

## COURTSHIP BEHAVIOR OF THE GREATER BIRD OF PARADISE

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IN September 1909, 48 Greater Birds of Paradise (*Paradisaea apoda apoda*) of unknown sex were released on 280-acre Little Tobago Island (11°18' N, 60°30' W) in the southern West Indies (Ingram, 1911). The birds had been obtained on the Aru Islands south of New Guinea and were placed on Little Tobago in the hope of establishing a population safe from the plume hunting that threatened their existence in their native home. Augmented by three more birds by 1912 (Ingram, 1913), the population apparently fluctuated in numbers for the next 20 years, but no one censused them carefully (Ingram, 1917, 1918; Baker, 1923; Guppy, 1931). The island became a sanctuary in 1928, but by 1955 only 11 *apoda* were thought to survive (Ingram, 1956). E. T. Gilliard (1958, and MS field notes) thought perhaps 35 birds were present in 1958 but he was certain of only 15. A hurricane in 1963 may have caused a further reduction in the population. Thus although the Little Tobago population has survived, it has never thrived as originally hoped.

I spent 9 months on Little Tobago studying this species in 1965–66. In that time I located only 7 *apoda*; 4 full-plumaged males, 1 subadult male, and 2 birds in the chocolate brown plumage worn by both females and young birds. At least one of these was a female.

I watched *apoda* on Little Tobago almost daily from 23 September 1965 to 4 July 1966. Roldan George, a resident of nearby Tobago, helped in the field work and continued observations through 30 September 1966. The period reported on here is 1 October 1965 through 30 September 1966. We worked mainly at several display grounds that the birds used extensively and in particular one that seemed to be the center of activity. We used natural hiding places and took extensive field notes on the courtship behavior.

As *apoda* are extremely wary, I made no attempt to capture or mark any of them, but I could distinguish adult males by differences in the color and length of the side plumes. I actually watched the birds for about 364 hours and secured additional information over many hours when I could only hear them. In all I watched 304 courtship displays and heard an additional 168.

Knowledge of the courtship of *apoda* has heretofore been based largely on a few brief descriptions. Wallace in his classical account (1869: 466) describes how 12 to 20 full-plumaged males on the Aru Islands assembled to play and dance in lofty, large-leaved forest trees,

raise up their wings, stretch out their necks, and elevate their exquisite plumes, keeping them in a continual vibration. Between whiles they fly across from branch to branch in great excitement, so that the whole tree is filled with waving plumes in every variety of attitude and motion. . . . the wings are raised vertically over the back, the head is bent down and stretched out, and the long plumes are raised up and expanded till they form two magnificent golden fans.

No one since Wallace has described the display of *apoda* from the Aru Islands. Baker's description (1923) of its display on Little Tobago is similar to that of Wallace. Crandall (1936) photographed and briefly described the display of captive birds and Iredale (1950) also has brief notes on the display.

Gilliard (MS field notes) wrote the best previous description of the display of *apoda* on Little Tobago. He noted that males gathered at edges of a display area, each on a secondary perch. Here each bird called and rapidly flapped his wings against his sides in short, rapid wingbeats.

From there the birds moved to the main display limbs where, with body held upright, they extended their wings forward and erected the plumes over the back. Then abruptly the tail was depressed, the head, wings, and body were lowered so that the body was close to the limb, and the plumes were still held erect over the back. In this position the bird moved along the limb, sometimes prancing on stiff legs and at other times charging rapidly. The bird then stopped abruptly and assumed a frozen posture, the bill pointing down, wings spread, and plumes erect. Gilliard called this the "flower" position and considered it the climax of the display.

Gilliard observed that when no females were present, the males charged back and forth on the limbs, often in synchrony. However, when females were present, they assumed the "flower" position. This position was only assumed on the central or main dancing stages (courts). He also thought that the male with the longest plumes tended to assume the central position in the court and other males assembled around him, each with a private perch.

#### DISPLAY GROUNDS

I located four main display grounds (the tree or trees used for displaying by one or more males) on Little Tobago. I occasionally saw displays at trees outside of these four, but the use of these trees was too irregular and infrequent to ascertain any exact usage pattern. Three of the display grounds were within 63 m of each other on a wooded hillside. Each seemed to have one plumed male in regular attendance. The three birds could easily hear and probably often see each other. They often visited each other's display grounds, but the regular male at each used a centrally located court (the limbs of trees used repeatedly for displaying)

while the others seemed to use peripheral perches and courts. The fourth adult male had short side plumes and probably had just reached maturity. This bird apparently had no court he attended regularly and was seldom seen. The fourth display ground was 365 m from the others and seemed to be used transiently. The two most frequently used display grounds were on the west slope of a hill and thus were not exposed to the early morning sun.

Elsewhere I have described in detail the limbs used as courts and/or perches (Dinsmore, 1967). In general the principal requirements for a court seem to be a horizontal or gently sloping leafless branch, 8 cm or less in diameter, under a fairly thick canopy cover. Perches seem to require thicker canopy. When deciduous trees dropped their leaves in the dry season, the birds deserted perches there and established new perches in thick-canopied evergreen trees. Most courts and perches were in understory trees such as *Eugenia* sp. and *Mayepea caribaea*.

Three of 13 courts had lateral scratch marks or small holes on them, apparently from bill-wiping and pecking, but none was worn smooth of bark. I never saw birds clearing leaves from the courts. Rather they seemed to choose limbs or parts of limbs that were naturally clear of leaves.

#### CALLS

The basic call note of *apoda* is a deep loud "wauk" or "wonk." This note is delivered in a number of calling patterns. Several of these patterns along with a few other calls are associated with courtship display. The courtship display, described in the next section, consists of five main phases (wing pose, pump, bow, dance, and mounting).

*Rising call.*—In this call four or sometimes five deliberate "wauks" are repeated at about 1-second intervals, the first two notes of equal intensity and the rest successively louder and higher. Birds give this call, at the rate of about one per minute, most often in early morning from near their display grounds. They often give a similar call in late afternoon before they roost.

*Rapid wauk call.*—This call is a series of rapid, equal pitch "wauk" notes delivered in short bursts of several per second, usually accompanied by synchronous short wingbeats, the wing tips being moved about 2 inches from the bird's sides and then flapped back against the sides with each note. It is usually given when a female is near the display ground and, with the following call, accompanies the wing pose phase of the display.

*Wing pose call.*—This call, given with the wing pose phase of the display, is a shrill sliding "eee-ak" note, often repeated several times. While calling the bird throws the wings forward into the wing pose position. Birds often alternate this and the preceding call, delivering rapid "wauk"

notes with the wings held forward rather than flapped against their sides as previously described.

*Pump call.*—This consists of a series of very rapidly given “wauk” notes of equal pitch, even faster than the rapid “wauk” call described above. The notes often are run together so that it sounds more like “wa-wa-wa-wa.” Lasting up to about 10 seconds, the pump call is given without break during the pump phase of the display.

*Baa call.*—At the conclusion of the pump call, the bird usually gives one or several drawn-out, harsh nasal “baa” notes as it tips the body forward and down.

*Click call.*—During the dance phase of the display, the birds utter a slow and rhythmic “click” at about 1-second intervals, much like the sound made when a person clicks his tongue against the roof of his mouth. Between “clicks” I sometimes heard a faint nasal “bonk” note as the bird raised the wings for another dance step.

*Nasal call.*—Similar to the “baa” call but more abrupt and nasal, this call is given most commonly after a display, either as the bird bill-wipes or moves from tree to tree tearing off leaves.

*Chugich call.*—This call, heard only a few times, is a rather harsh, guttural “chug’-ich,” “chug’-a,” or “chug’-a-la” note. It is given in two quite different contexts and may be two distinct but similar calls. Males give it while bouncing along the court prior to giving the “click” call and starting the rhythmic bouncing of the dance. I also heard it just after a bird left a display ground but was still nearby, usually as he was about to move to his evening roost.

#### COURTSHIP DISPLAY

I recognize five main phases in the courtship display of *apoda*. They are described in the sequence in which they usually were given. A more thorough description of the sequence is presented later in Table 1. Although the term “dance” often has been used in reference to the entire display of *apoda*, in this discussion dance refers to only the fourth phase of the display.

*Phase 1. Wing pose.*—The display begins with one or more males calling from near or on their display grounds. At the approach of another male, a female, or often in the absence of another *apoda*, the male flies to his court, either directly or with several brief stops at perches on the way, usually giving rapid “wauk” calls as he flies. Upon arrival at his court, he continues the rapid “wauk” calls together with wing pose calls. In conjunction with the latter call, the bird extends and holds his wings in a rigid position in front of the body for a few seconds, then continues the rapid “wauk” calls. Throughout the performance he holds the plumes

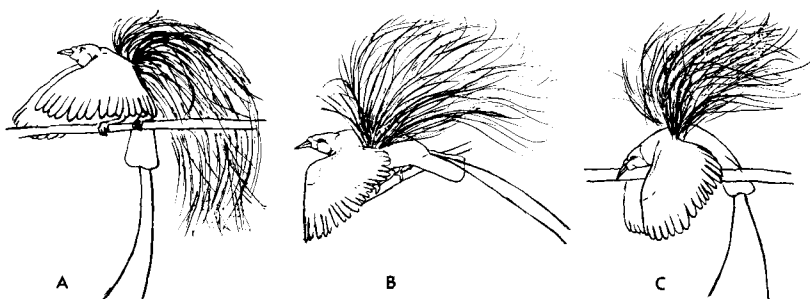


Figure 1. A, position of bird of paradise while in wing pose phase of display. B, position in pump phase of display. C, position in bow phase of display.

erect over the back, tucks the tail forward under the perch, and orients the body perpendicular to the perch (Figure 1A).

In lengthy displays, which occurred most often when a female came near but did not land on the dance limb, he holds the wing pose for several seconds, then gradually drops the wings to the sides and flaps them rapidly there, accompanied by rapid "wauk" calls. Then with a new burst of activity, the bird again gives a wing pose call and posture. This cycle might be repeated every 10–20 seconds without interruption with some bouts lasting 30 minutes or more.

With a female present, the calling in this phase seems louder and more excited. The performance apparently functions to attract the female to the court.

*Phase 2. Pump.*—In the next phase of the display, the body is lowered and turned almost in alignment with the display limb, the wings are extended and cupped slightly around the branch, the plumes are erected almost vertically, and the head and bill are pointed down (Figure 1B). In this position the bird rapidly hops along the court giving the pump call as he bounces up and down. The vertical motion is exaggerated by flexing the legs, and the tail is moved rapidly sideways with each bounce. The body's motion adds to the splendor of the cascade of plumes above and behind the bird. Often the bird moves from branch to branch while giving the pump but usually returns to the court. A single pump phase lasts at the most 10 seconds, but the phase is often repeated several times.

This phase often is given as soon as a female arrives at the court. With the body lowered, the plumes are more evident than in the wing pose and thus this phase may serve to keep the female at the court once she has arrived. This phase (which Gilliard called charging) is given most often in male only displays.

*Phase 3. Bow.*—At the end of the pump, the body is tipped far forward

and down so that the head is below the limb and the back humped. The wings are held out and cupped down around the limb, the tail is brought forward and under the limb opposite the head, and the plumes are held erect over the back (Figure 1C). If a call is given in this position, it is the "baa" call. The bow is held rigidly from a few seconds to more than a minute. This is apparently Gilliard's "flower" position which he considered to be the climax of the courtship display. Females weren't necessarily present during this phase, although the bow invariably was given when females landed at the court.

Often the display ends at this point. The bird gives a few rapid bill-wipes, raises up, and shakes his wings as he lowers his plumes. Frequently the wing pose-pump-bow cycle is repeated several times without appreciable interruption although the bow is often left out.

*Phase 4. Dance.*—The dance phase usually but not always follows the wing pose-pump-bow sequence. It usually starts from the pump position, although in about one-fourth of the cases the wings are held against the body. From this crouched position the bird slowly and rhythmically bounces and shuffles back and forth along the court with leg flexion exaggerating the vertical motion. Both feet are off the branch simultaneously as he bounces along. The "click" call is given instead of the "pump" call, and the movement in the dance is slow and rhythmic while in the pump the motion is rapid and somewhat jerky. Gilliard (MS field notes) describes a shuffling movement by the birds but doesn't distinguish the distinctive "click" call and rhythmic bouncing of this phase.

I saw two variations of the dance, a silent dance without "click" calls and a dance with the plumes lowered and the wings held against the sides.

The dance may last from a few seconds to more than a minute but usually takes less than 30 seconds. Birds commonly pause briefly to wipe the bill and then continue to dance. At the end of the dance the bird usually bill-wipes several times, shakes his wings, and lowers his plumes.

*Phase 5. Mounting.*—I saw only six mountings. Five occurred before 08:00, the other at 17:25, and all involved the same male. Once a second male was present when the female arrived, but he left before the other two copulated.

The mean interval from the time the male first began giving rapid "wauk" calls in response to a female's arrival on the display ground until she landed and remained on the dance limb was 14 minutes (range 4–30,  $n = 6$ ).

The complete sequence of events leading to mounting is sketched below as I observed it on these six occasions. First the male gave a series of rapid "wauk" calls, flapping his wings against his body and holding wing poses with erected plumes (phase 1). The sight of a female near the

display ground apparently triggered this, although I couldn't always see the female until she came very close to the court. The rapid "wauks" continued as the female moved around near the dance tree. While approaching the display ground, she moved quietly but actively from tree to tree.

Usually the male drove the female off the court the first few times she landed there; once he did this five times. Eventually she landed at the distal end of the display limb and then moved up to the distal end of the court. Twice the male gave a pump (phase 3) when the female landed at the court, once holding a long bow while facing away from her. More commonly the pump and bow were omitted and the male moved to the proximal end of the dancing surface, turned and danced toward her, usually with wings spread and giving the "click" call, always with the plumes erected. When he reached her, he turned so his body was alongside but at a slight angle to her, their heads close together. He then danced in position, plumes erect, wings spread, and the body bouncing in time with the "click" calls.

The male usually obscured the female from view at this point, but once I had a clear view of her. On this occasion I saw that the male's wing next to the female was extended over her body and as he flapped his wings he held her close alongside his body. The male also repeatedly rubbed his bill against her bill, bit at her bill, and stretched his head and neck beneath hers and rubbed his bill on the far side of her head, all as he continued to dance. I clearly saw wing-holding and billing only once, but they are probably typical components preceding mounting.

After about 20 seconds of dancing in contact with the female, the male mounted, still flapping his wings. Four times copulation appeared successful while the other two times the female flew before the two could mate. In the dismount the female always flew out from under the male and he dropped to where she had been perched.

While the female was on the court before mounting, she sat quietly, usually crouching as the male came toward her. Occasionally after he had mounted she looked up at him, and once she turned her head, rubbed bills, and bit at his throat. I heard no audible calls by the female while she was on the court. The female stayed on the court only 1 to 2 minutes.

After the female flew away, the male stayed near the dance limb for a few minutes, giving a few nasal calls, preening, and once dancing again briefly. In most cases he left about 10 minutes after the female. The same general sequence took place on several occasions when a female landed at the court and flew before mounting occurred.

These five phases, with their calls and movements, seem to form the main features of the courtship display of *apoda*, but I did note several

other display elements described below. Besides bill-wiping, birds occasionally pecked at their perch or preened feathers, including the plumes, during a break in the display.

On 11 occasions a male tore off sections of leaves in or near the display ground, nearly always the large fan-shaped leaves of the palm *Coccothrinax australis*. Harsh nasal calls invariably accompanied this behavior. The bird landed directly on the leaf, his weight pulling it over so that he hung upside down. He then tore off sections of the leaf and dropped them. He commonly moved back and forth between a palm and his court, repeating this leaf-tearing, and once carried a section of a leaf to his court to drop there. One *Coccothrinax* near a court had several leaves completely frayed from this activity. Baker (1923) mentions a similar activity.

Such behavior is suggestive of the habits of some of the bowerbirds (Marshall, 1954). Leaf-tearing by *apoda* usually occurred in association with but did not appear to be an integral part of a display. It usually came after a partial display prompted by a very brief visit and departure of a female.

Besides hanging while leaf-tearing, five times a male hung upside down from a limb for about 5 seconds, always shortly after he had displayed and nearly always accompanied by nasal calls. Once while upside down he released one foot and hung by the other.

One other time a male hung upside down briefly while another male displayed nearby. Although both *P. rudolphi* and *P. guilielmi* regularly hang inverted in their display (Crandall, 1921, 1932; Stonor, 1936), such behavior was certainly not a regular component of the courtship display of *apoda* on Little Tobago.

Often during a display a bird left the court briefly to move rapidly from limb to limb nearby, sometimes giving rapid "wauk" calls.

I analyzed all of the display elements in a sample of 97 displays (out of a possible 304), in which I saw most or all of the display elements without disturbing the birds. The number of times each element followed each other element was tabulated (Table 1) and the usual sequence of the display elements was then determined by inspection. A single element repeating itself was considered as one. The elements are listed in Table 1 in their order of sequence, insofar as that could be determined.

#### SEASONAL ACTIVITIES

The number of displays seen or heard reached a maximum of 123 in March and dropped to only a few in June and July, although birds displayed in every month (Table 2). From April through August birds were molting and seldom displayed. Molt was first noted on 14 March 1966



TABLE 1  
ORDER OF OCCURRENCE OF ELEMENTS IN 97 COURTSHIP DISPLAYS OF *P. APODA* ON LITTLE TOBAGO

Immediately preceding element	Ensuing element <sup>1</sup>														Totals
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	
Start	20	12	43	4	0	0	3	1	4	0	8	0	0	2	97
1. Rapid "wauk" calls	-	23	26	3	0	0	1	2	1	0	7	0	3	0	69
2. Wingbeats	5	-	31	5	1	0	5	0	3	0	4	0	1	3	64
3. Wing pose	33	4	-	86	0	0	8	7	2	0	14	0	2	0	160
4. Pump	2	0	5	-	49	63	3	1	3	0	1	0	0	0	129
5. Bow	1	0	4	5	-	16	7	2	4	0	2	0	2	4	57
6. Bow with "baa"	0	5	5	10	6	-	23	0	3	0	8	0	3	6	79
7. Bill-wiping	2	13	6	2	1	0	-	3	16	0	20	0	5	8	86
8. Female arrives	2	1	4	8	0	0	0	-	4	0	2	0	1	0	23
9. Dance	0	1	6	0	0	0	21	5	-	5	2	0	7	7	61
10. Mounting	0	0	0	0	0	0	0	0	0	-	0	0	4	0	5
11. Limb-hopping	1	1	23	3	0	0	11	2	19	0	0	0	4	2	70
12. Leaf-tearing	1	1	0	0	0	0	1	0	1	0	0	-	0	0	5
13. Nasal calls	2	2	5	3	0	0	3	0	0	0	2	3	-	9	43
14. Preening	0	2	2	0	0	0	0	0	1	0	0	2	11	-	23
Totals	69	64	160	129	57	79	86	23	61	5	70	5	43	41	97

<sup>1</sup> Read across, i.e. out of 69 rapid "wauk" calls, 20 came at the start of the display, 33 followed directly after a wing pose, etc.

TABLE 2  
MONTHLY FREQUENCY OF DISPLAYS ON LITTLE TOBAGO IN 1965-1966

Month	No. of displays		Birds present <sup>2</sup>					Times display included	
			No. of Males						
	Seen	Heard <sup>1</sup>	1	2	3	4	Female	Dance	Mounting
October 1965	10	5	8	3	4	0	0	8	0
November	12	7	12	5	0	2	4	12	0
December	48	11	46	8	5	0	11	21	0
January 1966	38	20	53	5	0	0	5	7	0
February	50	45	80	14	0	1	6	28	0
March	58	65	106	16	1	0	10	42	2
April	40	8	47	1	0	0	4	32	2
May	18	2	20	0	0	0	4	8	2
June	0	2	2	0	0	0	0	0	0
July	0	1	1	0	0	0	0	0	0
August	9	2	11	0	0	0	0	1	0
September	21	0	20	1	0	0	3	6	0
Totals	304	168	406	53	10	3	47	165	6

<sup>1</sup> Displays in which the bird could be heard giving display calls but couldn't be seen.

<sup>2</sup> Number of occasions on which 1, 2, 3, or 4 males were present at the display ground together and those on which a female was present.

when one male pulled out several side plumes. After 5 April 1966 only one male still had plumes. He continued to display until he started his molt 16 May 1966. During molt the birds' activities were greatly reduced and they seldom called, displayed, or were seen.

By late August new plumes had grown and displaying gradually increased. From then until the next molt, each male's activities were quite regular and predictable, being centered around a well established display ground.

On 30 November and 1 December 1965 a female flew several times in rapid succession between two ridges, carrying what appeared to be dry grass in her bill. I saw no other evidence of nest building and although I carefully searched the area she flew to, I did not find a nest. The only record of a bird of paradise nest on Little Tobago is the questionable record by Baker (1923) but the nest he found may well have belonged to another species.

#### DAILY RHYTHM OF DISPLAY

During the display season, males spend much of their time at or near their display grounds. They start calling shortly before sunrise and move, in several short flights, to the edge of the display ground where they call and preen at habitual perches. Except for a brief feeding break around 07:00, they often stay near the display ground until 11:00, their calling becoming more sporadic after 08:00. More commonly they leave the dis-

TABLE 3  
TIME OF OCCURRENCE OF DISPLAYS ON LITTLE TOBAGO IN 1965-1966

Time	No. of displays		Birds present <sup>2</sup>					Times display included	
	Seen	Heard <sup>1</sup>	No. of Males				Female	Dance	Mounting
			1	2	3	4			
Before 06:00	4	1	4	0	0	1	2	4	1
06:00-07:00	88	23	86	17	7	1	26	33	3
07:00-08:00	57	15	64	6	2	0	8	35	1
08:00-09:00	11	3	11	2	0	1	0	4	0
09:00-10:00	6	1	7	0	0	0	1	2	0
10:00-11:00	10	4	11	3	0	0	1	9	0
11:00-12:00	2	1	3	0	0	0	0	1	0
12:00-13:00	1	3	2	2	0	0	0	2	0
13:00-14:00	1	15	13	3	0	0	0	0	0
14:00-15:00	10	21	29	2	0	0	1	8	0
15:00-16:00	18	19	31	6	0	0	2	8	0
16:00-17:00	42	26	61	6	1	0	4	25	0
17:00-18:00	50	31	75	6	0	0	2	30	1
After 18:00	4	5	9	0	0	0	0	4	0
Totals	304	168	406	53	10	3	47	165	6

<sup>1</sup> Displays in which the bird could be heard giving display calls but couldn't be seen.

<sup>2</sup> Number of occasions on which 1, 2, 3, or 4 males were present at the display ground together and those on which a female was present.

play ground around 08:00 and spend the hot midday hours on heavily wooded slopes some 460 m away.

By 13:00 they are moving back toward the display grounds, often displaying briefly from near the display ground as they approach. Normally they call or display from 14:00 to 17:00. As sundown approaches, they move again, often displaying before they fly swiftly to individual widely separated roosting areas. A similar pattern has been noted for *P. minor* (Gyldenstolpe, 1955).

Table 3 gives the time of occurrence of 472 displays seen or heard in 1965-66 and indicates peaks between 06:00-08:00 and 16:00-18:00.

#### DISPLAYS BY OTHER *PARADISAEA*

Short descriptions of the courtship displays of the other six species of *Paradisaea* (following the classification of Rand and Gilliard, 1968) have been published. Males of both *guilielmi* (Crandall, 1932, 1936; Stonor, 1936; Wagner, 1938) and *rudolphi* (Crandall, 1921, 1932) hang inverted to display. The display of *decora* is less known but apparently similar to that of *raggiana* (Stonor, 1936; Iredale, 1950) while *rubra* apparently displays by hopping along a sloping branch, the wings extended and vibrating and the plumes slightly elevated (Crandall, 1937).

Ogilvie-Grant (1905) describes three stages in the display by *minor*. These are similar to phases 1-3 of the display by *apoda*, and Crandall

(1936) has photographs of the first and third stages. Gilliard and LeCroy (1961) note the similarity between *minor* and Little Tobago *apoda* and also that the wings are "rowed" forward rather than thumped over the back as by *raggiana*.

The display of *raggiana* has been described for at least two subspecies, *salvadorii* and *augustaevictoriae* (Crandall, 1936; Dharmakumarsinhji, 1943; Iredale, 1950: 130–131; Gilliard, 1954; Mayr and Gilliard, 1954). Generally this species displays by holding the body horizontally, spreading the wings, and arching the plumes over the back and then hopping stiff-legged along the limb. Crandall (1936) notes that at the climax the bird tips forward, much as in the bow (phase 3) by *apoda*. Mayr and Gilliard (1954) and Gilliard (1954) note that the males thump their "wrists" over their back rather than throwing the wings forward as *apoda* does in phase 1.

Thus of the six, *apoda* differs most from *rudolphi* and *guilielmi* and seems closest to *minor* and *raggiana*. Still *apoda* differs from *raggiana* in lacking the thumping of the wings over the back. Although both *minor* and *raggiana* hop along the limb before tipping the body forward, none of the descriptions mention the distinct "click" call and rhythmic dance of *apoda*. Mounting has not been described for any of the six and several of the accounts are of captive birds so it is likely that parts of the display have not been described. Both Iredale (1950) and Mayr and Gilliard (1954) saw a male *raggiana* hang inverted during a display and a female landed above him and pecked at him, a behavior similar to that described for *guilielmi* (Wagner, 1938).

Indeed the similarity in the displays of *apoda*, *raggiana*, and *minor* is not surprising as Mayr (1962) considers the subspecies of *raggiana* to be conspecific with *apoda*, and *minor* has been known to hybridize with *apoda*.

#### DISCUSSION

The Greater Bird of Paradise has long been included with some manakins, cotingas, hummingbirds, grouse, shorebirds, and other birds of paradise as a species having a communal type of display. This apparently dates back to Wallace who described dance parties on the Aru Islands (1869: 466). His report evidently was based largely on the reports from local people although he did get a glimpse of such a performance (1869: 449). Gilliard (1958) was convinced that the Little Tobago birds did indeed perform as Wallace had described.

Generally communal display refers to a situation in which two or more males come together, display for an extended period, and meet only briefly with the females to mate. Promiscuity, lack of a pair bond, and mutual

stimulation by the males often occur in this situation but all have not been shown satisfactorily for all supposed communally displaying species. In these situations, birds often compete for favored (usually centrally located) positions on the display ground and these birds usually do most of the mating (Scott, 1942; Snow, 1962). Within these communal display grounds individual ownership of the various courts is evident. Snow (1962) with *Manacus manacus*, Hogan-Warburg (1966) with *Philomachus pugnax*, Gilliard (1962) with the Cock-of-the-Rock (*Rupicola rupicola*), and Mayr and Gilliard (1954) with *P. r. salvadorii* all note that each male had his own court that he defended, even when several males had gathered to display.

I found that *apoda* on Little Tobago did display in groups, but this occurred only occasionally and mostly early in the display season (October–December). Of 472 displays seen or heard, only 53 involved two males, 10 three males, and 3 had four males (Tables 2, 3). In perhaps half of the single bird displays, the calls of one or two other males could be heard by the displaying male, but otherwise the birds were not involved in the display.

The male at the display ground I observed most often appeared to have the longest and most colorful side plumes. This male nearly always displayed on the most centrally located court while other males, when present, used other courts in that tree or perched high on limbs in the immediate vicinity. I am not sure if males defended these other limbs.

As the display season progressed at this display ground other males appeared to recognize that the area belonged to the one male and they made less use of it. Most of the two-bird displays involved this male and one from the nearest display ground. Multiple-bird displays also were observed at other display grounds, but again the pattern of usage was not determined.

Several times I saw a male defend a court on Little Tobago. One male regularly permitted other males in his display ground, but consistently drove them off if they landed at his court; the same bird also drove females away several times before allowing them to remain at the court.

Twice two males came together in a tree about midway between their respective display grounds. Each time they grasped each other and fell from the tree, twirling in a tight ball until a few meters from the ground, where they separated and each flew toward his own court. They appeared to be scuffling, although I am not sure if wings, feet, or bill were used. Baker (1923) described a similar encounter.

Among *Paradisaea*, both *minor* (Gyldenstolpe, 1955; Gilliard and Le-Croy, 1961) and *raggiana* (Simson, 1907; Iredale, 1950; Gilliard, 1954; Mayr and Gilliard, 1954) display in groups. For *raggiana salvadorii*, a

situation similar to that noted for Little Tobago *apoda* has been described (Gilliard, 1954; Mayr and Gilliard, 1954). They saw males defend dance limbs from others, including about 10 females and young males that had gathered around the adult males. The males charged the intruders with a mock attack, the plumes in disarray over the body. They saw up to three adult males simultaneously in one tree, but each seemed to have an individual limb.

Although multiple-bird displays were often quite intense on Little Tobago, they also were usually brief. It is of interest that of the six mountings observed, three occurred when only one plumed male was present and no opportunity existed for stimulation from other males displaying. Also all the observed mountings involved the one most colorful male.

Gilliard (1963) used the term "exploded arena" to describe the situation for some birds in which the group has widely separated courts but still can hear each other. Although I have used the term display ground synonymously with Gilliard's arena, I believe that this exploded arena concept fits quite well for the three regularly occupied display grounds on Little Tobago. There each male has his own display ground with courts which he defends from other males. Still at times the birds from these separate display grounds gather and display together on one bird's display ground.

Thus *apoda* does have a communal display, but in a somewhat different manner than usually suggested. Most of the calling and activity takes place at somewhat separated courts and perches, but occasionally the males do gather together to display.

There also appeared to be two aspects to the courtship display, a social one early in the season when the birds often came together and gave the pump and bow phases, and a sexual aspect later in the season. In this second period, the pump and bow were commonly omitted and birds seemed to go directly from the wing pose to the dance and then to mounting and copulation. Also at this time, group displays were rare and each male seemed more attached to his own display ground and less apt to move than early in the season.

Snow (1962), in his thoughtful discussion of how communal displays could have evolved in *manacus*, thought that if adequate food could be obtained rapidly, nest predation was high, and clutch size was low, it would be advantageous for the males to be released from nest care so that the nest would have more chance of success. Then males would be free to attract and mate with as many females as possible and selection would favor elaborate display structures and movements. If several males displaying together had a greater stimulatory effect on females than did

a single male, group displays would also be favored. Snow's discussion was based on a thorough knowledge of the ecology of *manacus*.

For *apoda* less is known about important phases of the life history, especially the nesting biology. As Snow (1962) has pointed out, the tropical forest habitat has many of the birds known to display communally (e.g. cotingas, hummingbirds, and manakins). A common characteristic of these species is that they are frugivorous or nectarivorous and are able to obtain adequate food in a short time. Snow points out that generalizing the situation found in *manacus* to all tropical communally displaying birds is premature. Still some of my findings with *apoda* fit the pattern quite well and will be mentioned here.

First, *apoda* is primarily a fruit eater (Dinsmore, 1967) and although I saw some evidence of a food shortage during the dry season (February through mid-April), the birds still were able to spend hours daily either displaying or resting and seemed to get adequate food in a few brief feeding forays each day. The few records of eggs indicate that the usual clutch is one or two but possibly three (Simson, 1907; Ogilvie-Grant, 1912; Sims, 1956). No adequate studies of predation have been made, but on several occasions in this study a Broad-winged Hawk (*Buteo platypterus*) flew near or over *apoda* as one displayed or was at a display ground. In each instance the *apoda* either dove into nearby brush or ceased calling until the hawk left and then resumed his calling. Thus in these few cases the bird was still alert, even when occupied with display. A similar response to the presence of a hawk has been noted before and *apoda* remains have been found in a hawk's nest (Baker, 1923).

A final word of caution on the present study is needed. Even though the Little Tobago *apoda* are free living, they still form a small introduced population. They have survived more than 50 years on Little Tobago and thus must have found the environment suitable, but they still are not indigenous to the region. A display such as theirs should remain relatively unchanged, even in a new habitat, but we can not be sure whether or not any behavioral change has occurred in this small population through genetic drift.

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#### SUMMARY

A 12-month study of the courtship display of the remnant population of *Paradisaea apoda* on Little Tobago Island, West Indies showed that that population now consists of four males, two females, and one sub-adult male. In that period 304 courtship displays were seen and 168 were heard. Each of four display grounds used regularly had several courts and calling perches within it. Three of the display grounds had one individual male in regular attendance, each of which seemed to defend some perches from other males although often other individuals used peripheral perches and courts during group displays.

The courtship display consists of five main phases (wing pose, pump, bow, dance, and mounting), all of which are described together with associated calls. Displays occurred in every month with March having the maximum (123). Most occurred in early morning or late afternoon.

Of the other *Paradisaea*, the *apoda* display most resembles those of *raggiana* and *minor*. Communal displays occur most frequently several months before mating occurs. Only one male was seen to mount a female (six occasions) and three of these occurred after the other males had started molt and were no longer active at display grounds. No nests or signs of nesting were found. Several aspects of the bird's ecology that may have permitted the evolution of its elaborate courtship display are discussed.

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