Why hummingbirds have such large crops

F. LYNN CARPENTER*, MARK A. HIXON††, ANDREA HUNT and
ROBERT W. RUSSELL
Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92717, USA

Summary

Male Anna's Hummingbirds (*Calypte anna*) defend territories that contain a predictable food source, floral nectar. For such a hummingbird, the meal size that maximizes long-term net energy intake is less than the maximal crop volume. Smaller meals must be consumed more frequently, but larger meals increase body mass and therefore flight cost. Individuals without territories or with inadequate territories do not have easy access to nectar and intrude on territories owned by other *C. anna*, where they may be chased at any time. It was predicted that these intruders should minimize the number of potentially risky intrusions necessary for maintenance by ingesting as much nectar as possible whenever they manage to feed without being chased (usually when owners are temporarily absent). Therefore, relative to uninterrupted feeding by owners, uninterrupted intruders should feed longer and take larger meals. Field observations supported these predictions. Intruders apparently filled their crops in all seasons, whereas owners ingested smaller amounts (0.21–0.22 ml) and fed for lengths of time consistent with the prediction of an optimization model (0.21 ml). Thus, owners may energetically optimize meal size whereas intruders fill their crops whenever they are not chased. Under most conditions, hummingbirds only fill their crops one-tenth to one-third full, leading to the question why hummingbirds have such large crops. This study demonstrates that a large crop volume may be of survival value when an individual lacks a territory or has inadequate access to resources and must poach on others' territories.

Keywords: Foraging behaviour; meal size; crop size; optimization; energetics; territoriality; intruders; hummingbirds

Introduction

A territory is a defended area in which the resident restricts access to resources by other individuals. Male Anna's Hummingbirds (*Calypte anna*) establish feeding territories throughout the year, and they perform breeding displays on these territories from about October or November to April (Stiles, 1973). We studied foraging behaviour on feeding territories defended by male Anna's Hummingbirds around artificial feeders. These territories are well defined and vigorously defended (Ewald and Carpenter, 1978). We were interested in differences in feeding behaviour between territory owners and intruders on those territories. In particular, we hypothesized that territory owners should be more able to pursue behaviours that maximize long-term net energy gain than intruders. In this paper, 'meal size' refers to the mass or volume of food ingested during a single feeding bout, and 'feeding duration' refers to the duration of a single feeding bout.

Large meals in birds may add significantly to body mass thereby increasing the energetic cost of flight and decreasing the rate of net energy gain from one foraging bout to the next (DeBenedictis *et al.*, 1978; Hainsworth, 1978). The energetically optimal meal size for an energy-maximizing

* To whom correspondence should be addressed.
†† Current address: Department of Zoology, Oregon State University, Corvallis, OR 97331, USA.

hummingbird, i.e. that which maximizes the rate of net energy gain, is predicted to be considerably less than the bird's maximal crop volume (DeBenedictis *et al.*, 1978). Therefore, a bird with exclusive access to a food source should ingest relatively small but frequent meals. Territorial Rufous Hummingbirds (*Selasphorus rufus*) in the field regulated meal size at about 10% of the crop volume (Hixon and Carpenter, 1988; Hixon *et al.*, unpublished data).

Many male *C. anna* meet their entire daily energetic requirements on their own territory. However, individuals whose territories are inadequate or who do not have a territory may intrude on defended areas for all or part of their food (Stiles, 1973). Defence is usually effective, but occasionally owners leave their territories briefly undefended. These are the times when intruders are most likely to feed successfully. An intruder can obtain 10% of its daylight requirements in a single successful feeding at a feeder (Ewald and Carpenter, 1978). However, if the intruder is immediately chased by the owner of the territory, its net energy gain from that poaching bout is negative. One would predict that the most beneficial feeding pattern for an intruder on a territory would be, contrary to that of the territory owner, to fill its crop completely whenever possible. Filling the crop would reduce the number of feeding bouts and, therefore, risky intrusions necessary for the intruder to meet its energetic requirements.

We tested these predictions on feeder-based territories by measuring feeding durations of both territory owners and intruders and, in a few cases, by directly measuring meal mass. The results supported the predictions by demonstrating that intruders on a territory have significantly longer feeding durations than the territory owners. Moreover, in the cases where meal sizes were measured, intruders completely filled their crops, but the one owner measured did not. This owner ingested an amount very close to the energetic optimum predicted by DeBenedictis *et al.* (1978) for an energy maximizer.

Methods

This study was conducted at the Tucker Wildlife Sanctuary in Modjeska Canyon, California, on three days in late October 1983 and during three 3- to 4-day periods between November 1988 and May 1989. The site consists of riparian woodland, where there are no nectar-producing flowers in the immediate vicinity. Year-round, sanctuary personnel maintain many artificial feeders consisting of small glass jars upended with rubber stoppers pierced by a curved glass tube. The feeding tubes are kept filled with a red-dyed sucrose solution. This constant food supply attracts Anna's Hummingbirds to the area and sustains them throughout the year (Ewald and Carpenter, 1978).

We removed all but three feeders from the sanctuary, and separated the three so that each was defended by one male *C. anna*. Three observable territories were thereby established. We captured birds in mist nets, weighed them with a Pesola spring balance, determined their sex according to their plumage, and individually colour-tagged them. The tags were vinyl flagging cut into 0.2 × 3 cm strips and attached with 'superglue' to the bare skin at the base of the neck between two tracts of feathers. These tags remained attached for the 2 weeks of study in 1983 and the 6 months of study in 1988–89, and facilitated distinguishing territory owners from intruders. Birds were assigned 'owner' or 'intruder' status based on behaviours characteristic of territory owners, including defence of the territory by vocalizations, gorget displays made from specific perches around the periphery of the territory, and chases of intruders who attempted to feed.

In 1983 we erected an electronic perch-balance (field accuracy 0.01 g, Carpenter *et al.*, 1983) at each feeder. By weighing birds just before and after each feeding bout, we measured meal sizes. Feeders were regulated at concentrations of 15, 20, or 25% sucrose, and 2 mm plastic artificial corollas were added to the ends of the glass tubes. Feeding durations at the feeders were measured with stopwatches. Ambient temperatures were taken at the beginning and end of each

observation period. In 1988–89 we did not use balances or artificial corollas, and sucrose concentrations were 20%.

For hummingbirds using feeders in the laboratory there is a tight linear relationship between feeding duration and meal size (Wolf and Hainsworth, 1977). In 1983 our limited mass data gave the same result. It required over 200 person-hours to obtain relatively few mass data in 1983 because owners rarely perched to feed and successful intrusions are rare in nature. Because of this and because feeding durations reflected meal sizes, we subsequently collected only feeding duration data, refining our techniques.

In 1983 we timed the entire time a bird was at a feeder without subtracting intervals when the bill was not inserted. However, the feeding activity of a hummingbird at an artificial feeder is discontinuous. Therefore, in order to more accurately measure feeding durations in 1988–89, we used a cumulative stopwatch to sum only the intervals in a bout during which the bird's beak was inserted in the feeder tube. In both 1983 and 1988–89, data from feedings of owners or intruders that were interrupted by chases or other distractions were discarded.

The study was conducted primarily in the late afternoons but before dusk, when owners sometimes take very large meals and often no longer defend their territories (Calder *et al.*, 1990; Carpenter and Hixon, unpublished data).

Treatment of data

Because not enough of our individuals were marked in either year to always assign particular feeding bout data to particular individuals across dates, we had to pool our data, assuming that individual values were independent of each other. Hixon and Carpenter (1988) suggested, without analysis, that such measurements may not constitute pseudoreplication because of the dynamics and energetics of hummingbird behaviour. We now analyse this claim for our data set.

In hummingbirds, variation between measurements on a single individual often exceeds variation between means of different individuals (personal observations). Although duplicate measurements of the same individuals inflate our error degrees of freedom in tests of statistical significance, the high intra-individual variation relative to inter-individual variation inflates our error sum of squares, resulting in an error mean square (i.e. the denominator of the *F*-ratio in significance tests) that may be increased by repeated measures.

We examined the potential consequences of pooling our data using the 1983 data set, which was obtained over 1 week and included feeding duration measurements of individually separable birds on three days. On two of the days the total MS was less than the between-individual MS, while on one day the total MS was greater than the between-individual MS (Table 1). On average, daily pooling of these data would result in a seven-fold inflation of degrees of freedom and a 50% inflation of *F* statistics in significance tests of treatment effects.

These potential biases should only represent worst-case figures with respect to analyses of the larger 1988–89 data set, since those data were obtained over a long time period and likely represented largely different individuals. Significance levels reported in this paper for the 1988–

Table 1. Variation in 1983 feeding duration data (s). Degrees of freedom are given in parentheses. Ratio is total mean square (MS) divided by between-individual MS.

	October 18	October 20	October 25
Between-individual MS	198.1 (1)	134.4 (2)	21.1 (2)
Within-individual MS	74.1 (9)	80.5 (12)	33.7 (6)
Total MS	86.5 (10)	88.2 (14)	30.5 (8)
Ratio	0.44	0.66	1.45

89 data are high (0.01 or less), and were not affected even when a hypothetical adjustment was made for the potential inflation of error degrees of freedom and F values discussed above. Because the 1983 sample sizes were small, we did not apply statistical tests to them.

Results

Feeding durations and meal masses in 1983

In 1983, intruders sat on the perch-balances during three uninterrupted feedings. The average uninterrupted feeding duration for intruders was 93.3 s and the associated average meal mass was 0.90 g (Table 2A and B). The volume equivalent of 0.90 g of 20% sucrose (0.58 M) is 0.84 ml. The predicted crop volume of an Anna's Hummingbird is 0.65 ± 0.15 ml, calculated from the regression equation in Hainsworth and Wolf (1972). Obviously, the intruders were filling their crops.

Table 2. Meal masses in grams (A) and feeding durations in seconds (B) (mean $\pm$ S.D. (n)). Except for data on owner 'Green', the number of individuals is uncertain, and all measurements are pooled. In A, the last column gives the volume equivalent (ml) of the mean meal mass (g) in the first column. The value for total owners (third row) is calculated from the feeding duration in Table 2B using 'Green's' feeding efficiency.

	(A) Meal masses (1983)	
	Mean (g)	Volume equivalent (ml)
Intruders	0.90 $\pm$ 0.12 (3)	0.84
Owner 'Green'	0.24 $\pm$ 0.09 (5)	0.22
Total owners	0.23 (35)	0.21
	(B) Feeding durations (s)	
	1983	1988–89
Intruders	93.3 $\pm$ 27.4 (3)	21.2 $\pm$ 9.3 (24)
Owner 'Green'	18.0 $\pm$ 5.7 (5)	–
Total owners	16.9 $\pm$ 9.8 (35)	9.1 $\pm$ 5.3 (95)

In contrast to the intruders, only one territory owner sat on the perch-balance. Others refused to sit on it even when it was positioned so that their hovering feeding posture was awkward. The one territory owner who sat on the perch-balance, 'Green', had a mean feeding duration of 18.0 s. The associated mean meal mass was 0.24 g, only about one-quarter that of the intruders (Table 2A and B). The volume equivalent for 'Green's' mean meal size is 0.22 ml.

Overall in 1983, we obtained 35 uninterrupted feeding bouts for owners. Sugar concentration, varying from 15 to 25%, had no detectable effect on feeding duration. The mean duration of the 35 bouts pooled was 16.9 s. If the same feeding efficiency calculated for 'Green' (0.0227 h ml^{-1}) pertained for all 35 owners' bouts, this pooled mean feeding duration would have been associated with a mean meal mass of 0.23 g, or 0.21 ml (Table 2A).

Thus, the territory owners were filling their crops one-quarter to one-third full, depending on whether actual crop volume is closer to the upper end (0.80 ml) or mean (0.65 ml) of the calculated crop volume.

Table 3. Assumptions and values for parameters used in calculating optimal meal volumes (v) for territorial Anna's Hummingbirds defending feeders in the field according to the model by DeBenedictis *et al.* (1978, Equation 18).

Criterion assumption: maximizing rate of net energy gain from one feeding bout at least to the next when interbout sitting cost is unaffected by meal mass:

$$V = \frac{-t_T\phi D + ((t_T\phi D)^2 + 2(b+c)t_T\phi D \times \{E_N - E_f t_T D/2 - W[\lambda - (b+c)E_f]\})^{1/2}}{(b+c)\phi D}$$

b = Feeding rate^{-1} (h ml^{-1}) = 0.0227 (this study, observed in 1983 territory owner).

c = Crop-emptying rate^{-1} (h ml^{-1}) = 1.3667

D = Density of sugar water (g ml^{-1}) = 1.074 for 20% (0.58 M) sucrose.

E_f = Energetic cost of forward flight (cal (g − h)$^{-1}$) = 183 as assumed in DeBenedictis *et al.* (1978).

E_H = Energetic cost of hovering (cal (g − h)$^{-1}$) = 215 as assumed by DeBenedictis *et al.* (1978), which is valid because Anna's Hummingbirds have average wing-disc loading according to the values for body mass and wing length in Johnsgard (1983).

E_N = Energy content of sugar water (cal ml^{-1}) = 849.12 for 0.58 M, assuming 4 cal mg^{-1} for sucrose (Brody, 1964).

E_q = Energetic cost of flying during interbout period (cal (g − h)$^{-1}$) = 196 as assumed by DeBenedictis *et al.* (1978).

E_S = Sitting cost (cal (g − h)$^{-1}$): at 10°C, E_S = 106.1, and at 25°C, E_S = 63.5 as calculated in Ewald and Carpenter (1978) for Anna's Hummingbirds.

q = Proportion of interbout period spent flying = 0.262 for non-breeding season, calculated from Ewald and Carpenter (1978, p. 285). For breeding season, q triples (Stiles, 1973) to 0.786.

t_T = Time (h) spent in transit to and from feeder during one bout = 2 s = 0.0006 h.

T_A = Ambient temperature (°C) = 10 in December–March 1989, 25 in October 1983 and May 1989.

V = Optimal volume of meal (ml).

W = Body mass (g) = 4.63 (this study, mean of 20 individual adult males).

ϕ = $E_H b + qE_q c$

λ = $E_H b + [qE_q + (1 − q)E_s]c$

Between-season changes:

V (October 83, breeding, 25°C): q = 0.0786, ϕ = 25.935, λ = 105.899, V = 0.21.

V (December 88–March 89, breeding, 10°C): q = 0.0786, ϕ = 25.935, λ = 159.545, V = 0.19.

V (May 89, non-breeding, 25°C): q = 0.0262, ϕ = 11.899, λ = 96.410, V = 0.31.

Comparison with predicted optima

We compared these 1983 observed and estimated meal sizes with predicted optima from a model assuming long-term maximization of rate of net energy gain (DeBenedictis *et al.*, 1978). Activity between feeding bouts is an important parameter in this model and depends on breeding status in Anna's Hummingbirds (Stiles, 1973). In late October 1983, adult males had shifted to breeding activity, including displays and chases, so we calculated the optimum based on the heightened activity of breeding. Incorporating the parameter values in Table 3, the model predicted that the optimum meal volume for a bird with the body mass and activity patterns of our territorial Anna's in October 1983 is 0.21 ml. Thus, whereas the intruders were filling their crops, owners were taking meal sizes close to the predicted optimum (Table 2A).

Relation between meal mass and feeding duration

Owner 'Green' showed a tight linear relationship between meal mass and feeding duration (Fig. 1). The intruders fell somewhat below this line. However, one would not expect intruder feeding efficiency to equal that of owners because they spend more time with their bills out of the feeder tubes acting alert and agitated. A similarly tight relationship between meal volume and feeding duration was found in the laboratory (Wolf and Hainsworth, 1977). Our meal mass data therefore serve primarily to support the assumption that feeding duration reflects meal size, and the bulk of our analysis is on refined feeding duration data obtained subsequent to 1983.
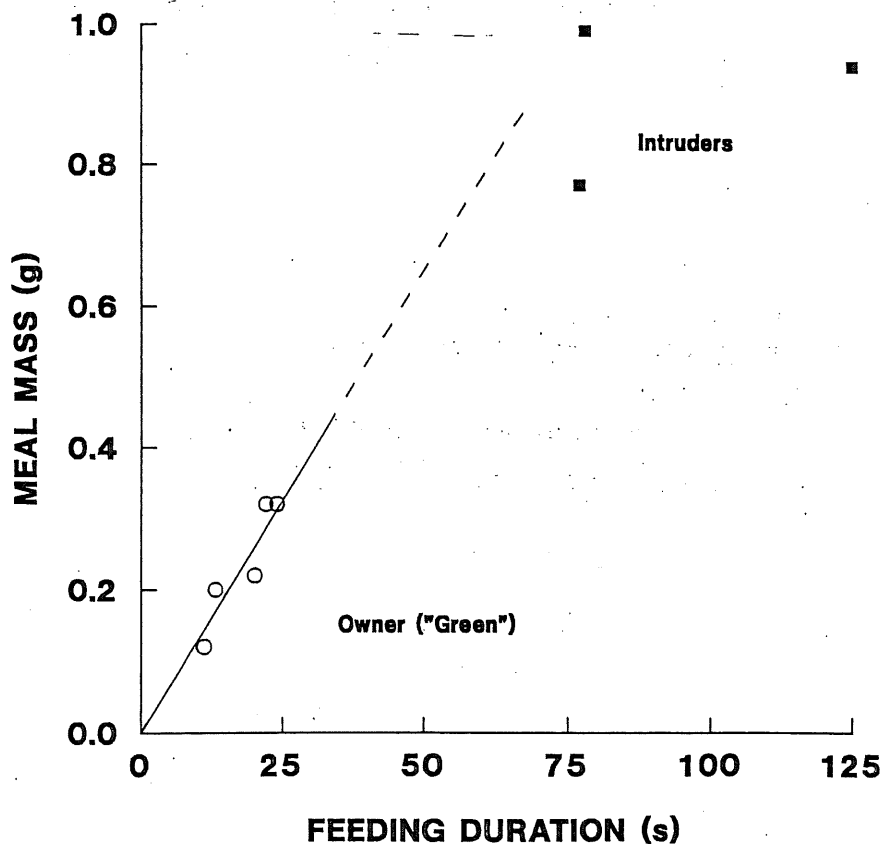

Figure 1. Ingested meal mass (g) as a function of feeding duration (s) by one territory owner ('Green') and during three intrusions made by unmarked hummingbirds. All data were taken at feeders with 20% (0.58 M) sucrose solutions on 25 October 1983. The regression equation calculated for 'Green' only is given by $Y = 0.013\,X$ ($R^2 = 0.986$, $p < 0.001$).

Feeding durations in 1988–89

We obtained a larger database on feeding durations in December 1988 and in February–March and May 1989. The average time a territory owner spent ingesting a single uninterrupted meal was 9.1 s compared to 21.2 s for intruders (Table 2B). The fact that these means were shorter than in 1983, especially for intruders, probably reflects the differences in our methods. In 1983 the 2 mm artificial corolla may have slowed intake rate. More importantly, in 1983 we timed the entire bout at the feeder without subtracting the intervals when birds removed their bills from the tubes. This difference is particularly important for intruders, who back out of the feeder tube frequently.

The variances in owner and intruder feeding durations were not equal (Table 2B): owners fed for much less variable durations than intruders (*F*-test, $p < 0.005$). In order to correct for heteroscedasticity, analysis was carried out on square-root transformed data.

A two-way ANOVA showed that feeding durations were significantly longer in intruders than in owners ($F_{1,113} = 55.3$, $p < 0.001$; Table 4). Our confidence in this difference is not diminished

Table 4. Analysis of variance of mean meal length (s) (square-root transformed).

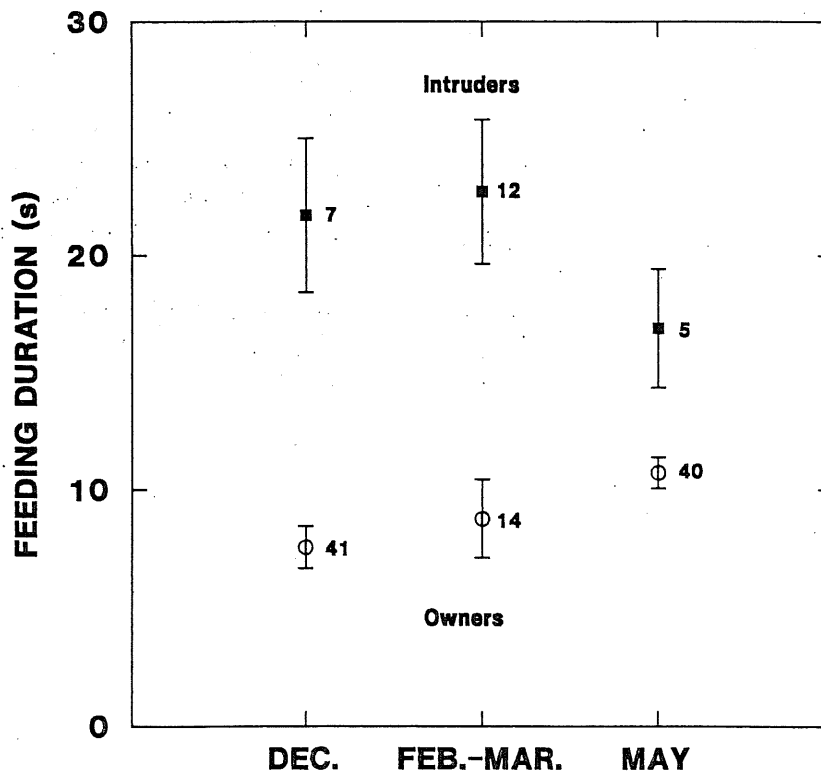| Source of variation	df	MS	F	p
Territorial status	1	40.021	55.313	<0.001
Season	2	0.139	0.192	0.826
Status × season	2	2.033	2.810	0.064
Error	113	0.724		

Figure 2. Feeding duration (*s*) of intruders and owners during three periods from December 1988 to May 1989. Data points represent means ± one standard error (untransformed data). Data collection periods were 3–5 December 1988, 23 February–6 March 1989, and 9–18 May 1989.

when we make a hypothetical adjustment for the potential seven-fold inflation of error degrees of freedom and 50% inflation of F discussed earlier ($F_{1,16} = 36.8$, $p < 0.001$). Although there was no significant overall seasonal effect or interaction between the two effects, there was a suggestion of a seasonal-status interaction. Figure 2 shows that in May, the mean meal size in intruders seemed to decrease and that of owners to increase. Linear contrasts of seasonal means for intruders and owners indicated that in May, feeding durations for intruders were not significantly different than during the winter months ($p = 0.185$); there was, however, a significant increase in feeding durations of owners in May ($p < 0.01$), amounting to a rise of about 40%.

Discussion

Owner and intruder meal sizes

These results support the prediction that intruders, when uninterrupted, have longer feeding bouts than do territory owners. Furthermore, our limited data on actual meal masses suggest that intruders fill their crops whereas owners take frequent small meals very close to the predicted optimum for energy maximizers. The almost exact coincidence of predicted and observed meal sizes occurred despite the fact that our observations were 'blind': the data were collected before the predicted optimum was calculated. However, we believe this coincidence is fortuitous. One of the most sensitive parameters in the model is q, which we did not measure in our study but took from the literature.

Crop-filling is not usually predicted by the energy-maximization model (DeBenedictis *et al.*, 1978). Does this mean that intruders are not energy maximizers? It is possible for the energy maximizer model to predict full-crop meal sizes given extreme values of some parameters. There are only two sensitive parameters in the model (Table 3): that, first, we assumed were equal between intruders and owners; and second, reasonably could differ enough between intruders and owners to predict full-crop meals for intruders. These are q (the proportion of the interbout period spent flying) and t_T (transit time to and from the feeder). If q decreases, predicted meal size increases. However, q for our owners was already small and q for intruders likely would be no smaller because they frequently initiate unsuccessful intrusions. Thus on the basis of this frequent intrusive activity, one would predict equal or smaller meal sizes for intruders than for owners, assuming energy maximization.

Transit time of intruders must be over an order of magnitude larger than that of our owners to yield a prediction of full-crop meal size, meaning that intruders would have to consistently come from a long distance to poach. This is possible for our intruders. However, they could be seen frequenting the fringes of territories waiting to intrude, and since the surrounding habitat is devoid of flowers, intrusion from long distances seems unlikely.

It is possible that, instead, our intruders fit the prediction of the 'time minimization' model of DeBenedictis *et al.* (1978), because owners drastically restrict the amount of time per day that intruders can feed. When time for feeding is limited, this model predicts that birds should fill their crops at each feeding. In this case, time available for feeding is limited by aggressive behaviour of other individuals. Normally, time minimization is considered a strategy for maximizing time available for non-foraging activities (Schoener, 1971; Hixon, 1982). The impact on optimal meal size will be the same in either case. In sum, we need more information about intruders to be able to judge whether they are energy maximizers.

The fact that owners fed for much less variable durations than intruders (with their 'backing out' time subtracted) is consistent with the idea that owners are regulating meal mass around an energetic optimum, whereas intruders are feeding opportunistically and beginning their successful feedings with varying pre-existing crop contents. Together with this greater observed variance in

intruder feeding durations, the fact that mean feeding durations did not differ significantly between seasons for intruders strongly suggests that they always take the largest meals possible.

Seasonal effect on meal size

The hypothesis that territory owners optimize meal size is also supported by the 40% increase in feeding duration from the winter breeding season to the spring non-breeding season in owners in 1988–89 (Fig. 2). The predicted optimal meal size for an energy maximizer calculated from the DeBenedictis *et al.* (1978) model increases 60% (from 0.19 to 0.31 ml) with the change from cold breeding season to warm non-breeding season (see Table 3). About 10% of this increase is due to seasonal warming from 10°C to 25°C. The remaining 50% is accounted for by tripling of interbout activity during the breeding season (Stiles, 1973). These changes, then, probably account for the May increase in the owners' feeding durations as shown in Fig. 2, assuming that the increased feeding durations were associated with proportionately increased meal sizes. The seasonal trend therefore lends further support to the idea that territory owners take meals of optimal size, and is based on the more plentiful feeding duration data.

Effect of artificial feeders on activity level and meal size

When activity is low, as is often true for birds defending feeder-based territories, predicted optima for meal sizes can be large relative to those for birds on flower-based territories who are much more active (e.g. Hixon and Carpenter, 1988; Calder *et al.*, 1990; Hixon *et al.*, unpublished data). This is because heavy meals cost relatively little when there is little flying. In fact, the predicted and observed optimum meal volume for our Anna's Hummingbirds defending feeder-based territories, calculated from the model of DeBenedictis *et al.* (1978), is over twice as large as that predicted and observed for Costa's Hummingbirds (*Calypte costae*) and Rufous Hummingbirds defending flower-based territories (Hixon and Carpenter, 1988; Hixon *et al.*, unpublished data.)

Why do hummingbirds have such large crops?

DeBenedictis *et al.* (1978) were puzzled by the large crop volumes of hummingbirds, and speculated that final feedings of the day might account for the phenomenon. In support, field data have shown that hummingbirds may fill their crops during the final few feeding bouts of the day (Calder *et al.*, 1990; Carpenter *et al.*, unpublished data). Analogously, in a migratory species territory owners may fill their crops just before resuming migration (Carpenter *et al.*, unpublished data.)

Our observations of wild hummingbirds at artificial feeders reveal another circumstance under which large crop size is probably of survival value, namely, whenever an individual lacks a sufficient territory and is forced to poach. We found that intruders ingest large meals whenever they have a chance to feed uninterrupted within a territory. In addition to being an adaptive response to infrequent and unpredictable opportunities to feed, this behaviour reduces the cost of foraging by reducing the number of intrusions necessary and therefore the likelihood that the intruder will be chased by the owner before having the chance to feed. In contrast, owners with easy access to food resources have shorter feeding bouts and take much smaller meals almost identical in size to the theoretical energetic optimum.

Every individual hummingbird probably spends some portion of its life forced to intrude on defended areas to feed. We suspect that this factor may be largely responsible for the fact that crop size is 3–10 times larger than are most measured meal sizes (Hixon and Carpenter, 1988; Calder *et al.*, 1990; Hixon *et al.*, unpublished data). Large crop size in hummingbirds therefore may be, at least in part, an adaptation to episodic rather than commonplace circumstances.

Our results suggest that behavioural contingencies such as temporary loss of access to resources may be important selective factors in the evolution of morphologies.

Acknowledgements

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