THE IMPACT OF SEASONAL FLOWERING ON THE BIOLOGY OF SOME TROPICAL HUMMINGBIRDS

LARRY L. WOLF

Department of Zoology
Syracuse University
Syracuse, New York 13210

In most parts of the Neotropics the annual cycle of climate usually is broken into two distinct phases, wet and dry seasons. Characteristically many of the woody plants undergo sexual reproduction during the dry season while vegetative growth occurs during the rainy season (Janzen 1967). This seasonal flowering has a marked effect on organisms which are directly dependent on vegetative or reproductive phases of plant growth. One group of tropical birds, the hummingbirds (family Trochilidae), are thought to be closely tied to flowers through most or all of their life cycle. Plants are presumed to be the most important food source for many species, even though evidence is accumulating that many species are to some degree insectivorous. Even these species may be tied to flowering seasons through the increased feeding efficiency of visiting flowers as rich, localized sources of insect food.

If flowering is important in the economy of hummingbirds, and if this flowering is limited largely to a single season of the year, it would follow that, to cope with this, there must be some major adjustments in the ecology and behavior of the birds. The present study was undertaken to discover two things about the habits of several species of hummingbirds living in such a wet-dry seasonal climate. It was hoped, first, to discover the relative importance of flowers as food sources for the birds, and, second, to understand the importance of seasonal flowering activity in the evolution of techniques for biological exploitation of the dry lowlands of Middle America, and especially the influence on the territorial systems of the hummingbirds.

ENVIRONMENT

The Granja Experimental Jiménez study site is located approximately 14 km SW of Las Cañas, Guanacaste Province, Costa Rica (10° 20′N, 85° 09′W). The entire surrounding region is tropical dry forest (Tosi 1965). Figures 1 and 2 present weather data from Finca La Pacifica, located about 4 km NE of Cañas. Although there are definite, but usually minor, differences in timing of climatic events, especially rainfall, between the two sites, La Pacifica has the most reliable weather station in Guanacaste Province.

The actual study area was on a hillside near the buildings of the experimental farm operated by the Ministerio de Agricultura y Ganadería of Costa Rica; the elevation ranges from 11–45 m. The vegetation of the hillside would be called tropical deciduous forest, following the scheme outlined for México by Leopold (1950). It is dominated by such tree genera as *Bursera, Bombacopsis, Cochlospermum, Quazuma, Samanea, Enterolobium, Genipa, Luhea,* and *Tabebuia.* During the height of the dry season the ground was nearly devoid of green herbaceous vegetation and the trees were almost all leafless (fig. 3). However, after the first rains in late April some ground vegetation appeared and the trees began to leaf out. The rains then stopped until late May, at which time there was a burst of vegetative growth by both woody and herbaceous plants (fig. 4). During the late part of the dry season several small fires were started in the area by Ministerio personnel, but these had little effect on the important food plants of the hummingbirds.

A second portion of the study area, visited irregularly, is along a road ("river road") adjacent to the stream bed at the base of the study hill. This road passes through limited riparian evergreen forest which is much more extensive on the other side of the river.

The flowering seasons for plants observed being used by the hummingbirds were scattered throughout the study period (table 1) with relatively little overlap of important species. In the dry forest area, few species flower at any one time and the flowering season for each species is relatively synchronous and short.

METHODS

Visits to the area were made on the following 1967 dates: 19–20 January, 28 February–2 March, 24 and 26 March, 19–21 April, 17–19 May, 20–22 June, and 13 July. On each of the visits, except that in July, at least two 2-hr. censuses were made in the early morning, normally from 06:00 to 08:00, along a dirt

The Condor, 72:1–14, 1970

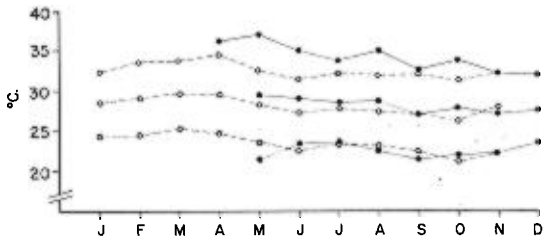

FIGURE 1. Monthly temperature data (mean maximum, mean minimum, monthly mean) from Finca La Pacifica, 5 km NE Cañas, Guanacaste Province, Costa Rica. Open circles are 1964, dots are 1965.

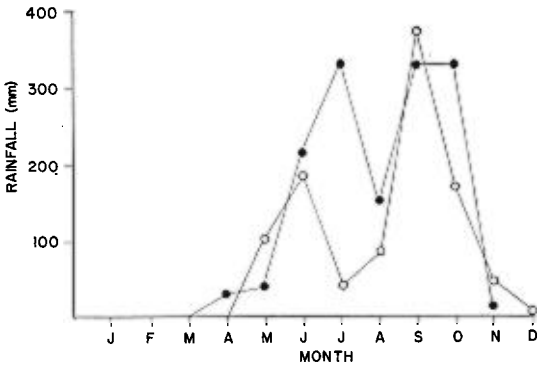

FIGURE 2. Monthly rainfall at Finca La Pacifica, 5 km NE Cañas, Guanacaste Province, Costa Rica, 1965 (open circles) and 1964 (dots).

road winding down the hillside from the offices of the experimental farm to the Río Higuerón (fig. 5). One census usually covered about 0.7 km. On each trip at least some observations were made along the river road. An attempt was made to identify each hummingbird encountered and to record the activity of the bird at the time of observation. No attempt was made to follow individuals for extended periods during these censuses. By moving fairly rapidly along the census route it was hoped to avoid much duplication of individuals in the census figures. Unavoidably, there were varying numbers of birds that I was unable to identify on these censuses, so the results have been presented only as relative values for each species (table 2). All species regularly using the hillside during the study period probably were recorded. The species composition was checked each visit by prolonged observations in various localities at other times of the day.

Following the censuses, several places on the hillside were selected for more intensive observations for the rest of the study period. Where possible, these were areas of bird concentrations, usually around a feeding source. Observations generally were made until 12:00 and then later for another 2–3 hr. until 18:00. This eliminated the hot part of the day from the study time but should not affect the results reported here.

Records were kept of the major tree species in bloom and of all plants at which hummers were observed foraging (table 3).

FIGURE 3. View on study hillside during dry season, April 1967. Note bare trees and absence of ground vegetation.

FIGURE 4. View on study hillside during early part of rainy season, June 1967. Most of trees have leaves and ground vegetation has appeared.

SPECIES OF HUMMINGBIRDS RECORDED

General characteristics of range, breeding season, degree of sexual dimorphism, and habitat at Granja Jiménez for the hummingbird species observed on the study area are listed in table 4. Several size characteristics of the nine species are recorded in table 5. There are roughly three size classes of species: *Archilochus, Phaethornis,* and *Chlorostilbon* are relatively small, the three species of *Amazilia* are intermediate, and *Phaeochroa, Anthracothorax,* and *Heliomaster* are the largest species. *Phaeochroa* averages longest in all three measurements, except for the longer bills of *Anthracothorax* and *Heliomaster.* As with many of the larger species of hummingbirds, the males, in general, are larger than the females, although this may not hold for the smallest species (Lasiewski and Lasiewski 1967). Usually the bill of the female is slightly longer than that of the male.

TABLE 1. Flowering seasons at Granja Jiménez.

Species of plant	Jan.	Feb.	Mar.	Apr.	May	June	July
Pombacopsis Fendleri	x[a]	x	–	–	–	–	–
Combretum farinosum	x	x	x	–	–	–	–
Tabebuia crysantha	–	X	–	x	–	–	–
Samanea saman	–	x	x	x	x	–	–
Vine (Bignoniaceae) (possibly several sibling species)	–	–	X	x	–	–	x
Genipa caruto	–	x	–	x	x	X	X
Inga vera	–	–	X	X	–	–	–
Bromelia pinguin	–	–	–	–	X	–	–
Manihot utilissima	–	–	–	–	–	x	X
Muntingia calabura	x	x	x	x	x	x	x

[a] X indicates relatively more flowering than x; X's account for >50 per cent of flowering in an observation period.

Little Hermit. *Phaethornis longuemareus.* A relatively common species in evergreen forests around Granja Jiménez, it did not venture onto the open, dry forest hillside. There were no singing assemblies on the hillside and only single, quietly foraging birds were encountered during the census.

Scaly-breasted Hummingbird. *Phaeochroa cuvierii.* This is an uncommon species which may be migratory or nomadic in the Granja Jiménez region since it was not recorded on the hillside until May. It was first recorded in the general area during the study period in an evergreen forest approximately 5 km from Granja Jiménez on 29 March (D. R. Paulson, pers. comm.). In the study area it

FIGURE 5. Portion of census road from buildings of experimental farm looking toward Río Higuerón at base of hill, June 1967.

was prominently associated with two abundant flowering plants, *Bromelia* and *Genipa*. Its appearance on the study hillside coincided with the leafing of the trees and the growth of herbaceous vegetation.

The Green-breasted Mango. *Anthracothorax prevostii*. Although recorded in the study area from January-April, it was not found after April in several visits to evergreen riparian forest and to other dry forest localities nearby (G. H. Orians and D. R. Paulson, pers. comm.).

The Fork-tailed Emerald. *Chlorostilbon canivetii*. It is generally an uncommon species of the dry forest area, and seldom encountered in riparian forest, although it may visit the forest edge. It is probably more common at slightly higher elevations (Slud 1964). It was recorded on all but two visits to the area.

Blue-vented Hummingbird. *Amazilia saucerottei*. This is one of the two common resident hummingbirds of the tropical dry forest region of Costa Rica. However, it is more common than *A. rutila* on the central plateau of Costa Rica in the vicinity of San José. It also makes "a limited entry to the Caribbean slope" (Slud 1964) and in general seems to inhabit slightly moister conditions than *A. rutila*. It probably is slightly more common than *A. rutila* in the study area. None of the adults collected in May and June were in breeding condition.

Cinnamon Hummingbird. *Amazilia rutila*. Although common on the dry-forested hillsides in the Granja Jiménez region, it is much less common in or at the edge of the riparian forest than is *A. saucerottei*. Although the

TABLE 2. Relative numbers of hummingbird species observed on monthly censuses at Granja Jiménez.[a]

Species	Jan.	Feb.	Mar.	Apr.	May	June
Amazilia rutila	2	2	1	1	4	4
Amazilia saucerottei	3	3	1	4	3	4
Phaeochroa cuvierii	0	0	0	0	2	2
Anthracothorax prevostii	2	1	1	1	0	0
Heliomaster constantii	1	1	0[b]	0	1	0
Archilochus colubris	2	3	1	0	0	0
Amazilia tzacatl	0	0	0	0	1	0
Chlorostilbon canivetii	0	1	0[b]	3	1	2
Phaethornis longuemareus	0	0	0	1	0	3
All species	5	6	4 + 2	5	6	5

[a] Numbers per visit refer to the following categories: 0 = no birds recorded on that visit; 1 = 1–2 birds recorded; 2 = 3–5; 3 = 6–10; 4 = 10 or more.

[b] No individuals recorded on the regular censuses, but at least one was seen during other observations at that visit.

TABLE 3. Species of flowering plants visited by hummingbirds at Granja Jiménez.

Plant species	Hummer species[a]									Total
	A.c.	*A.s.*	*A.r.*	*P.c.*	*H.c.*	*A.t.*	*A.p.*	*C.c.*	*P.l.*	
Tabebuia chrysantha[b]	X	X	X		X		X	X		6
Muntingia calabura			X					X		2
Genipa caruto[b]		X	X	X	X	X				5
Samanea saman		X						X		2
Verbenaceae ? (herb)	X									1
Combretum farinosum		X	X				X			3
Bromelia pinguin[b]		X	X	X	X	X		X	X	7
Bignoniaceae (vine)	X	X	X		X		X	X	X	7
Shrub	X							X		2
Convolvulus sp.	X									1
Bursera simaruba		X?								1?
Inga vera[b]		X	X				X			3
Bombacopsis Fendleri	X	X	X							3
Legume-like herb	X									1
Tree sp.	X									1
Helicteres guazumaefolia									X	1
Manihot utilissima[b]		X		X				X		3
Total flower species visited	8	9	8	2	5	2	4	7	3	
Total numerically important flower species visited	2	6	5	2	5	2	3	3	2	
No. shared with other species	5	9	8	2	5	2	4	6	2	

[a] *A.c.* = *Archilochus colubris*; *A.s.* = *Amazilia saucerottei*; *A.r.* = *A. rutila*; *P.c.* = *Phaeochroa cuvierii*; *H.c.* = *Heliomaster constantii*; *A.t.* = *Amazilia tzacatl*; *A.p.* = *Anthracothorax prevostii*; *C.c.* = *Chlorostilbon canivetii*; *P.l.* = *Phaethornis longuemareus*.

[b] Numerically important species (see table 1).

two species do occur together to some extent throughout suitable habitat in the region of geographic overlap, they seem to be partly separated ecologically by this habitat difference. G. Orians (pers. comm.) found a nest at Granja Jiménez in mid-February and birds taken in May and June (mostly males) had small, inactive gonads.

Rufous-tailed Hummingbird. *Amazilia tzacatl.* This species was recorded on the hillside study area on only a single occasion when one or two individuals were foraging at *Genipa* and *Bromelia.* It was probably more common in the moister riparian forest along the Río Higuerón.

Plain-capped Starthroat. *Heliomaster constantii.* This uncommon species occurred from the edge of the moist forest along the river onto the dry forest hillside during both the dry and rainy seasons. Wetmore (1944) found them at the borders of heavy woodland or along brush-lined roadways near Liberia, Costa Rica.

Ruby-throated Hummingbird. *Archilochus colubris.* A winter migrant to Central America, arriving in Costa Rica "probably in October" and departing in late March or early April (Slud 1964), its main wintering area in Costa Rica is the tropical dry forest zone of the Pacific lowlands. In the Finca Jiménez area it was common on the dry hillside, but not in the evergreen riparian forest.

DEFINITIONS

Before presenting the results of this study it is imperative to define several terms which appear frequently in the text. "Resident" is used here to mean an individual which restricts its activities to one site for a period of several hours or more at a time. It is possible that a resident individual might occupy several subsections of a tree during its period of residency. "Territory" is used in the sense of an area within which the resident controls or restricts use of one or more environmental resources. These hummingbirds were defending an area in which a food source was localized. This definition differs slightly from that of Pitelka (1959) in that emphasis is switched from space per se to some presumably limited environmental resource contained within the space. This implies that intruders may be allowed to penetrate the territorial space provided they do not attempt to utilize the defended resource. It does not imply that space might not be the resource being defended. To complete the definition of territory one should add the behavioral parameter of dominance on the territory and loss of dominance when the bird leaves the territory (Willis 1967).

TABLE 4. Some general characteristics of the nine species of hummingbirds recorded at Granja Jiménez.

Species	Range[a]	Breeding season	Degree of sexual dimorphism	Habitat at Jiménez
Phaethornis longeumareus	México into South America	Rainy season[b]	Slight	Evergreen forest; occasionally on dry hillside.
Phaeochroa cuvierii	Guatemala to Colombia	Rainy season[c]	Slight	Dry forest.
Anthracothorax prevostii	México to northern South America	Dry season?	Marked	Dry forest.
Chlorostilbon canivetii	México to South America	Dry season?	Marked	Dry forest; edge of evergreen forest.
Amazilia saucerottei	Nicaragua, Costa Rica, and northern South America	??	Slight	Dry forest; edge of evergreen forest.
Amazilia rutila	México to Costa Rica	Dry season?	Slight	Dry forest.
Amazilia tzacatl	México to South America	??	Slight	Evergreen forest; occasionally on dry hillside.
Heliomaster constantii	México to Costa Rica	??	Marked	Dry forest.
Archilochus colubris	temperate 'Breeds in North America, winters in Middle America	————	Marked	Dry forest.

[a] Slud 1964.
[b] Skutch 1951.
[c] Skutch 1964.

RESULTS

SUMMARY OF MONTHLY OBSERVATIONS

January. Although the last substantial rainfall occured in late October 1966, some of the trees which later would be bare still had leaves in late January. There was no rain and the sky was generally clear during this observation period. I estimated that more than 50 per cent of the trees on the study hillside were bare, and most of the remainder were losing their leaves. At the same time the ground vegetation was drying out. Only two tree species, *Cochlospermum vitifolium* and *Bombacopsis Fendleri,* were blooming in abundance. *Cochlospermum* was not being visited by hummingbirds but was visited by insects. This species may be bee- or bat-pollinated (Janzen 1967). *Bombacopsis* is primarily night-blooming and pollinated by moths (Janzen, op. cit.) and probably by bats. Hummingbirds, especially *Amazilia rutila,* visited the *Bombacopsis* flowers for several hours in the early morning until the last flowers dropped off the tree. In addition to these trees, the shrub, *Combretum,* and a small purple-flowered herb were blooming. Both were visited by hummingbirds, the herb especially by *Archilochus.* Despite the lack of flowers throughout the area, hummingbirds were more abundant on the hillside than along the river.

Flycatching or insect gleaning from foliage or spider webs was the common foraging method among the individuals I watched. There were no areas of concentration of hummingbirds and little evidence of territorial defense at a food source. A few *Bombacopsis* trees were defended during the early morning hours by individuals of *Amazilia rutila.* Even with little spatially organized aggression, there were numerous intra- and interspecific chases throughout the area.

February. By late February and early March most of the hillside trees and shrubs were completely bare of leaves; the major exceptions were the few species and individuals which retained their leaves throughout the dry season. The most abundant and obvious of the tree species in bloom was the yellow-flowered *Tabebuia chrysantha.* I estimated that 50–75 per cent of the individuals visible from the census road were in some stage of flowering at this time. The number of open flowers per tree ranged from fewer than 100 to more than 3000. In general, the *Tabebuia* with the largest number of fresh flowers were most actively visited by the birds (table 6) and were the activity centers for the greatest number of insects. A few *Bombacopsis* were still flowering. *Samanea,* a legume which retained its leaves throughout the dry season and which probably is pollinated by bees (Janzen 1967), was coming into bloom and remained in bloom at least through June. Some *Genipa* trees had a few blooms and were being visited by several species of hummingbirds. There were also a few *Combretum* still in bloom, but there was no evidence that they were being visited by hummingbirds.

Hummingbird foraging activity was concentrated on the dry hillside around the flowering *Tabebuia chrysantha* (table 7); all

TABLE 5. Size characteristics of the nine hummingbird species recorded on the study area; appendage measurements from Ridgway (1911).

Species	Sex	Measurements (mm) Wing	Tail	Bill	(n)	Weight (g)	(n)	% *P. cuvierii*[a] Wing	Tail	Bill	♂ as % of ♀ Wing	Tail	Bill
Amazilia saucerottei	M	55.0	30.9	19.1	10	5.1	4	74.9	69.9	85.6	104.4	103.0	99.0
	F	52.7	30.0	19.3	10	4.7	5	76.7	68.2	82.5			
Amazilia rutila	M	55.9	34.6	21.8	10	5.1	9	76.2	78.2	97.8	105.5	101.8	94.8
	F	53.0	34.0	23.0	11	4.8	3	77.1	77.3	98.3			
Phaeochroa cuvierii	M	73.4	44.2	22.3	10	10.2	2	100.0	100.0	100.0	106.8	100.4	95.3
	F	68.7	44.0	23.4	10	8.5	1	100.0	100.0	100.0			
Amazilia tzacatl	M	57.4	34.3	22.2	4	5.3	28[b]	78.2	77.6	99.6	103.8	103.0	97.8
	F	55.3	33.3	22.7	3	4.7	24[b]	80.5	75.7	97.0			
Heliomaster constantii	M	68.0	34.4	35.2	10	8.0	1	92.6	77.8	157.8	103.5	105.5	99.2
	F	65.7	32.6	35.5	10			95.6	74.1	151.7			
Archilochus colubris	M	38.5	27.0	15.9	10	3.40	3[b]	52.4	61.1	71.3	87.5	105.5	87.4
	F	44.5	25.6	18.2	10	3.36	3[b]	64.8	58.2	77.8			
Anthracothorax prevostii	M	65.9	35.3	24.4	9			89.8	79.9	109.4	101.1	99.7	96.1
	F	65.2	35.4	25.4	10			94.9	80.4	108.5			
Chlorostilbon canivetii	M	46.0	31.5	14.4	10	3.1	3[b]	62.7	71.3	64.6	101.1	118.4	95.4
	F	45.5	26.6	15.1	10	3.2	13[b]	66.2	60.4	64.5			
Phaethornis longuemareus	M	37.6	33.3	21.7	10	2.5	7[b]	51.2	75.3	97.3	97.9	95.4	99.1
	F	38.4	34.9	21.9	10	2.7	4[b]	55.9	79.3	93.6			

[a] Same sex.
[b] Data from Hartman (1961).

six species seen in the area during this visit were recorded in the *Tabebuia*. *Amazilia saucerottei*, *Archilochus colubris*, and *Anthracothorax prevostii* were recorded almost entirely from *Tabebuia*. *Amazilia rutila* was found at *Tabebuia* and *Bombacopsis*. *Heliomaster* and *Chlorostilbon* were recorded too infrequently to characterize the focal point of their activities.

After several extended periods of observations at *Tabebuia*, it was obvious that the hummingbirds were foraging much more by catching insects than by probing flowers. Estimates for *Archilochus*, *Anthracothorax*, and *Amazilia saucerottei* were 70 per cent or more of foraging time spent flycatching, 30 per cent or less probing flowers. Even when probing flowers they may have been taking insects. During hour-long observations at *Tabebuia* I found no evidence that any of the birds were defending territories in the tree or remaining in the tree for more than 5–10 min. Numbers of species and individuals fluctuated rather widely, even during 10-min observations. When more than one bird occurred simultaneously in a tree, there were few chases except when two birds met while foraging. Although foraging areas could change with little interaction, the individuals normally foraged in separate sections of the tree. Several *Amazilia saucerottei* repeatedly chased one or more *Archilochus* from *Tabebuia chrysantha* trees which were just coming

TABLE 6. Relation between flower abundance and number of hummingbirds visiting *Tabebuia chrysantha* on 1 and 2 March 1967 at Granja Jiménez, Costa Rica.

No. birds in tree	No. flowers on *Tabebuia chrysantha* 1–50	51–100	101–250	251–500	501–1000	>1000
0	11	6	1	1	1	1
1	1	4		2	1	
2				2	1	
3					1	1
4						1

TABLE 7. Summary of foraging sites of hummingbird species recorded on censuses at Granja Jiménez on 1 and 2 March 1967.

Bird species	Foraging site[a] Foliage	*Tabebuia*	Tree sp.	*Bombacopsis*	*Combretum*
Archilochus	1	9	1		
Amazilia saucerottei		6		2	
Amazilia rutila		3		3	1
Anthracothorax		2			
Chlorostilbon		1			
Totals	1	21	1	5	1

[a] Birds at foliage were flycatching; the others were at flowering plants collecting either nectar or insects.

into flower. However, it appeared that a tree was defended only a few minutes before the "resident" left. The larger area from which birds were chased, the entire tree, probably reflected the small number of open flowers in the tree.

March. During late March, near the end of the dry season, the hillside was very dry. The few hummingbirds observed were foraging mostly at a bignoniaceous vine with light purplish flowers. This plant was uncommon and there were few other flowers to attract hummingbirds to the hillside. Most of the hummingbirds were found along the river in the evergreen riparian vegetation. No birds were observed going to two *Tabebuia pentaphylla* near the bignoniaceous vine which had flowers similar in color, general shape, and size to those of the vine.

Only four species of hummingbirds were observed during the censuses but six species were recorded during observations at the bignoniaceous vine. Although *Archilochus* foraged at the vine it did not normally probe into the corolla tubes, but caught insects flying near the flowers. *Amazilia rutila* had the shortest bill of the species which regularly probed into the flowers. As at *Tabebuia* in February, the birds were using the vine as a localized feeding area which they visited at intervals for short term foraging. No individuals were holding territories in the flowering vine, but there were some chases of new arrivals by birds that were already foraging; these chases usually involved the two frequent visitors, *Archilochus* and *Amazilia rutila.* I am uncertain of the total area from which the birds came to forage at the vine.

April. As we arrived at Finca Taboga on 18 April there was a short but hard localized rainstorm. According to Ministerio personnel the first rain of the season fell on 16 April. Throughout the April visit it was generally overcast and cooler than on previous occasions. The number of tree species in bloom was greater than at the end of March, but few of these species were being visited by hummingbirds. This was especially true of *Guazuma* and *Bursera,* which were in full bloom yet had no birds regularly foraging in them. Both species probably are pollinated by bees (Janzen 1967). *Muntingia, Samanea,* and the bignoniaceous vine were blooming and hummingbirds were foraging at each. *Chlorostilbon,* the commonest hummingbird on the hillside, foraged primarily at the *Muntingia* which were common along a short length of the census route. A few *Amazilia saucerottei* and *A. rutila* foraged at the bignoniaceous vine; *A. saucerottei* also was recorded occasionally in *Samanea.*

Most of the hummingbirds were concentrated on the floodplain of the river around flowering *Inga vera* trees. Beyond the sphere of direct influence of these scattered trees there were few hummingbirds, even along the river. Only *A. saucerottei* was resident in the *Inga,* although A. *rutila, Anthracothorax prevostii* and *H. constantii* occasionally visited the trees to forage. Individuals of *Amazilia saucerottei* seemed to hold definite territories in the trees, which were defended intraspecifically and, to a limited extent, interspecifically. In one *Inga vera* tree containing approximately 15,000 ft^3 of space occupied by foliage, there were seven resident territorial *A. saucerottei. Anthracothorax* was able to feed freely in the trees. It usually was attacked by the resident, but the attack either was rebuffed or ignored.

May. When we arrived at Granja Jiménez on 16 May there had been no recent rain, but the sky was overcast and the temperature did not go as high each day as during the dry season. It remained cloudy most of the time we were at Taboga and there were a few light sprinkles of rain. The advent of leafing out of most of the trees was correlated with the April rains. At the same time the ground vegetation began to look more verdant. The few common plants in bloom during this visit were *Guazuma, Muntingia, Genipa, Bromelia,* and *Helicteres.* Of these, all except *Guazuma* were visited by hummingbirds. *Genipa,* which was just beginning to bloom, had not flowered since February when a few flowers were produced. *Helicteres,* a shrub, never occurred in large clumps or produced many flowers at one time and was used only sporadically. *Muntingia* was still a focal point for activity for *Chlorostilbon.*

Most of the birds observed during this visit were on the hillside. A few *Amazilia tzacatl* and *Phaethornis longuemareus,* both evergreen forest species, had moved onto the hillside. This was the only time that *A. tzacatl* was recorded away from the evergreen forest, while *Phaethornis* also was noted part way up the hill in June. The major foci of feeding activity by all the species were the large clumps of *Bromelia pinguin* which were blooming during the observation period (fig. 6). The flowering period of this species is very restricted at this site; two weeks after my observations the plants had completely finished blooming, the attendant hummingbirds had left the area, and they were feeding at other plant species (D. R. Paulson, pers.

FIGURE 6. Large clump of flowering *Bromelia pinguin* at which extended observations were made, May 1967.

comm.). Only *Chlorostilbon* was observed to flycatch actively.

All six hummingbird species recorded during the May censuses also were found feeding or attempting to feed at the *Bromelia*. At least five *Amazilia rutila*, all males, were resident in one bromeliad patch I watched intensively. Two or three *Phaeochroa*, including at least one female (collected), and one *A. tzacatl* also held territories in the same bromeliad patch. Although *Heliomaster* and *Chlorostilbon* foraged at the bromeliads neither species held territories. In several instances an *A. saucerottei* held a territory where earlier in the day an *A. rutila* had been in control. It seemed that some, although not all, of the *A. rutila* individuals occasionally left their territories for short periods, usually less than one hour. During this time an *A. saucerottei* would be able to utilize the area unless it was preempted by another *A. rutila*. However, at no time was an *A. saucerottei* able to retain a territory in the face of persistent pressure by an *A. rutila*, nor was an *A. saucerottei* able to force an *A. rutila* to relinquish a territory.

P. cuvierii was the dominant species at the bromeliad patches; *A. tzacatl* was next in the hierarchy (table 8). Both were present in limited numbers, enabling *A. rutila* to control areas not utilized by the other two. At the same time the territorial *A. rutila* were able to defend areas against the remaining species and remained in control of most of the areas throughout the observations. Two *P. cuvierii* used the same feeding areas as two of the resident *A. rutila*. In one of these territories I could follow most of the activity. The *P. cuvierii* normally perched near the *A. rutila;* whenever the *P. cuvierii* went to feed, it either flew at the resident *A. rutila*, or ignored the aggressive actions of the resident. In either situation the *P. cuvierii* was able to use the food resources in the territory with little

TABLE 8. Aggressive encounters among hummingbird species[a] at flowering *Bromelia pinguin* on 17, 18, 19 May 1967.

	Loser							
Winner	*A.s.*	*A.r.*	*P.c.*	*C.c.*	*A.t.*	*H.c.*	Total	Interspecific
A.s.	0	1	0	1	0	0	2	2
A.r.	70	54	0	0	0	1	125	71
P.c.	12	27	2	2	0	0	43	41
C.c.	1?	0	0	0	0	0	1?	1?
A.t.	2	0	0	0	0	0	2	2
H.c.	0	0	0	0	0	0	0	0

[a] Species abbreviated as in table 3.

effort expended in defense. The area was defended by the resident *A. rutila* at essentially no energetic cost to the *P. cuvierii*. This system would work effectively only when the resource being used and defended was renewed fast enough that the food required by one species would make little impact on the total amount of food available to the other.

June. Throughout the June visit it was generally cloudy; there were several periods of light rain but no heavy rain. There were few species of trees and shrubs blooming commonly in the study area; particularly abundant were *Genipa* and *Muntingia*. Most hummingbird feeding activity was centered around the yellow-flowered *Genipa* trees. A few trees which bloom in mid- to late July were not in bloom at this time. Details of the utilization of *Genipa* by the hummingbirds are reported by Stiles and Wolf (in press) and so will not be repeated here. Suffice it to say that individuals of *A. rutila*, *A. saucerottei*, and *P. cuvierii* maintained essentially continuous territorial holdings in a single *Genipa* which was watched intensively for parts of three days. The highest number of resident birds recorded was 19. There was a rapid increase in the number of territorial individuals in the early morning, but the number declined gradually through the late afternoon until no territorial residents were present 30–60 min before sunset. *P. cuvierii* was dominant over *A. rutila*, which was dominant over *A. saucerottei*. However, the total number of territorial *A. saucerottei* exceeded that of the other two species. That some female *A. saucerottei* and *A. rutila* were holding territories in the tree was established fairly conclusively. Both territorial *P. cuvierii* were males.

July. Only a 2-hr observation period was possible in July. From 08:00 to 09:00 I made a census covering about 0.7 km. Just prior to this, I visited another portion of the hillside behind the experimental farm, where there was a patch of flowering *Manihot* and where as many as 10 *A. saucerottei* were defending small areas. I saw no other species resident at *Manihot*. A single *H. constantii* which came to feed at the *Manihot* was chased from the area almost immediately by the resident *A. saucerottei*. Two *Chlorostilbon* and other *A. saucerottei* were persistently chased from a single *Manihot* (D. R. Paulson, pers. comm.).

Most of the dry hillside behind the houses was now verdant. All, or most, of the trees had leaves and the forest presented a much more closed appearance than it had in the dry season. In this part of the woods I found no hummingbirds while I walked slowly along a path from 07:00 to 08:00. I found several small flowering shrubs and herbs (*Helicteres* and others), but no flowering trees. The herbs and shrubs were sufficiently scattered and produced such a small number of flowers that they provided only a scanty food source.

NUMBERS OF HUMMINGBIRDS USING THE AREA

As can be seen from table 2, the lowest relative numbers of birds were recorded on the March censuses; the other months were more nearly equal. The number of species remained fairly constant, but there was some turnover in actual species present. Variation in total individuals was due to fluctuations of numbers within species. Much of this variation in numbers of individuals reflects changes in numbers of the two most common species, *Amazilia rutila* and *A. saucerottei*. There seemed to be no clear-cut relation between the number of plant species in bloom which were visited by hummingbirds and the number of hummingbird species; this did not hold for individuals within species. The numbers of *A. rutila* were consistently low throughout the study until May and June, when they increased enormously. This rise paralleled the advent of flowering of *Bromelia* and *Genipa*. The increased numbers in April are almost entirely accounted for by the concentrations of *A. saucerottei* around a few flowering *Inga vera* trees along the river and an increase in abundance of *Chlorostilbon* around the flowering *Muntingia* on the study hillside.

The population of hummingbirds on the hillside was large only at the beginning of the dry and rainy seasons. There was a general decline in numbers from January to March. This seemed to be correlated with generally severe climatic conditions from the middle to the end of the dry season. By the middle of April the climate had ameliorated slightly following some light rains. Thus, the harshest dry season conditions were probably encountered during March and early April.

The decline during the dry season occurred despite the fact that several tree species visited by hummingbirds were in bloom throughout all or most of the period (table 1). However, these continuously flowering plants were species around which one rarely found territorial birds, and never concentrations of hummingbirds. The plants seemed to be used only infrequently as food sources. *Samanea* did not produce concentrations of flowers at one time, and birds generally were

TABLE 9. Summary of the aggressive encounters between hummingbirds[a] observed on the study area from January–June 1967.

Winner	Loser								Total	% Inter-specific	Dominance level[b]
	P.c.	*A.p.*	*A.t.*	*A.r.*	*A.s.*	*H.c.*	*A.c.*	*C.c.*			
P.c.	3	0	0	44	46	0	0	2	95	96.8	1
A.p.	0	0	0	1	1	0	0	0	2	100.0	1
A.t.	0	0	0	1	2	0	0	0	3	100.0	1
A.r.	3	0	0	156	320	3	5	5	492	68.3	2
A.s.	0	0	0	55	491	0	14	4	564	12.9	3
H.c.	0	0	0	0	0	0	0	0	0	0.0	?
A.c.	0	0	0	0	0	0	7	4	11	36.4	4
C.c.	0	0	0	0	0	0	0	2	2	0.0	5
Total	6	0	0	257	860	3	26	17	1169		
% Inter-specific lost	3.2	0	0	23.2	83.5	100.0	82.6	100.0			

[a] Species abbreviated as in table 3.
[b] Range: 1 = top or dominant species, 5 = most subordinate species. Since insufficient data are available to differentiate among several of the species, three species are placed at the top level.

not present in trees with only a few flowers. The peak of hummingbird activity, mostly *Amazilia saucerottei,* at these trees was during April, suggesting that when most of the other plants on the hillside were not flowering, the birds turned to these secondary food items.

The numerical increase in May and June was almost entirely due to the attraction of large numbers to *Bromelia* and *Genipa.*

I did not find increased numbers of hummingbirds in the more mesic riparian vegetation to correspond with the dry season decline on the hillside. G. Orians and D. Paulson (pers. comm.) did not notice any marked increase in another mesic forest area about 5 km away and also surrounded by dry forest. It is not known where the birds go when they desert the dry hillside.

Thus, although this may be the peak of flowering for many of the tree species in the Granja Jiménez area, the hummingbirds generally shun the most extreme environmental conditions unless there is a very abundant food source, such as at *Tabebuia* in February. Most of the tree species which are highly attractive to hummingbirds and which produce large numbers of flowers at one time bloom primarily at the end of the rainy season as the trees are beginning to lose their leaves or at the start of the rainy season. Only in areas with supplementary sources of moisture, such as along the rivers, do the tree species highly attractive to hummingbirds bloom late in the dry season.

RELATION OF NORTH AMERICAN MIGRANT TO OTHER SPECIES

Archilochus colubris was the only migrant hummingbird from the North Temperate Zone in the area. It was fairly common from January through March. It was probably in the area from September or October until about the end of March, the months during which Slud (1964) reported that it occurred in Costa Rica. Its numbers were exceeded only by those of *Amazilia saucerottei* during January and February.

The generally subordinate position of the ruby-throat is documented by the results of interspecific chases given in table 9. Although Willis (1966) reported that other species of North American migrants in the tropics also tended to be dominated by the resident species, the ruby-throat fit nicely into the dominance hierarchy of species which seemed to be based almost entirely on size (table 10). The ruby-throat was able to dominate the slightly smaller (in body weight) *Chlorostilbon,* which was a resident member of the hummingbird community. The dominance of *Archilochus* over *Chlorostilbon* might help explain the apparent increase in abundance of the latter after the ruby-throat migrated north in the spring.

In general the ruby-throat tended to utilize

TABLE 10. Relation of dominance to size in eight hummingbird species at Granja Jiménez.

Species	Size rank of male[a]	Dominance level[b]
Phaeochroa cuvierii	1	1
Heliomaster constantii	2	?
Anthracothorax prevostii	3	1
Amazilia tzacatl	4	1
Amazilia rutila	5	2
Amazilia saucerottei	6	3
Chlorostilbon canivetii	7[c]	5
Archilochus colubris	8	4

[a] Based on wing length.
[b] Data taken from table 9.
[c] *C. canivetii* weighs less than *A. colubris* even though wing length relationship is reversed.

either a portion of the food resources which was not heavily used by the resident species, or was able to fit into a complex of species using a localized, but very abundant, food source. Sometimes it was able to feed in areas of residency of larger species. The utilization of several species of plants that were not visited by other hummingbird species is shown in table 3. A purple herb seemed to be commonly used as a food source by the ruby-throat. The extent to which it fed on insects rather than nectar was impossible to document. In most of the feeding time which these birds spent around *Tabebuia* they engaged in active pursuit behavior which appeared to be flycatching. At other times they seemed to be probing for nectar; subsequent inspection of other flowers on the same plants revealed no accumulations of insects in the flower corollas. I suspect that these birds normally feed on the insects attracted to the main flowering species, but they can and do use nectar at times.

Slud (1964) remarked that the occurrence of the ruby-throat in this dry forest habitat would surprise people familiar with the species in the North Temperate Zone, where it is found in much more mesic habitats. The large population of ruby-throats in the study area probably was related to factors influencing the availability of food. In dry forests there is a definite peak of flowering activity among the native plant species during the dry season (Janzen 1967). In the wet tropics, flowering seasons probably are less synchronized so that a peak in food supply is not of the magnitude found in dry forest areas. If these assumptions are correct, the ruby-throat is using a portion of the tropics in which there is the greatest chance that food will be available in sufficient quantities that it can not be utilized completely by the resident species. Thus, if *Archilochus* is physiologically able to inhabit the area, the dry forest might provide the best foraging conditions for it. Lack (1965) and Moreau (1966) suggested similar reasons for the primarily open country distribution of Palearctic migrants in Africa during the winter.

DISCUSSION

During the first three months the birds seemed to be taking mostly insects. There were few trees in abundant bloom, and of these only *Tabebuia* was visited regularly by hummingbirds in any numbers. Only short periods of territoriality were seen during this time. In the early morning during January, individuals of *Amazilia rutila* defended *Bombacopsis* trees which retained a few flowers from the previous night. Around *Tabebuia crysantha* in February there were individuals which focused much of their activity on a specialized food source. However, even in trees with several thousand flowers no birds were observed holding territories, although some did maintain individual distance perimeters while feeding. There were clear dominance hierarchies among the species present at a *Tabebuia*, but apparently no continuously defended areas. In a few *Tabebuia* just starting to bloom, a single *Amazilia saucerottei* chased away conspecifics and *Archilochus* for short periods, but there was no evidence of continual occupancy for long portions of a day. These observations suggest that food supplies were not stable enough in time and/or space to provide sufficient advantages for establishing and defending territories. Both *Bombacopsis* and *Tabebuia* lost their flowers in a relatively short time.

From April to July non-reproductive territories centered around abundant food supplies were common. In each case the territories were in a single plant species which differed from month to month. In April and July *Amazilia saucerottei* were the only territorial individuals observed, although several other species used the sources in very low numbers. In May and June *Phaeochroa* and *A. rutila* were the predominant territorial species. *A. saucerottei* established territories in plants in which the behaviorally dominant *A. rutila* did not control all potential feeding areas.

Although there is a general peak of flowering during the dry season in this area, the peak for each major species visited by the birds tended to be temporally distinct from similar peaks of other species. This pattern of temporally and spatially shifting food sources has led to the establishment of shifting territorial patterns among the hummingbirds. Generally the territories are small, probably related to the defendability of the source in terms of numbers of individuals attempting to use the source (Brown 1964). The small size of the territories and the continual shifting of territorial locations has led to the evolution of behavioral means of defense which are less expensive energetically than the spectacular aerial displays found among north temperate species. Calling was probably the least expensive active mode of defense. The reliance on vocal displays and finally on motion-oriented chases has reduced the selection pressure for brightly colored plumages among these hummingbirds; *Amazilia rutila* and *Phaeochroa cuvierii* are rel-

atively dull-colored. Probably the subordinate position of *A. saucerottei* in relation to the other two species has forced it to retain as many aggressive signals as possible for territorial defense. This might explain the bright plumage coloration of this species.

The lack of sexual dimorphism in plumage coloration probably is a result of selection in the two sexes for similar aggressive signals when both sexes hold territories (Wolf 1969). Females as well as males of *A. saucerottei, A. rutila,* and *P. cuvierii,* among the species in this study, have been found to hold territories.

During the early part of the dry season the birds apparently take mostly insects. From April to July they probably take large amounts of nectar in addition to insects, but the hummingbird species are not thought to be important as pollinators even for these nectar-producing plants (Janzen, pers. comm.). In each case there is strong evidence that insects are the important pollinators. Thus, it appears that the birds have not been important selective agents in determining the timing of reproductive activity among these plant species. Rather they seem to have secondarily entered a coevolving system of plants and their insect pollinators, i.e., the behavioral and morphological adaptations evident in these bird species are being forced on them as adaptations to prevailing ecological conditions. This contrasts strongly with the presumed importance of birds in producing the temporal pattern of fruiting of *Miconia* on the island of Trinidad (Snow 1966). Judging from the increased importance of vertebrates as dispersal agents for plants in the Cañas area (Janzen 1967), it is not unlikely that the situation is similar to that in Trinidad. However, the hummingbirds are probably not important members of this coevolving system.

The similarity of the territorial systems of the Granja Jiménez hummingbirds and those reported for some north temperate species on migration (Pitelka 1942; Armitage 1955) probably results from a similar relation in the two groups of species of the spatial and temporal patterns of food availability and the time and energy available for defense of territories. In both cases there is limited time for defense. In north temperate species this results from the short-term residency of an area by migrating individuals. Many of these reports of territorial migrants are of birds clustered around a concentrated food source. This tends to increase the number of potential and actual encounters involved in territorial defense, and increases the time and energy required to defend a food supply large enough to satisfy the energy requirements of the territory holder. It is not surprising to find similar territorial systems in the north temperate and tropical areas where the temporal and spatial pattern of availability and utilization of food is so similar.

SUMMARY

The feeding and territorial activities of nine species of hummingbirds were studied in the dry lowlands of Costa Rica, near Cañas, Guanacaste Province, during the period of January-July 1967. Monthly censuses and intensive observations were made in areas where birds were concentrated. There was a peak of flowering during the dry season and the start of the rainy season. Each burst of flowering activity by a plant species regularly visited by hummingbirds tended to be temporally distinct from other species. From January to March it appeared that most of the birds were relying on insects for food. There was little territoriality and a gradual decline in numbers of birds on the dry forest hillside as the dry season progressed. From April to July several of the numerically and/or behaviorally dominant species maintained a shifting pattern of short-term territoriality around flowering individuals of a different plant species each month.

The impact of this type of territorial system on the behavior and morphology of the birds is considered. It is concluded that these tropical hummingbirds entered the ecological system secondarily and that they were being forced into their territorial adaptations by the prevailing ecological conditions, rather than being part of a coevolving complex. Comparisons are drawn with the short-term territories which have been reported for North American hummingbirds on migration.

ACKNOWLEDGMENTS

Financial support for this study came from an Elsie Binger Naumberg fellowship from the American Museum of Natural History. Logistic and administrative support in Costa Rica were provided by the Organization for Tropical Studies. G. H. Orians and D. R. Paulson kindly shared with me their transportation to the study area and provided me with their data on hummingbirds recorded in the areas of Granja Experimental Jiménez and Puntarenas, Costa Rica. The kind hospitality of the Granja Jiménez personnel, especially the two resident managers, Ing. Mauro Molina U. and Henry R. Giralt, is especially appreciated. Many of the plants were identified for me by Ing. Alfonso Jimenez of the Museo Nacional de Costa Rica. M. Mathias and D. Janzen were very patient in teaching me some of the flora of Costa Rica. My wife, Janet, aided in the field work. D. H. Janzen, G. H. Orians, D. R. Paulson, R. B. Root, and F. G. Stiles kindly read the manuscript.

LITERATURE CITED

ARMITAGE, K. B. 1955. Territorial behavior in fall migrant Rufous Hummingbirds. Condor 57: 239–240.

BROWN, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76:160–169.

HARTMAN, F. A. 1961. Locomotor mechanisms of birds. Smithsonian Misc. Coll. 143:1–91.

JANZEN, D. H. 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. Evolution 21:620–637.

LACK, D. 1965. Evolutionary ecology. J. Anim. Ecol. 34:223–231.

LASIEWSKI, R. C., AND R. J. LASIEWSKI. 1967. Physiological responses of the Blue-throated and Rivoli's Hummingbirds. Auk 84:34–48.

LEOPOLD, A. S. 1950. Vegetation zones of Mexico. Ecology 31:507–518.

MOREAU, R. E. 1966. The bird fauna of Africa and its islands. Academic Press, New York. 424 p.

PITELKA, F. A. 1942. Territoriality and related problems in North American hummingbirds. Condor 44:189–204.

PITELKA, F. A. 1959. Numbers, breeding schedule, and territoriality in Pectoral Sandpipers of northern Alaska. Condor 61:233–264.

RIDGEWAY, R. 1911. The birds of North and Middle America. U. S. Natl. Mus., Bull. 50, Pt. V. 859 p.

SKUTCH, A. F. 1951. Life history of Longuemare's Hermit hummingbird. Ibis 93:180–195.

SKUTCH, A. F. 1964. Life history of the Scaly-breasted Hummingbird. Condor 66:186–198.

SLUD, P. 1964. The birds of Costa Rica. Bull. Amer. Mus. Nat. Hist. 128:1–430.

SNOW, D. 1966. A possible selective factor in the evolution of fruiting seasons in tropical forest. Oikos 15:274–281.

STILES, F. G., AND L. L. WOLF. In Press. Hummingbird territoriality at a tropical flowering tree. Auk.

TOSI, J. 1965. Life zone map of Costa Rica. Trop. Sci. Center, San José, Costa Rica.

WETMORE, A. 1944. A collection of birds from northern Guanacaste Costa Rica. Proc. U. S. Natl. Mus. 95:25–80.

WILLIS, E. O. 1966. The role of migrant birds at swarms of army ants. Living Bird 5:187–231.

WILLIS, E. O. 1967. The behavior of bicolored antbirds. Univ. Calif. Publ. Zool. 79:1–127.

WOLF, L. L. 1969. Female territoriality in a tropical hummingbird. Auk 86:490–504.

Accepted for publication 15 July 1968.