

Perhaps other hummingbirds did not feed at these trees because sap holes are usually in the upper part of the tree. Of the nine resident species in Finca Merenberg, only Buff-tailed Coronets and Long-tailed Sylphs are canopy species. Other species, such as the Booted Raquet-tail, may feed in the canopy only occasionally. Also, Buff-tailed Coronets strongly defend their territories against intruders and are always dominant over other species. Only Greenish Pufflegs (*Haplophaedia aureliae*) are almost as aggressive, and they sometimes chase coronets. Snow and Snow (1980) found that Buff-tailed Coronets carried on their activities at higher levels and were more aggressive than other hummingbirds.

Second, Acorn Woodpeckers seemed to tolerate the activities of the coronets, whereas sapsuckers usually defend their sap trees against all other animals (Foster and Tate 1966). Acorn Woodpeckers in California do not tolerate hummingbird intruders, and Anna Hummingbirds (*Calypte anna*) enter their sap trees almost exclusively when the woodpeckers are absent (MacRoberts and MacRoberts 1976). These woodpeckers in Colombia are less interspecifically aggressive, perhaps owing to the lack of intruders competing for sap. We never recorded any bird or mammal, other than the hummingbirds mentioned above, visiting sap holes. Our observations are not sufficient to support any speculation on the evolutionary significance of the relationship between Acorn Woodpeckers and Buff-tailed Coronets. We nevertheless conclude that in the areas where both species occur together, the behavior of Buff-tailed Coronets is greatly affected by the activities of Acorn Woodpeckers.

This study was made while we were students at the Universidad del Valle, Cali, Colombia. We thank H. Alvarez for his constant advice and encouragement, and G. Buch for his hospitality at Finca Merenberg. The manuscript benefited from comments by M. MacRoberts, F. G.

Stiles, P. Feinsinger, and M. F. Lawton. Financial support was provided by Comité de Investigaciones, Universidad del Valle, and an Exxon fellowship from the Smithsonian Tropical Research Institute.

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*The Condor* 87:543-546  
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## SONGS, DISPLAYS, AND OTHER BEHAVIOR AT A COURTSHIP GATHERING OF BLUE-BLACK GRASSQUITS

TOM WEBBER

At 19:05 on 28 June 1983, J. W. Hardy and I encountered a group of at least 20 male Blue-black Grassquits (*Volatinia jacarina*) in Guerrero, Mexico. Surprised to see such a flock in the middle of the grassquits' breeding season, which in Mexico lasts from about April to about November (Miller et al. 1957 and data in the collection of the Western Foundation of Vertebrate Zoology), I returned to the same site on three evenings and two mornings in the following week. Each time, I found many grassquits displaying in a dense congregation unlike anything described to date. In some ways, this congregation resembled a lek.

The grassquits gathered in a shallow basin on a hillside that sloped to the sea, about mid-way between Pie de la Cuesta and Acapulco. The basin was about 30 × 40 m, at an elevation of about 100 m, and was about 400 m inland. Grass (ca. 1 m high), dotted with bushes (up to 3 m high), grew over the hillside and basin.

Each morning and evening, I found between 20 and 30 males in the basin, more than 90% of which were within

an area about 25 m in diameter. Because they often changed perches before I could describe the locations and activities of all the birds present, I resorted to making occasional estimates of the overall distribution of the birds, and concentrated on following individuals until I lost sight of them. The grassquits perched and displayed on the grass and bushes, on bare spots in the grass, and on a one-lane asphalt road that crossed the basin. They perched singly or in clumps of up to ten birds; I saw as many as seven grassquits in a single bush about 1 m in diameter. The number and size of these clumps changed often. The grassquits on the road spaced themselves more evenly than those in the vegetation. Fewer than half of the grassquits stood on the road at any time; my presence may have kept others from joining those on the road.

Males sang several versions of their short, buzzy song, which has been aptly phoneticized as *szeeyew* (Slud 1964) and *weezit* (Peterson and Chalif 1973). I recorded three major song types (Fig. 1a-c), and several minor variations on one of them, in about 20 min. Males sang while they perched and while they performed their flight display: with tails spread, they flew straight up to a height of about 0.5 to 1 m; as they descended, they faced head-down and tail-up, righting themselves just before they returned to the perch. Some authors, such as Dickey and van Rossem (1938) and Haverschmidt (1968), have said that the displaying grassquits "leap" or "jump" into the air; all of the ones that I saw obviously flew. As they launched into the air, they often made a series of distinct snapping sounds (Fig. 1d) with their wings before they began singing. Songs usually ended at the tops of display flights. I can find no differences in my recordings between songs that were delivered while the birds perched and while they flew. I saw

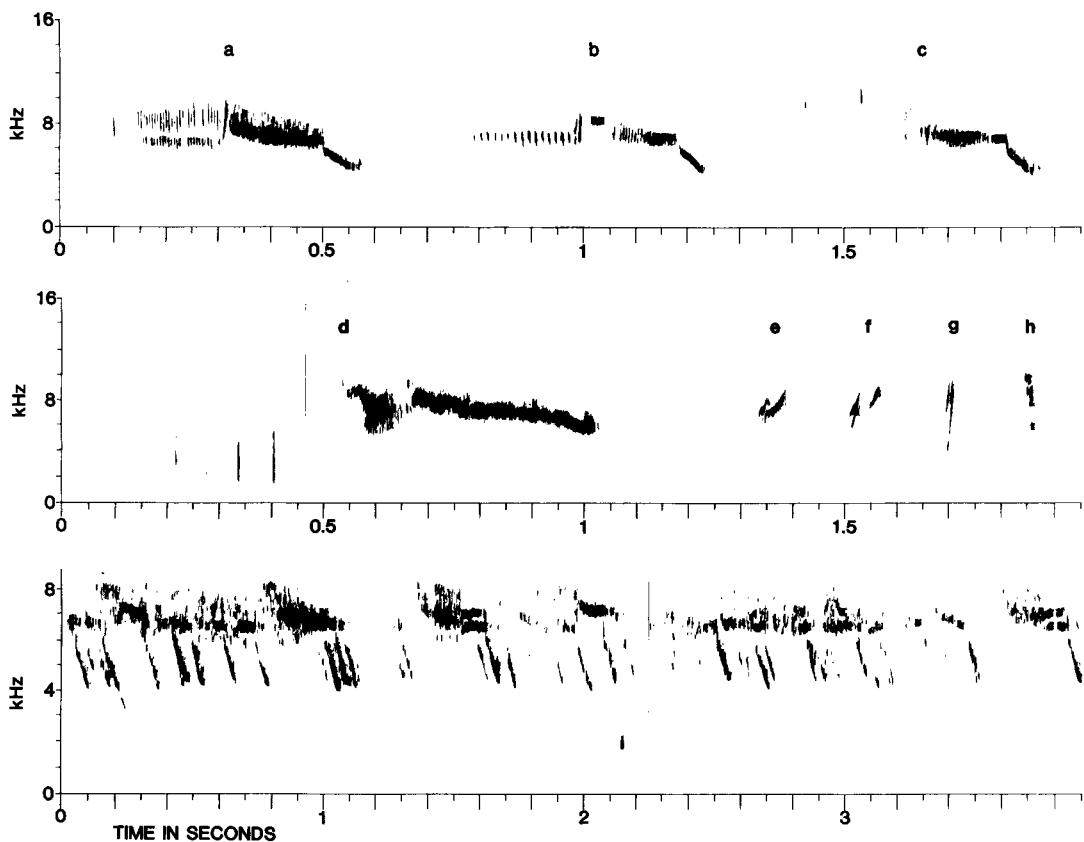


FIGURE 1. Wide-band sonograms of Blue-black Grassquit sounds. (a–c) Three versions of the primary song performed by the grassquits in the basin. I reproduced the two introductory chips in (c) at a setting 6 dB higher than the rest of the song. (d) A song preceded by a series of six snapping sounds that are produced by the grassquit's wings in a display flight. These wing sounds are clearly audible on many of my recordings made in the basin, but this sonogram is from a recording made at Zihuatenejo, Guerrero, that shows the sounds with special clarity. I reproduced the wing sounds at a setting 8 dB higher than the song. (e, f) Two *seep*<sup>2</sup>-like calls, and (g, h) two *chip*-like calls that were given by the grassquits as they settled into the grass in the evening and as they arose in the morning. (i) The dawn chorus of the massed grassquits. Note the difference between this and the other sonograms in their time and frequency scales. All recordings are in the Bioacoustic Archives of the Florida State Museum.

no displays such as the one Edwards and Lea (1955, p. 53) saw in Chiapas, Mexico: "Without actually leaving the perch the tiny [male] bird bounced vigorously up and down with flapping wings, uttering a strange, shrill buzzy note at each upward bounce."

About half of the males present at the peak of activity (but none of the few males in parti-colored juvenal plumage) performed flight displays. Birds that performed flight displays changed perches often and seemed not to hold mutually exclusive display sites. I saw three attempts, two of them successful, to take over another's display or song perch.

It was sometimes apparent that more than one male sang in the distinct clumps of birds in the vegetation, but I never saw more than one perform flight displays in such a clump. Other males in these clumps watched the male performing the flight displays. Some males certainly alternated between singing while perched and while in flight, but I do not know whether any alternated between performing flight displays and acting as watchers. In this account, I use the term "flight displayer" to refer to grassquits that I saw performing flight displays, regardless of anything else they might have done. Flight displayers often perched with their torsos erect, their crowns fluffed, and sometimes with their upper flank feathers fluffed as well. The birds who watched them often perched with their torsos nearly

horizontal and their plumage sleeked, facing the flight displayer at a distance of less than 1 m. Five times, I saw watchers follow flight displayers that had just flown more than 3 m away from them; in the one instance in which I could see where the flight ended, the watcher landed close to the flight displayer and resumed scrutinizing him. Once, a flight displayer flew a mere 60 cm to a new perch, and his watchers immediately moved so as to stay as close to him as before. Three times, I saw flight displayers chase their watchers when there were no females nearby. Flight displayers seemed to ignore their watchers most of the time. Four times, I saw males visit a flight displayer, watch him closely, and then leave. I never saw a flight displayer follow a watcher that left him. In general, the watchers seemed to ignore one another; only once did I see one chase another.

The ratio of visible males to visible females was perhaps ten to one. Females usually stayed inconspicuously in the grass. Nine times, I saw one or more females emerge from the grass, fly to one or more males (often a flight displayer and his watchers), and perch there quietly within about 1 m (sometimes within 40 cm). Three times, I saw males fly to a female's perch.

Males performed three kinds of displays to females when they met at close range. At least 17 times, I saw males approach females by scrambling slowly over the branches

in a crouched posture, with their crowns fluffed, bowing down first to one side and then to the other at a rate of about one or two bows per second, while opening and closing their tails with each bow. Twice, males performed flight displays within 30 cm of a perched female; one male's flights were only 15 cm high. One male on the road walked in a circle less than 25 cm in diameter around a female, with his crown fluffed, his tail spread, and his wings drooping to the ground. Females usually stood quietly when males displayed to them at close range. One female jabbed with her bill at an approaching male, who then retreated.

Of the five times I saw flight displayers, watchers, and females close together, a flight displayer chased his watchers only once. Once, a flight displayer and his sole watcher performed bowing displays to a female at the same time. Four times, two or more males performed the bowing display to one or more females in groups that had no flight displayers. In the remaining five instances of close-up courtship, single males performed the bowing display to one or more females.

Seven times, a female left the male or males and flew directly into the grass, where one or more of the males followed immediately. In one of these instances, a female left a flight displayer and his sole watcher, and only one of the males followed, but I could not see which one it was. In the other six instances, the males that followed females away from the perch were lone flight displayers (three times), males that had been in clumps with no flight displayers (twice), and a flight displayer that first chased away his watchers. Twice, males left females and flew into the grass and bushes, where one or more of the females immediately followed. I always lost sight of the birds as they flew into the vegetation. Five times, clumps of males and females broke up without any appearing to follow others. Once, a male pursued a female out of the grass and over the road in a fast, twisting chase, after which they fought on the ground. Reicherdt (1973) described his captive Blue-black Grassquits chasing one another in a somewhat similar way during courtship. I saw no copulations.

When I visited the basin at 16:00 (29 June), 11:00 (30 June and 2 July), and 08:45 (3 July), there was never more than one male singing there. At these times, singing males were scattered widely over the hillsides.

One evening I arrived at 18:30, once at 19:05, and once at 19:10; each time the maximum number of grassquits was already there. The singing and displaying continued until dark. As darkness descended, the grassquits stayed in the basin and settled into the grass to roost. Before they chose a final roosting place, many grassquits tried several sites in the basin, alternately skimming over the top of the grass and plunging in. They gave a variety of calls (Fig. 1e-h) from the grass, perhaps as they contended for perches. Some roosted singly, others in clumps of three or four at the bases of bushes. By 19:25, when it was dark, all of the grassquits had taken their places in the grass and had fallen silent.

Twice, I arrived at the basin before dawn. By 05:46, when it was still dark, the grassquits began to sing from deep in the grass. As the first light showed, they began to take up perches on the bushes and the road. The chorus of song reached a sustained crescendo (Fig. 1i) by 05:56, before all of the males had arisen from the grass. By about 06:00, the grassquits were arrayed over the basin, singing and displaying as they had done the evening before. By 06:11, grassquits started to leave the basin, some flying fast and straight over the crest of the hill to points unknown. By 06:30, only one or two males remained in the basin. On the morning of 3 July, the remaining male chased out several stragglers as he gave chips of the type shown in Fig. 1g.

Was this courtship gathering a lek? Bradbury (1981) and Oring (1982) defined leks as mating systems in which (1) males provide no parental care, (2) there is an arena of

displaying males that females visit for mating, (3) the arena contains nothing of value to the females except the males, and (4) females have a choice of mates at the arena.

I do not know whether the spread-out sites on which the males displayed during the daytime were territories, or whether the males may have attended nests or young there, but others have found evidence that male Blue-black Grassquits care for young. Miller (1952) thought that he had flushed a male from a nest in Colombia, and Alderton (1963) found males in Panama building nests, incubating, brooding, and feeding young. Reicherdt's (1973) captive male gathered nest material and fed young. I do not know whether certain males in the basin may have controlled favorable roosting sites of value to females. I saw nothing that obviously prevented females from choosing among males; most of the time, males met females when the females approached them.

Even though they are not definitive features of leks, the presence of males (some in subadult plumage) who stood by and watched the displayers, and even the absence of the birds at mid-day, resemble, to some extent, characteristics of leks in several other species of birds, including birds of paradise (LeCroy 1981) and grouse (Oring 1982).

Several authors have described gregarious roosting or inklings of group courtship by Blue-black Grassquits and their relatives. Skutch (1954) found a roost of White-collared Seedeaters (*Sporophila torqueola*), Variable Seedeaters (*S. aurita*), Blue-black Grassquits, and Thick-billed Seed-Finches (*Oryzoborus funereus*) in Costa Rica that numbered, at times, in the hundreds. At least the White-collared Seedeaters, the most abundant birds, roosted there during the breeding season. They arrived at the roost about an hour before sunset. Skutch described no courtship behavior, but said that occasionally a burst of song spread through the congregation.

Murray (1982) found ten male Blue-black Grassquits singing, performing display flights, and holding territories in an area of 0.4 ha in Costa Rica. Other males were present who did not sing or display, but the territory-holders chased them as soon as they showed themselves. Murray concluded that he had seen either a lek or some of the smallest territories known among passerines. The grassquits he watched were not so concentrated as the ones I saw, apparently did not roost together, and spent virtually all day in their territories. Barnard (1956) saw a male in Panama performing flight displays in the presence of a female, while another male in the same garden (size not specified) "seemed to imitate his every move."

Skutch (1954) often saw two or three Yellow-faced Grassquits (*Tiaris olivacea*) in Costa Rica singing "close together," two sometimes within 30 cm of one another, and, on one afternoon at the peak of the breeding season, he saw five singing in the same bush. Although Yellow-faced Grassquits often form flocks in Costa Rica (Skutch 1954), they are "strictly territorial" in Jamaica and never occur in flocks there (Pulliam et al. 1972). Aggregations of Blue-black Grassquits such as the one I have described may occur at only one or a few places in the range of this widespread species.

Oring (1982) listed only 18 species of passerines that are known or strongly suspected to form leks: two are cotingas, eight are manakins, and the rest are birds of paradise. If Blue-black Grassquits do indeed form leks, they are the only New World oscines, and the only grassland passerines, known to do so. Even if the aggregation that I have described was not a lek, the combination of a roost with a courtship arena and what may be territoriality (those spread-out, mid-day display sites) amounts to a richly-detailed avian oddity that ought to repay further study.

I thank J. Cox, J. W. Hardy, L. McKean, J. Robinson, and K. Winnett-Murray for criticizing the manuscript, L.

Baptista for providing a reference, and L. Kiff for providing breeding dates. The American Philosophical Society generously provided a grant to J. W. Hardy for our trip to Mexico.

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*Florida State Museum, University of Florida, Gainesville, Florida 32611.* Received 30 March 1984. Final acceptance 30 May 1985.

*The Condor* 87:546-547

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## LATERAL ASYMMETRY OF THE BILL OF *LOXOPS COCCINEUS* (DREPANIDINAE)

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Unlike the claws of crustaceans, the shells of snails, or flatfish that lie on one side, few bird species show lateral asymmetry in external morphology. Asymmetries have been described in ears, legs, and bills: (1) several species of owls have asymmetric, feather-covered external ears (Newton 1896, p. 178 and 675; Norberg 1977); (2) asymmetry of leg and foot bones associated with predominant use of a given limb has been reviewed by McNeil et al. (1971); (3) lateral bending of the bill has been noted in Charadriiformes: the bill of the Wry-billed Plover (*Anarhynchus frontalis*) of New Zealand bends to the right (Johnsgard 1981, p. 204-206), and in at least four species of oystercatchers (*Haematopus* spp.), a minority of individuals have bent bills, most of which are bent to the left (Hockey 1981); (4) crossbills (*Loxia* spp.) have crossed mandibles; and, (5) the Akepa (*Loxops coccineus*), a small, endangered species of the Drepanidinae (Hawaiian finches, formerly honeycreepers) has crossed mandibles that resemble those of crossbills. The Akepa is small (wing 59-69 mm, culmen 9-11.5 mm; Amadon 1950) and is found on the islands of Hawaii, Kauai, Maui, and formerly Oahu. The island populations differ considerably in color and morphology but all show the characteristic bill-asymmetry. The populations were formerly more numerous but are now rare and of limited distribution. Most of the museum specimens were collected in the period 1890 to 1900.

The Akepa's bill-crossing, although slight and inconspicuous, is likely to be related to the feeding habit of the species. Richards and Bock (1973) reported (from four specimens) that the asymmetry is confined to the horny rhamphotheca and does not involve the underlying skel-

eton. They suggested how the asymmetry functions in prying apart closely imbricated structures. Preliminary evidence suggested to me that the sexes might differ in the direction of laterality and, perhaps, present a novel form of sexual niche-diversification (Selander 1966). The acquisition of these specialized foraging skills is presumably contingent upon development of the appropriate structures. Thus, it is valuable to compare the bill-crossing between Akepas of different ages.

Here, I report the direction of bill-crossing in Akepas from different islands in relation to age and sex, and the magnitude of lateral asymmetry in relation to age for males from one population.

I examined all available, undamaged skins in the following collections: American Museum of Natural History, New York (105); Bernice P. Bishop Museum, Honolulu (87); British Museum, Tring (57); Museum of Comparative Zoology, Harvard University (20). These comprise 71% of all specimens reported to exist in collections (Banko 1979).

For each specimen, I recorded from the label(s) age, sex, and details of collection, and from the skin, the direction of asymmetry (position of lower mandible with reference to sagittal plane), and plumage color. For the majority of specimens, I measured (under a microscope) the lateral separation of the tips of the mandibles (i.e., extent of asymmetry). Some of the Akepa skins had been damaged or distorted during collection or preparation, but the direction of laterality was rarely obscured. Some severely distorted skins were rejected for measurements of tip separation.

All females (and males from Kauai) cannot conveniently be aged by plumage color. Other males were classified into three age-classes by the extent of orange (or red) plumage: (a) juveniles (without any orange), (b) sub-adults (orange incomplete), (c) adults (fully orange). The timing of these transitions in plumage is not yet known, but they are believed to represent an increasing age sequence. Males are significantly more numerous than females in the collections ( $\chi^2 = 18.6$ ,  $P < 0.005$ ).

Right-billed birds predominated, especially in adult males (58%), and the only groups with a majority of left-billed birds were females from Maui and the six males