

## TERRITORIAL DEFENSE AGAINST HUMMINGBIRDS AND INSECTS BY TROPICAL HUMMINGBIRDS

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Studies of time and energy budgets generally require measuring the division of time among an animal's various activities and then converting these values to appropriate energetic costs. For highly mobile animals, such information is often difficult to obtain because of problems of observing them at close range and the variability of their behavior.

Territorial hummingbirds are ideally suited for the study of time and energy budgets for the following reasons. (1) Their daily activities are usually quite localized. (2) They are not affected by the presence of a quiet observer and consequently can be observed at close range. (3) They feed almost exclusively on nectar from flowers on their territories. The caloric content of their food is therefore easily assessed. (4) Most of their daily activities in the wild are spent at two basic metabolic levels, hovering flight and resting (perching). The energetic costs at both these levels have been measured and appear to be similar for most hummingbird species studied (Lasiewski 1963, Hainsworth and Wolf 1972a).

Many studies describe hummingbirds defending flowers from other hummingbirds, but reports of birds chasing insects from their territories are rare (Pitelka 1942, Stiles and Wolf 1970, Lyon 1974, Primack and Howe 1975). In addition, information on the frequency of insect chasing by territorial hummingbirds, its role in territorial defense, and its importance with respect to competition for nectar resources is scant. In this paper I investigate the significance of insect chasing through a consideration of the time and energy budgets of territorial hummingbirds. I also test some predictions of optimal behavior in hummingbirds defending flowers from intruders of different sizes.

### THEORY

I hypothesize that a hummingbird should defend a feeding territory whenever the distribution of flowers and the quality and abundance of nectar on the territory are such that the bird is more than repaid the energy it expends in self-maintenance and defense. Each potential competitor that invades the territory should, in theory, be chased by the bird, providing that the energy represented in nectar thus saved outweighs the energetic expense of chas-

ing. In nature, whether or not an intruder is pursued should also depend on the frequency of invasion of the territory by other classes of intruders and the amount of time and energy available for defense. The threat posed by a competitor should depend on its size, appetite, foraging efficiency and ability to displace the territory-defender. The frequency, distance and duration of chases of intruders of different classes should correspond to the threat that each poses to the territory. Different types of intruders visiting the territory simultaneously should be chased in the order of the threat they pose—for nectar depletion or territorial displacement—the intruder posing the greatest threat being chased first.

### STUDY AREA AND METHODS

Most of this work was conducted at Morgan's Gardens, 5 km N of Balboa, Canal Zone from 23-25 June 1974. The main study site was a feeding territory consisting of seven flowering bushes of the Pagoda Plant (*Isertia hankaeana*, Rubiaceae), covering an area 8 m × 4 m × 3 m that was defended by a single Rufous-tailed Hummingbird (*Amazilia tzacatl*). In addition, I observed a White-vented Plumeleteer Hummingbird (*Chalybura buffonii*) defending a feeding territory of ten *I. hankaeana* bushes at a woods trail 2 km W of the Bridge of the Americas near Panama City, Panama on 3 July 1974. All discussion which follows refers to the territory defended by *A. tzacatl* unless stated otherwise.

I watched the Rufous-tailed Hummingbird over several periods totaling 11 h 43 min. These periods were generally between 06:30-12:00 because of unpredictable weather conditions and a general decline in the activity of pollinators in the afternoon. The bird's activities were recorded by two people using stopwatches. Activity categories recorded were: Perching, Change of Perch, Display, Feeding, Chasing Birds, Chasing Bees and Gone. The last category includes time the hummingbird was out of sight. No flycatching or foliage gleaning for insects was observed during this study.

### RESULTS AND DISCUSSION

The most common insect visitors to the territory were the long-tongued euglossine bees (*Eulaema nigrita* and *E. cingulata*) and carpenter bees (*Xylocopa* spp.). Other occasional visitors included small euglossines (e.g., *Euglossa mixta*, *E. cyanapsis*) and butterflies. Both large and small euglossines fed on *Isertia* nectar for I saw several individuals probing the flowers with their tongues. Similarly, I

observed carpenter bees perforating flower corollas at their base to obtain nectar.

*I. hankaeana* is native to Panama and its flowers from May to mid-September. The flowers have long tubular corollas, and are initially yellow, gradually changing to reddish-orange over several days. Only the newer yellow flowers are visited by hummingbirds and insects.

The defended area contained 104 inflorescences, each bearing an average of 66 new flowers ( $S = 3.78$ ,  $N = 20$ ). The average volume of nectar per flower (new) at the beginning of each day (06:30) was  $1.5 \mu\text{l}$  ( $S = 3.24$ ,  $N = 60$ ). Sugar content of the nectar, measured in the field with a Bausch and Lomb hand refractometer, averaged 22.1% by weight ( $S = 1.24$ ,  $N = 36$ ). The nectar was analyzed with the aid of paper chromatography in the laboratory and the sugar was primarily sucrose.

The average nectar content of the territory at the beginning of each day was estimated at 10,296  $\mu\text{l}$ . I calculated the energy content of *Isertia* nectar as follows: a 22.1% sucrose solution by weight is equivalent to 0.87 Molar. To convert this to calories, I used a value of 1349.6 cal/ml for 1 M sucrose (or 1174 cal/ml for 0.87 M; see Hainsworth and Wolf 1972b). The average energy content of the territory at the start of each day was thus estimated at 12,087 cal.

The oxygen consumption by *A. tzacatl* during forward and hovering flight was assumed to be 43 ml/g/h (see Wolf et al. 1972). This is equivalent to 5 cal/ml of  $\text{O}_2$  consumed at a Respiratory Quotient (R.Q.) of 1 (see Hainsworth and Wolf 1972b).

The crop capacity of all invading hummingbirds was assumed to be equivalent to that of a 5 g hummingbird (684  $\mu\text{l}$ ), while the honey-stomach capacity of all *E. nigrita*, *E. cingulata* and *Xylocopa* bees was assumed to be equivalent to that of a bumblebee of comparable size (100  $\mu\text{l}$ ; Hainsworth and Wolf 1972a, Heinrich 1975b). The smaller euglossines were not quite honeybee size and were assumed to have a honey-stomach capacity of 25  $\mu\text{l}$  (honeybee capacity = 40  $\mu\text{l}$ ; Heinrich 1975a).

A total of 599 hummingbirds (primarily conspecifics) and 236 large bees (*E. nigrita*, *E. cingulata* and *Xylocopa* spp.) visited the *Isertia* territory during the entire study (Table 1). Other flower visitors during this period included 41 small skipper butterflies (Hesperiidae), 16 small euglossine bees, and three large butterflies (two *Phoebis sennae*, one *Heliconius erato*). Of these, 588 humming-

TABLE 1. A summary of actions by a single *Amazilia tzacatl* hummingbird defending a feeding territory against other hummingbirds and bees.\*

	Intruder	
	Humming-birds	Large bees
No. chased	588	131
No. not chased	11	95
Chase with vocal display	433	5
Chase w/o vocal display	155	126
Feeding after chase	46	66
No feeding after chase	542	65
$\bar{x}$ distance of chase (m)	5.44	0.68
$\bar{x}$ duration of chase (s)	7.24	2.53
$\bar{x}$ no. cal/chase (roundtrip)	2.16	0.75

\* Other insects intruding on the territory during this period are discussed in the text.

birds were pursued by the defending *A. tzacatl* while only 131 large bees were chased. The three large butterflies were chased away immediately upon landing on flowers, but none of the smaller skipper butterflies or small euglossine bees visiting flowers on the territory were pursued. The Rufous-tailed Hummingbird did not respond to other insects flying over or landing on the territory (e.g., dragonflies).

When intruder groups were ranked by size (hummingbirds, large bees and butterflies, small bees and butterflies), the frequency of chases relative to the total number of invasions differed among size classes significantly. Hummingbird chases by *A. tzacatl* occurred with significantly greater frequency than did chases of large bees and butterflies ( $\chi^2 = 233.3$ ,  $P < .001$ ). Large bees and butterflies were chased with significantly greater frequency than were small bees and butterflies ( $\chi^2 = 62.76$ ,  $P < .001$ ). Thus the frequency of aggression shown by the defending hummingbird towards different intruder groups appeared to depend on their size and hence the potential threat that they posed for depletion of nectar resources on the territory.

An alternative explanation for the chasing of intruders is that the bird was responding to the overall numbers of intruders rather than to their size. Many more hummingbirds visited the territory than did large bees, and many more large bees visited the territory than did small bees and butterflies. This explanation seems unlikely, however, because only three large butterflies visited the territory and they were immediately pursued, whereas none of the 41 small skippers or 16 small euglossines was chased.

The White-vented Plumeleteer defended its

territory primarily from butterflies. During a 3 h period, it chased 24 large butterflies, six small butterflies, two large bees, one wasp and three hummingbirds from its territory. The butterflies chased included 18 *Parides sesostris*, five *P. arcus* (Papilionidae), one *Phoebis sennae* (Pieridae), and six *Eudamus* spp. (Hesperiidae). The bees were *Eulaema nigrita*, the wasp was not identified, and the hummingbirds were two Fork-tailed Emeralds (*Chlorostilbon canivetii*) and one *Chalybura buffonii*.

Primack and Howe (1975) observed a Rufous-tailed Hummingbird defending a territory of *Stachytarpheta jamaicensis* flowers primarily from skipper butterflies in Costa Rica. If skipper butterflies (and small bees) are worth pursuing, the fact that they were not chased by the *A. tzacatl* I observed can be explained by the high frequency of invasion by other intruders with a greater potential to deplete the territorial resources. According to energetic theory, visitors should be chased in order of the potential threat that they pose in terms of nectar depletion and territory displacement. As many large bees were not chased from the territory and chases of large bees should take priority over chases of small bees and butterflies, the fact that small bees and butterflies were not pursued appears to make good 'energetic sense'. In contrast, hummingbirds defending territories with less frequent invasion and fewer intruders, such as the plumeleeter I observed and possibly the Rufous-tailed Hummingbird observed by Primack and Howe may, as a result, be able to extend their defense repertoires to include chasing smaller intruders.

The behavior of *A. tzacatl* in response to intruding hummingbirds and bees was quite different. The defending bird pursued all hummingbird intruders, with the exception of larger, more dominant species and those individuals who visited the territory during its absence. Bees, however, were generally pursued only when hummingbirds were not invading or feeding on the territory. This 'lesser priority' of bee chases (also evident in the data on the frequency of chases of these two intruders groups) corresponds to energetic theory. The defending bird also spent significantly more time feeding during the periods when hummingbirds were not invading ( $\chi^2 = 147.49$ ,  $P < .001$ ). By chasing bees and feeding more during these periods, the defender was presumably exhibiting 'optimal behavior' because probably much less nectar was removed from the territory than would have been the case had it performed these ac-

tivities during peak periods of hummingbird invasion.

Another habit that seemed to be related to the frequency of hummingbird invasion was the perching position of the defending bird on the territory. During periods of intense invasion by hummingbirds, the defender generally returned to one of two perches in the center of the territory, whereas, during periods when few or no hummingbirds were invading, its perch sites on the territory were more varied. By perching in a central location, the defending bird may have been able to see intruders more readily and maintain a more effective defense.

Bees were rarely chased beyond the bounds of the territory ( $\bar{x} = 0.68$  m), while hummingbirds were usually chased well beyond them ( $\bar{x} = 5.44$  m;  $t = 4.62$ ,  $P < .001$ ). The differences in these distances may merely indicate that a bee is more easily intimidated by a hummingbird than is another hummingbird and that it is not necessary to pursue a bee as far as a hummingbird to achieve the same effect. However, the pursuit of bees up to, but rarely beyond, the territorial boundary also left the defending bird in a position to ward off possible hummingbird intruders.

The amounts of vocal display by the defending bird during pursuit of hummingbirds and bees differed significantly ( $\chi^2 = 219.35$ ,  $P < .001$ ). *A. tzacatl* most often emitted a shrill chattering trill during hummingbird chases but made no vocalizations during most bee chases. These observations also appear to correspond with 'energetic logic'. Vocalizations directed towards bees by a territory-holding bird would seem to be an unnecessary energy expenditure because bees cannot hear and therefore are not likely to respond to such signals. Vocalizations directed towards hummingbirds, on the other hand, advertise the presence of the territory-holding bird and may serve to deter some individuals from invading the territory.

## THE ENERGETICS OF DEFENSE

I did not assess the impact of intruders on the total nectar resources available on the territory defended by either hummingbird because of the difficulties of monitoring the activities of different intruders visiting the territory simultaneously and in assessing quantities of nectar they extracted. However, it was possible to make some general energetic predictions based on the calculated energy expenditure by *A. tzacatl*, estimates of the honey-stomach capacity of intruders, and mea-

TABLE 2. Time budget and calculated energy expenditure for a single *A. tzacatl* hummingbird defending a feeding territory against hummingbirds and insects.

	Perching	Feeding	Chasing birds	Change of perch	Chasing bees	Display	Gone	Total
Minutes	402.55	125.65	70.93	9.67	5.51	3.08	85.58	702.97
% of total time	57.26	17.87	10.09	1.38	0.78	0.44	12.17	100
Calories expended	716	2251	1271	173	99	55	—	4565
% of total calories expended	15.7	49.3	27.8	3.8	2.2	1.2	—	100

The number of calories expended perching was calculated for a 5-g hummingbird at Resting Metabolic Rate (RMR) by using the equation of Herreid and Kessel (1967) relating thermal conductance to body weight and assuming a constant body temperature of 41°C at an ambient temperature of 30°C,  $RMR = 106.7 \text{ cal/h}$  (see also Hainsworth and Wolf 1972a). Energy expenditure in all other categories is based on hovering flight for a 5-g hummingbird ( $43 \text{ ml O}_2/\text{h} \times 5 \text{ cal/ml O}_2 \times 5 \text{ g} = 1075 \text{ cal/h}$ ); (Hainsworth and Wolf 1972b, Wolf et al. 1972).

surements of the nectar resources available on the territory.

In examining the energetics of defense, it first seems necessary to determine whether the territory occupied by *A. tzacatl* was energetically worth defending, secondly, whether a hummingbird or a bee was energetically worth pursuing, and finally, whether these intruders could be considered serious competitors for nectar on the territory.

The area defended by the Rufous-tailed Hummingbird was relatively small, and the distribution of the inflorescences was such that the defending bird appeared to have little difficulty seeing or driving off intruders. Sucrose concentration in *Iserertia* nectar falls within the range (20–25%) determined by Baker (1975) for hummingbird flowers. The calculated amount of energy expended by the hummingbird in defense and self-maintenance during a 10.3 h period (4565 cal) was much less than that available on the territory at the start of each day (12,087 cal) (Table 2). Thus, the distribution, quality and abundance of the resources appear to be such that the area was energetically worth defending.

The calculations in Table 1 show that an average of only 0.75 cal was expended by the defender in chasing a bee from the territory and 2.16 cal was expended per hummingbird chase. By these estimates, a hummingbird stealing only 2  $\mu\text{l}$  of nectar (2.34 cal) or a bee stealing as little as 1  $\mu\text{l}$  of nectar (1.17 cal) would be worth pursuing. As most hummingbirds and bees would probably visit many florets if allowed to forage undisturbed and could potentially remove 1.5  $\mu\text{l}$  of nectar from each floret, both types of intruders should be worth pursuing. This would be especially true if a hummingbird or a bee was able to forage on the territory until it filled its crop or stomach. Under such conditions a hummingbird could potentially remove a maximum of 684  $\mu\text{l}$  (803 cal) and a bee a maximum of 100  $\mu\text{l}$  (117 cal). These figures suggest that the potential amount of energy represented in

nectar saved by chasing hummingbirds and bees from the territory greatly outweighs the energetic expense incurred by *A. tzacatl* in chasing either type of intruder.

The 599 hummingbird and 226 bee visits to the territory probably represent repeated intrusions by smaller numbers of individuals. However, regardless of the total number of intruders, my calculations indicate that if each of the hummingbird visitors had been allowed to forage on the territory until it had filled its crop to 5% of capacity, or each of the bee visitors had filled its honey-stomach to 90% of capacity, either group would have totally depleted two-thirds of the nectar resources available on the territory over a three-day period (30,888  $\mu\text{l}$ ). Thus, both hummingbirds and bees appear to represent a serious threat to the resources on the territory. In a situation where two intruder groups occur, each with the potential to seriously affect nectar resources, the best defense in energetic terms for a defending hummingbird should be exactly what this Rufous-tailed Hummingbird did, i.e. to defend against both hummingbirds and bees as defense against only one group might prove futile.

I speculate that chasing hummingbirds should take priority over chasing bees because a hummingbird generally forages more efficiently than a bee, can remove more nectar per visit than a bee and also may be able to displace the territory-defender (see Hainsworth and Wolf 1972a, Heinrich 1975a).

Table 3 gives estimates for the length of time that Rufous-tailed Hummingbirds of different weights with a full crop of *Iserertia hankaeana* nectar could exist at Hovering (HMR), Resting (RMR) and Standard (SMR) Metabolic Rates. To arrive at these theoretical values, I assumed 100% utilization of crop-storage energy and rates of nectar extraction by *A. tzacatl* at flowers of *I. hankaeana* similar to those measured by Wolf et al. (1972) for *A. tzacatl* visiting flowers of *Heliconia imbricata*. Foraging times in this table include

TABLE 3. Theoretical estimates of the energy value of a full crop of *Isertia hankaeana* nectar for *A. tzacatl* hummingbirds of different weights, and time required to use that amount of nectar at Hovering, Resting, and Standard Metabolic Rates.

Wt. (g) <sup>a</sup>	Crop vol. (ml) <sup>b</sup>	Time to fill crop (min) <sup>c</sup>	Energy value of a full crop (cal) <sup>d</sup>	HMR (cal/h) <sup>e</sup>	Time at HMR (h)	RMR (cal/h) <sup>f</sup>	Time at RMR (h)	SMR (cal/h) <sup>g</sup>	Time at SMR (h)
4.5	.638	2.46	749.0	967.5	0.77	101.5	7.4	65.4	11.45
5.0	.684	2.63	803.0	1075.0	0.75	106.7	7.5	70.8	11.34
5.5	.730	2.81	857.0	1182.5	0.72	111.3	7.7	75.8	11.30
6.0	.776	2.99	911.0	1290.0	0.71	116.2	7.8	80.8	11.27

<sup>a</sup> Weights approximate those measured for *A. tzacatl* by Wolf et al. 1972 (4.3–6.1 g,  $\bar{x}$  = 5.0 g).

<sup>b</sup> Calculated as in Hainsworth and Wolf (1972a).

<sup>c</sup> Calculated by using the equation for nectar extraction efficiency of *A. tzacatl* at *Heliconia imbricata* (Wolf et al. 1972).

<sup>d</sup> Based on a nectar concentration of 0.87M by weight = 1174 cal/ml.

<sup>e</sup> Based on an energy expenditure of 215 cal/g/h.

<sup>f</sup> Calculated by using the equation of Herreid and Kessel (1967) relating thermal conductance to body weight and assuming a constant body temperature of 41°C and an ambient temperature of 30°C (see also Hainsworth and Wolf 1972a).

<sup>g</sup> Calculated from the equation for SMR for nonpasserines, Lasiewski and Dawson (1967).

only time when a bird had its bill inserted into a corolla, not hovering time between flowers, as do the values in Table 2. The weights of birds approximate the range measured by Wolf et al. (1972) for *A. tzacatl*.

The values in Table 3 demonstrate the presumed adaptive advantages of defending or robbing a territory. A defending individual of *A. tzacatl* weighing 5 g can obtain enough energy in 2.63 min of foraging on its territory to survive for 45 min at HMR, 7.5 h at RMR, or 11.3 h at SMR. Similarly, another individual with the same weight may obtain enough calories in 15 s of feeding on another bird's territory to survive 4 min at HMR, 41 min at RMR or 62 min at SMR.

## SUMMARY

Data presented here on a single Rufous-tailed Hummingbird (*Amazilia tzacatl*) defending a feeding territory from hummingbirds and insects correlate quite well with predictions of 'optimal behavior' based on time and energy considerations. The majority of time spent in defense was in chasing hummingbird intruders. Less time was spent chasing large bees and butterflies; small bees and butterflies were not chased from the territory. The amount of time spent chasing different types of intruders appeared to correspond to their size and hence to the potential threat that they posed to the territory in terms of depletion of nectar resources and displacement.

My calculations indicate that the territory occupied by the hummingbird was worth defending because the average amount of energy available there at the beginning of each day was approximately three times the amount used by the bird during 10.3 h of active defense. Comparisons of the amount of energy expended by the defender in chasing hummingbirds and large bees, and the amount of

energy in nectar that these visitors could potentially steal from the territory indicate both types of intruders to be worth pursuing. The defender's behavior when chasing hummingbirds differed from that when chasing bees. Hummingbird chases were more frequent, longer, and consequently, required significantly greater energy expenditures than bee chases. The observations on *Amazilia* and *Chalybura* hummingbirds presented here also support the conclusion that insect chases by hummingbirds may occur with greater regularity and frequency than previously suspected and may represent an important component of defense against competitors at some types of feeding territories.

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## LITERATURE CITED

- BAKER, H. G. 1975. Sugar concentrations in nectars from hummingbird flowers. *Biotropica* 7: 37–41.
- HAINSWORTH, F. R., AND L. L. WOLF. 1972a. Crop volume, nectar concentration, and hummingbird energetics. *Comp. Biochem. Physiol.* 42:359–366.
- HAINSWORTH, F. R., AND L. L. WOLF. 1972b. Power for hovering flight in relation to body size in hummingbirds. *Am. Nat.* 106:589–596.
- HEINRICH, B. 1975a. Energetics of pollination. *Annu. Rev. Ecol. Syst.* 6:139–170.
- HEINRICH, B. 1975b. The role of energetics in

- bumblebee-flower interrelationships. In: Co-evolution of animals and plants. Univ. of Texas Press, Austin.
- HERREID, C. F., AND B. KESSEL. 1967. Thermal conductance in birds and mammals. *Comp. Biochem. Physiol.* 21:405-414.
- LASIEWSKI, R. C. 1963. Oxygen consumption of torpid, resting, active, and flying hummingbirds. *Physiol. Zool.* 36:122-140.
- LASIEWSKI, R. C., AND W. R. DAWSON. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69:13-23.
- LYON, D. L. 1974. Territorial and feeding activity of Broad-tailed Hummingbirds (*Selasphorus platycercus*) in *Iris missouriensis*. *Condor* 75: 346-349.
- PITELKA, F. A. 1942. Territoriality and related problems in North American hummingbirds. *Condor* 44:189-204.
- PRIMACK, R. B., AND H. F. HOWE. 1975. Interference competition between a hummingbird (*Amazilia tzacatl*) and skipper butterflies (Hesperiidae). *Biotropica* 7:55-58.
- STILES, F. G., AND L. L. WOLF. 1970. Hummingbird territoriality at a tropical flowering tree. *Auk* 87:467-491.
- WOLF, L. L., F. R. HAINSWORTH, AND F. G. STILES. 1972. Energetics of foraging: rate and efficiency of nectar extraction by hummingbirds. *Science* 176:1351-1352.

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