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*The Courtship of Gould's Manakin (*Manacus vitellinus*  
*vitellinus*) on Barro Colorado Island, Canal Zone*

BY FRANK M. CHAPMAN

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**Article VII.—THE COURTSHIP OF GOULD'S MANAKIN**  
**(*MANACUS VITELLINUS VITELLINUS*)**  
**ON BARRO COLORADO ISLAND,**  
**CANAL ZONE**

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<sup>1</sup> In this connection read Noble and Vogt's 'An experimental study of sex recognition in birds' (The Auk, LII, 1935, pp. 278-286).

## THE FAMILY PIPRIDAE

The Passerine family Pipridae, to which the manakins belong, contains about 50 species and 60 subspecies. With the exception of four species inhabiting the Andean subtropics, they occupy the American Humid Tropical Zone from southeastern Mexico to eastern Paraguay, excluding the Antilles.

Manakins are small birds, averaging less than five inches in length. As a rule, the males are strongly or brightly marked while the females are uniform olive-green. In some species the male is further distinguished from the female by concealed colors, a lengthening of the feathers of the head, throat, or tail, or by modifications in the shape or structure of the wing and tail-feathers.

So far as our very limited knowledge of the habits of manakins goes, these characters of the male are functional and are used for display or sound-production in his courtship of the female. But there are also species which have pronounced courtship customs not dependent upon the possession of special structure. For example, in *Chiroxiphia caudata* of southeastern Brazil, aside from color, the plumage of the male differs notably from that of the female only in its slightly longer and narrower central tail-feathers. Nevertheless this bird and its congeners are among the best known of so-called bird dancers. Of it von Jhering writes:

“The ‘Dansador’ or ‘dancing bird.’ This name refers to the remarkable, as it appears, little known dances of these birds. It is the males, at most three or four in number, which in the spring perform their dances before the females who sit by quietly and look on. They require for this a thin horizontal or slightly inclined twig upon which they hop up and down. Unfortunately, I myself have observed this beautiful performance only once, and not long enough, as we were soon observed. According to the assurance of many acquaintances, one of the animals is said to make the music for the dance and later, with a beating together of the wings, by a loud sharp *Pfiff* gives the signal for the breaking up of the play. Also, they are said often to use the place regularly for a long time.” (Zeitschrift für die Gesamte Ornithologie, 1885, volume II, pp. 138, 139.)

In *Chiroxiphia linearis* of Central America the central tail-feathers are much longer, the wing more rounded than in *C. caudata*, but in the appended account of the habits of this bird in Nicaragua by C. C. Nutting, these characters do not appear to function:



" . . . One day, while hunting through the dense forest, the profound silence was suddenly broken by the regularly repeated note of 'El Bailador,' and softly making my way toward the spot whence the sound proceeded, I witnessed one of the most remarkable performances it has ever been my lot to see.

"Upon a bare twig which overhung the trail at a distance of about four feet from the ground, two male 'Bailadors' were engaged in a 'song and dance' act that simply astounded me. The two birds were about a foot and a half apart, and were alternately jumping about two feet into the air and alighting exactly upon the spot whence they jumped. The time was as regular as clock-work, one bird jumping up the instant the other alighted, each bird accompanying himself to the tune of 'to-lé-do-to-lé-do—to-lé-do,' sounding the syllable 'to' as he crouched to spring, 'lé' while in the air, and 'do' as he alighted.

"This performance was kept up without intermission for more than a minute, when the birds suddenly discovered that they had an audience, and made off." (Proc. U. S. Nat. Mus., 1883, VI, p. 384.)

The male of the yellow-crested manakin (*Neopelma pallescens*) of eastern Brazil differs from the female only in having a larger crown-patch; nevertheless, without further external sexual characters it has a well-developed courtship "dance." H. Snethlage writes:

"One finds the male at the time of the first rains sitting quietly on a horizontal loop of a creeper about half or a meter above the ground. It suddenly utters a peculiar note which sounds like *de ray*, and jumps three to four times, one after the other, quickly into the air, landing regularly again on the creeper. During this display it spreads the feathers of the head and droops the wings and spreads the tail-feathers like a fan. This dance is repeated again and again. I have shot the dancer in three cases and these specimens have been identified by Hellmayr as belonging to this species." (Journal für Ornithologie, 1928, Heft 4, volume LXXVI, p. 711.)

We come now to a species (*Pipra mentalis*) in which, in addition to color, the male possesses marked structural sexual characters. Its secondaries are enlarged, curved and stiffened, as in *Manacus*, its rectrices stiffened, its thighs yellow and its tarsi more feathered than in the female. My notes on the habits of the form of this species (*Pipra mentalis minor*) inhabiting Panama show that all these characters are functional. I quote from 'My Tropical Air Castle' (p. 176):

"December 25, 1926. A bright Christmas morning. As I reached the Shannon Trail where yesterday I met Lawrence's Wren, a Red-

headed Manakin [= yellow-thighed manakin, *Pipra mentalis minor*] passed, *buzzing*, *whirring*, and *snapping*. He showed no fear and several times perched quite near me. He seemed much excited and his erratic dartings here and there proved to have a focal point of interest about fifteen feet from the ground on the thin, horizontal limb of a slender tree. Reaching this limb, he jumped from side to side for a distance of about fifteen inches as rapidly as it was possible for him to move, varying this performance by sliding over this space with whirring wings; or, with his feet barely touching the perch, he made rapid sideway steps like a ballet dancer on tip-toe. After half-a-dozen jumps and a teetering slide or two, he would dart off, buzzing and snapping, going about fifty feet and then returning to the dance-perch. I now saw that the lure was a little greenish bird who was perched quietly at the junction of the display limb with its trunk. She took no active part in the performance and after two displays changed her place, the male at once following her to repeat his exhibition."

At 8 o'clock on the morning of December 27, when next I visited this place, the tireless little lover was still ardently pressing his suit. He used the same limb, and the female occupied the same position as before. "Evidently," my notes read, "she is a willing observer of his wooing and takes a position where she may see and be seen. As before, the male jumped sideways, back and forth, at the rate of about two jumps to the second; he also vibrated along the limb over the same space and as he approached the female his head was down, his tail elevated at an angle of about 45°, while the hind part of the body was raised to the limit of his leg-length, showing conspicuously the usually hidden yellow of his legs. To these evolutions he now added a half-whirling pivot, facing first forward then backward, and punctuating each turn with a *whir-r-r*. He must have changed his footing with each change of position, but he moved with such rapidity it was impossible to see him do it. The following day the courtship was continued with undiminished enthusiasm. Then the birds disappeared—let us hope to nest."

Casual observations in 1935 showed that, on occasion, several males and females unite in these demonstrations and return for weeks to the same place to perform them.

The members of the genus *Manacus* are among the most specialized of manakins. In all the species of this genus the primaries, as well as secondaries, and also the gular feathers function in the male's courtship procedure. In spite of the fact that the species of this group are

the most common, widely distributed, and hence best known of manakins, very little has been recorded concerning their habits.

Of *Manacus manacus interior* in eastern Peru, that excellent field naturalist, Jean Stolzmann, wrote:

"I first met this bird at Balza-Puerto, later often in the neighborhood of Yurimaguas; they evidently have favorite spots where they can almost always be found. Such a spot was in the low bushes at the edge of the forest. At a hundred paces one could recognize the presence of the birds by their snapping and their characteristic voice. In its habits this bird offers one detail that is very curious, the more so because it is found also in another so different bird, *Loddigesia mirabilis*. On examining these two birds, one finds a peculiarity common to them in the development of the stiff and flattened secondaries. These organs fulfill the same function in the present species as do those of *Loddigesia*. Striking its remiges against one another, *Manacus* produces a sort of snapping like that heard when hooking the nail of the middle finger against that of the thumb. *Loddigesia* produces a similar sound, but that of *Manacus* is much louder. Moreover, the latter bird can produce a combination similar to the noise of a child's rattle.

"The habits of *Manacus* are peculiar. They always keep in small bands, where the males seem more numerous. Suddenly their snapping begins on all sides, accompanied by a flute-like call composed of two notes. It seems to me that only the males make the snapping, accompanied by singular movements of the wings, as if the folded remiges were raised one over the other and then in falling, one after the other, produced the vibration." (Tacz., 'Orn. Pérou,' 1884, II, p. 349.)

Stolzmann is one of the few field naturalists who correctly attributed the manakin's snapping to the striking together of the remiges, and his statement, that "they evidently have favorite spots" in which to snap, suggests that, like their near relative, *Manacus vitellinus*, they also have courts.

To our knowledge of the habits of *Manacus manacus* I add an extract from my journal of April 5, 1893, recording a brief observation on the actions of *Manacus manacus gutturosus* in Trinidad:

"An interesting bit of bird-life had for its actors four manakins (*Manacus*). Three were in adult male plumage, the fourth was in female plumage but, to my surprise, proved on dissection to be an immature male. This shows the value of dissection and the ease with which a false conclusion may be reached.



"The birds were in the lower bushes at the edge of the forest. They were all calling in an excited way their sharp twittering chirp which is like a young bird's first efforts at song. At the same time they were jumping back and forth from bush to bush, *buzzing* and *whirring* at every wing stroke, and frequently with each jump making the sharp snapping sound which I have heard before but have been unable to identify. Sometimes two birds would engage in desperate combat, at others the activity of all would reach a maximum and the result was the strangest chorus of bird 'music' I ever listened to. As the 'female' was not a female I am at a loss to know what the disturbance was about."

While the needs of the collector evidently terminated this incident, and also prevented such prolonged, intensive observations as are recorded beyond, it must be admitted that the gun here supplied definite information concerning sex that I should have welcomed at times in my more recent studies.

This necessarily brief survey shows us that, in spite of our limited knowledge of manakins, what we know at least suggests that there exists throughout the group, without regard to sexual differences of color or form, a widespread impulse for sexual display.

In *Neopelma* the sexes are nearly alike in color and form; the male is without special characters but, nevertheless, has a "dance" in which its somewhat larger yellow crest is widely spread.

The male of *Chiroxiphia* differs from its olive-green mate in color and, in some species, its tail is longer. This character, however, apparently does not function in the courtship "dance" in which several males take part.

The male of *Pipra mentalis* possesses structural characters in the feathers of the wings and tail which enable it to accompany the display of its yellow thighs and its amazing actions with remarkable sounds, while *Manacus*, as we shall see beyond, still better equipped, produces an even more impressive and diversified performance. So we may feel assured that *Machaeropterus*, for example, finds a use for its singularly developed secondaries and that doubtless other species besides *Neopelma*, in which the sexes are essentially alike, also have well-marked ways of winning a mate.

We may also here recall that the manakins' large relative, the cock-of-the-rock (*Rupicola*), is noted for its courtship, though I am unable to find an adequate description of it.

But, although the best equipped birds are the authors of the most striking displays, it should be noted that they depend chiefly on their bodily activity with which to express themselves. The arboreal gyrations of *Pipra mentalis minor*, described above, and the "court" acrobatics of *Manacus vitellinus vitellinus*, described beyond, are not the product of their specialized tail or wing-feathers, but of that sexual inspiration to which we may look for the origin of these courtship demonstrations, which, presumably through the action of natural or sexual selection, are responsible for the development of the color and structural characters that distinguish their authors.

When we find specialized behavior, like the so-called "dancing" of manakins, exhibited by the strongly differentiated, widely distributed members of a family, we conclude that the habit has its root in the origin of the family and is as much a part of its evolution as form. If this be true, the study of the habits of a single member of a group can be only a small contribution toward the solution of problems of this nature. Such a contribution I have attempted to make in the following pages.

#### THE GENUS *MANACUS*

The fact that the genus *Manacus* ranges throughout the greater part of the Humid Tropical Zone, from southeastern Mexico to eastern Paraguay, and is everywhere more or less numerous, may be accepted as evidence that it successfully meets the requirements of its environment.

Aside from *Manacus coronatus*, known from a single Bogotá specimen in the Paris Museum and considered by Hellmayr to be a hybrid between *Manacus manacus* and an unknown species, the genus contains three groups:

- 1.—*Manacus candei*, one species, southeastern Mexico to northeastern Costa Rica;
- 2.—*Manacus vitellinus*, five forms, southwestern Costa Rica to western Colombia; and
- 3.—*Manacus manacus*, eleven forms, from northwestern Colombia to eastern Paraguay.

Without regard to the closeness of their resemblance, these seventeen forms are apparently representative of each other and, so far as I am aware, in only one instance do any two of them occur at the same place. This is in Antioquia, Colombia, whence we have specimens of both *Manacus vitellinus milleri* and *Manacus manacus abditivus* from Puerto Valdivia on the lower Cauca. Sclater records them from

Remedios. Of their past history or existing relations there we know nothing, but it is more than probable that their present characters were acquired prior to their meeting and that, although they now associate as species, they have a common origin. In this connection, however, we are concerned merely with the fact that the members of the wide-ranging genus *Manacus* so closely resemble each other in form and structure and in pattern of coloration that it is more than probable they all have essentially similar habits.

#### GOULD'S MANAKIN

Gould's Manakin [*Manacus vitellinus vitellinus* (Gould)], the form with which we are here concerned, inhabits the tropical forests of Central Panama from Coiba Island on the Pacific side and the Rio Calovevora on the Caribbean side, eastward to Darien.

On Barro Colorado it is a common species known to most visitors as "the bird that *snaps*." It is generally distributed over the island but, during the nesting season, at least, is perhaps more frequently found near the shore line than in the heart of the forest. Doubtless because it is more or less confined to the vicinity of its courting grounds, the male is far more often heard than seen, while the female, because of her dull coloring and comparative silence, is even less often observed.

Both their courting and nesting are conducted on or near the ground and both sexes, therefore, belong in the lower zone of forest bird-life, but either may ascend to the tops of tall trees for their fare of small fruits.

Their flight is as direct as that of a bee and is accompanied by a slight whirring sound produced probably by the rapid motion of the small, rounded wings rather than by the incised feathers.

#### The Color of Specimens

ADULT MALE.—Entire crown, foreback, scapulars, wings and tail black; throat, breast, and connecting nuchal collar lemon-chrome to light cadmium, in some specimens more or less irregularly washed with cadmium yellow; rump and upper tail-coverts olive or warbler-green; underparts, including lower tail-coverts and legs, greenish or sulphine yellow; lesser wing-coverts more or less yellow; lining of wing whitish; bill black; tarsi dull scarlet.

ADULT FEMALE.—Warbler to olive-green, paler below, yellower abdominally; wing-lining yellowish white; bill black; tarsi dull scarlet.



YOUNG MALE.—Resembles the female, apparently acquiring adult plumage at the postjuvenile molt. I have no specimens of *Manacus vitellinus vitellinus* in this plumage, but two examples of the closely, perhaps racially, related *Manacus aurantiacus* show this plumage-change satisfactorily. One was taken at El General, Costa Rica, June 24, 1908; the other at Cerro Montosa, Cape Mala Peninsula, Panama, August 5, 1925.

#### Color in Life

Viewed in the hand the male of *Manacus vitellinus* seems to be brightly colored and hence to be an exception to the rule that tropical forest birds living on or near the ground wear dull plumage. But in life this species is far from conspicuous. Its broken pattern of marking makes its yellow area seem more like a yellow leaf than part of a bird, and its habit of occupying the same perch for comparatively long intervals adds to the difficulty with which it is seen when at rest. But when in motion, as with all other birds, without regard to color, it is readily observed. It, therefore, seems surprising that the courting males, which day after day for months, by both voice and action, do their best to attract attention to themselves, do not become the victims of predatory animals. In only one instance has a court under observation lost its owner, evidence that, in practice, the performing birds are not unduly exposed to danger. In any event it seems obvious that, since one male may fertilize a number of females, his life is of far less importance in maintaining the existence of the species than that of the female.

At 9:32 A.M., on February 15, 1932, while watching Court No. 3 of the Laboratory Group, a young puma entered it just as its owner, having finished a performance, flew into the forest. The bird was not, apparently, aware of the puma's coming. Whether the animal was attracted by the bird I am unable to say. It remained in the court for one minute eyeing me and occasionally sniffing the ground. Then it turned and lightly bounded whence it came. Later I discovered in Court No. 1 what was doubtless the puma's "kill"—the body of a three-toed sloth with the viscera partly eaten. During the day this was dragged about thirty feet from the court and further consumed; during the night it disappeared.

Doubtless my arrival at the group, at 6:20 A.M., had disturbed the puma at its meal, to which attraction of food had induced it to return when, normally, it would have been in retirement for the day. Possibly the usually crepuscular or nocturnal habits of the Felidae may

be one of the reasons that performing manakins seem exempt from their attack.

### The "Beard"

The feathers growing from the throat and chin of the adult male Gould's manakin are more or less elongated, those from the latter region reaching a length of twenty or more millimeters.

At times of sexual excitement these feathers are erected and the degree of stimulation may be measured by the extent of their elevation. The maximum extent of their display is attained when the bird visits "court." At such times this tuft of feathers is not only erected but projected forward, and the surrounding yellow areas are so expanded that the black cap seems a comparatively small spot widely surrounded by yellow. This action completely transforms the appearance of the bird.

### The Wings

The completely expanded wings of both male and female Gould's manakin are shown in the accompanying photographs. These reveal their proportion, and shape, but not, adequately, the texture of the

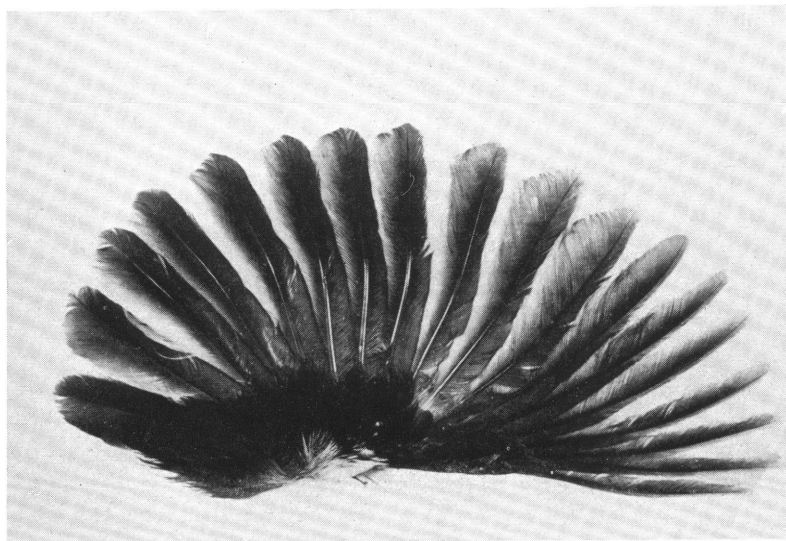


Fig. 1. Photograph of wing of male Gould's manakin.

(Natural size)

Note incised outer primaries, enlarged and slightly curved shafts, and broader, firmer webs of secondaries as compared with corresponding feathers in wing of the female.

feathers. The shafts of the male's secondaries are not only laterally curved and stouter than those of the female, and their vanes, particularly the outer one, broader, but the vanes themselves are much heavier and the wing, in consequence, stiffer. It is also flatter and less arched than in the female.

In *Machaeropterus deliciosus* the secondaries reach an extreme of development, as figured in the accompanying cut from Selater's description of this bird, of whose habits we know nothing. Selater appends to his description of *deliciosus* the interesting statement:

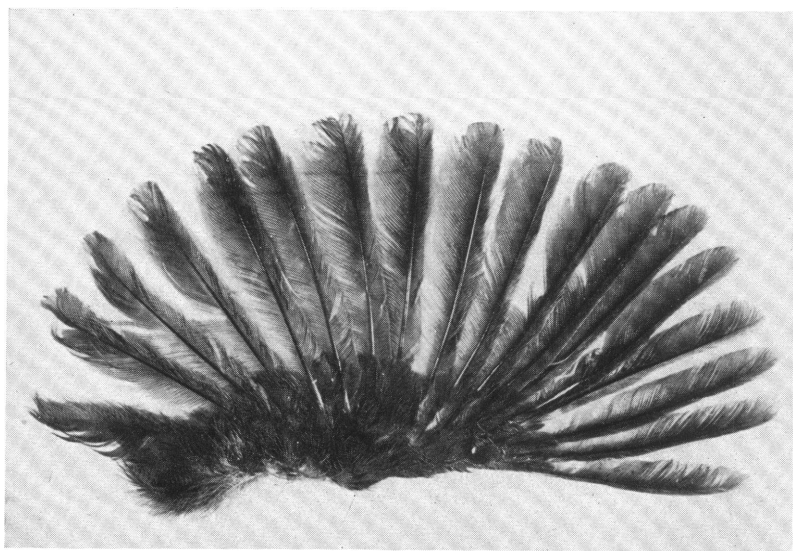


Fig. 2. Photograph of wing of female Gould's manakin.  
(Natural size)

For comparison with wing of the male.

"The same deviation from ordinary characters is observable in other species of the allied group *Chiromachaeris* [= *Manacus*] (e.g. in *C. manacus*, *C. gutturosa*, *C. candei*, etc.). I believe it is this structure which enables them to make the extraordinary noise for which they are noted." (P.Z.S., 1860, p. 91.)

Darwin ('Descent of Man,' first edition, 1871, II, pp. 65, 66) quotes Selater's description of the wing of *Machaeropterus* and adds "These little birds make an extraordinary noise the 'first sharp note being not unlike the crack of a whip.'" This enclosed quotation, however, does not refer to *Machaeropterus* but to *Manacus candei* as described by Salvin (*Ibis*, 1860, p. 37).



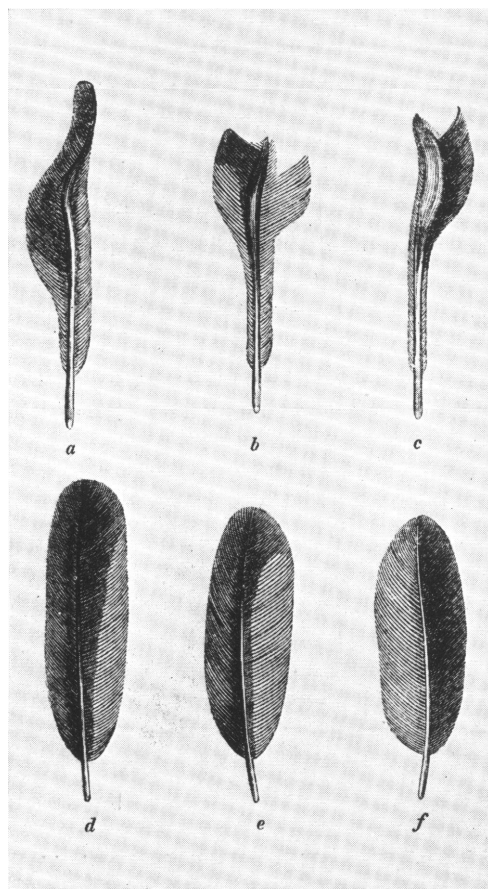


Fig. 3, *a, b, c*. Fifth, sixth, and seventh secondaries of the male of *Machaeropterus deliciosus*, the first two from above, the last from below. *d, e, f*. Corresponding views of same feathers in wing of female.

(After Selater, P. Z. S., 1860, p. 91.)

		Size <sup>1</sup>			
		WING	TAIL	EX. CULMEN	TARSUS
15 males	Panama	50-55 (52.8)	27.5-31 (29.6)	10.5-11.5 (10.09)	20-21.5 (20.8)
5 females	"	51.5-55 (54)	29.5-35 (30.9)	11-11.5 (11.1)	19-20 (19.5)

<sup>1</sup> From Ridgway, Bull. L, U.S.N.M., 1907, IV, p. 733.

## MY STUDIES ON BARRO COLORADO

My studies of Gould's manakin were made on Barro Colorado Island, in the Canal Zone, between January 20 and March 24, 1932,<sup>1</sup> and December 9, 1934 and April 17, 1935. In 1932, observations were made on 43 days; in 1934-1935 on 62. They were usually begun at

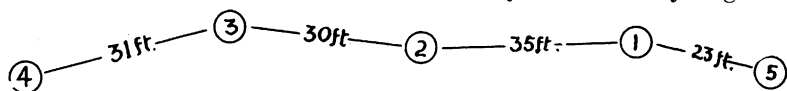


Fig. 4. Position of "Courts" in the Laboratory Group. 1932.

7:30 to 7:45 and continued until 9:30 to 10:00 A.M. Occasionally I was afield soon after daybreak, also at mid-day and in the late afternoon.

In 1932, manakin court groups were found on the small peninsula 300 yards east of our laboratory pier (Laboratory Group); on the slopes west of the upper part of Fuertes Estero (Fuertes Group); near

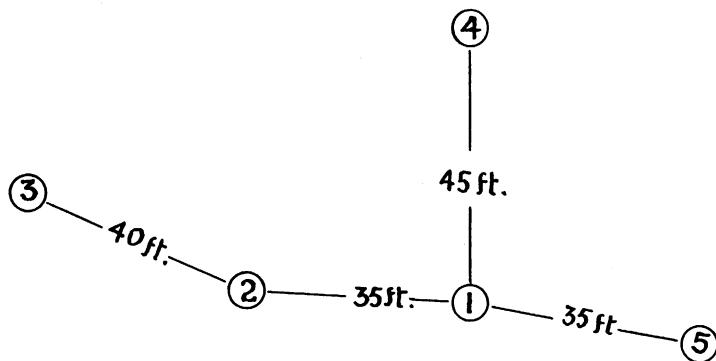


Fig. 5. Position of "Courts" in the Laboratory Group. 1935.

the end of the Miller Trail (Miller Group); at No. 23 Armour Trail (Armour Group); and (by Dr. Ray Carpenter) on a small peninsula

<sup>1</sup> An abridged, popular report of these observations was published in 'Natural History,' Nov.-Dec., 1932, pp. 470-480.

west of No. 6 on the Fairchild Trail (Fairchild Group). Studies were made chiefly at the Laboratory and also at the Fuertes Group. Both contained five courts.

In 1935, thanks to the stable conditions that prevail on Barro Colorado, the Laboratory, Fuertes, Armour, and Fairchild Groups were again active. A group was found at No. 2, Donato Trail, which may have been occupied in preceding years. The location of the Miller Group was not re-visited. Studies were made chiefly at the Labora-

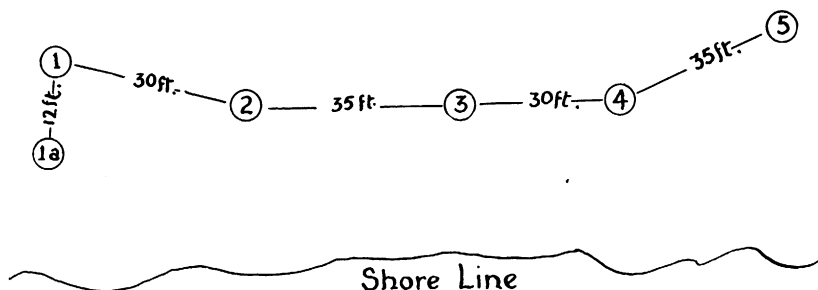


Fig. 6. Position of "Courts" in the Fairchild Group. 1935.

tory Group (5 courts), Fairchild Group (7 courts), and Donato Group (5 courts).

Male Gould's manakins, when at their courts, can be approached to within a distance of eight to ten feet. Beyond the cover afforded by the vegetation, no concealment, therefore, was required in the study of these birds. It should be obvious, then, that whatever merit this study

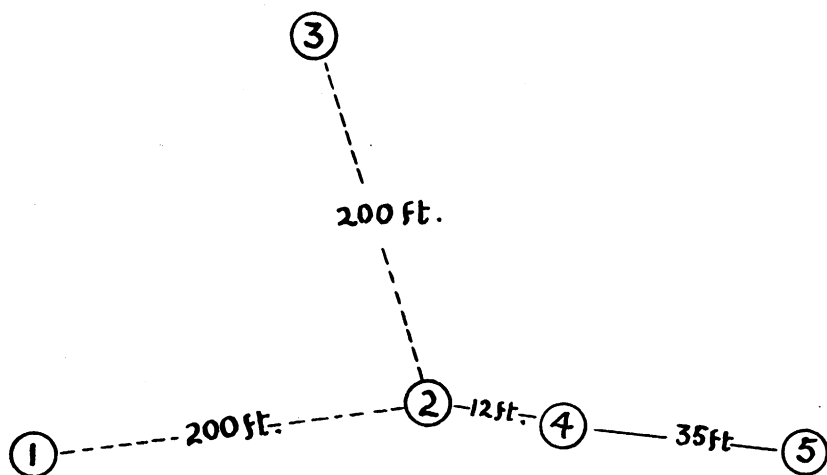


Fig. 7. Position of "Courts" in the Fuertes Group. 1932.



of manakins may possess is due in no small part to the coöperation of the birds themselves. Observations were recorded in a field book as they were made and were subsequently "posted" on sheets under the subject heading to which they belonged.

In addition to notebook, pencil, and field-glass, my equipment consisted of a leather-bound cushion, which provided a comfortable, dry, and comparatively insectless observation post, a "snapper," with which to imitate the sounds made by the birds, and mounted specimens of both sexes of Gould's and the yellow-thighed manakins, with feathers and Duco cement with which to modify them, the use of which is described beyond. I employed also, with only indifferent results, both "still" and motion cameras.

The weather records of Barro Colorado as a meteorological station have been used in preparing this report.

#### OUTLINE OF COURTSHIP HABITS

In order that the more detailed descriptions of the courtship habits of Gould's manakin here presented may be considered in relation to the whole of which they form a part, I present an outline of the bird's activities and organization during the breeding season, as I understand them.

Like the ruff (*Machetes pugnax*), and certain, perhaps all, hummingbirds, some grouse, Paradise-birds, and other birds, Gould's manakin conducts its courtship at a *lek*, or regularly frequented locality. Here, during a mating period of not less than eight months, several males gather and are visited by females. At such localities, always in the forest, each male clears a small space on the ground (here called the "court") which becomes the focal point of his existence. Here his rights are rarely disputed, here he produces certain sounds and presents certain performances in order to attract the attention of the female and induce her to take part in his display as a means of stimulating her sexually and securing her consent to coition.

Beyond this connection, at a time when her eggs are doubtless ready for fertilization, it is believed that the adult female has no other association with the male. In the sense of pairing, like the ruff, grouse, and hummingbirds, she has no mate. Unaided, she builds her nest, incubates her two eggs, and rears her young.

It will be seen that this type of courtship organization, with the court as the daily frequented center of sex life, offers an exceptional opportunity for the prolonged and continuous study of both individual

and group life. The male's claim to ownership of a clearly marked area demonstrates a phase of territorialism, while the visit by the female to the male in his court seems equally well to illustrate the theory of sexual selection.

#### EXTENT OF BREEDING SEASON

In 1932 I did not begin to study manakins until January 20, when their breeding season was well under way. In 1934 I reached Barro Colorado on December 7. On the 11th, manakins were first discovered on their courtship grounds, but it was not until the 25th that their courtship *whirrs* and *snaps* were noticed. Between that date and the 28th these sounds were heard at four different localities, indicating that, on Barro Colorado, Gould's manakin begins to court the first half of the last week in December, in other words, at what is usually the beginning of the dry season.

Of interest in this connection is the fact that in both 1926 and 1934 the yellow-thighed manakin (*Pipra mentalis minor*) was first seen courting on December 25.

In 1935 my observations ceased on April 17. While some individuals then seemed less responsive, sexually, than they had been earlier in the season, group activity suggested that the courtship season was far from ended.

Whether more than one brood is raised is unknown, but observations made on Barro Colorado show a high percentage of nest fatality. It is more than probable, therefore, that many females make at least two, perhaps more, attempts at nesting during the same season, and thereby prolong the nesting period.

The activities of courtship are exhibited both in the morning and afternoon. Early in the season they cease at about 9:30 A.M.; later they continue until about eleven o'clock. An essentially similar variation is shown in the afternoon.

The males may be found at or near their courts throughout the day. At intervals of two or three hours they may absent themselves for as many minutes in order to secure food. (See beyond.)

My own incomplete observations, supplemented by those of Drs. Gross and Van Tyne on Barro Colorado and by Mr. Harrower at Gatun, presented beyond, show that courtship and nesting season extends at least to the latter part of August. It covers, therefore, a period of not less than eight months and includes both dry and wet seasons. When we discover that the intense, competitive sexual life

of these birds requires that they be ever ready to respond to the wants of the female, this is indeed a surprisingly long period. It is true we have no data to show that the same male functions continuously during this time. But my daily observations of the same individual show that he is sexually active for nearly four months, and it is not impossible that he may continue to function to the end of the nesting season. On the other hand, it is not impossible that different individuals may have different nesting dates and hence that this eight-month period may represent the nesting season of the species rather than of the individual. But the stability of group and court organization during my nearly four months of continuous observation is not in favor of this theory.

#### SEASONAL VARIATION IN TIME

In 1934-1935 my studies of Gould's manakin began December 9, about two weeks before the inauguration of the nesting season, but, unfortunately, in 1932 they were not begun until January 20. So far as season is concerned, therefore, comparison of the two years cannot properly be made before the last-named date. Moreover, the stuffed female used in these studies throughout the 1934-1935 season was not available in 1932 until February 16, thereby further restricting the comparable periods. Nevertheless, enough comparable data remain to show that there was a marked difference both in the dates and the character of the development of the two seasons, the phenomena of 1932 appearing earlier and being, on the whole, more pronounced than in 1935. Thus, as before stated, the date on which coition with a stuffed female was first attempted in 1932 was February 16; in 1935, March 11. Moreover, the ardor displayed by the male of February 16, 1932, warrants the belief that he would have accepted the stuffed bird at an earlier date. Other activities of court-life seemed to have been performed with greater enthusiasm, and the responses to the mounted bird were more evident in 1932.

This delay or indefiniteness in the advance of the season was also manifest in the blooming of certain trees. Thus the flowering of neither the guayacan (*Tabebuia guayacan*) nor jacaranda (*Jacaranda copaia*) reached its usual climax. Of the former we saw only scattered trees from time to time. At no period could more than half-a-dozen flowering trees be seen from the laboratory on the mainland across the lake, while in former seasons as many as 140 inflorescent trees have been counted at one time. Of the jacaranda only scattered blooms were

noted; not one tree acquired the mass of flowers so characteristic of this species.

It was the emphatic opinion of those of us who were working on the island during the winter of 1934-1935 that the season was exceptionally wet and cold. On the whole the records of our rainfall and temperature seem to warrant the strength of our impression. I append the data.

#### Rainfall

	December	January	February
Average.—1927-1933	8.81	1.71	0.86
1931-1932	2.67	1.20	0.97
1934-1935	15.35	1.66	5.91

#### Temperature

	December	January	February	March
Mean.—1931-1932	?	80.6	80.3	81
1934-1935	80.2	79.6	79.4	?

Compared with the average and also with the season of 1931-1932, it will be observed that the rainfall of December 1934 and February 1935 is much higher, while that of January is essentially the same. It seems possible, however, that the effects of the very heavy rainfall of December may not have been apparent until January and that the birds were further affected by the unusual precipitation of February.

Add the slightly lower temperature of 1935, as compared with that of 1932, and we have, in my belief, sufficient cause to account for the differences observed in the habits of manakins during these two seasons.

Opposed to this theory, however, is the fact that manakins nest until August and thus, well into the wet season. Hence the variation above recorded may be due to other than climatic causes or to insufficient data.

#### THE MANAKIN AND MIGRATION

While the manakins of Barro Colorado, as species, are permanent residents, and, as individuals, probably do not leave the island, the regular return to their mating grounds, at approximately the same time each year, to establish territories to which the female will be invited, is prompted by fundamentally the same motive that induces a migratory bird to return to its nesting grounds. Indeed, a migration in miniature may be observed when the male, inspired solely from within, leaves its perch to visit the heart of its territory for the purpose of

sexual display and possible mating and, this purpose accomplished, returns to the place whence he started.

#### THE COURTSHIP GROUNDS AND COURT

The courtship grounds of Gould's manakin find an equivalent in the *lek* of the ruff. They are situated in the forest, the same locality being used year after year. The males return, or migrate, to them about two weeks before they begin to clear the spaces on the ground in which they display their courtship activities. During this preliminary period I have heard only their vocal notes, *chee-póoh* and *pée-yuk* and its variants, and have seen no evidence of competition for possession of the spot in which the "court" is to be situated.

What I have termed the "court" of Gould's manakin is a space on the forest floor cleared by the bird of all moveable material (see Fig. 11). The making of the court indicates the arrival of the nesting season and it at once becomes the focal point of its owner's life. To induce the female to come to court is now the chief object of the male's existence. His jurisdiction over his court is rarely questioned. If he can induce a female to visit his court, he not only supplies the suggestive background for his advances but also surroundings in which he need fear no competition.

Courts vary in size and shape but are usually irregularly elliptical in outline and average two and a half feet long by twenty inches in width. They are placed in forests with an undergrowth of small saplings, several of which grow at or near their borders.

The bird removes leaves and other material from its court with its bill. This act seems to be more or less sexual in character and often terminates the court display of snapping. Small leaves are carried to a height of about three feet and dropped at an equal distance from the court. Large ones are taken in a more direct line to the border of the court. One that I saw removed measured  $10\frac{1}{2} \times 3\frac{3}{8}$  inches; it was therefore slightly more than two and a half times as long as the bird that carried it.

The court is not only cleaned but kept clean. Leaves that I placed in courts were soon removed. To test the bird's possible sense of color I introduced into a court, at the same time, scarlet petals of the passion flower (*Passiflora vitifolia*) and green leaves of about the same size. There was no regularity in the order of their removal. Sometimes one, sometimes the other was taken first, indicating that the bird was no more responsive to red than to green.

Courts are associated in groups of from four or five to seven and possibly more, and are placed at varying distances from each other. Two courts of the Fuertes Group were only twelve feet apart, but two others of the same group were each 200 feet away from them in different directions. In 1932 the five courts of the Laboratory Group were set at approximately equal distances of about thirty feet from each other. In 1935 some of these courts were near to or on the sites occupied in 1932, but the plan of the group as a whole was different.

The least distance at which we have found court-groups, or *leks*, separated is 300 yards. The intervening area was occupied by very dense growth and included a bit of water about twenty-five feet wide and a difference in elevation of approximately fifty feet. The birds of one court were not heard by me from the other, but it is probable that females occupying the intermediate territory were within hearing of both groups.

Observation indicates that the same localities are used by courtship groups year after year. For example, groups were found 300 yards east of our landing; at the head of Fairchild Cove; at Armour Trail No. 23; and on the slopes above Fuertes Estero in 1932 and 1935. No observations were made in 1933 or 1934, but it seems probable that the localities named were also occupied in those years.

In view of the habit that prompts the female to seek the male, rather than the reverse, it is obvious that a group of males is more likely to attract the female than is a single bird. It also seems clear that unless the members of such a group are organized under laws which all observe, the confusion resulting from ungoverned competition on the occasion of a female's visit would defeat the aims of both sexes. Hence, the company and the court, the continuity of court location, and the law and order of court life.

#### NOTES AND CALLS

The male Gould's manakin is the author of many sounds of which none, in a musical sense, can be called a song. Some are of vocal, others of mechanical origin. The former are probably uttered throughout the year but doubtless possess additional significance during the breeding season. The latter appear to be restricted to the period of courtship.

The principal vocal notes are *pée-you* and *chee-póoh*. Both are high-pitched, clearly uttered, and of sufficient volume to be heard in the forest, under favorable conditions, at a distance of about 200 feet.



Of *pée-you* there are many variants. It may be given as *pée-yur* or *pée-yuk*, with the final syllable slightly trilled, as a pensive *pee-a-a* or a plaintive *pee-e-e*. *Pée-you* or *pée-yuk* is a note of awareness, address and response, or of inquiry or protest. In the latter sense it is invariably used when a mounted male is placed in a bird's court. At such times it expresses excitement and it may be uttered twenty-five to forty times a minute.

*Chee-póoh* is a note of address and response, never of protest or alarm. It frequently follows the rolling *whirr* and, like a signal, is repeated from court to court. It is a well-defined call and subject to little variation.

In addition to these calls the bird utters a variety of single syllabled *chees* and *pees* and fragmentary rolls, all more or less conversational or responsive in character. *Chee*, for example, a low, fine note, is uttered as a rhythmic response to the snap in court of a near or distant neighbor. The calling bird shows no excitement, utters its *chee* after each snap, when it seems to express awareness of and sympathy with the snapping bird's activity.

The mechanical calls of Gould's manakin are given only by the male, and, apparently, only during the breeding season, and hence function as songs. They include a *snap* or *crack*, a *snip*, a snapping *whirr*, and a reedy *whirr*, and are all made with the wing feathers.

The *snap* or *crack* is given only as the bird jumps from one perch to another, distant usually from two to four feet. It has somewhat the character of the sound produced by the explosion of a percussion cap and is apparently made by the sudden, violent impact of the secondaries, one upon the other, which evidently can be secured only by the muscular effort accompanying the act of jumping. As a rule the bird snaps only in or near court. A single *snap* is given with each jump and the frequency of production is determined by the length of the jump, whether the route travelled is around or across the court, and the rapidity of the bird's movements.

It is difficult to believe that so loud and so hard a noise as the snap can be produced by an object as soft as a feather. Doubtless, for this reason, it has often been attributed to a snapping of the mandibles. But if this were true we should expect to find the bill of the male heavier or otherwise different from that of the non-snapping female. Furthermore, if the snap were made by the bill it would not, presumably, be necessary to jump when snapping. On the other hand, the somewhat large, slightly curved and stiffened shafts and broad webs of the sec-

ondaries in the male are doubtless of functional value in producing the *snap*, and represent a stage of development which in *Machaeropterus*, as before stated, has reached its known maximum.

The *snip* is a restrained or nascent snap. It is also, in my belief, produced by the secondaries but does not call for the effort required by the *snap* and, hence, can be given while its maker is perched. It accompanies the arched jump over the court and is heard when several males in the tree tops are pursuing each other or are in joint pursuit of a female. At such times the effect of their combined *snips* resembles the sound produced by an exploding pack of diminutive firecrackers.

In the whirring or rolling *snap* the perching bird throws itself slightly forward, raises its wings above its back until they are within less than an inch of one another, but do not touch, snaps its secondaries and rotates its primaries in such a way as to produce a combined *snap* and *whirr*. This is done with a single effort lasting not more than a second or two, during which the wings are held aloft and the outline of their outer margin can be clearly seen while that of the feathers is blurred.

This sound, while not so loud as the jumping snap, is a surprising sound, and also denotes sexual excitement. It may be uttered anywhere, in court or out, and usually announces the return of that condition which prompts court display. It is frequently followed by the vocal call *chee-póoh* and is answered in kind by birds throughout the group.

The reedy *whirr*, the fourth of the mechanical calls produced by the male of Gould's manakin, is a comparatively low, short, vibrant call without a trace of snap, and, in my opinion, is produced by its deeply incised outer primaries. It usually follows a round of court snapping as the bird flies upward to a perch near the court; but it can be produced in less resonant tone by the perching bird. At such times the wings are half-raised.

Of these mechanical calls the *snap* and the snapping *whirr* are the loudest and hence doubtless the most important. On a still morning, over water, I have heard them at a distance of 300 yards. When courting, the males are confined by habit to an area a few square yards in extent and it is therefore essential that they have some effective means of announcing their presence to the females who may be in need of their attention. Lacking a voice of much volume, like many other birds, they use their wings to produce sounds that will notify receptive

females of their location and invite them to share the functions of the court.

#### THE OBSERVANCE OF TERRITORIAL BOUNDARIES<sup>1</sup>

The success of the *Manacus* system of courtship is based on a rigid observance of territorial rights. With the exception of the two unusual instances, described under "Interrelations of Males," no living male manakin was seen in another's court and experiment shows that territorial boundaries extend a well-defined distance beyond the border of the court itself. When the courts are comparatively near one another the intervening area is divided between their owners, the amount belonging to each being in apparent relation to the birds' sexual development. Both distance and development were measured by the use of mounted birds. In 1932 only a female was available. In 1935 both sexes were employed, but the male provoked a greater response.

From many experiments I select the following: Courts 1 and 1-a of the Fairchild Group were but twelve feet apart. Their owners had no relations with one another, each perching near its own court. On March 12, a stuffed female was placed in Court No. 1 and a few minutes later was removed to Court 1-a. She aroused a similar and only slight response from each court owner and was soon replaced by a stuffed male, first in No. 1, then in 1-a. This bird was attacked in both courts, No. 1 acting more vigorously than 1-a. The stuffed male was then placed at different distances between the two courts when it was found that No. 1 attacked it up to a distance of seven feet from his court, No. 1-a remaining in his territory; but beyond seven feet it was attacked by No. 1-a, while No. 1 did not go beyond the seven foot line. March 17 this test was repeated with essentially similar results.

This division of the space between courts was found to occur up to a distance of seventy feet. In the Donato Group, this distance separated Courts Nos. 1 and 2. There, on March 8, 1935, the owner of Court No. 1 responded to the introduction of a mounted male in his court chiefly by the assumption of a pose of nine minutes duration. The owner of No. 2, on the contrary, was far more aggressive and, after jumping and snipping, just outside court, flew at the mounted male, perched on his head and picked at it furiously. This action was at

<sup>1</sup> Since writing this section I have read Dr. Ernst Mayr's classification of territories in his paper on 'Bernard Altum and the Territory Theory' (Proc. Linn. Soc. N. Y., 1933-1934, p. 33) from which it is clear that, as a territorialist, *Manacus vitellinus* belongs in Section "II. Mating station, but not feeding ground. (b). Not connected with nest (Ruff, many Tetraonidae, Paradisaeidae)."

once repeated whenever the bird was driven off and permitted to return.

When the mounted male was moved gradually from Court No. 2 to Court No. 1 it was found that No. 2's interest extended up to forty-five feet while No. 1 did not appear until the mounted bird was within twenty feet of his court.

An unusual illustration of the recognition of territorial boundaries was supplied on February 26, 1935, by the owners of Courts No. 3 and 4 of the Fairchild Group. At 8:53 A.M. a mounted female was placed in Court No. 4. At 8:54 the male returned, *whirred*, hopped about with beard partly extended, but made no close approach to the mounted specimen. This slight demonstration attracted the attention of No. 3 who came from his court, distant thirty feet, and perched about midway between the two courts. Meanwhile a living female appeared in Court 3 (whether in the male's absence or after his return I am unable to say) and jumped with its owner who *snapped* loudly. This more pronounced demonstration attracted the attention of No. 4, who now left his court, with its stuffed female, and went about halfway toward Court No. 3. There he *whirred*, *snapped*, and twisted his head in a peculiar spasmodic manner, indeed showed more excitement than he had before, but did not venture beyond what he evidently considered his territorial boundary.

Later study of these two birds showed that No. 3 possessed much greater sexual ardor. He indeed was one of the few males who in 1935 attempted to mate with a mounted female and, correlated with his condition, a test with a mounted male showed that he claimed two-thirds of the distance between his court and that of No. 4.

Wider territory was claimed not only by the most sexually active bird, but, as might be expected, by the dominant bird. This was shown by tests made with a mounted female between Courts Nos. 2 and 4 of the Fuertes Group, which were twelve feet apart, and between Nos. 2 and 3 of the Laboratory Group, which were thirty feet apart. In each case the dominant's territory was about fifty per cent greater than that of the submissive's.

In these, and many similar tests, it was observed that in no instance did the neighboring birds both claim the mounted bird at the same time, nor did either one trespass on the territory of the other. This recognition of boundaries makes for law and order. No time or energy is lost in futile disputes or needless conflicts and the birds may devote

themselves to winning the attention of the female, now the chief object of their lives.

The disruptive effects of trespass are clearly shown by the prompt and vigorous response to the introduction of the mounted male in court, as shown in the succeeding experiments.

#### INTERRELATIONS OF MALES

When one considers the intense sexual ardor of the males and the fact that the mating activities of a number of individuals are conducted in a comparatively limited area, the fact that conflicts between them rarely occur is a tribute to the effectiveness of their group organization.

In the earlier part of the courtship season, before the attachment to their courts is fully developed, two to six males have been observed and heard actively jumping, *whirring*, and *snipping* twenty to thirty feet from the ground in the upper part of small trees. Rarely a female, of which the males seemed to be in pursuit, was observed, and on at least one occasion a male appeared to give chase to another, but, normally, no actual contact between males has been observed. A male's court is his castle and with rare exceptions I have not, under normal conditions, seen his right of possession disputed.

When neighboring courts are comparatively near each other the owner males, during periods of sexual inactivity, often occupy perches within six or more inches from one another. At such times one bird, and always the same, may try to win the attention of the other by actions which, in a measure, suggest the courtship of the female yellow-thighed manakin by the male. With short, mincing hops, the "courting" bird self-consciously approaches the "courted" bird, occasionally half-flitting his wings and quickly bowing his head; this manoeuvre is preceded or followed by a rapid, nervous turn of the head from side to side through an arc of about 120 degrees. At times this motion becomes so pronounced that the bird turns its entire body halfway around and back again. Not a note is uttered, but the beard of the "courting" bird is extended and in periods of extreme activity he appears to be much excited. At all times his attitude toward the male he is addressing is one of supplication or submission and I have called him, therefore, the "submissive." Meanwhile, the bird addressed makes no response and, beyond an occasional change of position, makes no acknowledgment of the apparent homage that is being paid to him. This demonstration may occur at frequent intervals. I have

called the bird addressed the "dominant." In three out of four cases his yellow areas were darker than those of the submissive bird.

In only one instance has any question of court ownership been noted. This occurred in 1932, in Court No. 1 of the Laboratory Group. For a period of over a month (January 20–March 1) this court was occupied by two males; at the end of that time apparently one of them (I did not ascertain which, if either) formed a new court twenty-three feet beyond No. 1. One of these males was the darker and in my notes they appear as "Dark" and "Pale." At times Pale acted as a submissive to Dark, courting it as described above. At other times it seemed to be a rival of Dark, snapping and performing in the court as though it were the owner. Always it retreated before Dark who was ever the aggressor in pursuit. Again, for long periods, the two birds perched within a foot or two of one another. But in these apparently peaceful intervals Pale was on guard and, at any movement of Dark, half-raised its wings in anticipation of attack. This situation continued until, as I have said, a new court was formed beyond No. 1, I assume by either Dark or Pale, but without seeing them together I was unable to say which of the two remained in No. 1. On March 24, 1932, when a mounted female was placed in Court No. 1 the owner did not appear, but the owner of the new court, No. 5, came to it, evidence supporting my belief that this court had been built by one of the two birds which had claimed No. 1.

It is interesting to record that three years later a court was still placed at position No. 5 and one within twelve feet of position No. 1, and that No. 1 was submissive to No. 5, their relations being more pronounced than in any other observed case of this type of homosexuality.

When, in 1935, a mounted male of Gould's manakin was placed in Court No. 1, not only No. 1 responded but it was joined by its dominant No. 5 who showed his relations to No. 1 by threatening the mounted bird as actively as did No. 1, the owner of the court. Although, as related under the section on "Territorial Rights," the presence in court of an alien male was, as a rule, vigorously resented, the assistance by No. 5 to No. 1 was accepted by the latter in good part, as in apparent conformity with his relations as a submissive to No. 5.

#### THE ACTIONS OF THE COURTING MALE

The wide variation in the actions of courting males doubtless depends primarily on their sexual development, as that is affected by the time of the year and the character of the season. But they are also



influenced by the nature of the stimulation to which they are subjected, and probably also by temperament and by age.

In 1932, sex-life seemed better organized and its manifestations more pronounced than in 1935; the female more often visited court and there appeared to be less pursuit of her out of court. In the belief that high rainfall and low temperature checked the development of the breeding phenomena of 1935, I use here my observations of 1932 as more nearly representing the normal habits of the species.

While waiting for the appearance of a female, the event of supreme importance in his life at this season, the male perches quietly near his court. Should he have a close neighbor, the two birds often sit within a few inches of one another when there may arise between them the dominant-submissive relation described above.

Should the waiting bird be alone, he squats in relaxed pose on his red toes and seems to be dozing. But his wide open eyes and the frequent movement of his head show that he is constantly on the alert.

To the snapping in court of another member of the group he may, without changing his position, reply with a sympathetic *chee*, repeated rhythmically after each snap. A snapping *whirr* arouses more interest and, raising his wings, he replies in kind. If this signal spreads through the group, indicating that the alarm is not a false one, he proceeds to his own court to perform, or, when court-life is not fully organized, he may take part in a disorderly pursuit of the female, through the tree tops, by several *whirring*, *snipping* males.

On occasion he appears to be aroused by an inborn emotion. Without apparent cause he suddenly calls *chee-póoh*, becomes more alert, partly erects his beard, and raises his wings for a *whirring snap*. Meanwhile he has moved toward his court, his excitement increases, his beard is thrust forward, and with a series of cracking *snaps* he makes the round of the perches about his court.

Six to ten *snaps*, delivered as rapidly as two to the second, may leave him on the ground in court with beard still extended and yellow areas fully expanded; then, with head on one side, or with bill pointed upward, he assumes a rigid, gaze-pose and holds it for from several seconds to a minute or more.

After this rest, inspired to fresh exertions, he may jump rapidly forward and backward across court and, no matter how short the distance, in some invisible way, he turns in the air to alight, facing the point of departure.

The display is usually ended by an upward jump to a nearby perch, which is accompanied by a low-toned, reedy *whirr*. This sound, rarely heard at other times, is without trace of *snap* and is made, I assume, by the narrowed primaries.

To this exhibition, No. 3 of the 1932 Laboratory Group added what I have called the dirigible pose. 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, 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. In spite of this remarkable demonstration, which was not infrequently repeated and seemed to imply the possession of much virility, its author, No. 3 of the Laboratory Group, was submissive to No. 2.

When the male has been prompted to visit court by the presence of the female, this demonstration is evidently designed to induce her to visit him in court. But in her absence it apparently is inspired by cumulative, ungratified sexual desire, and we may think of his snapping dash around or to and fro across court as a pursuit of an imaginary female, while the subsequent display is a further outlet for excess sexual emotion.

His ineffective attempts to mate with a stuffed female so stimulated No. 3 of the Fairchild Group that he often left the mounted bird to jump and *snap* about his court.

When the performer was not sufficiently stimulated to *snap*, the jump from perch to perch was arched and accompanied by only a *snip*, and at times it was wholly noiseless.

This demonstration is supposed to indicate that the male is ready to "dance" with a female should she come to him. Whether the dance will lead to coition depends doubtless primarily on the condition of the female. But the failure of the male of March 20, 1935, in the Fuertes Group to respond to a stuffed female, but to repeatedly mate with a living one, indicates that in some instances the male, as well as the female, requires the stimulation of the dance to induce coition.

Whether during his long period of court-life, which may last for eight months, the male at times is not in condition to mate, I am unable to say, but it is difficult to believe that he would submit to the restrictions of court-life if he were not at all times ready to perform its functions. The males that mated with a stuffed female were *always* ready to mate with her.

## THE ACTIONS OF THE FEMALE AND HER RELATIONS TO THE MALE

The female of Gould's manakin is obscurely colored, her single call-note, *pée-you* or *pée-yuk*, is not often uttered, she apparently visits courts rarely, in short, her mating habits are so difficult to observe that my notes on them are far from satisfactory.

It seems clear that when the female is in condition to have her egg or eggs fertilized she visits the *lek* to receive proper attention from a male. Whether she visits it at other times I am unable to say. I have seen birds in female plumage in the trees above the courts whose presence did not excite the males. They may have been young males, they may have been unripe females. If, however, the males are able to recognize the oestrous female, why are they so often deceived by a mounted female, as described beyond? On the other hand, it seems improbable that a female would nest in a *lek* within forty feet of the nearest occupied court without being annoyed by the males, who were doubtless at all times conscious of her presence, unless, in some way, she could inform them that she did not wish to be courted.

Usually I was made aware of the presence of the female by the activity of the males. Presumably the first male to see her produces his snapping *whirr* often followed by the vocal *chee-póoh*. The significance of this demonstration seems to be understood and it is repeated by bird after bird throughout the *lek*. One or more of the birds then goes to court and snaps. It will be observed that under these conditions the male does not go to the female, but to his court, in an apparent attempt to induce the female to visit him there. In court he will not have to meet the competition of other males; in court the stage is set for the performance which may lead to the consummation of his desires. For whatever be the sexual condition of the female, she apparently must be courted before she will receive the male.

Producing, therefore, their loudest sounds from fixed localities, the males issue their invitation and, in accepting one of the several available, the female seems to select her partner. But before giving her consent to coition she apparently is to be further stimulated by a performance which may be called the mating dance. At its full development this is a rhythmic jumping across court, or its immediate surroundings, in which, facing one another, the two birds jump at the same moment, pass in midair, and repeat from the same or new perches. While the birds act in unison and thus give to their actions the character of a concerted performance, this so-called "dance" is possibly a mock pursuit in which the female, instead of making a genuine effort to escape

the male, keeps just beyond him and possibly thereby increases his desire to secure her. The male *snaps*, the female is silent; there is an air of excitement about this performance which often produces no observable result, may lead to coition in court, or may be terminated by what appears to be a mating flight in which the two birds disappear.

It will be seen, then, that the completed cycle of this joint demonstration requires (1) that the sexual condition of the female prompts her to seek the male of whose suggestive calls she may be within hearing. (2) Arrived at the *lek*, the more evident and urgent invitations of the males further arouse her desires until she is induced to visit the court of one of her ardent wooers; an apparent instance of sexual selection. (3) Not yet aroused to the point of sexual consent she evades the male's advances by jumping across court as he springs toward her, but if the excitement of the chase sufficiently stimulates her she may mate with the male in court one or more times, or coition may follow the end of a mating flight.

When court organization is neither complete nor binding, or, possibly, when the female is not sufficiently developed to respond to the invitations of the male to visit his court, the males leave their courts and with much *snipping* pursue the female in the tree tops. The result is confusing and apparently the ends of neither sex are served.

I quote from my field notebook several of the observations on which these generalizations are based:

January 29, 1932. Laboratory Group. "8:10 A.M. No. 1 calls and hops. No. 2 calls a little. 8:15 a female comes to No. 1. They jump and either one or both snaps to bare place, then to perch, back and forth, crossing one another. Female perches 6 feet up quietly, then disappears. Male, alone, jumps to and fro, calling."

January 30, 1932. Laboratory Group. "8:30 A.M. As I arrived No. 2 was 'dancing' with a female back and forth over court, changing places regularly about eight times. Apparently only one snapped, very fast. Female leaves; returns in five minutes; scene repeated. Between visits male *whirrs* with wings erect."

February 6, 1932. Laboratory Group. "9:05 A.M. Female alights over Court No. 2; stays 3, 4 seconds, finds no one there; disappears toward No. 1; nothing happens. 9:09 No. 2 returns; takes perch female just left."

February 11, 1932. Fuertes Group. "9:00 A.M. While crouching near No. 1, see female *Manacus* on ground apparently drinking from large circular basin, like fallen leaf, 5 feet away. Male pays no

direct attention to her but is exceedingly active, whirring and snapping out of court as well as in. I reach a good position about 12-15 feet from court. Male comes repeatedly, but makes no attempt to clean court, which is not well kept, and only once alights on it, near edge. No side gazing, no reverse jumping, just jumping and snapping with beak forward. Female appears and joins male in court, jumping to and fro with him in an orderly manner. It is a two-part performance; he jumps and snaps, she jumps only and does not make any noise, so far as I can tell. Nor did he attempt to pursue her. Once he left court while she remained perched directly above it (20 inches). He went only to the edge for a few seconds, then returned and their jumping was renewed for 15-20 seconds more. Then they disappeared."

February 13, 1932. Laboratory Group. "8:30. All active; female comes to No. 3. They dance."

February 17, 1932. Laboratory Group. P.M. "Female comes to No. 2 and quickly departs. Comes again, goes; No. 2 snaps."

February 29, 1932. Laboratory Group. "3:30 P.M. No. 2 dances with female in usual manner. Stops as I land. He goes into rigid upward gaze. She flies away. He snaps in court repeatedly, flies to left and returns to snap. Much activity to left."

March 13, 1932. Fuertes Group. "8:10 A.M. A female appears in No. 2 and jumps with male; intense excitement in Nos. 4 and 5, both snapping and jumping. No. 4 ventures near No. 2 and is at once driven away. Female disappears and males perch quietly over courts."

March 15, 1932. Laboratory Group. "8:22 A.M. Nos. 1 and 2 call and answer actively, each from court. No. 2 *whirrs* and gazes one half a minute. A female appears in No. 2; they dance, crossing 6 or 8 times. He mounts her; they fly off. He returns alone. Two minutes later female comes, they dance again briefly, and he pursues her into the tree-tops. Snapping in the other courts."

December 31, 1934. Laboratory Group. No courts had as yet been cleared and the numbers refer to birds in or near the spots they subsequently occupied. "8:15 A.M. Females in Nos. 1 and 2 and much (full) excitement. One dances with No. 2 and apparently chases him to and fro. A second male appears and there is much confusion. Is there a court? Female and male 15 feet up; much unlocalized calling."

January 21, 1935. Laboratory Group. "8:05 A.M. A female and two males beyond No. 1. Much general excitement."

February 1, 1935. Laboratory Group. "7:45 A.M. Much, at times, almost constant activity in 1, 2, 5, and 4. Female comes to 2; he goes to court, *snaps* and *whirrs* around her but she makes no response and soon flies. He does not follow."

February 4, 1935. Laboratory Group. "8:00-8:15. Much *snipping* and *chee-pooking* in trees. A female over my head up hill hops about for two minutes; silent. Much *snipping* toward No. 5 but no one pays attention to her. A great deal of disorganized out-of-court activity, difficult to follow and still more difficult to understand. Four males all *snipping*, *whirring* and jumping around in trees and bushes, not near court, presumably after female which I do not see."

February 9, 1935. Laboratory Group. "9:25 A.M. "A female (?) appears but causes no excitement or interest."

February 15, 1935. Laboratory Group. "7:45 A.M. Nos. 1, 2, 3, 5 all snapping actively in courts. A female visits No. 1 and dances with him. He snaps. No visible results."

February 23, 1935. Laboratory Group. "8:30 A.M. Place mounted female in No. 5. He calls a little. A living female comes; he snaps a little and she jumps with him but no real excitement or result."

February 26, 1935. Laboratory Group. "9:00 A.M. Female comes to No. 3. He jumps with her. No result. No. 4 comes halfway but no farther, *whirrs*, half-snaps; gives a singular half twist to head."

March 4, 1935. Laboratory Group. "8:10 A.M. A female in No. 5 flies beyond No. 1 and perches for 10-15 seconds. Nos. 1 and 5 snap in court but none goes to her and she flies away."

March 16, 1935. Donato Group. "9:00 A.M. Three or four males in pursuit of one female; they *whirr* and *snap* a bit 10-12 feet up."

March 18, 1935. Laboratory Group. "8:05 A.M. A female seen in the tree tops; general whirring. She disappears."

March 20, 1935. Fuertes Group. "8:20 A.M. Place mounted female in group near water (a second bird 30-35 feet distant). 8:25. Male returns, also living female comes. They hop to and fro above and about court but no excitement. She goes and he perches quietly, paying no attention to mounted female. 8:28. Living female comes twice. She jumps with him in a disorganized, half-hearted way; he snaps some. 8:50. Female comes again; they jump; he snaps; she perches 4-6 inches below stuffed female and they mate. 8:55. Actions of 8:50 repeated. 8:57. Quiet. 9:00. Female returns; jumping and calling only. 9:08. Male sits quietly, alone. No attention paid



to stuffed female. 9:14. Living female returns, they act as at 8:50 and 8:55; she perching as before, below stuffed female, where he mates with her. She disappears. He perches quietly. 9:23. He *whirrs*; perching 18 inches above stuffed female but paying no other attention to her. 9:30. Stuffed female replaced by stuffed male. Response immediate and pronounced. Living male calls *pee-yur*, or *pee-yuk* about 30 times to the minute; hops actively about stuffed bird but does not attack it. Neighbor (who before has been silent) now seems interested and calls. 9:50. Remove male and go."

The infrequency with which the cycle is completed suggests that, at times, the male, as well as the female, must be sexually stimulated.

#### THE ACTIONS OF THE YOUNG MALE

February 29, 1932. Laboratory Group. 8:00 A.M. Two birds in female plumage, twenty feet up, call *pee-yuk* repeatedly in weak voices and make a slight, short wooden *whir* as they jump in short jumps from place to place. An adult male *whirrs* and *snaps* behind me, but no attention is paid to these "females."

Here then, the juvenile male, possessing a power that the stuffed female lacks, presumably informed the adult male of its sex and was not, therefore, courted as a stuffed female or, doubtless, a stuffed juvenile specimen would have been.

The fact that the juvenile male cannot be distinguished from the female in plumage makes it difficult to secure authentic information in regard to its habits. However, on several occasions, when I have seen birds in female plumage on the courtship grounds which produced a slight wooden *whirr* or an insignificant *snip* and were ignored by the adult males, I have assumed that they were juvenile males. See, for example, the following observation.

#### FEEDING HABITS OF THE COURTING MALE

I speak here of the feeding habits of Gould's manakin only as they are related to its courtship methods. The impulses of the breeding season confine the male to his court and its immediate vicinity in order that he may always be prepared to receive a visiting female. The food of this bird, so far as I have observed, consists of small berries or berry-like fruits similar to that of the mangabé (*Didymopanax moratotoni*). I have not seen food of this nature growing in or near a court and the birds under observation have, therefore, been obliged to go beyond the range of vision to secure food. This they did at intervals of two or

three hours, flying away with a direct objective flight and returning in a few minutes. In one instance the returning bird carried a berry in its bill, which was subsequently swallowed.

Near my home on Barro Colorado there are several trees about 30 feet in height which for the first ten days in March, 1935, bore clusters of small black berries. These were eaten by several species of tanagers and by Gould's manakin. When there were several manakins of both sexes in the trees it was not unusual to hear the males, doubtless stimulated by the presence of the females, *snap* and *whirr*. But the calls were half-hearted and did not seem to be of functional importance.

A male, which was observed perching quietly for a period of about fifteen minutes, was evidently in no hurry to return to court, if he had one. Possibly, he was not breeding.

#### NESTING

On March 9, 1932, I found my first and only nest of Gould's manakin. It was a rather lightly constructed, shallow bowl, or deep saucer, hung in a forked branch about five feet from the ground, and contained two whitish eggs heavily streaked with reddish brown covering most of their surface. From it the males in the nearest courts, distant about 100 yards, could be heard snapping.

Until March 14 this nest was under observation for three periods, but no male was seen near it. At this time I left the island, but Dr. Robert E. Enders reports that the nest was later abandoned.

Fortunately, I am not dependent on only my own observations for information concerning the nesting of Gould's manakin. Data of the first importance have been generously contributed from Barro Colorado by Drs. Alfred O. Gross, Jocelyn Van Tyne, and Alexander Skutch, and from Gatun by Mr. David E. Harrower. Dr. Gross also sends photographs.

Dr. Gross writes of three nests found near the mouth of the brook that parallels the Lutz Trail and enters the lake at the easterly side of the Laboratory dock. From his data I select the following:

"No. 1.—Found July 10, 1925, by F. Drayton; contained two eggs. The bird remained incubating until I was within two feet of the nest. July 22, 1930, A.M. One egg hatched. July 24. Nest and young destroyed during the night.

"No. 2.—Found July 22, near No. 1, about four feet from the ground; two eggs."



Fig. 8. Nest and eggs of Gould's manakin.  
Barro Colorado, C. Z., July 22, 1925.  
Photographed by Alfred O. Gross.

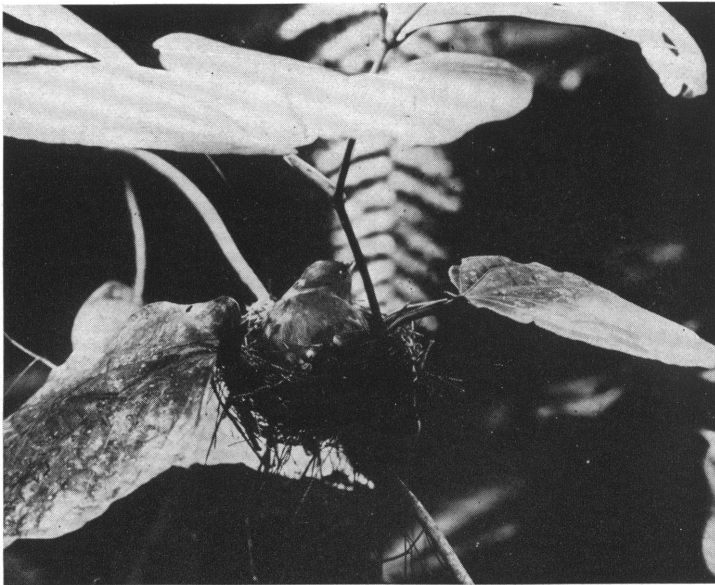


Fig. 9. Gould's manakin on nest.  
Barro Colorado, C. Z., July 22, 1925.  
Photographed by Alfred O. Gross.

Dr. Van Tyne also studied nest No. 1 and, in addition, he reports the discovery on July 12, 1925, of a nest about "200 feet farther up the brook" and on August 1, 1925, of one "in the forest just west of the laboratory." The first contained eggs which hatched on the 14th. It was under daily observation until July 18 when it was found destroyed. The second contained one egg on August 1, two on the 3d. They hatched on the 22nd, after an incubation period, therefore, of nineteen days. Dr. Van Tyne also records the taking of an incubating female on August 26.

Both these observers state that males were neither seen nor heard near the nests observed by them.

In 1935, Dr. Alexander Skutch discovered four nests and contributes the following data concerning them. In no instance was a male seen near them.

"February 27. To-day I found a recently begun nest of this species, in the horizontal fork of a small sapling growing in a rather open space in the woods. It is only 20 inches above the ground, and quite near some 'courts' of the males (40 ft. from the nearest).

"March 4. The nest appears to be finished.

"March 16. Still no eggs. Apparently abandoned.

"March 16. Nest 31 inches above the ground in a horizontal fork of a sapling growing in second-growth forest, near the same 'courts' as No. 1, but on the other side of the trail and somewhat more distant. It is a shallow, open cup of brown fibres, the meshwork so loose that the ground may be seen through the bottom, attached at its margin by cobweb and some fibres passed over the arms of the fork. It measures  $2\frac{1}{8}$  inches in internal diameter and  $1\frac{1}{8}$  inches deep. 1 egg, whitish, very heavily marked with brown, chiefly in the form of irregular longitudinal marks on the sides.

"March 19. The egg has vanished. I never saw a bird on the nest, for no matter how carefully I approached, the nest would be vacant when I arrived within sight of it; but the warm egg told that she had just flown. The identification of this nest depends upon its similarity to nest 1, and the description of the eggs given me by Dr. Chapman."

Dr. Skutch also found nests on April 17 and May 7, 1935, both about 300 yards from the Donato courts. The first contained a single egg on the 19th, which was present on the 20th, but on the 21st it was missing. The second contained one egg when found and this number had not been increased on the 13th. On the 14th the nest was empty.

Dr. Skutch writes that the males were still "snapping freely" when he left Barro Colorado at the beginning of June.

Mr. Harrower's notes from Gatun, given below, include a record of the distance from the nest of courting males and also the leaving of the nest by the young:

"Nest 1. July 23, 1933. Below the dam at Gatun. Nest hung in the fork of a small tree at the edge of a partial clearing in second-growth forest, six feet up. A shallow cup resembling the nest of the Acadian flycatcher, composed of plant fibres, fine strips of material like bark, grass, etc., lining scarcely finer. Eggs 2, cream heavily blotched and streaked with different shades of rich brown tending towards purple. Apparently fresh.

"The female flushed from the nest when approached within a hundred feet and flew low into the neighboring jungle. She was so shy that I was compelled to make several attempts at identification before I was certain of her identity, though I suspected it on finding the nest. During the three weeks in which I watched this nest I never once observed the male in the vicinity, though I made no special study of it. Even with the young hatched the female remained surprisingly shy, and disappeared completely when the nest was approached.

"About two hundred feet away was a small thicket in the center of the clearing where several males congregated at times and went through their characteristic antics and displays.

"July 29. Two small young.

31. Young OK.

"Aug. 5. Young partially feathered.

7. Young crowding in nest.

12. Young gone.

"Nest 2. July 27, 1933. Along 'Hill Trail' up Gatun Hill beyond dam. Nest hung in the fork of a small bush along trail, four feet above the ground. In no detail of importance differing from Number 1. Contained two rather well-fledged nestlings.

"Female did not appear to be nearly as shy as Number 1, and remained close at hand in the jungle while I was at the nest. She hopped about in the low growth in a manner that at times suggested a warbler.

"July 29. Young nearly ready to leave nest.

"Aug. 2. Nest empty.

"Nest 3. August 17, 1933. On the top of a small ridge running out to top of Gatun dam across spillway. In dense second-growth jungle, not at edge of clearing or trail. Nest in fork of small bush,

about three feet from ground. Contained two fully fledged nestlings which flew out of nest at my approach and vanished in the low jungle. Female was again in evidence, scolding from thicket. As I recall it, she uttered one note."

The facts pertinent to the subject of this paper contained in the preceding observations are (1) the extension of the nesting season of Gould's manakin to at least late August, and of the courtship season to at least August 12; (2) that the nest may be as near as forty feet to an occupied court; (3) that the male takes no part in nest life.

From a more general standpoint, these data show that in none of the nests discovered on Barro Colorado did young reach maturity; while in all the nests found at Gatun young were successfully developed. Can it be possible that nest enemies, e.g. coatis, have become abnormally abundant on Barro Colorado? The abundance of Gould's manakins on the island and the continued existence of their courting grounds would, however, seem to indicate no recent decrease in their numbers.

#### REACTIONS OF THE MALE TO A STUFFED FEMALE

Discovering in January, 1932, that the courtship of Gould's manakin was conducted day after day at the same place, and could therefore be observed continuously, I sent to the Museum for a mounted female to be used in the study of the habits of this species. After its arrival on February 15, it was constantly used in my field-work. In 1935, as before stated, females and males of both Gould's and the yellow-thighed manakin were employed.

Unfortunately, I had no stuffed male of Gould's manakin in 1932 and, in this connection, comparison of the two seasons' work can be made only on the basis of the responses to the stuffed female. The surprising differences in these responses has been commented on under "Seasonal Variation in Time." Here it may merely be said that in 1932 the reaction to the mounted female was much earlier and far more pronounced than in 1935. This fact will be made apparent by quotations from my field-notes for the two years.

The results of tests with a mounted female to determine territorial boundaries have already been presented. I give here those which illustrate sexual relations.

#### 1932

It may be remembered that in 1932 Court No. 1 of the Laboratory Group was claimed by two males, one of which (Dark) was dominant



Fig. 10. Male Gould's manakin approaching stuffed male (left) and stuffed female to which has been added a red crest. Note the unerected "beard." Barro Colorado, C. Z. Left, No. 3 Fairchild Group, March 26, 1935. Right, No. 2 Donato Group, April 17, 1935.

Photographed by F. M. C.



Fig. 11. A manakin "Court." Note the area from which the leaves have been removed. Court No. 3, Laboratory Group, 1932.

Photographed by F. M. C.



to the other (Pale). To test the relations of these birds to one another, as well as to the stuffed female, on February 16 at 7:35 A.M. the latter was placed on a perch about 12 inches from the ground, in the court they occupied.

Dark immediately snapped as an apparent invitation to the female to dance with him. There being no reply, he at once attempted to mate with her. In the course of the succeeding three hours he mounted her 163 times. During this period Pale was not permitted to enter court. Dark returned to the female 85 times the first hour, 58, the second, and 20, the third. With this decrease in ardor there was an apparent change from sexual desire to anger or frenzy at the non-responsiveness of the stuffed bird. I quote from my notes:

"8:00 Ardor undiminished.

"8:02 Flies away; Pale driven off.

"8:05 Returns.

"8:10 Perches on female's back, picks at her head and eyes.

"8:34 *Whirrs*.

"8:40 *Snaps*. Perches and picks with increased force and with anger (?).

"8:46 Drives Pale away.

"8:50-8:59 Mounts 15 times.

"9:14 Flies northwest.

"9:18 Returns, *whirrs*. Picks at female's rump. Flies at Pale. Hangs head down with feet clasped around female's neck; throbs convulsively; voice weak."

From this time there was a gradual decrease in Dark's reaction to the mounted bird which at 10:35 was removed. At 10:36 Dark returned to court but showed no apparent concern at the absence of the stuffed female. Pale was now permitted to perch at the side of the court.

No. 2 of the Laboratory Group was equally responsive to the stuffed female. My notes for February 22 read:

"7:56 Place female 30 feet from court No. 2, 25 feet from No. 1.

"8:00 No. 2 *whirrs* and *snaps*.

"8:10 No. 2 mounts female, knocks her from her perch, six feet up, follows her to the ground to continue attempted coition there. I advance and he leaves reluctantly, perching within four feet; then returns to court. Dark and Pale of Court No. 1 appear to have seen female

before No. 2 did and came halfway toward her but chased one another away.

"8:27 Female in new position.

"Dark discovers her but flies back to drive Pale away. Does this ten times, perching one foot from female, barely alighting, then hurrying back toward Pale."

This observation illustrates the frustration attending incomplete organization. The almost immediate awareness of the males to the presence of the stuffed female, at distances up to forty feet, gives some conception of their sexual alertness, as well as of the keenness of their sight. The mounted bird was of course voiceless and motionless as well as scentless, so far as any odor attractive to manakins was concerned. Nevertheless, as the following extracts from my field-notes indicate, its appearance was at once observed.

March 12, 1932. Fuertes Group. "8:15 A.M. Remove female from box and hold her exposed at 30 feet from No. 2. Within less than 30 seconds he sees her and begins to call and hop excitedly, coming toward me. I return bird to box but No. 2 has apparently been understood; No. 4 *snaps* in court. For the first time No. 5 *snaps* and No. 2 now goes to court and *snaps*. 8:29. Display female again; No. 2 at once sees her and acts as before.

"March 13, 1932. Fuertes Group. 8:27. Place female up hill 40 feet<sup>1</sup> from No. 2. Within 30 seconds Nos. 2, 4, 5, 3 were snapping, whether because of mounted bird I cannot say; but in six minutes No. 2 came to female and, calling, hopped about her."

### 1935

In 1934 a stuffed female of Gould's manakin was first used in my study of the courtship of this species on December 28. In 1932 it was not employed until February 16. It is not, therefore, until the latter date that the results obtained in the two seasons are strictly comparable.

At once it may be said that while in 1932 an attempt to mate with the stuffed female was made on February 16, and doubtless would have been made earlier, in 1935 a similar attempt was not made until March 11. Meanwhile, beginning December 28, 1934, the stuffed female was shown in four groups of manakins, both in court and out.

I speak first of the Laboratory Group, where, between December 31 and February 19, the female was placed on twenty-three mornings in the same spot, about midway between Courts Nos. 1 and 2. But on

<sup>1</sup> Forty feet, because of the density of the undergrowth, was near the limit at which the female could be seen.

only one occasion did it appear to attract attention. This was on January 9 when my notes read: "8:00. Put out female. . . . 8:25. Female discovered by No. 1 (?); he flies about, perching within six feet, first on one side and then on the other, calling *pée-you* once, *chee-póoh* twice and more; No. 2 interested and calls variously, snaps in court but does not leave his territory. There is a general snapping and whirring in at least four places, but nothing happens, and at 8:40 quiet returns."

When exposed in a court it was not until January 23 that the stuffed female attracted attention. Then my notes read: "8:25. Remove female to No. 5 where owner has just been snapping. 8:30. No. 5 flies about; no excitement; mildly interested; *chee-póoh* only note. 8:37. No. 2 *whirrs*, No. 5 follows. 8:40. No. 5 *whirrs* alone, still hopping about stuffed female, interested but embarrassed. Does not snap or go to court. No invitation to dance, but continues to hop and flit around silently."

This was much the reaction of No. 5 to a stuffed female throughout the season. On occasion he exhibited somewhat more excitement but not once did he attempt coition. The owner of Court 1, who was submissive to No. 5, showed even less interest in the stuffed female.

On February 16 the female was placed in Courts Nos. 1, 3, and 4 without response, while No. 5 reacted as before.

On February 17, when the stuffed female was placed in Court No. 1, the owner showed some response, snapped once, and with beard extended assumed the entranced "gaze" posture, but he soon flew to a nearby vine to "court" his dominant No. 5, as elsewhere related, and for the next half hour his attention was divided between the two.

Court No. 4 of the Laboratory Group of 1935 was not contained in this group in 1932. It is placed up the hill, forty feet from No. 1 of this group, and was not visited until February 16. I am not, therefore, familiar with the early history and origin of this court, and consequently am not in a position to explain various incidents observed there. The claims of the bird that occupied it appeared to have been disputed by birds on each side and one in the court, and there resulted a confusion which well illustrates the importance of order in manakin sex life. The results of tests in this court also show a wide range of response to the stuffed female.

At 9:18, March 5, a stuffed female was first placed in this court. At 9:23 a male appeared, hopped about, and, with beard well out,

*whirred, snapped*, and called *chee-póoh* in evident response to the presence of the female, with which, however, he made no attempt to mate.

At 8:03, March 11, the stuffed female was again displayed in Court No. 4 and for the succeeding hour it appeared to be the indirect cause of much general activity in other courts. My notes read: "Since 8:03 there has been almost continuous activity centering about Court No. 4. No. 4 snaps in court frequently and *whirrs* at the border. There is a male toward Court 5 and one toward Court 3 that *snap* and *whirr*, and a third just outside the court has been active. No. 4 sometimes perches within four feet of him but pays no attention to him. Sometimes, however, he rushes at the birds toward Court 3 and sometimes at the one toward Court 5. Always the call is *chee-póoh*. Meanwhile no attention is paid to the female.

"At 9:32 I replaced the female with a male. The call of No. 4 at once changed to *pée-yuk* and the males toward Nos. 2 and 5 disappeared.

"At 9:55 I restored the female, leaving the male. There followed more excitement, and the call *chee-póoh* was heard again. At 10:03 No. 4 mounted the female and was driven off by the second male in court with him, and at 10:05 this action was repeated. The bird from toward Court 3 now appeared. At 10:12 there was snapping in Court 4 while one bird attempted coition and the other drove it away."

I have recounted this incident because it is the first and only time that an attempt at coition was made in the Laboratory Group during the season of 1935. It appeared to be in part due to the stimulation of jealousy. Thereafter, No. 4 was left in possession of the court and although he responded to the presence of the stuffed female by whirring, snapping, and jumping, he did not again attempt to mount her.

I turn now to the Donato, Fuertes, and Fairchild Groups. In the former, tests were made at only two courts, known as Nos. 1 and 2. They were separated from one another by about seventy feet and, as related under the section on territorialism, No. 2, as the more sexually active bird, was responsive to the stuffed female over the greater part of this distance.

The female was first placed in Court 1 on February 27. The male was at once aware of its presence, flitted about, snapped some, partially extended its beard, but made no attempts at coition. Essentially the same response was made by this bird to similar tests during the remainder of the season.

On the same date the female was exposed in Court 2 from 8:40 to 9:00 but aroused no response. On March 7 this bird (No. 2) jumped

and snipped outside court but made no attempt to mate with the stuffed bird. But on March 27, when this experiment was repeated, No. 2, without snapping or whirring, mounted the females of both Gould's and the yellow-thighed manakin. Thereafter, it never failed to mate with the female of Gould's manakin, and, as recorded under "The Males Reactions to Artificial Females," it also attempted coition with a much altered female of that species.

During 1935 my only visit to the Fuertes Group was made on March 20. On that day, as I have before related, a stuffed female exposed in a court of that group from 8:20 until 9:30 was ignored by the owner of the court, who, however, during the first fifty minutes of this period, danced and mated with a living bird three times. Obviously, therefore, a male which did not react to a stuffed female did react to a living one; from which we may conclude that either the male recognized the stuffed bird as such (which does not seem likely) or that the male, as well as the female, may at times require the stimulation of the courtship dance to induce it to mate. Also, the fact that a bird does not attempt coition with a stuffed bird is not to be taken as evidence that it is not prepared to mate.

The Fairchild Group of six courts was first visited December 27, but it was not until February 26 that intensive observations were made there. With the exception of the owner of Court 3, all the birds in this Group made the average 1935 response to the stuffed female. That is, they exhibited more or less interest in the mounted bird, whirred some, snapped less, and jumped about her, but made no attempt to mate with her.

On February 26 and March 3 this was the reaction of No. 3 to the stuffed female although on the latter date it vigorously attacked a stuffed male. But on March 12, when a stuffed male and female were placed in Court 3, while the former was attacked, the latter was accepted and repeated attempts were made to mate with her.

March 17 the same results were obtained, No. 3 attacking the stuffed male but mounting the stuffed female; that is, it would alight on the head of the male and peck at its eyes, while its actions with the female were those of coition. On March 26 the same results were obtained and on April 6, as recounted under "The Males Reactions to Artificial Females," the male of No. 3 while refusing to mount with a stuffed female of Gould's manakin, to which a red crown and black helmet had been added, mated with it, both in court and out, twenty-seven times in forty-five minutes after these disguises had been removed.

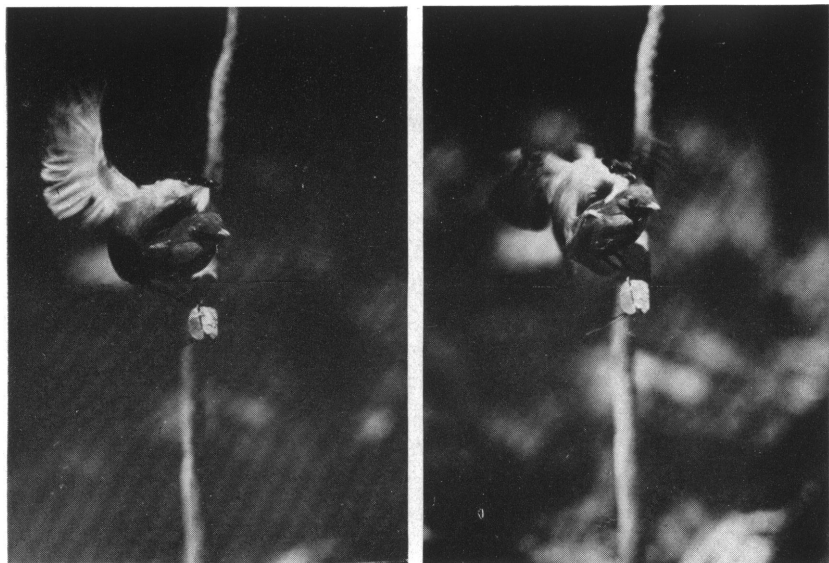


Fig. 12. Male Gould's manakin in attempted coition with stuffed female. Note partially erect "beard." Court No. 2, Donato Group. Barro Colorado, C. Z., April 17, 1935.

Photographed by F. M. C.

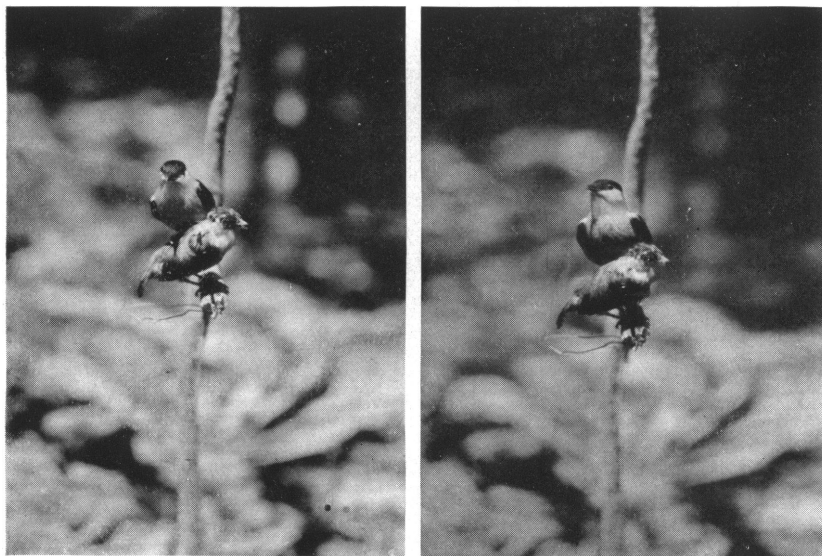


Fig. 13. Male Gould's manakin pausing between attacks on stuffed male. Court No. 2, Donato Group. Barro Colorado, C. Z., April 17, 1935.

Photographed by F. M. C.

Dr. A. A. Allen's remark that he "had learned from experiment that a male [ruffed grouse] would mate with a stuffed bird at least four different times during the day" indicates that, as compared with a manakin, a grouse, sexually, is a comparatively non-responsive bird.

Summarizing these tests, and many others of a similar character, it may be said that, with one exception, every male before which a stuffed female was displayed sooner or later responded to it.

This response varied widely in its date, its character, perceptivity, and intensity.

In 1932 it was made earlier in the year and was more pronounced than in 1935.

The living bird, as a rule, aroused a greater response than the stuffed one.

In most instances males that refused to attempt mating with a stuffed female continued this refusal, but male No. 2 of the Donato Group, after refusing a female on February 27 and March 7, accepted one on March 27 and thereafter.

So far as observed, attempted coition did not occasion emission of sperm.

#### REACTIONS OF THE MALE TO A STUFFED MALE

A stuffed male of Gould's manakin was not available in 1932 and the following observations relate, therefore, solely to 1935. In this year, beginning March 3, the male was exhibited on many occasions, both in court and out. It was rarely ignored and, in most instances, it aroused more attention than a stuffed female for which, apparently, it was never mistaken. That is, when the living male, in or near whose court the stuffed male was displayed, came into actual contact with it, his actions were those of a fighting, not a mating bird. Furthermore, it was greeted with the questioning *pée-you* or *pée-yuk*, rarely or never with the more sexual *chee-póoh*. Details are supplied by the following extracts from my field-notes:

March 3, Fairchild Group. "8:15 A.M. Placed female in No. 4 where there has been no activity. 8:24. No. 4 returns, *whirrs*, jumps across court, calls *chee-póoh*, which is repeated in other courts. 8:37. Male placed with female. Call changes from *chee-póoh* to *pée-you*. No. 4 perches near male but does not attack. Nos. 3 and 5 each come halfway to No. 4. 8:50. Move female to No. 3. He acts like No. 4. 9:05. Add male in Court 3. *Pée-you*, is called all around. No. 3 returns, sits near male quietly, calls *pée-you*, *pée-you*. 9:10. No.

3 flies at male, alights first on back, then on head, and pecks vigorously, making twenty-nine visits, until, at 9:20, to prevent destruction of my specimen, I remove it. The stuffed female, meanwhile, was ignored." (As recorded elsewhere, it was not until March 12 that she was accepted in this court.)

The stuffed birds were now moved to Court 5, distant about sixty-five feet, where the response was much the same. My notes read: "9:30. Female placed in 5. 9:35. Male returns, *whirrs*, calls *chee-póoh*. 9:37-9:39. Jumps, snips, beard out, perches above female. 9:45. Male added to female. No. 5 at once returns and attacks male, clinging below and furiously biting and pecking head; female ignored."

The following day, March 4, the stuffed male was first displayed in the Laboratory Group, where, it will be remembered, the response to the stuffed female in 1935 was so faint-hearted. At 7:55 a female was placed in Court 1 without producing visible result. At 8:19 a male was added, when, as recorded under "Interrelations of Males," two males appeared, one Pale, one Dark (probably No. 1 and his dominant, No. 5). Both acted alike, jumping about with some excitement and calling *pée-yuk*.

At 8:35 the stuffed female was placed in Court 5 without arousing response. At 8:47 the male was added. At once No. 5 called *pée-yuk* excitedly (at the rate of twenty-six times to the minute) and jumped about the mounted male, making occasional feints, and once actually hitting it in passing. At 9:40, possibly as a result of the excitement created by the male's presence, the female, which had been previously ignored, was picked at in passing; also an occasional *chee-póoh* was interspersed in the almost constantly uttered *pée-yuks*.

March 5, Laboratory Group. "8:45. Female placed in Court 5; usual lack of definite response. 8:50. Male of yellow-thighed manakin added. No. 5 calls *pée-yuk* about four times to the minute; perches and looks. 9:00. Replace male of yellow-thighed with male of Gould's. Immediate change in actions of No. 5; he calls *pée-yuk* about twenty-seven times a minute and jumps about more excitedly. 9:10. Male of yellow-thighed returned, male Gould removed. No. 5 at once perceives change; less excited and calls *pée-yuk* only three times in two minutes."

March 7, Donato Group. "8:38. Female placed in Court 2. 8:40. No. 2 returns, beard out, jumps, snips, just outside court, the female untouched. 8:45. Add male; No. 2 calls *pée-you* at once. Flies about male. 8:48. Alights on head and furiously pecks, same



as No. 5 of Fairchild Group. 8:50. Remove male. 8:55. Return male; attack renewed."

March 12, Fairchild Group. "8:05. Female placed in Court 1. Male at once returns, calls *chee-póoh*, whirrs, jumps about. 1*a* snaps. 8:16. Move female to court 1*a*, distant 12 feet. 8:18. No. 1*a* returns, acts much like No. 1. 8:26. Place male in No. 1. 8:28. Male returns; calls *pée-yur*. 8:40. Hits stuffed male and knocks it off its perch." Then followed a territory test, as already recorded.

I have before spoken of the confusing relations of No. 4, of the Laboratory Group, to his neighbors. They are illustrated by his actions on March 18 when, at 8:25, a stuffed male and female were placed in his court. His slight response apparently attracted males from Nos. 5 and 3 where, venturing too near, were driven away by No. 4, although no attention was paid to the stuffed male in his court.

I have also recorded the actions of the male in the Fuertes Group, who, on March 20, ignored a stuffed female but mated three times with a living female, and subsequently, with excitement, called *pée-yuk* thirty times to the minute when a stuffed male was placed in his court.

Other tests amply confirmed those here recorded and all appeared to show that the presence in or near court of a stuffed male aroused more response than the presence of a stuffed female in similar situations. Sexual jealousy, therefore, was apparently stronger than sexual ardor.

It should be especially noted that the male's attack on the stuffed invader of his court was not restricted to a vocal protest but was often so effective that I was at times forced to remove my specimen to save it from destruction. Under the normal conditions of courtship, therefore, the males are at peace with each other, not because they are of a peaceful disposition and do not know how to fight, but because they are so well organized and observe the laws of court-life so rigidly that the occasion for conflict does not arise.

The courting male obviously distinguishes a stuffed male from a stuffed female of its own species, but it does not distinguish a stuffed female or a stuffed male of its own species from living birds of corresponding sexes; nor does it distinguish a stuffed female of the yellow-thighed manakin from a stuffed female of its own species.

But, unless it is often deceived, it presumably distinguishes a living juvenile male of its own species from a living female of its own species, although the two are so alike in plumage that as specimens they cannot be told apart. The experiment was not tried, but there

can be no doubt that in view of the male's indiscriminating response to a badly mutilated mounted female of its own species, and a less-worn, mounted female of *Pipra mentalis*, it would also have responded with equal readiness to a mounted juvenile male. Unless, therefore, the adult male courts the juvenile male, which seems unlikely, the living bird must have some means of conveying a knowledge of his sex to the courting male which a stuffed bird does not possess. I have also suggested that a female, which nested so near an inhabited *lek* that she was doubtless frequently seen by the courting males occupying it, must have had some means of protecting herself from their attentions when she did not desire them.

That the stuffed female did not possess this means of self-protection was obvious whenever it was placed within the territory of a courting male, whether in court or out.

#### THE MALE'S REACTIONS TO ALTERED FEMALES

There is obviously no limit to the number and nature of the tests one may make with stuffed birds to which have been added feathers from other species. I have restricted my tests to those males of Gould's manakin that attempted coition with the normal stuffed female. Their definite response to this type of stimulation supplied a basis for comparison with their subsequent action toward stuffed specimens whose color or form had been altered. The results are inconclusive but at least show definite, if variable, response.

For example: At 8:18 A.M., March 29, a normal stuffed female was placed in Court No. 2 of the Donato Group. The owner of the Court at once returned and, with beard extended, jumped about his court. At 8:20 he snapped and mounted the stuffed bird and repeated this performance twice in the succeeding minute.

The bird was now removed and, after receiving a large cap of red-feathers, was replaced at 8:23. With apparent slight hesitation it was mounted at 8:24 and 8:25. Again it was removed, and to the red cap a long curving black helmet (alula of *Agapornis taranta*) was added. Returned to the court at 8:35, No. 2 at once attempted coition as before. Green feathers were now inserted on the back of the stuffed bird and at 8:40 it was replaced in the court. No. 2 now perched on its head and pecked at its eyes. Presumably, the stuffed bird had now been transformed into something to be attacked, but when I replaced it with a normal, unadorned stuffed female, that also was attacked, and this action suggests that, without regard to the changes in color and

form in the stuffed bird, its failure to respond changed sexual desire to anger.

The latter theory seems supported by a test made in this court eleven days later. On this occasion (April 9, 8:32 A.M.), when the female of Gould's manakin with red crown, black helmet, and green back was placed in Court No. 2, coition was at once attempted and the attempt repeated several times.

At 8:42 the artificial female was replaced with a normal male of the yellow-thighed manakin which was attacked as a male, No. 2 perching on its head and picking at its eyes.

At 8:44 the yellow-thighed male was replaced by a normal female of Gould's manakin. Number 2 now exhibited more excitement than it had before exhibited. It snapped, jumped actively and mated ardently.

At 8:50 the female was replaced by a normal male Gould's manakin. No. 2 immediately perched on this bird's head and picked it vigorously.

In short, the unchanged male and female of Gould's manakin were treated as such; the altered female was accepted as a female and the male of *mentalis* was treated as a male.

At 8:25, on the morning of April 6, the red-crowned, helmeted female was placed in Court No. 3 of the Fairchild Group. During the succeeding fifteen minutes the male *snapped* and *whirred* somewhat and hopped about the stuffed bird but made no attempt to mate with it. At nine o'clock, after the red crown and helmet had been removed, the stuffed female was placed about half way between Courts Nos. 3 and 4. It was apparently at once recognized as a female by the owner of Court No. 3 who, between 9:05 and 9:19, mounted it twelve times.

In this case, therefore, the disguised female was not recognized, but when the disguise was removed she was known at once.

#### REACTION TO THE MALE AND FEMALE OF THE YELLOW-THIGHED MANAKIN (*Pipra mentalis minor*)

In addition to Gould's, the yellow-thighed manakin is the only member of the family Pipridae known from Barro Colorado. This species is slightly smaller than Gould's manakin; the male is glossy black with a bright red crown, cheeks, and nape, yellow legs, and isabelline tarsi and toes; the female is olive-green, with tarsi and toes as in the male. The former, therefore, is quite unlike the male of Gould's manakin, but the females of the two species are so alike in color that in

life they can be distinguished only by their differently colored toes and tarsi. This difference is so slight that it is not recognized by the male of Gould's manakin, and a stuffed female of the yellow-thighed manakin was treated as though it were a female of Gould's. This fact might lead us to expect the occurrence of hybrids in this sexually emotional group, but it should be remembered that the males of the same locality are markedly unlike one another and that it is the *female* who selects.

The male of the yellow-thighed species, however, was apparently at once distinguished from the male of Gould's, as the following extracts from my notes show:

March 5, Laboratory Group. "8:50. Place male of yellow-thighed manakin in Court 5; No. 5 perches and looks; no excitement; calls *pée-yuk* four times to the minute." 9:00. "Replace male of yellow-thighed with male of Gould's; immediate change in actions of No. 5; more excited; calls of *pée-yuk* rise to twenty-nine a minute. 9:10. Male of Gould's removed, male of yellow-thighed returned; No. 5 evidently at once aware of change, shows less excitement; within two minutes calls drop to three in two minutes."

March 7, Donato Group. "8:45. Male, Gould's added to female in Court 2; No. 2 calls *pée-yuk* at once; flies about. 8:48. Alights on head and furiously pecks. 8:59. Remove male Gould's and put out male yellow-thighed; No. 2 returns; calls *pée-you* for a few seconds but does not attack."

Further tests brought essentially similar results. Apparently the presence in court of the male of another species is not resented.

#### SUMMARY

The manakins (family Pipridae) are small, passerine birds inhabiting the American tropics and subtropics exclusive of the Antilles. They number about fifty species and sixty subspecies. The males are usually conspicuously marked and, in many instances, further distinguished from the females by elongated throat and tail-feathers and by the form and structure of the remiges and rectrices.

The little that is known of these birds in nature indicates that as a group, they possess notable courtship behavior which in the physically better equipped species becomes complex, coöperative, and well organized. The existence of fundamentally similar habits among the strongly differentiated, widely distributed members of the same family, and their development with structure, indicates that they are rooted

in the origin of the family itself and are as much a part of its evolution as form.

The wide range and large numbers of Gould's manakin and its representatives indicate that in their physical characteristics and manner of life they successfully meet the requirements of their environment.

The fact that the male takes no part in the activities of the nest, and that a single male can supply the sexual needs of a large number of females, makes his life of far less importance in maintaining the existence of his species than that of the female.

Studies made on Barro Colorado Island, Panama, show that the nesting season of Gould's manakin extends from the end of December to at least the latter part of August. It therefore includes the dry season and at least four months of the wet season.

It is possible that both in time and degree of development the activities of courtship may be strongly governed by seasonal climatic variation.

About two weeks before the inauguration of courtship activities the males begin to gather at a yearly frequented *lek* or courting-ground in the forest. This periodic movement is inspired by the same motive that sends a warbler from its winter home in the Tropical Zone to its breeding ground in the North Temperate Zone and therefore appears to demonstrate the existing cause and object of bird migration.

The arrival of the breeding season is marked by the making of the "court." This is a small space on the forest floor, from which the male removes all loose material. This at once becomes the focal point of his life; to induce the female to visit him in court for the purpose of mating now becomes the chief object of his existence.

Five to seven courts placed, usually about thirty to forty feet from each other, constitute a group or *lek*. This association of several males is more likely to attract the attention of the female than the efforts of a single bird.

The vocal powers of the males are limited and, to announce the location of their courts to the females, they produce with their wing-feathers loud snapping and whirring sounds which can be heard at surprising distances. With rare, and generally explicable, exceptions territorial rights are rigidly observed. The extent of court boundaries is determined by the relations of the males concerned, but the court itself is usually inviolate. Only under certain rare and special conditions does one male enter the court of another. Hence, once the female is in

court, there is no competition for her favors. The continuity of court location and the stability of life secured by court organization must go far in promoting the success of *Manacus vitellinus* as a species.

At times several males may pursue a female in the tree tops when some competition may follow but, as a rule, the males appear to be on peaceful terms with each other. During periods of inactivity, owners of adjoining courts may perch side by side. Under this circumstance one apparently pays court to the other, developing a submissive-dominant relation which, although pronounced, appears to have no actual significance.

At irregular intervals the male enters his court to present his supreme invitation to the female to visit him there. This visit may be self-motivated; it may be inspired by the notes of other males, or by the presence of the female. In the latter event the other males of the group may have gone to their respective courts. Simultaneously they whirr, snap while jumping around and across court, and perform a variety of acrobatic feats, all designed to attract the attention of the female. Should she be in condition for fertilization she apparently selects the court of the male who appeals to her most strongly. Then may follow a "dance" or mock pursuit, leading to coition in court or to an apparent mating flight.

Although the young male resembles the female in color, he evidently makes his sex known to the courting male and presumably is not mistaken for a female.

The courting male has not been seen to feed near court. At intervals of several hours he leaves court to secure the small fruits that form his fare.

The nest, a rather frail saucer-like structure built in a forked branch from twenty inches to five feet from the ground, is usually placed a hundred yards or more from the nearest court, but in one instance it was distant only forty feet, in another sixty feet. Two eggs are laid. They are incubated only by the female who, unaided, rears the young, the male taking no part in the life of the nest.

There appears to be a higher mortality among nesting birds on Barro Colorado than on the mainland.

With one exception,<sup>1</sup> a stuffed female was accepted as a living bird. It was detected up to a distance of forty feet from court, beyond which the density of the undergrowth concealed it. A male's usual response to its presence in or near his court was *whirring*, *snapping*, jumping,

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<sup>1</sup> March 20, 1935, Fuertes Group.

and calling *chee-póoh*. In some cases this was followed by attempts at coition and these, in turn, by attack, the anger of the male apparently being aroused by the failure of the stuffed bird to respond to his advances. In one instance the male mounted the stuffed female 163 times in a period of three hours.

In most instances males that refused to mate with a stuffed female continued to refuse, while those that accepted it always accepted it. So far as observed, attempted coition did not occasion emission of sperm.

The failure of the stuffed female to move in the so-called "dance" or invitation to pursuit is possibly the reason why some males which, though evidently excited by her presence, were not sufficiently aroused to mate with her. It may follow, therefore, that, in some instances, the male, as well as the female, needs the stimulation of the chase to induce coition.

A stuffed female of the yellow-thighed manakin was not distinguished from a stuffed female of Gould's manakin.

A stuffed male juvenile of Gould's manakin was not available, but in view of its close external resemblance to the female of the species it is my belief that it would have been accepted as such. Hence, in order to prevent such an occurrence in life, it seems probable that the juvenile male makes its sex known.

It also seems probable that in order to avoid undue attention, a female, nesting so near occupied courts that she is frequently observed by courting males, can acquaint them with her condition.

A stuffed male of Gould's manakin when placed in or near an occupied court aroused more response than a stuffed female for which it was never mistaken. That is, the living male instead of attempting to mate with it attacked it, at times so furiously that I was forced to remove my specimen to prevent its destruction. The note of challenge or attack of the male is *pée-you* or *pée-yuk*, instead of the *chee-póoh* with which it addresses the stuffed female. Sexual jealousy apparently exceeds sexual ardor.

Tests with a stuffed female of Gould's manakin, altered by the addition of feathers from other birds, were not conclusive. In some instances it was mated with, in others attacked.

The male of a stuffed yellow-thighed manakin (*Pipra mentalis minor*) was distinguished from the male of Gould's manakin. The presence of the former in court was not resented, the owner bird showing no excitement and calling the protesting *pée-yuk* only three or

four times a minute. When it was replaced with a male or Gould's manakin there was considerable excitement and the protesting calls rose to twenty-nine a minute.

Summarizing this summary: in *Manacus vitellinus* it appears that natural selection, working through the performance of the fundamental sexual relation, has developed specialized structures and coöperative habits which, rigidly followed throughout an extended breeding season, overcome the high mortality of tropical nest-life and produce a successful species.









