

August 1971

PROPOSAL

Ecological Strategies of Resource Utilization Among the Birds of a Colombian Tropical Forest

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I. INTRODUCTION

Much of the present understanding of tropical avian ecology is based upon studies of single species (e.g. Skutch 1954, 1960, 1969; Miller 1962, 1968) or species groups (Willis 1967; Wolf 1970). Miller (1963) made a substantial contribution but, because of the method used (primarily collecting), was able to document his ideas adequately in only a very few species. Recent studies using mist nets, such as those initiated in Brazil by Humphrey and Lovejoy, or in Panama by Loften (neither study is extensively published) lack vital observational data and consistent day-to-day, year around effort in gathering capture data, Howell (1971) on the other hand relied almost entirely on visual census, without the knowledge of the individual in the population. The works of Snow and Snow (1964), Karr (1971), and Terborgh (e.g. 1971) combine, at least in part, both methods and are thus probably approaching the ideal in the study of a tropical bird population.

Despite the latter studies, long-term investigations of the dynamics of the total avian population within a given community are still lacking. For example, it is known that North American migrants compose ten to twenty-five per cent of the avifauna of certain tropical communities during the winter months. It is not, however, quantitatively known to what extent this migrant population competes with the resident population or constrains foraging niches or breeding seasons. In addition, the ecological roles (for instance their feeding niches) that many tropical birds are assumed to play are roles that have been defined from work in temperate zone communities, roles that may not apply or even exist in tropical communities. This "temperate zone bias" can only be corrected by extensive population-community studies in the tropics, fully as extensive as those completed or underway in the temperate zone.

The major goal of this study, therefore, is to provide baseline data, throughout an entire year, on the dynamics of the avian population of a tropical forest community. Special attention will be devoted to the following topics: the timing of the breeding and molt cycles of the resident species; the impact of North American passerine migrants; the movements of mixed feeding flocks; and the number and impact of transient tropical species. An attempt will be made to correlate these data with the available food supply. Specific food-web relationships will not be delineated; rather the insect, fruit, seed, and nectar supplies will be monitored throughout the year to determine their cycles.

II. LOCATION OF STUDY

We propose to carry out this study in the vicinity of Cali, Colombia, located in the upper Cauca Valley in the southwestern part of the country, at approximately 3° N. Through the cooperation of the Colombian ornithologist, Professor F. Carlos Lehmann V. of the Museum of Natural History in Cali, we have received assurances of a suitable field

site. This site will be located in the upper tropical, lower subtropical region at about 5000-6000 feet in the western range of the Andes, near that area studied so productively by Miller (1961, 1962, 1963, 1968). One of us (Ralph) spent four weeks in the vicinity in 1971 and has established contacts with the Department of Biology at the Universidad del Valle at Cali, where facilities are available through Professor Jose Ignacio Borrero H., an ornithologist in the department.

This location would be the best for our study for several reasons. First, approximately fifteen per cent of the avifauna of this area during the North American winter is composed of temperate passerine migrants (Miller 1963). Second, by being at 3°N we can take advantage of two wet and two dry seasons each year (Richards 1964:139 and Miller 1962), one when migrants from North America are present, and one when they are not. This situation, therefore, provides a unique field laboratory in which the effect of migrants upon the breeding population might be measured. Moving further north, one rapidly begins to lose the wet season during the North American winter and, by the time one reaches Panama, this wet season is virtually nonexistent. On the other hand, as one moves further south, numbers of North American migrants drop off rapidly and few winter south of the equator. Finally, the proximity of a university and museum at Cali with their available expertise will greatly facilitate our studies.

The field portion of this research will begin in the late fall of 1972 and continue through at least the entire year of 1973 to insure the coverage of at least one annual cycle.

III. SPECIFIC PROGRAM PLAN

A. Population Monitoring

The main focus of the avian population monitoring study will be the capture with mist nets, and processing of birds on a systematic and regular schedule. Mist netting is an especially sensitive technique to sample transients in an area and thereby detect this extremely important component of the tropical avian population. Most species of tropical birds do not exhibit the long distance seasonal migrations of north temperate species. Rather, it is presumed that they move in response to local seasonal factors such as fruiting trees or moisture gradients. Documentation of such movements is virtually non-existent and will be a major focus of this work. Mist netting by itself, however, is incapable of assessing the total population of an area. Towards this end, a regular weekly census of the entire study area will be conducted by visual and auditory means. The combination of the census, the netting and the in-depth studies outlined below, will enable an accurate estimate of the total avian biomass in the study area throughout the year.

Only through the use of mist nets, however, can there be accurate and complete documentation of the various molt and breeding cycles of the avifauna. It must be emphasized that virtually nothing is known about these cycles, especially molt, in tropical species. As Snow and Snow (1964) pointed out, "...knowledge of the season of moult is perhaps even more important than knowledge of the breeding season, as it seems to be the less variable of the two and may be more directly connected with the annual cycle." In addition, the extent and timing of the molt of North American migrants while in the tropics is still undocumented.

More or less continuous breeding in the tropics has been shown or suspected in several land bird species (e.g. Miller 1955, Moreau 1950, Snow and Snow 1964), but in only a few is it well documented. A double annual breeding cycle superimposed upon

apparent year-round breeding activity has been adequately shown in only one species (Miller 1959). With the data obtained from mist netting and from the in-depth studies, we will be able to pinpoint more accurately the timing of breeding cycles. With this information we can then perhaps gain some insight into the external mechanisms which control these cycles.

Moreau (1966) has estimated that there are approximately 40 times more migrants per unit area utilizing the American tropics than the African tropics. Although this estimate is probably too high (Ralph, MS), such an influx of migrants might inhibit breeding in residents during the winter season if food is limited. This has not yet been adequately documented. Near Cali, approximately equal climatic conditions prevail both when migrants are present and when they are absent, our study should be able to demonstrate the influence of the migrants upon the breeding avifauna.

To gather data as outlined above, mist nets will be set in at least two circles approximately 1.5 km. in circumference, and individual nets will be set approximately 50 meters apart, alternately oriented north-south and east-west. Each net set will sample various levels of the vegetation ranging from ground to canopy. This method of net placement results in the best assessment of dispersion, dispersal, territory or home range size, and it samples the largest area possible under the limitations of time and personnel as outlined in Ralph (MS). Such a net arrangement samples the birds on approximately 40 to 50 ha, and is effective in capturing more than 90 per cent of the residents. On each of the 30 net sites there will be a vertical arrangement of one to three nets for a total of 50 nets in operation per day covering all levels. A capture rate of from 0.5 to 1.0 birds per net per day is common in tropical situations when permanent sets are made (Ralph, unpublished data and Lovejoy, pers. comm.). With allowances for adverse weather and other factors, this would produce at least 10,000 captures in one year. Based on the work quoted above, approximately 80 per cent of these would be of 20 species for an average of some 30 captures per month of these 20 species. A sample size this large would be quite adequate for the purposes of documenting cyclic phenomena in these species. We know that this ideal will not be realized in all the 20 species in all the months, but it is felt that it will be obtained in most species.

Each bird captured by netting operations will be individually marked. The extent and location of molt, subcutaneous fat, weight, certain mensural characteristics, breeding condition (both externally and, when conditions require, internally), and the location and height of capture will be recorded.

B. In-depth Studies of Selected Species

Individual color marking of certain selected species will enable the investigators to follow more fully the interactions of these individuals, especially in resident feeding flocks and during breeding. Accurate assessment of the timing and duration of breeding seasons as outlined above will require knowledge of an individual's activities in addition to that produced by the sampling technique of mist netting. Various plots within and near the netting areas will be studied intensively, where all residents as well as established migrants have been color marked. Observational data from this portion of the study will aid us in determining the absolute numbers of individuals utilizing the areas, their feeding habits, breeding success, movements into or out of the area, and the types of social interaction common to each species (territorial, flocking, etc.). These

data will be gathered both during the breeding and non-breeding seasons and will thus provide the information necessary to properly assess the role of the individual bird in the population sampled by mist netting. As one of us has shown, this technique can provide great insight into the ecology of different species (Ralph 1967, 1969, MS; Ralph and Pearson 1971).

C. Foraging Niche Determinations

An understanding of the diverse ways the energy resources of a community are divided by its members is one of the primary goals of this study. A very useful observational technique for this end is the definition, in time and space, of the foraging niches of various species in the community (e.g. Morse 1968, Williamson 1971). Such a definition involves the recording of the foraging actions of individual birds and the characterization of these actions in terms of their type, frequency, and duration as well as in terms of their location in the microhabitat. Such a program was fruitfully used in delineating North American wood warbler niches as long ago as 1958 (MacArthur), but has received little use in the tropics, presumably because of the density of the foliage and the difficulty in following small birds. One of us (DeSante) has had experience with this problem in the tropics and has found that the use of a portable tape recorder alleviates this difficulty by allowing the observer to devote full attention to the bird. Individual actions of even such small birds as warblers can be recorded, even in quite dense foliage.

After choosing appropriate species or species groups to focus our attention on, a number of interesting problems will be investigated using this technique.

(1) The amount of foraging niche overlap between the wintering North American migrants and the related resident tropical species.

Presumably, this overlap could vary from a considerable percentage to virtually none as in the case of a migrant occupying either a seasonal or marginal niche (Willis 1966a). In the first case, the overlap of foraging niches of tropical resident species with North American migrants could prevent these tropical residents from undertaking any activities requiring high energy, such as breeding or molting. These foraging niche determinations therefore can be directly correlated with the molt and reproductive data obtained through mist netting. An example of the second case is DeSante's (MS) observations that in one area of Costa Rica, over eighty per cent of the foraging of the Tennessee Warbler (*Vermivora peregrina*) was on the inflorescences of the winter blooming *Combretum* vine. This niche was only shared with other North American migrants such as Baltimore (*Icterus galbula*) and Orchard Orioles (*I. spurius*).

(2) Seasonal changes in the foraging niches of certain resident species and their correlation with physiological or populational changes.

In the temperate zone, for example, it has been shown that most species of passerines, even granivores, feed their young on a nearly exclusive insect diet (Bent 1968). This often necessitates a change in foraging niche, particularly in those species whose breeding cycle is synchronized with a local bloom of insects. Near Stanford, California, DeSante (MS) has observed that the Oregon Junco (*Junco oreganus*), a typical temperate zone terrestrial granivore, takes up an arboreal foraging niche during April and May when it has young in the nest. There, feeding on oak moth larvae, it is in potential

competition with the migrant Orange-crowned Warblers (Vermivora celata) and resident Chestnut-backed Chickadees (Parus rufescens). Although such changes in foraging niche have seldom been demonstrated among tropical birds, (Wolfe 1970), these changes probably occur and play an important part in the dynamics of the avian population. The many fruit eating tanagers will be an ideal group to study in this respect, especially the many closely related species of the genus Tangara (Willis 1966b).

(3) The effect of the mixed feeding flock on the foraging niche of a given species.

This determination can be made by comparing the foraging niche of that species under various conditions of interaction with feeding flocks (e.g. Willis 1966c). For example, a species may leave the flock on a seasonal basis, perhaps at the onset of the breeding season. Another example is when an individual temporarily joins a flock that is passing through its feeding territory (Moynihan 1962, McClure 1967).

(4) The collection of comparative data on the foraging niches of tropical birds.

This can be an end in itself since such data are needed to lay the groundwork for any reasonable theories of competition and species diversity among tropical birds (e.g. Snow and Snow 1971 and Karr 1971). These concepts are indispensable for a comprehensive understanding of speciation and evolution in the tropics.

D. Monitoring of Available Energy Sources

The three previous sections of this study basically define the way in which the energy available to the avian population is utilized. It then remains to estimate the seasonal change in the total energy for this system. Miller (1962), with little data, contended that the abundance of food was constant throughout the entire year near Cali. However, this seems unlikely, and should be investigated. Our studies of the available food resources will describe these seasonal changes and thus their possible relation to the avifaunal cycles.

For the purposes of this study, determination of the absolute quantity of this energy is not necessary; however we will measure the changes in this energy. Fluctuations in the energy supply should be reflected in fluctuations in the consumers, either in their numbers or in the amount of energy that each consumes. These two alternatives will be reflected in the avian population, in the first case, by the emigration or immigration of a segment of the population or, in the second case, by the onset or culmination of breeding or molting processes. The energy sources that will be monitored are the fluctuations in the insect population, and in the quantity of fruit, seeds and nectar.

The insect population will be monitored by a regular schedule of sweeping at several levels and the operation of appropriate traps for flying insects. This monitoring will supply an approximate index to abundance, and thus should document the presence of cycles in the insect biomass.

The monitoring of the fruit, seed, and nectar quantity will be ascertained by very generalized methods of sampling. Species of plants that appear to be in fruit or flower and to be possible energy sources will be closely watched to record fluctuations in these food supplies.

Presumably any seasonal fluctuations in this energy supply result from a cyclic

nature of the climate. The extent and timing of climatic cycles will be measured by recording: rainfall and fog drip; humidity; daily temperature variations; and wind speed and direction. Except for precipitation, these variables have been shown to vary little in this area on an annual basis. However, another variable, cloud cover, may be one of the major exogenous factors influencing photosynthesis and thus plant growth and reproduction. This in turn will affect the food supply available to both herbivores and indirectly, insectivorous birds. Therefore careful measurements of fluctuations in cloud cover will be made with appropriate instruments.

IV. LOGISTICS

The project will be carried out by the principal investigators, assisted by four undergraduate volunteers, who will provide for their own transportation to Colombia but, once there, will be provided with room and board. If funding permits, local help will be utilized in some of the routine tasks.

The working schedule of the six people will include the following. The netting operations each day will include three people in the morning and two in the afternoon. The in-depth studies and the foraging niche determination study will involve, on the average, two people per day. The food monitoring will include the efforts of three people twice a week; one afternoon for insect sampling and one for assaying gross plant production. This amount of effort will reveal the presence or absence of cycles in these food resources.

All data from capture and observation operations will be entered on appropriate key punch forms. Key punch facilities are available at the University in Cali.

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SCHEDULE (per day week)

Netting Operation

3 people in morning, 2 in afternoon every day.

Insect Sampling

3 people in afternoon once a week one in morning to empty traps.

Plant Monitoring

3 people in afternoon once a week.

Misc'l Monitoring

3 people in late afternoon, early morning and midday for 1 hour each every two weeks. One person one day every two weeks (to catalogue).

Niche and In-Depth Studies

Approximately 7 man days available of principal investigators' time. 8 man-days assistants' time.

BUDGET

A. Scientific Expenses

Capture Equipment

poles for mist nets	\$ 1000.00	
mist nets (\$4 ea.- 250)	1000.00	
rigging (including canopy nets)	504.00	
bands (10,000)	450.00	
weighing balance	100.00	
misc'l tools, etc.	125.00	
record forms	100.00	3275.00

Other Equipment

tape recorders (3)	300.00	
tape and supplies	100.00	
vegetation survey equipment	100.00	
insect monitoring equipment	100.00	
weather station	200.00	
laterns, head lights, etc.	50.00	
misc'l equipment	100.00	950.00

Services

shipment of supplies	800.00	
data processing and punch	2000.00	
local help (2 assistants)	1800.00	4600.00

Transportation

4-wheel drive vehicle	4000.00	
carne de passage	1000.00	
gas and oil	800.00	

maintenance	350.00	
insurance	450.00	
misc'l equipment (winch, chains, etc.)	225.00	
trail bike	300.00	
upkeep of bike	<u>100.00</u>	7225.00