Weight gain and adjustment of feeding territory size in migrant hummingbirds

(energetics/field measurements/migration/optimization/territoriality)

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ABSTRACT   Rufous hummingbirds periodically establish and defend territories along their summer southward migration route. Using artificial perches attached to spring or electronic balances in the field, we were able to measure daily weight changes in undisturbed, individually marked birds. The territory size (number of flowers) of individual birds varied from day to day. Four of five intensively studied birds adjusted their territories to that size which was associated with the fastest sustained rate of weight gain attained at any stable territory size. The one exception was explicable on the basis of its unusually high weight. These results are consistent with the assumption of optimization theory that animals are capable of assessing when their behavior (e.g., territory size) is suboptimal and then making adjustments toward an optimum. The results also suggest, although not conclusively, that these birds are selected to maximize their rate of weight gain on each stopover prior to resuming migration.

Studies of animal energetics are usually necessarily confined to the laboratory, with the resulting data having unknown relevance to the situation in the field. A central question in many recent ecological studies of energetics is whether animals forage in a way that maximizes net energy gain over a specified interval (1, 2). Most of these studies have involved either laboratory tests (e.g., refs. 3–5) or pure theory (e.g., refs. 6–8). A practical problem in testing such ideas in the field is the difficulty of measuring net energy gain under natural conditions. We have devised a technique that measures weights of birds undisturbed in the field over intervals as brief as a single foraging bout. Weight changes then can be used to calculate the net energy gain of individuals using different foraging or territorial strategies.

Territoriality occurs when an animal defends an area and thus any included resources against other animals. Studies of feeding territoriality have focused recently on the factors that determine territory size (e.g., refs. 8–13). Most of these models are cost-benefit analyses that predict the existence of an optimal territory size that an animal should defend in order to maximize its rate of net energy gain. These models assume that (i) maximization of net energy gain over some time period is adaptive and is what the animals are selected to do and (ii) an individual in nature is capable of assessing when its territory size is in fact optimal and can make adjustments toward that optimum. Employing an unusually tractable field system and technique, we have obtained data that support the second assumption directly. The data also support the first assumption, albeit indirectly and for a rather special system.

METHODS

We have studied diurnally active nectar-feeding rufous hummingbirds (*Selasphorus rufus*) in the California Sierra Nevada Mountains for several summers (13–18). This species migrates south through the mountains, peaking in numbers at our study site from late July through August. Our studies to date have shown that birds weighing 3.0–3.5 g establish individual territories in flowering meadows and gain 1.5–2.0 g before resuming migration (17, 18). In our study site 27 km northwest of Bishop, Inyo County, California, the birds defend flowers of Indian Paintbrush, *Castilleja linariaefolia* (Scrophulariaceae). Territories are held for 1–2 weeks and contain about 600–4,000 flowers. Our birds supplement their nectar diet by hawking very abundant small insects about 1% of the day (nectar-feeding requires about 20% of the day). We have never seen birds persistently hawk or defend insects as a resource. Thus, nectar seems to be all-important to these migrant birds at this stage of their life cycle.

In 1980–1982 we netted new territory owners, weighed and color-marked them, and selected observable individuals to study until they resumed migration. We could judge easily when individuals resumed migration by their greatly increased allocation of time to feeding the hour before departure (18) and by their characteristic flight path upon departure, generally high and due south for as long as we could hold them in binocular view. These flights generally began between 0600 and 0800 hr. Every day until migration, we mapped territory boundaries (defended areas), noting any changes that occurred by the end of the day and counting all fresh and open flowers within each area as a measure of territory size. About every 3 days we bagged a sample of 15–20 flowers on each territory and measured nectar production per flower according to established methods (19). Mean per-flower nectar production over 24 hr multiplied by the number of flowers on the territory gave a rough measure of food production on each individual's territory.

To determine how territory size affects the rate of weight gain, we had to weigh each individual repeatedly. Netting hummingbirds to weigh them has disadvantages: a bird that has been captured, color-marked, and released is impossible to recapture at fixed intervals to determine rates of weight change. Also, netting an owner interferes with its ability to defend its territory for about 1 hr. Therefore, in 1980 we devised a technique to weigh birds undisturbed on their territories. We modified Pesola spring balances (capacity, 10 g with 0.2-g divisions) so that they would function by being depressed from above (Fig. 1). A dowel perch was fixed to the piston and the scale was recalibrated. Territorial rufous hummingbirds sit about 75% of

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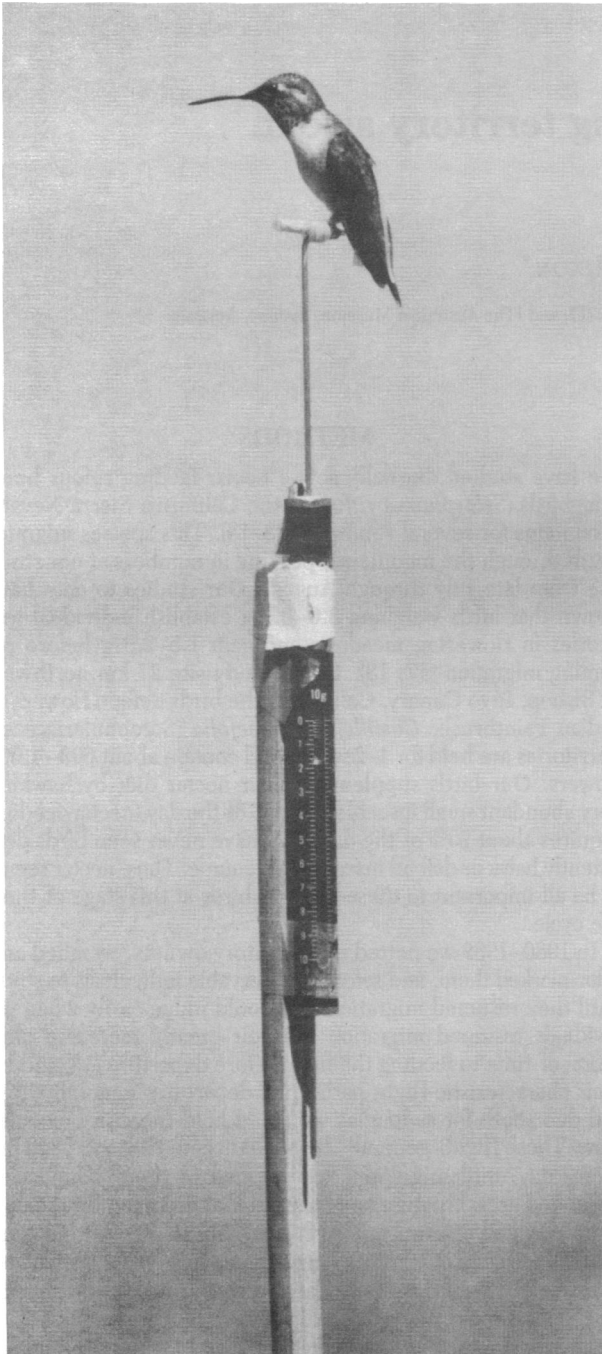‡ Present address: Department of Zoology, University of South Australia, Adelaide, Australia.

FIG. 1. Rufous hummingbird weighing itself on a spring perch-balance. The colored streamer on the back identifies the individual.

FIG. 2. Rufous hummingbird weighing itself on an electronic perch-balance. The mechanism is protected inside the white box. The flowers are Indian paintbrush (*C. linariaefolia*).

the day (18) on one or two perches, so we removed these natural perches and substituted our perch-balances. The scale was calibrated and readable through a telescope to 0.05 g. The birds seemed undisturbed by our observations and by the balances, which they used repeatedly. Whenever possible, we measured weights five times a day: before 0730, at 1030, 1330, 1630, and 1930 hr. We used only those readings made when the bird perched in the center of the artificial perch in order to avoid inaccurate measurements due to friction within the balance cylinder.

In 1982 we increased accuracy by using Mettler PE-200 electronic balances. We removed the pan and fixed a vertical rod topped with a small horizontal perch directly to the weighing

mechanism (Fig. 2). These balances can be tared easily for the weight of the rod and perch. Weights are accurate to 0.01 g and were not affected by the position of the bird on the perch. This balance is ideal for field use because it is rugged, does not have to be calibrated after moving, and has attachments that enable remote reading. A remotely controlled integration device averages weights over 5 s, reducing variability caused by the bird's movements or by moderate breezes. The increased accuracy of the Mettler system enabled us to obtain the change in bird weights after single foraging bouts and even to weigh defecations by subtraction. Successive measurements of single individuals over short time spans were highly repeatable.
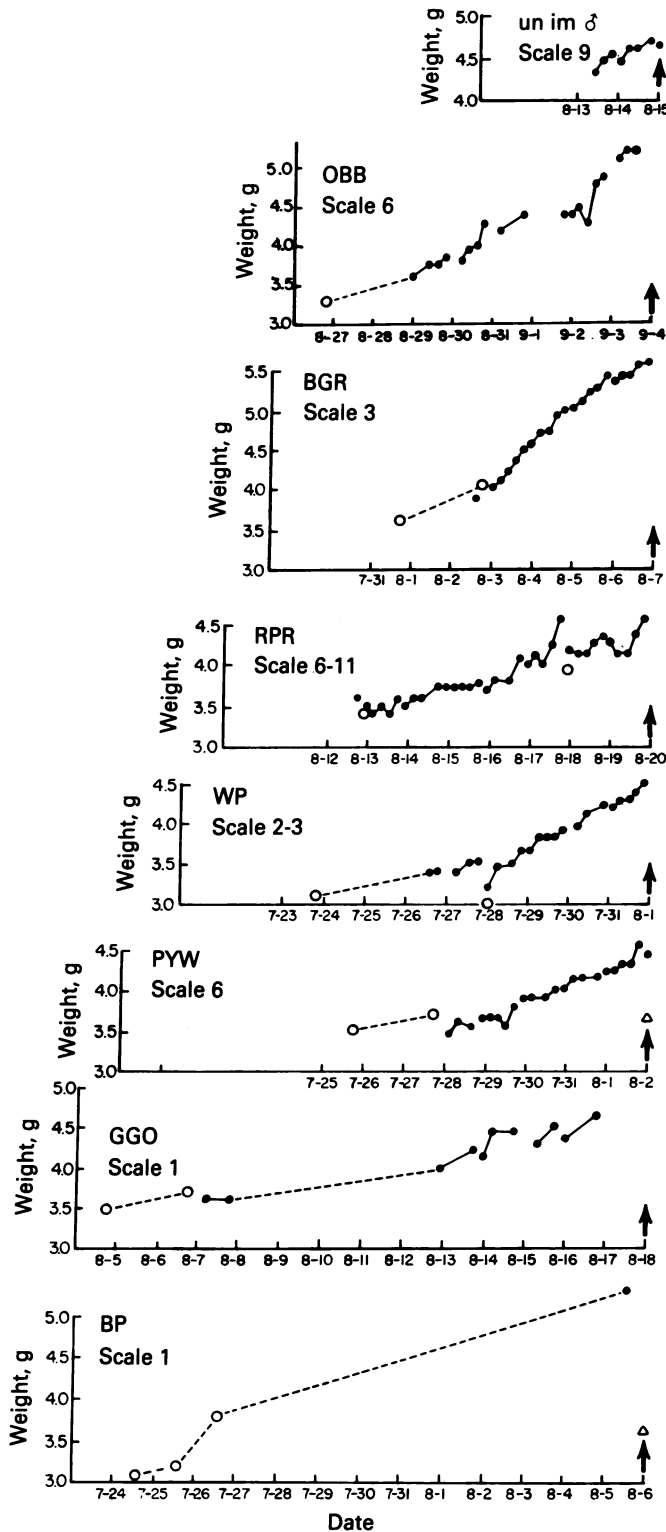
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RESULTS AND DISCUSSION

Fig. 3 shows the progress of weight change in eight individuals from the day that each was first netted and marked to the day that each resumed migration. The data are plotted so that all right margins align on the morning of migration. To our knowledge these are the only weight data collected on undisturbed adult animals in the field showing weight changes in known individuals over short periods of time. They show that net energy gain as measured by weight changes usually varies erratically during the day, contrary to the constant smooth accumulation of energy demonstrated for hummingbirds in simple laboratory environments with food ad lib (20, 21). Variations in nectar availability, intruder pressure, and other natural complexities undoubtedly account for the difference.

Fig. 4 plots the daily weight change measured from one evening to the next, as a function of number of flowers on the territory, in the five birds for which we measured weights as well as territory size on four or more consecutive days. These birds adjusted territory size considerably, and their rates of weight change varied from day to day.

Bird WP (Fig. 4A) occupied a very large range of territory sizes, beginning with a relatively small territory and low weight gain on days 1 and 2. It almost doubled its territory size on day 3 but only slightly increased its weight gain. On days 4 and 5, this bird relinquished about half of the flowers it had added,

FIG. 3. Weight measurements on one unmarked and seven color-marked rufous hummingbirds. ○, Weights obtained from netted birds using unmodified spring scales; ●, perch-balance weights of free birds on their territories; ▲, dates when the birds resumed migration; △, weights of new birds taking over the territories upon their abandonment. The perch-balances were given numbers and these are shown for each bird; two birds switched scales midway through their observation periods. Weights taken during a single day are connected with solid lines; dashed lines interpolate when successive weights were one or more days apart; gaps between days show overnight changes in weight. Calendar days are indicated on the abscissa by numerals (month first, day second).
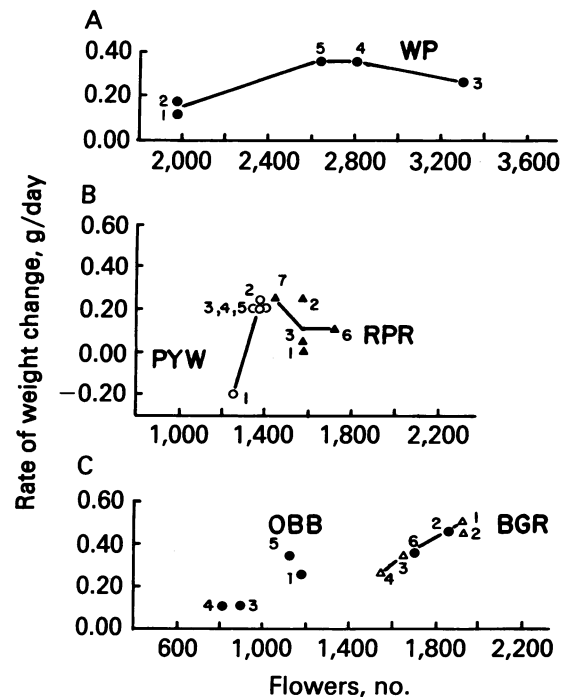
FIG. 4. Daily weight change of five color-marked individuals as a function of the number of flowers on the territory. Weight change was measured as the weight at 1930 hr on day *n* minus the weight at 1930 hr on day *n* − 1, except on a few days when weights were erratic at the end of the day. In these cases, 24-hr weight change was measured from 0630 hr on day *n* to 0630 hr on day *n* + 1. Numerals by data points indicate succeeding days on territory, beginning with the first day of intensive observations and ending on the evening before migration. For clarity, individuals are separated into three graphs: the divisions on both the abscissa and ordinate are the same scale on all three graphs; however, from *A* to *C* the abscissa shifts in terms of territory size. The points for bird OBB (●) are not connected with lines because the number of flowers on its territory continually fluctuated, both because flowering was declining and because OBB made two attempts to expand its territory (day 2 expansion was not successfully sustained).

yet attained its highest rate of weight gain on these intermediate territory sizes.

Birds PYW and RPR (Fig. 4B) adjusted their territory sizes over smaller ranges, but these adjustments were associated with more dramatic changes in weight gain than was the case with WP. PYW began with a small territory and rapid weight loss on day 1, increased its territory by about 10% on day 2, and then was able to sustain moderately high rates of weight gain over four days at this territory size. RPR began with a moderate-sized territory that was associated with variable but usually low rates of weight gain for three days. It then attempted to expand its territory on days 4 and 5 but its boundaries were in such constant flux that its territory size could not be measured. Its rates of weight gain also were difficult to measure accurately over those two days because its weight fluctuated greatly during the day, especially toward evening (August 16–17, Fig. 3). On day 6 (August 18) when it finally successfully established a larger territory in a shifted location, it showed a lowered rate of weight gain over 24 hr (Fig. 4B). On the seventh and last day, it reduced its territory to a size below the original, gained weight at a rate matching the fastest rate it had ever before attained at any established territory size, and then migrated the next morning.

OBB (Fig. 4C) occupied its territory at the end of the season (Fig. 3) when flowering was in rapid decline. It had a core area with a small number of flowers on August 28 and August 29 (our "day 1"), and initially its weight gain was moderately high (Fig. 4C). On day 2, a neighbor departed and OBB attempted to add its flowers, thereby almost doubling both its territory size and rate of weight gain. However, it could not maintain the acquisition in the face of competitors and lost it that evening, returning to its original core area for all of day 3. This area had lost flowers in the meantime and, as a result, territory size and rate of weight gain were lower than on day 1. A small area enlargement, but continued decline in flowers and low rate of weight gain, occurred on day 4. On day 5, OBB considerably expanded area and added flowers, attaining its highest rate of weight gain of any day except day 2. This expansion and high rate of weight gain continued on day 6, and OBB migrated on day 7.

These four birds all behaved similarly: all increased territory size at some point; all attained and maintained their fastest sustained rates of weight gain one (RPR) to several (WP, PYW, OBB) days immediately before resuming migration; these fastest sustained rates were all similar (0.25–0.35 g/24 hr); and all four birds migrated at similar final weights (Fig. 3).

The fifth bird, BGR, behaved differently. It showed the highest sustained rates of weight gain (up to 0.50 g/24 hr, △ in Fig. 4C, days 1 and 2) of any bird, until two days before it resumed migration. Beginning on day 3, it weighed 4.9 g in early morning, more than most birds weigh when they resume migration. Over that day and the next, it continually relinquished territory, eventually halving its rate of weight gain (Fig. 4C). The evening before it migrated, BGR weighed 5.55 g, a record for any bird in our system. It seems reasonable to suggest that these birds reach an asymptote of benefit gained by adding weight. BGR probably gave up territory and reduced its rate of weight gain the last 2 days because it already had reached suitable weight for migration. Why it did not migrate earlier at a weight more comparable to that of the other birds is unknown. Perhaps some physical condition, such as wind direction, was unfavorable earlier.

The birds appear to use a simple rule of thumb: if, initially, daily weight gain is low and total weight is less than migratory weight, expand the territory. Subsequent fine adjustments are variable, depending on the situation of each bird and on what

is gained by the expansion. In light of such a rule, BGR is not an exception and all five birds behaved consistently.

As suggested by the mostly shallow slopes of the curves in Fig. 4, daily weight gain in these birds usually changes slowly with variations in territory size as measured. The only major exception to this trend is PYW (Fig. 4B). Such individual variation in slopes may be explained by differing rates of nectar production per flower in patches added or deleted from territories. Because nectar measurements in *C. linariaefolia* destroy the flowers (19) and therefore affect territory size, our flower samples from each territory were necessarily too small to test this possibility.

However, the rough estimates for mean nectar production for each territory that we did obtain shifted the relative positions of individuals along the abscissa in Fig. 4. Thus, when weight gain is plotted as a function of daily nectar production rather than number of flowers, BGR and WP exchange places, and PYW and RPR exchange places. Even after territory sizes are converted to an energy basis, our results show that some individuals gain weight faster at small territory sizes than do others. The explanation for such variable responses probably lies in a multitude of factors that we cannot yet extricate: flower densities, intruder pressure, the owner's defense abilities, foraging efficiency, as well as its characteristic metabolic rate, and a certain amount of methodological error, especially in nectar measurements.

Two birds (WP, RPR) experienced a reduction in rate of weight gain at their largest territory sizes, and four birds (WP, OBB, PYW, BGR) showed a reduction in rate of weight gain at small territory sizes. These relative proportions are expected because territorial expansion often is resisted by contiguously territorial neighbors, whereas contraction is not resisted. These data suggest that for each individual, an intermediate territory size may exist, which maximizes the rate of weight gain, and that a hump-shaped curve (see WP) of daily net energy gain theoretically exists for each individual. The existence of hump-shaped curves would substantiate the basic approach of existing models of optimal feeding-territory size (e.g., refs. 8–13). Below the "optimum" territory size, the rate of weight gain is limited by the available food supply; above the optimum, increased intruder pressure and consequent defense requirements may (*i*) cause increased defense costs to exceed the gross energetic benefit gained by the increase over optimum size (9–11), (*ii*) cause the amount of territory production lost to intruders to exceed the energetic benefit potentially gained by the increase over optimum size, or (*iii*) reduce the amount of time available for foraging and therefore reduce net energy gain (8, 13). The latter possibility is most consistent with previous data we have gathered on our system (13).

In conclusion, these data show that individual birds are capable of trial-and-error adjustment of territory size in a way that ultimately maximizes their rate of energy gain. Because most individuals in our small sample did make such adjustments and because the one exception (BGR) made sense in terms of its exceptionally high weight, by inference this result suggests that energy maximization is a strategy that natural selection has favored in this particular system (6, 13, 22). We believe that rapid weight gain is adaptive in these migrating birds because of the unpredictability of weather along their mountainous route of southerly migration. From late July through early September, rain, hail, and windstorms periodically occur and can be severe enough to prevent feeding and cause extreme weight loss or even to destroy a large proportion of flowers (23). These birds are probably under pressure to reach the more moderate climate of their wintering grounds in Mexico as soon as possible. Furthermore, they are not constrained by preda-

tion, reproductive needs, or nutrients other than energy at this season. Thus, they make ideal subjects for studying the assumptions as well as predictions of current foraging optimization theory based on energetics.

To our knowledge, a technique to repeatedly weigh adult active animals undisturbed in the field has not been reported previously. The Mettler system is particularly modifiable for many kinds of animals in many environments, and we have only begun to utilize its unprecedented potential in our system. Any animal that returns periodically to one or a few spots in its home range is a likely candidate for study of weight change. Such field measurements will be a powerful way to answer questions of optimal foraging, territoriality, migration, nesting success, competition for food, physiological adaptations including those related to water loss, and many others. These weighing devices are likely to be a technological breakthrough for field ecology and environmental physiology.

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