobile flocks. The latter behavior is apparently associated with periods when local food supplies may be unreliable and territory defense is not economical.

Temporal dynamics of tropical forest avifaunas also present significant problems. In addition to a variety of locally stable, but not classical territorial species, many tropical forest species travel over wide areas in search of their mobile and/or patchy food resources (Willis 1973). This makes reliable censuses on small study plots very difficult.

Often movements that are so common in tropical forest birds appear random when data bases are derived from short-term studies. However, many of these apparently random patterns are precisely timed movements. Local movements on diurnal, seasonal, and year-to-year time scales are clear (Karr, in press). Further, the patterns on these time scales are not always consistent among days, seasons, and years due to lean seasons that vary in severity or to bottlenecks in resource availability that limit species and their distributions. All in all, these patterns are exceedingly complex; they do not lend themselves to use of a single census procedure that is equally applicable for all species, seasons, years, and habitats.

Another temporal dynamic is associated with arrival and departure of migrants (Keast and Morton 1980). In some cases there are long distance migrants, while in other cases they may be local movements on altitudinal or other (e.g., rainfall) gradients. Transients also may be very common for short periods.

Another methodological problem is variability in census results from one period to another. I have censused a forest study plot on one morning and been hard pressed to detect more than 6 to 10 species of birds. On the very next day and under the same weather conditions, I may detect 50 or more species on the same area. This magnitude of variability defies easy classification and development of reliable census procedures.

High cicada densities also may create problems. During the dry season, the din of calling cicadas can effectively prevent any census activity that depends on hearing bird vocalizations. This may seem a trivial problem, but presence of the problem for weeks on end can result in major blanks in valuable and otherwise contiguous data records.

Intensity of predation pressure on tropical forest birds, especially during their breeding season, may have selected for cryptic behavior patterns. Many species are very effective at avoiding detection because of their secretive behavior. In addition, effectiveness of nest concealment also is a result of similar selective pressures. This limits success in searching for nests

to confirm breeding on the study area. As an example, despite long studies by Willis on the Ocellated Antbird (*Phaenostictus mcleannani*) on Barro Colorado Island, Panama, he has still not discovered the nest of the species (Willis 1973).

SOLUTIONS

Regrettably, there are no simple solutions to the problem of censusing birds in tropical forest. The best advice is to use an array of procedures selected to provide the most comprehensive information for the objectives of the study. The problem is easiest to solve when the subject of the study is a small set of closely-related species. Under this circumstance, a procedure(s) can be selected to optimize quality of results.

However, when community level objectives are a top priority and/or when time is limited, I have grave doubts about the possibility of producing reliable census data across a wide spectrum of species. This pessimistic view is substantiated by comments and qualifications invariably included in papers on tropical avifaunas. Anyone anticipating attempts to census birds in tropical (especially forest) areas should carefully review their objectives in light of the comments and cautions of Orians (1969), Terborgh and Weske (1969), Howell (1971), Karr (1971, 1976c, In press), and Hespenheide (1980).

Several widely recognized census procedures have been used in tropical environments, including singing male, transect or trailside counts, mist nets and banding, and point counts. All have strengths and weaknesses.

Singing-Male Counts

This is, in my opinion, the least reliable procedure. Lack of breeding synchrony and limited singing activity of many species makes this procedure inappropriate. Several early studies (MacArthur et al. 1966; Howell 1971; Karr 1971, 1976c) depended heavily on this procedure. A large proportion of species is missed on any individual census, so there is a tendency to grossly underestimate species richness. In addition, use of this technique by persons inexperienced in identifying tropical birds also results in underestimates of species richness. Reliability of density estimates is no doubt low, although when supplemented with monitoring of banded birds, reliability may improve (Karr 1971, 1976c).

Due to the large number of rare and/or rarely encountered species in tropical areas, the suggestion, based on temperate work, that 5–6 censuses are sufficient to census an avifauna accurately must be viewed with caution. A more comprehensive census effort is essential.

Transect Counts

Transect counts also have been popular with researchers in tropical forest areas although they rarely include the type of corrections for sighting distance discussed by Emlen (1977a). Pearson (1977) used this procedure as did Orians (1969), Hespenheide (1980), and Fodgen (1972). All of these researchers recognize the inadequacy of a procedure which centers on the naive assumption that encounter probabilities are proportional to local density. Since species conspicuousness varies considerably (e.g., the tanager *Tachyphonus delatrii* vs. the wren *Microcerculus marginatus*), care must be used to standardize comparison of results from several areas. Variability among observers in knowledge of voices and sight identification may create real problems. Further, observer bias toward flocks (Hespenheide 1980) may significantly bias transect counts against solitary or quietly foraging species.

Mist Nets

Mist nets, in my opinion, are the best procedure available for "censusing" bird populations in tropical forest. They avoid the bias of inadequate knowledge of the resident avifauna and provide a random, unbiased sample of birds moving in the space sampled by nets. They do not, however, randomly sample the entire fauna. Species that walk on the ground, large and very small species, and species active at levels above net operation are undersampled. Very mobile species are captured out of proportion to their local density.

These disadvantages notwithstanding, I still feel more comfortable using nets to develop quantitative information on selected components of a tropical avifauna. Use of numbered or colored bands in combination with mist nets further enhances the value of mist-net counts. In addition, other data can be collected in concert with netting operations. Excellent examples of the use of bands to understand avian population dynamics include the detailed studies of antbirds by Willis (Willis and Oniki 1978), antwren flocks by Gradwohl and Greenberg (1980), and studies of moult by Fodgen (1972).

Point Counts

Point counts have rarely been used in tropical forest. Its only use to my knowledge was by MacArthur et al. (1966). MacArthur recognized the weakness of that study long ago. Recent census experience in temperate areas with this procedure suggests to me that its use should increase in the tropics. Without doubt, sample sizes and duration will have to be expanded con-

siderably relative to the conventional use of point counts in temperate habitats.

All of these procedures have strengths and weaknesses, and thus must be used, and their results interpreted, with caution. The bottom line for tropical censuses is intimate knowledge of birds to be studied and design of a complex of census protocols selected to provide the greatest amount of information in the context of the purpose of the investigation. It is important to identify species with peculiarities in behavior or ecology. The situation is very different from that in the temperate zone, where most species have "normal" spacing and territorial systems. Census procedures, as well as interpretation of data, must reflect that reality. To attempt to establish a uniform protocol at this time would limit reliability of census data in years ahead.

DISCUSSION

Decisions about census procedures are perhaps the most important and complex decisions to be made by an ornithologist wanting to assess an avian population or community. During the past decade considerable effort has been made to examine techniques and biases in censusing birds in temperate regions. In contrast, systematic, comparative studies to evaluate census methodology in tropical areas are lacking; most tropical censuses have been conducted by researchers with limited time and a primary focus on research objectives unrelated to evaluation of census procedures. Short-term visits by temperate-based scientists are not likely to fill that gap in the near future. As a result, census results will often be less reliable than is desirable.

To minimize the problem created by inadequate information on census procedures in tropical areas, I suggest that four primary questions should be asked and carefully answered before censusing is initiated: Why? Who? What? How? (The same logic obtains for efforts to census birds at higher latitudes.)

WHY?

Why is the research program being initiated? What are the study objectives and/or the specific hypothesis to be tested?

WHO?

Emphasis in this question is determination of the species to be censused. Is it a single species or all of the birds in the assemblage? What are the important natural history attributes of the species in question? How will those attributes affect census results? In general, the who question will come second in studies of a disciplinary orientation, such as ecology or behavior. More applied efforts may have the "Who" question imposed by concern, for example, for specific rare or endangered species.

WHAT?

The what question is concerned with the type of information needed to attain project objectives. Are absolute or relative densities required? How essential are data on sex and age structure? To what extent are data on foraging behavior and ecology or other natural history data required?

HOW?

Finally, the "How" question should be asked. Identification of suitable procedures must consider time and funds available for the study as well as information on study objectives and natural history of study organisms. At this point the researcher must evaluate the presumed reliability of his results from a variety of census procedures in the context of objectives, organisms, and environmental constraints.

Lack of knowledge of environmental constraints, species attributes, and census biases makes decisions about census procedures especially difficult in the tropics. At the very least, I urge caution in the uncritical acceptance and application in tropical areas of procedures designed for censusing in the temperate zone. Indeed, I have some doubts about the extent to which the common assumptions of the temperate-based procedures are satisfied by the biology of temperate-zone birds; those concerns have been reinforced by my tropical experience and are now being raised by others in this symposium. This is not to suggest that census efforts should be abandoned; rather, thoughtful evaluation of results must include assessment of census biases and reliability.

My own work in censusing tropical birds has led me to the following general approach:

(1) Use a composite of census procedures selected to provide the best possible data for a variety of species. Tropical habitats, especially tropical forest, are a microcosm of the most vexing problems for censusing terrestrial birds. As a corollary for this, recognize that the problems of accurate assessment of abundance for all species are overwhelming. I prefer to target my efforts to development of reliable information on a selected set of species (e.g., undergrowth avifauna with mist netting) even if it means little or no information on other species (e.g., canopy species) within the community.

(2) Select procedure(s) which do not depend on some seasonal phenomenon like breeding for their effectiveness.

(3) Identify exceptional species and use special procedures to improve knowledge of their

abundances if such knowledge is essential to project objectives.

(4) There is no substitute for knowledge of the organism under study.

(5) Keep in mind the constraints placed on these thoughts by variability in study objectives.

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