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C. N. Lotz · C. Martínez del Rio · S. W. Nicolson

Hummingbirds pay a high cost for a warm drink

Abstract Endotherms must warm ingested food to body temperature. Food warming costs may be especially high for nectar-feeding birds, which can ingest prodigious volumes. We formulated a mathematical model to predict the cost of warming nectar as a function of nectar temperature and sugar concentration. This model predicts that the cost of warming nectar should: (1) decrease as a power function of nectar concentration, and (2) increase linearly with the difference between body temperature and nectar temperature. We tested our model on rufous hummingbirds (*Selasphorus rufus*). A typical experiment consisted of feeding birds nectar of a given concentration at 39°C (equivalent to body temperature) and then at 4°C, and vice versa. We used the percentage change in metabolic rate between the two food temperatures to estimate the cost of warming nectar. The model's predictions were accurately met. When birds had to hover rather than perch during feeding bouts, estimated food-warming costs were only slightly lower. The cost of warming nectar to body temperature appears to be an important yet overlooked aspect of the energy budgets of nectar-feeding birds. Hummingbirds feeding on 5% sucrose solutions at 4°C have to increase their metabolic rate by an amount equivalent to that elicited by a 15°C drop in ambient temperature.

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C. N. Lotz · C. Martínez del Rio (✉)
Department of Zoology and Physiology,
University of Wyoming, Laramie,
WY, 82071-3166, USA
E-mail: cmdelrio@uwyo.edu
Tel.: +1-307-7662623
Fax: +1-307-7665625

S. W. Nicolson
Department of Zoology and Entomology,
University of Pretoria, 0002
Pretoria, South Africa

Abbreviations AE assimilation efficiency · *C* nectar concentration · *H'* cost of warming food to body temperature · SDA specific dynamic action · T_a ambient temperature · T_b body temperature · T_n nectar temperature

Introduction

Like most animals, nectar-feeding birds exhibit compensatory feeding: they increase food intake with caloric dilution of nectar and with increasing energy demands (reviewed by Martínez del Rio et al. 2001). The relationship between volumetric nectar intake and sugar concentration has been well characterised as a steep inverse power function (e.g., McWhorter and Martínez del Rio 1999, 2000; Nicolson and Fleming 2003). When nectar sugar concentration is high, intake is low. As concentration decreases, intake increases to satisfy energy requirements. At low concentrations like those often found in natural floral nectars (5–35% sugar; Pyke and Waser 1981), birds ingest prodigious volumes (up to five times body mass daily; McWhorter and Martínez del Rio 1999; Nicolson and Fleming 2003). Indeed, hummingbirds and other nectar-feeding birds have daily water fluxes that exceed the values predicted from allometry by large factors (Weathers and Stiles 1989; Goldstein and Bradshaw 1998; Lotz and Nicolson 1999; McWhorter and Martínez del Rio 2000; Beuchat et al. 1990; Williams et al. 1993). A spate of recent papers has emphasised the digestive and osmoregulatory challenges that energy-dilute and watery diets pose to nectar-feeding birds (reviewed by Martínez del Rio et al. 2001). Here we emphasize an aspect of feeding on nectar that has been largely overlooked: the cost of warming food.

The effect of ambient temperature (T_a) on hummingbird thermoregulation has been studied frequently both in the laboratory and in the field (e.g. Powers 1991; Calder 1993; Schuchmann and Schmidt-Marloh 1979; Beuchat et al. 1979; Prinzinger et al. 1992; Gass et al. 1999). Nevertheless, researchers have ignored a potentially

important factor. In the wild and in the laboratory, birds always feed on nectar with temperatures below body temperature (T_b). Because birds may feed on nectars that are not only cold but also dilute, the cost of warming nectar may be substantial. This cost is an overlooked, but likely important, aspect of hummingbird energy budgets. The impact of food warming on energy budgets is likely to be highest for hummingbirds living in cool climates. Rufous and broad-tailed hummingbirds (*Selasphorus rufus* and *S. platycercus*) are good examples. These species breed at both high latitudes and altitudes in the Rocky Mountains (Calder 1993, 1994) where T_a and hence nectar temperature (T_n), is low. In the central Rocky Mountains of southern Wyoming, we have found that T_n lower than 10°C is not uncommon, and on cool spring mornings we have even observed broad-tailed hummingbirds sip icy sugary slush from hummingbird feeders (B.H. Bakken and C.N. Lotz, unpublished data).

To investigate the cost of warming nectar, we formulated a simple mathematical model. Our model relates the energy needed to warm nectar to T_b, to T_n and concentration (C). We tested the predictions of this model on captive rufous hummingbirds. As a first step, we conducted all experiments on hummingbirds that fed while perching. In a subsequent set of experiments, we also explored the possible effects of substitution of heat produced during hover feeding into food warming.

The model

The amount of energy required to warm nectar is a function of three factors: (1) the volume of nectar consumed, (2) the specific heat of the sugar solution, and (3) the difference between T_b and T_n. Our model integrates these factors in a single algebraic expression. If birds regulate nectar intake to achieve a constant rate of energy intake (m in grams of sucrose per unit time), the volume of nectar imbibed (I in milliliters per unit time) is reciprocally related to nectar concentration (C in mass of sugar/volume of nectar solution, g ml^{-1}; Martínez del Rio et al. 2001):

$$I = \frac{m}{[C(AE)(SDA')]} \qquad (1)$$

AE and SDA' in Eq. 1 are the efficiency with which energy (sugar) is assimilated and the fraction of energy that remains to fuel metabolism after specific dynamic action, respectively. AE is approximately 0.95 in nectar feeding animals (Jackson et al. 1998 and references therein), and for animals feeding primarily on carbohydrates SDA' equals approximately 0.94 (Peters 1983). Thus,

$$I = \frac{m}{0.89C} \qquad (2)$$

The cost (E in kJ) of warming up I mL of nectar from a given temperature (T_n) to T_b equals the product of three terms: the volume imbibed (I), the specific heat of

sucrose solutions ($S(C)$ in kJ ml^{-1} °C^{-1}), and the difference between the bird's temperature (T_b) and that of the nectar (T_n; $\Delta T = T_b - T_n$),

$$E = (I)S(C)\Delta T = \frac{mS(C)\Delta T}{0.89C} \qquad (3)$$

If k equals the energy content of sucrose ($k = 16.6$ kJ g^{-1}), then the fraction of the energy acquired used to warm up nectar (H) equals

$$H = \frac{E}{km} = \frac{S(C)\Delta T}{0.89kC} \qquad (4)$$

The amount of energy that birds must consume (m) must be increased to account for the energy used to warm food. For every m g of energy the bird will have to ingest mH grams more. In a similar fashion, to pay for the cost of warming up these additional mH g ingested the bird will have to increase its intake by mH^2. Thus, the total energy requirements (m') including the cost of warming up nectar are given by the series

$$m' = m + \lim_{i \to \infty} \sum_i mH_i = m + \frac{mH}{1-H} \qquad (5)$$

Substituting Eq. 4 into Eq. 5 yields the cost of warming nectar (H') relative to the cost of feeding on nectar at T_b:

$$H' = \frac{H}{(1-H)} = \frac{S(C)\Delta T}{((0.89kC) - S(C)\Delta T)} \qquad (6)$$

Figure 1 illustrates the predicted relationships between H' and C and temperature (for clarity we express H' as a percentage). The relationship in Fig. 1 assumes that the bird's T_b is 39°C (Calder 1993; C.N. Lotz, unpublished data) and that the specific heat of sucrose solutions, $S(C)$, is approximately $[4.182-(0.022766C)] \times 10^{-3}$ kJ ml^{-1}°C^{-1} (Watson 1989). Although the specific heat of sucrose solutions depends on both sucrose
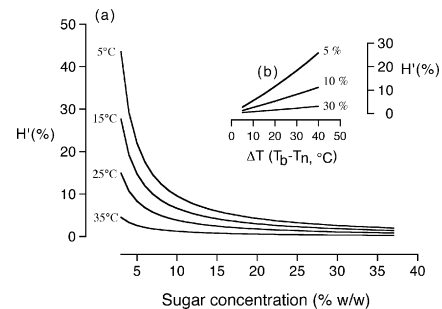

Fig. 1 A simple model of the cost of warming nectar to body temperature (T_b) makes two predictions: (1) when nectar temperature (T_n) is constant, this cost will decrease as a power function of sugar concentration (*panel a*), and (2) when sugar concentration is constant, this cost will increase roughly linearly with the gradient between T_b and T_n (*panel b*). The cost of warming nectar (H') is measured as the percentage by which birds increase their metabolic rate relative to their metabolic rate when nectar is at T_b

concentration and temperature, the effect of temperature on $S(C)$ is very small and does not change the output of the model significantly. Figure 1 portrays the two dominant influences on the cost of warming nectar: because birds decrease volumetric intake as C increases, H' decreases approximately as a reciprocal function of C. Because the energy needed to warm nectar increases linearly with the difference between T_b and T_n, H' decreases roughly linearly as T_n increases.

Materials and methods

Bird capture and maintenance

We captured rufous hummingbirds (body mass = 3.3 ± 0.1 g during experiments, mean ± SE, $n = 12$) in mist nets in Albany County, Wyoming (41° 20'N, 106° 15'W). Between experiments, hummingbirds were maintained in 61 cm×61 cm×61 cm gauze cages in an air-conditioned laboratory (≈20°C). Birds were fed a balanced artificial maintenance diet (130 g Nektar Plus, Nekton-Produkte, Germany and 50 g of commercial grade table sugar per liter of water). Birds either maintained or increased body mass in captivity.

Experimental protocol

During experiments, T_a (20 ± 1°C) and photoperiod (10L:14D, lights on at 0800 hours) were kept the same as between experiments. We measured H' (the cost of warming nectar to T_b), as changes in oxygen consumption of hummingbirds with changes in food temperature. We measured oxygen consumption of individual hummingbirds at 10-min intervals for 24 h, starting at 1700 hours. At noon the following day, we changed the T_n. We calculated average metabolic rates between 1100 and 1200 hours (before the change in T_n) and between 1500 and 1600 hours (after the change in T_n). By these times, metabolic rates had stabilized well after the transition from night to day, and after the change in T_n at noon (Fig. 2). This was in accordance with our system's expected and estimated washout time of less than 94 min, given a system volume (including tubing) of 3,080 ml, and a flow rate of 150 ml min^{-1} (Lasiewski et al. 1966). For each nectar concentration and individual bird, we changed T_n from the birds' T_b (≈39°C; Calder 1993) to a lower temperature, and vice versa. We then used the average change in metabolic rate (H') for both treatments. Birds were weighed before and after each 24-h experimental period. We kept T_a constant during all experiments, because confounding variables would make it impossible to test our model if we co-varied T_a and T_n to mimic the field situation.

Three randomized experimental blocks were used. In the first two blocks, birds did not have to move to feed (the perch was close enough to the feeder to preclude hovering). First, we varied sugar concentration (5%, 15%, 25% or 35% weight of sucrose/total weight of solution), while changing food temperature from 39 to 4°C (i.e., $\Delta T = 35°C$) or vice versa. We fed birds these sucrose concentrations because they span the range of nectar concentrations commonly occurring in the field (Pyke and Waser 1981). Second, we fed birds 5% sucrose and used three values of ΔT (0, 17.5 or 35°C) to examine the effect of ΔT on H'. Finally, we fed hummingbirds 5% sucrose and maintained ΔT constant (35°C), but varied whether birds perched or hovered during feeding bouts. To hover-feed, birds had to fly 10 cm from their perch and had to feed in flight.

Respirometry

Hummingbirds were placed individually in a 3-l glass chamber which was part of a flow-through respirometry system. The chamber was inside a constant-environment cabinet set at 20 ± 1°C.
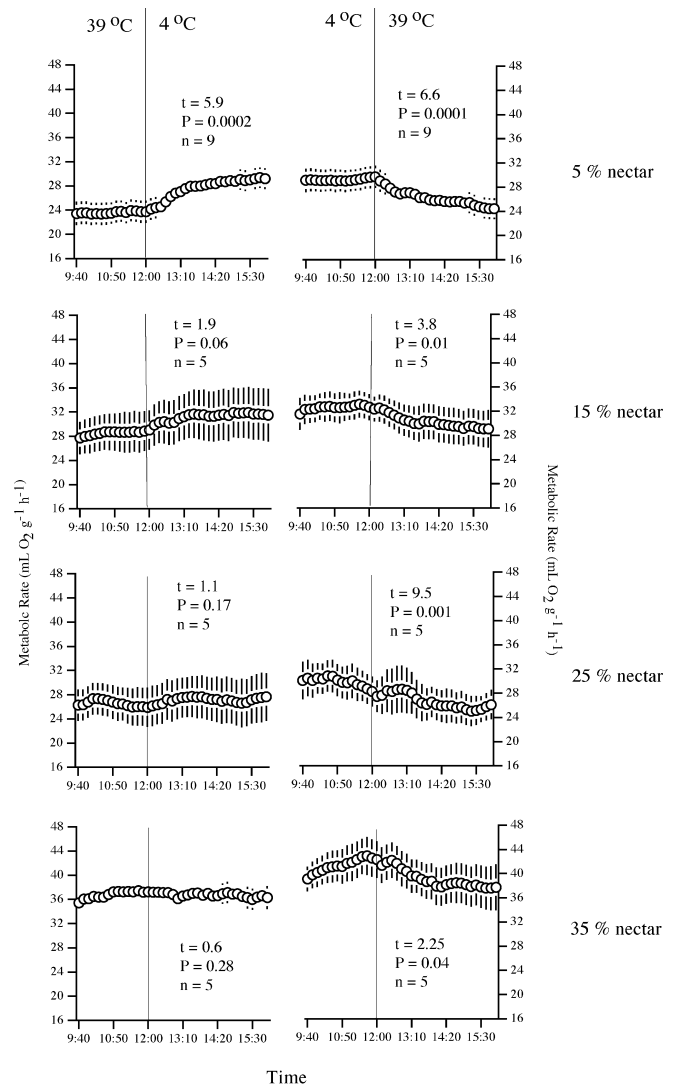

Fig. 2 The daytime metabolic rates (mean ± SE at 10-min intervals) of rufous hummingbirds (*Selasphorus rufus*) increased when food temperature was reduced by 35°C at noon (*vertical lines*) and vice versa, the effect weakening with increasing nectar concentration. Values for paired sample *t*-tests comparing the average metabolic rates from 1100 to 1200 hours with those from 1500 to 1600 hours are shown on each graph

During the day (hummingbirds did not feed at night), birds used a glass feeding tube that allowed us to warm or cool the food. The feeder was enclosed within a glass jacket through which ethylene glycol coolant was continuously circulated with plastic tubing, from a temperature-controlled bath. Only the bottom of the feeder (which contained the feeding hole) extended into the bird's chamber; the rest of the feeding apparatus was outside the chamber.

Air was pulled through the system at 150 ml min^{-1} by a pump. Fresh air was drawn through bev-a-line IV tubing (used for the entire respirometry setup) from outside the constant environment cabinet, through soda lime (to absorb carbon dioxide), then through Drierite (self-indicating anhydrous $CaSO_4$; 10–20 mesh; to absorb water vapor), then through a coil of copper tubing in a water bath to buffer the T_a beyond the capabilities of the cabinet. Air was dispersed as it entered the top of the chamber by a halved (length-wise) tube of silicone rubber tubing (diameter 4 cm; length 14 cm) containing 5-mm-diameter holes. This tube was glued horizontally over the air inlet. Air exited the chamber on the bottom, diagonally opposite corner of the chamber, before being

pulled through soda lime, Drierite, and then into an S-3A/I Applied Electrochemistry O_2 analyzer. The oxygen analyzer was set to read 20.96% O_2 when dry, CO_2-free air was flowing through the system prior to a bird being added, and we checked that the system reverted to 20.96% O_2 after completion of each experiment. After the oxygen analyzer, the air passed through the pump and finally into a bubble flow meter for accurate measurement of flow rate. T_a and ambient pressure were monitored at the air pump outside the constant environment cabinet for conversion of gas volumes to STPD. Instantaneous O_2 percentage values were recorded automatically on computer (Sable Systems, Salt Lake City, Utah) every 5 min. Metabolic rate $\dot{V}_{O_2}$ was calculated (in ml O_2 h^{-1}) as:

$$\dot{V}_{O_2} = \frac{(\dot{V} \times 60) \times (F_iO_2 - F_eO_2)}{(1 - F_i - O_2)} \tag{7}$$

where flow rate ($\dot{V}$) is in ml air min^{-1}, and F_iO_2 and F_eO_2 are the fractional concentrations of O_2 in the incurrent and excurrent air, respectively (Bucher and Chappell 1997). Values were then divided by body mass averaged between the start and end of each experimental run, to yield mass-specific values (ml O_2 g^{-1} h^{-1}).

Statistical analyses

Paired t-tests were used to compare metabolic rates of birds before and after changes in food temperature (Zar 1996). We compared the average metabolic rates from 1100 to 1200 hours with those from 1500 to 1600 hours. We also used paired t-tests to compare metabolic rates of hover- versus perch-feeding birds. The effect of control variables (C and T_n) on H' were analysed by regression using linear models. We used individual birds as components in these models, to avoid pseudoreplication (Hurlbert 1984). We calculated r^2 values for our H' data fitted to a priori model, as well as to linear and power curves (Mendenhall 1975). Unless otherwise stated, data are given as mean $\pm$ SE.

Results

Body masses of rufous hummingbirds measured during experiments averaged 3.3 ± 0.1 g ($n = 12$). The nighttime metabolic rates that we measured in hummingbirds while not torpid (0.86 ± 0.03 ml O_2 min^{-1}, $n = 11$) compared well with the resting metabolic rate for this species at 20°C of 0.85 ml O_2 min^{-1} reported by Calder (1993). As expected from our model, daytime metabolic rates increased when T_n was changed from 39°C to 4°C (at noon) and decreased when T_n was changed from 4°C to 39°C. The was very marked when birds fed on dilute food (Fig. 2).

When fed dilute (5%) sucrose, metabolic rates changed (1) dramatically when T_n was changed by 35°C at noon, (2) less markedly when changed by 17.5°C, and (3) not at all when T_n was kept constant (Fig. 3), again in accordance with our model. Figure 4 summarizes the data from Figs. 2 and 3 values, calculated as the percentage change in metabolic rates (%$H' = 100H'$) from 1100 to 1200 hours compared with those from 1500 to 1600 hours. Figure 4a shows the relationship between %H' and sugar concentration for nectar at 4°C, whereas Fig. 4b shows the effect of varying T_n and maintaining concentration constant (%$C = 5$%). Calculated %H' values were strongly affected by both nectar concentration (repeated measures ANOVA, $F_{21,23} = 18.6$,
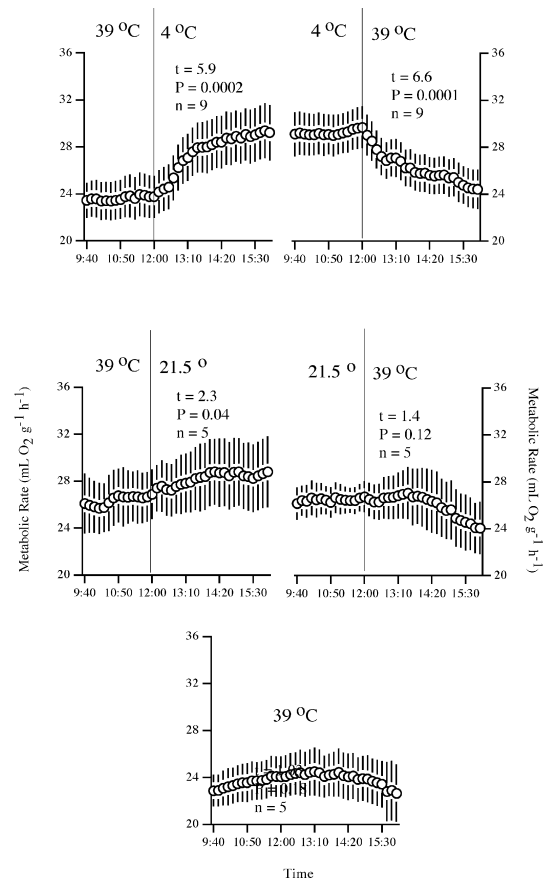

Fig. 3 The daytime metabolic rates (mean $\pm$ SE at 10-min intervals) of rufous hummingbirds (*Selasphorus rufus*) fed 5% sucrose changed (1) markedly when food temperature was changed by 35°C at noon (*vertical lines*), (2) less markedly when food temperature was changed by 17.5°C, and (3) not at all when food temperature remained unaltered. Values for paired sample t-tests comparing the average metabolic rates from 1100 to 1200 hours with those from 1500 to 1600 hours are shown on each graph

$P < 0.0002$), and by T_n (repeated measures ANOVA, $F_{17,19} = 56.6$, $P < 0.0001$).

Fitting our data on the effect of nectar concentration on H' to our model and to a power function, yielded r^2 values of 0.49, and 0.42, respectively. Similarly, fitting our data on the effect of T_n on H' to (1) our model, and (2) a linear function, yielded r^2 values of 0.71 and 0.77. The values of the functions fitted by least squares and by our model were very similar (Fig. 4).

The metabolic rates of both hover- and perch-feeding hummingbirds fed 5% sucrose changed dramatically with 35°C changes in T_n (Fig. 5). Although metabolic rates of hover-feeding birds were higher than metabolic rates of perch-feeding birds, the differences were not significant. The %H' values of hover-feeding hummingbirds (20.3 ± 3.8%) feeding on 5% sucrose and with a 35°C temperature change were slightly but significantly lower than those of perch-feeding birds (24.5 ± 2.6%; Mann-Whitney U-Test, $U_{(1),6,6} = 31$, $P < 0.005$, $n = 6$).
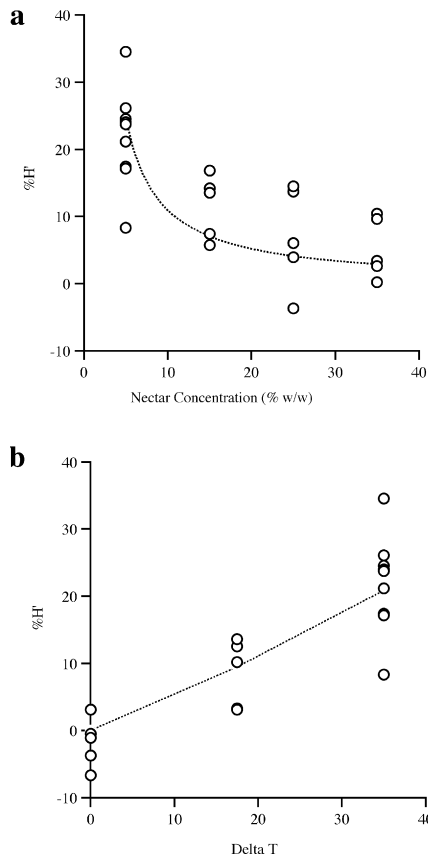
Fig. 4 The cost of warming nectar to body temperature ($\%H'$) in individual rufous hummingbirds (*Selasphorus rufus*) increased with decreasing nectar concentration (**a**), and with the difference between T_b and T_n (5°C, **b**), in accordance with the expectations of our model (*dashed lines*). The cost of warming nectar (H') was measured as the change in metabolic rate due to a change in T_n. The *dashed lines* depict the predictions of our a priori model, whereas the *solid lines* represents a power ($y = 90.1x^{-0.87}$) and a linear function ($y = 0.68x + 2.30$) in **a** and **b**, respectively

Discussion

The cost of warming nectar to T_b in rufous hummingbirds increased dramatically with nectar dilution, and with the difference between T_b and T_n. Measured values were very similar to those expected from our model. Perhaps more importantly, the cost of warming nectar was often high, suggesting that the cost of warming food may be biologically significant for nectar-feeding birds. For example, birds that were fed 5% nectar at 4°C used over 20% more energy than when they were fed nectar at T_b. Even when birds were fed cold nectar at an intermediate sugar concentration (15%), they spent more than 10% more energy than when their food started at T_b. We begin our discussion by examining the significance of our findings for studies of thermoregulation. We then discuss the possible role of substitution of heat produced from hovering during feeding bouts into food warming. Finally, we discuss the ecological implications of our findings.
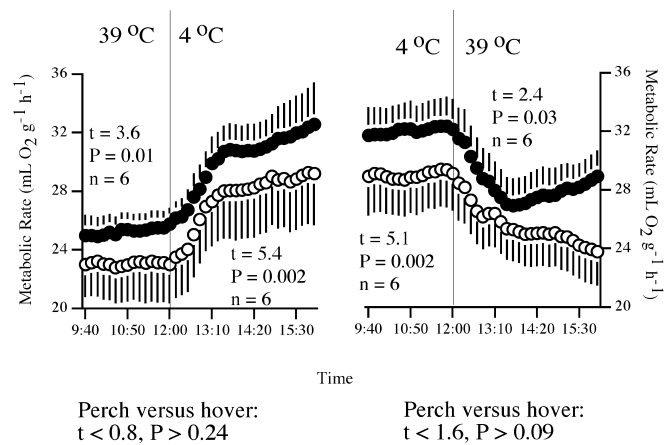

Fig. 5 The daytime metabolic rates (mean ± SE at 10-min intervals) of rufous hummingbirds (*Selasphorus rufus*) fed 5% sucrose increased markedly when food temperature was reduced by 35°C at noon (*vertical lines*) and vice versa, irrespective of whether birds perch-fed (*open circles*) or hover-fed (*closed circles*). Values for paired sample t-tests comparing the average metabolic rates from 1100 to 1200 hours with those from 1500 to 1600 hours are shown. Although the metabolic rates of hover-feeding birds were higher than those of perch-feeding birds, paired sample t-tests revealed no significant differences either from 1100 to 1200 hours or from 1500 to 1600 hours

Significance for thermoregulation

Few studies of vertebrate thermoregulation (with the exception of recent studies on aquatic birds) have considered the effect of food warming as a potential confounding variable. For example, there have been numerous studies demonstrating increasing food intake, or increasing energy expenditure, with reduction in T_a. Among these studies are many on nectar-feeding birds (e.g., Schuchman and Schmidt-Marloh 1979; Leon and Nicolson 1997; Beuchat et al. 1979). However, almost all of these studies have ignored the fact that T_a effects must be confounded by co-varying food temperature, especially when food is energetically dilute. Tufted ducks (*Aythya fuligula*) feeding on mussels consume three times their body mass daily of food (which includes large amounts of indigestible shells), and de Leeuw et al. (1998) calculated that these ducks must use 13–20% of their daily energy intake to warm food during winter. Prior to our study, Wilson and Culik (1991) were apparently the only authors who actually measured (and not just calculated) food warming costs. They found that food-warming costs of Adelie penguins were relatively unimportant (only 2.5% of total energy intake), because penguins feed on energy-rich food (krill). Lotz and Nicolson (2002) found that nectar dilution increases metabolic rate in lesser double-collared sunbirds (*Nectarinia chalybea*), and that this increase in metabolic rate could be entirely accounted for by estimated food warming costs.

Like studies of the effect of T_a on metabolic rate, most studies of specific dynamic action (SDA) have ignored food warming as a contributing factor to the

observed increase in metabolic rate after a meal. These numerous studies do not report food temperatures, making it impossible to guess the fraction of SDA that may be accounted for by the cost of food warming. A few authors have calculated food-warming costs and subtracted them from the total increase in metabolic rate due to feeding. For example, Hawkins et al. (1997) reported that 30% of the increase in metabolic rate after fish ingestion in Brunnic's guillemots (Uria lomvia) was due to food warming. In two studies of SDA in Adelie penguins, food (krill) was pre-warmed to T_b before being fed to birds: Wilson and Culik (1991) could not detect SDA in adult penguins, whereas Janes and Chappell (1995) measured a substantial SDA (10% of ingested energy) in penguin chicks. Other studies of SDA in endotherms feeding on cold food may have to take into account that some fraction of the heat increment attributed to SDA may be the result of food-warming costs.

The role of thermal substitution

Thermal substitution of heat produced from activity may affect how food-warming costs are estimated. For example, "waste" heat produced by foraging activity in verdins (Auriparus flaviceps) substitutes for heat that is otherwise produced solely for thermoregulation at low temperatures (Webster and Weathers 1990). We found a surprisingly small decrease in food warming costs from activity-produced heat substitution when hummingbirds were forced to hover rather than to perch during feeding bouts. The amount of heat produced by activity that is available for warming cold food probably varies with other demands for heat. For example, at low T_a, heat produced during activity may substitute for thermoregulation rather than food warming. We predict that heat produced from activity will be used for thermoregulation at T_a below that used in our experiments (20°C), and thus that there will be little "excess heat" left for food warming. Indeed, SDA in house wren (Troglodytes aedon) chicks is considerably reduced when T_a is decreased (Chappell et al. 1997).

Food warming and the temperatures of floral nectar

Our laboratory experiments suggest that T_n and concentration are important influences on food warming costs and hence on hummingbird energy budgets in the field. Assessing the relevance of our results for the energy budgets of wild hummingbirds requires data on both T_n and concentration. The importance of nectar concentration has been long recognized and there is an enormous amount of data on nectar concentration in the field (e.g., Baker 1975; Nicolson 2002; Pyke and Waser 1981; Stiles and Freeman 1993). Curiously, there are almost no published data on T_n. Presumably the lack of data on T_n is the result of the perception that this measurement is uninteresting. It is tempting to assume that T_n will simply track T_a. However, because many flowers use a variety of behavioural and morphological devices to collect the radiant energy of the sun for thermoregulation (reviewed by Kevan 1989), and conversely because nectar may be cooled by evaporation (Corbet et al. 1979), this simplifying assumption is risky. Apart from reducing food-warming costs, increasing T_n also leads to a reduction in nectar viscosity, making hummingbird licking and therefore nectar harvesting rates faster (Heyneman 1983).

The cost of warming nectar is considerably smaller when its concentration is higher, so in cooler climates birds should prefer more concentrated nectar (as hypothesised by Calder 1979). Thus, pollinator food warming costs may sometimes pose a selective pressure on plants to produce more concentrated nectars. In light of the large effect of sugar concentration on the cost of warming nectar, it is surprising that the nectars of bird-pollinated flowers world-wide tend to be dilute, averaging only 23% (w/w), and sometimes being as low as 5–15% (Nicolson 2002; Pyke and Waser 1981).

Hummingbirds that breed at high latitudes or altitudes will be challenged the most by food-warming costs. Rufous hummingbirds are a good example. They breed high in the Rocky Mountains of Canada and Alaska and they conduct a remarkable migratory journey along the length of North America in spring and fall, when temperatures are low (Calder 1993). Given the challenges of low T_a, cold nectar, and migration, perhaps it is not surprising that rufous hummingbirds use torpor extensively in addition to hyperphagia to accomplish pre-migratory fattening (Calder 1994; Carpenter and Hixon 1988; Carpenter et al. 1993; Gass et al. 1999). Several other hummingbirds that breed far north in the United States and high in the Andes must also be severely challenged by the cost of food warming.

Similarly, a number of nectar feeding birds in South Africa (sunbirds and sugarbirds) and Australia (honeyeaters) breed in winter when low ambient (and hence nectar) temperatures (≈4°C) may last for several days (Williams et al. 1993; Jackson 1998). For these birds the situation is aggravated when nectars are diluted by winter rain both directly in the many non-tubular flowers that birds use in these regions, and indirectly because of high relative humidities (Tadey and Aizen 2001).

Like nectarivores, frugivores sometimes consume energetically extremely dilute food (Peters 1983). Boreal frugivores may incur a large additional cost that nectarivores do not: they eat frozen food (C. Martínez del Rio, personal observation). The latent heat of fusion is very high (335 J g^{-1} for pure water; Withers et al. 1979). Thus, food-warming costs will be doubled when food has to be melted and then heated, rather than simply heated, from 0°C to T_b.

Our results suggest that warming food to T_b is costly for hummingbirds, and hint at a missing element in the study of thermoregulation in these animals. So far,

research on the effect of T_a on metabolic heat production has largely ignored food temperature as a determinant of metabolic expenditures. Rufous hummingbirds feeding on 5% sugar solutions at 4°C have to increase their metabolic rate by an amount equivalent to that elicited by a 15°C drop in T_a (Calder 1993). We suspect that further research will reveal that the cost of warming food is an important ingredient of the energy budgets not only of hummingbirds, but also of many other animals that feed on cold and energy-dilute foods. We also suspect that T_n will prove to be a factor that can shape the interaction between plants and the birds that feed on, and pollinate, their flowers.

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