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The hummingbird's restraint: A natural model for weight control[1]

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Summary. By day, a breeding male hummingbird gives priority to aerial performance over energy security, minimizing body weight gain to expedite flight activity. We observed behavior and monitored weight via perches on electronic balances in a territory with unlimited resources (artificial feeder). The male restricted his first feeding to less than 1/6 of crop capacity. In the ensuing 15 h, his body weight increased only 1% despite an unlimited resource of artificial nectar. This facilitated acceleration for pursuit and courtship flights and reduced energy cost. In 20 min at dusk, an intake of 34% of body weight provided adequate energy for temperature regulation all night. In July, cessation of territorial activity was accompanied by a regular upward drift of dawn weight, suggesting that weight had been regulated previously as a balance between expenditure and intake, perhaps without involving set-points.
Key words. Weight control; energetics; foraging; territory.

Causes of human weight problems and eating disorders are often unknown[2,3]. A fundamental issue is whether body weight is stabilized without reference to set-points via a simple balance between intake and expenditure, responding independently to exogenous and endogenous factors[4,5] or via servo-regulation to specific 'set-points'[6-8]. In the latter, obesity would represent an elevated set-point, anorexia a depressed one. We describe a case of natural control in terms of these models. (Although the gram is a unit of mass, we revert here to customary reference to 'weight control', appropriate in this case because flying requires lift to balance weight.)

Birds are 'useful models for studying control of appetite and obesity'[9]. This should be especially true of hummingbirds, whose quantifiable activity yields unambiguous patterns amenable to mechanistic interpretation. Small size and high energy costs of hovering [41.5 ml oxygen/ (g body mass × h)] and temperature regulation[10,11] result in intense metabolism and rapid energy turnover. This would seem to necessitate a progressive day-long increase in stored energy as survival insurance.

Progressive gain is also implied in an assumption of optimal foraging theory, in which hummingbirds have been important, that reproductive fitness increases linearly

with net energy intake rate[12]. This assumption is testable only during the breeding season. Foraging data are commonly collected in mid-July when western flower meadows are crowded with southbound migrant *Selasphorus rufus*[13-16]. Their intense feeding is easily observed, though hardly related to reproductive fitness. By this time, the local male broad-tails have also abandoned territorial and reproductive goals to concentrate on self-survival until the next year. Hence information on foraging intake or the weight changes due to this foraging have not been described for breeding hummingbirds. Hixon and Carpenter[17] hypothesized that maximization of time for courtship takes precedence over energy storage. Our observations test this.

We weighed broad-tailed hummingbirds (*Selasphorus platycercus*) during natural behavior at 2910 m in seral meadow and *Populus tremuloides* at Gothic, Colorado, using electronic balances with perches[13]. Two banded, marked males, XHLK (1987) and X49154 (1988) adopted a perch on a Mettler PE-300-SE remote balance (accuracy ± 10 mg checked with standard weights; 5 s averaging of wind and respiratory transients). A Scientech 3300 balance (also ± 10 mg) registered arrival weight and meal size of birds drinking 36–38% aqueous sucrose from an artificial feeder. Because the male often shuttled between weighings on the feeder and territorial perches, we could determine that the first and last readings during a 'meal' were stable and free of artifact. The sucrose concentration approximated the average solute concentration of nectars used by local hummingbirds. In midday, the male came to the feeder less often, and we could observe him feeding on natural flowers and insects, presumably to obtain other nutrients such as protein and minerals.

X49154 habitually perched but hesitated before his first feeding at dawn (0515–0529 h), allowing us to record his fasted mass, consistently 2.96 g (± 0.031 SD; n = 18). Although he had been fasting for twenty times his daytime inter-meal interval and now had ad libitum access to the feeder, his first feeding was a remarkably restrained 80 mg (± 26 SD), only 14% of his estimated crop capacity[18] of 580 mg when filled with 37% sucrose solution. Feeding throughout the day (fig.) was also very modest. Individual meals averaged 60 mg (± 30 SD; n = 45), less than a sixth of intake by females who were probably on recess from nests at the time (400 mg ± 147 SD; n = 17).

X49154 used territorial perches to watch for other hummingbirds. He courted arriving females with a series of climbs and powerdives[19]. He chased other males away. From 05:30 to 20:00 h, this activity and modest intake maintained an almost constant body weight (mean 3.04 g ± 0.054 SD; maximum 3.20 g; n = 261). The advantages of restraint in feeding are probably related to his territorial performance. This we analyzed in 1989, when X49154 returned to reclaim the territory and follow a nearly identical pattern in body weight. We estimate

that his hourly average of 41.3 chases and 43.1 climb-dive displays to heights of 18.3 m [± 6.37 SD, n = 39; determined by clinometer (PM5 Suunto) and triangulation] would have required 3.4 kJ energy per day. For the calculations, we used a partial efficiency of 23% in flight and climbs[20] and assumed that the work of first climb was 3.04 g × 18.3 m × 0.0098 J/(g·m) with recovery of 50% of the kinetic energy in a dive for subsequent climbs in series. We figured that each chase attained a kinetic energy of 1/2 mass × velocity^2, using a velocity of 9.39 m/s[21]. A weight increase would increase these costs in direct proportion, but might have an even more serious effect on aerial performance. Pursuit entails acceleration from his perch to match or exceed the intruder's velocity. Acceleration equals force divided by mass, so greater mass would decrease the acceleration possible from his muscular force-generating ability. Following Schoener's distinction between foraging patterns of energy-maximizers and time-minimizers[22-24], breeding male hummingbirds appear to maximize not energy intake, but territorial time and performance. A cost-benefit model[25] predicts greatest net energy gain for a 3 g hummingbird by taking 40 to 60 µl meals (~ 50 to 70 mg of 0.5 to 1.0 M sucrose). Average meal size was also 60 mg for migrant *S. rufus*, body mass 3–4 g[17].

Nevertheless, sufficient energy had to be obtained to fuel his 24-h cycle. Almost concealed within the 3.04 g mean weight was a slight but significant rise of 2.15 mg/h (± 0.59 SD; F = 13.15; p < 0.001) over the 15-h day, accumulating a total of 32 mg (see fig.). (In 1987, the territorial male XHLK had gained 3.40 mg/h ± 1.66 SD; n = 38; F = 4.23, p < 0.05). With his initial breakfast gain of 80 mg, X49154 accumulated a total of 112 mg. If this was fat, 1.63 kJ was stored. We estimate that 0.47 kJ would sustain the bird minimally through 8 1/4 h of nocturnal torpor (hypothermia) while 6.75 kJ could maintain his body at 39°C all night (8.25 h of temperature regulation at a metabolic rate balancing 7.9 mW loss

TERRITORIAL MALE BROADTAILED HUMMINGBIRD
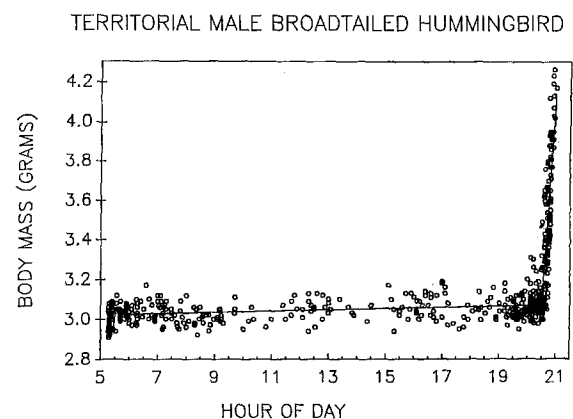
The body mass of a male hummingbird recorded from his territorial perch, 1 June–10 July, data pooled as a function of daytime. The feeder was available and defended by this bird, so absence of marked increase until dusk's anticipation of night fasting seems to be weight control by voluntary restraint.

per C body-ambient temperature difference [calculated for size from Calder[26]; body = 39 °C or in torpor 12 °C[27]; ambient 10 °C from records in roosting area). To evaluate the unlimited sucrose resource artifact, we compared weight patterns with males using weighing-perches for look-out posts on natural territories (no feeders). Presumably because natural feeding takes more time, later a.m. arrival and earlier p.m. departure shortened the territorial day (our weight-monitoring opportunity) by 1.6 h. Two males gained 6.4 mg/h and 10.7 mg/h ($\pm$ 2.43, 3.49 SD, n = 78, 38, p < 0.02, 0.01, respectively). The other two showed no statistically significant trends (p > 0.1). Field captures of males in the population also showed a diurnal trend in weights of 8.8 mg/h, but variability in individual bird size overshadowed any statistical significance in this trend (SD 0.103, n = 68, F = 0.24, p > 0.1).

At dusk, restraint was replaced by hyperphagia[28, 29], the physiological basis of most energy-maximization (fig.). The more extensively documented X49154 tripled his meal size (to 190 mg $\pm$ 93 SD, n = 48) and he fed more often. Though he still chased intruder males, courtship flights were discontinued. In 20 min before flying to roost, his weight increased 1.04 g ($\pm$ 0.100 SD, n = 18 nights), 179% of calculated crop capacity in the time required to empty the crop once[30]. This amount of sucrose solution provided enough energy (6.6 kJ) to preclude the need for hypothermic torpor. The very small net gain during the 15-h day and the dramatic intake at dusk were completely utilized by dawn, so on the scale of a daily cycle, gains for the male are for his own survival. Similar postponement of weight gain until late in the day was predicted in models which give priority to song or risk-aversion rather than feeding[31, 32]. Had total energy storage from the dusk burst of hyperphagia been inadequate, or had unusually high daytime metabolic demands depleted reserves to a threshold (perhaps indicated by plasma glucose or lipid level[33]), hypothermic torpor[34−36] could have slowed energy depletion and weight loss markedly. Torpor duration was correlated inversely with mass of 19 males captured in the hour before dusk and placed in a gradient chamber to study temperature preferences (one bird per night; 15 entered torpor later at night [Calder, unpubl.]). After 9 July 1988, X49154 abandoned his territorial claim. He continued to come to feed at dawn and at odd intervals through the day, but ceased to chase intruder males or perform dive-displays. From our estimates (above), this should have reduced his energy costs by 3.4 kJ/d. Linear regression of his daybreak weight showed a regular gain of 27 mg/d ($\pm$ 2.0 SD, n = 18, t = 13.14, F = 173, p < 0.001). Had his daily energy intake remained the same while reducing expenditures by 3.4 kJ/d, he would have gained about 70 mg fat/d (at 84% efficiency in conversion to fat containing 39.7 kJ/g[37]. Since he gained only 2/5 of this per day, he must have reduced his food intake, but to a lesser extent than his activity reduction.

This weight regulation could be explained as a combination of a) feedback from maneuvering ability in territorial chases and climbs, b) energetic demands of daytime territorial activity, c) crop and gut capacity, and d) sensing, perhaps biochemically, an approach to some lower limit ('energy threshold'[34, 35]) for onset of hypothermia to curtail further depletion.

We commented on (b) and (c) above, so now turn to (a) and (d). In May, when few males had arrived to claim territories, they frequently dived on sparrows and warblers that posed neither competitive nor predatory threat. Training activity on 'irrelevant' birds would burn off residual migratory fat until aerial performance felt best. Continued territorial activity could then have reinforced the 'training weight'. Prorated weight losses from first seasonal capture to acceptance of weighing perch were 27 mg/d (male XHLK, 1987) and 29 mg/d (male X49154, 1988), rates similar to the 27 mg/d post-territorial gain rate of X49154, when the activity decreased. Crop and gut capacity and behavioral patterns must have evolved to approximate food requirements without excess maintenance cost; either deficiency or excess should lower fitness[38]. Within such bounds, a series of sequential weight set-points per se are unnecessary to explain this complex but consistent daily cycle in body weight of territorial males. Alternatively, we consider the pattern in terms of set-points. Dynamic or kinesthetic sensations in muscular activity might be sensed more effectively than static load and thus serve as set-points. A set-point drift of 2 to 10 mg/h would fit the patterns monitored from birds on feeder and natural territories. Then at dusk, the set-point would be overridden to allow energy maximizing hyperphagia. Intake would be limited only by nectar availability and volume of digestive tract. Another set-point could be the threshold for energy-conserving torpor[34, 35]. This set-point would be reset or overridden when hummingbirds fatten for migration[39]. Human weight control problems are complicated by artificial uncoupling of feeding from functional needs. Physical exertion has been reduced by 'labor-saving' devices, while food intake is influenced by media and peers. The very slow nature of gains and reductions also hampers study. The typical gain of 11 kg in women from age 25 to 65 averages only 350 mg/d[33], an increment for which physiological detection would require five times the proportionate sensitivity of an electronic balance (350 mg/55 kg = 6 parts per million). Revelation of weight control principles might be expedited with fast results obtainable on a short time scale in species still relying on counterbalancing effects of natural feeding and activity, such as hummingbirds.

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Intercellular dye-coupling in intestinal smooth muscle. Are gap junctions required for intercellular coupling?

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Summary. The dye Lucifer Yellow was injected into single smooth muscle cells in the guinea pig small intestine in order to study intercellular coupling. Dye-coupling was observed in both the circular and longitudinal muscle layers and was markedly reduced when the intercellular pH was lowered. These results suggest the presence of gap junctions among intestinal muscle cells, but are inconsistent with previous ultrastructural studies that failed to demonstrate such junctions in the longitudinal muscle.

Key words. Gap junctions; dye-coupling; Lucifer Yellow; intestine; smooth muscle.

In most types of smooth muscle, adjacent cells are connected by gap junctions which allow the passage of ions and small molecules. Gap junction proteins (termed 'connexins') have been cloned in both heart and uterus muscle[1]. Gap junctions are believed to be the basis for electrical propagation in smooth muscles and for maintaining coordinated mechanical activity[2,3]. Gap junctions have been demonstrated ultrastructurally in intestinal circular muscle of various mammals. However, they have not been found in the longitudinal muscle layer of the same intestinal segments[4,5]. These observations raise the question as to the mechanism of propagation of electrical activity in the longitudinal muscle layer. In the present study we have examined the coupling of intestinal smooth muscle cells by intracellular injection of Lucifer Yellow, a dye that crosses gap junctions[6]. This technique has been previously used to demonstrate coupling among aortic smooth muscle cells in culture and the results were correlated with the presence of gap junctions and a low resistance intercellular pathway[7].

Materials and methods

Adult guinea pigs of either sex, weighing 400–800 g were used. Detailed description of the dissection and the electrophysiological methods has been published[8-10]. The preparation consisted of the longitudinal muscle layer from the guinea pig small intestine (dudenum and ileum)