

AMERICAN MUSEUM  
*Novitates*

PUBLISHED BY  
THE AMERICAN MUSEUM  
OF NATURAL HISTORY

CENTRAL PARK WEST AT 79TH STREET  
NEW YORK, N.Y. 10024 U.S.A.

NUMBER 2606

SEPTEMBER 20, 1976

LARRY L. WOLF

Avifauna of the Cerro de la Muerte Region  
Costa Rica





# AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY  
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024

Number 2606, pp. 1-37, figs. 1-8, Tables 1-7

September 20, 1976

## Avifauna of the Cerro de la Muerte Region Costa Rica

LARRY L. WOLF<sup>1</sup>

### ABSTRACT

Records are summarized of the birds occurring above 2900 meters in the vicinity of Villa Mills, Costa Rica, at the northern end of the Talamanca Cordillera of Costa Rica and western Panama. Most of the records are from the period of 1965-1967; a few are from 1968-1969. Passerines are disproportionally represented among the resident or breeding avifauna, and nonpasserines are more represented among the transients, including migrants passing through the region to and from the North Temperate zone. Levels of endemism of breeding species are investigated in relation to source areas and lower altitudinal limits of distribution of each species. The area

supports a high level of endemism, and can be analogized to an island in that most of the resident species must cross uninhabitable lowland areas as they move between the Talamancas and surrounding highland areas that reach above 2000 meters and provide suitable habitat. Food habits, foraging zones, breeding, and molting seasons are discussed where data are available. In general, most of the species are insectivorous or frugivorous, breeding is mostly from March through June, and molting occurs shortly after breeding. The nectarivores depart from this pattern, breeding principally in August through February when flowers are abundant.

### INTRODUCTION

The avifauna of Costa Rica is fairly well known taxonomically and distributionally, perhaps as well known as that of any of the Middle American countries, primarily through the research of Slud (1964). However, the composition of local faunas is poorly documented. Many statements in Slud's report are general and, understandably, in many cases vague. So far little attempt has been made to follow changes in a local bird fauna throughout most or all of a year; but it is only in this way that we can build a background of information

on seasonal movements, breeding periodicity, seasonality of food supply, and impact of migrants. Short studies have been done in various areas, but these mostly have yielded lists of species occurring in an area at one time of year or at several scattered periods. The only detailed work on a local fauna in Costa Rica was a one-year study in the eastern lowlands by Slud (1960). The present report concerns the avifauna of the Cerro de la Muerte region (hereafter referred to as Cerro or Villa Mills) of central Costa Rica. The birds of this area are noted for their endemism

<sup>1</sup>Department of Biology, Syracuse University.

the degree of which is similar to that reported by Mayr and Phelps (1967) for a series of isolated mountains in Venezuela. Herein I attempt to analyze the general ecological characteristics of the fauna, the phenology of the fauna, and the zoogeographic history of the birds.

Field work was accomplished during three periods: August, 1965; August and early September, 1966; and December, 1966, to early July 1967. A few observations are from later years. This project, however, was secondary to studies of the ecology and social behavior of hummingbirds in the same area. As a consequence, no attempt was made to sample systematically either species or areas throughout the study period. Detailed daily observations of species were noted during December to July. At other times, general notes were kept, especially of the more common species and of the occurrence of unusual birds. Some specimens were collected; all are deposited in the American Museum of Natural History. In addition, I obtained information from specimens collected in this area by Morse, which are currently in the Louisiana State University Museum of Zoology (LSU). I have also seen most of the material collected in the area by Slud; much of this material is deposited in the Museum of Zoology at the University of Michigan (UMMZ).

#### ACKNOWLEDGMENTS<sup>1</sup>

This study was supported financially by the Frank M. Chapman Memorial Fund and an Elsie Binger Naumberg Fellowship from the American Museum of Natural History. Logistical aid was provided by the Organization for Tropical Studies, especially Mr. Jorge Campabadal and Ms. Liliana Echeverria. Ms. Janet Wolf and Dr. F. Gary Stiles helped with the field work. Stiles also provided extremely helpful comments on an earlier draft of the manuscript. This help is not to be construed as agreement with all ideas and emphases in the report. The Ministerio de Agricultura y Ganaderia provided the necessary collecting permits. Finally, the owners of the

Pension Georgina, Villa Mills, gave us comfortable living conditions and allowed us to store field equipment in their living quarters.

#### PHYSICAL ENVIRONMENT

This study was carried out in the vicinity of Villa Mills, along the Pan American highway between Cartago and San Isidro del General, Costa Rica, near the northwestern end of the Talamanca Cordillera (fig. 1). The bulk of observations were made between km. post 96 and post 99. The cordillera extends to the southeast from near Cartago, Costa Rica, to Panama where it effectively terminates at Volcan Chiriqui in western Panama. A series of mountains of decreasing height extend to the east from Chiriqui toward the Canal Zone. The northernmost peak of the Talamanca Cordillera, Cerro de la Muerte or Cerro Buena Vista, reaches its maximum height of 3491 meters near km. 91 where the Pan American highway reaches its highest elevation in Central America, 3335 meters. The Talamanca range is long and narrow. Its very steep slopes coupled with passes between major peaks probably facilitate movement across the mountains by some species of more lowland affinities (e.g., *Spizaetus ornatus*). The site of the study was between 2900 and 3200 meters, along the spine of the cordillera. Although a scattering of records was obtained from other areas mostly lower on the cordillera, I restricted the species records in the present paper to those from 2900 meters or higher in order to limit the fauna to highland forms.

Government weather data for this area were collected at a weather station about 2 miles northwest of Villa Mills. Rainfall is very seasonal although averaging between 2500 and 3000 mm. per year (fig. 2). There is considerable annual and monthly variation in total rainfall; but the general trend is still readily apparent. Rainfall from December through April is usually less than 100 mm. and in February and March is often less than 25 mm. March is consistently the driest month of the year with rainfall less than 15 mm. The rainy season is May to November with a slight decline in July and August. The rainiest months are June, October, and November.

<sup>1</sup>The present paper is dedicated to the memory of Dr. Hugh C. Land, who first introduced me to Neotropical birds.



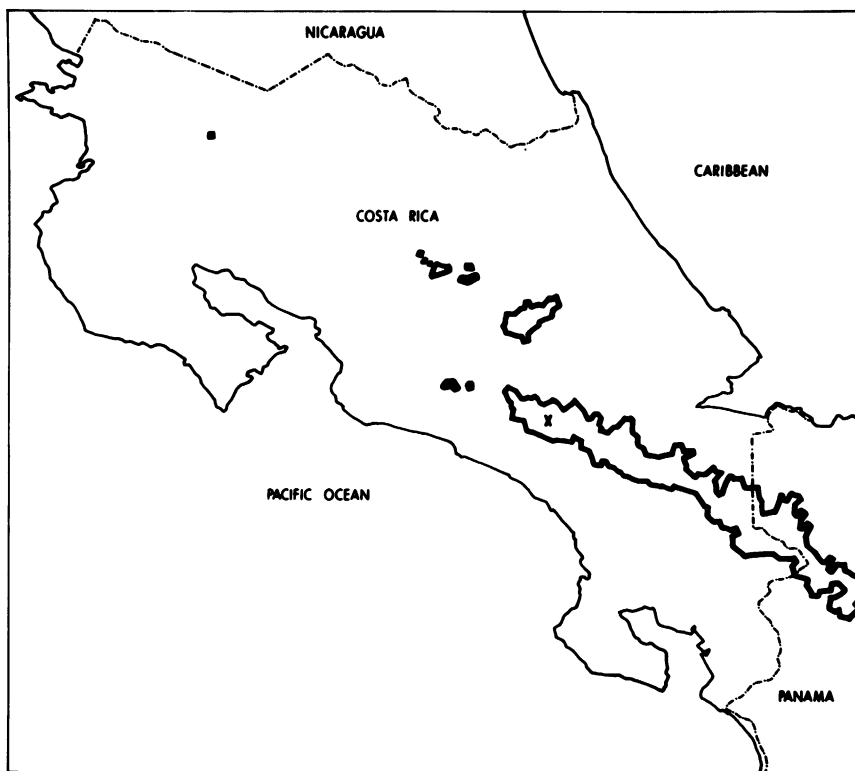


FIG. 1. Map of Costa Rica and adjoining areas of Nicaragua and Panama. 2000 m. elevation in Costa Rica and adjacent Panama is indicated by the dark line. Location of study area is represented by X.

The mean monthly temperature (all data from 1965) fluctuated about  $11^{\circ}\text{C}$ .; only for January did the mean temperature drop below  $10^{\circ}\text{C}$ . (fig. 3). The mean maximum reached a high plateau about March to July, whereas the high values for mean minimum were slightly above  $5^{\circ}\text{C}$ . from May to November. December to April were characterized by low absolute minimum temperatures and March to May by high absolute maximum temperatures. Thus the consistency of the mean monthly values was produced by offsetting trends in the maximum and minimum throughout the year. The highest and lowest temperatures occurred during the dry months.

Wind is continual on the Cerro. The prevailing winds come from the Atlantic slope and bring most of the precipitation. There are frequent strong winds from the Pacific especially at the

onset of the rainy season. At this point on the Cerro there are no protective barriers to the winds sweeping inland from either coast.

#### GEOLOGIC HISTORY OF THE TALAMANCA CORDILLERA

The following information is from Lloyd (1963) and Weyl (1956) on the general history of the range and on the possible occurrence of glaciation on the higher peaks of the cordillera.

According to Lloyd, the present-day mountains first appeared as volcanic islands during the late Oligocene. By the Upper Miocene the range was fairly well developed with some vulcanism still occurring; the mountains were still an isolated series of islands. Not until the Pliocene were the mountains connected via lowland areas

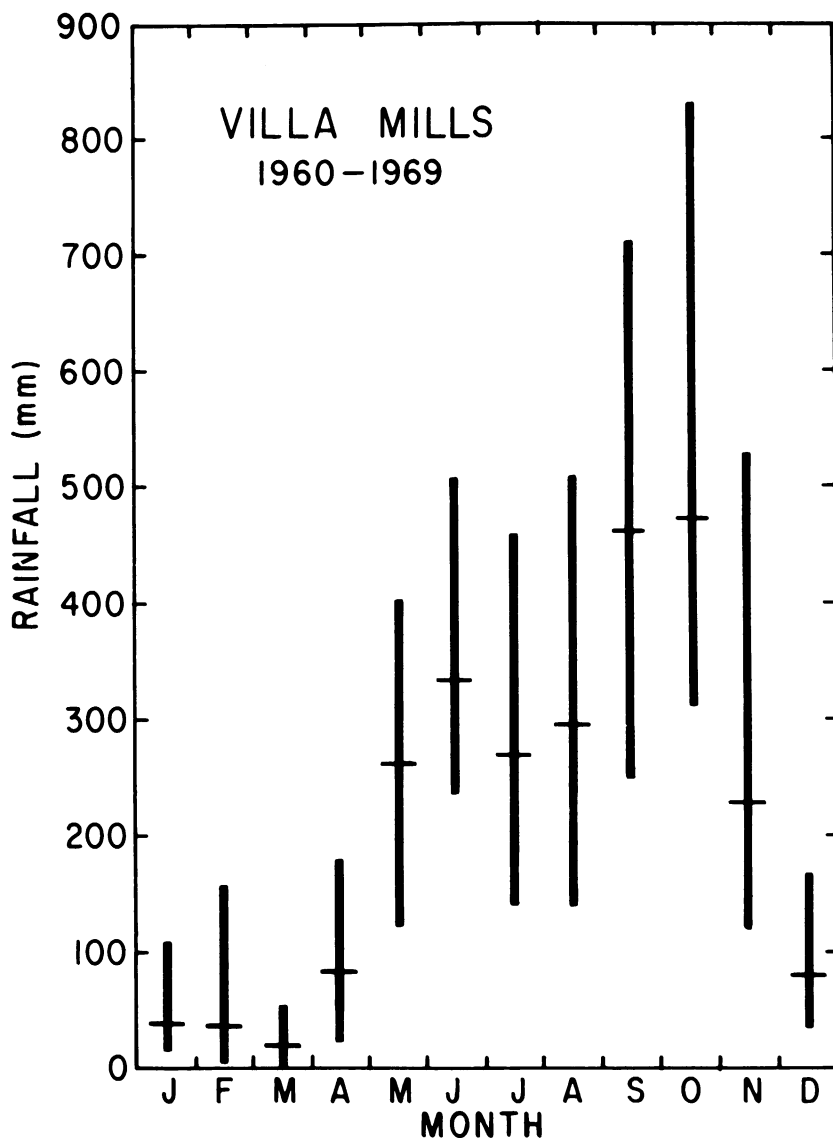


FIG. 2. Rainfall records from the Villa Mills weather station 1960-1969. Vertical bars are ranges, horizontal bars are means for 10 years. Data from the Servicio Meteorológico, San Jose, Costa Rica.

to the other montane systems of Central America and northern South America. At the end of the Pliocene or in the early Pleistocene an extensive series of faults was produced, possibly related to the contemporaneous origin of the vulcanism that today extends from northwestern Nicaragua

into the central highlands of Costa Rica. The closest volcanoes to the Talamanca range are those of the central highlands—Poás, Barba, Irazú, and Turrialba. The intervening lowlands range to about 1550 meters at the Continental divide and the birds would have to descend to



this elevation to cross the lowland gap without making a continuous flight.

According to Weyl (1956), there is good evidence that some of the peaks of the Talamanca Cordillera were glaciated; probably during the Wisconsin age of the Pleistocene. He thought that on Cerro Chirripo, the highest point in the Cordillera, the glaciers might have extended to as low as 3400 meters. Although the Cerro de la Muerte extends about 100 meters higher it may never have been glaciated. The lowering of temperatures, however, which accompanied this formation of ice certainly lowered the temperatures a biologically significant amount. There are

remnants of a subparamo or paramo flora in a bog area at km. 83 (2800 meters); today this flora is limited to the highest peaks in the cordillera. If, on the average, the lowering of vegetation zones was of the order of 300 meters it means that the present montane flora would have extended at least to 2500 and possibly down to 2000 meters. However, even with this amount of lowering, a continuous band of montane vegetation would not have formed in the low areas between the volcanoes and the cordillera. It appears that the cordillera has probably been isolated from other areas of montane flora and fauna since its inception. Even a lowering of the

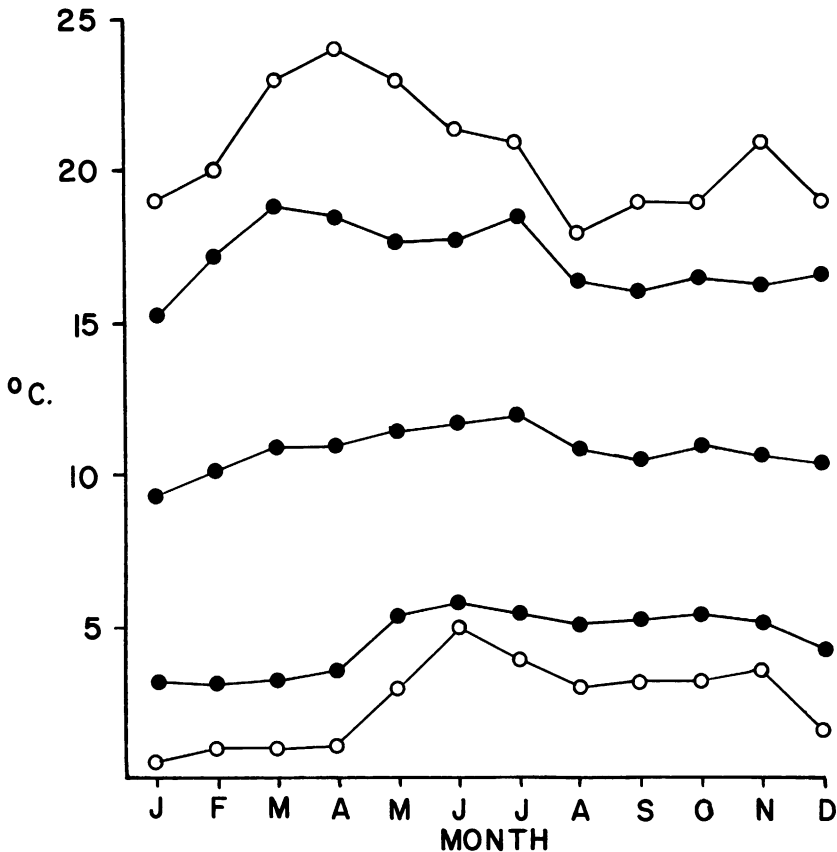


FIG. 3. Temperature records throughout 1965 recorded at Pension Georgina, about 4 km. NE Villa Mills, elevation 3100 m. Mean values (maximum, minimum, and grand mean) are shown as dots, extreme values for each month are shown as circles. Data from Servicio Meteorológico, San Jose, Costa Rica.

flora and accompanying fauna to the 2000 meter level would not decrease by more than 20 percent the distance that the species must travel to reach other high montane areas. This evidence suggests that most of the colonization by highland species must have been by long-distance dispersal or short-distance movement through several habitat types.

#### SOURCE AREAS

The closest highland areas that could serve as sources for immigrants are the volcanic highlands of central and northwestern Costa Rica and adjacent Nicaragua. These highlands have been available as a region only since the beginning of the Pleistocene (Lloyd, 1963) and probably received many immigrants from the nearby Talamancas, which had been in existence since the late Oligocene. This initial one-way flow of immigrants probably fairly quickly was replaced by bidirectional movement of potential colonists.

The montane source regions to the north for the volcanic-Talamanca system were in Nuclear Central America, which had been in existence prior to the Miocene, and at least since the Cretaceous. Thus in Nuclear Central America there was sufficient time to evolve a distinctive fauna, parts of which could then move across the Nicaragua depression once the land connection had formed in the Pliocene (Lloyd, 1963). With the appearance of the volcanic ranges in northern Costa Rica and Nicaragua, the actual extent of intervening lowlands was somewhat reduced, perhaps facilitating flow of colonists.

The nearest high montane areas to the south and east that could provide colonists for the Talamanca range is the extension of the Andes into eastern Panama. This area has been in existence since before the Miocene (Lloyd, 1963). If we consider the 2000 meter level as the lowest at which a potential montane flora might have existed, then the closest connection between the montane areas of eastern Panama and the Talamanca Cordillera would be approximately 500 kilometers. This is a much more formidable barrier for montane birds to cross than the gap between volcanoes of the Central highlands and the northern end of the cordillera.

One source of the fauna not affected by the distance separating the highland areas is the

adjacent lowland regions. Both Monroe (1968) and Griscom (1932) noted that many of the species found today in the cloud forests of Honduras and Guatemala, respectively, are forms probably derived from groups of South America that originally inhabited lowland tropical regions. The progenitors of the present cloud forest forms presumably moved north through the lowlands once they became continuous in the Pliocene (Lloyd, 1963). To invade montane areas would require either that the species have a wide tolerance for climatic and habitat variables or that they have made the necessary genetic and physiological adjustments.

A more immediate source of the montane avifauna would be species which only use the area for breeding and "winter" at lower levels in the mountains. For these species the effective gap between adjacent montane areas would be reduced by a factor reflecting the potential continuity of areas in the lowlands. To maintain a resident population in the mountain region would then require physiologic and ecologic adjustments to the highland habitat, perhaps only at climatically optimal seasons. So far there is little information available on the physiological tolerances of highland birds in the tropical regions of the world.

#### VEGETATION

The study area is in the Montane Rain Forest Life Zone (Tosi, 1965). Throughout the study area the climax vegetation is oak forest with the trees covered with epiphytic growth (fig. 4). Most of the undisturbed mature oak forest is either well away from the Pan American highway or is on rather steep slopes that are more difficult to clear (fig. 5). In some places the forest has been cut a half-mile or more from the road. In places where the forest has been removed naturally, such as in ravines, much of the successional vegetation is bamboo (*Chusquea* sp., fig. 6). The same species of bamboo predominates in the bottoms of the ravines and also is common on the slopes and on more level ground above the ravines. Tree ferns 15 feet or more are also found in these ravines and scattered throughout the area, principally in second-growth rather than primary forest. There are a few pasture areas.

The disturbed vegetation of the Cerro area is a



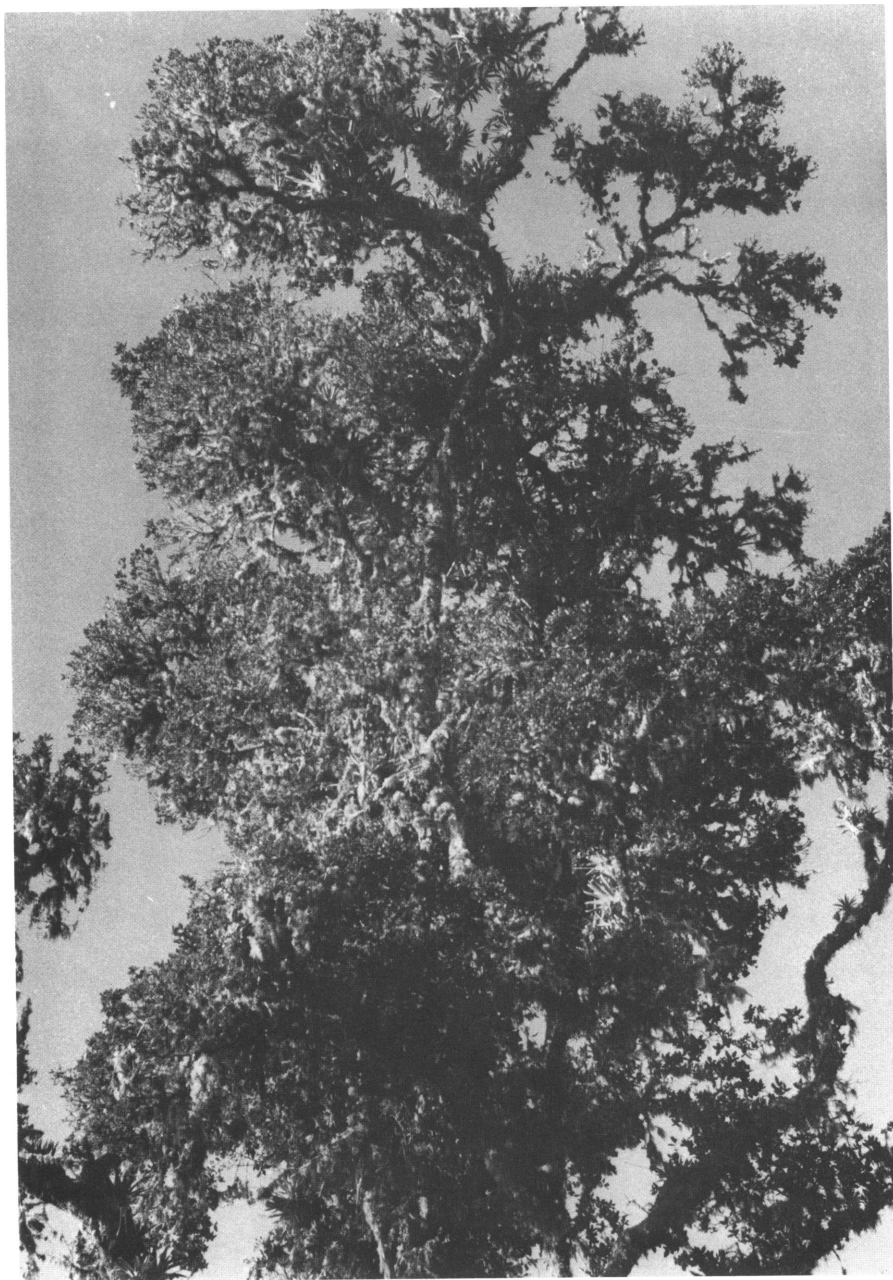


FIG. 4. Canopy of oak (*Quercus* sp.) on the Cerro with heavy growth of bromeliads and lichen. Photo by F. G. Stiles.

series of patches of different stages of succession and in some places remnants of the original oak forest (fig. 7). Most of the second-growth areas

are dominated by shrubs of the family Ericaceae and small trees of the genus *Miconia*. Both groups produce nectar and abundant fruits,

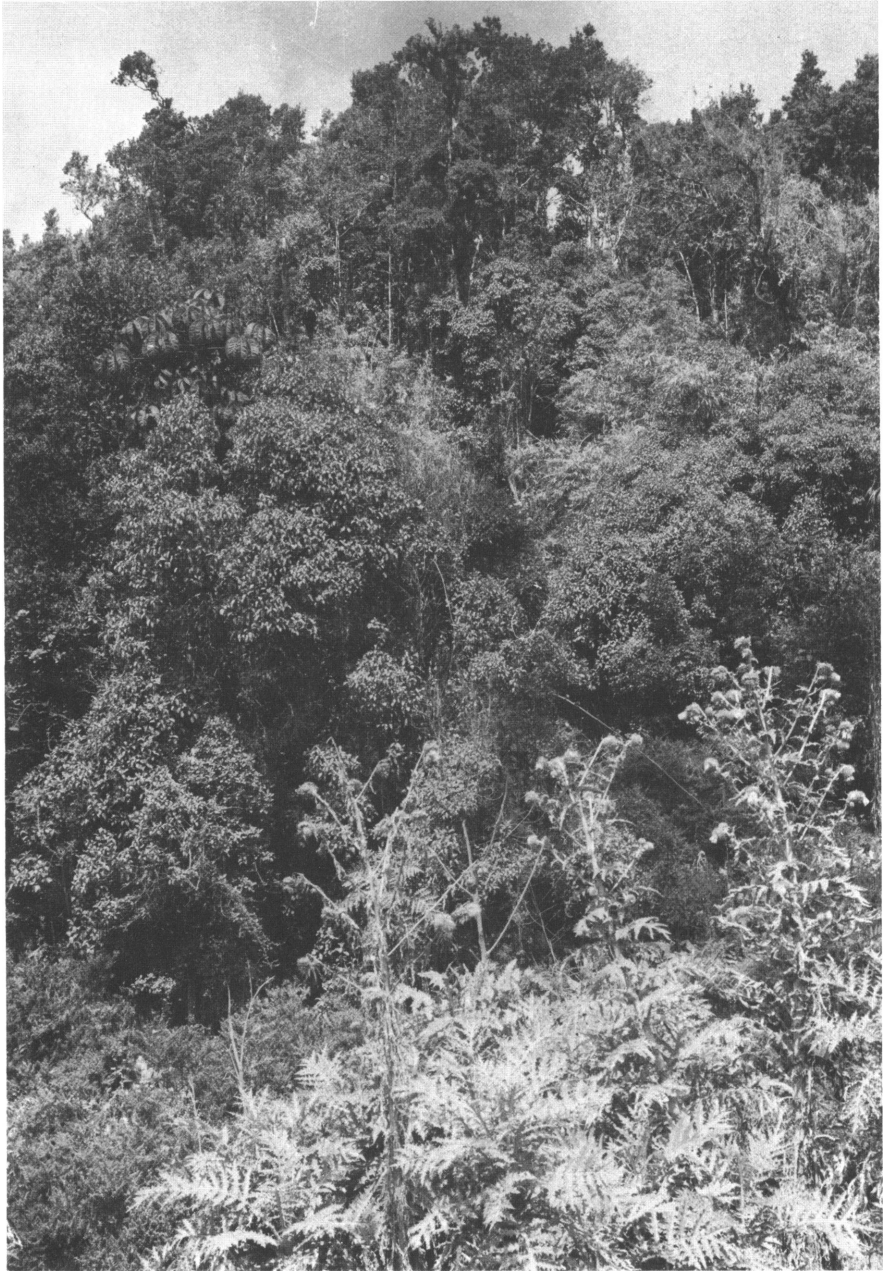


FIG. 5. Steep hillside on the Cerro with second-growth at base and on hillside with remnants of the oak forest on the hilltop. Photo by F. G. Stiles.

which are major food sources for many birds. Other dominant second-growth shrubs include two species of *Centropogon*, which provide

nectar for the hummingbirds and *Diglossa* and fleshy seed pods for several species of passerines. Another common food source is the lorantha-



ceous epiphyte *Gaiadendron poasense* that produces both bright yellow flowers and fleshy yellow fruits.

Most of my observations were made in the second-growth areas, as the hummingbirds I was studying were found almost exclusively in this type of vegetation. Periodically, I made a special effort to visit relatively undisturbed oak forest to observe species that were primarily limited to this habitat type. I probably recorded most, if not all, of the species that occurred there, but the number of observations is lower than if I had worked regularly in this habitat. In part this may account for the few records of such species as *Chamaepetes unicolor*, *Myioborus torquatus*, and several others.

It must be emphasized that this report, although dealing with the birds of the Cerro, cannot make any definitive statements about the avifauna of the area prior to the arrival of man or in nearby areas that are still fairly undisturbed by

man. It is very likely that the relative abundances of several of the species have markedly changed in the 20 years since the Pan American highway penetrated this area. Species such as *Pharomachrus mocinno* and *Chamaepetes unicolor* probably are being reduced in numbers. At the same time, species such as *Zonotrichia capensis*, *Turdus nigrescens*, *Catharus gracilirostris*, the four breeding hummingbirds, and others probably now are able to maintain larger populations than before major clearing activities.

#### SPECIES ACCOUNTS

*Coragyps atratus*. Black Vulture. I saw only one. Although Slud (1964) stated that the species occurs in Costa Rica to the mountaintops it probably occurs around Villa Mills only when a wandering individual crosses the ridge going between the Atlantic and Pacific slopes.

*Cathartes aura*. Turkey Vulture. I saw no indi-



FIG. 6. Ravine in clearing in oak forest on the Cerro showing bamboo, *Centropogon* and *Miconia*. Photo by F. G. Stiles.



FIG. 7. Clearing in oak forest on the Cerro looking toward the Caribbean slope. The thick under-story is principally ferns and *Centropogon*. Photo by F. G. Stiles.



viduals that appeared to be resident. On March 15 single birds flew by with flocks of migrating *Buteo* hawks at 0830 and 0930 and four vultures went past at 1000. Lone individuals sailed over going northwest on March 19. Although these birds appeared to be migrating it is possible that they were residents moving from the Pacific to Atlantic slopes. Slud (1964) reported this species from the tops of mountains but did not specify whether these were migrating and/or resident individuals.

*Elanoides forficatus*. Swallow-tailed Kite. Seen on five occasions, each time probably resident individuals moving up the Caribbean slope and along the eastern side of the crest of the Talamancas. The records (March 31, April 7, May 1, 7, June 4) are scattered throughout the observational period and give no hint of regular movements. Generally the lone individual or sometimes a pair would appear and circle for some time just above the level of the tallest oaks before moving off along the crest of the ridge; they seemed to be actively foraging or trying to gain altitude.

*Accipiter (striatus?)*. Sharp-shinned Hawk. On March 5, a single individual passed overhead from south to north as if migrating along the crest of the ridge. Although I could not identify it to species, it probably was a Sharp-shinned Hawk, which is a regular winter visitor in lower elevations of the country. *Accipiter cooperi* is decidedly rare or accidental and has been recorded only once in Costa Rica (Slud, 1964).

*Buteo jamaicensis*. Red-tailed Hawk. Identified positively only once when on January 8 a bird soared overhead for a short time. Some unidentified hawks in the migrating flocks of Broad-wings and Swainson's may have been this species.

*Buteo platypterus*. Broad-winged Hawk. A lone winter visitor stayed in a pasture area for part of January 15. This may have been the species seen on several occasions when birds sailed overhead under such poor lighting conditions that it was impossible to identify them. The migratory flights in which this species participates are already well known from the reports of Skutch (1945) and Slud (1964). In the Cerro area I saw groups of birds moving along the spine

of the ridge in a generally south to north direction on the following days: March 15-18, 21, 22. On March 17, there were only a few individuals of *B. platypterus*. On the other days there were several flocks, often exceeding 50 birds; no flocks exceeded about 400 birds.

*Buteo swainsoni*. Swainson's Hawk. Seen only in migratory flocks during the spring. All birds were moving from south to north near the crest of the ridge on the Caribbean slope. Groups were seen on the following days: March 15, 16, 22, and April 6. In addition, individuals not positively identified as either *B. platypterus* or *B. swainsoni*, were identified in several flocks of migrant hawks.

*Spizaetus ornatus*. Ornate Hawk-eagle. On January 27, a single bird flew in and sat for approximately a minute before flying downhill on the Caribbean side. This bird probably was moving from the General Valley to the Caribbean slope as Slud (1964) predicted they do at times.

*Circus cyaneus*. Marsh Hawk. Lone individuals were seen about 1000 on March 16 and 17, moving from south to north along the ridge. I did not identify any Marsh Hawks in the migrating flocks.

*Chamaepetes unicolor*. Black Guan. I saw individuals only twice during the study period. Several other individuals and a small group were reported to me during March and August. In my experience, this is strictly a bird of oak forests at this elevation. Both times I saw it standing parallel to the branch on a large oak limb near the trunk. As oak forests are cut, this species probably is declining.

*Charadrius vociferus*. Killdeer. Seen twice in late December around a small, temporary pond. In January and early February the ponds dried up eliminating any suitable habitat for these birds. Slud (1964) had no highland records for Costa Rica.

*Capello gallinago*. Common Snipe. One flushed from thick ericaceous shrubs near some small, temporary ponds.

*Odontophorus guttatus*. Spotted Wood Quail. I never saw any quail in this area. However, calls

sounding phasianid-like were fairly common from the dense second-growth thickets and brush on the hillsides. Calls tentatively assigned to this species were heard throughout my stay on the Cerro. The most common note, and one which is easily recognizable, sounds like a flock of Whip-poor-wills (*Caprimulgus vociferus*) chorusing with not quite complete calls. I could not discover if this was a single bird or several in a covey calling at the same time.

Several people reported seeing quail in this area. Roy McDiarmid obtained two adults and a small chick from a family group on March 22. The adults were made into skeletons after being identified as this species by Joseph Jehl, Jr.

*Columba fasciata*. Band-tailed Pigeon. This is a bird of the treetops of the Cerro. First seen mostly in groups in February, and generally as individuals or pairs until June and July when the birds were in flocks again. The species seemed to be more common through most of the year at slightly lower elevations. On the Cerro the pigeons became more frequent by early March as if they moved into the area for breeding. However, this impression might have been due in part to the increased activity associated with courtship and reproduction. I first heard continuous calling, especially the nuptial hoot, in early March. The birds were essentially quiet again by early June. The calls of this species have already been well-described by Peeters (1962) and Slud (1964). The only additional call was a very raven-like "raank" given by lone birds during the nuptial flight or by perched birds before or after a flight display.

Only two Cerro specimens are available. They were taken, apparently together, on March 27. One is a male with the "t(estes) g(reatly) e(nlarged)"; the other is a juvenile with the tail about one-half grown. Using nesting data from Peeters' study (1962) of this species in California the egg from which the juvenile hatched probably was laid sometime in early February.

*Columba subvinacea*. Ruddy Pigeon. This was another species frequently heard but infrequently seen. The call is a four-noted, mellow hooting, the first two notes on about the same pitch, the third going up and the fourth down. Most of my records are from after the

time the birds started calling in March. I saw a nearly full-grown young with two adults on June 11. It probably is an uncommon resident of the area.

*Geotrygon* (*costaricensis*?). Buff-fronted Quail-Dove. A single individual tentatively identified as this species was observed in thickets of second-growth on May 5, apparently as it moved from lower on the Caribbean slope toward the crest of the ridge. Later in the month I heard pigeons call from the upper slopes of the General Valley below where I was working. The call was a long series (sometimes 30 seconds or more) of hoot notes repeated at intervals of slightly less than one per second. Gordon Orians (personal commun.) identified this call as belonging to *G. costaricensis* in a study area about 25 road miles from Villa Mills. I never heard this call in my study area; the main center of distribution in the mountains of Costa Rica is to about 8000 feet or slightly higher.

*Pyrrhura hoffmanni hoffmanni*. Sulphur-winged Parakeet. Seen almost daily from February into early July. They were less frequent in late December and January. In four visits to this same area during August and September in 1965, 1966, and 1969 I saw this species only once. It is normally very conspicuous and probably is not regularly present on the Cerro at this time. This suggests some sort of vertical migration in this part of the range. Slud (1964) apparently thought that this species did not regularly range this high in the mountains.

The species normally occurs in flocks of from four to more than 25 individuals. The size of the flocks decreased somewhat from March to July. The flocks seemed to have an area that they patrolled regularly. What I thought was a single flock operated along about one-half mile of roadway around km. 97 for several months. The movements of this flock were so regular that I collected several specimens by waiting for the flock to fly through a clearing which it usually did at about 1600. From March through June, it appeared that the resident flock visited the same fruiting *Miconia* trees on several days in succession. At each visit the birds stayed only about 10 minutes before moving to another feeding site. This time was not sufficient to strip the tree of

fruit nor apparently to take enough fruit to make it inefficient to visit the tree the next day. This pattern of feeding may reduce time wasted in searching for new sites without feeding on later days while at the same time covering a sufficiently broad area of the available habitat to increase chances of encountering new food sources as they become available. In terms of the energy required to search out food items this may be the most efficient method of exploiting a food resource that is localized on individual trees and yet scattered temporally and spatially.

I collected two males on April 27, 1967. One had very worn plumage and testes only slightly enlarged (6 by 2, 4 by 2 mm.); the other had fresh plumage and smaller testes (4 by 1, 3 by 1 mm.). Probably the worn bird was a post-breeding adult and the freshly plumaged bird a young of the year. Morse collected an adult male (LSU 32441; testes, 6 by 2.5, 4.5 by 2 mm.) on April 3. The food of the two birds I collected was entirely vegetable, primarily black seeds, some white seeds, and fleshy parts of a fruit. All the seeds were less than a millimeter long.

*Bolborhynchus lineola lineola*. Barred Parakeet. Although most authors consider this a rare species in Central America, it was common in the Cerro area at certain times. It occurred in flocks of up to 150 or more individuals during three one-week periods in August and September, 1965 and 1966. The birds did not forage on the Cerro. In the early morning small groups would fly over very high (200 or more meters up) going from the Caribbean slope to the Pacific slope. In the evenings shortly before dusk, flocks would begin to congregate in the valleys below the summit on the Pacific slope. One could stand on the summit and listen to the birds calling and occasionally, when the clouds would break, the flock, sometimes more than 200 birds, could be seen flying back and forth a mile or more away and several thousand feet below. At intervals some birds would break from the flock and, as a smaller flock, fly up and over the crest onto the Atlantic slope and disappear downhill. The uphill progress of the flock could often be followed by listening to the calling. Most of the birds flew very close to the ground; we erected mist nets 7-10 feet aboveground and caught numerous

parakeets as they flew through a small saddle between two hills. For several nights in a row the birds used the same area as a passageway across the ridge. Crossing of the mountains from one valley to another is seasonally restricted to the late summer and fall.

During December to July the birds were much less frequent. They were seen infrequently in December to April, rarely in May and June, and apparently were beginning to increase in abundance in early July when we left the area. The infrequent records in the spring generally were of birds flying very high in directions opposite to those of the summer period. These movements probably are related to the spatial and temporal distribution of abundant food sources, especially fruits. The only food items which I recorded were ericaceous fruits.

The following gonad information was obtained from specimens: males—August 10, testes 6 by 2 mm.; August 11, 5 by 2 mm. and 6 by 4 mm.; females—August 10, follicles less than 1 mm. and ovary postbreeding; August 11, ovary of two birds slightly enlarged. Miller (1963) judged testis lengths of 4 to 4.5 mm. of this species in Colombia to be nonbreeding level.

*Glaucidium jardinii*. Andean Pygmy Owl. This uncommon species was recorded when calling. The only sight observation was of a bird sitting about 75 feet up near the trunk of an oak on a lichen-covered branch. Numerous hummingbirds, mostly *Panterpe insignis* and possibly one *Eugenes fulgens*, were mobbing this bird. These are the only hummingbirds that regularly forage at this height in the Cerro area. The other two hummingbird species, *Colibri thalassinus* and *Selasphorus flammula*, were present within 50 yards of the owl, easily within the range of some hummingbirds that were mobbing the owl, and yet the other two species gave no sign of recognition of the owl. *Colibri* and *Selasphorus* forage almost entirely below 25 feet. Several Sooty Robins (*T. nigrescens*) gave some alarm calls when the owl flew in and began calling, but the robins made no attempt to mob the owl. Again, *T. nigrescens* is a species that rarely ventures into the trees.

As reported by Miller (1963) the call is a double-noted hoot, repeated at intervals of about

1 second. The first and second notes are on different pitches. A calling bout may last several minutes.

*Caprimulgus saturatus*. Dusky Nightjar. This uncommon species probably is resident on the Cerro. My infrequent records, except the collected specimens, are of calling birds usually at dusk. Calling birds were usually in wooded areas with a nearby patch of open ground.

A female was netted in the early morning of May 6 by MacGuire about 4 feet aboveground in a clearing. The stomach contained insects. The ovary and oviduct were slightly enlarged; the bird may have been incubating. A male (UMMZ 210636), taken on March 22, had only slightly enlarged testes.

*Streptoprocne zonaris*. Collared Swift. Seen on 17 occasions generally as it flew across the spine of the Talamanca Cordillera from one slope to another, probably without feeding. Early in the year it was most often in large swirling flocks; in April and May it was seen in pairs or small groups. Occasionally I saw very fast, direct "chases" involving two or three birds usually accompanied by a chittering call. Another characteristic flight call was a nasal "beent." On June 2, I saw a group of about 25 flying directly from the Pacific to the Atlantic slope; later the same day I saw a lone pair go over.

*Cypseloides* sp. Several times, mostly in April and June, I saw swifts that were smaller than *Streptoprocne* but obviously larger than *Chaetura*. Unfortunately, I never was able to make a positive identification. The birds looked all dark with no obvious lighter marks. The call was very like the chittering of *Streptoprocne* but the manner of flight was more fluttery, like that of the smaller *Chaetura*. Several species of *Cypseloides* might be found in these mountains.

*Colibri thalassinus*. Green Violet-ear. The ecology and behavior of this species and similar accounts of the other three species of hummingbirds (*Panterpe*, *Eugenes*, and *Selasphorus*) that were regular inhabitants of the Cerro will be covered in more detail elsewhere (Wolf, Stiles, and Hainsworth, In Press).

The Green Violet-ear generally was found at the edge of woods in thickety second-growth

areas. The only flower regularly defended was *Centropogon valerii*. To my knowledge only males defend these sources. Females regularly return to the same flowers, but there is no evidence that they defend food sources.

This hummingbird was common in December and remained so through mid-March when the numbers declined coincidentally with cessation of calling by the males. In early September, 1966, I saw a single bird on the Cerro, but none was reported during two one-week visits in early August, 1965, 1966. In late August, 1969, *Colibri* was regular, but uncommon. Apparently the main influx of birds is after early September prior to the breeding season. A similar situation occurred on Volcán Barba at 6300 feet elevation (B. Mlecko, personal commun.). Skutch (1967) noted that this species migrated vertically to the higher elevations to breed. The evidence is strong for such a migration, but a few individuals remain most or all of the year.

Singing was in full force when we arrived in late December and continued through the middle of March. Skutch (1967) reported that the birds sing slightly longer at about 7000 feet on Volcán Barba. The only evidence of breeding is an adult gathering nesting material ("down" of *Cirsium*) in late December.

*Panterpe insignis*. Fiery-throated Hummingbird. A very common species and probably increasing in abundance as the forests are cleared. It feeds from about 1 inch aboveground (only rarely) to well up in the large oaks left standing in cleared areas or at the edges of woodland. Although individuals flycatch at times, the major source of food is nectar from herbs and second-growth trees and shrubs that bloom profusely in this area. This species is fairly broad in the range of flowers that it will visit during the course of a year (Wolf, Stiles, and Hainsworth, In Press). However, at any one time the individuals concentrate on one or a few of the more common flowering species. Both sexes hold territories, the females only when not breeding (Wolf, 1969b; Wolf and Stiles, 1970).

Males with testes 3 mm. or more long can be found during most of the year. The largest testis was only 4 mm. long, suggesting that some birds may be in breeding condition throughout the



year. It is possible that the large size of the testes of these birds is not indicative of breeding condition, but Williamson (1956) found that in the Anna Hummingbird (*Calypte anna*), a slightly smaller bird, testes of even 1.5 to 2 mm. long produced sperm. None of the females collected were in breeding condition. The few nests were found in August (fig. 8).

There apparently are two periods of molt. Most of the population has a complete molt in August to December, extending for a few individuals into January. In March and April, some individuals, probably juveniles, molt body and flight feathers.

*Eugenes fulgens spectabilis*. Magnificent Hummingbird. A migratory species on the Cerro. It was very common in December and remained so until early April when numbers declined. A few individuals apparently stayed throughout the year. From May to September we have scattered records of female-plumaged birds.

The habitat is fairly open second-growth, especially where thistles (*Cirsium*) and *Centropogon gutierrezii* (= *C. talamancensis*; Colwell, 1973) are in bloom. *Eugenes* is fairly specific in the flowers it visits. The range of flower species visited is less than for *Panterpe* or *Selasphorus*, but is slightly greater than for *Colibri*. Only the males hold territories around flowering plants. While most foraging is at flowering plants, *Eugenes* also flycatches for insects.

I have no data on the breeding period of this species in the Cerro area. Some birds handled in September and April were apparently engaged in a complete molt.

*Selasphorus flammula*. Volcano Hummingbird. A common species. Males hold territories at least from August into February. After February, the numbers decline until about the first of July when the birds begin to return to the Villa Mills area. This movement probably is a vertical migration; if so, the timing is slightly different from



FIG. 8. First reported nest of *Panterpe insignis*, the Fiery-throated Hummingbird. Found August, 1969, about 2 km. NW Villa Mills. Photo by F. G. Stiles.

that of the two other migratory species of hummingbirds in the area.

*Selasphorus* is an inhabitant of open, second-growth areas where there are many flowering shrubs and herbs. This is the only one of four common hummingbirds that is a regular inhabitant of the subparamo area of the highest points near the summit of Cerro de la Muerte where the major flowers are small herbs and some species of *Hypericum*. It visits the broadest range of flowers of any of the four common hummingbirds. It also is the subordinate species of the hummingbird assemblage and territorial males cannot keep intruders of the other species from visiting the resources they are defending. Volcano hummingbirds do some flycatching.

The males have a characteristic dive display that is very similar to that of its North American congeners, *S. rufus* and *S. sasin*. This display is given on the feeding territories of the males.

The only evidence of breeding was a nest that we found on January 13. The female was still adding lining material. On January 15, she was feeding young. The nest probably was started late in December.

*Lampornis castaneiventris cinereicauda*. White-throated Hummingbird. A very rare species in the Cerro and probably accidental. I caught a female on August 26, 1969, and a male on September 2, 1966, in a net set on partly cleared hillside. Stiles (personal commun.) saw a male on August 27, 1969, and on May 6, 1967, I saw a female of this genus, either *L. castaneiventris* or *L. calolaema*.

The taxonomic status of *L. castaneiventris* and *L. calolaema* is still in doubt. The male I collected had a white throat although some feathers at the periphery of the throat patch had purple tips. Similar birds apparently are found in other parts of the range of the white-throated form (Blake, 1958). Slud (1964) gave the range of *L. castaneiventris* as along the Talamanca Cordillera at least to Volcán Chiriqui. The purple-throated form occurs from Nicaragua to the northern slopes of the Talamancas and reappears on Chiriqui; it is fairly common at 7500 feet about 1 km. from El Empalme, Costa Rica (Orians, 1969). The distribution of the two forms along the slopes of the Talamancas still needs to be defined.

*Pharomachrus mocinno*. Quetzal. Although I saw this species on only 14 days, there probably were one or two resident pairs in the study area. I occasionally saw a male, and later in the year a male and female, moving through the same area in the early morning. Although I saw them mainly in open areas between patches of relatively heavy forest, they appeared to be moving from one forest patch to another. I saw no foraging.

*Melanerpes formicivorus*. Acorn Woodpecker. A species of open and semiopen areas. Although the birds forage to the edge of the forest they rarely venture into it. Most foraging was by probing and pounding on trunks and large branches in the tall oaks. They rarely came down to within 25 feet of the ground but even then they were on large stubs. I never saw them flycatching. They did not join mixed flocks. I estimated that in the study area there were approximately four pairs along 2 km. of roadway.

The only evidence of breeding was in late May and early June when two adults were feeding young in a hole about 50 feet up in a living oak. I saw pairs apparently inspecting nest holes as early as February and March. The birds may remain paired throughout the year. When we arrived in December they were already in pairs and actively calling. Nesting was just finished when we left in July and they were still in pairs.

*Dendrocopos villosus extimus*. Hairy Woodpecker. This species and the Acorn Woodpecker were about equally abundant. It also was found in the fairly open areas and rarely, if ever, entered the mature forest. Usually it was seen singly, occasionally in pairs. The species foraged from on the ground up to more than 50 feet aboveground, mostly from about 5 to 30 feet up. The typical foraging area was the thinner branches of a small tree, the stalks of the large thistle (*Cirsium*) or the woody stalks of a common species of *Senecio*. *Dendrocopos* does most of its foraging by hammering. There is very little overlap in foraging sites between this species and *Melanerpes*.

The food of this woodpecker is predominantly insects; Otvos (1967) reported that the food was 95 percent insects and both of my specimens contained only insects.

I found a single nest with a well-grown young on May 25. The female was actively feeding the young. Later the same day the young was killed and removed from the nest by a weasel (*Mustela*). For over an hour the female woodpecker continued to bring food to the nest tree and to call from a perch near the hole. The next day, more than 24 hours after the young was killed, I saw the female at the nest tree with food. The male of this nest probably was the bird that I collected nearby on May 24. I saw full-grown young on June 3 and 9.

*Lepidocolaptes affinis neglectus*. Spot-crowned Woodcreeper. An uncommon or accidental species in the Cerro area; it may be a vagrant from lower on the mountain. I saw it only twice, both times in the open at the edge of a wooded area. I did not encounter it in the forest. Slud (1964) reported that this species was common in the montane belt to timberline. The only specimens from this area were a female obtained on April 27, and one, sex unreported, collected in July or August (Otvos, 1967). The female had no brood patch and the ovary contained ova to 1 mm. long.

*Margarornis rubiginosus rubiginosus*. Ruddy Treerunner. This species is a fairly common resident in the Villa Mills region. Treerunners were often seen with mixed species flocks organized around *Chlorospingus pileatus*. Usually one or two individuals, rarely three, moved with a *Chlorospingus* flock. They were most frequently seen with flocks from December to March and again from late May to July. In April and part of May they tended to occur alone or in pairs.

Treerunners foraged mostly in epiphytic vegetation, such as moss clumps, bits of lichen, bromeliads, and the lichen-covered aerial "bulbs" of *Macleania*. They worked equally well on both vertical and horizontal branches. I rarely saw them hike up a tree in the manner of a woodpecker, and there was no indication that they used the stiff tail as a brace. Occasionally, an individual clinging to a trunk or branch with one foot used the other foot to raise a patch of moss to search underneath. The only food items recorded were insects.

Testes of two males were enlarged (8 mm. by 5 mm., 5 mm. by 5 mm.) by March 15. A speci-

men from April 1 (LSU 32485) had only moderately enlarged testes (4 by 3). A juvenile I collected in the company of an adult on May 24 had an unossified skull. On September 2, I collected a fresh-plumaged female with small ova. A female taken on January 7, with some body molt, suggests that some individuals may have a limited prenuptial molt.

I never heard this species sing. The most frequent vocalization was a note very similar in pitch to the flocking call of *Chlorospingus*, perhaps this similarity promoted cohesion of the mixed flocks.

*Pseudocolaptes lawrencii lawrencii*. Buffy Tufted-cheek. Although this species was recorded infrequently through March it is probably resident in the area. Once the birds began calling, probably as the breeding season approached, two or three pairs were seen or heard regularly along about 2 km. of highway where earlier I had seen the birds infrequently. There probably was no migration into the area for the breeding season. This species was seen in fairly open oak woodland where 50 percent or more of the oak trees had been removed. They often occurred with *Chlorospingus* flocks until about early April after which they occurred either singly or in pairs. They were normally in pairs in the mixed flocks and may be permanently paired.

The primary food items in two specimens were insects, although one had some *Miconia* berries. Tufted-cheeks forage in organic detritus around epiphytes on the branches of the larger trees, primarily the oaks, from about 4 feet aboveground to near the tops of the oaks. Individuals often moved from one epiphytic bromeliad to another without visiting intervening moss and lichen clumps that are often visited by the Ruddy Treerunners. I did not see the tail used as a brace.

I found no nests, but did see adults carrying food, probably to feed young, on May 6. A male (LSU 32486) taken on April 4 had small testes (3 by 2.5). On May 24, 1967, one adult was already in postnuptial molt.

The calling period extended from early April into late May. The predominant species' call during the breeding season, and one which can be heard for more than 400 meters is "spink,

spink," followed by a rising chatter and then several "chink" notes, or a series of "chink" notes, slightly lower in pitch than the final notes of the chatter.

*Scytalopus argentifrons argentifrons*. Silvery-fronted Tapaculo. Except for the single bird caught in a mist net in a pasture at the edge of a ravine this species was found only in the thick bamboo (*Chusquea* sp.) growth in the ravines. Until I caught the male in the net, I was unaware of the presence of this very shy bird. Shortly thereafter, I heard calls in several ravines and was able to obtain one other specimen. The birds are probably resident in the area, but would be nearly impossible to locate regularly when not calling. I heard them calling only in April and May. The call is adequately described by Slud (1964).

Both specimens contained only insects in the stomach. I have no nesting information. The male taken on May 4, had enlarged testes (7 by 4 mm.) and the female on May 10, undoubtedly from a different pair, had an enlarged oviduct, a new brood patch, and one old ruptured follicle. She had recently laid an egg. Both breeding adults had unossified skulls.

*Pachyrhamphus versicolor*. Barred Becard. Seen only on December 28, 1966, when a female-plumaged bird was with a mixed flock of passerines, including several *Chlorospingus pileatus*. The flock ranged to 40 to 50 feet aboveground but the becard stayed within 3 to 4 feet of the ground, in the lower branches of trees and shrubs in a area of thickety second-growth at the edge of an oak woods.

This is the first published record from the Talamanca Cordillera although Dickerman collected a male from a mixed flock on March 10, 1967, approximately 12 km. from El Empalme, at an elevation of about 8500 feet. The flock was in the interior of a selectively cut oak wood.

*Nuttallornis borealis*. Olive-sided Flycatcher. A regular migrant through the area but apparently does not winter in the highland regions of Costa Rica in any numbers. The first fall migrants were seen and heard on September 3, 1966. None was seen or heard again until mid-

April. It was reported sporadically from then until May 13. The birds were most often seen or tall exposed perches, usually dead stubs, in the middle of an open area.

The two spring specimens, both males, were fat and had small gonads.

*Contopus (sordidulus?)*. Pewee. Two birds, probably migrants, were seen separately on May 7.

*Contopus ochraceus*. Ochraceous Pewee. Uncommon, probably resident in the Villa Mills area. My records are the first published for the Talamanca Cordillera although Slud (1964) predicted that this large flycatcher would eventually be found there. It was seen only sporadically from December to July; the bulk of the records were in the spring months. Gary Stiles reported a single individual from the same area in early September, 1966. The birds usually occurred singly although several times from late April to mid-May I saw pairs.

The habitat was open, cut-over oak woods with second-growth of small trees (often *Miconia*) and shrubs. This pewee perches in exposed positions at or near the tip of small branches from 15 to 30 feet aboveground. Foraging is by sallies from this perch, often returning to the same or a nearby perch. These sallies varied from 15 to 45 feet long. The two specimens had only insects in the stomach, including some fairly large flying insects of a type not found in the stomachs of the much smaller *Empidonax atriceps*.

Only two male specimens were collected. One on May 10 had testes measuring 9 by 5 mm.; the other on June 14 had testes 7.5 by 4 mm. The breeding season probably is April and May, possibly into June.

The calls I heard from this species are: "wheep," which sometimes sounds like a single note and at other times a double note. It is given with a rising inflection and is sharply delimited at the end. The only other call was given by one of two birds engaged in a chase and sounded like a series of "drrrrt" notes.

*Empidonax atriceps*. Black-capped Flycatcher. Common; seen almost daily. It is most common



in open areas where there is some shrubby second-growth. It seldom ventures into the oaks even at the edge of the woods. The species forages from near the ground to, rarely, 50 feet up. It rarely attempts to capture flying insects. The main foraging technique is a typical flycatcher sally from exposed stationary perch, but the substrate from which food is most often taken is the foliage of small trees and shrubs. The diet seems to consist of small insects and other arthropods gleaned from the foliage.

Whenever I have been in the study area the birds were paired, and I suspect that they either are permanently paired or maintain long-term bonds. Each pair seemed to patrol circumscribed areas throughout the year.

Slud (1964) has adequately described the common call of this species. A two-parted call, "pit-ah," is heard much less often and may be a sort of song. It is often repeated in series, sometimes after two birds have been chasing each other.

The breeding season probably varies somewhat each year. A specimen taken on March 15, 1964 (LSU 32539) had an egg in the oviduct, but there was no evidence of breeding in 1967 until late April. A female taken on April 12, 1967, had no brood patch, but a female netted on April 30, 1967, while she was collecting feathers had a brood patch and apparently was in the early stages of nesting. By June 17, I saw the first nearly full-grown young of the year. On the same day I collected an adult not yet in the postnuptial molt. An immature taken on July 3, was in the final stages of the postjuvenile molt and probably was hatched more than two months previously, perhaps as early as March.

*Elaenia frantzii frantzii*. Mountain Elaenia. Most common in the nonforested areas or at the edge of partly cleared oak forests where there is an abundant second-growth of small trees and shrubs. It was seen very rarely until March when it became very common and from then was reported almost daily until July when I left the area. It was very uncommon on the three visits in August and September. Although it was more conspicuous during the calling period from early March to late May, I still believe that there was a

movement of individuals into the area for the breeding season. Skutch (1967) also suggested that there may be some seasonal movement by this species in Costa Rica.

Foraging is by typical flycatcher sallying but with the important difference that most of the sallies were to fruits and not to flying insects. Perhaps 95 percent of the active foraging maneuvers were aimed at obtaining fruits and originated within a fruiting tree, whereas only about 5 percent originated from an exposed perch and went to the air as if they were chasing insects. The predominant food items in the stomachs of the four specimens collected were fruit. One collected in late December also contained some flying insects.

I found no nests of this species but have gonadal evidence of breeding capability for five individuals. One bird had enlarged testes by March 17 (8 by 4 mm.) and they were still large in another male on May 24 (10 by 5 mm.). A male taken in late December had small testes (3 by 5 mm.) as did another male taken on March 15 (5 by 3.5 mm.; LSU 32547). A female collected on May 4 with an edematous brood patch probably was incubating.

The female from May 4 and the December male had skulls that were only partly pneumatized; some individuals must take one year or slightly longer to achieve a fully ossified condition.

Each of the five species of flycatchers that have been reported in this area has a slightly different status. There is one large species (*Nuttallornis*, 29 gms.), two medium-sized species (*Contopus ochraceus*, 22 gms.; *Elaenia frantzii*, 21 gms.), and two small species (*Contopus* sp., 14 gms.; *Empidonax atriceps*, 8-9 gms.). The large species is a transient that apparently moves into the area in small numbers and stays for one or a few days. One of the medium-sized species, *Elaenia*, is a breeding resident and most individuals migrate to lower elevations by the end of the breeding season. The other medium-sized species, *Contopus ochraceus*, is a rare resident. One of the small species is an uncommon transient; the other is the only common flycatcher on the Cerro.

There are two major dichotomies in terms of

the food resources utilized by these species. *Elaenia* is primarily frugivorous, whereas the other four are strictly or predominantly insectivorous. Of the insectivorous species one is a foliage gleaner and three are species that primarily eat flying insects. The height of the foraging flights differs among two of the three species. *Nuttallornis* and *C. ochraceus* occur at nearly exclusive levels in the relatively open areas of the study site. I did not see *Contopus* sp. forage on the single day it was present.

The primarily frugivorous species *Elaenia frantzii* becomes more common when many of the trees and shrubs are in fruit and may leave either as the local supply of fruits declines or as the supply increases in other areas. The only species that remains as a permanent resident in numbers is the small foliage gleaner species *Empidonax atriceps*. It may compete mostly with the migrant Wilson's Warbler, the other predominantly foliage gleaner foraging fairly low in open second-growth.

*Hirundo rustica*. Barn Swallow. Seen only on April 6, when four groups, containing about 30 birds of at least two species of swallow, flew across the ridge between the Pacific and Atlantic slopes in a northeasterly direction about 100 to 150 feet aboveground.

*Stelgidopteryx ruficollis*. Rough-winged Swallow. On May 7, a loose flock of more than 20 birds flew overhead going from the Pacific slope toward the Caribbean slope. These were probably migrants. It is possible that this species was with barn swallows in the flocks on April 6.

*Pygochelidon cyanoleuca cyanoleuca*. Blue-and-white Swallow. The Blue-and-white Swallow is a resident around Villa Mills. These birds forage only in the air at heights from about 6 inches to greater than 75 feet aboveground. The majority of foraging is between 20 and 50 feet. Foraging birds sweep back and forth over a fairly restricted area, sometimes in a linear swath about 200 yards in extent. Pairs of birds often forage together during the breeding season but small flocks may occur around nest sites at any time of the year. Groups often gather when a nesting pair gives an alarm call.

Nests have been found in rocky crevices and

at the end of an 18-inch tunnel in the side of a recent road cut about 2 feet above ground level, but apparently there is no excavation of a burrow. Skutch (1960) also thought there was no active excavation. I saw no colonial nesting and Skutch (1960) did not indicate that the species is markedly colonial, although there may be some grouping of nests where suitable sites are grouped.

Skutch (*op. cit.*) has summarized most of the nesting data for most of Costa Rica. None of his records are from the altitude of Villa Mills where laying probably starts in late March or early April. A female collected on April 6, had a large yolk in the oviduct and a follicle about ready to break. By May 25, there were full-grown young accompanying adults. The eggs in one nest hatched about June 8. In 1965, I found a nest with young on August 11. From the data of Skutch (1960) I calculated that these young hatched from eggs that were laid in early July. These two nests were probably second broods.

I found nests with clutches of three and two eggs. In several the young, in most cases two, were of markedly unequal size when they were ready to leave the nest.

*Cyanolyca argentigula argentigula*. Silvery-throated Jay. I saw this species twice during the study and once in August, 1969. It also was recorded twice in March and April, 1964, by D. Morse (in lett.) who collected the second specimen from the Costa Rican portion of the cordillera. The only previous specimen was the type, which probably came from the vicinity of Pico Blanca near the Panamanian border (Pitelka, 1951).

The birds I saw were in small flocks of five and eight to 10 birds, moving through the subcanopy of tall oaks in partly cleared areas. On July 5, there were several full-grown young of the year in a group of eight to 10 birds. The two birds I collected had been eating insects.

A female had a slightly enlarged ovary in April, whereas a male had small testes (5 by 3 mm.) on July 5 and was in the midst of postnuptial molt. A juvenile taken on July 5 was undergoing the postjuvenile molt.

There is apparently little movement by these birds to the Cordillera Central in central Costa

Rica. Specimens from Villa Mills at the northern end of the Talamancas are essentially identical with the type from Pico Blanca, whereas Cordillera Central specimens are distinctly silvery throated and markedly different from the Talamanca birds.

*Troglodytes ochraceus*. Ochraceous Wren. I have only one record for this species from the Cerro area. One was searching about 20 feet up in crevices and fissures of the bark of the trunk of a large oak in early September, 1966. Stiles (personal commun.) reported one bird foraging in a similar manner in early August, 1966. The species is fairly common at slightly lower elevations (7500 feet) about 25 miles closer to the northern end of the cordillera (Orians, 1969).

*Thryorchilus browni basuloti*. Timberline Wren. A common resident of the Cerro in second-growth thickets and bamboo clumps. It rarely, if ever, ventures far into open areas and seldom is seen in the interior of undisturbed woods. It was in pairs in mid-December and still in August and September; they probably are permanently paired. It seemed that the birds occupied restricted areas in suitable habitat throughout the periods of observation, suggesting that they also may be permanently territorial.

Foraging is by active search in brush, shrubs, and trees. Generally they search in the moss on twigs, branches, and lichens rather than glean foliage. They also forage on vertical trunks on which they stand sideways. Foraging height ranges from near the ground to higher than 15 feet, but seldom higher than 20 feet. This foraging beat overlaps somewhat with that of *Margarornis* at the lower foraging level of the latter.

An adult male taken on December 29 had a small testis (1 mm.) and was in fairly fresh plumage. By March 15, the testes of a male were 3 by 3 mm., which is at or near the breeding level for this species. Males taken during the height of the breeding period (April 27, 29) had testes 4, 3.5, 4, 3, 5, and 4 mm. long. On April 1, 4, and 12 females had ovaries that were slightly enlarged but not yet ready to ovulate. A female taken on May 10 had an enlarged oviduct and an early stage brood patch; she probably was incubating. A male on June 1 had moderately

enlarged testes (3 by 2.5 mm.), whereas a female on June 7 had only a slightly enlarged ovary and a brood patch. Both of these birds probably were through breeding for the year. Full-grown young were seen on June 8 and 10. The breeding season probably extends from sometime in mid- to late-April to the end of May or early June.

The specimen on June 7 had not started the postnuptial molt.

One call that adds to those described by Slud (1964) was given while two birds foraged in thick brush. I transcribed it as "tee, cheee, cheee, cheee, cheee," and often ending with a "peer, peer." A whisper version of the regular song is given in moderate alarm situations.

*Henicorhina leucophrys*. Gray-breasted Woodwren. This shy, little wren is presumably a permanent resident although I was not aware of its presence until early March when it began calling or singing. The usual habitat was dense second-growth dominated by shrubs, trees, and bamboo. Judging from the songs in the several densely vegetated ravines, which I regularly visited, this species is probably not uncommon despite the few observations.

*Turdus grayi*. Clay-colored Robin. Found primarily at low to middle elevations in Costa Rica (Slud, 1964). I have two records above 9500 feet in the Talamancas. On April 13, a bird I heard singing like *T. migratorius* was tentatively identified as *grayi* since the Sooty and Mountain Robins have very different songs. On April 24, I again heard this song and found two adults moving through the tops of shrubs, apparently from one patch of forest to another about 200 yards away.

*Turdus plebejus*. Mountain Robin. Although this species was recorded in every month except February from December to July, there were few records until about the first of April, after which it was recorded in substantial numbers daily until the end of June when it declined in frequency. The birds seemed to move into the area for the breeding season, probably from lower elevations. During three periods of about four days each in August and September of 1965 and 1966, in this same area I recorded but a single individual. Skutch (1967) also thought there was a seasonal

migration in the highlands of Costa Rica. The birds generally were seen individually. No flocks of *plebejus* were recorded in the study area and there were few records of pairs.

Mountain Robins spend most of their time either in fruiting trees or in the canopy and sub-canopy of the remaining tall oaks. I saw very few *plebejus* foraging. I saw several birds that looked to be foraging along oak limbs fairly high up. Several were seen foraging in fruiting trees, mostly *Miconia* or *Solanum*, and one was collected while it foraged in the organic accumulation in an epiphytic bromeliad. The birds were never observed foraging on the ground and rarely came lower than 15-20 feet. I saw little interaction between *Turdus plebejus* and *T. nigrescens* although there were a few encounters in fruiting trees. The two species seemed to be isolated by both vertical separation within a habitat and by predominant habitats utilized.

There are relatively few specimens from the Cerro area. Morse collected an adult female on March 15, 1964, which had a slightly enlarged ovary, but was not in breeding condition. A male on April 1, 1967, had very enlarged testes (14 by 10 mm.) and probably was in breeding condition. The only positive evidence of breeding were females taken on May 3 and June 3 with edematous brood patches. A female on April 30 had an enlarged ovary. No young or nests were found. The breeding season of *plebejus* probably extends from early April into late May or early June. This means that the breeding seasons of the two *Turdus* overlap extensively but *nigrescens* breeds somewhat earlier than *plebejus*. The song of this species sounds like a run-together "song" of the Green Violet-ear Hummingbird (*Colibri thalassinus*), and is very unlike that of *T. migratorius*.

*Turdus nigrescens*. Sooty Robin. One of the most common birds in the Cerro region, especially in open, second-growth habitats. It was frequently encountered as a dooryard bird and often fed in the early morning on moths that had collected during the night around lighted areas below the windows of the hotel. Although this species could be found at the edge of the forest and sometimes moving through treetops in a forested area, the principal habitats were cleared

pastures and shrubby second-growth. The birds were in pairs throughout the December-July period. Although several birds might gather at a locally abundant food source I never saw any flocks. At various times I saw aggressive encounters that appeared to be territorial disputes. The species is resident in the area.

Adults were primarily frugivorous throughout the observation period and foraged mostly in small trees and shrubs that were in fruit. The major fruits taken, including *Miconia*, *Pernettya*, and *Solanum*, were very abundant and fruit was available the year-round. The adults spend some time foraging on the ground apparently for insects. Several that I watched feeding at half-dry cow flocs would tear them apart by pulling off pieces with the bill, and catching the insects exposed at the still-moist lower surface. Other individuals used the bill to throw aside dry leaves and other detritus on the ground to expose insects.

Egg-laying extends from early March into May. Some young still are in juvenal plumage in early July. An adult male from late December had a small testis (3 mm.) and a female from mid-March had a slightly enlarged ovary. By early April a female had two ruptured follicles; at least one of the eggs was laid in late March. The presence of a nearly full-grown juvenile on April 15 suggests that egg-laying began in 1967 by the middle of March. A nest with eggs was found on April 6. On April 15, and May 26, 27, and June 7 adults were watched feeding young in different nests. There is sufficient time for some pairs to raise two broods, but there was no definitive evidence that any did.

To mid-May none of the birds handled showed any evidence of molt. After that there were no data until August 11, 1965, when an adult was in late stages of postnuptial molt. Birds were in fairly fresh plumage in December and became more worn as the season progressed. There apparently was no prenuptial molt.

The breeding period corresponds rather well to the recorded song period, which extended from January and February, when there was sporadic singing, through mid-May. After mid-May there was little or no singing although the birds were still very common. When singing was at its peak one could hear song at almost any



time of the day, but during periods of decreased singing the birds normally sang only during the early morning and late afternoon. Slud (1964) provided a good description of the song.

*Myadestes ralloides*. Andean Solitaire. Seen only rarely, but heard fairly regularly from early May to early June. There was a definite increase in sight records after the birds started singing. Whether this represented a general increase in activity associated with breeding or a movement of birds into the area is not known, but probably some birds migrate to this higher elevation for breeding. Almost all my sight records were glimpses of individuals sitting for a short time on bare branches about 25 feet aboveground. I never saw this species foraging, but Wallace (1965) reported that in Colombia the species primarily was frugivorous throughout the year.

The period of greatest song activity, early May to early June, probably was the major breeding period. Miller (1963) thought the breeding season in Colombia extended from March to June.

*Hylocichla ustulata*. Swainson's Thrush. I saw this species on each of 14 days from April 5 to May 10. Three was the highest number seen on one day. All the birds probably were moving through the area on the way north. I heard no singing.

*Catharus gracilirostris*. Black-billed Nightingale-thrush. One of the commonest species in the Villa Mills area. I recorded it daily, usually more than 10 individuals. There is no evidence for migratory movements. It seemed to be equally common in August and September and in January to July. The nightingale-thrush usually is found in the open or semiopen, often around second-growth trees and shrubs, but it will venture into bamboo thickets to forage in the thick litter. Several individuals foraged at my feet in litter that I had recently disturbed. Nightingale-thrushes normally forage on the ground, but they will move into trees. Individuals rarely forage higher than 20-30 feet, and 50 feet was the highest that I saw a bird foraging. They hopped on the ground searching in open areas or in moss or litter for insects. I did not see the bill used to move ground debris aside. Often they

hunted on open ground as much by watching for movement as by active searching. It was not uncommon to watch a bird scan an area and try to capture an insect that just had landed or flown up a short distance away. The birds usually foraged singly, sometimes in pairs. I never saw this species in flocks. Several individuals may use the same feeding area simultaneously even during the breeding season. It appears that territories may not be determined by strict boundaries, but rather in terms of dominance as Young (1951) reported for the American robin. I often saw aggressive encounters among feeding individuals, but no bird maintained a fixed area from which it excluded other individuals. The pair bond in this species may persist beyond the breeding season as pairs still were present in September.

Insects were the major food items. Some specimens had fruits as well as insects in their stomachs, but fruits formed only a minor part of the diet, at least from December to July.

Enlarged gonads were found in males by mid-March. Two adults netted on March 21 showed no evidence of breeding (no enlarged cloacal protuberance or brood patch). Several specimens had small testes or ovaries in early April. Egg-laying probably starts in late April; a female on May 1 had a very edematous brood patch indicative of an incubating bird. Another female, taken on April 30 had recently laid an egg. The only nest was found on May 5 on a live leaf of a *Cirsium subcoriaceum* about 6 feet tall. It contained two bluish eggs with rather blurred brownish spots over most of their surface. The nest was on a lower leaf that gradually drooped, tipping the nest, until the eggs fell to the ground. The first evidence that I obtained for the presence of young was an adult collecting food, presumably for nestlings on May 10. By June 1, there were full-grown young begging from adults and I saw a juvenile begging from an adult as late as July 3. The breeding season probably extended from sometime in April to May or early June. A bird on September 1, 1966, was in the final stages of the postnuptial molt.

As Slud (1964) reported, the song of this species is very similar to that of the Hermit Thrush (*Hylocichla guttata*) of North America. This is a fairly common song mode in the genus *Catharus*, being found at least in *C. occidentalis* and *C.*

*frantzii* among the species with which I am familiar. Some other species, however, which are placed in the same genus, have markedly different songs (e.g., *C. aurantirostris*, Miller, 1963). I recorded the following call notes: a high, thin "tzee," a "drrr" that sounded like a gravelly mew-o and maybe the buzzy "chrr" which Slud (1964) reported. The adults also make a high, thin "whreet," which is similar to a sound made by *Zeledonia*. A young bird stranded on the roadway made a nasal "rannk."

Active singing started in mid-January, was declining in early July, and was very reduced in August and September.

*Zeledonia coronata*. Wrenthrush. I have little information to add to the account of the biology of this species published by Hunt (1971). Hunt's observations were made in the same area as the present study.

On June 15, I collected a young with a nearly full-grown tail. The accompanying female, which was still feeding the young, had an old brood patch, but had not started the postnuptial molt. Insects and other arthropods are the usual food items; the female collected on June 15 was carrying a spider in her bill. One other female I collected had a few seeds in the stomach.

*Ptilogonys caudatus*. Long-tailed Silky-flycatcher. Silky-flycatchers were present throughout the year. They normally occurred in the semiopen, first in small groups, and as the breeding season approached, in pairs. Skutch (1965) has already described many aspects of the life history of this species and my information from the Cerro area adds relatively little.

The diet is predominantly fruits, but flycatching increased during the breeding season. The fruiting plants visited included *Miconia* and *Gaiadendron*; some purple berries were taken from the stomach of one bird. Aggressive chases sometimes occur in feeding areas.

The testes of a male taken on March 16 were enlarged (7 by 5 mm.), whereas those from June 4 were only moderately enlarged (4 by 3 mm.). The only female specimen was taken on April 27 and had a brood patch. There was no molt on the specimen taken on June 4.

*Phainoptila melanoxantha*. Black-and-Yellow

Silky-Flycatcher. This species is much less common than *Ptilogonys* and was recorded on only 12 days. It normally forages in thick foliage of second-growth trees; apparently taking only berries. Most of my foraging records were of birds in *Miconia* trees. It was fairly regular in December to early February, but irregular in May and June after several months with no records. The May pair, which apparently was breeding, was collected and the species was not seen again until a pair appeared in June. Skutch (1965) suggested a downward movement for breeding that would be in the opposite direction from most species in the highlands which migrate to higher areas for breeding.

A male from March 24 had enlarged testes. The male of a pair had enlarged testes (9 by 6 mm.) on May 3, and the female, taken on May 4, had an edematous brood patch and follicles to 2 mm.; it probably had laid fairly recently.

*Vireo carmioli*. Yellow-winged Vireo. I observed this species on approximately 80 percent of the field days. Most field days for which there was no record were during the season when the species was not singing. I assume that it was a permanent resident in the area. I usually saw it in or near oak woodland, foraging from the tops of the tallest oaks down into second-growth trees to approximately 25 feet aboveground. I collected one in a mist net about 4 feet aboveground in a clearing. Most foraging is a slow, deliberate foliage-gleaning similar to other species in the genus. Most of my sight records were from the spring and early summer during the breeding season and it is possible there may be a habitat shift following breeding.

The singing period on the Cerro extended from early February at least to early July. I did not hear songs in August and September and my only record at these times is the bird I netted.

The only available specimens from the area are from April, June, and September. Birds on April 1 and 4 had testes 3 mm. long.

A male from April 27, had testes slightly larger (4 by 3 mm.) and was in the midst of a light body molt. Two females, one on June 7, and the other on June 14, had small, inactive ovaries and were in postnuptial molt.

*Diglossa plumbea*. Slaty Flower-piercer. This

small nectar and insect feeder was a common resident of the Cerro area usually found in shrubby second-growth where there was an abundance of flowering shrubs. It normally foraged within 10 feet of the ground, occasionally higher. I did not see it traveling with mixed foraging parties. Usually it foraged singly; sometimes it was with a family group of one or two young. Two recognizable individuals recurred regularly for more than one month in one of my study areas, often at the same bushes, and using fairly regular routes of foraging. Although individuals continually returned to the same bushes, there was no attempt to defend a bush over a long period of time. It appeared that each *Diglossa* foraged in a large area that probably was defended against other *Diglossa*. When they visited a bush being defended by a hummingbird there was usually a conflict. The hummingbirds seemed able to force the *Diglossa* to leave, but not immediately. During several periods in late spring, a foraging *Diglossa* was able to displace successfully the defending hummingbird and feed undisturbed. The foraging technique of *Diglossa* has been described by Skutch (1954). The *Diglossa* is a slower forager than any of the four sympatric hummingbird species and tends to forage actively in the same bush for a much longer period of time (see Colwell et al., 1974 for a more complete discussion of the *Colibri-Diglossa* interaction at *Centropogon valerii*).

All the stomachs examined contained only insects although several collected individuals leaked a sweet (by taste) fluid from the bill. It was impossible to determine what percentage of the diet was composed of nectar and insects. In checking flowers *Diglossa* visited, I rarely, if ever, found the same insects as those found in the stomach; the usual arthropods in the flowers were very soft-bodied whitish mites (Colwell, 1973), whereas the insects found in stomachs usually were dark-bodied, flying insects.

The only singing I heard was for a short period in January. We found no nests. When we arrived in late December I encountered a single juvenile that was starting the postjuvenile molt. In March we found several juveniles still traveling with adults. Males in April had testes of 3 mm. and 5 by 4 mm., and two males in May had testes of 4 by 3 and 3.5 by 2.5 mm. respectively. The

only females were collected in late December and early April and both showed ovaries which were slightly enlarged (follicles to 1 mm.). It appeared that males were in potential breeding condition throughout the study period and that actual breeding depends on the timing of the female cycle. Some birds in December and January appeared to be in the midst of a molt, probably a complete molt, following a breeding period. From these limited data it appears that this species has a remarkably long breeding period.

*Vermivora peregrina*. Tennessee Warbler. Although this species is a common winter visitor in much of Costa Rica (Slud, 1964), it is only occasional at the highest altitudes. I saw individuals only twice, on January 28 and on April 16. The first bird was foraging along the under-surface of thistle leaves about 4 feet from the ground.

*Vermivora gutturalis*. Flame-throated Warbler. Although presumed to be a permanent resident in the area, this species was seen infrequently. The main habitat was oak woods where the birds foraged through the canopy singly or in pairs. It probably is strictly a foliage gleaner.

I heard no song which I associated with this species. Skutch (1967) reported a song which was a "weak, dry, rather harsh buzz." I cannot corroborate the statement of Moynihan (1962) that this is a noisy species that moved with mixed flocks. It was seen only infrequently with mixed flocks, but this might reflect its limited abundance in relation to other flocking species rather than a geographic difference in flocking tendency.

I saw a young bird on June 15 and 17 (probably different individuals). Each one had the tail about three-quarters grown. A male taken on April 1 had the testes only slightly enlarged (4 by 2 mm.) in comparison with a male taken on May 7 (7 by 5 mm.). A female on March 21 showed no ovarian enlargement, whereas an April 4 female had the ovary slightly enlarged. By June 14, a single individual was undergoing the postnuptial molt. It appears that the breeding period for this species extends from late April or early May possibly into June.

*Dendroica virens*. Black-throated Green

Warbler. Recorded only on December 30, when I saw an individual in a shrubby second-growth area. It probably is much more frequent at lower elevations.

*Wilsonia pusilla pileolata*. Wilson's Warbler. The earliest record for this species on the Cerro was on September 2, 1966. From December to July it was seen in numbers daily until mid-May. The last record was a single bird on May 25. It was by far the most common parulid in the area. The habitat was second-growth areas in which individuals normally foraged singly, although single birds sometimes might join a mixed flock. The birds foraged by flycatching, foliage gleaning, and dropping to the ground to pick up items, possibly ones that fell or were flushed from the foliage. Individuals seemed to use spatially restricted foraging areas, but there seemed to be no rigidly defined territories as such. However, none of the birds were individually recognizable so this could not be documented fully. I saw several chases as two foraging birds approached each other. I also watched two or three individuals forage through the same tree within 6 to 8 feet of each other with no sign of aggressiveness.

I heard no singing.

*Myioborus torquatus*. Collared Redstart. Seen generally in pairs, either alone or with young. Skutch (1967) also reported that they occur in pairs the year-round. The species was restricted to oak forests or to the edge of such forests. They foraged primarily by capturing foliage insects in the canopy of the oaks, acting very much like such redstarts as *Setophaga* or *Myioborus miniatus*.

I heard no songs that I connected with this species.

A male taken on April 1 had testes that were only slightly enlarged (4 by 2.5 mm.). By the end of April a male (UMMZ 153325) had fully enlarged testes (8 by 5) and a male on May 10 had similarly sized gonads (9 by 6 mm.). Two females were in quite different stages of breeding although taken at about the same time; one on April 27 was labeled by the collector as breeding, but a female that I took on May 10 had no brood patch and had not initiated breeding for

the year. The breeding season probably is restricted mostly to May.

Stiles (personal commun.) saw a single *M. miniatus*, the Slaty-throated Redstart, moving with *M. torquatus* and other species in a mixed flock on August 1, 1966.

*Basileuterus melanogenys melanogenys*. Black-cheeked Warbler. An uncommon species in the Cerro area and like the redstart it seemed to be paired the year-round. In contrast to the canopy foraging redstart, the black-cheeks primarily foraged in thickets within 15 feet of the ground. I once saw a pair in the canopy or subcanopy of oaks approximately 50 feet up where they seemed to be working around clumps of lichens and mosses. An active forager, this warbler is not nearly so active as the redstart. The only food items in stomachs were insects.

The testes of a male taken in mid-March were small (2 by 2 mm.). The gonads of some mid-March and early April males were slightly enlarged (5 by 3 mm., 4 by 3 mm.). A female taken on June 16 had an old brood patch but had not yet started to molt.

*Amblycercus holosericeus holosericeus*. Yellow-billed Cacique. This species probably has the greatest altitudinal range of any resident forms in Costa Rica. It is known from sea level up to about 3100 meters. On the Cerro it is limited to thickets, primarily of bamboo, in the ravines. It is very shy, although it will respond to "squeaking," and is much more often heard than seen. Once the call was known it was obvious that there were probably six to eight pairs in the series of ravines that I normally visited. Calling started by early February and was still heard in early July when we left. There was no calling recorded in either August or September.

Most foraging was done by probing in crevices in the vegetation such as nodal sheaths and basal areas of leaf projections in the bamboo plants. Normally the birds were encountered as pairs foraging independently, but within easy vocal contact. Calls back and forth were repeated frequently.

One female, from late April had the ovary greatly enlarged, and one from late May had a brood patch with the ovary and oviduct enlarged.



This was probably the height of the breeding season.

*Chlorophonia occipitalis callophrys*. Blue-crowned Chlorophonia. Records of this species were scattered throughout the December to July study period. Most of the birds were encountered in pairs in *Gaiadendron* clumps on oak trees either in open woods or where there were scattered trees. The birds were feeding on the *Gaiadendron* berries.

The only specimen was a female taken on December 22; the ovary was not enlarged and the skull was not yet completely ossified.

*Tangara dowii*. Spangle-cheeked Tanager. Recorded only 10 times during the study period. All the records were from December to early February, suggesting that the birds may come higher into the mountains in the winter months and then returned to lower elevations, the site of most records (Slud, 1964). Two birds, probably a mated pair, were collected on December 23. When the species was present in the area, most of the records came from a single clearing in which the birds were visiting a large fruiting clump of *Gaiadendron*. These are the first records from this altitude in the Talamanca Cordillera where it previously had been reported only on the Caribbean slope at the northern end. It previously was known from this elevation in the Cordillera Central.

*Chlorospingus pileatus pileatus*. Sooty-capped Bush-tanager. One of the few really abundant species on the Cerro. It was normally seen in groups of more than two adults. The only time that I saw pairs of adults consistently separated from the flocks was when I investigated a nest with young. Here there seemed to be only two adult birds attending. No others came around when the adults gave an alarm call while I checked the nest contents.

The major habitat occupied is open to fairly dense second-growth. These birds forage both for insects and fruits and are continually on the move. A flock seemed to follow a regular route that included returning to the same area periodically throughout the day. The normal foraging beat is low in the second-growth shrubs, but I did

see some flocks moving through the canopy of some of the taller oaks; this was especially noticeable at the end of the breeding season. I regard this species as an active nuclear species (see Moynihan, 1962, for definition) in this area with many calls between individuals and many species tending to follow them. In fact this is the only regular flocking species on the Cerro; the other species rarely flock except as one or two, sometimes three individuals as in the case of *Margarornis*, and never form intraspecific flocks. During the breeding season of most of the other species in the area, which normally were seen in the mixed flocks, the numbers of individuals and species joining the flocks decreased markedly. This decline was reversed and the flocks reformed after the breeding season ended.

This species sang mostly in the early morning and late evening, except at the peak of the breeding season. Singing was almost entirely absent out of the breeding period.

Laying began at least by early March, as I found a nest with two young on March 21. There were full-grown young moving with flocks of adults by May 5. Some adults in the population were beginning the postnuptial molt by May 13. A young of the year was in heavy postjuvinal molt in June. Probably the breeding period ended by late April or sometime in early May. This means that the breeding period of this species began and ended earlier than for many other species in the area.

*Spinus xanthogaster xanthogaster*. Yellow-bellied Siskin. I have no records of this species on the Cerro from mid-December to early March when one was reported to me by a reliable observer. The species became fairly regular in early April and was still common when I left in early July. However, I have but one record for three weeks of observations in August and September. It seems that the birds come into the area, probably for the breeding season, and leave soon after breeding is completed. I infrequently heard birds singing during the breeding period; most often they gave a flight note which was very similar to that given by *Spinus tristis*. The birds were normally found in relatively open areas where some large oaks remained. Usually

they stayed in or near the tops of these oaks; occasionally they came down to some of the lower shrubs and trees. Apparently most feeding is done in the canopy of the oaks. They were most often in small groups of from four to 10, rarely more, individuals.

Two males collected on May 10 were in breeding condition (testes 5 mm., 7 by 4 mm.) and were with two female-plumaged birds when collected. The stomachs contained seeds and buds.

*Spodiornis rusticus*. Slaty Finch. I have only two records for the Cerro area. These records are the first for the Costa Rican portion of the Talamanca Cordillera, along which it was to be expected as Eisenmann (reported by Slud, 1964) had found it in the Volcan district of Chiriqui which is continuous with the Costa Rican portions of the cordillera. A female was caught on May 4 in a mist net placed across a path in a small grassy area in an overgrown pasture dominated by shrubby second-growth. There were signs that cattle grazed in the area periodically, which probably helped to keep some of the ground cover in grass rather than a solid mass of shrubs. An immature male caught on August 23, 1969, is more fully reported by Stiles and Hespenehede (1972).

*Acanthidops bairdii*. Peg-billed Finch. The first record of this species in the Talamanca Cordillera was an individual collected on December 29, after being observed foraging in a *Vaccinium* bush in shrubby second-growth. Following this encounter the species was recorded a total of 11 more times until our departure in early July. Generally, only a single individual was seen, but pairs were also recorded. Usually the birds, whether male or female, were foraging through flowering trees or shrubs in second-growth areas. I did not see them in the oaks. I carefully watched several individuals as they visited flowers but was unable to see precisely how they were foraging. They appeared to be working at the front of the flowers. Since I only saw them at flowers with short corolla tubes I believe that they must probe the front of the corolla for the nectar that collects at the base. The birds were most often seen at *Vaccinium* bushes, but they also visited *Macleania* (Erica-

caee), *Weinmannia* (Cunoniaceae), and *Solanum*. One male was observed hopping along the ground, where it seemed to be searching in the moss growing on a road bank, acting very like *Junco vulcani*. When birds foraged in *Macleania*, they seemed to search for insects and did not visit flowers or fruits. Similarly, in *Weinmannia*, the activity was of a foliage gleaning bird rather than a flower visitor. Only once did I see an individual engage in what appeared to be an attempt at flycatching. In general the birds foraged much more slowly than did *Diglossa*, and they often stayed for considerable time in a single tree or shrub.

The bicolored bill is very noticeable in the field and serves as a good field mark to distinguish this bird at a glance from the similarly colored *Diglossa*.

The stomach contents of two specimens, which I collected, were all insects or other arthropods (Stiles and Hespenehede, 1972). One bird, which had been actively feeding just before being collected, had its esophageal diverticulum crammed with food. As far as I know this sort of storage system is not known for *Diglossa* to which *Acanthidops* likely is closely related (Storer, personal commun.).

Three specimens were collected on the following days: December 29, a female with moderate to heavy fat deposits, no molt, and a granular ovary; May 1, a female with a fully ossified skull, the ovary only very slightly enlarged, and with a light amount of body molt; June 7, an adult male with testes 2 mm. long, flight and body molt.

*Pezopetes capitalis*. Large-footed Finch. In thickety areas of second-growth where there is leaf litter this is the common ground-foraging finch. It is much more abundant than the more shrub-oriented *Pselliophorus* and is found in denser situations than *Zonotrichia*. This species foraged to a lesser extent in small trees and low shrubs in second-growth areas. While foraging on the ground, the birds often scratched backward in a hopping motion employing both feet simultaneously. In December the birds were already in pairs, although I was not always sure that the pairs represented one of each sex. Once I saw what I initially thought to be some sort of sexual chase only to catch both birds and discover that they were females. This strengthened

the belief I held after watching other encounters that both sexes in a pair were active in defense, but I was never sure that defense was oriented around a fixed area. Pairs could often be found in about the same area day after day and seemed to restrict their activities, but more than one pair could be found feeding in the same area. It appeared that the foraging areas might be shared to some extent and the encounters served to keep the pairs separated.

Songs and duetting were essentially as described by Skutch (1967). The song is rather infrequently heard; the common vocalization is the squeal duet. It normally is given when two individuals of a spatially separated pair come together and it can, therefore, properly be called a reunion duet. The only other call I heard I described as soft lilting notes. These were given by one of two birds, a male and a female, which were chasing each other in a small *Miconia*. I was able to collect one bird and then the other. After I shot the first the second stayed in the tree jumping from branch to branch with its crown-feathers raised. They were both in heavy annual molt and this may have represented pair formation behavior.

Females taken on March 15 had slightly enlarged follicles (to 2 mm.), preparatory to breeding. I collected a female on May 4 with an edematous brood patch. By May 26, I saw two pairs of adults each with a single full-grown young begging from, and being fed by, the adults. Young were seen with adults as late as June 29. Although I never found any nests of this species, I saw one young with each of five or six pairs of adults. Carriker (1910) reported one egg as the usual clutch in this species. If this is actually the case it would be an unusual occurrence for a New World passerine and further investigation might provide interesting information on the factors regulating clutch size in birds.

The major food items that I recorded were insects, seeds, and fruits, especially of *Pernettya*.

*Pselliophorus tibialis*. Yellow-thighed Finch. A species of brushy second-growth areas, but normally found foraging in bushes or small trees rather than on the ground as was *Pezopetes*. I saw individuals apparently foraging as high as 50 feet. The birds did not regularly enter forested areas. Foraging was a methodical search as in

vireos. The major food items recorded were seeds, insects, and fruits. I watched one adult pecking at a hanging seed pod of *Centropogon valeri* from which it removed a few pieces of fleshy material in which the tiny seeds were imbedded.

The song of this species, which is rarely heard, was described by Skutch (1967). The squeal duet usually was given as a pair reunion vocalization, but also may be a territorial call, suggesting that it is rather similar in quality and function to the squeal duets given by several species of sparrows in the genus *Aimophila* (Wolf, In press) and towhees in the genus *Pipilo* (Marshall, 1964).

Males were in breeding condition in mid-March (testes 11 by 7 mm.). Another adult male taken on May 6 was already through breeding (testes 2 mm.) and was starting the postnuptial molt. A female on June 7, was also in the postnuptial molt. I never saw any young with adults. The breeding season probably extended from March to April and is slightly shorter than for *Pezopetes*.

*Junco vulcani*. Volcano Junco. The Volcano Junco is nearly restricted to open areas of grass and small shrubs on the Cerro. They foraged in dense shrubs 6 to 10 feet high, but most foraging was done in the open. However, I saw birds foraging as high as 10 to 15 feet on large horizontal branches of oaks. They usually foraged singly or in pairs and may be paired the year-round. A foraging bird normally walks while moving slowly over the ground. Quick movements of some distance on the ground are by hopping.

The predominant food items taken from the stomachs of collected birds were insects and seeds. One adult pecked at a hanging pod of *Centropogon valeri*.

Song perches were either on the ground or on rocks; much less frequently the singing bird would move into a shrub. The song is a series of repeated notes and phrases on variable pitches and is more similar to the type recorded by Marler and Issac (1961) for the Yellow-eyed Junco (*Junco phaeonotus*) of the southwestern United States and Mexico than for the Dark-eyed Junco (*Junco hyemalis*) of North America. Each singing individual repeated the same song for 10 or more times.

This species has a long breeding season. The first eggs are laid by early to mid-March as I saw a young with tail approximately half-grown out of the nest on April 14. A nest discovered in a road bank on April 15, held young only a few days from fledging. They were being fed by two adults. I found another nest on June 2 containing two well-grown young, about 3 feet up in a *Pernettya* bush growing out of a road bank, and I found a nest with two eggs that were being incubated by an adult on July 30. We were not able to determine when these eggs hatched. A bird collected on July 3 was in the midst of the postnuptial molt.

*Zonotrichia capensis costaricensis*. Rufous-collared Sparrow. This species occupies the same sort of pasture and open shrubby second-growth as was reported for other areas in Costa Rica (Wolf, 1969a). Most of the foraging is done on the ground. The major food items were seeds and insects.

The birds were in pairs when we arrived December 20 and were still in pairs when we left in July. Singing started in mid-January and continued for several months before declining to a low level in mid- to late June.

Nesting began in February. Dickerman reported a young on March 6, which appeared to be just out of the nest. By late May most individuals that I observed closely in the field were engaged in postnuptial molt. The population seemed to be very synchronous in initiating this molt which coincided with a marked decline in singing. A young taken on June 1 was nearly through the postjuvinal molt; following the aging system of Miller (1961) it must have been at least 70 days old, meaning that the eggs that produced this individual were laid around mid-March. I have no evidence of a second breeding period following the complete molt in June and July as was found in a population around Vara Blanca (Wolf, 1969a).

## DISCUSSION

### MORPHOLOGICAL DIVERGENCE

There are many factors influencing the rate of evolutionary divergence of an isolated population from its parental stock. The amount of morphological divergence, however, as reflected in taxonomic designations, which the endemic forms show, may provide some insight into the rate and timing of colonization as well as providing information about actively evolving forms and gene flow into the area.

The ratio of nonpasserines to passerines breeding in the area is 15:34, or 31 percent nonpasserines. The 69 percent passerines is a higher figure than any reported in Slud (1960) for other Neotropical areas. The most similar figure was 61 percent passerines in the resident avifauna at a locality in southeastern Nicaragua (Howell, 1957). Eight other nonpasserines, but only four other passerines breed at slightly lower elevations which suggests that the evolutionary more recent passerines are more capable of successfully invading the highland tropics than the nonpasserines.

Endemism first will be viewed at the geographic level of the Costa Rica-Panama highlands, which includes the northwestern and central volcanic ranges in Costa Rica and the Talamanca

Cordillera. As noted in the section on source areas there is little geographic separation of montane areas among these ranges, but wide separation between these ranges and the next major mountain masses to the north and southeast. The level of endemism in taxonomic categories among the 49 species that have been recorded breeding in the Cerro area varies from no taxonomically recognized endemism, even at the subspecific level, to a single endemic form, the wren-thrush, that is placed in a monotypic family, Zeledoniidae, by some authors (Van Tyne and Berger, 1959; Wetmore, 1960). It undoubtedly will be found that the wren-thrush should be merged with another family, in or near perhaps the group containing the wood warblers (Parulidae) (Sibley, 1968, 1970). For the present I retain the family level of endemism.

There are five genera, each monotypic, endemic to the Costa Rica-Panama highlands. One, *Panterpe*, belongs to the Trochilidae, a family presently overburdened with small, even monotypic genera (Sibley, 1957), and badly in need of revision. Another endemic genus is the wren, *Thryorchilus*, which Peter's checklist (Paynter, 1960) merged into the genus *Troglo-*

*dytes*, probably a correct decision. A further generic endemic is the monotypic silky-fly-catcher, *Phainoptila*. The relations of this form are still in doubt, especially since so little is known of the living bird (Skutch, 1956). The other two endemic genera are both finches, one of which, *Pezopetes*, seems to be related rather closely to the *Atlapetes* group of finches and may not warrant generic distinction. *Acanthidops*, the peg-billed finch, is rather unusual in bill structure, but is so poorly known as to not warrant speculation about the taxonomic importance of the divergence.

At the specific level, 21 forms are endemic to the highlands of Costa Rica and adjacent Panama; of these 17 are passerines and only four nonpasserines. The 81 percent of the endemic forms at the species level or above that are passerines is somewhat higher, but not significantly ( $\chi^2 = 1.31$ ), than the percentage of the total breeding fauna that is passerine (69%). This high proportion may reflect greater gene flow from other populations for the nonpasserines as compared with passerines or perhaps the nonpasserines have broader environmental tolerances that reduce selective pressures for morphological divergences of isolated populations.

One might expect a similar relationship among the passerine and nonpasserine subspecies endemic to the highlands. In fact, the 17 endemic subspecies are nearly equally divided between passerines and nonpasserines although the endemic subspecies comprise twice the proportion of the total of nonpasserine to passerine forms. Since the number of and percentage of nonendemic forms in the passerines and nonpasserines is also approximately equal it suggests that the passerines in this area are under stronger selective pressures for obvious morphological divergence or that they have been isolated longer; the latter is not a likely possibility.

There is some subspecific differentiation among the species occurring around Villa Mills that are endemic to the Costa Rica-Panama highlands. Ten of the 27 species have taxonomically recognized races that appear to be valid; of the 10 only one, *Thryorchilus browni*, has more than two recognized forms. Most of the 10 have races that are similar throughout the Talamanca Cordillera, but have a different form on the

lower mountains in eastern Chiriqui Province in Panama. *Pyrrhura*, *Thryorchilus*, and *Basileuterus* each have a form on Volcan Chiriqui that is taxonomically distinguished from the birds at the northern end of the Talamanca Cordillera. There is little reason to doubt that any of the three are not continuously distributed along the Cordillera. When the birds along the Cordillera are better known, this probably will prove to be another case where two ends of a cline have been named.

*Cyanolyca argentigula*, which occurs on the central volcanic highlands as well as the Talamanca Cordillera, is the only species that has been differentiated subspecifically in those two areas. Birds from the cerro are essentially identical to the type near the Panama border (Pitelka, 1951) and Chiriqui, but differ strikingly from the silvery throated birds from Irazu.

The degree of endemism might also be considered in terms of the altitudinal distribution of the species. Using information from Slud (1964) although he does not always give a specific distributional range in meters above sea level, I recorded approximate lower limits of distribution for all the species breeding in the Cerro area. Even though 49 of the species are considered to breed in the area, several migrate after breeding, mostly to lower elevations. In each case, the lowest regular occurrence was taken. On this basis there was a significantly higher proportion of endemics at the species level and above which were restricted to the lower montane and montane life zones, whereas the majority of endemics from the subtropical and tropical zones showed limited morphological divergence from allopatric populations (tables 1, 2).

The degree of morphological divergence generally increased as the lower limit of distribution increased. An index was derived of the level of endemism for species with lower distributional limits in each zone. Values were assigned to each species ranging from 4 for endemism at the family level to 0 for no endemism. Summing these values for each zone and dividing by the number of species per zone gave the average endemism per species (table 3).

The increasing endemism with increasing altitude suggests that the level of divergence depends on the degree of isolation of the populations rather than the age of the mountain mass.



TABLE 1  
Endemism Level Among Breeding Species Relative to  
Lowest Life Zone of Regular Occurrence

Lowest Regular Occurrence	Family	Genus	Level of Endemism		None	Total
			Species	Subspecies		
Montane	0	2	3	0	0	5
Lower Montane	1	3	10	2	1	17
Subtropical	0	0	8	14	3	25
Tropical	0	0	0	1	1	2

TABLE 2  
Comparative Levels of Differentiation Among  
Breeding Birds Relative to Lowest Life Zone  
of Regular Occurrence

Life Zone	Level of Endemism	
	Species and Above	Subspecies and None
Montane and Lower Montane	19	3
Subtropical and Tropical	8	22

$\chi^2=15.77$ , 1 d. f.,  
 $p<0.005$

The possible causal factors are twofold, both relating to the ability of the birds to reach the mountains. As has already been discussed there is good evidence for glaciation on the cordillera, probably accompanied by a lowering of the limits of the life-zones during the Pleistocene. At the same time the lower elevations today are potentially more continuous for birds than the higher life-zones would be. The level of divergence then reflects the time of arrival of a population and the probability that subsequent colonists of the same species will arrive sufficiently regularly to retard morphological divergence of the resident population. On the other hand, species that arrive with a set of morphological characters that, for whatever reasons, is not subject to strong directional selection in the environment would also not be expected to diverge taxonomically. For the Cerro birds the evidence strongly points to the importance of the degree of isolation of the populations from gene flow rather than homeostasis of the morphotype.

However, as noted by Gill (1973), even moderate selection pressures can override the effects of fairly high levels of gene flow.

ECOLOGY OF THE CERRO SPECIES

There was great diversity among the 76 species that have been recorded on the Cerro in the temporal exploitation of the resources of the montane habitats. Twelve (16%) of the species are only occasional visitors to the area from lower in the mountains. Of the 12, two-thirds are nonpasserines and four are passerines although 40 percent of the entire fauna is nonpasserines. This means that a disproportionate number of the nonpasserines are only visitors ( $\chi^2 = 4.4$ ;  $p < 0.05$ ).

Sixteen of the species were classed as migrants on the Cerro. Several of these species were present only on one or several days in small numbers and have very little impact on the total resource exploitation. Only *Hylocichla* and *Wilsonia*, of the 16 migrants, were present on more than 10 days in the December to July period and could be important in the ecological organization of the avian community. *Wilsonia* is very common while in the area, generally outnumbering the total population of all the other warbler species. The total time that *Wilsonia* was in the Cerro region was in excess of the amount it spends in the North Temperate zone. On a strictly time basis it was equally or more important than several warbler species that breed in the area and leave during the nonbreeding season. Numerically it probably created a much greater impact on available resources than many of the breeding residents. In considering the organizational structure of tropical communities one should take into account the impact of the

TABLE 3  
Average Degree of Endemism Relative to  
Lower Limit of Life Zone Distribution

Life Zone	Average Endemism <sup>a</sup>	Number of Species
Montane	2.2	5
Lower Montane	2.1	17
Subtropical	1.2	25
Tropical	0.5	2

<sup>a</sup>See text for explanation of endemism index.

winter residents (Miller, 1963; Fretwell, 1972) although this is not usually done in current studies (MacArthur, Recher, and Cody, 1966).

The remaining 49 species, which have been recorded on the Cerro, are breeding residents. Eleven of these species leave the Cerro following the breeding season, presumably for lower elevations. This leaves 38 species which are year-round residents on the Cerro.

In addition to residency status the birds might also be grouped ecologically in terms of the food resources they utilize and the foraging zones they occupy. It is difficult to make much of the non-quantitative differences in foraging behavior as reported in this study, except where foraging behavior specifically limits certain types of exploitation within a general class. This is mentioned, where known, under each of the species accounts.

With our present knowledge of tropical birds, it is nearly impossible to consider in detail the relative amounts of each food type that are utilized by each species or the seasonal variation in food type. Consequently, each species was recorded as exploiting a food type when my own data or literature information confirmed utilization, regardless of amount and independent of season. It must be kept in mind that each species could be listed as exploiting more than one food type. The data for food utilization are presented in table 4. Arthropods are important food items for the greatest number of species of the total avifauna. For most of these species, insects form the major part of their diet. The next most common item is vegetable material, either fruits or buds. Seeds, which were segregated from other vegetable material, were taken by about the same

number of species as were foraging on nectar. Of the remaining categories, predators on vertebrates and scavengers, only Skutch's report (1944) of limited predation on reptiles by the Quetzal suggests predatory foraging by resident birds. The data for *Glaucidium* are limited, but it is likely that the pygmy owl was also predatory to some extent. The abundance of the lizard, *Sceloporus malachiticus*, and small birds seems to provide sufficient biomass to support a resident species of bird that eats these organisms, especially a *Micrastur* or *Accipiter*-type. This seems to be an unfilled exploitation zone suggesting that the Cerro fauna is still unsaturated, even if migrants and nonbreeding visitors are included.

The predominance of insectivores in the avifauna is undoubtedly related to the relative and temporal availability of food types. On this view it is interesting that the altitudinal migrants that breed in the area were primarily frugivorous or nectarivorous, although many feed insects to their young. Of these migrants only the three hummingbirds when adult seem to use major quantities of insects. This suggests that there is a marked seasonal fluctuation in fruit either in the Cerro area (which is my impression) or perhaps lower on the mountain, which would make it advantageous to leave the Cerro even when plenty of fruit is still available. The cycling of fruit availability is not of such magnitude that there are no permanently resident species that are primarily frugivorous. The only common frugivorous residents are the Sooty Robin and Sooty-capped Bush-Tanager, both of which also utilize insects.

In addition to food differences species can also divide the area in terms of foraging zones. I established a classification of foraging zones,

TABLE 4  
Food Utilization by Species on the Cerro

Food Type	Number of Species
Insects	58
Fruits and Buds	23
Seeds	6
Nectar	7
Vertebrates	4
Scavengers	2

partly based on similar classifications of Slud (1960) and Miller (1963). The distribution of foraging zones among families and species is presented in tables 5 and 6. In general, families with one or more permanent resident or common species tended to occupy more foraging zones than families with few or uncommon species. A few species essentially monopolize one foraging zone and were quite frequent (e.g., *Pygochelidon*). As expected, families with broad foraging zones in other areas successfully maintained a larger species composition than families with narrow foraging ranges.

The best documentation of differences in foraging beats among species in the same guild (Root, 1967) that are reflected in differences in food items taken is for the four regular hummingbird species. There is fairly clear differentiation of flower species at which each of the bird species forages as well as differences in the

TABLE 5  
Utilization of Foraging Zones by Resident Bird Families on the Cerro

Family	Number of Species	Foraging Zones <sup>a</sup>
Phasianidae	1	1,4
Columbidae	2	3,6
Psittacidae	2	6,9
Strigidae	1	3,6
Apodidae	2	12
Trochilidae	4	3,4,5,7,8
Picidae	2	5,6,7,8,10
Dendrocolaptidae	1	5,6,8,9
Furnariidae	2	5,6,8,9
Rhinodryptidae	1	4,5
Tyrannidae	3	5,6,7,8,9
Hirundinidae	1	12
Corvidae	1	6
Troglodytidae	2	4,5,7
Turdidae	4	3,4,5,6,7,8,9,10
Zeledoniidae	1	4
Ptilonotidae	2	6,8,9
Vireonidae	1	3,5,6
Coerebidae	1	5,7,8
Parulidae	4	2,3,4,5,6,7,8,9,10,11
Icteridae	1	4,5
Thraupidae	3	6,7,8,9
Fringillidae	7	3,4,5,6,7,10,11

<sup>a</sup>See table 6 for classification of foraging zones.

TABLE 6  
Principal Foraging Zones of Resident Species

Foraging Zone	Number of species
Forest	
1 <sup>a</sup> 0-5 feet	1
2 5-25 feet	2
3 > 25 feet	9
Dense Second Growth or Open Forest	
4 0-5 feet	11
5 5-25 feet	24
6 > 25 feet	25
Open Second-Growth	
7 0-5 feet	17
8 5-25 feet	19
9 > 25 feet	13
Pastures	
10 ground	7
11 aboveground	3
12 Aerial	3

<sup>a</sup>Numerical code for foraging zone.

total number of plant species visited by each of the hummingbird species. More details are presented elsewhere (Wolf et al., In press). Three pairs of other species that forage for similar food items divide the habitat in terms of where each species searches for food. *Pezopetes* and *Pseliophorus* tend to divide the second-growth vegetation vertically with *Pseliophorus* foraging much more aboveground, whereas *Pezopetes* forages mostly on the ground. The two woodpecker species, *Melanerpes* and *Dendrocopos*, divide the habitat both vertically and in terms of size of branch on which they forage. *Dendrocopos* tends to forage lower and on much smaller branches than does *Melanerpes*. The two furnariids, *Pseudocolaptes* and *Margarornis*, are somewhat more subtle in the apparent mechanism of habitat division. Both forage in the same general zone and work the same trees. However, *Margarornis* forages principally on the trunks and branches searching for insects in the moss and lichens, whereas *Pseudocolaptes* searches for insects in the debris accumulated in epiphytes.

The foraging range and food taken must be coupled with ability to utilize disturbed environ-

ments that were predominant on the Cerro as a result of clearing of the forest. The relative numerical composition of the avifauna undoubtedly has changed markedly in the last 25 years, since the completion of the Pan American highway. It is not at all unreasonable to assume that all the common second-growth forms were present before the forests were cleared, but the relative numbers of these birds undoubtedly increased greatly since clearing commenced. At the same time, the abundance of forest birds probably has declined in the study area. The predominance at present of second-growth forms is clearly seen in the distribution of species in foraging zones (table 6). The greatest numbers of species forage in dense or open second-growth, although not so many forage on or near the ground in dense second-growth as in other zones in second-growth. The least commonly used foraging zones are inside the forest from the ground to about 25 feet and the frequency is much lower than recorded by either Miller or Slud from localities at lower elevations. In large part these forest-interior birds on the ground are frugivorous at low elevations. In the highlands climatic conditions are such as to reduce the diversity of trees until the forest is dominated by oaks. The acorns with a hard exterior are quite different from the fruit types normally utilized by tinamous, pigeons, etc. and may partly

account for the reduced avifauna. The lack of insectivorous birds at low heights in the montane forest interior probably reflects the general lack of insects in this zone, partly because of reduced primary production (Orians, 1969) and partly because the vegetation which is there probably is more resistant to insect damage than in second-growth areas. In other areas many of the low foraging insectivores are common in dense vegetation resulting from tree falls or small clearings made by man. Another group of species forage to varying degrees on insects that are flushed from the forest floor by army ants, which are missing from the highland forests.

#### BREEDING SEASONS

There are few data to substantiate the timing of breeding for any species. On the basis of gonad size, brood patches, presence of young, and carrying of food by the adults I have been able to postulate breeding periods or months in which breeding undoubtedly occurs for 34 of the 49 resident breeding species (table 7). The bulk of breeding occurs in April and May and is timed to coincide with the end of the dry season and the onset of the rains. A few species begin breeding in March and a few, primarily the nectarivorous species, breed in August through January. There was some indication that the frugivorous

TABLE 7  
Number of Species Breeding Each Month of the Year on the Cerro

Month	Number Breeding Species <sup>a</sup>	Principal Food(s) <sup>b</sup>			
		Insect	Fruit	Nectar	Seeds
January	2	—	—	2	—
February	3	—	—	1	2
March	10	8	6	0	3
April	22	20	10	0	3
May	19	16	6	0	2
June	4	3	2	—	—
July	2	2	1	—	—
August	1	—	—	1	—
September	1	—	—	1	—
October	1	—	—	1	—
November	1	—	—	1	—
December	2	—	—	2	—

<sup>a</sup> All species initiating laying during month; one species may occur in several months.

<sup>b</sup> One species may have more than one principal food type.

residents began breeding slightly earlier than did the foliage-gleaning insectivores, but documentation of this relationship requires more detailed information than I obtained.

#### LITERATURE CITED

- Blake, E. R.  
1958. Birds of Volcan de Chiriqui. Fieldiana: Zool., vol. 36, pp. 499-577.
- Carriker, M.  
1910. An annotated list of the birds of Costa Rica, including Cocos Island. Ann. Carnegie Mus., vol. 6, pp. 314-915.
- Colwell, R. K.  
1973. Competition and coexistence in a simple tropical community. Amer. Nat., vol. 107, pp. 737-760.
- Colwell, R. K., B. J. Betts, P. Bunnell, F. L. Carpenter, and P. Feinsinger  
1974. Competition for the nectar of *Centropogon valerii* by the hummingbird *Colibri thalassinus* and the flowerpiercer *Diglossa plumbea*, and its evolutionary implications. Condor, vol. 76, pp. 447-452.
- Fretwell, S.  
1972. Populations in a seasonal environment. Princeton Monogr. Popul. Biol. no. 5. New Jersey, Princeton Univ. Press.
- Gill, F. B.  
1973. Intra-island variation in the Mascarene White-eye *Zosterops borbonica*. Amer. Ornithol. Union Monogr., no. 12, 66 pp.
- Griscom, L.  
1932. Distribution of bird-life in Guatemala. Bull. Amer. Mus. Nat. Hist., vol. 64, pp. 1-439.
- Howell, T.  
1957. Birds of a second-growth rain forest area of Nicaragua. Condor, vol. 59, pp. 73-111.
- Hunt, J. H.  
1971. A field study of the Wrenthrush, *Zeledonia coronata*. Auk, vol. 88, pp. 1-20.
- Lloyd, J. J.  
1963. Tectonic history of the south Central-American orogen. In Backbone of the Americas. O. E. Childs and B. W. Beebe (eds.), Amer. Assoc. Petrol. Geologists, Memoir No. 2. pp. 88-100.
- MacArthur, R., H. Recher, and M. Cody  
1966. On the relation between habitat selection and species diversity. Amer. Nat., vol. 100, pp. 319-332.
- Marler, P., and D. Isaac  
1961. Song variation in a population of Mexican juncos. Wilson Bull., vol. 73, pp. 193-206.
- Marshall, J. T.  
1964. Voice in communication and relationships among brown towhees. Condor, vol. 66, pp. 354-356.
- Mayr, E., and W. H. Phelps  
1967. The origin of the bird fauna of the south Venezuelan highlands. Bull. Amer. Mus. Nat. Hist., vol. 136, pp. 273-327.
- Miller, A. H.  
1961. Molt cycles in equatorial Andean sparrows. Condor, vol. 63, pp. 143-161.  
1963. Seasonal activity and ecology of the avifauna of an American equatorial cloud forest. Univ. California Publ. Zool., vol. 66, pp. 1-78.
- Monroe, B. L., Jr.  
1968. A distributional survey of the birds of Honduras. Ornith. Monogr. no. 7, pp. 1-458.
- Moynihan, M.  
1962. The organization and probable evolution of some mixed species flocks of neotropical birds. Smithsonian Misc. Coll., vol. 143, no. 7, pp. 1-140.
- Orians, G.  
1969. The number of bird species in some tropical forests. Ecology, vol. 50, pp. 783-801.
- Otvos, I.  
1967. Observations on the feeding habits of some woodpeckers and woodcreepers in Costa Rica. Condor, vol. 69, pp. 522-525.
- Paynter, R. A., Jr.  
1960. Troglodytidae. In Check-list of Birds of the World. E. Mayr and J. C. Greenway, Jr. (eds.), vol. IX, pp. 379-440.
- Peeters, H. J.  
1962. Nuptial behavior of the Band-tailed Pigeon in the San Francisco Bay area. Condor, vol. 64, pp. 445-470.
- Pitelka, F. A.  
1951. Race names in the Central American jay, *Cyanolyca argentigula*. Jour. Washington Acad. Sci., vol. 41, pp. 113-115.
- Root, R. B.  
1967. Niche exploitation patterns of the Blue-gray Gnatcatcher. Ecol. Monogr., vol. 37, pp. 317-350.

- Sibley, C. G.  
 1957. The evolutionary and taxonomic significance of sexual dimorphism and hybridization in birds. *Condor*, vol. 59, pp. 166-191.  
 1968. The relationships of the "Wren-thrush," *Zeledonia coronata* Ridgway. *Postilla*, vol. 125, pp. 1-12.  
 1970. A comparative study of the egg-white proteins of passerine birds. *Peabody Mus. Nat. Hist., Bull.*, vol. 32, pp. 1-131.
- Skutch, A. F.  
 1944. Life history of the Quetzal. *Condor*, vol. 46, pp. 213-235.  
 1945. The migration of Swainson's and Broad-winged Hawks through Costa Rica. *Northwest Sci.*, vol. 19, pp. 80-89.  
 1954. Life histories of Central American birds. 1. *Pacific Coast Avif. No. 31*. Cooper Ornithol. Soc.  
 1960. Life histories of Central American birds. 11. *Pacific Coast Avif. No. 34*. *Ibid.*  
 1965. Life history of the Long-tailed Silky-flycatcher, with notes on related species. *Auk*, vol. 82, pp. 375-426.  
 1967. Life histories of Central American highland birds. *Publ. Nuttall Ornith. Club*, no. 7.
- Slud, P.  
 1960. The birds of Finca "La Selva," Costa Rica: a tropical wet forest locality. *Bull. Amer. Mus. Nat. Hist.*, vol. 121, pp. 49-148.  
 1964. The birds of Costa Rica. *Ibid.*, vol. 128, pp. 1-430.
- Stiles, F. G., and H. A. Hespenheide  
 1972. Observations on two rare Costa Rican finches. *Condor*, vol. 74, pp. 99-101.
- Tosi, J., Jr.  
 1965. Ecological map of Costa Rica, provisional edition. Tropical Science Center. San Jose, Costa Rica.
- Van Tyne, J., and A. J. Berger  
 1959. *Fundamentals of ornithology*. New York, J. Wiley and Sons. 624 pp.
- Wallace, G. J.  
 1965. Studies on neotropical thrushes in Colombia. *Publ. Mus., Mich. State Univer., Biol. Ser.*, 3, pp. 1-47.
- Wetmore, A.  
 1960. A classification for the birds of the world. *Smithsonian Misc. Coll.*, vol. 139 (No. 11) pp. 1-37.
- Weyl, R.  
 1956. Spuren eiszeitlicher Vergletscherung in der Cordillera de Talamanca Costa Ricas (Mittelamerika). *Neues Jahrb. Geol. und Paläontol.*, vol. 102, pp. 283-294.
- Williamson, F. S. L.  
 1956. The molt and testis cycle of the Anna Hummingbird. *Condor*, vol. 58, pp. 342-366.
- Wolf, L. L.  
 1969a. Breeding and molting periods in a Costa Rican population of the Andean sparrow. *Condor*, vol. 71, pp. 212-219.  
 1969b. Female territoriality in a tropical hummingbird. *Auk*, vol. 86, pp. 490-504.  
 [In Press.] Species relationships in the avian genus *Aimophila*. *Amer. Ornithol. Union Monogr.*
- Wolf, L. L., and F. G. Stiles  
 1970. Evolution of pair cooperation in a tropical hummingbird. *Evolution*, vol. 24, pp. 759-773.
- Wolf, L. L., F. G. Stiles, and F. R. Hainsworth  
 [In Press.] The ecological organization of a highland, tropical hummingbird community. *Jour. Animal Ecol.*
- Young, H.  
 1951. Territorial behavior in the eastern robin. *Proc. Linn. Soc. N.Y.*, nos. 58-62, pp. 1-37.













