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Thermoregulation in endothermic dung beetles (Coleoptera: Scarabaeidae): Effect of body size and ecophysiological constraints in flight

J.R. Verdú[a],*, L. Arellano[b], C. Numa[a]

[a]*Instituto de Biodiversidad CIBIO, Universidad de Alicante, 03080 Alicante, Spain*
[b]*A.C. Departamento de Biodiversidad y Ecología Animal, Instituto de Ecología, Apartado Postal 63, Xalapa 91000, Veracruz, Mexico*

Abstract

We explore the physiological constraints of body temperature as related to body mass and ambient temperature during flight in endothermic dung beetles showing a mass-related breakpoint where species show strong vs. weak endothermy. We found two different strategies in the dung beetles prior to flight; larger beetles (>1.9 g) elevate and maintain their body temperature (T_b) at levels well above ambient temperature (T_a) whereas smaller beetles' (<1.9 g) T_b tends to conform with T_a. Physiological constraints analysis revealed a constant maximum tolerated temperature (in flight) of 42 °C and a minimum temperature for flight of around 25 °C. These, with body mass, may play a role in thermal niche partitioning and geographical distribution patterns.
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1. Introduction

Animals are considered endothermic if they elevate their body temperature using internally generated heat (from flight muscles, for example). In endothermic insects preflight warm-up behaviour can be observed and is a modification of flight in which most of the thoracic muscles are activated by the central nervous system relatively synchronously rather than alternately (Kammer, 1968). From a metabolic point of view, flight is the most demanding activity known in insects. Insects generate a lot of heat when they fly and the heat produced is a function of body mass. In dung beetles, the true relationship between size and body temperature is not known. The only attempt to address the subject was made by Bartholomew and Heinrich (1978). They observed a positive relationship between metathoracic temperature and body mass up to about 2.5 g, and virtual independence

from body mass above 2.5 g. This apparent discontinuity in the relationship between the two variables was not fit to any model, though they did analyse the data below 2.5 g by means of a simple regression analysis (Bartholomew and Heinrich, 1978, Fig. 5, p. 71).

In order to regulate body temperature, insects don't just have to worry about increasing body temperature (T_b) but also must decrease it at times in order to stay within the limits of physiological activity. The temperature of heat shock is generally narrowly defined as 45–47 °C in flying insects (May, 1976, 1978; Heinrich, 1993; Chown and Nicholson, 2004), while the upper end of lethal temperature normally spans 50–53 °C (Christian and Morton, 1992; Wu et al., 2002). Many endothermic insects cannot fly if their thoracic temperature is below 25 or 30 °C and flight performance increases with T_b near 40 °C. Data on isolated muscles suggest that maximum performance might be limited by temperatures of 40 °C or more (Machin et al., 1962; Heinrich, 1979).

In dung beetles, several observations suggest that different thermoregulatory strategies are controlled by

*Corresponding author. Tel.: +34 965903400; fax: +34 965903815.
E-mail address: jr.verdu@ua.es (J.R. Verdú).

adjusting habitat selection and the timing of flight (Caveney et al., 1995; Verdú et al., 2004). These thermoregulation patterns together with thermal constraints may play a role in niche partitioning and geographical distribution patterns of insects (Blouin-Demers and Weatherhead, 2002; Chown et al., 2002; Chown and Nicolson, 2004).

The main objectives of this study are to explore (1) the relationship between body temperature and body mass of endothermic dung beetles, and (2) to obtain the physiological constraints of body temperature as related to ambient temperature during flight. Owing to phylogenetic proximity, we started with a broad-scale comparative analysis to explore the physiological constraints on endothermic dung beetles (see Chown, 2001). We evaluated whether the distribution of endothermy data is significantly restricted in relation to surrounding or environmental temperature using a null model analysis. We used temperature excess (T_{ex}), measured as the difference between thoracic temperature and ambient temperature, as the extent of endothermy.

2. Material and methods

2.1. Body temperature and body mass measurements

Body temperature was measured during flight and immediately after the landing with Ni–Cr($+$)/Ni–Al($-$) Type K thermocouples (Thermocoax^{TM}) threaded into hypodermic needles (0.25 mm in diameter). Intrinsic response time of thermocouples was 7 ms and mean sensitivity 41 μV/$^{\circ}$C. Temperatures were read using MMS3000-T4^{TM} Multi Measurement System^{TM} (COMMTEST INSTRUMENTS Ltd.), with an accuracy of 0.5 $^{\circ}$C. Body temperatures were measured as they arrived at fresh human, horse, sheep and cow dung (for coprophagous); and fish and chicken corpses (for necrophagous). To obtain thoracic temperature, the thermocouple was inserted into the centre of the metathorax. We arrived in the field at the study sites 2 h before the beetles became active and left 2 h after the last observation. Body temperatures and ambient temperature during flight (T_a), were recorded within 1–3 s of capture and double latex dissection gloves were used to protect the beetles from heat transfer. A total of 506 measurements of body temperature were obtained in the field. Of these data, 331 were recorded in the present study (a total of 13 species) and the rest of the data were obtained from the literature (a total of 11 species) (see Table 1). In addition, complementary measurements ($n = 97$) were recorded in climate chambers under laboratory conditions varying the environmental temperature from 15 and 40 $^{\circ}$C.

2.2. Body mass

After body temperature was measured each specimen was numbered and immediately frozen to $-20\,^{\circ}$C. Beetle mass (fresh weight) was measured with an AND$^{\circledR}$ HM-202 high-precision balance (accuracy of 0.1 mg).

2.3. Thermal constraints in endothermic dung beetles

A piecewise linear regression model was used to test the possible discontinuous relationship between body temperature (T_b) and body mass (W_T) for 591 individuals belonging to 24 species of dung beetles (see Table 1) from Mexico, Kenya (Bartholomew and Heinrich, 1978) and Spain (Mena, 1999; Verdú et al., 2004, unpublished data). This method allowed us to adjust the equation obtained to reflect a 'knot' (breakpoint) in the regression lines. A homogeneity of slopes (or parallelism) test by means of covariate interactions in a GLM analysis was used to test whether there was a statistically significant difference between the two slopes obtained.

A second piecewise linear regression model was used to test the relationship between body temperature (T_b) and body mass (W_T), eliminating the possible influence of ambient temperature (T_a) on T_b. For this, first a simple linear regression analysis was carried out for T_b and T_a. Next, the residuals obtained were analysed again with body mass using the same procedure. The resulting piecewise model represents the relationship between T_b and W_T, but without the entire effect of T_a. This produced a new breakpoint. Finally, a new homogeneity of slopes test was used to determine whether there was a statistically significant difference between the new slopes obtained with the model. The models were fit using a least-squares procedure and analyses were carried out using the Statistica software package (Statsoft Inc., 1997).

To test for the existence of body temperature constraints in endothermic dung beetles, three different analyses were carried out by plotting the distribution of body temperature excess data (T_{ex}), as an indicator for the extent of endothermy and ambient temperature during flight (T_a). A total of 603 individuals belonging to 24 species were used to construct the original matrix. First, the observed T_{ex} (in ordinates) and T_a (in abscises) data were submitted to the 'boundary test', using EcoSim 7.0. software (Gotelli and Entsminger, 2003). The objective of this test was to obtain an interval of body temperature data points on two-dimensional plots and to determine the upper and lower boundaries of the measurements. Two a priori hypotheses about boundaries were established according to the literature and our observations: (a) *For the upper boundary*: Dung beetles that show strong T_{ex} cannot fly when the surrounding temperature is elevated because they overheat. (b) *For the lower boundary*: Dung beetles that show weak T_{ex} cannot fly when ambient temperatures are very low. The null hypothesis was that heat generation in dung beetles is independent of ambient temperature.

The original matrix was randomized and a specified number of simulated matrices (1000 in this case) were created by the boundary test analyses of the thermal data. The observed and expected metric, the probability value and the histograms for the simulated data sets are shown

Table 1
The 24 species of dung beetle studied from Mexico, Kenya and Spain

Species	Weight (g)	Functional group	Habitat	Region	b	n
Scarabaeidae						
Bubas bubalus (Olivier)[a]	0.47 ± 0.17	T–C–N	Dehesa	Palaearctic	0.30	30
Canthon cyanellus Le Conte	0.06 ± 0.02	R–N–D	Rainforest	Neotropical	0.70	20
Canthon femoralis (Chevrolat)	0.03 ± 0.003	R–C–D	Rainforest	Neotropical	0.93	21
Canthon humectus (Say)	0.20 ± 0.06	R–C–D	Mountain grassland	Nearctic	0.45	22
Canthon indigaceus chevrolati Harold	0.06 ± 0.02	R–C–D	Coastal grassland	Neotropical	0.72	25
Coprophanaeus telamon Harold	1.19 ± 0.39	T–N–N	Rainforest	Neotropical	0.71	20
Deltochilum lobipes Bates	0.86 ± 0.29	R–N–N	Rainforest	Neotropical	0.49	34
Deltochilum mexicanum Burmeister	0.54 ± 011	R–N–N	Pine/Oak Forest	Neotropical	0.96	31
Deltochilum pseudoparile Paulian	0.10 ± 0.02	R–C–D/N	Rainforest	Neotropical	0.67	21
Deltochilum scabriusculum Bates	0.84 ± 0.17	R–C–N	Rainforest	Neotropical	0.65	12
Dichotomius amplicollis (Harold)	0.47 ± 0.08	T–C–N	Rainforest	Neotropical	0.59	14
Gymnopleurus flagellatus (F.)	0.17 ± 0.04	R–C–D	Dehesa	Palaearctic	0.64	106
Heliocopris dilloni Harold[b]	9.37 ± 3.17	T–C–N	Savannah	Afrotropical		29
Kheper aegyptiorum (Latreille)[b]	2.23 ± 0.79	R–C–D	Savannah	Afrotropical		58
Kheper platynotus (Bates)[b]	3.72 ± 0.83	R–C–D	Savannah	Afrotropical		83
Onitis belial F.[a]	1.10 ± 0.40	T–C–D	Dehesa	Palaearctic	0.33	7
Phanaeus amethystinus Harold	0.70 ± 0.23	T–C–D	Cloud forest	Neotropical	0.23	76
Scarabaeus catenatus Gerstaecker[b]	1.63 ± 0.50	R–C–D	Savannah	Afrotropical		129
Scarabaeus cicatricosus (Lucas)[c]	1.14 ± 0.25	R–C–D	Coastal shrubland	Palaearctic	0.20	47
Scarabaeus laevistriatus (Fairmaire)[b]	3.30 ± 0.72	R–C–N	Savannah	Afrotropical		137
Scarabaeus laticollis L.	0.67 ± 0.14	R–C–D	Dehesa	Palaearctic	0.43	20
Scarabaeus sacer L.[c]	2.57 ± 0.54	R–C–N	Coastal shrubland	Palaearctic	0.15	47
Geotrupidae						
Geotrupes ibericus Baraud[a]	0.68 ± 0.23	T–C–N	Dehesa	Palaearctic	0.39	21
Geotrupes mutator Marsham[a]	0.70 ± 0.27	T–C–N	Dehesa	Palaearctic	0.51	18

Abbreviations: R = roller; T = tunneller; C = coprophagous; N = necrophagous; D = diurnal; N = nocturnal; b = slope from simple linear regression between T_b and T_a; n = number of individuals studied.
[a]Mena (1999).
[b]Bartholomew and Heinrich (1978).
[c]Verdú et al. (2004).

for each boundary tested. The 'data-defined' constraint option was selected following the recommendations of Gotelli and Entsminger (2003).

Second, a least-squares regression technique was used to estimate the slopes of the upper and lower boundaries (Blackburn et al., 1992; Scharf et al., 1998). Data were divided into size classes representing equal increments (or ranges) of T_a (independent variable). Since a rectangular distribution of the data is assumed, functions were estimated by pairing the maximum and minimum T_{ex} values (dependent variable) with each of the values corresponding to T_a for each size class (the range of the latter is practically identical to that of the dependent variable). We defined these linear regressions as 'R' models in the results section.

Third, based on the same regression technique, two functions were estimated by pairing the maximum or minimum values considering all the ranks of T_a. The values were selected according to the maximum and minimum body temperatures (T_b) suggested in the literature (May, 1976, 1978; Heinrich, 1993) and our observations. For the upper boundary, values over 42 °C were selected (near heat shock) and for the lower boundary values below 27 °C were selected (near the minimum temperature required for

takeoff). We defined these linear regressions as "M" models in the results section.

Finally, measurements of T_b in the field are often necessary to give an accurate pattern of the thermoregulation mechanism. Thus the relation of body temperatures to ambient temperature for each species is summarized by a linear regression that indicates the level at which body temperature is regulated, the degree of independence between body temperature and ambient temperature (a slope of 1 suggests no thermoregulation, a slope of zero perfect thermoregulation) and the degree to which factors other than ambient temperature may influence body temperature (May, 1985).

3. Results

3.1. The relationship between flight body temperature and body mass

Body temperature (T_b) was highly correlated with body mass (W_T) ($R^2 \times 100 = 92.09\%$, breakpoint = 1.98) (Fig. 1a):

Weight below or equal to 1.98 g : $T_b = 29.55 + 2.82 W_T$,

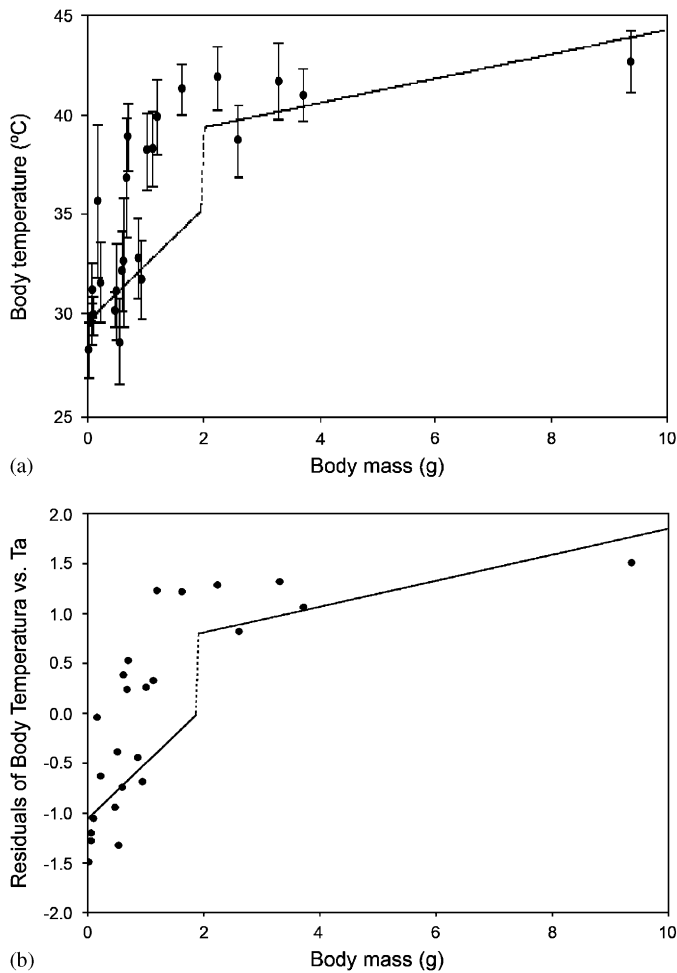Weight above 1.98 g : $T_b = 38.10 + 0.61 W_T$.

Fig. 1. The relationship between body temperature and body mass for 24 species of dung beetles (a) with the influence of ambient temperature where a significant breakpoint occurs at 1.98 g (the bars show the standard errors of T_b along T_a range) and (b) excluding the effect of ambient temperature where a significant breakpoint occurs at 1.90 g.

The homogeneity of slopes model showed significant differences between both slopes obtained in the piecewise model (effect of slope × W_T: $P < 0.001$). So, it is necessary to fit the separate-slopes model (piecewise linear model in this case) to explain the relationship between T_b and W_T.

Without the effect of T_a, T_b was also highly correlated with W_T ($R^2 \times 100 = 85.00\%$, breakpoint = 1.90) (Fig. 1b):

Weight below or equal to 1.90 g : $T_b = -1.06 + 0.56 W_T$,

Weight above 1.90 g : $T_b = 0.55 + 0.13 W_T$.

The homogeneity of slopes model showed significant differences between both slopes obtained by the piecewise model (effect of slope × W_T: $P < 0.001$).

As seen in Fig. 1, a similar pattern was obtained using both piecewise models. Also, the relationship between both breakpoints is very close, which demonstrates the existence of two different physiological patterns in the endothermic dung beetles that we studied.

In both piecewise models (Fig. 1), body temperature increased markedly from the species with the lowest body mass (0.03 g) to a significant breakpoint at 1.98 g (with influence of T_a) or at 1.90 g (without control of T_a). In both cases our breakpoints were near the intuitive point of 2.5 g suggested by Bartholomew and Heinrich (1978). Above 1.98 g or 1.90 g, body temperature increased slightly with a slight slope that indicated a second pattern of endothermy and this is corroborated by the existence of significant differences between the slopes.

3.2. Physiological constraints on flight

Fig. 2 shows a well-defined bivariate pattern between the lower and upper physiological boundaries. The boundary test confirmed the existence of this pattern in the general distribution of the data. Both the upper and the lower boundaries were corroborated by the 'boundary test' ($P < 0.0001$, in both cases). The results of the least-squares regression were highly significant in both cases (Fig. 2). First, the equal range technique (R_1 and R_2 models) produced a significant estimate of both upper (range = 7 °C; $R^2 = 0.92$; $F = 36.93$; df = 1.3; $P = 0.008$) and lower boundaries (range = 15 °C; $R^2 = 0.94$; $F = 32.24$; df = 1.2; $P = 0.03$). In addition, estimates of the boundaries by means of maximum and minimum T_b selection (M_1 and M_2) showed a significant result at both the upper ($R^2 = 0.99$; $F = 2593.15$; df = 1.11; $P < 0.001$) and lower boundaries ($R^2 = 0.96$; $F = 267.48$; df = 1.11; $P < 0.001$). The first model (R_1) indicates a slight increase in the maximum ambient temperature tolerated during flight. In contrast, there was a slight reduction in the minimum body temperature to flight with respect to the ambient temperature in the R_2 model. The M_1 model revealed a constant maximum tolerated temperature of 42 °C. The M_2 model showed a minimum temperature to flight of around 25 °C.
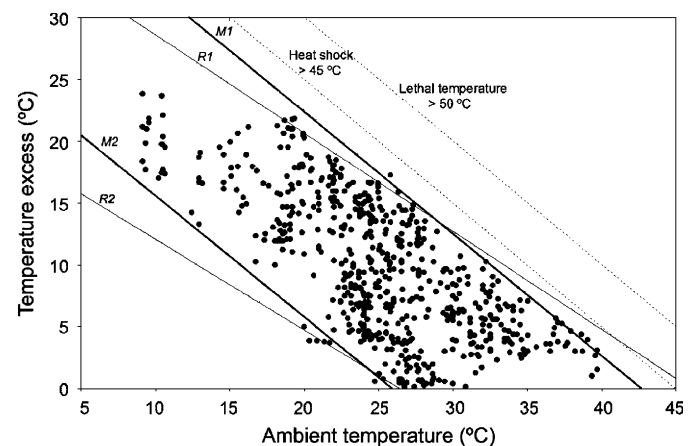

Fig. 2. The relationship between environmental temperature and temperature excess. The upper and lower boundaries from the R_1 and R_2 models are shown. Also given are the estimates of the maximum and minimum T_b (M_1 and M_2).

4. Discussion

4.1. Body mass and body temperature

Bartholomew and Heinrich (1978) suggested that only insects weighing more than 2.5 g are able to thermoregulate with precision over a wide range of ambient temperatures. These authors observed that there was a truncated distribution of the body mass and endothermic capacity data. After analysing this relationship, a breakpoint near the value proposed by those authors was obtained. There is highly significant statistical support for this value, both 'with the ambient temperature effect' (breakpoint = 1.98 g), and 'without the ambient temperature effect' (breakpoint = 1.90 g). These breakpoints indicate the existence of two different strategies in endothermic dung beetles. According to Heinrich's (1993) observations and our data, species that weigh more than 1.98 g must all be great endotherms (with body temperatures constantly higher than that of their surroundings) and thermoregulators with respect to their range of flight temperatures (see slopes near to zero obtained from T_b vs. T_a relation; in Table 1), and could be homeothermic in some cases (Morgan and Bartholomew, 1982). The ability to regulate and maintain a body temperature independent of ambient temperature during flight may provide competitive benefits. Nevertheless, species with smaller body sizes (below ~2 g), are different with respect to the variation in body temperature relative to environmental temperature. According to our observations, dung beetles weighing less than ~2 g are not able to maintain a high body temperature relative to environmental temperature, and 'small endothermic' dung beetles exhibit a variation in body temperature that depends on the ambient temperature (see slopes near to 1 obtained from T_b vs. T_a relation; in Table 1). In these cases, the linear functions of thoracic temperature are practically parallel to the straight line of theoretical poikilothermy ($T_b = T_a$), showing slopes near to 1. This tendency is related on the gradual decrease in weight (see Fig. 3 and Table 1). In the most extreme cases, we have recorded species that come near to theoretical poikilothermy, such as *Canthon femoralis* (0.025 g and 0.93 of slope; Table 1). Thus, beetles less than ~2 g clearly tend towards being thermoconformers (poikilotherms) and this tendency gets stronger for the smaller beetles. This pattern forces these species to fly during 'benign' periods of the day, with relative high temperatures and mainly during the midday. Therefore, even though these species show the typical dung beetle endothermic behaviour patterns— shivering of flight muscles prior to flight—they can actually not be considered as functional endotherms.

What are the implications of these different patterns for the ecology of this group of animals? Temperature and body size are primary determinants of biological rhythms and ecological roles. Metabolic rates depend primarily on body size and temperature (Gillooly et al., 2001). In dung beetles, heat gain is chiefly a result of metabolism,
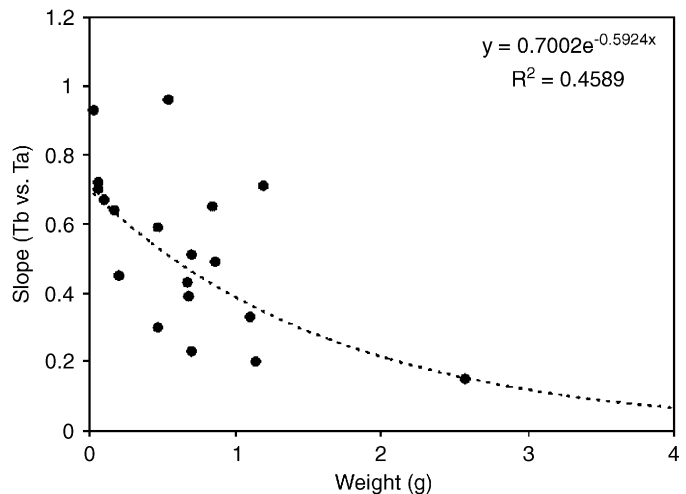

Fig. 3. The relationship between slope (T_b vs. T_a) and weight (g).

particularly the contraction of flight muscles. Radiant loss of body heat during cool nights and at dawn may explain why smaller species (< 0.4 g) fly only during the day or early dusk. Many of the larger insects would remain grounded if they did not actively increase the temperature of their flight muscles prior to flight (Heinrich, 1974). Nocturnal species are clearly endothermic immediately before and during flight, but not when walking; and they reach thoracic temperatures 15 °C higher than ambient temperature (Bartholomew and Heinrich, 1978), which presumably extends the daily temperature range over which they are able to forage. By foraging on the wing in the dark, many dung beetles are able to exploit herbivore dung voided at night before it is encountered by the species that fly at dawn and during the day. Yet nocturnal scarabs must be able to see well enough to avoid obstacles while flying rapidly over long distances in near-pitch darkness. Small body size may restrict long-range flight in a crepuscular-nocturnal beetle in at least two ways: by limiting the beetle's ability to sustain a high thoracic temperature during cool nights and at dawn, and by limiting the beetle's ability see well enough to navigate while flying at night (Caveney et al., 1995). The importance of T_b on the spatial and temporal segregation of sympatric groups of species has been documented for diverse organisms. For example, in *Micrathyria* dragonflies, larger species can shift their major activity peaks to early or late in the day, reducing competitive interactions with smaller species that are restricted to midday (May, 1985). In the *Scarabaeus* genus (*S. sacer* and *S. cicatricosus*, concretely), some mechanisms for thermoregulation may explain how closely related sympatric species respond to environmental temperature, and how this favours their coexistence (Verdú et al., 2004). This same pattern was observed between *Scarabaeus sacer* and *Scarabaeus laticollis* in Central Spain (JRV unpublished data).

Thermoregulation is likely to be one of the determining factors in habitat selection. However, it is not known how species use their thermoregulatory capacity or how species

behave according to the thermal quality of the habitat, particularly in the case of the endothermic insects. In burying beetles, body size and some morphological features (such as wing loading and insulation) affect their thermoregulation pattern and activity times (Merrick and Smith, 2004). In Canthonina assemblages (including *Canthon* and *Deltochilum* species from Table 1), a made study along an altitudinal gradient showed a guild structure based on diverse thermal niches that it diminished activity time overlap and competition, subsequently (Verdú et al., in preparation).

Thus, the relationship between body size and ambient temperature is important for determining the characteristics of the thermal niches of species, though it is necessary to learn more about the reaction of these species to thermal variations in microhabitats as well as their responses to these changes. However, in order to address this in greater detail, we must first determine the physiological boundaries of the thermal niches for endothermic dung beetles.

4.2. Ecophysiological constraints

There are doubts about the validity of temperature measurements obtained under laboratory conditions instead of directly in the field (Heinrich, 1993). In this study, practically all the measurements of body temperature were made in the field and this allowed us to determine that the maximum thoracic temperature of endothermic dung beetles during flight was approximately $42\,°C$ (Fig. 2). Our results seem to indicate that such maxim temperature is approaching heat shock and triggers a behavioural response in the insect to actively maintain T_b below this limit for as long as possible.

With respect to the lower limit of temperature, our results show that endothermic dung beetles need to warm their flight muscles up to at least $25\,°C$ for successful takeoff. This coincides with the $25–30\,°C$ range observed by other authors for other groups of insects (May, 1976, 1985; Heinrich, 1993; Chown and Nicholson, 2004). From a physiological point of view, we know that the neuromuscular system of the wings requires a minimum temperature to work properly. However, the existence of a minimum temperature for neuromuscular operation around $25\,°C$ does not imply that all endothermic dung beetles have this same temperature requirement for takeoff. Like dragonflies (May, 1976), in dung beetles there is a positive relationship between takeoff temperature and body mass (Bartholomew and Heinrich, 1978; unpublished data). In tropical beetles, oxygen consumption increases with body mass (Bartholomew and Casey, 1977). Additionally, there is a positive relationship between metabolic rate and altitude (related to the mean maximum temperature of the environment) (Davis et al., 2000), which explains why many medium-sized and large dung beetles require body temperatures at takeoff that are much higher than $25\,°C$. This allows them to both takeoff successfully and fly continuously and effectively. In most taxa, body size increases with altitude,

suggesting that factors acting to constrain body size might be weaker at high elevations (Brehm and Fiedler, 2004).

The available data on the relationship between body mass and body temperature indicates that there are two groups of endothermic dung beetles. The distribution of the T_{ex} data defines two physiological boundaries. In this study endogenous heat production in dung beetles ranged between 25 and $42\,°C$. Future research should be directed towards the search of new relationships between body size, endothermy vs. wing-loading, diel activity and geographical distribution, and also the verification of the variables related to flight (minimum takeoff temperature, thermal niche, *maximum voluntary tolerated* temperature, etc.) that could be influencing the interspecific interactions and the spatial distribution of species.

Acknowledgements

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