

## HUMMINGBIRD TERRITORIALITY AT A TROPICAL FLOWERING TREE

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INTERSPECIFIC competition is generally a subtle phenomenon that must often be inferred rather than observed directly. Hummingbirds are unusual among birds in that competition for food is frequently demonstrated by overt aggression between individuals of different species. Males of many species of hummingbirds defend territories at feeding sites against all other hummingbirds, regardless of species or sex. Such feeding territories typically center about flowering plants, whether these yield insects, nectar, or both. A territory is defined as a spatially limited site in which the resident restricts use of environmental resources (here, nectar) to satisfy its own requirements (Wolf, 1969).

The distribution of flowers in time and space can be expected to influence the outcome of intra- and interspecific competition among hummingbirds. The density and richness of food sources may affect the minimum territory size required to control sufficient energy resources. The actual extent of a defended area probably also depends on such factors as foliage density and the availability of display perches, which affect the bird's ability to advertise, scan, and defend its territory. Both the length of the blooming season and the availability of alternative food sources will influence the duration and rigidity of the territorial system (Wolf, 1970).

Interspecific territoriality may result in the exclusion of weaker or less aggressive species from the food source and/or in a partition of the feeding area between two or more competing species. Instances of exclusion in hummingbirds are numerous in the literature (e.g. Bent, 1940; Pitelka, 1942; Skutch, 1961); the usual situation appears to be for larger species to drive out smaller ones. Partitioning of a feeding area may be viewed as a dynamic equilibrium that varies with the relative numbers and pugnacity of the hummingbird species concerned. Small interspecific differences in foraging habits could contribute to or reinforce such a partitioning, especially if the flowering area is heterogeneous. In particular, different feeding height preferences could lead to a stable stratification of hummingbird species in flowering trees.

This paper presents observations of territorial interactions of the hummingbirds *Amazilia rutila*, *A. saucerottei*, and *Phaeochroa cuvierii* at a tropical flowering tree, *Genipa americana*, of the Rubiaceae. They were made in 2 successive years at the same locality, and in large part at the

same tree. We found many similarities and certain notable differences in the territorial situations in the 2 years, and shall try to account for these in terms of the factors mentioned above.

#### ECOLOGY OF THE STUDY AREA

Our work was done at or near the Granja Experimental Enrique Jiménez Núñez, a government farm 5½ km east of Taboga, Guanacaste Province, Costa Rica. Stiles made his observations 6 July and 13–17 July 1966, Wolf made his from 20 to 22 June and 13 July 1967.

The province of Guanacaste in northwestern Costa Rica is at the southern limit of the Tropical Dry Forest, a vegetational formation that extends north along the Pacific slope of Middle America into Mexico (Slud, 1964). Much of Guanacaste is covered by savanna maintained by grazing and periodic burning. Granja Jiménez sits on a low hill rising out of the surrounding savannas. The vegetation of the hill is chiefly tropical dry forest, which is continuous at the base of the hill with gallery forest along the Río Higuierón. The elevation at the farm is 53 meters; at the river, 11 meters.

The climate is characterized by a severe dry season extending from November to April (Janzen, 1967). Most dry forest trees flower during the dry season; Janzen lists only 8 of 64 common tree species at a nearby locality that produce flowers or fruit during the first 3 months of the rainy season (June to August). During the period of our work, the amount and variety of flowers available to hummingbirds were very low, and the few trees in bloom were frequently the foci of large hummingbird concentrations.

*Genipa americana* is a widespread neotropical tree ranging from southern Mexico to Peru and Brazil; the Guanacaste variety is *G. a. caruto* (Standley, 1937–1938). At Granja Jiménez *Genipa* is fairly common, growing in loose groups in the hillside dry forest. It becomes uncommon as one approaches the wetter conditions along the Río Higuierón. Mature *Genipa* trees average 30 to 40 feet in height; a few individuals reach 50 feet or more. At the time of flowering most *Genipa* have their full complement of leaves, although they are essentially bare during the dry season. The major blooming period begins after the rains start, perhaps permitting flowering and vegetative growth to coincide without a prohibitive drain on water resources. A flowering season that is delayed until the rainy season starts may have the further advantage of reducing competition for pollinators with other plant species (Janzen, 1967).

Leaves and flowers of *Genipa* are clustered at the tips of the twigs. When a flower first opens it is creamy white, but by the second day it has begun to wither and turn a dull yellow. Old withered flowers may per-

TABLE 1  
MENSURAL CHARACTERISTICS OF THREE HUMMINGBIRD SPECIES HOLDING  
TERRITORIES IN THE OBSERVATION TREE

Species	Sex	Wing <sup>1</sup>	Tail <sup>1</sup>	Culmen <sup>1</sup>	Body wt. <sup>2</sup>	N
<i>Amazilia rutila</i>	M	55.9	34.6	21.8	5.17	10
	F	53.0	34.0	23.0	4.92	11
<i>Amazilia saucerottei</i>	M	55.0	30.9	19.1	5.12	10
	F	52.7	30.0	19.3	4.83	10
<i>Phaeochroa cuvierii</i>	M	73.4	44.2	22.3	10.22	10
	F	68.7	44.0	23.4	8.51	10

<sup>1</sup> Wing, tail, and culmen are lengths in mm.

<sup>2</sup> Body weight in grams.

sist on the tree for several days, thus each cluster usually contains a graded series of flowers of various ages. Only fresh white flowers have nectar, and hummingbirds visit these flowers almost exclusively. The nectaries are about 15 mm deep in the corolla tube, and are thus easily accessible to the common hummingbird visitors (Table 1).

The flowers of *Genipa americana* provided by far the most important floral food resource for hummingbirds during most of our study. The only other flowering tree visited extensively was *Luehea spectabilis* (Tiliaceae), which bloomed prior to *Genipa* in 1966. By 13 July 1966 *Luehea* was no longer flowering and many *Genipa* trees were coming into full bloom. In 1967 *Luehea* has not yet begun to bloom at Granja Jiménez as of 13 July, although many were in flower at La Pacífica, some 25 km northeast. Approximately half the *Genipa* trees in the study area were blooming on 20–22 June 1967; by 13 July these had ceased flowering and other individuals appear to be coming into bloom, although none were in full flower at the time.

The few other plants in bloom during our study periods did not seem to constitute an important food source for the three hummingbird species that held territories in *Genipa*. The large, tubular, red-orange flowers of the perennial herb *Lamorouxia viscosa* (Scrophulariaceae) were visited occasionally by *Amazilia rutila* in 1966. In both years we saw hummingbirds visit the crimson flowers of the straggling shrub *Helicteres guazumoeifolia* (Sterculiaceae). Stiles saw *A. saucerottei* visiting the yellowish inflorescences of *Calathea macrocephala* (Marantaceae) on several occasions, but few plants of this common forest herb were in bloom. In 1967 Wolf watched *saucerottei* piercing the rolled-up leaves of *Calathea* for either water or small insects that collected in the inner rolls. D. R. Paulson (pers. comm.) found a few *saucerottei* at a patch of *Manihot* (Euphorbiaceae) near the farm buildings, and this was the only major site of

hummingbird territorial activity on 13 July 1967. Other species blooming in 1967 but not visited by the three species that utilized *Genipa* were *Muntingia calabura* (Tiliaceae) and *Solanum* spp. (Solanaceae).

#### HUMMINGBIRD ECOLOGY AND BEHAVIOR

The two commonest hummingbirds at Granja Jiménez during our stays were *Amazilia rutila* and *A. saucerrottei*. *A. rutila*, represented by the nominate race, is characteristic of Tropical Dry Forest, and reaches its southern limit in Guanacaste (Slud, 1964). The distribution of *A. saucerrottei* is unusual; the species is found in Nicaragua and Costa Rica, is absent from Panama, and reoccurs in Colombia and Venezuela. The Costa Rican population, *A. s. hoffmanni*, is common in Tropical Dry Forest and on the largely deforested central plateau (Slud, 1964).

Both *Amazilia* species could be found in practically all the more open habitats around Granja Jiménez, but *rutila* seemed most common at scrubby forest edges and did not often enter gallery forest. Stiles frequently encountered *saucerrottei* in open gallery forest along the Río Higuierón. Both Carriker (1910) and Slud (1964) consider *saucerrottei* a nonforest species, but mention that it may enter forested areas along openings or clearings.

Territorial behavior in both species was primarily vocal, but visual components were involved as well. Both have a shrill, chattering trill given on territory while perched or flying that appears to serve an advertising or intimidating function. The trill of *rutila* is lower-pitched and buzzy, that of *saucerrottei* shriller and squeakier. Both species give a high, piercing squeak when engaged in a chase. Visual display consisted largely of side-to-side head movements. In *rutila* the head is rotated, and the bright red bill waves to and fro. In the corresponding display of *saucerrottei* the blackish bill always points straight ahead and the head moves rhythmically sideways. The feathers of the head and breast are raised, thereby presumably presenting their brilliant green iridescence to the rival with maximal effect. In both species these displays were seen only when the bird was perched and close to a conspecific rival. By climbing a *Genipa* and waiting until the resultant disturbance among the hummingbirds died down, Stiles was able to watch these displays from extremely close range. Twice he saw one *saucerrottei* repel another solely by visual and vocal displays. Skutch (1931) noted the presence of vocal display in the congeneric *A. tzacatl*, but he does not mention visual displays. The visual elements mentioned above are apparent only at very close range.

Least common of the three hummingbird species holding territories in *Genipa* was *Phaeochroa cuvierii*. Widespread in Caribbean Central

America, this species occurs on the Pacific slope only in Costa Rica and western Panama (the race *maculicauda*). *Phaeochroa* is apparently migratory in Guanacaste, being absent for almost the entire dry season; where it spends this part of the year is not known (Wolf, 1970). At Granja Jiménez the species appeared restricted to Tropical Dry Forest. *Phaeochroa* is noted for the complexity of its song, most unusual for a hummingbird (Skutch, 1964; Slud, 1964). Wolf heard this species sing in a *Genipa* apparently the same warbling song Skutch describes. The species also gives a sharp, piercing "cheet," apparently an aggressive note. As Table 1 shows, *Phaeochroa* is a considerably larger bird than the two *Amazilia*, but all three have bills of rather similar length.

Both species of *Amazilia* usually probed flowers while hovering, but frequently lit on a projecting leafblade and probed from this perch; *Phaeochroa* invariably hovered while feeding. Small flying insects were plentiful around *Genipa* trees, and all three hummingbird species frequently engaged in aerial flycatching. Stiles found practically no insects in *Genipa* blossoms he dissected, hence nectar is probably the major food offered by the flowers themselves. Stomachs of birds collected at *Genipa* trees contained nectar and insects, the latter predominating. As the digestion of nectar is extremely rapid and continues for some time after death, this probably does not adequately indicate the proportion of nectar in the diet.

The other hummingbird species we saw in the vicinity during our observations did not appear to affect the territorial situation at *Genipa*. Of these only the very large and long-billed *Heliomaster constantii* was ever noted feeding at *Genipa*. The single *Heliomaster* visit came just after Wolf had collected many of the residents from a *Genipa*; perhaps the bird was attracted by the commotion. *Chlorostilbon canivettii* was seen once in 1966 and often in 1967, but the only flower it visited was *Muntingia*. *Phaethornis longuemareus* was rather common in the gallery forest understory, but visited flowers only rarely and probably seldom encountered the other local hummingbird species.

#### DISTRIBUTION OF HUMMINGBIRDS BETWEEN FLOWERING TREES

The local distribution of the two *Amazilia* species and *Phaeochroa* was strikingly polarized about stands of *Genipa*. Height and degree of flowering appeared to determine the amount and frequency of hummingbird exploitation of any given tree. Table 2 lists the results of a survey of *Genipa* trees for height, flowering, and hummer visitation. Relatively more of the taller trees were flowering, and of those trees in bloom, hummingbirds tended to prefer the taller ones. Of the two common

TABLE 2  
HEIGHT, PRESENCE OF FLOWERS, AND HUMMINGBIRD VISITATION OF *GENIPA AMERICANA*  
TREES AT GRANJA JIMÉNEZ 14-15 JULY 1966

Height in feet	Numbers of trees	Number and % of trees with flowers	Number and % of flowering trees supporting humming- birds	Number of trees supporting:		
				<i>A. rutila</i>	<i>A. saucerrottei</i>	<i>P. cuvierii</i>
0-10	8	0 (0)	—	—	—	—
10-20	7	3 (43)	0 (0)	—	—	—
20-30	13	8 (62)	3 (38)	3	1	1
30-40	15	11 (73)	8 (73)	7	4	0
40-50	11	9 (82)	7 (78)	6	5	2
50+	1	1 (100)	1 (100)	0	1	0
TOTALS	56	32 —	19 —	16	11	3

species, *rutila* was present at more trees than was *saucerrottei*. Generally *rutila* could be found at smaller trees as well as larger ones, while *saucerrottei* showed a stronger preference for the taller trees.

A quantitative index of flowering was devised to account for the variation in hummingbird numbers at blooming trees. As *Genipa* leaves and flowers occur in terminal clusters, one can compute a flowering percentage by counting the number of such clusters per 100 taken at random over the tree, that contain fresh, white flowers. Table 3 shows that those *Genipa* with higher flowering percentages do indeed support more hummingbirds, both relatively and absolutely. Moreover three *Genipa* growing very close together supported between them relatively more birds than their relatively low flowering percentages would lead one to expect on an individual basis; here again, the total amount of food present was large. These data suggest a preferential clustering of hummingbirds about richer food sources.

At those *Genipa* whose flowering percentage had been estimated, Stiles also counted numbers of hummingbirds of different species. Of 37 *A. rutila* recorded 17, or nearly half, were at poorer feeding sites—trees of lower flowering percentage, supporting fewer birds. By contrast, 20 of the 29 *A. saucerrottei* and 2 of the 3 *P. cuvierii* seen were at the richer, more heavily exploited trees. These data also suggest that *saucerrottei* tended to concentrate more at the most productive foraging sites, while *rutila* was distributed more widely. General observations in both years support this conclusion. The total numbers of birds seen in this survey give a fairly accurate idea of the relative numbers of the three species in the study area in 1966.



Figure 1. Photograph of the observation tree taken 21 June 1967. Note the clustering of leaves and flowers, most evident in the lower parts of the tree.

On 20 and 22 June 1967, Wolf made general censuses of hummingbird numbers and activity along the road running from the farm about 1 km down to the Río Higuerón. Each census began at 06:00 and lasted about 2 hours. Walking at a fairly constant rate to ensure uniform coverage,

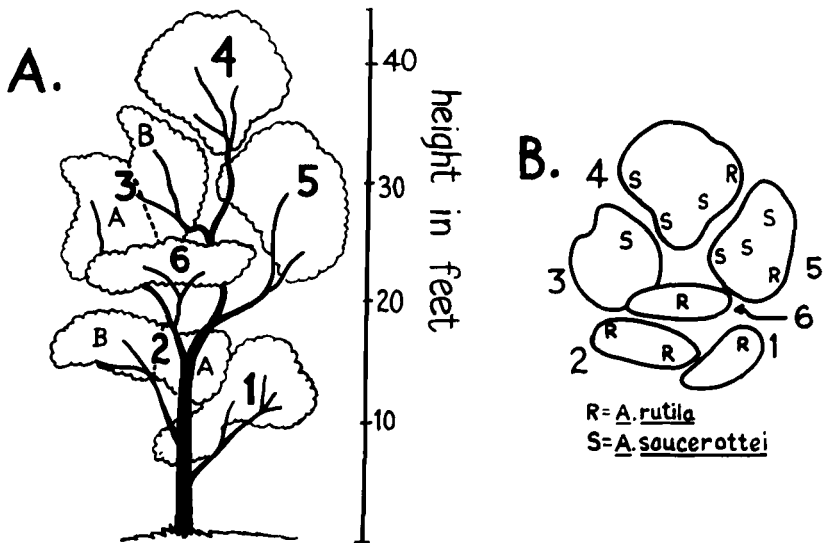


Figure 2. A, the division of the observation tree into sections to facilitate censusing and observation of territorial hummingbirds. B, a representative census of territorial hummingbirds in the observation tree, plotted on a foliage map as used in 1966.

he listed all birds seen and their activities at the time. In these censuses he recorded a total of 33 *A. saucerrottei*, 25 *A. rutila*, and 5 *P. cuvierii*. Of the 32 perching and foraging birds seen, 27 (85 per cent) were localized about flowering *Genipa* trees. The remaining 31 sightings were nearly all of birds engaged in long flights or chases away from feeding areas. The only other hummingbird recorded on these censuses was *Chlorostilbon canivettii*, which was localized about flowering *Muntingia*.

#### HUMMINGBIRD TERRITORIALITY AT THE OBSERVATION TREE

We made our most intensive observations on hummingbird territoriality at a single 45-foot *Genipa* growing on the hillside a short distance below Granja Jiménez (Figure 1). In both years this tree was flowering profusely and was attracting a large and noisy concentration of territorial hummingbirds. Stiles spent portions of 14 and 15 July and most of 16 and 17 July 1966 at this tree; Wolf watched at the tree parts of 20 and 22 June and most of 21 June 1967. A major objective of these observations was to obtain quantitative data on the daily rhythm of territorial behavior, and on the relative amounts of interspecific and intraspecific aggression.

*Methods of observation.*—To facilitate the handling of data, Stiles divided the observation tree into six sectors according to the major foliage masses, as shown in Figure 2A. At regular intervals through the day he



TABLE 3  
FLOWERING PERCENTAGES, HEIGHT, AND NUMBER OF HUMMINGBIRDS RESIDENT IN *GENIPA AMERICANA* AT GRANJA JIMÉNEZ 14-15 JULY 1966

Height in feet	Trees not supporting hummingbirds		Trees supporting 1-5 hummingbirds						Trees supporting more than 5 hummingbirds						
	No.	Mean and range flow- ering %	No.	Mean and range flow- ering %	No. trees with		No. birds (total)		No. Flowering %	No. birds					
					<i>A. r.</i>	<i>A. s.</i>	<i>P. c.</i>	<i>A. r.</i>	<i>A. s.</i>	<i>P. c.</i>	<i>A. r.</i>	<i>A. s.</i>	<i>P. c.</i>		
10-20	1	70	0	-	-	-	-	-	-	-	0	-	-		
20-30	4	18 (0-36)	2	30 (16-44)	2	2	0	4	2	0	1	46	3	4	0
30-40	4	2 (0-4)	4	36 (24-46)	4	2	1	6	2	1	0	0	6	8	0-1
40-50	3	4.7 (4-10)	3	43 (32-50)	3	2	0	7	3	0	1	76 <sup>2</sup>	6	8	0-1
50+	0	-	1	36	0	1	0	0	2	0	0	-	-	-	-
TOTALS	12	14 (0-70)	10	37 (16-50)	9	7	1	17	9	1	2	61 (46-76)	9	12	1

<sup>1</sup> Not included here are: a) one tree in thick scrubby forest that supported 5 *A. r.*, 5 *A. s.*, 1 *P. c.*; dense foliage prevented Sities from obtaining a flowering percentage; b) 5 trees of 32, 18, 14 flowering percentage within 13 feet of each other, that together supported 6 *A. r.*, 3 *A. s.*. There was considerable traffic of birds between the trees, and where the crowns of two almost touched, a *Ysitha* appeared to be defending an area in both trees.  
<sup>2</sup> The observation tree; flowering percentage was 62 on 17 July.

TABLE 4  
CENSUS RESULTS: BIRDS PRESENT AT OBSERVATION TREE 14-17 JULY 1966

Day and hour	No. birds present			Day and hour	No. birds present		
	<i>A.r.</i>	<i>A.s.</i>	<i>P.c.</i>		<i>A.r.</i>	<i>A.s.</i>	<i>P.c.</i>
14 July				16 July			
05:00	0	0	0	14:00	5	7	0
05:14	1?	0	0	15:00	5	4	0
05:23	2	3	0	16:00	3	2	0
05:29	5	6	0	17:00	1	2	0
05:32	7	8	0	17:30	1	0	0
05:36	8	8	0	17 July			
08:30	7	7	0	05:40	7	10	0
11:30	7	7	0	07:00	6	8	0
14:00	6	7	0	08:00	6	7	0
16:30	2	0	0	09:00	5	8	0
18:00	0	0	0	10:00	6	7	0
15 July				11:00	5	7	0
12:30	6	7	0	12:00	5	7	0
16 July				14:00	6	3	1
06:00	4	10	0	15:00	5	2	0
07:30	6	7	0	16:00	1	2	0
09:00	5	7	1	17:00	2	2	0
10:30	4	7	0	17:30	2	1	0
12:00	5	7	1	18:00	0	0	0

counted all hummingbirds present on the tree and plotted their positions on a diagrammatic map of the foliage; Figure 2B shows a representative census plot. During most of the day, hummingbirds on the tree were localized on feeding territories, and the census results refer to these "resident" birds. During early morning and late afternoon territoriality tended to break down, and birds shifted around considerably. Under these conditions it was difficult to plot positions reliably, and the hummingbirds present were simply counted.

To obtain a quantitative measure of aggressive activity, Stiles counted the vocalizations and chases occurring over the entire tree in a timed 5-minute interval once each hour. No attempt was made to distinguish species, the objective being to measure aggressive levels among all birds present. To clarify the dominance relations between *rutila* and *saucerrottei*, he counted all chases originating in the various foliage masses over two 15-minute intervals on 16 July. For these counts he determined the species of both birds involved in each chase.

Feeding activity was estimated at different times of day for comparison with data on aggression. As a measure of the overall amount of feeding, Stiles counted foraging birds on two visual scans over the entire tree, taken 1 minute apart. The counts were thus weighted in favor of those birds engaged in long-sustained bouts of feeding.

Wolf used the same foliage divisions as had Stiles, save that he sub-

TABLE 5  
NUMBERS OF BIRDS PRESENT AT OBSERVATION TREE AT VARIOUS TIMES OF DAY  
20-22 JUNE 1967

Day and census interval	No. birds present			Day and census interval	No. birds present		
	A.r.	A.s.	P.c.		A.r.	A.s.	P.c.
20 June				21 June			
14:40-15:30	5	7	2	17:00-17:03	4	6	0
15:40-16:00	5	8	0	17:05-17:08	4	4	0
16:13-16:20	5	7	0	17:10-17:13	1	7	0
16:40-16:50	3	7	0	17:15-17:18	1	5	0
17:00-17:10	3	8	0	17:20-17:23	2	4	0
17:15-17:25	3	8	0	17:25-17:28	2	6	0
21 June				17:30-17:33	2	6	0
05:30-05:40	3	3	1	17:35-17:38	2	5	0
07:00-07:40	5	8	2	17:40-17:43	2	5	0
08:00-08:40	7	8	2	17:45-17:48	2	1	0
09:00-09:40	7	8	2	17:50-17:53	0	3	0
10:00-10:40	7	9	2	17:55-17:58	0	2	0
11:00-11:40	8	10	1	18:00-18:03	0	0	0
15:00-15:40	3	10	2	22 June			
16:00-16:40	4	8	0	09:15-09:55	6	11	2
				10:10-10:50	5	10	2

<sup>1</sup>40-minute census intervals consisted of 8 consecutive 5-minute observation periods, one in each region of the tree (see text).

divided sectors 2 and 3 to obtain a total of eight regions (cf. Figure 2A). He divided each hour spent at the tree as follows: a) the first 10 minutes he spent counting the total number of chases in the tree without regard to identifying the participants; b) during the next 40 minutes, 5 minutes were devoted to watching each of the eight regions; c) the last 10 minutes were spent in general observations. During the 5-minute periods at each region he counted the number of chases originating therein, and recorded the species of both birds involved whenever possible. Numbers and species of resident birds having most of their territory in the given region were recorded at the end of each 5 minutes.

*Census results.*—Tables 4 and 5 give the numerical results of the various censuses of hummingbirds present at the observation tree for 1966 and 1967 respectively; total numbers of birds present are graphed against time of day in Figure 3. The overall daily pattern of hummingbird activity was fairly similar in both years, but some quantitative differences existed. Approximate times of dawn and dusk were 05:30 and 18:00.

Early morning observations in 1966 showed a rapid rise in numbers of birds present, reaching a maximum about ½ hour after dawn. This early morning peak corresponds to a period of intense foraging and low aggression, with many of the birds present for only a brief time. Territorial activity increased rapidly thereafter, and within an hour or two a steady level of 12 to 14 (1966) or 17 to 19 (1967) territorial birds had been

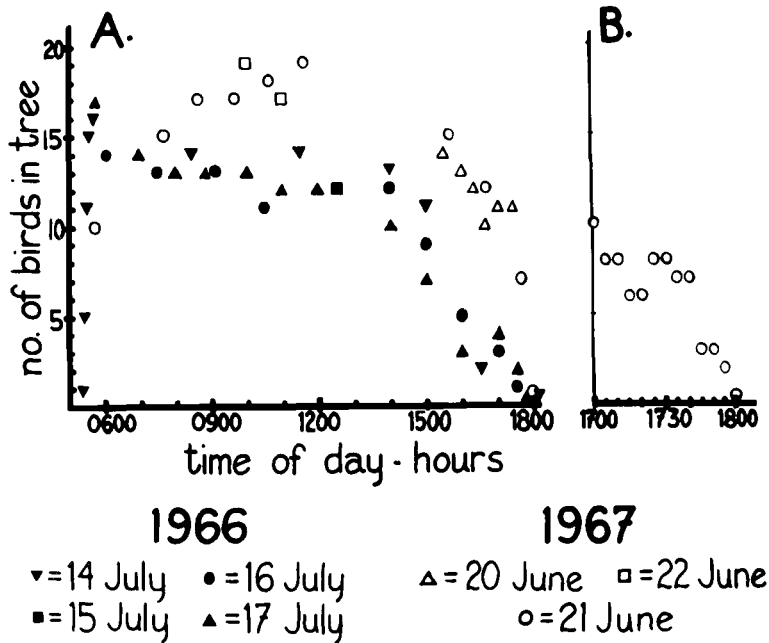


Figure 3. A, number of hummingbirds of all species present in the observation tree at different times of day, 14–17 July 1966 and 20–22 June 1967. B, changes in the number of hummingbirds at the observation tree during the last hour of activity on 21 June 1967.

reached. No further marked change in numbers occurred until birds began leaving the tree in midafternoon. This decline was most marked between 15:00 and 16:00. Between 16:00 and 17:30 numbers stayed fairly stable at 3 to 5 (1966) or 10 to 12 (1967); all birds left the tree by 18:00. During this last hour or two of the day, no birds were resident in the tree. This produced a pattern of continuously shifting short-term territories and fluctuating numbers of each species.

During the 1966 studies the flowering of the observation tree declined from 76 per cent on 14 July to 62 per cent on 17 July. The decline was correlated with a decrease in resident birds (14 on 14 July to 12–13 on 17 July), and a hastening of the afternoon departure of birds from the tree (cf. Table 4 and Figure 3). In 1967 the number of territorial residents was considerably higher, and more birds remained at the tree later into the evening. Taken together these observations suggest that the tree was blooming more vigorously in 1967.

## TERRITORIAL BEHAVIOR

The hummingbirds present during the midday hours were highly territorial. Each bird controlled a segment of the canopy with its associated flowers and repelled all intruding hummers by visual or vocal displays or by chasing. Within each territory were certain favored perches upon which a hummingbird spent most of its time. Birds left these posts chiefly to feed or to repel intruders. Most feeding took place within the territory, but the commonest cause of chases was the wandering of a feeding bird into another's holdings; sallies after flying insects very often ended in chases. Short flights from perch to perch within the territory were also frequent, especially by *saucerottei*. These flights, usually accompanied by aggressive displays, were apparently to confront a potential trespasser.

Virtually all the aggressive activity by hummingbirds in the tree was directed solely at other hummingbirds. The various other birds that visited the tree were almost never attacked. The honeycreeper *Cyanerpes cyaneus*, a frequent visitor to *Genipa* flowers (and a probable competitor for nectar), was never molested. Various large tyrannids (*Pitangus*, *Myiodynastes*, *Myiarchus*, *Megarhynchus*) from time to time hawked flying insects in the tree, frightening or dislodging hummingbirds in the process. Sometimes upon the arrival of one of these flycatchers many hummers left the tree. Their return, after absences of up to a minute, was usually accompanied by an increase in chases as territorial boundaries were established. Wolf noted a similar exodus when a Turkey Vulture (*Cathartes aura*) flew overhead. The only nonhummingbirds that elicited aggressive responses from hummers were the common, large, blue-black bees. Pitelka (1942) and others have suggested that the hum or buzz of rapidly-beating wings releases aggressive behavior in hummingbirds. These bees were probably not serious competitors for nectar; their major activity at the tree appeared to be gathering pollen.

The spatial arrangements of the resident territorial *Amazilia* were remarkably constant throughout the 1966 observations. Two individually recognizable birds, one of each species, held the same positions in the tree for at least 3 days. Figure 2B gives a representative picture of the territorial pattern. Sectors 1, 2, and 6 were controlled by *rutila*; 3, 4, and 5 were mostly occupied by *saucerottei*, but 4 and 5 each contained one *rutila* territory. In general, the *saucerottei* held small, close-packed territories on the inside of the crown. Territories of *rutila* were larger and occupied the lower foliage masses and parts of the outside of the crown.

*P. cuvierii* visited the observation tree at irregular intervals in 1966, and fed exclusively in foliage masses 1 and 2. In 1967 this species held

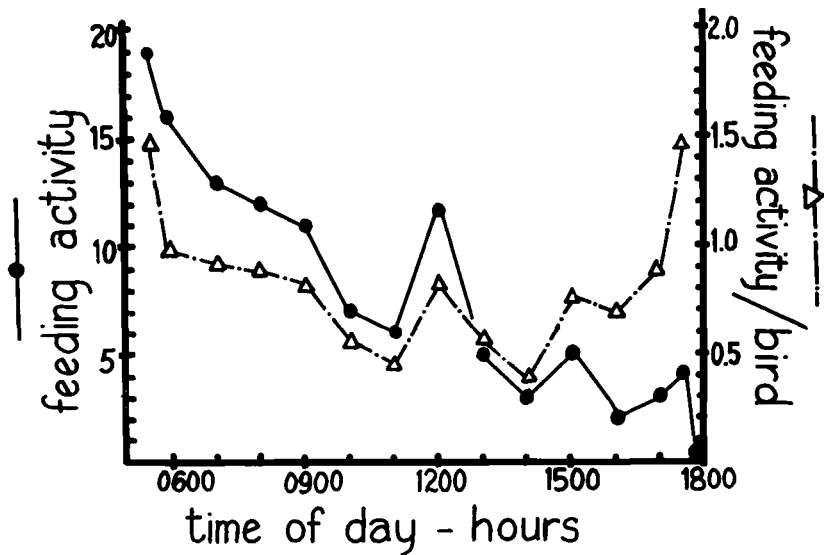


Figure 5. Changes in feeding activity, and feeding activity per bird present, over the course of 16 July 1966, at the observation tree. Feeding activity equals the sum of foraging birds recorded on two scans of the entire tree, taken 1 minute apart.

territories fairly consistently, again in sectors 1 and 2. The presence of residents in 1967 probably reflects the tree's more vigorous flowering rather than an increase in abundance, as the relative numbers of *Phaeochroa* and the *Amazilia* species recorded in the study area were similar in the 2 years.

The spatial arrangements between the *Amazilia* species in 1967 were fairly similar to those of 1966, allowing for the upward displacement of *rutila* and consequent shifting of *saucerottei* by the continued presence of *P. cvierii* in sectors 1 and 2. Areas 4 and 6 were utilized almost exclusively by *saucerottei*, while *rutila* controlled 3A; 3B and 5 held territories of both species. When *Phaeochroa* was absent, *saucerottei* utilized 2B while *rutila* held 1. The largest territories were held by *P. cvierii*; the smallest, by *A. saucerottei*.

Figure 4 shows variations in aggressive activity, measured as chases per minute, with time of day. The early morning was a period of intense foraging and low aggressive levels, during which *rutila* and *saucerottei* mingled freely in all sectors. Shortly thereafter, aggression increased sharply as the territorial pattern was reestablished and "floaters" were driven out. By 07:00 to 07:30 territories had been defined, and aggression



TABLE 6  
INTRASPECIFIC AND INTERSPECIFIC CHASES ORIGINATING IN VARIOUS FOLIAGE MASSES OF  
THE OBSERVATION TREE FOR TWO TIMED 15-MINUTE INTERVALS 16 JULY 1966

Time	Foliage masses in which chase originated	No. resident birds		Chaser-chased			
		<i>A.r.</i>	<i>A.s.</i>	<i>A.r.-A.r.</i>	<i>A.r.-A.s.</i>	<i>A.s.-A.r.</i>	<i>A.s.-A.s.</i>
07:30-07:45	1, 2, 6	4	1	3	10	2	2
	3, 4, 5	2	6	0	3	4	24
TOTALS		6	7	3	13	6	26
11:30-11:45	1, 2, 6	3-4 <sup>1</sup>	1	5	5	0	0
	3, 4, 5	2	6	3	7	6	24
TOTALS		5-6	7	8	12	6	24
GRAND TOTALS		Avg. 5-6	7	11	25	12	50

<sup>1</sup> One *rutila* present for only about one-half of the observation period.

Below a certain level of illumination, aggressive behavior may be inhibited by the birds' inability to distinguish the colors and markings important in display. The burst of feeding at dusk, seen in many species of hummingbirds, is also usually accompanied by a decrease in belligerence. Because such small homeotherms must feed well at dusk and dawn to accumulate and replenish the energy reserves utilized during the night, it is clearly advantageous for aggression to be minimized at these times.

The daily patterns of aggressive activity were quite similar in the 2 years; the higher number of chases in 1967 can be related to the greater number of birds present. Figure 6 shows that the number of recorded chases per minute was directly and exponentially related to the number of birds in the tree, which is not surprising in that as the number of birds rises the unoccupied or intermittently occupied volume in the tree decreases. Full occupation of the tree (the maximum number of territories the tree will hold) probably represents a balance between the food requirements and competitive ability of the individual birds. Periods of intense feeding activity and/or low territoriality show lowered aggressive levels (cf. the early morning values in Figure 6A). The tree supported more birds longer when it had more flowers (see above), but apparently few or no birds defended a territory large enough to contain a full day's food. We have no evidence of any changes in territory sizes between the 2 years.

*Dominance relationships.*—Tables 6 and 7 present the data on intraspecific vs. interspecific chases. Clearly *rutila* was dominant to *saucerrottei*, even in those foliage regions where the latter was more numerous. More-over *rutila* chased *saucerrottei* more often than other *rutila*, while most



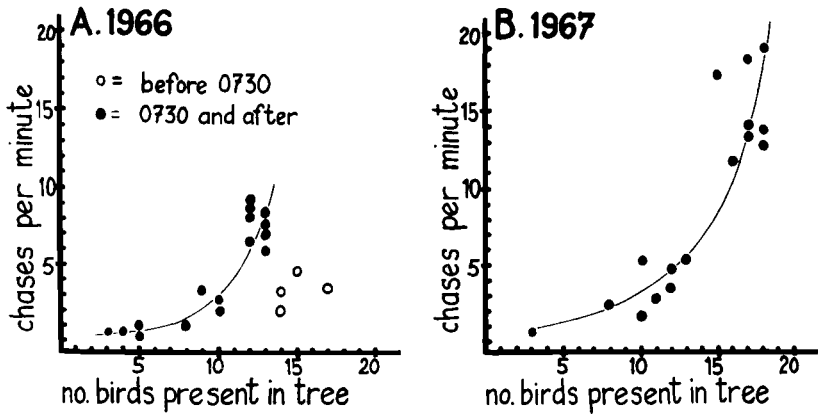


Figure 6. Variation in levels of aggression with number of birds present at the observation tree.

*saucerottei* aggressive activity was directed against its own species. The large numbers of *saucerottei-saucerottei* chases were due chiefly to this species' small, closely-packed territories; often a chase would cross several territories, with the respective owners joining in—3- and 4-bird chases were not uncommon. This “ganging” effect may also have helped *saucerottei* to maintain their positions against *rutila*. When the latter was the aggressor, the chases were nearly always 2-bird affairs, often prolonged and involving actual fighting.

*Phaeochroa* was clearly dominant to both *Amazilia* in 1967 (Table 7), when it held territories in the observation tree. In 1966 individual *P. cuvierii* visited the tree several times a day, fed in areas 1 and/or 2 for 5 to 20 minutes, and left. The larger *Phaeochroa* consistently dominated the established *Amazilia*, and not infrequently forced a *rutila* from its territory temporarily. In one 7-minute visit near noon on 15 July, a *P. cuvierii* chased *rutila* five times, *saucerottei* once, and was once chased by *rutila*.

TABLE 7  
TOTAL NUMBERS OF CHASES RECORDED IN OBSERVATION TREE IN WHICH BOTH BIRDS INVOLVED WERE IDENTIFIED 20-22 JUNE 1967

Chaser	Chased			Totals
	<i>A.s.</i>	<i>A.r.</i>	<i>P.c.</i>	
<i>A.s.</i>	410	50	0	460
<i>A.r.</i>	223	59	3	285
<i>P.c.</i>	33	16	0	49
TOTALS	666	125	3	794

## BIRDS COLLECTED IN THE STUDY AREA

Late in the afternoon of 17 July 1966, Stiles collected three *A. rutila* (♂ ♂ ♀), four *saucerottei* (♂ ♂ ♀ ♀), and one *P. cuvierii* (♂) from three other nearby *Genipa* trees. These birds were probably not representative of the midday territorial assemblage at the observation tree. One of the female *saucerottei* was giving a typical aggressive vocalization when shot, suggesting that females as well as males may be territorial.

At the conclusion of his observations at 11:00 on 22 June, Wolf tried to collect a representative sample of the resident territorial assemblage at the observation tree. Five minutes before starting to collect, he made a census of the residents, and in each region of the tree he removed no more birds than the census indicated were resident there. He shot only birds sitting on perches known to be used regularly by residents. After each shot he allowed the birds to calm for a minute or two and resume normal activities. The *Amazilia* species repopulated the tree very quickly, and birds Wolf took after he was no longer sure which the original residents were, he considered to have arrived after the collecting began.

Table 8 summarizes the data from Wolf's collecting. The strikingly rapid repopulation of the tree by the *Amazilia* species suggests a considerable floating population. Moreover the census data showed that collecting and its attendant commotion altered the spatial arrangements between the *Amazilia* species remarkably little, in spite of the turnover of individuals. One of the three definitely resident *A. rutila* collected was a female; two of the four resident *saucerottei* were females. This establishes that females are involved in the territorial system at *Genipa* trees and appear to hold and defend feeding territories on an equal basis with males.

None of the birds we collected showed any gonadal evidence of breeding. Skutch (1940, 1950) states that most Middle American hummingbirds breed early in the dry season (roughly November to January), and this appears to be the case for *A. rutila* (Wolf, 1970).

For *P. cuvierii* the situation is problematical. This species breeds during the rainy season in southwestern Costa Rica (Skutch, 1964), but we obtained no evidence of breeding at Granja Jiménez as late as mid-July; perhaps it breeds still later. The fact that Wolf heard *P. cuvierii* sing in May and June is even more perplexing, although the relationship between song and breeding in many hummingbirds may be complex (Pitelka, 1942).

## DISCUSSION

## ECOLOGICAL AND BEHAVIORAL RELATIONSHIPS

We have noted the existence of a linear dominance hierarchy among the three species territorial at *Genipa* trees. Theoretically it should be possible



for *Phaeochroa* to eliminate or reduce the numbers of the *Amazilia* at *Genipa*, and for *rutila* to act likewise upon *saucerottei*. The question is, then, how do these three species manage to coexist in the study area, and even in the same tree?

Two possible reasons why *Phaeochroa* does not eliminate the *Amazilia* species are its relatively low numbers in the area, and its strong preference for lower foraging heights. The factors limiting the numbers of *P. cuvierii* in the study area as a whole are unknown, although it may be significant that the species is apparently a transient in the Granja Jiménez area. In the observation tree, we found that *Phaeochroa* confined virtually all of their foraging to sectors 1 and 2, leaving the whole upper part of the tree to the *Amazilia*. The maximum number of *P. cuvierii* simultaneously present at the observation tree was two.

Territoriality may be of little advantage to a large, dominant, uncommon hummingbird such as *Phaeochroa*, unless the food source to be defended is rich enough to satisfy its greater energy needs. The observation tree may have answered this requirement in 1967, but not in 1966. At other times *P. cuvierii* may best satisfy its energy needs by moving between good feeding areas, which it can invade with impunity because it is dominant to the other hummingbirds likely to have established territories there.

Because of their commonness, close relationship, and wide ecological overlap, *A. rutila* and *saucerottei* were probably the most intense competitors at *Genipa* trees. Part of the reason for their coexistence may stem from somewhat different patterns of distribution in the study area. *A. rutila* occupied more *Genipa* trees with relatively more individuals at sparsely flowering trees, while *saucerottei* tended to cluster more at the richer food sources (Tables 2 and 3). Perhaps *rutila* has more intraspecific intolerance, but no such difference was manifested in the number of chases recorded. Conversely *saucerottei* may be more gregarious and/or better able to tolerate small, close-packed territories. At other times of year *saucerottei* shows a stronger tendency to congregate at certain flowers such as *Inga* or *Manihot* than does *rutila* (Wolf, 1970).

Despite the wide overlap in observed foraging heights between *rutila* and *saucerottei*, some average differences may exist that are reinforced when the two species come together. In 1966 when *P. cuvierii* was absent, most *rutila* territories were in the lower parts of the observation tree and *saucerottei* occupied most of the crown. Table 2 indicates that *rutila* occurred at relatively more of the small *Genipa* in the study area; *saucerottei* was virtually confined to trees over 30 feet in height. Wagner (1946) gives indirect evidence that *rutila* prefers lower foraging heights. In a large flowering tree in Chiapas, he found the lower parts occupied by

*rutila*, while *Anthracothorax prevostii*, a species probably dominant to *rutila* (Wolf, 1970), occupied the upper half. Thus *rutila* may, on the average, prefer to forage lower than *saucerotteei*. However, *rutila* is also sufficiently dominant to establish territories in the crown as well. Although lacking quantitative data, we both had the impression that these *rutila* territories contained the richest feeding areas in the crown.

None of the other three species of hummingbirds recorded in the study area appeared to have any appreciable effect on the territorial situation at *Genipa* trees, or upon the ecological and social relationships of *Phaeochroa* and the two *Amazilia*. *Phaethornis longuemareus* was seldom seen beyond the gallery forest, where *Genipa* was rare; in any case, it always kept to the understory. *Heliomaster constantii* was present in very low numbers, and probably visited *Genipa* trees rarely if at all under normal circumstances. *Chlorostilbon canivetii*, fairly common in 1967, visited only *Muntingia* flowers, which play little or no role in the ecology of the other local hummingbirds. Wolf (1970) has shown that this species is subordinate to other hummingbird species at Granja Jiménez. *Muntingia* has small flowers, and since more dominant hummers ignore it, it probably is a relatively poor food source that only very small species like *Chlorostilbon* can utilize effectively. Conversely this species may avoid sites like *Genipa* trees where more aggressive hummingbirds congregate.

#### FACTORS INFLUENCING TERRITORIALITY

The importance of *Genipa* as a hummingbird food source must now be viewed in terms of general factors that influence aggregation and territoriality at floral feeding sites. The two most important of these are the richness and localization of the food source, relative to the amount and distribution of alternative foods. If several such alternatives were available, one might expect the various hummer species of a region to segregate by flower type, presumably with dominant species controlling the richer sources. To some extent this may have occurred at Granja Jiménez, with *Chlorostilbon* being restricted to *Muntingia* blossoms. With flowers highly localized and few alternatives available, several species may congregate at a feeding site. The number of species that can fit in depends upon relative aggressiveness and numbers, and also upon whether or not the food source is diverse enough to include subsectors that can be utilized by different species. The coexistence of three hummingbird species at *Genipa* trees probably resulted from a combination of different numbers, local distribution patterns, and foraging height preferences of the species concerned.

The importance of territoriality under such circumstances probably

varies with the ratio of energy saved by gaining exclusive use of a feeding area to energy expended in defending that area (Brown, 1964). The energy expenditures of defense are greatest when competitors are numerous. When alternative food sources are rare or widely scattered, holding a territory can be of considerable advantage. Few alternatives often imply many competitors, and the food source must be very energy-rich to permit territoriality under such conditions. The extremes of both situations can be reached at artificial feeding stations: copious and concentrated food, and hordes of competing hummers. Under these circumstances territoriality at low bird densities gives way to individual aggressiveness, without defense of the feeders at high densities. The situation at *Genipa* trees is probably intermediate in both respects, with *Genipa* blossoms apparently supplying enough nectar to support territorial defense. Territorial aggregations occurred only at those *Genipa* trees with large numbers of flowers. The afternoon breakdown of territoriality at the observation tree probably reflected the exhaustion of the tree's nectar supply.

Length of the blooming season may also influence the pattern of hummingbird utilization of a floral food source. A short blooming season may produce a tendency for aggregation at richer food sources, while over a longer flowering period the birds may spread out until their distribution parallels that of the food. It is perhaps significant that most of the hummingbirds discussed here probably breed at the time when many flowers are available for the longest period: the early dry season. During June and July the two *Amazilia* species and *Phaeochroa* probably engage in local movements in response to the comparatively short blooming seasons of plants like *Luehea* and *Genipa*. So more birds held territories in the observation tree than the tree could support for a whole day, perhaps the short blooming season of *Genipa* is insufficient to permit more even spacing of the birds with respect to the available flower supply.

Nomadic wandering in response to shifting flower abundance is generally considered typical of tropical hummingbirds during the nonbreeding season. It is noteworthy that feeding territoriality almost exactly comparable to that described here, has been reported in several North American species during migration (Unglish, 1933; Armitage, 1955). In several accounts of feeding concentrations of migrating hummers aggression figures prominently but territoriality as such is not mentioned (numerous examples in Bent, 1940; Stott, 1942). Similar to these last are Skutch's (1958, 1961) descriptions of feeding aggregations of tropical hummingbirds at *Stachytarpheta* hedges. These data suggest that during the nonbreeding season no major difference exist in the kinds of feeding territoriality between tropical and temperate-zone hummingbirds (see also

Pitelka, 1942). Moreover most "temperate-zone" hummingbirds merely breed there; for up to 6 months a year they are as "tropical" as any *Amazilia*. Wolf (1970) further shows that such species on their wintering ground may adopt the nomadic existence of "typical" tropical hummingbirds.

The presence of females of both *Amazilia* species in the territorial assemblages at *Genipa* trees brings up some interesting questions. When food sources are localized or rare, and/or when energy needs are high, intraspecific as well as interspecific competition may be severe. Males usually being dominant to females in hummingbirds, one way to alleviate some of the pressure on the weaker sex is by ecological separation, either in food or habitat. Both of these are seen, for example, in temperate-zone hummers in the breeding season. Evidence exists in several of these species for a separation of the sexes during migration (Bent, 1940). Alternatively, if habitat or food diversity is limited, it may be advantageous for females to equal males in dominance. Pitelka (1942) has mentioned that female hummingbirds approach males most closely in territorial behavior at feeding sites. In the present instance, female and male *A. rutila* and *saucerrottei* appear to be competing on essentially an equal basis at *Genipa* trees. The lack of sexual dichromatism in these and other tropical species may be a result of selection for equal dominance of the sexes during periods when food is scarce (Wolf, 1969).

Because of the short data-gathering periods, this study can shed little light on the time dimension of hummingbird feeding and territoriality, but its results do have general applicability to the problems of resource partitioning in space. Their very small size and limited capacity for energy storage make it imperative for hummingbirds to respond quickly to changes in the spatial distribution of food within the habitat. Hummingbirds not in the special physiological state associated with migration must feed very frequently and literally live from hour to hour. Thus the distribution of food at any one time is the factor to which they must respond. In this context, we believe that our attempt to investigate and quantify some of the factors influencing territoriality has general validity.

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#### SUMMARY

Flowers are scarce during the early rainy season in the lowlands of northwestern Costa Rica, and hummingbirds gather into highly territorial aggregations at the few trees in bloom. During July 1966, and June 1967, we made observations on the territoriality of the hummingbirds *Amazilia rutila*, *A. saucerrottei*, and *Phaeochroa cuvierii* at the tree *Genipa americana*, the only important floral food source at the time. The two *Amazilia* species were common, and females as well as males held territories. *A. saucerrottei* tended to cluster at the richer feeding sites, while *rutila* occurred in smaller numbers at most of the available flowering trees. *P. cuvierii* occurred in low numbers at scattered trees. No birds collected were in breeding condition. We made detailed, quantitative observations at the same *Genipa* tree in both years. During most of the day the tree was occupied by a highly territorial aggregation of hummingbirds. Birds began leaving the tree in midafternoon, and the territorial system was reestablished each morning after a period of nonterritorial foraging at dawn. Levels of aggressive activity varied exponentially with the number of birds present in the tree. A linear interspecific dominance hierarchy was evident: *P. cuvierii* over *rutila* over *saucerrottei*. Coexistence of the three species in the tree and in the study area was ascribed to differences in numbers, distribution patterns, aggressiveness, and foraging height preference.

Territorial defense is advantageous when alternate food sources are scarce, but expensive in both time and energy when competitors are numerous. Selection for equal dominance of the sexes, correlated with decreased sexual dichromatism, may occur during times when food is scarce. During the nonbreeding season, tropical and temperate-zone hummingbirds show no important differences in territorial behavior.

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