

A Field Study of the Black and White Manakin, *Manacus manacus*, in Trinidad^{1, 2}

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(Text-figures 1-21)

INTRODUCTION

THE BLACK AND WHITE Manakin (*Manacus manacus*) is one of the commonest forest birds in Trinidad. It is also one of the easiest to study in the field, and it was this fact, combined with the outstanding interest of its communal courtship displays, that led me to devote much of my time to it during 4½ years' residence in the Arima Valley, the site of the New York Zoological Society's Tropical Field Station in the center of the Northern Range of Trinidad (Text-fig. 1).

It is a small, stockily built bird, with short wings and relatively long, strong legs (Text-fig. 2). The sexes differ markedly, the male being black and white and the female olive-green; the legs are orange in both sexes. Though it occurs in forest of all kinds, it probably reaches its greatest abundance in secondary forest. Like other manakins, it subsists largely on fruit which it takes in flight. It bathes in shallow streams, and drinks occasionally from streams but usually from water collected in the leaves and bracts of plants. Though it will feed on occasion in the tops of lofty trees, most of its life is spent within 25 feet of the ground. In particular, it nests only a few feet above the ground, and displays on and within a few inches of the forest floor. It is communal in its courtship; each male displays at a cleared "court" on the forest floor within a few yards, or even a few feet, of his neighbors. Groups of courts constitute "display grounds," which are used year after year. The

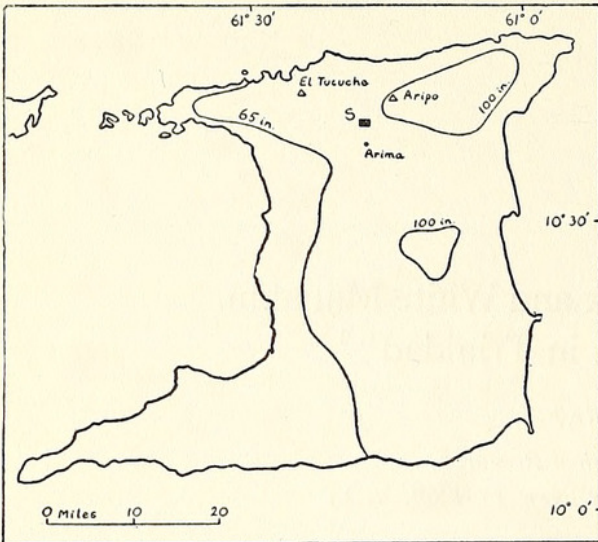
females visit the display grounds to mate. No pairs are formed, and the male takes no part in the nesting.

One other member of the family occurs in Trinidad, the Golden-headed Manakin (*Pipra erythrocephala*). Both occur in the same habitats and have largely the same feeding and nesting habits. The Golden-headed Manakin, however, displays 25 feet or more up in the trees, and also tends to feed and nest higher than the Black and White Manakin, so that, although it is even more abundant, it is less suitable for detailed study. A shorter account of its biology will be presented in a later publication.

There have been some previous accounts of the biology of *Manacus*. Chapman's pioneering study of the courtship of Gould's Manakin (*M. vitellinus*) in Panama was the first detailed study of any of the Pipridae (Chapman, 1935). Although there had been some earlier accounts, it was this paper which first drew attention to the extraordinary development of courtship behavior in the family. Working on specimens sent to him by Chapman, Lowe (1942) described the musculature of the wing-feathers and other specializations responsible for the loud mechanical noises made by the males during their displays. In Trinidad, Chapman (1894) had earlier made some brief observations on the display of *M. manacus*, and subsequent writers have occasionally referred to the males' courtship gatherings. A preliminary account of the present study, dealing only with display, has already been published (Snow, 1956). Darnton (1958) has also published some observations made at a Trinidad display ground of *M. manacus*. Finally, Sick (1959) has dealt with *Manacus* among other genera in his review of displays in the Pipridae as a whole.

¹ Contribution No. 1015, Department of Tropical Research, New York Zoological Society.

² This study has been supported by National Science Foundation Grants G4385 and G21007.



TEXT-FIG. 1. Trinidad, showing the study area (S) and the annual isohyets. The Northern Range extends along the whole of the northern side of the island, the two highest points being shown (Aripo and El Tucuche).

It may be noted that, although *M. manacus* and *M. vitellinus* have usually been treated as separate species, there are no important differences in behavior between them (Appendix 1) and morphologically they differ only slightly, *M. vitellinus* having the plumage suffused with orange-yellow which is lacking in *M. manacus*. They would thus reasonably be considered as conspecific, but for evidence that they are sympatric in Colombia (de Schauensee, 1950).

The present study is based on observations continued over 4½ years. Display was watched, and filmed, from hides at display grounds, the most complete observations being made at one display ground that was visited regularly over the whole period and weekly, except for a few gaps, from June, 1958, to September, 1961. Trapping was an important part of the work; a total of 271 individuals were caught in mist-nets in the study area, many of them repeatedly. Some 150 more were trapped in other parts of Trinidad, mainly in connection with the work of the Trinidad Regional Virus Laboratory. Each bird trapped in the study area was given a different color combination, and many of them were seen subsequently in the field. Many of the males occupying courts at the display grounds under observation were eventually color-ringed. Trapped birds were also examined for moult and other details of plumage, and were weighed. Breeding was studied by systematically searching for nests along certain stretches of forest stream, and recording their fate. Searching was continued in all months of the year, not only at seasons when manakins were known to be nesting. Twenty-eight birds were ringed as nestlings.

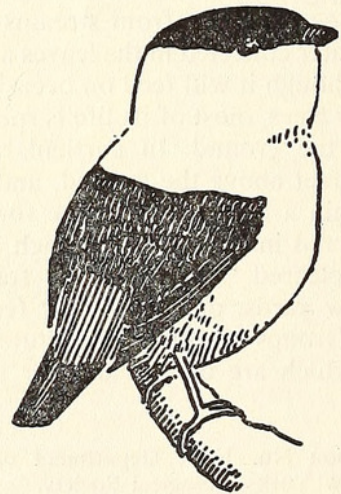
Some observations on behavior at the nest were made from a hide. Food was studied by direct observation of birds feeding, and by collecting the regurgitated remains of food from display grounds and from below nests.

Throughout the work, attention was directed to certain problems of general biological interest concerning the ecology of birds in tropical forest. These include: numbers, reproductive rate and the control of the population; the food supply throughout the year; the breeding season and the factors controlling it; the function of communal displays.

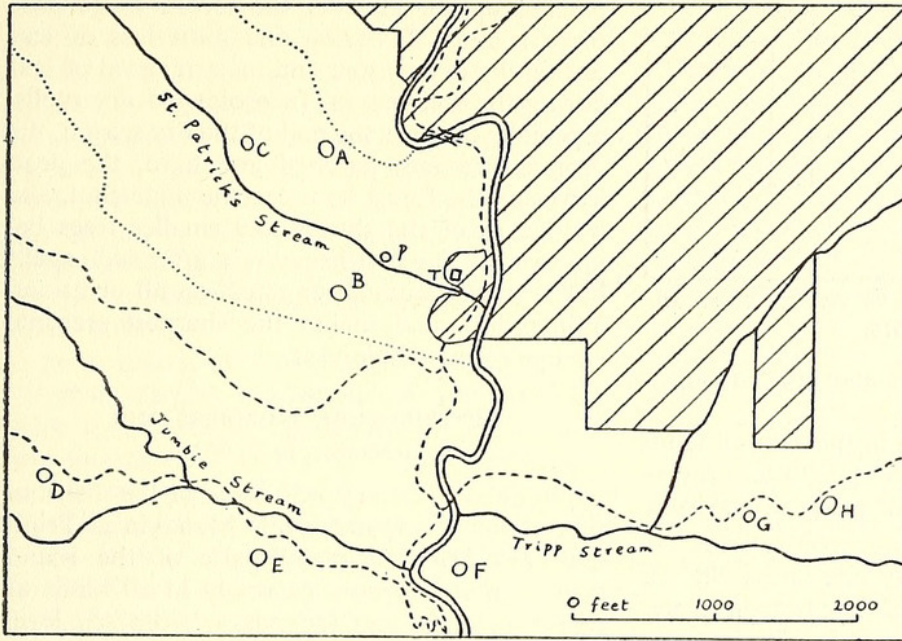
I am much indebted to my wife for help in the field work, especially the trapping and the finding and inspection of nests; to Dr. William Beebe and Miss Jocelyn Crane for placing at my disposal all the facilities of the New York Zoological Society's Tropical Field Station; to Dr. W. G. Downs and Dr. T. H. G. Aitken for the opportunity to examine birds trapped during the field studies of the Trinidad Regional Virus Laboratory; and to Mr. N. Y. Sandwith, Mr. N. W. Simmonds and Dr. J. J. Wurdack for many plant identifications. My thanks are due also to Dr. N. P. Ashmole, Mr. R. E. Moreau and Dr. D. Lack for valuable criticisms of the paper in draft. The whole work was generously supported by the National Science Foundation.

THE ENVIRONMENT

The lower part of the Arima Valley at 400-1,800 feet above sea level, the site of the study area (Text-fig. 3), has a natural vegetation transitional between lower montane rain forest and lowland seasonal forest (Beard, 1946). As most of the area is government forest, the greater part of this natural vegetation remains little altered except for a limited amount of lum-



TEXT-FIG. 2. Male Black and White Manakin; resting posture.



TEXT-FIG. 3. The study area. Manakin display grounds are shown as circles and are lettered. Dotted line: boundary between St. Patrick's Estate and Government Forest. Broken lines: pathways and roads. Hatched area: unforested country.

bering, which has reduced the number of large trees of the economically important species (especially *Cordia alliodora*, *Cedrela mexicana* and *Carapa guianensis*). The forest is rich in tree species, many of which bear berries of suitable size for manakins to eat. The country is hilly and steep, the underlying rocks being rather soft schists.

The main Arima River flows with a gently winding course down the valley and is joined by numerous steep-sided tributaries, which in turn are joined by numerous deep side-gullies. The whole area is thus divided and subdivided into numerous ridges. The main river and the larger side-streams have water all the year round, while the gullies fill up only after heavy rain. Along the side-streams and in the gullies the dampest conditions are found; the vegetation includes tree-ferns and many smaller ferns, *Carludovica*, *Cyclanthus bipartitus* and species of *Heliconia*. At the other extreme, up on the well-drained ridges there is a thinner forest of trees tolerant of desiccation, among which the Yellow Poui (*Tabebuia serratifolia*) is prominent during the dry season, when it loses its leaves and produces its yellow blossoms in two or three bursts of flowering. In the dry season there is a marked contrast between the ridges, where the forest includes an important deciduous element, and the lush vegetation along the stream bottoms.

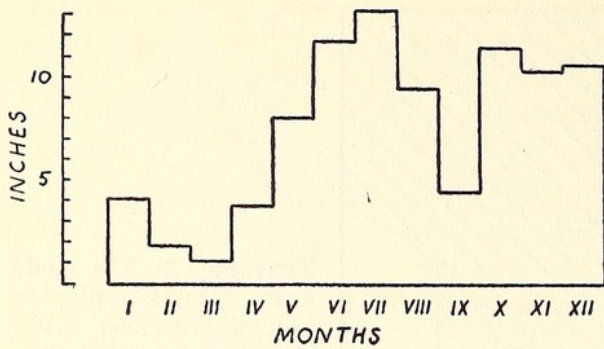
The main road up the valley follows the river. As a consequence, the forest along the river has been much opened up and the natural vegetation modified. In particular there are great clumps of an introduced bamboo.

St. Patrick's Estate, where the two main display grounds that were studied were situated and

all the trapping was carried out, is an area of secondary forest adjoining the government forest. Some large trees remain, but mostly the trees are in various stages of growth, up to a height of about 60 feet. This secondary forest is even richer in berry-bearing trees and shrubs than the primary forest. Melastomaceae are especially abundant, being represented by twelve common tree species and several shrubs. Among the lower-story trees and shrubs, in both primary and secondary forest, the berry-bearing Rubiaceae are important and are represented by many species.

Along the Northern Range the rainfall increases steadily from west to east. Port-of-Spain, at the foot of the hills at the western end, has an average annual precipitation of 55 inches, while at the eastern end the average is well over 100 inches (Text-fig. 1). The Arima Valley, half way along, has an intermediate rainfall, but closer to that of the eastern end than to the western. The average precipitation at Verdant Vale Estate, adjoining St. Patrick's, for the six years 1935-40 was 108.1 inches. The four years 1957-1960 were considerably drier, the average being only 89 inches (Text-fig. 4). Probably a long-term average would be around 100 inches at an altitude of 500 feet above sea level.

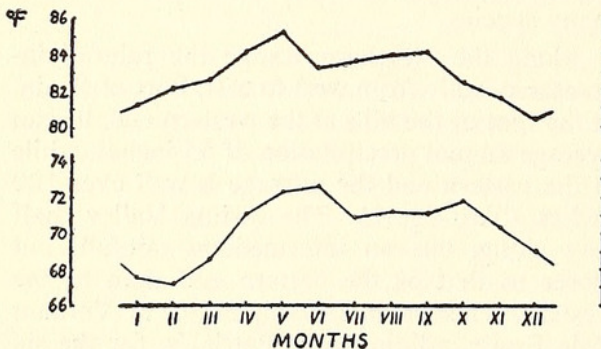
There is one main dry and one main wet season. The dry season begins in January and ends variably, usually in May. The wet season lasts for the rest of the year, but is usually broken by a spell of dry weather in September or October (the "petit carême"). Monthly totals of only one or two inches, sometimes less, are recorded in February and March; in the wet season totals of 15 inches or more are common. There is, how-



TEXT-FIG. 4. Mean monthly rainfall, 1957-1960.

ever, considerable variation in the rainfall from year to year, especially in the length and severity of the dry season. At all times of the year there is much sunshine.

Shade temperatures rarely rise above 88° F. and on wet and cloudy days they remain in the seventies. Nightly minima are usually between 65° and 75°, falling a few degrees lower on the coldest nights of the months December-March. Mean temperatures rise steadily from December to May, remain steady from May to September, then fall more rapidly from October to December (Text-fig. 5). Relative humidity is very high at nights, being always close to saturation; the day minimum varies much with location, season and weather. In two years' records an absolute minimum of 43% was recorded in March at Simla, half a mile from the study area (Beebe, 1952).



TEXT-FIG. 5. Mean monthly temperatures. St. Patrick's Estate. Upper line: mean daily maxima. Lower line: mean daily minima.

The seasons affect the appearance of the forest strikingly. Most of the trees have well-defined flowering and fruiting seasons, and all the trees of any one species are usually well synchronized. Thus when the Yellow Poui flowers, towards the end of the dry season, the forest for a few days is dotted with patches of brilliant yellow. A little later another common tree, the White Olivier (*Terminalia obovata*), loses its leaves and comes into flower, and pale yellow

patches appear all over the forest. In general, there is most flowering and most loss of leaf during the dry season, and most renewal of leaf during the wet season. In prolonged dry spells, especially towards the end of the dry season, the ground becomes parched and hard, the dead leaves on the forest floor crackle underfoot, and the leaves of the shrubs and smaller trees begin to wilt. The first heavy rain after such spells has a greatly stimulating effect on all plant and animal life, and makes the sharpest seasonal change of the whole year.

DISTRIBUTION, NUMBERS AND GENERAL ECOLOGY

No detailed survey was made of the distribution of the Black and White Manakin in Trinidad, but visits to many parts of the island showed that it occurs generally in all kinds of forest, primary and secondary, from sea level to about 2,000 feet, except for the dry forests at the western end of the Northern Range to the west of El Tucuche (Text-fig. 1). It is especially abundant in the forests of the central and eastern parts of the Northern Range, at moderate altitudes, and in the adjacent low-lying forests. This is the sector of highest rainfall, up to 100 inches or more. Above 2,000 feet, where the rainfall is considerably higher and the forest changes to the montane type, the Black and White Manakin becomes rather rare. The two highest display grounds found were on Aripo at about 2,000 feet and on El Tucuche at about 2,200 feet. Very few birds were seen on walks through the mountain forests above 2,000 feet.

Where manakins are common, display grounds are scattered at intervals through the forest. In the hilly country of the Northern Range they are mainly situated on ridges, either on the crest or a little way down one of the sides. Those in the study area (Text-fig. 3) were situated on minor side-ridges not more than two or three hundred feet above a stream bed. In low-lying country, however, display grounds are common in perfectly level forest. The preference for a situation on a ridge, where it is available, may be due to the commanding position of such a display ground over the streams below, along which the females prefer to nest.

More critical than the position of the display ground with respect to ridge or stream bed is the structure of its lower vegetation. The Black and White Manakin depends for its display on small upright saplings up to about 20 mm. in diameter. As will be seen later, two or more of these must be available within a few feet of each other to allow a bird to display fully. Further, a communal display ground cannot be established

unless there are many such groups of saplings within a few yards of each other.

The same display grounds seem to be used as long as the vegetation remains unchanged. All those that were under observation persisted for up to 4½ years, and local information indicated that they were already old. During a visit to Panama in 1958 the display ground of *M. vitellinus* studied by Chapman in 1932 was found to be active exactly in the position which he described.

In the course of the 4½ years' observations at the main display ground that was studied, the same individual saplings continued to be used, and though they were not measured when observations began they showed no apparent growth. In this, as in other respects, the tropical forest is an extremely constant, unchanging habitat. Only a few courts were abandoned, due to the fall of a mass of vines or a small tree, and some new ones were cleared, but these new ones were mainly peripheral and they did not all last long. The central nucleus of courts remained almost the same.

Text-figure 3 shows the distribution of display grounds in the area of forest, comprising some 450 acres, that was most thoroughly covered. It is unlikely that any large display grounds were not found, but small, intermittently-used display grounds (the "practice display grounds," p. 80) may easily have been missed. From the number of courts at these main display grounds it is possible to assess the number of adults in the area.

There were approximately 205 courts at the seven main display grounds known in the area. At the display ground studied in most detail (A in Text-fig. 3) it was found that in addition to the established adult males there were about a quarter as many unestablished adults. Thus 205 courts probably corresponds to some 250 adult males. Trapping showed almost exact equality between the sexes (p. 97). Thus there were probably about 500 adult birds in the 450 acres of forest.

There was no evidence for any considerable change in numbers in the course of the study. The main display ground under observation usually had from 24 to 28 active courts over the four years, and another that was observed less closely (B in Text-fig. 3) had from 30 to 33 over three years.

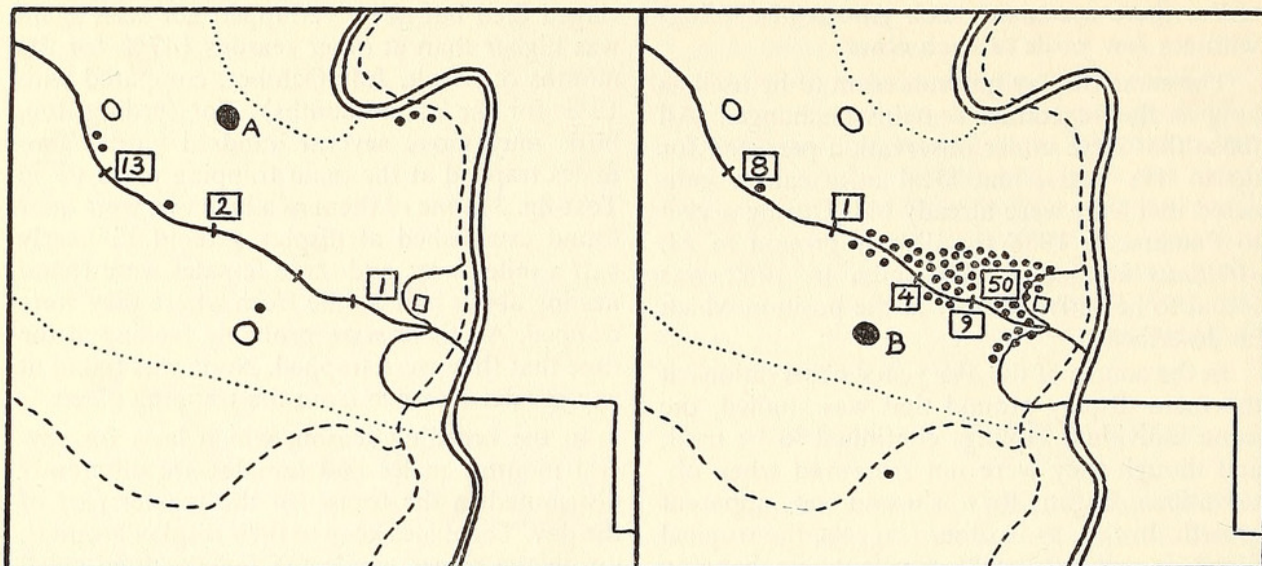
Although individuals are in general sedentary, there was nevertheless too much local movement for the trapping figures to be used for an independent assessment of the population. Especially during the moult there must be some individual wandering, as the proportion of birds

ringed then but never retrapped nor seen again was higher than at other seasons (47% for the months of moult, July-October, compared with 19% for the other months). For feeding, too, birds may move several hundred yards. Two males trapped at the main trapping place (T in Text-fig. 3), one of them as a juvenile, were later found established at display ground E, nearly half a mile away, and three females were found nesting about half a mile from where they were trapped. All these were probably feeding at the time that they were trapped. None was found at any greater distance from the trapping place.

In the breeding season, which lasts for several months, males and females are differently distributed in the forest for the greater part of the day. The males keep to their display grounds, up on the ridges, while the females hold small territories along the streams and gullies by which they mostly nest. The sexes meet when feeding and bathing, and also, for short periods, at the display grounds.

When feeding and bathing, males from the two display grounds A and B kept mainly to separate areas (Text-fig. 6). Thus at the main trapping place (T) many males from display ground B were trapped while feeding, most of them repeatedly, but only one male from display ground A was ever trapped there, once only. No males from display ground A were ever seen at the two bathing places nearest to T, but males from display ground B were seen bathing at them 13 times. At the bathing place nearest display ground A, on the other hand, there were 13 records of males from A bathing, and only 8 of males from display ground B.

Though no figures are available for comparison, there is little doubt that the density of the manakin population in the forests of the Arima Valley, and probably over much of Trinidad, is unusually high. *Manacus* was found to be much more sparsely distributed in various forest habitats in British Guiana, Surinam and Panama, and the published accounts from other areas are in agreement. Two factors are probably responsible for the high Trinidad population. First, the forest in Trinidad is much broken up, and there is a high proportion of second growth. Clearings, paths and roads are numerous. Where lumbering is carried out, the trees that are removed are mostly species whose fruits are unsuitable for manakins to eat (especially *Cordia alliodora*, *Cedrela mexicana*, *Carapa guianensis*, *Sterculia earibaea* and *Mora excelsa*). Many of the manakins' main food trees are characteristic of secondary forest and of road-edges, being relatively rare in untouched forest; this is particularly true of the most important family of



TEXT-FIG. 6. Foraging and bathing ranges of 9 males from display ground A (left) and 13 males from display ground B (right). Figures in squares: numbers of observations at bathing and trapping places. Dots: sight records of feeding birds.

all, the Melastomaceae, which flourish in second growth in areas of high rainfall and reach a great abundance in the wetter parts of Trinidad. Thus a moderate amount of clearing and lumbering benefits the manakin population. Secondly, with a reduced avifauna, compared with neighboring parts of Venezuela, Trinidad shows to some extent the phenomenon characteristic of islands: few species, but large populations of those species that are present. This must be attributed to reduced competition from other species, but the way in which this reduction of competition operates is far from clear.

DISPLAY

FIRST IMPRESSION OF A DISPLAY GROUND

It is difficult to describe the activities at a display ground of Black and White Manakins in terms suitable for a scientific journal and at the same time give any adequate impression of the total effect of the bizarre postures and movements, the sharp snaps and cracks, and the extraordinary vivacity of the whole performance. Yet undoubtedly this combined effect is of paramount importance, for communal display would not have evolved if the effect of a group of males displaying at close quarters had not, for the female manakin, greater attractive power than that of a single male displaying by itself.

The first impression is bewildering. Spaced only a few feet apart (if the courts are well concentrated), a group of small black and white birds are seen leaping about and performing other evolutions with extraordinary rapidity, within a few inches of the ground. Accompanying these movements, some of which are too rapid to fol-

low in detail by eye, are a variety of sharp cracks, like percussion caps exploding, rolling snaps, and whirring and grunting noises, as well as a chorus of excited high-pitched calls.

Closer inspection shows that each bird is performing on and around a small area of bare soil and rootlets, which shows up plainly against the surrounding leaf litter, and that two or three saplings around the edges of each cleared area are the chief perches of the displaying birds. More prolonged observation shows that the birds' bewildering evolutions can be resolved into a number of highly stereotyped movements. Surprisingly, the whole performance may be taking place, and may continue to do so, without the presence of a single female. But if a female does appear, the intensity of display will at once increase.

ANATOMICAL SPECIALIZATIONS OF THE MALE AND THE MECHANICAL SOUNDS

Lowe (1942) made a detailed examination of the plumage and musculature of *Manacus vitellinus* and described the structures responsible for its specialized displays. In its morphology *M. manacus* seems to be identical with *M. vitellinus*, and its displays are almost identical. Here only a short summary will be given of the anatomical findings. It is still not certain how all the mechanical sounds are made. As Sick (1959) remarks, full elucidation will depend on experiments on birds displaying in aviaries.

Both the primaries and secondaries are modified in the male. The four outer primaries are very narrow and stiff, the outer webs especially

being extremely narrow. Due to this, the male makes a grasshopper-like whirring in level flight which is automatic and not a part of any display. Females and young males, which have unspecialized primaries, make only a low whirr when they fly, and moulting males that have lost some of their outer primaries also fly comparatively silently. However, the attenuated outer primaries are probably also responsible for the sound made during "fanning," a display to be described later.

The secondaries are more highly modified. Their shafts are unusually thick, and the outer webs very stiff. In addition, the ends of the quills are not attached to the ulna but pass dorsally to it and are loosely attached to a tendon that runs along the dorsal side of the radius. The muscle slips attached to the bases of the secondaries are very highly developed. The secondaries thus have great mobility.

These modifications of the secondaries are undoubtedly responsible for the two loudest mechanical noises made in display, the single "snap" and the "rolled snap." A single "snap" is made each time the displaying bird jumps from one perch to another; it is also made, much less often, by perched birds. In either case the wing movement is much too rapid for the details to be seen. The "rolled snap" is also made when perched or just before taking off for a leap or short flight. As it is made the wings can momentarily be seen raised above the back and vibrating rapidly. Both in the single and the rolled snap the actual sound is probably made by the stiff outer vanes of the secondaries brushing against one another rapidly as the wing is opened and closed, partly through the action of their muscles and partly due to the nature of their attachment along the radius.

More general muscular modifications are also important for the display. In particular there is a great development of the pectoral musculature (responsible for the very rapid wing-actions needed for "snapping"), the thigh musculature (responsible for the powerful leaps from perch to perch), and the muscles moving the tail (connected with the rapid turning about in mid-air during jumps between perches).

The appearance of the head is much altered during display. Most striking are the elongated feathers of the throat, which are puffed out to form a white "beard" protruding beyond the tip of the beak. Connected with this, Lowe reported a noticeable development of the unstriated muscles activating these feathers, and also of the muscles of the hyoid apparatus. The neck feathers, and the feathers of the sides of the head, are also greatly puffed out, so that the black cap

is transformed from a broad oval to a narrow slip of black tapering to a point at the posterior end. Seen from the front the bird appears all white with a small black lozenge in the middle. Probably the neck feathers too are provided with a specialized musculature.

VOICE

Black and White Manakins utter a variety of rather simple, mainly monosyllabic, calls. Undoubtedly the very loud mechanical snaps have functionally replaced the loud and more complex calls of some other manakins and the related Cotingidae. Nevertheless some of the calls are quite loud, and they make up an important part of the total volume of sound heard at an active display ground.

The only call of the adult that is unconnected with display and uttered by both sexes is a rather plaintive monosyllabic "peerr," slightly trilled at the end. It is uttered by alarmed birds, such as females whose nests have been approached or males disturbed at a display ground, by solitary birds away from display grounds or nests, and by males sitting quietly at the display ground between bouts of display. In aggressive encounters between males, it is uttered by the subordinate bird.

As the excitement of a male mounts, his calls change from the unexcited "peerr" to a louder, higher-pitched and untrilled "chwee." This is the dominant vocal sound made during the outbursts of calling and snapping which greet the arrival of a female at a display ground.

The "peerr" call has other variants that sound like "pee-you" or "pee-yuk," being more disyllabic, with the trilled ending modified into a more distinct separate note. Chapman described these as "notes of awareness, address and response, or of inquiry or protest"; certainly they have a varied social significance that cannot be simply defined. They are uttered by males at display grounds in a variety of circumstances, but not in the immediate presence of a female.

A quite distinct call, a disyllabic "chee-poo," typically marks the beginning of a bout of display. Frequently it follows immediately after a rolled snap. It is not uttered in other circumstances.

Juvenile males, when displaying, sometimes utter a rather soft, plaintive "pu." In *M. vitellinus* this call is associated with a stereotyped display (Appendix 1), but in *M. manacus* it seems almost to be obsolescent, since it was rarely heard, and then only from juveniles when engaged in uncoordinated display with other young birds.

The begging calls of young birds, in the nest

and when being fed after leaving the nest, are described elsewhere (p. 89 and 90).

THE COURT

The general character of the display ground has already been described, and the constancy of the courts from year to year mentioned. The spacing of the courts at different display grounds is variable. If there are sufficient suitable saplings, most courts may be within a few feet of each other and clusters of two or three may be in contact with each other. If groups of suitable saplings are fewer, courts may be many yards apart. At the largest display ground seen in Trinidad (H in Text-fig. 3) there were some 70 courts, many of them almost touching each other, within an area of about 20 by 10 yards. More commonly courts are on average from one to five yards apart. The display grounds of *M. vitellinus* studied by Chapman in Panama were far more scattered, and also very small, with not more than five courts spaced as much as 200 feet apart. This situation is probably unusual; at another display ground in Panama visited in 1958, the spacing of the courts was the same as in Trinidad.

The size of a court is also variable. Most are roughly oval and measure about 3 by 2 feet. From this area all dead leaves are carried away and most of the rootlets are stripped white by the owner's continual picking at the bark. All that remains is bare earth, rootlets and such sticks as are too large for the bird to carry away.

One of the upright saplings growing round the court is more important than the others, in that some of the main displays, and mating itself, take place on it. This "main upright," as it will be called, must be fairly straight and smooth; those that were measured were not less than 6 mm. or more than 20 mm. in diameter near the ground. Its bark is usually worn smooth by the continual rubbing of the bird's feet, and below it the ground is kept especially well cleared.

The birds clear their courts at intervals throughout the day, usually during bouts of display. Typically, the bird jumps down onto the ground beside the object, picks it up and flies to a perch a few feet away, dropping it as it lands. Or it may lean down from a low perch at the base of a sapling, pick up an object and fly away with it. Less often, a bird flies down and without alighting, or alighting for only a fraction of a second, picks up a leaf and flies off with it, the whole movement being so rapid that it is impossible to see in detail.

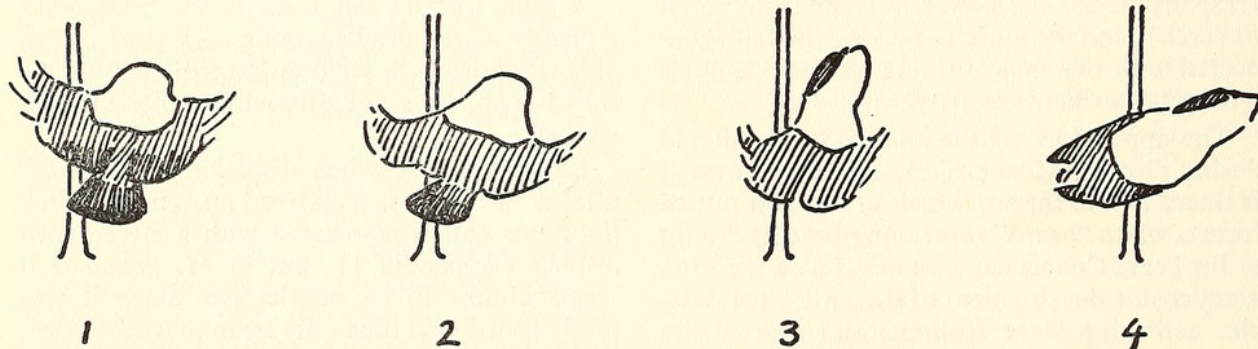
THE ELEMENTS OF THE DISPLAY

The different displays were seen very many times and were recorded on 16 mm. movie film, usually at 24 frames per second (the light at the display grounds was not good enough for exposures shorter than 1/50 second). This account differs to some extent from previous accounts of the display of *M. manacus*. Previous observers have not seen all the displays, and their accounts of some that they have seen have been inaccurate. This is not surprising; conditions of observation are often not easy, and in any case very fast display movements need to be seen many times, and over a long period, before their exact nature becomes clear.

There are also some differences between this account and Chapman's account of the display of *M. vitellinus*. Some of these seem to represent real differences between the behavior of the two species; they are dealt with fully in Appendix 1.

The "snap-jump"

This is the most frequently used of the display movements. Typically, the bird perches in a horizontal position across one of the upright saplings round its court, with its head thrust forward and beard extended, then suddenly with a loud snap leaps to another perch, reversing its position as it reaches the other perch so that it lands facing the way it came from (Text-fig. 7). The complete leap from one perch to an-



TEXT-FIG. 7. The "snap-jump": a male turning in the air and landing after the jump. The bird approaches the perch in an upright position (1), tucks tail under, at the same time turning head and neck (2 and 3), and lands facing the way it came from (4). (Drawn from movie film.)

other usually lasts from one-sixth to one-quarter of a second, depending on the distance between the two perches. During the jump, the whirring noise made during normal flight is not heard.

Many snap-jumps may be repeated in quick succession, so that the bird crosses and recrosses its court with great rapidity. When more than two perches are available, there is a tendency for the sequence of snap-jumps to follow a fixed pattern from one perch to another.

Because the snap and the jump are simultaneous, it would seem that the snap depends on the wing-movements involved in the leap. Very occasionally, however, a bird makes a snap and remains perched, but such snaps are less loud than those accompanying a jump.

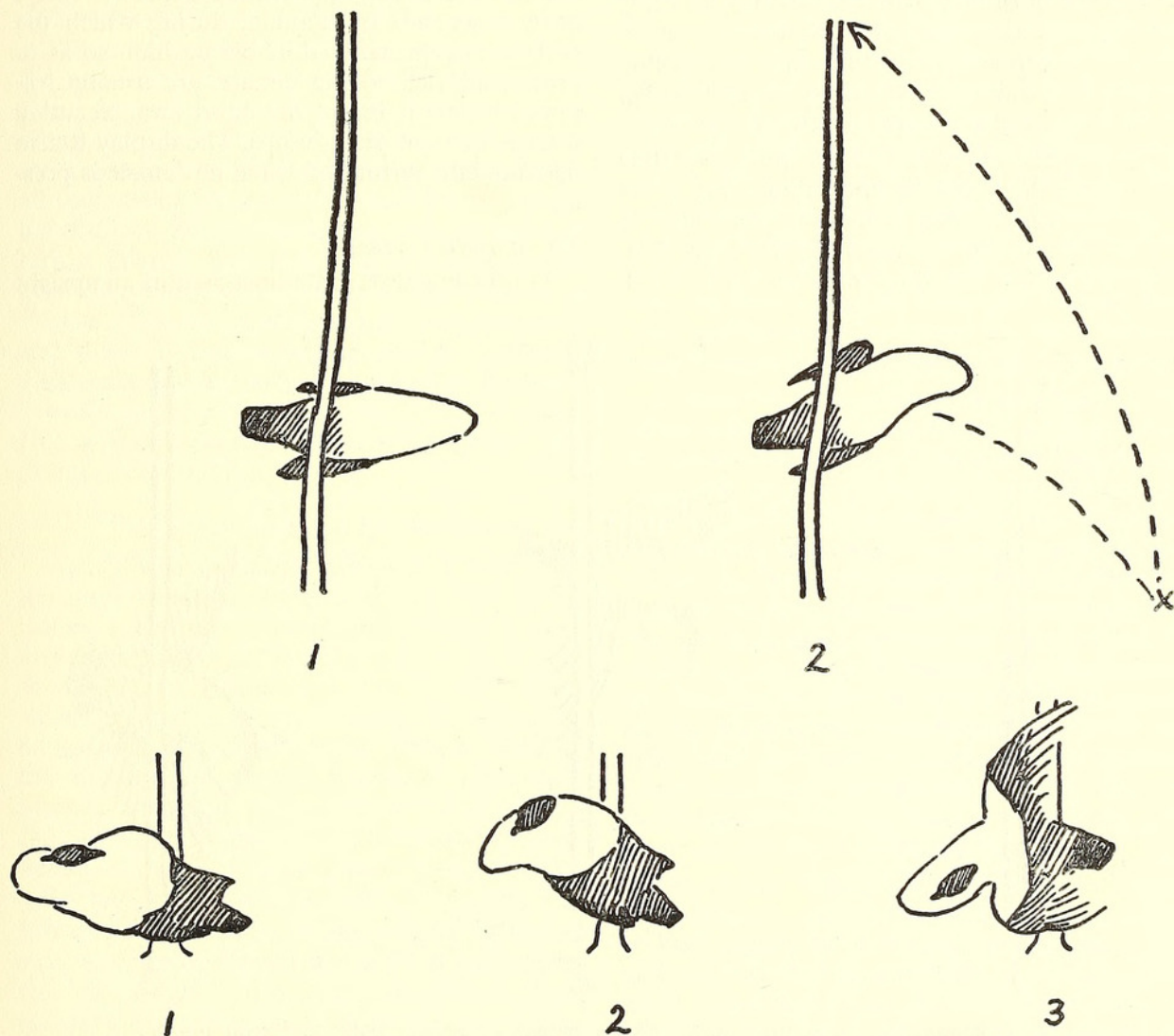
The "rolled snap"

The bird leans forward on its perch, raises its wings above the back, and with a vibrating movement that is almost too rapid to see emits

a loud rolling snap, like a succession of single snaps run together. It frequently takes flight immediately afterwards, or if it does not fly utters a call, "chee-poo," indicative of mounting excitement. The rolled snap typically introduces a bout of display after a period of inactivity.

The "grunt-jump"

This follows after a sequence of snap-jumps between the saplings round the court. The bird jumps or flies to the "main upright," landing transversely on it within a few inches of the ground, then with beard extended, body tensed and even quivering slightly, as if bracing itself for the effort, it leaps down to the ground, turning in the air as it does so, lands momentarily on its feet facing the perch, and leaps back to a higher position on the same perch (Text-fig. 8). As it leaves the ground it emits a curious sound between a grunt and a whirr. The whole sequence, from leaving the perch to landing on it



TEXT-FIG. 8. The beginning of the "grunt-jump," from two viewpoints, showing the bird's trajectory (right, upper). Just before jumping, the bird raises its head and neck and half-opens its wings. (Drawn from movie film.)

again higher up, is extremely rapid and difficult to follow by eye; it lasts just over one-third of a second.

The same grunting sound is occasionally made by perched birds, and is accompanied by a sudden humping up of the back, the head being held forward and rather low. At the same time the wings are moved, but too rapidly for the details to be seen. The grunting sound thus made is a little lower-toned, lasts longer and is more vibrant than that made on an upward jump. A sound approaching the grunt is also made when a bird rapidly flies upward from the ground to a perch, or from one perch to another. Thus the sound is certainly mechanical in origin but it is not clear how it is made.

The "slide down the pole"

Immediately after landing on the main upright, after the "grunt-jump," the bird may move down the perch for several inches in a head-downward position, with the wings beating, moving with such short steps that it appears to slide. As it approaches the bottom of the sapling it turns to a more horizontal position (Text-fig. 9). This display is comparatively infrequent.

The "grunt-jump" followed by the "slide down the pole" represent the culminating phase of the courtship display in that they immediately precede copulation, as described later (p. 77). The male "slides down the pole" on to the back

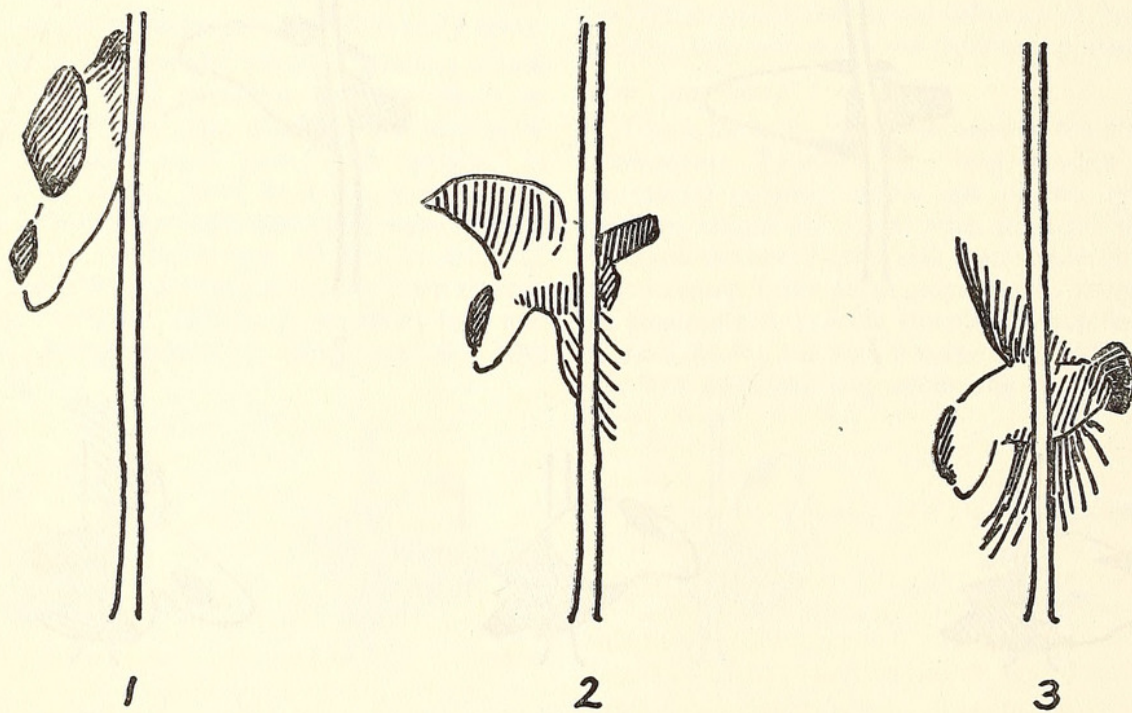
of the female, who perches below him on the sapling.

"Fanning"

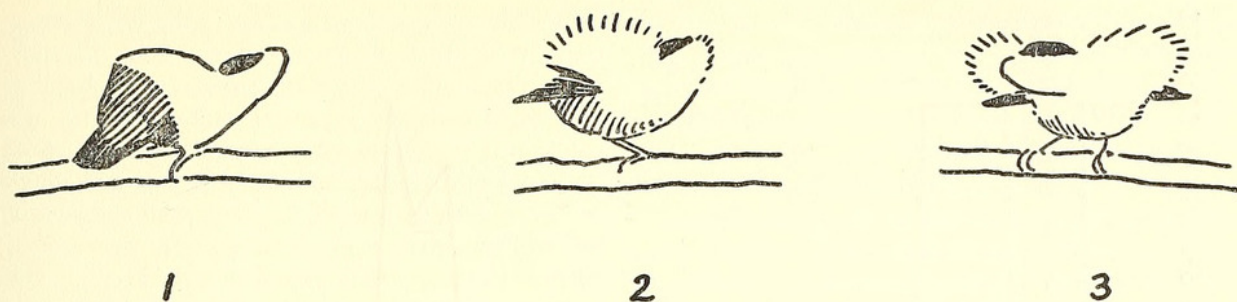
This is a very distinct display. The male leans forward on his perch, holding his head low, with the neck retracted and the beak pointing slightly upwards, and sways his body from side to side. At the same time he holds his wings out from the body and beats them at the rate of five times per second, raising and depressing the tail and the whole hind end of the body synchronously. The beating of the wings makes a low-frequency whirring sound, easily distinguishable from the flight whirr. Apparently due to the retraction of the head between the "shoulders," as the wings are raised the feathers of the hind-neck are pushed forwards and upwards so that they stick out as two flickering white puffs behind the bird's head at either side (Text-fig. 10). This display is most often directed at a female which has approached a male's court. Several seconds of fanning, during which the male may repeatedly shift his position so as to present himself to the female, are usually followed by his flying to the court and executing a series of rapid snap-jumps. The display is also occasionally performed when no female is present.

The upright posture

Displaying birds sometimes assume an upright



TEXT-FIG. 9. The "slide down the pole." (1) the beginning of the slide, just after landing from the "grunt-jump." (2) half way down. (3) near the end of the slide, the body becoming more horizontal and the tail fanned. (Drawn from movie film; no attempt has been made to show the feet, which move too fast to appear on the film.)



TEXT-FIG. 10. "Fanning." Left, (1) and (2): wings closed and wings raised. Right (3): wings raised, seen from the front. (Drawn from movie film.)

posture when perched, with the head pointing upwards and beard extended. This posture does not seem to play an integral part in any of the main display movements described above, though it sometimes follows a bout of snap-jumps. The posture may be held for several seconds.

Aggressive displays between males

When two males are perched close together, the dominant one may extend his beard, turn about frequently on his perch, give little jumps along the perch, hold his head low and turn it from side to side, or raise and vibrate his wings, all these being incomplete forms of normal sexual displays. Sometimes he may fan his tail and turn it towards the other bird. The subordinate bird sits quietly, with throat and body plumage sleeked; when threatened he may flick his wings and suddenly fan and close his tail, probably flight-intention movements. Aggressive behavior between males may culminate in prolonged flight chases round and round the display ground and in fights on the ground.

THE DAILY RHYTHM OF DISPLAY

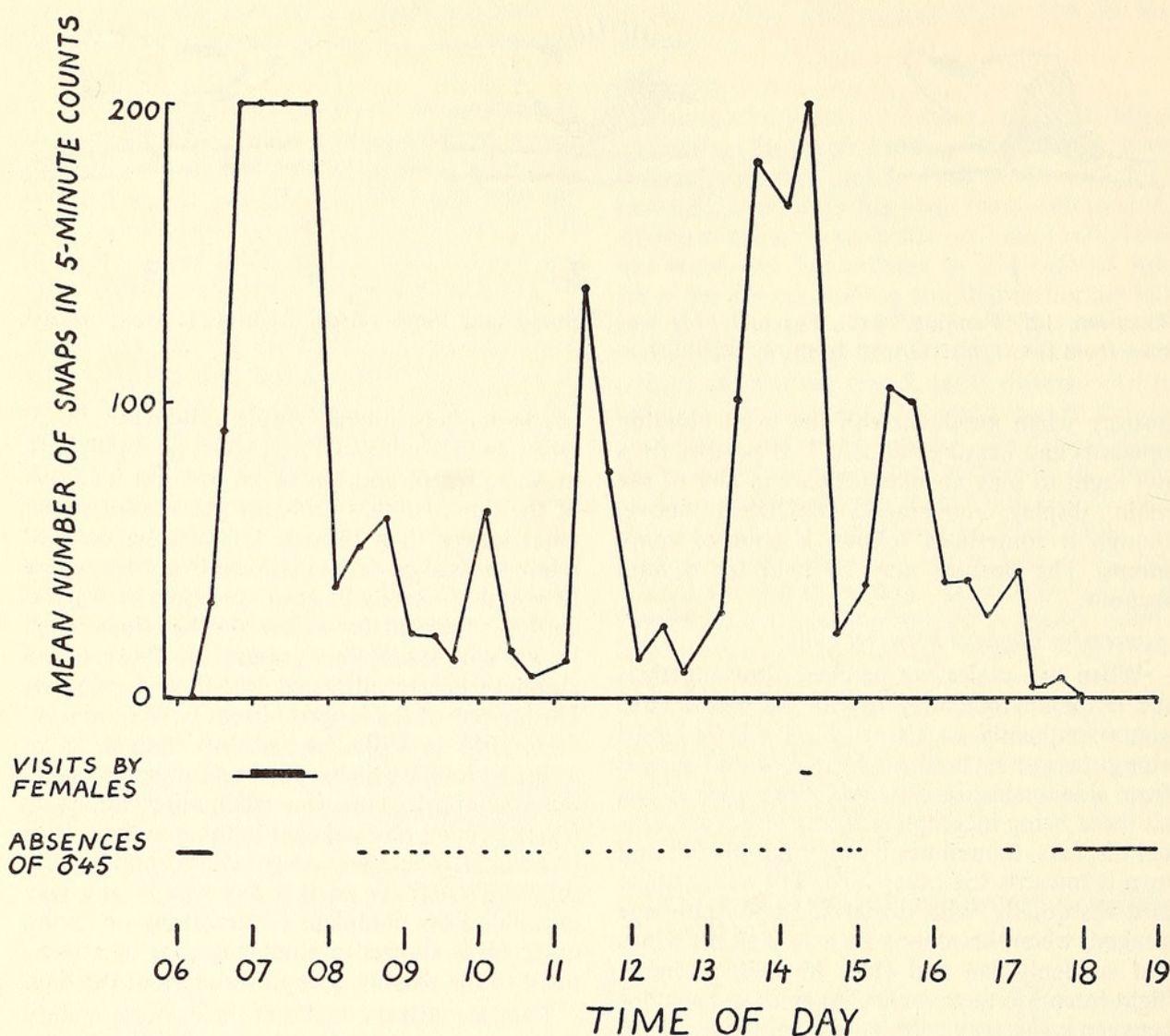
Apart from the weeks when he is moulting, the adult male manakin is at all times closely attached to the display ground. Almost as soon as it is light enough to see, the first males appear at their courts. Display soon begins and reaches a peak, then after an hour falls off to a low point between 0900 and 1100 hours. In late morning the intensity of display increases again and reaches a second peak around 1400; it then falls off again gradually and by 1700 has practically ceased. The males gradually move away, a few late ones remaining until about 1800. The precise times of the beginning and end of display vary somewhat, depending on the times of sunrise and sunset and on the variations in light intensity due to weather and the forest canopy.

Text-figure 11 shows the results of a continuous watch on a single ringed male throughout the daylight hours of January 27, 1960, a day

of moderately intense display. Between 0625, when he arrived, and 1747, when he finally left, he was present and under observation for 90% of the time. He was probably present for somewhat longer than this, as at times he perched a few yards away from his court in a place where he could not easily be seen, and thus he was recorded as absent for a few short periods when he was almost certainly present. His 24 recorded absences nearly all lasted less than 5 minutes. During one of the longest absences, of 6 minutes from 1659 to 1705, he certainly bathed, as he returned looking dishevelled and preened vigorously (and this is the time when observations by forest streams showed that bathing activity is at its height). There was no reason to suppose that this bird's activity on this day was in any way unusual. Less complete observations on many other birds showed a similar degree of attachment to the display ground throughout the day.

Females visit the males at their courts mainly during the two periods of intense display (0630-0800 and 1330-1500). Intensity of display by the males and the presence of the females are of course interrelated, in so far as the presence of a female stimulates the males, and intense display by the males attracts the females. But apart from this, the males' daily cycle of display is to a great extent independent of the females, as it is equally marked at seasons when the females are visiting them hardly or not at all. On the day when a continuous watch was kept, only one visit by a female was recorded in the afternoon. This was unusual; typically as many females are seen visiting the males in the afternoon as in the early morning period.

Text-figure 11 shows that the male under observation left the display ground, presumably to feed, mainly at times when display was slack, and that his first absence took place soon after 0800, when the early period of intense display was over. Trapping and observation away from the display grounds confirmed that these are the main feeding times. In particular, trapping at a feeding area (T in Text-fig. 3) regularly



TEXT-FIG. 11. The activity at display ground A, January 27, 1960. Intensity of display measured by number of snaps in 5-minute periods (snaps in excess of 200 omitted). Female visits: thin line, one female present; thick line, several females present.

showed a period of great activity in the hour between 0800 and 0900. Text-figure 12 shows the numbers of males, known to have courts, that were trapped in this area in the different hours of the day.

It was also found that, at least occasionally, males may feed intensively in the short period between first light and their arrival at the display ground. This may depend on the availability of fruiting trees in the forest canopy or in open places along the forest edge, where the light allows feeding at such an early hour.

DISPLAYS BETWEEN MALE AND FEMALE

Males display vigorously and perform all the display movements described above when no female is present, as already mentioned. But the arrival of a female leads to especially intense and sustained display. Indeed the observer is

usually first made aware of the presence of the cryptically colored female by the upsurge of display and calling.

Her arrival is usually greeted by an outburst of rolled snaps, as males fly to their courts to display, by an intensification of the single snaps, as males that are at their courts perform rapid snap-jumps, and by a change in the calling from an occasional "peerr" to a chorus of excited "chwee" calls. If the female approaches a male's court, he may fly to her and, landing beside her, give a prolonged display of "fanning," after which he will usually fly down to his court and perform a series of rapid snap-jumps.

There is always a strong tendency for the males to fly towards the female as well as to go to their courts and display. Sometimes several males will fly towards her while she is still at the edge of the display ground, and though

quantitative observations on this point would be difficult and were not made, the tendency seemed to be strongest in the first weeks after the moult, and in those males that were less settled at their courts. The tendency for males to fly towards a female is also strong when, as sometimes happens, she flies in high and perches well above the courts. Several males then often fly up to her and call and snap excitedly, but in such cases the female appears unwilling to go down to the courts. Females that are ready to join the males at their courts fly in only a few feet above the ground.

Usually males do not approach a female until she is within a few yards of their court, and they then perform the fanning display at her. Fanning is a clear indication that the female is within the male's sphere of influence, even though she may still be several feet from his court. Two males were never seen fanning simultaneously at the same female.

The behavior of the females when they first arrive at the display ground is quiet and almost secretive. They flit from perch to perch, within a few feet of the ground, and show signs of initial nervousness. Early in the season, before breeding has begun, they often arrive in groups of up to five together; later they more often come singly.

Early in the season they not only arrive together but also go down to the courts in groups, and a rather confused display develops. The male displays hard, but at the same time seems somewhat "taken aback" by the number of females present. They perch on the surrounding saplings and on his court, frequently flitting from one perch to another and changing places with each other, keeping clear of the male and yet plainly attracted to his court.

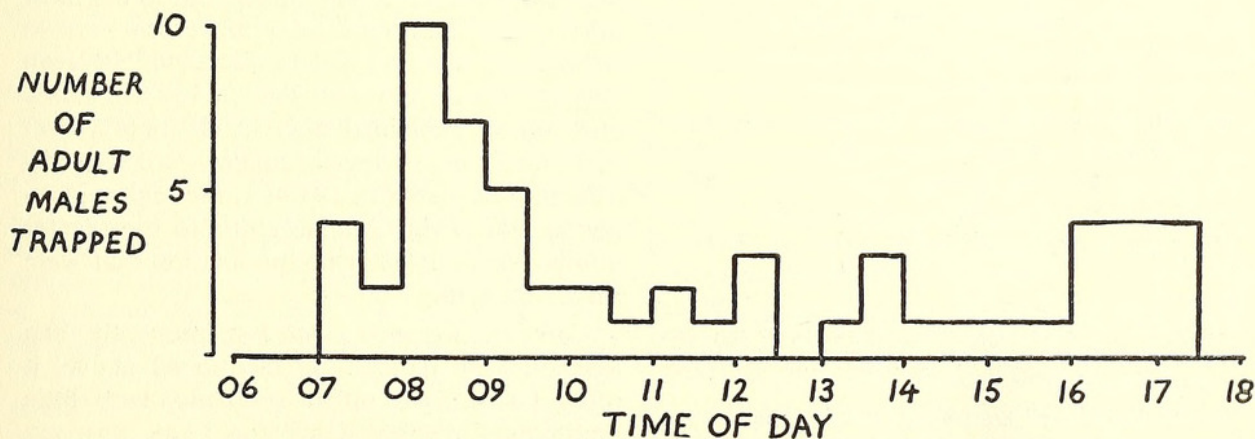
But when a single female visits a male at his court a well coordinated display or dance may take place, which may culminate in copulation.

These dances become commoner as the breeding season approaches. As would be expected, all transitions may be seen between the confused situation with several females present at a court and the highly coordinated dance between the male and a single female.

A full sequence of the precopulatory display is as follows. The female approaches the court; the male flies to her and "fans" for several seconds; the male then flies down to his court and executes a rapid series of snap-jumps; the female soon follows, landing on one of the upright saplings; a mutual dance then takes place, with the male doing repeated snap-jumps across the court and the female crossing him in mid-air and landing at the place which he has just left; after a series of these jumps, the female lands on the "main upright;" the male jumps and lands below her on it, then immediately executes a "grunt-jump," going down to the ground and back up onto the main upright above the female; he then "slides down the pole" onto her as she is perched crosswise on it, and copulation takes place; during copulation the male has one foot on the perch and one on the female's back.

More often, only a part of this sequence is seen. In particular, the preliminary fanning, which serves to attract the female to the court, is usually given only to hesitant females, and such birds, when they do go down to the court, usually do no more than a few jumps with the male. On the other hand, females that are ready to copulate often fly straight to the main upright and the male at once follows with the sequence "grunt-jump"—"slide down the pole"—mounting. It was sometimes observed, and is probably usually the case, that these birds had recently visited the male and had danced with him several times.

When females first dance with a male they are nervous, and the males in their turn sometimes behave aggressively towards them. The female tends, when flying to the perch that he has just



TEXT-FIG. 12. Numbers of adult males with courts trapped at a feeding area throughout the day.

left, to keep a little higher. Thus the two birds cross in mid-air with the female a little above. This tendency to keep above the male is undoubtedly an indication that the female is not ready to mate, to do which, as described above, she must allow the male to land above her on the same upright. If the male, perched below her on the main upright, does a "grunt-jump" to land above her, the female, if not ready to mate, at once flies to another perch.

The females that visit the same display ground probably have a mutually stimulating effect upon one another. As already mentioned, they tend to come to the display ground in small groups, especially at the beginning of the season, and at all times the outburst of display that accompanies the visit of one female to the display ground must help to attract other females. As a result, there is a tendency for the nests near any one display ground to be better synchronized with each other than with nests near other display grounds (Table I).

TABLE I. SYNCHRONIZATION OF NESTINGS OF FEMALES ALONG THE SAME STRETCHES OF STREAM, 1961

| | Number of nests started along different stretches of stream (see map, Text-fig. 3) | | |
|----------------|--|-------------|------------------|
| | Tripp Stream | Arima River | St. Pat's Stream |
| Feb. 26-Mar. 1 | 3 | 1 | — |
| Mar. 2-6 | 2 | 1 | — |
| Mar. 7-11 | — | — | — |
| Mar. 12-16 | 1 | 4 | 2 |
| Mar. 17-21 | 1 | — | 1 |
| Mar. 22-26 | — | — | — |
| Mar. 27-31 | 1 | — | 1 |
| Apr. 1-5 | 2 | — | — |
| Apr. 6-10 | 3 | — | 2 |
| Apr. 11-15 | 1 | — | 1 |
| Apr. 16-20 | 2 | 2 | — |
| Apr. 21-25 | 1 | — | — |
| Apr. 26-30 | — | — | — |
| May 1-5 | — | — | 1 |
| May 6-20 | — | — | — |
| May 21-25 | — | — | 1 |
| May 26-30 | — | — | 1 |
| May 31-June 4 | — | — | 2 |
| June 5-9 | 4 | — | 3 |
| June 10-14 | 5 | — | 1 |
| June 15-19 | 1 | 4 | 1 |
| June 20-24 | — | 1 | 1 |
| June 25-29 | 1 | — | — |

Notes. A small number of nests started after the end of June are omitted.

The "Arima River" nests were all situated along the 600-foot stretch west and south of display ground F, at the lower edge of Text-fig. 3.

CHOICE OF DISPLAY PARTNER BY VISITING FEMALES

At the main display ground, 39 color-ringed females were seen visiting the courts and dancing with males, most of which were themselves color-ringed. Three of the females were seen visiting the display ground in three successive years, and eight in two successive years.

There was no evidence for any kind of pair-formation at the display ground. Without exception, all those females that were seen visiting more than once (21 out of the 39) visited and danced with more than one male. Usually in the course of a single visit females went from one male to another. They all undoubtedly went to many more males than they were seen to visit, since they are difficult to follow as they flit silently from court to court in the undergrowth.

Certain males were outstandingly successful in attracting females, especially ♂ 45, whose court was close to the hide. Twenty of the 39 color-ringed females visited him, as well as many unringed females. The large number seen visiting him was only partly due to the fact that his court was easy to observe, as only four color-ringed females were seen to visit an adjoining court, and at two other close courts, also easy to observe, only 9 and 12 were seen. In the early part of the season ♂ 45 was regularly visited by four or five females together, while the males displayed persistently but vainly at neighboring courts. Within the area under detailed observation, two other males were also very successful, but because their courts were farther from the hide and the undergrowth round one of them was rather thick, only 17 and 4 color-ringed females were identified visiting them.

There was no obvious reason for ♂ 45's success. He was an old bird, established when trapped in 1958. He was constantly at his court, but not more so than many other males, and his court was not obviously more suitable than many others. He displayed vigorously, but so did most other males, and the display movements are so stereotyped that no differences could be seen between his display and that of his neighbors. His success remained high in all three years: 7, 7 and 11 color-ringed females were seen visiting him in the years 1959-61, the higher number in 1961 being probably due to the greater number of females in the population that were ringed by then.

Copulation is seen much less frequently than the courtship dances. As mentioned above, it often takes place rather suddenly, with little preliminary display. Only for ♂ 45 was any worthwhile record obtained. He was seen copu-

lating with two different color-ringed females and 15 times with unringed females. At the least he must have copulated with three different birds in a single season, and undoubtedly with many more, since observations were usually made on only one morning a week.

RELATIONS BETWEEN MALES AND THE OWNERSHIP OF COURTS

During most of the year there is little overt aggressive behavior between the males. With the ownership of their courts uncontested, neighboring males perch and display close to each other without hostility. Nevertheless competition for courts is strong, and when one falls vacant it is usually soon taken over by another bird, either an unestablished bird or one that has been occupying a less suitable court.

Some males remained unestablished for months. Such birds often display for periods at one of the outlying courts of a display ground, but they do not occupy them permanently. They shift frequently, and when an opportunity arises move to a more central court. It is because males do not remain satisfied with outlying courts that the courts in the central nucleus of the display ground remain much the same year after year, while the number and positions of the outlying courts change.

Unestablished males sometimes hang about for days round the edges of an occupied court, coming down to it and displaying when the owner is away and vacating it as soon as he returns. There were also several cases of what appeared to be joint ownership of a single court. This situation was usually short-lived, except at one court where it continued for 7 months. The two males would sit together within a few inches of each other on the court. However, one (a ringed bird) was dominant and it alone displayed when both were present, the other bird only when it was alone, and then only hesitantly. The two birds had a strong tendency to leave the court together and return together.

In such cases, as long as one bird is clearly dominant and the other subordinate, there is no open hostility between them, aggressive behavior being limited to the posturing described above (p. 75). But it occasionally happens that an intruding male actively tries to oust the owner and does not assume a subordinate position. Then prolonged flight-chases may take place, the owner pursuing the intruder, who does not leave the display ground but flies round and round. Or the two birds may come to grips and roll together interlocked on the ground. The main display ground under observation was on such a steep slope that when this happened the two

birds would roll helplessly downhill over their neighbors' courts.

During the moulting season temporary changes of ownership are frequent as old birds abandon their courts, and newcomers, in many cases young males who have completed their moult earlier (p. 85), take them over. But when the moult is over and the old birds have returned, the courts normally revert to their original ownership and the position becomes stabilized. It is then rather rare for an established bird to be ousted by another. Only one such case occurred in the part of the display ground, comprising some 16 courts, that was under the most detailed observation, and the ousting was only temporary. The aggressor, ♂ 109, though an old bird, was of unsettled habits. From March, 1959, when he was trapped, to May, 1960, he had held one court, abandoned it and disappeared for three months, and had then occupied another court. At the end of May he abandoned this court too and began to hang about round the edges of the court of ♂ 45, already mentioned as an outstandingly successful old bird who had been in possession of his court for at least two years. On May 31 these two were apparently involved in a fight, which unfortunately was not seen. ♂ 109 was seen in the afternoon at one of the bathing places, with the side of his head bloody and his plumage dishevelled. On the next morning he was in possession of ♂ 45's court and ♂ 45 was not present. But a week later ♂ 45 was back in possession. ♂ 109 was again hanging about round the edges of the court and later he shifted back to his second court, which he retained for over a year until observations ceased.

Once a male is well established at a court, his tendency to keep to it still needs constant reinforcing by the presence of his neighbors at the surrounding courts. This is particularly clearly seen in the early part of the moulting season. The display ground is then largely abandoned except for some of the later males which have not yet begun to moult. These birds move about and display freely at courts at which they have never been seen displaying before. A little later, when the young males that have completed their moult come to the display ground and try to establish themselves, they too move from court to court and seem unable to settle at one court while others remain unoccupied.

Unestablished males occasionally shift from one display ground to another. Ten color-ringed males were seen frequenting two different display grounds (A and B, and in one case A and C; Text-fig. 3). Seven were known to be young birds that had not yet settled, three of them

being still in juvenile plumage. Two others were adults, but were unestablished and had probably only recently moulted into adult plumage. The tenth was an old male (adult when ringed a little over a year earlier), which, having tried unsuccessfully for a year to establish himself at display ground A, shifted to another (C), where he acquired a court.

Though they are aggressive towards each other, males have a strong tendency to sit within a few inches of each other on neutral ground between their courts, especially between bouts of display. Sometimes, but by no means always, slight movements and postures show that one is mildly dominant to the other. The same is also seen when one male is hanging about round the edge of another bird's court; the two spend much time sitting together when display is slack. Also in the case of apparent joint ownership described above, the two males would sit for long periods close together. As a result of this tendency, at times when display is slack the owners of courts that are close together spend much more time at the display ground than the owners of the more isolated courts.

Obviously, this strong social tendency is essential to the maintenance of a communal display ground. Aggressiveness and sociability are so balanced as to result in a compact group of constantly maintained, individual territories.

Mutual stimulation is also of great importance in raising the intensity of display and so more effectively advertising the display ground. Though display is inhibited when two males are too close together through competition for the same court, in the normal situation display by the owner of one court conspicuously stimulates the neighbors to display. In the absence of females display thus tends to occur in bursts, one bird starting and setting off the others. The chorus of rolled snaps that introduces these bursts is one of the characteristic sounds of a display ground.

THE SETTLING DOWN OF YOUNG MALES AT THE DISPLAY GROUNDS

Juvenile males moult into adult plumage in their second summer, between June and September. Before this they are indistinguishable in color from the females, but their behavior differs and it is not difficult to tell the sex of a female-plumaged bird when it has been watched a few times in the field.

From as early as twelve weeks after leaving the nest they begin to make incipient display movements. They become highly social and move about in small groups which may be seen performing uncoordinated display, often in com-

pany with one or two males in adult plumage. Often they display well away from a display ground, but they also regularly visit the display grounds and hang about round the periphery, where they are often joined by the unestablished adult males attached to the display ground. They perform all the display movements of the adult males, but as their wing-feathers are unmodified the mechanical sounds are softer, the "snap" being reduced to a "snip." The displays are also more confused. When displaying together, they have a strong tendency to fly to a perch that another bird has just left; thus they are continually changing places. At times they utter a distinctive call heard only in this context, a plaintive "pu" (p. 71).

In the study area there was a small tract of secondary forest where juvenile males and unestablished older males displayed so regularly that several small courts were created, 10 to 20 yards apart, some of which remained more or less clear for months, while one remained for nearly three years. Altogether, 18 different color-ringed males were seen displaying at these courts, as well as many unringed birds. Nearly all were juveniles or birds known to have only recently moulted into adult plumage; the two exceptions were adult males from a neighboring display ground. In addition, four females were seen displaying with the males; three of these were known to have nesting territories very close at hand. The use of this "practice display ground," as it may be called, became a tradition in the local population. During the period of observation none of the courts was ever occupied continuously for any length of time by a single male. No other practice display grounds were found, but their intermittent use would make them difficult to find except in areas which are under regular observation.

While moulting into adult plumage the young males stay away from the display grounds and, like the moulting adults, become inconspicuous. When their adult plumage is complete they reappear and become bolder, temporarily occupying courts vacated by moulting adults. But they cannot maintain their ownership when the adults return, and there begins a usually prolonged unsettled period, during which they try to establish themselves at a court.

Fairly complete information was obtained on 11 color-ringed birds during this period, and less complete information on several others. All these were watched first as juveniles, and then for at least a year after their moult into adult plumage. All moulted into adult plumage in the months June-October.

There was a strong tendency for all these

birds to occupy courts temporarily and shift for no obvious reason, and it was never possible to be sure if a court, once occupied, was going to prove permanent or not. Of the 11 birds, one was established by the following April, one by the following June, and one not until the second February after its moult. Another held a court in the February following its moult, but in December moved to another court, which at the time observations ceased appeared to be permanent. Another was definitely not established in the second February after its moult but established itself two months later. Thus these five birds established themselves approximately 8, 10, 16, 18 and 20 months after their moult to adult plumage. The remaining six birds were less successful; all were still unestablished after periods ranging from 12 to 24 months.

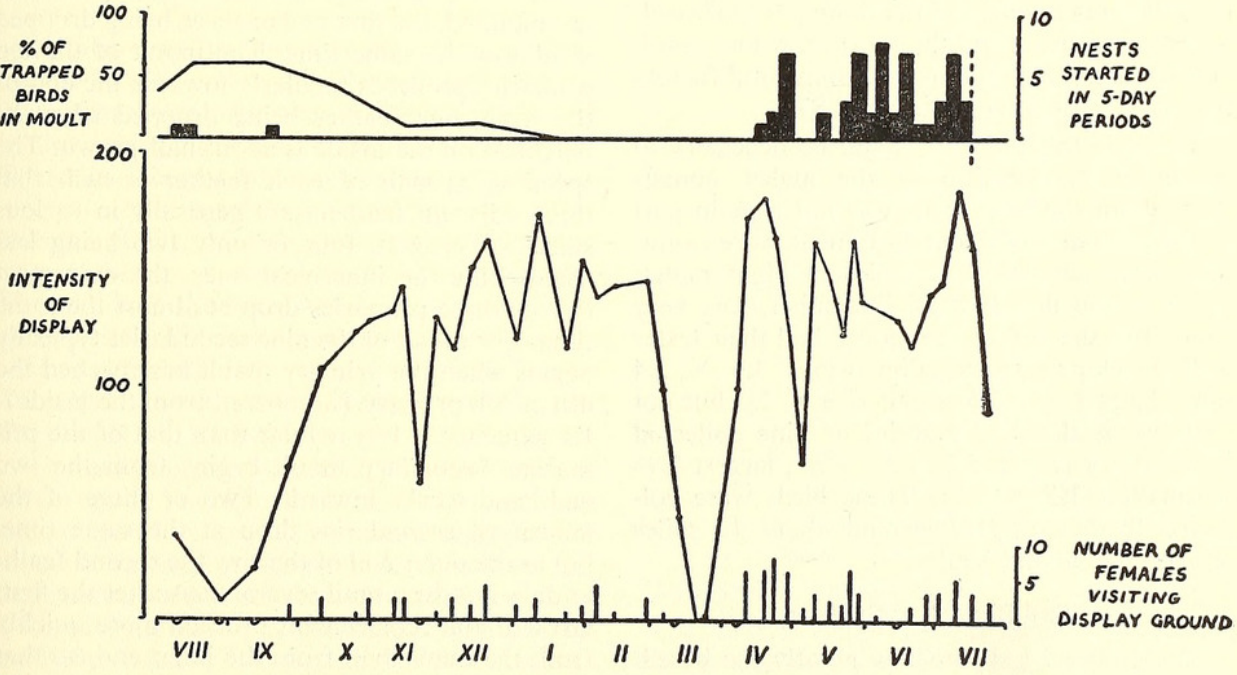
The history of ♂ 114, the bird that established itself in the second February after its moult, was known in some detail. It hatched in August and left the nest on September 2, 1958. It was re-trapped in April, 1959, and color rings were added to the numbered ring that it had been given as a nestling. It was subsequently seen three times in June, once displaying at the practice display ground with another probably juvenile male, and once at one of the outlying courts of display ground A with several other probably juvenile males. It was last seen in juvenile plumage on June 24, being seen again in full adult plumage on October 31, when it was again displaying at the practice display ground. From November onwards, though it was seen displaying five more times at the practice display

ground, it frequented display ground A more and more. Usually it appeared nervous and hung about round a group of central courts. In March, 1960, it tried unsuccessfully to clear a court in a rather unsuitable, but central, place in the display ground. From the end of June to mid-October it was not seen and was undoubtedly moulting. It reappeared on October 18 and from then onwards was constantly present, sometimes displaying at unoccupied courts and sometimes hanging about. In February, 1961, at 2½ years old, and 1½ years after moulting into adult plumage, it began to clear a new court a few yards from the central nucleus of courts, and though the site was not very suitable it successfully cleared it and held it until the second week of September, when it again disappeared for the moult.

THE ANNUAL CYCLE

THE ANNUAL CYCLE OF DISPLAY

As already mentioned, except when they are moulting the adult males are normally present at the display ground throughout the year. From the beginning of August, 1958, to the end of July, 1959, an early-morning watch was made each week at the main display ground under observation, and a quantitative record was kept of the intensity of display by counting the snaps accompanying each display jump. Text-figure 13 shows the intensity of display as thus recorded through a complete year, based on the average number of snaps per 5-minute period recorded in the hour of most intense display. The figure also shows the numbers of females recorded as visiting the display ground during the



TEXT-FIG. 13. The annual cycle of display, breeding and moult, August 1958 to July 1959.

early-morning watches, the numbers of nests found in the neighboring forest, and the percentage of adults trapped in the vicinity that were undergoing wing-moult, and thus provides a conspectus of the annual cycle of the species for this one year.

It will be seen that display did not cease completely at the season of moult, but was merely much reduced. This was because individual males moulted at rather different times, so that by the time that the latest ones had abandoned their courts some of the early ones were back again. More striking was the almost complete cessation of display in the second half of March, probably due to a temporary food shortage, as discussed later. It did not occur in other years, but in 1960/61 there was a more prolonged cessation of display in December and early January, the cause of which was not clear and which also was not recorded in other years (p. 87). Thus the normally continuous cycle of display may show occasional and irregular interruptions.

Text-figure 13 also shows that small numbers of females visited the display ground from the end of the moulting period onwards, but that, as would be expected, the greatest numbers were recorded at and shortly before the start of breeding.

As shown in more detail later, the breeding season did not start at the same time in each year. In the five seasons of observation, the beginning of breeding varied from one to six months after the ending of the moult. Probably in every year the males are ready to mate over a very long period, from shortly after the end of the moult until shortly before the beginning of the following moult, and the timing of the breeding season depends on the females, whose readiness to nest is affected by environmental factors that vary from year to year (p. 87).

To settle this point, it would be necessary to make an examination of the males' gonads throughout the year. This was not a main part of the present study, but specimens were examined when available. A series of eight males, taken in the first half of December, *i.e.*, very soon after the end of the moult, had their testes well developed (mean dimensions 3.6×2.4 mm.; largest 5×3.5 , smallest 3×2), but not so large as those of a series of nine collected in February (mean 5.2×3.4 mm.; largest 7×5 , smallest 3.5×2.5). These birds were collected from a display ground about 12 miles east of the Arima Valley.

THE BREEDING SEASON

Text-figure 14 shows how greatly the breeding season varied in the five years. In 1957, apart

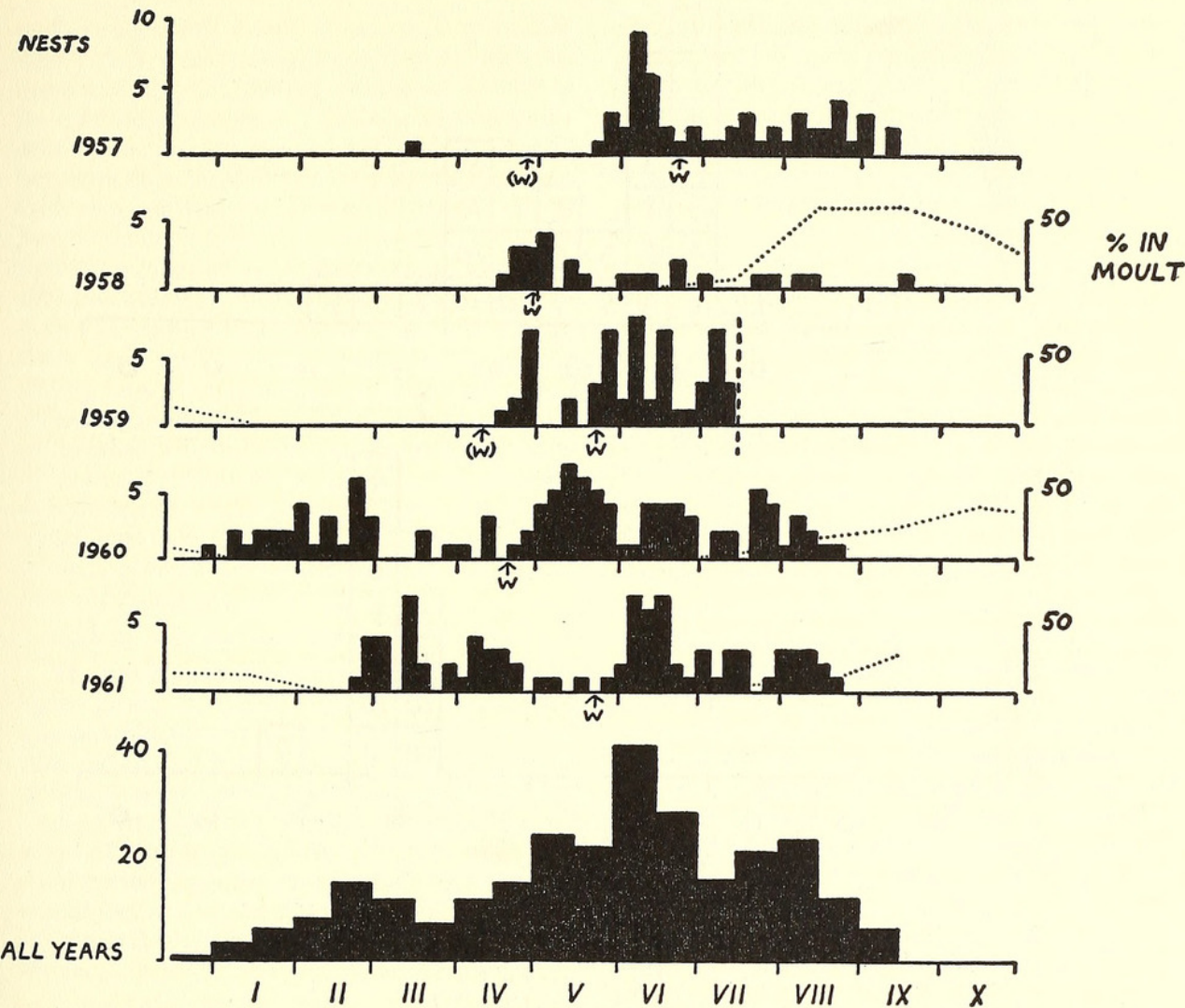
from a single nest in March, breeding was first recorded at the end of May and quickly reached a peak in early June. It then continued steadily until early September. In both 1958 and 1959 breeding began abruptly in mid-April. In 1960 the start was in early January, with a single nest at the end of December, 1959, and in 1961 breeding began in the latter half of February. In all years, the start of breeding was well-defined, many nests being built and getting their eggs within a fortnight, while observations at the display ground at and shortly before this period showed intense activity resulting from the visits of numerous females, and more copulations were seen then than at any other time. There was a little evidence, as can be seen from Text-fig. 14, that nesting ended rather later in 1957 and 1958, when it began late, than in the early breeding seasons of 1960 and 1961. The breeding season lasted from 4 to 8 months in the different years.

The relation of the breeding season to weather and other environmental factors is considered in a later section (p. 85).

THE MOULT

Sequence of moult

The full post-breeding moult follows a sequence similar to that of other passerine birds. Replacement of the wing-feathers follows a consistent pattern. It begins with the dropping of the secondary major coverts. Typically the outer ones drop a little before the inner ones, so that as the new feathers grow they are in a graded order of length from outside inwards. While the coverts are growing, the innermost primaries are moulted, the first two or three being dropped at almost the same time. The moult of the ten primaries proceeds regularly towards the end of the wing, one feather being dropped when its neighbor on the inside is about half grown. The speed of growth of each feather is such that three adjacent feathers are generally in various stages of growth, four or only two being less usual. Like the innermost ones, the outermost two or three primaries drop at almost the same time. The moult of the nine secondaries typically begins when the primary moult has reached the 4th or 5th primary (numbered from the inside). Its sequence is less regular than that of the primaries. Secondary moult begins from the two ends and works inwards. Two or three of the innermost secondaries drop at the same time, but at the outer end of the row the second feather does not drop until several days after the first. Growth and replacement proceed more quickly from the outer than from the inner end, so that although two or three of the innermost second-



TEXT-FIG. 14. The breeding seasons, 1957-1961. Histograms: nests started in 5-day periods. Dotted lines: percentages of trapped birds undergoing wing-moult. W: beginning of wet season. (W): rainfall, followed by further dry weather.

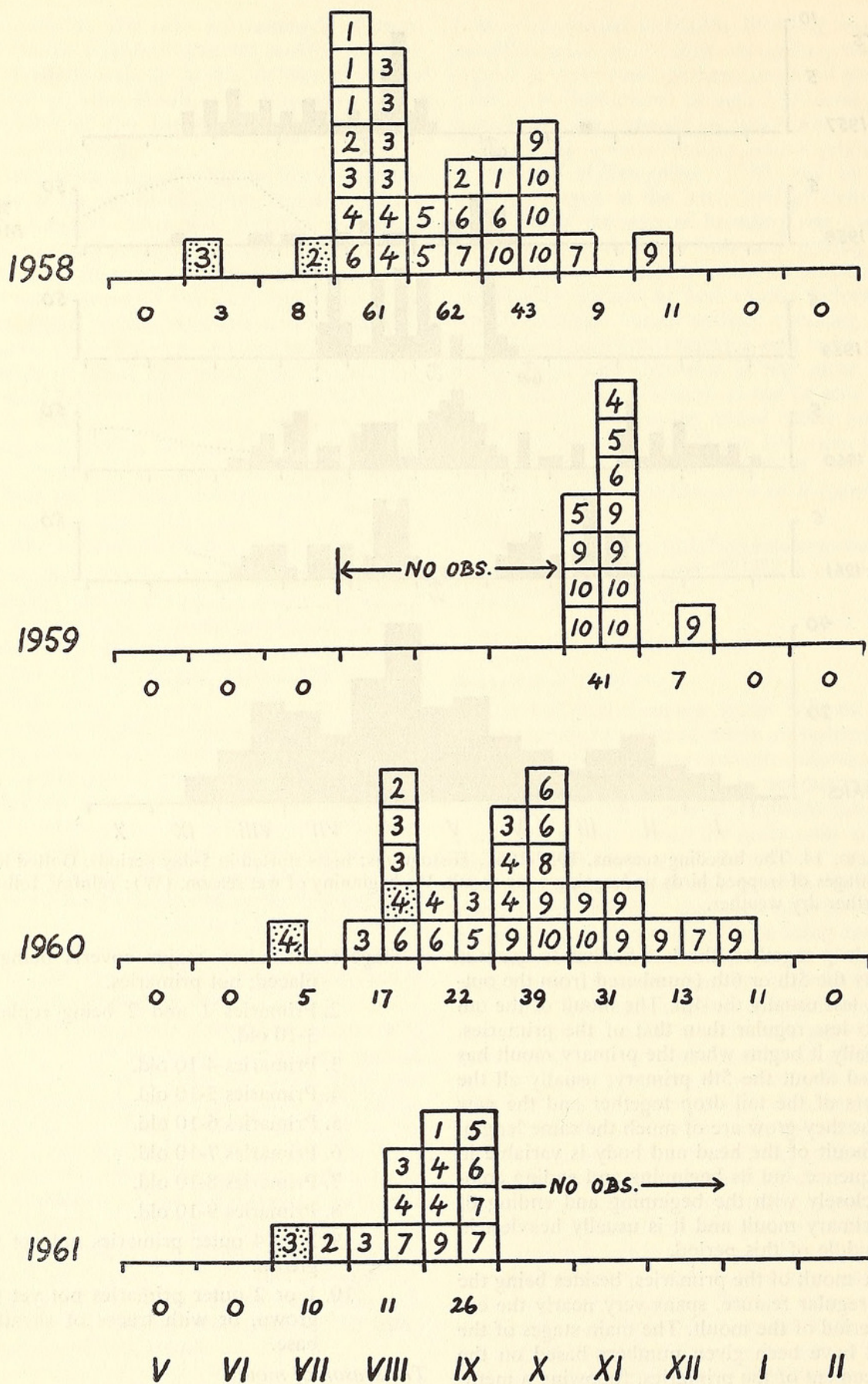
aries drop together, the last feather to grow is usually the 5th or 6th (numbered from the outside), less usually the 4th. The moult of the tail is also less regular than that of the primaries. Typically it begins when the primary moult has reached about the 5th primary; usually all the feathers of the tail drop together and the new ones as they grow are of much the same length. The moult of the head and body is variable in its sequence, but its beginning and ending coincide closely with the beginning and ending of the primary moult and it is usually heaviest in the middle of this period.

The moult of the primaries, besides being the most regular feature, spans very nearly the entire period of the moult. The main stages of the moult have been given numbers based on the replacement of the primaries, following a method used by Miller (1961), and these numbers have been used in Text-fig. 15. The stages recognized are as follows:

- Stage 1. Secondary major coverts being replaced; not primaries.
- 2. Primaries 1 and 2 being replaced; 3-10 old.
- 3. Primaries 4-10 old.
- 4. Primaries 5-10 old.
- 5. Primaries 6-10 old.
- 6. Primaries 7-10 old.
- 7. Primaries 8-10 old.
- 8. Primaries 9-10 old.
- 9. 3 or 4 outer primaries not yet full-grown.
- 10. 1 or 2 outer primaries not yet full-grown, or with traces of sheath at base.

The season of moult

In contrast to the breeding season, the season of moult in all probability varies very little. Text-fig. 14 shows the percentages of trapped birds



TEXT-FIG. 15. Moulting seasons, 1958-1961. Each square represents one individual trapped at the stage of moult indicated by the number. Dotted squares: juvenile males moulting into adult plumage. Figures below the line: percentages of the total number trapped that were undergoing wing-moult.

undergoing wing moult in the four years for which data were collected, and in Text-fig. 15 these moulting individuals are shown according to their stage of moult. It will be seen that the moult extends over the six months July-December, with most birds in moult in August-October. Only one individual was found to be moulting in June and one in January, and none in the months February-May. In the four years, the moult began and ended at approximately the same time.

In calculating these percentages, all trapped birds have been included. However, as will be shown later, the moult of juveniles into adult plumage, in their second autumn, takes place on average a few weeks earlier than the moult of adults. It has not been possible to separate the age-groups in Text-fig. 15, because juvenile females moulting in their second autumn cannot be distinguished from older females, but the five juvenile males are indicated.

Length of time taken to moult

The trapping of five individuals twice, and two three times, in the course of a single moult, showed that, except for the innermost and outermost primaries, two or three of which drop more or less together, the primaries drop at intervals of 8 to 10 days, and that the complete replacement of the primaries takes about 80 days. The total period from the dropping of the secondary major coverts to the completion of the growth of the last wing-feather must take a few days longer.

Observation at the display ground provided an independent assessment of the length of time taken to moult. It has already been mentioned that the males are usually present at all times except when moulting. Their disappearance before moulting and reappearance afterwards are quite sudden, and in nine cases the period of absence was known accurately to within a few days. All were between 76 and 85 days.

The moults of juveniles

Mainly in their first autumn and winter, juveniles undergo an apparently prolonged moult which is not heavy at any time, involving the head, body, lesser coverts and, at least sometimes, some of the inner secondary major coverts. All but 4 of the 35 records of this moult were in the months August to January.

In their second autumn the moult to adult plumage takes place. Unless the past history of the individual is known, this moult is recognizable only in the male, since the female and juvenile plumages are the same. What follows therefore concerns only the males.

The moult to adult plumage takes place rather earlier than the subsequent moults, being usu-

ally complete by the end of October and often by the beginning of September. The most extensive information comes from field observations of 20 young males which were seen when in juvenile plumage, most of them for the last time in June, and then again when they had completed their moult into adult plumage, at which time they are rather conspicuous as they display persistently and try to establish themselves at display grounds. Fifteen of these birds had completed their moult by the end of October, four of them as early as mid-September. It was not of course certain that they were seen as soon as they had completed their moult, so these dates are the latest possible. More exact but less abundant evidence comes from the trapping of five males during their moult into adult plumage, as shown in Text-fig. 15.

Annual variations in the moulting season

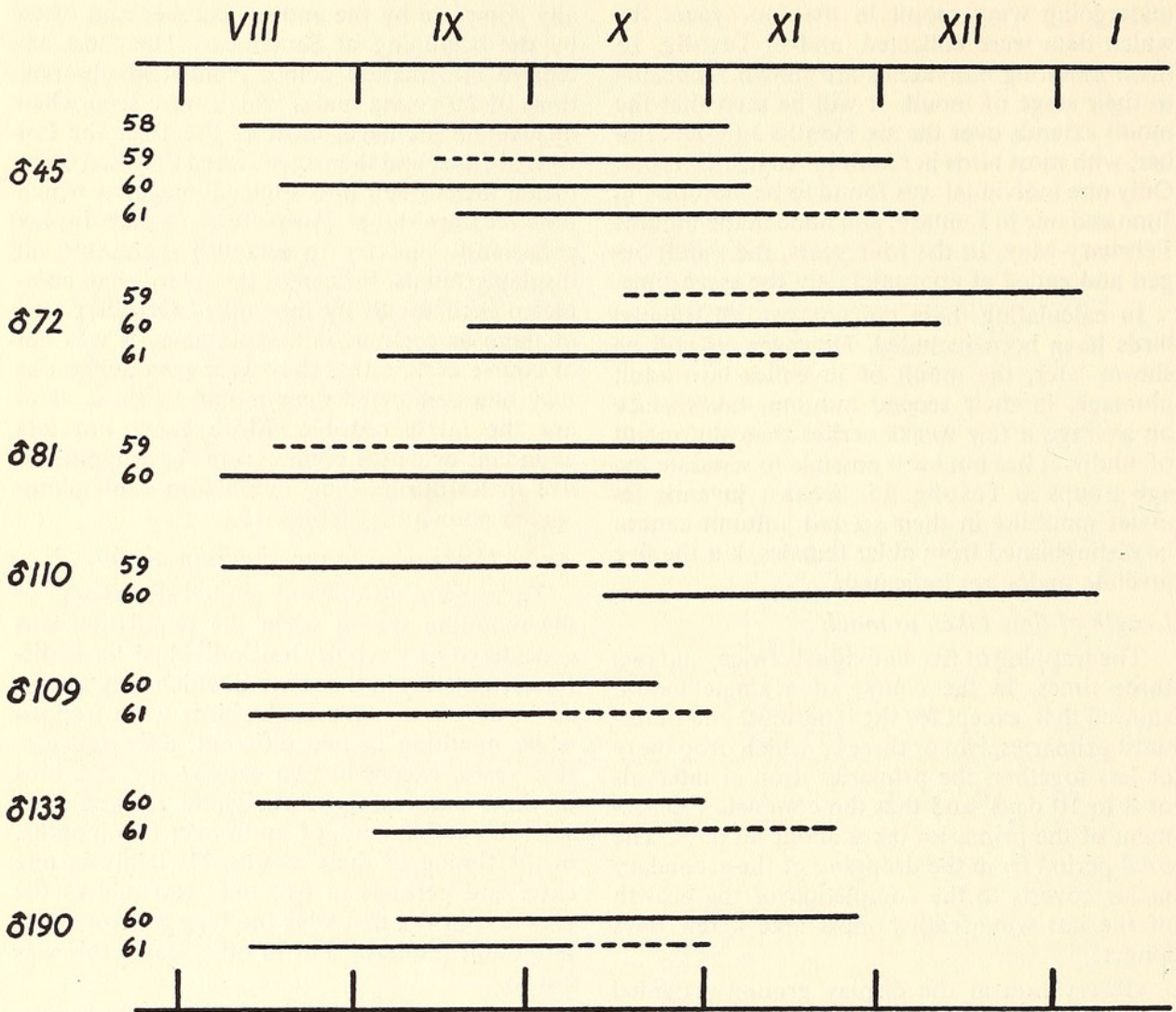
There were no obvious annual differences in the moulting season when the population was considered as a whole, but individual birds differed markedly in the times at which they moulted in different years. Eight birds were trapped while moulting in two different years (successive years, except in two cases), and one bird in three successive years. These showed considerable differences, of up to over two months, in the timing of their moults. Certainly in one case, and perhaps in two, this was due to the fact that in the first year the bird was moulting into adult plumage, but in other cases this was not so.

Observations at the display ground showed the same thing. The moulting periods of five adult males were found in two successive years, one in three successive years, and one in four successive years. These showed considerable variations from year to year which could not be attributed to the age of the bird (Text-fig. 16). The cause of these variations is considered in the next section.

ENVIRONMENTAL FACTORS AND THE ANNUAL CYCLE

In view of the annual variation in the breeding season and the relative fixity of the moult, it seems likely that the manakins' annual physiological cycle is, as it were, anchored to the yearly cycle of the seasons by their response to environmental factors initiating the moult. Consideration of the juveniles strengthens this supposition. Young birds may leave the nest in any month from January to October, yet all, as far as known, moult into adult plumage in the months June-September of the year following their year of birth.

In seeking the external regulator which year



TEXT-FIG. 16. Moulting periods of seven males in successive years. Broken lines indicate that the beginning or ending of a period was not exactly known.

after year maintains the timing of the birds' physiological cycle, keeping all the individuals more or less synchronized, we cannot consider the Black and White Manakin in isolation. Almost all other Trinidad birds, so far as known, sea birds, swamp birds and land birds, moult at approximately the same season as the Black and White Manakin (Snow & Snow, in preparation. 2). and this is of course the moulting season of northern hemisphere birds generally. It is most reasonable to suppose that the same external regulator is operating for all of them, and that this regulator is day-length, even though in Trinidad, at 10° N., the annual variation in day-length is only 74 minutes.

If day-length is the main regulator, other more variable environmental factors may still exercise important modifying or secondary effects on the timing of the different phases of the annual cycle. The data are not inconsistent with the hypothesis that the ending of the breeding

season and the start of the moult are in fact partly controlled by the onset of the wet season, though they do not follow for several weeks. The wet season began on the following dates in the four years for which there was information on the moult (parentheses indicating heavy rainfall followed by a further dry spell):

1958—April 29
 1959—(April 9), May 22
 1960—April 20
 1961—May 22

The trapping data do not show any appreciable differences in the time of moult in these four years (Text-fig. 15), but the samples are not large and they are composed mainly of different individuals. The data on moulting dates of the same individuals over successive years show a more consistent pattern, though here again, as would be expected, there are inconsistencies. The date of moult was known for four individuals in both 1958 and 1959: all moulted

later in 1959. The dates were known for eight individuals in both 1959 and 1960: six of them moulted earlier in 1960 than in 1959. The dates were known for five in 1960 and 1961: three of them were later in 1961 than in 1960. (One individual, whose first moult was from juvenile to adult plumage, has been omitted). Thus of 17 annual differences in date of moult, 13 agreed with the differences in the date of onset of the wet season. The data for ♂ 45, the only bird whose moulting dates were known in all four years, agree exactly with the weather data (Text-fig. 16). Clearly more records would be needed, for more individuals and more years, for an adequate test, but these data are at least suggestive.

The environmental factors concerned in the onset of breeding are still obscure. Of most obvious apparent importance is the weather. The period from January to late May, during which breeding may begin, is generally dry except at the end, when heavy but irregular precipitations may occur. Towards the end of this period, in April and May, especially if there has been little recent rainfall, the ground becomes extremely parched, even in the forest, and the leaves of many herbs, shrubs and even large trees wilt. In such a case, the first heavy rainfalls stimulate many birds, including manakins, to build nests and lay eggs (as also in northern Venezuela, a short distance to the west of Trinidad; Gilliard, 1959). This occurred in 1959, when heavy rain on April 9-10 was followed by an outburst of nest-building and the first manakin eggs were recorded on April 20. But in 1957 heavy rain at the end of April had no effect, while in 1958 breeding began at the same time as in 1959 although there had been no heavy rain for several weeks. The early start in 1961 might be attributed to the weather in January and February, which was wetter than usual, but the very early start in 1960 took place before the dry season had properly begun and cannot be easily attributed to weather.

Once the breeding season has started, fluctuations in activity may be pronounced and some of these were certainly due to weather. Thus in 1961, after an early start, with steady nesting from February to the end of April, there was an almost complete cessation in May, followed by a great outburst in early June. The second half of April and most of May were exceptionally dry in this year, and it was not until May 22 that heavy rain fell.

Clearly other factors besides weather must contribute to the timing of the breeding season. Some observations suggest that fluctuations in the availability of food may play a part in some years. As will be shown later (p. 93), fruit grad-

ually becomes more plentiful from January to April; in the first three months of the year the number of species of Melastomaceae in fruit is at its lowest, and annual variations in the fruiting seasons of the various species may result in temporary gaps, when no species is in fruit. It seems probable that such annual variations in the food supply during this period may help to determine whether the manakins start breeding early or late. The only marked food shortage was recorded in March, 1959. In mid-March there was a sudden decrease in activity at all the display grounds visited in the Arima Valley. The courts were deserted and became covered with leaves. No Melastomaceae were found in fruit—an exceptional situation, to judge from later observations—and manakins visited the guava trees in our garden and even fed on the fallen fruit. This situation lasted two or three weeks, after which display was resumed and returned to normal. As mentioned above, there was rain on April 9-10 and nesting began soon after.

In the winter 1960/61 there was an even longer period of cessation of display. Activity declined at all display grounds in December and at the main display ground under observation several males which had returned after finishing their moult disappeared again. The cessation of display by *Pipra erythrocephala* was even more complete. Display was gradually resumed during January and was normal by the end of the month. The data from the Arima Valley alone suggested a correlation between this cessation of display and food shortage. The great crop of Matchwood (*Didymopanax*) fruit, which is an important part of the manakins' food in November and December, was nearly at an end, while two important melastomes, *Miconia kappleri* and *M. myriantha*, had also recently finished, after a good crop. Another melastome of importance at this season, *M. guianensis*, was not yet ripe. There was in fact a gap in the sequence of the main fruits. However, during the same period *Pipra* ceased displaying equally completely in a locality 6 miles away on the north side of the Northern Range, in an area of forest where food was abundant. These observations emphasized the danger of generalizing from the situation in one locality only.

The problem of the start of breeding in the Black and White Manakin becomes clearer when it is considered in a wider context. There is a common pattern to which the annual cycles of most Trinidad land birds conform (Snow & Snow, in preparation. 2). As already mentioned, the months from July to October or November are occupied by the moult. After the moult,

there may be a minor peak of breeding, followed by a decline in December and then a gradual increase in breeding activity to a peak in April-June. Seen against this common pattern, the situation in the Black and White Manakin may be better understood. Immediately after the moult there is no actual breeding, though males display hard and females pay preliminary visits to the display grounds. From the end of December onwards the readiness to breed gradually increases. Early in this period of increasing readiness, especially good conditions of weather, food, or perhaps other environmental factors not obvious to the observer, are necessary to stimulate breeding. Later, nesting may be stimulated by quite slight environmental changes as long as the weather is not too dry. Towards the end of the dry season, if the drought has been severe, the onset of nesting, or its resumption after an earlier start, depends upon and follows quickly after the first heavy rainfall. Whatever the initiating factors, the start is abrupt, involving many birds at the same time, almost certainly due in part to the intense social stimulation to which manakins are exposed both at and away from the display grounds.

It must be emphasized that the details of the breeding seasons, as shown in Text-fig. 14, apply only to the Arima Valley. Visits to an area of more humid forest 10 miles to the east showed in each of three years that breeding began earlier than in the Arima Valley, in one year several weeks earlier. The difference was probably due to the different climate, and suggests a reason for the variable breeding season in the Arima Valley. Rainfall decreases steadily from east to west along the Northern Range. Concomitantly, towards the west, with an increasingly severe dry season there is an increasing tendency for birds to delay breeding until the wet season begins. In the Arima Valley, half way along the range, it appears that environmental factors favoring early or late starts are nicely balanced; hence the great variations in different years.

NESTING

THE FEMALE AND HER TERRITORY

The age at which the females start to breed was not determined. Juvenile females were seen visiting display grounds when they were not more than five months old, but no information was obtained on the first nesting of a color-ringed bird. The only female of known age found nesting was nearly three years old.

Breeding females occupy small territories along the streams and gullies where most of the nests are found. Soon after the moult is over they advertise their presence by persistently call-

ing the monosyllabic "peerr"; this behavior then declines, to be renewed again as the breeding season approaches. A few observations of aggressive behavior between two females at what appeared to be territory boundaries suggested that the territories are defended against neighboring females, but competition for a nesting territory does not seem to be intense. Territories are small and probably highly compressible, as occupied nests may be found within a few yards of each other. As mentioned earlier (p. 78), nests along the same stretches of stream tend to be more closely synchronized with each other than with nests along other streams, probably because the females visit the same display ground in company.

Although the females' wing-feathers are unmodified, in aggressive encounters with other females and in the presence of intruders near the nest they may give typical male displays, but with softer sounds. The beard is protruded, though the feathers are not very long, and little jumps may be made from perch to perch, each accompanied by a soft "snip." Occasionally they may make a soft "rolled snap."

Observations were made on 14 color-ringed females nesting along the section of stream that was most frequently watched, and on two nesting further afield. In general these birds remained, and so far as known nested, within the same small area during the period of observation. One bird remained in the same territory for 3½ years, and others for shorter periods. There were two known cases of change of territory. One of these birds was found nesting, within an area of about 40 by 20 yards, once in 1958, probably in 1959 (behavior suggesting nesting, but nest not found), and twice in 1960. Half way through the breeding season of 1961 (whether she had already attempted to nest or not was not known), she shifted 320 yards upstream, where she was found nesting for the fourth time. The other bird also shifted in the middle of the breeding season, in this case only 150 yards.

THE NEST

The nest is built within a few feet of the ground, usually at a height of between 1½ and 5 feet. It is of typical manakin type, a rather thinly woven shallow cup, slung between horizontal supports. A large number of nests (38% of the total) were slung between two side frondlets of a fern frond, and most of the others were slung in forks between the side twigs of small saplings or shrubs. Over 95% of all the nests found were on or near the banks of streams or gullies, many of them overhanging the water.

The outer cup of the nest is made of rootlets and black fungal hyphae (probably *Marasmius* sp.; see Sick, 1957), with occasionally a few dead leaves. Some of the rootlets used are very long (29 inches in one case), and being wound round and round, inside and outside the supporting twigs, they bind the nest firmly to its support. A little cobweb is also used to secure the nest to its supporting twigs.

The lining is of different material. The great majority of all nests examined were lined with the branching panicles of *Nepsera aquatica*, a small herbaceous member of the Melastomaceae. The rich brown stalks of these panicles are very fine, smooth and shiny; each of the branches into which they are subdivided ends in a small fruit capsule. Due to the branching and to the terminal capsules, they adhere to each other when interwoven so that if pulled out the lining usually comes away from the rest of the nest intact.

Nepsera aquatica grows along forest edges and road-sides, not in the forest itself. In spite of this, it was the usual nest-lining of nests found well within the forest as well as those nearer the edges. At the main trapping place on the edge of secondary forest, six females were trapped carrying nest-material in the 1961 breeding season, and in every case it was *Nepsera aquatica*. In spite of regular searching in the neighboring secondary forest towards which they were flying when trapped, none of the nests of these six birds was found, which suggested that most of them at least were flying some distance with the nest-material, as indeed it is clear that many birds must nest far from a forest edge. No birds were trapped carrying nest-material in other years, suggesting that *Nepsera* was unusually scarce elsewhere in 1961.

Unfortunately the identity of the nest-lining was not discovered until late in the study. Incomplete observations made subsequently suggested that *Nepsera* flowers mainly in the dry season, from December to April, and that the dead or fruiting panicles are mainly available from March to August. In support of this suggestion, it was several times noted that early nests were lined with other less suitable material, sometimes finely branched dead grass-heads. But observations on this point were inadequate to show whether the availability of *Nepsera* could be a factor in the timing of the breeding season, and the point requires further study.

For three nests an interval of four days was recorded between the beginning of building (a few strands only in place) and nest completion, and for seven others intervals of 5-7 days were recorded. Nests sometimes remain half com-

pleted for days, apparently because the female is not ready to lay.

INCUBATION AND FLEDGING

Detailed observations from a hide were made at only one nest. These are the basis of the account of behavior at the nest given here. The rest of the data in this section were obtained in the course of repeated visits to many nests.

The clutch, normally of two eggs, is usually laid soon after the nest is complete. In every case in which there was information on the point, the second egg was laid two days after the first. Though visits were not usually frequent enough to give an exact time of laying, the time of laying of eleven eggs was known within a few hours and all were laid round the middle of the day, mostly between 1000 and 1400 hours, none being earlier than 0750 or later than 1545.

Apparently complete clutches of one egg are not rare. The clutch was regarded as complete when the number of eggs present remained the same for three days or more and the bird was known to be incubating. Of the 244 complete clutches thus recorded, 22 consisted of only one egg.

The female does not usually sit until the second egg is laid. Thereafter she is regularly on, except for periodic absences during which she must feed. At the nest under observation from a hide, during three hours' watching in the morning in fine weather, three days before the eggs hatched, the female sat for 71% of the time. Two completed periods on the nest lasted 46 and 53 minutes, and two recesses lasted 14 and 26 minutes. As incubation proceeds, the female sits more and more tightly. Early in incubation she usually flies from the nest when the observer is still several yards away; in the last two or three days before hatching she usually remains on the nest until the observer is very close and then flutters away close to the ground giving distraction display.

The incubation period (from the laying of the second egg to the hatching of the second young) was ascertained at seven nests to be $19 \pm \frac{1}{2}$ days and at two nests to be $18 \pm \frac{1}{2}$ days.

The young hatch with a thin covering of down. At the nest under observation, when they were one day old they were brooded for 34% of the time during a watch of nearly two hours in the morning. When they were five days old they were brooded for 41% of the time during a watch of one hour 40 minutes, but the next day they were not seen to be brooded at all. They are generally very silent. Small nestlings utter soft cheeping calls audible for only a few feet; no calls were heard from large nestlings.

The young are fed by regurgitation, mainly on fruit with a small proportion of insect food. The bird under observation from a hide normally arrived with no food in the beak, perched on the edge of the nest, and produced a succession of fruits which she would give to the two young alternately. The feeding rate was recorded on five days and showed a steady increase, from one feed every 28 minutes when the young were one day old to one feed every 18 minutes at 13 days.

Like the adults, the nestlings are capable of swallowing surprisingly large fruits. At the nest under observation, some of the fruits brought to the young were not only very large but consisted mainly of a large seed only partially enclosed by a small aril. After swallowing the fruit the young regurgitate the larger seeds, and nests with young are often found to have one or two seeds lying in the nest-cup. At the nest under observation, the female picked up these seeds and usually swallowed them, but occasionally carried them away. She also swallowed the faeces of the young up to the tenth day; on the thirteenth day she sometimes swallowed them, and sometimes the young defaecated over the nest-edge.

Thus as the young grow larger an accumulation of regurgitated and defaecated seeds, together with a few insect hard-parts, spatters the ground and leaves below the nest. Examination of many of these piles of remains, as well as observations from the hide, showed that the young are fed on the same fruits as the adults themselves eat, except for some of the largest kinds.

The young remain in the nest for 13-15 days. For six nests with two young the periods were: 13 and 14; 14; 14; 14; at least 14; 14 and 15 days. For two nests with one young the periods were 13 and 14 days.

After they have left the nest the young are extremely difficult to see. They perch in low vegetation, move little, and either do not call or call very seldom. Later they accompany the female but are still not easy to locate because

they are so silent. It was remarkable that the juvenile's begging call, a loud and distinctive "weeee-e-e," rather plaintive and slurred at the end, was only heard on one occasion, from two full-grown juveniles accompanying a female. Thus little information was obtained on the post-fledging period by direct observation, but data on the interval between the fledging of young and the start of the next clutch (Table V) suggest that the young are attended by the female for three or four weeks.

BREEDING SUCCESS AND REPRODUCTIVE RATE

In calculating nesting success, only those nests have been used that were found before the clutch was complete; most were in fact found while they were being built. (For a discussion of the bias introduced if nests found at a later stage are included, see Snow, 1955). In this way we can obtain figures for the percentage of all nests started (*i.e.*, in which eggs were laid) that reached the hatching and fledging stages, and for the number of young produced for each nest started. Table II summarizes the results of the five seasons' observations.

Like other tropical forest birds (Skutch, 1945), *M. manacus* has a very high rate of nest failure. Combining all the years, 40% of all nests started reached the hatching stage, and 19% produced fledged young; each nest started produced an average of 0.33 fledglings. There were considerable differences between the years, but the significance of these is uncertain. Analysis by months shows that late nests were considerably more successful than early nests (Table III).

Most nests fail early, apparently through predation (Table IV). Predation also falls heavily on the 40% that reach the nestling stage. In all, 86% of all nest losses were attributed to predation. In nearly every case predation can only be presumed, as there was no evidence except a clean, empty nest. Indirect evidence suggests that the chief predators are snakes, of which there are several known or potential egg-

TABLE II. BREEDING SUCCESS

| Year | Number of nests | Reached hatching | Reached fledging | % reaching fledging | Number of young fledged |
|-----------|-----------------|------------------|------------------|---------------------|-------------------------|
| 1957 | 29 | 18 + 3? | 12 | 41 | 22 |
| 1958 | 19 | 3 | 3 | 16 | 5 |
| 1959 | 30 | 7 + 2? | 4 | 13 | 8 |
| 1960 | 79 | 39 + 11? | 18 | 23 | 28 |
| 1961 | 70 | 13 + 6? | 7 | 10 | 11 |
| All years | 227 | 80-102 | 44 | 19 | 74 |

Note. Queries in the hatching column indicate that the nest failed just before or just after hatching, the exact time not being known.

TABLE III.
ANALYSIS OF BREEDING SUCCESS BY MONTHS

| Month | Number of nests | Reached fledging | Number of young fledged | Number of young per nest |
|-------|-----------------|------------------|-------------------------|--------------------------|
| Jan. | 6 | 0 | 0 | } 0.14 |
| Feb. | 16 | 2 | 3 | |
| Mar. | 14 | 2 | 4 | } 0.13 |
| Apr. | 34 | 2 | 2 | |
| May | 43 | 10 | 17 | } 0.35 |
| June | 63 | 11 | 20 | |
| July | 25 | 9 | 15 | } 0.55 |
| Aug. | 26 | 8 | 13 | |

eating species frequenting low growth in the forest. The fact that no traces of chewed egg shell were ever found in or near a nest seems to rule out small mammals as important predators. Neither have birds been implicated. The toucan *Ramphastos vitellinus*, the only Trinidad representative of a family known to be nest-robbers (Skutch, 1944), rarely comes within 20 feet of the ground. The large cacique *Psarocolius decumanus* and the larger flycatchers may occasionally rob nests, but there was no evidence that any of these could be important nest-predators near ground-level in the forest.

Frequently nests are found not only empty but partly dismantled only a day or two after they had been occupied. This is not however due to a predator. The nest-material is much in demand, not only by other manakins but by the flycatcher *Pipromorpha oleaginea*, so that abandoned nests may soon be reduced to a mere framework.

Inadequate construction or support of the nest caused 6% of all the failures. In particular, nests are sometimes slung between side-fronds of a fern which after a time wither, so that the

TABLE IV. CAUSES OF NEST FAILURE

| Cause of failure | Number of nests |
|-------------------------------------|-----------------|
| Eggs predated | 105 |
| Eggs deserted | 3 |
| Eggs lost through collapse of nest | 11 |
| Eggs or small young predated | 24 |
| Young predated | 29 |
| Young lost through collapse of nest | 1 |
| Nest flooded | 7 |
| Tree fell on nest | 1 |
| Human disturbance | 2 |

nest tilts and the eggs or young fall out. Natural catastrophes were the only other regular cause of failure (4% of the total); in several cases nests placed low over streams were flooded or swept away after heavy rain, and once a nest was destroyed by a natural tree-fall. Loss by flooding was the only cause of failure which showed seasonal variation; all cases occurred in the wet months June-August.

Reproductive rate

Individual females nest more than once in the course of the long breeding season, but it is not easy to find out the average number of nesting attempts made by each bird. Observations at the display ground showed that known females visited and displayed with the males at intervals throughout the beeding season, but were too few to throw any certain light on how many times a single female attempted to nest in the season. More satisfactory information comes from observations on the repeated use of the same nests.

As already mentioned, the females usually occupy fixed territories throughout the breeding season. Thus when a nest is used more than once, or when a new nest is built within a few feet of the site of a previous one, it is likely that the same female is involved. Also, in such cases the intervals between the ending of one nesting attempt and the laying of the next clutch show certain consistencies (Table V), which further supports the belief that the same bird is involved. Fortunately, repeated use of the same nest or nest-site is rather common.

TABLE V. INTERVALS BETWEEN BROODS

| | Number of days between end of one breeding attempt and laying of first egg of next clutch | | | | |
|-----------------------------|---|-------|-------|-------|-----|
| | 0-10 | 11-20 | 21-30 | 31-40 | 41+ |
| After loss of eggs or young | 4 | 10 | 5 | 5 | 7 |
| After successful fledging | — | — | 3 | 4 | 1 |

In 1957 and 1958, when the breeding seasons were rather short, 11 nests or nest-sites were used twice. In 1960, with a very long breeding season, 12 nests or sites were used twice, 3 three times, 2 four times, and there was a single case of a succession of five nestings in two nests, the second nest, which was used twice, being built within a few feet of the first, which was used three times. In 1961, with a fairly long breeding season, 11 nests were used twice and 3 three times.

These observations suggest that two to four nesting attempts during the breeding season are usual, two being commoner in a short season and three or four occurring more often in the longer breeding seasons. If three is provisionally accepted as the average number, then, with each nest started producing on average 0.33 fledglings, each female will on average rear approximately one fledgling a year.

In the years 1957-60 15 nestlings were ringed along the section of stream where intensive trapping was carried out, and all, as far as known, left the nest successfully. Of these, four were later trapped and became fully adult (*i.e.*, reached their second autumn) and a fifth was seen several times, up to nearly a year after it had left the nest. The other ten were never trapped nor seen. Though a small sample, this suggests that at least one-third of the birds which leave the nest survive to become adult. Thus if each breeding female rears on average one fledgling a year, she will contribute on average 0.33 to the next year's adult population.

FOOD

FEEDING HABITS

The Black and White Manakin is predominantly a fruit-eater, taking a great variety of fruits from trees, shrubs and even low herbs. Typically the bird makes a rapid sally from its perch, plucks a fruit in flight, lands with it in its beak, and then swallows it whole. But fruits are sometimes plucked from a perched position if they are accessible. Manakins do not hop about to feed, nor do they cling to the bunches of fruit on which they are feeding, as do the tanagers and honeycreepers which are often seen feeding with them.

Almost all the fruits eaten are small berries, but a few exceptions were noted. Sometimes pieces are plucked from the fruiting catkins of *Cecropia peltata*, sections are taken from the compound fruit of the introduced rubber tree *Castilloa elastica*, and during the period of food shortage mentioned earlier manakins came down onto the ground and fed on fallen fruits of the cultivated guava (*Psidium guajava*).

They have a wide gape and can swallow very large fruits for their size. They often have to "juggle" large fruits in the beak for some time before they can swallow them; probably the fruit is softened during the process and so made easier to swallow. With the largest fruits of all, this juggling may go on for a minute or more, while it seems to the observer that the bird cannot possibly succeed in getting the fruit down. The three largest fruits that manakins were seen eating, after much juggling, were the following:

Coussarea paniculata (Rubiaceae), length 19, diameter 16 mm.; *Protium guianense* (Burseraceae), length 15, diameter 11 mm.; and *Cordia lockhartii* (Boraginaceae), length 15, diameter 10 mm. Undoubtedly the wide gape is of great importance to the species in making available a greater range of fruits than could normally be eaten by such small birds. Thus Black and White Manakins can feed on fruits that cannot be eaten by considerably larger birds such as the tanagers *Tangara mexicana* and *T. gyrola*.

A small quantity of insect food is taken, also in flight. Not uncommonly manakins follow army ants and take the insects disturbed by them, plucking them in flight from a leaf or tree trunk. Occasionally a manakin is seen, when feeding on berries, to pluck a small object, probably a resting insect or spider, from the underside of a leaf. When termites swarm after the heavy rains which bring the dry season to an end, manakins hawk for them from exposed tree-top perches, as do many other birds.

A greater proportion of insect food is fed to the young than is eaten by the adults themselves. Thus insect remains were found in eight of 15 food samples collected from below nests with young, but in only four of 93 samples collected from display grounds. Nearly all the insect remains consisted of hard parts of the imagines of small Coleoptera and Diptera; remains of a small damselfly (Odonata, Zygoptera) were also found in three of the samples. The fact that insect larvae were never found in the samples may not be significant in itself, as they would probably not be distinguishable among the food debris. However, the birds' behavior when feeding suggests that they would rarely be taken.

Black and White Manakins drink regularly from the water that collects in the large colored bracts of the abundant banana-like plant *Heliconia* cf. *wagneriana*. Less often, they drink from streams.

COMPOSITION OF THE FOOD

Altogether, Black and White Manakins were seen feeding on the fruits of 66 species of plants (40 trees, 13 shrubs, 7 vines, 6 others), of which 4 (3 trees, 1 vine) remained unidentified. Collections of seeds from display grounds and below nests brought the total to 105 species, of which 32 remained unidentified. Most of the unidentified species were represented by only a few seeds, and comprised a very small fraction of the total food. The identified fruits, and the months in which they were found to be eaten, are listed in Appendix 2.

As already noted, one family of plants, the

Melastomaceae, is of especial importance. 47% of all records of manakins observed feeding were from Melastomaceae. All except nine of the 108 samples collected from display grounds and below nests contained melastome seeds, which often far outnumbered everything else; seven samples contained only melastome seeds. Records were obtained of manakins feeding on at least 17 species of melastomes, nearly all of them trees and shrubs of the genus *Miconia*. Several other less common species were probably fed on. The berries of these melastomes contain large numbers of very small seeds which show little difference between the species. Except for one species with unusually large seeds, they were not distinguished in the samples collected from display grounds and below nests.

The family Rubiaceae was easily second in importance to the Melastomaceae. At least 15 species of this family were found to be eaten, and 14% of all observations of birds feeding were from them. The remainder of the identified food plants belonged to a variety of families, with few species in each. The Euphorbiaceae and the Moraceae, both with 4 species, were the most important tree families in number of species. The greatest number of records for single tree species were from *Didymopanax morototoni* (Araliaceae) and *Ficus clusiifolia* (Moraceae).

Records were obtained from a variety of smaller plants, the only apparent requirement being that they should bear fleshy berries of the right size. Among these were aroids of the genera *Monstera* and *Philodendron*, *Costus spiralis* (Zingiberaceae), *Stromanthe tonckat* (Marantaceae), two species of *Heliconia* (Musaceae) and the grass *Lasiacis sorghoidea*. There were no records of manakins feeding on the fruits of aroids of the genus *Anthurium*, the epiphytic cactus *Rhipsalis*, or any of the mistletoes. They are all common, and were fed on by some other fruit-eating birds. They are translucent berries, with a rather tough skin enclosing a sticky pulp, and perhaps are not easily digestible by manakins.

The Melastomaceae.—Trees and shrubs of the genus *Miconia* are a conspicuous feature of the secondary vegetation of the Arima Valley. They also occur, but not so abundantly, in primary forest. They range in size from shrubs a few feet high to 70-foot trees, but apart from their size they are all rather similar in appearance and all bear, in conspicuous terminal panicles, roundish berries which are from 3 to 10 mm. in diameter and contain numerous very small seeds embedded in pulp. Three other genera of melastomaceous shrubs, *Clidemia*, *Conostegia*

and *Platycentrum*, have similar fruits, but as food for manakins, at least in the study area, they were of minor importance. There was also one record of a manakin picking pieces from the much larger fruit of a melastomaceous tree of the genus *Henriettea*.

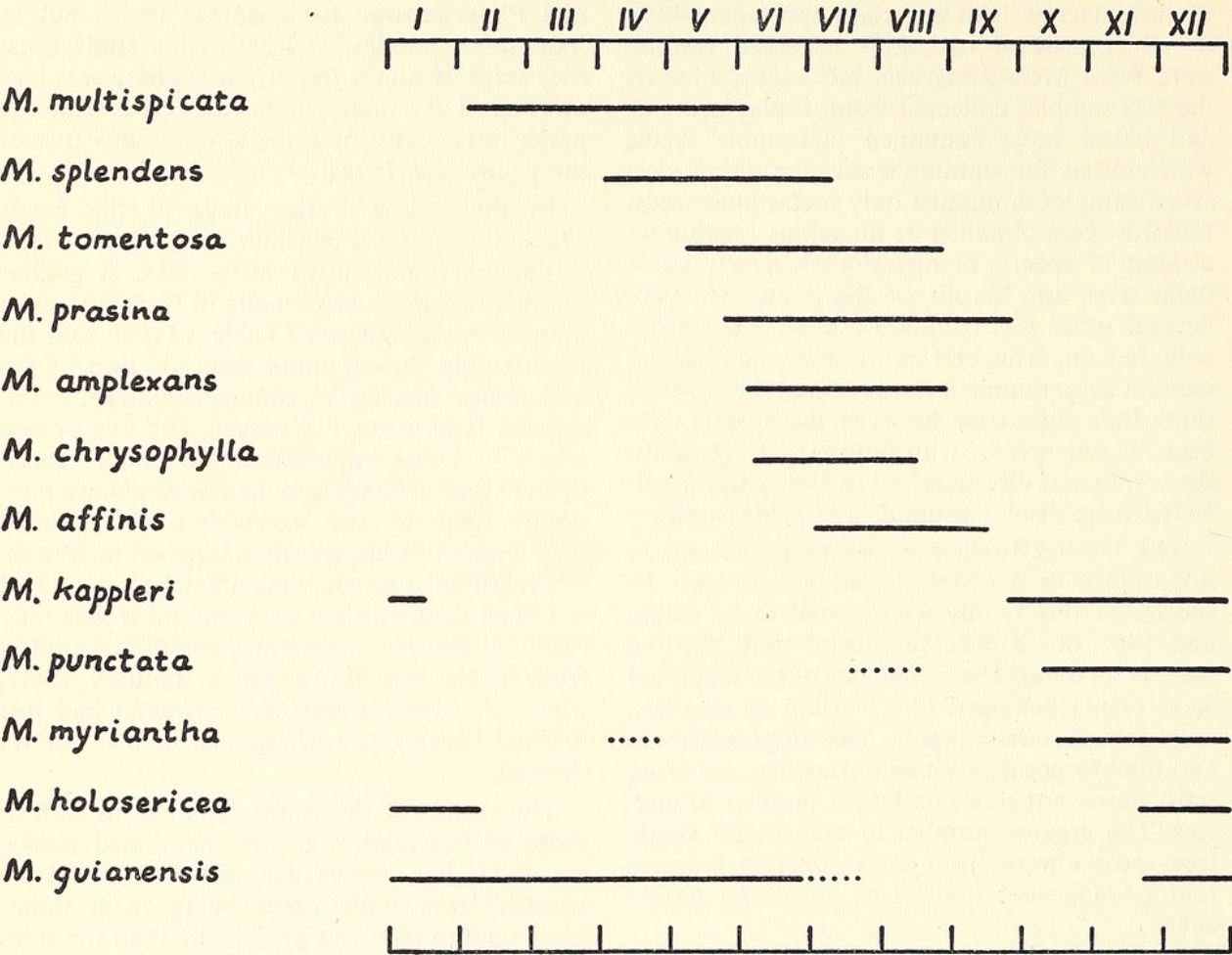
In the Arima Valley trees of the genus *Miconia* produce a constant succession of fruit throughout the year (Text-fig. 17). A greater number of species are usually in fruit in the wet than in the dry season (Table VI), so that the food supply then is more assured. Two of the commonest species, *M. guianensis* and *M. multi-spicata*, fruit in the dry season, and one or two others of lesser importance, but annual variations in their fruiting seasons can produce a temporary gap in the succession. As already mentioned, this apparently happened in March, 1959, but unfortunately the different species had not been distinguished by then and it was only recorded that no melastomes could be found in fruit. There was also a gap in January, 1961, when *M. kappleri* and *M. myriantha* had just finished fruiting and *M. guianensis* had not yet ripened.

The shrubs of the genus *Miconia*, as well as those of the related genera mentioned above, are of far less importance, only 4% of all the records from melastomes being from them. They tend to fruit less prolifically than the trees and to spread their fruiting over a longer period. Thus few berries are available on one plant at one time, and manakins do not pay much attention to them when the more abundantly fruiting trees are available. They fruit more in the wet season than the dry (Table VI).

The Rubiaceae.—In the forest a large number of the small trees and shrubs belong to this family. The identification of some of them is not easy, and a few more than the 15 recorded species may have been involved. Like the melastomes, many of them bear fruit conspicuously in terminal panicles. Their fruits are more diverse in appearance, many of them being rather larger than those of the melastomes. They contain in most species one or two, in a few species several, seeds embedded in pulp; some species have arillate fruit. Like the melastomes, the tree species have mainly well-defined fruiting seasons, while the shrubs fruit over a long period but mainly in the wet season. Thus they also provide a more or less continuous food supply throughout the year, but far less abundantly than the Melastomaceae.

AVAILABILITY OF FOOD THROUGHOUT THE YEAR

Text-figure 18 shows that there were well-marked seasonal changes in the numbers of



TEXT-FIG. 17. Fruiting seasons of *Miconia* tree species, Arima Valley, October 1959 to September 1961. (Since most of the species did not fruit at exactly the same time in the different years, the fruiting periods for any one year were mostly a little shorter than shown.)

kinds of fruit recorded as taken in the different months, with a marked peak in April and a minor one in November-December. But the high figures in the period February-July are partly caused by the inclusion of samples collected from below nests, which included various small seeds not found at the display grounds and perhaps taken because the small berries containing them were specially suitable as food for nestlings. A truer picture of the variety of food available is probably presented by Text-fig. 19, which shows the average number of different kinds of fruit in the collections made at display ground A, and thus eliminates variation due to locality and the requirements of nestlings. Again

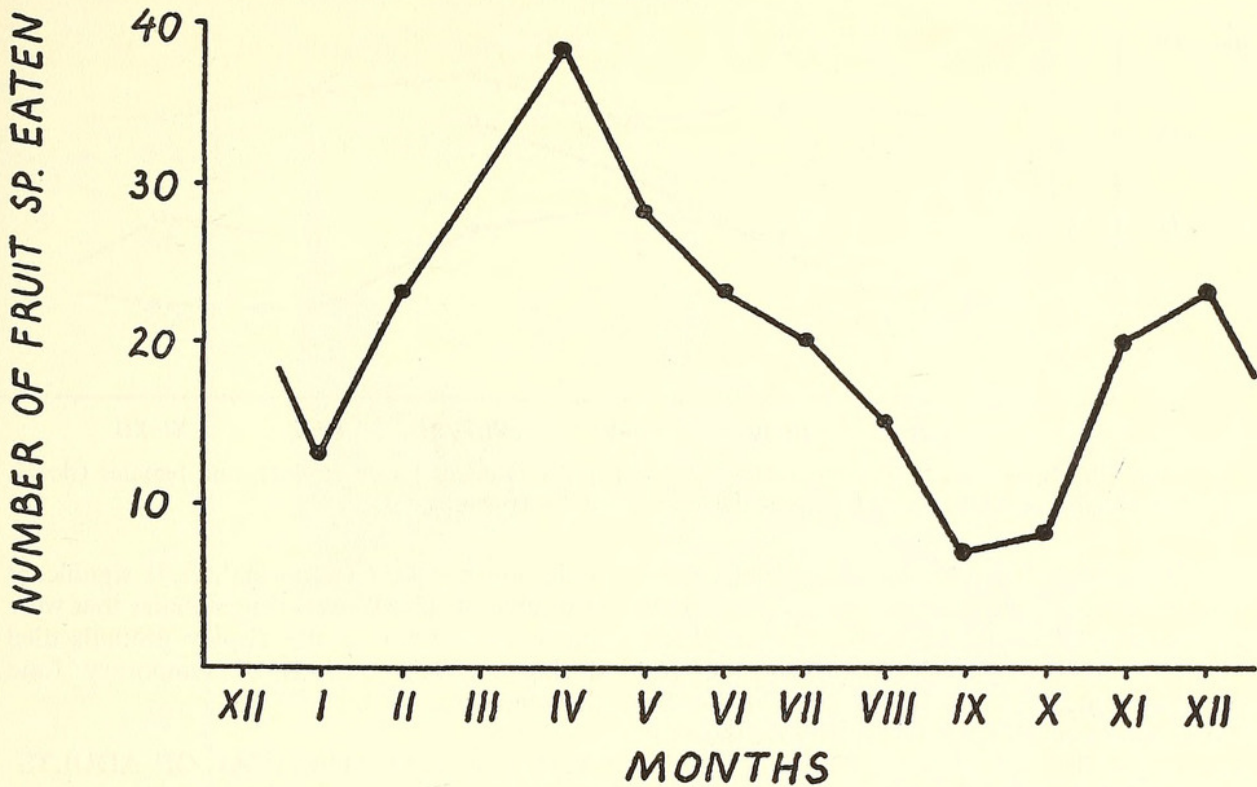
the figure shows that there was a steady increase in variety from January onwards, with the greatest variety between March and June and the least from August to October. It has already been shown that the date at which breeding starts is variable, ranging from early January to late May. In relation to the food supply, it starts at some time in the period when the variety of food available is steadily increasing. Food conditions are by no means the same in each year, and it seems reasonable to suppose that their variation may affect the time at which breeding starts.

Though no quantitative assessment of insect food has been made, it appears almost certain

TABLE VI. NUMBER OF SPECIES OF MELASTOMACEAE IN FRUIT IN DIFFERENT MONTHS

| | Jan. | Feb. | Mar. | Apr. | May | June | Jul. | Aug. | Sep. | Oct. | Nov. | Dec. |
|--------|------|------|------|------|-----|------|------|------|------|------|------|------|
| Trees | 3 | 3 | 3 | 3 | 5 | 8 | 7 | 5 | 3 | 4 | 6 | 6 |
| Shrubs | — | — | — | — | 2 | 4 | 4 | 5 | 5 | 5 | 3 | 1 |

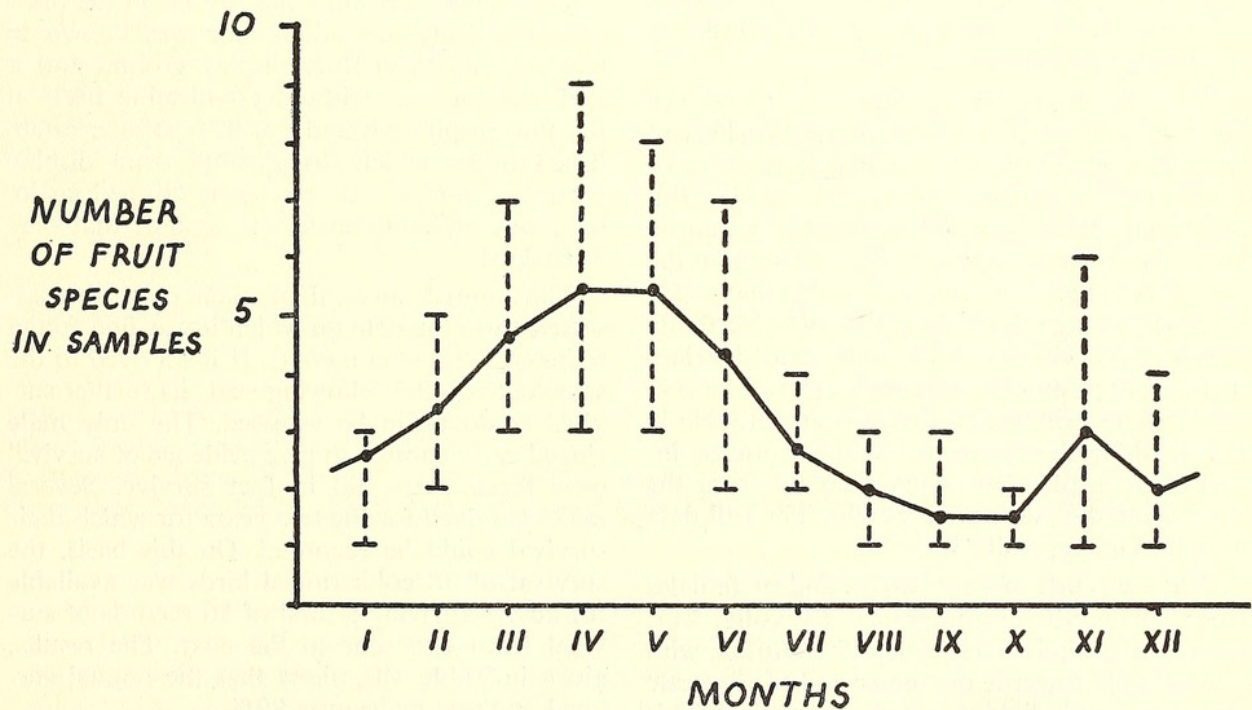
Note. Especially in the shrubs, there is a little out-of-season fruiting. This has been omitted; figures indicate regular and abundant fruiting.



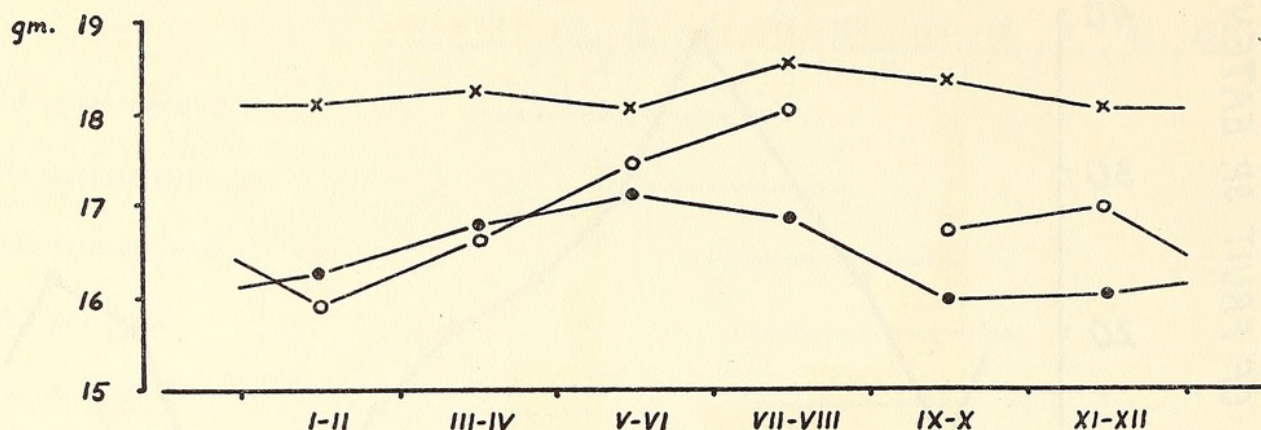
TEXT-FIG. 18. Total numbers of fruit species found to be eaten throughout the year.

that insects are available in greatest numbers in the early part of the wet season. It is then that termites swarm, mosquitoes increase, and most Lepidoptera are breeding. Thus the early part of the manakins' breeding season probably coincides with the period of greatest abundance of insects as well as fruit. By the time that breeding ceases, in August and September, the variety of fruit is decreasing and approaching its minimum.

Although temporary, perhaps local, food shortages may occur, it seems that for the Black



TEXT-FIG. 19. Number of fruit species in food samples collected from display ground A, showing the range (broken line) and the mean.



TEXT-FIG. 20. Mean weights of adult males (crosses), juvenile males (open circles), and females (dots), grouped in two-monthly periods. (From the data given in Appendix 3.)

and White Manakin there is no regularly recurring period of food shortage such as plays such an important part in the ecology of northern birds. This is of course what might be expected; the generalization has often been made by writers on tropical forest birds, without the support of detailed data. For the Black and White Manakin, the evidence from an analysis of the food, given above, is further supported by observations at display grounds and from the weights of trapped birds.

As already mentioned, adult males can feed themselves in less than 10% of the daylight hours. And the food collected in this short period suffices for regular bouts of intense activity at the court. This applies to all months of the year, since even at the height of the moult some early or late individuals are usually present at the display grounds.

Analysis of weights lends further support. All known birds which undergo annual periods of food shortage lay down in advance reserves of fat to meet the shortage (Lack, 1954). But adult male Black and White Manakins showed no significant variation in weight throughout the year (Text-fig. 20). Adult females showed a seasonal change in weight that was certainly due to enlargement of the ovary and development of eggs, and juvenile males showed a seasonal increase in weight that was attributable to the gradual development of the muscles involved in display, bringing them up from the juvenile to the adult male weight. The full data are given in Appendix 3.

When weights of adult males and of females from all months are combined (Text-fig. 21), both show a similar frequency distribution, with a long "tail" towards the upper end of the scale and very few individuals at the lower end. This suggests that during the period of the study few individuals in the population could have been

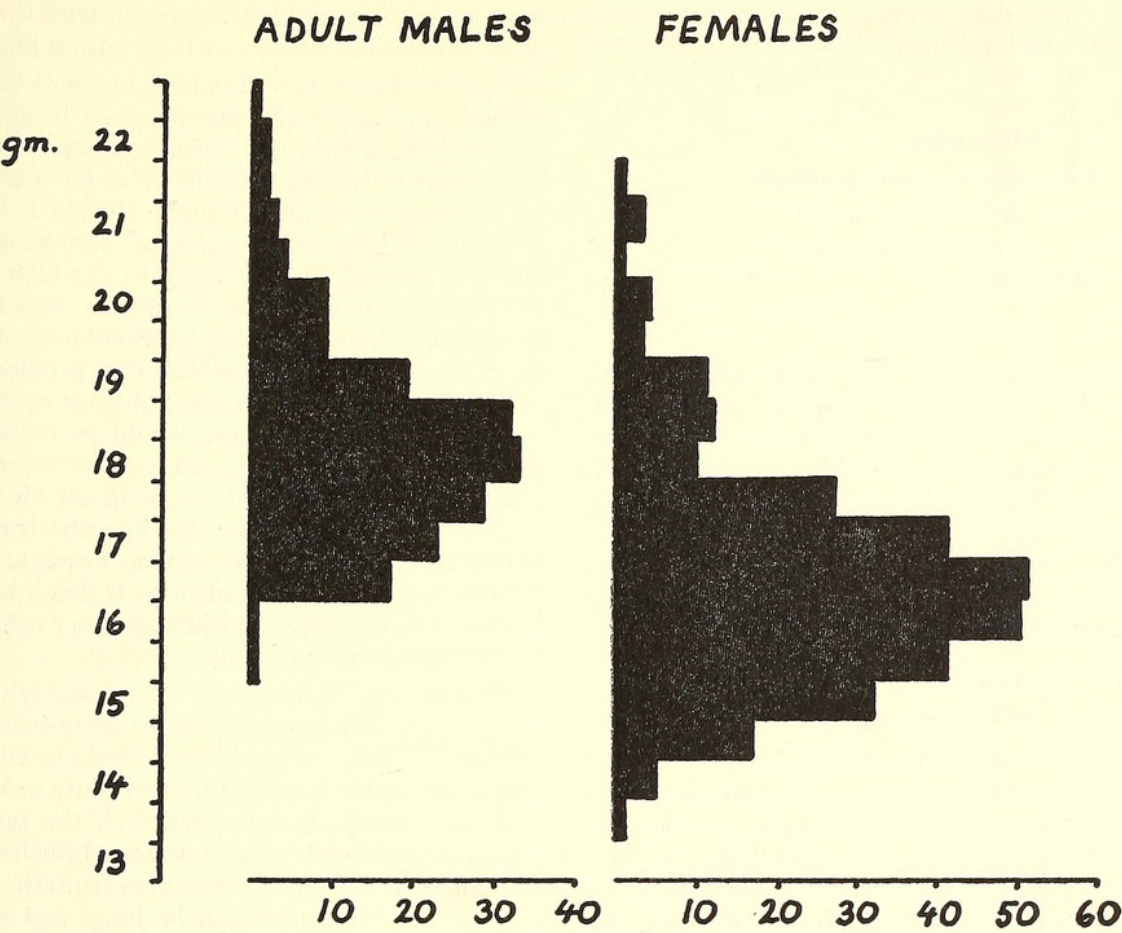
undernourished or subnormal. It is significant that none of the 38 color-ringed males that were under observation at the display grounds died during the two periods of temporary food shortage.

THE ANNUAL SURVIVAL OF ADULTS

Because adult males normally retain their courts indefinitely, once they have settled down, it is comparatively easy, by observing color-ringed males at display grounds over a long enough period, to find the annual mortality. The figure so obtained must of course be a maximum, since if a bird shifts its court to another display ground it may not be found again and will be recorded as dead. In fact this source of error is almost certainly not serious in the present case. Only one adult male was known to have shifted to another display ground and it had spent a year without establishing itself at the first display ground (p. 80). Of the established males which disappeared from display grounds, none was ever seen or trapped again, so it was probably correct to assume that they were dead.

The annual survival of each male was assessed from the date on which it was first found to be established at a court. If it survived to the same date on the following year, its further survival could again be assessed. The only male ringed early enough to give evidence of survival over three years did in fact survive. Several males survived for the two years for which their survival could be recorded. On this basis, the survival of 38 color-ringed birds was available for analysis, giving a total of 56 records of survival from one year to the next. The results, given in Table VII, show that the annual survival of these males was 89%.

The annual survival of adult females could not be assessed in the same way. Though they



TEXT-FIG. 21. Combined weights of all adult males and females, all months.

hold breeding territories, these are shifted more often than the males' courts, and the disappearance of a female from a small area could not be taken as evidence of death. However, the trapping data showed a high rate of survival. Thus of the first eight females trapped, in June, 1958, one was never retrapped nor seen again, but the other seven were known to have survived for an average of over 2½ years, five of them being alive at or shortly before the time when observations ceased, in September, 1961.

The trapping data also showed that the sex ratio of the adults was equal or nearly so, which implies that the females' survival rate must be about as good as the males'. Table VIII gives an analysis of the first 100 birds trapped at a feeding area away from the display grounds. Forty-two of them were males, 40 of them females,

and the sex of 18 birds in female or juvenile plumage was not determined. This last category must have consisted of juvenile males, and adult and juvenile females, the females preponderating as they included two age-classes. The sex-ratio of this sample must therefore have been near 50:50. The figures for the second hundred are similar, except that the undetermined category was greater as there was not so much time for subsequent observation and re-trapping (known males 40, known females 35, undetermined 25).

An annual survival of 89% is far higher than that of any other small bird whose survival rate is known (Lack, 1954). But very high survival rates may well be general in tropical forest birds. If, as seems usual, their reproductive rate is very low, it follows that their annual survival must

TABLE VII. ANNUAL SURVIVAL OF ADULT MALES

| | | | |
|--|----|-------------------|----|
| Ringed early enough for survival over one year to be recorded: | 38 | Number surviving: | 35 |
| Ringed early enough for survival over 2nd year to be recorded: | 17 | " " | 14 |
| Ringed early enough for survival over 3rd year to be recorded: | 1 | " " | 1 |
| All observations: | 56 | " " | 50 |

TABLE VIII. ANALYSIS OF SEXES OF TRAPPED BIRDS (First hundred individuals trapped at feeding and bathing places away from display grounds)

| | |
|-------------------------------------|----|
| Trapped as adult males | 28 |
| Trapped in female/juvenile plumage: | |
| later known to have been males | 14 |
| later known to have been females | 40 |
| sex not determined | 18 |

be high. For the Black and White Manakin the figures for reproductive rate and survival balance as well as could be expected. With 89% annual survival, if the population is to remain stable each female must contribute annually an average of 0.22 adults to the next year's population. This figure is reasonably close to the 0.33 independently estimated for the reproductive rate (p. 92).

DISCUSSION: THE EVOLUTION OF COMMUNAL DISPLAYS

Advertisement and courtship displays of males have evolved to an extreme degree in many species of tropical forest birds—especially hummingbirds, cotingas, manakins, bowerbirds and birds of paradise. In several species of manakins, a few hummingbirds and cotingas, and at least one bird of paradise, communal or "lek" displays have been evolved. Such behavior is of course known in birds of other habitats (e.g., Ruff *Philomachus pugnax* and species of grouse), yet there can be no doubt that the tropical forest environment is especially favorable to the evolution of elaborate group displays.

The present study throws light on the ecological factors favoring communal display in the Black and White Manakin. To apply the conclusions reached here beyond this species and other small manakins would be rash; nevertheless it is probable that similar ecological circumstances have been important in the evolution of the sexual behavior of the other tropical forest families mentioned above.

In the Black and White Manakin we find the following. The food supply is rather uniform throughout the year, with no regular period of food shortage. Normally an individual can satisfy its food requirements in a very short time in each day (at most, 10% of the daylight hours). The breeding season is long, and variable in its time of onset. Clutch-size, and consequently family-size, is low, and it seems unlikely that a female normally finds it difficult to supply the needs of one or two young ones. Nesting success is very low, most of the losses being due to predation. The expectation of life

of the adult is very high compared with that of other small birds whose mortality rate is known.

The manakins' low clutch-size cannot be regarded as in any way consequent on its special way of life. Almost all other species building open nests in the same habitat also lay a clutch of two eggs (see also Skutch, 1949). I agree with Skutch in attributing the low clutch-size of birds in tropical forest mainly to the high rate of predation, which gives a selective advantage to nests which need visiting very seldom and are as inconspicuous as possible. The problem is essentially a quantitative one, whether on average more, or fewer, young would be reared if the clutch were larger. As yet, neither for manakins nor for any other tropical forest bird are there critical data enabling the hypothesis to be tested. For the present argument, however, the importance of the low family-size is that it is one of the ecological prerequisites for the evolution of the manakins' communal display.

Where nest predation is heavy and clutch-size low, the emancipation of the male from attendance at the nest presents obvious advantages, especially if he is more brightly colored than the female. This is possible if the female does not need much time to find food for herself and her family. Thus her absences from the nest during incubation need not be long, and when the eggs hatch she will have no difficulty in feeding two nestlings as well as herself. Selection will thus favor the progressive dissociation of the male from the care of the nest and young.

Once the male is free of nesting duties, the pair bond can be broken and he becomes free to mate with as many females as he can attract. Thus sexual competition between the males will intensify, and selection will promote the development of all structures and behavior enhancing the effectiveness of the male's display. The ability to find food quickly will enable the male to devote a great part of his time to attracting prospective mates. If the female's breeding season is a long one, natural selection will ensure that the male's period of display is at least as long.

Probably the fundamental requirement is a food supply which enables the individual to get its nourishment in a short time in each day. Thus the manakins, and those cotingas and birds of paradise with similar behavior, are all primarily fruit-eaters. No primarily insectivorous groups have evolved along these lines. Of the huge family of New World flycatchers (Tyrannidae), which includes many species inhabiting tropical forest, one species, *Pipromorpha oleaginea*, is known to have evolved this kind of behavior (Skutch, 1960; personal obs.): the males spend most of their time calling and displaying in fixed

places in the forest and take no part in the nesting. Of all the small flycatchers observed in the Arima Valley, this was the only species found to eat fruit regularly; Skutch has recorded that fruits are also fed to the young. The mainly nectarivorous hummingbirds, whose communal displays are highly developed, can also feed themselves in a very short time in each day (Snow & Snow, in preparation. 1). Once this requirement is met, the emancipation of the male from the nest becomes possible and all further developments can follow.

Whether or not evolution leads to communal or "lek" displays depends on other factors. Thus the bellbirds are sexually highly dimorphic and the males spend much of their time in display, but they display in scattered groups within earshot but not within sight of each other (B. K. Snow, 1960), and in some manakins the situation is similar. But the bellbirds have extremely loud calls and can advertise their presence to females a long way off. For a small bird in thick forest, traditional display grounds, which the females know and can visit when they are ready to mate, are an obvious advantage. Almost certainly, however, this is not the main advantage of a lek over a solitarily displaying male. A single manakin displaying at a solitary court in the forest would soon become known to the local females and they would have no difficulty in finding him. Other species of manakins have display perches well apart from their fellows. The crucial point is that a group of males displaying together must have a much greater attraction for the female and a greater stimulating effect on her, once she has arrived, than a solitary male. Otherwise it would seem advantageous for males to display at some distance from their fellows, where competition for the attention of the female would be less intense.

If the conspicuousness of males at communal display grounds made them more liable to predation, we should have an important selective factor working against the evolution of communal displays. But the evidence for the Black and White Manakin is against such a hypothesis, as the annual survival rate of males with courts is extremely high and probably nearly the same as that of the females, which are far less conspicuous.

Strong sexual selection will lead to the extreme development of display structures and exaggerated display movements, and as Sibley (1957) has pointed out, the more distinct the displays and structures are in related species, the more effective they will be as isolating mechanisms. But the extreme ritualization of the display movements probably has another important

function. In a species in which no pair bond is formed, the female has no opportunity to become acquainted with her mate over a long period. Ethological studies have shown the importance of the agonistic elements as well as the sexual in relationships between the sexes, especially in the early stages. When pairs are formed, the hostile responses are gradually overcome; in such species copulation is not usually preceded by very elaborate displays. But when pairs are not formed and the two sexes meet only briefly for mating, the coordination between male and female necessary for successful copulation needs to be brought about in some other way. Hence the importance of the male's precisely ritualized display movements, to which the female responds with synchronized movements. Thus a highly coordinated mutual dance achieves in a few seconds what in a paired bird needs a prolonged period of mutual adjustment.

SUMMARY

The Black and White Manakin, *Manacus manacus*, a small, sexually dimorphic, mainly frugivorous passerine bird, was studied for 4½ years in an area of tropical forest in Trinidad.

There was an estimated adult population of some 500 birds in 450 acres of forest. It is considered that this density is considerably greater than is usual on the mainland of South America.

Males display at communal display grounds, where each bird clears a "court" on the forest floor. Each court has two or more saplings around its edges, which are used by the male in his display. Six display movements are described, and the accompanying mechanical sounds made by the specialized wing-feathers. Display goes on all through the day, with a marked peak soon after dawn and another peak in early afternoon.

Females visit the display grounds and join the males in a highly coordinated dance over the court. To mate, the male "slides down" one of the saplings onto the back of the female.

Observations on color-ringed birds showed that no pairs are formed. The males are polygamous and the females to a great extent promiscuous.

The communal display grounds result from the balanced social and aggressive tendencies of the male. There is keen competition for courts, and those near the center of the display ground are favored. Young males take many months to obtain a court.

Display continues all year, but is much reduced during the moult. The start of breeding varied in the five seasons by up to five months, but the season of moult did not vary appreciably.

The moult lasts for about 80 days for each bird. Juveniles moult into adult plumage in their second year, a little earlier than the adults.

The start of breeding is probably affected by food supply and weather, and its ending appeared to be correlated with the time of onset of the wet season.

The nest is attended by the female alone. The incubation period was 18-19 days, the fledging period 13-15 days. Only 19% of nests started produced fledged young. Females usually start 2-4 nests per season. Each female is estimated to rear on average one young per year.

Berry-bearing trees of the families Melastomaceae and Rubiaceae are of especial importance in the manakins' diet, producing a succession of fruit throughout the year. There was evidence of two periods of temporary food shortage. The breeding season coincides with the period of greatest availability of food.

The annual survival of adult males was 89%, and survival of females was also very high.

The evolution of communal displays is discussed.

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APPENDIX 1

THE DISPLAY OF GOULD'S MANAKIN (*M. vitellinus*)

In March, 1958, the display of Gould's Manakin was studied on Barro Colorado Island and neighboring areas in Panama. Most of the observations were made at the display ground studied by Chapman in 1932 and 1935. As far as could be seen by field observations and by examination of motion picture film, its display was in general identical with that of *M. manacus*, with the following differences.

(1) "Fanning" was never seen, nor does Chapman mention it.

(2) The rolled snap, followed by "chee-poo," though the same as in *M. manacus*, appeared to be a more stereotyped and commoner display pattern. Chapman also remarked that it was a well-defined display.

(3) The "slide down the pole," following the "grunt-jump," was much more commonly performed by the individuals under observation than is normal in *M. manacus*. Twice a male was seen to slide down onto a female and copulate with her, after a preliminary dance similar to that of *M. manacus*; the sequence was filmed. Analysis of motion picture film shows that in one case, at the end of the slide, the bird remained head downward near the bottom of the perch for about a second, fanning its wings and vibrating its body somewhat as in the fanning display of *M. manacus*. The male that copulated also vibrated its body in the same way.

These observations provide a clue to the very puzzling "dirigible pose" described by Chapman. He described this display, which he saw performed by only one individual, as follows: "With bill touching the end of a slender, broken sapling the size of a pencil and about eighteen inches high, it fluttered its wings while holding a horizontal pose; then, with bill still pressed to the sapling, it slid down to the court and, with bill now touching a root, wings still fluttering, seemed to be standing on its head." Aerodynamically it is difficult to see how a manakin could flutter its wings and remain motionless in the air head downwards, since in such a position the force generated by its wings would have no down-

ward component. It seems almost certain that what Chapman saw was the "slide down the pole" (during which the bird's feet grip the perch, though this is not easy to see), followed by wing-fluttering at the bottom of the perch. In the poor light of the forest floor it is often difficult to see the details of these very rapid display movements.

(4) During low-intensity to-and-fro jumps across the court, without the initial snap and with normal whirring flight, a low "flup," clearly a wing noise, was often made on landing. The same sound was heard on two occasions when a bird landed after "snap-jumps," and was also occasionally heard made in mid-flight. It was never noted in *M. manacus*.

(5) Juvenile males, engaged in uncoordinated display behavior in the trees around the display ground, were several times seen to perform a display that was not recorded in *M. manacus*. Perched on a horizontal twig, the bird would look downwards, then with an initial little jump upward would jump down to a lower perch, uttering a weak plaintive "pu" on jumping. The same "pu" call was occasionally heard from juvenile males of *M. manacus* (p. 71), but it was not seen to be associated with a jump.

APPENDIX 2

FRUITS EATEN BY THE BLACK AND WHITE MANAKIN

This list includes all the identified fruits found to be eaten by Black and White Manakins, by direct observation and by collection of regurgitated seeds from below nests, from display grounds, and in a few cases from trapped birds. The numbers following each plant name indicate the months in which the fruit was found to be eaten. These figures are used in Text-fig. 18, with the addition of the follow-

ing numbers of unidentified fruits in each month: January, 2; February, 5; March, 5; April, 16; May, 2; June, 4; July, 3; August, 1; September, 1; November, 3; December, 3.

I am much indebted to Mr. N. Y. Sandwith and Dr. J. J. Wurdack for help with many of these determinations.

| | |
|---------------|--|
| Podocarpaceae | <i>Podocarpus</i> sp., 12 |
| Gramineae | <i>Lasiacis sorghoidea</i> (Desr.) Hitchc. & Chase, 1 |
| Araceae | <i>Monstera pertusa</i> (L.) de Vriese, 11 <i>Philodendron</i> sp., 2 |
| Liliaceae | <i>Smilax</i> sp., 4 |
| Musaceae | <i>Heliconia</i> cf. <i>wagneriana</i> O. G. Peters, 11 <i>Heliconia hirsuta</i> L.f., 4, 6 |
| Zingiberaceae | <i>Costus spiralis</i> Rosc., 12 |
| Marantaceae | <i>Stromanthe tonckat</i> (Aubl.) Eichl., 12 |
| Moraceae | <i>Castilloa elastica</i> Cerv., 6, 7 <i>Cecropia peltata</i> L., 6, 7, 9 <i>Ficus citrifolia</i> Mill., 2 <i>Ficus clusiifolia</i> Schott ex Spr., 2-7, 10, 11 |
| Urticaceae | <i>Trema micrantha</i> (L.) Blume, 1, 5 |
| Nyctaginaceae | <i>Pisonia eggersiana</i> Heimerl., 7, 8 <i>Pisonia</i> sp., 7, 8 |
| Lauraceae | <i>Ocotea canaliculata</i> (Rich.) Mez, 3-5 <i>Ocotea oblonga</i> (Meissn.) Mez, 3, 5, 6 <i>Phoebe elongata</i> (Vahl) Nees, 4, 5 |
| Connaraceae | <i>Rourea surinamensis</i> Miq., 3-7, 11 |
| Burseraceae | <i>Protium heptaphyllum</i> (Aubl.) March., 7, 8 |

| | |
|----------------|---|
| Euphorbiaceae | <i>Alchornea triplinervia</i> (Spr.) Müll. Arg., 12 <i>Hieronyma caribaea</i> Urb., 6-8, 10, 11 <i>Maprounea guianensis</i> Aubl., 11 <i>Richeria grandis</i> Vahl, 3, 4 |
| Aquifeliaceae | <i>Ilex</i> sp., 12 |
| Sapindaceae | <i>Cupania rubiginosa</i> (Poir.) Radlk., 3-5 <i>Paullinia fuscescens</i> H. B. K., 10, 11 |
| Tiliaceae | <i>Sloanea laurifolia</i> (Bth.) Bth., 3 <i>Sloanea stipitata</i> Spruce ex Bth., 5 |
| Dilleniaceae | <i>Doliocarpus dentatus</i> (Aubl.) Standl., 4-8 <i>Pinzona calineoides</i> Eichl., 2-5 |
| Flacourtiaceae | <i>Laetia procera</i> (Poepp. & Endl.) Eichl., 2 |
| Myrtaceae | <i>Myrcia leptoclada</i> DC, 4, 5 |
| Melastomaceae | <i>Clidemia</i> sp., 8, 12 <i>Henriettea</i> sp., 8 <i>Miconia acinodendron</i> (L.) Sweet, 11 <i>Miconia affinis</i> DC, 6-9 <i>Miconia amplexans</i> (Crueg.) Cogn., 7 <i>Miconia chrysophylla</i> (Rich.) Urb., 5 <i>Miconia guianensis</i> (Aubl.) Cogn., 1, 2, 5-7, 12 <i>Miconia kappleri</i> Naud., 11, 12 <i>Miconia mucronata</i> (Desr.) Naud., 1, 2 <i>Miconia multispicata</i> Naud., 1-6 <i>Miconia myriantha</i> Benth., 10-12 <i>Miconia nervosa</i> (Sm.) Tr., 5, 7 <i>Miconia prasina</i> (Sw.) DC, 4-10 <i>Miconia punctata</i> (Desr.) D. Don, 10-12 <i>Miconia racemosa</i> (Aubl.) DC, 2 <i>Miconia splendens</i> (Sw.) Griseb., 4 <i>Miconia tomentosa</i> (Rich.) D. Don, 5, 6 |
| Araliaceae | <i>Didymopanax morototoni</i> (Aubl.) Dcne. & Planch., 1-3, 10-12 |
| Boraginaceae | <i>Cordia bicolor</i> A. DC, 7, 8 <i>Cordia curassavica</i> (Jacq.) R. & S., 2, 4, 5, 12 |
| Verbenaceae | <i>Aegiphila integrifolia</i> (Jacq.) Jacks., 12 <i>Lantana camara</i> L., 2, 5 |
| Solanaceae | <i>Cestrum latifolium</i> Lam., 2, 4, 5 |
| Rubiaceae | <i>Amaioua corymbosa</i> H. B. K., 2, 4-8 <i>Cephaelis muscosa</i> (Jacq.) Sw., 1, 5, 6, 8 <i>Cephaelis tomentosa</i> (Aubl.) Vahl, 2, 5, 6, 8, 9 <i>Cephaelis</i> sp., 1 <i>Chiococca alba</i> (L.) Hitchc., 11, 12 <i>Coussarea paniculata</i> (Vahl) Standl., 1 <i>Gonzalagunia spicata</i> (Lam.) Gómez, 1, 12 <i>Lacistema aggregatum</i> (Berg) Rusby, 5-7 <i>Malanea macrophylla</i> Bartl., 2, 4 <i>Palicourea crocea</i> (Sw.) DC, 1, 12 <i>Psychotria cuspidata</i> (Bredem. ex Willd.), 4-6 <i>Psychotria marginata</i> Sw., 4, 11, 12 <i>Psychotria trinitensis</i> Urb., 4, 5, 11 <i>Psychotria undulata</i> , 2, 4, 6, 8-11 <i>Rudgea freemanii</i> Sprague & Williams, 11 |
| Compositae | <i>Wulffia baccata</i> (L. fil.) Kze., 9 |

APPENDIX 3

WEIGHTS AND MEASUREMENTS

Weights

All trapped birds, unless they were wet, were placed in a cloth bag and weighed immediately after being caught. A spring balance, accurate to 0.5 gm., was used and was kept regularly calibrated. Altogether, 774 weights were obtained.

Eighteen birds were trapped and weighed more than once on the same day, two of them three times

and the remainder twice. Analysis of their weights showed that individuals increase their weight slightly in the course of the day, by approximately 0.75 gm. from 0700 to 1700 hours. For the analysis of seasonal weight-changes, weights taken from 1100 onwards need to be reduced by 0.5 gm. to make them comparable with those taken earlier. This has been done in the tables that follow. In the case of birds trapped more than once on the same day, the first weight has been used.

The mean of 185 weights of adult males was 18.20 gm. (range 15.5-22.5 gm.) The mean of 310 weights of females was 16.45 gm. (range 13.5-21.5 gm.). Juvenile males were intermediate, the mean of 59 weights being 17.02 gm. (range 13.5-19 gm.). (A considerable number of weights of birds in

female plumage have not been used, as it was not known whether they were females or juvenile males.)

Seasonal changes in weight have been discussed in the body of the paper (p. 96).

Weights of adult males

| gm. | Jan.-Feb. | Mar.-Apr. | May-Jun. | Jul.-Aug. | Sep.-Oct. | Nov.-Dec. |
|------|-----------|-----------|----------|-----------|-----------|-----------|
| 22.5 | | | | 1 | | |
| 22 | 1 | | | | 1 | |
| 21.5 | 1 | | | | | 1 |
| 21 | | | 1 | 2 | | |
| 20.5 | | | 2 | 2 | | |
| 20 | 2 | | 1 | 2 | 4 | |
| 19.5 | 1 | | 1 | 1 | 1 | 5 |
| 19 | | 5 | 4 | 4 | 4 | 2 |
| 18.5 | 5 | 5 | 9 | 4 | 5 | 4 |
| 18 | 4 | 4 | 10 | 6 | 4 | 5 |
| 17.5 | 2 | 4 | 11 | 4 | 2 | 6 |
| 17 | 4 | 1 | 5 | 5 | 6 | 2 |
| 16.5 | 6 | | 5 | 1 | 1 | 4 |
| 16 | | | | | 1 | |
| 15.5 | | | | | | 1 |

Weights of juvenile males

| gm. | Jan.-Feb. | Mar.-Apr. | May-Jun. | Jul.-Aug. | Sep.-Oct. | Nov.-Dec. |
|------|-----------|-----------|----------|-----------|-----------|-----------|
| 19 | | | 3 | 3 | | |
| 18.5 | | 1 | | 3 | 1 | |
| 18 | | 1 | 1 | | | |
| 17.5 | | 2 | 7 | | | 2 |
| 17 | | 1 | 2 | 2 | 1 | 7 |
| 16.5 | | | 3 | | 4 | |
| 16 | 4 | 1 | | | 2 | |
| 15.5 | 1 | | 1 | 1 | | 1 |
| 15 | | 3 | | | | |
| 14.5 | | | | | | |
| 14 | | | | | | |
| 13.5 | | | | | | 1 |

Weights of females

| gm. | Jan.-Feb. | Mar.-Apr. | May-Jun. | Jul.-Aug. | Sep.-Oct. | Nov.-Dec. |
|------|-----------|-----------|----------|-----------|-----------|-----------|
| 21.5 | | | 1 | | | |
| 21 | | | 2 | 1 | | |
| 20.5 | | | 1 | | | |
| 20 | 1 | | 1 | 2 | | |
| 19.5 | | | 3 | | | |
| 19 | 2 | 2 | 5 | 1 | | 1 |
| 18.5 | 1 | 2 | 6 | 2 | | 1 |
| 18 | 1 | 1 | 6 | 2 | | |
| 17.5 | 4 | 2 | 9 | 7 | 3 | 2 |
| 17 | 3 | 5 | 11 | 13 | 4 | 5 |
| 16.5 | 3 | 4 | 9 | 14 | 10 | 11 |
| 16 | 5 | 2 | 12 | 13 | 7 | 11 |
| 15.5 | 3 | 3 | 8 | 11 | 8 | 8 |
| 15 | 4 | 2 | 8 | 8 | 5 | 5 |
| 14.5 | 2 | 1 | 1 | 2 | 5 | 6 |
| 14 | 3 | | | 2 | | |
| 13.5 | 1 | | | | | |

Measurements

The wings of nearly all the birds trapped were measured (the wing being held in the naturally closed position and not flattened). In addition the width of the outermost (10th) primary was measured 5 mm. from the tip in a smaller number of

Wing-lengths

| mm. | Adult males | Juvenile males | Females |
|-----|-------------|----------------|---------|
| 57 | | 2 | 2 |
| 56 | | 10 | 15 |
| 55 | 3 | 16 | 27 |
| 54 | 4 | 8 | 28 |
| 53 | 20 | 3 | 6 |
| 52 | 17 | 2 | |
| 51 | 11 | | |

individuals, in order to find out if juvenile males are distinguishable from females by the degree of modification of the primaries (p. 70). The results, tabulated below, show that the wing-length of adult males averaged 2 mm. less than that of juvenile males and females, which did not differ appreciably from each other. Juvenile males, however, had slightly wider (less specialized) outer primaries than females.

Width of outermost primary

| mm. | Adult males | Juvenile males | Females |
|-----|-------------|----------------|---------|
| 3.5 | | 2 | |
| 3 | | 9 | 13 |
| 2.5 | | 3 | 14 |
| 2 | 17 | | 3 |
| 1.5 | 5 | | |



Snow, David W. 1962. "A field study of the black and white manakin, *Manacus manacus*, in Trinidad." *Zoologica : scientific contributions of the New York Zoological Society* 47(8), 65–104. <https://doi.org/10.5962/p.203324>.

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