

Energy, predators and the behaviour of feeding hummingbirds

STEVEN L. LIMA*

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, USA

Summary

Current evidence suggests that many animals trade off energy gain against the risk of predation while feeding. In contrast, energetic considerations alone have proven successful in explaining and predicting the behaviour of feeding hummingbirds. This success may reflect the relative lack of natural predation on hummingbirds, but this study suggests that it may additionally reflect the lack of studies taking a predation perspective. In particular, when Anna's hummingbirds (*Calypte anna*) are faced with an obstructed view of their surroundings, they engage in behaviour suggestive of anti-predatory vigilance. In doing so, they voluntarily reduce their rate of energy intake. These birds also forgo better feeding opportunities that occur close to the ground, where observations suggest they are wary of opportunistic predators such as roadrunners (*Geococcyx californianus*). While energy-based concepts will remain useful in the study of hummingbird feeding behaviour, the lack of predation on these birds should not be equated with an insensitivity to the risk of predation. This realization may lead to further insights into hummingbird–plant interactions, and hummingbird biology in general.

Keywords: Foraging behaviour; hummingbirds; plant–pollinator interactions; predation risk.

Introduction

The small size and high metabolic rate of hummingbirds leaves them closely 'linked' to their energy supplies (Stiles, 1973; Hainsworth, 1981). Many studies have explored the nature of this link in feeding-territoriality (e.g. Gass *et al.*, 1976; Kodric-Brown and Brown, 1978; Carpenter *et al.*, 1983), foraging behaviour (e.g. DeBenedictis *et al.*, 1978; Gass, 1978; Montgomerie *et al.*, 1984; Gass and Sutherland, 1985), and the physiology of feeding (e.g. Wolf *et al.*, 1972; Hainsworth, 1981; Diamond *et al.*, 1986). These studies collectively present a strong case that most aspects of a hummingbird's life are inextricably linked to energy. In fact, virtually all such behavioural studies have focused upon energy as the sole criterion, or currency of fitness (Schoener, 1971), upon which hummingbirds base their decisions, although the precise nature of this currency has varied from thermodynamic efficiency (e.g. Pyke, 1979), to energy intake rate (Pyke, 1978), to energy per unit volume ingested (Montgomerie *et al.*, 1984).

In contrast, energy-based currencies of fitness often fail to predict behaviour in a host of creatures which are potential prey for others (Lima and Dill, 1990). This failure results from a fundamental conflict between efficient feeding and predator avoidance: basically, that which enables feeding efficiency often detracts from predator avoidance, and vice versa. Perhaps the success of energy-based currencies in hummingbirds reflects their low rate of being preyed upon,

*Present address: Department of Life Sciences, Indiana State University, Terre Haute, Indiana 47809, USA.

as suggested by Miller and Gass (1985). However, as Lima and Dill (1990) point out, an apparent lack of predation does not necessarily imply a lack of behavioural sensitivity to potential predators. Thus this study examines whether energy-based currencies of fitness can explain hummingbird feeding behaviour even in situations that other birds might perceive as high in predation risk. The overall goal is not to deny the utility of energy-based models of hummingbird behaviour, but to examine whether the predator sensitivity so prevalent in other animals is actually absent in hummingbirds.

Two basic lines of evidence suggest that Anna's hummingbirds (*Calypte anna*) do perceive a risk of predation while feeding. First, these hummingbirds avoid feeding close to the ground. Second, they engage in behaviour which suggests anti-predatory vigilance when the view of their surroundings is compromised by feeding; vigilance directed towards hummingbird aggression appears unable to fully explain this behaviour. Observations suggest that these birds are wary of certain terrestrial predators, particularly the carnivorous roadrunner (*Geococcyx californianus*).

Methods

This study was conducted during January and February, 1988 in the foothills of the Tucson Mountains west of Tucson, Arizona. The study site was located in habitat dominated by foothills paloverde (*Cercidium microphyllum*), creosote bush (*Larrea tridentata*), and saguaro cactus (*Cereus giganteus*). Hummingbirds were attracted to the study site using artificial feeders, containing a 20% sucrose solution (determined on a weight-to-total-weight basis), for three weeks prior to the beginning of data collection.

Two types of artificial feeders were used throughout this study, both derived from plastic centrifuge tubes 10 cm in height and approximately 1.2 cm in width. Hummingbirds gained access to the sugar solution through a hole 3 mm in diameter drilled near the feeder's bottom. A small tube of red plastic (1.7 cm in length and 0.8 cm in diameter) was fastened to each feeder such that a hummingbird had to insert its bill and tongue into it to reach the hole and the sugar solution. The two feeder types differed with respect to the presence of a large, conical piece of red plastic that mimicked the corolla of a large flower. The feeders are depicted in Fig. 1 and referred to as the F (flower) and NF (no-flower) feeders, respectively.

The feeders were presented to hummingbirds by clamping them to a thin metal support pole (1.5 m high) that was hammered perpendicular to the ground 0.5 m away from, and midway between, a large prickly-pear cactus (*Opuntia* spp.) and century plant (*Agave parryi*). A feeder was positioned either 1.3 or 0.2 m above the ground (measured from the bottom of the feeder); these are referred to as the upper and lower positions, respectively. Regardless of its positioning, the NF feeder always contained the 'standard' solution of 20% sugar, while the F feeder contained either the standard solution or one with double the concentration (40%), depending upon the experimental treatment.

One or more of the experimental feeders were available at the study site during each entire day throughout the study. However, a daily experimental session lasted only 4 h, starting at 09:30 and ending at 13:30. During a session, a continuously-running video camera equipped with a 12:1 zoom lens recorded hummingbird visits from within a building 6 m from the feeder(s). Height position and/or feeder identity changed each hour during a session, depending upon which of the eight experimental treatments was in effect. These treatments are discussed below in detail, and summarized in Table 1 for the reader's convenience.

The data gathered during Treatment 1 concerned the details of hummingbird behaviour during a feeding bout (one visit to the site). During this treatment, only one feeder was available at a given time. Each of the four possible combinations of feeder type and height positioning was available during each session; the order of their presentation varied over the course of this four-

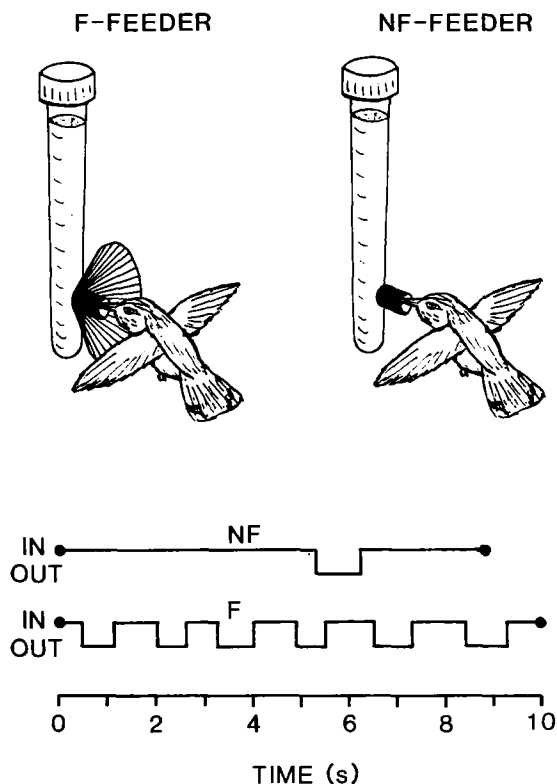


Figure 1. The two types of feeders and representative feeding bouts for female Anna's hummingbirds. 'In' refers to probes into the feeder, and 'out' refers to the birds hovering 5 to 15 cm away from the feeder. Objects are drawn to scale.

session treatment such that each combination was available during the 1st, 2nd, 3rd, or 4th hour of a session. Following each session, a feeder was present for the remainder of the day, and its position and identity were changed periodically. Note also that Treatment 1 was preceded by six days of 'training' during which the birds were familiarized with the basic routine of feeder and position changes as per the above protocol. The standard sugar solution was available in both feeders throughout Treatment 1.

Treatment 2 assessed the hummingbirds' preference for the F vs the NF feeder. Here, both feeders were attached side-by-side (20 cm apart) to a thin piece of wood clamped to the support pole. Two tandem arrangements were used each session, one with the F and NF feeders on the 'right' and 'left' sides, respectively, and vice versa. The tandem feeders were available at either the lower or upper positions, thus there were also four feeder-type-height combinations during this treatment. As in Treatment 1, each combination was available for a 1 h period during a session. Note that Treatment 2 was preceded by a two-day training period during which hummingbirds were familiarized with the tandem feeders and the basic experimental protocol. Both F and NF feeders contained the standard sugar solution throughout training and experimentation.

Treatment 3 was essentially a repeat of Treatment 1, where only one feeder was available at a given time. No training period preceded Treatment 3.

As in Treatment 2, Treatment 4 also involved a pairwise preference test, but here the two feeder types were simultaneously available in the upper and lower positions, respectively. There

Table 1. Summary of experimental treatments.

Treatment	Reeder presentation	Sessions	Dates (1988)
Training	As in Treatment 1	—	19–24 Jan
1	One feeder at a time; $F = NF^*$	1–4	25–28 Jan
Training	As in Treatment 2	—	29–30 Jan
2	Pairwise choice: F and NF feeders simultaneously available side-by-side, $F = NF$	5	31 Jan
3	One feeder at a time; same as Treatment 1	6–9	1–4 Feb
Training	As in Treatment 4	—	5 Feb
4	Pairwise choice: One feeder in upper height position, other in lower position, $F = NF$	10–11	6–7 Feb
Training	As in Treatment 5	—	8 Feb
5	Pairwise choice: Feeders side-by-side, $F = 2 \times NF$	12–13	9–10 Feb
Training	As in Treatment 6	—	11 Feb
6	Pairwise choice: Feeders in upper and lower height positions, $F = 2 \times NF$	14–15	12–13 Feb
Training	As in Treatment 7	—	14 Feb
7	Pairwise choice: F and NF feeders side-by-side, $F = NF$	16–17	15–16 Feb
Training	As in Treatment 8	—	17 Feb
8	Pairwise choice: feeders in upper and lower height positions, $F = NF$	18–19	18–19 Feb

* Comparison of sugar concentration in F and NF feeders; NF always contained standard 20% sugar solution.

were only two distinct feeder positionings (the F and NF feeders in the upper and lower positions, respectively, and vice versa) and both were available during two (alternating) 1 h periods per session. A given feeder positioning started the first session of the treatment, and the other started the second one. Both feeders contained the standard sugar solution throughout this treatment.

Treatments 5 through 8 all involved pairwise preference tests with the feeders available either side-by-side (Treatments 5 and 7) or simultaneously in the upper and lower positions, respectively (Treatments 6 and 8). The experimental protocols used during these treatments were as outlined above for the preference tests in question, with the exception that during Treatments 5 and 6, the sugar concentration in the F feeder was twice that of the standard (20%) solution in the NF feeder. Each new treatment was preceded by a one-day training period to refamiliarize birds with the upcoming experimental situation.

All data were taken from analyses of the video tapes. Data gathered during Treatments 1 and 3 concerned the 'probes' into the feeder (i.e. periods of ingesting sugar solution) and 'pull-outs' from the feeder (which involved flying backwards and hovering 5 to 15 cm away from the feeder). These events were timed using the video equivalent of frame-by-frame analysis (29 'frames' per second). Data gathered during the pairwise preference tests concerned the identity of the feeder initially chosen during a bout, and whether any subsequent switch occurred. All feeding bouts ended prematurely by aggression were excluded from the analysis; this involved only 5% of all bouts. All statistical tests are as in Sokal and Rohlf (1981).

The data below pertain only to female Anna's hummingbirds since only these birds were consistently present at the study site. Other birds occasionally feeding at the site were male Anna's and female Costa's hummingbirds (*Calypte costae*). Hummingbirds were not individually marked, but on each day at least three female Anna's hummingbirds visited the study site as

judged by simultaneous sightings. Note also that the 'owner' of the feeder (or the most dominant individual present) was always a female Anna's, but it appeared to spend less than 20% of its time at the site.

Results

Data gathered during Treatments 1 and 3 showed that within-bout foraging behaviour differed markedly according to feeder-type. As seen in Fig. 1, hummingbirds repeatedly 'pulled out' of the F feeder about every second or so, whereas at NF feeders the pull-outs were much less frequent; in fact, there were no such pull-outs during 49% of the 90 recorded visits to NF feeders. These basic patterns held for every visit to the respective feeder-types for not only female Anna's hummingbirds, but also for the male Anna's and female Costa's hummingbirds present at the study site.

Figure 2 summarizes several aspects of within-bout behaviour of female Anna's hummingbirds during Treatments 1 and 3. Data are summarized according to the four possible feeder presentations, where U and L signify upper and lower positions of the F and NF feeders,

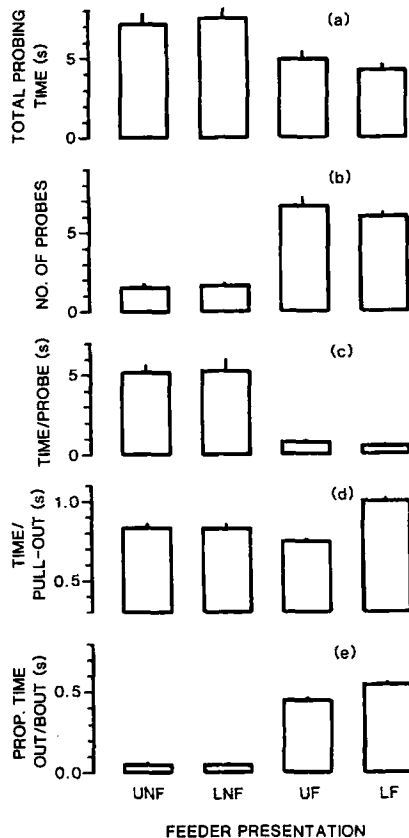


Figure 2. Within-bout behaviour of female Anna's hummingbirds during Treatments 1 and 3 (see text) as a function of feeder placement; NF and F denote 'no-flower' and 'flower' feeders, respectively, and U and L denote the upper and lower feeder positions, respectively. Data for each behavioural measure are given as averages (bars) and SEs (lines on bars). Note that for the time/pull-out data gathered at NF feeders, only bouts with one or more pull-outs are included in a given average.

respectively. These data result from a conservative data summation process which avoids potential non-independence in behaviour within a session (particularly within a bout). This process involves first determining the average value in question over an individual bout, and then averaging these values over the bouts of an entire session to obtain an 'observation'. Thus, each of the averages in Fig. 2 is based upon 8 observations, corresponding to the 8 sessions during Treatments 1 and 3.

Once again, the major behavioural differences indicated in Fig. 2 are between the NF and F categories, regardless of the upper or lower presentations. Generally, while at an NF feeder vs an F feeder, female Anna's hummingbirds spent more total time probing (Fig. 2a), made fewer overall probes (i.e. pulled out less often, Fig. 2b), and spent much more time per probe (Fig. 2c). Generally, most probes at NF feeders exceeded 5 s, whereas probes at F feeders rarely exceeded 1 s (the longest being 2.3 s). In addition, hummingbirds spent far less time per bout out of NF than F feeders (Fig. 2e). The average times per pull-out (Fig. 2d) were more compatible between the NF and F feeders. However, all possible pairwise comparisons between the NF and F feeder categories were significantly different within this behavioural measure (*t*-tests, all $p < 0.05$), as they were within the other four measures *t*-tests, all $p < 0.01$).

The behaviour of female Anna's hummingbirds feeding at NF feeders was very similar at the upper and lower positions, and no statistically significant differences were indicated for any behavioural measures in Fig. 2. In contrast, all pairwise comparisons between the upper and lower F feeder categories were significant (*t*-tests, all $p < 0.05$); total probing time, number of probes per bout, and time per probe were reduced in the lower position relative to the upper position, while both the time per pull-out and total per-bout time spent out of the feeder increased.

Figure 3 presents the results of the NF vs F feeder preference tests when feeders were presented side-by-side (left panel) or simultaneously in both the upper and lower positions (right panel). Recall that there were three side-by-side (SBS) and three 'upper/lower' (UPLOW) preference test treatments (Table 1), and that during the second treatment in each sequence, the F feeder contained twice the sugar concentration of the NF feeder. Hence, for convenience, the top, middle and bottom subfigure in each panel refer to the first, second and third presentation of the preference test in question. The subfigures themselves show two frequency distributions of the number of times a bout was spent solely at the NF or F feeder, or was mixed between the two feeders (where the initial choice is as indicated). For the SBS tests, the solid and open bars refer to the tandem feeders in the upper and lower position, respectively; solid and open bars refer to the F feeder in the upper and lower position, respectively, for the UPLOW tests.

The hummingbirds greatly preferred the NF feeder during the first SBS test (Treatment 2, Fig. 3a), and feeder choice distributions were statistically indistinguishable between the upper and lower positionings of the feeders (Kolmogorov-Smirnov (K-S) test, $p \geq 0.05$). Very different behaviour was observed during the next SBS test (Treatment 5, Fig. 3b) where the F feeder contained twice the sugar concentration of the NF feeder. With the tandem feeders in the upper position (solid bars), most bouts took place at the F feeder, or started there before a switch to the NF feeder (where hummingbirds usually probed briefly before leaving). With the tandem feeders in the lower position (open bars), however, most bouts were mixed, starting at the NF feeder and ending at the F feeder (most feeding usually took place at the NF feeder). These two choice distributions differed significantly (K-S test, $p < 0.001$). Feeder choices also differed significantly between the first and second SBS tests (K-S tests, all $p < 0.001$ for all pairwise comparisons).

The third SBS test (Treatment 7, Fig. 3c) was essentially a repeat of the first one (Treatment 2, Fig. 3a), and acted as a control to test for preference stability over time. As in the first SBS test, most bouts in the third one took place solely at the NF feeder, regardless of the upper or lower positioning of the feeders. Feeder preferences appeared stable, since there were also no statistical

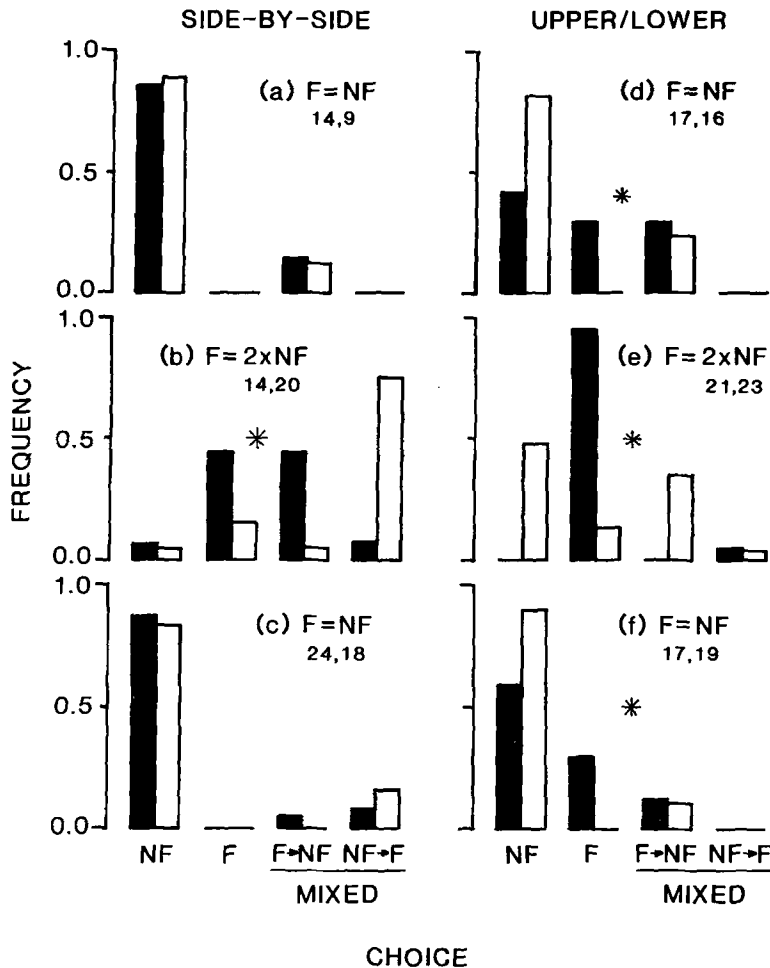


Figure 3. Results from the feeder preference tests during Treatments (a) 2, (b) 5, (c) 7, (d) 4, (e) 6, and (f) 8. Each sub-figure shows two frequency histograms of feeder choice (including any switches) corresponding to the two possible feeder presentations. For the side-by-side preference tests (left panel), solid bars = tandem feeders in the upper position, open bars = tandem feeders in the lower position. For the upper/lower preference tests (right panel), solid bars = F feeder in upper position (with NF feeder in the lower one), and open bars = F feeder in the lower position. The pair of numbers in each sub-figure represent sample sizes for the solid (left) and open (right) histograms. The relative concentration of sugar in each sub-figure is as indicated. Statistical significance between histograms within a sub-figure is indicated by an "*" (all $p < 0.025$; Kolmogorov-Smirnov tests, see text).

differences between the two choice distributions during this third SBS test (Fig. 3c), or between any two choice distributions when comparing this and the first SBS test (Figs 3a and 3c). Overall, the SBS tests revealed a preference for the NF feeder that could be overridden by adding more sugar to the F feeder.

Feeder positioning had marked effect on behaviour during the first UPLOW preference test (Treatment 4, Fig. 3d). Most bouts started at the F feeder when it was in the upper position (solid bars), though many ended at the NF feeder (in the lower position). The majority of bouts took

place solely at the NF feeder when it was in the upper position (open bars). These two choice distributions differed significantly (K-S test, $p < 0.025$).

The second UPLOW test (Treatment 6, Fig. 3e) involved the doubling of the sugar concentration in the F feeder. Here, virtually all of the feeding took place at the F feeder when it was in the upper position (solid bars). With the F feeder in the lower position (open bars), however, about 50% of the bouts took place solely at the NF (upper) feeder, and relatively few bouts were completed at the F feeder. These two choice distributions differed significantly (K-S test, $p < 0.01$). All other possible pair-wise comparisons of choice distributions between the first and second UPLOW tests (Figs 3d and 3e) also differed significantly (K-S tests, all $p < 0.05$).

The third UPLOW test (Treatment 8, Fig. 3f) acted as an additional control to test for stability in preferences over time. This preference test was a repeat of the first UPLOW test (Treatment 4, Fig. 3d), and the observed preferences were broadly similar between these two treatments. As in the first UPLOW test, the two choice distributions in the third one differed significantly (K-S test, $p < 0.005$), and there were no significant choice differences between these two tests (Figs 3d and 3f) for a given feeder positioning, although there was a somewhat greater preference for the NF feeder during the third UPLOW test. Overall, the results of the UPLOW tests, taken in conjunction with the SBS tests, revealed a preference for the NF feeder that could be overridden by placing the F feeder in the upper position, as well as by doubling the sugar concentration in the F feeder.

Discussion

Energy-based currencies of fitness have proven useful in the study of hummingbird foraging behaviour. However, two general results herein suggest that such currencies will not be uniformly successful. First, the hummingbirds voluntarily lowered their energy intake rate at F feeders by repeatedly pulling-out during a feeding bout. Perhaps the most obvious aspect of an F feeder is its potential for blocking a hummingbird's view of its surroundings (Fig. 1). When faced with similar situations in which feeding and vision are mutually exclusive, several species of birds voluntarily interrupt feeding to scan their environment; a great deal of evidence suggests that this 'vigilance' is anti-predatory in nature (Elgar, 1989; Lima and Dill, 1990). Since a hummingbird with its view obstructed by the large 'corolla' of an F feeder may be vulnerable to opportunistic attack by predators (see below), the repeated pulling out of F feeders may represent anti-predatory vigilance. If so, then the trade-off between vigilance and feeding should be influenced by factors determining the risk of attack (Lima, 1987); the hummingbird's tendency to pull-out (or 'scan') more often and for longer periods of time while feeding closer to the ground suggests that proximity to the ground is one such factor. Note the strong resemblance of this result to that in Lendrem (1983), where anti-predatory vigilance in blue tits (*Parus cearuleus*) increased as the birds fed closer to the ground and potential predators, such as cats.

An F feeder blocks not only the view of predators, but also the view of potentially aggressive hummingbirds. Undoubtedly, some of the pulling out of F feeders was devoted to detecting such aggression from feeder 'owners' (Paton and Carpenter, 1984; see also Waite, 1987). However, such anti-aggression vigilance seems unable to explain fully why pulling out increased with decreasing distance to the ground (Fig. 2). Also, recall that every bout at an F feeder involved repeated pull-outs, thus the feeder owner was also engaging in such behaviour. Perhaps the owner was pulling out to detect 'intruders', but it is not clear why it would be so concerned with detecting intruders that it would pull-out every second as do the intruders.

Independently of vigilance considerations, the large corolla of an F feeder may have induced subtle aerodynamical problems (e.g. turbulence) the overcoming of which required repeated

pulling out. However, it is not clear how this alternative could account for the distance-to-ground effect. Note also that the pull-outs themselves involved an abrupt, often startled retreat away from the feeder up to a distance of 15 cm (occasionally more), which appears too far for aerodynamical considerations alone.

Second, the feeder preference tests also suggest that hummingbirds voluntarily lowered their energy intake rate as a response to the risk of predation. The hummingbirds' preference for the visually non-obstructive NF feeder over the F feeder (at equal sugar concentrations) follows from the above arguments concerning anti-predatory vigilance: the NF feeder allowed for simultaneous feeding and vigilance, while the F feeder did not. Doubling the concentration of sugar in the F feeder reversed the hummingbirds' feeder preference (Tamm and Gass, 1986), but only when the F feeder was in the position farther from the ground (Fig. 3). This again implies that the hummingbirds were sensitive to a perceived threat that increases towards the ground (Lendrem, 1983). A perceived risk of feeding too close to the ground might also help explain the strong tendency for 'mixed' bouts during the second side-by-side preference tests with the feeders in the lower position (Fig. 3b). Perhaps most bouts began at NF feeders in an attempt to assess the presence of potential predators simultaneously while feeding, before switching to the (then) more energetically profitable F feeder (c.f. Lima, 1988).

While the behaviour of Anna's hummingbirds appears consistent with a trade-off between energy gain and predator avoidance, it is nonetheless clear that predation on hummingbirds is relatively rare (Miller and Gass, 1985; Stiles, 1978). This might seem contradictory, but one should not equate the lack of predation with the lack of response to potential predators (Lima and Dill, 1990). Potential hummingbird predators at the present study site included cats, American kestrels (*Falco sparverius*), loggerhead shrikes (*Lanius ludovicianus*), *Accipiter* hawks, and roadrunners. In fact, Anna's (and Costa's) hummingbirds would not feed at the site if a roadrunner was anywhere near the feeder. Instead, they would 'chatter nervously' before leaving the site (W. A. Calder describes similar behaviour in hummingbird/roadrunner encounters, personal communication). This wariness seems justified as reports exist of roadrunners feeding opportunistically on hummingbirds (Spofford, 1976) and several passerine birds (Zimmerman, 1970; Binford, 1971; Barclay, 1977). The curve-billed thrasher (*Toxostoma curvirostre*), a large omnivorous passerine common at the study site, may also be a potential predator, for in one instance a thrasher lunged at a feeding Costa's hummingbird. In general, hummingbirds would not feed if thrashers were within a few metres of the feeder; smaller passerines and even larger birds such as doves elicited no such response. Thus, even though hummingbirds are nimble flyers and probably difficult to capture, they nonetheless seemed aware of the predatory tendencies of the many animals in the area, and their behaviour suggests this was incorporated into their decisions while feeding.

In conclusion, a greater consideration of the influence of predators on hummingbird decision making may lead to greater insight into hummingbird biology in general. In this regard, it is tempting to speculate that the long, tubular flowers (offering very little visual obstruction) typical of hummingbird-pollinated plants (Brown and Kodric-Brown, 1979) evolved (in part) in response to a hummingbird's 'desire' for an unobstructed view of its environment while foraging.

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