

FEMALE TERRITORIALITY IN THE PURPLE-THROATED CARIB

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THE potential kinds of competitive interactions among individuals, regardless of species, can be classified as contest and scramble (Nicholson 1957) or interference and exploitation (Miller 1967). The two sets of terms refer to approximately equivalent phenomena. Presumably the type of competition an individual displays depends in large part on the characteristics of the limited resource (McNaughton and Wolf 1973). A resource that can be defended advantageously, in the evolutionary sense, will result in selection for contest or interference competition. One possible behavioral outcome of contest competition is territoriality, the restriction of use of a potentially limited resource in a spatially fixed area to meet the biological requirements of the individual that defends the resource (Pitelka 1959, Rand 1967, Wolf 1969). Territoriality might be expected to evolve among all classes of individuals in a species for which the cost of defending the resource does not exceed the gain achieved by the defense (Brown 1964, Cody 1974). For hummingbirds, a potentially limited resource is nectar they use as an energy source. Theoretically most individual hummingbirds might be expected to exhibit territorial behavior under appropriate conditions of nectar availability and competitor pressure (Wolf et al. 1975, Gill and Wolf 1975).

The literature contains numerous reports of territoriality of male hummingbirds, but reports of female territoriality except around nests (Legg and Pitelka 1956, Wolf and Wolf 1971, Stiles 1973) or on migration (Armitage 1955, Cody 1968) are very limited (Wolf 1969). In *Panterpe insignis*, the Fiery-throated Hummingbird, I reported that female territoriality during the nonbreeding season in a nonmigratory species was correlated with brightly monomorphic plumage coloration and similarities in bill length between the sexes (Wolf 1969). To establish if these correlations held for other species of hummingbirds I studied the Purple-throated Carib, *Eulampis jugularis*, during the breeding and nonbreeding seasons on the island of Dominica, British West Indies. I also made incidental observations on the Green-throated Carib, *Sericotes holosericeus*.

I found that both species, which are sexually monomorphic in color, are territorial around certain flower species and that females of both species hold territories during the nonbreeding season. The relationships of the sexes and of the territories held were somewhat different than

for *Panterpe* (Wolf 1969). Most of the data reported here concern *Eulampis*, as I concentrated on that species. In addition to adding these further examples of female territoriality in hummingbirds during the nonbreeding season, this report explores environmental, morphological, and behavioral factors related to female territoriality.

METHODS AND MATERIALS

Eulampis jugularis is a brightly colored, moderately large, sexually monochromatic species that occurs nearly throughout, but restricted to, the Lesser Antilles (Bond 1971). *Sericotes* has a somewhat larger range and tends to occur in drier parts of each island than *Eulampis*. Both species apparently are resident throughout their respective ranges.

The two species are among about 20 species of hummingbirds (in a family of birds with about 320 species; Van Tyne and Berger 1959, Austin 1971) in which both sexes are brightly colored and have identical, or nearly identical, plumage patterns and colors (Wolf MS).

Mensural and weight characteristics of *Eulampis* are summarized in Table 1. In addition to a longer bill the females also have decurved bills while the males' bills are more nearly straight. Sex in *Eulampis* is easy to recognize in the field, which is the main reason I concentrated on that species. In some cases the sex of a territorial individual was corroborated by collecting the bird from its territory and examining the gonads. *Sericotes* is slightly smaller (5.1–6.6 g) than *Eulampis* and has a similar bill dimorphism, but the difference in bill length and shape between the sexes is less pronounced and less obvious than in *Eulampis*.

I also made observations on territoriality in the Antillean Crested Hummingbird, *Orthorhyncus cristatus*. This is a smaller species (2.2–3.2 g) than *Eulampis* and *Sericotes* and a species with the usual pattern of hummingbird sexual dichromatism—bright male and dull female. The species has a distribution similar to that of *Sericotes*. *Orthorhyncus* has the broadest habitat range of the three species (Lack 1973), but it tends to occur more than the other species in open spaces and regularly in arid regions, which the other two species, especially *Eulampis*, use less frequently.

Most of the data reported here were collected on three visits to the island of Dominica. We spent June, July, August 1968, parts of December 1968, January, March, and April 1969 on the island, principally studying the social behavior and ecology of the hummingbirds. Normally two persons were involved in the fieldwork with one watching the birds and the other recording the activities. The birds were studied through 7× binoculars or with the unaided eye at distances generally less than 50 feet. Incidents were timed with a stopwatch or the second hand of a wrist watch.

Few birds were marked for individual recognition, but during the course of one day or one period of observations the resident of a territory could be kept in view most of the time. Other observations on marked birds showed that, once established, a resident normally remained on a territory with sufficient flowers unless driven out by an intruder. With the few marked birds we also determined that the same bird returned from day to day to a territory in which nectar was still available, though day-to-day continuity of individuals is not essential to what follows.

Territoriality already has been defined in a general sense. Behaviorally, territoriality in *Eulampis* and the other species was manifested by chases, calls, and perched displays, all of which served to displace an individual from a set of flowers or to reduce the possibility that an intruder would stop at the flowers the resident was

TABLE 1
MENSURAL AND WEIGHT CHARACTERISTICS OF *Eulampis jugularis* ON THE ISLAND OF
DOMINICA, BRITISH WEST INDIES

		Mean	SE	Range	N
Wing (mm)	Male	75.6	0.46	71.8-78.6	15
	Female	69.6	0.21	67.2-72.5	33
Tail (mm)	Male	42.7	0.61	38.1-46.2	15
	Female	38.7	0.24	36.3-41.0	30
Bill (mm)	Male	19.8	0.36	18.4-23.6	13
	Female	26.6	0.12	25.2-28.1	36
Weight (g)	Male	9.9	0.22	8.8-10.9	13
	Female	7.9	0.09	7.1- 8.6	20

using. In general for a bird to be classified as territorial I also required that site specificity be continued for at least 30 consecutive min; observation periods ranged from 30 min to 11.5 h.

RESULTS

Resource base of territoriality.—With a single exception (female's nest defense; Wolf and Wolf 1971) territorial behavior by *Eulampis* always centered around flowers. During the course of a morning the size and shape of a territory centered around banana flowers changed as the flowers fell to the ground where the hummingbirds did not, and probably could not, visit them.

Aggressive interactions among individuals hawking for insects in the same area were very rare. In one case one to two intruder male *Eulampis* even used the same perch for flycatching as the resident male, and they often sat within 6 inches of each other. If an intruder male left this flycatching group and went to the flowers that the resident male defended, the resident male immediately chased the intruder from the vicinity of the flowers.

Seasonal distribution of female territoriality.—Although we were in the field almost daily from 10 June to 28 August we did not find non-breeding females territorial until 24 July, when the first territorial female was located in a clump of flowering *Heliconia caribea* plants where several males had been territorial several days earlier. On the same day we also found a female territorial in the late afternoon in an *Inga vera* tree. From then on throughout our fieldwork until mid-April 1969, we continually found females territorial around a variety of plant species. Table 2 shows the distribution of territorial females at plant species through time. While we did not regularly search the island for territorial females the data in the table indicate quite clearly that terri-

TABLE 2
MONTHS DURING WHICH FEMALE *Eulampis jugularis* WERE TERRITORIAL AT
PARTICULAR PLANT SPECIES

Plant species	1968				1969		
	June	July	August	December	January	March	April
<i>Heliconia caribea</i>		X (1) ¹	X (3)				
<i>Inga vera</i>		X	X (1)				
<i>Spathodea</i> sp.				X	X		
<i>Musa</i> sp.				?	X	X	X (2)
<i>Ichnosiphon</i> sp.					X	X	X
<i>Tabebuia pentaphylla</i>						X	X

¹ Figures in parentheses indicate number of territorial females for which sex was verified by examining gonads.

toriality in females is seasonally prolonged and widespread in relation to possible nectar sources.

The only season when we did not find some females territorial around flowers was during the nesting period in June and early July (Wolf and Wolf 1971). During this period females were regular intruders into territories held by male *Eulampis*, which, except for mating sequences (Wolf 1975b), regularly and quickly chased the females from the territories. Even in areas males used only irregularly we could find no territorial females. It seems likely that during the breeding season no females hold flower-centered territories.

Relative dominance of male and female Eulampis.—In most intersexual interactions the male *Eulampis* was dominant over the female. This dominance was evident in the male's ability to displace a female in a territory or at a feeding site, even a site the female was defending. Only during the middle stages of courtship (Wolf 1975b) was a female able to remain in a male's territory, to feed at his defended flowers, or to dominate the male. A female (apparently the same individual from day to day) that held a territory for several weeks in a patch of *Ichnosiphon* was displaced for parts of 2 consecutive days by an intruding male that forced her to an unused portion of the patch. Two days later the male was gone and a female had returned to, and reoccupied, the territory successfully. Males often visited banana flowers defended by a female even though she tried to displace the male. A male *Eulampis* occupying a portion of a *Spathodea* tree throughout the morning began to expand the area he defended as flowers fell from the tree. Eventually he displaced an adjacent female and took over her territory. Another male entered this tree late in the morning and displaced a resident female from her feeding territory. The few times a

TABLE 3
CHARACTERISTICS OF *Eulampis jugularis* TERRITORIES CENTERED AT BANANA FLOWERS

Date	Area (ft ²)	No. stalks	Peak No. flowers	Ft ² /flower
Females				
28 March	4820	10	202	23.9*
15 January	3650	7	135	27
17 January (A)	150	3	52	2.9
17 January (B)	125	3	46	2.7
30 March	*1150	7	116	—
Males				
5 April	1100	9	151	7.3
7 April	1430	15	222	6.4
11 January	550	7	175	3.1
12 January	1250	11	190	6.5

female displaced a male in the *Spathodea* tree was always when the two held adjacent territories and always early in the morning, when the male probably had sufficient nectar in his own territory.

Territory characteristics.—As males were dominant over females, the males' territories should be of higher quality than those the females defended, provided the males were sufficiently abundant and dispersed to control the high quality territories. Table 3, comparing the characteristics of territories of both sexes, shows female territories averaged much larger than those of males in relation to the number of flowers available or they were about the same size as the males' territories, but had many fewer flowers, providing less total energy in the territory. The number of flowers per unit area should indicate how much energy must be expended by the bird to reach a source to obtain a unit of nectar (see Smith 1968).

Relatively richer territories should require less foraging time for a given body size to meet the energetic needs of the resident (Wolf and Hainsworth 1971, Wolf et al. 1975). Females and males of *Eulampis* had similar time budgets for foraging (Table 4). A difference in weight of male and female *Eulampis* means that females extracting less nectar per unit time from a territory could achieve equivalent foraging efficiencies as the males because of the reduced foraging costs per unit time for the females (about 80% that of the males; Hainsworth and Wolf 1972). If both sexes adjust foraging time equivalently in relation to the short-term reward characteristics of the territory (see Wolf 1975a) then the similar foraging times for males and females in banana, *Heliconia*, and *Inga* territories means that the territory quality was somewhat higher for the males (Wolf et al. 1975). In this context, note that the females feeding at *Ichnosiphon* tended to have higher foraging time budgets than

TABLE 4
TIME BUDGETS FOR TERRITORIAL MALE AND FEMALE *Eulampis jugularis*¹

Flower species	Sit	Forage	Fly-Catch	Chase	Hover	Change perch	Gone	Total min
<i>Heliconia caribea</i>								
Male	88.3 ²	7.0	1.3	1.4	0.4	0.6	8.5	3565.4
Female	89.2	6.9	2.0	0.9	0.4	0.4	25.3	1841.8
<i>Musa</i> sp.								
Male	86.6	7.8	0.6	3.5	0.9	0.5	4.5	1889.4
Female	90.8	6.8	0.4	0.9	0.6	0.4	15.6	1349.5
<i>Inga vera</i>								
Male	86.5	4.8	1.3	6.4	0.1	0.8	8.3	392.1
Female	92.6	4.3	2.9	—	—	0.2	11.2	384.1
<i>Ichnosiphon</i> sp.								
Female	90.5	8.3	0.2	0.4	0.2	0.4	14.8	703.1

¹ Data for males from Wolf and Hainsworth 1971.

² Percentages for known activities are calculated from total time after time gone is removed.

females at the other flowers for which data were available (Table 4). The lack of male territoriality at *Ichnosiphon* (see earlier) suggested that these were poorer quality territories and this tended to be confirmed by the lower foraging time budgets of females in the other flower species.

Territoriality in female Sericotes and Orthorhyncus.—The sexes of *Sericotes* were much more difficult to distinguish in the field and I spent little time watching territorial individuals. I did find a single non-breeding female territorial around *Lantana* bushes; the sex was verified by dissection. The female and a male held separate territories that divided three *Lantana* bushes at which they foraged and each regularly chased a male *Orthorhyncus* that tried to feed there.

Orthorhyncus cristatus is sexually dichromatic, and the sexes were very easy to distinguish in the field. Although we have many observations of territorial behavior of males (> 30 h), principally around *Lantana* bushes, we never found a territorial female. Males territorial at *Lantana* often were displaced by feeding *Sericotes* and we watched a *Sericotes* take over a cluster of *Lantana* bushes defended by a male *Orthorhyncus*. I conclude that female *Orthorhyncus* never held territories whereas males did so regularly, and that territorial males were easily displaced by and clearly subordinate to *Sericotes* (and *Eulampis*) of either sex (c.f. Leck 1973).

DISCUSSION

To be effective in defense of a resource an individual must be able to chase off efficiently actual or potential intruders. If aggressive signaling

is sufficient, less energy would be required for actual chases thereby improving the energy balance of the territorial bird. Aggressive signaling also might reduce the amount of time a territorial bird is gone from the area if chases extended well beyond the boundary of the territory as often happens in hummingbirds. Finally an individual that can displace an intruder by aggressive signaling can eliminate the minor possibility of injury that accompanies physical aggressive encounters. Earlier I suggested (Wolf 1969) that many of the bright iridescent colors of hummingbirds, especially those related to sexual dimorphism in males, were probably important as aggressive signals. Aggressive signals in hummingbirds should be closely associated with territoriality, especially defensive behavior.

The Fiery-throated Hummingbird, *Panterpe insignis*, of the mountains of Costa Rica and Panama, is not sexually dichromatic, and both sexes have bright iridescent throat and crown patches that probably serve as aggressive signals (Wolf 1969). I postulated that the evolution of this bright monomorphism was probably a result of the selection for female territoriality associated with the limited food supply during a portion of the nonbreeding season, mostly at a time when *Panterpe* was the only species of hummingbird regularly exploiting the area. From this hypothesis we would expect that in other species of brightly monomorphic hummingbirds the females should hold territories during some time of the year. Our demonstration of female territoriality in *Eulampis*, and at least sometimes in *Sericotes*, coupled with the lack of female territoriality in *Orthorhyncus cristatus*, lends support to the hypothesis.

Female territoriality produces selection pressure for appropriate aggressive signals in the female. But why should these signals be similar to the signals evolved by the male? A mechanistic hypothesis would be that these colors are carried in the genome of the female, but the genetic expression is suppressed in most hummingbird species by female hormones, and dull female characters are produced. This type of dual color system in the phenotype built on a single color in the genotype is characteristic of many species of birds (Witschi 1961).

A second, but not mutually exclusive hypothesis, raises the possibility that the similar coloration is a kind of automimicry (Brower et al. 1970) in hummingbirds. Males are territorial throughout the year when resource distribution is appropriate. This means that potential competitors are continually exposed to the aggressive signals of the regularly dominant males. Females then might be at a distinct advantage if they used the same aggressive signals, as many potential intruders would have associated this color pattern with territorial defense.

Mimicry increases the problem of sex recognition in sexual encounters

by reducing the number of obvious sex identification signals emanating from the female. Reduced sexual differentiation by color or pattern places special importance on behavioral signals during the short period of pair formation associated with mating in most species of hummingbirds (Wolf 1975b). *Panterpe* probably has a fairly long period of pair formation associated with its long pair bond (Wolf and Stiles 1970). The longer time during which the male and female associate prior to nesting reduces the requirement for the easily recognized visual signals frequently correlated with obvious plumage dimorphism (Hamilton 1961, Hamilton and Barth 1962).

Eulampis has a typical hummingbird mating system that involves promiscuous pair relations and very short mating sequences (Wolf and Wolf 1971, Wolf 1975b). Females of *Eulampis* carry another visual signal, the decurved bill, that immediately differentiates them in the field from males, at least for a human observer. Presumably the bill also could serve as a sex recognition character during courtship (Jehl 1970), but the bill difference does not seem to reduce the aggressive reaction of a male to a female's initial intrusion into his territory, even though the intrusion finally leads to mating (Wolf 1975b).

The bill dimorphism in *Eulampis* could also increase the range of flower types that the species exploits (Selander 1966, Snow and Snow 1972, Wolf et al. 1972). I suggested earlier (Wolf 1969) that the similar bill length of the sexes of *Panterpe* was probably related to the importance of a single flower species, *Centropogon valerii*, in the energetic economy of *Panterpe* at certain times of the year, including times when the females are territorial (see also Wolf et al. 1975). The length of the bill also is probably a compromise between a very long and very short bill that permits *Panterpe* to exploit efficiently a relatively wide range of plant species that are available to hummingbirds in the region where we studied *Panterpe* (Wolf et al. 1975). *Eulampis* females, unlike females of *Panterpe*, always have numbers of alternative flowers available to them throughout the year. As a consequence selection pressure is less stringent for a bill of similar length to that of the male. On the other hand, disruptive selection probably is acting continually to maintain different bill lengths between the sexes (Selander 1966, 1972).

Of the $320 \pm$ species of hummingbirds about 20 show the phenomenon of brightly monomorphic plumage coloration. From the hypothesis presented here one would expect each of these species to show female territoriality some time during the nonbreeding period. So far the situations where this has been studied have been essentially islands in the broad sense of the word. *Eulampis* is limited to islands and *Panterpe*

is limited to the high elevations of two adjacent mountain masses that are widely separated from other mountains and have few hummingbird species. Female territoriality and bright monomorphism is not found among species in diverse avifaunas such as the tropical lowlands of Costa Rica. The limitation of the female territoriality to island situations probably is related to the decreased diversity of hummingbirds in these places. Fewer species of birds means fewer other species to dominate the potentially territorial females at the limited number of plants available. The size-related dominance hierarchy of sympatric hummingbirds (Wolf 1970, Stiles 1973) generally reduces the possibility of female territoriality to females of large species or to species that are the only residents in the habitat, although other species may occupy it for longer or shorter periods.

On Dominica the females of one and probably two species of the three that regularly co-occur exhibit female territoriality in the non-breeding season. *Eulampis* is the largest species of hummingbird on Dominica and the females can dominate males of the smaller species. The most subordinate of the three and the one presumably working the poorest quality flowers was strikingly dimorphic and the females were never seen to be territorial. Our limited data suggest that female territoriality may be less common in *Sericotes* than in *Eulampis*. The single documented case of female territoriality in *Sericotes* was in a cluster of *Lantana* bushes that normally would be defended by a male *Orthorhyncus*. It appears possible that regular occurrence of female territoriality is related closely to the relative dominance of the species, as this reflects the availability of good quality nectar resources and the ability to defend a set of flowers successfully.

In a diverse hummingbird fauna such as in the Caribbean lowlands of Costa Rica (Slud 1960) the females of the behaviorally dominant species (Bronze-tailed Plumeleeter, *Chalybura urochrysis*) are grayish below and much duller than the males. The females apparently never hold territories (pers. obs.) but migrate elsewhere when food supplies decline. Female territoriality and bright monomorphism, then, seems to be associated with species that are resident in a region where food supplies become seasonally limiting, where the females can dominate rich food sources by virtue of their size, or because there are no other species present. The alternative strategy is for a female to search out places where sufficient flowers are available that are not being defended by more dominant birds. If population pressure is high for a limited number of flowers, these will usually be scattered flowers that are economically undefendable by a territorial individual.

A separate question is why bright monomorphism has not evolved in those North American species of hummingbirds for which female territoriality is known, albeit only on migration. I suggest that the lack of bright monomorphism results from stronger selective pressures for dull females with few aggressive signals as compared to the selective pressure for bright monomorphism or other strong aggressive signals for the short period of each year during which the female holds a territory. The counter selective pressure might relate to sex recognition in pair formation, especially among migrant hummingbirds (Hamilton and Barth 1962), but we know so little about pair formation in these species that it is hard to evaluate this hypothesis. Another possibility is that the bright colors increase the predation pressure sufficiently to produce counterselection. Finally, depending on the sympatric species of hummingbirds during the short periods of female territoriality, the relative size of the female may function sufficiently to promote territoriality. It is generally conceded that males migrate first, meaning that the females will not have to hold territories against males, unless these are less experienced and potentially less aggressive individuals.

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SUMMARY

Females of the Purple-throated Carib, *Eulampis jugularis*, regularly hold flower-centered territories during the nonbreeding season. The females are subordinate to conspecific males and generally hold territories of inferior quality. Territorial occupancy is controlled by availability of nectar and ability to defend the flower from other nectarivores. Females of *Sericotes holosericeous*, the Green-throated Carib, at least occasionally hold flower-centered territories in the nonbreeding season. Females of *Orthorhyncus cristatus*, the Antillean Crested Hummingbird, apparently never are territorial around flowers.

Both *Sericotes* and *Eulampis* are brightly monochromatic in plumage. *Orthorhyncus* has the typical hummingbird sexual dimorphism with a brightly colored male and relatively dull colored female. Brightly monochromatic plumage in the hummingbirds studied so far is closely cor-

related with nonbreeding territoriality in females and it is argued that the bright, iridescent colors of hummingbirds are aggressive signals. The sex differences in *Eulampis* bill length and shape probably result from selection to partition resources between the sexes of this dominant species in the nectarivore guild.

Bright monochromatism, and probably female territoriality in the nonbreeding season, are found in about 20 species of hummingbirds, mostly species inhabiting ecological islands. It is suggested that only in such situations is there strong selection for female territoriality, probably in relation to the small numbers of competitors, limited food supplies, and enforced residency.

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