FEMALE TERRITORIALITY IN A TROPICAL HUMMINGBIRD

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THE latest summary of territoriality in hummingbirds (Pitelka, 1942) reports that females of some species defend a spatially circumscribed area during the breeding season. The available data suggest that defense is limited to an area surrounding the nest site, with the possible inclusion of certain feeding areas near the nest. Females of a few species may hold temporally and spatially limited territories around localized feeding sites during and after the breeding season. Several recent studies refer to females defending a nest area (Dorst, 1962) or birds on migration defending a small area in a locally common food source (Armitage, 1955; Cody, 1968). Recent studies in arid tropical lowlands in Costa Rica suggest that females of several resident species hold nonbreeding territories similar to those of the males (Stiles and Wolf, 1969).

The present study documents female territoriality in a highland tropical hummingbird, *Panterpe insignis*, during the nonbreeding season. (Unfortunately nothing is known of the territorial system in this species during the breeding season.) This report also suggests possible ecologic factors that produce selective pressures for female territoriality and some possible morphological and behavioral consequences of this territorial social system in hummingbirds.

The Fiery-throated Hummingbird, *Panterpe insignis*, the only member of its genus, is distributed throughout high montane central and southern Costa Rica and western Panama (Slud, 1964) where it is limited almost entirely to elevations above 2,000 meters. The primary habitat is clearings where secondary succession has reached the shrubby stage. The birds also enter partly cleared forests where epiphytes (Bromeliaceae, Ericaceae, Loranthaceae) grow on the large oaks that dominate the woodlands at this elevation. More detailed accounts of the ecology and behavior of this species, especially its ecological and behavioral relations with the sympatric complex of nectar-feeding birds, are being prepared.

Panterpe is a brightly colored hummingbird in which both sexes are so similarly colored that Ridgway (1911: 511 footnote) was unable to "find . . . even an *average* difference of coloration between the sexes, some of the most brightly colored specimens being females, while some of the dullest are males." Near the middle of the major study period (April) I was able to sex most individuals I handled in the field, and later collected, on the basis of a slight size difference (Table 1) and sometimes by a difference in the degree of feather wear on the lower abdomen. The difference in wear left the lower belly of some females slightly grayer than the males.

TABLE 1
SIZE CHARACTERISTICS OF *PANTERPE INSIGNIS*

Character	Sex	Mean	SD	SE	No.	Female as per cent of male	Range
Wing length (mm)	M	65.6	1.9	0.4	21		63.6–68.2
	F	61.5	2.4	0.5	25	93.7	56.2–67.9
Tail length (mm)	M	43.3	1.5	0.3	22		41.3–45.8
	F	40.2	2.0	0.4	24	92.9	37.9–47.4
Bill length (mm)	M	19.3	0.2	0.05	23		18.3–19.9
	F	19.5	1.0	0.2	22	101.1	17.8–21.8
Weight (g)	M	6.2	0.4	0.08	33		5.5– 7.0
	F	5.3	0.4	0.1	15	85.8	4.9– 6.5

This, the only consistent color difference I could find between the sexes, is evident only at limited times of the year, probably following incubation and prior to the next body molt.

I was unable to find any nests of *Panterpe.* Gonad data from the females do not identify the breeding season, and size data from the male gonads suggest that some individuals may be in potential breeding condition throughout most of the year. The breeding season may start by early September, when Stiles (pers. comm.) and I saw what may have been attempted copulations, and may continue into December and January.

METHODS

Most of the critical observations on which this report is based were made between December 1966 and early July 1967. Additional field studies were made in June and August 1965 and 1966 and early September 1966. The study area was the vicinity of Villa Mills, a small collection of houses on the southwestern side of the Cerro de la Muerte at the northern end of the Cordillera de Talamanca in central Costa Rica. Elevations of the study sites ranged from 2,900 to 3,200 meters. Most of this region originally was dominated by oak forest, but when the Pan-American Highway opened it to human exploitation, lumbering operations destroyed much of the forest near the highway; cutting is still proceeding. Many of the first lands cleared have now grown up in shrubs and small trees, especially members of the Ericaceae and the genus *Miconia* of the Melastomaceae. Many of the data reported here were obtained in a limited number of locations within the general study area. The primary factors in choice of study sites were the presence of *Panterpe* and the ease of watching the activities of birds that occupied the site.

At the beginning of the study, individuals of *Panterpe* were caught in mist nets and marked on the back with a spot of airplane dope. The marked birds were watched for 1 week or more on their territories. I had hoped to collect most of these birds near the end of the study period in June and July, but the birds often deserted the territories at unpredictable times, and once a bird had left its territory I was rarely able to locate it again. Thus it was difficult to follow birds over periods longer than several days and still be certain of collecting them for positive sex determination. Also some of the birds molted in March and April and lost their paint markings. I therefore decided to watch unmarked birds for periods of at least 2 hours until positive territorial defense was noted and then to collect these individuals before leaving so that I could be certain of collecting the resident on which the observations

TABLE 2
GENERAL SUMMARY OF TERRITORIAL *PANTERPE INSIGNIS* COLLECTED NEAR VILLA MILLS, COSTA RICA

Sex	Date	Gonads[1]	Molt	Active defense seen	Marked
M	15 March	t. 1 mm	Light on head	Yes	Yes
F	6 April	o. s. e.	Adventitious	Yes	No
M	7 April	t. 1 mm	Flight, body	No	Yes
F	14 April	o. s. e.	Flight	Yes	No
F	15 April	o. v. s. e.	None	Yes	Yes
M	16 April	t. 2 mm	Slight on head	Yes	No
M	30 April	t. 2.5 mm	Body, flight	Yes	Yes
M	13 May	t. 2 mm	Body, flight	Yes	Yes
F	27 May	o. v. s. e.	Body	Yes	No
M	27 May	t. 1.5 mm	None	No	No
M	11 June	t. 1.5 mm	Light body	Yes	No
M	10 June	t. 3 mm	Light body	Yes	No
F	8 June	o. n. e.	Light body	Yes	No
M	8 June	t. 2 mm	Light body	Yes	No
F	16 June	o. n. e.	Light body	Yes	No
M	17 June	t. 1 mm	Light body	Yes	No
M	3 July	t. 2 mm	None	Yes	No
F	4 July	o. v. s. e.	None	Yes	No
M	5 July	t. 2.5 mm	None	Yes	No

[1] t = length of left testis in mm; o. s. e. = ovary slightly enlarged; o. v. s. e. = ovary very slightly enlarged; o. n. e. = ovary not enlarged.

were made. I tried to watch marked birds for several days before collecting them. In addition to data on the birds I collected, I have data from many other birds, often individually marked, that were not collected. The data on female occupancy of territories are derived only from individuals that were collected on their territories (Table 2).

RESULTS

Observations on marked individuals that were not collected showed that most territorial birds were present on their defended areas through most or all of a day, but that they left each evening. Strongly territorial birds returned to the territory about ½ hour after sunrise the next morning. Normally a marked individual held a territory for more than a week, but once it deserted the territory, the individual rarely reappeared in the vicinity, with two exceptions. One individual, marked on a territory where it remained for several weeks, moved to an adjacent territory on which it was finally collected. The other exception was a bird, caught and marked in the same general area, that remained on a recently abandoned territory for only one day. No other individuals subsequently occupied the territory, probably because a decline in floral food sources made it too unproductive. Most other marked birds maintained their territories for several days and usually longer. Thus I assumed that unmarked birds defending a certain place 2 or more hours were probably resident.

Characteristics of territorial birds and territories.—The only activities of

TABLE 3
SEXUAL COMPOSITION OF SAMPLES OF *PANTERPE INSIGNIS*

Type of collecting	Number of individuals		Female as per cent of total
	Male	Female	
General	9	5	36
Territorial	12	7	37

the residents in these territories, at least during this study, were maintenance, feeding, and defense. No evidence suggested that the territories served any reproductive function. Most or all feeding took place on the territory. Sometimes other hummingbird species were tolerated in these territories until they began to forage at the flowers. Defense of food was thus the primary function of the territoriality. Pitelka (1942) comes to a similar conclusion regarding territoriality among males of most species for which he has adequate data. Ecologically, then, a territory might be defined as a spatially limited site in which the resident restricts use of environmental resources by other individuals in order to satisfy its own requirements (these include mating and resources for young).

No data on sex in relation to territoriality were collected prior to mid-March; most data were obtained in April, May, and June. Possibly females hold feeding territories only during this season. It is assumed that during the reproductive period females of *Panterpe*, in common with most other species of hummingbirds, probably do most or all of the work associated with nesting and rearing of the young (Pitelka, 1942). These activities place increased demands on the female's time and energy and would reduce the effectiveness of her territorial defense. Although I was unable to document the breeding season of *Panterpe* and have no data on nesting activities, one might expect only male territoriality during the breeding period, unless females defend the vicinity of the nest as has been reported for other species (Pitelka, 1942). None of the territorial birds collected showed evidence of breeding; several were molting.

Of the territorial birds collected, 7 of 19 (37 per cent) were females (Table 3). To compare this result to the sex ratio of the entire population, birds were collected at irregular intervals in several sectors where continuous observations were not being made. I tried to collect each *Panterpe* that I encountered, hoping thereby to approximate random sampling. On this basis I determined the sex ratio of the population to be 36 per cent females (Table 3), almost identical to that of the territorial birds. These ratios do not differ significantly from 50:50.

This fact is surprising because in other species of hummingbirds for which sex ratios have been estimated, females outnumbered males (Nicholson,

TABLE 4
SEX OF *PANTERPE* SPECIMENS COLLECTED AT THE SEVERAL TERRITORIAL SITES

Location[1]	No. males	No. females	Total
Km 96	2	0	2
Km 96–97	0	3	3
Km 97	1	0	1
Km 97+	1	1	2
Km 97–98 (clearing)	1	0	1
Km 97–98 (hilltop)	3	0	3
Km 99 (near road)	2	1	3
Km 99 (soccer field)	2	2	4
TOTAL	12	7	19

[1] Locations are referred to kilometer sign posts along the highway.

1931; Schlag, 1939; Legg and Pitelka, 1956). A preponderance of females is to be expected in a group of birds in which the males are normally more conspicuous and the mating system is based on short, if any, pair bonds and probably promiscuity (Selander, 1965). A promiscuous mating system decreases the selective pressure for an equal adult sex ratio as one male can fertilize several females.

Several explanations are possible for the unbalanced sex ratio in favor of males in the population samples of *Panterpe*. The most obvious reason is that the sampling was biased by more conspicuous behavior of the males. It also is possible that the species makes some postbreeding migratory movement, and the movement pattern of the two sexes may be somewhat different.

In an effort to establish the similarities of these territories for males and females, several characteristics of the territories were compared. I have deliberately omitted the most obvious parameter—size—in these characteristics. Territory size in *Panterpe* varies with the distribution and species composition of the major food sources visited. Territories that centered around widely dispersed food sources, such as scattered trees with epiphytes, tended to be large; several territories exceeded 20,000 square feet. Small territories encompassing as little as 550 square feet were found in habitats such as shrubby second growth where the food supply was concentrated. In addition one territory might contain several species of food plants making it hard to judge the total energy value of the territory. At the same time many other parameters, such as numbers of other hummingbirds, weather, and nectar production, probably influence the actual size of the territory. It seemed beyond the scope of the present study to investigate precisely these determinants of territory size.

Males were more widespread among the territorial stations sampled than were the females (Table 4). At five territorial sites only one sex was

TABLE 5

FOOD PLANTS REGULARLY VISITED BY TERRITORIAL *PANTERPE* COLLECTED IN THIS STUDY[1]

Food plant	Territorial individuals visiting food plant		
	No. males	No. females	Total
Macleania	6	0	6
Tillandsia	2	0	2
Centropogon valerii	9	7	16
C. gutierrezii	4	1	5
Fuchsia splendens	1	0	1
F. microphylla	3	1	4
Symplocos irazuensis (?)	2	0	2
Rhamnus sp.	1	0	1
Miconia sp.	0	1	1
TOTAL	28	10	38

[1] A territorial individual may regularly visit more than one species of food plant.

taken; males occupied four of the five. As not all territorial birds in a given area were collected, possibly females were more widespread than the data indicate.

The types of food plants the territorial residents visited are listed in Table 5. No attempt is made in this table to reflect relative utilization of each plant species; some resident individuals are listed under more than one food item. The predominant food species in terms of utilization was *Centropogon valerii.* Most large clumps of this shrub had a resident *Panterpe* at this time of year. Earlier (December to March) when other plant species, such as *Gaiadendron, Macleania, Vaccinium,* and *Tillandsia* were blooming more commonly, these same clumps of *C. valerii* had no, or very few, territorial *Panterpe,* and some clumps were controlled by territorial *Colibri thalassinus,* the Green Violet-ear.

By March many of the other plant species that had served as food sources for *Panterpe* had finished blooming. At the same time *Colibri* disappeared almost entirely from the region and *Panterpe* began to control the *Centropogon* clumps. Most of the other plant species that the territorial individuals used from April to July were either just finishing the flowering period (*Macleania, Tillandsia*) or were species whose flowering declines markedly as the rainy season starts (*Fuchsia microphylla*). Other species such as *Fuchsia splendens, Symplocos irazuensis,* and *Rhamnus* sp. were just starting to bloom, but were not common enough or clumped enough to provide by themselves a suitable food source.

Centropogon gutierrezii is not used regularly, partly because it is relatively less common and has fewer flowers per clump than *C. valerii,* but primarily because its longer corolla tube (50 mm) is more difficult for the relatively short-billed *Panterpe* (20 mm) to use than that of *C. valerii*

(29 mm). The only hummingbirds of the four resident species that regularly fed at *C. gutierrezii* flowers were female *Eugenes fulgens* which have a 36-mm bill. *Panterpe* sometimes probed at the outside of the base of the *gutierrezii* corolla tube. Thus the abundance of clumps and the large numbers of flowers per clump of *C. valerii*, added to the lack of other suitable flowers at this time of year, apparently led *Panterpe* overwhelmingly to use *valerii*. *Panterpe*'s use of *valerii* during only a restricted period (April to July) and the quick establishment of territories around other plant species as they begin to bloom suggest that *valerii* is not a preferred source at all times of the year, but is utilized when other flowers are scarce or lacking.

Simultaneous with this shift in food sources was a general departure, probably an altitudinal migration, by most individuals of the other three hummingbird species in the area. *Eugenes* and *Selasphorus flammula* left as the flowers they had been using decreased in abundance. *Colibri* may have left as the result of the switch by *Panterpe* to *C. valerii* as a primary food source, producing a strongly competitive situation in which *Panterpe* won most of the encounters seen. In general it appeared that the hummingbirds were reacting to a decline in food supply throughout the Villa Mills region.

For all territorial females that were collected *C. valerii* was the predominant food source in the territory and the plant visited most frequently. The males were distributed slightly more widely in terms of food items and several individuals defended territories that included no, or only minor amounts of *C. valerii*, particularly early in the sample period before most other plants had stopped blooming completely. The restricted pattern of use by females may have been a result of male dominance over females, but in one well-documented case two males and a female were taken at different times from the same territory. A male held this territory initially; a female took it over when the first male was collected, and a second male finally claimed it when I collected the female. Both the last two occupants were previously excluded from the territory and held adjacent territories. Another case involved three birds with linearly adjacent territories, a female in the center one. At least one aggressive interaction was observed at each territorial boundary; neither bird chased the other, and each returned to its respective territory after a short period of hovering and calling. This center territory was held for several days before I collected the resident female. As she was not marked, I cannot be sure that the same bird held it throughout this period, but the boundary disputes were observed on the day all three birds were collected. Neither of these observations supports the notion that females were dominated by males.

The territories that included the *Centropogon valerii* as the dominant food plant were often among the smallest territories, because of the shrub's clumped growth pattern. It may be that territories centered around *Centropogon* are relatively easy to maintain because of their small size and the generally inferior quality of the food source. At the same time the territories that were most diverse florally tended to be largest; perhaps only a very dominant bird can defend a large territory successfully.

Territorial defense.—Willis (1967: 102) defines a territory behaviorally as "a space in which one animal or group generally dominates others which become dominant elsewhere." Unlike many north temperate hummingbird species, *Panterpe* has evolved no spectacular dives or pendulum displays for territorial defense. Once a territory was established, the resident announced its occupancy vocally only infrequently, usually by a "chit" or "chittering" call given from a perch within the territory. These calls seemed to be given most often when another hummingbird flew nearby, even if the intruder continued out of the territory. The territorial individuals sometimes sat on exposed perches, but about as often they perched in partly hidden places and thus made little active announcement of a territory either visually or vocally.

A persistent conspecific intruder elicited a direct encounter with the resident. This most often began with a "chitter" and led to a hovering flight by one or both birds. If both were hovering they often faced each other about 10 inches apart at about the same height. Usually such a confrontation ended in an upward flight of several feet or more whereupon the intruder turned and flew out of the territory. The resident often followed in a rapid chase well beyond the boundary of the territory. At other times one or both birds sat on an exposed perch while the other hovered; if only one sat it was usually the resident. The intruder hovered a short distance away, sometimes within 3 inches, slightly above and to the front of the resident. The resident usually kept its body slightly depressed on the perch, its plumage slightly fluffed, and its bill pointed at the intruder. Sometimes this type of encounter ended with the intruder flying rapidly out of the territory, chased by the resident; more often the resident began to forage as the intruder left. The most active type of encounter by the resident was a simple, rapid chase, normally caused by an intruder foraging within the territorial boundaries. This usually was accompanied by a call of some sort, normally a "chitter."

The commonest type of encouter with other species of hummingbirds was a simple chase during which *Panterpe* was usually silent. Encounters with the Slaty Flower-piercer (*Diglossa plumbea*) varied from simple chases to hovering flights near the intruder. The type of reaction seemed to depend on the dominance of *Panterpe* in relation to *Diglossa*. If the *Panterpe* normally was able to chase a *Diglossa* from the territory, it usually did so immediately. However, some *Panterpe* of both sexes, especially later in the year, seemed to be subordinate to an intruding *Diglossa* even though the *Panterpe* otherwise controlled the area. In these cases the usual encounter was a hovering flight near the intruder, which either showed little or no reaction or, more frequently, flew at the *Panterpe* and drove it to another part of the territory.

Within this relatively simple framework of behavioral patterns I was unable to differentiate sex in the field on the basis of behavior. Except for a rarely-used dry rattle call that I heard only during encounters in which the resident was a male, all other aspects of territorial defense seemed not to differ between the sexes. Each participated in the dual hovering flights, the hovering by the intruder with the resident sitting (sometimes when the intruder was a male and the resident a female), and the chases. Both sexes seemed to use the same repertoire of calls (except the dry rattle call) in similar situations. The defensive displays did not seem nearly so spectacular or specialized as those found among the north temperate species (Bent, 1940; Pitelka, 1942) or even in the resident *Selasphorus flammula* on the Cerro de la Muerte. This latter species, presumably a close relative of the Allen (*S. sasin*) and Rufous (*S. rufus*) Hummingbirds of North America, has a dive display very similar to the corresponding behavior of its congeners.

DISCUSSION

To my knowledge this is the first documented report of female hummingbirds holding long-term territories during the nonbreeding season; these territories differ in no significant manner from those held concurrently by males of the same species. As noted earlier, female territoriality is reported around a nest, but no good data exist on the extent of nesting territories or their spatial relationship to dispersion patterns of the available food supply (see Wagner, 1945, for a suggested relation of *Colibri thalassinus* nests to dispersion patterns of *Salvia mexicana*). Territories in which a nest is defended should be differentiated from those of female *Panterpe* in which a food source is defended. In most nesting territories any defense of a food source apparently is strictly secondary and depends on the chance distribution of certain food items within defensible range of the nest site.

In a few other species of hummingbirds the females apparently defend a spatially restricted food source for short periods during the nonbreeding season. Among north temperate species, females on migration occasionally hold territories in a locally abundant food source (Pitelka, 1942; Armitage, 1955; Cody, 1968). Female territoriality apparently also occurs in some hummingbird species of lowland tropical regions, at least in Costa Rica (Stiles and Wolf, 1969). The territories were in trees that flowered abundantly in a particular locality for only a short time. In each case the tree was the major species most of the local hummingbirds were visiting, and several territories were crowded into these spatially and temporally restricted food sources. The territories of these females also do not seem to differ from those of the males. Maintenance of territories by females seems to vary seasonally (Wolf, 1969). These territories also serve no reproductive function.

The territoriality of north temperate migrant and lowland tropical female hummingbirds is similar in several respects. In both cases the territories are usually short-term, but for different reasons. In the case of the migrants, the birds soon leave the area en route to their wintering or breeding grounds. For the lowland tropical forms, the specific flowers they visit are usually available for only a few days. Other individuals of the same plant species may bloom slightly asynchronously in a locality, but a shift to another tree or patch of shrubs requires a redefinition of the territorial boundaries and results in a shifting pattern of territories maintained throughout the habitat. In both types of territorial systems the plants on which the birds depend often are locally plentiful, but in scattered clumps. Thus groups of hummingbirds tend to gather at one point and the territories are often small. This leads to intense territorial aggressiveness, but defense over short periods is advantageous because of the abundance of food being defended.

The territories of migrant and lowland tropical hummingbirds differ from those reported here for *Panterpe*, which are centered around plant species, especially *C. valerii*, that have a long, nearly continuous flowering period and hence provide a continual food supply. Furthermore, the territories of *Panterpe* are usually larger and less actively defended. The size of the territory and the decrease in time required for defense results from the more dispersed spatial distribution of *valerii*, and in fact for most of the plant species on which *Panterpe* feeds.

The appearance of food-centered territoriality among females in the present study may have been correlated with restricted or declining food supplies. In this way these territories did not differ significantly from those of migrating females. As no intruding individuals normally are allowed to feed freely at defended sources, seemingly as the number of undefended areas decreases, pressure increases for a female either to defend a territory or to leave the region completely and search elsewhere for a more plentiful source of food. As at least some females remain around Villa Mills, the declining food supply may be a selective force producing territorial defense by females. Whether this is the major selective factor depends in part on whether the females are also territorial at other times of the year, especially when food is plentiful.

Morphological and behavioral correlates of territoriality in Panterpe.—In *Panterpe* territorial defense initially is much less active than in many other species of hummingbirds that have been studied. In general the resident rarely announces its presence either vocally or visually and it has no specialized dive displays. Yet plumage characteristics seem to play an important part in inter- and intraspecific aggressive encounters involving *Panterpe*. In a species in which the females are also territorial the sexes might be expected to behave similarly in territorial defense; this was found to be the case.

Pitelka (1942) notes that for many north temperate species the primary methods of territorial defense are vocal and/or visual behavior and he comments on the apparent difference between several north temperate and tropical species in this regard. Males of most north temperate species defend their territories by sitting on exposed perches in the open and by a ritualized chase that normally takes the form of dive displays. Only Anna's Hummingbird among North American species uses vocal defensive behavior to any important extent (Pitelka, 1942). Even while calling, the male Anna's normally sits on an exposed perch providing visual signals at the same time. Among several tropical species that Skutch (1940) studied, vocal announcement of territories is more important, although several of the species normally sit on exposed perches within the territory. Further studies (Skutch, 1951, 1964), especially of forest dwelling hermits (*Phaethornis* spp.), reveal an overriding importance of vocal communication in territories that have been established as areas for attracting mates and have little or nothing to do with feeding.

In many hummingbirds the bright iridescent patterns of the males of sexually dimorphic species seem to have evolved as functional parts of the visual communication patterns associated with territorial defense. The male Anna's flashes his bright gorget at the base of the dive displays, many of which seem to be oriented to produce the proper alignment to the sun to achieve this flash (Hamilton, 1965), and also flashes it when he is perched in an exposed position in his territory. Even females seem to be treated aggressively when they first intrude on the male's occupied territory during the breeding season (Pitelka, 1942). Although the male's displays may lead to courtship and eventually to mating, the sequence rarely has been observed (Wagner, 1954; Skutch, 1958), and possibly other behavioral patterns are more closely associated with postaggressive mating behavior. In any case the primary, initial reaction of a territorial bird to an intruder of whatever sex or species is usually aggressive. Thus one might expect to find a similarity of plumage pattern signals in the sexes in those species in which female territoriality is known, and in which visual signals are important in aggressive displays.

Among the resident tropical species in which female territoriality is known or strongly suspected (*Phaeochroa cuvierii, Amazilia rutila*, and *A. saucerottei* in the lowlands and *Panterpe insignis* in the highlands) one common denominator is the lack of marked sexual dimorphism in plumage color. The rufous venter of *A. rutila* females tends to be slightly duller than in males, but otherwise the sexes of each species are nearly identical in color (Ridgway, 1911). Of these four species, two (*A. saucerottei* and *Panterpe* have bright iridescent patches on the plumage in addition to the general iridescent green of the back found in many species. This suggests that in species in which female territoriality has evolved it has been accompanied by a convergence (or nondivergence) of those parts of plumage patterns and coloration that may play an important role in aggressive displays associated with territorial defense.

This is not the case among north temperate species in which the females are much duller than the breeding males and in general lack the bright flash patterns. Most reports of territoriality during fall migration are of females or young males, all in essentially the same plumage (Pitelka, 1942; Armitage, 1955; Miller and Stebbins, 1964). The aggressive encounters normally involve calling and flitting chases. As both sexes generally are in the same plumage, although dull, little selective pressure probably is exerted to produce a strikingly colored plumage for this relatively short period of the year when territoriality is an important and relatively common phenomenon. Among wintering Ruby-throated Hummingbirds (*Archilochus colubris*) in Costa Rica we saw no adult males in breeding plumage and little evidence of territorial establishment, although most individuals maintained a distance barrier wherever they happened to be feeding. During spring migration, although both males and females hold territories (Cody, 1968), the sexes still are strongly dimorphic in plumage coloration. This may relate to the importance of rapid sex recognition and the facilitation of mating once the species arrive on the breeding grounds (see Hamilton, 1961, for a similar possibility among migrant species of certain families of North American passerines). The reasons for the marked dimorphism in plumage of the resident Anna's Hummingbird of California are not clear at this time.

Other species of hummingbirds that have similar plumage convergence between the sexes also might show female territoriality at some season of the year. At the current state of our knowledge of social systems of hummingbirds, it seems best to restrict this hypothesis to those species in which visual signals are important components of aggressive behavior patterns. The species of hummingbirds in which the plumage is sexually monomorphic, but dull, might also show certain convergences to accompany

TABLE 6
SEXUAL DIMORPHISM AND FEMALE HUMMINGBIRD TERRITORIALITY[1]

	Per cent deviation[2]			
	Species	Wing	Tail	Bill
Resident females holding nonbreeding territories	*Phaeochroa cuvierii*	— 6.4	— 0.5	+ 4.9
	Amazilia saucerottei	— 4.2	— 2.9	+ 1.0
	Amazilia rutila	— 7.1	— 6.1	+ 5.5
	Panterpe insignis	— 6.3	— 7.1	+ 1.1
	Average value	— 6.0	— 4.2	+ 3.1
Resident females NOT holding nonbreeding territories	*Eugenes fulgens*	— 5.5	— 9.6	+17.1
	Selasphorus sasin	+10.0	— 3.5	+11.9
	S. flammula	+ 4.5	— 4.7	+10.2
	Archilochus colubris	—15.6	+ 5.2	+14.4
	Calypte anna	— 1.2	—13.1	+ 3.3
	Average value (absolute)	7.2	7.2	11.4

[1] Each figure for a species is the deviation of the length of the appendage of an average female from an average male, which was taken as 100 per cent.

[2] Data from Ridgway (1911).

female territoriality, if present, but these would be more likely to occur in the vocal communication patterns.

One group of hummingbirds in which many of the species are monomorphically dull is the genus *Phaethornis* and the closely related genera of hermits. Possibly females of these species might be territorial, but they probably are not (Skutch, 1951, 1964). More likely the coloration of these birds of the dark forest understory is protective or concealing and the primary territorial and mating signals are vocal. In at least some of these species the males gather into singing assemblies in which scattered and apparently territorial males sing most of the day at certain seasons. The actual significance of these singing assemblies is not well-documented although Skutch (1951, 1964) feels that they are primarily courtship and mating grounds, or a vocal form of lek display.

A further morphological correlate of female territoriality might be expected in bill length (Selander, 1966), an important component of the feeding apparatus. If these female territories, at least among resident tropical species, are important primarily during periods of limited food supply when both sexes tend to use the same food plants, one might expect the feeding apparatus of the two sexes to be selected for more similarity than among hummingbirds in which the selective pressure on females seems to be to enable them to use sources the territorial males do not normally exploit. In general the species in which female territoriality is known or strongly suspected do indeed show marked similarity between the sexes in the length of the bill (Table 6). In most species of hummingbirds the bill of the female averages longer than that of the male, even though the female, at least of the larger species, is often smaller. Thus the male and female of *Calypte anna* might frequently exploit the same food species, which seems to be the case around Los Angeles during the breeding season (Stiles, pers. comm.).

Selection, then, among these species that show female territoriality, probably has increased the effectiveness of the aggressive signals of the female and in the process has increased the sexual monomorphism of plumage coloration in those forms in which plumage plays an important communicative role in aggressive encounters. At the same time the declining food supplies encourage selection for similarity of bill length, probably toward the length most effective for exploiting the common food plants when both sexes exhibit territorial behavior.

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SUMMARY

Studies were conducted of territoriality in the brightly monomorphic hummingbird, *Panterpe insignis,* in the mountains of Costa Rica in 1965–67. Collections of territorial birds from March to July 1967, a nonbreeding period, revealed that females were holding relatively long-term feeding territories generally centered around *Centropogon valerii* as the primary food source. It is suggested that this female territoriality may be causally related to declining food supplies at this time of year.

Female territoriality in *Panterpe* is compared to that of other species in which females hold territories during the nonbreeding season. In general the type of territoriality reflects the temporal and spatial distribution of the food sources and the residency status of the birds.

Finally, it is suggested that female territoriality in hummingbirds is accompanied by strong selection for sexual monomorphism in plumage coloration as advantageous in aggressive encounters, and for sexual similarity in bill length as advantageous for efficient utilization of the limited food sources.

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