DUAL SINGING BY NEW GUINEA BIRDS

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A relatively uncommon but intriguing form of bird song, the significance of which is imperfectly understood, is synchronized duetting between a mated male and female. Most reports of birds engaging in this come from the tropics, with examples from Central America (Skutch, 1940), South America (Haverschmidt, 1947), Africa (Moreau, 1941; Thorpe, 1963; Grimes, 1966), Madagascar (van Someren, 1947), and Malaya (Young, 1942). A few examples from the temperate zone have also come to light among owls, Himalayan (Osmaston, 1941) and Australian (Robinson, 1947: 14–17) passerines, and the Canada Goose (*Branta canadensis*) (Collias and Jahn, 1959), Carolina Wren (*Thryothorus ludovicianus*), and three species of quail (Stokes and Williams, 1968) of North America. A selected list of species may be found in Van Tyne and Berger (1959: 140). The present paper is an analysis of all instances known to us of duetting by New Guinea birds, based largely on our previously unpublished field observations. As it has been suggested that the incidence of duetting may correlate with type of habitat, possibilities for visual contact between singers, or sexual dimorphism of plumage, these points are considered in each species discussed.

Duets may be divided conveniently into three categories. (1) The leader (generally the male) sings one phrase, and at its conclusion the second bird (generally the female) sings another phrase. Often the follower begins so precisely upon cessation of the leader's phrase that the result may easily pass for a conventional single song, unless the observer can see the singers or is close enough to hear that different notes come from different places. For example, the Marbled Wood-Quail (*Odontophorus gujanensis*) calls a rapidly repeated "corcorovado," in which "corcoro" is always sung by one member of a pair and "vado" by the other (Chapman, 1929: 275; Armstrong, 1963). The term "antiphonal singing" has been used for this type of duetting, in which male and female sing alternately rather than simultaneously. In this category belong the Central American wrens described by Skutch (1940) and *Amaurornis olivaceus*, *Pitohui kirhocephalus*, and *Philemon novaeguineae* (see below) of New Guinea. (2) Members of a pair sing different phrases simultaneously. The synchronization between the two phrases may nevertheless be very exact; the female may begin only a fraction of a second after the male. In New Guinea the duets of *Megapodius freycinet*, *Campochaera sloetii*, and *Coracina montana* are of this type. (3) The male and female sing virtually identical phrases in unison. Such unison duets are practiced by *Centropus toulou* (Cuculidae) of Madagascar (van Someren, 1947), *Aspatha gularis* (Momotidae) of Central

America (Skutch, 1945: 495), and other species listed by Power (1966) but not, to our knowledge, by any New Guinea species.

The physiological problems posed by synchronized duetting are well illustrated by Thorpe's (1963) studies on the shrike *Laniarius erythrogaster* of Africa. In this species the duetters are up to 20 yards apart in dense brush and out of visual contact, but their calls are nevertheless delivered almost simultaneously: a *yoick*-like sound from the leader and a "tearing hiss-like" sound from the follower. Sound recording showed that the second bird may begin as little as 72 milliseconds after the first, the exact duration of the interval being characteristic of a given pair. This is several times shorter than the fastest acoustical response time for man. For any given pair the variation of this interval is very slight, the standard deviation being 5 to 12 milliseconds, or several times less than the comparable figure for man (20–55 milliseconds). Similar acoustical response times have been determined from duets for the related species *Laniarius barbarus* (Grimes, 1965) and for the Orange-chinned Parakeet (*Brotogeris jugularis*) (Power, 1966). Thus, synchronized duetting demands an ability both to react rapidly to an acoustical stimulus and to time an interval accurately.

Duetting between a paired male and female resembles acoustically, but has a very different significance from, another class of dual singing, namely the several kinds of countersinging between males. When the pauses between successive phrases of a territorial song are longer than the phrases of the song itself, two males on adjacent territories may tend to sing alternately, thus giving each the opportunity to hear the other's song during the pause. Such countersinging occurs frequently in the European Wren (*Troglodytes troglodytes*) (Armstrong, 1944) and, in our experience, in many species of South American antbirds (Formicariidae). Males that meet at the borders of their territories may both sing loudly and simultaneously to threaten each other. In some species, when one male begins to sing other males in territories within hearing distance begin to sing at more or less the same time. A bizarre instance of a male–male dual song that is identical in form to the third (unison) type of male–female duet is provided by the Blue-backed Manakin (*Chiroxiphia pareola*) of South America; display in front of a female is routinely carried out by two males which perch side-by-side, almost touching each other, and call in unison (Snow, 1956: 90). Apart from this special case, male–male countersong can generally be distinguished from male–female duetting by the fact that in the former, coordination is generally imprecise and the two singers have identical phrases, whereas male–female duetting is usually precisely coordinated and the partners often sing very different phrases. However, some male–female duets involve no more precise coordination than does some countersinging, and in some duets the male and female give identical phrases. For these reasons the distinction between duetting and countersong cannot always be made with certainty in monomorphic species if one has not collected both singers. We have therefore discussed, in addition to all presumed instances of duetting in New Guinea, five cases that we assume at present to represent countersong, but of which one or two may possibly turn out to be male–female duets.

METHODS AND LOCALITIES

The observations described here were made during three separate expeditions to New Guinea. One of the purposes of these expeditions was to study altitudinal distribution of bird species by taking censuses at different elevations above sea level. These censuses were based to a large extent on song, and it thus became necessary to track down and observe repeatedly the songs of as many species as possible. Field work was carried out by both of us from June to September of 1964, and by one of us (J. M. D.) from June to September of 1965 and 1966. Observations were made at the following localities, all in the eastern (Australian-mandated) half of the island: Port Moresby and vicinity on the southeast coast; the area from Lae to Bulolo on the Huon Gulf, and the lower Markham Valley; the eastern highlands between Kainantu, Okapa, Karimui, and Goroka; Wewak on the north coast; the North Coastal Range (Prince Alexander, Torricelli, and Bewani Mountains); and the northern edge of the Sepik Basin. All major types of habitat and a range of elevations from sea level to 12,300 feet were covered. In addition we have included for comparative purposes some observations on Australian birds made in Queensland and New South Wales, and on South American birds made in the Department of Ayacucho, Peru. The identification of all New Guinea species for which we observed dual singing is supported by specimens deposited in the American Museum of Natural History and the Harvard Museum of Comparative Zoology. Tape recording was not undertaken, and the descriptions are based on field notes.

RESULTS

During these studies we identified the songs of 217 New Guinea species (146 passerines, 71 nonpasserines). Of this total 3 were found to practice regularly some kind of dual singing that might have been duetting, 4 occasionally, 1 rarely, and 209 not at all (this does not include some obvious cases of countersong that could not possibly have been confused with duetting). In addition, E. T. Gilliard once observed a duet in *Philemon novaeguineae*, a common species that we encountered many times but never found engaging in dual singing, and in a megapode whose vocalizations we never heard (Gilliard and LeCroy, 1966). Details of these instances of dual singing follow under the individual species concerned. No other possible examples of duetting in New Guinea have come to our attention.

Megapodius freycinet. Common Scrub-hen.—This is a species of the forest floor, occurring most commonly in the lowlands but ranging occasionally up to 6,000 feet. It is well known for constructing huge mounds of rotting vegetation in which the eggs are laid and incubated by the heat of decay. The male and female are identical in appearance. While we have had no first-hand experience of its vocalizations, E. T. Gilliard (Gilliard and LeCroy, 1966: 254) observed it to engage in dual singing in the area of the middle Sepik River and described the performance as follows:

> Male (?), "kok, nyacal, nailleue" (ascending to a high screech). Female (?), a stutter delivered in duet with the peal of the male and beginning just after the male began and continuing throughout the call "nu-nu-nu-nu-nu-." These duetted calls were heard at all hours of the day and night, but were most prevalent on moonlit nights. Often at night the birds called within 200 feet of my tent (which was just outside the forest and about 150 feet from an occupied mound) and from sound orientation I determined that the birds kept closely together in pairs. In fact, it was only rarely that the call of the female seemed to emanate from a distance of more than 10–20 feet from that of the male. Most times, the sound seemed to come from birds standing almost side by side.

From this description it seems likely that the male and female are in visual contact during many of the diurnal duets, though probably not for the nocturnal ones.

Amaurornis olivaceus. Rufous-tailed Moorhen.—We encountered this rail in tall, dense grass bordering native gardens, roads, and fields; other observers have also found it in swamps (Mayr, 1941). It sleeps in low trees but otherwise remains on the ground. The male and female are identical in appearance.

Most vocalizations of *Amaurornis olivaceus* are duets between two individuals concealed in the grass. The first bird gives a catlike wail that remains on nearly the same pitch, and as this wail starts to drop in volume, the second bird begins a similar wail at about the same pitch. Each bird then alternately wails from a few to a dozen times, each wail lasting between one-half second and a second but overlapping both the preceding and following wails of the other singer, so that the effect is of a continuous sound. Sometimes the series appears to be on the verge of dying away when the duet is suddenly pursued with renewed vigor for several more alternations. The series may be introduced by hen-like clucks which accelerate and crescendo before breaking into the wails. Because of the dense grass in which the performance takes place, it is rarely possible to watch the singers, but they appear to be from 4 to 10 feet apart and to move about as they sing. They are surely out of visual contact throughout the performance, which may be heard at any time of day and infrequently at night as well. The duets given by birds from the Karimui Basin (*A. o. ruficrissum*) and from the north coast (*A. o. molucannus*) are indistinguishable to our ears.

Although the duet is the commonest kind of vocalization in this species, solitary individuals may also give a series of clucks. The wails, however, are never heard outside of a duet. On one occasion we heard a call *bk-bk-bk* from the grass which we assumed to be a native chicken, until we spotted an adult and a juvenile *Amaurornis*. The adult was probing for food and clucked when it found a morsel, whereupon the juvenile would come up and receive it.

Dacelo gaudichaud. Gaudichaud's Kingfisher.—This small kookaburra is noisy and common in the middle story of second-growth and sometimes in the forest from the lowlands up to 2,000 or 3,000 feet. The male and female differ only in the color of the tail.

The commonest vocalizations are a short bark repeated at one-second intervals on the same pitch, and a short trilled bark repeated at one-second intervals on successively lower pitches. The barking of one individual frequently stimulates another at some distance (generally well out of visual range) to begin barking at the same time. On one occasion we observed two individuals barking simultaneously in an isolated tree standing in a garden. There is no synchronization in such cases. One singer may cease well before the other, or the two may bark at different rates, so that the two series become progressively out of phase. These are generally considered typical features of male–male countersong. The Blue-winged Kookaburra (*Dacelo leachii*) of the south New Guinea savannah has a very similar trilled bark, and Rand (Mayr and Rand, 1937) described several individuals calling simultaneously, much as with *Dacelo gaudichaud*. In the remaining member of the genus as well, the Laughing Kookaburra (*Dacelo gigas*) of Australia, several individuals perched next to each other on the same limb may call simultaneously.

Campochaera sloetii. Golden Cuckoo-shrike.—The isolated, brilliantly colored, and monotypic genus *Campochaera* is endemic to mainland New Guinea, where it is distributed erratically in the lowlands and hills up to about 3,600 feet and is nowhere common. Its habitat is the crowns of tall forest trees.

The usual vocalization is a duet carried out by groups of two to four individuals. The leader delivers a rapid series of half-a-dozen musical spitted notes, all on the same pitch. Simultaneously with the last several notes, a second individual gives a whistled slur which may be a simple upslur, a downslur, or up to two or three slurs. Some common patterns are depicted in Figure 1. The duet is given repeatedly as the birds chase each other in flight just above the crown of a tree, or else as they perch in the treetops. The notes are high and melodious, and the effect is most attractive. After perhaps one-half minute in one tree the group flies off to an-

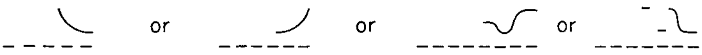

Figure 1. Patterns of duetting by *Campochaera sloetii*. The repeated notes (lower line) are given by one bird, while the slurs (upper line) are given by a different bird.

other tree 100 to 500 feet away, duetting as they go or else uttering rapid repeated notes on one pitch similar to the leader's part in the duet. The performance is then repeated in the next tree. A group can readily be followed by sound as they progress down the ridge of a mountain or gradually describe a wide circle through the forest. The singers remain in close visual contact throughout the whole performance.

The male and female differ slightly in plumage, the throat being black in the male but gray in the female. Singing groups contain individuals in both plumages, but we have not been able to determine whether the leader is a male and the follower a female, because the singers are in the forest crown and often in rapid motion. The performance generally takes place in the morning (never at night or as part of the dawn chorus) at any time from an hour after sunrise until noon. The birds then become silent and settle down to feeding. As described below, two other New Guinea campephagids (*Coracina schisticeps* and *Coracina montana*) conduct strikingly similar communal displays, and that of *C. montana* also involves duetting. A purpose of the displays may be to assert and maintain a territory held communally by the group (see p. 69).

Coracina montana. Mountain Cuckoo-shrike.—This is a conspicuous, fairly common species of mid-montane forest from about 3,500 to 8,000 feet, usually found in the upper story but occasionally descending to the middle story to feed. In the male the plumage is blue-gray above, while the wings, tail, and underparts from chin to tail are black. The female and immature male differ in that while the lores, chin, wings, and tail are black, the underparts are blue-gray as the upperparts.

The song of *Coracina montana* is a loud duet that carries considerable distances and forms part of a stereotyped display similar to that of *Campochaera sloetii.* The display is carried out by a group of usually three or four, sometimes only two, birds, and the group seems always to include at least one female and one adult male. The group alights in a conspicuous position in the crown of a tall tree, either a dead one or one with a commanding view. The members typically perch within a few feet of each other, often immediately next to each other on the same branch, and always in unhindered visual contact. In a typical pattern (Figure 2,A) the male gives an upslurred whistle succeeded immediately by a downslurred whistle, followed at short intervals by several more such pairs, then at longer intervals by single upslurs. Immediately after the beginning of each slur the female commences a series of either three or four unmusical, harsh notes on the same pitch (*kek* or *chuck*), which are completed within the time span of the male's slur. Common variations are that the performance may begin with single slurs rather than pairs, and that the concluding series may be downslurs rather than upslurs or else pairs of slurs. In the

Figure 2. Patterns of duetting by *Coracina montana*. The slurs (upper line) are given by the male, while the repeated notes (lower line) are given by the female. Patterns (a) and (b) are the usual ones in the eastern highlands, while (c), (d), and (e) are characteristic of the North Coastal Ranges.

North Coastal Range the initial slurs may be virtually disyllabic, whereas in the eastern highlands the units are always simple slurs. Figure 2 gives some of the common patterns. Among New Guinea dual singers the song of this species involves the finest synchronization and would offer interesting material for an analysis of time relations, similar to that carried out by Thorpe (1963) for *Laniarius erythrogaster*. It should be stressed that although we have heard the duet on several hundred different occasions in seven different areas, we have not encountered a single instance of the male singing alone.

The singers are always perched when the *Coracina montana* duet is given, whereas in *Campochaera* the duetting group may either be perched or else whirling above the crown. The duet may be followed by some uncoordinated groups of *keks* similar to the female element of the duet but softer. Groups usually remain only a minute or two in a tree before flying off together to another tree 200 to 1,000 feet away. In flight the group utters loud groups of unmusical *keks* but no slurs. When they alight in the next tree, the duet is repeated, and so on in successive trees, with a burst of *keks* in flight between the trees. The progress is easily followed by ear, and it is our impression that a given group uses the same duetting trees and follows a prescribed route each day. Usually the route will take a group along a mountain ridge for a vertical distance of up to 1,000 feet, then into the adjacent valley and perhaps across to the next ridge if it is sufficiently close. On one occasion we observed a group following a circular route a few hundred feet in radius and returning to the same tree within one-half hour. When not engaged in this performance, the birds are in-conspicuous and remain silent while feeding. The duetting is confined to daylight hours beginning well after sunrise, most commonly in the morning but occasionally in the afternoon. We have never heard it either at night or as part of the dawn chorus.

As noted above, the displaying group usually consists of three or four individuals, and all appear to contribute to the *keks* in flight, although only one male and one female carry out the duet. Regarding the composition of the groups, we succeeded once in collecting a complete group of four, and found it to consist of two adult males, one adult female, and one immature male molting from the female-like to the male plumage. On five occasions our native collectors brought in three birds that had been together, but may have had a fourth partner that escaped, with the following composition: one adult male and two adult females; one adult male, one adult female, and one unsexed immature bird in female-like plumage; one adult male, one adult female, and one immature male in female-like plumage; two adult males and one adult female; and three adult males. On eight occasions the native collectors obtained two birds together, possibly from larger groups, and seven of these pairs consisted of one adult male and one adult female, while the eighth was an adult male and an unsexed bird in female-like plumage. In one pair both the male and female had enlarged gonads, but this was generally not the case. All our specimens were obtained between June and September, and we suspect from the reports of natives that this species generally breeds from November to February where we collected in New Guinea.

It is possible that in *Coracina montana* and in *Campochaera sloetii* the duetting behavior not only strengthens bonds between the participants but also represents a communal territorial display. Each group may jointly hold a feeding territory, to which it maintains its claims by circling the territory once or twice a day while displaying. While we have not observed definite territorial confrontations between adjacent groups, this interpretation is suggested by the selection of conspicuous perches and by the use of established and more or less circular routes. Functions of duetting in territorial behavior have previously been indicated for *Laniarius barbarus* (Grimes, 1966) and *Brotogeris jugularis* (Power, 1966). The following account of the display of *Coracina schisticeps* suggests an additional significance of duetting by *Coracina montana.*

Coracina schisticeps. Grey-headed cuckoo-shrike.—This species does *not* engage in dual singing and is discussed here for comparison with *Coracina montana.* The male is largely blue-gray, with the lores and most of the wings and tail blackish, thus resembling female or immature male *C. montana* in pattern. The female (and immature male) is largely brown, with the head and much of the tail gray and the wings black. In addition, this species is smaller than *C. montana* (wing, 108–120 mm, *vs.* 123–135 mm for *C. montana* in eastern New Guinea). It occurs from sea-level to about 3,000–4,000 feet in the upper story (sometimes the middle story) of the forest, and apparently replaces *C. montana* at lower altitudes. In all, 11 superficially rather similar members of the genus *Coracina* occur in New Guinea (5, including *montana* and *schisticeps*, are sometimes separated under the generic name *Edolisoma*). From our own familiarity with the behavior of nine of these species, and from published accounts of the other two, it appears that *schisticeps* and *montana* are the only ones that practice the distinctive group tree-top displays described in this paper. The vocalizations of the other species are also rather different, ranging from a crescendoing series of buzzes, progressively increasing in volume, in *C. morio*, and a parrot-like *whee-chew* in *C. papuensis*, to harsh chirps and screams in *C. caeruleogrisea.*

The display and song of *C. schisticeps* are similar to those of *C. montana* except that the female does not reply to the slurred whistles of the male and thus there is no duet. In the display, groups of two to four birds, consisting of both males and females, occupy conspicuous perches close together in the crown of a tree and remain there a few minutes before flying on to the next tree a few hundred feet away. When perched, the male delivers a series of slurs, of which some representative patterns are given in Figure 3. The similarity to the patterns of *Coracina montana* (Figure 2) is obvious, and the quality is also similar, varying from a musical whistle to a whistle more nasal than that of *C. montana.* Some male vocalizations of *C. schisticeps* are practically indistinguishable from those of *C. montana* except for the absence of a female reply (compare Figures 2,B and 3,C).

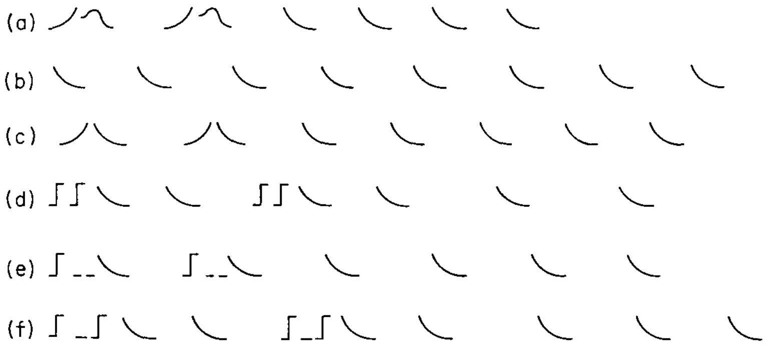

Figure 3. Song patterns of *Coracina schisticeps.* The whole song is given by the male, and no duet is involved. Patterns (a) and (b) are from the North Coastal Ranges; (d), (e), and (f) from the eastern highlands; and (c) from both the North Coastal Ranges and the eastern highlands.

At the end of the series of male slurs, several birds join in with a rapid, low, harsh, and less loud *chuck-chuck-chuck*. Finally the group flies off to the next tree, with several birds simultaneously and noisily calling *chuck-chuck-chuck* in flight. We collected one group of four *in toto* and found it to consist of one adult male, two adult females, and one immature male molting from the female-like to male plumage. On four occasions we obtained three birds that may or may not have had a missing partner: two males and a female twice, one male and two females, and three males. The gonads were generally not enlarged. Thus the display is in all respects similar to that of *C. montana* except for the slurred whistles of the male being unaccompanied.

Among New Guinea birds a number of congeneric species inhabit altitudinal bands nearly or completely exclusive of each other (e.g., *Crateroscelis murina* and *C. robusta* [Timaliinae], *Peltops blainvillii* and *P. montanus* [Muscicapinae], *Epimachus fastosus* and *E. meyeri* [Paradisaeidae], *Amblyornis macgregoriae* and *A. subalaris* [Ptilonorhynchidae], and *Ptiloprora perstriata* and *P. guisei* [Meliphagidae]). Presumably the members of such pairs have rather similar ecological requirements, so that they cannot share the same area any more than can the members of a superspecies group. Whereas the members of a superspecies are separated by a geographical boundary, the members of an altitudinal pair meet at a contour line on many or all the mountain ranges of New Guinea. *Coracina schisticeps* and *C. montana* provide an additional example of two species with mutually exclusive altitudinal preferences, such that the presence of each species seems to offer the principal barrier to the other's altitudinal range. On different mountains the transition takes place at various altitudes between 2,700 and 4,200 feet. For example on the northwest ridge of Mt. Karimui in the eastern highlands, a flat volcanic plain on the north side of the mountain permits many tropical species to spread upwards to higher altitudes than usual elsewhere in New Guinea. Consequently the highest altitude at which *C. schisticeps* was observed was 4,030 feet, and the lowest altitude for *C. montana* was 4,115 feet. In the North Coastal Range the transition was studied on Mt. Somoro, Mt. Nibo, Mt. Menawa, and Mt. Turu. On Mt. Somoro *C. montana* extended regularly down to 2,990 feet, and *C. schisticeps* was encountered only below this altitude except for a pair collected at 3,100 feet. On Mt. Nibo the transition occurred at some altitude between 2,700 and 3,000 feet. On Mt. Menawa, *C. montana* was found down to 2,650 feet, and *C. schisticeps* occurred only below this altitude except for one specimen at 2,775 feet. On the fourth and lowest mountain, Mt. Turu, only 3,750 feet high, *C. montana* was missing entirely and *C. schisticeps*, apparently freed from the competition with *montana*, occurred all the way up to the summit, 800 to 1,000 feet higher than on the other mountains of the North Coastal Range. Thus, the altitudinal ranges of these two species are complimentary with only marginal overlap, i.e., the lowest occurring group of *montana* and the highest occurring group of *schisticeps* appear to invade each other's areas by little more than 100 feet.

Consideration of present distributions of other New Guinea altitudinal pairs suggests that these pairs originate when one population of a polytypic species or superspecies group reinvades the range of a related population that has developed a slightly different altitudinal preference during geographical isolation. Many of these altitudinal pairs are rather similar morphologically but have very different songs, suggesting an important role of voice in the isolating mechanisms (e.g., *Peltops blainvillii* and *P. montanus*, *Epimachus fastosus* and *E. meyeri*). Thus, it can be suggested speculatively that the fine synchronization between male and female in the duet of *C. montana* may function in addition to the plumage differences as one of the isolating mechanisms between it and *C. schisticeps*. The duet could readily have evolved from a *schisticeps*-like song, as the female element of the duet is already present in the song of *C. schisticeps* as the group notes delivered after the male slurs and in flight. In addition the example of duetting by *Campochaera* as well may suggest some predisposition towards duetting in New Guinea campephagids, unless these two similar duets evolved quite independently.

Pitohui kirhocephalus. Greater Wood-shrike.—This common species of lowland forest ranges up to about 3,500 feet and is found in the lower and middle story of the forest and in second-growth, particularly among dense tangles of vines and other vegetation. No other New Guinea bird shows such geographical variation in plumage, its subspecific color variation encompassing the whole range of patterns found among the other five species of the genus. The male and female are identical in the races we have studied, though this is not true of some other races.

Because of its loud voice and preference for the interior of thickets, *Pitohui kirhocephalus* is much more often heard than seen. The vocalizations are rather varied, common elements being upslurred whistles, connected pairs of notes on different pitches, a dry series of rattled notes proceeding upscale, and clear, whistled, staccato notes. The quality varies from mellow to harsh. A typical song will be introduced by a whistled pair of notes, followed after a short pause by two more pairs in quick succession, and then by a disorganized jumble of notes and slurs in irregular rhythm. The first singer may be answered by one or two other birds within a distance of 20 feet, delivering the same kinds of chatters at the some time but without any detectable organization or synchronization. The singers are certainly out of visual contact. Finally one may hear a loud whirring of wings and observe several birds fly out of the thicket and chase each

Figure 4. Patterns of duetting by *Pitohui kirhocephalus.* In pattern (a) one bird gives the upslur, and a different bird gives the single note *tup* which follows it after a variable delay or sometimes is omitted. In pattern (b), which is given repeatedly separated by pauses, one bird gives the upslur and another the second note, but it is uncertain which bird gives the last two notes or whether they are given by a third individual.

other into a nearby thicket. The fact that all the singers use the same kind of "song," and that there is no fine synchronization but simply several chatters going on simultaneously, suggests that this common performance is an example of countersinging between rival males, not of duetting between a mated male and female. We have heard this kind of singing both in the eastern highlands (*P. k. brunneiceps*) and in the North Coastal Range (*P. k. brunneicaudus*).

In addition an entirely different kind of dual singing, which we have heard only on the north coast, is surely a male–female duet. The leader delivers a single upslurred whistle that is generally answered at an interval of one to three seconds by a mellow staccato *tup* from another bird 10 to 30 feet away. The upslur and *tup* are then repeated several seconds later with the singers apparently not having changed position (Figure 4, A). The interval between the slur and the *tup* varies, however, on successive repetitions. Sometimes the *tup* is omitted entirely in response to one slur but is then given after the next. (Another instance of an "optional" female reply is provided by the duet of the Australian Whip-bird (*Psophodes olivaceus*), in which a long whistle of the male, that increases explosively in volume, may or may not be followed by *chew-chew* from the female.) In a more complicated variant of three elements, the slur and *tup* are followed at an approximately equal interval by a pair of notes (Figure 4, B). We were unable to determine which of the singers gives this pair of notes or whether it is given by a third individual, in analogy to the "trio-singing" of *Laniarius aethiopicus* and *Cossypha heuglini* (Thorpe and North, 1965). The three-element performance is most often heard as part of the dawn chorus, when it may be repeated a dozen times or more. On one occasion we heard two groups carrying on the three-element duets simultaneously from adjacent thickets; the two duets were not synchronized with each

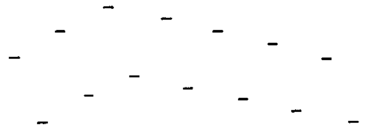

Figure 5. Dual singing by *Melidectes rufocrissalis*, heard on only one occasion. One bird (upper line) gave a series of caws, and a second bird (lower line) gave a similar series such that each note appeared in the pauses between the notes of the first bird.

other. The two-element duet (slur plus *tup*) may be heard at any time in the morning or afternoon. The species does not sing at night.

Thus, *Pitohui kirhocephalus* apparently engages in both countersinging and, in at least one race, duetting. The dense thickets the species inhabits ensure that the singers are not ordinarily in visual contact. The duet also differs from that of *Campochaera sloetii* or *Coracina montana* in that the time relations between the first and second singer are variable and in that most of this species' vocalizations do not involve duetting.

Melidectes rufocrissalis. Yellow-browed Honey-eater.—This honey-eater is a common and noisy inhabitant of the forest interior and forest edge from 4,500 to 8,500 feet, and is found in the middle and lower story. It has attracted interest because it hybridizes readily with its congener *M. belfordi* in areas of disturbed ecology (Mayr and Gilliard, 1952; Gilliard, 1959; Diamond, 1967). The male and female are identical in appearance.

A common call is a series of nasal and piercing, or else hoarse and raucous, *caws*, either on the same pitch or slightly ascending or descending. Another call is a series of bugled notes which are alternately on two different pitches. We observed dual singing in this species on only one occasion, by two birds perched on the same limb two feet apart and facing each other. Each individual gave a descending series of *caws* at the usual rate (two or three per second), but the note of one bird occupied the pause between the preceding and following note of the other bird (see Figure 5). The performance was not repeated. While a distinct possibility exists that this was a duet between male and female, competitive singing between two rival males appears to us the more probable interpretation. The fact that the notes did not get out of phase on this one occasion may have been due to chance and need not imply fine synchronization.

Oreornis subfrenatus. Sub-bridled Honey-eater.—A species of erratic distribution, this honey-eater is locally common from 4,500 to 8,500 feet in the forest middle story but is absent in many apparently suitable areas. The male and female are identical in appearance.

The song is a rapid, loud, bubbling, and cheerful series of notes which first rises and then falls in pitch, progressively decelerating and sometimes

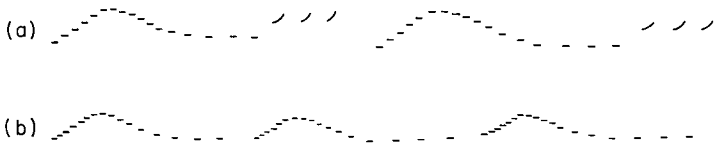

Figure 6. Two typical song patterns of *Oreornis subfrenatus*. Dual singing, which is the exception rather than the rule, consists of two birds giving the same pattern at the same time, the second bird starting a few notes behind the first bird.

concluding in three slurs on the same pitch, after which the pattern is immediately repeated one or two times (Figure 6). About one-quarter of the renditions involve dual singing. A second bird perched in the same tree as the first, 3 to 10 feet from it, and generally in sight of it, delivers an identical song beginning a short time (i.e., several notes) after the leader starts. Both the single and dual songs are heard frequently in fruit trees where several individuals have come to feed. The fact that both individuals deliver the same song, which is more often heard as a solo, suggests that competitive singing between males is involved, though male–female duetting remains a possibility.

Xanthotis chrysotis. Brown Xanthotis.—This is one of the most abundant birds of the New Guinea lowlands, becoming progressively less common with increasing altitude, until it drops out around 5,000 feet. It may be seen at any height in a tree, though more often in the lower and middle stories than in the treetops. The male and female are identical in appearance.

In the eastern highlands (*X. c. rubiensis*), the vicinity of Port Moresby (*X. c. guilanettii*), and the vicinity of Lae (*X. c. madaraszi*) the song is based on a pattern lasting about two seconds and consisting of three notes separated by pauses. The pattern is immediately repeated without change a half-dozen times in succession. On the north coast (*X. c. philemon*) the song differs by being delivered at least twice as fast. Dual singing occurs occasionally. After one singer has given the three-note pattern once, another singer may join him for the second delivery of the pattern on the same pitch and in approximate synchrony, and the two continue on for several deliveries, though one may stop before the other. Sometimes three birds may sing at the same time. The singers are never close together, generally 50 to 200 feet apart, and of course out of visual contact. It seems a reasonable assumption that the singers are males maintaining adjacent territories.

Philemon novaeguineae. New Guinea Friar-bird.—This large honey-eater is common in the lowlands, ranging occasionally up to 2,000 or 3,000 feet. It is found in the middle and upper story of trees, much more often in second-growth and around villages than in the forest. The sexes are identical.

The song is based on a repeated pattern of three or four loud nasal slurs, and the pattern is repeated a few to a dozen times in immediate succession. We never noted dual singing in this species, but Gilliard (Gilliard and LeCroy, 1966: 273) observed that on at least one occasion the pattern was divided between two birds:

> The leatherhead (*Philemon novaeguineae*) has a repertory of bugled notes that are so clownish they almost defy description. These are delivered very often from semi-concealed perches high up and commanding an extensive view. "Stick-ta-ba-co," rapidly repeated, is a common call; "ka-kek-ka-ke-kek-ku" is another loud call, as is "yes-joe-joe-jup-kip-jup." Behind Bogadjim I confirmed what I had long suspected, that this species sings antiphonally; as I watched, one called "ki-kor-rik," to which another, directly overhead, added "queww." They did this a number of times. I would have taken the call for that of one bird had I not been standing where I was.

After learning of Gilliard's observation, we paid particular attention to this species and had the opportunity to observe it at Port Moresby, Lae, and Wewak, and at many localities on the southern slopes of the North Coastal Range. In every instance when we tracked down the origin of a song, the whole of the song came from a single individual. Thus duetting in *Philemon novaeguineae* must be regarded as a relatively uncommon or perhaps a geographically localized practice. On the basis of Gilliard's description and of the kinds of trees which *Philemon* frequents, it is highly probable that the pair observed by Gilliard were in visual contact.

Basically, Gilliard's observation was that a given pattern which is normally delivered as a solo by one bird may also be divided between two singers as a duet. At least two similar cases exist among Australian birds. First, the *chew-chew* that follows the male's explosive whistle in *Psophodes olivaceus* (see earlier) may be given either by the male or by the female. Second, the song *pee-o-wit—te-he* of the Magpie-lark (*Grallina cyanoleuca*) may be delivered as a solo, or else *pee-o-wit* may come from the male and *te-he* from the female, or vice versa (Robinson, 1947: 14–17). Thorpe and North (1965; 1966) cited additional examples.

DISCUSSION

Most of the 10 New Guinea species that have come to our attention as dual singers do not exhibit sexual dimorphism of plumage. Hence in only one instance can we be positive about the sex of the singers (*Coracina montana*, where a male leads and a female follows). The following reasoning makes it probable, however, that male–female duetting is occurring in six species and male–male countersinging in five:

In the cases of *Megapodius freycinet*, *Campochaera sloetii*, *Coracina* *montana*, and *Philemon novaeguineae* both distinguishing characteristics of male–female duetting are present; the vocalizations of the leader and follower differ, and their time relations are rigidly defined. In the *Pitohui kirhocephalus* "duet" the singers have somewhat flexible time relations but entirely different notes, while in *Amaurornis olivaceus* the leader and follower sing similar phrases but in a strict time relation. These six vocal performances also share in common the fact that they form an unbreakable unit, i.e., half of the duet is not given as a solo. Thus presumed duetting between male and female occurs regularly in four species (*Megapodius freycinet*, *Amaurornis olivaceus*, *Campochaera sloetii*, and *Coracina montana*), occasionally in one species (*Pitohui kirhocephalus*), and rarely in one species (*Philemon novaeguineae*).

The remaining cases (*Dacelo gaudichaud*, the double chatter of *Pitohui kirhocephalus*, *Melidectes rufocrissalis*, *Oreornis subfrenatus*, and *Xanthotis chrysotis*) resemble each other and differ from the male–female duets in that both singers give the same phrase and in that these identical phrases are much more often heard as solos. Countersong is the only reasonable interpretation for the dual singing in *Dacelo gaudichaud* and *Xanthotis chrysotis*. The degree of synchronization in the cases of the *Pitohui kirhocephalus* double chatter, *Oreornis subfrenatus*, and *Melidectes rufocrissalis* leaves duetting as a distinct, though still a less likely, possibility.

The incidence of duetting among New Guinea birds is therefore about 3 per cent (6 out of 217 species, assuming these 217 to be a representative sample). The songs of most of these species were observed sufficiently often and closely to make it unlikely that undetected duetting was occurring and that the true incidence differs much from this 3 per cent figure. Among the 217 species, the songs of 141 were heard more than 10 times (hundreds of times in many cases), the songs of 173 more than 4 times, and of 196 more than once. At best among this group a few more cases may turn up of birds that duet infrequently or only in certain geographical areas, as *Pitohui kirhocephalus* and *Philemon novaeguineae*.

The 6 New Guinea duetters belong to 6 different genera, 5 different families, and 3 different orders, so that duetting must have evolved independently many times. Why did duetting evolve, and what is its biological significance? Probably there is more than one explanation, as the New Guinea duetters share little in common. Their habitats may be tall grass, the forest floor, dense vegetation of the lower and middle story, second-growth trees, the forest middle and upper story, and the crowns of tall trees. Some live in the lowlands and others in the mid-montane zone. One of the duets takes place most often on moonlit nights, another during the dawn chorus, two during presumed territorial displays, and two at any daylight hour. The singers are always in immediate visual contact in two species, generally or sometimes in visual contact in two or more species, and entirely out of sight of each other in the other two species. Two of the species show sexual plumage dimorphism, four do not. Five species have dull plumage, one (*Campochaera sloetii*) is brilliantly colored. Perhaps the only common denominator is that all are more or less social birds. *Coracina montana* and *Campochaera sloetii* are always encountered in groups of two to four; *Megapodius freycinet* and *Amaurornis olivaceus* frequently, but by no means always, in pairs; and *Pitohui kirhocephalus* and *Philemon novaeguineae* in abundant, loosely organized populations of frequently interacting individuals.

The significance of some cases of duetting is suggested by the facts that duetting is much commoner in the tropics than in the temperate zone, and that many tropical duetters are birds of dense vegetation, in which the singers remain out of visual contact. This correlation has been well expressed by Thorpe (1961: 50):

> The explanation suggests itself that birds living in the dark and tangled undergrowth of tropical forests, conditions which are likely to hinder the development of mutual visual displays, are the more likely to replace these by the elaboration of vocal displays. It is perhaps also significant that in Europe the only group which seems to employ antiphonal vocalization persistently is the owls which are, of course, mainly nocturnal.

Among the species that sing duets out of sight in tropical undergrowth are *Laniarius erythrogaster* (Thorpe, 1963) and *Laniarius barbarus* (Grimes, 1966) of Africa, several Central American species discussed by Skutch (1940), and the Coraya Wren (*Thryothorus coraya*) of South America. The duets may have a specific role in maintaining contact between members of a pair as they move about. For example, the male and female of *Saltator intermedius* sing a simple duet throughout the year, while the male alone sings a very different song in the nesting season (Skutch, 1940). At least two temperate-zone duetters, *Psophodes olivaceus* of Eastern Australia and *Thryothorus ludovicianus* of North America, also live in dense thickets where the singers cannot see each other. Two of the six New Guinea duetters fit very well into this pattern: *Amaurornis olivaceus* (in tall grass) and *Pitohui kirhocephalus* (in dense undergrowth). Whether *Megapodius freycinet* belongs in the same category is more doubtful; the singers may be out of sight when they duet on the forest floor on moonlit nights, but this may not be true for their daytime duets.

The other three New Guinea duets cannot be explained on this basis, for the singers definitely maintain close visual contact in *Campochaera sloetii* and *Coracina montana* and probably do so in *Philemon novaeguineae*. This finding also applies to some duetters from other parts of the world, such as the Canada Goose of North America (Collias and Jahn, 1959) and

Brotogeris jugularis (Power, 1966) and *Monassa nigrifrons* (Bucconidae) of South America. In the last-named species, an inhabitant of clearings and second-growth, members of a pair engage in a prolonged and raucous antiphonal duet while perched on the same or nearby branches. Similarly some Australian duetters, such as *Grallina cyanoleuca* and several of the Cracticidae, are birds of open country and in visual contact as they sing. Armstrong (1963) has pointed out that these Australian species gear their breeding seasons to the onset of the rains, which come at unpredictable times of year. In order to begin nesting as soon as the rains arrive, the birds must already be paired and may in fact remain in pairs and maintain territories throughout the year. Thus duets may be one possible behavioral device involved in maintaining pair-bonds for prolonged periods in anticipation of a favorable time for nesting. Such a role of duetting is also suggested by evidence that details of the duet enable members of a pair to recognize each other as individuals. For example, Thorpe (1963) found that the interval between the beginning of the male's and the female's note in *Laniarius erythrogaster* is characteristic of each pair, and different pairs of *Laniarius barbarus* (Grimes, 1966) and *Grallina cyanoleuca* (Robinson, 1947) can be distinguished by a characteristic repertoire of patterns. Studies on captive birds have made it clear that a pair of birds learns to duet in perfect synchrony only after many months of practice (Thorpe and North, 1966; Power, 1966). Thus the great majority of duetting species, regardless of habitat and geographical range, prove to be species with stable pair-bonds that remain intact outside of the breeding season. This and the previous explanation of duetting are not mutually exclusive—both may apply simultaneously to birds of tropical thickets in areas of somewhat unpredictable seasons. Skutch (1940) noted that the wrens and other species of Central American thickets that practiced duetting were also species that remain in pairs throughout the year, and the same can be said from our experience of the South American Coraya Wren.

Too little is known of breeding seasons in New Guinea birds to make a final assessment of this hypothesis, viz. that duets are characteristic of species that must remain paired for much of the year because their nesting depends on unpredictable climatic changes. However the available information is compatible with the hypothesis. In the eastern highlands in 1964 and 1965 June, July, and August were the driest months, and December and January the wettest months, but this varies greatly from year to year. A preliminary analysis of gonad size in specimens we collected, plus information gathered from natives and local Europeans in New Guinea, suggests that many birds of the grasslands and forest lower story breed in dry periods, many fruit-eating birds breed in rainy periods, and some species breed more or less at random throughout the year. Ripley (1964) also observed seasonal breeding patterns in western New Guinea. All specimens of *Campochaera sloetii* we collected, and almost all *Coracina montana*, had the gonads in nonbreeding condition. This was to be expected, as our collections were made in the dry season and both species feed to a large extent on fruit (Mayr and Rand, 1937: 95; Rand, 1938: 2; 1942: 463; Gilliard and LeCroy, 1961: 46; Terborgh and Diamond, MS). Nevertheless both species showed markedly territorial behavior and went about strictly in pairs or small groups containing both sexes. Thus the stereotyped duetting displays of these campephagids may well have played a role in preserving pair bonds in readiness for the rains and the nesting season.

A third possible role of duetting is the one discussed for *Coracina montana*, whose duet may serve as an isolating mechanism against its non-duetting altitudinal representative *Coracina schisticeps*. This can best be regarded as an additional or incidental role of duetting in *C. montana*, as *Campochaera sloetii* performs a very similar duetting display despite its position as a distinct monotypic genus, while all other New Guinea species with altitudinal representatives maintain reproductive isolation by vocal or other means without resort to duetting.

On the one hand duetting cannot be assigned a unique explanation nor, on the other hand, can it be regarded as a unique behavioral response to one or more sets of conditions. Far more New Guinea birds inhabiting just as dense vegetation as *Amaurornis olivaceus* and *Pitohui kirhocephalus*, and whose nesting is just as dependent upon unpredictable seasonal changes as that of *Campochaera sloetii* and *Coracina montana*, maintain contact or remain mated without engaging in duets. The evidence in most cases where duetting does occur suggests it to be one means that may evolve to cement permanent or semipermanent pair-bonds, and that this particular form of intra-pair communication and recognition is more likely to arise in habitats where visual displays would have much less value for these purposes.

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SUMMARY

Synchronized vocal duets between a mated male and female, such as have been reported for species from most other parts of the tropics, are described and analyzed for New Guinea birds. Four New Guinea species (*Megapodius freycinet*, *Amaurornis olivaceus*, *Campochaera sloetii*, and *Coracina montana*) duet regularly, one (*Pitohui kirhocephalus*) occasionally, and one (*Philemon novaeguineae*) rarely. In addition, five examples of dual singing are described (*Dacelo gaudichaud*, *Pitohui kirhocephalus*, *Melidectes rufocrissalis*, *Oreornis subfrenatus*, and *Xanthotis chrysotis*) which appear to represent competitive countersinging between males, but of which one or two may prove to be male–female duets. The incidence of duetters among New Guinea species is about 3 per cent.

The most interesting examples involve the campephagids *Campochaera sloetii* and *Coracina montana*, which duet in the course of similar stereotyped displays, possibly of a communal territorial nature. A close relative of *Coracina montana*, *C. schisticeps*, has an altitudinal range just below that of *C. montana* and exclusive of it. The song of *C. schisticeps* is very similar to that of *C. montana* except for lacking the female element of the duet, so that the duet might act as an isolating mechanism between these closely related species.

The singers are out of sight of each other in the cases of *Amaurornis olivaceus* and *Pitohui kirhocephalus*, sometimes or generally in sight in *Megapodius freycinet* and *Philemon novaeguineae*, and always in immediate visual contact in *Campochaera sloetii* and *Coracina montana*. It is suggested that duetting may arise in response to two different situations: the need for birds living in dense vegetation where visual contact is difficult to evolve intricate vocal displays rather than visual displays, and the importance for birds whose nesting season depends upon unpredictable climatic changes, such as the start of the rainy season, to become and remain paired long in advance of breeding.

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