

TERRITORY AREA, FLOWER DENSITY, AND TIME BUDGETING
IN HUMMINGBIRDS: AN EXPERIMENTAL AND
THEORETICAL ANALYSIS

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If a locality produces a great deal of food . . . the territory sizes may be reduced to some extent (Altum [1868]).

Territoriality occurs when an animal defends an area against other animals, thus gaining nearly exclusive access to resources within that area. The potential regulatory effect of territoriality upon local population density has received much theoretical and empirical attention (e.g., Brown 1969; Fretwell and Lucas 1969; Watson and Moss 1970; Maynard Smith 1974). The critical factors in this regulatory role are those affecting the size of the individual territory. Of these factors, food density is of predominant importance in many systems. Controlled field manipulations of naturally occurring food sources have demonstrated a general inverse relationship between food availability and territory area for an intertidal limpet (Stimson 1973), two fishes (Hixon 1981, in prep.), and a bird (Miller et al. 1970). Laboratory experiments (e.g., Symons 1971; Slaney and Northcote 1974); field manipulations involving artificially dispersed food additions (e.g., Krebs 1971; Simon 1975; Franzblau and Collins 1980); and an experiment lacking unmanipulated controls (Ebersole 1980) have yielded less consistent results.

In an effort to elucidate the behavioral and energetic mechanisms by which territory size responds to changes in food availability, we have experimentally investigated the interrelationships between territory area, flower density, time budgeting, and other parameters in nectar-feeding hummingbirds. After comparing our results with available theoretical predictions, we discuss our findings in terms of a general model on the determinants of feeding-territory area (Hixon 1980) modified for hummingbird systems. We conclude that, in response to variations in flower density, migrant hummingbirds adjust territory area and time budgeting in a manner consistent with maximizing daily net energy gain.

Hummingbirds are excellent subjects for investigation of the economics and dynamics of feeding territoriality because: (1) they are readily observable for time-

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budget analyses in the field (e.g., Pearson 1954; Stiles 1971; Wolf and Hainsworth 1971); (2) they must at least balance their energy budgets on a daily basis (e.g., Calder and Booser 1973; Carpenter 1974), and in many systems (including the one discussed here) they have been shown to be nectar limited (Carpenter 1978, 1983; Montgomerie and Gass 1981), so they can be expected to respond rapidly to experimental manipulations of nectar availability; and (3) their energy allocations are directly proportional to their time allocations involved in different behaviors (e.g., Stiles 1971; Wolf and Hainsworth 1971; Hainsworth and Wolf 1972*b*; Ewald and Carpenter 1978), so time-budget analyses reflect underlying energetic relationships. Furthermore, a general inverse correlation has been observed between territory area and flower density (or similar nectar standing-crop measures) in these and other nectar-feeding birds (Wolf 1969; Gill and Wolf 1975; Carpenter and MacMillen 1976; Gass et al. 1976; Lyon 1976; Kodric-Brown and Brown 1978; Gass 1979). Of these studies, however, only Kodric-Brown and Brown (1978) have reported experimental manipulations of flower densities. After the number (and thus mean density) of flowers within three rufous hummingbird territories was halved, one territory apparently remained unchanged in area, the second occupant abandoned its territory, and the third expanded its territory, taking the area abandoned by the second. We have replicated these manipulations of the same species at another site, using a more refined experimental design and obtaining more consistent results.

METHODS

The Study Animal

From June to September of each year, rufous hummingbirds (*Selasphorus rufus*) migrate from breeding areas located between Oregon and Alaska to wintering areas located in Mexico (Skutch and Singer 1973). During this southward journey they travel along the Cascade-Sierra Nevada and Rocky Mountain Ranges (Grant and Grant 1967), with adult males preceding females and juveniles (Phillips 1975; personal observation). Along this route, migrant individuals establish feeding territories within isolated mountain meadows, defending various flower species mainly against conspecifics for periods of up to 2 wk (Armitage 1955; Cody 1968; Gass et al. 1976; Gass 1978*b*, 1979; Kodric-Brown and Brown 1978; Carpenter et al., MS). Recent field observations indicate that these stops allow the birds to replenish their fat stores in preparation for continued migration (Carpenter et al. 1981, MS).

The Study Site

Our study site was a stream-fed meadow occupying several hectares at the eastern base of the Sierra Nevada Mountains 27 km NW of Bishop, California (37°30'N lat., 118°30'W long., 1,700 m elevation). Although this site was visited almost exclusively by rufous hummingbirds, we also occasionally captured Allen (*Selasphorus sasin*) and calliope hummingbirds (*Stellula calliope*). The meadow

was situated on an alluvial slope dominated by sagebrush (*Artemisia tridentata*). A small stream supported dense stands of small willow trees (*Salix* spp.), which were bordered by a broad zone of grassland interspersed with various small shrubs. The flowering plant utilized by the hummingbirds was the herbaceous perennial *Castilleja linariaefolia* (Scrophulariaceae), patches of which were fairly evenly distributed within the grass zone and covered roughly half the meadow. The weather remained fair and stable throughout our study. Air temperature (ranging on average from 15.3° C to 29.7° C each day) and relative humidity (14.8% to 43.9%) followed nearly constant daily cycles.

Experimental Design

The experiments took place in August 1979 during the peak of the annual 2-mo flowering period of *Castilleja*. The basic experimental design involved comparisons of territory area and time budgeting before and after manipulations of flower density within "established" territories (*sensu* Copenhaver and Ewald 1980). Prior to each replicate, we captured resident birds in mist nets, identified their sex and maturity according to the key in Stiles (1972), and tagged them with small strips of colored surveyor's flagging glued to the center of the back. These tags caused no observable deleterious effects. Each of three experimental replicates involved a test-control pair of immature male birds, for a total of six individuals. Each pair of birds was selected on the basis of initial similarity of territory areas and number of territorial neighbors. None of the territories in the meadow were contiguously surrounded by neighbors on all sides, and flowering plants did occur outside well-established territories.

We ran two sequential and reciprocal manipulations during each experimental replicate (fig. 1). Following 1 day of baseline observations (day 1), we uniformly halved flower density (number of fresh and open flowers) within the test bird's territory at dawn by covering inflorescences with transparent plastic bags. To control for the presence of the plastic, the same number of bags was used to cover nonflowering stems in the control bird's territory. After another day of observation (day 2), we removed the bags from both territories, which had two effects: (1) The number of available flowers within the test bird's original territory was restored; and (2) the initial mean standing crop of nectar within those flowers was significantly increased because nectar had accumulated while the flowers were covered (table 1). We then observed the territory occupants for a final day (day 3).

During the experiments, we measured nectar volumes and concentrations (percent sucrose equivalents) within covered and uncovered flowers with 10 μ l capillary tubes and temperature-compensated hand refractometers (Carpenter 1976). Taking into account the density of different sugar solutions (Bolten et al. 1979), we subsequently calculated nectar standing crops (mg of sucrose equivalents per flower).

During each experimental replicate, we simultaneously measured the amount of time each control and test bird allocated to different activities. The birds were active from approximately 0600 to 2000 h each day. We observed each bird during two consecutive half-hour periods at 0630, 0930, 1230, 1530, and 1830 h, for a total

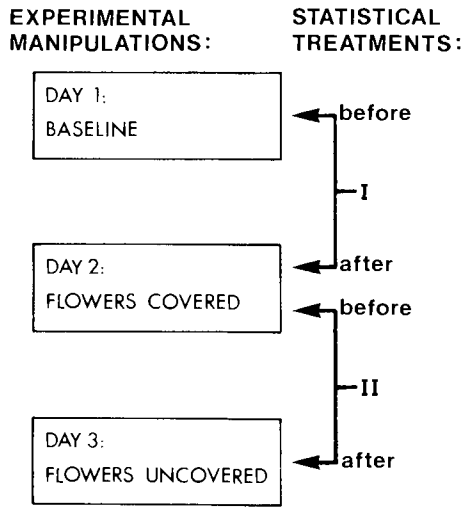


FIG. 1.—Design of the experimental manipulations of flower density and subsequent statistical analyses. Each block represents one day of time-budget data following the given manipulation of half the flowers within the original test territory. Simultaneous observations were made of the occupant of a control territory. Changes in time budgeting were tested by statistical comparisons between days before and after: (I) halving the mean density of flowers and thus the initial standing crop of nectar within the test territory; and (II) increasing the mean density of flowers and standing crop of nectar within the test territory. See text for further explanation.

of 10 sample periods per bird per day. Using binoculars and stopwatches at elevated observation posts (car roofs and ladders), we measured the amount of time the birds spent in the following activity categories (cf. Stiles 1971; Wolf and Hainsworth 1971): (1) foraging, which included mostly nectar feeding, but also occasional short bouts hawking insects, as well as time flying to, from, and between flowers; (2) defense, which included obvious agonistic interactions with intruding hummingbirds, as well as several encounters with bumblebees (see Carpenter 1979); (3) sitting, which included perching, preening, and relatively rare bouts flying between perches; and (4) lost, which included periods when the bird was out of sight. We suspect that most lost time was spent perching in nearby trees. We added observation time to each sample period to compensate for lost time, which averaged 2.8 min/h during a grand total of 90 h of observation.

Territory boundaries were readily mappable in this system because the entire territory was visible and each bird clearly limited its daily defense to a specific group of flowering plants. Changes in territory area induced by the manipulations invariably occurred in the morning and stabilized by midday. We therefore measured territory area at the end of each day by plotting the distances and angles between the outermost defended flowers of a bird's range, and measuring the resulting polygon with a planimeter. Thus, "territory area" accurately reflected the actual "defended area" (*sensu* Noble 1939). After each measurement, we tallied the number of fresh and open flowers within the territory.

TABLE 1

EFFECT OF COVERING FLOWERS UPON STANDING CROPS OF NECTAR WITHIN THE THREE TEST TERRITORIES (replicates 1 to 3)

TREATMENT	MEAN STANDING CROP OF NECTAR (mg sugar/flower)		
	Replicate: 1	2	3
A. Covered one day	3.20 (20) ^{***}	2.04 (20) [*]	2.65 (10) ^{***}
Open control54 (20)	.57 (20)	.49 (10)
B. Uncovered one day69 (20) ^{NS}	.53 (20) ^{NS}	.52 (10) ^{NS}
Open control52 (20) ^{NS}	.50 (20) ^{NS}	.36 (10) ^{NS}

NOTE.—Test A compares flowers covered one day to nearby control flowers within the same territory. Test B compares formerly covered flowers (which were subsequently exposed for one day) to the controls. Means were compared by approximate *t*-tests (Sokal and Rohlf 1969). Sample sizes are listed parenthetically.

* = $P < .05$.

*** = $P < .001$.

NS = not significant ($P > .05$).

Two control birds and one test bird emigrated before completion of the experiments. The test bird emigrated at the end of day 1, and its territory was immediately reoccupied by another bird that subsequently maintained the same baseline (i.e., premanipulation) territory area. The control birds, however, emigrated on the morning of the final (third) day of the experiments and were replaced by neighbors that shifted their territories into the vacated areas. Therefore, we used the territory-area data on the new test bird (T1 in fig. 2) in our analyses, but not those on the new controls (replacing C1 and C2 in fig. 2). Time-budget data gathered for all three new individuals were comparable to those gathered in analogous replicates and thus were included in subsequent analyses.

Because *F*-max tests indicated homogeneity of variances (Sokal and Rohlf 1969), we pooled the time-budget data on each activity category from all three experimental replicates for comparison by two-way analyses of variance (4 treatments vs. 5 times of the day). The statistical "treatments" (fig. 1) consisted of before- and after-manipulation data on both control and test birds (i.e., control: before, control: after, test: before, test: after). Thus, each ANOVA included 20 cells with 6 half-hour time-budget samples per cell. The rationale behind these analyses was the assumption that uncontrolled environmental nonstationarities had affected each pair of test and control birds in the same ways and at the same times of the day. Thus, the two-way ANOVA design should be capable of detecting additional nonstationarities in the pooled data imposed by the experimental manipulations (see Sokal and Rohlf 1969). Two such ANOVA's were run for each activity category (foraging, defense, and sitting): Comparison I (fig. 1) tested the effect of halving the number of flowers and thus the initial total standing crop of nectar within the territory; and comparison II (fig. 1) tested the effect of increasing the number of flowers and the initial mean standing crop of nectar within those flowers. In all cases but one, the ANOVA's indicated highly significant differences among treatments, and in every case, lack of significant

TABLE 2

ANALYSES OF VARIANCE COMPARING: A, PERCENT FORAGING TIME; B, PERCENT DEFENSE TIME; AND C, PERCENT SITTING TIME AMONG FOUR TREATMENTS AND FIVE TIMES OF THE DAY FOR EACH EXPERIMENTAL COMPARISON (I and II) DESCRIBED IN FIG. 1

Source	df	MS	Fs
A. Foraging time			
I. Flower density decrease			
Treatments	3	335.6923	7.011 ***
Times of day	4	202.2122	4.223 **
Interaction	12	27.4541	.573 NS
Residual	100	47.8791	
II. Flower density increase			
Treatments	3	595.9990	14.242 ***
Times of day	4	88.3349	2.111 NS
Interaction	12	38.8624	.929 NS
Residual	100	41.8468	
B. Defense time			
I. Flower density decrease			
Treatments	3	36.8276	5.504 **
Times of day	4	10.9429	1.636 NS
Interaction	12	6.0593	.906 NS
Residual	100	6.6906	
II. Flower density increase			
Treatments	3	15.0747	1.486 NS
Times of day	4	9.5566	.942 NS
Interaction	12	7.9897	.787 NS
Residual	100	10.1455	
C. Sitting time			
I. Flower density decrease			
Treatments	3	391.8319	6.776 ***
Times of day	4	188.7790	3.265 *
Interaction	12	30.4894	.527 NS
Residual	100	57.8222	
II. Flower density increase			
Treatments	3	469.0714	9.731 ***
Times of day	4	125.6497	2.607 *
Interaction	12	27.9090	.579 NS
Residual	100	48.2042	

* $P < .05$.

** $P < .01$.

*** $P < .001$.

NS = Not significant ($P > .05$).

interactions between treatments and times of the day (table 2). This allowed us to compare simultaneously by a priori F -tests (Sokal and Rohlf 1969) the percentage of time the test birds spent in each activity after each manipulation (test:after) to that spent before the manipulation (test:before) and to that spent by the control birds during both periods (control:before and control:after). Thus, all tests for changes in the time budgeting of the test birds incorporated the responses of the control birds, and controlled for both environmental differences between days as well as intrinsic differences between individual birds.

RESULTS

Flower Density and Territory Area

Twofold ranges existed in unmanipulated baseline and control territory areas (114.0 to 235.2 m²) and number of included flowers (1,595 to 3,961). Thus, we present experimentally induced changes in the territory area, the mean density of flowers within the territory, and the number of defended flowers in figure 2 as percentages of respective baseline values.

Territory area varied inversely with mean flower density. When half the flowers in each test territory were removed, these territories expanded to 175%, 199%, and 562% of their baseline areas, while all control territories remained well within 20% of their original areas (fig. 2A). One test bird (T3) expanded its range into neighboring territories, with territory boundaries remaining in dispute throughout the day. In this particular replicate, therefore, our measurement of "territory area" actually reflected a disputed foraging range. While both (T3) and another test bird nearly doubled the area of their territories in response to the removal of half their nectar-producing flowers, the third bird (T1) more than quintupled its area. Unlike the others, this individual, whose territory was on the edge of the meadow, expanded its range from a relatively dense patch of flowers into the surrounding sagebrush, which contained many fewer flowering plants. During the flower additions, all test territories decreased in area (fig. 2A). Two birds contracted their ranges to 12.8% and 18.6% below their baseline sizes. The individual that had expanded into the sagebrush (T1) retained a considerable portion (13.4%) of its recently acquired area, presumably because this area cost relatively little to defend.

By adjusting the areas of their territories, the test birds usually compensated for the experimentally induced changes in mean flower density (fig. 2B), such that relatively little proportional change occurred in the number of nectar-producing flowers per individual territory (fig. 2C). The number of flowers within all control territories remained within 10% of their baseline values, while those within one test territory remained within 5% and another within 15% of their original values (fig. 2C). The third test bird (T2) experienced a sustained net loss of over 30% of its baseline number of flowers throughout both manipulations, despite extensive changes in the area of its territory. A possible explanation for this discrepancy is that this individual may have been about to resume migration. During such periods, the birds sometimes relinquish portions of their territories after most of their fat stores have been replenished (Carpenter et al. 1981, MS).

Time Budgeting

Throughout the experiments the three control birds exhibited relatively stable time budgeting, with an overall average of 19.4% of the day spent foraging, 2.8% defending their territories, and 77.8% sitting. These values closely compare with those reported for other hummingbird species (see Stiles 1971; Wolf and Hainsworth 1971; Ewald and Carpenter 1978). Figure 3 depicts average changes in the time budgets of the three test birds relative to their baselines and controls. The left-hand pie diagrams show the average time budgets of the test birds before the

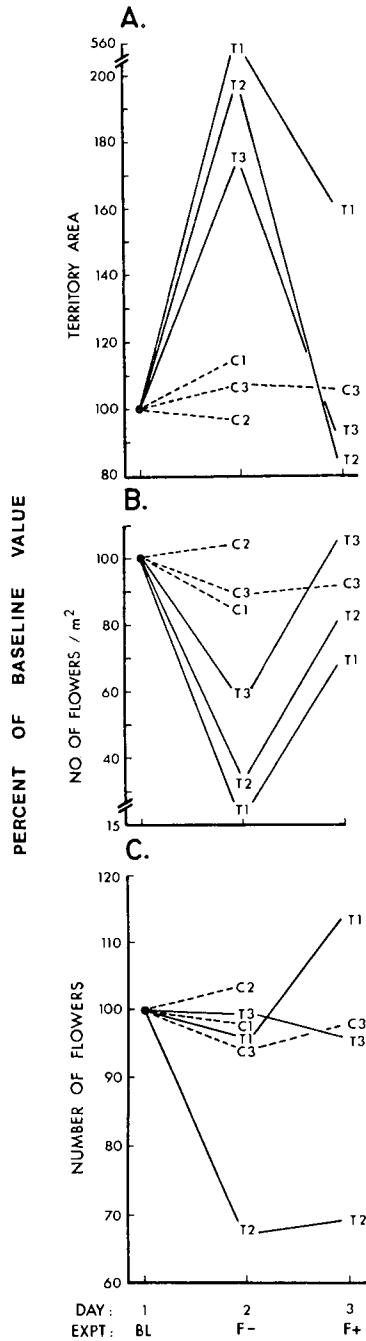


FIG. 2.—Changes in: A, territory area; B, mean density of flowers within the territory; and C, number of flowers included within the territory of each test (T) and control (C) bird at the end of each treatment day: BL, baseline (day 1); F-, flower removal (day 2); and F+, flower addition (day 3). Data are standardized as percentages of respective baseline values. Control birds C1 and C2 emigrated on the final day of the experiment. See text for further explanation.

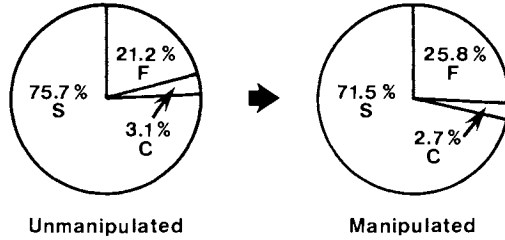
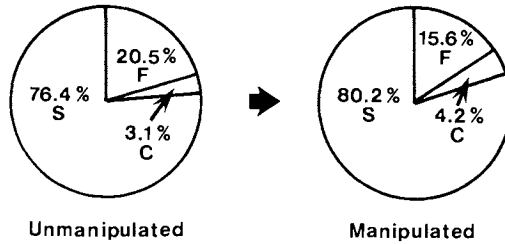
I. FLOWER REMOVAL:**II. FLOWER ADDITION:**

FIG. 3.—Mean daily time-budgeting patterns of test and control birds during the flower removal (I) and addition (II) experiments described in fig. 1. Each left-hand pie diagram represents the mean percentage values of the unmanipulated birds in each case (test:before, control:before, control:after), calculated from 45 h of observation pooled for 6 different individuals. Each right-hand pie diagram represents the mean percentage values of the manipulated birds in each case (test:after), calculated from 15 h of observation pooled for 3 different individuals. F, foraging (nectar-feeding); C, chasing (defense); S, sitting. See tables 2 and 3 for analyses of the data from which these means were derived.

given manipulation pooled with those of respective control birds before and after the manipulation. These averages reflect the unmanipulated system during the experiments, controlling for both temporal and between-individual variation. The right-hand pie diagrams show the average time budgets of the test birds after the given manipulation. These averages reflect the manipulated system. To test for significant changes in time budgeting, we compared the data from which these means were derived.

The *F*-test comparisons of the test birds to their baselines and controls revealed that foraging time varied inversely with flower density and thus with the initial mean standing crop of nectar within the territory. When the density of flowers was halved experimentally, percent foraging time increased by a significant absolute average of 4.6 ($P < .01$, table 3) from 21.2% to 25.8% (fig. 3), which corresponded to a proportional increase of 21.5%. Conversely, when flower density was increased, percent foraging time decreased by a significant absolute average of 4.9 ($P < .001$, table 3) from 20.5% to 15.6% (fig. 3), which corresponded to a proportional decrease of 24.0%.

TABLE 3

F-TESTS COMPARING MEAN TIME BUDGETING OF TEST BIRDS AFTER MANIPULATIONS OF FLOWER DENSITY (test:after) TO THOSE OF UNMANIPULATED CONTROLS (test:before, control:before, and control:after) FOR EACH EXPERIMENTAL COMPARISON (I and II) DESCRIBED IN FIG. 1

Activity	Flower Density Manipulation	Activity Δ%	MS(=SS)	F _{S_{1,100}}
Foraging	Decrease (I)	+4.6	468.0840	9.776 **
	Increase (II)	-4.9	542.4322	12.962 ***
Defense	Decrease (I)	- .4	4.2902	.641 NS
	Increase (II)	+1.1	35.0314	3.453 NS
Sitting	Decrease (I)	-4.2	381.7180	6.602 *
	Increase (II)	+3.8	302.3167	6.272 *

NOTE.—“Activity Δ%” is the difference between the mean percentage value of the test:after data (fig. 3, right) and that of the pooled controls (fig. 3, left). Statistical values were derived from the respective analyses of variance presented in table 2. See text for further explanation.

* *P* < .05.

** *P* < .01.

*** *P* < .001.

NS = Not significant (*P* > .05).

TABLE 4

MEAN FREQUENCY AND DURATION OF NECTAR-FEEDING BOUTS BY CONTROL AND TEST BIRDS ON EACH EXPERIMENTAL DAY (Each value summarizes data from 3 different birds)

FLOWER DENSITY MANIPULATION	FREQUENCY (no./30 min)†		DURATION (sec)‡	
	Control	Test	Control	Test
Baseline (day 1)	9.5	9.5	38.8	44.2
Decrease (day 2)	7.1	7.9	38.7	53.6
Increase (day 3)	8.6	7.6	40.5	35.3

NOTE.—See tables 5 and 6 for analyses of the data from which the bout-duration means were derived.

† *n* = 30 each (10 half-hour sample periods × 3 birds).

‡ *n* = 150 each (5 full-hour sample periods × 10 randomly selected bouts per period × 3 birds).

Changes in foraging time can result from alterations of the frequency and/or duration of foraging bouts (Hainsworth 1978; Hainsworth et al. 1981). Average bout frequency, measured as the number per half-hour sample period, was nearly identical for the control and test birds on each day of the experiments (table 4). Analyses of variance and *F*-tests of this parameter revealed no significant difference among or between treatments throughout the experiments. Foraging-bout duration was analyzed similarly using random subsamples of 10 bouts (allowing equal statistical sample sizes) from each hour-long sample of each control and test bird during each experimental replicate. The averages of these subsamples suggested that, while the control birds remained nearly unchanged, the mean foraging-bout duration of the test birds was strongly affected by the manipulations of flower density (table 4). ANOVA's of this parameter revealed significant differ-

TABLE 5

ANALYSES OF VARIANCE COMPARING FORAGING BOUT DURATION AMONG TREATMENTS AND TIMES OF THE DAY FOR EACH EXPERIMENTAL COMPARISON (I and II) DESCRIBED IN FIG. 1

Source	df	MS	F _s
I. Flower density decrease			
Treatments	3	7316.691	5.150**
Times of day	4	3563.394	2.508*
Interaction	12	1970.697	1.387 NS
Residual	580	1420.641	
II. Flower density increase			
Treatments	3	9583.896	7.958 ***
Times of day	4	1993.506	1.655 NS
Interaction	12	2017.375	1.675 NS
Residual	580	1204.365	

* $P < .05$.** $P < .01$.*** $P < .001$.NS = Not significant ($P > .05$).

TABLE 6

F-TESTS OF CHANGES IN MEAN FORAGING BOUT DURATION OF TEST BIRDS RELATIVE TO CONTROLS, AS DESCRIBED IN TABLE 3 AND SUMMARIZED IN TABLE 4

Flower Density Manipulation	Foraging Bout Δ (sec)	MS(=SS)	F _{s1,580}
Decrease	+ 13.01	19019.001	13.388 ***
Increase	- 8.99	9076.536	7.536 **

NOTE.—Statistical values were derived from the respective analyses of variance presented in table 5.

** $P < .01$.*** $P < .001$.

ences among treatments and lack of significant interactions between treatments and times of the day (table 5). Subsequent *F*-tests showed that, relative to their baselines and controls, the test birds increased the duration of each foraging bout a significant average of 13 s during the flower removals, and shortened each bout a significant average of 9 s during the flower additions (table 6).

In the remaining activities, average defense time showed no significant changes during both the flower removals and additions (table 3), though there was a tendency to decrease during the flower removals and increase during the flower additions (fig. 3). Finally, sitting time decreased significantly during the flower removals and increased significantly during the flower additions (table 3). (Of course, these final tests were not statistically independent of the others, since the entire time budget necessarily totaled 100%.)

DISCUSSION

To our knowledge, these data represent only the second time an inverse relationship between territory area and the availability of naturally occurring food has been demonstrated experimentally for birds. After fertilizing the food plant *Calluna vulgaris*, Miller et al. (1970) observed an eventual decrease in the territory areas of red grouse (*Lagopus scoticus*), although a time lag suggested that the mechanisms involved were indirect.

The results of our experiments with immature migrant hummingbirds indicated that within 1 day following a 50% decrease in flower density: (1) Territory area usually about doubled; (2) the number of defended flowers usually was restored to near the premanipulation value; (3) foraging time increased as a result of an increase in foraging-bout duration, with bout frequency remaining unchanged; (4) sitting time decreased; and (5) defense time did not change significantly. These patterns reversed within 1 day following a subsequent recovery of flower density, except that territory area usually decreased slightly below its original baseline size and foraging time decreased slightly more than it had previously increased.

To what extent can these patterns be explained by current territoriality theory? Formal models of feeding-territory size published to date have been largely descriptive, suggesting which factors interact to determine the optimal defended area (e.g., Davies 1978; MacLean and Seastedt 1979; Tullock 1979; Wittenberger 1981). Other approaches have been to determine which foraging strategy best fits an observed territory size and time budget (Pyke 1979), or to consider territory size in terms of "evolutionarily stable strategies" (Parker and Knowlton 1980). Those optimization models that are predictive have attempted to foresee mainly how territory size itself will respond qualitatively to changes in food benefits (Covich 1976; Ebersole 1980), defense costs (Kodric-Brown and Brown 1978), or both (Schoener 1971, 1977; Schoener and Schoener 1980; Myers et al. 1981; but see Dill 1978 for quantitative simulation analyses). Although heuristically useful, a problem with single qualitative predictions is that, because only three outcomes are possible (i.e., territory size will decrease, increase, or remain unchanged following a given environmental variation), an experimental verification of that single prediction quite easily may be the result of chance alone and may or may not reflect biological reality.

In an effort to provide a more rigorously testable theory capable of generating multiple simultaneous predictions, Hixon (1980) developed a set of models that investigated the effects of both food and competitor density upon both territory size and daily time budgeting for different types of foragers (see below). Each environmental variation, then, resulted in a specific set of predicted changes in territory area, defense time, feeding time, and sitting time. Schoener (1983) extended these and other models into the same format, providing a large matrix of predictions for different types of foragers under different sets of circumstances. If we compare the results of our experiments to both Hixon's (1980) and Schoener's (1983) sets of qualitative predictions, we find that no single set of predictions is entirely supported by our data. The reason for this outcome is that all these

models are too simple in their original forms to adequately mimic the hummingbird system.

In the following sections, therefore, we develop what we presently believe to be the most realistic predictive model of hummingbird territory size. We first review evidence allowing us to classify migrant hummingbirds as a specific type of forager. We then modify Hixon's (1980) model for this type of forager to incorporate crucial aspects of hummingbird foraging and territoriality that were not included in the original version. We stress that the revised model is still a greatly simplified abstraction of a complex reality, incorporating what we believe to be the major relevant factors in a multifactorial system (cf. fig. 8-1 in Gass and Montgomerie 1981). Nonetheless, we show that the modified model generates independent a priori predictions that are corroborated closely in direction by our experimental results. Finally, we use some of our field data to refine a single factor in the model more realistically. The resulting a posteriori version generates quantitative predictions that are much more closely comparable in both direction and magnitude to our experimental results, suggesting that the dynamics of hummingbird territoriality validly may be considered an optimization process.

Migrant Hummingbirds as Energy Maximizers

Because Hixon's (1980) model generates different predictions for different types of foragers, we must first categorize migrant hummingbirds as being basically either energy maximizers or time minimizers (*sensu* Schoener 1971). This section both summarizes and extends previous ideas on this problem detailed by Hixon (1982).

Assuming both these forager types maximize their rate of net energy gain when actually foraging (Pyke et al. 1977), then the essential difference distinguishing them is the relative amount of available time each spends foraging. "Available time" for territorial migrant hummingbirds can be considered one daylight period minus the required daily defense time and any time spent sheltering during foul weather. (Because these birds are nonbreeding and we observed no potential predators at our study site, no time is required for reproductive activities and very little if any for avoiding predation.) Since energy maximizers should spend all available time foraging, such birds would spend an entire day during favorable weather either foraging or defending their territories, thus maximizing their daily net energy gain. On the other hand, since time minimizers should stop foraging after obtaining some fixed daily energy requirement, such birds would exhibit "spare" sitting time each day.

At first glance, categorizing migrant hummingbirds using these criteria seems straightforward: Because they spend about 75% of the day sitting, they should obviously be considered time minimizers (Hixon 1980; see also Wolf et al. 1975). However, two lines of recent evidence suggest independently that sitting time may not be "spare" time and that these birds are in fact energy maximizers. First, preliminary field measurements of weight changes of birds in our system have shown that they not only gain weight while on their territories, but also are capable of individually selecting territory areas that result in an apparently max-

imum rate of weight gain (Carpenter et al., MS). We believe that rapid weight gain is adaptive in these birds because the weather along their mountainous migratory route can be unpredictably harsh. From late July through early September, periodic thunderstorms occur which can be severe enough to prevent foraging (personal observation) or even destroy a large portion of the flowers (Gass and Lertzman 1980). These birds are probably under pressure to reach the more moderate climate of their wintering grounds in Mexico as soon as possible.

Second, combined theoretical and laboratory studies suggest that the duration of a nectar-feeding bout in hummingbirds is constrained by the increasing energetic costs associated with the increasing weight of the meal (DeBenedictis et al. 1978; see also Wolf and Hainsworth 1977). By limiting their meal sizes to nectar volumes less than the maximum crop volume, and interspersing feeding bouts with nonfeeding activities, they are apparently able to maximize their rate of net energy gain during successive foraging bouts over the course of a day (DeBenedictis et al. 1978). These findings suggest that all or part of sitting time constitutes crop-emptying time between successive nectar-feeding bouts. This crop-emptying time may be considered part of the necessary "handling" portion of total foraging time (*sensu* Holling 1965). Thus, despite the fact that hummingbirds spent most of the day sitting, they are actually energy maximizers to the extent that sitting time is required for crop-emptying. Given that it takes about 30–40 min for some hummingbirds to empty a full crop in the laboratory (Hainsworth and Wolf 1972a), and that each of our birds may fill about half its crop during one nectar-feeding bout (Carpenter et al., MS) and averages about 16 bouts per h (table 4), it seems reasonable that most if not all of the 75% of the day spent sitting is required for emptying the crop of nectar obtained during the 20% of the day spent nectar feeding.

In the following section, therefore, we modify Hixon's (1980) model of optimal territory area with the basic tentative assumption that migrant hummingbirds are energy maximizers whose sitting time is required for crop emptying. In the terminology of Schoener (1983), we consider these birds to be energy maximizers with both time constraints and food-processing constraints.

A Model of Optimal Territory Area

Assumptions.—In order to make Hixon's (1980) energy-maximizer model more realistic for the present system, two important aspects of hummingbird foraging and territoriality must be incorporated as assumptions that were not included in the original version. First, previous data indicate that "foraging efficiency" (defined here as the amount of nectar consumed per unit nectar-feeding time) varies directly and reversibly with the available standing crop of nectar per flower (Wolf et al. 1975), which in turn varies directly with the number of flowers in the territory (Kodric-Brown and Brown 1978). Second, local increases in food availability attract nearby hummingbirds to an area (personal observation; see also Yeaton and Laughrin 1976; Lyon et al. 1977; Ewald 1980; Norton et al. 1982), so manipulations of nectar standing crops within a territory are probably accompanied by concurrent changes in the intrusion rate of competitors and thus the

required defense time (see Stiles and Wolf 1970; Wolf 1978). It appears, then, that food availability and intruder pressure are linked in hummingbird systems, which has been demonstrated previously for some territorial animals (e.g., Myers et al. 1979), but refuted for others (e.g., Mares et al. 1982). Note, however, that because hummingbirds typically spend small portions (less than 5%) of the day overtly defending their territories, any absolute changes in defense time accompanying changes in nectar availability will probably be small (see below).

The major assumptions of the original model retained in the new version are that: (1) the territories are noncontiguous and occupy a homogeneous habitat, a simplifying assumption which is approached fairly closely by our system; (2) all intruders are detected and chased, which is almost invariably true in our system (Paton and Carpenter, in press; personal observation); (3) the entire daily food production within the territory is consumed, which is commonly true in our system (Carpenter 1978, 1979; see also table 1); and (4) travel time is not an important constraint, which is certainly true for the short distances our birds fly within their territories.

Development: the baseline system.—The development of the modified model closely follows that of the original version; the reader may refer to Hixon (1980) for additional details and justification of basic assumptions. For a territorial energy maximizer, one daylight period (T_{tot}) is divided into two basic activities:

$$T_{\text{tot}} = T_c + T_f \quad (1)$$

where T_c is the percentage of the day required to chase intruding competitors from the territory, and T_f is the foraging time required to consume and handle the daily nectar production within the territory. Within the time constraint imposed by T_{tot} and because the territory is basically two-dimensional, the required T_c should increase linearly with territory area (A) and local competitor density (C) which, as discussed above, should increase with flower density (F). For simplicity, we assume an approximately linear increase in C with increasing F over the range of parameter values we encountered. Hence, equation (2a) of Hixon (1980) can be modified and summarized as:

$$T_c = k_1 CA = k_2 FA \quad (2)$$

where all k 's are conversion constants.

The required T_f consists of two components, nectar-feeding time [$T_{f(n)}$] and nectar-handling (crop-emptying) time while sitting [$T_{f(s)}$]. Within the time constraint imposed by ($T_{\text{tot}} - T_c$), the value of $T_{f(n)}$ should increase linearly with the number of flowers visited (FA) and decrease with increasing foraging efficiency (E), as discussed above. Hence, equation (3b) of Hixon (1980) can be modified and summarized as:

$$T_{f(n)} = k_3 FA/E. \quad (3)$$

Within the same time constraint, we assume that the value of $T_{f(s)}$ increases linearly with the amount of nectar produced and consumed within the territory, which as discussed above, is a function of (FA). Hence:

$$T_{f(s)} = k_4 FA. \quad (4)$$

When plotted as functions of territory area, these relationships form the linear curves depicted in figure 4B. In summary, at any given values of F and E , the larger the territory area becomes, the more time is required to defend that area adequately and to consume and handle the daily nectar production within that area. Beyond some critical territory area, foraging time (T_f) must decrease as defense time (T_c) increases simply because available time ($T_{\text{tot}} - T_c$) becomes limiting (fig. 4B).

The energetic analogues of these time relationships can be derived from the fact that the energy-budget components of hummingbirds are each linear functions of their respective time-budget components (e.g., Stiles 1971; Wolf and Hainsworth 1971; Hainsworth and Wolf 1972*b*; Ewald and Carpenter 1978). Thus, if we define ΔE as the daily difference between the total energy gained while nectar feeding and the total energy lost while defending the territory, a time analogue is provided by ΔT , defined as $[T_{f(n)} - T_c]$ and indicated on figure 4B. Therefore, given that the assimilation of nectar sugar by hummingbirds is virtually 100% (Hainsworth 1974), ΔT reflects the daily net energy gain (ΔE) available for both maintenance costs and storage for migration, which provides the ultimate criterion for optimal territory area in this system. As depicted, the ΔT of an energy maximizer (ΔT_{max}) reflects the maximum possible daily net energy gain (ΔE_{max}), which occurs at the smallest territory area (\hat{A}) where $(T_c + T_f)$ exactly equals T_{tot} (fig. 4B). Thus, \hat{A} is the optimal territory area. To the left of this optimum, a bird would have "spare" time (T_s in fig. 4B) after defending and consuming the daily nectar production of a smaller territory. To the right of the optimum, the bird would not have enough time after necessary defense activities to consume and "handle" the added nectar production of a larger territory. In either case, ΔT and thus ΔE would not be maximized, so the bird would not be a true energy maximizer. Recent observations suggest that, to the extent daily weight gain reflects ΔE , such a peak in ΔE over a range of territory areas, as depicted in figure 4B, does in fact exist (Carpenter et al. MS).

The baseline system illustrated in figure 4B has been drawn so that the daily time budget at the optimal territory area (\hat{A}) is the same as that commonly found in nature (see Stiles 1971; Wolf and Hainsworth 1971; Ewald and Carpenter 1978), as exemplified by our baseline data depicted in the upper left pie diagram in figure 3: about 3% daily defense time (\hat{T}_c), 21% nectar-feeding time ($\hat{T}_{f(n)}$), and 76% "sitting" time ($\hat{T}_{f(s)}$). Before calculating the changes in this system following a decrease in flower density, we must first derive several more equations. Let F and E represent the values of flower density and foraging efficiency, respectively, in this unmanipulated system. It follows that equations (2) and (4), respectively, can be expressed in terms of equation (3):

$$T_c = (3/21)T_{f(n)} \approx (0.14)T_{f(n)} \quad (5)$$

$$T_{f(s)} = (76/21)T_{f(n)} \approx (3.62)T_{f(n)}. \quad (6)$$

By substitution, equation (1) at the baseline optimal territory area (\hat{A}) becomes:

$$T_{\text{tot}} \approx (0.14)T_{f(n)} + T_{f(n)} + (3.62)T_{f(n)} = (4.76)T_{f(n)} = (4.76)k_3 F\hat{A}/E.$$

Therefore, \hat{A} can be expressed as:

$$\hat{A} \approx T_{\text{tot}}E/(4.76)k_3F. \quad (7)$$

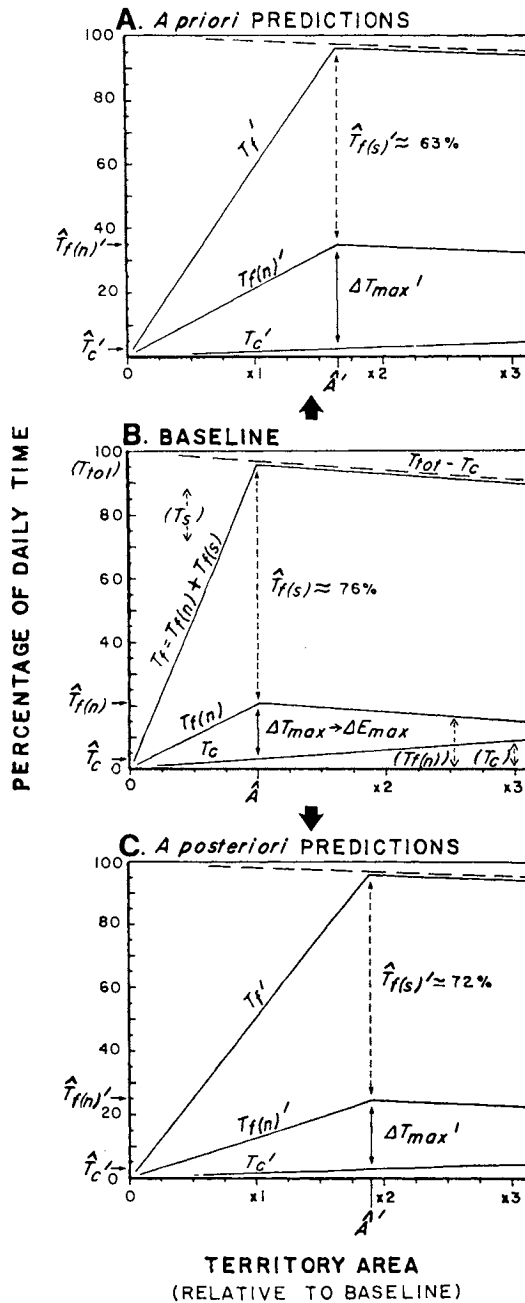


FIG. 4.—Graphical representation of the model depicting predicted changes in territory area and daily time budgeting of a migrant hummingbird one day after a 50% decrease in flower density. The central graph, *B*, depicts the unmanipulated baseline system, while graphs *A* and *C* show alternative changes in the manipulated system predicted by the a priori and a posteriori versions of the model, respectively. The plotted curves show (*continued*)

Equations (2), (3), and (4), respectively, can also be rewritten to express \hat{A} as:

$$\hat{A} = (3)/(k_2F) \quad (8)$$

$$= (21)E/(k_3F) \quad (9)$$

$$= (76)/(k_4F). \quad (10)$$

Let us now consider the changes that will occur in this baseline system following a 50% decrease in flower density.

A priori predictions: the right direction.—Following a 50% decrease in flower density, three concurrent events should interact to change the baseline system depicted in figure 4B. The first event is a decrease in the attractiveness of the territory to intruders. We assume simplistically that a 50% decrease in local flower density should result in about a 50% decrease in the per unit area intrusion rate of competitors. Thus, the required T_c should also decrease by about 50% at any given territory area. That is, equation (2), combined with equation (5), becomes:

$$T'_c = k_2(0.5)FA \approx (0.07)T_{f(n)}. \quad (11)$$

This effect is illustrated in figure 4A, where the slope of the new T'_c curve is half that of the original T_c curve in figure 4B.

Second, the $T_{f(s)}$ required to handle the consumed daily nectar production within the territory should also decrease by about 50% at any given territory area. This is simply because half as many flowers are present in any given area, so only half as much nectar is consumed and passed through the crop. Thus, equation (4), combined with equation (6), becomes:

$$T'_{f(s)} = k_4(0.5)FA \approx (1.81)T_{f(n)} \quad (12)$$

as illustrated in figure 4A.

Third, the decrease in flower density should initially result in the occupant increasing its return rate to individual flowers within the original territory (see Gill and Wolf 1979), causing a decrease in the standing crop of nectar (Kodric-Brown and Brown 1978), a subsequent decrease in foraging efficiency (Wolf et al. 1975), and thus an eventual increase in the average foraging-bout duration required to obtain a given meal size (Wolf and Hainsworth 1977), as we observed (table 6). If the bird subsequently expanded its territory into areas previously undefended and exploited by nonterritorial birds, it would probably encounter flowers with similar reduced standing crops (see Gill and Wolf 1975). Thus, the bird should

FIG. 4. (continued)—daily defense time (T_c) and foraging time (T_f) as functions of territory area, where T_f is divided into time spent nectar feeding ($T_{f(n)}$) and nectar handling (crop emptying) while sitting ($T_{f(s)}$). As illustrated in the lower right corner of graph B, T_c and $T_{f(n)}$ at any given territory area are both measured from the abscissa, while $T_{f(s)}$ is measured as the distance between the $T_{f(n)}$ and cumulative T_f curves. The optimal territory area (\hat{A}) provides an energy maximizer the maximum possible difference between $T_{f(n)}$ and T_c , defined as ΔT_{\max} , which provides the maximum possible daily net energy gain (ΔE_{\max}). The daily time-budget values at this optimum (\hat{T}_c , $\hat{T}_{f(n)}$, and $\hat{T}_{f(s)}$) are indicated along the ordinate. T_s in graph B illustrates the "spare" time that would be experienced by a bird defending a territory area smaller than the optimum, such that $T_c + T_f < T_{\text{tot}}$. See text for further explanation.

experience reduced average foraging efficiency throughout the first day following the manipulation. Because the extent of the decrease in foraging efficiency depends upon the initial standing crop of nectar in any flowers that are added to the territory, as well as the rate at which those flowers are added, an accurate a priori prediction of this decrease cannot be made. We thus assume an approximate 50% decrease in average foraging efficiency. Hence, equation (3) becomes:

$$T_{f(n)'} = k_3(0.5)FA/(0.5)E = k_3FA/E = T_{f(n)}. \quad (13)$$

That is, because both flower density (F) and average foraging efficiency (E) decrease by 50%, equation (3) remains unchanged, as illustrated in figure 4A.

Summarizing the above three events, a 50% decrease in flower density should cause specific changes (or lack of change) in the rates at which T_c , $T_{f(s)}$, and $T_{f(n)}$ increase with territory area. This is illustrated by comparing figure 4A with the baseline system depicted in figure 4B.

The interaction of these events in determining the new optimal territory area (\hat{A}') can be predicted by substituting equations (11), (12), and (13) into equation (1):

$$T_{\text{tot}} \approx (0.07)T_{f(n)} + T_{f(n)} + (1.81)T_{f(n)} = (2.88)T_{f(n)} = (2.88)k_3F\hat{A}'/E.$$

Therefore, \hat{A}' can be expressed as:

$$\hat{A}' \approx T_{\text{tot}}E/(2.88)k_3F. \quad (14)$$

Combining equations (7) and (14), it follows that:

$$\hat{A}' \approx (1.65)\hat{A}. \quad (15)$$

That is, the a priori model predicts that territory area should increase about 65% in area following a 50% decrease in flower density, as illustrated in figure 4A.

As for predicted changes in time budgeting, by combining equations (8), (11), and (15), the new percent defense time is:

$$\hat{T}_c' \approx k_2(0.5)F(1.65)\hat{A} = k_2(0.5)F(1.65)[(3)/(k_2F)] \approx 2\%.$$

By combining equations (9), (13), and (15), the new percent nectar-feeding time is:

$$\hat{T}_{f(n)'} \approx k_3F(1.65)\hat{A}/E = k_3F(1.65)[(21)E/(k_3F)]/E \approx 35\%.$$

Finally, by combining equations (10), (12), and (15), the new percent nectar-handling time while sitting is:

$$\hat{T}_{f(s)'} \approx k_4(0.5)F(1.65)\hat{A} = k_4(0.5)F(1.65)[(76)/(k_4F)] \approx 63\%$$

so that $T_{\text{tot}} = 100\%$ by equation (1). These patterns are illustrated in figure 4A.

Table 7 compares these a priori predictions with the results of the flower removal experiments. The model accurately predicted the direction of changes in the system following a 50% decrease in flower density, but failed to accurately predict the magnitude of those changes. Given the deterministic simplicity of the model, the latter result is not surprising, and we conclude that our general approach to predicting territory area and time budgeting changes is tenable. We now show in hindsight where the model erred, and how a refined a posteriori

TABLE 7
 VALUES OF TERRITORY PARAMETERS FROM FIELD EXPERIMENTAL DATA COMPARED WITH THOSE
 PREDICTED BY TWO VERSIONS OF THE MODEL FOLLOWING A 50% DECREASE IN
 FLOWER DENSITY (See fig. 4 and text)

TERRITORY PARAMETER	EXPERIMENTAL DATA		PREDICTED RESULTS	
	Baseline System	Observed Results	A priori Model	A posteriori Model
Territory area†	1.00x	T1: 5.62x T2: 1.99x T3: 1.75x	1.65x	1.90x
Number of flowers†	1.00x	T1: .96x T2: .67x T3: .99x	.83x	.95x
Defense time (\hat{T}_c)‡	3%	3%	2%	3%
Nectar-feeding time ($\hat{T}_{f(n)}$)‡	21%	26%	35%	25%
Sitting time ($\hat{T}_{f(s)}$)‡	76%	71%	63%	72%

† Measured relative to baseline value (x). Experimental results are listed for three separate replicates (see fig. 2). Predicted number of flowers calculated as predicted territory area times 50% reduction in flower density.

‡ Measured as percentage of the day (see fig. 3 and table 3).

version of the model further validates our optimization approach to hummingbird territoriality.

A posteriori predictions: closer to reality.—As noted above, perhaps the weakest assumption of the a priori model involved the presumed magnitude of changes in foraging efficiency. We could predict in advance that foraging efficiency would decrease following a decrease in flower density, but the extent to which it decreased depended upon factors we could not measure in advance. We therefore assumed a 50% decrease in foraging efficiency. In this section, we revise this estimate in hindsight, leaving the rest of the model the same as the a priori version.

From table 4, the average foraging-bout duration of the test birds increased from 44.2 s to 53.6 s, or 21.3%, during the flower removal experiments, while the control birds remained virtually unchanged. Assuming a nearly constant meal size (nectar volume consumed per foraging bout), as suggested by recent field measurements (Carpenter et al. MS; see also Wolf and Hainsworth 1977; DeBenedictis et al. 1978), these data suggest that the average foraging efficiency of the test birds decreased by about the same extent, roughly 20%. That is, each unit of nectar-feeding time after the manipulation represented about 80% the nectar intake as previously. Thus, the appropriately numbered equation (13) must be revised to read:

$$T_{f(n)}' = k_3(0.5)FA/(0.8)E = (0.625)k_3FA/E = (0.625)T_{f(n)}. \tag{16}$$

This revision is illustrated in figure 4C. Revising the remainder of the model, by substituting equations (11), (12), and now (16) into equation (1):

$$T_{\text{tot}} \approx (0.07)T_{f(n)} + (0.625)T_{f(n)} + (1.81)T_{f(n)} = (2.505)T_{f(n)} \\ = (2.505)k_3F\hat{A}'/E.$$

Therefore, \hat{A}' can now be expressed as:

$$\hat{A}' \approx T_{\text{tot}}E/(2.505)k_3F. \quad (17)$$

Combining equations (7) and (17), it follows that:

$$\hat{A}' \approx (1.90)\hat{A}. \quad (18)$$

That is, the revised model predicts a posteriori that territory area should almost double following a 50% decrease in flower density, as illustrated in figure 4C.

Similar to the previous model, by combining equations (8), (11), and (18), the new percent defense time becomes:

$$\hat{T}'_c \approx k_2(0.5)F(1.90)\hat{A} = k_2(0.5)F(1.90)[(3)/(k_2F)] \approx 3\%.$$

By combining equations (9), (16), and (18), the new percent nectar-feeding time becomes:

$$\hat{T}'_{f(n)} \approx (0.625)k_3F(1.90)\hat{A}/E = (0.625)k_3F(1.90)[(21)E/(k_3F)]/E \approx 25\%.$$

Finally, by combining equations (10), (12), and (18), the new percent nectar-handling time while sitting becomes:

$$\hat{T}'_{f(s)} \approx k_4(0.5)F(1.90)\hat{A} = k_4(0.5)F(1.90)[(76)/(k_4F)] \approx 72\%$$

so that $T_{\text{tot}} = 100\%$ by equation (1). These patterns are illustrated by comparing figure 4C with the baseline system in figure 4B.

Table 7 shows that these a posteriori predictions, generated by estimating a single factor in the a priori model more realistically, approach the results of the flower removal experiments quite closely. The only major disparity is that the model predicted a near doubling of territory area, while one test bird (T1) more than quintupled its area. Recall, however, that this bird expanded its territory into sparsely flowered marginal areas. In fact, this individual and one of the other test birds ended with nearly the same number of flowers as before the manipulations (fig. 2), as predicted by the model (table 7). As discussed above, the test bird (T2) that ended with a substantial net loss of flowers after expanding its territory may have been about to resume migration. (Note that, because the model assumed a homogeneous distribution of flowers, the predicted change in the number of defended flowers assumed that flower density was halved both inside and outside the original territory. In reality, our experiments reduced flower density inside the original territory only. However, the areas into which the bird expanded naturally exhibited similarly low flower densities [fig. 2B], so the prediction is still roughly applicable.)

In any event, these discrepancies suggest two important conclusions. First, they reveal the inadequacy of this simple model to deal with spatial heterogeneity in flower density. Second, because both the number of defended flowers and the required defense time were less labile than the defended area during the course of these experiments, these hummingbirds may perceive territory "size" more in

terms of number of defended flowers than in terms of area per se. Future theoretical explorations should incorporate these ideas.

Finally, note that the predictions of the model would reverse following a subsequent return of flower density to its original value. However, our experimental design not only recovered flower density to near the baseline value (fig. 2*B*), but also greatly increased the initial standing crop of nectar within the flowers that had been covered during the previous day (table 1). This added nectar availability would act to slightly increase the magnitude of the predicted decreases in both territory area and nectar-feeding time relative to their previous increases. In fact, during the flower addition experiments the previous changes in time budgeting and territory area not only reversed in direction, but also differed as predicted in relative magnitude. In particular, territory area usually decreased somewhat below its original baseline size (fig. 2*A*), and nectar-feeding time decreased slightly more than it had previously increased (table 3).

CONCLUSIONS

We interpret these combined experimental and theoretical findings as an indication that territoriality in migrant hummingbirds can be modeled at least roughly in terms of the maximization of daily net energy gain. The often precarious energetic balance and rapid response of hummingbirds suggests that selection for foraging optimization has probably occurred more intensely in these systems than in many others. Although nectar-feeding birds provide excellent model systems for field experiments, the extent to which our findings can be generalized to other systems is unknown. Moreover, we accept our simple model of territory area and time budgeting with necessary caution, given that it represents a deterministic abstraction describing a naturally stochastic and heterogeneous biological system. It is obvious that our understanding of the economics and dynamics of hummingbird territoriality is far from complete, particularly at the level of physiological and behavioral cues and feedback mechanisms. Hummingbirds certainly exhibit extensive decision-making capabilities involving a variety of cues (Gass and Montgomerie 1981; Pyke 1981). However, most advances in understanding the workings of these capabilities have necessarily occurred under confined laboratory conditions (e.g., Wolf and Hainsworth 1977; DeBenedictis et al. 1978; Hainsworth 1978; Hainsworth et al. 1981), although complex artificial environments hold great potential (Gass 1978*a*). Such investigations combined with more detailed field experiments will ultimately allow a closer approach to essence of these mechanisms, and thus more realistic models. At present, we accept the premise that the size of a migrant hummingbird's territory reflects an energy-maximizing optimization process capable of responding to short-term interacting variations in flower density, competitor density, foraging efficiency, and time budgeting.

SUMMARY

While migrating southward each summer along the Sierra Nevada Mountain Range in California, nectar-feeding rufous hummingbirds (*Selasphorus rufus*)

establish feeding territories within isolated meadows. We investigated the effect of variable food density upon territory area and time budgeting by controlled removals and additions of flowers of *Castilleja linariaefolia* within the territories of immature birds. The experiments were replicated three times with generally consistent results.

Within one day following a 50% decrease in flower density: (1) territory area usually about doubled, resulting in (2) the number of defended flowers remaining similar to the premanipulation value; (3) foraging time increased significantly from about 21% to about 26% of the day as the result of (4) a significant increase in foraging bout duration, with (5) bout frequency remaining unchanged; (6) daily sitting time decreased significantly from about 76% to about 71% of the day; and (7) daily defense time did not change significantly at about 3% of the day. These patterns reversed within 1 day following subsequent experimental increases in flower density.

Recent evidence suggests that migrant hummingbirds are energy maximizers that gain weight as rapidly as possible while on their territories. By modifying a simple model of feeding-territory area for such foragers (Hixon 1980) to incorporate previously described aspects of hummingbird foraging, a priori predictions of changes in territory area and time budgeting were generated. The direction of these predictions were independently corroborated by the experimental results. Refining a single factor of the model using our field data produced quantitative a posteriori predictions that very closely approached the experimental results in magnitude as well as direction. These findings tentatively suggest that, in response to short-term variations in food availability, migrant hummingbirds are capable of adjusting territory size and time budgeting in a manner consistent with maximizing daily net energy gain.

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