

Original Article

Hummingbirds choose not to rely on good taste: information use during foraging

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To increase their chances of survival and reproduction, animals must detect changes in food quality and then decide if, and how quickly, to adjust their behavior. How quickly an animal responds to change will depend on the information available (cognitive, sensory, or physiological) and how it weights those types of information. Surrogate measures of meal size suggest that sensory information is used to make initial choices about how much to eat following changes in resource quality, choices are subsequently altered and refined as further information becomes available. Using direct measures, we investigated the amount of food consumed, the time taken to feed, and the interbout intervals between visits to a feeder of rufous hummingbirds, before and after changes in sucrose concentration. The hummingbirds did not change how much they drank at first experience of a new concentration but then rapidly adjusted meal sizes toward optimal for that concentration over a few feeding visits. Thus, it seems the hummingbirds used both cognitive and physiological information to decide how much to drink but appeared to ignore sensory information, such as taste. The early responses animals make to changed resources enable us to determine the types of information on which they rely most in their decision making. *Key words:* decision making, foraging, hummingbirds, information. [*Behav Ecol* 22:471–477 (2011)]

INTRODUCTION

Food availability (amount and quality) varies in both space and time, and we expect animals to respond to changes in food quality in a timely manner. Changes in food quality pose a problem for animals because while tending to prefer higher quality food, they require less of it to maintain their body condition than poorer quality food, so they should control their intake (e.g., Tamm and Gass 1986; Sclafani 2004). Like weight loss, weight gain can have negative consequences including, in the case of birds, increased flight costs, reduced manoeuvrability, and increased predation risk (DeBenedictis et al. 1978; Gosler et al. 1995; Macleod et al. 2005). Therefore, where access to food is unrestricted, animals should consume relatively less when preferred high-quality food is available than they do when food quality is lower.

Animals base decisions about where to forage and how much to eat on both expectations of resource quality and current information (Cole et al. 1982; Bacon et al. 2010). A combination of recent and more distant memories are used to form expectations about current conditions, with more weight given to more recent information (Shettleworth and Plowright 1992; Hirvonen et al. 1999). By comparing current information with these memories and expectations, foragers can detect changes in patch quality and change their behavior appropriately, neither too hastily nor too slowly (Hirvonen et al. 1999; Lara 2006; Vasquez et al. 2006; Hall et al. 2007). Prior knowledge of patch types and their frequency in the

environment can be used by animals alongside current sampling information to form an estimate/expectation of patch quality and inform, for example, decisions on when to leave a patch (e.g., McNamara 1982). This is referred to as Bayesian, or Bayesian like, decision making and has been described in multiple species (e.g., Valone and Brown 1989; Valone 1991; Biernaskie et al. 2009).

An animal gains information about the current foraging situation in 2 ways: sensory input and physiological feedback. Each of these may vary in how readily the animal can access the information: Orosensory information, such as taste, is available immediately on encountering an item of food, whereas physiological information from postingestive feedback becomes available only after a temporal delay as the meal is digested (Sclafani 1994; Yearsley et al. 2006).

How much an animal consumes in a foraging bout might be considered in terms of how much it likes/wants the food on offer (often referred to as its hedonic value; Sclafani 2004). This value is based on the sensory attributes of the food and the animal's body condition. Foods that are better than normal are more desirable (hedonically positive) and vice versa. Following changes in food quality, the hedonic value of the food is updated as physiological feedback becomes available via "incentive learning," such that animals take an appropriate amount and do not over or under eat (Costa et al. 2007). However, reductions in preferences for (the hedonic value of) higher quality foods do not always happen, which can lead to obesity (Sclafani 2004).

By knowing the previous experience and the delay between meals, we can use an animal's behavioral responses following a change in resource quality to determine the relative importance of different kinds of information, as they become available over time, in animals' decisions about how much to consume of a changed resource (Sclafani 2004). This allows

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us to determine if animals regulate their food intake using learned or innate preferences for certain flavors (e.g., sweetness) rather than from direct information about food quality obtained from physiological feedback (Sclafani 1987; Sclafani 1994; Ackerman et al. 1992). For example, in rats, preferred flavors can induce increased consumption and weight gain independently from the actual nutrient content of the reward received (Sclafani 2004).

Models of decision making suggest that in general animals should use more reliable types of information such as post-ingestive feedback in preference to information such as taste, which is only indirectly related to a meal's physiological consequences (Koops 2004; McLinn and Stephens 2006). However, little is known about the sequence of adjustments animals may make to their behavior as different sorts of information become available when resource quality changes. In this experiment, we examined the behavioral responses of territorial male rufous hummingbirds (*Selasphorus rufus*) to changes in resource quality (sucrose concentration), in order to determine whether the kind of information a bird uses to decide how much to drink on encountering a change in resource quality differs with increasing experience of the changed resource. Rufous hummingbirds are particularly suitable for this experiment as their optimal meal sizes differ with food quality such that they should drink less of preferred higher concentration sucrose solutions than of less preferred lower sucrose concentrations (DeBenedictis et al. 1978; Tamm and Gass 1986). The concentrations in hummingbird flowers range from as low as 7.3% to more than 60% (Pyke and Waser 1981) with a mean value in the order of 24–25% (Pyke and Waser 1981; Ornelas et al. 2007). As in nature floral nectar varies within and between plants and species as well as over time, therefore, hummingbirds will often encounter different concentrations sequentially (Pleasants 1983; Ha et al. 1990; McDade and Weeks 2004; Herrera et al. 2006).

Meal size is a result of trade-offs between the energy consumed and the additional flight costs of carrying the meal (DeBenedictis et al. 1978). The sucrose concentration we provided was either 14% (low) or 25% (high), a difference that these birds can easily detect using taste when presented with multiple options simultaneously (they can discriminate between solutions differing by 1–3%: Blem et al. 2000). Being able to remember, and to detect and respond to changes in, the reward values of different flowers allows territorial and traplining species, including hummingbirds, to forage and defend resources more efficiently than do individuals that lack such local knowledge (e.g., Sandlin 2000; Ohashi et al. 2008).

The first time birds encounter a new sucrose concentration they would only have 2 sorts of information available to them to decide how much to drink: taste and past experience (memories of the previous concentration and of their previous behavior). As hummingbirds can learn the position of more rewarding flowers, we assume that the birds can remember taste and would use this information to determine the expected taste of food during subsequent bouts at the same location (Hurly and Healy 1996).

Hummingbirds typically prefer stronger nectar concentrations (Gass et al. 1999; Blem et al. 2000) and, thus, the taste of a higher concentration is expected to be more rewarding than that of the preceding lower concentration (i.e., would have a higher hedonic value). Therefore, if the hummingbirds use taste alone to decide how much to drink at the first experience of 25% sucrose after feeding on 14% sucrose, they should drink more of the 25% sucrose. Likewise, at the first experience of 14% sucrose, taste-alone decisions would lead to birds drinking less than they had been drinking of the

preceding 25% solution. Such behavior would be similar to that of animals choosing among different quality rewards, rejecting a poor quality prey item because it pays the animal to wait for a better prey item (Berec and Krivan 2000). However, this would lead to the amount drunk at first experiences of poorer concentrations to be lower than the optimal meal size for that concentration, and the amount drunk at first experience of higher concentrations being larger than optimal for that concentration.

Conversely, as animals readily form associations between the taste of food and its post-ingestive consequences and will adjust their behavior accordingly (e.g., mollusks, Gelperin 1975; wolves, Gustavson et al. 1976; and ruminants, Provenza 1995), it is possible that hummingbirds learn that they should drink less of higher than of lower concentrations. We might then expect hummingbirds to modify how much they drank at a first experience of a new concentration in the direction of the optimal volume for that concentration.

Alternatively, hummingbirds may use only post-ingestive feedback to decide how much to drink. Post-ingestive feedback informs animals of their energetic state (Sclafani 2004; Yearsley et al. 2006), information that can become available between bouts when there is little delay between ingestion and its post-ingestive consequences, as for hummingbirds (Karasov et al. 1986; Tiebout 1989). As such information is not available at the first experience of a new concentration, the volume consumed should remain unchanged until later bouts. Sunbirds adjust their foraging behavior in response to changes in concentration within 5–10 min (equivalent to 2–5 feeding bouts: Kohler et al. 2008). Like sunbirds, hummingbirds have rapid meal transit times of around 5–15 min (Tiebout 1989; Downs 1997). As more than 50% of a hummingbird's first meal should have been fully digested between successive meals, the hummingbird would have at least some post-ingestive information by the second meal following a change in concentration (10–15 min; Tiebout 1989). Thus, if post-ingestive feedback but not taste was used to decide how much to drink following a change in concentration, changes in bout volume in the direction of the optimal meal size for that concentration would be expected from around the second meal onward. Based on unpublished data and the time sunbirds take to adjust their meal size, hummingbirds would be expected to be drinking roughly optimal volumes by around 5 bouts after a change in concentration. A summary of predictions for hummingbirds' initial responses to a new concentration is shown in Table 1.

METHODS

Twelve male rufous hummingbirds (6 in 2007 and 6 in 2008), which had been defending territories containing a 250-ml inverted bottle feeder (filled with 14% sucrose) for at least a week, were trapped, color-marked, banded for individual identification, and released. The field site was the Westcastle river valley in the Rocky Mountains, Alberta, Canada (lat: 49.349024, long: -114.410902).

Not less than 3 days after trapping birds were trained to feed from an artificial flower containing 14% sucrose during the course of a day (6–9 h). The "flower" was a red cardboard disk (diameter 4.5 cm) with a syringe cap inserted through its center to act as a well. The flower was taped with red tape to the top of a cane (1 m), which was pushed into the ground within 5 m of the usual position of the feeder. Observers sat at least 10 m from the flower.

Following training, there were 2 experimental days: Treatment 1 and Treatment 2, which weather permitting immediately followed the training day. As on the training day, the feeder was removed and replaced with the artificial flower.

Table 1
Hypotheses about the types of information hummingbirds may employ and associated predictions regarding drink volumes in the first feeding bout at a new concentration (F1)

Hypothesis	Prediction on F1
Taste alone + higher hedonic value for 25% sucrose	14–25 increase volume 25–14 decrease volume
Taste alone + association between concentration and optimal meal size	14–25 decrease volume 25–14 increase volume
Postingestive feedback alone	14–25 same volume 25–14 same volume

Hummingbirds have different optimal bout volumes for different concentrations and are therefore expected to respond differently to an increase from the way they respond to a decrease in concentration. Thus, we provide predictions for behavior at (F1) following changes from 14% to 25% (increase) and changes from 25% to 14% sucrose (decrease).

In Treatment 1 (low, high, and low), the flower contained 14% sucrose for the first 3 h, 25% sucrose for the next 3 h, and 14% sucrose for the final 3 h. In Treatment 2 (high, low, and high), the flower contained 25% sucrose for the first 3 h, 14% sucrose for the next 3 h, and 25% sucrose for the final 3 h. Half the birds received Treatment 1 first and the other half Treatment 2 first.

The volume drunk and the timing and duration of each of a bird's visit to the flower were recorded during both training and treatment days. Volumes were measured by refilling the syringe cap using a repeating pipette accurate to 10 μ l. Duration of a feeding bout was the interval between the first insertion of the bird's bill into the flower and the last withdrawal from the flower before flying away.

RESULTS

We first determined whether birds' foraging behavior (volume drunk, interbout intervals, and drinking duration) differed between the 2 years of testing with a maximum-likelihood mixed-model in the statistical package JMP. The data were averaged for each bird for each experimental concentration. The model included bird (as a random effect), year, and concentration. There was no effect of year on the amount the birds drank (analysis of variance: $F_{1,10} = 1.42$, $P = 0.26$), interbout intervals ($F_{1,10} = 1.22$, $P = 0.29$), or duration of the feeding bout ($F_{1,10} = 0.26$, $P = 0.62$). Given no effect of year in these analyses, year was excluded from the subsequent analyses.

To investigate initial responses and the speed of behavioral adjustments following changes in concentration, we required more than just the first and later feeding bouts following changes in concentration. As birds were expected to adjust their behavior within 5 bouts, we grouped the data into 3 foraging periods: the first feeding bout (F1) to assess initial responses, when only sensory information would be available; a mean of feeding bouts 2, 3, and 4 (F2–4), when postingestive feedback from the previous meals of the new concentration would be available and we expected a period of fairly rapid behavioral adjustment; and thirdly, the mean of feeding bouts 5 onward (F5+), when behavior was expected to be relatively stable. We included a single mean value for each bird for each foraging period such that all foraging periods had equal weight in analyses (12 subjects \times 2 concentrations \times 3 foraging periods = 72 mean values).

The following data were analyzed with Multivariate analysis of variance repeated-measures tests in the statistical software pack-

age JMP. The Mauchly criterion test was used to test for sphericity and, where data were nonspherical, we used Greenhouse–Geisser–adjusted degrees of freedom and P values. Paired t tests (two-tailed) were used to make further comparisons.

Volume consumed

To determine whether birds changed the amount they drank during their first experience of a new concentration, we compared the volume of the first feeding bout with the volume consumed during feeding bouts 5+ of the previous concentration. Birds did not change the amount they drank on their first visit to the feeder containing the new concentration. On both high and low concentrations, the birds drank a similar volume during F1 compared with the volume drunk during F5+ of the previous concentration ($t_{11} = 1.8$, $P = 0.10$) and ($t_{11} = 0.64$, $P = 0.53$), respectively.

We then investigated whether birds changed how much they drank with increasing experiences of a new concentration, both for increases and decreases in sucrose concentration by comparing the means of F1, F2–4, and F5+ for each concentration. There was no effect of concentration ($F_{1,11} = 0.23$, $P = 0.63$) or the number of feeding bouts since the concentration change ($F_{2,22} = 0.76$, $P = 0.48$). However, there was a significant interaction between concentration and the number of bouts following the change in concentration such that the volume consumed of the high concentration decreased from F1 to F5+, whereas the volume consumed of the low concentration increased from F1 to F5+ ($F_{2,22} = 5.72$, $P = 0.01$; Figure 1). Decreases in bout volume with increasing experience between F1 and F5+ of the high concentration were significant ($t_{11} = 3.43$, $P < 0.01$), whereas increases in bout volume between F1 and F5+ of the low concentration were nearly significant ($t_{11} = 2.04$, $P = 0.06$).

Having found that following changes in concentration birds altered how much they drank with increasing experiences of the changed resource, we looked at this pattern in more detail to determine how many bouts occurred before the birds took a fairly stable amount for that concentration. To do this, we compared the volume of F2–4 when birds may still have been adjusting how much they drank to the volume taken on

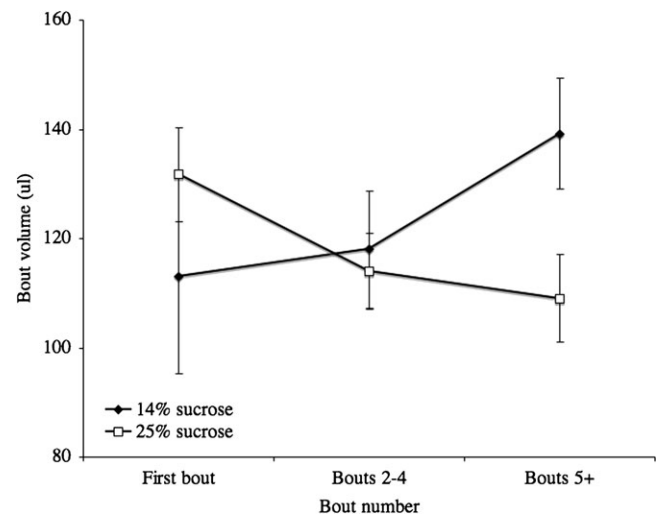


Figure 1

The average volume of the first feeding bout, the second to fourth bouts, and feeding bouts 5 onward, following changes from 25% to 14% sucrose (black diamonds) and 14% to 25% sucrose (open squares). Data are means and standard errors, $N = 12$.

F5+ by which stage we expected them to have reached a stable volume. If birds adjusted their behavior in fewer than 5 bouts, then the volumes of F2–4 were expected to be similar to the volumes of F5+. On the high concentration, the adjustment of the amount drunk was complete by F2–4 (comparison F2–4 with F5+: $t_{11} = 0.66$, $P = 0.52$). However, the adjustment of the amount drunk on the low concentration was slower: the volumes of F2–4 were still significantly less than the volume drunk during F5+ ($t_{11} = 2.48$, $P = 0.03$).

Time of day effects

To test if birds behaved differently throughout the day, we compared the mean volume the birds drank in F5+ for each concentration at each time of day (AM, noon, and PM). Birds drank larger volumes of the low concentration than of the high concentration (mean low = 126 ± 12 SE μl , mean high = 112 ± 10 μl ; $F_{1,11} = 5.21$, $P = 0.04$), and they drank more of both concentrations as the day progressed (mean morning = 99 ± 2 μl , mean afternoon = 138 ± 5 μl ; $F_{2,22} = 10.69$, $P < 0.01$). There was no interaction between concentration and time of day ($F_{2,22} = 1.09$, $P = 0.35$).

Feeding bout duration

To see if birds changed the length of their feeding bouts at the first bout on a new concentration, we compared the duration of the first feeding bout with the mean of feeding bouts 5+ of the previous concentration. The duration of F1 on the low concentration was significantly shorter than it was for F5+ of the previous high concentration period ($t_{11} = 2.68$, $P = 0.02$). The duration of F1 on the high concentration was significantly longer than it was for F5+ of the previous low concentration period ($t_{11} = 2.14$, $P = 0.05$).

Overall, the duration of each feeding bout was longer on high than on low concentrations ($F_{1,11} = 7.71$, $P = 0.02$), but there was no overall effect of the number of feeding bouts since the change in concentration (F1 through F5+; $F_{2,22} = 0.44$, $P = 0.65$). The interaction between concentration and number of feeding bouts was significant ($F_{2,22} = 5.87$, $P = 0.01$) indicating that following changes to the high concentration the duration of feeding bouts decreased from F1 to F5+, but conversely, increased from F1 to F5+ following changes to the low concentration (high F1 [mean = 8.9 ± 0.8 s] vs. high F5+ [mean = 7.6 ± 0.8 s], $t_{11} = 3.09$, $P = 0.01$; low F1 [mean = 6.4 ± 0.8 s] vs. low F5+ [mean = 7.8 ± 0.8 s], $t_{11} = 3.12$, $P < 0.01$; Figure 2). It is apparent that the concentration effect on bout length was due to differences in the early bouts and that bout lengths were essentially identical by F5+ ($t_{11} = 0.35$, $P = 0.73$; Figure 2).

Intake rates

We calculated the mean intake rate of sucrose (bout volume/bout duration, microliters/second) for F1, F2–4, and F5+ within each concentration. Intake rates tended to be greater when birds were drinking the low concentration rather than when drinking the high concentration (mean high = 14.93 ± 1.00 $\mu\text{l/s}$, mean low = 19.14 ± 2.93 $\mu\text{l/s}$; $F_{1,11} = 3.89$, $P = 0.07$). Intake rates did not differ with increasing overall experience ($F_{2,22} = 0.82$, $P = 0.45$) nor did experience interact with concentration ($F_{2,22} = 0.10$, $P = 0.90$).

Interbout intervals

We compared the means of interbout intervals following F1, F2–4, and F5+ for each concentration. Interbout intervals on

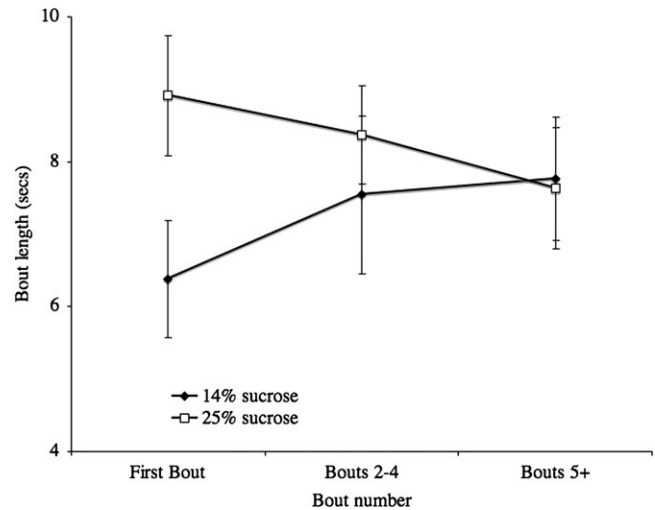


Figure 2

The average duration of the first feeding bout, the second to fourth bouts, and feeding bouts 5 onward, following changes from 25% to 14% sucrose (black diamonds) and 14% to 25% sucrose (open squares). Data are means and standard errors, $N = 12$.

the low concentration were shorter than when birds were feeding on the high concentration ($F_{1,11} = 78.55$, $P < 0.01$). There was a significant interaction between concentration and the number of feeding bouts ($F_{1,25,13,72} = 9.73$, $P < 0.01$; Figure 3). Interbout intervals decreased from F1 to F5+ on the high concentration but increased from F1 to F5+ on the low concentration (high F1 [mean = 16.28 ± 2.30 min] vs. high F5+ [mean = 11.62 ± 0.09 min], $t_{11} = 2.83$, $P = 0.02$; low F1 [mean = 5.52 ± 0.57 min] vs. low F5+ [mean = 7.78 ± 0.59 min], $t_{11} = 7.33$, $P < 0.01$).

We then looked to see how rapidly birds adjusted their behavior following increases and decreases in sucrose concentration. If birds had adjusted how much they drank before feeding bout 5 then the interval for F2–4 would be similar to the interval for F5+. On the high concentration, the decrease in interbout intervals occurred during F2–4 (F2–4 vs.

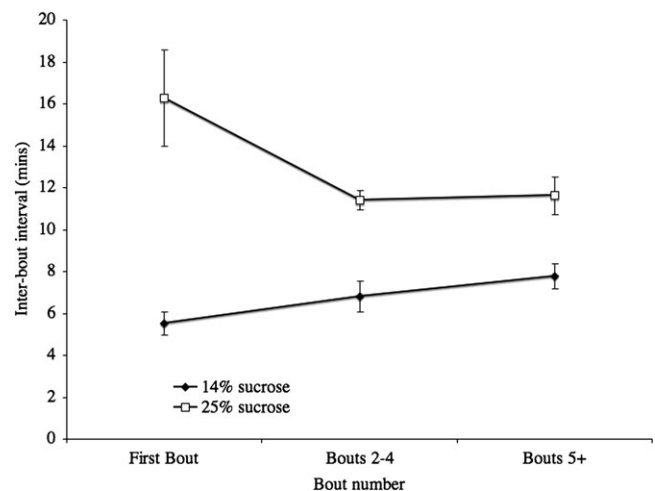


Figure 3

The average interbout interval following the first feeding bout, the second to fourth bouts, and feeding bouts 5 onward, for changes from 25% to 14% sucrose (black diamonds) and 14% to 25% sucrose (open squares). Data are means and standard errors, $N = 12$.

F5+: $t_{11} = 0.31$, $P = 0.76$). On the low concentration, the adjustment of interbout intervals was slower, as interbout intervals 2–4 were significantly shorter than were interbout intervals 5+ (F2–4 vs. F5+: $t_{11} = 2.74$, $P = 0.02$).

Time of day effects

We used interbout intervals 5+ for each concentration at each time of day to investigate if interbout intervals changed across the day. Interbout intervals were shorter when the birds were drinking the low rather than the high concentration (Means: 14% = 7.78 ± 0.59 min, 25% = 11.62 ± 0.90 min; $F_{1,11} = 56.70$, $P < 0.01$). Interbout intervals increased across the day (Means: morning = 13.29 ± 0.83 min, midday = 14.93 ± 1.09 min, and afternoon = 17.63 ± 1.75 min; $F_{2,22} = 8.85$, $P < 0.01$) for both concentrations (interaction: $F_{2,22} = 1.87$, $P = 0.17$).

To estimate whether changes in interbout interval and the amount the birds drank across the day were affecting the birds' rate of energy intake, we calculated the average joules consumed by birds per unit time for each time of day. Birds consumed a similar number of joules per minute (a function of volume of sucrose per feeding bout/interbout interval) on both concentrations ($F_{1,11} = 1.55$, $P = 0.24$; Figure 4) and all times of day ($F_{1,38,15,21} = 1.44$, $P = 0.25$). There was no significant interaction between concentration and time of day ($F_{2,22} = 0.19$, $P = 0.83$).

In order to test whether increasing experience of a new concentration affected the energy available to birds in subsequent interbout intervals, we calculated the mean energy available to them per minute following F1, F2–4, and F5+ for changes to high and low concentrations. There was no effect of increasing experience ($F_{2,22} = 0.33$, $P = 0.72$) or of concentration ($F_{1,11} = 0.16$, $P = 0.70$), and the interaction was not significant ($F_{2,22} = 1.08$, $P = 0.36$).

The relationship between interbout interval and the volume consumed

We used a mixed effects model fitted by a restricted maximum likelihood approach in the statistical package JMP to investigate whether the volume birds drank was better explained by the time since their last meal or the time until they fed again (preceding vs. subsequent interval). The data were log transformed for normality, and bird was included as a random effect. Both intervals were longer when the bird drank more (Adjusted $R^2 = 0.31$; preceding interval: $F_{1,1397} = 20.62$, $P < 0.01$, Effect size estimate = 0.01; subsequent interval: $F_{1,1396} = 75.31$, $P < 0.01$, Effect size estimate = 0.02). Despite the relationships between drink volume and both the preceding and the subsequent intervals, the 2 intervals were not significantly related to each other ($F_{1,1397} = 0.52$, $P = 0.47$). However, the effect size of the interval following the feeding bout of interest was nearly twice that of the interval preceding the bout. It appears that the volume drunk affects the subsequent interbout interval more strongly than that volume is affected by the previous interbout interval.

DISCUSSION

Unexpectedly, birds did not change the amount they drank at their first experience of a new concentration. As we know they can detect much smaller changes in concentration using taste within a bout, it seems very unlikely that the hummingbirds did not detect the large changes in concentration albeit experienced some minutes apart between bouts (Stiles 1976; Stromberg and Johnsen 1990; Roberts 1996; Blem et al. 1997; Blem et al. 2000). It would also be surprising if they could not detect a change in concentration approximately half of the mean

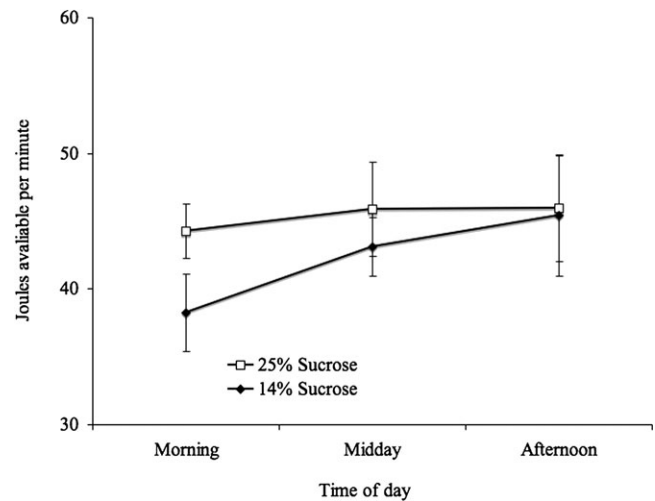


Figure 4

The average joules consumed per minute at different times of day for 14% sucrose (black diamonds) and 25% sucrose (open squares). Data are means and standard errors, $N = 12$.

nectar concentration of hummingbird-pollinated flowers (ca. 24%; Ohashi and Thomson 2005; Ornelas et al. 2007). Birds did, however, adjust drink volumes subsequent to this first experience of a new concentration. There are 2 possible explanations for this delay in volume adjustment. Firstly, from a single experience, the bird cannot be sure that the change in sucrose concentration is more than transitory. There may be little cost associated with taking one drink of a suboptimal volume so birds may simply have ignored the change. This possibility we consider unlikely because the birds are expected to capitalize on one-off, or first, experiences of higher concentrations by drinking more, or to decrease the amount they drink, depending on the optimal drink volume for that concentration. Animals' acceptance of poor food items is low if the energy gained from those food items is less than that gained by waiting for a larger reward (Stephens and Krebs 1986). This possibility, then, does not explain why they did nothing in response to a change.

The second more plausible explanation is that although birds can detect the change using taste, they required further information to assess the magnitude and the energetic consequences of the change. They would then be expected to drink the same amount as previously and to wait for post-ingestive feedback from that meal before deciding whether and by how much to adjust the amount they drink at the next meal, thus avoiding overshooting the optimal meal size of the new concentration. Indeed, starlings use taste to inform their foraging decisions only when it reliably informs them about the food's content (Skelhorn and Rowe 2010). The post-ingestive information available from the new concentration would have been considerable by the time the bird came to feed for a second time (Tiebout 1989). It is also possible that birds further delayed reaching a final decision on the appropriate amount to drink so as to confirm that the change was stable (Shettleworth and Plowright 1992). This may be why birds took up to 4 experiences to adjust how much they drank following changes to 14% sucrose. The delay to respond until after the first foraging bout suggests that taste is not important in making decisions about meal size at least when foraging from fairly constant resources, although it may be important for detecting changes in food quality.

The way in which birds responded depends on which behavior was measured. Birds drank for longer on their first encounter of the higher concentration and for less time

when they encountered the lower concentration for the first time. Had bout duration been the sole measure we used, we would have concluded that birds, in fact, drank more on first experiences of high concentrations and drank less on first experiences of lower concentrations and, consequently, that birds did not wait for postingestive feedback before adjusting the amount they drank. The discrepancy between this surrogate measure of drink volume and our direct measure may be explained by differences in the viscosity of the 2 solutions: the higher the viscosity, the longer it takes a hummingbird to obtain the same volume (Roberts 1995). Indeed, intake rates (microliters/second) were somewhat, but not significantly, higher when birds were drinking 14% sucrose than when they were drinking 25% sucrose. Surrogate measures of food intake, such as bout lengths and average bite masses, are frequently used and are fairly accurate over multiple bouts. However, they may be inaccurate as measures of the amount consumed within a bout, particularly where several food types are being eaten (Agreil et al. 2005; Magrath et al. 2007). This inaccuracy could lead to misinterpretation concerning the information animals employ to respond to a changed resource.

The frequency at which birds came to the flower took several visits before stabilizing at new values. The first interbout interval following an increase in concentration was the longest and that following a decrease in concentration the shortest. This was expected as the time between meals is largely dependent on the time required to digest most of the sucrose in the previous meal (Wolf and Hainsworth 1977; DeBenedictis et al. 1978; Hainsworth 1989). Indeed, the amount birds drank was strongly correlated with both the time since the previous feeding bout and the time until they fed again, and the energy available to them per minute did not change with increasing experience of a new concentration. Of these 2 time periods, however, the amount drunk was most strongly related to the interval following the current feeding bout. The most parsimonious interpretation is that interval depends on digestion of the previous sucrose intake as discussed above. However, this relationship also opens up the possibility that hummingbirds might be able to plan their near-future activities (Clayton et al. 2003; Raby et al. 2007), taking a larger drink in preparation for being away from the flower for longer.

We can use the pattern of behavioral responses associated with changes in food quality to determine what information hummingbirds use to make foraging decisions. They probably use taste to detect changes (but do not necessarily then respond), memory to compare past and present conditions (to drink the same amount as before at first experiences of new concentrations), and physiological postingestive feedback over several experiences to fine-tune how much they drink. Decision-making models are typically based on the assumption that animals use the most reliable types of information available (Koops 2004; van Bergen et al. 2004). However, we have shown that animals may, at least initially, ignore what is a very accurate indicator of the relative quality of their food (concentration of the sucrose). It may be that some animals generally prefer to delay changing their behavior until they have several types of information on which to base their decisions. If so, then detailed data about the amount and sorts of information animals require and prefer to use to make decisions may greatly improve the resolution with which we are able to model and interpret animal decision making not only with regard to initial responses to change but also to the time animals may take to reach a stable response level. Finally, it appears that care should be taken when using surrogate measures of meal size especially where the questions being addressed concern an animal's responses to changes in food resources.

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REFERENCES

- Ackerman SH, Albert M, Shindlecker RD, Gayle C, Smith GP. 1992. Intake of different concentrations of sucrose and corn-oil in pre-weanling rats. *Am J Physiol.* 262:R624–R627.
- Agreil C, Fritz H, Meuret M. 2005. Maintenance of daily intake through bite mass diversity adjustment in sheep grazing on heterogeneous and variable vegetation. *Appl Anim Behav Sci.* 91:35–56.
- Bacon IE, Hurly TA, Healy SD. 2010. Both the past and the present affect risk-sensitive decisions of foraging Rufous hummingbirds. *Behav Ecol.* 21:626–632.
- Berec L, Krivan V. 2000. A mechanistic model for partial preferences. *Theor Popul Biol.* 58:279–289.
- Biernaskie JM, Walker SC, Gegear RJ. 2009. Bumblebees learn to forage like bayesians. *Am Nat.* 174:413–423.
- Blem CR, Blem LB, Cosgrove CC. 1997. Field studies of rufous hummingbird sucrose preference: does source height affect test results? *J Field Ornithol.* 68:245–252.
- Blem CR, Blem LB, Felix J, van Gelder J. 2000. Rufous hummingbird sucrose preference: precision of selection varies with concentration. *Condor.* 102:235–238.
- Clayton NS, Bussey TJ, Dickinson A. 2003. Can animals recall the past and plan for the future? *Nat Rev Neurosci.* 4:685–691.
- Cole S, Hainsworth FR, Kamil AC, Mercier T, Wolf LL. 1982. Spatial learning as an adaptation in hummingbirds. *Science.* 217:655–657.
- Costa RM, Gutierrez R, de Araujo IE, Coelho MRP, Kloth AD, Gainetdinov RR, Caron MG, Nicolelis MAL, Simon SA. 2007. Dopamine levels modulate the updating of tastant values. *Genes Brain Behav.* 6:314–320.
- DeBenedictis PA, Gill FB, Hainsworth FR, Pyke GH, Wolf LL. 1978. Optimal meal size in hummingbirds. *Am Nat.* 112:301–316.
- Downs CT. 1997. Sugar digestion efficiencies of Gurney's sugarbirds, malachite sunbirds, and black sunbirds. *Physiol Zool.* 70:93–99.
- Gass CL, Romich MT, Suarez RK. 1999. Energetics of hummingbirds foraging at low ambient temperature. *Can J Zool.* 77:314–320.
- Gelperin A. 1975. Rapid food-aversion learning by a terrestrial mollusk. *Science.* 189:567–570.
- Gosler AG, Greenwood JJD, Perrins C. 1995. Predation risk and the cost of being fat. *Nature.* 377:621–623.
- Gustavson CR, Kelley DJ, Sweeney M, Garcia J. 1976. Prey lithium aversions in coyotes and wolves. *Behav Ecol.* 17:61–72.
- Ha JC, Lehner PN, Farley SD. 1990. Risk-prone foraging behaviour in captive grey jays, *Perisoreus canadensis*. *Anim Behav.* 39:91–96.
- Hainsworth FR. 1989. Evaluating models of crop emptying in hummingbirds. *Auk.* 106:724–724.
- Hall CL, Humphries MM, Kramer DL. 2007. Resource tracking by eastern chipmunks: the sampling of renewing patches. *Can J Zool.* 85:536–548.
- Herrera CM, Perez R, Alonso C. 2006. Extreme intraplant variation in nectar sugar composition in an insect-pollinated perennial herb. *American Journal of Botany.* 93:575–581.
- Hirvonen H, Ranta E, Rita H, Peuhkuri N. 1999. Significance of memory properties in prey choice decisions. *Ecol Model.* 115:177–189.
- Hurly TA, Healy SD. 1996. Memory for flowers in rufous hummingbirds: location or local visual cues? *Anim Behav.* 51:1149–1157.
- Karasov WH, Phan D, Diamond JM, Carpenter FL. 1986. Food passage and intestinal nutrient absorption in hummingbirds. *Auk.* 103:453–464.
- Kohler A, Verburt L, Fleming PA, Nicolson SW. 2008. Changes in nectar concentration: how quickly do whitebellied sunbirds (*Cinnyris talatala*) adjust feeding patterns and food intake? *J Comp Physiol B.* 178:785–793.

- Koops MA. 2004. Reliability and the value of information. *Anim Behav*. 67:103–111.
- Lara C. 2006. Temporal dynamics of flower use by hummingbirds in a highland temperate forest in Mexico. *Ecoscience*. 13:23–29.
- Macleod R, Barnett P, Clark JA, Cresswell W. 2005. Body mass change strategies in blackbirds *Turdus merula*: the starvation-predation risk trade-off. *J Anim Ecol*. 74:292–302.
- Magrath MJL, Janson J, Komdeur J, Elgar MA, Mulder RA. 2007. Provisioning adjustments by male and female fairy martins to short-term manipulations of brood size. *Behaviour*. 144:1119–1132.
- McDade LA, Weeks JA. 2004. Nectar in hummingbird-pollinated neotropical plants I: patterns of production and variability in 12 species. *Biotropica*. 36:196–215.
- McLinn CM, Stephens DW. 2006. What makes information valuable: signal reliability and environmental uncertainty. *Anim Behav*. 71:1119–1129.
- McNamara JM. 1982. Optimal patch use in a stochastic environment. *Theor Popul Biol*. 21:269–288.
- Ohashi K, Leslie A, Thomson JD. 2008. Trapline foraging by bumble bees: V. Effects of experience and priority on competitive performance. *Behav Ecol*. 19:936–948.
- Ohashi K, Thomson JD. 2005. Efficient harvesting of renewing resources. *Behav Ecol*. 16:592–605.
- Ornelas JF, Ordano M, De-Nova AJ, Quintero ME, Garland T. 2007. Phylogenetic analysis of interspecific variation in nectar of hummingbird-visited plants. *J Evol Biol*. 20:1904–1917.
- Pleasant JM. 1983. Nectar production patterns in *Ipomopsis aggregata* (Polemoniaceae). *Am J Bot*. 70:1468–1475.
- Provenza FD. 1995. Postingestive feedback as an elementary determinant of food preferences and intake in ruminants. *J Range Manag*. 48:2–17.
- Pyke GH, Waser NM. 1981. The production of dilute nectars by hummingbird and honeyeater flowers. *Biotropica*. 13:260–270.
- Raby CR, Alexis DM, Dickinson A, Clayton NS. 2007. Planning for the future by western scrub-jays. *Nature*. 445:919–921.
- Roberts WM. 1995. Hummingbird licking behavior and the energetics of nectar feeding. *Auk*. 112:456–463.
- Roberts WM. 1996. Hummingbirds' nectar concentration preferences at low volume: the importance of time scale. *Anim Behav*. 52:361–370.
- Sandlin EA. 2000. Foraging information affects the nature of competitive interactions. *Oikos*. 91:18–28.
- Scalafani A. 1987. Carbohydrate taste, appetite, and obesity—an overview. *Neurosci Biobehav Rev*. 11:131–153.
- Scalafani A. 1994. How food preferences are learned—laboratory-animal models. *Proc Nutr Soc*. 54:419–427.
- Scalafani A. 2004. Oral and postoral determinants of food reward. *Physiol Behav*. 81:773–779.
- Shettleworth SJ, Plowright CMS. 1992. How pigeons estimate rates of prey encounter. *J Exp Psychol Anim Behav Process*. 18:219–235.
- Skelhorn J, Rowe C. 2010. Birds learn to use distastefulness as a signal of toxicity. *Proc R Soc B Biol Sci*. 277:1729–1734.
- Stephens DW, Krebs JR. 1986. Foraging theory. Princeton (NJ): Princeton University Press.
- Stiles FG. 1976. Taste preferences, color preferences, and flower choice in hummingbirds. *Condor*. 78:10–26.
- Stromberg MR, Johnsen PB. 1990. Hummingbird sweetness preferences: taste or viscosity. *Condor*. 92:606–612.
- Tamm S, Gass CL. 1986. Energy-intake rates and nectar concentration preferences by hummingbirds. *Oecologia*. 70:20–23.
- Tiebout HM. 1989. Tests of a model of food passage rates in hummingbirds. *Auk*. 106:203–208.
- Valone TJ. 1991. Bayesian and precient assessment: foraging with pre-harvest information. *Anim Behav*. 41:569–577.
- Valone TJ, Brown JS. 1989. Measuring patch assessment abilities of desert granivores. *Ecology*. 70:1800–1810.
- van Bergen Y, Coolen I, Laland KN. 2004. Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. *Proc R Soc Lond B Biol Sci*. 271:957–962.
- Vasquez RA, Grossi B, Marquez IN. 2006. On the value of information: studying changes in patch assessment abilities through learning. *Oikos*. 112:298–310.
- Wolf LL, Hainsworth FR. 1977. Temporal patterning of feeding by hummingbirds. *Anim Behav*. 25:976–989.
- Yearsley JM, Villalba JJ, Gordon IJ, Kyriazakis I, Speakman JR, Tolkamp BJ, Illius AW, Duncan AJ. 2006. A theory of associating food types with their postingestive consequences. *Am Nat*. 167:705–716.