SHORT COMMUNICATIONS

WITHIN-TERRITORY DIVISION OF FORAGING SPACE BY MALE AND FEMALE AMAKIHI (*LOXOPS VIRENS*)

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AND

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Whenever a foraging nectarivorous bird visits a flower that contains no nectar, it has wasted time and energy. Therefore, one would expect nectar-feeding birds to minimize visits to flowers that were recently depleted of nectar. An individual bird can forage more efficiently by excluding intruders from a feeding territory and not revisiting flowers within the territory. This pattern of behavior occurs in sunbirds (Gill and Wolf 1977), some hummingbirds (Gass and Montgomerie 1981), and honeycreepers (Kamil 1978).

When a breeding pair of nectar feeders maintains a nesting and feeding territory, it may be important for one member to avoid flowers recently depleted of nectar by its mate. Amakihi (*Loxops virens*) are nectar-feeding Hawaiian honeycreepers that maintain type A territories within which copulation, nesting, and foraging occur (Hinde 1956), and from which conspecifics are excluded (van Riper 1978). Within these territories, individuals avoid flowers from which they have recently taken nectar (Kamil 1978). In this paper, we present data which suggest that pairs of honeycreepers subdivide their territories while foraging, and that this division ceases as the female spends less time at the nest.

METHODS AND RESULTS

Our observations were made on the island of Hawaii, at approximately 2,130 m elevation on the southwestern slope of Mauna Kea in the Kaohe Game Management Area. The dry, open parkland forest is dominated by two native trees, *Sophora chrysophylla* (Leguminosae) and *Myoporum sandwicense* (Myoporaceae); see van Riper (1980) for a detailed description of the area. Amakihi breed in this forest from winter to early spring, and during this time feed extensively upon *Sophora* nectar (van Riper, pers. observ.). We collected data during February, March, and April, 1975, when the territorial boundaries of pairs in a color-banded population of Amakihi had been delineated. We first observed the division of the feeding area among members of a pair while collecting data on the pattern of flower visitations by individual birds in territory 16-75. This territory included two *Sophora* trees in heavy flower located next to each other. Each day, 70–90 flower clusters on the southeast side of the larger of the two trees were noted. We had placed five colored markers in the tree several days earlier so that we could identify each flower cluster on the basis of its position with respect to a marker. When a bird visited one of these clusters, we recorded its identity, the flower cluster that it visited, and the time of the visit (see Kamil 1978, for details). Both resident birds frequently foraged in the two trees, but only the female used the area of the larger tree where the numbered clusters were located. During 25.9 h of observations (over a five-day period), the female initiated 86 feeding bouts, while the male initiated 83 bouts. However, the female made 241 visits to the marked clusters (a visit was defined as probing one or more flowers in a cluster),

whereas the male made only six. This difference is highly significant ($\chi^2 = 215.3$, df = 1, $P < 0.0001$) assuming that the expected number of visits to any specific set of clusters is proportional to the number of feeding bouts. Although the female fed throughout both trees, she concentrated her foraging in the area containing the experimental clusters, an area within which the male almost never foraged.

We found similar division of food supply in two other territories. During 9.8 h of observation (over two days) of the single feeding tree in territory 70-75, the female initiated 74 feeding bouts, the male only 34. The female visited 191 experimental clusters, the male only 39 ($\chi^2 = 22.49$, df = 1, $P < 0.001$). During 14.7 h (over three days) in territory 23-75, the female initiated 61 feeding bouts, the male 60. The female visited 120 experimental clusters, the male only 77 ($\chi^2 = 8.04$, df = 1, $P < 0.01$).

In each of these cases the female made a disproportionately large number of visits to the clusters under observation. In territory 16-75, nearly all the experimental clusters were within the area used only by the female. In the other two territories, the boundary separating the area used by the female from the area used by both birds seemed to run through the area of the experimental clusters, and consequently sexual differences in foraging pattern were less obvious. However, in all cases only a few hours of observation sufficed to enable us to discern a line that the male rarely crossed for foraging purposes. Unfortunately, surrounding vegetation made it impossible to collect data directly from the female's area within these two territories. However, it seemed clear to us that the male on each territory avoided foraging in a spatially defined area that was used heavily by the female.

We also observed the same behavioral pattern under somewhat different circumstances in two other territories. In the three territories that we described above, the nests were located in trees containing no bloom. But in territories 40-75 and 37-75, they were in *Sophora* trees that contained some flowers, although the major sources of nectar were in other trees. The females on these two territories made heavy use of the clusters near the nest, which the males almost never used while incubation was in progress.

We studied temporal changes in the division of feeding areas in more detail at nest 45-75. All flower clusters near the nest were marked. In 24 h of observation during late incubation and the early nestling period, we found a close correlation between the time that the female spent on the nest and the exclusiveness of her foraging area (r = −0.895, df = 5, $P < 0.01$; Table 1). Early in the breeding cycle, when she was incubating eggs or young for extended periods, her feeding area was rarely visited by the male (Fig. 1). However, as she spent more and more time off the nest, this pattern disappeared. By day 5 of the nestling period (30 April), the male foraged throughout the area containing marked flower clusters.

DISCUSSION

Our data suggest that a female Amakihi has exclusive use of some of the flower clusters within a territory. While this pattern gives her sole access to the nectar produced by these flower clusters, it also makes the pattern of nectar distribution more predictable. She tends to visit flowers that she has not previously visited (Kamil 1978); these are virtually certain to contain nectar, since they were not emptied by the male, and other Amakihi are effectively prevented from foraging on the territory by the residents.

Sexual differences in avian foraging behavior have often been reported (e.g., Holmes and Pitelka 1968, Morse 1968, Williamson 1971, Feinsinger and Chaplin 1975, Williams

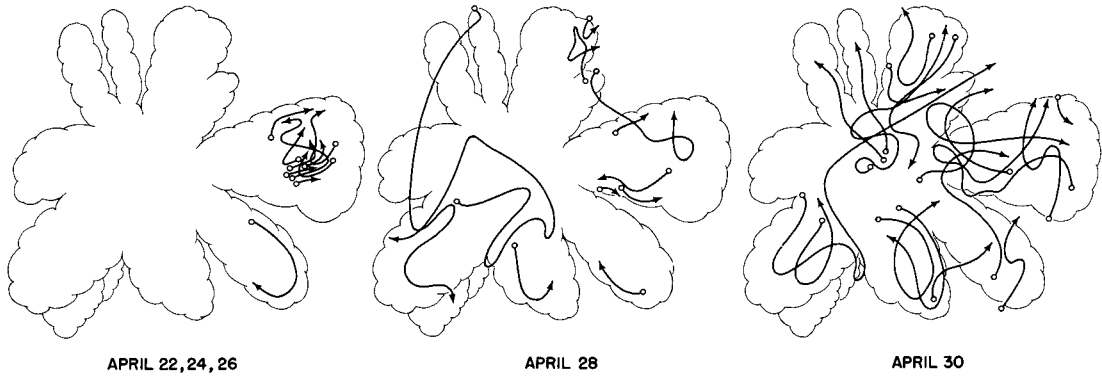**APRIL 22,24,26**   **APRIL 28**   **APRIL 30**

FIGURE 1.   Diagrammatic representation of changes in the use of feeding space by the resident male Amakihi on territory 45-75. Lines depict the foraging path of the male at marked flower clusters in a *Sophora chrysophylla* tree during late incubation (22 and 24 April) and the early nestling period (26 April = day 0; 28 April = day 3; 30 April = day 5).

1980). These behavioral dimorphisms are sometimes associated with sexual dimorphism, and as a result of such differences the diets of the males and females sometimes differ significantly (Selander 1966, Holmes and Pitelka 1968). In other cases, females tend to forage near the nest, while males forage at greater heights, near perches from which they sing (Morse 1968, Williamson 1971), increasing foraging efficiency by reducing the time spent travelling to and from foraging areas.

These factors seem relatively unimportant in the present case. Male and female Amakihi are monomorphic, and both obtained nectar from *Sophora*. While the foraging area of the female was generally near the nest, males had no song perches. Because individual flowers are a stationary and depletable source of nectar, territorial partitioning may improve foraging efficiency by increasing the predictability of the location of food for an individual forager. Division of the territory may be especially important in cases where male and female diets do not differ. For example, male and female Henslow's Sparrows (*Ammodramus henslowii*) tend to forage in different directions from their nest, but feed the same food to nestlings (Robins 1971).

Other evidence also suggests that subdividing food resources in this way increases foraging efficiency. As Wolf and Stiles (1970) pointed out, foraging efficiency may be particularly critical for an incubating or brooding female. Minimizing the amount of time needed to obtain food will

maximize the time she can spend at the nest. This interpretation is consistent with the foraging patterns that we observed on territory 45-75 (Fig. 1), where the food supply was no longer divided after the female's attendance at the nest decreased.

Several proximate mechanisms could maintain the division of food sources between a pair of territorial Honeycreepers. For example, if the female routinely feeds on particular flowers, the male may learn to avoid them because they contain little nectar. However, we witnessed several male-female encounters, which suggest that the female actively defends her foraging area against her mate. On two occasions, once in territory 16-75 and once in territory 45-75, the female flew directly at the male, displacing him, almost immediately after he entered and began to feed in her exclusive foraging area. Because the male Amakihi engages in most of the territorial defense, including defense of the female's foraging area (van Riper 1978), this female behavior was particularly striking, and supports Smith's (1980) suggestion that female intrapair dominance is common among monogamous species during the breeding season.

TABLE 1.   Foraging patterns of male and female Amakihis on territory 45-75, and time spent on the nest by the female during the breeding cycle.

Day of the breeding cycle	Period of observation (h)	Number of feedings at marked flowers		Time spent by female on nest (% total observation time)[a]
		Male	Female	
Incubation period				
Day 13	1	0	24	77.6
Day 15 (hatching)	4	17	28	57.6
Nestling period				
Day 0	5	14	77	57.7
Day 1	6	11	85	63.3
Day 3	4	51	102	48.8
Day 5	4	51	34	29.6

[a] Data modified from van Riper (1978).

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TERRITORIAL BEHAVIOR OF THE BLUE-BLACK GRASSQUIT

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Although the Blue-black Grassquit (*Volatinia jacarina*) is a common species from northern Mexico to northern Argentina and Chile, it has been studied in some detail only in Panama (C. C. Alderton, Condor 65:154–162, 1963). In 1970 I had the opportunity to study the territorial behavior of this species at Finca Taboga near Cañas, Guanacaste Province, Costa Rica, where it occurred singly in openings at the forest edge or in dense groups in open areas. Because the territorial behavior of tropical birds is poorly known, the following observations may be of interest.

On 13 July I mist-netted and color-banded three adult male (all black), two "subadult" male (black mixed with
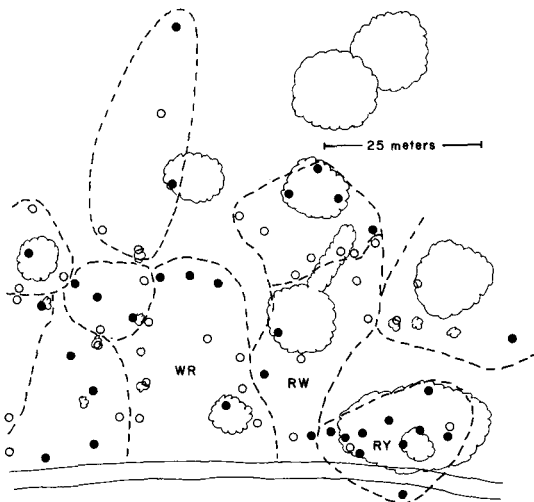

FIGURE 1. Map of territories of Blue-black Grassquits. The dashed lines indicate territorial boundaries as determined from positions of singing and displaying individuals (black circles) and other positions of the same birds (open circles). WR, RW, and RY are color-marked birds. The wiggly lines represent the crowns of individual trees.

brown; perhaps these were adults that had not completed their molt), and one female (all brown) grassquits. During the next three days I was able to watch the activities of the three all-black males, as well as several unmarked males and females. I mapped my study area (approximately 3,750 m² or 0.4 ha) by establishing a transect along a road and triangulating the major features of a field with scattered trees (Fig. 1). The three marked males maintained separate territories from which they chased intruders and within which they were the only individuals to sing and display. Hence, I assumed that other singing and displaying males, although unmarked, were territory holders. By plotting the activities and movements of these unmarked birds, their territories could also be mapped.

The area under observation supported 10 resident males (Fig. 1), none with mixed black and brown plumage. The smallest territory was about $1/5$ the size of the largest. Only the resident male displayed within its territory, giving its short, buzzy song every 3.5 to 4.5 s for up to 5 min at a time, with or without its unique aerial display, that is, jumping into the air about a foot or so, exposing the white patches under the wings, and returning to its perch (Alderton 1963; P. Slud, Bull. Am. Mus. Nat. Hist. 128:1–430, 1964). Other males were often present but neither sang nor displayed and were almost immediately chased by the resident. From time to time a resident left his territory for several minutes, flying high over intervening territories to some point out of my sight.

The small territories and the conspicuousness of the distinctive vocal and aerial displays of male Blue-black Grassquits gave the appearance that the birds were on a display arena. These habits typify species with lek behavior and imply polygamous mating relationships. Alderton, however, reported that this species in Panama was monogamous with the male participating in nest building, incubation, and caring for the young. D. E. Davis (Bird-Banding 12:93–97, 1941) mentioned that it was "typically" territorial, and A. H. Miller (Auk 69:450–457, 1952) thought that he had flushed a male from a nest in Colombia. If these reports are correct, and if the territories I observed in Costa Rica were typical of the Blue-black Grassquit in Panama and Colombia, then the territories of this species are among the smallest reported among passerines.

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