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Distinguishing Energy Maximizers from Time Minimizers: A Comparative Study of Two Hummingbird Species[1]

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Synopsis. The potential reproductive success of a food energy maximizer increases with foraging time, while that of a foraging time minimizer increases with time spent in nonforaging activities given a set energy requirement has been met. How can these foraging "goals" be distinguished for nonbreeding animals in the field? If individuals of two species occupying the same habitat consume the same foods, face similar foraging constraints, and have similar meal sizes (food intake per foraging bout), then relative to a time minimizer, an energy maximizer should: (1) spend more time foraging, with greater foraging-bout frequency, but no difference in foraging-bout duration; (2) spend less time sitting, with lower sitting-bout duration yet greater sitting-bout frequency; (3) gain mass more rapidly, if net energy intake results in mass accumulation; and (4) exhibit no other differences in time budgeting. These assumptions and predictions were verified by population- and individual-level comparisons of immature males of two species of nectar-feeding hummingbirds studied over three field seasons. The results suggest that, relative to each other, migrant Rufous Hummingbirds are energy maximizers and nonmigrant Costa Hummingbirds are time minimizers. Despite significant differences in time budgeting, by far the most striking difference between the species was that the Rufous gained mass four to eight times as rapidly as the Costa. This was due to the Rufous entering torpor at night, resulting in relatively little overnight loss in body mass. These patterns underscore the importance of measuring net energy intake as directly as possible (in this case by fat accumulation) in testing foraging theory. Indirect measures (such as time budgets) may not always provide the resolution necessary to detect important energetic differences between different foragers.

Introduction

A major area of study where energetics and animal behavior interface is foraging theory. Indeed, in virtually all foraging models, energy is considered to be the "currency" relating inherited behavior to reproductive success (recent reviews by Krebs and McCleery, 1984; Pyke, 1984). A fundamental requirement for testing such models is to determine the forager's "goal," which defines the limit to which increasing net energy gain increases potential fitness. Schoener (1969, 1971) introduced and contrasted two broad goals, which can be distinguished by considering an animal's net energy gain ($\boldsymbol{E}$) over some arbitrary time period ($\boldsymbol{T}$) spent foraging (T_f), being inactive ("sitting," T_s), and performing other activities (T_o), such that:

$$\boldsymbol{T} = T_f + T_s + T_o. \qquad (1)$$

Food *energy maximizers* are animals whose potential reproductive success increases with net energy intake during $\boldsymbol{T}$. Such animals are selected to maximize $\boldsymbol{E}$ and thus T_f (consequently minimizing T_s and T_o). Therefore, energy maximizers spend as much time as possible foraging, subject to any constraints requiring other behaviors. On the other hand, feeding *time minimizers* are animals whose reproductive success is not limited by energy intake during $\boldsymbol{T}$ beyond some set requirement. Once this requirement is met, such animals are selected to spend time in nonforaging activities. That is, $\boldsymbol{E}$ is a fixed quantity, so these foragers are selected to minimize the

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T_f required to obtain $\boldsymbol{E}$, thereby maximizing T_s or T_o.

While energy maximizers are selected to minimize both T_s and T_o, time minimizers maximize one or the other of these parameters depending upon their reproductive state. During the breeding season, they presumably maximize T_o in terms of time spent in courtship and other behaviors directly related to reproduction (Schoener, 1971; Hixon, 1987). Between breeding seasons, time minimizers seem to maximize sitting time (T_s), thus minimizing exposure to predators and other sources of injury or mortality (see Herbers, 1981).

Nonbreeding vertebrates typically spend most nonforaging time sitting rather than in other activities (review by Herbers, 1981). For such animals, the only practical difference between the two foraging goals is that, because an energy maximizer spends all available time foraging, it sits only when required to do so by internal or external constraints (Hixon, 1982). A nonbreeding time minimizer sits as much as possible—more than required by such constraints. Thus, the duration of a sitting bout ($\boldsymbol{S}$) consists of two components, time required by constraints (S_c) and "spare" time (S_s), such that:

$$\boldsymbol{S} = S_c + S_s. \tag{2}$$

For either forager, S_c may be zero or positive, but is probably positive for most animals, including the subjects of this paper, hummingbirds (see below). By definition, S_s equals zero for energy maximizers and is positive for time minimizers. Thus, an animal that spends no time sitting, foraging constantly except when interrupted by behaviors of higher priority (such as predator avoidance), is self-evidently an energy maximizer (Hixon, 1982). If, as more commonly observed, an animal alternates its behavior between foraging time and sitting time (review by Herbers, 1981), then S_c and/or S_s are positive and the foraging goal is not self-evident.

Thus, the intuitive appeal of the energy maximizer–time minimizer dichotomy belies the difficulty of its application. In addition to problems concerning sitting time, consider some of the key terms in the previous paragraphs. How can one measure "net energy intake"? How is one to know whether an animal is sitting because it has met some "set" energy requirement (time minimizer) or because it has faced some "constraint" (energy maximizer)? Indeed, what are the "constraints" that face a foraging animal? Such questions are not trivial. Determining net energy intake requires either direct physiological measurements, or, if the intake is stored as fat or other tissue, repeated measurements of body mass without disturbing the animal. Because of the logistic problems associated with such measurements, time budgets are often assumed to reflect underlying energy budgets. However, observing animals only while they are foraging does not allow foraging goals to be determined. In particular, Pyke *et al.* (1977) argue that both energy maximizers and time minimizers should maximize the rate of net energy intake as much as possible while actually foraging (*i.e.*, during T_f), and thus should have similar foraging rates *ceteris paribus.*

Constraints are even more problematical, ranging from internal limits on the rate of food handling and processing to external conflicts between foraging, predator avoidance, competitive interactions, maintenance, and social/reproductive behaviors. Such constraints can even modify foraging goals. For example, energy maximization can be subject to "risk minimization" in terms of predator avoidance (Sih, 1980), and time minimization can be subject to "area maximization" in terms of sexual selection operating on territorial males (Hixon, 1980, 1987).

How, then, can nonbreeding energy maximizers and time minimizers be distinguished in the field? Previous approaches have employed either absolute or relative determinations. Absolute determinations consider the foraging goals to be precise points within a universe of possible behaviors. Such studies require accurate measurements of constraints, costs and benefits, and explicit quantitative predictions associated with each goal. Although labor intensive, this approach has been applied successfully to a variety of terrestrial herbivores by Belovsky (1978, 1984*a*, *b*, 1986).

His linear programming techniques indicated that various insects and mammals select diets predicted for energy maximizers. Similarly, Pyke (1979) generated alternative quantitative predictions of time budgeting for a variety of foraging goals and found that sunbirds budget time as predicted for "energy cost minimizers" (similar to time minimizers).

Relative determinations consider the foraging goals to be positions along a continuum of possible behaviors, where one individual or species can be considered more or less of an energy maximizer than other individuals or species, depending upon its position relative to the other's. For example, Schoener (1971) suggested that, within species, females would be energy maximizers relative to males (and conversely, males would be time minimizers relative to females). The resulting prediction that females should spend more time foraging than males was tested experimentally for sex-changing coral-reef fish by Hoffman (1983). Fish that were induced to change sex from female to male decreased their foraging time, suggesting that males were indeed time minimizers relative to females. A variety of observational evidence from other systems supports this general conclusion (review by Hixon, 1987).

For relative comparisons between species, distinguishing foraging goals can be difficult if the species are dissimilar functionally or ecologically. This is because constraints and local environments are likely to differ between the species, resulting in differences in behavior unrelated to foraging goals. However, if the species occupy the same habitat and are closely related or otherwise similar morphologically, physiologically, and ecologically (*e.g.*, are congeneric members of the same foraging guild), then the constraints facing the two species are likely to be comparable and relative predictions are possible. Moreover, the assumed similarities between the species can be tested along with the predicted differences, providing sufficiently strong inference for distinguishing relative foraging goals. The purpose of this paper is to develop such means of distinguishing energy maximizers from time minimizers at a relative level for similar species. The predictions include both time-budget parameters and changes in body mass. We present a case study testing these predictions observationally for two species of nectar-feeding hummingbirds.

PREDICTED DIFFERENCES BETWEEN ENERGY MAXIMIZERS AND TIME MINIMIZERS

Consider nonbreeding individuals of two diurnal species of the same foraging guild occupying the same habitat. The animals consume the same kinds of food, and alternate their behavior between foraging and sitting, with occasional bouts of other activities. If the species are similar morphologically and physiologically, then they are likely to have similar metabolic rates and face the same internal constraints while foraging. External constraints (risk of predation, competitive behavior, etc.) can be documented provided the animals can be observed adequately. Assuming the constraints are comparable, the goal is to determine the relative positions of the two species along the energy maximizer–time minimizer continuum.

The simplest prediction is that energy maximizers should spend more time foraging than time minimizers (Hixon, 1982). However, more detailed predictions are also possible and testable by observation. If both species forage with similar efficiencies (food intake per unit foraging time, e) and have comparable meal sizes (food intake per foraging bout, m), then they should have comparable foraging-bout durations ($\boldsymbol{F} = m/e$). Available evidence suggests that the subjects of our study, hummingbirds, are capable of optimizing meal size (DeBenedictis *et al.*, 1978), so individuals of similar body size and morphology are likely to exhibit fixed and similar meal sizes. Thus, if all constraints and resulting foraging efficiencies are comparable, the two species should exhibit the same meal sizes, foraging efficiencies, and foraging-bout durations *regardless of their respective foraging goals.*

The differences between forager types should lie in other parameters. As argued

TABLE 1. *Assumed similarities and predicted differences between energy maximizers and time minimizers compared with observations of 5 Rufous and 6 Costa hummingbirds during 1985 and 1986 ("Population-level") and 1 Rufous and 1 Costa which occupied the same territory sequentially during 1983 ("Individual-level").*[a]

	Predicted		Observed					
			Population-level			Individual-level		
Mean parameter value	Energy maximizer	Time minimizer	Rufous	Costa	P	Rufous	Costa	P
Meal size, m (g nectar):	-- no difference --		0.06	0.05	ns	0.06	0.05	ns
Foraging efficiency, e (g/min):	-- no difference --		0.05	0.05	NA	0.04	0.04	NA
Foraging time, T_f (min/hr):	high	low	12.6	10.8	*	19.1	13.2	***
Bout duration, $\boldsymbol{F}$ (min):	-- no difference --		1.1	0.9	ns	1.6	1.2	***
Bout frequency, f (no./hr):	high	low	11.4	12.0	NA	11.9	11.0	NA
Sitting time, T_s (min/hr):	low	high	36.8	40.8	**	33.2	35.4	ns
Bout duration, $\boldsymbol{S}$ (min):	low	high	4.6	5.0	ns	4.0	5.1	***
Bout frequency, f (no./hr):	high	low	8.4	8.2	NA	8.3	6.9	NA
Rate of weight gain (g/d):	high	low	0.23	0.03	***	0.23	0.06	***
Other parameters (T_o):								
Defense time (min/hr):	-- no difference --		2.1	3.0	*	2.2	3.0	ns
Insect-hawking time (min/hr):	-- no difference --		0.7	1.0	ns	0.7	0.7	ns
Perch changing time (min/hr):	-- no difference --		1.7	1.8	ns	0.5	0.3	*

[a] See text for sample sizes and statistical tests used. P values: ns, >0.05; *, <0.05; **, <0.01; ***, <0.001; NA, not applicable (values calculated from and therefore not independent of other parameters).

above, energy maximizers should by definition exhibit shorter sitting bouts ($\boldsymbol{S}$) than time minimizers, being S_c rather than $(S_c + S_s)$ in duration (eq. 2). Consequently, they should have a greater foraging-bout frequency (f_E) than that of time minimizers (f_T). Ultimately, this should result in energy maximizers gaining mass at a greater rate, assuming that net energy gain is stored as fat or other tissue over the duration of the study. Because energy maximizers feed more frequently than time minimizers, they should also sit more frequently ($f_E > f_T$), each foraging bout necessarily being followed by a nonforaging bout and sitting presumably being the primary nonforaging behavior for nonbreeding animals. This assertion assumes that nonforaging, nonsitting activities (T_o) interrupt foraging and sitting bouts with equal frequency, a simplifying but not essential assumption. The result is that energy maximizers should have shorter, but more frequent, sitting bouts than time minimizers. Overall, energy maximizers should spend more time foraging (T_f) and less time sitting (T_s) each day than time minimizers.

If the species are truly similar in all respects except their foraging goals, then the amount of time they spend in each nonforaging, nonsitting behavior each day (collectively, T_o) should be the same. This prediction is important in testing the assumption of similarity of the species independent of their respective foraging goals.

Thus, in simplest terms a nonbreeding energy maximizer's total time is partitioned such that:

$$\boldsymbol{T} = f_E(m/e + S_c) + T_o, \qquad (3)$$

and that of a nonbreeding time minimizer is partitioned such that:

$$\boldsymbol{T} = f_T(m/e + S_c + S_s) + T_o, \qquad (4)$$

where $f_E > f_T$, and assuming the animals are identical in every way except for their foraging goals. The left side of Table 1 summarizes these assumed similarities and predicted differences between energy maximizers and time minimizers.

Study species: Constraints and hypothesized goals

Hummingbirds are excellent candidates for testing foraging theory because they and their food (flower nectar) are easy to observe, measure, and manipulate. Moreover, these birds respond rapidly to manipulations of their natural food supplies, so hours and days provide realistic time scales for measuring and comparing foraging parameters (Hixon *et al.*, 1983). Also, we are confident that we have identified the major constraints facing these birds at our study site, where we have worked since 1976. The external constraints are few: (1) We study the birds during the nonbreeding season (mid-July to early September), so reproductive constraints are unimportant. (2) This particular study included only immature males, thus removing any differences in constraints due to sexual differences. (3) Predators were not present during our study, and in general North American hummingbirds appear to be largely immune to predation (Miller and Gass, 1985). (4) Besides during storms, there are no foraging constraints due to weather. Except for one day (discussed below), this study was conducted during weather which did not inhibit foraging. (5) Any nutrient constraints from nectar-feeding are ameliorated by the birds hawking superabundant small insects several minutes each day. (6) The only potentially significant external constraint that interrupts foraging by our birds is competition for nectar with other birds (and occasionally bumblebees [Carpenter, 1979]). Consequently, our birds are both interspecifically and intraspecifically territorial, spending about 5% of the day chasing intruders from their territories (Hixon *et al.*, 1983). Together, territorial defense and insect-hawking represent the major components of T_o in eqs. 3 and 4.

Hummingbirds do face an important internal foraging constraint: the rate of emptying nectar from the crop into the digestive system (Karasov *et al.*, 1986; summarized by Diamond *et al.*, 1986). The birds fill their crop while foraging much more rapidly than the crop empties, so they are constrained to spend some time sitting between foraging bouts. Conceptually, this crop-emptying time while sitting is analogous to handling time while foraging (Hixon, 1982; Hixon *et al.*, 1983), and represents S_c in eqs. 3 and 4.

The two species we compared were the Rufous Hummingbird (*Selasphorus rufus*) and the Costa Hummingbird (*Archilochus* [formerly *Calypte*] *costae*). Immature males are similar morphologically, exposed culmen lengths and body sizes overlapping and Rufous having slightly shorter wings (Johnsgard, 1983). In terms of energetic cost of flight, the greater wing disc loading of Rufous (ratio of body mass to area swept by wings) may confer a territorial advantage in maneuverability during aggressive encounters, yet a compensatory disadvantage in hovering while probing flowers (Feinsinger and Chaplin, 1975). The torpid, resting, active, and flying metabolic rates of the species are comparable over a broad range of temperatures (Lasiewski, 1963), as are their body temperatures, heart and breathing rates, and evaporative water loss (Lasiewski, 1964).

Overall, the major differences between the species are behavioral. The Rufous occur at our California study site as long-distance migrants en route to their wintering grounds in Mexico from their breeding areas between Oregon and Alaska (Johnsgard, 1983). The birds stop periodically and replenish their fat stores in preparation for continued migration (Carpenter *et al.*, 1983). During refattening, virtually 100% of their increase in body mass above 3.5 g is fat (C. A. Beuchat, personal communication). Because flower nectar is often limiting (Carpenter, 1978), the birds typically maintain individual feeding territories during their one- to two-week tenure at our site (Carpenter *et al.*, 1983; Hixon *et al.*, 1983). Being the aggressive dominant, Rufous displace Costa and other species when they are abundant, which occurs most years.

The Costa at our site are relatively nonmigratory, although they do make short-distance movements in the southwestern United States (Johnsgard, 1983). At our study site, they have been sufficiently abundant to study during three years while we were present (1980, 1983, and 1986). During other years, either the Rufous arrived and displaced the Costa early or the Costa were rare for other reasons. When present at our site, Costa also defend feeding territories, but usually do so less effectively than Rufous.

In our previous studies, we have argued that migrant Rufous are energy maximizers, selected to reach their wintering grounds as soon as possible. First, because they fledge their young late in the year, the weather during their migration is starting to deteriorate, and storms can prevent foraging, with potentially fatal consequences (Gass and Lertzman, 1980). Second, the birds adjust their territory sizes both naturally (Carpenter *et al.*, 1983) and following manipulations of flower density (Hixon *et al.*, 1983) in ways that are consistent with energy maximization. Third, recently the assumption of energy maximization was tested more directly. In the absence of significant external constraints, a sitting hummingbird that was an energy maximizer with a crop-emptying constraint would resume foraging as soon as the crop emptied sufficiently (Hixon, 1982). This prediction was verified tentatively by Karasov *et al.* (1986; summarized by Diamond *et al.*, 1986), who concluded from physiological measurements that the frequency of foraging bouts in Rufous captured from our site was the maximum possible given the amount of time required for crop-emptying while sitting. This result supported the assertion that S equals only S_c for energy maximizers (eq. 2).

Thus, our previous data supported our hypothesis that migrant Rufous were energy maximizers. Because Costa at our site were not long-distance migrants, we hypothesized further that, relative to Rufous, they were time minimizers. Comparing these species at the same site provided an opportunity to test the hypothesized foraging goals more closely by evaluating the assumed similarities and predicted differences in meal size, foraging efficiency, time budgeting, and rate of mass gain listed on the left side of Table 1.

METHODS

Study site

Our permanent study site is a stream-fed meadow occupying several hectares at the eastern base of the Sierra Nevada 27 km NW of Bishop, California (37°30′N lat., 118°30′W long., 1,700 m elevation). The meadow is situated on an alluvial slope dominated by sagebrush. A small stream supports dense stands of small willow trees, which are bordered by a broad zone of grassland interspersed with various small shrubs. The flowering plant used by the hummingbirds is the herbaceous perennial Indian Paintbrush (*Castilleja linariaefolia*, Scrophulariaceae), small patches of which are fairly evenly distributed within the grass zone. See Hixon *et al.* (1983) for a more detailed description of the site.

Time budgets

Individuals of both species were active from approximately 0600 to 2000 hr each day. To control for potential intrinsic cycles or environmentally induced variations in behavior during the course of the day, we time-budgeted each study bird during one-hour observation periods beginning at 0630, 0930, 1230, 1530, and 1830 hr, for a total of 5 hr per day. Each time budgeter observed one bird from a ladder or car roof located outside the territory, and recorded data on Observational Systems battery-powered event recorders. Periodically, the data were transferred directly to a portable minicomputer for storage on diskettes. The event recorders enabled us to gather and store detailed time and frequency data without taking our eyes off the study birds.

The timed variables were: (1) nectar-feeding at various locations, (2) thieving nectar from neighboring territories, (3) hawking insects (averaging less than 1 min/hr), (4) perching at various locations, (5) preening (while perching), (6) flying between perches (usually less than 1 min/hr), (7) chasing intruders, (8) being chased by other birds, and (9) lost from sight (usually less than 3 min/hr). For the present analyses, we pooled variables 1 and 2 as "foraging" (*i.e.*, involving energy intake, as opposed to the nutrient intake of insect-hawking), variables 4 and 5 as "sitting," and variables 7 and 8 as "defense." Time "lost" was not analyzed so that the other timed variables could be considered statistically independent (*i.e.*, totalling less than the entire observation time).

Weight gain

We weighed each study bird repeatedly by replacing its favorite natural perch with an electronic perch-balance. The apparatus, described and illustrated in Carpenter *et al.* (1983), is basically a Mettler PE-200 or PE-300 top-loading balance with a perch attached to the pan. The balance is accurate to 0.01 g, has a mechanism for damping variations due to a fidgeting bird or a slight breeze, and is powered by batteries charged by solar panels. The balance interfaces with the event recorder by cable, allowing body-mass data and time-budget data to be recorded simultaneously.

The perch-balances allowed us to record three parameters. First, meal size (grams of nectar) was measured as the difference in the mass of a sitting bird just before and just after an uninterrupted foraging bout. If the bird defecated during the bout, resulting in an unusually low reading (0.01 g or less, sometimes negative), the value was ignored. Second, rate of body-mass gain (g/day) was measured by averaging all masses during observation period 3 (1230–1330 hr) and comparing averages between sequential days. (Period 2 or 4 was used in several cases when no mass data could be gathered during period 3.) Third, overnight body-mass loss (g) was estimated as the difference between the latest reliable mass measurement at dusk (period 6: 1830–1930 hr) and the earliest measurement at dawn the next morning (period 1: 0630–0730). The birds did forage after period 6 and before period 1, but we were unable to weigh the birds on their nocturnal roosts, so these estimates were useful only for comparative purposes. For all three parameters, a study bird would occasionally not use its perch-balance during an entire period, precluding any mass data.

Other measurements

Although largely unreported here, we also measured the territory area of each bird, the number of flowers within the territory, and nectar productivity (volume/flower/day) and concentration (mass of sucrose equivalents/volume), which provided direct measures of the dynamics and availability of food energy (see Carpenter, 1983; Hixon *et al.,* 1983). Nectar concentration did not change substantially within each studied territory, and was not appreciably different between territories.

Testing assumptions and predictions

Drawing conclusions from observational tests of hypotheses can be risky because so many potentially important factors are uncontrolled. This is especially true for hummingbirds, which respond rapidly and dramatically to environmental changes. Therefore, we compared the two species at two complementary and independent levels: "population" and "individual." At the population level, we compared 30 days (150 observation periods) of data equally distributed between 5 Rufous and 6 Costa individuals studied during the 1985 and 1986 field seasons. This analysis had the advantage of sampling a representative number of individuals for a substantial period of time, but the disadvantage of each bird facing a unique local environment in terms of the number of flowers it defended, the spatial distribution of those flowers, the number of territorial neighbors, the density of nonterritorial intruders, and other factors.

Complementing the population-level comparison, we had an unusual opportunity during the 1983 field season which provided a so-called "natural experiment" for comparing the species at an individual level. We studied an immature male Costa intermittently over a 6-day period. We then observed an immature male Rufous of the same body mass displace the Costa and maintain virtually the same territory (Fig. 1) for the next 6 days until it resumed migration. Thus, we were able to compare the use of the same flower patch by individuals of the same sex, maturity, and initial mass belonging to different species. This opportunity provided an independent and more detailed individual test of the assumptions and predictions associated with the hypothesized foraging goals.

Statistical analyses

Data for each time-budget parameter (min/hr) were grouped by the five daily observation periods for each species. The grouped data were tested for normality by probability plots, and for homogeneity of variances by F-max tests. Data that met these assumptions before or after trans-

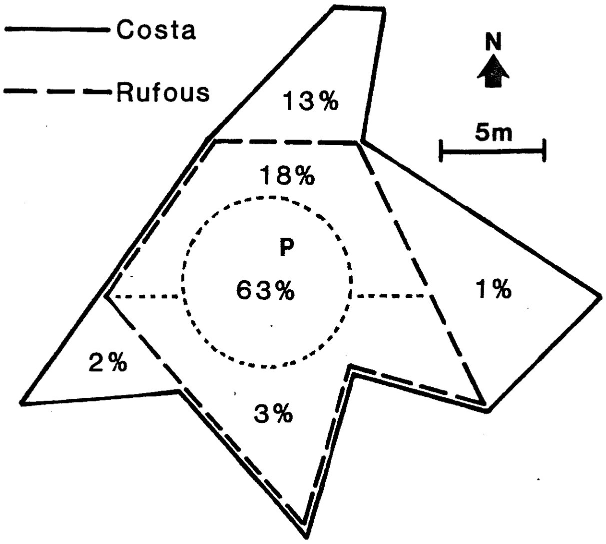

FIG. 1. Map of the areas sequentially defended by an immature male Costa Hummingbird and an immature male Rufous Hummingbird during 1983 (individual-level comparison). Concavities in the territory boundaries were areas containing no flowering plants. The percentages denote the approximate distribution of flowers by arbitrary sections, based on complete flower censuses. The circular section delimits the core patch of flowers. The "P" indicates the position of the electronic perch balance.

formation were analyzed by parametric methods, and those that did not were analyzed by nonparametric analogs.

Values of each parameter were plotted against observation period for each species. All trends were linear. Linear regression analysis of each parameter on observation period was run for each species, and subsequently compared between species. In each case, if the slopes of both regressions were not significantly different from zero, then the data were analyzed by 1-way ANOVA or nonparametric Kruskal-Wallis tests. If the slopes of both regressions were significantly different from zero, but not from each other, then ANCOVA was used. Otherwise, 2-way ANOVA or nonparametric Friedman tests of species by observation period was employed. None of the 2-way ANOVAs detected a significant interaction term.

Data on uninterrupted bout durations (min) and meal sizes (g nectar) were not sufficiently abundant to allow grouping by observation period for the individual-level comparisons. These data were compared by *t*-tests or nonparametric Mann-Whitney *U*-tests. Rates of daily body-mass gain (g/day) and overnight body-mass loss (g) were compared by *t*-tests.

By definition, bout frequency (no./hr) is total time (min/hr) divided by bout duration (min). Because the event recorders readily provided total times and uninterrupted bout durations for foraging and sitting, average bout frequencies were calculated rather than measured directly. Similarly, average foraging efficiency (g/min) was estimated as average meal size (g) divided by average foraging-bout duration (min). Because these calculated parameters were not independent of the measured parameters, statistical comparisons were not justified.

We argue that these analyses did not involve so-called "pseudoreplication." This was a study of behavior, which necessarily occurs through time. Each bird represented a "population" of behaviors which were sampled systematically. We maintain that our one-hour observation periods constituted independent, replicate samples because of the nature of hummingbirds. Having among the highest metabolic rates known, these birds respond within an hour to environmental changes (Hixon *et al.*, 1983), so samples separated by 2 hr arguably record independent sets of behaviors.

RESULTS AND DISCUSSION

Population-level comparisons

We recorded 7,188 behavioral bouts during the 75 hr we observed 5 Rufous immature males, and 8,962 bouts during the 75 hr we observed 6 Costa immature males during 1985 and 1986. Comparing the species largely supported the assumptions and predictions associated with the hypothesis that the migrant Rufous were energy maximizers and the basically nonmigrant Costa were time minimizers. Considering the assumptions and predictions in the sequence listed in Table 1 (except for bout frequencies, see below):

(1) The assumption that the average meal sizes of the species were not significantly different was verified (Rufous: 0.06 g, n = 164; Costa: 0.05 g, n = 176; $P > 0.05$, 1-way ANOVA).

(2) The assumption that foraging efficiencies were comparable was verified by our calculated estimates of 0.05 g nectar/min for both species.
(3) As predicted, the Rufous spent more time foraging than the Costa on average (Rufous: 12.6 min/hr, n = 75; Costa: 10.8 min/hr, n = 75; $P < 0.05$, 1-way ANOVA).
(4) The assumption that the average uninterrupted foraging-bout durations were not significantly different was verified (Rufous: 1.1 min, n = 75; Costa: 0.9 min, n = 75; $P > 0.05$, Kruskal-Wallis 1-way ANOVA).
(5) As predicted, the Rufous spent significantly less time sitting than the Costa on average (Rufous: 36.8 min/hr, n = 75; Costa: 40.8 min/hr, n = 75; $P < 0.01$, 2-way ANOVA).
(6) Although the average uninterrupted sitting-bout duration of the Rufous was less than that of the Costa, as predicted, the difference was slight and not significant (Rufous: 4.6 min, n = 75; Costa: 5.0 min, n = 75; $P > 0.05$, Kruskal-Wallis 1-way ANOVA).
(7) The prediction that the Rufous should gain mass at a greater rate than the Costa was strikingly verified. The Rufous gained an average of 0.23 g/day (n = 12), while the Costa gained an average of only 0.03 g/day (n = 9). The difference was highly significant ($P < 0.001$, *t*-test).
(8) The assumption that there should be few differences between the birds in other behaviors was verified (Table 1), especially considering insect-hawking and perch-changing time (n = 75 each per species; $P > 0.05$, Kruskal-Wallis 1-way ANOVAs). Although average defense times were also similar, they were nonetheless significantly different (Rufous: 2.1 min/hr, n = 75; Costa: 3.0 min/hr, n = 75; $P < 0.05$, Friedman 2-way ANOVA).

Individual-level comparisons

We recorded 2,696 behavioral bouts during the 22 hr we observed the immature male Costa, and 2,816 bouts during the subsequent 28 hr we observed the Rufous that occupied the same territory in 1983. Comparing the behavior of these birds further bolstered the conclusion that the Costa was a time minimizer and the Rufous was an energy maximizer. Again considering the assumptions and predictions in the sequence listed in Table 1 (except for bout frequencies, see below):

(1) The assumption that the average meal sizes were not significantly different was verified (Rufous: 0.06 g, n = 39; Costa: 0.05 g, n = 12; $P > 0.05$, *t*-test).
(2) The assumption that foraging efficiencies were comparable was verified by our calculated estimates of 0.04 g nectar/min for both birds.
(3) As predicted, the Rufous spent more time foraging than the Costa on average (Rufous: 19.1 min/hr, n = 28; Costa: 13.2 min/hr, n = 22; $P < 0.001$, ANCOVA).
(4) Although average uninterrupted foraging-bout durations were similar, as predicted, they were nonetheless significantly different (Rufous: 1.6 min, n = 160; Costa: 1.2 min, n = 82; $P < 0.001$, Mann-Whitney *U*-test).
(5) Although the Rufous spent less time sitting than the Costa on average, as predicted, the difference was not significant (Rufous: 33.2 min/hr, n = 28; Costa: 35.4 min/hr, n = 22; $P > 0.05$, 1-way ANOVA).
(6) As predicted, the average uninterrupted sitting-bout duration of the Rufous (4.0 min, n = 202) was less than that of the Costa (5.1 min, n = 108; $P < 0.001$, Mann-Whitney *U*-test).
(7) The prediction that the Rufous should gain mass at a greater rate than the Costa was again strikingly verified. As illustrated in Figure 2A, the Costa gained 0.38 g over 6 days, an average of 0.06 g/day, while the Rufous gained 1.17 g over 5 days, an average of 0.23 g/day. The difference in rate of mass gain was highly significant ($P < 0.001$, *t*-test). Note that the Rufous lost mass during its first full day on the territory (18 August, Fig. 2A), when heavy rainfall from a passing storm prevented foraging. This loss did not affect the

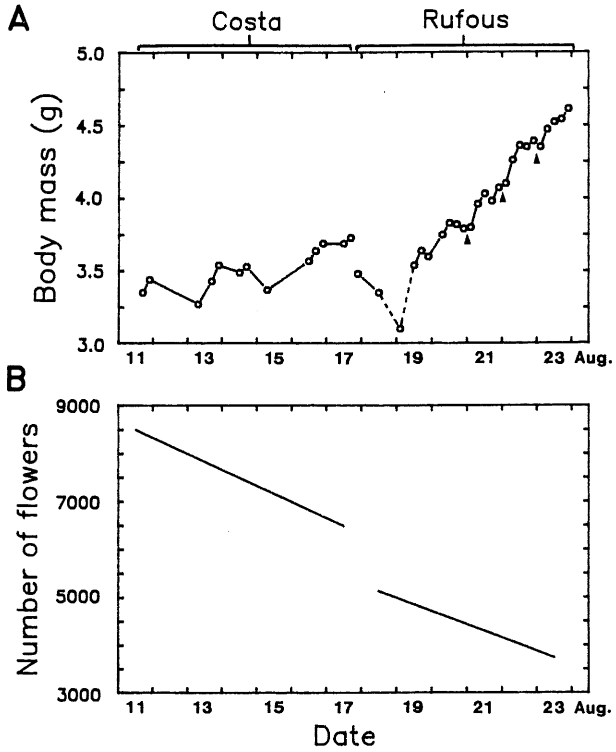

FIG. 2. A. Average body mass of each territory occupant by observation period over the duration of the 1983 study. Arrows indicate times when body masses were obtained at both dusk and the following dawn. Heavy rainfall prevented birds from foraging during August 18. One measure was made with a hand-held spring balance when the Rufous was captured in a mist net the morning of August 19 (dashed line). B. Regression lines of number of flowers in the territories depicted in Figure 1 over the duration of the 1983 study. Note that the Rufous defended fewer flowers yet gained mass more rapidly than the Costa.

average mass gain because the bird managed to gain mass at a normal rate between period 3 on 18 August and period 3 on 19 August, the periods we used to calculate 24-hr mass gain. The lowest recorded mass, 3.1 g during period 1 on 19 August, was measured with a Pesola spring balance after the bird was captured in a mist net. The subsequent unusually high rate of mass gain during the morning of the 19th may have been partly due to replenishing water loss, and in any case compensated for the continuous decline during the 18th. If we calculated mass gain from this lowest measurement, the average rate of mass gain was even greater (0.30 g/day; Carpenter and Hixon, 1988).

(8) The assumption that there should be few differences between the birds in other behaviors was verified (Table 1), especially considering defense time (Rufous: n = 28; Costa, n = 22; $P > 0.05$, Kruskal-Wallis 1-way ANOVA) and insect-hawking time (Rufous: n = 28; Costa: n = 22; $P > 0.05$, Friedman 2-way ANOVA). Although mean perch-changing times were also similar, they were nonetheless significantly different (Rufous: 0.55 min/hr, n = 28; Costa: 0.34 min/hr, n = 22; $P < 0.05$, 2-way ANOVA).

Environmental changes during the study

During the two weeks of the 1983 study, the only major environmental change was a continuous natural decline in flower abundance. This decline is illustrated in Figure 2B as regression lines for the number of flowers each bird defended through time. Note that the regressions are largely extrapolations from four complete counts of the flowers in the area made between 22 and 31 August ($r^2 = 0.92, P < 0.05$). We suspect that flower abundance declined in an accelerated rather than linear fashion, so that the earliest extrapolations (*i.e.*, for the Costa) are overestimates. In any case, it was clear that the Costa defended more flowers than the Rufous. Combined with the facts that the Costa defended a larger area than the Rufous (290.0 m^2 *vs.* 189.9 m^2, Fig. 1), and defended more flowers without significantly greater defense cost (3.0 min/hr *vs.* 2.2 min/hr, Table 1), this trend should have favored the Costa gaining mass more rapidly than the Rufous. The fact that the Rufous gained mass more rapidly than the Costa despite this trend bolsters the conclusion that the Rufous is an energy maximizer.

Comparisons between years

Assumptions concerning bout frequencies. Considering both the population- and individual-level comparisons, the assumption that foraging- and sitting-bout frequencies would be greater for the Rufous (f_E in eq. 3) than the Costa (f_T in eq. 4) was clearly verified in only one of four cases (sitting-bout frequencies in the individual-level comparison, Table 1). Moreover, the assumption that the frequencies of foraging and sitting bouts would be the same within each species was falsified; for each species, calculated foraging-bout frequencies were greater than calculated sitting-bout frequencies (Table 1). These results indicate, first, the probable inaccuracy of calculating bout frequencies; second, the possibility of defense and other nonforaging, nonsitting bouts interrupting foraging bouts more often than sitting bouts; and third, the simplistic nature of eqs. 3 and 4. However, the fact that these assumptions were violated to similar degrees by both species apparently resulted in the relative differences between the species remaining unchanged with respect to the predictions.

Between season differences. The 1983 field season was unusual in that the abundance of birds at our site was very low (Carpenter *et al.*, 1988). In normal years, each bird defends about 2,000 flowers. The two birds in the 1983 individual-level comparison spent virtually the same time in defense as those studied during 1985–1986 (Table 1), but managed to secure several times as many flowers as in normal years (Fig. 2B). This result suggests that nectar was not limiting for these individuals, and, indeed, most other birds were not territorial during this part of the 1983 season.

Nonetheless, within each species, the birds studied during the more typical 1985 and 1986 seasons had identical average meal sizes, had nearly the same estimated foraging efficiencies, and gained mass at virtually identical rates as those in 1983 (Table 1). For the Rufous, the average rates of mass gain were nearly identical to those observed during other years (Carpenter *et al.*, 1983). These recurring patterns suggest that different individuals of each species, studied during different seasons, faced fundamentally similar constraints (probably physiological) and/or made fundamentally similar behavioral decisions. Overall, the similarity of the results of the 1985–1986 population-level and 1983 individual-level comparisons suggests that birds of each species exhibited the same foraging goal between years.

An anomaly and its resolution

Considering both the population- and individual-level comparisons, one apparent anomaly was that, although the Rufous spent 17% to 45% more time foraging than the Costa, the Rufous gained mass four to eight times more rapidly (Table 1). This was despite the fact that the other significant differences in the time budgets of the two species could not account for the striking differences in rate of mass gain (Table 1).

A clue to solving this anomaly was the fact that the Rufous appeared to lose very little mass overnight. During the 1983 individual-level comparisons, there were three occasions we were able to weigh the Rufous at dusk one day (period 5) and at dawn the next morning (period 1); the overnight change in mass averaged zero (range: -0.04 to $+0.03$ g; Fig. 2A). Unfortunately, we were unable to obtain comparable data for the Costa in 1983, but it is evident from Figure 2A that this bird lost mass between days, resulting in a more "stepped" body-mass trend than that of the Rufous. During the 1985–1986 population-level comparisons, the Rufous lost an average of 0.09 g (± 0.02 SE) overnight, significantly less than the average 0.27 g (± 0.03 SE) overnight loss of the Costa ($n = 14$ each; $P < 0.001$; *t*-test).

The anomaly was resolved when we fortunately found the Rufous studied in 1983 roosting in dense willow trees the night before it migrated. This was a very rare observation, the first and only time we have located a sleeping bird during 11 years of study. Amazingly, this healthy, fat bird was torpid, suggesting that Rufous may use torpor (nocturnal hibernation) to conserve fat in preparation for resuming migration (Carpenter and Hixon, 1988). The Costa's disproportionally low rates of daily mass gain and high rates of overnight mass loss would be explained if this species did not use nocturnal torpor. The fact that the Costa is physiologically capable of entering torpor in the lab (Lasiewski, 1963), yet apparently did not do so in the field during this study, is consistent with the conclusions that (1) the Costa is a time minimizer relative to the energy-maximizing migrant

Rufous, and (2) the migrant Rufous enters torpor by behavioral choice rather than physiological necessity (Carpenter and Hixon, 1988).

Conclusions

Our population-level comparisons of immature males during 1985 and 1986, combined with observations of individual immature males that sequentially occupied the same territory in 1983, supported virtually all predictions indicating that, relative to each other, migrant Rufous Hummingbirds are food energy maximizers and the basically nonmigrant Costa Hummingbirds are feeding time minimizers (Table 1).

Clearly, hummingbirds are ideal candidates for determining relative foraging goals. To what extent can the assumptions and predictions developed here be tested for other animals? The basic requirements are that the constraints facing the animals be known, the animals be readily observable in the field, and for predictions concerning net energy intake, the amount of food energy assimilated be measured repeatedly or the animals be weighed repeatedly without disturbance. These are not easy tasks for most species. In some cases, simple comparisons of time budgets can be employed, but cautiously (Hixon, 1982). In any case, testing assumptions as well as predictions is essential. Particularly important for such comparative studies is testing the assumption of *ceteris paribus*: "all else being equal." If dissimilar species are compared, many differences independent of foraging goals could be erroneously attributed to differences in foraging goals.

One important lesson learned from the present study is the necessity of determining the relative net energy intake of animals as directly as possible. In this case, differences between species in time-budget parameters were not nearly as great as differences in the rate of daily mass gain and overnight mass loss (Table 1, Fig. 2A). The rate at which an animal gains mass (fat in this case) can be a much more direct measure of net energy intake than the amount of time the animal spends foraging. Had our study not included measurements of body mass, the differences in time-budget parameters would not have strikingly distinguished the two species. The fact that the Rufous lost little mass overnight, combined with our observation of a fat, healthy bird entering torpor at night, suggests fundamental differences between migrant and nonmigrant hummingbirds. These differences include not only relative foraging goals, but also ways in which net energy intake is utilized. Migrant birds apparently are selected to gain fat as rapidly as possible and conserve that fat until migration. Nonmigrant birds may be selected to support small amounts of fat as an emergency energy store. In this case at least, the theoretical energy maximizer–time minimizer dichotomy has a particularly firm basis in reality.

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NOTE ADDED IN PROOF

During the two years this paper was in press, we discovered that some Costas are not displaced from their territories by Rufous for several days. During this time interference competition is intense and Costas' daily energy intake declines. They compensate by using nocturnal torpor. Thus, some Costas shift from time-minimizing to relative energy-maximizing. We also have some evidence that under special circumstances, some Rufous may shift toward time-minimizing the final day on territory. Thus, these foraging behaviors may shift in a given individual even from day to day (manuscript in preparation).

REFERENCES

Belovsky, G. E. 1978. Diet optimization in a generalist herbivore: The moose. Theor. Pop. Biol. 14: 105–134.

Belovsky, G. E. 1984*a*. Snowshoe hare optimal foraging and its implications for population dynamics. Theor. Pop. Biol. 25:235–264.

Belovsky, G. E. 1984*b*. Summer diet optimization by beaver. Am. Midl. Nat. 111:209–222.

Belovsky, G. E. 1986. Optimal foraging and community structure: Implications for a guild of generalist grassland herbivores. Oecologia 70:35–52.

Carpenter, F. L. 1978. A spectrum of nectar eater communities. Amer. Zool. 18:809–819.

Carpenter, F. L. 1979. Competition between hummingbirds and insects for nectar. Amer. Zool. 19: 1105–1114.

Carpenter, F. L. 1983. Pollination energetics in avian communities: Simple concepts and complex realities. *In* C. E. Jones and R. J. Riddle (eds.), *Handbook of experimental pollination ecology,* pp. 215–234. Van Nostrand Reinhold, New York, New York.

Carpenter, F. L. and M. A. Hixon. 1988. A new function for torpor: Fat conservation in a wild migrant hummingbird. Condor. (In press)

Carpenter, F. L., D. C. Paton, and M. A. Hixon. 1983. Weight gain and adjustment of feeding territory size in migrant rufous hummingbirds. Proc. Nat. Acad. Sci. U.S.A. 80:7259–7263.

DeBenedictis, P. A., F. B. Gill, F. R. Hainsworth, G. H. Pyke, and L. L. Wolf. 1978. Optimal meal size in hummingbirds. Am. Nat. 112:301–316.

Diamond, J. M., W. H. Karasov, D. Phan, and F. L. Carpenter. 1986. Digestive physiology is a determinant of foraging bout frequency in hummingbirds. Nature 320:62–63.

Feinsinger, P. and S. B. Chaplin. 1975. On the relationship between wing disc loading and foraging strategy in hummingbirds. Am. Nat. 109:217–224.

Gass, C. L. and K. P. Lertzman. 1980. Capricious mountain weather: A driving variable in hummingbird territorial dynamics. Can. J. Zool. 58: 1964–1968.

Herbers, J. M. 1981. Time resources and laziness in animals. Oecologia 49:252–262.

Hixon, M. A. 1980. Food production and competitor density as the determinants of feeding territory size. Am. Nat. 115:510–530.

Hixon, M. A. 1982. Energy maximizers and time minimizers: Theory and reality. Am. Nat. 119: 596–599.

Hixon, M. A. 1987. Territory area as a determinant of mating systems. Amer. Zool. 27:229–247.

Hixon, M. A., F. L. Carpenter, and D. C. Paton. 1983. Territory area, flower density, and time budgeting in hummingbirds: An experimental and theoretical analysis. Am. Nat. 122:366–391.

Hoffman, S. G. 1983. Sex-related foraging behavior in sequentially hermaphroditic hogfishes (*Bodianus* spp.). Ecology 64:798–808.

Johnsgard, P. A. 1983. *The hummingbirds of North America.* Smithsonian Institution Press, Washington, D.C.

Karasov, W. H., D. Phan, J. M. Diamond, and F. L. Carpenter. 1986. Food passage and intestinal nutrient absorption in hummingbirds. Auk 103: 453–464.

Krebs, J. R. and R. H. McCleery. 1984. Optimization in behavioural ecology. *In* J. R. Krebs and N. B. Davies (eds.), *Behavioural ecology: An evolutionary approach,* pp. 91–121. Sinauer Associates, Sunderland, Massachusetts.

Lasiewski, R. C. 1963. Oxygen consumption of torpid, resting, active, and flying hummingbirds. Physiol. Zool. 36:122–140.

Lasiewski, R. C. 1964. Body temperatures, heart and breathing rate, and evaporative water loss in hummingbirds. Physiol. Zool. 37:212–223.

Miller, R. S. and C. L. Gass. 1985. Survivorship in hummingbirds: Is predation important? Auk 102: 175–178.

Pyke, G. H. 1979. The economics of territory size and time budget in the golden-winged sunbird. Am. Nat. 114:131–145.

Pyke, G. H. 1984. Optimal foraging theory: A critical review. Ann. Rev. Ecol. Syst. 15:523–575.

Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: A selected review of theory and tests. Q. Rev. Biol. 52:137–154.

Schoener, T. W. 1969. Optimal size and specialization in constant and fluctuating environments: An energy-time approach. Brookhaven Symp. Biol. 22:103–114.

Schoener, T. W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2:369–404.

Sih, A. 1980. Optimal behavior: Can foragers balance two conflicting demands? Science 210:1041–1043.