DIFFERENCES IN NECTAR USE POTENTIAL IN A GUILD OF BIRDS: A GUT'S VIEW

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Resumen. - Las aves nectarívoras han sido utilizadas como modelos para estudiar tanto ecología de comunidades como ecofisiología. Curiosamente estas dos áreas del conocimiento no han sido relacionadas. Diversos ecofisiólogos han encontrado que los mecanismos que controlan la asimilación de los azúcares presentes en el néctar limitan el consumo de alimento de los animales nectarívoros, pudiendo afectar su comportamiento en campo. En este trabajo cuantifiqué la capacidad para digerir sacarosa de una comunidad de 10 aves nectarívoras de las montañas del occidente de México (siete colibríes, dos chipes y una diglosa). Utilicé un modelo matemático para predecir el consumo máximo de energía (CME) de las aves y lo comparé con sus tasas metabólicas de campo (TMC), las cuales calculé utilizando ecuaciones alométricas. El CME de los colibríes fué igual o mayor que sus TMC. Estas aves tuvieron capacidades digestivas máximas que superaron entre un 10 y un 70% el consumo de alimento. Las tres especies de paserinos presentaron resultados diferentes. La diglosa (Diglossa baritula) y un chipe (Vermivora ruficapilla) tuvieron CME dentro del límite inferior del intervalo de confianza del 95% de su TMC, mientras que el otro chipe (V. celata) tuvo CME menores a su TMC. La digestión de sacarosa parece limitar la tasa de ingestión de alimento en los paserinos, más no en colibríes. Aunque *V. celata* se alimenta de forma importante de flores en campo, mi análisis indica que debe enfocar su forrajeo en especies con nectares que contengan poca sacarosa, y/o adicionar su dieta con insectos. Mis datos sugieren que las capacidades digestivas pueden brindarnos información sobre el uso de recursos por los miembros de una comunidad.

Abstract. – Diferencias en el uso potencial de néctar por una comunidad de aves: una mirada desde la tripa. - Nectar-feeding birds have been used as models to study both community and physiological ecology. However these two areas have not been linked in the past. Physiological ecologists have found that the mechanisms by which nectar sugars are assimilated can impose limits to the food intake of nectar-feeding animals, affecting their behavior in the field. In this study I quantified the ability to digest sucrose of a community of 10 nectar-feeding birds from the highlands of Western Mexico (7 hummingbirds, 2 warblers and 1 flowerpiercer). I used a mathematical model to predict the birds' maximal capacity to assimilate sucrose, and linked these predictions with ecological parameters. I compared the birds' predicted maximal rate of energy intake with their field metabolic rates (FMRs) estimated from allometric equations, and with their food intake. Hummingbirds' predicted maximal energy intake was either equal to or greater than their expected FMRs. In these birds, maximal digestive capacities exceeded observed food intake by 10 to 70%. The three species of passerines presented different results. Flowerpiercers (*Diglossa baritula*) and Nashville Warblers (*Vermivora ruficapilla*) had predicted maximal energy intake values within the lower 95% confidence interval of their predicted FMRs, and predicted energy intakes of Orange-crowned Warblers (*V. celata*) were lower than their FMRs. Flowerpiercers ingested roughly the same amount of sucrose as expected a priori from intestinal enzyme measurements. Digestion of sucrose seems to limit ingestion rate in passerines but not in hummingbirds. Although *V. celata* individuals feed heavily on flowers at the study site, my analysis indicates that they need to focus on plant species that produce hexose-rich nectars and/or complement their diet with insects. I suggest that knowledge of interspecific variation in digestive capacities can inform community-level studies of resource use.

Key words: Digestion, *Diglossa*, Hummingbirds, Nectarivory, Physiological Constraint, Spare Digestive Capacity, Sucrose, Warblers.

INTRODUCTION

Ecologists and physiologists have often used nectar-feeding birds to study both community and physiological ecology. Traditionally, community ecologists have emphasized competition and the partitioning of floral resources among bird species (Stiles & Wolf 1970, Colwell 1973, Stiles 1975, Feinsinger 1976, 1978; Wolf *et al.* 1976, Gill & Wolf 1978, Brown & Kodric-Brown 1979, Feinsinger *et al.* 1979, 1985; Des Granges 1979, Stiles 1995, Sandlin 2000). These studies relied on foraging observations and/or on morphological measurements as proxies for use and dependence of birds on different plant species as nectar sources. At the same time that ecologists were conducting community-level research with nectar-feeding birds, physiologists were researching their energetics (Stiles 1971, Wolf & Hainsworth 1971, Hainsworth & Wolf 1972, Wolf 1975, Wolf *et al.* 1976, Weathers & Stiles 1989, Tiebout 1991, 1993; Powers & Conley 1994). Because data on energetic demands are crucial for understanding the resources needed by birds (Hainsworth 1974, Wolf *et al.* 1976, Wolf *et al.* 1976, Beuchat *et al.* 1979, Nagy 1987, Nagy *et al.* 1999), these two research programs were complementary.

During the last 15 years, physiological ecologists working with nectar-feeding birds have shifted their attention from energetics to digestive processes (Diamond *et al.* 1986, Karasov & Diamond 1988, McWhorter & Martínez del Rio 2000, Levey & Martínez del Rio 2001, Suarez & Gass 2002). The focus on the digestive tract has revealed that the mechanisms by which nectar sugars are digested and absorbed can influence food selection and foraging patterns of nectar-feeding birds (Diamond *et al.* 1996, Martínez del Rio 1990a, 1990b, 1994; McWhorter & Martínez del Rio 2000, Schondube & Martínez del Rio 2003a, 2004). We have learned that digestion can be a determinant of the types of sugars preferred by these birds (reviewed by Lotz & Schondube 2006) and can impose limits on the amount of food that they can consume (Kersten & Visser 1996, Winter 1998, Gass *et al.* 1999, McWhorter & Martínez del Rio 2000, Schondube & Martínez del Rio 2003a). Here I describe an approach that allows digestive physiology to be linked with community ecology. I suggest that an understanding of digestive processes can provide a more complete perspective not only on the foraging behavior of nectar-feeding birds, but also of their roles in ecological communities.

One recent advance that allows physiological digestive mechanisms to be linked with ecological patterns is the development of mathematical models that permit the prediction of food intake from the physiological and morphological traits of birds and the characteristics of nectar (e.g. quantity of nectar available, and its sugar composition, and concentration; Jumars & Martínez del Rio 1999, McWhorter & Martínez del Rio 2000, Martínez del Rio *et al.* 2001). These models integrate biochemical and anatomical measurements to estimate the upper limits on food intake imposed by digestive processes. Here I investigated potential differences among the members of a community of syntopic nectar-feeding birds in the capacity to digest sucrose, and hence to rely on sucrose-rich floral nectar. My study included seven hummingbird species (*Archilochus alexandri*, *Colibri thalassinus*, *Eugenes fulgens*, *Hylocharis leucotis*, *Lampornis clemenciae*, *Selasphorus platycercus* and *Selasphorus rufus*), a nectar robbing passerine (the Cinnamon-bellied Flowerpiercer, *Diglossa baritula*), and two species of warblers that are often observed extracting nectar from flowers (Orange-crowned and Nashville warblers, *Vermivora celata* and *V. ruficapilla*) found in the highlands of Western Mexico. All these species are found in the same locality feeding on the same plants (Calder & Contreras-Martínez , Schondube pers. observ.).

Although my study is comparative, it has an ecological focus. My goal was to assess the

capacity of birds of each species to rely on nectar to satisfy energy demands relative to other members of the guild of nectar feeding birds. Comparative studies that focus on evolution and that attempt to infer adaptation must rely on phylogenetic information (Felsenstein 1985, Garland & Adolph 1994, Losos & Miles 1994). Because my objective was strictly ecological, I ignored phylogeny.

METHODS

Study area
I collected all birds at Nevado de Colima National Park (located between 19°33'45" and 19°30'40"N and 103°36'30" and 103°37'30"W) in the state of Jalisco, Mexico. Nevado de Colima is an inactive volcano, and the highest mountain in western Mexico (4,264 meters above sea level). Des Granges (1979) and Calder & Contreras-Martínez (1993) described the climate and vegetation of the study area. My study site was located at 3,100 meters elevation on an east-facing slope with bunchgrasses and alders on exposed ridges and a mesic fir-oak forest at the bottom of ravines. The community of nectar feeding birds present at this site includes a total of 11 hummingbirds, one flowerpiercer and two warblers. Of these we collected the most common species (10 out of 14), missing only some hummingbirds that have very low abundances (*Amazilia beryllina*, *A. violiceps*, *Atthis heloisa*, and *Lampornys amethystinus*). The sampled species represent more than 98% of the bird abundances inside the community (Schondube pers. observ.). The principal flowering plants used by the nectar-feeding bird community at this site include *Salvia elegans*, *Salvia gesneriflora*, *Ribes ciliatum* and *Senecio angulifolius* (Des Granges 1979, Des Granges & Grant 1980, Gonzalez-Villarreal & Perez-de-la-Rosa 1987, Schondube pers. observations). Both the species of nectar-feeding birds and the floral resources that they use at

the Nevado de Colima, are common to the temperate mountain habitats of Western Mexico (Gonzalez-Villarreal & Perez-de-la-Rosa 1987, Hutto 1992, Cuevas 1994, Ornelas & Arizmendi 1995, Santana Castellon 2000).

Collection of samples
Birds were captured with mist nets, euthanized by thoracic compression and their intestines immediately removed. Intestines were chilled in ice-cold 0.9% saline and slit longitudinally, unfolded flat, and its length and width measured to obtain an estimate of its "nominal" area. The tissue was then blotted, weighted and stored in liquid N_2. Birds were collected with permission from the National Institute of Ecology (INE), Mexico and sample sizes reflect permit constraints (see Appendix 1).

Modeling food and energy intake as a function of sucrose hydrolysis
I used a mathematical model described in detail by McWhorter & Martínez del Rio (2000) and Martínez del Rio *et al.* (2001) to predict the maximal food intake capacity of individuals of the 10 study species. To use this model, I assumed of that sucrose was the only sugar present in nectar. Because specialized nectar feeding animals (hummingbirds and phyllostomid bats) ingest identical amounts of food when feeding on sucrose or hexose solutions, this assumption works well for most of the species in this study (Schondube & Martínez del Rio 2003a, Lotz & Schondube 2006, Ayala *et al.* 2008). McWhorter & Martínez del Rio (2000) model assumes that the intestine of nectar feeding birds functions as a plug flow chemical reactor (Penry & Jumars 1987) in which digesta flow unidirectionally (Jumars & Martínez del Rio 1999), and in which the rate at which sucrose is hydrolyzed in the intestine follows simple Michaelis-Menten kinetics:

$$-r_s = S_{max} C_s (K_m + C_s)^{-1} \qquad (1)$$

where S_{max} equals the rate of hydrolysis along the intestine (in μmol min^{-1} μl^{-1}), K_m is sucrase's Michaelis-Menten constant (in μmol μl^{-1}), and C_s is the concentration of sucrose (in μmol μl^{-1}) down the intestine or with time (Jumars & Martínez del Rio 1999). Equation (1) can be integrated to yield the throughput time (τ, also called mean retention time) required to reduce the initial sucrose concentration (C_{s0}) to a given final value (C_{sf}):

$$\tau = (S_{max})^{-1}(K_m Ln(C_{s0}C_{sf}^{-1}) + (C_{s0} - C_{sf})) \quad (2)$$

In plug flow reactors, if one knows τ and the volume of gut contents (G in μl), maximal food intake rate (v_0 in μl min^{-1}) can be estimated as:

$$v_0 = G\tau^{-1} \quad (3)$$

This model predicts maximal food intake capacity of sucrose solutions in a variety of nectar-feeding species remarkably well (McWhorter & Martínez del Rio 2000, Martínez del Rio et al. 2001, Schondube & Martínez del Rio 2003a, Ayala et al. 2008). I want to emphasize that the model predicts maximal intake. Often, the observed nectar intake of birds tends to lower than their predicted maximal intake, but when birds are challenged to increase their demand for energy (for example, by exposing them to lower ambient temperatures), they ingest the amounts predicted by the model (McWhorter & Martínez del Rio 2000, Ayala et al. 2009, T. J. McWhorter pers. com.).

I used in vitro measurements of sucrase activity and kinetics (Appendix 1) and intestine morphology data (gut luminal volume) to predict maximal food intake capacity of sucrose nectar as a function of sucrose concentration. Sucrase activity and kinetics were measured from gut tissue homogenates following Martínez del Rio (1990a) as modified by Schondube et al. (2001). Intestinal volume was estimated from the average circumfer-

ence of the small intestine measured at 0.5 cm intervals along the length of the intestine. Sucrose assimilation efficiencies for hummingbirds and D. baritula were assumed to be 99% (Hainsworth 1974, Martínez del Rio 1990b, McWhorter & Martínez del Rio 2000, Schondube & Martínez del Rio 2003a). For the two warblers I assumed an assimilation efficiency of 90% based on personal field measurements (Schondube pers. obser.). This value is simmilar to that obtained for the Yellow-rumped Warbler (Dendroica coronata) by Afik & Karasov (1995).

Sucrose is the most abundant sugar in the floral nectar of the plant genera that are commonly visited by nectar-feeding birds at Nevado de Colima (Salvia, Ribes; Baker et al. 1998, I. Baker unpublished data; see Table 1). In order to use McWhorter & Martínez del Rio (2000) digestive model to predict maximal food intake capacity and maximal energy intake I assumed that the dominant sugar in the diet of nectar-feeding birds in my study site was sucrose. The implications of this assumption for my conclusions are considered in the discussion section. Because nectar sugar concentration of most hummingbird-pollinated plants is close to 20% weight/volume (584 mmol/L; Stiles 1976, Pike & Waser 1981; Freeman et al. 1984), I used the model to predict volumetric intake at this concentration. Maximal energy intake predicted by the model was calculated as the total sucrose ingested in a 12 h day, making the assumption that 1 g of ingested sugar renders 16.6 kJ (Yudkin et al. 1971).

Field metabolic rate calculations, data sources, and data analysis
To compare predicted maximal energy intake with energy demands, I assumed that birds had to ingest enough energy to match their field metabolic rates (FMR). I estimated FMR for hummingbirds with Nagy et al.'s (1999) allometric equations for Apodiformes (FMR = 5.54(Body Mass)$^{1.212}$). For the flowerpiercer

Table 1 - Sucrose content in floral nectar of the most common plant genera visited by nectar-feeding birds at the Volcan de Colima.

Genus	No. of species in dataset	% sucrose content in nectar (mean)	Range % (max., min.)	Species present at study site	Relative abundance	Source for nectar composition
Malvaviscus	1 (*M. arboreus*)	44		M. arboreus	R	Baker *et al.* 1998
Penstemon	8	51.3	63, 34	P. roseus	L	Baker, I. unp. data
Castilleja	1	55		C. scorzoneifolia	R	Baker, I. unp. data
Salvia	4	68.7	87, 34	S. elegans	A	Baker, I. unp. data
				S. gesneriflora	A	Baker, I. unp. data
Circium	1	69.2		C. sp.	M	Baker, I. unp. data
Ribes	2	52.5	43, 62	R. ciliatum	VA - dominant	Baker, I. unp. data
Fuchsia	7	74.5	84, 36	F. mycrophylla	L	Baker *et al.* 1998

Abundance: VA - Very Abundant, A - Abundant, M - Medium, L – Low, R – Rare.

and the warblers, I used Nagy *et al.*'s (1999) equation for Passerines (FMR = 10.4(Body Mass)$^{0.68}$). To determine the relationship between energetic demands (measured as the amount of food ingested/day) and digestive capacity, I compared the predicted intake values with published and unpublished observed intake values for six species (*D. baritula, A. alexandri, S. platycercus, S. rufus, E. fulgens* and *L. clemenciae*) feeding for 12 hours (on a 20% sucrose diet at an ambient temperature of 20°C; see Appendix 1) in cages big enough to allow them to flight normally.

RESULTS

Sucrase activity standardized by intestinal area in hummingbirds was higher that in either *D. baritula* or the two species of warblers (Fig. 1). Sucrase activity in all species followed Michaelis-Menten kinetics. Gut nominal area increased with body mass and the two warblers appeared to have relatively larger intestinal areas than the hummingbirds and *D. baritula*. The flowerpiercer had an intestinal area similar to that of a hummingbird of equivalent body mass (Fig. 1). Appendix 1 lists the biochemical and morphological measurements that I used as input for the model.

In hummingbirds, predicted maximal energy intake was equal to or higher than predicted field metabolic rate (Fig. 2). Both *D. baritula* and *V. ruficapilla* had predicted maximum energy intake values that were lower than the field metabolic rates expected for passerines of their mass. Their estimated maximal intakes, however, were within the 95% confidence interval of the line predicting FMR as a function of body mass. The predicted maximal intake of *V. celata* was lower than the expected FMR and outside the 95% confidence intervals of the allometric prediction line.

To compare digestive capacity with energetic demands, I plotted maximal intake predicted by the model ("capacity") on the X axis, against energetic demands, estimated by observed intake ("demand"), on the Y axis (Fig. 3). Although predicted digestive capacity exceeded observed food intake in all hummingbirds (Fig. 3), there was notable variation among species in the ratio of demand to capacity. The 95% confidence interval of the predicted intake values for *A. alexandri* overlapped with the Y = X line, suggesting that the energetic demands of this species are close to the limits imposed by its sucrose digestive capacity. Four hummingbird species fell below the 1:1 energy intake:digestive capacity line (*E. fulgens, L. clemenciae, S. platycercus* and *S. rufus*). At 20°C, the model predicted digestive capacities that exceeded observed food intake by about 30% in *S. rufus, S. platycercus* and *E fulgens*. Expected intake in *L. clemenciae* exceeded observed intake by about 70%. *Diglossa baritula* was the only passerine for which I could obtain intake data. In this species, the amount of nectar ingested was indistinguishable from the maximal amount predicted by the model.

DISCUSSION

The hummingbirds and passerines included in this study had contrasting capacities to digest sucrose. The model predicted that hummingbirds feeding on sucrose at a 20% (wt/vol) could ingest enough nectar to match or surpass their field energetic demands. In contrast, the maximal predicted energy intake while feeding on a sucrose diet of one of the passerines, *V. celata*, was lower than that required to match predicted field metabolic rates. *Vermivora ruficapilla* and *D. baritula* had digestive capacities that barely matched field metabolic rates. Because *D. baritula* is considered a specialized nectarivore (Skutch 1954, Vuilleumier 1969, Arizmendi *et al*. 1996, Schondube & Martínez del Rio 2003a, 2003b), this result is notable. The comparison between digestive capacity and field metabolic rate was mirrored by the comparison between observed intake and
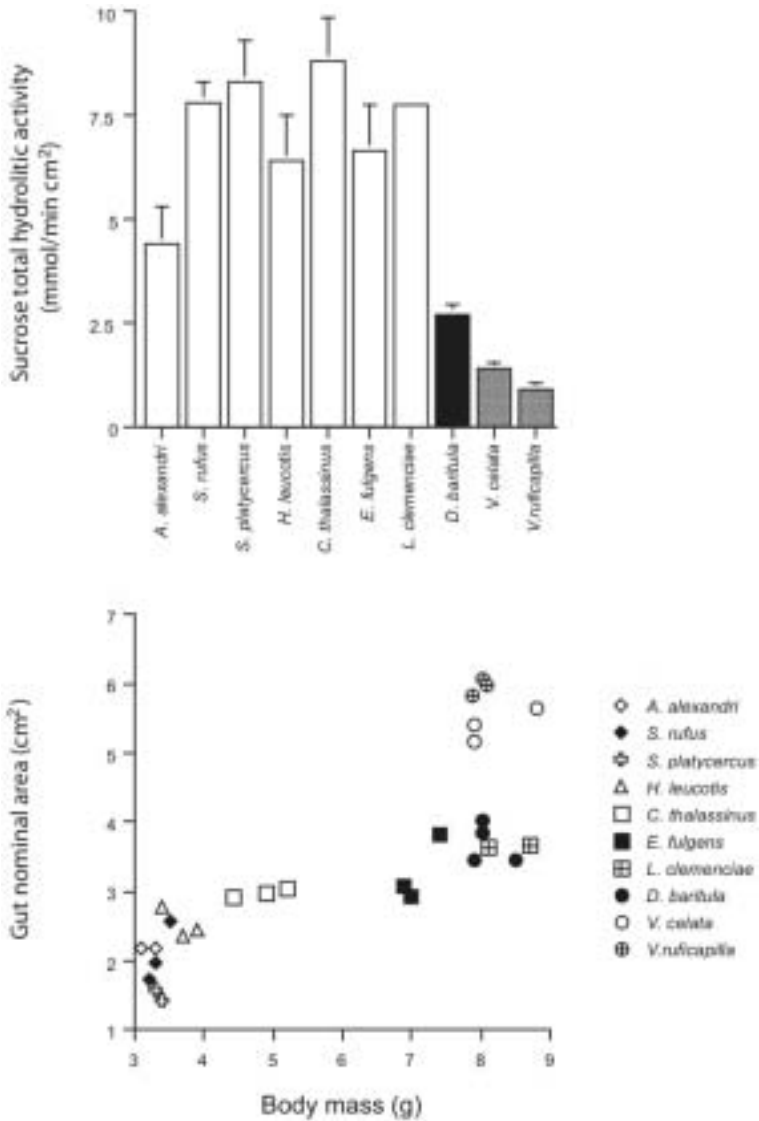
Figure 1. Sucrase activity standardized by intestinal area was higher in hummingbirds than in either *D. baritula* or the two species of warblers (upper panel; values are means ± SE). Gut nominal area increased with body mass (lower panel). The two warblers appeared to have larger intestinal areas than *D. baritula* and the hummingbirds. *D. baritula* had an intestinal area similar to that of a hummingbird of equivalent body mass.

predicted maximal food intake. This comparison suggested larger "spare digestive capacity" (*sensu* Diamond 1991, and Diamond & Hammond 1992) in hummingbirds than in *D. baritula*. Because my results are based on a model with a variety of assumptions, this discussion focuses on the significance of these assumptions. In a final section, I discuss the relevance of these results for how we perceive the behavior of the different species that form the
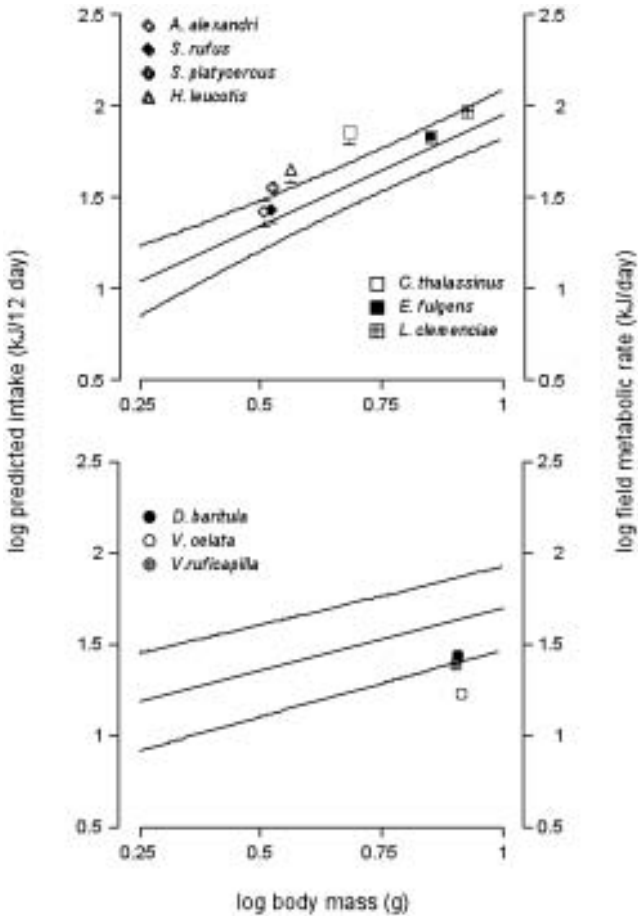
Figure 2. In hummingbirds, predicted maximal energy intake (symbols) was equal to, or higher than expected field metabolic rate (FMR; regression line, upper panel). Both *D. baritula* and *V. ruficapilla* had predicted maximal energy intake values that fell within the lower 95% confidence interval of the allometric prediction line of their FMR (dashed lines, lower panel). The predicted maximal intake of *V. celata* was lower than its expected FMR (lower panel)

community of nectar-feeding birds in the Nevado de Colima and the implications of this functional approach for the study of nectar-feeding bird communities.

To be assimilated, sucrose has first to be hydrolyzed by the enzyme sucrase into its monosaccharide components, glucose and fructose (Dahlqvist 1968, Semenza & Corcelli 1986). The model assumes that sucrose hydrolysis is the rate-limiting step in the assimilation of nectar and that sucrose is the main sugar in nectar. Although I measured most of the model's parameters directly, I used published values to estimate others. In the following paragraphs I consider the potential impact of inaccuracies in these estimates for my inferences. Other more general assumptions of the model (e.g., that the intestine functions as a plug flow reactor in which sucrose is hydrolyzed by a Michaelis-Menten saturating process) have been
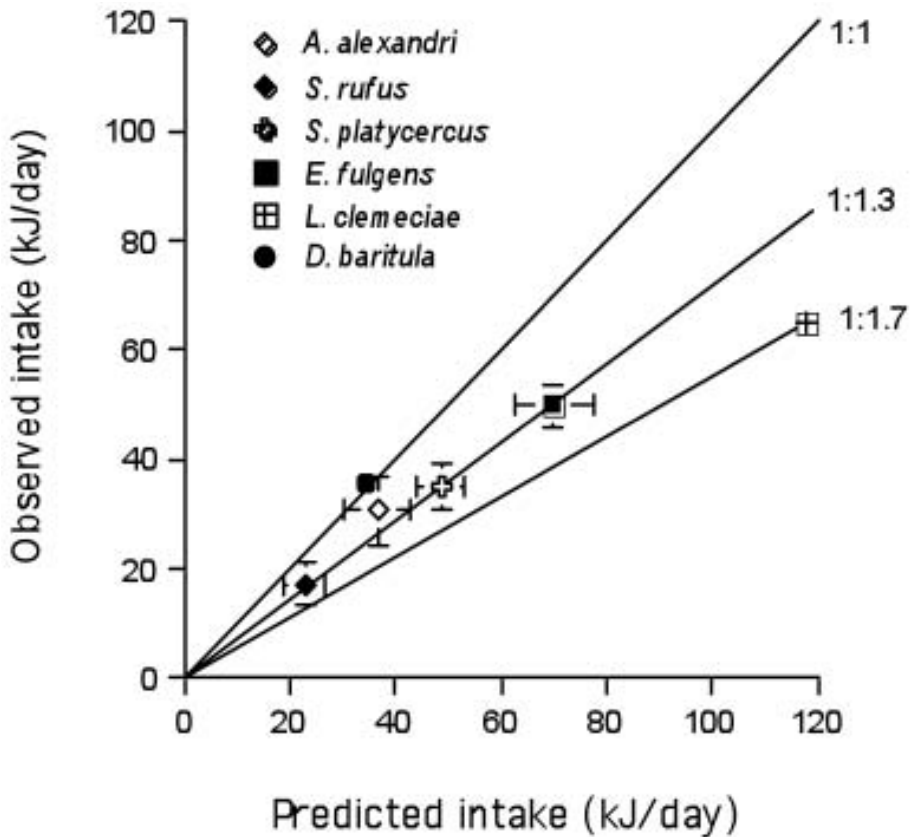
Figure 3. Digestive capacity exceeded observed food intake in all hummingbirds. The 95% confidence interval of the predicted intake values for *A. alexandri* overlapped with the Y = X line, suggesting that the energetic demands of this species are close to the limits imposed by its capacity to digest sucrose. The model predicted digestive capacities that exceeded observed food intake by about 30% in *S. rufus*, *S. platycercus* and *E fulgens* and by 70% in *L. clemenciae*. In *D. baritula*, the amount of nectar ingested was indistinguishable from the maximal amount food intake predicted by the model.

discussed in detail by McWhorter & Martínez del Rio (2000), and I will not consider them here.

Effects of floral nectar sugar composition
Most floral nectars do not contain a single sugar, but rather mixtures of sucrose, glucose, and fructose in variable proportions (Percival 1961, Baker & Baker 1982, Barnes *et al.* 1995, Baker *et al.* 1998). Glucose and fructose, in contrast with sucrose, do not require hydrolysis by intes-

tinal disaccharidases before absorption. Thus, their assimilation rate is presumably limited by the rate at which they are absorbed in the intestine (Karasov & Diamond 1983, Karasov *et al.* 1986). The model that I used to estimate maximal intake assumes that sucrose is the only sugar in nectar. What is the consequence of this assumption? For hummingbirds, sugar composition has no effect on estimated maximal sugar assimilation rate. Schondube & Martínez del Rio (2003a) and Fleming *et al.* (2004) found that

maximal assimilation rates of 1:1 mixtures of glucose and fructose and equicaloric sucrose solutions were indistinguishable in two species of hummingbirds (*E. fulgens* and *S. platycercus*) and one sunbird (*Nectarinia talalata*, Nectarinidae). In these birds sucrose intake is paired to hexoses intake, and it can be accurately predicted using sucrase activity and gut morphology as suggested by McWhorter & Martínez del Rio (2000). *Diglossa baritula* assimilated about 10% more glucose and fructose than sucrose per unit of time (Schondube & Martínez del Rio 2003a). Thus, in this species the model underestimates energy intake when the birds are feeding on real floral nectars (made up by a mixture of hexoses and sucrose) by at most 10%.

How do the presence of glucose and fructose in nectar affects the total energy intake of the two warbler species? Since the effect that sugar type has over the food intake of these birds is unknown, I can only made an educated guess. Natural history observations suggest that warblers can increase their food and energy intake rates when they feed on hexose-rich nectars. Migrating warblers such as *V. ruficapilla* and *V. celata* are the primary visitors to several Neotropical plants species that secrete hexose-rich nectars (Alvarez del Toro 1963, Toledo 1975, Des Granges 1979, Des Granges & Grant 1980, Stiles 1981, Gryj *et al.* 1990, Calder & Contreras-Martínez 1993). Although the model presented here may underestimate energy intake when warblers are feeding on hexose-dominated nectars, it probably makes accurate predictions at my study site. The flower species that these birds feed on at the Nevado de Colima (species of *Ribes* and *Salvia*) have nectars that average 70% sucrose (Baker *et al.* 1998, I. Baker unpublished data; see Table 1). If warblers have the capacity to assimilate the glucose and fructose present in these nectars while they are also digesting sucrose (i.e., if their capacity to absorb hexoses exceeds their maximal sucrose hydrolysis rates), they will be able to increase their en-

ergy intake rates by 30%. If this is the case, the predicted energy intake of individuals of *V. celata* would be closer to, but still lower, than their predicted FMR. However, if the warblers focus their foraging on abundant plant species that have lower sucrose content, like *Ribes*, their energy intake could be enough to fuel their field metabolic rate.

Digestive capacity and the ecology of nectar-feeding birds

The model predicts that hummingbirds are able to satisfy their energetic demands in the field using sucrose rich nectars. The model also predicts that most hummingbird species have some spare digestive capacity. The capacity of hummingbirds to fuel their field metabolic demands using sucrose rich nectars, explains why these birds tend to use sucrose-rich nectars in the field as have been reported by several authors in the past (see Lotz & Schondube 2006 and references therein). Because sucrose digestion rate seems to be paired with glucose and fructose assimilation rates in hummingbirds (Schondube & Martínez del Rio 2003a, Fleming *et al.* 2004), hummingbirds are able to use both sucrose or hexose rich nectars with the same efficiency. This should make them capabe to use all nectar sources regardless of their sugar composition, allowing them to act as ecological generalists.

D. baritula individuals were able to satisfy their energetic demands using sucrose rich nectars, but their maximal predicted sucrose digestive capacity matches their energy intake at 20°C. This result suggests that energy intake could be limited under more demanding environmental conditions. Although *D. baritula* is considered a specialized nectarivore, when feeding on sucrose-rich nectars these birds live at the edge of negative energy balance. The other two species of passerines also had limited capacities to hydrolyze sucrose. *Vermivora ruficapilla* individuals were barely able to satisfy their energetic demands while feeding on su-

crose rich-nectars, whereas *V. celata* individuals appear not to be able to subsist on sucrose dominated nectars. Although members of this species feed heavily on the flowers of different plant species at my study site, my analysis suggests that they should focus on plants with hexose rich nectars, or to obtain additional energy from other food sources like insects.

The different digestive capacities to use sucrose rich nectars of the members of this nectar-feeding bird community indicates the existence of a continuum in digestive traits that has "specialized" nectarivores at one extreme and "non-specialized" nectarivores at the other. The specialized nectarivores can be defined as those that have the digestive traits that allow them to fuel their metabolic expenditures with any kind of nectar. While non-specialists can use nectar, but must focus on plant that secrete hexose rich nectar and/or supplement their diet with other foods sources to satisfy their energy demands. Stiles (1981) outlined a semi-quantitative system to ascertain the relative degree of specialization of nectar-feeding birds. He used a weighted index that scored the degree of specialization in several morphological traits (body size, beak, tongue and gut morphology) to determine degree of specialization. Stiles (1981) characterized hummingbirds as highly specialized (they received a score of 2.6 out of a maximum of 3), and flowerpiercers as slightly less specialized (with a score of 2.0). He scored *Vermivora* warblers as minimally specialized and gave them a score of 0.62. Although my analysis is consistent with Stiles' (1981) assessment, I found that there is a surprising amount of heterogeneity in the capacity to assimilate sucrose in floral nectars among the non-specialists. Although individuals of *V. celata* were clearly limited in their ability to subsist on sucrose rich floral nectars, *V. ruficapilla* individuals had almost the same hydrolytic capacity as the flowerpiercer *D. baritula*.

Based on the data present in this study, I constructed a conceptual model relating sucrose digestive capacity and ecological specialization in birds. In this model, nectar-feeding birds that are able to obtain enough energy from sucrose rich nectars to satisfy their FMR should be considered as physiologically more adapted to handle a diverse nectar diet (Karasov & Diamond 1988, Karasov 1990, Martínez del Rio and Karasov 1990, Karasov and Hume 1997, Martínez del Rio *et al.* 2001, Schondube & Martínez del Rio 2004). Physiologically adapted nectarivorous birds (in this case hummingbirds) have higher sucrase activity and higher glucose transport rates than birds that are less adapted to this diet (most passerines; Martínez del Rio 1990, Schondube & Martínez del Rio 2004, Lotz and Schondube 2006). The high sucrose activity of these physiologically adapted birds should allow them to satisfy their energetic needs using nectars with any sugar composition. As a result of this, they could have a wider breadth of diet (Levey and Martínez del Rio 1999, Lotz and Schondube 2006). On the other hand, birds physiologically less capable to obtain energy from sucrose rich nectars should benefit from feeding mostly on hexose rich nectars. By doing so, they should have more restricted diets and act as ecological specialists. A similar model to explain resourse partition has been proposed recently for a community of nectar-feeding bats (Ayala & Schondube 2011).

Observations I conducted in the field support this model of differences in resourse use by nectar-feeding birds. At my site in Nevado the Colima, both hummingbirds and flowerpiercers used the flowers of different plant species in relation to their abundance, spending more time visiting the more abundant plant species, acting as ecological generalists. However *V. celata* spent more time visiting the flowers of one of the plants with more hexoses in its nectar (*Ribes ciliatum*) than expected based on the flower abundances, acting like as an ecological specialist (Schondube pers. observ.). While this topic requiresfurther exploration, the existence of a sucrose digestion capacity gradient among the species that compose this nectar-feeding bird community,

and the data related to their foraging strategies and dietary breath, suggest that the partition of plant resources among nectar-feeding birds could be directed by their gut capacities.

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Appendix 1. Sucrase hydrolytic activity and gut morphology values for the study species.

Species	Sample size	Body mass (g)	Gut nominal area (cm^2)	Gut volume (μl)	Sucrase V_{max} total (μmol/min)	Sucrase Km (μmol/L)
Hummingbirds						
Archilochus alexandri[1]	2	3.2 ± 0.1	2.19 ± 0.01	82.8 ±	9.76 ± 1.9	38.1 ± 1.3
Colibri thalassinus[2]	3	4.8 ± 0.2	3 ± 0.3	170.1 ±	26.42 ± 3.2	59.2 ± 2.1
Eugenes fulgens[2]	3	7.1 ± 0.1	3.27 ± 0.28	206.6 ±	21.43 ± 2.4	32.5 ± 1.4
Hylocharis leucotis[2]	3	3.6 ± 0.1	2.52 ± 0.13	103.7 ±	16.04 ± 2.1	59.2 ± 4.4
Lampornis clemenciae[1]	2	8.4 ± 0.3	3.66 ± 0.02	162.35 ±	28.54 ± 0.02	30.64 ± 0.1
Selasphorus platycercus[3]	2	3.3 ± 0.1	1.52 ± 0.07	115.7 ±	12.71 ± 2.2	52.35 ± 5.4
Selasphorus rufus[2]	3	3.1 ± 0.1	2.07 ± 0.29	115.7 ±	10.73 ± 1.8	74.27 ± 4.2
Passerines						
Diglossa baritula[2]	4	8.1 ± 0.1	3.51 ± 0.14	242.1 ±	10.16 ± 0.9	38.9 ± 3.2
Vermivora celata[2]	3	8.2 ± 0.3	5.42 ± 0.13	276.5 ±	4.84 ± 0.9	37.8 ± 4
Vermivora ruficapilla[2]	3	8 ± 0.2	6.06 ± 0.22	263.7 ±	8.37 ± 1.1	36.4 ± 1.3

[1]McWhorter unp. data, [2]this study, [3]McWhorter & Martínez del Rio 2000.
Note: Values are means ± SEs.

Appendix 1. Continuation

Species	Sucrase pH optimum	Sucrose hydrolysis efficiency (%)	Observed intake (kJ/day)	Predicted FMR (kJ/day)
Hummingbirds				
Archilochus alexandri[1]	6.5	99	30.64 ± 6.42	22.68
Colibri thalassinus[2]	6.5	99		37.43
Eugenes fulgens[2]	6.5	99	49.8 ± 3.32	59.82
Hylocharis leucotis[2]	6.5	99		26.71
Lampornis clemenciae[1]	6.5	99	65.13 ± 3.12	73.41
Selasphorus platycercus[3]	6.5	99	35.22 ± 0.69	23.98
Selasphorus rufus[2]	6.5	99	17.26 ± 2.34	20.12
Passerines				
Diglossa baritula[2]	6.5	99	35.52 ± 2.12	43.13
Vermivora celata[2]	6	90		43.49
Vermivora ruficapilla[2]	6	90		42.76

[1]McWhorter unpublished data, [2]this study, [3]McWhorter & Martínez del Rio 2000.
Note: Values are means ± SEs.

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