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# The integration of diet, physiology, and ecology of nectar-feeding birds

## La integración de la dieta, fisiología, y ecología en aves nectarívoras

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## ABSTRACT

Balance between energy acquisition and expense is critical for the survival and reproductive success of organisms. Energy budgets may be limited by environmental factors as well as by animal design. These restrictions may be especially important for small endotherms such as hummingbirds, which have exceedingly high energy demands. Many nectar-feeding bird species decrease food intake when sugar concentration in food is increased. This feeding response can be explained by two alternative hypotheses: compensatory feeding and physiological constraint. The compensatory feeding hypothesis predicts that if birds vary intake to maintain a constant energy intake to match energy expenditures, then they should increase intake when expenditures are increased. Broad-tailed hummingbirds (*Selasphorus platycercus*) and Green-backed fire crown hummingbirds (*Sephanoides sephaniodes*) were presented with diets varying in energy density and exposed to various environmental temperatures. Birds decreased volumetric food intake in response to sugar concentration. However, when they were exposed to lower environmental temperatures, and hence increased thermoregulatory demands, they did not increase their rate of energy consumption and lost mass. These results support the existence of a physiological constraint to the energy budgets of hummingbirds. Digestive and peripheral organ function limitations may impose severe challenges to the energy budgets of these small endotherms, and therefore play a significant role in determining their distribution, ecology, and natural history.

**Key words:** energetics, digestion, feeding behavior, hummingbirds, nectarivory.

## RESUMEN

El balance entre la adquisición y el uso de energía es crítico para la reproducción y sobrevivencia. Los presupuestos energéticos de los organismos pueden estar limitados tanto por factores ambientales como por su fisiología. Estas restricciones pueden ser especialmente importantes para pequeños endotérmos como los colibríes (picaflores) que tienen costos energéticos altos por unidad de masa. Muchas especies de aves nectarívoras reducen el consumo de alimento cuando la concentración de azúcar aumenta. Esta respuesta puede ser explicada por dos hipótesis alternativas: compensación alimenticia y restricciones fisiológicas. La primera hipótesis predice que las aves varían el consumo para mantener la ingesta de alimento ajustada a sus gastos energéticos. Por ende, cuando los gastos energéticos aumentan, el consumo debe aumentar. Colibríes vibradores (*Selasphorus platycercus*) y picaflores (*Sephanoides sephaniodes*) fueron alimentados con dietas de contenido energético variable y expuestos a varias temperaturas ambientales. Las aves redujeron el volumen consumido en respuesta a un incremento en la concentración de azúcar. Sin embargo, cuando fueron expuestos a bajas temperaturas, y por lo tanto a mayores demandas de termoregulación, no aumentaron su consumo de energía y perdieron masa corporal. Estos resultados indican la existencia de una limitante fisiología que restringe a los presupuestos energéticos de los colibríes. Limitaciones funcionales (digestivas o periféricas) pueden imponer seríos dilemas para los presupuestos de energía de estos pequeños endotérmos y por lo tanto jugar un papel significativo en su distribución, ecología, e historia natural.

**Palabras clave:** energética, digestión, conducta de alimentación, picaflores, nectarivoría.

## INTRODUCTION

Nectar feeding animals provide physiological ecologists with relatively simplified systems in which to study the interaction of diet, physiology, and ecology. Hummingbirds are among the most intriguing subjects because they are among the smallest endothermic vertebrates and have extremely high mass-specific metabolic rates (Pearson 1950, Lasiewski 1963, Bartholomew & Lighton 1986). The energetic cost of hovering flight employed by foraging hummingbirds

(Managed by F. Bozinovic)

(Suarez 1992) sets them apart from other nectarivores and in combination with their small size makes them especially sensitive to energy stress (Tooze & Gass 1985, McNab 1988). In addition to confronting the problems of endothermy at small body sizes, hummingbirds often face large fluctuations in energy availability and energetic demands (Gass & Lertzman 1980, Montgomerie & Gass 1981). Furthermore, many species of hummingbirds that breed in temperate, high latitude areas face the additional energetic cost of migrating long distances between breeding and wintering grounds (see for example Calder 1993). The ability of the digestive system to obtain energy to meet demands and peripheral organs to transform energy to work must be tightly coupled in hummingbirds. The simultaneous regulation of energy intake and energy use has the potential to limit physiological, behavioral and ecological capacities in these animals (Beuchat et al. 1990, McWhorter & Martínez del Río 1999).

Although hummingbirds are able to modify their behavior (Ewald & Carpenter 1978, Gass 1978, Tiebout 1991) and utilize energy saving strategies, such as torpor, to enhance their ability to deal with energetically adverse conditions (Calder 1994 and references therein), they still appear to live teetering on the edge of the chasm of negative energy balance. What factors influence the energy budgets of small endotherms such as hummingbirds? In addition to potential ecological constraints on energy budgets (i.e. resource availability and competition), the idea that physiological limitations may restrict the energy budgets of animals has gained support over the past decade (Weiner 1992, Hammond & Diamond 1997). Physiological constraints include limits to both rates of energy acquisition (foraging, food ingestion, digestion and absorption) and energy expenditure (work, heat production and tissue growth, Weiner 1992). Animals may maintain energy balance by dynamically regulating nutrient uptake capacity and energy expenditure (i.e. changing the relative importance of central versus peripheral limitations) based on the conditions they experience. Despite the considerable flexibility that hummingbirds exhibit in their energy management, physiological constraints may be important in determining their life histories.

In this paper we review the interplay of diet, physiological constraints, and ecology as determinants of food intake. Specifically, we examine some of our recent research on the physiological and behavioral responses of hummingbirds to manipulation of environmental energy availability and energetic demands. In addition, the modeling of gut function based on chemical reactor theory is presented as a tool to understand the digestive physiology of nectar-feeding animals. We argue that adopting an integrative, mechanistic approach to the study of the physiological ecology of hummingbirds is key to understanding their behavior, ecology and distribution.

## CASE STUDIES

A major goal in physiological ecology is to understand the factors that may influence the ecological roles and abilities of animals. For hummingbirds, energy budgets and constraints thereof are undoubtedly among the most important influences. Because their nectar diets are relatively energy dilute and their mass-specific metabolic rates so high, physiological limitations to energy acquisition and energy utilization may be equally important. We are going to begin to examine the factors that influence the energy budgets of hummingbirds by introducing a behavioral feeding pattern and its ecological correlates. We will then introduce a series of experiments designed to differentiate between possible explanations for this pattern and determine the nature of potential physiological constraints.

### *Effects of sugar concentration on hummingbird feeding and energy use*

The energy content of food and its spatial and temporal availability determine both the net energy that a foraging hummingbird can obtain and how it manages its daily energy budget (López-Calleja et al. 1997). Nectar sugar concentration, therefore, probably has a strong effect on hummingbird foraging behavior. Indeed, foraging time and resource removal rates are functions of feeding rate, which is dictated by digestive capacities and ultimately the energy demands of the animal (Karasov 1990). López-Calleja et al. (1997) experimentally varied nectar sugar concentration and investigated the effect on feeding patterns and energy use in hummingbirds, using captive Green-backed firecrowns (*Sephanoides sephaniodes*). Their work tested the assumptions and predictions of a model of hummingbird feeding that assumes gut processing rates are linearly correlated with sugar concentration in food (Martínez del Río & Karasov 1990). The model makes several predictions about how hummingbirds should respond to sugar concentration if their goal is to maximize energy gain. The predictions examined by López-Calleja et al. (1997) are the following: (a) Hummingbirds should assimilate the sugars in their diets essentially completely, regardless of sugar concentration; (b) Increased sugar concentration should lead to increased rates of energy intake; and (c) Meal retention times, and hence inter-meal intervals, should increase linearly with sugar concentration. Note that the second prediction in particular follows from the assumption that hummingbirds behave to maximize their rate of energy intake.

The feeding behavior and digestive performance of hummingbirds supported several of the predictions of the model (López-Calleja et al. 1997). Hummingbirds assimilated the sugars in their food almost completely, regardless of sugar concentration. This pattern is common to all of the hummingbird species that have been examined thus far (Karasov et al. 1986, Hainsworth 1988, Martínez del Río 1990b, McWhorter 1997) and suggests that assimilation efficiency is independent of sugar concentration (López-Calleja et al. 1997). Processing time index (PTI), proposed by Martínez del Río (1990b) as an indirect measurement of meal retention time, increased with sugar concentration. Inter-meal intervals also increased linearly with sugar concentration. Energy assimilation was not, however, correlated with sugar concentration as predicted. Despite a ten-fold variation in food intake between 0.25 and 0.75 M sucrose solutions, energy assimilation remained constant at about 35 kJ/day (López-Calleja et al. 1997). This result falsified perhaps the most important prediction of Martínez del Río and Karasov's (1990) model, which is that energy intake would be positively correlated with sugar concentration. This can be interpreted either as evidence that hummingbirds do not function as "energy maximizers" (sensu Schoener 1971) at the temporal scale of a day, or that gut processing rates somehow constrain the rate of energy assimilation (Karasov et al. 1986, Levey & Martínez del Río 1999). Many observations have suggested that at the temporal scale of a day hummingbirds regulate energy intake at a relatively constant level (Hainsworth 1978, 1981, Hainsworth & Wolf 1983). Discerning whether hummingbirds are defending a constant rate of energy assimilation or are constrained to a maximal rate of energy assimilation requires that they be exposed to environmental conditions that force them to increase their rate of energy expenditure (López-Calleja et al. 1997). Such conditions include low temperature (Kendeigh et al. 1969), unpredictable resource availability or temperature (Caraco et al. 1990, Elkman & Hake 1990), and long distances to food sources (Tiebout 1991). The next section describes experiments designed to differentiate between these possible explanations using acute exposure to low ambient temperatures.

### *Does gut function limit hummingbird food intake?*

Hummingbirds respond to experimentally increased sugar concentration in food by decreasing volumetric intake (Fig. 1, see also López-Calleja et al. 1997, McWhorter 1997). This inverse relationship between intake and sugar concentration is common to many nectar-feeding birds (Collins 1981, Downs 1997, Lotz & Nicolson 1999). Similar reciprocal relationships between nutrient/energy density and food intake have been described in a variety of animals (Montgomery & Baumgardt 1965, Batzli & Cole 1979, Simpson et al. 1989, Nagy & Negus 1993, Castle & Wunder 1995). The widespread occurrence of such intake-response patterns has often been attributed to compensatory feeding (Simpson et al. 1989). This explanation supposes that animals regulate food intake to maintain a constant flux of assimilated energy or nutrients (Montgomery & Baumgardt 1965, Slansky & Wheeler 1992). Animals compensate for decreased energy density in food by increasing intake. An alternative explanation is that intake is constrained by the ability of animals to assimilate the nutrients contained in food (see above, Karasov et al. 1986, Levey & Martínez del Río 1999). McWhorter and Martínez del Río (in press) address the question of whether the intake-response relationship observed in hummingbirds is the result of compensatory feeding or a digestive constraint to energy assimilation. Animals must be exposed to environmental conditions that acutely increase their energetic demand in order to discern between these possibilities, because chronic cold exposure in endotherms is often accompanied by increased digestive and metabolic capacities (Konarzewski & Diamond 1994 and references therein).

The resting metabolic rate of Broad-tailed hummingbirds (*Selasphorus platycercus*) is considerably higher at 10°C than at 20°C (Bucher & Chappell 1988). Based on this observation McWhorter and Martínez del Río (in press) hypothesized that for a given food energy density, birds exposed to lower temperatures would show increased food intake. An increase in sugar intake under energetically demanding conditions would support the compensatory feeding explanation. Conversely, the opposite result would provide evidence that a physiological process limits sugar assimilation. Broad-tailed hummingbirds were exposed to 10°C and 22°C and fed diets ranging in sugar concentration from 292 to 1168 mmol/L sucrose. Birds exhibited the expected reciprocal relationship between intake and food energy density, but did not significantly increase food consumption when exposed to low environmental temperatures (McWhorter & Martínez del Río in press). This failure to increase food intake when acutely challenged by cold temperatures was interpreted as evidence for the existence of a physiological constraint to energy assimilation. The conclusion that broad-tailed hummingbirds were unable to increase their food intake to meet increased energetic demands was supported by two additional observations. First, birds lost significantly more body mass at the lower temperature. Second, birds exposed to 10°C were often observed emerging from torpor in the morning and exhibited behaviors commonly associated with energy conservation (ptiloerection, decreased flying time, feet held close to body in flight, Gass & Montgomerie 1981, Udvardy 1983). Regardless of any energy conserving mechanisms employed, it appeared that acutely cold-exposed hummingbirds could not process energy fast enough to compensate for their higher energy demands. Increased torpor use by cold-exposed hummingbirds highlights the subtle interrelation of their digestive and metabolic traits. Balancing their precarious energy budget may require hummingbirds to use energy conserving strategies when energetic demands are increased and energy acquisition is constrained (McWhorter & Martínez del Río in press).

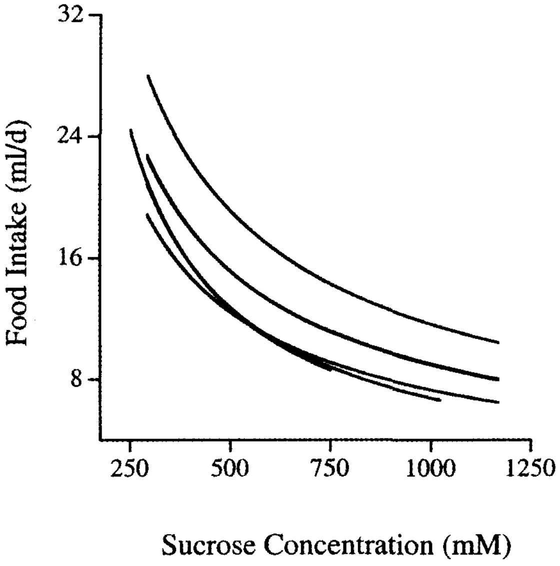

*Fig. 1.* The relationship between volumetric food intake and sugar concentration in hummingbirds and flower-piercers. This reciprocal relationship is common to a wide variety of animals and has often been attributed to compensatory feeding. Data are well described by power functions with slopes ranging from -0.71 to -0.95. Interestingly, the slope is significantly less than one in some cases and does not appear to be correlated with taxa. Intake (I) decreased significantly with increased sucrose concentration in diet (C) as follows: *Selasphorus platycercus* $I = 1502.0\ C^{-0.77}$; *Archilochus alexandri* $I = 1582.7\ C^{-0.75}$; *Eugenes fulgens* $I = 1697.3\ C^{-0.76}$; *Lampornis clemenciae* $I = 1606.2\ C^{-0.71}$; *Sephanoides sephaniodes* $I = 4638.6\ C^{-0.95}$; *Diglossa baritula* $I = 3789.9\ C^{-0.92}$.

Relación entre la ingesta volumétrica de alimento y la concetración de azucar en picaflores y mieleros-serranos. La relación recíproca es común a una amplia variedad de animales y se ha atribuido a alimentación compensatoria. Los datos se describen por una función potencial con pendientes que varían entre -0,71 y -0,95. Interesantemente, la pendiente es significativamente menor que uno y en algunos casos no está correlacionada con los taxa. La ingesta (I) disminuye significativamente con un aumento en la concentración de sacarosa en la dieta ( C) de la siguiente manera: *Selasphorus platycercus* $I = 1502{,}0\ C^{-0{,}77}$; *Archilochus alexandri* $I = 1582{,}7\ C^{-0{,}75}$; *Eugenes fulgens* $I = 1697{,}3\ C^{-0{,}76}$; *Lampornis clemenciae* $I = 1606{,}2\ C^{-0{,}71}$; *Sephanoides sephaniodes* $I = 4638{,}6\ C^{-0{,}95}$; *Diglossa baritula* $I = 3789{,}9\ C^{-0{,}92}$.

The apparent inability of hummingbirds to increase energy assimilation when subjected to higher energetic demands led McWhorter & Martínez del Río (in press) to speculate about the factors potentially imposing an upper limit to food intake. Physiological processes that determine rates of sugar assimilation are important potential limiting factors because the vast majority of energy acquired by hummingbirds comes from dietary sugars. Sugar ingestion can be limited by rates of sucrose hydrolysis or transport of the resulting monosaccharides (Karasov et al. 1986, Martínez del Río 1990a), and by rates of sugar catabolism or biosynthetic processes (Suarez et al. 1988, Suarez et al. 1990). McWhorter & Martínez del Río (in press) focused on the potential role of digestive processes in limiting energy assimilation. Because previous methods developed to compare the capacity of the intestine to hydrolyze and absorb nutrients with ingested loads appear to overestimate digestive capacity, an alternative model of sucrose hydrolysis in hummingbird guts was developed. This method relies on modeling the intestine of hummingbirds as a plug-flow chemical reactor (Penry & Jumars 1987), and was described in detail by McWhorter & Martínez del Río (in press). Sucrase activity measurements in vitro, sugar assimilation rates and intestinal morphology were used to predict intake rates for four experimental sucrose concentrations. The intake rates predicted using this model slightly overestimated observed intake rates, but there was a remarkable qualitative resemblance between the model's output and bird behavior. The safety factors (defined as the ratio of capacity to load) estimated using this method are considerably lower than those predicted by integrating the maximum capacity of intestinal hydrolases along the length of the intestine as proposed by Diamond and Hammond (1992). Because the model developed by McWhorter & Martínez del Río (in press) includes greater physiological detail than previous methods, it may lead to a less biased estimate of hydrolytic capacity. Most significantly, the model takes into account the decline in sucrose concentration along the gut that accompanies hydrolysis. The lower safety factors predicted by the model indicate that broad-tailed hummingbirds ingested as much sucrose as they had the ability to process. Consequently, when they were faced with increased energetic demands, they were unable to increase energy assimilation to meet them.

The cold exposure experiments performed by McWhorter & Martínez del Río (in press) were specifically designed to differentiate between compensatory feeding and constraints to energy acquisition. Cold exposure was acute in these experiments because chronic exposure to increased energy demands leads to increased intake and is typically accompanied by increased digestive and metabolic capacities (Konarzewski & Diamond 1994). For example, Hammond et al. (1994) demonstrated that the higher intake shown by cold-acclimated mice is accompanied by hypertrophy of the gastrointestinal tract. It would make sense that hummingbirds are similarly capable of increasing intake and assimilation. McWhorter & Martínez del Río (in press) showed that the physiological capacities of hummingbirds are well matched to the loads that they experience normally. When energy demands were increased, birds were unable to match them and lost body mass. Based on these results, we hypothesized that chronic cold exposure would lead to up-regulation of the ability to assimilate energy and to a new match between demands and capacities. If this hypothetical scenario is correct, it leads to an important ecological consequence of the tight matching of physiological capacities and ecological demands. The energetic savings provided by not having a large spare digestive capacity could come at the cost of short-term behavioral flexibility. In hummingbirds, such tight matches between the ability to assimilate energy and the normal energetic demands of the environment can result in periods during which the animals lose mass. In the next section, we describe experiments that explore the factors accounting for the regulation of energy budgets when hummingbirds are chronically exposed to low environmental temperatures and energy dilute diets.

### *What factors impose a ceiling to the energy budget of hummingbirds?*

Physiological constraints to the energy budgets of animals may include limits to either the energy-supplying physiological machinery (central limitation hypothesis), the energy-consuming machinery (peripheral limitation hypothesis), or both (Kirkwood 1983, Petersen et al. 1990, Koteja 1996a, 1996b). Central limitations include aspects directly related to the assimilation of nutrients and energy. Digestive capacities, such as nutrient hydrolysis and uptake rates, influence food ingestion rate and ultimately foraging behavior (Karasov 1990, Martínez del Río 1990a). Peripheral limitations involve pathways through which absorbed nutrients are converted to work, heat production and growth (Weiner 1992). Limitations to the catabolism of absorbed sugars and/or shunting into biosynthetic pathways has the potential to limit feeding rates (Suarez et al. 1988, Suarez et al. 1990). Physiological limitations are undoubtedly of primary importance to small endothermic vertebrates such as hummingbirds. The studies that we have previously described focus mainly on establishing the existence of physiological constraints, and to some extent exploring the factors responsible for those constraints. We believe that peripheral limitations, which these studies did not explore, may be as important as central limitations for hummingbirds.

López-Calleja & Bozinovic (pers. comm.) explored the influence of energy acquisition and expenditure on the energy and time budgets of captive *S. sephaniodes*. Their study was designed to provide a quantitative assessment of the factors (central versus peripheral limitation) responsible for regulating and limiting the energy budgets of hummingbirds. Birds were tested using two experimental diets (high and low energy density) and two environmental temperatures (within their thermoneutral zone and low temperature), and were acclimated to these conditions for 15 days before experiments began. Volumetric food intake, body mass, time budgets and metabolic rates were measured during the experimental period. After experiments, birds were killed in order to measure organ masses and fat content. In agreement with other studies on hummingbirds (López-Calleja et al. 1997, McWhorter 1997, McWhorter & Martínez del Río in press), volumetric food intake was negatively correlated with sugar concentration, independent of thermal conditions (López-Calleja & Bozinovic pers. comm.). Birds in their thermoneutral zone feeding on the high quality diet (higher quality defined as higher energy density; HQ-TNZ) maintained body mass throughout the experimental period. Birds challenged with lower quality diets and cold temperatures (LQ-LT) decreased their body mass. Birds in the remaining two treatment groups (HQ-LT and LQ-TNZ) showed slight decreases, but body mass stabilized toward the end of the acclimation period. Since rates of sugar assimilation are limiting when hummingbirds are subjected to increased energetic demands over the short term (McWhorter & Martínez del Río in press), these decreases in body mass make functional sense. If the input side of an energy budget cannot be increased, then the output side must be decreased. Reduced body mass is accompanied by lower net energy demands. The observation that birds lost mass when challenged with energy-dilute food and/or cold temperatures chronically confirms a physiological constraint to their energy budgets. A closer look at patterns of energy use and changes in organ mass was necessary, however, to discern whether the limitation is central or peripheral.

Fat free carcass mass (including the flight muscles, which may compose up to a third of a hummingbird's body mass) increased significantly in cold-exposed birds, as did heart and lung mass (López-Calleja & Bozinovic pers. comm.). In addition, significant increases in intestinal nominal area and kidney mass were detected in birds fed the low quality diet. The overall decrease in body mass observed in cold-exposed birds was presumably due to decreased fat stores. Daily energy expenditure (DEE) and the proportion of energy used for thermoregulation increased significantly in cold-exposed birds (López-Calleja & Bozinovic pers. comm.). The time budgets of birds also changed as a consequence of energy challenges. Cold-exposed birds spent less time flying and feeding and used torpor much more frequently and for longer periods than birds at milder temperatures (López-Calleja & Bozinovic pers. comm.).

What do these observations say about physiological constraints to the energy budgets of hummingbirds? Changes in the time budgets of birds, such as decreased flying time and feeding frequency, and increased torpor use indicate the existence of an energetic constraint, but not where it may lie. The increase in energy-consuming organs (flight muscles, heart, lungs) may reveal that the higher metabolic rates observed in cold-exposed birds required a concomitant increase in organ size (Konarzewski & Diamond 1995). It is conceivable that the combined energetic demands of hovering flight and increased thermoregulatory costs exceeded the capacity of the energy-consuming organs to produce work and heat, which indicates a peripheral limitation. The increase in the absorptive surface area of the intestine, on the other hand, indicates a central limitation. It appears that both central and peripheral limitations are important influences on the energy budgets of hummingbirds.

The energy supplying and energy consuming physiological machinery of hummingbirds are without doubt closely matched. Hummingbirds are nevertheless subject to rapid and unpredictable fluctuations in environmental temperatures and resource availability (Gass & Lertzman 1980, Montgomerie & Gass 1981). Such tight matches between the ability to assimilate energy and the normal energetic demands of the environment result in periods during which birds are in negative energy balance. The energetic savings provided by not having a large spare digestive capacity indeed appeared to come at the cost of short-term behavioral flexibility. Birds subjected to low temperatures and energy dilute foods utilized torpor to a much greater extent than other birds, but the energy savings provided by this strategy were not adequate to prevent negative energy balance and significant mass loss (López-Calleja et al. 1997, McWhorter & Martínez del Río in press, López-Calleja & Bozinovic pers. comm.). Chronic cold exposure, however, led to a new balance between energetic demands and the ability to assimilate and utilize energy. We propose that the relative importance of central or peripheral limitations changes dynamically, based on the conditions experienced by the animal. The considerable flexibility that hummingbirds exhibit in their energy management over the long term is critical for their survival and reproductive success, and greatly broadens the ecological role that they may occupy.

## GENERAL DISCUSSION AND NEW DIRECTIONS

Interest in physiological constraints to the energy budgets of animals stems from the conjecture that many animals routinely operate at near maximum intensity (Weiner 1992). Kirkwood (1983) computed an allometric equation that predicts the maximum metabolizable energy input for a variety of animals. The predictions of this allometry imply that the energy budgets of animals are limited, often to levels equal to or only slightly higher than rates of energy expenditure observed in the field (Nagy 1987). Apparently, some animals operate with little safety margin between energetic load and capacity. Physiological limitations may therefore be more important than environmental constraints, such as resource availability, for the energy budgets of animals (Weiner 1992). Indeed, many authors have suggested that knowledge of the digestive and metabolic physiology of birds is a crucial, albeit neglected, component in understanding their behavior and feeding ecology (Karasov et al. 1986, Karasov 1990, Petersen et al. 1990, Weiner 1992, Martínez del Río & Restrepo 1993, Martínez del Río 1994, Karasov 1996, Sabat et al. 1998). The observation of sucrose avoidance in passerines in the *Sturnidae-Muscicapidae* lineage that lack the enzyme sucrase (Martínez del Río et al. 1988, Karasov & Levey 1990, Martínez del Río 1990a) is an excellent example of how physiological traits determine behavior and resource utilization in birds. Previous research on hummingbirds has emphasized the regulation of energy budgets in the face of changing energy demands and availability without directly examining the underlying physiological mechanisms involved (Calder 1975, Hainsworth 1978, Hainsworth 1981, Hainsworth & Wolf 1983, Calder 1994). We argue that avoiding such "black box" approaches by asking broad, integrative questions about the physiology of hummingbirds can lead to a greater understanding of the factors that determine their behavior and ecology.

Hummingbirds are perhaps the most specialized nectarivorous vertebrates. They exhibit remarkably high rates of sucrose hydrolysis (Martínez del Río 1990a) and the highest rates of carrier-mediated glucose transport reported among vertebrates (Karasov et al. 1986). Their digestive systems appear extremely well suited to digest and absorb a sucrose rich diet. Likewise, their energy consuming metabolic machinery is well matched to their energetically demanding lifestyle. Hummingbirds have high lung oxygen diffusing capacities, cardiac outputs, mitochondrial volume densities, cristae surface densities and concentrations of enzymes involved in energy metabolism (Suarez 1998 and references therein). Although it is clear that hummingbirds are impressively equipped for their energetically demanding lifestyles, the specific factors responsible for imposing a ceiling to their energy budgets were previously unclear. The studies we have reviewed in this paper provide support for the notion that both central and peripheral limitations are significant influences on the energy budgets of hummingbirds (López-Calleja et al. 1997, McWhorter & Martínez del Río in press, López-Calleja & Bozinovic pers. comm.). The concept of symmorphosis would argue that all structures of an organism are precisely tuned to one another, so that the functional capacity of one structure does not exceed any other (Weibel et al. 1991, Weiner 1992). Although we agree that the functional capacities at each step in linear pathways are probably well matched (i.e. that there is not a single rate limiting step, Suarez 1998), we suggest that the relative importance of central or peripheral limitations changes dynamically. Regardless of the specific limitations in effect in any given situation, the putative effects of physiological limitations to energy budgets define the ecological capacities of hummingbirds, and undoubtedly contribute to the establishment of the lower size limit for endothermic homeotherms.

The integrative approaches adopted by the studies reviewed in this paper provide a mechanistic bridge between ecological patterns and physiological capacities at organism, tissue and cellular levels. This type of approach may be particularly useful for identifying the nature of physiological constraints and testing under what conditions these constraints have an ecological function (Karasov 1986). The ongoing process of developing and testing mathematical models of digestive function has been an indispensable tool for understanding the digestive physiology of nectar-feeding animals. The remarkably accurate predictions of sugar intake made by McWhorter & Martínez del Río's (in press) model highlight the usefulness of this approach. We have made the assumption that the digestive limitations documented for hummingbirds in captivity operate in the field. Models of digestive function lack relevance if their predictions are not testable under natural conditions. Hummingbirds present an unparalleled opportunity to test the usefulness of these models for understanding the ecology and behavior of nectar-feeding animals. Daily energy expenditures can be measured using standard methods (Powers & Nagy 1988, Tiebout & Nagy 1991) and digestive capacities can be estimated from floral nectar composition and the model presented by McWhorter & Martínez del Río (in press). Clearly, a better understanding of the digestive and metabolic traits of nectar-feeding birds, and how these factors influence each other, is necessary. It has been concluded based on previous research that the assumption of energy maximization is probably inappropriate for nectar-feeding animals that are not growing, storing fat, or reproducing (Karasov & Cork 1996, López-Calleja et al. 1997). The understanding of physiological limitations to the energy budgets of these animals may, however, be especially important under just those conditions. Additional laboratory and field studies are necessary to provide a complete picture of how and when physiological constraints are ecologically relevant for hummingbirds. Examination of the physiological traits of nectar-feeding birds can also provide insight into their roles as selective influences on the characteristics of other animals and plants with which they interact (Martínez del Río et al. 1992, Martínez del Río & Restrepo 1993). Further study at all levels, from the biochemical to organismal, as well as continued work towards integration, is necessary to clarify the relationships between capacities and loads in these animals (Suarez 1998). Adopting an integrative approach to the study of the physiological ecology of hummingbirds is key to understanding their behavior, ecology and distribution.

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