

BULLETIN

of the
FLORIDA STATE MUSEUM
Biological Sciences

Volume 22

1977

Number 4

ECOLOGY AND BEHAVIOR OF THE JAMAICAN WOODPECKER

ALEXANDER CRUZ



UNIVERSITY OF FLORIDA

GAINESVILLE

Numbers of the BULLETIN OF THE FLORIDA STATE MUSEUM, BIOLOGICAL SCIENCES, are published at irregular intervals. Volumes contain about 300 pages and are not necessarily completed in any one calendar year.

OLIVER L. AUSTIN, JR., *Editor*

RHODA J. RYBAK, *Managing Editor*

Consultants for this issue:

OLIVER L. AUSTIN, JR.

JEROME A. JACKSON

Communications concerning purchase or exchange of the publications and all manuscripts should be addressed to: Managing Editor, Bulletin; Florida State Museum; University of Florida; Gainesville, Florida 32611.

This public document was promulgated at an annual cost of \$2,193.63 or \$2.193 per copy. It makes available to libraries, scholars, and all interested persons the results of researches in the natural sciences, emphasizing the circum-Caribbean region.

ECOLOGY AND BEHAVIOR OF THE JAMAICAN WOODPECKER

ALEXANDER CRUZ¹

SYNOPSIS: Jamaican Woodpeckers (*Melanerpes radiolatus*) occur wherever habitats are suitable, from sea level to high elevations. Their presence depends on the occurrence of trees necessary for feeding, nesting, and roosting. Highest densities were recorded in a wooded pasture and a mesophytic forest, with an average of 22 and 20/km, respectively. The high figures for these locales are possibly related to their structural complexity—well developed vertical stratification, high tree species diversity, and numerous epiphytes, all of which increase both the area available for foraging and the amount of foods present. Censuses in Jamaica and Florida indicate that in some habitats the Jamaican Woodpeckers maintain comparable or higher densities and biomass than do several species of Florida woodpeckers in comparable habitats. Possible explanations are: Jamaican Woodpeckers have more resources available in the absence of other species with similar habitats, Jamaica has fewer predators than Florida, Jamaican habitats are more complex than comparable Florida habitats, and primary productivity is probably greater in Jamaica than in comparable Florida habitats.

No selection pressure for differential niche use between the sexes appears to have acted on the Jamaican Woodpecker—the sexes are structurally monomorphic, forage in similar fashions, are syntopic, and take the same food. Food and foraging sites, which would be the two most important selective forces, appeared to be more abundant in Jamaica than on some other islands. When food is plentiful, both sexes profit by having a longer bill, for large predators (implied here by longer bill lengths in birds) eat either an equal or a greater range of foods than smaller predators. Bill size is also a good indicator of food size: birds with longer bills usually obtain larger prey items than birds with smaller bills. As greater prey size implies greater biomass, which in turn implies more calories and more energy, the sexes are thus equally efficient in obtaining energy from the environment. In addition one might argue that by decreasing both the body size and bill size of the female, the female will be less efficient in protecting the nesting hole against competitors, of which several species are present on Jamaica.

The predominant foraging methods of the Jamaican Woodpecker are fruit-eating (28%), probing (28%), and pecking (20%). Gleaning, sallying, and probing into bromeliads accounted for the remainder.

In the Jamaican Woodpecker's diet both animal and vegetable matter are well represented, comprising 58.2% and 42.7%, respectively, of the total volume. The large and varied numbers of foods taken strongly suggest that the Jamaican Woodpecker is diverse and opportunistic in its feeding habits. The foraging behavior diversity of the Jamaican Woodpecker and of seven species of Florida woodpeckers was measured by the Shannon-Weaver information theory formula. The foraging diversity index of the Jamaican Woodpecker was higher than any one species of the Florida woodpeckers studied, and was almost equivalent to the pooled foraging diversity indices of Florida woodpeckers, 1.59 to 1.72 respectively. No methods of feeding were noted in the Jamaican Woodpeckers that the mainland woodpeckers did not use, but the foraging methods were more evenly distributed in the different categories. There is no evidence that limitations in the range or amounts of available food resources is the factor underlying these changes in feeding methods, rather certain zones are incompletely exploited by other species in Jamaica; and hence it is profitable for *M. radiolatus* to extend into them.

Jamaican Woodpeckers occupy overlapping home ranges and territorial defense is restricted to the nest vicinity. The extended breeding season of at least 10 months is most likely a response to the more uniform tropical climate that provides sufficient food throughout the year.

¹ The author is Assistant Professor of Biology, Department of Environmental, Population, and Organismic Biology, University of Colorado, Boulder CO 80309. Portions of this paper were submitted earlier to the University of Florida in partial fulfillment of the Ph.D. degree (1973).

TABLE OF CONTENTS

INTRODUCTION	150
ACKNOWLEDGEMENTS	152
METHODS OF STUDY	152
DESCRIPTION OF STUDY AREAS	155
RESULTS AND DISCUSSION	159
DISTRIBUTION	159
HABITAT ANALYSIS	160
ABUNDANCE	162
FEEDING ECOLOGY AND BEHAVIOR	165
BREEDING BEHAVIOR AND BIOLOGY	184
VOCALIZATIONS	184
MECHANICAL COMMUNICATION	185
DISPLAYS	186
TERRITORY, TERRITORIALITY, HOME RANGE, AND NEST HOLE COMPETITION	186
THE ANNUAL BREEDING CYCLE	191
LITERATURE CITED	202

INTRODUCTION

The study of insular biogeography and ecology has contributed significantly to the development of evolutionary and ecological theories and concepts. By studying species on individual islands or groups of islands, biologists view a simpler microcosm of that seemingly infinite complexity of continental areas. By their very multiplicity and variation in shape, size, degree of isolation, and ecology, islands provide the necessary replications in natural experiments by which evolutionary and ecological hypotheses can be tested (MacArthur and Wilson 1967).

One of the basic tenets of island biology is that species diversity of island habitats is low in comparison to similar habitats on mainland regions (Darwin 1859, Wallace 1880). This concept has provided important opportunities for ecological investigations on competition, niche exploitation, and behavior patterns. Preston (1962), Hamilton and Rubinoff (1963), and MacArthur and Wilson (1963) have demonstrated that the number of species on an island depends upon diverse factors, the most important of which are: (a) the island's size, (b) its distance from a source of additional species, and (c) the structure of the habitat, which includes both topographic variation and the number of vegetational strata. MacArthur and Wilson (1967) expanded the above factors into an elaborate mathematical model of island biogeography, based on the tenet that the number of species of an island represents an equilibrium between immigration and extinction rates, the level of which depends primarily on the above factors. In the Greater Antillean region for instance, Cuba (the largest and closest island to the continental mainland) supports five resident species of woodpeckers, Hispaniola (the second largest) has two species, and the smaller islands of Jamaica and Puerto Rico each have one species. In contrast, 79 species of woodpeckers are found in South America and 39 species are found in North America (Meyer de Schauensee 1964).

Important studies of insular birds include those of Crowell (1961, 1962), Selander (1966), and MacArthur, Diamond, and Karr (1972) on Bermuda, Hispaniola, and Puerco Island respectively. Crowell's studies of three passerine bird species resident on both Bermuda and in the eastern United States demonstrated that absence of competition on the species-poor island of Bermuda has allowed these species to attain greater densities than they do in North America, although the total range of habitat use and feeding behavior lies within the range of their abilities in North America. Selander found that the Hispaniolan Woodpecker (*Melanerpes striatus*) has attained the ability to subdivide and perhaps expand the total feeding niche use of the population by evolving sexual dimorphism in the feeding apparatus (bill) accompanied by divergence in the foraging behavior of the sexes. In the more recent study on the Puerco Island avifauna, MacArthur *et al.* found that niche shifts between island and mainland (Panama) birds included habitat expansions, wider ranges of vertical foraging strata, and increase in numbers.

To test these important concepts, niche expansion and population density changes in the absence of related species and differential niche utilization between the sexes, and to examine the breeding biology and behavior of an insular species of bird, I studied the endemic Jamaican Woodpecker (*Melanerpes radiolatus*). Data for this study were obtained on six trips to Jamaica during the winter, spring, and summer (14 June-17 August 1969, 20-29 December 1969, 14 April-24 May 1970, 14 June-28 July 1970, 4 June-24 June 1971, and 7 June-15 June 1972). The main ecological emphasis was on various parameters of the Jamaican Woodpecker's niche. Hutchinson (1957) defined the niche as a multidimensional space with each parameter corresponding to a different requirement of the species. My study is a critical examination of parameters related to population size, habitat preferences, foraging patterns, niche expansion in the absence of other woodpeckers and birds of similar foraging methods, sexual differences in niche use and intra- and interspecific competition. My investigation of the Jamaican Woodpecker's breeding biology covered all aspects of the annual reproductive cycle, from pre-pairing to fledging of the young. Behavioral information was obtained on a variety of subjects, including foraging behavior, vocalizations, displays, agonistic behavior, territoriality, and reproduction. This is of interest because, although information is available on the breeding biology and behavior of the North American congeners (e.g. *Melanerpes carolinus* and *M. aurifrons*), little information is available on the insular species of this genus, specifically *M. radiolatus*.

Investigations of Florida woodpeckers (*Colaptes auratus*, *Dryocopus pileatus*, *Melanerpes carolinus*, *M. erythrocephalus*, *Dendrocopos villosus*, *D. pubescens*, and *D. borealis*) were undertaken during the spring and summer seasons of 1969-1972, mainly to compare the foraging behavior and population densities of mainland woodpeckers with those of the Jamaican Woodpecker.

ACKNOWLEDGEMENTS

I am indebted to the members of my supervisory committee, Archie F. Carr, George W. Cornwell, Dale H. Habeck, David W. Johnston, and Thomas H. Patton, for their encouragement and helpful criticisms during the course of this study. I am especially grateful to David W. Johnston, not only for his guidance and assistance as my supervisory committee chairman, but for the many helpful discussions of the project, and to Thomas H. Patton and Joshua C. Dickinson for making available the resources and facilities of the Florida State Museum and Worthy Park Field Station, without which field research in many parts of Jamaica would have been impossible. A number of people participated in field work—particularly Philip Clarke, Audrey Downer, Neil Jones, David W. Johnston, Jean Klein, T. H. Patton, Roger Smith, Robert Sutton, Lisa Salmon, and Michael Winegar. C. B. Lewis, Director of the Institute of Jamaica, was very helpful and made available the Institute facilities. C. D. Adams (University of West Indies) and George Proctor (Institute of Jamaica) aided in the identification of plant material, and John Carrol, Dale H. Habeck, Jonathan Reiskind, Joel Rodriguez, and Fred C. Thompson aided with the identification of animal material. The Clarke family of Worthy Park not only provided strategic lodging, but their friendly hospitality made the visits more pleasant.

Support during this investigation came from a National Institute of Health Grant awarded to T. H. Patton, American Philosophical Society Grant to David W. Johnston, and a Frank M. Chapman and Ford Foundation Fellowship awarded to me. To all the people of Jamaica, known and unknown, who gave me indispensable aid, this report is especially dedicated.

METHODS OF STUDY

DISTRIBUTION, HABITAT PREFERENCES, AND ABUNDANCE

I tried to analyze each habitat occupied by the Jamaican Woodpecker to see what components of the community might be consistently present in each of the places visited in order to determine its habitat preferences and requirements. Some of the factors considered included: ground cover, shrub layer, canopy height, tree species diversity, tree sizes, presence or absence of dead trees, and epiphytic growth.

The principal study areas were censused to obtain comparative data on woodpecker population densities. In addition, censuses were made on mainland woodpeckers in Florida in various communities to compare population densities and biomass between mainland and insular woodpeckers. The Florida counts were also supplemented by the published literature, but no published counts were found for the Jamaican Woodpeckers. Two census methods were used in Jamaica: (1) a linear strip count for all birds heard or seen along preselected routes, and (2) a census plot count for all birds in a given area. In Florida only the latter method was used. Censuses were conducted on foot during the morning when woodpeckers are usually most active. In each of the census areas, at least three counts were taken and then averaged.

FORAGING AND FEEDING METHODS

Detailed foraging and feeding observations of the Jamaican Woodpecker in the principal study areas were obtained during the spring, summer, and winter, but chiefly during the breeding season (spring and summer). Observations were carried out at all times of the day, although it was found that the woodpeckers fed most frequently in the morning and late afternoon. The specific technique involved walking along an undetermined path in the study area until a woodpecker was encountered. If the bird was foraging, information was recorded for foraging height, behavior, and zones used. The tree was divided into three main feeding zones, trunk, inner branches, and outer branches. Each of these main zones was in turn divided into three subzones (Fig. 1). Sex was also recorded. Observations on the foraging behavior of Florida woodpeckers were undertaken during the spring and summer of 1969-1972 in approximately the same fashion.

The percentage of the total number of times the woodpeckers were recorded in each discrete foraging zone was used to estimate the frequencies with which the woodpeckers used each of these zones. These percentages were calculated by summing the observations recorded in a particular foraging zone and dividing the total by the sum total of observations from all zones.

Feeding behavior patterns of the woodpeckers were categorized as follows:

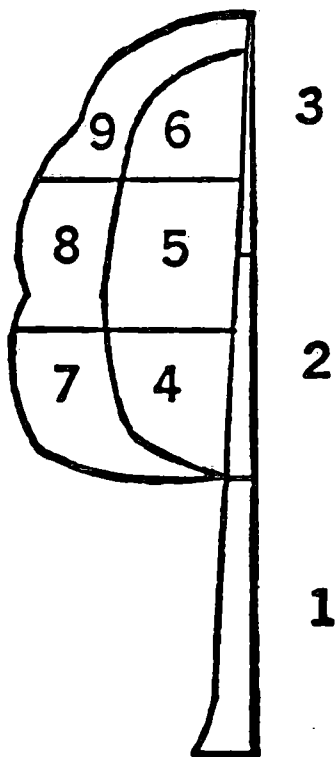


FIGURE 1.—Diagram of foraging zones. Numbers correspond to the following zones: (1) Lower trunk, below lateral branches of crown; (2) Middle trunk, lower half of trunk within region of crown; (3) Upper trunk, upper half of main stem within region of crown; (4) Proximal lower 1/3 of inner branches; (5) Proximal middle 1/3 inner branches; (6) Proximal upper 1/3 of inner branches; (7) Distal lower 1/3 of outer branches; (8) Distal middle 1/3 of outer branches; (9) Distal upper 1/3 of outer branches.

PROBING.—In probing, a bird inserted the bill, tongue, or both into cavities, such as holes, cracks, and crevices in the bark, weathered holes previously excavated by the woodpeckers, holes in dead stumps, cracks between trunks, and in accumulations of plant debris.

BROMELIAD-PROBING.—A special category of probing was into bromeliads and other epiphytes. As will be demonstrated quantitatively later, this special feeding category comprised a significant proportion for these woodpeckers.

SEARCHING AND GLEANING.—In searching and gleaning, the birds moved slowly along limbs and trunks, actively scanning the bark, epiphyte-covered branches, and clumps of leaves for animal prey, which were picked up with the bill and tongue.

FRUIT-EATING.—In this category are included the use of berries, fruits, and seeds as a food. The usual foraging procedure involved taking of fruits from a perching position and, less commonly, by hanging on the clumps of fruits.

PECKING.—Pecking (excavating) involved striking an object sharply with the bill. Usually it is a repetitious activity, with several blows delivered in rapid succession. In addition to pecking, the woodpeckers sometimes excavated in wood by prying off flakes of bark, especially in spots where the bark was rotten.

SALLYING.—Both bird and prey are on the wing at the time of capture.

The percentage of the total number of observations the Jamaican Woodpecker was in each foraging procedure was used to estimate the frequency with which the woodpeckers used

each of these methods. These percentages were calculated by summing all the observations recorded in a particular foraging method and then dividing the total by the sum of observations for all zones.

Foraging method is usually indicative of the food items sought. Although in some cases I was not able to see the food items taken, those identified were recorded. Observations on the food and foraging ecology of other bird species in the study areas were also recorded to determine the degree of feeding niche overlap and whether competition might exist for any particular food source.

FOOD ANALYSIS

In addition to obtaining information on the foraging behavior and zones the Jamaican Woodpecker used, 29 adults were collected and the stomach contents examined. The primary purpose was to determine foods taken, how the food items in the stomach correlated with foraging patterns, and to determine if any differences existed between the sexes with respect to food type. All woodpeckers were collected in the Worthy Park area in the summer of 1969, spring of 1970, and summer of 1971. The stomach and intestinal tract were removed soon after death and preserved in 75% alcohol. Later the food samples present were initially separated into food classes or groups (animal and vegetable) and analyzed both by volume and frequency of occurrence. The reason for using more than one method of food analysis is that the different methods provide indications of different aspects of the feeding ecology of the species. A food class with a high occurrence indicates that the food is consistently available (and attractive) to the bird, and so is a reliable food source. The frequency of occurrence alone gives little indication of the importance of each food in the birds' diet as it ignores the size of the food item. This problem is overcome by measurements of the volume of the various food classes in each sample to obtain indications of the relative general importance of the different food classes in the birds' diet. In addition the length of each prey item was measured to determine the importance of the various classes of prey size and to see if the sexes differed in prey sizes eaten.

In the volumetric analysis method, food volume was ascertained with reasonable accuracy by noting the displacement of water in a graduated cylinder accurate to 0.1 ml. The volume of the total items in each of the food and prey size classes was summed for each class, and expressed as percentage of the total volume of the food and prey size in all classes. The frequency of occurrence of each food class is presented as the percentage of samples in which the class was represented.

MORPHOLOGICAL ANALYSIS

Morphological data were obtained by standard mensural methods to see if any sexual dimorphism in body structures of possible ecological significance existed. Bill length was measured from the anterior margin of the nostril to the tip; the tarsometatarsus was measured from its posterior proximal end to the distal edge of the most distal unbroken scale crossing the bases of the two forward toes; and the outer front toe (number 3) was measured from its proximal end to the distalmost scute (not including claw). Body weights were obtained on all the specimens collected. Foot volume was measured in a graduated cylinder accurate to 0.1 ml. Linear measurements are in millimeters, weights are in grams, and food volumes in ml. All weights and measurements were usually taken on the day the bird was collected.

BREEDING BEHAVIOR AND BIOLOGY

Field studies of breeding Jamaican Woodpeckers were conducted primarily at the Worthy Park (Lluidas Vale) field station during the summer of 1969, spring and summer of 1970, and summer of 1971. The part of the annual cycle covered by the above field work extended from early April to late August. Some additional field work was conducted during December of 1969.

The primary method of study was by direct observation and recording data on breeding biology, vocalization, territoriality, and inter- and intraspecific behavior. To record the activities inside the nesting hole a rotatable mirror attached to the end of a rod and with a built-in light source was used. Reproductive condition was noted for all collected specimens.

To investigate factors involved in species recognition, territorial behavior, and territory size, I performed a series of experiments in which dummy male Jamaican Woodpeckers (study skins) were placed at varying points from the nesting hole, and the reaction thereto of the breeding pair was recorded. Presumably the points where the occupant pair fail to show aggression towards the visual representation of another woodpecker marks the boundary of the territory. These experiments were supplemented by noting the reactions of contiguous family groups of woodpeckers toward one another, and the reactions of nesting woodpeckers to artificial drumming produced by tapping a clip-board with a pencil. Home range size in the Jamaican Woodpecker was determined by measuring the distance traveled from the nesting hole by 12 breeding pairs in Worthy Park during the summer of 1969. The distances traversed were plotted on a field map, and the home range boundaries were determined by drawing a line through the extreme points where the woodpeckers were recorded (modification of the method used by Odum and Kuenzler 1955).

DESCRIPTION OF STUDY AREAS

PHYSIOGRAPHY

Jamaica lies at 18° N. Lat. in the western Caribbean, approximately 150 km south of Cuba and 200 km west of Hispaniola. The nearest mainland is Honduras, approximately 610 km southwestward. With an area of 11,740 sq km, Jamaica is the third largest island in the West Indies, exceeded in size only by Cuba and Hispaniola. Most of Jamaica is mountainous, with more than one-half of the island over 305 m (1000 ft) in elevation. The greater part of this area comprises the Central Upland plateau at 600-915 m, and the Blue and John Crow Mountain ranges in the east. The Blue Mountains, the highest in Jamaica (maximum height 2155 m), extend westward from the John Crow range in the eastern part of the island to Mount Telegraph (1275 m), approximately one-third the length of the island. In the Central Upland plateau are the Dry Harbor Mountains (St. Ann Parish) and the Mocho Mountains (Clarendon Parish), separated by the Main Ridge group. Farther westward is the Cockpit country, a succession of cone-like hills with alternating enclosed conical depressions or "cockpits," typical karst country with underground drainage, subterranean rivers, sinkholes, and caves. Mount Diablo (1000 m), in St. Ann and St. Catherine parishes, is a precipitous, calcareous plateau, similar to the Cockpit country. Dolphin Head (542 m) is an isolated limestone peak on the western end of the island. Along the southern coast of Jamaica from Morant Bay (eastern Jamaica) westward to Portland Ridge, a distance of over 80 km, lies an intermittent line of limestone hills, mostly under 300 m in elevation.

CLIMATE

Rainfall is the most important single factor affecting the vegetation. The island lies in the path of the moisture-laden easterly trade winds that blow throughout the year. The uplifting and cooling of the winds causes condensation that strikes first the high limestone John Crow Mountains and then the northern flank of the Blue Mountains. Hence Portland in the northeast is one

of the wettest parishes with an average annual rainfall of 381 cm. In contrast, the dry southern parish of St. Andrew has only 89 cm of rain. Another feature of the rainfall is its seasonal periodicity. Rainfall records for the island indicate that the heaviest rainfall occurs in May and June and again from August to November. The major dry period is from January to March (Asprey and Robbins 1953).

VEGETATION AND STUDY AREAS

The vegetation of Jamaica, except in the higher montane region, is tropical. In general the average annual temperature decreases with increase in ground elevation, whereas rainfall tends to increase from south to north and also with elevation. The annual mean surface temperature is 26°C at Kingston on the southern coast and 13°C at the Blue Mountain Peak (2255 m). These conditions (rainfall, elevation, and temperature) operate to bring about a very diverse vegetational pattern. The description of the following major communities and principal study areas follows the terminology of Asprey and Robbins (1953).

STRAND WOODLAND ASSOCIATION.—This association is characteristic of coastal Jamaica and occurs on both coral and sandy substrata. Characteristic trees are sea grape (*Coccoloba uvifera*) and seaside mahoe (*Thespesia populnea*). This is a low (3-6 m) scrubby, open community which may include palms and a mixture of other trees and shrubs. Field investigations on woodpeckers in this community were conducted at Morant Point (St. Thomas Parish), Negril (Westmoreland Parish), near Falmouth (Trelawny Parish), and various points in St. Elizabeth Parish.

COASTAL PLAINS PLANT COMMUNITIES.—Large low-lying coastal plains extend along the dry southern coast. They once supported several types of seasonal evergreen or deciduous forests. Man's activities have now produced successional communities that may lead to a secondary savanna type forest consisting primarily of mesquite (*Prosopis juliflora*), acacia (*Acacia lutea*), or logwood (*Haematoxylum campechianum*). Much of the area is under cultivation, primarily for sugar cane, bananas, and coconuts. Where irrigation is impractical, the land is used for grazing and has a savanna-like appearance that consists mainly of guinea grass (*Panicum maximum*) and guango trees (*Samanea saman*). Field investigations in the coastal plain were undertaken in various localities in the parishes of St. Thomas, St. Catherine, Clarendon, and St. Elizabeth.

MANGROVE WOODLAND.—In protected coastal areas where silt is deposited, mangrove woodlands develop in which four New World mangrove species are present. The red mangrove (*Rhizophora mangle*) usually forms pure stands on the seaward side, whereas white mangrove (*Laguncularia racemosa*), black mangrove (*Avicennia germinans*), and buttonwood (*Conocarpus erecta*) are characteristic of mud swamps and occur farther inland. One of the principal

study areas, near Falmouth (Trelawny Parish), was in this community. Characteristic trees of this mangrove community included white, black, and button-wood mangrove. Red mangrove was not present. The forest was low, the trees averaging approximately 4.5 m in height.

DRY LIMESTONE FOREST.—Asprey and Robbins (1953) recognized two distinct vegetational types on limestone rocks: dry limestone forest and wet limestone forest. Dry limestone forest occurs where the annual precipitation is less than 101 cm and is best represented along the southern coast of Jamaica, but also occurs at Negril on the extreme western end of the island and in the parish of Trelawny on the northern coast. Asprey and Robbins noted: "Dry limestone is a sparse, vegetation cover of low forest and tall scrub growing on bare limestone rock. No soil is present except for that deposited in small crevices or washed down to level areas. Leaf litter is almost nil and the floor is either a jumble of broken stones or a more or less continuous mass of jagged honey comb rocks." There is no distinct stratification and heights vary from low scrub to a thin forest with trees rarely exceeding 9 m in height with occasional emergence of red birch (*Bursera simaruba*) and cotton tree (*Ceiba pentandra*) up to and over 18 m. Many of the tree species are semi-deciduous during the dry season. Field investigations in this community were conducted at Portland Ridge (Clarendon Parish), Hellshire Hills (St. Catherine Parish), and near Discovery Bay (St. Ann Parish). Portland Ridge (152 m in elevation and one of the principal study areas) forms the western end of the intermittent line of limestone hills that occur along the southern coast from Morant Bay westward, a distance of approximately 80 km. This type of forest has been subject to much human interference in Jamaica, but the Portland Ridge region is relatively undisturbed. Some of its characteristic trees are red birch, torchwood (*Amyris balsamifera*), thatch palm (*Thrinax parviflora*), burnwood (*Metopium browni*), and dildo (*Cephalocereus* spp.) among many others.

WET LIMESTONE FOREST.—This community is developed on limestone rock where the rainfall is over 190 cm and may be as high as 380 cm. Most of this forest grows inland at elevations from 300-760 m. It is more mesophytic and luxuriant than the dry type, with more tree species, epiphytes, lianas, aroids, and bromeliads. Ground vegetation and leaf litter are more evident, although soil might be absent on the hillsides but deep in the valley. The canopy is dense and twice as tall as the dry limestone forest, with emergent trees up to 30 m or more. Investigations in this community were conducted in the Lluidas Vale (Worthy Park) and Mount Diablo area (St. Catherine Parish), Cockpit country (Trelawny Parish), and Dolphin Head Mountain (Hanover Parish). Investigations in Worthy Park (one of the principal study areas) were conducted both in forests and upland pastures at elevations ranging from 370 m in the valley to 950 m in the surrounding hills and mountains. Some of the characteristic trees are broadleaf (*Terminalia lati-*

folia), Jamaican cedar (*Cedrela odorata*), sweetwoods (*Nectandra* spp.), bulletwoods (*Daphnopsis* spp.), prickly yellow (*Fagara martinicensis*), and figs (*Ficus* spp.). In the upland pastures where some of the original vegetation has been removed, characteristic trees also include guango, pimento (*Pimento officinalis*), trumpet tree (*Cecropia peltata*), logwood, and citrus trees (*Citrus* spp.). Many of the trees in this region support epiphytes, bromeliads, and lianas growing in profusion.

LOWER MONTANE RAIN FOREST.—Floristically some relationships exist between the lower montane rain forest and the wet limestone forest; but the former occurs at higher elevations (up to 1070 m). Annual rainfall exceeds 250 cm and may reach nearly 700 cm. Although this community has been subject to much human disturbance, lower montane rain forest is still to be found in the Blue and John Crow mountains. Investigations in this community were conducted near Hardwar Gap (St. Andrew) and Corn Puss Gap (St. Thomas Parish). Corn Puss Gap, one of the principal study areas, lies at an elevation of 610 to 686 m on the southwestern slopes of the John Crow Mountains. This forest consists of many of the tree species found in the wet limestone forest and has a similar appearance. Characteristic trees of this region also include santa maria (*Calophyllum jacquinii*), rodwood (*Eugenia* sp.), mountain guava (*Psidium montanum*), coby wood (*Matayba apetala*), and many others. The tree fern (*Cyathea*) is also characteristic of this area.

MONTANE MIST FOREST.—One of the few tracts of original vegetation in Jamaica is the montane mist forest covering the upper reaches of the Blue Mountains, which form the central mountain system in the island's eastern end. It is a region of high atmospheric humidity with a high annual rainfall (over 200 cm) and mist covers it almost continuously. The mist forest is low-canopied, seldom exceeding 12 m. Much variation is found in the structural and floristic composition of the mist forest, and variations are almost entirely correlated with degree of exposure. The chief variation is between that of the deep sheltered ravines and that of the exposed ridges. In both structure and floristics the montane mist forest shows some temperate forest features (Asprey and Robbins 1953). Hardwar Gap, one of the principal study areas, lies at an elevation of 1220 to 1373 m in the Port Royal Mountains, a range subsidiary to the Blue Mountains. Dominant trees in this community are yacca (*Podocarpus urbanii*), bloodwood (*Cyrilla racemiflora*), jumba (*Alchornea latifolia*), and wild fig (*Clusia* spp.). Undergrowth shrubs and lower order plants, such as mosses and ferns, including the tree fern, are also abundant.

ELFIN WOODLAND.—In Jamaica elfin woodland grows on the exposed summits and northern ridges of the Blue Mountains at 1525 m and higher. It is an open woodland of gnarled and twisted trees, often short, windblown, and laden with mosses, lichens, ferns, and epiphytes. Elfin woodland is regarded as an open stunted fasciation of mist forest, brought about by more exposed conditions. Investigations in this community were conducted on Abraham's Peak, St. Thomas Parish.

FLORIDA STUDY AREAS

Observations on woodpeckers in Florida were made in various natural and man-modified communities in Alachua County. A description of the major Florida study areas follows.

MORNINGSIDE PARK.—This city park in eastern Gainesville is composed of two main vegetational types, longleaf pine-turkey oak sandhills and longleaf pine flatwoods. In the former the predominant trees are longleaf pine (*Pinus palustris*), turkey oak (*Quercus laevis*), and bluejack oak (*Quercus cinerea*). The undergrowth is sparse, but in places patches of saw-palmetto (*Serenoa repens*) occur. In the longleaf pine flatwoods the predominant tree is the longleaf pine, although slash pine (*Pinus elliotii*) was also present. There is a dense understory in which the most conspicuous plants are saw-palmetto, gallberry (*Ilex glabra*), and fetterbush (*Demothamus lucidus*). Canopy height in both areas is less than 15 m.

DICKINSON STUDY AREA.—A xerophytic hammock in southwestern Gainesville, characterized by the presence of large live oak trees (*Quercus virginiana*) exceeding 10 m in height. Also present were laurel oak (*Quercus laurifolia*), sweetgum (*Liquidambar styraciflua*), pignut hickory (*Carya glabra*), and many other trees.

SAN FELASCO STUDY AREA.—This extensive tract of climax mesophytic hammock 11 km northeast of Gainesville has, unfortunately, been cutover in some places, but it is still dominated by large trees and is the most extensive stand of mesophytic forest in Alachua County. Characteristic trees are southern magnolia (*Magnolia grandiflora*), laurel oak, pignut hickory, sweetgum, and many others.

MEDICINAL GARDEN STUDY AREA.—The medicinal garden on the University of Florida campus, Gainesville, was originally a mesophytic hammock, but the removal of some of the trees and the undergrowth gives it a park-like appearance. Characteristic trees include loblolly pine (*Pinus taeda*), pignut hickory, blue beech (*Carpinus caroliniana*), water oak (*Quercus nigra*), southern magnolia, sweet gum, and others.

LOBLOLLY PINE-PASTURE STUDY AREA.—This tract west of Gainesville near interstate highway 75 consisted of pasture land with loblolly pines, ranging in height from seedlings to 15 m.

RESULTS AND DISCUSSION

DISTRIBUTION

The Jamaican Woodpecker occurs throughout the island wherever suitable habitat is present, from sea level to high altitudes (Fig. 2). It occupies forests, mangrove woodlands, and various man-modified communities, such as wooded pastures, park-like areas, and tree crop areas. Destruction of the Jamaican forests, which began when Columbus discovered the island in 1497,

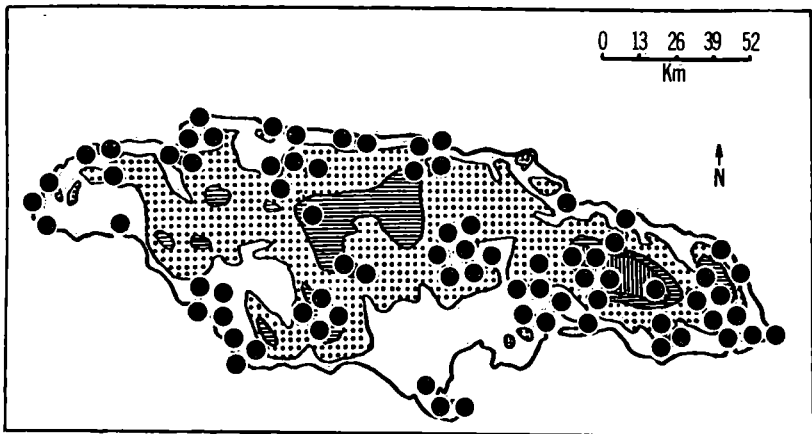


FIGURE 2.—Distribution of the Jamaican Woodpecker (*Melanerpes radiolatus*). Black circles = distribution of Jamaican Woodpecker based on field observations, museum specimens, published literature, and personal communications. Open area = 0–152 m, dotted = 153–610 m, horizontal = 610–1071 m, vertical above 1071 m.

has doubtless reduced the total range occupied by both the Jamaican Woodpecker and other predominantly forest-dwelling birds. Asprey and Robbins (1953) noted that the land area consists of 18% forest, 47% agricultural use, and 35% second growth scrub, thorn scrub, and mangrove woodland. Of the agriculture area, 8% can be classified as tree crops (cocoa, pimento, citrus, coconut, and bananas).

HABITAT ANALYSIS

Analysis of the structural components of the various communities visited (Table 1) shows that the presence of the Jamaican Woodpecker in a given habitat is directly related to the presence of trees necessary for feeding, nesting, and roosting. Communities visited that were composed primarily of shrubbery or scrub thickets, such as the dry limestone scrub and the elfin woodland, had no woodpeckers. Tree species diversity did not seem to be a factor in determining the presence or absence of woodpeckers, but it did seem to be correlated with the numbers of woodpeckers present. This aspect will be discussed under the census results. Woodpeckers were present in habitats ranging from low tree species diversity and foliage height, such as mangrove woodland and citrus groves, to areas of high tree species diversity and foliage height, such as wet limestone forest and lower montane rain forest. The presence of woodpeckers was not correlated with the presence of ground or shrub layers. Places visited where woodpeckers were present ranged from habitats without or with very little ground cover, such as mangrove woodland and dry limestone forest, to places with heavy ground cover, such as savanna (park-like) areas. Woodpeckers were also found in habitats ranging

TABLE 1.—HABITAT ANALYSIS OF COMMUNITIES VISITED.

	Ground ¹ layer	Shrub layer	Tree layer	Tree ² size	Tree species diversity	Dead trees ³ or branches	Epiphytes	Fruiting trees
Strand woods	2	2	3	S	1	U	R	U
Mangrove	1	1	3	S	1	U	R	R
Thorn scrub	1	3	1	-	-	-	R	-
Lowland savanna	3	2	2	M,L	1	C	R	U
Dry limestone scrub	1	3	1	-	-	-	R	R
Dry limestone forest	1	2	3	S,M	2	U	U	U
Wet limestone forest	1	1	3	M,L	3	C	C	C
Modified wet limestone forest	3	2	3	M,L	3	C	C	C
Upland tree crops	2	2	3	S,M	1	U	U	C
Montane rain forest	1	1	3	M,L	3	C	C	C
Montane mist forest	1	2	3	S,M	3	U	C	C
Elfin woodland	2	3	1	S	1	U	C	U

¹Strongly developed (3), moderately developed (2), poorly developed or absent (1)²Small (S) < 4.6 meters, medium (M) - 4.6 to 9.2 m, large (L) > 9.2 meters³Rare or absent (R), uncommon (U), common (C)

from zero or low shrub density (e.g. park-like areas and wet limestone forest) to those of high shrub density (mist forest and dry limestone forest). All these habitats contain gradients in types of food available, nest sites, microclimates, tree species diversity, and stratification, which help determine the size of the population present.

ABUNDANCE

POPULATION DENSITIES IN DIFFERENT HABITATS.—Table 2 lists the densities of Jamaican Woodpeckers in various natural and man-modified habitats in number of birds per km. The highest densities were recorded at Grass Piece, wooded upland pasture bordering on wet limestone forest (avg 22/km), and at Coco-Ree, wet limestone forest (avg 20/km). No woodpeckers were recorded on each of three visits made to the Port Henderson area (dry limestone scrub), Hellshire area (scrubby thickets), and Stoddard's Peak (elfin woodland). The number of individuals was lowest in the mangrove woodland (4/km) and dry limestone forest (6.8/km). The results of the other censuses varied from 9/km in the montane mist forest to 15/km in the induced guango savanna.

A species is probably found in greatest numbers in those habitats that best meet its ecological requirements. The density figures indicate that middle elevation wooded pastures and wet limestone forest are optimal habitats for the Jamaican Woodpecker. The absence of woodpecker occupation in the dry limestone scrub, scrubby thickets, and elfin woodlands indicate that these habitats do not meet the necessary minimal requirements, namely a well developed arboreal component. The low numbers in the mangrove woodland and dry limestone forest indicate that these areas are suboptimal for Jamaican Woodpeckers.

The high density figures for both the wooded pasture (which has the original wet limestone vegetation plus trees characteristic of more open areas) and wet limestone forest are possibly related to their structural complexity. Both areas have a well developed vertical stratification, high tree species diversity (including many fruiting trees), and numerous bromeliads, all of which increase the total area available for foraging. The results of the food and foraging behavior analysis (pp. 165-184) indicate that fruits form a significant portion of the foods eaten and that bromeliads and other epiphytes are important foraging sites. The high densities of Jamaican Woodpeckers in these places may also be related to the presence of large trees that furnish a variety of suitable sites for roosting, nesting, and foraging. In contrast the simpler forest structure of the mangrove woodland and the dry limestone forest (i.e. lower canopy, low tree species diversity—including fruiting trees, and little epiphytic development) apparently offers fewer sites for feeding, nesting, and roosting purposes. Although both areas have a simple forest structure, the less complex structure of the mangrove woodland probably

TABLE 2.—CHARACTERISTICS OF THE CENSUS AREAS AND THE RESULTS OF THE COUNTS.¹

Site	Community Type	Distance Censused (Kilometer)	Census Results Mean (Range)	Number of Censuses	Mean Number per Kilometer
Grass Piece	Wooded pasture bordered by wet limestone forest	0.6	14(12-15)	6	22
Coco-ree	Wet limestone forest	0.75	15(14-16)	4	20
Caymanas	Induced Guango savanna	0.3	4.5(4-5)	3	15
Corn Puss Cap	Lower montane rain forest	2.6	29(25-33)	3	14
Hardwar Cap	Montane mist forest	0.7	6.3(5-8)	3	9
Portland Ridge	Dry limestone forest	2.2	15(12-18)	3	6.8
New Falmouth	Mangrove woodland	0.5	2(2-2)	3	4
Stoddard's Peak area	Elfin woodland	0.6	0	2	0
Port Henderson	Dry limestone scrub	2.5	0	3	0
Hellshire	Scrubby thickets	1.75	0	3	0

¹All censuses were taken during the spring and summer (0800-1200)

TABLE 3.—COMPARISON OF WOODPECKER DENSITIES IN JAMAICA AND NORTH AMERICA (IN NUMBERS AND GRAMS PER 40 HA).

Species	Habitat	N/40 ha	Biomass (g/40 ha)	Source
Jamaican Woodpecker	modified mesophytic forest	36.4	3,942	This study
Florida woodpeckers ¹ (five species)	modified mesophytic forest	31.2	2,962	Dennis (1951)
Florida woodpeckers ² (two species)	modified mesophytic forest	34.0	2,330	Woolfenden and Rohwer (1959)
Jamaican Woodpecker	mesophytic forest	30.3	3,281	This study
Florida woodpeckers ³ (four to six species)	mesophytic forest (average for four areas)	31.5 (27 to 42)	2,598 (2,359-3,075)	Dennis (1951) Kale and Webber (1968), and this study

¹*Colaptes auratus*, *Dryocopus pileatus*, *Melanerpes carolinus*, *M. erythrocephalus*, and *Dendrocopos pubescens*.²*Colaptes auratus* and *Melanerpes carolinus*³*Colaptes auratus*, *Dryocopus pileatus*, *Melanerpes carolinus*, *M. erythrocephalus*, *Dendrocopos pubescens*, and *D. villosus*

accounts for the lower number of woodpeckers recorded there. In addition, the Jamaican Woodpecker uses mainly dead trees or dead branches of live trees for excavating nesting and roosting holes. An examination of over 100 woodpecker holes in various communities showed that they are usually placed higher than 4.6 m and excavated in trunks or branches at least 15 cm in diameter. Although trees meeting these requirements are present in both the dry limestone forest and the mangrove woodland, they are not common. The other communities censused (Table 2) showed a gradient of these factors.

COMPARISON OF WOODPECKER DENSITIES IN JAMAICA AND FLORIDA.—When a species occurs together with many similar species that exploit some of the same resources, one might anticipate that population numbers and niche breadth might be reduced, in contrast to the situation that would exist in the absence of the competitors (see Crowell 1962). Selander (1966) estimated that the Hispaniolan Woodpecker's population density was four to five times greater than that maintained in continental areas by any species of woodpecker with which he had field experience. Unfortunately no census counts were made in that study. The Hispaniolan Woodpecker shares its habitat with the Antillean Piculet (*Nesocittes micromegas*), a woodpecker that is very different in size, morphology, and habits.

The Jamaican Woodpecker is in a somewhat similar ecological situation. It is the only resident woodpecker on Jamaica, so that one might expect its population size to be greater than those of some of the mainland woodpeckers.

To test this assumption and to see whether the increase in numbers (if any) is sufficient to compensate for the absence of other woodpeckers, i.e. whether the total population density of Jamaican Woodpeckers is as high as the combined population densities of mainland woodpeckers, census counts were undertaken in Jamaica and Florida. The Florida counts were also supplemented by counts appearing in the literature, but no published census counts were available for the Jamaican Woodpecker.

These censuses (Table 3) indicate that in some habitats the Jamaican Woodpecker maintains comparable or higher densities than the combined population densities of several species of Florida woodpeckers. Thus Jamaica has 36.4 and 30.3 woodpeckers per 40 ha in modified mesophytic and mesophytic habitats respectively, and Florida has 32.5 (average for two plots) and 31.5 (average for four plots) per 40 ha in modified mesophytic and mesophytic habitats. Although number of individuals per unit area is the customary census unit, Salt (1957) and Crowell (1962) pointed out the value of biomass figures as an index of abundance of different species. Crowell (1962) noted: "when considering the amount of living matter supported by a unit area, it is weight which should be used." Standing crop biomass for woodpeckers in grams per 40 ha for Jamaica was calculated to be 3,942 for the modified mesophytic habitat, 3,281 for the mesophytic habitat, and for similar areas

in Florida it was 2,962 and 2,598. These data show that comparable (similar structure) Jamaican communities support a greater biomass of woodpeckers per unit area than do mainland habitats.

Some of the possible explanations for the high densities and biomass figures for Jamaica are the following. (1) More resources are available to Jamaican woodpeckers through the absence of other bird species (and animal groups) with similar habits. (2) The average weight of the Jamaican Woodpecker is 25% greater than the combined average weight (81 grams) of Florida woodpeckers (range 24.3 to 237.5 grams). In addition the larger species of Florida woodpeckers, such as the Pileated Woodpecker (*Dryocopus pileatus*), were not as common as the smaller species. The most common species was the Red-bellied Woodpecker (*Melanerpes carolinus*) with an average weight of 66.4 grams. (3) Apparently more energy is available to the avian segment of the community in Jamaica than in the North American mainland, because productivity is probably greater in Jamaican habitats than in comparable Florida habitats. Although no data are available for Jamaica, Odum and Pigeon (1970) found that the net productivity in a mature mesophytic forest in Puerto Rico was 13,000 kcal/m²/year, and Woodwell and Whittaker (1968) found that the net productivity of an oak-pine forest in North America was 5,000 kcal/m²/year. (4) Jamaican habitats are structurally more complex than comparable Florida habitats, evidently because more fruiting trees, epiphytes, lianas, and foraging niches are available in Jamaica (Asprey and Robbins 1953, Adams 1972). (5) Jamaica has fewer predators on birds than the mainland, where snake predation is one of the most common causes of woodpecker mortality (Kilham 1957, Nolan 1959, Stickel 1962, Jackson 1970, Dennis 1971). A hole-nesting bird such as a woodpecker, although having a safer nest in many respects and an easier nest to defend than birds nesting in the open, is still vulnerable to snake predation especially if surprised. Jamaica has five species of snakes, only one of which possibly preys on woodpeckers. This snake, the Jamaican boa (*Epicrates subflavus*), is very rare and consequently the numbers of woodpeckers it eats, if any, are probably negligible.

FEEDING ECOLOGY AND BEHAVIOR

This section describes feeding behavior and food habits in both a qualitative and quantitative manner, stressing the following aspects: sexual dimorphism, foraging heights, foraging zones (upper trunk, outer branch, etc.), foraging behavior (pecking, probing, etc.), food habits (based on stomach analyses and field observations), interspecific food competition, and structural adaptations relevant to foraging method. There follows a discussion of the morphological data obtained by standard methods to assess any sexual dimorphism in body structure with ecological significance.

LACK OF SEXUAL DIMORPHISM IN THE JAMAICAN WOODPECKER.—No statistically significant sexual differences were found between the sexes in

bill length, weight, and tarsometatarsal length at the 0.001 probability level (*t*-test). There was a difference in outer-front toe length at the 0.001 probability level. The data presented in Table 4 indicate that the Jamaican Woodpecker is monomorphic, with the males averaging slightly larger in culmen length, tarsometatarsal length, and outer-front toe length. The greatest differences between the sexes were in body weights, the male woodpeckers averaging 12 grams heavier than the female woodpeckers (114.8 to 102.0 respectively), and outer-front toe length, the male woodpecker averaging 1.55 mm longer than the female woodpeckers (24.3 to 22.75 respectively).

TABLE 4.—MEASUREMENTS OF *Melanerpes radiolatus*.¹

	Males			Females		
	N	Mean \pm S.D.	Range	N	Mean \pm S.D.	Range
Bill length ²	11	28.04 \pm .61	26.8– 29.1	14	27.01 \pm 1.05	25.8– 29.2
Weight	11	114.72 \pm 8.6	97.3–130.5	14	102.02 \pm 8.9	91.6–118.5
Tarsometatarsal	11	25.34 \pm .868	23.7– 26.7	13	24.80 \pm .65	23.6– 25.3
Foot volume	8	.8	.75– .85	9	.8	.75– .85
Outer front toe(3)	11	24.3 \pm .85	23.0– 25.5	12	22.75 \pm .97	20.7– 23.9

¹No statistically significant differences were found between the sexes either in bill length, weight, or tarsometatarsal length (.001 probability level, *t*-test).

²Measurements in mm, weights in g, and foot volume in ml.

These data contrast sharply with measurements on another insular species of woodpecker, *Melanerpes striatus* of Hispaniola (Selander 1966). In all linear dimensions and in weight, the male Hispaniolan woodpecker is larger than the female, usually with little or no overlap between the sexes. The greatest sexual differences were in bill length in which there was a 21.3% difference. Males use the longer bill to do more pecking and probing, whereas the shorter-billed females do more surface gleaning. This contrasts sharply with the Jamaican Woodpecker, where the bill of the female averages only 3.67% shorter than that of the male. In body weights females of *Melanerpes striatus* average 18.1% less than the male, but females of *M. radiolatus* average only 11.1% less than the male.

Selander's study demonstrated a relationship between the degree of sexual differences in foraging behavior and the degree of sexual dimorphism in the feeding apparatus. Davis (1965) and others suggested that "bill size would probably be the most important character involved" in determining the range of food items taken and the foraging techniques employed. One may reasonably ask whether males and females of structurally monomorphic species may exhibit differences in foraging and food items chosen, as such differences could be of a strictly behavioral nature (such as foraging heights or zones), rather than one directly correlated with differential morphological characters (Ligon 1968, Morse 1968, Williamson 1971).

FORAGING HEIGHTS.—Almost complete overlap in foraging heights for male and female woodpeckers is seen in the pooled data for all the study areas as well as in the data for individual study areas (Fig. 3). On the other

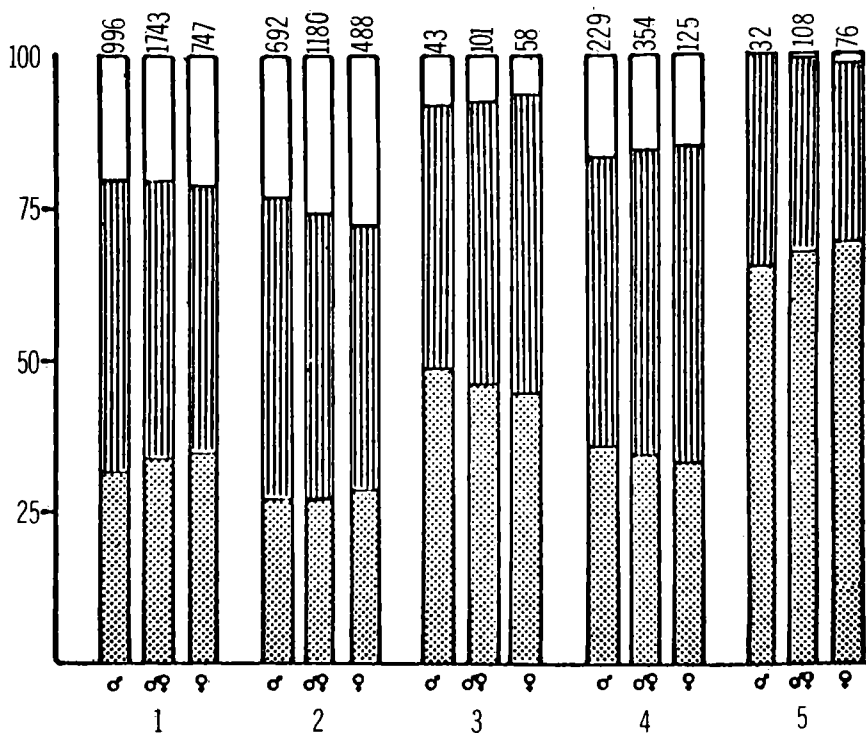


FIGURE 3.—Percent distribution of foraging heights in the Jamaican Woodpecker. (1) Pooled results for all study areas; (2) Modified wet limestone forest; (3) Dry limestone forest; (4) Montane mist forest; (5) Mangrove woodland. Stippled area = 0-4.6 m, vertical area = 4.6-9.2 m and white area = 9.2 m and over. Numbers at top of bar = number of observations.

hand, the foraging heights were correlated with the heights of the trees in the various foraging zones. In the Worthy Park study area, for example, the trees were usually taller than the trees in the other study areas, and this greater height is reflected in the foraging heights of the woodpeckers, 26% in the upper zone (greater than 9.2 m), 45% in the middle zone (4.6 to 9.2 m), 29% in the lower zone (less than 4.6 m). In the mangrove woodland the trees averaged considerably smaller, and consequently most of the foraging observations were recorded at lower heights: 68% in the lower zone, 30% in the middle zone, and 2% in the upper zone. In the other study areas tree heights on the average fell between the Worthy Park study areas and the mangrove woodland study area, averaging taller in the Hardwar Gap study area than in the Portland Ridge study area. In the Hardwar Gap area, 35%

of the foraging observations were recorded in the lower zone, 49% in the middle zone, and 16% in the upper zone; in the Portland Ridge study area, 46% were recorded in the lower zone, 46% in the middle zone, and 8% in the upper zone. The pooled results for all the study areas indicate that the lower zone was used 35%, middle zone 45%, and the upper zone 21%. These results indicate (1) an absence of stratal segregation between the sexes, and (2) that both sexes forage most commonly in the middle zone.

FORAGING ZONES.—Table 5 and Figure 4 summarize the percent of the total number of times the Jamaican Woodpecker was noted in the different foraging zones—trunk, inner, and outer portions. The Jamaican Woodpecker used different zones preferentially and both the pooled results for all the study areas and the results for the individual study areas show a nearly complete overlap in the foraging zones used by male and female woodpeckers.

The pooled data for both sexes for the different study areas indicate that almost one-half of the time (46%) was spent foraging in the inner portion, one-third (32%) in the outer portion, one-seventh (14%) on the trunk, and the remainder (8%) on the vines and in the aerial zones. These values varied from area to area, ranging from 38% for the inner zone in the Portland Ridge area to 57% in the mangrove woodland, 21% for the outer zone in the mangrove woodland area to 34% in the Worthy Park area, and from 10% for the trunk in the Hardwar Gap area to 22% in the mangrove woodland.

Within each major foraging zone (inner branches, outer branches, and trunks), different subzones were preferentially used (Fig. 4). The pooled data for the different study areas (Table 5) show that 20% of the foraging observations were in the middle inner branches, 13% in the middle outer branches,

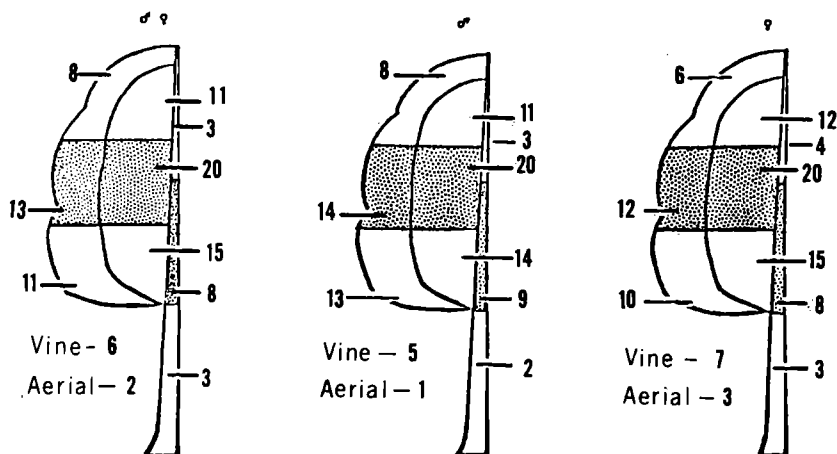


FIGURE 4.—Foraging zones of the Jamaican Woodpecker. The numbers represent the percent of the total number of observations. The subzones of greatest usage within each major zone are shown by stippling.

TABLE 5.—USE (IN PERCENT) OF VARIOUS FORAGING ZONES IN DIFFERENT HABITATS BY THE JAMAICAN WOODPECKER.

Study Areas	Number of Observations	Sex	Trunk			Inner			Outer			Vines	Aerial
			LT ¹	MT	UT	LIB	MIB	UIB	LOB	MOB	UOB		
Wooded pasture (Worthy Park)	725	♂	2	10	3	13	20	10	12	15	9	2	2
Dry limestone forest (Portland Ridge)	52	♂	4	8	4	16	14	10	12	12	6	4	—
Montane mist forest (Hardwar Gap)	259	♂	2	5	2	17	19	12	12	12	7	12	—
Mangrove woodland (New Falmouth)	32	♂	6	10	—	28	34	—	16	6	—	—	—
Pooled	1068	♂	2	9	3	14	20	11	13	14	8	5	1
Wooded pasture (Worthy Park)	552	♀	3	7	3	13	18	14	10	13	8	6	5
Dry limestone forest (Portland Ridge)	68	♀	3	13	6	10	19	7	6	15	6	15	—
Montane mist forest (Hardwar Gap)	141	♀	2	5	4	18	24	13	11	9	4	10	—
Mangrove woodland (New Falmouth)	76	♀	7	10	8	28	22	4	13	8	—	—	—
Pooled	837	♀	3	8	4	15	20	12	10	12	6	7	3
Wooded pasture (Worthy Park)	1277	♂ ♀	3	9	3	13	19	12	11	14	9	4	3
Dry limestone forest (Portland Ridge)	117	♂ ♀	3	11	5	13	17	8	8	14	6	15	—
Montane mist forest (Hardwar Gap)	400	♂ ♀	2	5	3	17	21	12	12	11	6	11	—
Mangrove woodland (New Falmouth)	108	♂ ♀	6	10	6	28	26	3	14	7	—	—	—
Pooled	1905	♂ ♀	3	8	3	15	20	11	11	13	8	6	2

¹Letter symbols same as in Figure 3.

and 8% in the middle trunk. The use of these subzones varied from area to area, ranging from 17% for the middle inner branches in Portland Ridge to 26% in the mangrove woodland, 7% for the middle outer branches in the mangrove woodland to 14% in both the Worthy park and Portland Ridge study areas, 5% for the middle trunk in Hardwar Gap to 11% in Portland Ridge (Table 5). Although some differences between the sexes exist with regard to the subzones used, a wide range of overlap is evident. The greatest differences between the sexes were in the use of the lower inner branches in the Portland Ridge region, 16% for the male and 10% for the female, and the middle inner branches in the mangrove woodland, 34% for the male and 22% for the female, a 6% difference in the former, and a 12% difference for the latter. In most of the subzones the range of overlap was from complete overlap to 3% differences. What is apparent is a correlation between the foraging zones used and the foraging behavior.

FORAGING METHODS.—Foraging by the Jamaican Woodpecker in the principal study areas is shown in Table 6. The pooled results for both sexes from all the study areas indicate that the predominant foraging methods are fruit-eating (28%), probing (28%), and pecking (20%). Probing into bromeliads (13%), gleaning (9%), and sallying (2%) accounted for the rest of the foraging procedures.

A comparison of the foraging patterns used by male and female Jamaican Woodpeckers (Table 6) shows that the area of overlap between the sexes was large and that neither sex used one method solely. The greatest difference noted between the sexes was in pecking—the combined results of the different study areas indicate that males do 5% more pecking than females, but this is not the complete picture. In some individual study areas (e.g. dry limestone forest) females peck more frequently than males (4% differences).

The results from the individual study areas indicate that certain feeding repertoires predominate in some places, whereas in others that same feeding repertoire plays a lesser role or is absent (Table 6). The high percentage of fruit in the diet of the Jamaican Woodpecker in some of the study tracts, for example, appears to be correlated with the diversity of fruiting trees that provide a variety and abundance of fruit at all seasons. Fruit-eating was highest in Worthy Park (33%) where an abundance of different fruiting trees occurs, and lowest in the mangrove woodland (0%) which was a low tree species diversity and few fruit-bearing trees.

Foraging pattern type was correlated with foraging zone used. For example, in Worthy Park where the incidence of fruit-eating was high, the use of the outer branches for foraging was also high (34%). This is obviously related to the fact that most of the fruit-bearing branches of the tree occurred in the outer zone. In the mangrove woodland, which has a low fruiting tree diversity, the predominant mode of foraging was pecking (58%), and this is reflected by the foraging zones used, the trunk and the inner branches (21%

TABLE 6.—USE (IN PERCENT) OF VARIOUS FORAGING METHODS IN DIFFERENT HABITATS BY THE JAMAICAN WOODPECKER.

Study Areas	N ¹	Sex	Pecking	Probing	Bromeliads	Gleaning	Fruit-eating	Sallying
Wooded pasture (Worthy Park)	731	♂	22	22	14	9	31	2
Dry limestone forest (Portland Ridge)	50	♂	30	28	—	10	32	—
Montane mist forest (Hardwar Gap)	259	♂	16	47	13	7	17	—
Mangrove woodland (New Falmouth)	32	♂	66	25	—	9	—	—
Pooled	1072	♂	22	29	12	9	27	1
Wooded pasture (Worthy Park)	552	♀	10	21	17	10	37	5
Dry limestone forest (Portland Ridge)	68	♀	34	29	—	9	28	—
Montane mist forest (Hardwar Gap)	140	♀	14	36	16	8	26	—
Mangrove woodland (New Falmouth)	76	♀	55	37	—	9	—	—
Pooled	836	♀	17	26	14	9	31	3
Wooded pasture (Worthy Park)	1283	♂ ♀	16	22	15	10	33	4
Dry limestone forest (Portland Ridge)	118	♂ ♀	32	37	—	10	21	—
Montane mist forest (Hardwar Gap)	399	♂ ♀	15	44	14	7	14	—
Mangrove woodland (New Falmouth)	108	♂ ♀	58	32	—	9	—	—
Pooled	1908	♂ ♀	20	28	13	9	28	2

¹Represents the number of observations.

and 57% respectively). In all the study tracts pecking was confined mainly to the trunk and the inner branches. The other study areas also showed a correlation between the foraging behavior and the foraging zones used.

PROBING.—Probing and fruit-eating were the most common foraging procedures used by the Jamaican Woodpecker, each accounting for 28% of the total. These values exclude probing into bromeliads, which is included in a separate section and accounts for 13% of the total foraging observations. Probing was used in all the study areas, ranging from 22% in the wet limestone forest (Worthy Park) to 44% in the montane mist forest (Hardwar Gap). A low frequency of probing for Worthy Park is possibly correlated with the availability of alternate food sources, such as fruiting trees and bromeliads. On the other hand, frequency of probing in the montane mist forest is possibly related to the presence of a large number of weathered holes and rotten branches (the result of high atmospheric humidity and rainfall) that provide many suitable sites for probing.

In probing both the bill and the tongue are used to explore a variety of natural cavities and accumulations of plant material. Cavities in which the woodpeckers probed included fissures and cracks in the bark, knot holes, weathered holes, holes previously excavated by woodpeckers, holes in ends of rotten or dying branches, and stumps. Accumulation of plant material included debris between trunks and lateral branches, spaces in and underneath mosses, lichens, and epiphytic growth on trees.

The long and protrusible tongue of the Jamaican Woodpecker, which extends almost 5 cm beyond the tip of the bill, is highly adaptive for probing. Kilham's studies (1963) on the use of the tongue by various woodpeckers showed that the tongue of the congeneric *Melanerpes carolinus*, while not as long as the tongues of *Colaptes* or *Dryocopus*, appears to function more adroitly in maneuvering objects at a distance, within crevices. Neither *Sphyrapicus varius* nor *Melanerpes erythrocephalus* has the long-distance control and adroitness of *M. carolinus*.

Kilham (1963) stated: "*C. carolinus* spends almost no time excavating holes when in search of grubs and other prey, but appears to accomplish the same objective by using bill and tongue to explore natural crevices. When I brought rotting logs from the woods to the aviary, the Pileated, Downy, and Hairy Woodpeckers, as well as the Yellow-shafted Flicker, and to a lesser extent, the sapsuckers, were immediately interested and each began pecking or hewing, in its individual style, to get ants, termites, or whatever might turn up. The strategy of *C. carolinus* was effective in this competitive situation . . . this species explored the logs with its tongue, occasionally twisting its head upside down to do so. In this manner it sometimes pulled out beetle larvae 2.5 to 5 centimeters long before any of the other woodpeckers had dislodged prey of any size. It may be that the tongue-probing of *Centurus*, in contrast to pecking and hewing methods, enables it to come upon its victims quickly and without disturbance."

My field observations on both the Jamaican Woodpecker and the Red-bellied Woodpecker in Florida bear out Kilham's observations, but the Jamaican Woodpecker does more pecking than the Red-bellied Woodpecker, in which pecking as a feeding method accounted for only 4% of its total foraging procedures. This low figure is possibly related to the presence of other woodpeckers in Florida that are more effective "peckers," whereas the higher pecking figure for the Jamaican Woodpecker is probably due to the absence in Jamaica of other woodpeckers that might compete with and be more efficient in using the pecking niche.

EPIPHYTES.—The use of this foraging niche was correlated with the quantities of epiphytes (particularly bromeliads) present. The mangrove woodland and the dry limestone forest support few bromeliads. In contrast the wet limestone forest and the montane mist forest have luxuriant growths of bromeliads and other epiphytes, and probing into bromeliads constituted 15% and 14.3%, respectively, of the total foraging methods for each of these habitats.

Foraging involved probing the inner and the outer leaves of the bromeliads, using the bill to push or throw aside debris or portions of the bromeliads until a suitable prey item was found. Foods seen taken from the bromeliads included snails (Gastropoda), spiders (Araneae), insects (Orthoptera, Coleoptera, larval lepidopterans, and other unidentifiable insects), frogs (*Hyla* spp.?), and an occasional fruit that had fallen into the bromeliad. The fauna of five bromeliads (two large, base diameter 20 cm; two medium, base diameter 13 cm, and one small, base diameter 5 cm) representative of the types used by the Jamaican Woodpecker consisted of snails (Gastropoda), earthworms (Oligochaeta), spiders (Araneae), insects (Tettigoniidae, Acrididae, Blattidae, Formicidae, unidentified hemipterans, larval and adult coleopterans, and lepidopterans), millipedes (Diplopoda), sowbugs (Isopoda), and frogs (*Hyla*).

PECKING.—The Jamaican Woodpecker has the family's structural specialization of obtaining food by pecking, but pecking does not play so prominent a role in its foraging as it does in some of the continental species (Table 11), other than its mainland congeners, *M. carolinus* and the *M. erythrocephalus*. Observations in Florida indicated that pecking accounted for 4% and 2% of the total foraging behavior of the Red-bellied and Red-headed woodpeckers, respectively. In contrast, pecking in the Jamaican Woodpecker accounted for 20% of the pooled results for the different study tracts, ranging from 15% in the montane mist forest to 58% in the mangrove woodland (Table 6). This difference between the insular species and its mainland congeners is probably related to the absence in Jamaica of other species of woodpeckers that would compete for the pecking niche. In Florida, for example, pecking plays a prominent role in the Pileated, Hairy, and Downy Woodpeckers, accounting for 62%, 91%, and 89% of the total foraging behavior (Table 11).

Pecking constituted a greater proportion of the foraging behavior in those

habitats where fruiting and epiphyte-laden trees were scarce, such as the mangrove woodland and dry limestone forest. In the wet-limestone and montane mist forests pecking played a minimal role.

Pecking for food was confined mainly to dead or dying portions of the tree, ranging from large tree trunks to the outer branches, and to the hollow branches of *Cecropia*. The latter, occupied by ants (Formicidae), was a favorite pecking site. This type of predation on ants living in *Cecropia* internodes is not peculiar to the Jamaican Woodpecker for it has also been reported by Skutch (1945) and Janzen (1969) for Central American woodpeckers. In addition this type of predation is not peculiar to ants living in *Cecropia*, for I have seen the Jamaican Woodpecker feed on the twig- and branch-inhabiting ants in other tree species, although it was not as common. The pecking procedure did not involve splitting the twigs, but punching a series of holes through the twig wall at approximately 2-8 cm intervals. The spacing and the size of the hole the woodpecker made varied according to the size and type of twig involved. Food items obtained by pecking, other than ants, included various woodboring larvae (e.g. Buprestidae).

In pecking the Jamaican Woodpecker assumes the woodpecker stance described by Spring (1965) for some North American woodpeckers. The whole body is held away from the tree trunk and the blow delivery momentum appears to come from regions posterior to the neck, although it appears that the neck also plays a role. While on a vertical surface (trunk), either pecking or climbing up, the toes are usually held in the position shown by Bock and Miller (1959) for the Hairy and Pileated Woodpeckers. While the fourth toe is directed laterally at right angles to the trunk, the second and third toes are held anteriorly and the hallux points down the trunk, and not in a zygodactyl position.

FRUIT-EATING.—Although the Jamaican Woodpecker is structurally specialized to obtain food by pecking, fruit-eating constitutes a greater proportion of the pooled foraging behavior than pecking, the former accounting for 28% and the latter for 20%. In addition, the results of the stomach analysis indicate an even greater use of fruits (41%). The use of fruits as food was directly correlated with the presence, abundance, and diversity of fruiting trees. In the mangrove woodland few fruiting trees were present and none was bearing fruits during my visits, and therefore no fruit-eating was recorded. The wet limestone forest had a diversity and abundance of fruiting trees (Table 7), and fruit-eating accounted for 33% of the total. In both the montane mist forest and dry limestone forest fruiting trees were also present, but not in the abundance or diversity of the wet limestone forest, which is reflected in the lower numbers of fruit-eating observations reported there (Table 7).

Melanerpes radiolatus showed considerable agility in moving over the outer branches of trees where most of the fruits grew. Birds often balanced

TABLE 7.—RECORDS OF FRUIT-EATING BY *Melanerpes radiolatus*.

Trees and Shrubs		Limestone Forest		Montane Mist
Family	Species	Wet	Dry	Forest
Ulmaceae	<i>Trema micranthum</i> ¹	5	—	—
Moraceae	<i>Trophis racemosa</i>	10	—	—
	<i>Cecropia peltata</i>	138	—	—
	<i>Ficus trigonata</i>	70	—	—
	<i>Ficus pertusa</i>	21	—	—
	<i>Ficus citrifolia</i>	—	2	—
Lauraceae	<i>Ocotea</i> sp.	20	—	—
	<i>Nectandra antillana</i>	15	—	—
	<i>Nectandra coriacea</i>	11	2	—
Rutaceae	<i>Citrus aurantium</i>	4	—	—
	<i>Fagara martinicensis</i>	8	—	—
Simaroubaceae	<i>Picrasma excelsia</i>	57	—	—
Burseraceae	<i>Bursera simaruba</i>	—	6	—
Euphorbiaceae	<i>Alchornea latifolia</i>	—	—	26
Anacardiaceae	<i>Mangifera indica</i>	8	—	—
Thymelaeaceae	<i>Metopium browni</i>	—	12	—
Thymelaeaceae	<i>Daphnopsis americana</i>	48	—	—
Flacourtiaceae	<i>Casaeria hirsuta</i>	10	—	—
	<i>Casaeria nitida</i>	—	1	—
	<i>Laetia thannia</i>	4	—	—
Araliaceae	<i>Dendropanax arboreus</i>	—	—	19
Sapotaceae	<i>Bumelia salicifolia</i>	—	2	—
	<i>Pouteria multiflora</i>	2	—	—
	<i>Chrysophyllum cainito</i>	5	—	—
Symplocaceae	<i>Symplocos octopetala</i>	—	—	10
Boraginaceae	<i>Cordia collococca</i>	4	—	—
Verbenaceae	<i>Petitia domingensis</i>	4	—	—
Solanaceae	<i>Dunalia arborescens</i>	—	—	19
Total number of observations		429	25	80

¹Botanical names taken from Adams (1972).

between two limbs, with legs spread apart, holding one branch with each foot, and reaching out for the fruits. Sometimes individuals flew to a clump, clung to the fruits, and plucked them. Occasionally I saw the birds hang upside down with the body parallel to the ground to reach an otherwise inaccessible fruit.

Small fruits (<25 mm) were plucked and swallowed and if the fruit was very small (5 mm), it was not uncommon to see woodpeckers with more than one fruit in the bill at a time (up to seven in one instance). If the fruit was large (> 25 mm) (e.g. ripe mango), the bird first pecked a hole in it, and then used the bill and tongue to probe and feed on the fleshy pulp. In feeding on *Cecropia* catkins (up to 6 cm), the birds broke off terminal pieces and swallowed them whole.

I recorded 29 different types of fruit eaten by the Jamaican Woodpecker. Fruit from trees of the family Moraceae accounted for one-half of the fruits they ate in the wet limestone forest. In the dry limestone forest and montane mist forest, where fewer cases of fruit-eating were recorded, *Alchornea*, *Dunalia*, and *Dendropanax* fruits accounted for more than three-fourths of the fruits eaten in the latter, and *Metopium* accounted for nearly one-half of those eaten in the former (Table 7).

GLEANNING.—Gleaning accounted for 9% of the total foraging behavior recorded. This consisted of searching along the limb and trunk surfaces for invertebrate or vertebrate prey. On trunks and larger branches, gleaning Jamaican Woodpeckers move in a fashion characteristic of most woodpeckers, using their stiff rectrices as a prop and the laterally directed toes acting in juxtaposition as a pincer. This stance was used while gleaning on horizontal and vertical surfaces and even when moving along the underside of large branches. On vertical branches, gleaning birds usually moved outward from the trunk and then usually flew back to where another branch joined the trunk and repeated the process. The identifiable animals taken by gleaning included tree snails (Gastropoda), insects (Orthoptera, Coleoptera, and larval Lepidoptera), and *Anolis* lizards.

SALLYING.—Jamaican Woodpeckers rarely engaged in sallying flights (Table 6), which usually took place in late afternoon from the tops of trees. The flight pattern took the form of a circle or a loop and the bird returned to the same perch or part of the tree.

STOMACH ANALYSES.—Tables 8 and 9 list all food items found in the stomachs of Jamaican Woodpeckers, as well as frequency and volume percentages of each prey taxon in the diet. Figure 8 shows the size distribution of intact animal prey.

In the Jamaican Woodpecker diet both animal and vegetable matter are well represented, comprising 58.2% and 42.7%, respectively, of the total volume. A striking general result of the present study is the demonstration of the major role played by vegetable material (fruits) in the diet of a member of a family considered primarily insectivorous.

The animal food embraced 3 classes, 7 orders, and 11 families. Insects were most important in the woodpecker diet, comprising 48.6% by total volume. The most important taxa were Orthoptera, Lepidoptera, and Coleoptera, accounting for 18.2%, 14.2%, and 11.5% of the total volume, respectively.

The low percentage of wood-boring larvae and limb or twig dwelling insects, accounting for (at the most) 10% of the total volume, is in agreement with the results of the foraging behavior where pecking accounted for 16% of the total in Worthy Park. Included here are the wood-boring larvae of Coleoptera (Buprestidae) and twig-dwelling ants (Formicidae). Most of the invertebrate prey taxa (48%) live on wood surfaces, in crevices, in accumulation of plant material, and in epiphytes. They included tree snails (Poma-

TABLE 8.—ANIMAL FOODS IN THE STOMACHS OF *Melanerpes radiolatus*.

Prey Taxon	Percent Occurrence			Percent Volume		
	♂ (15)	♂ ♀	♀ (14)	♂ (15)	♂ ♀	♀ (14)
Mollusca						
Gastropoda						
Pomatiasidae	—	6.9	14.2	—	2.0	4.7
Helicinidae	—	3.4	7.1	—	0.6	1.5
Undetermined	6.6	6.9	7.1	2.8	2.4	1.9
Arthropoda						
Arachnida						
Heteropidae	6.6	6.9	7.1	1.4	3.6	6.6
Undetermined	6.6	6.9	7.1	0.3	0.2	0.2
Insecta						
Undetermined	13.3	6.9	—	2.5	1.5	—
Mallophaga						
Menoponidae	6.6	3.4	—	0.3	0.1	—
Orthoptera						
Locustidae	26.7	22.1	21.4	5.3	7.7	11.0
Tettigoniidae	13.3	13.8	14.3	7.0	6.7	6.3
Gryllidae	6.6	6.9	7.1	2.3	3.7	5.7
Coleoptera						
Buprestidae	13.3	6.3	—	6.3	3.6	—
Cerambycidae	6.6	3.4	—	2.5	1.5	—
Undetermined	26.6	31.0	35.7	2.6	3.6	4.9
Lepidoptera						
Noctuidae	20.0	13.8	7.1	11.3	9.1	5.9
Undetermined	13.3	10.3	7.1	6.0	5.2	4.0
Hymenoptera						
Formicidae	33.3	34.4	35.7	4.9	5.1	5.3
Undetermined	—	7.1	13.8	—	0.2	0.4
Subtotal: Animal	—	—	—	55.5	58.2	58.4
Subtotal: Plant	—	—	—	44.2	42.7	41.0

tiasidae and Helicinidae), spiders (Heteropidae), grasshoppers (Locustidae and Tettigoniidae), crickets (Gryllidae), beetles (Cerambycidae and others of undetermined families), most of the lepidopteran larvae (Noctuidae), and possibly some of the ants. These prey items are obtained primarily by nonpecking means, such as probing and gleaning. The Noctuidae larvae, for example, belong to a group that is active during the night, but during the day hides underneath the bark, in crevices, and plant accumulation (Dale H. Habeck, pers. comm.). The proportion of the invertebrate prey obtained by nonpecking means (48%) is in close agreement with the results obtained in the foraging methods section, where foraging patterns other than pecking and fruit-eating accounted for 51% of the total volume.

Plant materials consisted of fruits and seeds, representing three identified families and ten genera. The family Moraceae was the most important in the diet, their fruits and seeds accounting for 25.4% of the total volume. The most important taxa were *Cecropia* and *Ficus* spp., accounting for 17.5%

TABLE 9.—VEGETABLE FOODS IN THE STOMACHS OF *Melanerpes radiolatus*.

Plant Taxon	Percent Occurrence			Percent Volume		
	♂ (15)	♂ ♀	♀ (14)	♂ (15)	♂ ♀	♀ (14)
Moraceae						
<i>Cecropia</i>	51.7	44.8	42.9	23.5	17.5	9.3
<i>Ficus</i>	26.6	20.6	14.3	7.7	7.3	6.6
<i>Trophis</i>	6.6	6.8	7.1	0.5	0.6	0.8
Lauraceae						
<i>Baileismidia</i>	-	3.4	7.1	-	2.4	5.7
<i>Nectandra</i>	6.6	6.8	7.1	0.8	1.3	1.9
<i>Ocotea</i>	6.6	6.8	7.1	4.9	5.6	6.7
Simaraubaceae						
<i>Picrasma</i>	-	3.4	7.1	1.1	0.6	-
Flacourtiaceae						
<i>Casaeria</i>	-	3.4	7.1	-	1.2	2.8
Thymelaeaceae						
<i>Daphnopsis</i>	13.3	13.8	14.3	5.3	5.3	5.1
Araliaceae						
<i>Dendropanax</i>	6.6	6.8	7.1	-	0.2	0.6
Undetermined	6.6	6.8	7.1	0.4	0.9	1.5
Subtotal: Plant	-	-	-	44.2	42.7	41.0
Subtotal: Animal	-	-	-	55.5	58.2	58.4

and 7.3% of the total volume. Both of these trees were visited by large numbers of birds to feed on their fruits. In Worthy Park I counted 11 species of birds feeding in a single *Cecropia peltata* tree and 19 species in a single *Ficus trigonata* tree (Cruz 1974). Other plants important in the diet (in percent of total volume) were fruits and seeds of the families Lauraceae 7.0%, Thymelaeaceae 5.3%, and Simaraubaceae 3.1%.

Figure 5 shows the distribution of prey in different size classes by percent frequency. The prey ranged from small ants (4 mm) to large caterpillars (45 mm). Most of the prey items taken by both sexes were in the 1-10 mm range, but as only intact prey items were measured and the prey capturing technique fractured proportionately more prey items, the sampling is biased against larger prey items (greater than 10 mm). Figure 5 shows a large prey size overlap between the sexes, so they are not selecting different prey sizes.

The large and diverse numbers of animal and plant species taken strongly suggest that the Jamaican Woodpecker is exceedingly diverse and opportunistic in its feeding habits, taking nearly all the animal and fruit material (within a certain size range) that it encounters while foraging. Fruit size is probably not of great importance, as the woodpecker uses its tongue and bill to feed on the fleshy pulp of larger fruits. If one assumes that woodpeckers forage in a manner that maximizes energy intake per unit of time and energy expended (MacArthur and Pianka 1966, Emlen 1966), it is unlikely that their

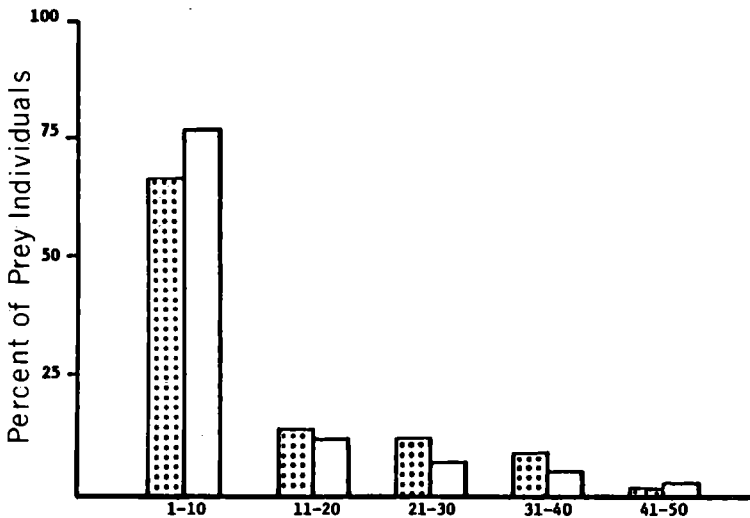


FIGURE 5.—Percentage of prey individuals in five categories of prey size for the Jamaican Woodpecker. Data are based on intact prey items found in the stomachs of 114 males and 141 females. Open bar = females; dotted bar = males. Food size in mm.

rate of energy intake could be increased, or even maintained by selectively discriminating against certain prey items unless they are highly unsuitable for other reasons, i.e. toxic, distasteful, or hard to catch.

All three of the techniques of measurement and analysis (percent occurrence, percent volume, and prey size distribution) showed an overlap in the kinds of foods male and female Jamaican Woodpeckers eat (Tables 8, 9 and Figure 6). Usually not only were the same families present but the same prey species of both animals and plants.

INTERSPECIFIC FOOD COMPETITION.—Orians and Willson (1964) suggested that in cavity-nesting birds the two resources most likely to be limiting and thus subject to interspecific competition are nest sites and food. On Jamaica interspecific competition for nesting holes was apparent and is discussed below, but in contrast I found little direct evidence that interspecific competition for food existed, though the feeding habits of the Jamaican Woodpecker overlapped in varying degrees with those of some of the species occurring in the same habitat. Table 10 shows the various bird species that were seen feeding either on similar foods or with similar foraging techniques. In all cases, however, the species that overlapped the Jamaican Woodpecker were morphologically or behaviorally adapted to obtain foods not available to the Jamaican Woodpecker, and conversely, the woodpecker's adaptations for pecking and probing enable it to forage and obtain foods not available to the other species in this table.

LACK OF DIFFERENTIAL NICHE UTILIZATION BETWEEN THE SEXES.—No selection pressure for differential niche utilization between the sexes appears

TABLE 10.—NICHE AND MORPHOLOGICAL CHARACTERISTICS OF BIRDS THAT OVERLAPPED IN THEIR FOODS AND FORAGING TECHNIQUES WITH THE JAMAICAN WOODPECKER.¹

Species	Body ² size	Bill ³ length	Feeding ⁴ heights	Foraging ⁴ methods	Foods ⁵ taken	Mean
<i>Columba leucocephala</i>	3	3	2	4	4	3.2
<i>Aratinga nana</i>	3	3	2	4	4	3.2
<i>Saurothera vetula</i>	2	2	1	4	4	2.6
<i>Hyetornis pluvialis</i>	2	2	1	4	4	2.6
<i>Platypsaris niger</i>	3	2	1	3	3	2.4
<i>Tyrannus caudifasciatus</i>	3	2	2	4	3	2.8
<i>Corvus jamaicensis</i>	3	4	1	3	2	2.6
<i>Turdus jamaicensis</i>	2	2	3	3	2	2.4
<i>Turdus aurantius</i>	2	2	3	3	2	2.6
<i>Myadestes genibarbis</i>	4	3	1	3	3	2.8
<i>Vireo altiloquus</i>	4	3	1	3	3	2.8
<i>Coereba flaveola</i>	4	4	2	4	4	3.6
<i>Euneornis campestris</i>	4	3	2	4	3	3.2
<i>Pyrrhuphonia jamaica</i>	4	4	1	4	4	3.4
<i>Spindalis zena</i>	3	3	1	4	4	3.0
<i>Icterus leucopteryx</i>	3	2	1	2	2	2.0
<i>Nesopsar nigerrimus</i>	3	2	1	2	3	2.2
<i>Loxigilla violacea</i>	3	3	3	3	3	3.0
<i>Loxipasser anoxanthus</i>	4	4	3	4	4	3.8

¹Differences: 1 = Poorly developed, 2 = moderately developed,
3 = moderately well developed, 4 = strongly developed.

²Body size based on weights taken in the field and measurements from Ridgway (1902-16).

³Bill length from Ridgway (1902-16).

⁴Feeding heights and foraging methods based on field observations.

⁵Foods based on field observations and stomach analyses.

to have acted on the Jamaican Woodpecker—both are structurally monomorphic, forage in similar fashions, are syntopic, and take the same food. Food and foraging sites, which would be the two most important selective forces, appeared to be abundant in Jamaica as opposed to some other island situations (Grant 1968). The main reasons for the abundance of food and foraging sites in Jamaica are topographic and climatic diversity, which in turn produce a number of distinct habitats with an abundance of fruiting trees, bromeliads, and other microforaging sites. In addition interspecific competition for food or foraging sites is slight in the absence of other woodpeckers, birds of similar foraging behavior, and other true frugivores.

As in the case of *Asyndesmus lewis* (Bock 1971), the Jamaican Woodpecker appears to be an opportunistic feeder concentrating on temporarily abundant food sources. A pair of Jamaican Woodpeckers that made over 20 trips in one day to a fruiting *Ficus trigonata* abandoned it after 2 days when its fruits were depleted and responded to the availability of a new food source, *Daphnopsis* fruits, and made 25 trips in one day to the latter tree. During the same periods the two woodpeckers also engaged in generalized probing, probing into bromeliads, pecking, and gleaning. Bock (1971) noted that: "Niche dimorphism is unlikely in these instances on theoretical grounds,

since selection should favor the ability of both sexes to exploit the full range of food types. That is, if most important prey species or food sources become abundant sequentially or are generally evenly distributed, each sex should be unspecialized enough to feed upon all types." Bock further noted: "It is important to realize that the selection pressure of intraspecific competition can act only to increase an already established sexual dimorphism. In a theoretical monomorphic population, a large female would have the same advantages as a large male in exploiting foods unavailable to the bulk of the population. While individual variability might increase there would be no reason to expect sexual dimorphism to occur."

In a situation where food is not scarce both sexes will profit by having a longer bill, for Schoener (1967) noted that very large predators (implied here by longer snout lengths in *Anolis* lizards and bill lengths in birds) eat either an equal or a greater range of foods than smaller predators. In addition bill size is a good indicator of food size: birds with longer bills in general obtain larger prey items than birds with smaller bills (Grant 1968). As greater prey size implies greater biomass, which in turn implies more calories and more energy, both sexes would thus be equally efficient in obtaining energy from the environment.

In addition one might argue that by decreasing both the body size and bill size of the female, the female will be less efficient in protecting the nesting hole against competitors, of which a number of species are present on Jamaica. Another disadvantage, which may be of greater importance on the mainland than in insular regions, is the likelihood of predation. Islands usually have fewer predators so that larger size as a defense against predation may not be as important, but larger size may still confer a selective advantage. Possible predators of the Jamaican Woodpecker would be the Red-tailed Hawk (*Buteo jamaicensis*), Kestrel (*Falco sparverius*), Barn Owl (*Tyto alba*), and the Jamaican Owl (*Pseudoscops grammicus*). Hence the possible disadvantages of competing less with the male is counterbalanced by other selective advantages for the female.

COMPARISON OF WOODPECKER FORAGING DIVERSITY ON JAMAICA AND ON MAINLAND FLORIDA.—As some related sympatric species of land birds reduce competition through compression of their foraging niches (Gibb 1954, Haftorn 1956, MacArthur 1958, Dixon 1961, Brewer 1963, and Newton 1967), one might expect that a species occurring in an area with no related species that might compete for the same resources would have a broader feeding niche. To test this hypothesis, the foraging behavior of the Jamaican Woodpecker was compared to the foraging behavior of resident Florida woodpeckers. Foraging behavior diversity was measured by the information theory formula (Shannon-Weaver formula), $-\sum p_i \ln p_i$ where p_i is the percentage of the total foraging behavior located in the i th interval (MacArthur and MacArthur 1961, Crowell 1962, MacArthur, Recher, and Cody 1966).

The results of the comparison of the foraging behavior of the Jamaican Woodpecker with Florida woodpeckers (Table 11) indicate that the foraging diversity index of the Jamaican Woodpecker was almost equivalent to the pooled foraging diversity indices of seven Florida woodpeckers, 1.59 to 1.72 respectively. In addition the foraging diversity index of the Jamaican Woodpecker was higher than any one species of mainland woodpecker. The highest mainland foraging diversity indices were those of the related Red-bellied and Red-headed Woodpeckers, 1.27 to 1.35 respectively. The lowest mainland foraging diversity indices were those of the *Dendrocopos* woodpeckers (Downy, Hairy, and Red-cockaded), which had values ranging from 0.36 to 0.61.

No feeding methods were noted in the Jamaican Woodpecker that the mainland woodpeckers did not use, but the foraging methods were more evenly distributed in the different categories in the Jamaican Woodpecker. Thus while both the mainland Red-headed and Red-bellied woodpeckers have the same number of feeding categories as the Jamaican Woodpecker, the distribution was not as equitable. Approximately one-half the foraging of both species were in one foraging category, probing in the Red-bellied and fruit-and-mast-eating in the Red-headed Woodpeckers. An even more striking example is furnished by the Red-cockaded Woodpecker, which has one less feeding category than the Jamaican Woodpecker, but one (pecking) was used 84% of the time. These results show that the Jamaican Woodpecker has a more diverse foraging niche than any one of the mainland woodpeckers.

No evidence suggests that limitations in the range of available food resources are factors underlying these results. Rather certain feeding zones are incompletely exploited in Jamaica because of the depauperate nature of its avifauna, and hence it is profitable for *Melanerpes radiolatus* to extend into them. Thus while on the mainland, pecking as a foraging method is rarely used by the Red-bellied and Red-headed woodpeckers, presumably because other mainland woodpeckers can peck more effectively and they (Red-bellied and Red-headed) are better adapted to obtain food by other means; the related Jamaican Woodpecker uses pecking to a greater extent (20% of total).

For example, Jamaica has a sufficient diversity of habitats to support several species of woodpeckers and birds of similar foraging types, as in continental habitats and islands near the mainland. For instance, the smaller island of Trinidad (2,980 sq km) has six species of woodpeckers and five of woodcreepers. Consequently Jamaica has unoccupied niches that permit niche expansion by species able to exploit the vacant habitats and niches as well as their own preferred ones (Crowell 1962, Selander 1966). This is achieved not by species abandoning their former way of life, but by their becoming increasingly diversified in food and foraging behavior as has the Jamaican Woodpecker.

An interesting and somewhat parallel situation was reported by Zusi (1969)

TABLE 11.—FORAGING BEHAVIOR OF THE JAMAICAN AND RESIDENT FLORIDA WOODPECKERS.

Species	No. ¹	Pecking	Probing	Gleaning	Vegetable	Ground	Sallying	Epiphytes	Scaling	FDI ²
Red-bellied	632	4 ³	53	21	16	1	—	5	—	1.27
Red-headed	248	2	5	26	47	6	14	—	—	1.35
Yellow-shafted	386	5	3	2	8	82	—	—	—	0.69
Pileated	149	62	18	3	16	—	—	1	—	1.04
Downy	127	89	8	3	—	—	—	—	—	0.41
Hairy	34	91	6	3	—	—	—	—	—	0.36
Red-cockaded	315	84	1	2	4	—	—	—	9	0.61
Total	1891	29	21	12	15	18	2	2	1	1.72
Jamaican	1908	22	29	9	27	—	1	12	—	1.59

¹Number of observations²Foraging diversity index³Percent of total observations

on Dominica where no woodpeckers or woodcreepers occur. There the Trembler (*Mimidae*, *Cinlocerthia ruficauda*) feeds on a variety of animal and plant foods, but does most of its feeding among epiphytes and clumps of dead leaves, and takes food from crevices on trunks or tangled vines. Zusi stated: "In forests of the mainland, members of the *Dendrocolaptidae* and *Furnariidae* forage among epiphytes and leaf trash and on tree trunks. Neither family is present on the Lesser Antilles, and no mimid has a comparable foraging niche on the mainland. The Trembler's feeding adaptations probably evolved largely on the islands in the absence of species specialized for arboreal rummaging." In a similar fashion, the Jamaican Woodpecker's use of bromeliads and other epiphytes may be related to the absence of *Dendrocolaptidae* and *Furnariidae*.

Thus through a diversification in its foraging patterns, the Jamaican Woodpecker is able to use foods and foraging zones of species that are absent, and to exploit its insular environment to a degree that in continental habitats is achieved only by the combined efforts of several species of woodpeckers and birds of similar adaptive types.

BREEDING BEHAVIOR AND BIOLOGY

The Jamaican Woodpecker has an extensive communications and display repertoire, the former by both vocal and mechanical means. Both sexes take part in the vocalization, drumming, and displays discussed below. In contrast to the situation described by Kilham (1961) for the Red-bellied Woodpecker in which the males are the more active participants, the female Jamaican Woodpecker appears to be almost as active a performer as the male. The categories used below are based on Kilham (1961), Lawrence (1967), and my interpretations of their meanings based upon the circumstances attending their communications and displays on repeated occasions.

VOCALIZATIONS

LOCATION CALL.—A loud *kaa* that may be repeated two or three times in succession. This call is heard throughout the year, but is heard more frequently during the breeding season. The location call is used to reveal a bird's presence and location to another woodpecker or to its young. Upon hearing it, one or more Jamaican Woodpeckers usually answer with the same call, or signal a response by drumming and, depending upon the circumstances, one of the participants may fly toward the other.

TERRITORIAL CALL.—A very loud *kaaaah* that usually includes shaking or vibrating of the entire body. Its use is to advertise the territory, and it is also given when disturbed by a human intruder. Upon hearing it one or more woodpeckers answer with the same call or signal a response by drumming.

LOW INTENSITY ALARM CALL.—The low intensity alarm call *kao* is usually expressed singly but is sometimes repeated in a continuous and scolding

fashion. It suggests, as Lawrence (1967) noted, alertness to danger, to the unexpected, unusual, or strange. Birds uttered it, for example, when I surprised an individual feeding, or came too close to a nesting tree or to an adult bird with a juvenile.

HIGH INTENSITY ALARM CALL.—The high-intensity alarm note, a loud *wee-cha wee-cha*, is usually uttered in intraspecific encounters between woodpeckers not belonging to the same family group.

BREEDING CALL.—Whereas the above calls were heard during December, the breeding call, *krirr, krirr*, and the following mutual recognition call were heard only during the breeding season. The breeding call was heard throughout the reproductive period, but was uttered more frequently during the early reproductive period before egg-laying. It is somewhat reminiscent of the *kwirr* note of the North American Red-bellied Woodpecker, although harsher. It appears to have the same functions as in the Red-bellied Woodpecker, namely to bring the sexes together and to establish and maintain pair bonds during the breeding season (Kilham 1958, 1961, Stickel 1965).

MUTUAL RECOGNITION OR CONTACT NOTES.—A low intimate *whirr-whirr* sound was given by members of a pair and apparently functions in mutual recognition and to reinforce the pair-bond. This sound was heard during courtship and when one member of the pair alighted near its mate to relieve it from excavation or incubation duties.

MECHANICAL COMMUNICATION

Mechanical means of communication are important in this species, as they are in many other woodpeckers. They serve a variety of functions, i.e. expressing excitement, territorial dominance, or displacement.

DRUMMING.—Drumming is the burst of very closely spaced taps produced when the woodpecker's bill hammers on any resonating structure, such as a dead or hollow branch. Drumming in the Jamaican Woodpecker appears to have the same function as in other woodpeckers (Kilham 1959, 1961, Lawrence 1967, Bock 1970, 1971), that is, the assertion of territorial dominance and the attraction of a mate. In contrast to the Red-bellied Woodpecker, in which drumming is far less common and is used frequently or solely by the male (Kilham 1961), both sexes of the Jamaican Woodpecker drum.

RITUAL AND MUTUAL TAPPING.—Ritual and mutual tapping were noted in the Jamaican Woodpecker and appear to serve the same function as in the Red-bellied Woodpecker, the strengthening of the pair bond (Kilham 1958). The arrival of the mate while the partner is in or near the nest hole appears to be necessary for the performance of ritual or mutual tapping, and it may be enacted either by the male or female in response to the appearance of its mate. In ritual tapping the mate begins tapping in one spot upon the arrival of the partner at the nest hole. Tapping may either take place outside or inside the nesting hole. Outside the nest hole, tapping usually takes place just

below the lower rim of the hole. An elaboration of ritual tapping is mutual tapping in which both members of a pair tap together.

DISPLACEMENT TAPPING.—Displacement tapping is the tapping produced under stress or confusion. This was witnessed, for example, when a dummy Jamaican Woodpecker skin was put near the nest hole while the woodpeckers were away. Upon arrival the male was confused, did not enter the nesting hole, and circled the dummy woodpecker. Instead of attacking the dummy bird (as it did later), it flew to the base of a large bromeliad and tapped for 50 seconds.

DISPLAYS

CREST-RAISING.—Crest-raising was done alone or accompanying other displays. It is usually indicative of a disturbed or excited condition.

BILL-WAVING.—The bill-waving display is usually done in conjunction with either low or high intensity alarm calls. The woodpecker, with rectrices spread and crest raised, swings its head from side to side in a 180 degree angle. Lawrence (1967) described similar types of displays in the Hairy and Downy woodpeckers, Yellow-shafted Flicker, and Yellow-bellied Sapsucker, but it has not been reported in other *Centurus* woodpeckers.

RESTING MOTIONLESS.—Members of a pair or a family group may cease all activities and remain motionless within close proximity of each other for periods of up to 20 minutes. This form of behavior has also been observed in the Red-bellied and the Hairy Woodpeckers by Kilham (1966); and in palearctic woodpeckers by Pynnönen (1939). Kilham noted: "for such active, energetic birds, these . . . motionless periods are a striking form of behavior."

TERRITORY, TERRITORIALITY, HOME RANGE, AND NEST HOLE COMPETITION

DEFINITIONS.—A territory in this study is defined as a space within which an animal is aggressive toward and usually dominant over certain categories of intruders (Emlen 1957), whereas the home range is the total area that a bird habitually occupies and normally confines its movements to (Burt 1943). In some birds home range may be the same as the territory if the bird defends the whole area, and in other birds the territory may be restricted to the nesting area (for a fuller treatment of territories see Nice 1941, Hinde 1956, Brown 1964). I found that the Jamaican Woodpecker occupies overlapping home ranges and that territorial defense is restricted to the vicinity of the nest.

HOME RANGE.—Home ranges of 12 breeding pairs of Jamaican Woodpeckers obtained during the 1969 breeding season are given in Figure 6. The size of the home range in the Worthy Park area (modified wet limestone forest) varied from .74 to 2.6 ha (\bar{x} = 1.4 ha). The size of the home range appears to depend upon the suitability of the area for foraging. For instance pair No. 1, which occupied a more open area with fewer trees, had the largest home range. In contrast, pair No. 3, which occupied a heavily wooded area

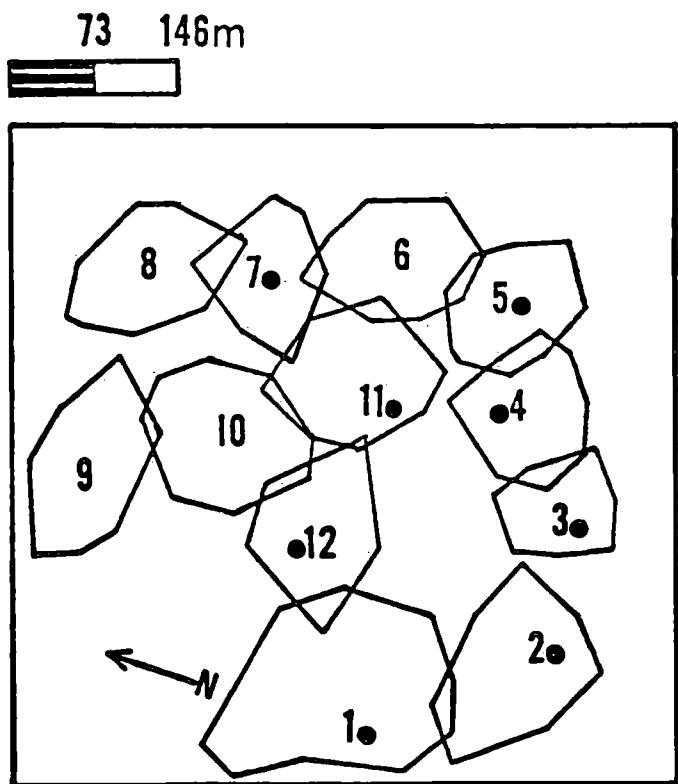


FIGURE 6.—Home ranges of 12 breeding pairs of Jamaican Woodpeckers during the 1969 breeding season in Worthy Park. Circles indicate nesting tree. Those ranges without circles are for family groups with postfledgling young.

with many fruiting trees and foraging sites, had the smallest home range. Frequently (27 observations) pairs occupying neighboring home ranges fed within full view of one another and no aggressive behavior was detected. In one instance (30 June 1969), the male and female of pair No. 5 and the male of pair No. 4 fed without conflict in the same fruiting tree.

TERRITORIAL UNIT.—In the Jamaican Woodpecker, the territorial unit consisted of the nest tree and its immediate surroundings. Using the nest tree as the approximate center, the territory appears to have a maximum radius of approximately 40 meters. The principal elements of the territorial behavior included (Lawrence 1967): (1) calls and drumming, expressing challenge or protest; (2) display, elaborate conspicuous movements expressing protest and having the effect of threat; (3) pursuits, taking the form of stalking, chasing, or supplanting attack (in which the attacker dislodges the trespasser by flying at him and taking his place); and (4) fighting, involving bodily contact.

TERRITORIAL DEFENSE.—Adjacent pairs often fed within full view of one

another in the area of home range overlap, but if a strange or neighboring woodpecker intruded the vicinity of the nest area (black circles in Fig. 6), the resident woodpecker actively defended it. The size of the defended area was difficult to quantify because intrusion of the territorial boundary of nesting woodpeckers by another woodpecker was rarely recorded. In three seasons of nesting observations, territorial conflicts were recorded only nine times—six of the conflicts took place when a strange woodpecker landed on a tree adjacent to the nest tree. In each case the intruder was repelled by either chasing or supplanting attacks. The minimal distance that an intruding bird was chased was 15 m and the maximal distance was 40 m. In one instance the resident male chased an intruding male for approximately 30 m before flying back to the nest tree. The intruding male flew to an exposed branch on a tree 50 m from the nest and remained for approximately 5 minutes; although the intruding bird was still in the home range and in full view of the resident male, no further territorial behavior was recorded.

An example of territorial behavior is taken from my field notes. On 7 July 1969, a strange male landed on the tree where the Swansea pair was brooding the young. The resident male arrived momentarily. Instead of entering the nest hole, he flew to a dead branch on the same tree and started to drum. The intruding male remained close to the branch and did not respond to the drumming. The resident male with crest raised flew toward the intruding male (supplanting attack), which flew off to another branch on the same tree. Next a series of pursuits began, the resident male chasing the intruding male from one limb to another or following him around the tree trunk. This lasted for approximately 3 minutes, culminating with the resident male chasing the intruder off the tree and following him for approximately 35 m. During this time, the female did not join in the chase, but flew to an exposed dead branch on the nest tree and began uttering high-intensity alarm notes.

EXPERIMENTS WITH DUMMIES.—Before describing the experiments with dummies and mechanical stimuli, I must emphasize that while these experiments are useful and helpful in gaining insight into woodpecker behavior, specifically territorial behavior in this case, the results, if not corroborated with the action of live woodpeckers, might be misleading in some cases. For instance Lawrence (1967) noted: "The woodpecker's encounters with dummies . . . which elicited ferocious attacks and pecking carried to the extreme, certainly give a distorted idea of the birds' normal way of life. In the wild the woodpeckers display to live opponents that move and never remain still in one place. Swiftly and impressively the woodpecker reacts to the sight of an aggressively displaying bird of its own kind and every one of its movements has, in turn, a crucial impact upon the latter's further behavior." Nevertheless, I feel that (bearing these limitations in mind) ex-

periments with dummies and mechanical stimuli are of value in gaining insight into behavioral phenomena that one has little opportunity to observe in nature.

I experimented with dummy woodpeckers on three different nesting pairs in the summers of 1969 and 1970. The following results obtained from a pair nesting in a prickly yellow tree are characteristic. On 2 July 1970 at 0900 I placed a dummy male Jamaican Woodpecker 1 m from the prickly yellow tree nest while the parents were away. At 0908 the male landed on the nest tree and saw the dummy. Instead of going into the nest hole as he normally did, he uttered high intensity alarm notes and moved his head from side to side (bill waving) and simultaneously started approaching the dummy. When he was 2 m from the dummy he flew to another tree and began tapping at the base of a bromeliad (displacement tapping). While he was tapping, the female landed on the nest tree, visibly agitated with crest raised, and uttered high intensity alarm notes. The male flew back to the nest tree with crest raised and began attacking the dummy with blows directed at the head region. The female did not join in the attack, but remained on the tree uttering high intensity alarm calls. The resident male's excitement was so great that he continued the attack while I was removing the pole with the dummy from its position. The pole with the attached dummy was next placed at distances of 5, 10, 15, and 20 m from the nest hole. At 25 m from the nest tree, the male discontinued the attack, but remained on the nest tree uttering high intensity alarm notes for 6 minutes, after which he entered the nest hole and resumed brooding the young. The female flew to the nest tree 18 minutes later and relieved the male. The male, completely ignoring the dummy, flew off the nest tree and began to forage.

TERRITORIAL DRUMMING.—The use of dummies was not the only way to elicit territorial defense. On many occasions tapping on a clip board with a pencil near the nesting hole excited the parents. For example on 14 July 1969, the female of the pair nesting in the guango tree was brooding young and the male was presumably foraging. At a distance of 5 m from the nest branch, I began tapping. Immediately the female stuck her head out, uttered a territorial call, flew to a dead branch on the nest tree, and began drumming. Momentarily the male joined the female on the tree, and began drumming and uttering high-intensity alarm notes. I repeated the tapping 15 m from the nest, the male flew toward me, landed on a vine 5 m from me, and with raised crest and bill-waving motions began uttering the high-intensity alarm call. I moved to 25 m from the nest and repeated the same procedure, again obtaining the same response from the male, but at a lower intensity. At 30 m from the nest, the resident male answered my tapping, but he remained on the nest tree. The following morning I repeated the same procedure, but this time started 45 m from the nest. No response was obtained at 45 or 40

m from the nest, but at 35 m the male responded by drumming. At 27 m from the nest the male not only responded to my tapping, but landed about 6 m from me and began uttering his high-intensity alarm note.

The results of the experiments with dummies and mechanical stimuli (tapping) were not unexpected in view of the previous observations on territorial behavior between resident and intruding woodpeckers, and served to reinforce and clarify those observations.

INTERSPECIFIC TERRITORIALITY.—Although the observations above demonstrate that the Jamaican Woodpecker exhibits intraspecific territoriality, I saw no interspecific aggressive behavior. On some trees containing active woodpecker nests other species of birds nested, and some even used unoccupied woodpecker holes. In one instance three hole-nesting birds, a Saffron Finch (*Sicalis flaveola*), a Starling (*Sturnus vulgaris*), and a Jamaican Woodpecker nested in different holes in the same branch. The Saffron Finch often chased the woodpecker as it entered or left the nest hole, but the woodpecker never reacted aggressively to either species.

On 14 occasions in a 3-day period I saw from one to three of the introduced common Parrotlets (*Forpus passerinus*) enter an active woodpecker hole containing young. Although in two instances the parent woodpeckers were on the nest tree, they watched the Parrotlets with indifference and made no efforts to drive them away. Another time I watched the male woodpecker land outside the nest hole with food while the Parrotlets were still inside the hole. Again the woodpecker acted indifferently and waited until the Parrotlets left. Apparently the Parrotlets did not harm the young because two juveniles fledged successfully from this nest, but because of its inaccessibility I was unable to determine the original number of young. Skutch (1948) also observed a similar lack of aggressive behavior between the Golden-naped Woodpecker (*Tripsurus chrysauen*) and other Central American birds.

Murray (1971) hypothesized that interspecific territoriality is misdirected intraspecific territoriality, and that it usually occurs in closely related species which share similar features that stimulate intraspecific territorial aggression. Thus Selander and Giller (1959) found that the Red-bellied and Golden-fronted woodpeckers (*Melanerpes aurifrons*) maintained exclusive territories where they occurred together near Austin, Texas. These two species resemble each other in plumage, vocalization, foraging, and nesting. The lack of interspecific territoriality in the Jamaican Woodpecker may be related to the absence of other species of similar morphology, vocalization, or habits that might otherwise stimulate territorial aggression.

DISCUSSION.—In the Jamaican Woodpecker territorial behavior is confined to the space around the nest and does not include the home range as it does in some mainland woodpeckers (Kilham 1958, 1961, 1968, 1969, Selander and Giller 1959, Ligon 1970). The reason for this seems to be that food is not a limiting factor in Jamaica and large territories are uneconomical,

in terms of time-energy budgets. In contrast, on the mainland where six or seven species of woodpeckers are sympatric, the species do not appear to have as diverse foraging niches as the Jamaican Woodpecker, and holding a large territory that includes the species' foraging zone may be advantageous. Brown (1964) noted that aggressive (territorial) behavior is generally employed by individuals in the acquisition of goals that tend to maximize individual survival and reproduction. Natural selection should favor aggressive behavior within a population when these goals are consistently and easily accessible through aggression, but should not favor it when they are not obtainable. For example when food is abundant or transient (fruiting trees) as appears to be the case in most Jamaican Woodpecker habitats, no territorial system is needed to defend foraging zones, and the territory if present is restricted to the space around the nest.

THE ANNUAL BREEDING CYCLE

Studies on the breeding biology of Jamaican Woodpeckers, primarily in Worthy Park, enabled me to complete a fairly accurate picture of their annual reproductive cycle. Figure 7 shows the combined breeding data of 19 pairs of woodpeckers. Most data (17 pairs) were obtained in a wet limestone forest, and the dates for certain events in the annual cycle may differ in other habitats or parts of the island. For instance, in New Falmouth (mangrove woodland) I saw a female woodpecker feeding a fledged bird on 11 May 1970; and Perkins (1970) saw a pair of woodpeckers in Trelawny excavating a nest hole in December 1933, from which young fledged in April. Snow and Snow (1964), in their work on the breeding seasons and annual

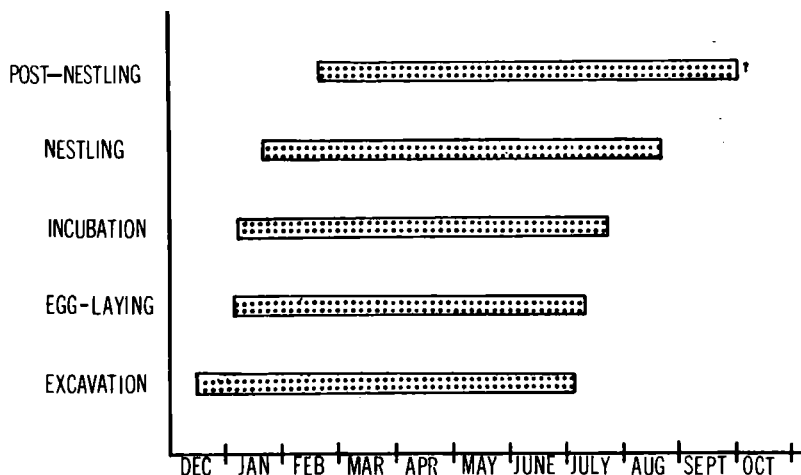


FIGURE 7.—The annual breeding cycle of the Jamaican Woodpecker based on 17 pairs in Worthy Park (St. Catherine), one pair at Baron Hill, one pair at New Falmouth (both in Trelawny).

cycles of Trinidad landbirds, found that the breeding season varied locally, being longest in regions of high rainfall and probably shortest in the very dry parts of Trinidad.

The breeding season of the Jamaican Woodpecker (excavating to post-nesting) extends at least 10 months (December to September), which is probably longer than that of any mainland temperate woodpecker. Lawrence (1967) found that in the four species she studied (Hairy and Downy woodpeckers, Yellow-shafted Flicker, and Yellow-bellied Sapsucker) the breeding cycle (excavating to post-nesting) extended from 4 to 5 months. The extended breeding season in the Jamaican Woodpecker is most likely related to the more uniform tropical climate, which provides sufficient food for the nestlings and adults throughout most of the year. In temperate zones with their seasonal variations in weather, reproduction must be timed to a period of minimum stress on the adults and maximum probability for the survival of both parents and the young, usually in the spring and summer.

PAIR-BOND RELATIONSHIPS.—Although no birds were banded in these studies, the recording of male and female Jamaican Woodpeckers feeding together when no reproductive activities were under way in Worthy Park suggests that they maintain year-round pair bonds. During December 1969, I made 21 observations of 7 different male and female woodpeckers (presumably pairs) foraging together in the home ranges occupied by pairs 1, 3, 5, 7, 10, 11, 12 (Fig. 6). During this period male and female woodpeckers occupying the same home range kept in contact by using location calls. These results differ from those of Kilham (1958, 1961) and Stickel (1965) for the congeneric Red-bellied Woodpecker in which the sexes do not maintain a year-round bond and occupy different home ranges during the nonbreeding season. My data are similar to Skutch's (1969) observations on the Golden-fronted Woodpecker (*M. aurifrons*) in which the sexes remain together throughout the year.

NEST SITES.—Data on 68 nest sites in Jamaica (Table 12) show that the Jamaican Woodpecker prefers to nest in dead branches on live trees, such sites accounting for 53% of the total. Other sites, listed in order of preference, were dead trunks, dead branches in dead trees, and live branches. No nests

TABLE 12.—NESTING SITES OF THE JAMAICAN WOODPECKER.

Height of Nesting Hole	Live Tree			Dead Tree	
	Trunk	Live Branch	Dead Branch	Trunk	Branch
under 4.6 m	—	—	3	4	2
4.6-9.2 m	—	1	26	11	5
over 9.2 m	—	1	7	2	6
Total	—	2(3%)	36(53%)	17(25%)	13(19%)

were in live trunks. Aside from the existence of suitable dead trees or dead branches for nesting, the main reason for the preference of such sites is that the Jamaican Woodpecker belongs to a group of woodpeckers that are not structurally specialized for pecking (see Burt 1930, Bock and Miller 1959, Spring 1965). It thus avoids the use of the heavier live woods more difficult to dig into. Nest heights varied from 3 m to over 20 m, with an approximate average of 9 m.

Dimensions were measured at 16 nest holes. The shallowest hole was 15 cm deep (measured from lower rim of entrance hole) and the deepest hole was 60 cm, the average depth was 31 cm. (David Johnston told me of a hole 180 cm deep in a dead coconut palm in St. Andrew Parish.) The differences in depths could be related to the type of wood used, because the shallower holes were in live wood. In addition the preempting of nesting holes by Starlings probably forced the construction of hastily made second holes in some cases. Dennis (1969) noted that the unusually shallow nesting holes made by the Flicker on Nantucket Island were probably related to the fact that Starlings took over the original holes thus forcing the Flickers to construct a second hole quickly. The nest hole diameter of the 16 nests ranged from 47 to 77 mm, with a mean of 65 mm. Rarely was the same nest hole used for more than one season in Worthy Park. The most important factor involved in this appears to be the presence of aggressive nest-hole competitors such as Starlings and Saffron Finches. One nest hole in a heavy woodland, where no Starlings or Saffron Finches were present, was used by woodpeckers for three seasons.

NEST-SITE SELECTION.—Although most woodpeckers that I noted had already started their nest holes, in one pair that had not started excavating the male took the lead in nest-site selection. On 18 April 1970 I watched a male Jamaican Woodpecker moving up a dead prickly yellow tree, tapping it lightly with his bill. Upon reaching the top of the dead trunk, he began uttering his breeding call, and the female answered. A few minutes later the female landed on the tree about 3 m below the male. The male flew toward the female and landed approximately 0.5 m below her. He moved up toward the female and, when they were at approximately the same level, they engaged in mutual tapping. After mutual tapping three times, the female flew off followed by the male. The next day the male began excavating a nesting hole in the prickly yellow tree. These observations are similar to Kilham's (1961) report for the Red-bellied Woodpecker.

IMPORTANCE OF THE JAMAICAN WOODPECKER TO OTHER HOLE-NESTING BIRDS.—The Jamaican Woodpecker, by creating nesting and shelter sites for many species of Jamaican birds, plays an important role in the community. I have noted the following species using woodpecker holes for breeding: Sparrow Hawk, Yellow-billed Parrot (*Amazona collaris*), Common Parrotlet, Rufous-tailed Flycatcher (*Myiarchus validus*), Purple Martin (*Progne subis*),

Starling, and Saffron Finch. In addition the following birds, based on their nesting habits (Bond 1971), quite likely also use woodpecker holes: Black-billed Parrot (*Amazona agilis*), Barn Owl (*Tyto alba*), Jamaican Owl, Stolid Flycatcher (*Myiarchus tuberculifer*), and Dusky-capped Flycatcher (*M. barbirostris*). With the exception of the Starling and possibly the Saffron Finch, those species that I observed appeared to be using abandoned woodpecker holes and did not seem to compete with woodpeckers for active nest holes.

STARLING-WOODPECKER NEST HOLE COMPETITION.—Starlings were first introduced into Jamaica in 1903 near Annoto Bay (Saint Mary's Parish) and since then have become well established in many parts of the island, including Worthy Park. As is true for Europe (Howard 1920, Löhrl 1956) and North America (Kilham 1958, 1960, 1968, Lawrence 1967, Dennis 1969), Starlings are effective nest-hole competitors of some woodpeckers, and the same was also true in Jamaica. The following two accounts from the summer of 1969 demonstrate this competition and show the lack of interspecific aggression on the part of the Jamaican Woodpecker. On 17 June 1969 I found a pair of woodpeckers in the final stages of nest hole construction in a dead branch of a guango tree. By 22 June 1969 the pair had apparently completed the hole. That same day two Starlings arrived and perched on the branch containing the hole. The woodpeckers appeared to be disturbed, but showed no aggressive behavior toward the Starlings. The Starlings used an aggressive display involving various shrill calls and wing-flapping. The same day, when both woodpeckers were away from the tree, the Starlings went into the nest hole. When the male woodpecker arrived he made no attempt to take over the nesting hole, but remained on a nearby branch. As heavy rain began at this time, I was unable to continue watching. The next day the Starlings were taking nesting material into the woodpecker hole, and the woodpeckers were excavating a new cavity in the same branch. On 26 June 1969 I noted Starlings with young in a woodpecker hole in a dead branch of a guango tree. On another dead branch on the same tree a pair of woodpeckers were excavating a nest hole. The Starlings fledged their young before the woodpeckers finished their hole. The woodpeckers immediately stopped work on their hole, modified the Starlings' hole, and nested in it. Possibly the woodpecker originally built this hole, and the Starlings took it over. The fact that in both cases the woodpeckers were able to fledge young seems that (for the present) the Starlings are not an obstacle to the nesting success of the Jamaican Woodpecker. Subsequent increases in the Starling populations may pose a threat in the future, not only to the Jamaican Woodpecker but to other hole-nesting birds.

COPULATION.—Copulation in the Jamaican Woodpecker was observed 12 times in 4 different pairs. It occurred most frequently during the early part of the breeding cycle (excavation and egg-laying), but also once during incubation. In one pair it was seen approximately 28 days before egg-laying.

Copulation occurs in a manner similar to that described for other woodpeckers (Kilham 1958, Stickel 1965, Lawrence 1967, Bock 1970). The male, with wings fluttering, mounts the female, turns his body at a right angle to hers, and after copulation falls off to the left. Copulation always took place on a horizontal branch and lasted from 5 to 15 seconds. Mutual recognition notes were always exchanged as the male approached the female, but no sounds were uttered during copulation.

EXCAVATION PERIOD.—Both male and female Jamaican Woodpeckers excavate the nest hole. Of 1721 minutes spent watching the construction of four nests the male performed 62% of the excavating and the female 38%. The average working period for both sexes lasted 21.5 min. One excavation I watched from the start of nest-hole construction to completion took 21 days.

Lawrence (1967) divides the process of excavation into three stages: (1) boring the corridor that forms the entrance part of the cavity, (2) the curved link between the corridor and the cavity, (3) the cavity itself (for information on how each stage was determined see Lawrence 1967). For the nest mentioned above stage 1 took 9 days, stage 2 took 4 days, and stage 3, 8 days. The length of time spent in each stage is probably highly variable (as Lawrence noted), depending upon the condition of the wood (whether live or rotten) and the amount of disturbance. During nest-hole construction members of a pair maintained contact with one another through location and breeding calls and engaged in ritualistic and mutual tapping, both thought to be associated with the maintenance and strengthening of a pair bond.

CLUTCH SIZE.—Although most nest holes were inaccessible because of their height, I was able to determine the contents of two nests low in dead trees. The clutch size was three and four eggs, respectively. In addition the examination of 4 females revealed the presence of from 3 to 5 follicles on the surface of the ovary.

LENGTH OF INCUBATION.—Examining the inside of one nest with a rotatable mirror from the time of egg-laying to hatching revealed that one white egg was laid daily until a clutch of three was reached. The female laid each egg during the early morning hours. Hatching started 13 days after the first egg was laid and continued for 2 more days. These results are similar to the report of Skutch (1969) for the Central American *Melanerpes aurifrons*, a species with an incubation period of 12 days. Stickel (1965) reported an incubation period for *Melanerpes carolinus* of 11.5 days \pm approximately 6 hours.

ATTENTIVENESS.—Both sexes take part in incubation during the day, but only the male incubates at night. During 1955 minutes of observations on three nests at least one adult was inside the nesting hole 88% of the time, the average incubation session lasting approximately 31.7 minutes. The division of daytime attentiveness was 47% for the male and 41% for the female. Percent attentiveness in North American woodpeckers ranged from 68% in *Asyndes-*

mus lewis (Bock 1970) to "not less than 95% of the time during the day" in the four species studied by Lawrence (1967).

THE RELIEF RITUAL.—Nest relief in the Jamaican Woodpecker varied from no contact (one bird leaving before the other arrives) to elaborate ritualistic behavior involving mutual tapping and mutual recognition notes. In many instances when the incubating individual wanted to be relieved, it would look out the nest hole and utter its location call. The mate usually arrived at the nest shortly thereafter. The relieving woodpecker usually landed below the nest hole and moved toward the nest. Often it did not go directly into the nest, but inserted its body two or three times in intention movements into the cavity before entering. Lawrence (1967) noted that the number of intention movements performed by North American woodpeckers depends on the nervous state of the birds as well as on the situation outside of the nest. No or few intention movements denote quiet surroundings and a low level of nervous tension in the bird.

HATCHING DAY AND BROODING DURATION.—Lawrence (1967) reported that when the eggs begin to hatch "the brooding rhythm changes from the slow regular pattern of incubation to a chopped-up pattern of shorter, irregular brooding sessions." Table 13 compares the rhythm of incubation between the last day of incubation and hatching day, which was also the first day that food was brought to the nest. The date of hatching of the prickly tree pair was also verified by the use of a mirror. Whereas the duration of brooding per session decreased from incubation to hatching, no decrease in attentiveness was detected at either nest.

TABLE 13.—THE DIFFERENCE IN INCUBATION RHYTHM BETWEEN THE LAST DAY OF INCUBATION AND HATCHING DAY. DATA OBTAINED DURING MORNING HOURS (0800-1200).

Pair	Last Day of Incubation			Hatching Day		
	Number of Sessions	Average Minutes	Attentiveness Percent	Number of Sessions	Average Minutes	Attentiveness Percent
Guango tree Pair 1969	7	31.2	91	21	10.5	92
Prickly Pair 1971	6	35.3	88	23	9.4	90

These changes in rhythm are so distinct that, together with the initial food brought, they serve as reliable criteria for determining the duration of the nestling period (hatching day to fledgling). Because the nest of the guango tree pair, which was studied intensively during the summer of 1969, was in an inaccessible place, the nestling period and the fledgling time were determined by these criteria. The first nestling left the nest 29 days after hatching and the second nestling after 30 days. Stickel (1965) reported that the nestling

period for *M. carolinus* in Illinois varied from 22 to 27 days, and Kilham (1961) noted the nestling period for the same species in Maryland to be 26 days. Skutch (1969) reported that the young of *M. aurifrons* remain in the nest for about 30 days, and that the young of *M. rubricapillus* flew 31 and 33 days after the parents were first seen to take in food.

BROODING RHYTHM.—Both parents shared brooding the young during the day almost equally, 44% for the male and 56% for the female, based on 2,488 minutes of observation at three nests. During the night only the male brooded the young. Equal sharing of nesting duties during the day enables each parent to spend the maximum time possible away from the nest. Bock (1970) and Stickel (1965) reported similar brooding behavior in the Lewis and Red-bellied woodpeckers. Lawrence (1967) found that in the Yellow-bellied Sapsucker, the sexes share brooding almost equally, whereas in the Flicker and the Hairy Woodpecker the female, but in the Downy Woodpecker the male, assumes most of the duty.

In the Jamaican Woodpecker diurnal brooding attentiveness was sustained at a high level until the 10th day, ranging from 93 to 83%. By the 18th day, brooding was shortened to 41%, and brooding ceased entirely by the 26th day (Fig. 8), 3 days before the first young left the nest.

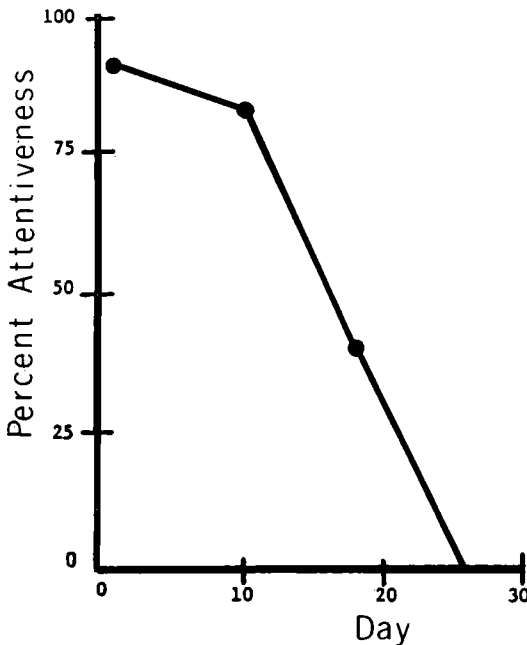


FIGURE 8.—Variation of diurnal brooding attentiveness in the Jamaican Woodpecker (based on 1853 minutes of observation in the guango tree pair). Percent attentiveness refers to the percent of the total period of observation that the parents were inside the nesting hole (presumably brooding).

FEEDING RATES.—Nesting pairs averaged 10.3 feedings of the young per hour ($N = 335$) with a range of 2 to 22. This feeding range is within the ranges reported in the literature for North American woodpeckers. Stickel (1965) found that the diurnal variation in the feeding rate for the Red-bellied Woodpecker was from 4.5 to 15.7 feedings per hour (no average given). Lawrence (1967) found that the average feeding rate of the Flicker was 2.2 feedings per hour, whereas that of the other three species varied from 8.8 in the Yellow-bellied Sapsucker to 14.8 in the Downy Woodpecker. For the Lewis Woodpecker, Bock (1970) reported feeding rates varying from 2 to 62 with an average of 15.1 feedings per hour.

The mean feeding rate per hour was 5.7 for the male and 4.6 for the female in the Jamaican Woodpecker. This same pattern was also present in Lawrence's (1967) study of North American woodpeckers and Pynnönen's (1939) study of European woodpeckers. Lawrence noted that this is due to the female's preoccupation with brooding and defense, activities for which she usually undertakes with greater responsibility. Although this may be true for the woodpeckers that she studied, there was no evidence that the female played a greater role than the male Jamaican Woodpecker in these activities.

In general the Jamaican Woodpeckers spent a greater proportion of the morning and afternoon hours foraging, and this variation in diurnal activity pattern has a direct bearing on the rate of feeding the young (Fig. 9), with peaks during the morning (0800-0900) and afternoon (1600-1700). Stickel (1965) observed a similar pattern in the feeding rates of *M. carolinus*.

The rate of nestling feeding was lowest during the first and last week and highest during the second and third week of the nestling period (Fig. 10). Lawrence (1967) found that in the course of the nestling period the Flicker's feeding rate increased gradually until it reached a level that was sustained to the end. The feeding rates of the other three species of woodpeckers studied by Lawrence (Hairy, Downy, and Sapsucker) showed a peak about the middle of nest life after which the feeding rates declined, reaching a low at the time of fledgling. The decline in the feeding rate toward the end of the nesting cycle is probably related to behavioral changes in the adults and may play a role in encouraging the nestlings to leave the nest.

RELIEF RITUAL.—The relief ritual described in the incubation section remained unchanged into the nestling period, but as the rate of feeding the nestlings increased, the meeting at the nest by the parents occurred less frequently, and as a consequence relief rituals were less frequently performed.

FOOD AND FEEDING BEHAVIOR.—Feeding of the young commenced almost immediately after the first egg hatched in the prickly yellow tree nest. Food items at first were small invertebrates and fruits, and the proportion of larger food items increased as the nestlings grew older. Analysis of 283 feeding visits in which the food items brought could be identified showed that animal foods accounted for 59% and vegetable foods 41%. Diets of the nestlings

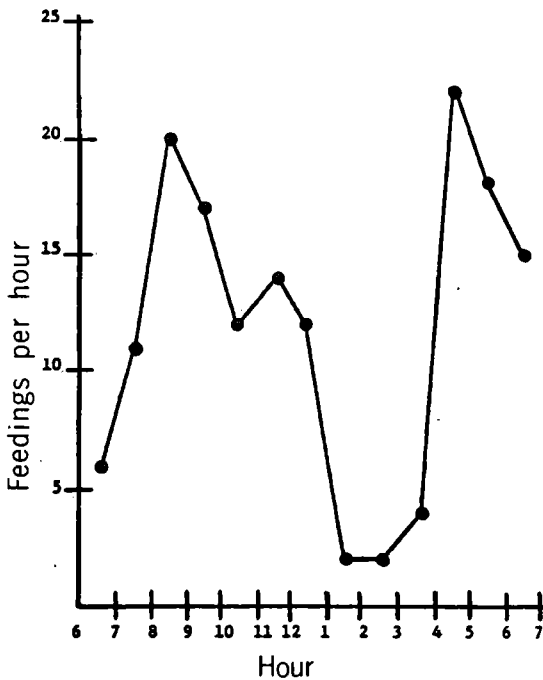


FIGURE 9.—All day observations of feedings by the Jamaican Woodpecker on the 18th day of the nestling period (based on 783 minutes observation of guango tree pair, 1969).

were almost as diverse as those of the parents, ranging from small fruits to insects to lizards, identified vegetable foods included fruits of *Cecropia*, *Ficus*, and *Daphnopsis*. On one day the guango tree pair (1969) brought the nestlings fleshy fruits of the *Daphnopsis* tree 35 times. Identified animal foods included snails, lepidopterans, orthopterans, ants, coleopterans, and small *Anolis*.

Lawrence (1967) divided the nestling period into three stages according to the method of feedings: inside feeding, corridor feeding, and outside feeding. She noted that each stage is determined by the phase in the development of the nestlings. These three stages were readily identified in the Jamaican Woodpecker where inside feeding, in which the parent goes all the way into the hole, lasted until the 17th day. As the nestlings grow older, they began climbing up to the entrance as soon as they heard the parents arrive. The parent bringing food met the nestlings in the corridor and fed them there. Outside feeding, in which the parents do not enter the hole, began on the 20th day.

NEST SANITATION.—During 1853 minutes of nestling observations, the parents removed fecal material from the nest 39 times, the male accounting for 65% of them. These observations differ from Kilham (1961) who never saw

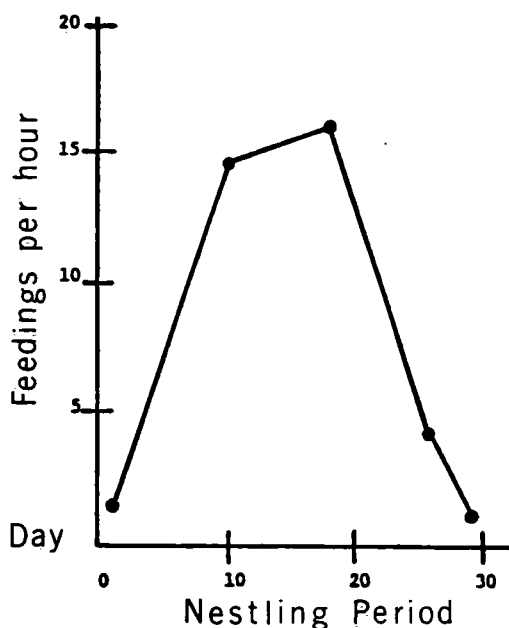


FIGURE 10.—The feeding rates of a pair of Jamaican Woodpeckers during the nestling period. Based on 15 hours of observations during five mornings (0800-1100).

M. carolinus remove fecal material, and from Stickel (1965) who saw only the male *M. carolinus* remove fecal material from the nest. Lawrence (1967) found that males of the Sapsucker, Flicker, and the Hairy and Downy woodpeckers played a greater role than the females in the removal of feces from the nest, the male accounting for 70% of the total observations. The feces of the nestling Jamaican Woodpeckers are enclosed in a whitish membrane that makes the droppings easy to carry. Similar types of membranes have been reported by Kilham (1962) for the Flicker and by Sielmann (1958) for the European Black Woodpecker (*Dryocopus martius*). In contrast the Sapsucker and Hairy Woodpecker have either a thin or no membrane around the feces (Lawrence 1967). The Jamaican Woodpecker never used a special disposal station, but each time flew in a different direction from the nest. This is similar to what Lawrence found for the Flicker but differs from the Sapsucker, which consistently deposited the excreta at a particular spot. Lawrence also reported that the woodpeckers she studied often ate the fecal material rather than removing it, but I noted no such behavior in the Jamaican birds.

POST-NESTLING PERIOD.—During the first 2 days after emergence from the nesting hole, the young made no attempt to reenter the hole at dusk, which the adult male now used for roosting. Skutch (1969) noted that in *M. rubricapillus* the parents repulsed the fledglings that tried to enter the roosting hole

with them. One juvenile Jamaican Woodpecker roosted in an abandoned woodpecker hole after the 6th day of fledgling life. I feel that juvenile Jamaican Woodpeckers probably use abandoned holes until they are sufficiently strong to excavate their own holes. The juvenile woodpeckers are approximately the same size as the adults, but their excavating tool (the bill) is 22% shorter (\bar{x} bill length = immature 21.5 mm, adult 27.5 mm). In Worthy Park there appeared to be enough abandoned woodpecker holes to afford the juvenile woodpeckers plenty of shelter. In other parts of Jamaica, such as the dry limestone forest and mangrove woodland, fewer holes were present, and probably a longer period must elapse before the young birds find proper shelter.

The two fledglings of the guango tree pair (1969) remained within 40 m of the nest tree during the first 2 days after leaving the nest. During this time they did not attempt to follow the parents, but kept in contact by means of location calls. Whenever the parents obtained food, they uttered a location call, the young answered, and the parents flew toward them. As the fledglings detected the parents approaching with food, their begging calls intensified. During this time the young made feeble attempts at pecking and probing, but apparently found no food. On the 3rd day the young began following the parents. Although the family more or less traveled together, one of the young followed the male, and the other the female. The juveniles did not travel as fast as the adults and often lagged behind. Once after 4 minutes of pecking into a dead logwood branch, the female removed a buprestid larva about 2.5 cm long. She began uttering location calls, and one of the young arrived within less than a minute. The adults fed the young both animal and vegetable matter.

During the first 2 weeks after emergence, the young of the guango tree pair relied upon the adults almost exclusively for their food. Although the young tried to obtain food during this period, they were apparently unsuccessful. On the 15th day after leaving the nest I saw the first successful food capture by a young bird when it removed a grasshopper-like insect from a bromeliad. After this the young fed more and more independently, but the parents still continued to feed them.

On the 21st day, I noted the first repulsion of a juvenile by the parents. While the adult female was feeding on *Ficus* fruits, the juvenile male approached her, and she made a stabbing lunge at him, causing him to fly off. After this day repulsions of the juveniles by the parents occurred more frequently, but they still continued feeding the young until the 24th day. After the 24th day, although the family group still remained together, no more feedings were detected. This particular family group (Guango Tree pair) remained together until I left Jamaica on 17 August 1969 (28th post-nestling day). Another family group first seen 19 June 1970 was still together when I left on 28 July 1970. Thus the young remain with the parents for at least a month. Kilham (1961) noted that in *M. carolinus* the young remained with

the parents for nearly 2½ months. He did not specify whether or not the young were completely dependent upon the parents. Lawrence (1967) found that for the Hairy, Downy, Flicker, and Sapsucker the period of dependence of the fledglings ranged from 1 to 3 weeks.

LITERATURE CITED

- Adams, C. D. 1972. The flowering plants of Jamaica. Glasgow, Scotland, The University Press. 848 p.
- Asprey, G. F., and R. G. Robbins. 1953. The vegetation of Jamaica. Ecol. Monogr. 23:359-412.
- Bock, C. E. 1970. The ecology and behavior of the Lewis Woodpecker (*Asyndesmus lewis*). Univ. Calif. Publ. Zool. 92:1-91.
- . 1971. Relations between Lewis' and Red-headed Woodpeckers in southeastern Colorado. Wilson Bull. 83:237-248.
- Bock, W., and W. DeW. Miller. 1959. The scansorial foot of woodpeckers, with comments on the evolution of perching and climbing feet in birds. Amer. Mus. Nov. 1931:1-45.
- Bond, J. 1971. The birds of the West Indies. Boston, Mass., Houghton Mifflin Co. 256 p.
- Brewer, R. 1963. Ecological and reproductive relationships of Blackcapped and Carolina Chickadees. Auk 80:9-47.
- Brown, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76:160-169.
- Burt, W. H. 1930. Adaptive modifications in the woodpeckers. Univ. Calif. Publ. Zool. 30:455-524.
- . 1943. Territoriality and range concepts as applied to mammals. J. Mammal. 24:346-352.
- Crowell, K. L. 1961. The effects of reduced competition in birds. Proc. Nat. Acad. Sci. 47:240-243.
- . 1962. Reduced interspecific competition among the birds of Bermuda. Ecology 43:75-88.
- Cruz, A. 1974. Feeding assemblages of Jamaican birds. Condor 76:102-119.
- Darwin, C. 1859. On the origin of species by means of natural selection. London, John Murray. 2 Vols.
- Davis, J. 1965. Natural history, variation, and distribution of Strickland's Woodpecker. Auk 82:537-590.
- Dennis, J. V. 1969. The Yellow-shafted Flicker (*Colaptes auratus*) on Nantucket Island, Massachusetts. Bird-Banding 40:290-308.
- . 1971. Species using Red-cockaded Woodpecker holes in northeastern South Carolina. Bird-Banding 42:79-87.
- Dixon, K. L. 1961. Habitat distribution and niche relationships in North American species of *Parus*. pp. 179-216. IN W. F. Blair, ed., Vertebrate Speciation. Austin, Univ. of Texas Press.
- Emlen, J. M. 1966. The role of time and energy in food preference. Amer. Natur. 100:611-617.
- Emlen, J. T. 1957. Defended area? A critique of the territory concept and of conventional thinking. Ibis 99:352.
- Gibb, J. 1954. Feeding ecology of tits, with notes on tree creeper and goldcrest. Ibis 96:513-543.
- Grant, P. R. 1968. Bill size, body size, and the ecological adaptations of bird species to competitive situations on islands. Syst. Zool. 17:319-333.
- Haftorn, S. 1956. Contribution to the food biology of tits especially about storing of surplus food. Pt. IV. Kgl. Norske Vidensk. Selsk. Skrifter. No. 4.
- Hamilton, T. H., and I. Rubinfoff. 1963. Isolation, endemism, and multiplication of species in the Darwin finches. Evolution 17:388-403.
- Hinde, R. A. 1956. The biological significance of the territories of birds. Ibis 98:340-369.
- Howard, H. E. 1920. Territory in bird life. London, William Collins and Sons, Ltd.
- Hutchinson, G. E. 1957. Concluding remarks. Cold Springs Harbor Symp. Quant. Biol. 22:415-427.

- Jackson, J. A. 1970. Predation of a Black Rat Snake on Yellow-shafted Flicker nestlings. *Wilson Bull.* 82:329-330.
- Janzen, D. H. 1969. Birds and the ant-acacia interaction in Central America, with notes on birds and other myrmecophytes. *Condor* 71:240-256.
- Kilham, L. 1957. Pilot Black Snake and nesting Pileated Woodpeckers. *Wilson Bull.* 71:191.
- . 1958. Pair formation, mutual tapping, and nest hole selection of Red-bellied Woodpeckers. *Auk* 75:318-329.
- . 1959. Behavior and methods of communication of pileated woodpeckers. *Condor* 61:377-387.
- . 1960. Courtship and territorial behavior of Hairy Woodpeckers. *Auk* 77:259-270.
- . 1961. Reproductive behavior of Red-bellied Woodpeckers. *Wilson Bull.* 73:237-254.
- . 1963. Food storing of Red-bellied Woodpeckers. *Wilson Bull.* 75:227-234.
- . 1966. Reproductive behavior of Hairy Woodpeckers. I. Pair formation and courtship. *Wilson Bull.* 78:251-265.
- . 1968. Reproductive behavior of Hairy Woodpeckers. II. Nesting and habitat. *Wilson Bull.* 80:286-305.
- . 1969. Reproductive behavior of Hairy Woodpeckers. III. Agonistic behavior in relation to courtship territory. *Wilson Bull.* 81:169-183.
- Lawrence, L. de K. 1967. A comparative life-history study of four species of woodpeckers. *Ornithol. Mono. No. 5*, Am. Ornithologists' Union, Lawrence, Kansas. 156 p.
- Ligon, J. D. 1968. Sexual differences in foraging behavior in two species of *Dendrocopos* woodpeckers. *Auk* 85:203-215.
- . 1970. Behavior and breeding biology of the Red-cockaded Woodpecker. *Auk* 87:255-278.
- Löhr, H. 1956. Der Star als Bruthöhlenkonkurrent. *Die Vogewelt* 77:47-50.
- MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* 39:599-619.
- , J. M. Diamond, and J. R. Karr. 1972. Density compensation in island faunas. *Ecology* 53:330-342.
- , and J. W. MacArthur. 1961. On bird species diversity. *Ecology* 42:594-598.
- , and E. Pianka. 1966. On optimal use of a patchy environment. *Natl. Acad. Sci. Proc.* 51:1207-1210.
- , H. Recher, and M. Cody. 1966. On the relation between habitat selection and species diversity. *Amer. Natur.* 100:319-327.
- , and E. O. Wilson. 1963. An equilibrium theory of island zoogeography. *Evolution* 17:373-387.
- , and E. O. Wilson. 1967. The theory of island bio-geography. *Mono. Popul. Biol. No. 1*, Princeton Univ. Press, Princeton, N. J. 203 p.
- Meyer de Schauensee, R. 1964. The birds of Colombia. Narberth, Pa., Livingston Pub. Co. 430 p.
- Morse, D. H. 1968. A quantitative study of foraging of male and female spruce-woods warblers. *Ecology* 49:779-784.
- Murray, B. G. 1971. The ecological consequence of interspecific territorial behavior in birds. *Ecology* 52:414-423.
- Newton, I. 1967. The adaptive radiation and feeding ecology of some British finches. *Ibis* 190:33-98.
- Nice, M. M. 1941. The role of territory in bird life. *Amer. Midl. Natur.* 26:441-487.
- Nolan, V., Jr. 1959. Pileated Woodpecker attacks Pilot Black Snake at tree cavity. *Wilson Bull.* 71:381-382.
- Odum, E. P., and E. J. Kuenzler. 1955. Measurement of territory and home range size in birds. *Auk* 72:128-137.
- Odum, H. T., and R. F. Pigeon (eds). 1970. A tropical rainforest. A study of irradiation and ecology at El Verde, Puerto Rico. *Natl. Tech. Info. Serv.*, Springfield, Va., 1678 p.
- Orians, G. H., and M. F. Willson. 1964. Interspecific territories of birds. *Ecology* 45:736-745.
- Perkins, L. G. 1970. Woodpeckers. *Gosse Bird Club, Broadsheet* 15: 14-16.
- Peters, J. L. 1948. Check-list of the birds of the world. Cambridge, Mass., Harvard Univ. Press, Vol. 6, 259 p.

- Preston, F. W. 1962. The canonical distribution of commonness and rarity: Part I. Ecology 43: 185-215; Part II. Ibid. 43:410-432.
- Pynnönen, A. 1939. Beiträge zur kenntnis der biologie Finisher Spechte. Pt. 1. Ann. Zool. Soc. Zoologicae-Botanicae-Fennicae Vanamo 7:1-66.
- Ridgway, R. 1902-16. The birds of North and Middle America. Parts 2-7. U. S. Natl. Mus. Bull. No. 50.
- Salt, G. W. 1957. An analysis of the avifaunas in the Teton Mountains and Jackson Hole, Wyoming. Condor 59:373-393.
- Schoener, T. W. 1967. The ecological significance of sexual dimorphism in size in the lizard, *Anolis conspersus*. Science 155:474-477.
- Selander, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. Condor 68:113-151.
- , and D. R. Giller. 1959. Interspecific relations of woodpeckers in Texas. Wilson Bull. 71:107-124.
- Sielmann, H. 1959. My year with the woodpeckers. London, Barrie and Rockcliffe, 139 p.
- Skutch, A. 1945. The most hospitable tree. Sci. Monthly 60:5-17.
- . 1948. Life history of the Golden-naped Woodpecker. Auk 65:225-260.
- . 1969. Life histories of Central American birds, Part III. Cooper Ornithol. Soc., 580 p.
- Snow, D., and B. K. Snow. 1964. Breeding seasons and annual cycles of Trinidad landbirds. Zoologica 49:1-40.
- Spring, L. W. 1965. Climbing and perching adaptations in some North American woodpeckers. Condor 67:457-488.
- Stickel, D. W. 1962. Predation on Red-bellied Woodpecker nestlings by a Black Rat Snake. Auk 79:118-119.
- . 1965. Territorial and breeding habits of Red-bellied Woodpeckers. Amer. Midl. Natur. 74:110-118.
- Stolpe, M. 1932. Physiologisch-anatomische Untersuchungen über die hintere Extremität der Vögel. J. F. Ornith. 80:161-247.
- Wallace, A. R. 1880. Island life. London, Macmillan.
- Williams, C. B. 1964. Patterns in the balance of nature and related problems in quantitative ecology. New York, Academic Press.
- Williamson, P. 1971. Feeding ecology of the Red-eyed Vireo (*Vireo olivaceus*) and associated foliage-gleaning birds. Ecol. Monogr. 41:129-152.
- Woodwell, G. M., and R. H. Whittaker. 1968. Primary production in terrestrial ecosystems. Amer. Zool. 8:19-30.
- Woolfenden, G. E., and S. A. Rohwer. 1969. Breeding birds in a Florida suburb. Bull. Florida State Mus., Biol. Sci. 13(1):1-83.
- Zusi, R. C. 1969. Ecology and adaptations of the Trembler on the island of Dominica. The Living Bird 8:137-164.

Contributions to the BULLETIN OF THE FLORIDA STATE MUSEUM, BIOLOGICAL SCIENCES SERIES, may be in any field of biology. Manuscripts dealing with natural history of systematic problems involving the southeastern United States or the New World tropics are solicited especially. Manuscripts should be of medium length—circa 35 to 200 pages (10,500-16,000 words). Examination for suitability is made by an Editorial Board.

The BULLETIN is distributed worldwide through institutional subscriptions and exchanges. It is considered the responsibility of the author to distribute his paper to all interested individuals. To aid in this the author(s) receive(s) 50 copies free, and he may purchase additional separates at cost if ordered when page proof is returned. The author is also responsible for any charges incurred for alterations made by him on galley or page proofs. The Museum will send an invoice to the author for this amount upon completion of publication.

PREPARATION OF MANUSCRIPT

Contributors should consult recent numbers of the BULLETIN for preferred style and format. Highly recommended as a guide is the CBE Style Manual, 3rd Edition, 1972 (Washington, D.C., Amer. Inst. Biol. Sci.).

MSS must be submitted in duplicate (please no onionskin) and satisfy the following minimal requirements: They should be typewritten, double-spaced (*especially* tables, figure captions, and "Literature Cited"), on one side of numbered sheets of standard (8-1/2 × 11 in.) bond paper, with at least one-inch margins all around. Figure legends and tables should be typed on separate sheets. All illustrations are referred to as figures. They must comply with the following standards: Photographs should be sharp, with good contrast, and printed on glossy paper. Drawings should be made with dense black waterproof ink on quality paper or illustration board. All illustrations should have a cover sheet. All lettering will be medium weight, sans-serif type (e.g. Futura Medium, News Gothic) in cutout, dry transfer, or lettering guide letters. Make allowance so that after reduction no lowercase letter will be less than 1 mm high (2 mm is preferred) nor any capital letter greater than 5 mm high. The maximum size for illustrations is 8-5/8 × 14 in. (twice typepage size); illustrations should not be less than typepage width (4-5/16 in.). Designate the top of each illustration and identify on the back with soft pencil by author's name, MS title, and figure number.

All manuscripts not submitted in BULLETIN format will be returned to the author for retyping.

Manuscripts and all editorial matters should be addressed to:

Managing Editor of the BULLETIN
Florida State Museum
Museum Road
University of Florida
Gainesville, FL 32611