

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 2549 OCTOBER 1, 1974

LESTER L. SHORT

Habits of Three Endemic West Indian
Woodpeckers (Aves, Picidae)

Habits of Three Endemic West Indian Woodpeckers (Aves, Picidae)

LESTER L. SHORT

*Curator, Department of Ornithology
The American Museum of Natural History
Adjunct Professor, City University of New York*

AMERICAN MUSEUM NOVITATES

NUMBER 2549, pp. 1-44, figs. 1-14

Issued October 1, 1974

Copyright © The American Museum of Natural History 1974

ISSN 0003-0082

Price. \$2.50

ABSTRACT

The Antillean Piculet (*Nesocittes micro-megas*), the Guadeloupe (*Melanerpes herminieri*), and Hispaniolan woodpeckers (*M. striatus*), little known, endemic West Indian woodpeckers, were studied during March, 1973. The piculet ranges widely on Hispaniola, in suitably dense undergrowth, mainly gleaning for insects more like a passerine species than a woodpecker. Five calls are described, including the Piping Call employed in antiphonal calling. Meager data on displays are presented. I advocate the tribal separation of monotypic *Nesocittes* (in the Nesocittini) from other piculets (Picumnini). The Guadeloupe Woodpecker, endemic to Guadeloupe, and the only picid in the Lesser Antilles, occurs in pairs mainly in western Guadeloupe. It forages diversely for insects and probably fruits. Regular drumming and demonstration drumming and Wa and Chur calls are described and compared with those of other melanerpine species. The Guadeloupe Woodpecker may be related to *Melanerpes portoricensis* or to continental species of the *M. chrysarchus* complex. Sharing Hispaniola with the Antillean Piculet is the much larger Hispaniolan Woodpecker, a variably social species that partly nests colonially and even may engage in communal nesting activity (nest sharing by birds other than a pair). The Hispaniolan Woodpecker's varied vocalizations are described. Demonstration drumming occurs sporadically near the nest site. Bowing and Swinging are the two most conspicuous displays, rendered separately and in different circumstances. A Bill Directing Posture, a Bill Raised Posture, a gliding Dihedral Flight Display, and Courtship Feeding also are described, and Wing Flicking possibly is a display. Up to 19 nests were found in a colony, but most Hispaniolan Woodpeckers probably nest in solitary pairs or in small, loose colonies of two or three pairs. Large colonies often are destroyed by humans who consider the birds a pest because of their depredations on fruits. Within colonies pairs defend variable areas near their nest. Helpers occurred at several nests. Communal nesting tendencies are indicated by one bird feeding at two nests, and by lack of territoriality between some pairs nesting almost side-by-side. Young are fed both indirectly by regurgitation (probably of small insects), and directly (held in the bill), involving large insects and berries. Courtship feed-

ing birds also utilize both feeding methods. The taxonomy of this woodpecker is assessed on its behavior, ecology, zoogeography, and external morphology. The evidence derived from these, points to the melanerpine relationship of this picid, contradicting evidence (Olson, 1972) from a few functionally obscure anatomical features purported to indicate that it is not so related. A brief consideration of the melanerpine woodpeckers, including the genera *Xiphidiopicus*, *Melanerpes* and *Sphyrapicus*, provides a framework for discussion and treatment of the Hispaniolan Woodpecker within *Melanerpes* (*M. striatus*).

INTRODUCTION

Twelve species of woodpeckers occur in the West Indies. Of the 11 resident species, three (on Cuba, the Bahamas, and adjacent islands) range into North America, and eight are endemic in the West Indies. During March, 1973, I was able to study the Antillean Piculet (*Nesocittes micromegas*), Hispaniolan Woodpecker (*Melanerpes striatus*), and Guadeloupe Woodpecker (*Melanerpes herminieri*). The piculet represents a monotypic genus with no close relatives; it is confined to Hispaniola and adjacent small islands. The Hispaniolan Woodpecker, also restricted to Hispaniola, has been separated from the genus *Melanerpes* by several authors (most recently Olson, 1972), and placed in the monotypic genus *Chrysarpes*. The Guadeloupe Woodpecker is the only woodpecker on Guadeloupe, and the only picid in the Lesser Antilles. Very little is known of the habits of the piculet and the Guadeloupe Woodpecker, and sparse behavioral data are available only from casual observations. The Hispaniolan Woodpecker has been studied, mainly ecologically (Selander and Giller, 1963; Selander, 1966; Wallace, MS), but its behavior is little known (for aspects of its natural history see Wetmore and Swales, 1931, pp. 291-295). These three woodpeckers are the most distinctive of the West Indian Picidae, with the exception of the Cuban *Xiphidiopicus percussus* and perhaps *Colaptes fernandinae*.

The present report treats the behavior and some aspects of the ecology of these three wood-



FIG. 1. Pine forest, Baorucu Mountains of southwestern Dominican Republic, elevation 4100 ft. Parts of forest bearing dense low shrubs, as shown here, support scattered Antillean Piculet pairs. Hispaniolan Woodpeckers occur throughout the pine forests, but population is not dense.

peckers, following methods discussed in my previous woodpecker studies (Short, 1970a, 1971b, 1971e, 1972, 1973a, 1973b). I concentrate upon the vocalizations, displays, foraging habits, individual and pair interactions, and, to some degree (Hispaniolan and Guadeloupe woodpeckers), the nesting habits of these woodpeckers. Some taxonomic inferences are drawn from these data. I hope that this presentation will stimulate workers to undertake further investigations of these and comparative studies of other West Indian woodpeckers.

In field observations I used 10 by 50 field glasses. I obtained tape recordings with a Uher 4000-L Report tape recorder and a Phillips directional microphone, the recorder operating at 7.5 inches per second. Representative vocalizations and instrumental signals were analyzed with a Kay Electric Company Sonagraph (sound spectrograph), using both narrow and wide band-pass filters. Available for comparison were specimens

of all West Indian woodpeckers and their relatives, examined in the American Museum of Natural History; I have seen additional material at many other museums in North America and Europe.

I am indebted to many people for their suggestions and diverse assistance. Field studies in the Dominican Republic were facilitated especially by Mr. and Mrs. Donald Dod of Santo Domingo. Study sites on Guadeloupe were suggested by Mr. Robert Guth. Various helpful comments on aspects of field work were provided by Mr. James Bond, Dr. Jean Delacour, Dr. Michael Gochfeld, Mr. Fred Sibley, Dr. John Terborgh, Dr. Charles Vaurie, and Dr. John Weske. Dr. Wesley Lanyon kindly read the manuscript, offering beneficial suggestions. Miss Marianna Neighbour typed the manuscript in her usual efficient manner. The staff of the Photography and Graphic Arts departments of the American Museum of Natural History expertly rendered the charts and



FIG. 2. Thorn forest and mixed thorn forest and desert northeast of Cabo Rojo, at 300 ft. elevation, southwestern Dominican Republic. Low population of Hispaniolan Woodpeckers and well-scattered pairs of Antillean Piculets occupy this habitat.

photographs. Background information was secured on earlier trips to the Neotropics, supported by the National Science Foundation (grant GB-5891). The Edward John Noble Foundation supported field studies on St. Catherines Island, Georgia, where I obtained tape recordings used for comparison herein. I am grateful to all of these individuals and agencies.

ANTILLEAN PICULET

The Antillean Piculet shares the island of Hispaniola with the much larger Hispaniolan Woodpecker (the Yellow-bellied Sapsucker, *Sphyrapicus varius*, winters on Hispaniola, hence three picids occur at that season). It is distributed throughout the island in suitable woodlands, namely those with a rather dense understory. In the Baoruco Mountains the piculet ranges up into the pine forests (fig. 1), to an elevation of at least 5800 feet, and down into

lowland thorn forest (fig. 2), but is most common in dense second growth at intermediate levels, for example, about Las Mercedes at an elevation of 1600 feet (fig. 3). It frequents brushier portions of the mixed desert scrub and thorn forest throughout the area south of the Baoruco Mountains. Scattered pairs occur in low, second-growth forests of limestone areas southeast of La Romana, and in wet, wooded hills between Sabana de la Mar and Seibo (figs. 4, 5) in the northeastern region, and the species is in low tangled forest with meandering small streams (fig. 6) along the Comate River northeast of Santo Domingo (12 miles north-northeast of Bayaguana). The studies reported here were conducted mainly near Las Mercedes, and along the Comate River.

This bird is by far the largest of piculets (subfamily Picumninae), and it is the only West Indian piculet. Un-woodpecker-like to the same degree or more so than the Old World wrynecks (*Jynx*, subfamily Jynginae), the Antillean Piculet



FIG. 3. Dense second-growth woodland at 1600 ft. elevation near Las Mercedes in southern foothills of Baoruco Mountains, Dominican Republic. Antillean Piculets were common in this habitat, and Hispaniolan Woodpeckers occurred wherever there were larger trees.

hops through bushes and low trees, and zigzags its way along branches without the usual woodpecker (and piculet) clinging. Indeed, in the field it is like a passerine species, almost vireo-like in demeanor. The bird's flight is fast and direct, without the undulations of many woodpeckers. In March when I was in Hispaniola the piculets were highly territorial, and there is no evidence for social breeding or flocking at any time of the year.

Ecology and Foraging Behavior

This piculet favors woodlands with tangled undergrowth and vines, especially in the vicinity of streams. Although it may wander into adjacent orchards and other wooded cultivated areas, it ordinarily shuns most fields and plantings such as palms. Within pine forest and more desertic arid scrub it is uncommon and restricted to local

areas of dense vegetation. Open forests are utilized only where adjacent to dense woodland. One seeks the piculet in places having vines and creepers, and dense low foliage where it is difficult for humans to walk. In such habitat the piculet may be found at various elevations and in diverse settings (e.g., in tangles along mountain streams amid pines, in thorn forest, and in dense second-growth bordering pastures). The bird moves about, usually alone or loosely in pairs, foraging over part of a tree or sapling, then flying rapidly to either a nearby site or one far off.

Foraging resembles that of a gleaning wood-warbler, vireo, or tanager, for it picks most of its food from the surface of bark and leaf bases. Occasionally the piculet taps sporadically, without bracing its tail or body against the surface of the tree, and when it taps it often perches crosswise on a branch. Its movements are not like those of a woodpecker or other piculets, which move generally parallel to a branch or trunk,



FIG. 4. Forest in wet zone along Sabana de la Mar-Miches road, near sea level, northeastern Dominican Republic. Hispaniolan Woodpeckers are common in pairs, and Antillean Piculets are scarce in undergrowth of such forests.

but, rather, the Antillean Piculet hops zig-zag, perching diagonally to the branch and often alternating direction with each hop. When tapping with its bill, the blows are weak and lateral in direction. In addition to gleaning and occasional tapping, probing frequently occurs about fruits and flowers, the bases of pine needles, and at leaf bases. Both sexes foraged similarly during my observations (females are larger and longer billed than males, and may feed somewhat differently at some time of the year). The birds move rapidly along a branch or vine, perhaps drop to a lower branch, move up into the crown of the tree, pause, then fly off. Their rapid movements are compensated for by occasional pauses, sometimes for several minutes, especially after a flight. These pauses, the rapid foraging movements, frequent flights, and often the dense vegetation make observation very difficult.

Sites used in foraging include vines, branches and branchlets of bushes and trees, weed stalks,

and tip leaflets and leaf clusters at all heights. Although this piculet ranges into the foliage of tall trees, it normally is found in the understory of forests (from near the ground to the tops of saplings, about 0 to 8 meters) or throughout second growth or thorn scrub. Vines, small branches, and branchlets are used more frequently than trunks of trees or saplings. The diet appears to be mainly insects, but some fruit is utilized. Wetmore and Swales (1931, p. 298) listed a centipede, ants, several earwigs, and many small beetles in the stomach of a Hispaniolan specimen, but (p. 299) only "seeds and pulp of some fruit" as stomach contents of a Gonave Island bird.

Vocalizations

Drumming and other instrumental signals are unknown in the Antillean Piculet. At least five vocalizations were heard and recorded on tape,



FIG. 5. Cutover forest near Miches along Sabana de la Mar road near sea level, northeastern Dominican Republic. Hispaniolan Woodpeckers are common to abundant and Antillean Piculets are rare in such habitat.

and these are described in detail for the first time.

Prit Call (fig. 7A). A sharp, mechanical note, prit, commonly heard from disturbed Antillean Piculets. Expressing mild alarm, this call often introduces or is otherwise associated with the other common call, the Piping Call. Sonagrams indicate that the Prit Calls are about 0.02 second in duration, in the form of a tight, inverted V, with a peak at 3 to 4 kilohertz, and another (harmonic tone), about equally emphasized, at 6 to 8 kilohertz. This form of note is frequent in woodpeckers (and many other birds), usually as a call note.

Prew Call (fig. 7A). Less frequent and longer, this call seems to express alarm, but is uttered usually in the presence of another piculet. About 0.1 second in duration, the call is in the form of a broad, inverted U, with a series of about five peaks between 2.5 and 5 kilohertz. The note somewhat resembles the Piping Call notes, but

shows more overtones, and is given singly or in very loose, irregular series.

Wiii Call (fig. 7A). A series of up to six (usually four to six) vertical notes given at about 14 per second. The weak, diffuse notes show vague, multiple peaks at diverse frequencies over a broad range. The notes are pritlike, but weaker and with ill-defined peaks; also they are delivered in series lasting one-third to one-half second. This low call is heard from piculets that approach each other closely, as when they (pair, presumably) are in the same bush or tree. Its function is unknown.

Yeh Call (fig. 7A). An almost continuous series of notes uttered by one or both of two male Antillean Piculets that had fallen to the ground at my feet, their legs tightly bound together, calling "yeh-yeh-yeh-yeh." This perhaps is equivalent to the Wicka Call of certain woodpeckers (see Short, 1971b, 1972), being somewhat similar in sound and occurring in a similar context

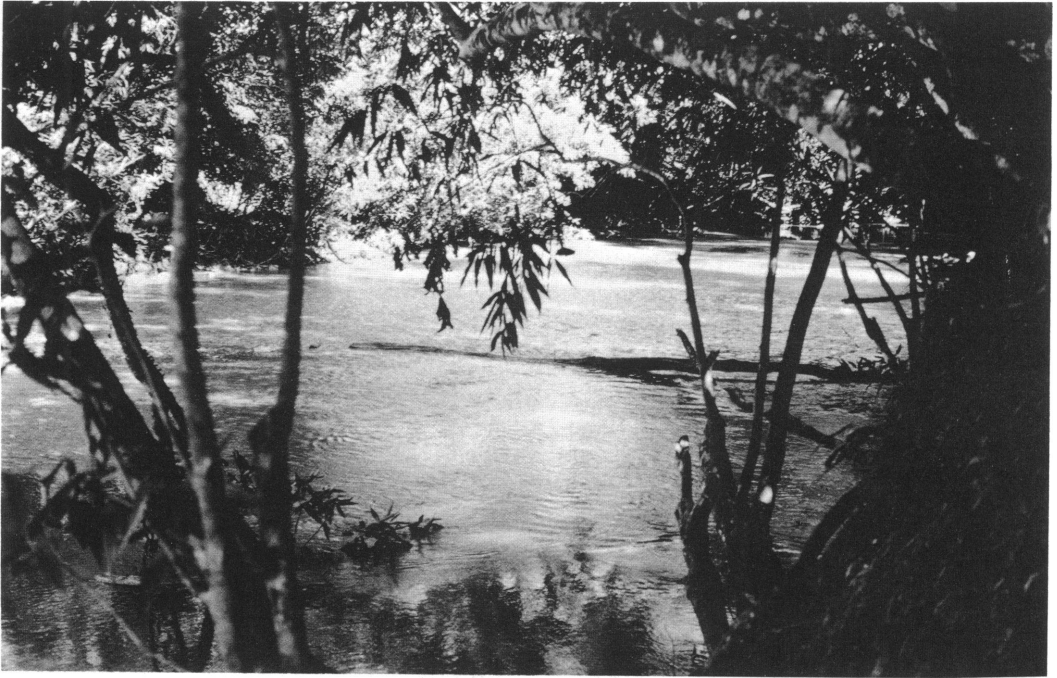


FIG. 6. Comate River, 12 miles north-northeast of Bayaguana (northeast of Santo Domingo), elevation 750 ft., Dominican Republic. Dense, tangled undergrowth in partly cutover forest amid hills provides favorable habitat for Antillean Piculets, which were common at the time of my visit, as were Hispaniolan Woodpeckers. The piculets especially favored areas beside the stream, perhaps because the undergrowth is densest there.

with a similar associated display (see below). The notes are long (one-quarter of a second), and are composed of several elements having multiple peaks between 1 and 8 or more kilohertz, but especially between 1.5 and 4.0 kilohertz. One continuous series lasted 4.5 second, during the same encounter. The composite call somewhat resembles woodpecker begging calls and Wicka Calls. Obviously an aggressive vocal display, the Yeh Call ought to be studied carefully and compared with woodpecker calls.

Piping Call (fig. 7B, C, D). The piculet's Spanish name, flautero, comes from this loud call—a series of two to eight notes, for up to three-quarters of a second. The tempo of the notes varies from 11 to 14 per second. The calls show considerable variation, but most consist of a group of nearly identical notes followed by a longer, lower pitched, but similar note (fig. 7B).

Often the initial note and sometimes the terminal note are short and low-pitched resembling Prit Calls (fig. 7C). Indeed one or a series of Prit Calls often precedes and follows a Piping Call (fig. 7C). The inverted, U-shaped notes have several peaks, the emphasized peak being between 2 and 3 kilohertz. In some calls the notes diminish in duration and pitch during the call. Antiphonal calling (fig. 7D) occurs frequently; a bird calls, and its mate (or another bird) responds in 0.2 to 0.5 second. Occasionally, apparently near territorial borders, as many as four birds may indulge in a calling bout, the sound of which carries a great distance. A series of two or three calls, each answered by a nearby mate, often elicited a distant response or two, or even a distant antiphonal calling bout. Antiphonal calling is not known otherwise in the Picidae. The Piping Call serves as a location call and in territorial proclamation,

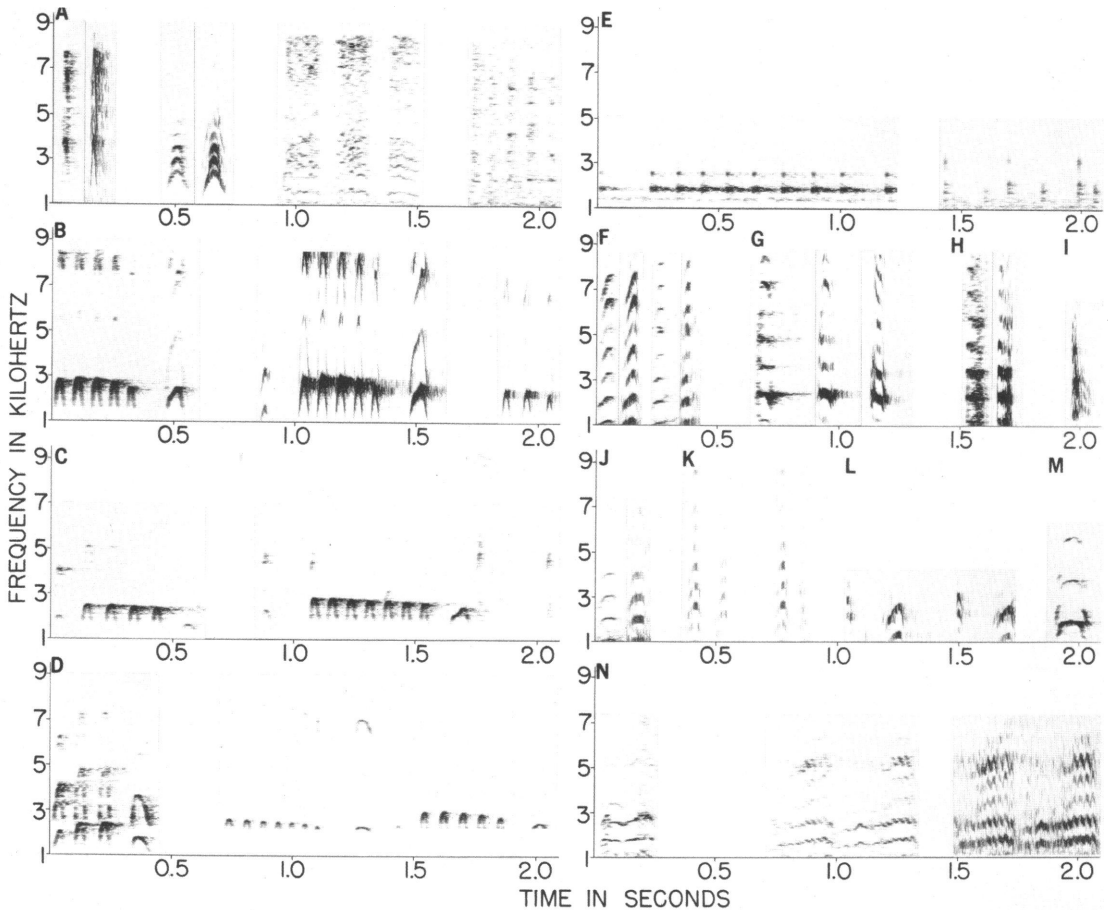


FIG. 7. Sound spectrographs of vocal and instrumental signals of *Nesocittes micromegas*, *Melanerpes herminieri*, *M. striatus*, *M. portoricensis*, *M. radiolatus*, and *M. carolinensis*. A. Prit Call followed by same call, WB, then Prew Call, same Prew Call WB, then 3 consecutive Yeh Calls, and finally 5 notes of a Wiii Call, all of *Nesocittes micromegas*. B. 6-note Piping Call followed by the same call (except for inclusion of an initial, low Prit Call), WB, and then an abortive, 3-note Piping Call lacking a terminal long note, WB, all of *N. micromegas*. C. Variant Piping Call with introductory pritlike note and very weak terminal note, followed by 8-note Piping Call with background (4 tall notes) Prit Calls of a second bird, both calls of *N. micromegas*. D. Variant 4-note Piping Call, then 2 Piping Calls delivered antiphonally, all of *N. micromegas*. E. 10-beat drumming burst of *Melanerpes herminieri*, followed by mutual tapping of a pair (low-pitched beats of one bird, high-pitched beats of the other) of *M. herminieri* at a presumed nest (please note that frequency for E is one kilohertz below that indicated). F. 2 Wup Calls of *M. striatus*, each followed by the same call, WB, showing variation in this call (compare with G, H, I). G. Pep Calls of *M. portoricensis*, one call followed by the same call, WB, then another example, WB. H. Chut Call of Jamaican *M. radiolatus*, then same call, WB (G and H from recordings by G. B. Reynard). I. Chup Call of *M. carolinus* from coastal Georgia, WB. J. Ta (or Wa) Call of *M. striatus*, then same call, WB. K. 2 consecutive double notes of Ta-a (Wicka) Call of *M. striatus*, WB, compare with next and previous. L. Wicka Call of *M. carolinus*, WB, from coastal Georgia. M. Preep Call of *M. portoricensis* (from recording by G. B. Reynard). N. Intermediate Ta-Waa call of *M. striatus*, followed by 2 consecutive Waa or Chur Calls of *M. striatus*, then the same Waa Calls, WB. Sonagrams are narrow band unless indicated wide band by WB.

that is, a song. The significance of the variation encountered may relate to these functions. The notes of the Piping Call are similar in form to many woodpecker rattle-like notes (see e.g., Short, 1971b, 1972, 1973b), but they are more musical in quality than any woodpecker sounds I have heard.

Displays and Other Behavior

The visual displays of the Antillean Piculet are virtually unknown. A close look at an encounter between two males provides the only details available. The males were seen in a sapling about 5 meters above ground, face to face at a distance of a half-meter. Both attacked simultaneously giving Yeh Calls, and clasped each other with their feet and tumbled to the ground. There was a brief flurry of wing and body movements, then a pause, as they lay clasping each other lying on their side with one bird apparently holding the other a trifle lower and pushing it into the ground. The dominant male raised its head, with bill pointed slightly above the horizontal, and then swung its head far to one side, paused, swung to the other side, and repeated the performance five or six times calling "yeh-yeh-yeh." Both may have called as I heard an almost continuous Yeh Call for five seconds or so (the birds were no more than 3 meters from my feet, and I had a clear view). The piculets then sped away in opposite directions. The Swinging Display resembled that of various woodpeckers but was more deliberate. Head positioning postures, such as perhaps a Bill Raised Posture (Short, 1971b), seem likely to occur as agonistic displays. I saw other brief encounters, but the birds were not visible, or they flew away rapidly.

Other habits, including nesting, are poorly known. Nests of which I have read, and those I have seen (the small holes could have been excavated by no other bird) all were below 5 meters, and often 1 to 2 meters from the ground. The five old cavities I ascribed to this piculet were in very rotten stubs and fence posts. Eggs are known to number two to four (Wetmore and Swales, 1931). Nests are solitary, not clustered. The feeding and care of the young, and occurrence and duration of family parties following nesting are unreported. It would be of interest to

know if the piculets remain territorial throughout the year, or are somewhat social and nonterritorial following the breeding season. Certainly they are highly territorial prior to nesting, although details of their territoriality (e.g., do both sexes defend the territory, and mainly against members of the same sex?) remain to be elucidated. It may be noteworthy with regard to territoriality that females are larger than males (unpublished data, all measurements) in this piculet.

Systematic Comments

The Antillean Piculet is placed in the monotypic genus *Nesocittes* apart from other piculets by virtue of its curved culmen with nostrils close to it, very short gonys, and long outer primary (Ridgway, 1914). Its coloration, green above with ventral streaks and yellow and orange crown spots is not approached by other piculets, and it differs from them in its much greater size. The soft tail and holaspidean planta tarsi resemble those of other piculets and the wrynecks (*Jyn-ginae*), and contrast with those of woodpeckers.

Antillean Piculet behavior is distinctive and sets it apart from other piculets. The bird infrequently taps as it forages, perches at a right angle to branches, and its movements bear some (probably superficial) resemblance to those of wrynecks. Certainly, the Antillean Piculet does not show the distinctive orientation (in landing, perching, moving about) to trunks and branches of trees that characterizes woodpeckers and piculets. The songlike quality of the Piping Call, and antiphonal singing of the bird also are distinctive. The Antillean Piculet does not drum as do most piculets and woodpeckers.

There is a possibility that *Nesocittes micromegas* is not related directly to the other piculets, that is, that the Picumninae is polyphyletic. *Nesocittes* may be a distant relative of, for example, the wrynecks. At any rate, *Picumnus* and *Sasia* (including *Verreauxia*), the other piculets, are interrelated closely, and *Nesocittes* appears to be at best only distantly related to them. Pending further comparative study of *Nesocittes* with other Picidae, I propose tribal separation of this genus (*Nesocittini*) apart from the other piculets (*Picumnini*) within the picid subfamily Picumninae.



FIG. 8. Forest edge and cultivated fields, 3 miles northwest of Vernou, Basse Terre, Guadeloupe, at 500 ft. elevation. Guadeloupe Woodpecker was common along the forest edge at the time of my visit.

GADELOUPE WOODPECKER

The Guadeloupe Woodpecker is the only species of its family in the Lesser Antilles, and is restricted to wooded areas of Guadeloupe Island. It is found from sea level up to an elevation of 3000 feet, but is absent from all but a few wooded locations (R. W. Guth, personal commun.) on the larger eastern island, Grande Terre. On the mountainous western island of Basse Terre it is common in hills back from the eastern shore, and it extends locally through the forested highlands and occasionally along the dry western slopes (e.g., above Marigot, R. W. Guth, personal commun.). It is not particularly shy, but is inconspicuous generally except when tapping or drumming. Birds frequently are seen flying across the roads in favored localities. Fruits form part of the food, and are sought in the tops of appropriate trees, but most foraging occurs along the trunks and major branches of trees between 8 and 20 meters from the ground. The sexes are

similar and cannot be distinguished in the field. Most of the data reported herein is based on about four pairs studied about 4 km. northwest of Vernou, on eastern Basse Terre, Guadeloupe (figs. 8, 9).

Ecology and Foraging Behavior

On the forested eastern slopes of Basse Terre I found the Guadeloupe Woodpecker, or *Tapeur* as it is known locally, common between elevations of 100 to 700 meters (fig. 10). It forages in adjacent cultivated areas that bear trees. Foraging sites include trunks, branches, and larger branchlets of trees, and fruit clusters in trees. Birds probe and tap, usually briefly along a branch, then fly to a site in another tree, continuing in this way from tree to tree. Visits to particular trees appear to be erratic, but fruiting trees may be visited regularly. I suggest that a site visited in a tree is used as an investigative survey point,



FIG. 9. Forest and tree stub about which Guadeloupe Woodpeckers were active, 4 miles northwest of Vernou, Basse Terre, Guadeloupe, at elevation of 600 ft. Several holes can be seen in the stub (V-arrows, center), the one on the left side (lower arrow) of the stub about in the middle of the photograph being that entered by a pair of woodpeckers in late March, 1973.



FIG. 10. Hill forest at an elevation of about 1700 ft., approximately 15 miles west of Vernou, Basse Terre, Guadeloupe. Scattered pairs of Guadeloupe Woodpeckers occupy this forest, especially feeding at arboreal bromeliads (center of photograph) and on *Cecropia* trees (at lower left).

from which the woodpecker scans adjacent parts of the tree, in addition to foraging actively. If fruit or other foods are found, these may be utilized at length, if not, the woodpecker confines

its activities to one site in the tree, and departs very soon.

One woodpecker foraged in five trees in seven minutes, and it did not tap within that time. It

paused frequently, appressing its body closely to the bark. At one tree it hung from a large blackish fruit, apparently unripe, that it examined briefly. Another woodpecker worked in one tree at a single site, tapping repetitively but weakly, and removed a large larva after which it flew to another tree. Most feeding seems accomplished by gleaning, probing, and tapping, in that order, and more on branches than on tree trunks. Presumably the woodpecker concentrates its foraging on fruits of certain kinds when these ripen. Danforth (1939, p. 33) remarked on the diet of the Guadeloupe Woodpecker based on analysis of four stomachs. He found a single seed and many insects, mainly cerambycid beetles and their larvae, and other Coleoptera, yielding a diet of 93 percent insects and 7 percent plant foods.

The flight of this picid across large open areas is less undulating than that of many woodpeckers, showing resemblance to the flight of such melanerpine species as *M. candidus* and *M. lewis* (Short, 1970a, p. 10).

Instrumental and Vocal Signals

This woodpecker employs both instrumental and vocal signals. Its drumming (fig. 7E) is loud, and rather slow, with a tempo of nine to 14 beats per second. Five tape-recorded bouts lasted 0.85 to 1.31 seconds, and contained 10 to 16 beats. The interval between beats varied from 0.07 to 0.11 second for regular notes, but the five drums recorded on tape (and others that I heard) contained either a delayed beat or (twice) two, or an initial beat issued before the others, or both. The "delayed" beats showed 0.03 to 0.06 second more time between them and other, regular beats than the duration between beats in the latter category. Other melanerpine woodpeckers drum more rapidly, as, for example, *M. erythrocephalus* (18 to 23 beats per second), *M. carolinus* (18 to 20 beats per second), and *M. radiolatus* (16 to 18 beats per second). This drumming seems to have a territorial proclamation function, but perhaps also acts as a location signal in mated birds.

Demonstration drumming ("tapping" ordinarily is used, but I would restrict tapping to the use of the bill in foraging) occurred on several occasions, twice by an incoming bird as the second bird was in the possible nesting cavity. The drum-

ming beats are given at four to six beats per second. They are relatively less strong than regular drumming beats, and number four to seven beats per burst. On at least two occasions the apparent pair drummed mutually, one bird within the cavity and the other outside. One such bout was recorded on tape (fig. 7E), the stronger beats of the outside bird numbering seven in 1.68 seconds (4.2 beats per second), and the weaker beats of the inside bird numbering six beats in 1.12 seconds. Demonstration drumming is known in other melanerpine woodpeckers, as, for example, *M. carolinus* (Kilham, 1958) and *M. erythrocephalus* (Kilham, 1959). Presumably it functions reproductively (e.g., in synchronization of breeding, pair maintenance).

I heard and recorded two vocalizations on tape. The Wa Call is a low series of notes, rendered "wa, wa, wa" or "wu, wu, wu" in my notes, and uttered when two birds are close together, or by one woodpecker as it flies into the nest when the other Guadeloupe Woodpecker is already there. Unfortunately, these notes were too weak to allow illustration of their sonagrams. There are two versions of the notes, a shorter ta version, and a longer wa version. The ta notes have a tall, diffuse form on sonagrams, with emphasis between 0.5 and 7 kilohertz, but especially from 0.8 to 2 kilohertz. These notes are 0.03 to 0.05 second in duration. The wa notes are 0.05 to 0.075 second in duration, and are similar to ta notes but tend to show vague peaks at 1.0 to 1.3 kilohertz. Three calls recorded on tape took 0.9 to 1.55 seconds, and contained seven to nine notes. The delivery is at six to eight notes per second. Three calls show mixed notes or, in one case, only wa notes. This call appears to represent an agonistic or agonistic-reproductive vocal display, perhaps a form of the Wicka Call (Short, 1971b, 1972). It is difficult to compare these notes with those of other species, but the Ta or Wa Call of *M. striatus* (fig. 7J) and wik notes of the Wicka Call of *M. carolinus* (fig. 7L) seem generally similar.

Various species of *Melanerpes* utter Chur Calls, and indeed these calls are characteristic of that genus. I heard the Chur Call of *herminieri*, a loud, usually repetitive "ch-arrgh," commonly in the area where I studied this woodpecker. Series of three to eight Chur Calls (fig. 11C, E) were

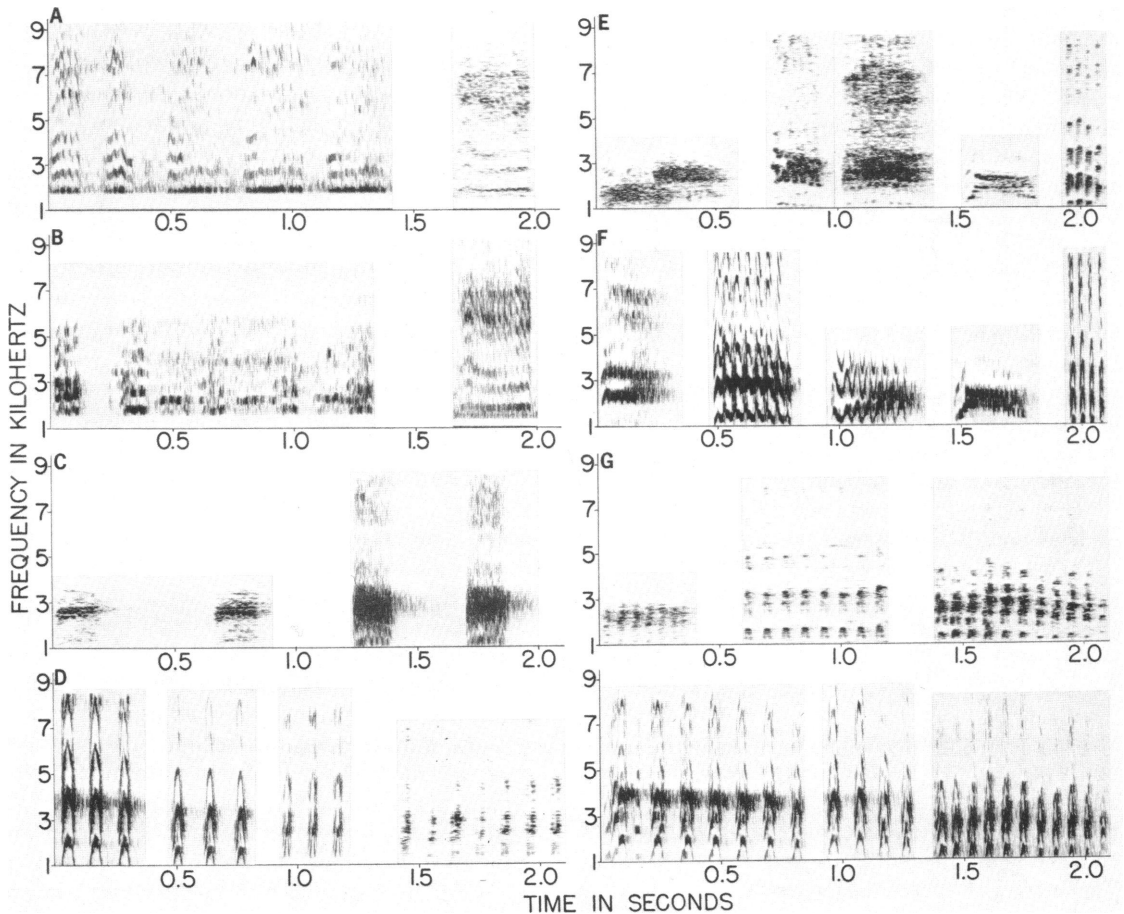


FIG. 11. Sound spectrographs of some melanerpine woodpecker vocalizations. A. Series of Waa Calls between Rattle Calls of *Melanerpes striatus* (compare with B), WB, followed by single Waa Call (note that frequency of A and B is 1 kilohertz lower than indicated). B. Series of low Waa Calls of *M. superciliaris* from Grand Cayman Island, WB (recording provided by G. B. Reynard), followed by same Waa Call of *M. striatus* shown at end of A, above, but WB. C. Last 2 consecutive Chur Calls of a series of 5 calls by *M. herminieri*, followed, WB, by calls 2 and 3 of an 8-call series of Chur Calls of *herminieri*. D. Parts of Slow Rattle Calls of *M. striatus*, first 3 notes from longer noted, higher pitched call, then 3 from a shorter noted call, and 3 notes from a short-noted, low pitched call, all WB, then 7 notes from same Slow Rattle Call as last 3, short notes. E. Simultaneous Chur Calls of pair of *M. herminieri* (notice lower pitch of first call, see text) followed by shorter and longer Chur Call of Jamaican *M. radiolatus* (recording provided by G. B. Reynard), then a Kweer Call of *M. erythrocephalus* from Georgia, and finally four-noted Bddt Call of *M. striatus* (see F). F. 5 calls, all WB, of Jamaican *M. radiolatus* (Chur Call, compare with A and B), *M. superciliaris* (Chur Call, Grand Cayman, these first 2 calls obtained from recordings by G. B. Reynard), *M. carolinus* (Chur Call, Georgia), *M. erythrocephalus* (Chur Call, Georgia), and *M. striatus* (Bddt Call, see E). G. Chur Call of *M. portoricensis* (recorded by G. B. Reynard), part of Moderate Rattle Call of *M. striatus* (see D), and 11-note Fast Rattle Call of *M. striatus* (see H below). H. All WB are an intermediate, 7-noted Slow Rattle-Long Call (compare with D), a mixed Moderate Rattle and Long Call (contains 4 notes, first two rattle notes, last 2 open V Long Call notes), and then same Fast Rattle Call shown at end of G, above, all of *M. striatus*. Sonagrams are narrow band unless indicated wide band by WB.

uttered at intervals by foraging birds, but especially near the nest site. Often one bird answered another, as when both members of a pair were near the nest. The notes are variable in length, from 0.18 to 0.55 second, including the tail of sound extending beyond them. Each call consists of a cluster of as many as 11 or even 13 vaguely peaked, diffuse elements at frequencies between 0.8 and 3.5 kilohertz. The tempo of calls varied from 0.9 to 2.17 per second. Few series were recorded in their entirety, for there usually was no warning that a call would be emitted. A full eight-call series lasted 3.68 seconds, the fastest series recorded on tape. Other series had a duration of 3.95 seconds (seven notes), 4.36 seconds (five notes), 4.57 seconds (five notes), and 4.73 seconds (five notes), and a few of more than five seconds long were heard. Some series diminished in tempo through the calls, but others did not.

There is evidence of a sexual difference in the pitch of Chur Calls, as members of one pair showed a consistent difference in this parameter. One woodpecker of this pair called at a higher frequency, with emphasis at 2 to 3 kilohertz, and the other at a lower frequency, with major emphasis at 1 to 2 kilohertz (fig. 11E). Whether or not such a difference generally holds within pairs remains to be determined.

The Chur Call of *herminieri* resembles the more diffuse-noted Chur Calls of such species as *radiolatus* (fig. 11E, F), and to a lesser extent *erythrocephalus* (Kweer Call, fig. 11E), rather than the Chur Calls of *superciliaris* (fig. 11F) and *carolinus* (fig. 11F), and the churlike Waa Call (fig. 11A, B) and Bddt Call (fig. 11E, F) of *striatus*. The last group of calls have discrete, connected notes with strong overtones, as does the Chur Call of the related Yellow-bellied Sapsucker (*Sphyrapicus varius*). The Chur Call of *herminieri* most resembles that of *radiolatus*, showing notes of about the same duration, a similar variation in duration of the notes, and notes of approximately the same frequency. Differences from the more diffuse calls of *radiolatus* include the weaker, more vague elements in calls of *herminieri*, which also lack overtones or have them but weakly developed.

Territorial proclamation and location functions are ascribed to the Chur Call of *herminieri*. It is likely that both sexes use this call in

territorial proclamation, and that members of a pair maintain contact with this vocalization.

Displays and Other Behavior

Several displays observed in late March remain to be investigated in detail. Visual displays included a Bill Raised Posture, Head Swinging, and Bowing. The Bill Raised Posture may be incorporated in Head Swinging, or it may be used separately, as at the end of a bout of Head Swinging. It consists of the holding of the bill upward from the horizontal, facing toward an antagonist. Head Swinging is a display involving side-to-side, slow movements of the head, with a brief pause at each end of the swing. The bill was held in a raised position during this display, which twice was directed at me, and once at the apparent mate of the displaying bird.

Bowing is an up-down movement of the head, usually repeated three or four times, but with a pause between bows. No swinging or tail spreading accompanied this display, which was given at the presumed nest cavity usually with an associated Wa Call. An incoming bird Bowed its head into the cavity on at least three occasions, and twice more as a mutual display to its mate within the nest. On one occasion, after Bowing to the bird within the nest, the woodpecker outside the nest passed food into the bill of its mate. This appears to be an example of courtship feeding.

These displays seem similar to those of other melanerpine species such as *M. cruentatus* (Short, 1970a).

Much activity centered about the presumed nesting cavity, but I was unable to establish the stage of breeding under way at the time of my visit. The cavity was oval at the entrance and much larger than necessary to admit the woodpeckers. It was 10 meters up a dead stub situated in the forest along a partly cleared new road. The cavity was the lowest of seven holes in the stub; at least one of these appeared to be fresh, and perhaps represented the roosting hole of the female. I was unable to establish which bird was in the nest nightly but one woodpecker was in the "nest" cavity on two mornings at daybreak. On March 29 a woodpecker was within the cavity at 06:00, and remained there as the sky became

brighter. At 06:40 the second bird arrived, displaying (Wing Spreading), and the other bird came out. Both Bowed and called (Wa Call) then flew. At 07:00 one bird returned and entered the cavity from which it gave a Chur Call at 07:10. At 07:30 the second bird returned, displayed, then fed the bird within the nest. Then the newly arrived woodpecker left the area. The bird in the nest left at 07:40. Both birds uttered Chur Calls nearby at 07:50. Another brief display occurred when both birds arrived at the nest at 08:30, then left. Other entries into the nest occurred sporadically through the day.

Nothing is known of the nesting of the Guadeloupe Woodpecker. I suspect that breeding was about to commence at the time of my visit in late March. One juvenile specimen taken in September and the occurrence of the annual molt in September and October suggest that the breeding season is mainly from May or June to August.

Systematic Comments

The Guadeloupe Woodpecker universally is treated as congeneric with melanerpine woodpeckers of the genus *Melanerpes*. At one time it was separated generically in *Linneopicus* Malherbe on the basis of its black plumage and long outer primary, and was maintained separately by various authors up to the time of Ridgway (who, although "splitting" *Linneopicus* from *Melanerpes*, found no cause to separate "*Centurus*" *striatus* from other species of "*Centurus*"). Melanerpine woodpeckers are highly variable in coloration, yielding some of the most striking and unique patterns (e.g., *Melanerpes lewis*, *M. candidus*, *M. formicivorus*, *Xiphidiopicus percussus*, and *Sphyrapicus thyroideus*) in the Picidae. Certainly the loss of pattern in favor of an all-black plumage is no cause for generic separation of *herminieri*, and I find its "long" outer primary barely, and only on the average, longer than in *M. portoricensis* and other melanerpines.

The all-black plumage of *herminieri* does, of course, present problems in ascertaining its relationships within *Melanerpes*. The reddish tinge of its underparts suggests the coloration of *M. portoricensis*, but its habits, and particularly its strong drumming and well-developed Chur Call suggest that it is not related very closely to *por-*

toricensis. The latter drums rarely (R. Wallace, MS), and has modified churlike calls, in contrast to both *herminieri* and *radiolatus*. There is a resemblance of *herminieri* to weakly color dimorphic *portoricensis* in its almost sexually monomorphic coloration. The very great sexual dimorphism in bill length of *herminieri* is fully equal to that found in *striatus* which is, however, color dimorphic.

I suspect that *herminieri* represents a very old relict, perhaps once widespread in the Lesser Antilles, and that *portoricensis* either evolved independently, or has diverged more from their common ancestor. The relationships of these two species to one another, and their relationship to mainland species (e.g., of the "*Tripsurus*" group, *M. chrysauchen* and its relatives) and to such West Indian species as *radiolatus*, are in need of study.

HISPANIOLAN WOODPECKER

The Hispaniolan Woodpecker is by weight three times the size of the Antillean Piculet, the only other resident picid on Hispaniola (Yellow-bellied Sapsuckers, *Sphyrapicus varius*, winter sporadically on the island). Hispaniolan Woodpeckers occur throughout Hispaniola wherever there are trees or cacti suitable for nesting. I found them absent from extensive sugar cane fields, but otherwise ubiquitous, even apparently occurring, as indicated by appropriate-sized woodpecker cavities, in the sparse palm trees of Columbus Plaza in downtown Santo Domingo. In most habitats this picid is common, or even locally abundant. Its abundance in some places is as great as that of any woodpecker, equaling such species as *Colaptes auratus* in some North American riparian situations, *C. campestris* in parts of the Argentine pampas, *Melanerpes erythrocephalus* in some riverine areas of the Great Plains, and *M. formicivorus* in certain California oakwoods. The Hispaniolan Woodpecker is colorful, somewhat social in habits, and vocally active, hence conspicuous. Several studies have concentrated on its sexual dimorphism, foraging habits, and colonial nesting (Selander and Giller, 1963; Selander, 1966; Wallace, MS). My observations took place in March, 1973, at various sites in the Dominican Republic, but especially about Miches

in the northeast, along the Comate River northeast of Santo Domingo, near Barahona in the southwest, and in the Baoruco Mountains and foothills of the extreme southwest.

Ecology and Foraging Behavior

Diverse forest, woodland, and scrub at all altitudes (figs. 1-6) are occupied by this woodpecker, which occurs as well in cultivated trees, especially palms. Even thorn forest and deserts (fig. 12) provide suitable habitat for this versatile species. It seems most numerous in cultivated areas having plenty of trees, especially adjacent to forests or woodlands. Certainly it is one of the picids with the broadest ecological tolerance, matched only by the Northern Flicker (*Colaptes auratus*) and perhaps the Cardinal Woodpecker (*Dendropicos fuscescens*).

Like other melanerpine woodpeckers, the Hispaniolan Woodpecker is omnivorous and diverse in its foraging modes. It eats various insects, berries and other fruits, and other plant materials. Widely regarded as a pest species, it is unprotected in the Dominican Republic because it eats various cultivated fruits, for example, extracting seeds from cocoa fruits, and gouging large holes in oranges (*Melanerpes candidus* similarly annoys South American farmers). It also feeds on corn (Wetmore and Swales, 1931, p. 292). Cherrie (1896) reported sapsucking by *M. striatus*. I saw a great many scattered, irregularly shaped holes in trees, unlike the even rows produced by *Sphyrapicus varius*, suggesting that Cherrie may have been correct. I saw one Hispaniolan Woodpecker investigating such holes, but it did not appear to feed.

Foraging of the Hispaniolan Woodpecker is as diverse as its diet. Most foraging for insects is accomplished by gleaning, probing, and pecking. Arboreal bromeliads are favorite foraging sites, the woodpeckers probing deeply into their bases. Large pieces of bark were pried loose from trunks of pines in the Baoruco Mountains, the woodpeckers then gleaning insects from the exposed surface. Several birds, hanging upside down and probing apparently for insects, fed from pine cones. Occasionally (12 cases) these woodpeckers engage in flycatching for insects from treetops. Foraging takes place down to the

bases of trees and saplings, but, except in deserts, it mainly occurs in middle and upper levels of trees. Fruits are taken in various ways. Berries are picked off trees or bushes. The woodpeckers cling to larger fruits, even hanging upside down and sometimes clasping with the feet, but not the tail, as they peck into the fruits. Flowers are investigated, and nectar, as well as insects, may be secured; cactus flowers are favored in arid areas. Foraging sites include the trunk, branches and branchlets of trees, bushes and vines, including cacti; fence posts and telegraph poles also are investigated, but probably provide little food. I did not see Hispaniolan Woodpeckers on the ground. Insect-foraging woodpeckers move frequently, often by flying, not spending much time at one site. Foraging birds fly some distance between trees, looking in flight like *Melanerpes cruentatus*. Perching is virtually always in typical picid fashion, that is, parallel to the branches even on vines and saplings.

Feeding often is social at fruiting trees, which may hold as many as 15 or 20 woodpeckers at a time. I once saw five birds on separate fruits within 1 square meter. Even when foraging for insects, two or three birds may feed in different parts of the same tree. Observations at a nesting colony disclosed that adult woodpeckers go out from the nest in different directions, thus feeding at different sites; the same adult consistently flew in the same direction four or five times in succession. Foods brought to the young are diverse, including large insects (e.g., a mayfly-like insect), small insects, and berries. The nestlings are fed both directly (large insects and fruits), and by regurgitation (presumably small insects).

Wallace (MS) found differences in foraging between the sexes of *Melanerpes striatus*, but the differences varied considerably between study areas in the Dominican Republic and in Haiti. Generally females foraged more by gleaning and less by probing and tapping than did males, with the differences most pronounced in the winter (dry season) and on palm trees (trees simple in form), and weaker or no differences in the breeding season and on broad-leaved trees. He also found that females tend to forage on smaller limbs and branches, and that the sexes differ in foraging heights (some populations at some seasons), but these differences need corroboration.

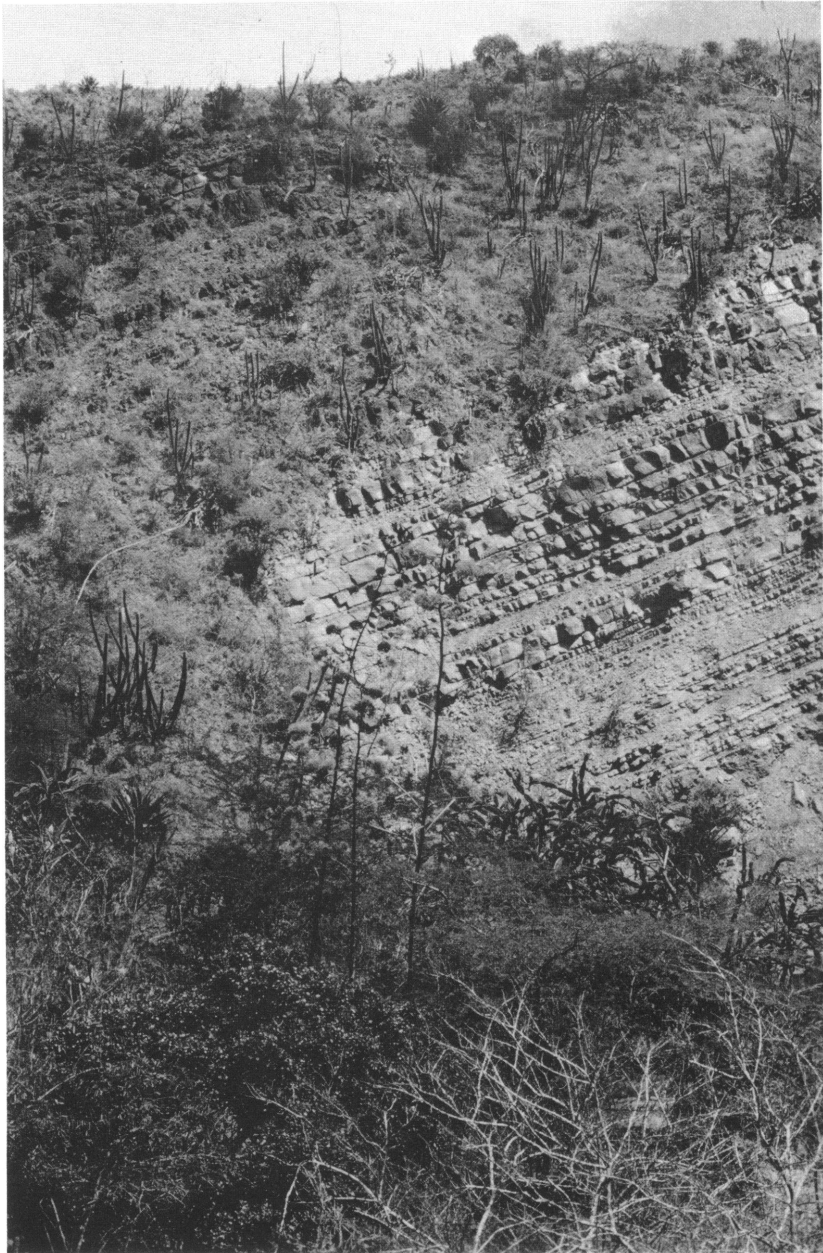


FIG. 12. Desert east of Azua, Dominican Republic, elevation about 500 ft. Habitat of Hispaniolan Woodpeckers; more dense (thorn forest-like) streamside vegetation in such deserts supports scattered pairs of Antillean Piculets, but these are scarce.

I note that parasites of Hispaniolan Woodpeckers have been mentioned prominently in various reports treating this picid. Sallé (1857) reported taking larvae of a parasitic anthomyid fly from *Melanerpes striatus*. Verrill and Verrill (1909), quoted by Wetmore and Swales (1931, p. 293), stated that the numbers of Hispaniolan Woodpeckers were kept down by parasitic worms infecting the throat and head and active in the breeding season of the woodpecker; he reported the ground beneath the woodpeckers' nests littered with dead or dying birds their throats laden with parasites. Danforth (1929) noted round worms in specimens of *M. striatus*. More recently, Wallace (MS) found that specimens of *striatus* he collected in the Dominican Republic were parasitized heavily by an undescribed species of large nematode. Although Verrill and Verrill's comments undoubtedly reflect a local situation, the frequent reports of parasitism suggest that this may be a major factor in limiting numbers of *M. striatus* and may also influence the degree of sociality and social nesting in this woodpecker.

Predation upon *M. striatus* may be minimal, and populations of *striatus* accordingly may be inordinately large. Wallace (MS) saw an American Kestrel (*Falco sparverius*) make a weak and unsuccessful attempt to secure a female *striatus*, but any such predation must be rare; other aerial predators are rare or lacking. Humans kill some woodpeckers because of their destructiveness to certain crops, and, according to several Dominicans, they particularly discourage nesting concentrations by use of shotguns (an active, large colony poses numerous inviting targets to a prospective gunner, and an irate farmer). My suspicion is that sufficient destruction of nesting colonies occurs to constitute a significant selective factor against colonial nesting in a single tree. Despite this predation and parasitism the woodpecker remains a common bird of Hispaniola.

Instrumental and Vocal Signals

The Hispaniolan Woodpecker is one of the most vocal of all woodpeckers, and perhaps correlated with this is that it drums infrequently. However, drumming varies among woodpeckers, and even among West Indian relatives of *M.*

striatus (*M. herminieri* drums regularly and rather loudly as I have discussed above, whereas *M. portoricensis* drums infrequently, its drumming having been noted only during intensive studies by Wallace, MS). I found that *M. striatus* occasionally (three instances, all near nests) performs demonstration drumming, the drumming bird holding its head close to the substrate and delivering a short but rapid burst of low drumming. On one occasion I heard the drumming from a palm tree in which two woodpeckers were perched (a nest was situated in that tree), but I could not see the drumming bird. In both of the other cases a male drummed below the entrance of its nest occupied by its mate. I could not hear a response from within the nest, but the drumming of the males was itself barely audible at 15 meters, so I could not be certain that there was no response. The drumming was not recorded on tape. As noted in the above discussion of *M. herminieri*, demonstration drumming is found commonly in melanerpine species.

Vocal signals of the Hispaniolan Woodpecker are among the most variable I have heard from woodpeckers. There are two calls given singly or in loose series, the Wup and Ta calls. Series calls basically are five, the Waa Call, the Ta-a Call, the Bdddt Call, the Rattle Call, and the Long Call. These vary, however, there being Short Rattle, Slow Rattle, Moderate Rattle, and Fast Rattle forms of the Rattle Call, and at least eight basic forms of the Long Call, in addition to various Rattle-Long Call mixtures and calls intermediate between several versions of the Rattle Call and five types of Long Call. I was unable to investigate individual variation in these mixed and intermediate calls, but variation is sufficient to allow for relatively distinct calls of individual woodpeckers. Whether or not each woodpecker has its own distinct form or several forms of Rattle and Long calls remains to be established.

Wup Call. Thirteen spectrographically analyzable Wup Calls were available for study. These calls average 0.053 second (range 0.04 to 0.07 second) in duration, and on sonagrams are short, peaked notes with a fundamental peak at 0.8 to 1.1 kilohertz and five to eight strong harmonic tones at intervals of 0.8 to 1.1 kilohertz (fig. 7F). The notes are inverted and V-shaped, with emphasis on the peaks and very little on the legs

adjacent to the peaks. Various harmonic tones, especially the first and the fourth to sixth, are dominant in various calls. Wup Calls are sharper and louder, they are often shorter, and they have stronger harmonic tones than the related Ta Call (see below).

Wup Calls are uttered singly or in loose series, often with Waa Calls when two woodpeckers are close, and intermixed with Rattle Calls and Long Calls. Functionally this call note seems equivalent to call notes of species of *Picoides* (Short, 1971b), that is, they are low intensity threat-alarm notes. Similar calls in other melanerpine woodpeckers include especially the longer (duration 0.1 second), higher pitched (fundamental tone peaks at 1.2 kilohertz) Chut Call of *M. radiolatus* (fig. 7H). This call has a terminal tail of sound lacking in the Wup Call of *striatus*, but its multiple harmonic peaks and similar pitch render it rather like the Wup Call. The Chup Call of *M. carolinus* (fig. 7I) is shorter than the Wup Call of *striatus*; it has weaker harmonic tones and a higher pitch (fundamental tone at 1.5 kilohertz), and it is more diffuse with a longer "tail." Other calls showing resemblance to the Wup Call of *striatus* are the Wu Call of *M. herminieri* and the Pep Call of *M. portoricensis* (fig. 7G).

Ta Call. The Ta Call (or Wa Call, sounding like "ta," "wa," or "wu") is very like the Wup Call, but is softer, with weaker overtones, and it is generally longer (fig. 7J, compare with Wup Call, fig. 7F). Spectrographic analysis of 19 examples shows that these calls average 0.07 second in duration (range from 0.04 to 0.12 second). The fundamental tone peaks at 0.7 to 1.0 kilohertz, but is dominant in only one of 19 examples, the dominant frequency usually being at the second harmonic tone peak (2.2 to 2.8 kilohertz, 10 cases) or on the initial harmonic tone (1.6 to 1.7 kilohertz, three cases), or at some other tone (five cases). Overtones are weak or absent above about 3.7 kilohertz. The form of the notes is like that of the Wup Call notes, but Ta Call notes are shallower, and more inverted U- than inverted V-shaped. The Ta Call is uttered singly or in loose, irregular series, or is intermixed with Wup, Waa, or Ta-a calls. It is frequently given by members of pairs, and individuals very close to one another, almost as a "conversational" note. It may be an agonistic call akin to the Wup Call,

which it resembles structurally, but emphasizing submissive rather than alarm and threat aspects.

As in the case of the Wup Call, the Wa Call shows resemblances to such melanerpine calls as the Chut Call of *M. radiolatus* (fig. 7H), the Chup Call of *M. carolinus* (fig. 7I), the Wu Call of *M. herminieri*, and the Pep Call of *M. portoricensis* (fig. 7G). There are also resemblances to the soft wik notes of the Wicka Call of *M. carolinus* (fig. 7L), which have weak harmonic tones and are comparable in duration and general form, and to the Preep Call of *M. portoricensis* (fig. 7M), which is flat-topped on sonagrams, is longer and higher pitched.

Long Ta Calls grade into Waa Calls, and these intermediates (fig. 7N) are as frequent as Ta Calls. Twenty-five examples show these intermediate calls to be longer, and to have multiple, short but connected peaks (see Waa and Ta-a calls below).

Waa Call. A long, multi-peaked call, usually uttered in series, and apparently constituting the equivalent of the Chur Call of other melanerpine species. Calls consist of three to 13 connected, peaked elements with a duration of 0.07 to 0.32 second (65 examples, see fig. 11A, B). The fundamental tone of the call is at 0.7 to 0.9 kilohertz, about as in Wup and Ta calls. Emphasized are various overtones and the fundamental tone, and as many as nine tones may receive moderate to strong emphasis. Dominance varies greatly among the tones from call to call. Individual peaks of the elements sometimes are weak or vague, the calls appearing almost horizontal at times.

Calls in series are uttered at rates varying from 2.5 to four calls per second, depending on the duration of the calls. I have heard Waa Calls in series lasting more than three seconds, but the longest recorded series was 2.27 seconds in duration, containing seven calls. The Waa Calls often are associated with other calls, including Wup, Ta, Rattle, and Long calls, and with visual displays (see below). Usually they characterize interactions between woodpeckers perched rather close to one another.

The connecting, peaked notes render the Waa Call very like Waa and Chur calls of other species of *Melanerpes*; there is no resemblance to calls of colapine or other picids. Most similar, perhaps, is the Waa Call of *M. supercilialis* (fig. 11B), similar in form, pitch, and duration to the Waa Call

of *M. striatus* and differing only in its relatively weaker overtones and somewhat less continuous peaks. The full Chur Call of *superciliaris* (fig. 11F) also is similar to the Waa Call of *striatus*, but tends to be longer, with stronger overtones, and higher pitched (fundamental tone at 1.4 kilohertz, emphasis on initial harmonic tone peak at 2.8 kilohertz). The Chur Call of *M. radiolatus* (fig. 11E, F) is usually longer and its notes are more diffuse than those of Waa Calls of *striatus* but (weak) harmonic tones often are evident and the pitch (fundamental tone at 1.1 kilohertz) is similar to that of the latter call. Other Chur Calls show similarities to the Waa Call of *striatus*, but are restricted in pitch to lower frequency tones. The Chur Call of *M. carolinus* (fig. 11F) is longer than the Waa Call of *striatus*, its fundamental tone is higher pitched (1.5 kilohertz), and tones above the legs of the second harmonic tone are suppressed. The Chur Call of *M. herminieri* (fig. 11C, E) has sound concentrated between 1.9 and 3.5 kilohertz and indistinct notes, but is similar in duration and its fundamental tone is similar (0.6 or so kilohertz, giving a narrow frequency interval between tones). Less similar to the Waa Call of *striatus*, but showing some resemblance are the Chur Call of *M. portoricensis* (fig. 11G) and the Kweer or Chur Call of *M. erythrocephalus* (fig. 11E, F). Except perhaps for the Waa Call of *M. superciliaris*, these calls of species other than *striatus* probably differ in function from the Waa Call of *striatus*, as they are louder and apparently are used in more distant communication unaccompanied by visual or other vocal displays. Appropriate studies of Chur Calls of various melanerpine species have not been accomplished; therefore further comparisons are impossible at this time.

Ta-a (Wicka) Call. Calls very similar to the Ta Call, but uttered in more or less regular series, and consisting of double notes form the Ta-a Call (fig. 7K) of *M. striatus*. Essentially the Ta-a Call is a Ta Call associated closely with a rather short, diffuse Waa Call. The "ta" notes are identical with Ta Calls in all respects, except that they tend to have stronger overtones when forming part of the Ta-a Call. The "a" notes are like Waa Calls, but have very few elements (usually two to four), and show diffuse sound connecting the various tones, rendering them indistinct spectro-

graphically. Some Ta-a Calls resemble intermediate Ta-Waa calls in that the initial "ta" is connected loosely to an "a" or "waa," forming a single note.

Series of Ta-a Calls are uttered at a rate of three to four notes per second (six series analyzed). The interval between notes varies considerably, even from 0.08 to 0.15 second within a single series, whereas the interval between elements of an individual call varies only between 0.02 and 0.05 second. The "ta" element may either precede or follow the "a" element.

More data and further analysis of the Ta-a Call are needed before it can be considered to represent a Wicka Call (Short, 1971b, 1972), which appears likely. Ta-a Calls were uttered during encounters chiefly between mated Hispaniolan Woodpeckers that were engaged in Bowing and other agonistic displays. The Wicka Call of *M. carolinus* (fig. 7L) bears similarity to the Ta-a Call of *striatus*, particularly in its lead ("ta") element. The second element ("wak" or "wik") of that species' Wicka Call is separated by a greater interval from its initial element than is the "a" from the "ta" in the Ta-a Call of *striatus*. The "wak" element of *carolinus* spectrographically seems unlike the "a" of *striatus* (e.g., the former element has weak overtones and but one major peak), but variant "wak" elements show an initial subpeak and a tail of sound that is irregular, suggesting additional peaks. These calls may be structurally and functionally related. Wicka Calls of various other woodpeckers (Short, 1971b, 1972, 1973b) do not have a multi peaked element, which may prove to characterize equivalents of the Wicka Call in melanerpine species.

Bdddt Call. Short series of rattle-like notes form the Bdddt Call, a low call heard from Bowing and otherwise displaying Hispaniolan Woodpeckers. This call (fig. 11E, F) resembles the Waa Call (fig. 11A) of *M. striatus* and churlike calls (fig. 11E, F) of other melanerpine species, but the individual elements are distinct notes not connected with one another. The notes are given at a rate of 20 to 30 per second (in 21 calls), and number two to six per call. The duration of the call varies from 0.10 (two notes) to 0.19 (five, six notes) second. Slower calls show distinct notes with peaks of the fundamental tone (at 0.8 to 1.3 kilohertz) and as many as seven harmonic

tones. Several calls show variation in pitch between notes, and in these calls the fundamental tone generally peaks at a higher pitch (between 1.6 and 2.5 kilohertz). The dominant tones are those at low frequencies, mainly the fundamental tone and initial harmonic tone. Faster calls spectrographically have less distinct notes with diffuse sound rather than clear peaks, but they do not connect with one another. Bdddt Calls are uttered singly (five examples) or in pairs of calls (eight cases recorded on tape).

The Chur Call of *M. portoricensis*, which has diffuse notes separate from one another, thus particularly resembles the Bdddt Call of *striatus*. The frequencies of its tones (fundamental tone peak at 1.1 kilohertz) also are similar to those of the Bdddt Call, but higher overtones are lacking in the Chur Call of *portoricensis*.

Bdddt Calls are not very loud, and they appear to be another agonistic call used in close communication between interacting Hispaniolan Woodpeckers. Their functional relation to Ta-a Calls remains to be established.

Rattle Call. The commonly heard Rattle Call is loud and carries a long distance. I recorded 47 examples of the four versions of this call, additional to intermediate or mixed Rattle-Long calls (see below). Rattle Call notes are peaked, inverted U-shaped, and they are not connected within a call. Their rate of delivery varies from 7.45 to 10 notes per second in Slow Rattle Calls, from 10.5 to 14.8 notes per second in Moderate Rattle Calls, and from 15.5 to 18.5 notes per second in Fast Rattle Calls. The 47 calls recorded on tape fall into these categories as follows: 20 Slow, 20 Moderate, and seven Fast Rattle calls. Presumably these were recorded approximately in relation to the frequency with which they were heard during my study in March, hence these numbers roughly indicate the relative use of the three forms of Rattle Call. Short Rattle Calls contain three to six notes, and have been included in the above totals, as they too can be categorized into Slow, Moderate, and Fast on the bases mentioned.

Short Rattle Call: Differs in form from longer calls only in having fewer notes, but it is apt to differ functionally from them. Short Rattle Calls are uttered singly (five cases) or more often (seven instances) in series of two or three. The Short

Rattle Calls can be categorized by the tempo of their notes into Slow, Moderate, and Fast Short Rattle Calls, as defined above. Of 22 Short Rattle Calls eight are the Slow type, 12 are Moderate, and two are Fast, showing proportionally more Moderate and fewer Slow and Fast calls than in longer Rattle Calls (although the differences are not significant). The Short Rattle Calls uttered in series were of about the same tempo in five series, but in two others there was a shift in tempo of the calls, from Fast to Slow in one case, and from Moderate to Slow in another series. The notes vary in duration from 0.025 to 0.05 second, and they tend to become shorter through a call (in 12 of 22 calls). There is great variation in the frequency of the notes, from 0.8 to 2.2 kilohertz at the peak of the fundamental tone. Most calls show a drop in pitch through a call, or at least on the last note, but there is considerable variation. One six-note call has consecutive frequencies for the peak of the fundamental tone at 1.8, 1.7, 2.2, 1.8, 1.6, and 0.8 kilohertz. Emphasis is on the peak of the initial harmonic tone, or on the peak of the fundamental tone, or on some combination of these two (e.g., both codominant, or emphasis on peak of fundamental tone and legs of initial harmonic tone). The Short Rattle Call is not figured, but its notes generally resemble comparable notes in respective Slow (fig. 11D), Moderate (fig. 11G), and Fast (fig. 11G, H) Rattle Calls of greater duration. Short Rattle Calls are uttered during conflicts, or other encounters. They sometimes are interspersed with longer Rattle Calls, but the latter tend to be delivered in flight, or as a "proclamation" call from a conspicuous perch, in addition to conflict situations when woodpeckers are in proximity to one another.

Slow Rattle Call: Twelve Slow Rattle Calls (fig. 11D) contain seven to 17 notes, and last 0.72 to 1.67 seconds (average 1.11 seconds). As noted above the tempo is 7.45 to 10 notes per second. Individual notes are 0.02 to 0.055 second in duration in most calls, but a few long-noted calls have notes as long as 0.09 second. One nine-note call shows the first note as 0.065 second, the second at 0.04 second, other notes then vary between 0.03 and 0.04 second, and the last note is 0.025 second. In four of 12 calls notes diminish in duration, but in others their duration

is irregular or invariable. Notes are peaked, inverted U-shaped, with a fundamental tone peaking at 1.4 to 2.6 kilohertz (average 1.9 kilohertz). Three to four overtones usually are prominent, and the peak of the initial harmonic tone usually is dominant (in 10 of 12 cases, the other two having the fundamental tone dominant). There tends to be a drop in the pitch (eight of 12 cases) of notes during a call, but often the highest pitched notes are in the middle of the call. I was unable to distinguish functionally between this and other versions of the longer Rattle Calls. Slow Rattle Calls were uttered by woodpeckers in flight, or from a perch when other conspecific birds were nearby, or occasionally when no other woodpeckers were evident in the vicinity.

Moderate Rattle Call: Nine Moderate Rattle Calls (excluded are Moderate Short Rattle Calls) contain seven to 26 notes and have a duration of 0.52 to 1.82 seconds, averaging 11.1 notes in 0.96 second. The tempo of the notes is 10.5 to 14.8 notes per second. Moderate Rattle Call notes (fig. 11G) resemble Slow Rattle Call notes but their peaks tend to have weaker legs. They also tend to be shorter, ranging in duration from 0.02 to 0.065 second, and lower in pitch, from 0.9 to 1.8 kilohertz. As in the Slow Rattle Calls, there are tendencies for notes to shorten, and to fall in pitch through a call (sounding like "wik-wik-wik-wik-ik-ik-ik-ik"), but there are exceptions. The initial harmonic tone, or occasionally the fundamental tone or second harmonic is dominant, and three or four overtones are evident in most calls. Two calls commence with a Wup Call note, or a Rattle-Wup intermediate note; these show more and stronger harmonic tones, and are low (0.8 and 0.9 kilohertz, fundamental tone) in pitch. The longest (26 note) Moderate Rattle Call almost forms two calls, as notes 15 to 17 are exceptionally weak, and are preceded and followed by stronger notes. Moderate Rattle Calls occur under similar circumstances as Fast and Slow Rattle calls.

Fast Rattle Call: Five Fast Rattle Calls of the long version (see Short Rattle Call above) last 0.43 to 1.33 seconds and contain seven to 22 notes, averaging 14 notes in 0.87 second (fig. 11G, H). The notes are delivered at rates of 15.5 to 16.5 notes per second in these five calls. Individual notes are short (0.01 to 0.03 second in

duration), and they show diffuse sound over a wide range of frequencies. Tonal peaks are weak in sonagrams, and the notes appear as almost vertical bars in most cases. The peak of the fundamental tone falls between 0.8 and 1.7 kilohertz, and the initial harmonic tone usually is dominant. The terminal note of a call often is the weakest note, and the lowest in pitch. One peculiar, perhaps Wuplike terminal note clearly shows five overtones and has a fundamental tone at 0.6 kilohertz, compared with two overtones and 0.8 to 1.2 kilohertz for other notes of that call. Fast Rattle Calls are uttered under circumstances similar to those resulting in other versions of the Rattle Call.

Rattle Call notes are structurally simple, inverted U-shaped notes that occur in many woodpeckers (Short, 1970a, 1971b, 1972, 1973b). The Rattle Call notes of *M. striatus* have no peculiarities facilitating comparisons, and hence its Rattle Calls are similar to some Rattle Calls of species of *Picoides* (Short, 1971b), *Meiglyptes* (Short, 1973b), and to simple Long Calls of *Colaptes* (Short, 1972), *Picus* (Short, 1973b) and other picids. Melanerpine species other than *striatus* also have similar calls. The Chip Series Call (fig. 13F) and Long Call (fig. 13F, G) of *M. carolinus* are composed of inverted U- or V-shaped notes, in the former case delivered at three notes per second, and in the latter call, at 11 to 14 notes per second. The fundamental tone of the notes in these two calls of *carolinus* respectively is at 1.5 and 2.4 kilohertz. *Melanerpes portoricensis* employs a Pep Series Call (fig. 13H), notes of which generally resemble those of Rattle Calls of *M. striatus*; the Pep Series Call is given at nine notes per second. The Red-headed Woodpecker (*M. erythrocephalus*) has a Chur-Rattle Call that I have not analyzed fully, but its notes (barely peaked, sound diffuse with fundamental tone at 1.0 kilohertz, duration 0.025 second, tempo of notes in call at 11 per second) resemble Rattle Call notes of *M. striatus*. It is clear that its melanerpine ancestry provided vocalizations from which the Rattle Call of *striatus* easily could have been derived.

Long Call. The evolution of an elaborate array of Rattle and Long calls is a significant feature of *M. striatus*. Long Calls seem structurally and functionally equivalent to Rattle Calls, and

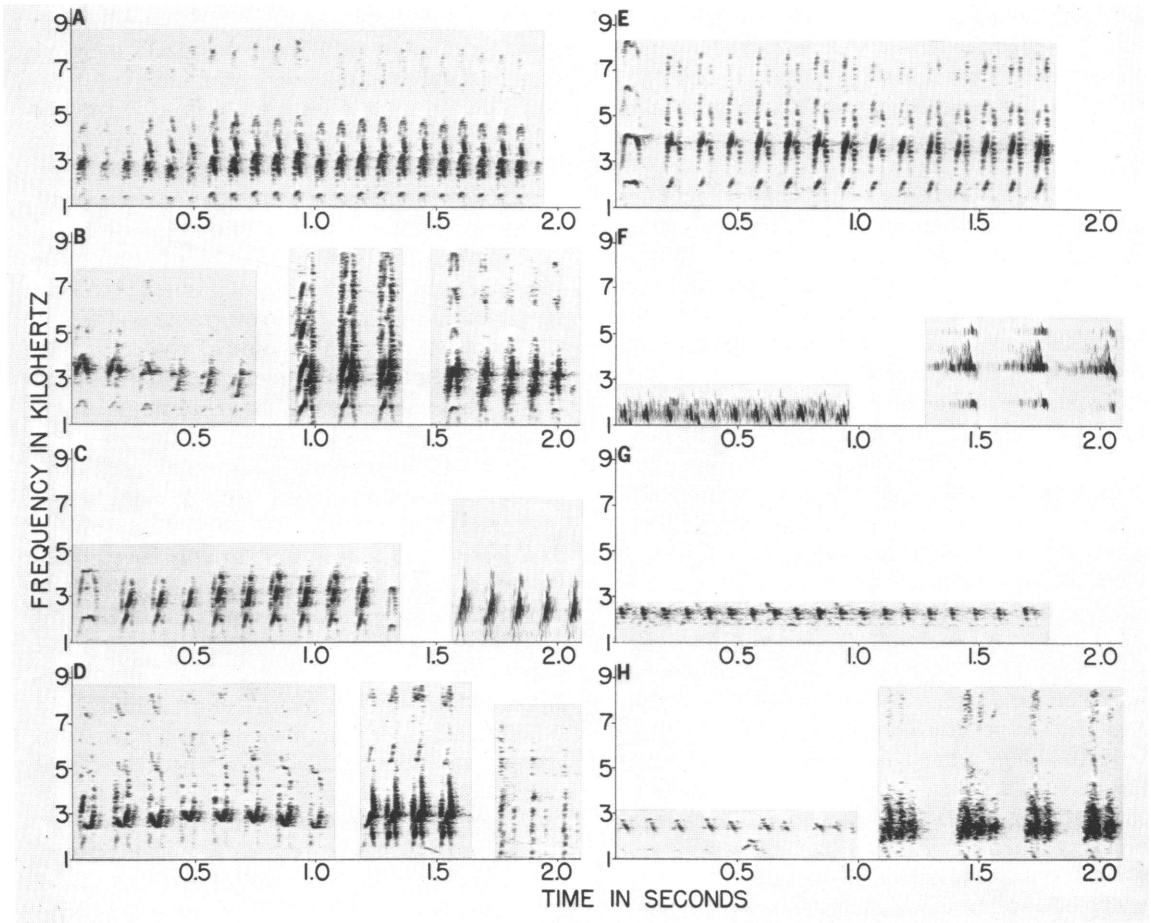


FIG. 13. Sound spectrographs of vocalizations of *Melanerpes striatus* and some other melanerpine woodpeckers. A. Full call of *M. striatus* intermediate between Moderate Rattle Call (see fig. 11G) and Long Call having dropping element of its notes. B. Partial mixed call of *M. striatus* showing switch from Slow Rattle Call notes (3 on left) to Long Call notes (3 on right) with a rising element, then 3 notes from a Long Call having open notes with a step in the rising element, and finally a full, short Long Call with initial and terminal Rattle Call notes surrounding 3 Long Call notes having a modified rising element. C. Full Long Call of *M. striatus* having a modified rising element of the notes (the peculiar initial note tends toward a Waa Call note, several of which preceded this call, and the terminal note is a Rattle Call note), then, WB, 5 notes of a typical rising-note Long Call of *M. striatus*. D. An 8-note Long Call having concave or J-shaped elements, then a short (4-noted) Long Call of the open V type, and lastly 3 notes from a Long Call having widely separated elements of each note, all calls of *M. striatus*. E. Full Long Call of *M. striatus* with notes having an initial fast-rising element (the lead note is an intermediate Waa-Long Call note). F. First 11 notes of Long Call of *M. carolinus* shown in G below, but here WB, then 3 notes from a Chip Series Call of *M. carolinus*, both recorded in Georgia. G. Full Long Call of *M. carolinus* (see F), from Georgia. H. Two series calls of *M. portoricensis* (recorded by G. B. Reynard), first 10 notes of Pep Series Call (disregard low-pitched note at 0.6 second), then 4 compound notes of Long Call, notes having both churlike and peaked Long Call-like aspects. Sonagrams are narrow band unless indicated wide band by WB.

they sound like Rattle Calls. Uttered at 6.8 to 10.9 notes per second they overlap in tempo with Slow and Moderate Rattle calls. Various mixed, and intermediate Rattle-Long calls commonly are used by Hispaniolan Woodpeckers (see below), clearly indicating the similarity of these calls. Generally, Long Calls may be conceived as Rattle Calls with notes broken at their peaks (gap between rising and falling legs), and otherwise somewhat modified.

I recorded on tape 33 Long Calls roughly categorized into 10 groups, in addition to nine calls intermediate between Rattle and Long calls, and 17 mixed Rattle-Long calls (see below). Long Calls average 7.39 notes per call (range two to 14 notes) delivered in 0.88 second (range 0.18 to 1.66 second) at a rate of 8.58 notes per second. Only three of 33 calls attain the tempo of a Moderate Rattle Call, and these three are in the low range of that call, at 10.3, 10.5, and 10.9 notes per second. The remaining calls were given at the same rate as Slow Rattle Calls. The following are the categories of Long Calls rather subjectively arranged by the form of the notes; doubtless there are other categories as yet unrecorded.

Open-noted Long Call: Two calls having basically peaked notes, with legs present on sonagrams, but there is a broad gap instead of a peak in each note. Figure 13D illustrates three notes from the middle of an eight-note call. The tall rising and falling legs are emphasized from 1 to 7 kilohertz; a fundamental tone peak, if present, would be at about 2.5 kilohertz. The initial two notes, not illustrated, show more of a peaked tendency, and the terminal note, also not shown, is a rattle note with a fundamental tone at 1.3 kilohertz. The call lasted 1.02 seconds, and individual notes are 0.055 second in duration.

Open V Long Call: Unpeaked notes in the form of an inverted V. One variant example of this version is shown in figure 13D; that four-noted call has connecting but dropping peaks between the legs in each note, with separate rising segments. These notes have a dominant fundamental tone, "peaking" at 2.5 to 3 kilohertz, and moderate harmonic tones. The notes are 0.06 second in duration, and the call is 0.40 second in duration (tempo 10 notes per second). Two other calls have the peak not quite formed, the fundamental tone nearly achieving a peak at 1.9

and at 2.4 kilohertz, and the second and first harmonic tone dominant, respectively. No two of the three calls are alike.

Open V, Rising Element Long Call: Five calls with notes spectrographically forming an open V and having a strong rising element at the peak of the inverted V. Emphasized are the legs below the rising element, the rising element, and the adjacent legs of the initial harmonic tone, all between 1.5 and 4 kilohertz. The highest frequency of the rising element varies from 3.0 to 3.5 kilohertz in the five calls. The initial note differs from the others in four of the calls, being longer, longer and peaked, shorter and weaker with a peak, or lacking the initial rise; thus the five calls are rendered distinctive.

Open V, Step-Rising Element Long Call: A step in the rising element or in the initial rise (see fig. 13B) distinguishes notes of this call from the previous version. Of six calls considered to represent this version, three have the step in the central rising element. One of the three has eight notes equally emphasized, and the other two show a decrease in strength and duration of the notes through the call (the last two calls differ in the tones stressed). The other three calls have the step in the initial rise, as shown in the three notes illustrated (fig. 13B). The "peak" marked by the rising element is between 2.5 and 3.0 kilohertz in these calls, which show differences on the order of those mentioned for the other three calls.

Initial Rise Long Call: A single call of 14 notes, the longest of the Long Calls, represents this version (fig. 13E). It is introduced by an intermediate Waa-Long Call note distinctly different from the other notes in the Long Call, which can be described as sounding like "Ka-wik-wik-wik-wik-ik-ik." The Long Call notes, uttered at 8.4 per second, show a lessened duration (from 0.065 to 0.05 second) of the notes throughout the call, and a corresponding but slight speedup in the delivery from the beginning to the end of the call. The initial harmonic tone is dominant, the upper frequency of the initial rising element being at 4.1 kilohertz (2.1 kilohertz in fundamental tone).

Rising-note Long Call: Represented by two calls in which there is a rising element emphasized far more than other parts of individual notes (fig. 13C). The rising element is between

1.5 and 3.0 kilohertz in the call figured (between 2.3 and 4.0 kilohertz in the second call), and the notes are rather short (0.025 second). The 12-note call was given in 1.36 seconds (8.8 notes per second, versus 10.5 notes per second in the other call).

Modified Rising-note Long Call: Eight calls, each different from the others in detail, have the strong rising element connecting with the falling leg in the broken, inverted V-shaped notes (fig. 13C). The 11-noted call that I have figured has an initial Waa-like note and a terminal rattle note ("Ka-wik-wik-wik-wik-----a"). The nine Long Call notes show emphasis on the rising element and adjacent lower legs of the initial harmonic tone and upper portion of the fundamental tone, between 1.5 and 3.8 kilohertz. Wide band analysis shows the rising element to connect with the dropping leg in the initial harmonic tone, reinforcing its sound. Other examples differ in having more or less emphasis on the initial rising leg of the notes, and in various other minor ways (e.g., only three of the calls show rattle- or Waa-like notes). Four of the eight calls show a decrease in duration of the notes through the calls. One of the eight calls actually represents three short bursts of three, four, and four notes. The four calls recorded near Barahona differ from the other four calls (recorded near Miches) in tending to have a step in the rising element, and in having most of the emphasis in a narrow frequency range about the rising element. The figured (13C) call was recorded near Miches. Two of the Barahona calls were uttered almost simultaneously, and, although similar, they differ markedly in the duration of the rising element, and the degree of emphasis on the initial rising leg.

Rise-Fall Long Call: One example of a four-note call with notes emphasizing a rising element (actually an extension of the initial rising leg) in the fundamental tone and a dropping leg of the next higher tone followed two calls, first an intermediate Slow Rattle-Open V Long Call, then a mixed Slow Rattle-Rise-Fall Long Call. The last part of the last-mentioned call is identical with a following Rise-Fall Long Call, and presumably was uttered by the same individual. The emphasized rising element is at 2.2 to 2.8 kilohertz and the falling portion emphasized is between 4.2 and 3.2 kilohertz. Disconnected Waa-like notes

were interspersed between the call described here and other "Long Calls" mentioned above.

H-noted Long Call: Two Long Calls, uttered consecutively, shows notes with a central rising element, the upper end of which has sound both preceding and following it, connecting the nearly vertical legs of the notes. Thus the tall notes are in the form of an H on a sonagram. The horizontal band of sound (crossing of H) is at 3.9 kilohertz. Notes diminish in duration by 33 percent through each call. The calls contained eight and five notes, delivered at 8.4 and 8.0 notes per second, respectively. Both calls have several notes tending toward the Concave-J Long Call (see below).

Concave-J Long Call: Three examples recorded on tape contain notes with a dropping then rising concave element strongly emphasized. In two calls the rising, terminal portion of the element reaches a higher frequency than the initial part, giving a J-shape to the element. The call illustrated (fig. 13D) differs from the other two in having an additional rising element parallel to the concave element, but entirely following the dropping leg of the note. The concave or J element is between 2.5 and 3.0, 2.2 and 2.7, and 2.2 and 2.8 kilohertz in the three calls. The initial note of two calls is peculiar in its greater duration and multiple peaks, tending toward a Waa Call. The tempo of the several calls varies from 7.4 to 10.6 notes per second.

Mixed Rattle-Long Call: Is represented by 17 examples containing notes of both call types, and of these, two involve Moderate Rattle, and 15 Slow Rattle calls. The Moderate Rattle Call notes were mixed with Open V, and Concave-J Long Call notes in the two instances. Slow Rattle Call notes were mixed with Open V (one call), Concave-J (two calls), Rise-Fall (five calls), Rising-note (four calls), and Modified Rising-note Long Call notes. I have not considered here the various Long Calls having one or two rattle-like notes, discussed under the Long Calls above. Notes of the mixed calls usually are clustered, but clusters of notes of one type often occur in several parts of a call. Mixed Calls frequently (two-thirds of instances) commence with Rattle Call notes, and terminate about as frequently with Long Call as with Rattle Call notes. One-third of the calls contain only one shift in notes, but 13 calls have two

or more (up to five) shifts from Rattle to Long Call notes, or vice versa. A mixed Moderate (Short) Rattle-Open V Long Call (fig. 11H) has two rattle notes, pitched lower and with complete peaks, followed by two higher pitched, open (nonpeaked) Long Call notes. Figure 13B shows notes two to seven of a nine-note mixed Slow Rattle-Rising-note Long Call. The first four notes, including the initial three figured, are peaked Rattle Call notes. The last five notes, including the final three figured, have the rising element (notice a slight step) of Rising-note Long Calls. A short (mixed) Slow Rattle-Modified Rising-note Long Call (fig. 13B, last call in sequence) has a long initial and short terminal, peaked Rattle notes surrounding three Long Call notes characterized by an intense rising element connecting with an equally intense falling leg of the initial harmonic tone. The 17 mixed calls contain more notes (average 12.08 versus 7.39 per Long Call), last longer (average 1.25 second versus 0.88 second) and tend to have a more rapid delivery (average 9.78 notes per second versus 8.58 notes, and seven of 17 are at Moderate Rattle tempo versus three of 33 Long Calls at that tempo) than do Long Calls.

Intermediate Rattle-Long Call: Nine calls contained notes mainly or entirely intermediate between Rattle and Long calls. Two such calls involved notes uttered at the tempo of a Moderate Rattle Call, one with intermediate Rattle and Open V Long Call notes, and the other with intermediate Rattle and Rise-Fall Long Call notes. The latter (fig. 13A) contains 23 notes uttered at 12 notes per second over 1.92 seconds; its notes are peaked but the peaks are skewed toward the end of the notes, forming a rising element that connects with a strong dropping leg of the second harmonic tone. The other seven intermediate Rattle-Long Calls involve the Slow Rattle Call and the Open V, Rising Element Long Call (one call), the Rising-note Long Call (five calls), and the Modified Rising-note Long Call (one call). The example of the intermediate Slow Rattle Call-Modified Rising-note Long Call (fig. 11H) has the rattle-like peaks of its notes, but there are rising elements as well, some with a step or gap in them. The terminal note of this call is a lower pitched, simple rattle note. The seven notes were given in 0.79 second (8.9 notes per second). The

intermediate calls show some variation among their notes, and the leading and the terminal notes especially tend to differ markedly from the others. The intermediate calls average as long as Long Calls (0.88 second duration), but tend to have more notes (8.5 versus 7.4 notes per call) delivered more rapidly (9.17 notes per second versus 8.58 notes per second for Long Calls). The intermediate Moderate Rattle-Rise Fall Long Call (fig. 13A) contained more notes than any Long Call or mixed Rattle-Long Call.

Long Calls may be regarded as modified Rattle Calls, uttered under circumstances (e.g., flying adult returning to nest or to a favored perch, distant conflicts) generally similar to those in which Rattle Calls are given, and in fact I found no difference in use of these calls. Their structural similarities, and the close association of their notes (e.g., Rattle notes in some Long Calls, mixed Rattle-Long Calls, intermediate Rattle-Long Calls) also suggest that they function similarly. Considered as modified Rattle Calls, Long Calls of *striatus* show resemblances like those of the Rattle Call to such melanerpine vocalizations as the Chip Series Call (fig. 13F) and Long Call (fig. 13F, G) of *M. carolinus*, the Pep Series Call (fig. 13H) of *M. portoricensis*, and the Chur-Rattle Call of *M. erythrocephalus* (see above discussion of Rattle Call).

The variation in Rattle and Long calls of *M. striatus* is exceedingly great (unsurpassed among picid calls), so much so that it suggests differences in calls between individuals. It remains to be established that distinct calls mark individual woodpeckers. The use of the Rattle-Long call complex in announcing the arrival of an adult at the nesting site suggests a function for such individual differences in social nesting woodpeckers. An incoming bird uttering its unique call apprises its mate at its nest and all adjacent nesting adults of its identity. This may serve to reduce the occurrence of conflicts among pairs, which are highly territorial about their nest sites. A study of the vocalizations of marked, paired birds at a social nesting site would be very rewarding.

Visual Displays

Displays of the Hispaniolan Woodpecker are numerous, and without detailed study it is im-

possible to do more than describe the visual displays and mention the circumstances under which they occur. Motion picture photography probably will be needed to clarify aspects of the displays mentioned below, and doubtless will permit the discovery of other displays (see, e.g., Short, 1970a, pp. 11-14 and fig. 3). I do not mean to imply that displays described below form a complete ethogram, or that there is a hierarchy in their order.

Bill Positioning Postures. Among the most common of picid displays (Short, 1970a, 1971b, 1972, 1973b, MSb). The Bill Directing Posture is a threat display in which the head is lowered and the bill is pointed at an antagonist. In *M. striatus* this posture emphasizes the sexual marking (crown color), presumably facilitating appropriate reactions. Two females in an encounter used Bill Directing Postures in between Swinging Displays as they moved at one another and gave the Ta Call. I observed Bill Directing when adults approached the nest of another pair; the bird defending the nest moved at the intruder using a Bill Directing Posture. For example, an intruding male approached the nest of another woodpecker, and the female inside that nest exited and, striking a Bill Directing Posture, moved toward the intruder driving him away. The Bill Directing Posture is incorporated into Bowing and Swinging displays (see below), and seems to be a threat display of less intensity than they are.

I saw Bill Raised Postures, in which the head and bill are held in a high, nearly vertical position several times during conflicts. This may be a submissive posture, as it occurred in submissive birds during encounters between members of a pair. Like Bill Directing, the Bill Raised Posture is incorporated into Bowing and Swinging displays.

Bill Directing has been noted in many picid species, including a few other species of *Melanerpes* (e.g., *M. carolinus*, personal observ., and *M. cruentatus*, Short, 1970a, pp. 11-12). Wallace (MS, p. 30) referred to "stabbing" in *M. striatus*, apparently a Bill Directing Posture used in attacking birds. I do not know of the Bill Raised Posture in melanerpine species other than *M. herminieri* (see above), but it probably will be found to occur in several other species of *Melanerpes*.

Swinging Display. Another frequent picid dis-

play is a side-to-side swinging of the body, and especially the head and bill. In *M. striatus* this movement incorporates the Bill Directing Posture when the swinging is in the horizontal plane, and the Bill Raised Posture when the swinging is accomplished with the head held high. These may reflect more aggressive and more submissive tendencies, respectively, in this ambivalent display. Wallace (MS, p. 30) reported "bill waving," that is the Swinging Display of *striatus*, during encounters. The mode of the side-to-side movements varies in woodpeckers, being rapid or slow, and repetitive or not. In *striatus* there is a rather slow swing from one side to the other, and sometimes back again, but the movement is neither rapid nor repetitive.

I saw Swinging Displays mainly in conflicts between birds of the same sex, as when two males or two females approached each other too closely. Ta Calls and a Bill Directing Posture accompanied Swinging Displays given by two females in conflict on a palm tree between their nesting trees near Barahona. Other Swinging Displays were accompanied by Ta and by Ta-a calls. Occasionally Swinging Displays were seen between individuals of the opposite sex, as when an intruding woodpecker ignored Bill Directing by a nesting bird and continued its advance. In several instances mated birds engaged in Swinging Displays. Once a female flew to its nest which the male occupied. The female gave a Swinging Display directed at the male inside the nest; the male came out supplanting the female, and gave a Swinging Display at her as she backed away.

Without analysis by use of motion pictures it is impossible to compare this display in detail with Swinging Displays of other picids, but that of *striatus* seemed similar to the Swinging Display of *M. cruentatus* (Short, 1970a, p. 14) and *M. herminieri* (Head Swinging Display, see above). In particular I failed to note a concomitant Tail Spreading Display, and indeed I have seen no Tail Spreading Display in melanerpine woodpeckers (Tail Spreading Displays are features of the display repertory of *Picoides* and its relatives, including the Campetherini, and of the Colaptini; Short, 1971b, 1972). Also, the hesitant swinging movements seem characteristic of at least some melanerpine species.

Bowing Display. Conspicuous displays of *M.*

striatus, particularly in nesting trees. The up-down movement of the head and bill, especially, incorporates a Bill Directing Posture and Bill Raised Posture into an ambivalent display. In contrast to the Swinging Display, Bowing Displays usually occur between birds of the opposite sex, and the up-down movements are repetitive. One male Bowed slightly as it uttered a Long Call at an approaching male, but otherwise Bowing occurred when at least one member of the opposite sex was present. Bowing Displays were common especially when one bird flew in calling to its mate at the nest. I note that Bowing birds usually hold their bill open, whether or not they are calling.

A male Bowed and called (Bdddt Call) as its mate came in uttering a Long Call. Often the bill was open as the woodpeckers Bowed, perhaps as they called. It was difficult to hear particular calls accompanying displays at social nesting sites, but Ta-a and Waa calls seemed most frequently given with Bowing Displays. A mate Bowed three or four times, its head projecting from the nest, as its mate flew in giving a Rattle Call. After landing, the incoming bird frequently Bowed, sometimes mutually with its mate. A female gave a Bowing Display with a Ta-a Call just preceding copulation with her presumed mate. Bowing also was common in mutual displays when several birds of both sexes were together.

Bowing Displays were not associated with Swinging Displays, and these seem functionally not related, in contrast to colapline woodpeckers (Short, 1972), in which Bowing (Head Bobbing, a more rapid form of Bowing) is closely associated with Swinging in composite displays. The Bowing Display of *striatus* seems similar in form to those of *M. erythrocephalus* (Kilham, 1958), of *M. cruentatus* (Short, 1970a; similar in form but used more in intense agonistic encounters), and of *M. herminieri* (see above).

Wing Flicking Display. I am doubtful as to whether Wing Flicking is a display. The rapid, but slight lifting of the wings, seen frequently, may be a simple, unrutalized intention movement. It is common in social nesting situations, and there may be a reflection of the high level of interactions that occur.

Dihedral Flight Display. A common display given in flight, it is marked by the wings being

held half-raised as the woodpecker glides to a perch. It was seen only in the vicinity of nests and characterizes the last 10 meters or so of the flight of an incoming bird when the mate is present at the nest. The most conspicuous of such displays were by females coming to the nest as it was being excavated by the mate, who responded by Bowing. At times the Dihedral Flight Displaying woodpecker may feed its mate after landing (see below). Calls associated with the Dihedral Flight Display are the Rattle Call, the Long Call, and the Bdddt Call. Moving pictures are needed to document the details of the Dihedral Flight Display in conjunction with recording of associated calls.

The Dihedral Flight Display is a gliding display of a Hispaniolan Woodpecker about to land, and is unlike the Flutter Flight Display of species of *Picoides* (Short, 1971b, 1973b, MSb), which employ stilted, fluttering wing beats in longer display flights. Other melanerpine woodpeckers known to have a similar, gliding form of display flight are *M. lewis* (Bock, 1970), and *M. carolinus* (Kilham, 1961); colapline woodpeckers seem not to have such flight displays (personal observ.).

Courtship Feeding. Seven clearly seen cases of courtship feeding document the occurrence of this activity in *M. striatus*. Five instances involved a female feeding a male, and two of a male feeding a female, all by regurgitation. I saw many other bill-touching episodes that may have involved feeding, but I could not be certain. All the observations took place as members of pairs replaced each other at nests. In several cases the incoming bird gave a Dihedral Flight Display as it landed, then, after Bowing or not the woodpecker fed its mate. In those instances in which the mate was inside the nest, the incoming bird after feeding its mate and a Bowing bout, replaced it within the nest. One female approached, Bowing, then fed her mate within the nest, backed away giving a Swinging Display, paused, and within one minute moved to the nest to feed the male again after which he gave a Swinging Display as he left the nest. She retreated, and he flew away; the female then entered the nest. Food was passed by regurgitation, and also single large items such as berries and large insects were passed to the mate inside the nest. In one case I saw a male in the nest pass

(regurgitated) food to its mate outside, although the latter had not fed the male, which had been inside the nest for some time with no access to food.

Courtship feeding has been documented for relatively few woodpeckers (e.g., *Dinopium raflesii*, Short, 1973b), and it would be premature to compare the few for which it is known. It is noteworthy that it also occurs in *M. herminieri* (see above), and should be looked for in other melanerpine woodpeckers.

Nesting and Sociality

Most nesting of Hispaniolan Woodpeckers occurs in the wet spring (February to October), but pairs remain together throughout the year, and may nest irregularly at other times (Wallace, MS). I saw nests that were solitary, groups of nests in adjacent trees, and nests in colonies (fig. 14) within a single tree. Social nesting has been reported by several authors, especially Selander (1966), Ashmole (1967), and Wallace (MS). Such sociality perhaps has been over stressed, for large colonies occur uncommonly and are local phenomena. This may to some degree reflect the destruction of conspicuous colonies by humans. Wallace (MS) found as many as 26 pairs nesting in a single tree, but pairs nested separately in his major study areas (one in Dominican Republic, one in Haiti).

My own data from March, 1973, probably are biased in favor of colonial nesting simply because such sites are more conspicuous; there are more birds, hence more activity about such colonies, and large colonies are situated in conspicuous dead trees. The data presented are from all areas that were visited in southern Dominican Republic. I found one large colony of at least 19 pairs in a single (fig. 14) tree, but the two next largest colonies contained only eight and seven active nests. Solitary nests totaled 39, there were 67 situations involving 166 nests in colonies of two or three nests, and 15 colonies, totaling 90 nests, with four to 19 nests per colony. Thus only 13 percent of the 295 occupied nests represented solitary nestings. Viewing the data in another way, it was seen that 117 of 295 nests were in trees containing no other cavities, the other 178 nests were in 55 trees. Of the 117 nests in indi-

vidual trees, 39 were solitary as far as I could determine, 20 (10 instances) were in "colonies" of two nests, 36 (12 cases) were in colonies with three nests, 12 (three situations) were in groups of four nests, and 10 (two cases) were in loose colonies of five nests.

Intense and repetitive interactions between birds representing different pairs occur much more often in large than in small colonies, but sometimes are seen when there are two or three nests in a tree, and when nests numbering three, four, or five are in separate trees that are in proximity. It is difficult to estimate how closely the proportions of nestings derived from my data approach those actually obtaining in the population. I suspect that large colonies are restricted to optimum conditions of habitat, and that vast areas of arid scrub, pine forests, and other habitats not able to sustain such large colonies mainly have solitary nests and small colonies. Thus the majority of Hispaniolan Woodpeckers probably does not have to undergo the frequent, intense interactions that mark large colonial gatherings.

Territories vary from the immediate vicinity of the nest site in colonies to at least the entire nesting tree in solitary nesting pairs and in loose colonies having each nest in a separate tree. In the last-mentioned situations it was obvious that visits to the nesting tree by other adults resulted in conflicts and the driving away of the latter birds by the nesting woodpecker pair. In the largest colony that I studied a very intricate territorial arrangement obtained. At places up to three nesting cavities were within about 2 meters of one another, and in these cases only the entrance to the nests was defended. In contrast, nests farther apart seemed to be so situated because their aggressive occupants kept other birds farther from the nest site. Conflicts arose most frequently in the upper part of the multi-branched nesting stub, where not only nests but tips of stubs were defended by nearby woodpeckers. Thus, an incoming, Long Calling woodpecker would land on such a perch, and out of a nearby nest would dart an attacking woodpecker who usually succeeded in driving the intruder away. Stubs far from nests, or equally far from two nests seemed to be shared by several pairs, or at least by several members of different pairs; these birds failed to attack one another



FIG. 14. Nesting colony of Hispaniolan Woodpecker in hills near Miches, northeastern Dominican Republic. By March 22 this tree contained at least 19 active nests. Several nesting cavity entrances can be seen, and birds at the holes, entering them (upper right), and within nests with head protruding (e.g., upper right; some seeming woodpecker heads are shelf fungi).

at the stub, but they drove away other intruders.

Some Hispaniolan Woodpeckers in the large colonies tended to dash out of the nest almost every time another woodpecker landed at all close. A conflict usually stimulated adults other than the combatants to peer out, or even call from their nests. Apparently nonnesting adults, perhaps attempting to locate a site in which to excavate a nesting cavity, frequented two of the largest colonies, and triggered many conflicts. Such birds were driven from one portion of the tree to another, and it was noted that they invariably were forced to the base of the nesting stub. There, sufficiently far below the lowest nesting pairs, they found sanctuary. Several newly excavated cavities I noticed late in my studies were in such low sites. These observations somewhat suggest a hierarchy in which more aggressive, dominant pairs occupy the upper, perhaps generally safer (from predators) part of the stub, whereas subordinate and late-nesting birds are relegated to lower nesting sites.

During my visit, most Hispaniolan Woodpeckers had completed excavation of their nests and presumably were laying eggs or incubating them. My observations suggest that more advanced nests, that is, those with large young, and especially those with young being fed at the entrance to the nest, largely were confined to nesting colonies. About half of the 19 nests in the Miches colony had adults feeding young by March 22, although four and perhaps five nests were newly excavated between March 10 and 22, or were being excavated on March 22. In contrast, most isolated nests seemed to have birds in the egg-laying or incubation stage. Nest sites include diverse live and dead trees, cacti (Wetmore and Swales, 1931), and telegraph poles. Palm trees and palm stubs are favorites, and the extensive palm-lined coasts (e.g., Santo Domingo eastward to the airport, and Barahona area) support up to two or three pairs per 100 meters of palms. In arid areas such as west of Azua every telegraph pole or every other one may have a nest of *M. striatus*. Evidently these poles are used year after year, for they often contained four, sometimes six or seven holes, yet most poles were used by only a single pair of woodpeckers. Nesting colonies seem invariably to occur in dead trees. Large colonies probably require a new stub yearly (the

19-nest Miches colony was initiated in 1973, according to local residents), as nesting cavities are newly excavated yearly, and a stub would be dangerously weakened with repeated use by many pairs. The availability of such stubs must limit severely the degree of social nesting, and likewise the yearly irregularity in availability of suitable stubs must cause great local fluctuation in the degree of social nesting.

Excavation of nests largely seems to be accomplished by the male, often with the female perched nearby. However, some females excavate, replacing their mates to take a turn. Excavating sessions of up to 95 minutes were noted. In some cases females waited beside the males for a time, then flew off, to return in Dihedral Flight Display and go through one or more Bowing and calling bouts with their mates. Occasionally copulation followed one of these displays, occurring in a tree near the nest. In one such case the female perched quietly for some time watching the excavating male, approached the male and Bowed; both then flew to a small tree 20 meters away. There both Bowed, especially the female, and called (Ta-a Call), and then the female turned crosswise on the branch, crouched, and was mounted for 20 seconds by her mate. The female then flew away and the male returned to the nest site and resumed his excavating. The six copulations that were observed all involved Bowing Displays, and pairs engaged in excavating nests. The general hubbub about nesting colonies prevented me from ascertaining the particular vocalizations that accompanied most of the copulations.

Four to five eggs comprise the clutch of *M. striatus* according to Wetmore and Swales (1931). Presumably the eggs in a nest are the products of but a single pair of birds. However, in three cases either more than two birds associated at one nest, or a woodpecker associated with two nests. On two consecutive days at the large Miches colony I saw one female Hispaniolan Woodpecker enter two consecutive nests situated 6 meters apart. One nest was occupied on the first day, and the female exchanged Bows, then entered the first nest, after which it moved to, and entered an unoccupied nest, in each case remaining inside very briefly. On the next day the second of the above nests was occupied, and the

female exchanged places with a male at that nest after having left the (unoccupied) other nest. Two other nests in that colony were entered by another female on March 10. Both of these nests were unoccupied at the time of her visits. I could see no food in the bills of these females, which, if feeding, must have done so by regurgitation. On March 15 at Barahona an isolated nest in a loose colony consisting of three nests in a palm grove separated from one another by 70 meters or more, was visited by two females at once. The male inside the nest at the time exited and left. The two females showed no overt aggression, but one, bearing something in her bill entered the nest. The other female waited beside the nest for nearly a minute and when the female in the nest came out and flew off, the other female entered the nest, remaining therein for eight minutes until the male returned; after Bowing to the male this female flew away. The last of these episodes might have been a helper situation, perhaps with a female from the brood of the previous year remaining with its parents to help in their next nesting effort. The other two cases suggest that individual birds occasionally may be active with respect to several nests, either as a helper or perhaps sharing more actively in the nesting endeavors. It is not inconceivable that two females sometimes actively are involved and lay eggs in the same nest. Communal nesting efforts involving participation of birds at more than one nest are known in the Picidae only among species of *Melanerpes* (see Short, 1970a, pp. 10-11, for discussion of *M. cruentatus* and *M. formicivorus*).

I have few data concerning incubation of eggs. At one nest in which incubation presumably occurred, the male and female replaced each other every 67 minutes on the average over a 270-minute period. Several other observations indicate approximately hourly replacement of the adults during incubation.

Newly hatched young were brooded by the adults, especially during rains. Fecal sacs were removed irregularly by the adults, and carried away from the nesting site. Both sexes participated in removal of fecal sacs.

Wallace reported (MS, pp. 31-32) that Hispaniolan Woodpeckers carry food materials to the young in the esophagus and buccal cavity, and feed them indirectly by regurgitation. In diverse

parts of the Dominican Republic I observed adults feeding nestlings both indirectly and directly. Often these methods were alternated, as for example by a female, away from the nest for an extended period of time. When she returned to the nest she regurgitated food to the young, then flew to a nearby shrub, pulled a large insect from a flower, and returned quickly to the nest to feed the item to a nestling. About half of the feeding was estimated to involve regurgitation, as inferred from there being no visible food items in the bills of adults returning, presumably to feed. Regurgitated food probably consists mainly of tiny insects. Of the food passed directly to the nestlings, about half was of individual large insects (e.g., a mayfly-like insect) and the remainder of individual berries or other fruits.

Both sexes employed the two means of feeding the young. In those few cases in which I was able to observe the feeding at a particular nest the female parent fed the young more often, indeed up to twice as often as the male. During seven morning hours, at five different nests, there were seven to 14 feedings per hour. One sequence at a nest is as follows (R denotes regurgitated food, I symbolizes a large, single insect fed directly, and F a berry or other fruit): Male: 07:33 (R), 07:51 (R), 07:53 (I), 08:33 (R). Female: 07:49 (R), 07:54 (I), 07:57 (R), 08:04 (F), 08:05 (I), 08:08 (R), 08:09 (I), 08:16 (I), 08:24 (R). After the 08:04 and the 08:08 feedings the female flew to a tree near the nest and soon was able to procure a large insect of some sort. Further data are needed in order to permit a full analysis of the role of the sexes in feeding the young.

I have no data concerning post-fledging feeding of the young (see Wallace, MS). Obviously Hispaniolan Woodpeckers are an excellent subject for studies in the development of sociality in family groups, especially families from the various-sized colonies.

The nesting habits and sociality of *M. striatus* bear comparison with those of the few other social woodpeckers. Among arboreal woodpeckers only two other melanerpine species nest so socially, namely *M. formicivorus* and *M. cruentatus* (Short, 1970a). Both of these species are communal nesters; several active nests in a colony are entered by various adults, there are no territories

effectively, and conflicts occur chiefly about favored perches. Indications of communal nestings are mentioned above for *M. striatus* (birds entering more than one nest, and more than two birds at one nest), and, although *striatus* largely maintains territories around nests in colonies, another tendency toward communal nesting is noted in the occurrence of some nests in proximity with little or no interactions among the pairs.

Other woodpeckers may cluster their nests somewhat, especially those nesting terrestrially (*Geocolaptes olivaceus*, Short, 1971a, 1971e; *Colaptes campestris*, Short, 1972), but only the terrestrial *Colaptes rupicola* (Short, 1972, see also Short, 1971a, 1971c) is social to the extent of placing numbers of nests close together in a dirt bank. There is no evidence that communal nesting behavior is exhibited by woodpeckers other than melanerpine species.

Among habits associated with nesting, the feeding of the young both directly and indirectly by *striatus* is unusual, but it simply reflects the varied diet of this woodpecker. Species of picids that regurgitate food to the young are those feeding on small insects, notably ants, whereas those species utilizing larger prey feed the young directly. The ability to employ both methods of feeding obviously is adaptively advantageous if plentiful foods of several types are available, particularly if predation is not severe. Regurgitation has the advantage of requiring fewer trips to the nest, whereas direct feeding requires more visits to the nest and greater risk of predation. Other factors enter the picture. One of these is the energy expenditure involved when woodpeckers fly perhaps greater distances to obtain small insects, when less energy is needed to obtain larger food items if these are available near the nest site. There also may be a social need for adults to visit their nest site more frequently; their presence and aggression may serve to discourage newcomers in their attempts to join the colony, thus maintaining adequate spacing of nests (too many nests may weaken the tree structurally, and may diminish seriously the available, accessible food supplies of the colony).

An interesting fact is the feeding of berries and other fruits to nestlings. Although species of *Picoides* are known to feed nuts to their young (e.g., *P. syriacus*, H. Winkler, personal commun.),

significant amounts of soft fruits are fed to the young only by *M. striatus* and other species of *Melanerpes* (*erythrocephalus*, Jackson, 1970, p. 8; *chrysauchen*, Skutch, 1967, p. 108; *carolinus*, Stickel, 1965, p. 115; and very probably *lewis*, Bock, 1970, *candidus*, Short, 1970a, and others such as *uropygialis* and *portoricensis*).

Systematic Discussion

The Hispaniolan Woodpecker universally was treated as congeneric with the "*Centurus*" group of *Melanerpes* until, during an era of excessive generic splitting, Miller (1915) erected for this species a monotypic genus, *Chryserpes*. His bases (p. 517) for such separation were what would be regarded today as trivial features of color pattern, plus the relatively straight, thick, sharply ridged culmen, stiff and compact crown and nape feathers, and very short upper tail coverts of *striatus* compared with species of "*Centurus*." The generic separation of *Chryserpes* did not find favor among taxonomists, who continued to treat *striatus* as congeneric with *Centurus*, or increasingly, with *Melanerpes* (see historical summary by Olson, 1972, p. 499).

Selander and Giller (1963), without field knowledge of *striatus*, concurred with Miller (1915) in the distinctiveness of this species. Again restrictedly comparing *striatus* with species of the *Centurus* group, Selander and Giller mentioned Miller's findings, and stressed these features of *striatus*: 1) the absence of barring on its flanks and under tail coverts; 2) the absence of a colored frontal region; 3) the short red upper tail coverts; 4) the olive and yellow body plumage; 5) the straight bill; and 6) its yellow or gold iris. Later, however, Selander studied *M. striatus* in the field, following which he reversed his stand, stating in a letter to James Bond (Bond, 1964, p. 7, quoted in Olson, 1972, p. 499-500) "I am sure that *striatus* is a melanerpine type, and . . . have no objection to putting it in *Centurus*." Both he and Bond pointed out that within *Centurus* the species *striatus* was somewhat aberrant.

Olson (1972), following a brief anatomical investigation, concluded on the basis of several anatomical features that *M. striatus* is not melanerpine, but is related to Cuban *Xiphidiopicus* and that these two genera are related to the campe-

therine-colapline picid assemblage. The anatomical features mentioned by Olson especially include a pneumatic opening in the head of the femur of "*Chrysperes*" and *Xiphidiopicus*, and the great development of a spur or flange on the otic cup in these two taxa, compared with *Melanerpes*. Other anatomical features mentioned by Olson do not seem to render *striatus* particularly distinctive. The search for characters supportive of his anatomical work prompted Olson (1972, p. 504) to overstress certain plumage characters (overlooking others, see below) of *striatus*, and to belittle (p. 500) the behaviorally based assessments of the relationships of this species rendered by taxonomists (i.e., Bond, Selander, and by implication Wetmore, who in Wetmore and Swales, 1931, pp. 291-292, 295, considered *striatus* to be melanerpine) having field experience with *M. striatus*.

I shall return to morphological aspects of the relationships of the Hispaniolan Woodpecker, but first I wish to consider the taxonomic implications of my behavioral and ecological data, and some zoological considerations.

Behavior and Ecology. A full and final appraisal of the taxonomic implications of the Hispaniolan Woodpecker's behavior and ecology is not possible, of course, for we need more study of this species and, especially, comparable data for other species of woodpeckers. Nevertheless, our current knowledge permits a preliminary appraisal. Under circumstances of limited available knowledge, it is best to concentrate attention on two categories of features that are apt to prove useful taxonomically. One category includes features that are highly unusual, and may be shared, derived traits, inferring relationship of the taxa bearing them. The other category includes sets of functionally related, complex traits present in various forms within a group, and differing substantially from (presumed) functional equivalents in other groups; a species having some or most aspects of a distinctive set of such traits, and lacking all aspects of equivalent sets in other groups is likely to be related to taxa with which it shares traits. Along these lines my data range from suggestive to compelling. The comments are offered within a framework of field experience with over 110 picid species representing all genera of Picidae but *Xiphidiopicus*.

General Appearance and Movements: The Hispaniolan Woodpecker, unlike most picids, is highly conspicuous, drawing attention to itself by frequent, loud vocalizations, by flights from tree to tree in the open, and by frequent interactions among individuals. In my experience melanerpine woodpeckers tend to be the most conspicuous, among the most vocal, and certainly the most interactive of picids. The flight of *striatus* resembles that of melanerpine species such as *M. cruentatus*. I regard this information as suggestive; *M. striatus* would be unusual in these respects within any assemblage of woodpeckers other than the melanerpine group.

Diet: Many picids consume fruits seasonally, but entirely subsist on insects during most of the year. The diet of *M. striatus* is highly variable, apparently throughout the year, and fruits are fed to nestlings in significant amounts. Melanerpine woodpeckers consume great quantities of plant materials, and some feed fruits to young birds. To my knowledge no other group of picids feed soft fruits regularly to young in the nest. Certainly colapline, and very probably campetherine woodpeckers do not feed fruits to nestlings, and they are less frugivorous (seasonally) generally than are melanerpine species. The omnivorous habits of melanerpine species probably are a reason why this group, to the exclusion of all picids except the Antillean Piculet (and *M. striatus* if it be excludable), successfully has colonized the West Indian islands south of Cuba (and Grand Cayman). The diet of *M. striatus* is suggestive of melanerpine relationships.

Demonstration Drumming: Unfortunately, little is known of demonstration drumming in woodpeckers, although it seems widespread among melanerpine species. It occurs in *M. striatus*. Demonstration drumming is unknown in colapline and campetherine woodpeckers. There is thus the merest suggestion that *striatus* is melanerpine-like in this feature. I should note that the apparent absence of typical drumming in *striatus* is not taxonomically useful information, although mentioned by Olson (1972, p. 504), because melanerpine species vary greatly in the amount of drumming utilized. *Melanerpes lewis*, for example, drums only seasonally (Bock, 1970), *M. portoricensis* long was thought not to drum (it does—very weakly and uncommonly,

Wallace, MS), and species such as *M. candidus* may never drum. Campetherine and colapline woodpeckers also vary in the extent of their drumming, some vigorously and others not at all (Short, 1971e, 1972).

Call Notes: The Hispaniolan Woodpecker has two single-noted calls, the Wup Call and the Ta Call. The first of these closely resembles the Chip-Chup-Chut call complex of various melanerpine species (see above). The Ta Call of *striatus* somewhat resembles the Wa Call of *M. herminieri* (see above), and through intermediate Ta-Waa calls, the Ta Call grades into the Waa Call (see below). Colapline woodpeckers generally have no call notes or notes unlike those of *striatus* (Short, 1972; a campetherine- or picoidine-like "pic" note is known for *Veniliornis spilogaster*, Short, 1970a, p. 18). Campetherine woodpeckers have a simple call note (Short, 1971e) unlike the Wup or Ta calls of *striatus*. I consider the call notes rather strongly suggestive of the melanerpine affinity of *striatus*.

Chur-like Calls: These calls are widespread within *Melanerpes*, and are unlike calls of other woodpeckers. As complex series of connected notes, these calls (Kweer, Chur, Waa; see discussion above), or calls like them are lacking in colapline woodpeckers. Among campetherine species, a somewhat similar (soft, nongrating "chuur") call was heard from *Campethera bennettii* (Short, 1971d) as a localization call between adults and young; no other of 12 campetherine species that I have heard had such a call. *Mulleripicus pulverulentus* employs a Whinny Call (Short, 1973b) having some resemblance in form to Chur Calls. The Waa Call of *striatus* very closely resembles the Waa Call of *Melanerpes superciliosus*, and resembles closely the Chur or Kweer calls of other melanerpine species also. The Bdddt Call of *striatus* (see above) shows some similarities to Churlike calls, especially the Chur-Rattle Call of *Melanerpes erythrocephalus*. I believe that the evidence from Waa and Bdddt calls is strongly suggestive of the melanerpine relationship of *striatus*. Overall, the vocal repertoire offers compelling evidence that *striatus* is a melanerpine woodpecker. There are resemblances to *Melanerpes* in details of all calls, and in the kinds of calls used. The Wup Call, the Ta and Waa call complex, and the Bdddt Call of *striatus* show no

similarities to calls of colapline woodpeckers. Further, the characteristic alarm call of at least some colapline species, and unusual calls (e.g., whistled calls) characteristic of species within that assemblage (Short, 1972) are not found in *striatus*. Vocal similarities between *M. striatus* and colapline species are found in the Ta-a (Wicka) Call, and the Rattle-Long Call of *striatus*, but similar calls also are found in such melanerpine species as *M. carolinus*, and indeed are widespread among woodpeckers (e.g., in *Picus*, *Dinopium*, *Meiglyptes*, *Dryocopus*, and others; Short, 1973b).

Bowing and Swinging: The Bowing and Swinging displays of *M. striatus* are separate displays, used in different circumstances. The Bowing Display is repetitive and the Swinging Display is slow and nonrepetitive. These displays occur in similar form in melanerpine woodpeckers. In colapline species the Bowing (Bobbing) Display is more rapid, the Swinging Display is more rapid also, and both are used simultaneously as a display complex in agonistic encounters (Short, 1970a, 1972); campetherine species are poorly known, but generally resemble colapline species (Short, 1971e). These displays in *striatus* suggest its relationship with melanerpine species.

Flight Display: The Dihedral Flight Display of *striatus* is a brief, essentially gliding display rendered in the last few meters before one bird lands beside another (usually its mate). This form of flight display is found in melanerpine woodpeckers. Colapline and campetherine species are not known to have flight displays. In other woodpeckers with flight displays e.g. in *Picoides* (Short, 1971b, MSb), the displays last longer, differ in form, and are given under different circumstances. The Dihedral Flight Display of *striatus* suggests its relationship to melanerpine species.

Courtship Feeding: This display is known for so few picids that it is barely worth mentioning, but I note that it is lacking in colapline species that I have studied, and it occurs in *striatus* and at least a few melanerpine species.

Social Nesting: The degree of social nesting indulged in by *striatus* is matched only by a few melanerpine species and by terrestrial *Colaptes rupicola*, and otherwise is approached only by terrestrial species of *Geocolaptes* (a campetherine genus) and *Colaptes* (see above). Communal nest-

ing is known only in melanerpine species, and a tendency toward it is found in *striatus*. Thus, there is a suggestion that *striatus* is melanerpine.

The available behavioral and ecological data are in accord with the view that *M. striatus* is related to, and not markedly different from, melanerpine woodpeckers. On the other hand, differences of *striatus* from colaptine and campetherine woodpeckers, and other picid assemblages insofar as they are known, are remarkable and numerous.

Zoogeographical Considerations. Aside from the Bahamas, on which is found the mainland North American *Picoides villosus*, the West Indies support 10 breeding woodpeckers (Bond, 1971) of these tribes: Nesotitini (one species); Colaptini (two species); Melanerpini (six species, including *M. striatus*); and Dryocopini (one species). Only the piculet tribe Nesotitini, with its monotypic species and genus, and the Melanerpini occur south and east of Cuba, the Isle of Pines, and Grand Cayman. On Cuba are five picids, the two Colaptini (partly terrestrial flickers *Colaptes auratus*, the same species of which occurs throughout North America, and *C. fernandinae*, an endemic, more terrestrial form), the single member of the Dryocopini (*Campephilus principalis*, barely subspecifically distinct from North American populations of this species), and two Melanerpini (the distinctive, endemic, monotypic genus *Xiphidiopicus* and *Melanerpes supercilialis*, which forms a superspecies with North American mainland *M. carolinus*).

Disregarding *M. striatus* for the moment, we are left knowing that only the piculet and species of *Melanerpes* have been able to colonize successfully the other large islands of the Greater Antilles beyond Cuba, even to the Lesser Antilles. *Melanerpes portoricensis* of Puerto Rico, *M. radiolatus* of Jamaica, and *M. herminieri* of Guadeloupe are the species involved.

Being broadly adaptable in regard to foraging and diet, and tending to be social in habits, it is not surprising that melanerpine species are the colonizers of the West Indies. Ant-foraging habits and partial terrestriality probably has discouraged colaptine species, and certainly species of that group derived from North America and Cuba, from colonizing other West Indian islands. On the other hand, given the melanerpine species

on Cuba, the Bahamas, Grand Cayman, Puerto Rico, Jamaica, and Guadeloupe, it seems likely that massive, ecologically varied, and centrally located Hispaniola would have been colonized by some melanerpine species. If indeed *M. striatus* of Hispaniola is entirely unrelated to the melanerpine group, and belongs "in or near the campetherine-colaptine assemblage" as Olson stated (1972, p. 505), then it is peculiar that Hispaniola should lack a melanerpine woodpecker, which presumably could coexist with as different a picid as *striatus* would be if Olson were correct.

It seems to me implausible that Hispaniolan *M. striatus* should be the only campetherine woodpecker outside Africa, and I reject that possibility. The only West Indian colaptine species are ant-foragers that have not colonized beyond Cuba and Grand Cayman. The Hispaniolan Woodpecker is not an ant-forager, and differs greatly in habits from the Cuban flickers. Typically arboreal Colaptini (*Piculus*, *Veniliornis*) have failed to reach the West Indies. The species of *Piculus* are ant-foragers with behavior very like *Colaptes*, from which *Piculus* barely is separable. *Veniliornis* is arboreally more specialized, but its species are small, and its morphology and behavior are colaptine (Short, 1970a). It seems unlikely that *striatus* represents a colaptine species. Rather it is reasonable to expect that Hispaniola, like its sister islands, was colonized by an ancestral melanerpine species that gave rise to *M. striatus*. It seems reasonable zoogeographically that the relatives of *striatus* should be sought nearby, in the West Indies, and not elsewhere in the Neotropics, or in Africa.

Morphology. Morphological features to be discussed can be categorized as internal anatomical, external structural, and plumage coloration. Not being an anatomist, I cannot discuss the anatomical characters of *striatus* described by Olson (1972). I am not certain of the taxonomic level at which these traits might be useful, and indeed I doubt that shallow, nonfunctionally based anatomical studies can provide taxonomically useful information concerning such a highly specialized family as the Picidae (specialized for "woodpecking"; many diverse character complexes are involved throughout the body of woodpeckers). This doubt is not removed when

it can be said of one of the anatomical features of *striatus* described by Olson (1972, p. 501), "It is difficult to perceive what advantages might accrue to *Chrysoperpes* and *Xiphidiopicus* by having this pneumatic modification of the femur." Olson's supposed anatomical evidence for setting *striatus* apart from the melanerpine assemblage, and within the campetherine-colapline group of picids seems meager, and needs reinterpretation viewed in light of contradictory evidence I present in this report. Bond (1973) recently has expressed similar doubts about Olson's (1972) findings regarding *striatus*, and relegates the anatomical features cited by Olson to no more than sub-generic importance.

Three external structural characters were stressed by Miller (1915; traits mentioned above) in establishing the new genus *Chrysoperpes* for *striatus*. I find the shape of the bill of the Hispaniolan Woodpecker to be at an extreme among species of *Melanerpes*, but it seems not to differ fundamentally from that of its congeners, especially because the bill varies considerably in this group. For example, within the superspecies *Melanerpes chrysauchen*, straight-billed *M. flavifrons* differs considerably (also approaching *M. striatus*) in bill shape from closely related *M. chrysauchen* and *M. cruentatus*. The rather stiff crown feathers of male Hispaniolan Woodpeckers, mentioned by Miller, are not highly modified in view of the considerable variation in feather structure among its congeners, as for example, *M. lewis* compared with related *M. erythrocephalus* and *M. formicivorus*. The short upper tail coverts of *striatus* are an interesting feature for taxonomic consideration at the species level, but hardly call for generic separation of *striatus*, especially since red feathers such as those of the upper tail coverts are more fragile and tend to be shorter than feathers bearing melanic pigments (e.g., see Short, 1970b, for discussion of red and black crest feathers in *Campephilus*). Miller's separation of *Chrysoperpes* from *Centurus* (which he clearly considered to include the closest relatives of *striatus*, see Miller, 1915, p. 519) must be viewed in the framework of other splitting that he advocated, including recognition of *Linneopicus* (for *Melanerpes herminieri*). Miller's extreme position is indicated by a footnote (*loc. cit.*) in which he expresses displeasure with asso-

ciation in one genus of *Melanerpes erythrocephalus* and *M. portoricensis*, "especially when the rather fine distinctions between the other genera of the group . . . are considered."

Plumage patterns of woodpeckers provide extremely useful taxonomic information, especially where complex patterns are involved. Particularly useful are consistent patterns of sexual dimorphism, and patterns of the foreparts and head, often employed in displays. In the current state of our anatomical knowledge of woodpeckers, I place greater taxonomic reliance on such plumage patterns, and on certain features of behavior than can be placed on anatomy.

The fact that, in the absence of comprehensive morphological studies, most avian taxonomists have allied *striatus* with *Melanerpes* (or "*Centurus*") rather clearly indicates that there is a basic overall plumage pattern similarity of *striatus* with melanerpine species. To state that the dorsal barring of *striatus*, shared with the *Centurus* group of *Melanerpes*, "has no doubt been the major factor masking the true affinities of *striatus*" (Olson, 1972, p. 504) is simplistic, for, in fact, the various patterns of the head, crown, underparts, and upperparts precisely resemble those found within *Melanerpes*. More particularly, the combination of these patterns is matched only by some melanerpine woodpeckers. Furthermore, this combination is similar to that of no other picid group.

The head pattern of *striatus* is that of a melanerpine woodpecker of the *Centurus* group. There are a crown and nape patch, broad superciliary stripes that restrict the crown patch, and a broad area, including the forehead and forecrown, outside of the crown patch in *striatus*. The forehead, superciliary stripes, sides of the head, lower neck and throat are concolored, as in *M. superciliaris*, *M. radiolatus*, and many other species of *Melanerpes*. Importantly, the sexes are distinguished, and presumably distinguish one another, by the presence of an anteriorly and laterally restricted red crown patch, connected to the red nape in males, and the presence of a black crown patch in females. There is no indication of malar markings, or of a difference in nape patch between the sexes, both of which are colapline patterns also found in campetherine species. West Indian colapline woodpeckers have a malar pattern of sex-

ual dimorphism; the loss of such a pattern, and assumption of a melanerpine-like crown pattern in a colaptine ancestry of *striatus* would have been unlikely. The restricted crown patch, differing in color between the sexes obtains in various melanerpine species, the female either having no patch (entire head concolored), or exhibiting a black patch (e.g., in *M. pucherani*) as in *striatus*. The nasal tufts are brightly colored in many melanerpine species, but others with a pale frontal patch lack such color (e.g., *M. formicivorus*, and even *M. uropygialis*), so the lack of yellow or red in the nasal tufts of *striatus* is not significant (see Miller, 1915, and Selander and Giller, 1963). The white streaking in the edges of the crown patch in some females of *striatus* (see Olson, 1972) is interesting in view of the white streaking occurring regularly in females of *Xiphidiopicus*, but may represent an ancestral picid condition (such spotting and streaking are common in piculets and in many woodpecker groups). In any event these markings neither suggest relationship of *striatus* and of *Xiphidiopicus* with some other picid group, nor preclude these species being melanerpine. The head patterning of *striatus* thus in itself is strong evidence for the melanerpine relationship of this picid.

The barred upperparts of *striatus* resemble those of many woodpeckers, but it is noteworthy that barred-backed melanerpine woodpeckers other than *striatus* occur in islands of the West Indies near Hispaniola. The yellow-green color of the paler barring is not found in melanerpine woodpeckers other than *striatus* and *Xiphidiopicus*, but *M. radiolatus* of Jamaica, and some *M. superciliaris* (e.g., *caymanensis*) show green tendencies. Green coloration occurs in piculets, and in various woodpeckers, including the colaptine and campetherine groups; it is apt to be retained in primitive picid groups, and to recur sporadically in various picid assemblages. One or more of the early, ancestral West Indian melanerpine species may have been greenish in color. At any rate, green coloration is insufficient reason to suggest relationship with other green-colored picid groups, as Miller (1915, p. 519) recognized in comparing, and rejecting relationship of *striatus* with the green-colored, colaptine *Chloronerpes* (= *Picus*). Likewise, the red upper tail coverts of *striatus* do not suggest relationship with picids

other than the melanerpine group, although unique in that group. Various picid assemblages sporadically have red-rumped species; among colaptine woodpeckers only two species, not closely interrelated and both in *Veniliornis*, have red in the rump or upper tail coverts, but this feature is treated properly as a species-level character in this group. Quite independently, Bond (1973, p. 6), criticizing Olson's (1972) conclusions, has made the same point, also citing *Veniliornis* as indicating that the red upper tail coverts of *striatus* "is of specific, not generic consequence."

The underparts of *striatus* are rather more olive than is found in other species of *Melanerpes*, but given the underpart color of *M. radiolatus*, and of *M. portoricensis* (posterior underparts only), I see no substantive difference between *striatus* and species of *Melanerpes* in this feature. The absence of barring on the flanks and abdomen of *striatus* has been stressed by the several authors considering the status of this woodpecker. Of course many species of *Melanerpes* lack barring on the abdomen (e.g., *M. lewis*, *M. erythrocephalus*, and West Indian *M. portoricensis* and *M. herminieri*). However, I note that many specimens of *striatus* have fine streaks on the abdomen and undertail coverts, some have strong streaking there, one has faint barring on the undertail coverts, and one (AMNH 487802) has distinct, although weak black barring on the flanks and sides of the belly (several specimens also show faint breast or throat streaks, reminiscent of those in *Melanerpes formicivorus* and *Xiphidiopicus percussus*). I suggest that the ancestor of *M. striatus* may have had a barred abdomen and streaking there or elsewhere on the underparts. Many species of *Melanerpes*, especially those of the *Centurus* group, show red, orange, or yellow coloration in the center of the abdomen. Of about 150 Hispaniolan Woodpecker specimens that I examined, nine show slight to moderate, and four show moderate to strong orange-red or reddish coloration on the belly. This abdominal color strongly suggests melanerpine relationship of *striatus*, as the trait is not that of other New World picids (absent in colaptine species); although several species have red in the abdomen, it is not particularly a feature of campetherine woodpeckers either.

The pale eyes of *striatus* are not unique in melanerpine woodpeckers, as *M. cruentatus* has similarly colored eyes. Eye color is not a very useful trait taxonomically in picids, for it may vary intraspecifically (e.g., in *Piculus chrysos-chloros*, Short, MSa). Likewise, the lack of white barring in the central tail feathers of *striatus*, found in many species of *Melanerpes*, is not useful taxonomically; other species of this genus, even West Indian *portoricensis* and *herminieri*, also lack these white marks.

The most striking color characteristic of *M. striatus* is its white and black neck patches. These are unique in picids, and therefore of no use in establishing relationships. Its red upper tail covert color is unusual. Other than these taxonomically not very useful traits, I see nothing distinctive in the coloration of *striatus*, and those aspects of its coloration that are suggestive of relationship all point toward relationship of *striatus* with *Melanerpes*.

Taxonomic Conclusions. Evidence derived from the behavior, ecology, zoogeography, and morphology of the Hispaniolan Woodpecker leaves little doubt that it is a melanerpine woodpecker. Only in several anatomical features, and in a few external morphological characters does this species differ from other melanerpine species (except in some cases *Xiphidiopicus*). These differences are apt to be insignificant taxonomically, and in fact they do not, alone or together, point toward relationship of *striatus* with other than the melanerpine assemblage. Having considerable evidence for a melanerpine relationship of *striatus*, and lacking evidence for any other relationship, I consider this species to be melanerpine.

Within the melanerpine assemblage I recognize the genera *Melanerpes*, *Xiphidiopicus*, and *Sphyrapicus*. Separation from *Melanerpes* of other, particularly monotypic, genera such as *Asyndesmus*, *Balanosphyra*, *Leuconerpes*, *Linneopicus*, and *Trichopicus* seems unwarranted; their recognition would obscure the greater distinction of *Xiphidiopicus* and *Sphyrapicus*. I find no valid reason for separation of, or points at which to separate the continuum *Centurus-Tripsurus-Melanerpes*, and extremes in this group differ from one another as much or more than do any of the genera mentioned above (other than *Xiphidio-*

picus and *Sphyrapicus*) from *Melanerpes*. Within this framework *striatus* seems to me no different from other *Melanerpes* than is, say *Trichopicus*, and hence I do not consider *Chryserpes* generically separable from *Melanerpes*. Apparently *striatus* has no living close relative, but it may have evolved from an early ancestor of the "*Centurus*" group. *Xiphidiopicus*, which is bizarrely plumaged, but shows some resemblance to such species as *Melanerpes formicivorus*, *M. cactorum*, and species of *Sphyrapicus* (and no resemblance to other picid groups; see also Bond, 1973) may have evolved earlier from stock that gave rise to the *Centurus* group and to *striatus*. I thus concur with Olson's (1972) contention that *Xiphidiopicus* and "*Chryserpes*" are related, but they fall within the melanerpine assemblage.

My broad generic concept has a function other than the suppression of all but the most distinct monotypic genera. Monotypic genera, unless highly distinctive, ought to be discouraged, simply because a genus consists of a group of related species and monotypic genera do not. I believe that within radiating groups such as the melanerpine assemblage, genera ought to represent truly distinctive groups, especially those showing a divergent ecology backed by its proof—radiation within the group (e.g., *Sphyrapicus*). In a genus undergoing radiation there ought to be different levels of distinctiveness among its species. A helpful aid to the appreciation of such levels is the occurrence of sympatry among congeners. One can use these levels, with other phylogenetic data, in establishing a taxonomic hierarchy within the genus, from subgenera, to species groups, to superspecies. Such an arrangement within *Melanerpes* is not possible at this time, because too little is known about many species. However, I prefer to stress the relationships within the melanerpine group, and not to mask its most distinctive taxa by recognition of various monotypic genera such as *Chryserpes*. It may be preferable to retain *Chryserpes* as a subgenus within *Melanerpes* (see Bond, 1973), but I am not convinced of that.

Melanerpes striatus is recognized as monotypic, although Miller (1915, p. 519) stated that "There is a little doubt that . . . [it] . . . consists of two or three races differing chiefly if not wholly in size." More particularly, Kaempfer

(1924) suggested that highland birds were larger, with heavier bills than lowland birds. Wetmore and Swales (1931, p. 295) found variation in this species to be "entirely individual." There is indeed great individual variation, even in seasonally comparable samples, but my examination of specimens so far has shown that the longest-winged birds consistently come from the highlands. As yet I have not seen enough highland specimens to establish whether the magnitude of the difference warrants subspecific recognition of the highland population. Certainly there are no trenchant features of this highland population, and I tentatively retain monotypic treatment of *Melanerpes striatus*.

LITERATURE CITED

- Ashmole, N. P.
1967. Sexual dimorphism and colonial breeding in the woodpecker *Centurus striatus*. *Amer. Nat.*, vol. 101, pp. 353-356.
- Bock, C. E.
1970. The ecology and behavior of the Lewis Woodpecker (*Asyndesmus lewis*). *Univ. California Publ. Zool.*, vol. 92, pp. 1-91.
- Bond, J.
1964. Ninth supplement to the check-list of birds of the West Indies (1956). *Acad. Nat. Sci. Philadelphia*, pp. 1-13.
1971. *Birds of the West Indies*. Second ed. Boston, Houghton Mifflin Co., pp. 1-256.
1973. Eighteenth supplement to the check-list of birds of the West Indies (1956). *Acad. Nat. Sci. Philadelphia*, pp. 1-12.
- Cherrie, G. K.
1896. Contributions to the ornithology of Santo Domingo. *Field Colombian Mus.*, publ. 10, ornith. ser., vol. 1, pp. 1-26.
- Danforth, S. T.
1929. Notes on the birds of Hispaniola. *Auk*, vol. 46, pp. 358-375.
1939. The birds of Guadeloupe and adjacent islands. *Jour. Agr., Univ. Puerto Rico*, vol. 23, pp. 9-46.
- Jackson, J.
1970. Observations at a nest of the Red-headed Woodpecker. *Niobrara* (1968-1969) (Ann. Rept. Univ. Kansas, Mus. Nat. Hist.), pp. 3-10.
- Kaempfer, E.
1924. Ueber das Vogelleben in Santo Domingo. *J.F. Ornith.*, vol. 72, pp. 178-184.
- Kilham, L. J. F.
1958. Pair formation, mutual tapping and nest hole selection of Red-bellied Woodpeckers. *Auk*, vol. 75, pp. 318-329.
1959. Mutual tapping of the Red-headed Woodpecker. *Ibid.*, vol. 76, pp. 235-236.
1961. Reproductive behavior of Red-bellied Woodpeckers. *Wilson Bull.*, vol. 73, pp. 237-254.
- Miller, W. DeW.
1915. Three new genera of birds. *Bull. Amer. Mus. Nat. Hist.*, vol. 34, pp. 515-520.
- Olson, S. L.
1972. The generic distinction of the Hispaniolan Woodpecker, *Chrysoperes striatus* (Aves: Picidae). *Proc. Biol. Soc. Washington*, vol. 85, pp. 499-508.
- Ridgway, R.
1914. The birds of North and Middle America. Part VI. Washington, Govt. Printing Office, xx + 882 pp.
- Sallé, M. A.
1857. Liste des oiseaux rapportés et observés dans la République Dominicaine. *Proc. Zool. Soc. London* (1857), pp. 230-237.
- Selander, R. K.
1966. Sexual dimorphism and differential niche utilization in birds. *Condor*, vol. 68, pp. 113-151.
- Selander, R. K., and D. R. Giller
1963. Species limits in the woodpecker genus *Centurus* (Aves). *Bull. Amer. Mus. Nat. Hist.*, vol. 124, pp. 215-273.
- Short, L. L.
1970a. Notes on the habits of some Argentine and Peruvian woodpeckers (Aves, Picidae). *Amer. Mus. Novitates*, no. 2413, pp. 1-37.
1970b. The habits and relationships of the Magellanic Woodpecker. *Wilson Bull.*, vol. 82, pp. 115-129.
1971a. Woodpeckers without woods. *Nat. Hist. Mag.*, vol. 80, no. 3, pp. 66-74.
1971b. The systematics and behavior of some North American woodpeckers, genus *Picoides*. *Bull. Amer. Mus. Nat. Hist.*, vol. 145, pp. 1-118.
1971c. The evolution of terrestrial woodpeckers. *Amer. Mus. Novitates*, no. 2467, pp. 1-23.

- 1971d. Notes on the habits of Bennett's Woodpeckers in Kruger Park. *Ostrich*, vol. 42, pp. 71-72.
- 1971e. Notes on South African woodpeckers. *Ibid.*, pp. 89-98.
1972. Systematics and behavior of South American flickers (Aves, *Colaptes*). *Bull. Amer. Mus. Nat. Hist.*, vol. 149, pp. 1-109.
- 1973a. Habits, relationships, and conservation of the Okinawa Woodpecker. *Wilson Bull.*, vol. 85, pp. 5-20.
- 1973b. Habits of some Asian woodpeckers (Aves, *Picidae*). *Bull. Amer. Mus. Nat. Hist.*, vol. 152, pp. 253-364.
- [MSa] The Green-barred Flicker and Golden-green Woodpecker of South America.
- [MSb] Habits and interactions of North American three-toed woodpeckers (*Picoides arcticus* and *P. tridactylus*).
- Skutch, A.
1967. Family life of the Golden-naped Woodpecker. *Animal Kingdom*, vol. 70, pp. 106-111.
- Stickel, D. W.
1965. Territorial and breeding habits of Red-bellied Woodpeckers. *Amer. Midland Nat.*, vol. 74, pp. 111-118.
- Verrill, A. E., and A. H. Verrill
1909. Notes on the birds of Santo Domingo, with a list of the species, including a new hawk. *Proc. Acad. Nat. Sci. Philadelphia* (1909), pp. 352-366.
- Wallace, R. A.
[MS.] Sexual dimorphism, niche utilization, and social behavior of insular species of woodpeckers. Ph. D. thesis (unpubl., 1969), Univ. of Texas, Austin, vi + 97 pp.
- Wetmore, A., and B. H. Swales
1931. The birds of Haiti and the Dominican Republic. *Bull. U. S. Natl. Mus.* no. 155, pp. 1-483.

