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Thermoregulatory cost affects territorial behavior in hummingbirds: a model and its application

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Abstract A common assumption in behavioral ecology is that the valuation of a resource by consumers depends on the energetic value of the resource itself. Nevertheless, the value of a resource may be relative to the condition of the organism, which is in turn related to the abiotic conditions such as ambient temperature. We developed a theoretical model—incorporating these untested assumptions—to predict a functional relationship between territorial aggression and ambient temperature for individuals sensitive to daily variations in energy availability. We evaluated our theoretical predictions against a field experiment carried out with the hummingbird *Sephanoides sephaniodes*. The model predicted a quadratic relation between aggression intensity and ambient temperature. Field data were better explained by a quadratic equation than a linear function, suggesting the existence of lower and upper thresholds of temperature which determine the intensity of territorial defense. Ambient temperature affects energy expenditure for thermoregulation, and therefore, it fixes the benefit level that must be produced by the territory to pay the costs of its defense. Our findings strongly suggest that abiotic conditions can change an animal evaluation of the yield of a resource and in turn influence the behavioral strategy which it adopts.

Keywords Resource value · Abiotic conditions · Territoriality · Hummingbirds

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Introduction

Territorial behavior may be affected by a number of factors such as defendability of resources, number of competitors, and abiotic environmental factors (Carpenter 1987; López-Sepulcre and Kokko 2005). The cost-benefit approach in behavioral ecology suggests that when the costs of defending a territory outweigh the benefits of exclusive use, territorial behavior ceases (Brown 1964; Hinsch and Komdeur 2010). The common assumption is that the value of a resource depends on the energetic value of the resource itself. Nevertheless, it is possible that the value of a resource could be subjective and related to the condition of the organism instead of the energetic content of the resource by itself (Mohamad et al. 2010). In turn, the condition of the organism could be related to biotic and abiotic factors such as ambient temperature. This situation would be expected more in individuals who are sensitive to daily variations in energy availability because they have a low capacity for energy storage. It could be a result of species-specific physiological and metabolic constraints or alternatively could be due to scarcity of resources at a population level, where individuals are unable to save energy and consequently making them sensitive to short-term variations in resource availability. In these cases, thermoregulatory costs might play a central role in resource defense.

Nectarivorous birds are useful organisms for studying territoriality because energetic benefits gained from defending nectar and energetic costs of territorial activities are quantifiable (Wolf and Hainsworth 1971; Gass et al. 1976; Gill and Wolf 1975; Pimm et al. 1985; Rosenzweig 1986). Hummingbirds maintain their feeding territories free of intruders by performing chases and vocalizations which are energetically expensive behaviors (Powers and Conley 1994). Following the cost-benefit approach, the energy derived from the exclusive access to the resources in the territory should be greater than the cost of the defense. Broad-tailed and rufous hummingbirds display more energetically expensive behaviors when defending high-quality sites, with longer chases, chip calls, and hovering (Camfield 2006). In the wild, hummingbirds often face short-term fluctuations in ambient temperature and energy availability (Cornet et al. 1979; Pyke and Waser 1981; Tamm 1989; López-Calleja and Bozinovic 2003). The challenge imposed by these fluctuations is accompanied by extremely high feeding costs (Suarez 1998; Winter 1998). The cost of hovering in feeding hummingbirds can reach the upper metabolic limit for vertebrates (Bartholomew and Lighton 1986; Chai and Dudley 1999; Suarez et al. 1991). Additionally, the maintenance of high and constant body temperature is costly for small endotherms (Bicudo 1996); thermoregulatory costs and basal rates of energy expenditure typically account for nearly 40% to 60% of total daily energy expenditure of small birds (Lasiewski 1963; Wolf et al. 2000). Moreover, hummingbird hovering is an energetically expensive flight style (Suarez 1992), and the convective cooling it produces due to wing and air movements could further exacerbate energy drain (Chai et al. 1998). Hence, to cope with low temperatures, hummingbirds must ingest large quantities of nectar (Lotz et al. 2003; López-Calleja and Bozinovic 2003).

Although appreciation of resource value by an organism may change depending upon the ambient temperature, it is difficult to make a simple prediction about how the thermoregulatory cost affects the organism's appreciation of the resources in its territory and how this fact affects the level of territorial aggression. In the present study, we developed a theoretical model predicting a functional relationship between territorial aggression and ambient temperature. Then we performed a field experiment with the goal of testing our model using the Green-backed Firecrown hummingbird (*Sephanoides sephaniodes*, Molina).

The Green-backed Firecrown is a migratory hummingbird that winters in central Chile. Males establish feeding territories and actively defend them using vocalizations and chases, while females are not territorial (González-Gómez and Vásquez 2006; González-Gómez and Estades 2009). In this region, hummingbirds can find nectar varying in quality (Smith-Ramirez 1993); the sugar concentration in the nectar of flowers in central Chile ranges from 0.25 to 1.21 M (Smith-Ramirez and Armesto 1998; Fraga et al. 1997). In addition to variation in food quality, this species experiences ambient temperatures ranging from 30°C (March) to −5°C (August) (di Castri and Hajek 1976), which results in a challenging scenario for hummingbirds.

Incorporating this natural history information in our theoretical model, we expected thermoregulatory costs and resource quality to affect the intensity of territorial behavior. In particular, we hypothesized that under conditions of higher ambient temperature, when the thermoregulatory cost for hummingbirds is relatively low and therefore there is higher energy availability, territorial individuals will display lower levels of resource defense. On the other hand, although non-territorial individuals have the visual certainty of particular resources existence, they have no information about the resource quality. Hence, probably they cannot determine the energetic intake as a result of an attack, and thus, their behavior will not be determined by the subjective resource value as it is for the territory owner. Therefore, it is reasonable to expect that non-territorial individuals will display more efforts to obtain resource access (and so, more resource attack) as the temperature increases (i.e., thermoregulatory cost decreases) and they have more energy available.

Methods

Theoretical model

When an aggression event is defined as the conjunction of an attack of a non-territorial individual and a defense of a territorial individual, the probability of an aggression event $P(\mathrm{Ag})$ is

$$P(\mathrm{Ag}) = P(\mathrm{At}) \cdot P(\mathrm{Df}|\mathrm{At}) \qquad (1)$$

where $P(\mathrm{At})$ is the probability of an attack and $P(\mathrm{Df}|\mathrm{At})$ is the conditional probability of a defense given an attack.

We suppose that the probability of attack of a non-territorial individual is directly proportional to its energy availability E, then

$$P(\mathrm{At}) = K_1 \cdot E \qquad (2)$$

where K_1 is a constant and we define $E = \mathrm{FMR} - \mathrm{MR}$ as the difference between the field metabolic rate (FMR) and the resting metabolic rate (MR), i.e., energy available for activity within an animal's energy budget, rather than energy available on the landscape. Field metabolic rate was understood as the metabolic rate of a free-living organism in the wild. Given that we carried on the experiments during non-reproductive season, we considered that the concept includes thermoregulatory expenditures, basic body functions, anti-predatory strategies, territory defense, and food searching, among others. Thus, Eq. 2 expresses the assumption that a fraction of energy that is not allocated to thermoregulation could be destined for territorial behavior. Thus, given that $\mathrm{MR}=C(T_\mathrm{b}-T)$ (McNab 2002), we obtain

$$P(\mathrm{At}) = K_1 C \cdot T + K_1(\mathrm{FMR_{At}} - \mathrm{CT_b}) \tag{3}$$

where C is thermal conductance, T_b body temperature, T ambient temperature, and $\mathrm{FMR_{At}}$ is the field metabolic rate of non-territorial individuals. In turn, there will be a temperature $T_\mathrm{At}{}^*$ where the probability of attack will be the lowest ($P(\mathrm{At})=0$) and a temperature $T_\mathrm{At}{}^{**}$ where the probability of attack will be the highest ($P(\mathrm{At})=1$), which according to Eq. 3 are, respectively:

$$T_\mathrm{At}{}^* = \frac{(\mathrm{FMR_{At}} - \mathrm{CT_b})}{C} \tag{4}$$

$$T_\mathrm{At}{}^{**} = \frac{1 - K_1(\mathrm{FMR_{At}} - \mathrm{CT_b})}{K_1 C} \tag{5}$$

Therefore, we can describe the probability function of attack by

$$P(\mathrm{At}) = \begin{bmatrix} K_1 C \cdot T + K_1(\mathrm{FMR_{At}} - \mathrm{CT_b}) & \text{when } T_\mathrm{At}{}^* < T < T_\mathrm{At}{}^{**} \\ 0 & \text{when } T < T_\mathrm{At}{}^* \\ 1 & \text{when } T > T_\mathrm{At}{}^{**} \end{bmatrix} \tag{6}$$

On the other hand, we assumed that the value of a resource to a territorial organism is lower as that individual's body condition improves (see "Introduction" section). In order to introduce this effect into the model, we supposed that the only relevant factor for the probability of defense is the subjective appreciation of resources. We predicted that the probability of a territorial individual defense given an attack decreased linearly with its energy availability. Then

$$P(\mathrm{Df}|\mathrm{At}) = K_3(1 - K_2 \cdot E)$$

Thus, according to the previous definition of E

$$P(\mathrm{Df}|\mathrm{At}) = -K_3 C \cdot T + (K_3 - K_2 K_3 \cdot \mathrm{FMR_D} + K_3 \mathrm{CT_b}) \tag{7}$$

where $\mathrm{FMR_D}$ is the field metabolic rate of territorial individuals and K_2 and K_3 are constants.

As before, there will be two critical temperatures, $T_\mathrm{D}{}^*$ and $T_\mathrm{D}{}^*$, where the probability will be the lowest and the highest, respectively ($P(\mathrm{Df}|\mathrm{At}) = 0$ and $P(\mathrm{Df}|\mathrm{At}) = 1$):

$$T_\mathrm{D}{}^* = \frac{(K_3 - K_2 K_3 \cdot \mathrm{FMR_D} + K_3 \mathrm{CT_b}) - 1}{K_3 C} \tag{8}$$

$$T_\mathrm{D}{}^{**} = \frac{(1 - K_2 \cdot \mathrm{FMR_D} + \mathrm{CT_b})}{C} \tag{9}$$

Thus,

$$P(\mathrm{Df}|\mathrm{At}) = \begin{bmatrix} -K_3 C \cdot T + (K_3 - K_2 K_3 \cdot \mathrm{FMR_D} + K_3 \mathrm{CT_b}) & \text{when } T_\mathrm{D}{}^* < T < T_\mathrm{D}{}^{**} \\ 0 & \text{when } T > T_\mathrm{D}{}^{**} \\ 1 & \text{when } T < T_\mathrm{D}{}^* \end{bmatrix} \tag{10}$$

Finally, combining Eqs. 1, 6, and 10, we obtain an expression for the relationship between the level of aggression and the ambient temperature:

$$P(\mathrm{Aggression}) = \begin{bmatrix} -\alpha T^2 + \beta T + \gamma & \text{when } T_\mathrm{At}{}^* < T < T_\mathrm{D}{}^{**} \\ 0 & \text{when } T < T_\mathrm{At}{}^* \\ 0 & \text{when } T > T_\mathrm{D}{}^{**} \end{bmatrix}$$

where

$$\alpha = K_1 K_3 C^2$$
$$\beta = K_3[CK_1(\mathrm{FMR_{At}} - \mathrm{CT_b}) + K_1 C(1 - K_2 \cdot \mathrm{FMR_D} + \mathrm{CT_b})]$$
$$\gamma = K_4(1 - K_2 \cdot \mathrm{FMR_D} + \mathrm{CT_b})\,(K_1(\mathrm{FMR_{At}} - \mathrm{CT_b}))$$

Therefore, the model predicts a quadratic functional relationship between aggression level and ambient temperature, determining a lower and higher critical temperature for the cessation of aggression $T_{\min} = T_{\mathrm{At}}^{*}$ and $T_{\max} = T_{\mathrm{D}}^{*}$, respectively.

Fitting experimental data to the theoretical model

The quadratic relationship found in the model was compared with the simplest alternative hypothesis, that is, the linear function. The three possible linear relationships, with slopes >0, =0, <0, represent the positive, null, and negative association between temperature and aggressive behavior, respectively. They could be biologically interpreted as the expression of just one of our main model assumptions (Eqs. 6 and 10), meaning that one of the two factors is much more relevant than the other one.

The Bayesian information criterion (BIC; Link and Barker 2006) and maximum-likelihood (Akaike information criterion, AIC; Burnham and Anderson 2002) estimation methods were used to evaluate the fit of field experimental data to three models: (a) a linear model considering nectar quality as independent variable, (b) a linear model with ambient temperature as independent variable, and (c) our quadratic theoretical model. We calculated the weighted BIC (wBIC) for model probabilities to be the best model for the data given the linear and quadratic models (Link and Barker 2006).

Field experiments

Species and study site

The study was carried out in July 2008 and July 2010 in the Andean foothills in the Mediterranean field station of the Universidad Católica de Chile at San Carlos de Apoquindo, central Chile (33°23′ S, 70°31′ W, 1,100 m elevation above sea level). Subjects were free-living male Green-backed Firecrown hummingbirds (*S. sephaniodes*), which had established feeding territories in the study site (see below) and actively defended territories. In order to identify the subjects, we could rely on their natural markings as well as their conspicuous territorial behavior. Territorial individuals are easily distinguishable as they display aggressive behaviors to protect their resources (see below). Subjects that were used for the analysis were those birds that were visible all the time during the trials. Since this species defends territories aggressively and because territories are of small size (around 200 m^2), we decided to study a subject's behavior within a half-day of activity and only when a subject could be followed entirely through his feeding territory by an observer (González-Gómez and Vásquez 2006). Therefore, trials were run between 7:30 and 12:00 h. The aggressive display consists of chases around the feeder accompanied by production of a distinctive shrilling sound. Furthermore, on a given day, we selected territories that were at least 40 m apart from each other. If during a trial we lost track of a subject, we ended the trial and these data were not used in the analysis. Observations were carried out from hidden places (behind vegetation) at least 10 m from the feeder.

Initial training

The experiments began with a training period in which the subjects got used to the feeders and defended them actively as part of their territories. In each year, we placed training feeders that contained 100 ml of 20% (weight/weight) sucrose in 20 different trees (*Quillaja saponaria*, *Lithrea caustica*, *Eucalyptus globulus*) 5–15 m high located in distinct territories where we had previously observed feeding hummingbirds. Nectar feeders were hung 1.5 m above the ground from an opportunistically selected branch. Within 2 days of training, males defended feeders actively as part of their territories; Only one dominant male per feeder was observed. An artificial feeder consisted of a commercial 100-ml glass water dispenser for squirrels enveloped with red paper. Each feeder was filled twice a day in order to prevent resource depletion and the consequent eventual loss of territorial defense (González-Gómez and Vásquez 2006).

Experimental protocol

We selected 20 territories for our experiments in 2008. In July 2010, we randomly selected 12 territories for our observations. Different sucrose concentrations were used to vary diet energy and thus territory quality. We assigned sucrose concentrations (15% and 30%, *w*/*w*) to territories randomly. Therefore, half of the feeders contained 15% nectar (i.e., ten territories in July 2008 and six in July 2010) and half had 30% nectar (i.e., ten in July 2008 and six in July 2010). Every territory was observed for 1 h. Observations were performed from 8:00 am to 12:00 am. We randomized the hour of observation at each feeder and quality to avoid temporal associations of activity levels and control for diurnal variation in territorial defense behavior. We considered a site to be defended if a single hummingbird fed at the feeder, perched nearby, and chased other hummingbirds (intruders) which entered the area. In each territory, we recorded the defense behaviors displayed by the owner (i.e., chip calls, chasing, or attacking other hummingbirds).

Aggression index

To assess the intensity of territorial defense, we developed an aggression index, composed of the three different territorial behaviors that we observed in *S. sephaniodes*: (a) chip calls (vocalizations, *V*), (b) chases (*C*), and (c) contacts (aggression, *O*), and their combinations. We weighted the behaviors by the energy used in the aggressive action, according to the following information. In other bird species, average metabolic rate during singing at 15–20°C is ~2·BMR in the same temperature range (Ward et al. 2003). Thus, we assumed that $V = 2 \cdot \mathrm{BMR}$. On the other hand, hovering is one of the most energetically costly activities for hummingbirds, in the order of ~10·BMR (Suarez 1992).

The strongest aggressive behavior that we observed combined vocalizations, chases, and contacts (*VCO*). We assumed that the cost of this behavior is equivalent to the cost of hovering, i.e., $VCO = 10 \cdot \mathrm{BMR}$. Finally, it has been reported that moderate/high speed forward flight is 5-fold BMR (Schroeder et al. 2009); accordingly, we assumed that $C = 5 \cdot \mathrm{BMR}$. With the system of three equations expressed above, we obtained that *V*/*C*/*O* has the relations 2:3:5, and therefore, we constructed the following aggressive index (AI):

$$\mathrm{AI} = V \cdot 2 + C \cdot 5 + VC \cdot 7 + CO \cdot 8 + VCO \cdot 10$$

Results

Field experiments

All the territorial individuals were males, while non-territorial individuals (attackers) were males and females. The presence of a dominant individual was not significantly influenced by nectar concentration (generalized non-linear model with binomial distribution and logit link function $W_{1,51}$=0.00, p=0.99). When aggression was recorded (N=27), the intensity of aggression was not significantly different between territories with low (N=13; X±SD=3,314.40±721.11 aggression level/observation period) and high nectar quality (N=14, X±SD=3,174.95±276.82; Mann–Whitney test, U_{26}=101.0, p=0.63, Table 1). On the contrary, temperature played a role in the intensity of aggression (see below).

Table 1 Parameter estimates (Bayesian posterior modes) for the three models of aggression in hummingbirds

Parameter	Linear model 1	Linear model 2	Quadratic model
Intercept	637.984	634.161	−1,962.52
Nectar quality	−4.937		
Ambient temperature		−8.137	401.22
Ambient temperature[a]		−15.533	−15.23
BIC	472.8405	473.0408	466.69
AIC	468.4433	468.6436	460.83
BIC weight	0.10	0.10	0.80

In the linear model 1, we incorporated the nectar quality as independent variable. In the second model (linear model 2), we included ambient temperature as independent variable. In the third model (quadratic model), we considered two ambient temperature terms, representing the second order polynomial

[a] Quadratic temperature term

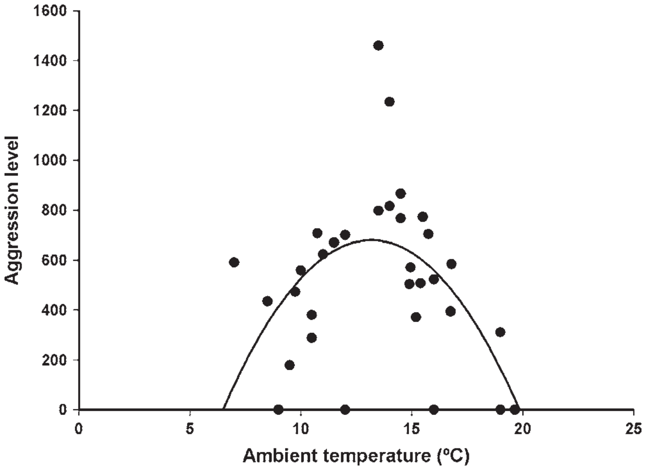

Fig. 1 Aggression levels displayed by males of *S. sephaniodes* at different ambient temperatures. The *line* represents the theoretical model while the *black dots* indicate field experimental data, represented by $y = -15.228x^2 + 401.224 \times -1,962.52$. The lower limit of thermoneutral zone for this species is 28°C

Fitting experimental data to the theoretical model

The Bayesian and maximum-likelihood estimation methods performed similarly (Table 1). Both the Bayesian approach

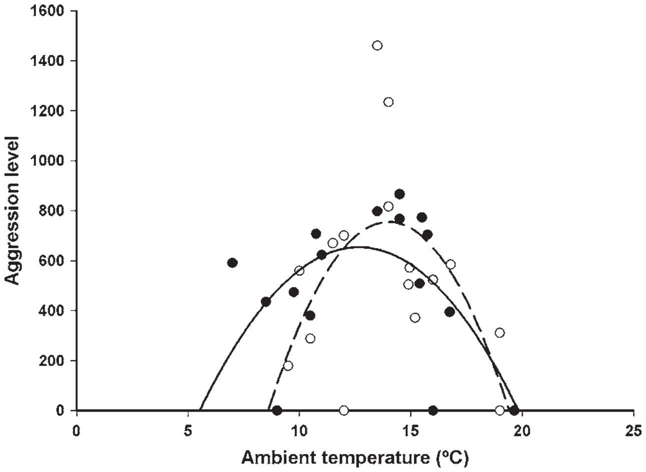

Fig. 2 Aggression levels of males of *S. sephaniodes* according to the resource quality at different ambient temperatures. The *solid line* and the *black dots* represent the high nectar quality territories (30%, w/w, $y = -11.594x^2 + 296.745 \times -1,252.74$), while the *dashed line* and *white dots* represent the low nectar quality territories (15%, w/w, $y = -30.288x^2 + 836.62 \times -5,009.2$)

and the maximum-likelihood favored the theoretical model that included the quadratic component of ambient temperature regarding the linear models including nectar quality and ambient temperature. Following the weighted BIC, the quadratic model has eight times higher probability to be the best model for the data in comparison with the linear models (Table 1; Fig. 1). A qualitative analysis of the incidence of nectar quality in the interplay between ambient temperature and aggression showed that the best nectar quality was defended in a wider range of temperature than the lower nectar quality (Fig. 2).

Model predictions

We inferred ecological parameters through the theoretical model. First we estimated the critical temperatures for the cessation of aggression by the extrapolation of the curve fit to field data. Taking the overall data, we obtained a lower temperature T_{min}=6.5°C and a higher temperature T_{max}=19.9°C. From Eq. 4 and assuming that $\mathrm{FMR_D}=\mathrm{FMR_{At}}$, we obtained $\mathrm{FMR}=C(T_{\mathrm{min}}+T_{\mathrm{b}})$; then using the values C=0.397 $\mathrm{mLO_2 g^{-1}\ h^{-1} {}^\circ C^{-1}}$ (López-Calleja and Bozinovic 1995) and T_{b}=41°C (Hainsworth and Wolf 1970; Wolf and Hainsworth 1972), we obtained FMR=18.70 $\mathrm{mLO_2 g^{-1}\ h^{-1}}$. Thus, the model predicts FMR as 5.9 times BMR (i.e., 3.17 $\mathrm{mLO_2 g^{-1}\ h^{-1}}$, López-Calleja and Bozinovic 1995). Using the high- and low-quality nectar data separately, we obtained T_{min}=5.3°C and T_{max}=20.3°C for rich territories and T_{min}=8.8°C and T_{max}=18.9°C for poorer territories. Thus, the range of temperatures for high-quality territory defense was 1.5 times greater than for low-quality territory defense.

Discussion

Classic frameworks dealing with behavioral and foraging ecology—including resource defense, use of patchy environments and handling time, among others—state that these behaviors depend mainly on the energy derived from the resource exploitation by itself (Charnov 1973; Krebs and Davies 1993). Nevertheless, the physiological condition of animals in combination with abiotic conditions can also have an important, albeit relatively unstudied effect on animal behavior.

We identified a novel strategy. We observed that the intensity of aggression was strongly related to ambient temperature, but not significantly with food quality, suggesting—against classical views—that an abiotic condition determining thermoregulatory costs may play a central role in territorial behavior among small-sized endotherms. Usually, it has been reported that territorial behavior increases with territory quality because high-quality sites yield a higher energetic return for the territory defender (Ewald and Carpenter 1978; Ewald and Bransfield 1987; Camfield 2006). A qualitative analysis of the tendency of the resource defense according to nectar quality suggests that richer territories are defended in a wider range of ambient temperatures which is expectable under a cost-benefit interpretation. In contrast, we did not observe significant differences in levels of aggression between high and low territory qualities. As a matter of fact, the maximum aggression level found for poorer territories was higher than in richer territories. A possible explanation for this behavior could be individual differences in the ability to secure and maintain high-quality feeding territories (Carpenter et al. 1993; Kasumovic et al. 2011). Individuals with greater ability to defend a territory have access to higher-quality territories and could display body signals (e.g., crown reflectance, body positions) that inhibit the attacker. As a result, individuals defending lower-quality territories may have to be more actively aggressive to hold the territory.

On the other hand, the individual appreciation of the resource value may change depending on the environmental abiotic conditions. Carpenter and MacMillen (1976) proposed the existence of lower and upper thresholds of food productivity for territorial behavior. In fact, they suggested that below a certain level of resources, there is an absence of territorial defense, since the benefit that results from territorial defense is insufficient to pay for the added cost of defense. In turn, in the “upper threshold,” the level of food productivity is so high that territoriality should disappear because food is not limiting and defense gains the animal nothing over non-territorial behavior. However, in nectar-feeding birds, cessation of defense on locally rich foraging areas occurred just when nectar was superabundant in the surrounding region relative to localized foraging areas (Carpenter 1987).

The existence of lower and upper thresholds of temperature determining the intensity of territorial defense could be explained with a similar cost-benefit approach. Ambient temperature plays an important physiological role in the costs of energy expended in thermoregulation, and therefore, it fixes the benefit level that should be produced by the territory to pay the costs of the defense, especially at the lower threshold. In fact, at 5°C, thermoregulatory cost for *S. sephaniodes* may be up to 4.87 times higher than basal costs (López-Calleja and Bozinovic 1995). Furthermore, the idea that food must be limiting to a population before feeding territoriality occurs (Carpenter 1987) may be understood as the energy available after to pay for the costs of thermoregulation determined by ambient temperature. This cost is related to territorial defense, both by the value of the defended resource to the territorial individual in an energetically limited environment and by the energy available for an intruder to attack a territory after paying the thermoregulatory cost (Carpenter and MacMillen 1976). A possible argument to explain our findings could be that under 5°C, hummingbirds are not active. Considering that the lower limit of the thermoneutral zone is 28°C, it could be argued that most of the birds were in torpor. Observations at individual feeders (10 min each, N=74, non-published data) performed between 0°C and 5°C showed an average of 6.3±0.83 non-territorial individuals (mean±SE, range of 0–41 birds) flying around one feeder. Just in four observations, none hummingbird was counted. These data support the ideas that bellow 5°C, hummingbirds are actively finding feeding sources but the cost of territorial defense is higher than the benefit.

The weakness of the linear fit of the data is consistent with the idea that below a certain temperature, the cost of the defense does not yield enough energy to maintain the behavior. Similarly, at the upper limit of temperature inferred (i.e., 22°C), the thermoregulatory cost is 1.36 times higher than BMR (López-Calleja and Bozinovic 1995), which is a negligible cost in comparison with the expenditure under cold conditions; the results strongly suggest that the benefit of the defense decreased until territorial behavior does not provide sufficient rewards to be energetically cost-effective.

As a subproduct of the theoretical model, we can predict that FMR in *S. sephaniodes* is 5.9 times higher than BMR. This prediction is very close to values already published for other hummingbird species, where the mean of FMR/BMR ratio is 5.92±0.79 (Weathers and Stiles 1989 and references within, Powers and Conley 1994). From the equation reported by López-Calleja and Bozinovic (1995), under cold conditions (i.e., 5°C), the thermoregulatory cost represents 0.65 times FMR; in contrast, at the upper limit of the territorial behavior (i.e., 21°C), this cost represents roughly 0.3 times FMR, which explains the relevance of ambient temperature in the value of resources. Our results strongly suggest that ambient temperature—though its effect on physiological cost—could play an equivalent role to the food productivity by itself as proposed by Carpenter and MacMillen (1976).

It is important to consider that our model makes some simplistic assumptions that could be relaxed. For example, we assumed that the probability of attack and defense are dependent on abiotic variables such as ambient temperature and organismal variables such as energy storage, but we assume that attack and defense probabilities are not interdependent. Nevertheless, it has been observed that a higher level of territorial display could increase intruder pressure and competition for a food source (Powers 1987; Marchesseault and Ewald 1991). Besides, to infer ecological parameters from the model predictions, we assumed that the FMR of territorial and non-territorial individuals is equal, but this assumption has not been tested. However, we opted for a perfectible but simplistic model, which does not exceed the complexity of natural phenomena in order to avoid overfitting as described by Ginzburg and Jensen (2004).

Our experiment was performed during the non-reproductive season where the aggressive behaviors displayed by territorial males are focused on males and females equally. Despite that possibly during the reproductive season it would be expectable a differential degree of aggression against males and females and consequently they should be modeled differently and the fact that hummingbirds are merely an ideal study system, the general message of this study holds. Mechanistic modeling of resource value and aggression costs using physiological principles give us better answers.

In summary, our model and our experimental results identified a novel behavioral and physiological strategy. Our results strongly suggest that subjects change the resource valuation depending on their energetic condition. Consequently, animals appear to shift their foraging strategy —including aggressive behavior—depending upon ambient temperature associated with thermoregulatory costs. All the above indicates that any particular behavior represents an integrated response to the biotic and abiotic environment and the physiological condition of the animal. The physiological constraints on the foraging ecology of animals—through changes in ambient temperature—are probably extremely important in determining when and how a food area should be used, defended, and a diet selected, which in addition to inter and intraspecific interactions would appear to be major components of the life history of endotherms.

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