

A MONTANE HUMMINGBIRD TERRITORIAL SYSTEM IN OAXACA, MEXICO

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Where common resources are exploited by 2 or more related species the concept of resource partitioning suggests that those conspecifics which compete least intensely with individuals of other species will be favored, thus the tendency is for initially competing species to diverge functionally in environmental use (MacArthur 1958). Many investigators, especially Lack (1954, 1966) and Mayr (1963), have regarded food as the critical resource and thus the one most likely to engender these changes; under certain conditions the protection of this potentially scarce resource is given selective advantage because the ratio of energy saved to energy expended is increased by excluding conspecifics (Brown 1964), and occasionally, seemingly contrary to the MacArthur prediction, other species as well (Orians and Willson 1964).

Wolf (1960) and Stiles and Wolf (1970) have reported on intraspecific and interspecific interactions in some Central American hummingbirds. Among the concepts advanced are: (1) distribution of the nectar resource in space and time will affect the outcome of territorial encounters, (2) length of the blooming season, and richness and degree of localization of nectar relative to alternative nectar sources will affect the formation, longevity, and rigidity of the territorial system, and (3) territoriality, both intra- and interspecific, is useful when alternative food sources are limited or widely scattered, but energy expensive when intra- and interspecific competitors are abundant. The purpose of this paper is to relate the above concepts of interspecific territoriality, system rigidity and longevity, and nectar distribution and partitioning to a montane hummingbird territorial system in the state of Oaxaca, Mexico.

STUDY AREA AND METHODS

The study was carried out during the summers (early June to early September) of 1967, 1968, and 1969 on Cerro San Felipe at 2500-3000 m in pine forest in the Sierra de Oaxaca north of the city of Oaxaca, Mexico. The area is classified as Montane Wet Forest according to the Holdridge (1947) scheme. This zone is characterized by summer wet and winter dry seasons, but the distinction between them is less well marked than at lower elevations. During the summer heavy thundershowers occur almost daily and lighter all-day rains are frequent. Temperatures range from 13-24°C during the day to 1-13°C at night. Near the summit (2800-2900 m) are well defined small meadows, most less than 2 ha, some slightly enlarged by lumbering and supporting dense stands of flowering plants during the summer and fall. Large numbers of hummingbirds were

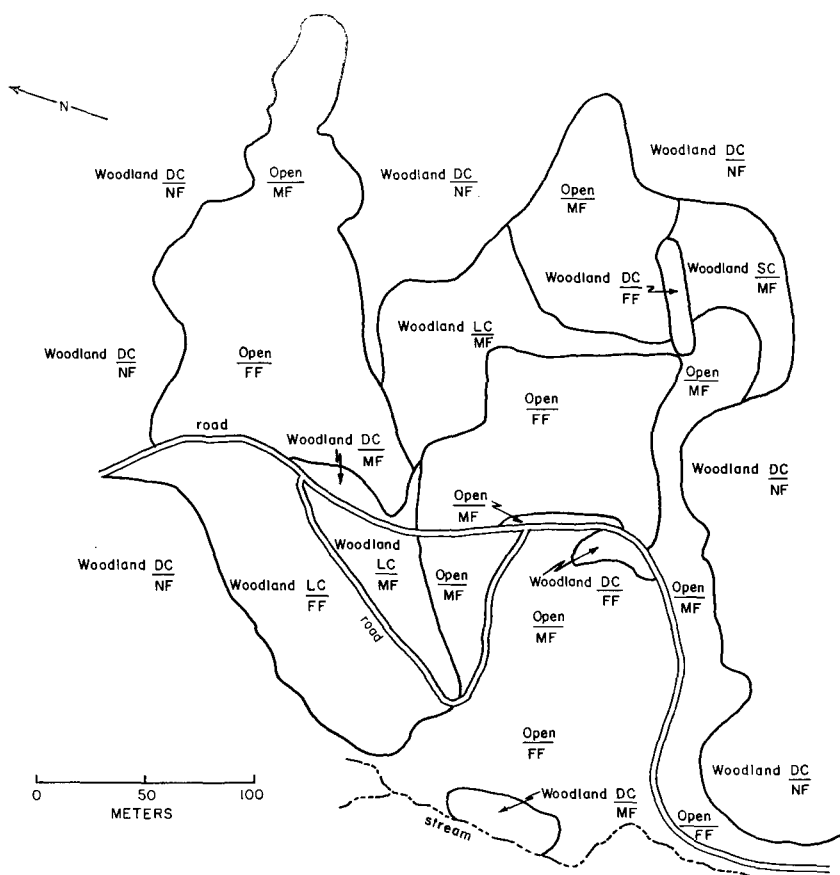


FIG. 1. Map of main meadow of study area indicating general vegetation pattern and flower abundance. LC = light canopy; DC = dense canopy. MF = many flowers; FF = few flowers; NF = no flowers.

attracted by the rich floral food source and it was in these meadows that most observations were made (Fig. 1).

In most meadows, trees were absent or widely scattered, but others resembled open parkland dominated by 20–25 m pines (*Pinus montezumae*, *P. pseudostrobus*, and *P. rudis*) and with a sparse understory of alder (*Alnus* sp.), oak (*Quercus* spp.) and madrone (*Arbutus* spp.). Small streams were present in some meadows, and willows (*Salix* sp.) and elderberry (*Sambucus* sp.) occurred along them locally. Border between meadow and dense forest was usually abrupt. Hummingbirds of all species were occasionally encountered within forest, but with the exception of White-ears (*Hylocharis leucotis*) most species were primarily restricted to meadows or meadow-forest ecotone.

Birds were captured for marking in 10 m, 4-shelf, nylon mist nets. In 1967 4 nets and

in 1968 and 1969 8 nets were in continual operation. Nets were placed around meadow edges where territorial chases were especially frequent. Locations were usually changed twice weekly. Various colors of "Pla" enamel chosen for high visibility were used to mark individual birds. Unmarked individuals were identified by distinctive physical or behavioral features, but near the end of the study period in all years most territorial birds were marked. Territory boundaries were determined by noting consistency of perch occupancy, and the frequency and location of chases and displays. Area of territories was determined by planimeter measurement from hand-drawn scale maps. During periods of observation of feeding activity various measurements of movement, location, and positioning of birds at plants and blossoms were obtained with a stopwatch and recorded on a tape recorder.

RESULTS AND DISCUSSION

Hummingbirds in the territorial system.—Six species of hummingbirds were important in the territorial system on Cerro San Felipe: Blue-throated (*Lampornis clemenciae*), Amethyst-throated (*L. amethystinus*), Rivoli's (*Eugenes fulgens*), White-eared, Violet-eared (*Colibri thalassinus*), and Bumblebee (*Atthis heloisa*) (Table 1). White-ears were probably the only abundant year-round residents in the study area judged by the general scarcity in early June of other species prior to the flowering season, although Blue-throats and Bumblebees may have been resident in small numbers. With the exception of Bumblebees which were relatively abundant in early June but rare the rest of the summer, other species were first observed in the study area in late May to mid-June and increased steadily in number until populations stabilized in July–August. Blue-throats and White-ears were the most abundant species in meadow areas as determined by general observation and the number captured in mist nets over the 3-summer period (Table 1). All species were observed in about the same proportions each year with the exception of Rivoli's which was common in 1967 and 1968, but uncommon in 1969.

Nectar resource.—Meadows on Cerro San Felipe supported a profusion of flowering plants during June–September, a large proportion of which were hummingbird-pollinated plants. *Penstemon kunthii* (Scrophulariaceae) and *Rigidella orthantha* (Iridaceae) (Fig. 2) were the most abundant and the major sources of nectar for most hummingbirds. *Rigidella* occurred in dense but scattered stands throughout the meadows, often near streams, but sometimes on drier sites along the meadow edge or under open stands of pine. During the major blooming period, May through June, recruitment of blossoms was rapid and stands showed little variation in blossom number from day to day. After mid-June, stands were in blossom only infrequently for short periods and often out of phase with each other. *Penstemon* began to bloom sporadically in late May, reached peak blossoming in early August and maintained this level from August (Fig. 2) into October (Rowley, pers. comm.). It thus was the most stable and dependable nectar source during my study

TABLE 1
NUMBER AND WEIGHTS OF CAPTURED HUMMINGBIRDS, 1967-1969

Species	Males			Females		
	n	Recap- tures	Wt. (g) $\bar{x} \pm SD^*$	n	Recap- tures	Wt. (g) $\bar{x} \pm SD^*$
Bumblebee	2	0	2.7 \pm 0.0	0	—	—
Violet-eared	31	3	6.3 \pm 0.2	11	0	6.0 \pm 0.3
Rivoli	119	38	7.7 \pm 0.4	24	8	6.4 \pm 0.5
White-eared	158	34	3.6 \pm 0.3	51	9	3.2 \pm 0.2
Amethyst-throated	21	1	6.8 \pm 0.8	5	0	6.6 \pm 1.3
Blue-throated	190	43	8.4 \pm 0.4	62	12	6.8 \pm 0.4
Totals	521	119		153	29	

*Includes recaptures.

and the primary factor in conferring stability to the territorial system. Like *Rigidella*, *Penstemon* was largely restricted to open situations, but was less clumped and more widely distributed.

Eleven other species of flowering plants were used by hummingbirds (Fig. 2), but only cuphea (*Cuphea jorullensis*) was sufficiently abundant to encourage territoriality. This plant sometimes occurred in scattered small stands throughout the larger meadows, but was most abundant at meadow edges or in small openings within forest. Average blossom size was small (ca. 2 cm long) and also presumably was nectar production—only White-ears and Bumblebees used it frequently and Violet-ears occasionally. The 2 most abundant plants in the meadows, *Penstemon perfoliatus* and *P. gentianoides*, were typical bee-pollinated species. Blossoms were seldom used by hummingbirds, apparently because nectar production was low relative to hummingbird-visited species. The Bumblebee Hummingbird was the most frequent user followed by White-ears. Blue-throats, and Rivolis were never seen to use these species.

The peak of nesting on the study area apparently occurred in late summer and early fall. Rowley (pers. comm.), during extensive monthly nest searches throughout the state of Oaxaca, recorded fewer nests in July and August at all elevations than at any other time of year, but above 2500 m the largest number was recorded in September and October after the rainy season was well under way. On Cerro San Felipe this period coincided with maximum flower abundance.

General aspects of territoriality and behavior.—The territorial system was dominated by males, an observation made frequently for other hummingbirds

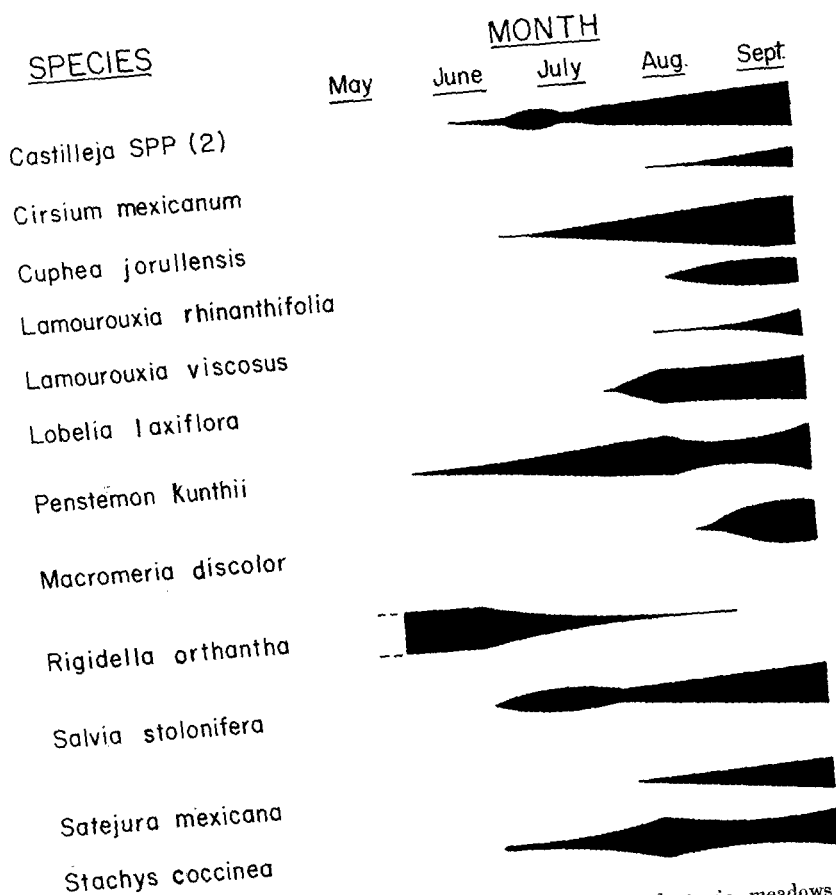


FIG. 2. Phenology of flowering of hummingbird-pollinated plants in meadows and adjacent areas of Cerro San Felipe, 2500-3000 m. Data on phenology determined from 25 10 × 20 m randomly selected plots in and contiguous to meadows supplemented by general observations from surrounding areas. Width of bars in figure proportional to density only within each species.

(Bent 1940, and others). A notable exception is the Fiery-throated Hummingbird (*Panterpe insignis*), a tropical montane species in Costa Rica and Panama in which female territoriality is well developed (Wolf 1969). I recorded female territoriality infrequently in Blue-throats, White-ears, and Rivolis, but in all cases territories were more temporary and usually smaller than those of males and the areas held frequently were deserted and reoccupied, usually by other female conspecifics. Except for Violet-ears and Amethyst-throats females were abundant in the meadows though never as numerous as males

(Table 1). Some seemed to be resident in the general area, but like non-territorial males, most were apparently transient and once netted and marked were not reobserved.

Dominance was directly proportional to body size. Territorial Blue-throats and Rivolis successfully invaded territories of other hummingbirds except conspecifics. Violet-ears and Amethyst-throats were dominant over White-ears and Bumblebees, and White-ears were dominant only over Bumblebees. Though Moore (1939) reported that in Sonora an individual White-ear was successful in repeatedly ejecting larger hummingbirds from its territory, including Blue-throats and Rivolis, I never observed this; White-ears were always subordinate to Blue-throats and Rivolis. In June, when *Penstemon* was beginning to bloom and the only important nectar source was *Rigidella*, all species except Bumblebees successfully invaded White-ear territories in *Rigidella*. Initially, territorial White-ears always attacked invaders regardless of size, but when the larger species persisted, White-ear aggression ceased and only conspecifics and Bumblebees continued to be harassed. Bumblebee Hummingbirds appeared to be neither inter- nor intraspecifically aggressive. Two or more individuals sometimes fed within a short distance of each other without aggression, but such occasions usually occurred within White-ear territories and this may have influenced behavior. I recorded no territories of Bumblebees during the 3 years of the study. Though Violet-ears and Amethyst-throats were intermediate in size and dominance, Violet-ears were much more persistent than Amethyst-throats in reentering territories of Blue-throats and Rivolis to feed. Amethyst-throats, when chased from a territory, seldom returned to attempt feeding immediately, but flew a short distance to a contiguous territory or unprotected area to forage. Some Violet-ears attempted to establish territories and were successful for short periods, but always eventually were displaced and the area incorporated in a new or already established Blue-throat or Rivoli territory. Unlike Violet-ears, Amethyst-throats did not attempt to establish territories. Both Amethyst-throats and Violet-ears, however, were dominant over White-ears and Bumblebees, invading the former's territories and frequently chasing both species from unprotected feeding areas.

The Blue-throated was the most successful territorial species in the meadow over the 3-year period judged by the number and size of territories maintained and the amount of *Penstemon* dominated (Table 2). This species gave both vocal and visual displays. While feeding in the territory it constantly gave a sharp "wheep" call at intervals of 2-3 sec and the tail flicked and spread outward at the same time exposing the white corner edgings of outer rectrices. Presumably these vocal and visual effects constituted an intimidation display. It was given most frequently by feeding territorial individuals, less often by

TABLE 2
TERRITORY SIZE BY SPECIES AND SEX, 1967-1969*

Species		Males	Females
Violet-eared	No. Territories	4	0
	Mean Size (m ²) ± SD	232.4 ± 229.6	—
Rivoli	No. Territories	16	5
	Mean Size (m ²) ± SD	722.6 ± 265.4	683.7 ± 158.8
White-eared	No. Territories	41	1
	Mean Size (m ²) ± SD	431.6 ± 88.5	70.8
Blue-throated	No. Territories	58	5
	Mean Size (m ²) ± SD	777.5 ± 442.2	444.8 ± 108.7

* For territories established after 1 June for White-ears, after 1 July for Violet-ears, and after 15 July for Rivolis, and Blue-throats. No territories of Bumblebees, Amethyst-throated, or female Violet-ears were recorded during the three years.

birds feeding in neutral areas with other hummingbirds, and seldom when feeding alone in these same areas (Table 3). This same call was also given by perched territorial birds, the frequency of the call usually increasing as a bird from an adjacent territory approached the territory boundary. All other territorial species demonstrated no obvious visual or vocal displays when their territories were invaded other than direct pursuit sometimes accompanied by rapid high-frequency "chittering," varying somewhat by species.

Territory stability varied by species due mainly to the persistence in blossoming of the flower resource controlled. Because *Penstemon* flowered from mid-June through August and Blue-throats and Rivolis controlled all large important stands, territories of these species tended to be held for as long as 12 weeks. Conversely, White-ear territories in *Rigidella* were much less stable, persisting for no more than 3-4 weeks. During early June when *Rigidella* was at peak blooming, territories appeared stable and were con-

TABLE 3
COMPARISON OF "TAIL-FLICKING" PER 200 TEN-SECOND OBSERVATION UNITS OF
MALE BLUE-THROATS IN 3 FORAGING SITUATIONS

Situation	Foraging alone within territories	Foraging with others in neutral areas	Foraging alone in neutral areas
Number "flicks"	176	83	19*
n	134	128	52

* $\chi^2 = 102.8$; $P < .005$.

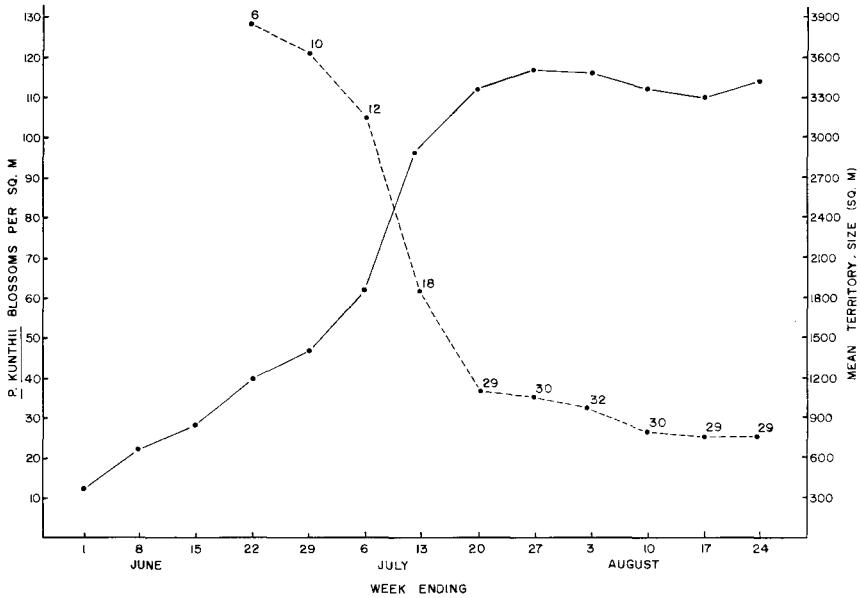


FIG. 3. Relation of territory size of Blue-throats to phenology of *Penstemon* blossoming, 1969. Solid line = blossom number; broken line = territory size. Numbers at points on broken line represent number of territories. Data on blossom density recorded from 25 2×2 m randomly selected plots in main meadow.

sistently held by the same individuals. In late June, however, the number of flowering plants decreased rapidly; blossoms might be abundant one day and almost absent the next, thus territories also fluctuated, disappearing and reforming with each major blooming pulse until blooming ceased in late July. Territory boundaries and control of areas by specific individuals changed daily as blooming resurgencies continued sporadically but at different locations within each *Rigidella* stand.

Violet-ears and Rivolis were present in the meadows only sporadically through June (Fig. 4) and thus missed the major blooming period of *Rigidella*. As blossom number declined only a few individuals made attempts to establish territories in *Rigidella*, but these were never defended for more than a day and the birds spent long periods away from the territory. Blue-throats, though present in relatively large numbers by mid-June, never established territories in *Rigidella*. Why this potential source of nectar was not used is not clear. Nectar quantity per blossom may have been low or extraction may have been more difficult for the larger species (Wolf et al. 1972). In addition, *Rigidella* seemed also to be best adapted to pollination by small,

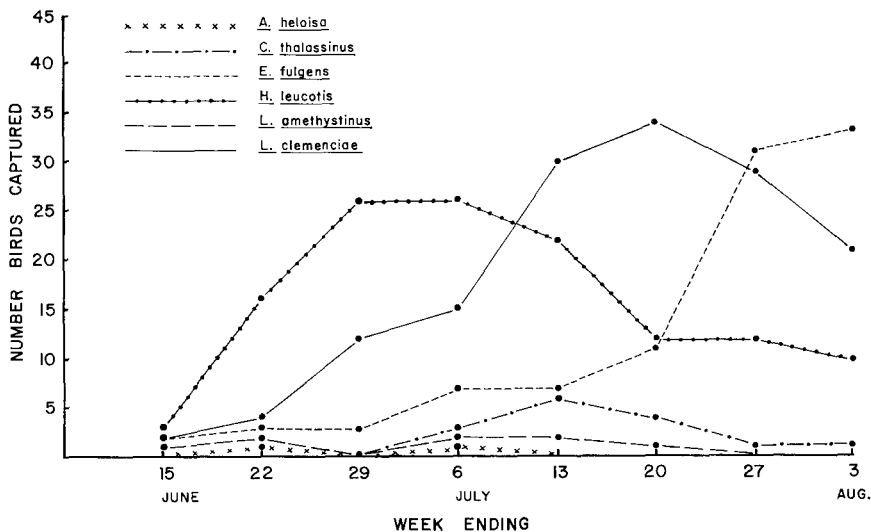


FIG. 4. Number of individuals of each species captured per week, 1968.

more mobile hummingbirds and the larger species had difficulty in maintaining feeding position while probing blossoms. These combined effects may have prevented Blue-throats and Rivolis from securing enough nectar to make more long-term territoriality energetically worthwhile.

Interspecific territoriality.—Territorial interaction in birds appears mainly to be restricted to conspecifics. It thus might be argued *a priori* that interspecific territoriality, if adaptive, should tend to be less well developed than intraspecific territoriality because competition for common resources among conspecifics would be more intense than between individuals of closely related species with similar ecological requirements. If interspecific territoriality was poorly developed, then in the present system in which the most important food source (nectar) is the focus of competition, birds of subdominant species should have an advantage over conspecifics of the larger dominant species because they could more easily invade territories of these species and satisfy a significant portion of their total nectar requirements from that source. For example, Violet-ears and White-ears could be less persistently expelled from Blue-throat and Rivoli territories than conspecifics and thus a degree of species coexistence could prevail despite the presence of a general interspecific aggressiveness on the part of all species.

I established criteria to attempt to differentiate among degrees of response to territorial invasion. The longer the invading bird was allowed to feed

before attacked, the more nectar that potentially could be consumed, and the less distant the chase, the less energy expended and the more quickly the invading bird could return to feeding. Judged by these criteria, territorial defense against conspecifics and others appeared equally well developed. No statistically significant differences in response of territorial individuals to invasion of territories were detected among species except for White-ears against conspecifics and Bumblebees (Table 4). White-ears seemed slightly more quick to respond to territory invasion by conspecifics, less quick in reacting to invasion by Bumblebees, and not so persistent in the chase. Thus except for the White-ear-Bumblebee interaction the nectar resource within territories appeared to be protected equally well against invading individuals of all species.

Despite domination of the large continuous stands of *Penstemon* by Blue-throats and Rivolis, numerous small stands of *Penstemon* existed in isolated and widely dispersed clumps throughout meadows and along forest-meadow edge. The largest of these were controlled by White-ears. Occasionally Violet-ears displaced White-ears, but did not return to the territory the following day. Blue-throats and Rivolis never attempted to control these stands. This suggests that nectar production was inadequate for the larger species, marginal for Violet-ears, but sufficient to encourage the establishment of territories by the smaller White-ear. The many remaining smaller, scattered, uncontrolled stands constituted undefended feeding areas in which hummingbirds of all species fed in close proximity with minimum conflict. These latter groupings of *Penstemon* appeared too widely scattered to permit effective defense, yet they provided an important source of nectar for nonterritorial birds.

Since many species of hummingbirds compete for the nectar resource, on the basis of MacArthur's (1958) prediction it would be expected that the most efficient use of flowers, especially the unprotected *Penstemon* stands, would occur through the evolution of species-specific feeding patterns and related behaviors. Potentially a minimum of 2 distinctive patterns of feeding seemed possible in the Oaxaca system and specialization in either could allow some measure of sharing of the food resource by various species of hummingbirds. In clumps of flowers some species could (1) feed on perimeter blossoms, others on interior blossoms, or (2) certain species could feed at upper levels of a stand, others at lower levels. The first of these possibilities seemed unlikely. Most individual plants were not sufficiently dense so that "interior" blossoms could be considered present. The second possibility was tested by recording the time in seconds each species spent feeding at upper, middle, low, and very low levels in *Penstemon* stands. Height classifications were visually estimated and relative between stands; some stands were taller than others and therefore intervals were somewhat larger than in shorter stands.

TABLE 4

COMPARISON OF INTRASPECIFIC AND INTERSPECIFIC TERRITORIALITY AS DETERMINED BY TIME LAPSE RESPONSES OF TERRITORIAL TO TRESPASSING BIRDS AND DISTANCE OF CHASE

Terri- torial Bird	Tres- passing Bird	Time Lapse Between Sighting & Chase (sec.)				Distance of Chase (m)				
		n	< 2	2-6	> 6	no chase	n	0-10	11-50	> 50
LC	→ LC	866	617	236	6	7	859	116	174	569
LC	→ EF	441	324	113	2	2	439	48	95	296
LC	→ LA	45	33	11	1	0	45	8	10	27
LC	→ CT	37	25	11	0	1	36	4	9	23
LC	→ HL	1023	708	296	8	11	1009	121	198	690
$\chi^2 = 9.34; P > .80$						$\chi^2 = 7.96; P > .60$				
EF	→ EF	292	230	61	0	1	289	33	68	188
EF	→ LC	410	305	95	7	3	397	46	77	274
EF	→ LA	24	15	9	0	0	24	3	5	16
EF	→ CT	30	22	6	1	1	29	4	6	19
EF	→ HL	483	323	156	3	1	477	48	89	340
$\chi^2 = 17.80; P > .25$						$\chi^2 = 13.50; P > .25$				
HL	→ HL	249	200	48	1	0	244	41	57	146
HL	→ AH	62	26	24	4	8	54	20	18	16
$\chi^2 = 80.23; P < .001^*$						$\chi^2 = 23.66; P < .001^*$				

AH = *A. heloisa*; CT = *C. thalassinus*; EF = *E. fulgens*; HL = *H. leucotis*; LA = *L. amethystinus*; LC = *L. clemenciae*. *Denotes significance.

However, since difference in total stand height between the tallest and shortest stands averaged no more than about 0.3 m, difference in interval size among stands was judged too slight to be important. I noted no significant differences in feeding levels either among species or by location except for White-ears (Table 5). The White-ear was also the only species that foraged in proportion to the numbers of flowers at the 3 levels. This was apparently due to its small size and ability to feed at lower-positioned blossoms than could the larger species. Further, White-ears showed a higher rate of blossom use at low levels when feeding within territories of Blue-throats and Rivolis than when feeding within its own territories or in unprotected areas (Table 5). This appeared to be a learned response to harassment by the 2 larger species when White-ears invaded territories to feed. The behavior was functional in that birds practicing it were able to feed for longer periods before discovery. Depending on the topography, density of the stand and associated vegetation, and the size of the invaded territory, some White-ears became adept at approaching and feeding within particular Blue-throat or Rivoli

TABLE 5
 PROPORTION OF TIME (SEC) HUMMINGBIRDS SPENT NECTAR FORAGING AT 4 HEIGHT CATEGORIES* IN *P. KUNTHII* STANDS¹

Species	Situation	Time (sec)/Height Category				Total	
		VL ²	L	M	H		
Blue-throated	Within territory	n	86.2	367.8	2023.8	2299.0	4776.8
		%	1.8	7.7	42.4	48.1	100.0
Rivoli	Within territory	n	8.8	205.6	1091.2	1550.8	2856.4
		%	0.3	7.2	42.4	48.1	100.0
White-eared	Within territory	n	36.2	72.4	295.5	199.0	603.1
		%	6.0	12.0	49.0	33.0	100.0
White-eared	In neutral feeding areas	n	45.8	164.9	448.8	247.3	906.8
		%	5.1	18.2	49.5	27.3	100.1
White-eared	In <i>L. clemenciae</i> or <i>E. fulgens</i> territories	n	338.6	658.4	733.6	169.3	1899.9
		%	17.8	34.7	38.6	8.9	100.0
Mean number of useable blossoms							
in each category			572	1050	5387	3341	10350
%			5.5	10.2	52.1	32.3	100.1

¹ Because time units were not independent (the feeding location in a given time might be influenced by its activity in the preceding time unit) the length of time spent foraging in the 4 height categories was not treated statistically.

² VL = very low; L = low; M = middle; H = high.

territories for various periods. During the 3 summers, I noted 9 such territories. In each case White-ears defended the area from a perch usually immediately outside the territory boundaries in an unprotected area. The most unusual example involved a marked individual which maintained a territory within a Blue-throat territory and defended it from a small tree approximately 50 m away. Though these territories-within-territories were uncommon and therefore of little importance in greatly increasing the total nectar supply available to White-ears as a species, raiding facilitated by low approach and feeding was frequent and undoubtedly permitted a higher consumption of nectar than would have otherwise been possible. Thus the White-ear has evolved a flexible feeding behavior repertoire which under the conditions on Cerro San Felipe may be as close to a species-specific feeding pattern as

could be expected to develop. Indeed, such flexibility in behavior may be the only possible way in which any significant ecological divergence in feeding can occur and probably is an important factor in the success of the White-ear in montane Mexico as judged by its reported wide geographical and elevational range and habitat tolerance.

Dynamics of territoriality in relation to habitat and phenology of flowering.—If territoriality is an adaptive behavior, it cannot be divorced from the range of evolutionary and extant environmental events which affected its development and presently work to maintain it. In hummingbirds, especially at times of the year when nectar is the major food, the phenology of flowering, particularly in nectar-rich hummingbird pollinated species of plants, is the major factor controlling the dynamics of territoriality. Not only the quantity of the nectar, the distribution and period of flowering, and richness in relation to alternative food sources (Wolf 1969, 1970, Wolf and Hainsworth 1971, Stiles and Wolf 1970), but also its “packaging” in blossoms of various shapes and sizes, and rate of production and decline of flowering are important in controlling the stability of the territorial system. In turn the territorial system is related to the pollination system involving both flowers and birds, and cannot be thoroughly understood without recognizing some of the details of operation of the pollination system. During the course of my study, the timing and extent of the major blooming periods of hummingbird flowers, and the phenology of territorial events in relation to them, made clear the degree of interaction and interdependencies in the 2 systems.

White-ears were present on Cerro San Felipe year-round, but because freezing temperatures commonly occur above 2500 m from late December through March, flowers were absent in the meadows during this period (Rowley, pers. comm.). White-ears must have been primarily insectivorous during this period or migrated to lower elevations where some plants may have continued to blossom through the winter. *Rigidella* was the first hummingbird plant to bloom in the spring. Flowering began in early May and the number of White-ears increased rapidly in the meadows. Territoriality was well developed by mid-May and continued into early June, but became temporary and sporadic in late June when the number and regularity of *Rigidella* in flower declined. During this same period the Bumblebee population was maximum and birds of this species were observed daily in *Rigidella* beds attempting to forage, but were under constant harassment by White-ears. Its small size, bee-like (*Bombus*) flight and buzz while hovering appeared to confuse territorial White-ears and allowed some Bumblebees to feed for relatively long periods before being discovered and chased. Occasional smaller isolated unprotected stands and clumps of *Rigidella* were heavily used by Bumblebees. As *Rigidella* blossoming declined, Bumblebees disappeared from

TABLE 6
CULMEN LENGTH OF *E. FULGENS* AND *L. CLEMENCIAE*

Species	Females		n	Males		n
<i>E. fulgens</i>	26.5	2.8	20	22.1	1.9	58
<i>L. clemenciae</i>	29.6	3.5	16	26.4	2.1	27

the meadows and surrounding areas and were observed only infrequently thereafter. Since Bumblebees were most abundant during the period of major White-ear territoriality in *Rigidella*, and its decline in numbers coincided closely with decrease in *Rigidella* flowering but was before the peak blooming of *Penstemon* and *Cuphea*, it is unlikely that White-ear, Blue-throat, or Rivoli territoriality was the main cause of its disappearance, although it may have been a contributing factor.

By early June *Penstemon* had begun to flower and the first Blue-throats arrived in the meadows and by mid-June had established territories. Most territories were large (1566 m² mean size prior to June 15, n = 24) yet were efficiently defended against all species except White-ears. This period coincided with flowering decline in *Rigidella*. The shift in White-ear foraging from *Rigidella* to *Penstemon* greatly increased the use of *Penstemon* as a nectar resource and resulted in an increased frequency of Blue-throat-White-ear chases. As territorial Blue-throats ejected and chased one White-ear, others invaded and fed in the unguarded territory. Thus though Blue-throat territoriality was already well developed and effective in controlling trespass of all other hummingbirds in this early June period, it was ineffective against White-ears. The effect of the rapid decline of *Rigidella* on White-ears was thereby minimized by increased blossoming of *Penstemon* despite attempts by Blue-throats to control it. However, by early to mid-July the steady influx of Blue-throats and increasing numbers of *Penstemon* in flower resulted in an increase in the number and a decrease in the size of Blue-throat territories (Figs. 3, 4). Trespassing in territories increased with increase in flowering, and the large territories established and successfully defended earlier when numbers of flowers were low could not be controlled when numbers of flowers were much higher. This resulted in the displacement of the territorial bird from part of the territory and the establishment of 2 or more new territories within the original. In all such cases the resident remained in and defended a smaller portion of the original territory; total displacement of the original tenant was never observed. In all situations involving the complete takeover of Blue-throat territories by conspecifics, the original bird had been absent

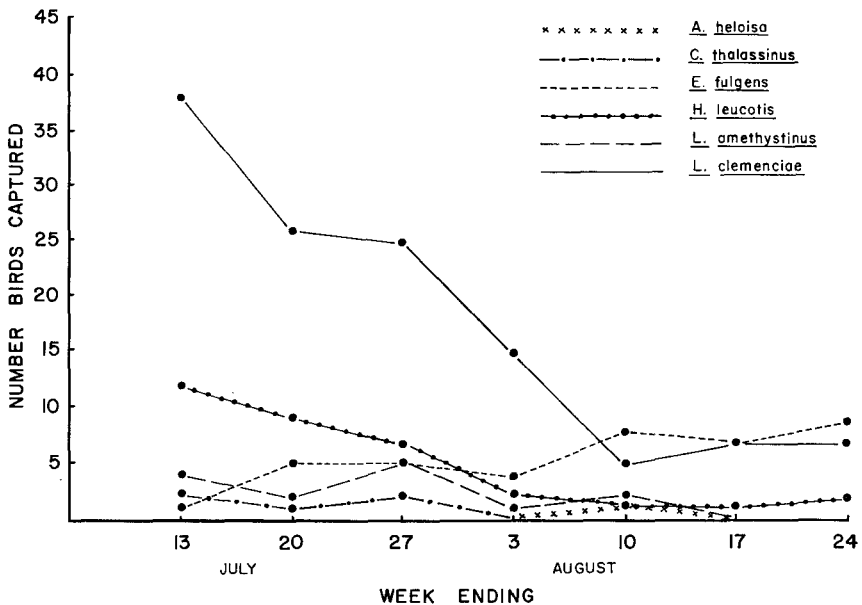


FIG. 5. Number of individuals of each species captured per week, 1969.

from the territory for at least one day and was unable to reclaim the territory upon returning, thus replacement appeared to be by default, not by expulsion. The reduction in territory size increased the effectiveness of exclusion of White-ears by Blue-throats. Thus the increase in numbers of *Penstemon* in flower, rather than alleviating the nectar shortage for White-ears, aggravated it because of the shrinkage in Blue-throat mean territory size.

During the same period in 1968 (early to mid-June) Rivolis were netted with increasing frequency (Fig. 4) and territorial confrontations between Blue-throats and Rivolis became more frequent. By mid-July all important stands were effectively controlled by Blue-throats and there was no further increase in the number of Blue-throat territories. Prior to this time Rivolis had been unable to establish territories, but on 17 July began the start of a 2 week period during which established territorial Blue-throats were replaced by Rivolis. Unlike the situation in which conspecifics were unable to completely displace territorial Blue-throats, displacement was total and Rivolis confiscated territories intact with no noticeable alteration in boundaries (Fig. 6). The actual event of displacement was not observed directly. Like other hummingbirds, Rivolis raided in Blue-throat territories and were consistently ejected. Often, upon return of the Blue-throat resident, a Rivoli was perched

or feeding in the territory and a second chase ensued. During some very active periods of raiding, certain territorial Blue-throats were in almost constant pursuit of thieving Violet-ears, White-ears, Amethyst-throats, and Blue-throats as well as Rivolis. None except Rivolis, however, attempted to perch at favorite perches of the Blue-throat resident. At the end of this 2 week period of intense interaction, 13 Rivolis had replaced Blue-throats and were feeding exclusively within the territories and defending them. Displaced Blue-throats usually were not observed or netted again; a few were present in the meadows for a few days and became part of the raiding population but then disappeared. None were able to displace territorial conspecifics or Rivolis. Twice, a newly territorial Rivoli was displaced by a conspecific but in each case this occurred within 2 days of displacement of the original Blue-throat resident. Once securely established, Rivoli territories remained stable and unchanged through the remainder of my study.

In 1969 displacement of Blue-throats by Rivolis did not occur. Although Rivolis were present and foraged in Blue-throat territories, the Rivoli population did not reach 1968 levels (Fig. 4). Thus there appeared to be a relationship between numbers of Rivolis and their ability to displace territorial Blue-throats, but the precise nature of the interaction is not clear. A minimum number of Rivolis was perhaps necessary to effect an increased frequency of chases and to allow some conspecifics to invade and temporarily occupy territories when resident Blue-throats were occupied in ejecting others.

In 1968 displacement by Rivolis by the end of July resulted in a distinct patterning of Blue-throat and Rivolis territories (Fig. 6). Blue-throats were restricted primarily to the edges of the meadows or open forest and Rivolis occupied all open areas that had suitable *Penstemon* densities. Why Rivolis were successful in displacing Blue-throats in open areas but not in others is not well understood, but it is clear that an ability to discern and discriminate subtle differences in habitat is present in one or both species. It also indicates the need to be cautious in making statements about dominance relationships in hummingbirds. Rising (1965) and others have commented on the consistent dominance of Blue-throats over Rivolis at feeders. My own observations in the Chiricahua and Huachuca Mountains in Arizona support these reports. Further, on Cerro San Felipe, Blue-throats were usually dominant over Rivolis in "neutral" undefended feeding areas. However, the interaction resulting in the displacement of Blue-throats by Rivolis suggests that observations made at feeders and other "neutral" sites may result in oversimplification of interspecies behavioral relationships and can be misleading.

By the end of July 1968 the territorial system had once again stabilized and remained unchanged to the end of the study period. Territorial Rivolis were as efficient as Blue-throats in defending against conspecifics and other

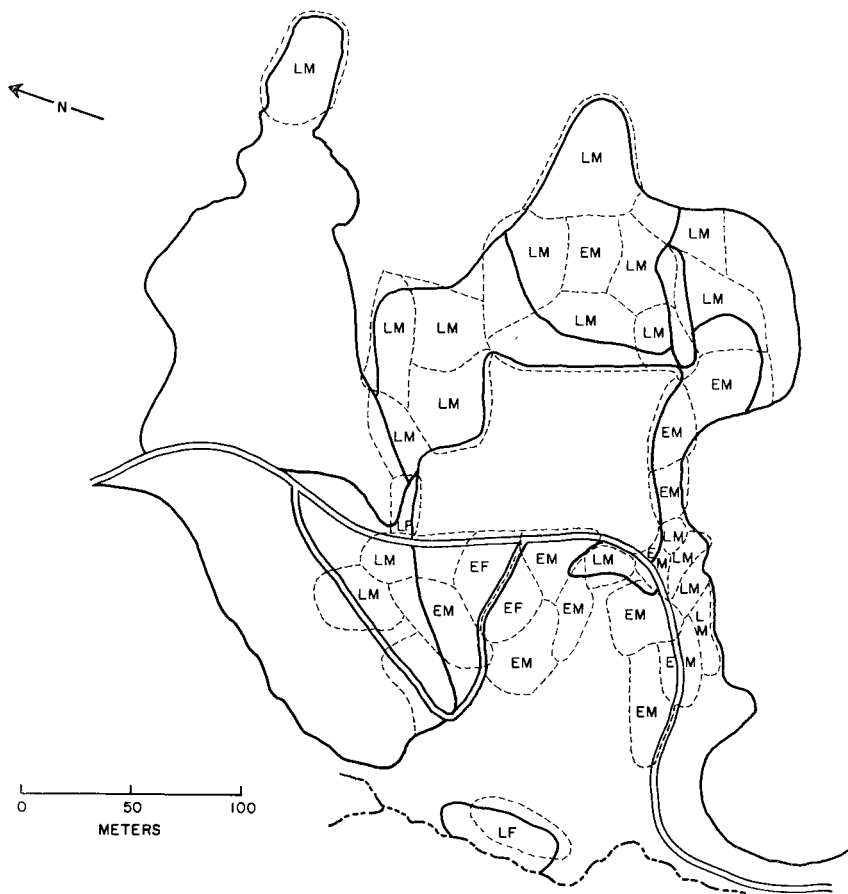


FIG. 6. Blue-throat and Rivoli territories in main meadow, late July 1968. In early July all territories shown here were already present but held only by Blue-throats. Compare territory placement of each species with vegetation pattern in Fig. 1. LM = Blue-throat male; LF = Blue-throat female; EM = Rivoli male; EF = Rivoli female.

species, and thus the final effect was a substitution of a portion of the territorial Blue-throat population by Rivolis but no additional pressure on the *Penstemon* resource. In 1968 the combined maximum number of Blue-throat and Rivoli territories was only 2 fewer than the maximum number of Blue-throat territories (30) in 1969 when no displacement of Blue-throats by Rivolis took place. This tends to further substantiate that Rivolis effectively substitute for Blue-throats and suggests that there exists a saturation level in numbers of territories of these species that the meadows will support, whether all of one

species or a mix of each, and that this level is determined primarily by the abundance of *Penstemon*.

The well-developed territoriality of Blue-throats and Rivolis also appeared effective in limiting the number of hummingbirds of all species which could feed in the meadows. With the exception of the multispecies territorial populations and a few nonterritorial frequently netted Blue-throats, Rivolis, and White-ears which were seen in the meadows daily, few marked individuals of any species were reobserved for more than 1 or 2 days after having been marked. Further, only 11% of the marked nonterritorial individuals in 1968 and 12% in 1969, were recaptured. Since birds were captured in large numbers throughout June and July in all years, a rapid turnover in the nonterritorial population must have occurred. Thus when the total number of birds using the meadows during the entire summer is considered, most were transients, though on any single day territorial birds constituted a large proportion of the population.

Toward the end of the summer study period, particularly in 1969, the number of birds captured of all species other than Rivolis declined rapidly (Figs. 4, 5). An additional indication of decline in total numbers was the distinct decrease in territorial chases during this period except during brief flurries of feeding activity immediately prior to sunrise and following sunset. Since the number of territorial individuals remained relatively constant during this same period, the decrease reflected a decline in numbers of transients, a reduction possibly initiated by the increase in blooming of other species of hummingbird-pollinated plants in areas outside meadows. Many of these bird flowers began blooming as early as *Penstemon* but did not reach peak blooming until late July. Still others did not begin to bloom until early August (Fig. 2). One of these, *Cuphea*, appeared to take up much of the slack for White-ears, but probably because of its small size was not used by the larger species. *Cuphea* was present early in small numbers scattered throughout Blue-throat and Rivoli territories and in undefended feeding areas, but it was most concentrated later in small openings within forest, and White-ears established territories in these areas. Some of these birds were marked and several had been territorial earlier in *Rigidella*. The other later-developing hummingbird-pollinated species were more dispersed and though used frequently by hummers seemed insufficiently clumped or abundant to encourage the establishment of territories. Most of these grew in isolated clumps or singly in light shade or, like *Cuphea*, in small forest openings. Marked nonterritorial Blue-throats, Rivolis, Violet-ears, and Amethyst-throats were observed occasionally at freshly blooming plants of these species, but because they were widely dispersed it was not possible to spend the long periods of observation necessary to determine the full extent of use by birds.

However, frequent examination of other locations indicated that flowering of these species was general throughout the Sierra de Oaxaca at this elevation and thus must have provided an increased nectar supply for nonterritorial birds.

SUMMARY

A study of an interspecific territorial system involving 6 species of hummingbirds (Bumblebee, *Atthis heloisa*; Violet-eared, *Colibri thalassinus*; Rivoli, *Eugenes fulgens*; White-eared, *Hylocharis leucotis*; Amethyst-throated, *Lampornis amethystinus*; Blue-throated, *Lampornis clemenciae*) was carried out between 2500 and 3000 m on Cerro San Felipe in the Sierra de Oaxaca north of the city of Oaxaca, Mexico. The basis of the system was a complex of 12 hummingbird-pollinated plants, the most important of which were *Rigidella orthantha* (Iridaceae) and *Penstemon kunthii* (Scrophulariaceae).

Blue-throats, Rivolis, Violet-ears, and White-ears were both intra- and interspecifically territorial, but Bumblebees, the smallest in the system, and Amethyst-throats, were non-territorial. Interspecific territoriality, as judged by the response of territorial individuals to thieving birds, appeared as well developed as intraspecific territoriality. Species' success in establishing and maintaining territories was directly proportional to body size. The 2 largest species and nearly equal in size, Blue-throats and Rivolis, dominated the richest nectar sources, but partitioned these sources on the basis of habitat. Initially, early in the season all significant *Penstemon* stands were held by territorial Blue-throats, but by mid-July in 1968 Rivolis had displaced territorial Blue-throats in all open meadow situations, yet were unable to do so in meadow-forest edge or open forest areas. In 1969 no displacement of Blue-throats by Rivolis occurred and this lack was associated with a much smaller population build-up of Rivolis compared to 1968. When it occurred, displacement was total, with Rivolis confiscating entire territories and with no noticeable alteration in boundaries.

The interspecific territoriality of Blue-throats and Rivolis also appeared effective in limiting the number of hummingbirds which could feed in the meadows. Most marked birds were seen for only short periods following their initial capture and few marked nonterritorial individuals were recaptured, indicating a rapid turnover in the nonterritorial population.

White-ears demonstrated the most flexible feeding behavior of any species in the system. They not only were able to use a wide range of blossom sizes, but also showed a functional and presumably learned raiding pattern involving secretive low approaches to *Penstemon* stands located within territories held by Blue-throats and Rivolis. Bumblebees were non-territorial but their small size allowed them to subsist on the blossoms of unprotected plants located outside territories. Also, their peculiar bee-like flight appeared to permit them to feed for long periods in stands of *Rigidella* within White-ear territories without being evicted.

The phenology of flowering was the main factor controlling the behavioral events and interactions among species of hummingbirds. In May and early June *Rigidella* was the most important nectar source for White-ears, but as flowering waned, White-ears were forced to feed increasingly on early blooming plants of *Penstemon* even though these stands were defended by territorial Blue-throats. However, because *Penstemon* blossoms were widely dispersed at this time, territories were necessarily large and defense, though efficient against most species, was inefficient against the raiding strategy of White-ears. As flowering continued with season, blossom density of *Penstemon* increased and was