ECONOMICS OF BREEDING TERRITORIALITY IN MALE CALLIOPE HUMMINGBIRDS

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ABSTRACT.—Several lines of evidence indicate that the territorial behavior of postbreeding North American hummingbirds can be explained in primarily energetic terms. The territoriality of breeding males, however, may be different in that it may play an important role in courtship. The results of this study on breeding male Calliope Hummingbirds (*Stellula calliope*) indicated that territoriality could not be explained either directly or indirectly in terms of defense of energy resources. Throughout the 2-month breeding season, flower sampling indicated that males could have obtained energy faster by foraging on nearby undefended areas than by foraging on their territories. In June there were no profitable flowers on the territories, and males did all or nearly all of their foraging away from their territories. In May, when territory nectar availability was fairly high, males did not leave, expand, or shift their territories in response to experimental exclosure of all profitable flowers on those territories. I suggest that males may have preferentially selected territory sites with prominent perches near females' nesting areas, and that these considerations outweighed the potential benefits of defending territories on areas with high-quality nectar resources. *Received 5 February 1986, accepted 26 October 1986.*

IF territoriality is an adaptive behavior in a particular situation, the costs associated with territory defense must be compensated for by some benefit or benefits. One class of adaptive explanations for territoriality comprises energy-based economic models, which view both the costs and benefits of territoriality in purely energetic terms (Carpenter and MacMillen 1976, Hixon et al. 1983, Schoener 1983, Carpenter 1987). These models may be particularly applicable in explaining the territorial behavior of hummingbirds (Hixon et al. 1983, Carpenter 1987). Hummingbirds feed on floral nectar, which provides little in the way of nutrients other than energy; they have rapid metabolic rates and have been observed to starve under natural conditions (Tyler 1940, Miller and Stebbins 1964, Kodric-Brown and Brown 1978).

Studies of postbreeding male, female, and juvenile North American hummingbirds have produced several lines of evidence indicating that their territorial behavior can be modeled in energetic terms. In locations where they have been studied, postbreeding hummingbirds defend territories that contain dense patches of flowers with copious nectar on which they do most or all of their feeding (Kodric-Brown and Brown 1978, Gass and Montgomerie 1981, Carpenter et al. 1983, Hixon et al. 1983, Paton and Carpenter 1984, Gass and Sutherland 1985). Where birds have been reported to defend areas with only marginally profitable flowers, richer flowers either were unavailable nearby (Lyon 1973) or were defended by other birds (Gass 1978). Postbreeding hummingbirds also defend territories around artificial feeders placed in areas not otherwise defended (Ewald and Carpenter 1978; Ewald 1980, 1985; Norton et al. 1982; Ewald and Orians 1983). Sizes of naturally occurring territories are inversely correlated with flower density (Gass et al. 1976, Kodric-Brown and Brown 1978, Gass 1979), and birds adjust territory sizes in response to natural (Gass 1979) or experimentally induced (Kodric-Brown and Brown 1978, Hixon et al. 1983) variation in flower density. When nectar becomes superabundant, birds may cease to be territorial (Carpenter 1987).

Although purely energy-based models may be sufficient to explain the territorial behavior of postbreeding hummingbirds, the costs and benefits of territoriality may be more complex during the breeding season. Among North American hummingbirds, only males hold territories during the breeding season, and these territories may play an important role in court-

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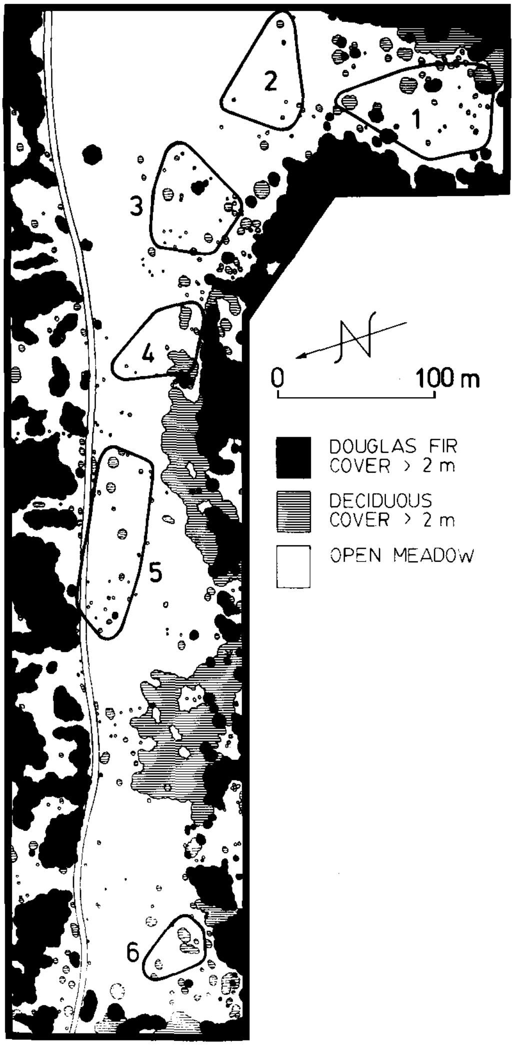

Fig. 1. Location of territories 1-6 on 1 June 1985. Territories were held by males during most of May and June. Females nest in conifers, primarily Douglas fir, immediately north of the meadow. See text for definition of territory boundaries.

ship. There is generally habitat separation between sexes; females usually nest in wooded areas and males hold territories in open meadows (Pitelka 1942, 1951; Legg and Pitelka 1956; Williamson 1956; Stiles 1973). Interactions between males and females are most often observed on males' territories, and the few copulations that have been observed occurred there. Most observations have indicated an absence of pair bonds and of parental care by males (Johnsgard 1983).

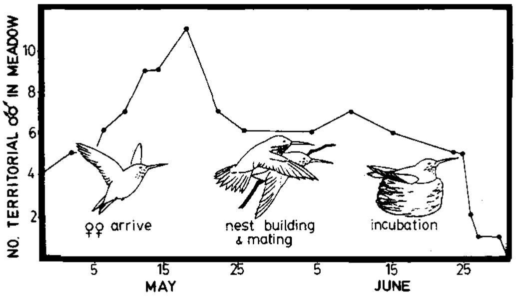

Fig. 2. Phenology of territoriality in the meadow, and approximate timing of reproductive activities. The influx of additional males during mid-May correlates with the peak of the *Ribes* flowering season.

Defense of nectar could benefit breeding males both by ensuring that they obtain their minimum energy requirements and by improving their immediate reproductive success. Because males are involved in energetically expensive activities during the breeding season (Stiles 1971), energy may be particularly important to them at that time of year. Improved access to nectar could increase male reproductive success in at least three ways. First, extra energy could allow males to perform energetically expensive courtship displays (Tamm 1985). Second, high nectar availability could attract females to territories to feed, and they might subsequently copulate with resident males (Stiles 1973). Third, territory nectar resources could comprise a secondary sexual characteristic, and act as a determinant of female choice (Selander 1965).

Because the above benefits relate directly to food energy, territoriality that involved only these benefits could be described by a purely energy-based model. Other benefits, however, might outweigh energetic considerations. First, by defending territories from other males, owners could secure exclusive access to any females that entered their territories. The best locations for encountering females might not always be those with the highest concentrations of flowers. Second, exclusive use of territories could allow males to court females without interruption. Third, some aspect of males' territories other than nectar resources could act as a secondary sexual characteristic.

I used two approaches to determine whether an energy-based model could account for the breeding territoriality of a group of male Calliope Hummingbirds (*Stellula calliope*). First, I measured the availability of nectar in flowers in bloom on territories and on nearby undefended areas. I used these data to determine whether males could obtain energy faster on their territories than on undefended areas, and whether they could obtain enough energy from their territories to meet their minimum energy requirements. Second, I performed an experiment to determine if males would leave their territories or otherwise change their behavior in response to exclosure of all territory nectar sources.

STUDY AREA

Calliope males defend territories on a strip of meadow about 100 m wide (Fig. 1) in a valley in the Ashnola Provincial Forest about 25 km southwest of Penticton, British Columbia (119°47′W, 49°18′N, elevation about 800 m). Various studies were conducted on the territorial males in this meadow during the 1983, 1984, and 1985 breeding seasons (Tamm 1985, Armstrong 1986). Males arrive in late April and defend territories through May and June (Fig. 2). Females arrive in early May and begin interacting with males on their territories soon after. Females nest in a Douglas fir (*Pseudotsuga menziesii*) stand north of the meadow (Fig. 1).

Males arrive about one week before the first suitable flowers begin to bloom. At this time, the only food males are seen to consume is small insects (Diptera, Lepidoptera, Neuroptera) that they hawk from their perches. Bushes of squaw currant (*Ribes cereum*) begin blooming in early May. *Ribes* is the only source of nectar available to birds through May, and is found on all territories in the meadow. During mid-May, when the number of territories peaks (Fig. 2), almost all bushes in the meadow are within or near territories. Dense aggregations of *Ribes* bushes also are found on undefended areas in and around the Douglas-fir stand north of the meadow, and on the north-facing slope of the valley south of the meadow.

Several other species bloom on and around the territories after *Ribes* finishes blooming in late May. These include lemonweed (*Lithospermum ruderale*), creeping mahonia (*Berberis repens*), larkspur (*Delphinium nuttalianum*), hound's-tongue (*Cynoglossum officinale*), and snowberry (*Symphoricarpos oreophilus* and *S. albus*). During preliminary observations in June 1984, I saw territorial males visit flowers of all these species, but noted that these visits accounted for less than 1% of their time budgets in 15 h of observation.

Indian paintbrush (*Castilleja miniata*) is common in the region during June, but is always sparse or absent in the meadow I studied. *Castilleja* is a typical ornithophilous plant (Grant and Grant 1968). Its flowers are red, secrete copious nectar, and have a long, tubular shape that makes them accessible to hummingbirds but not to most insects (Perkins 1977). In contrast, all species that bloom on the territories have shallow flowers that are accessible to insects as well as birds. Bees (*Apis mellifera*, *Bombus* spp., *Emphoropsis* spp., *Anthophora* spp., *Andrena* spp.) and hawk moths (*Hemaris diffinis*) are commonly seen feeding on the territories. The areas of dense *Castilleja* growth closest to the meadow are located on the steep portion of the slope 50–100 m south of and 50–100 m above the meadow. Calliope Hummingbirds frequently are seen feeding in these areas but almost never establish territories there. The few territories held in these areas from 1983 through 1985 were abandoned within a few days, and most were established after the breeding season.

In 1985, I studied 6 territories established by 6 May and defended throughout the breeding season. Territories 1, 3, and 6 (Fig. 1) each were defended by a single, clearly marked male throughout the season, whereas territories 2, 4, and 5 each were defended sequentially by at least two different males. I defined each male's territory on a given day in terms of the perches he used while surveying his territory on that day. Of 242 chases of intruding hummingbirds by territorial males observed in 1985, 228 (94%) were initiated when the intruder was within 10 m of the perimeter described by the perches used by the owner on that day. I used this criterion exclusively to define territory boundaries.

I. PROFITABILITY AND ENERGY PRODUCTION OF TERRITORIES

METHODS

Sampling design.—I sampled nectar from *Ribes* flowers on 4 territories (territories 1, 2, 4, and 5 in Fig. 1) and 2 undefended areas between 8 and 21 May 1985. I determined the locations of consistently undefended areas by mapping the positions of resident males in and around the meadow each day from 28 April to 7 May, and rechecked these areas throughout the sampling period. Because most *Ribes* bushes in the meadow were within or near the boundaries of a territory, I sampled the closest undefended areas with abundant *Ribes* north and south of the meadow. The first was an area approximately 50 × 350 m immediately north of and parallel to the meadow. The second was an area of similar dimensions 100–150 m south of and parallel to the meadow on the slope of the valley. The density of *Ribes* bushes on both undefended areas was approximately equal to that on the territories. Any other differences between the undefended areas and the territories presumably did not affect their energetic profitability.

Between 27 May and 25 June, I sampled nectar from flowers of all plant species that bloomed after *Ribes* on the territories. Because the density of these flowers was low, I treated all 6 territories as a single defended area. During this period I also sampled *Castilleja* on a 700-m^2 undefended area about 80 m south of and above the meadow. Although there were many isolated patches elsewhere, this was the largest area of fairly contiguous *Castilleja* growth. On 3 June it contained 1,615 *Castilleja* inflorescences, and the density remained fairly constant through most of June.

On and before 10 June I sampled 4 times daily, starting at 0600, 1000, 1400, and 1800. After 10 June I sampled 5 times daily, starting at 0500, 0900, 1300, 1700, and 2100. I divided each area into 10 sites, and measured nectar volumes of 3 flowers from each of 3 different treatments at each site. The first treatment was an uncovered branch available to all foragers. The second treatment was a branch that had been covered with a plastic screen bag since the last sampling session, and thus had been unavailable to foragers during that time. The third treatment was a branch covered with a wire bag with 3.2 × 2.5-cm hexagonal holes, which allowed insects to enter but excluded birds.

Sampling techniques.—I measured nectar volumes in flowers by extracting nectar with glass microcapillary tubes. I measured nectar concentrations with a temperature-calibrated sugar refractometer. Because a minimum volume was required before I could obtain a concentration reading (1-4 μl, depending on light conditions), I pooled nectar from several flowers. I chose flowers haphazardly with respect to appearance and position, but excluded old, withered flowers.

Measuring profitability.—I defined the profitability of an area as the rate at which a bird could obtain energy while foraging on that area over a specific time period. The amount of time the bird spent foraging must be specified to account for the effect of nectar depletion on energy intake rate. In this analysis I assumed males would spend 10% of the day foraging, and estimated rates at which they potentially could obtain energy while foraging during that time. I used 10% because it approximated the proportion of time males spent foraging on their territories during the peak of the *Ribes* flowering season in mid-May.

Instantaneous rate of nectar intake (W) at any time is a product of three factors: the nectar volumes of flowers birds visit (μl/flower), the sugar concentration of the nectar (J/μl), and the number of flowers visited over time (flowers/s). For each sampling session on the territories, I averaged nectar volumes of unbagged flowers at all 10 sites, and multiplied this by the average of all concentration readings to obtain a single estimate of the mean energy content per flower. For *Castilleja* I obtained at least one concentration reading for every second site. Therefore, for each sampling session I obtained 5 estimates of energy content per flower, with each estimate consisting of data averaged for 2 sites. To estimate the instantaneous rates at which males could obtain this energy, I recorded the number of flowers they visited over time whenever I observed foraging at close range. Flowers of each species occurred in patches of fairly consistent density, and thus I used a single average visitation rate for each species.

For each territory or undefended area, I used the estimates of potential energy intake rates to calculate the amount of energy a male could obtain while foraging for 10% of the day. As long as this amount was less than the estimated total energy production on the area, I assumed the instantaneous rate was a reasonable estimate of profitability. This was always the case throughout the *Ribes* season, and for the *Castilleja* area throughout June. On the territories in June, however, flowers of some species were so sparse that males could not have foraged on them for more than a few minutes each day. In calculating the potential profitability of the territories at that time, I assumed that males would spend as much time as possible foraging on the most profitable species on their territories, and then would allocate their remaining time to foraging on the second-best species, then the third-best species, and so on. This was a reasonable assumption, as flowers of different species generally occurred in separate patches.

Measuring energy production.—I estimated the average energy production per flower from the difference between the average energy content of flowers covered with screen bags and that of unbagged flowers at the same site at the last sampling session. To estimate 24-h energy production, I summed the estimates of production for all time periods between samples. This included an estimate of overnight production obtained by bagging flowers the night before each full day of sampling. I estimated the number of flowers of each species in each territory at least once each week, and from this estimated the total 24-h energy production of each territory.

For species other than *Ribes,* I counted all flowers on each territory. I estimated the number of *Ribes* flowers on each bush in bloom within each territory on the basis of the volume of the bush and its phenological stage. Most *Ribes* bushes are roughly hemiellipsoidal in shape. Therefore, I measured the longest and shortest horizontal axis and the height of each bush, and calculated the volume of a hemi-ellipsoid with those dimensions. I recorded the phenology of each *Ribes* bush by counting the number of flowers in bloom on the same sample branches twice each week. At the end of the season I divided the flower count for each date by the maximum number ever counted on that branch, and averaged the values of all branches on each bush. Throughout May I also counted flowers on sectors of 51 randomly selected bushes, with each sector making up $\frac{1}{16}$ of the bush volume. The number of flowers (f) was predicted ($r^2 = 0.60$) by $\sqrt[3]{f} = 0.4v + 2.3p$, where v is the

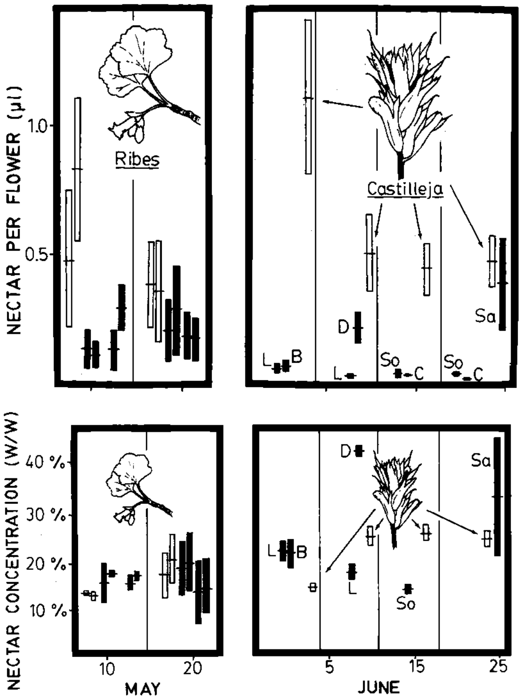

Fig. 3. Nectar volumes and concentrations of flowers blooming on (closed bars) and off (open bars) territories during the breeding season. Data for May are all for *Ribes*. Data for June are for *Castilleja* off territories and *Lithospermum* (L), *Berberis* (B), *Delphinium* (D), *Cynoglossum* (C), *S. oreophilus* (So), and *S. albus* (Sa) on territories. Horizontal and vertical bars indicate means and 95% confidence intervals, respectively. Observations are average nectar volumes at 10 sampling sites and average nectar concentrations at 4 or 5 times of day.

volume and p the phenological stage of the bush. By summing the predicted values for all *Ribes* bushes on each territory, I estimated the total number of flowers. The number of bushes on each territory varied over time, and ranged from 3 to 29 bushes.

Measuring the impact of insects.—I estimated the amount of nectar consumed by all foragers since flowers were bagged from the difference between the average nectar volume of flowers covered with screen bags and those left uncovered. I estimated the amount consumed by insects from the difference between the average nectar volume of flowers covered with screen bags and wire bags. If the rate at which nectar is harvested by insects is not affected by the wire bags, the ratio of these two differences provides an estimate of the proportion of nectar consumed by insects. I tested the assumption that wire bags did not reduce insect foraging by comparing insect visitation rates to bagged *Ribes* branches to rates observed immediately before or after these branches were bagged. Throughout the day of 16 May, I observed 72 branches for 30 min each both while bagged and unbagged. Based on logarithms of visitation rates, the ratio of visitation rates to bagged and unbagged flowers was 1.04 (95% confidence interval = 0.65–1.67), which indicates that the bags did not have a strong effect on insects.

TABLE 1. Flower visitation rates of male Calliope Hummingbirds foraging on 4 plant species. Values are means ± 95% confidence intervals.

	No. of bouts observed	Flowers per second
Ribes	9	1.0 ± 0.1
Lithospermum	8	0.8 ± 0.05
Delphinium	10	0.7 ± 0.1
Castilleja	31	0.6 ± 0.05

RESULTS

Profitability of territories.—During both weeks in May that I sampled *Ribes*, flowers on territories contained less nectar on average than those on the two undefended areas (Fig. 3). Nectar concentrations were similar on defended and undefended areas. From these data, and flower visitation rates for *Ribes* (Table 1), I estimated rates at which birds could have obtained energy while foraging on these areas. The estimates suggest that during both weeks males could have obtained energy faster by foraging on the undefended areas than by foraging on their territories ($P < 0.005$, ANOVA; Fig. 4).

Most flowers that bloomed on the territories in June contained little nectar, and far less than found in the undefended *Castilleja* flowers (Fig. 3). Flowers of *Delphinium* and *S. albus* on the territories contained approximately the same amount of energy on average as those of *Castilleja*. There were so few of these flowers, however, that territory owners could not have foraged on them for more than 3–4 min/day on average (Table 2). Estimates of profitability on the territories in June (Fig. 4) reflect the low nectar volumes of *Lithospermum*, *Berberis*, *Cynoglossum*, and *S. oreophilus*.

To estimate profitability of the territories in June, some assumptions were necessary. *Cynoglossum* nectar volumes were so low that I obtained no concentration readings. I made the generous assumption (see Fig. 3) that its nectar

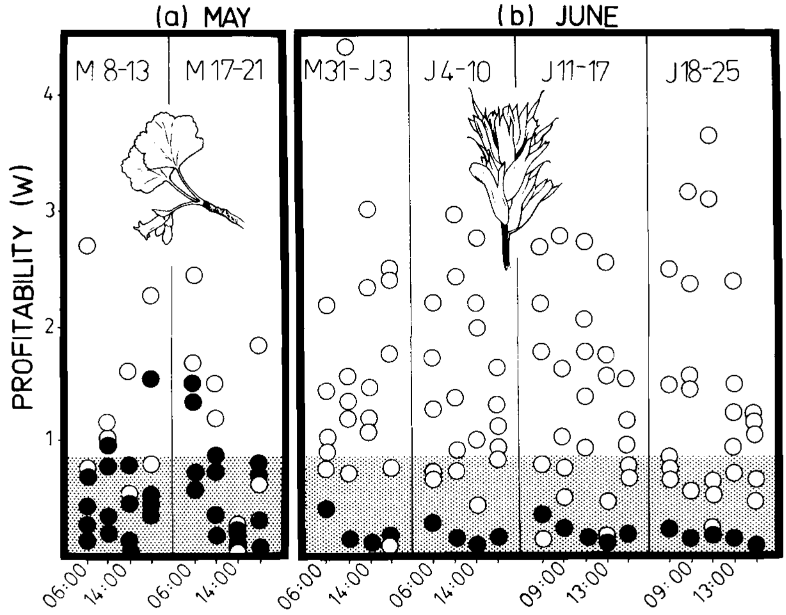

Fig. 4. Comparative profitability of nectar resources on (●) and off (○) territories at several times of day during the breeding season. Profitability refers to the gross rate at which a bird could obtain energy while foraging in a given area, assuming that it spent 10% of the day foraging. (a) Profitability of *Ribes* on each of 4 territories in May compared with that on 2 undefended areas north and south of the meadow. (b) Profitability of several plant species on the territories in June (see Fig. 3) compared with that of *Castilleja* on the slope south of the meadow. The top of the shaded region is an approximate value of the cost of hovering, based on Montgomerie's (1979) equations. If birds' rates of energy intake were below this value, they would lose energy while foraging.

was 40% sugar w/w. I obtained concentration readings for *S. oreophilus* during only one sampling session. For other sampling sessions, when nectar volumes were negligible, I assumed the average concentration was unchanged. Of the 6 species that bloomed on the territories in May, I observed birds foraging on only *Lithospermum* and *Delphinium*, and therefore could not measure flower visitation rates for the other species (Table 1). Because the morphologies of *S. oreophilus*, *S. albus*, and *Berberis* are fairly similar to that of *Ribes*, I assumed that flower visitation rates were similar. For *Cynoglossum* I used the average flower visitation rate observed for *Lithospermum*. For weeks during which there were too few flowers of a species to sample, I assumed nectar volumes and concentrations were equal to that on the closest preceding or succeeding week (Table 2).

The estimates of profitability on the territories for each week in June indicate that birds could not have obtained enough energy even to compensate for the cost of hovering while foraging (Fig. 4). This conclusion is insensitive to any realistic variation in my assumptions. It is not surprising that I observed few instances of birds visiting these species. In contrast, estimates of profitability for *Castilleja* on the slope indicate birds could have obtained energy rapidly from this source (Fig. 4). Throughout June, the bills of all 6 territory residents in the meadow usually were coated with the bright orange pollen characteristic of *Castilleja*, indicating that

TABLE 2. Total number of flowers of 6 plant species censused on territories each week during June. Boldface figures indicate insufficient flowers of that species to sample.

	27 May	4 June	11 June	18 June
Lithospermum	1,669	1,502	**357**	**38**
Berberis	1,068	**580**	0	0
Delphinium	0	253	**187**	**22**
Cynoglossum	**249**	**2,180**	6,051	3,853
S. oreophilus	0	**489**	5,570	698
S. albus	0	0	0	243

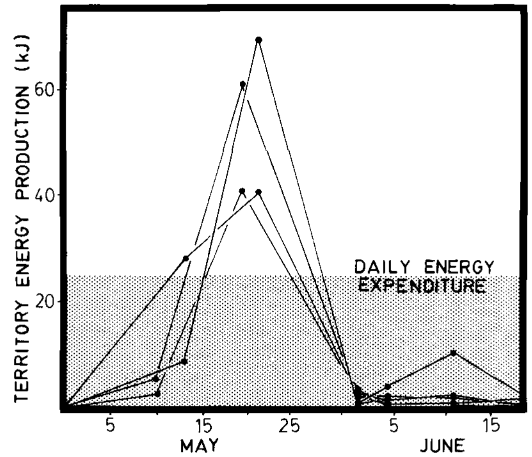

Fig. 5. Estimated daily energy production on 4 territories during May, and on 6 territories during June. Virtually all energy production throughout May was by *Ribes*. Estimates of territory energy production are products of 3 values: mean nectar volume/flower, mean nectar concentration, and estimated flower abundance. Daily energy expenditure was calculated from Montgomerie's (1979) equations, and the assumptions that birds remain perched for 16 h at 20°C and sleep for 8 h at 5°C. King's (1974) equation, which does not incorporate temperature, predicts a slightly lower value of 20.6 kJ.

they visited *Castilleja* somewhere off their territories.

Territory energy production.—I calculated minimum daily energy expenditures for males using King's (1974) and Montgomerie's (1979) allometric equations. Estimates of energy production by *Ribes* in mid-May were greater than males' minimum energy requirements (Fig. 5), but insects apparently consumed about 60% of this energy (Fig. 6). Nevertheless, males may have been able to obtain enough energy on their territories at that time to meet their minimum requirements.

In contrast, estimates of territory energy production in early May and throughout June were far below males' minimum requirements (Fig. 5), and insects apparently consumed most of this energy (Fig. 6). I estimated that insects removed more than 75% of the nectar produced by all species blooming on the territories in June except *Berberis*. This outlier resulted from 1 flower with an exceptionally high nectar volume out of 360 sampled. Conversely, data for *Castilleja* on the slope confirmed that all or nearly all nectar produced by this species was consumed by hummingbirds.

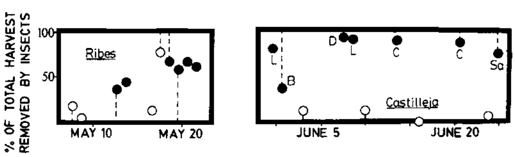

Fig. 6. Estimated proportion of daily nectar production removed by insects for plant species blooming on (●) and off (○) territories. Estimates were obtained by comparing nectar volumes of unbagged flowers with those of flowers enclosed in screen bags (hummingbirds and bees excluded) and wire bags (only birds excluded). Dotted lines indicate that nectar volumes of flowers in wire bags were not significantly different ($P > 0.05$; ANOVA) from those left unbagged (upward lines) or those in screen bags (downward lines). Data are not shown for *Ribes* on 10 May or for *S. oreophilus* because foragers did not significantly reduce nectar volumes.

Discussion

Throughout the breeding season, flowers on the territories were less profitable than those on nearby undefended areas. This suggests that a simple energy-based model could not explain the territoriality of the Calliope Hummingbird males in the meadow. Some caution, however, should be exercised in using data from random samples of flowers to infer rates at which birds could obtain energy on their territories. One factor not considered in such an analysis is that a territory owner may know which portions of its territory are most productive, and which portions it visited most recently. Consequently, a bird might obtain energy from its territory somewhat faster than if it foraged at random (Gill and Wolf 1977, Kamil 1978, Armstrong et al. 1987).

In June territories were not an important source of energy. Because insects consumed most of the nectar produced on territories, males probably could not have obtained energy faster than predicted on the basis of flower sampling. Further, estimates of daily territory energy production in June were far below males' minimum daily energy requirements.

In May *Ribes* was the only source of nectar in the area, and was abundant on the territories. I estimated that territories were less profitable than nearby undefended areas; however, given that the males apparently removed a significant portion of the *Ribes* nectar produced on their territories, their actual rates of energy acquisition may have been somewhat higher than estimated. Estimates of territory nectar production in mid-May exceeded calculated minimum energy requirements, and nectar production may have matched males' energy expenditures closely at that time.

To clarify the situation in May, I recorded the responses of Calliope males to experimental exclosure of all *Ribes* bushes on their territories. If territoriality is energy-based, one of several responses to such a manipulation should occur. Birds should leave their territories entirely, shift or expand them to incorporate peripheral sources, or challenge the owners of adjacent territories. If birds are defending some resource other than energy, they should remain on their territories. If territory nectar is nevertheless an important source of energy to birds, one of two types of responses should occur. Birds could increase their amount of time foraging off their territories to compensate for the loss of territory nectar. Otherwise, they could reduce their energy expenditure by perching in less exposed locations, or by reducing participation in energetically costly agonistic or courtship behavior.

II. RESPONSES OF MALES TO EXPERIMENTAL EXCLOSURE OF TERRITORY NECTAR SOURCES

METHODS

On or before 6 May 1985, I color-marked residents of territories 1-6 by catching them in a feeder-baited trap and painting their breast feathers. I removed feeders (Perky-Pet Brand) from territories immediately after males were trapped. Except for periods of a few hours when I placed feeders on territory 5 on 30 May and territory 6 on 2 and 16 June, there were no feeders on territories after 7 May.

On 9, 12, and 14 May I observed males on territories 1-6 for a total of 90 min each. The observations were divided into three sessions starting at 0630, 1100, and 1530. During each session I started with territory 1, and proceeded westward until I had observed each male for 30 min. During each 30-min observation session, I recorded the identity of the resident, all perches used, and various behaviors. I divided each bird's time budget into five component activities: perching, foraging for nectar, displaying to or chasing other birds, off the territory, and unaccounted for. If I observed a bird both fly away from and return to the territory, I considered the entire interim to have been spent off the territory. Time unaccounted for occurred most frequently when males flew behind vegetation or perched in inconspicuous locations.

On the evening of 14 May and throughout 15 May, I covered all *Ribes* bushes on or within 5 m of territories 3 and 6 with transparent plastic sheeting and secured the sheeting with staples. I repeated the observation procedure described above on these 2 experimental territories and the remaining 4 controls on 18, 20, and 22 May, and compared time budgets before and after *Ribes* exclosure. I left the plastic sheeting in place until 30 May, by which time *Ribes* had finished flowering. I conducted 3 further days of behavioral observations on 1, 9, and 15 June, and compared time budgets with those in May.

I analyzed behavioral observations with two-way ANOVA on time-budget data subjected to angular transformation (arcsin square root; Sokal and Rohlf 1981). The treatments compared were 9-14 May vs. 18-22 May (effect of *Ribes* exclosure) and 18-22 May vs. 1-15 June (effect of natural decline of territory nectar resources). The other factor in the ANOVA was variation between territories. To have a powerful method of detecting changes in behavior, I considered the 3 days in each time period to be replicates. Because these were pseudoreplicates in the sense that treatments were not repeated for each day (Hurlbert 1984), the changes in males' behavior should not be viewed as consistent effects of the different treatments.

RESULTS

Both of the males on experimental territories continued to defend them while the *Ribes* bushes were covered, and they remained on those territories until late in June. From 9 to 14 May, males spent on average 67% of their time perched visibly and 2.0% of their time displaying to or chasing other birds on their territories. From 18 to 22 May, while the *Ribes* bushes were covered, I obtained similar values of 61% for perching and 1.9% for displaying/chasing. Displays or chases or both were directed at male and female Calliope Hummingbirds, Rufous Hummingbirds (*Selasphorus rufus*), and passerines such as flycatchers (*Empidonax* spp.), Nashville Warblers (*Vermivora ruficapilla*), and Chipping Sparrows (*Spizella passerina*) (see Tamm 1985 for description and analysis of these behaviors).

The males did not shift their territories substantially after the *Ribes* bushes were covered. The overlap with the territories they defended on 9 May never fell below 50% on any subsequent day in May for either male, and their territories did not expand (Fig. 7). There were

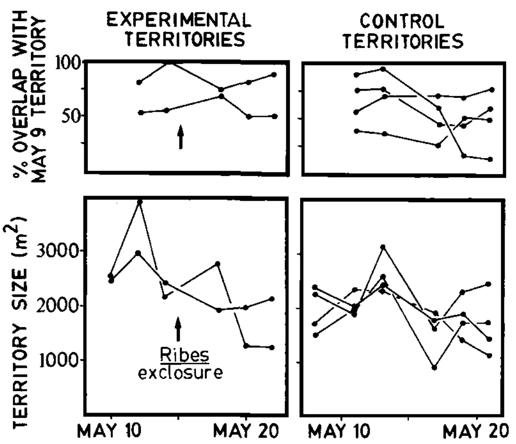

Fig. 7. Changes in positions and sizes of territories throughout May. Males continued to defend their territories after I covered all *Ribes* bushes on them.

several undefended *Ribes* bushes within 25 m of territory 6, whereas most of the uncovered *Ribes* bushes closest to territory 3 were defended by adjacent birds. The owner of territory 6 fed often on the nearby undefended bushes, but did not shift his territory boundaries to incorporate them. The owner of territory 3 sometimes stole nectar from bushes on adjacent territories, but never displayed aggression toward the owners or appeared to challenge them in any other way.

Only the amounts of time males spent foraging on their territories and spent off their territories changed significantly in response to *Ribes* exclosure (Fig. 8). The proportion of the time budgets spent foraging on their territories declined from 9.0% to 0.0% ($P < 0.0005$), while that spent off their territories increased from 3.3% to 14.5% ($P < 0.0005$). During the same time period I observed opposite trends in the males on control territories. The proportion of these males' time budgets spent foraging on their territories increased from 8% to 12% ($P < 0.05$) and that spent off their territories declined from 3.4% to 1.4% ($P < 0.10$). In June, time budgets of all 6 males were similar to those recorded in May for the 2 males whose *Ribes* bushes were covered. They spent 55% of their time perching, 1.6% displaying/chasing, 12% off their territories, and only 0.06% visiting flowers on their territories.

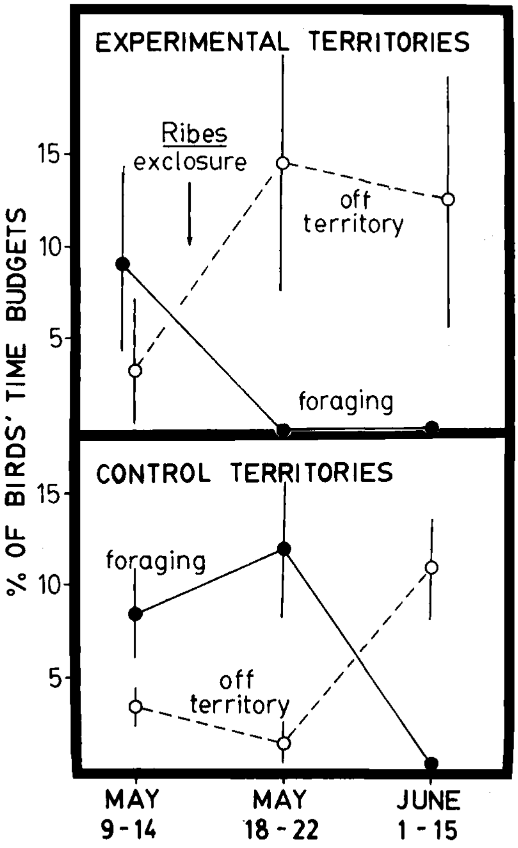

Fig. 8. Changes in time budgets of 2 males after I covered all *Ribes* bushes on their territories on 14 and 15 May. Similar changes occurred for 4 control birds in June after *Ribes* finished blooming. Each point shown is an average for 2 or 4 birds on 3 different days. Vertical bars indicate 95% confidence intervals based on arcsin square-root transformed data.

DISCUSSION

The fact that the males increased the amount of time they spent off their territories after exclosure of territory *Ribes* bushes indicates that these bushes were an important food source. It is possible that this increased time off their territories could have caused them additional effort in territory defense or caused them to lose courtship opportunities. The males continued to defend those territories, however, so that their territoriality in May as well as June probably was not related to defense of nectar. Ewald (1980) observed that nonbreeding Anna's Hummingbirds (*Calypte anna*) defended territories around artificial feeders after those feeders were removed, but this period of defense never exceeded 2 days, even if birds had previously held their territories for 10-30 days. In contrast, the birds in this study defended their territories for 15 days while the *Ribes* bushes were covered, and for about 25 additional days in June when their territories provided no profitable nectar resources.

In some cases defense of suboptimal habitat may be accounted for by long-term site tenacity (Wiens et al. 1986). Continuation of territory defense after *Ribes* exclosure and throughout June might be explainable in energetic terms if (1) males held the same territories over several breeding seasons and (2) the composition and density of flowers on territories was atypically poor during the 1985 breeding season. Neither of these conditions appears to have been the case. First, although many of the same areas of the meadow were defended during the 1983-1985 breeding seasons, there was extensive turnover of territorial males. Only 3 of the 6 males that defended territories during June 1985 had defended the same territory during any part of 1984. Second, the distribution and density of flowers was fairly similar during the 1983-1985 breeding seasons. The species composition on the territories in June 1985 was typical of all 3 years, and data from preliminary nectar sampling in 1984 were similar to those obtained in 1985. In all 3 years undefended *Castilleja* was available nearby.

I do not wish to imply that male Calliope Hummingbirds give no consideration to nectar resources when selecting breeding territory sites. If all other factors were equal, I suspect males would choose sites with abundant flowers on which they could feed. In the region surrounding the study site, I have observed Calliope males defending territories during June that contained abundant *Castilleja*. Also, different males may adopt different strategies in selecting territory sites. On my study site, a few additional males established territories during the peak of the *Ribes* flowering season each year (Fig. 2), and these males may have shifted the locations of their territories to follow nectar resources. My results indicate that an energy-based model cannot adequately explain the territorial behavior of at least some males during the breeding season. Therefore, if this territorial behavior were adaptive, these males must have gained some benefits from territory defense that outweighed energetic considerations.

A plausible hypothesis is that territoriality increases male reproductive success, and that this increase is not closely related to quality of territory nectar resources. I have seen females feeding on *Ribes* on males' territories, but these females either remained undetected by males or evaded them immediately after detection. I observed only 18 courtship encounters, and thus cannot rigorously compare encounter rates at times when territories did and did not provide nectar. Nevertheless, 5 of these 18 encounters occurred in June, and 2 of the remaining 13 occurred on experimental territories while *Ribes* bushes were covered. This is close to $\frac{1}{6}$ of those 13 encounters, as would be expected if they occurred evenly among territories and over time. These observations, along with the observation that males did not choose territories in areas with the richest nectar resources, suggest that the quality of territory nectar resources is not an important determinant of their reproductive success.

If territory defense benefits males simply by providing areas where they can encounter and court females without interference, there are several explanations for their choice of territory sites. First, the territories in the meadow are adjacent to an area where females nest (Fig. 1), so those females have easy access to the territories. Second, the meadow is devoid of vegetation except for low herbs and bushes, and a few prominent perches. Within the meadow, males defend areas with perches greater than 2 m high that are well separated from wooded areas (Fig. 1). From these perches they can observe intruders or females, and at the same time are visible to females. Third, by choosing sites without *Castilleja*, territory owners may reduce intrusion pressure from other males. Given that I observed interference by intruding males during 3 of the 18 observed encounters with females, it may be important for a male to maintain exclusive use of an area.

If territories primarily provide courtship areas, then the meadow can be described roughly as a lek. Classical lek behavior is common among male hermit hummingbirds (Phaethorninae) (Nicholson 1931; D. Snow 1968; B. Snow 1974, 1977; Stiles and Wolf 1979), which frequently vocalize and display in clear view of one another and sometimes in synchrony. In contrast, the Calliope males I studied defend territories that are well separated, especially during June. As long as each male remains in his own territory, there is generally little or no interaction among territory owners, and I doubt that a female could observe more than one male at a time. The term exploded lek (Bradbury and Gibson 1983) might provide the best description of the meadow in which these males reside.

ACKNOWLEDGMENTS

I thank Lee Gass for his time, enthusiasm, and financial support throughout this project, and Staffan Tamm for his advice and companionship in the field. This paper was strengthened considerably by critical reviews of earlier drafts by Lee Gass, Staffan Tamm, Don Ludwig, Jamie Smith, Judy Myers, Steve Paton, Peter Arcese, Gordon Orians, Lynn Carpenter, Paul Ewald, D. McCallum, and T. Breston. Lynn Carpenter sent two pertinent unpublished manuscripts, Don Ludwig and Peter Schumaker provided statistical advice, and Syd Cannings identified the nectarivorous insects. I also thank Si and Doreen Sieben for their hospitality during the 1984 and 1985 field seasons. Financial support was provided by a NSERC postgraduate scholarship, a University of British Columbia Graduate Fellowship, and a NSERC grant 67-9876 to C. L. Gass.

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