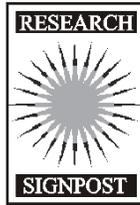


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# Ecophysiology of thermoregulation in endothermic dung beetles: Ecological and geographical implications

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## Abstract

*We examine the available information on thermoregulation in dung beetles also providing some new data to explore the relevance of heat production and dissipation temperature control mechanisms on the ecology and biogeography of these insects. We firstly examine the relationship between flight and thermoregulation to subsequently give some data on*

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*the variation in thermoregulation among species, populations and individuals. Lastly, we discuss the possible relevance of thermoregulation processes in explaining the geographical distribution of species, also providing some preliminary analysis. We show that both heat production and heat dissipation could be the consequence of evolutionary contingent adaptations related to the environmental conditions of the regions where the different lineages have evolved.*

## Introduction

Biodiversity consists of the variety of morphology, behaviour, physiology, and biochemistry in living things [1]. Physiological diversity is a complex component that should be applied from individuals to assemblages of species. This variability is found in numerous aspects such as regulation, maintenance and tolerance of certain physiological levels that are acceptable for the development and activity of a species [2]. Amongst these aspects, thermoregulation is one of the physiological mechanisms that have been studied most in insects. Studying thermoregulation patterns may help us to answer some questions about the ecology and biogeography of a species and, thus, about the basic requirements for the establishing of its populations and their conservation. Currently, the understanding of thermoregulation patterns can be a valuable tool to predict movements in the distribution of species that may be caused by climate change at different scales.

Thermoregulation is the ~~maintenance, using behavioural patterns or physiological responses of an organism~~ of its body temperature ( $T_b$ ) relatively independent from ambient temperature ( $T_a$ ), at least during part of its daily activity [3]. Although thermoregulation is not a continuous process, especially during flight, some large-sized Scarabaeidae, such as *Megasoma elephas* (Felder, 1775) have developed the ability to maintain certain homeothermy, although not related with flight, locomotion nor any other activity in this case, but with an oscillatory increase in the rate of oxygen consumption [4].

Some species have the ability to produce endogenous heat by using their wing muscles prior to take-off and during flight (endothermy). There have been many works describing different processes that regulate endogenous heat over a range of ambient temperatures since 1941, when endothermy in *Geotrupes stercorarius* (Linnaeus, 1758) was first registered [5]. These processes have been described according to the flight behaviour, size or morphology of each species [6].

Endothermy is of great importance in different aspects of the life of Scarabaeidae, as - apart from the ~~compulsory~~ relation that exists between this physiological process and flight - it has been shown that maintaining a high  $T_b$  during their other activities is an advantage in the presence of different behaviours that may create competition for a resource and even for establishing

reproductive pairs. In this sense, in ball-rolling Scarabaeidae, specifically in *Scarabaeus laevistriatus* Fairmaire 1893, it has been observed that the speed at which the ball of dung can be transported is proportional to the increase in  $T_b$  [7]; even in the same species, in cases where a fight develops over ownership of the ball of food, maintenance of this high  $T_b$  increases the probability of victory [8] and therefore a greater probability of finding a mate, as a ball of dung represents the nuptial gift for many species [9].

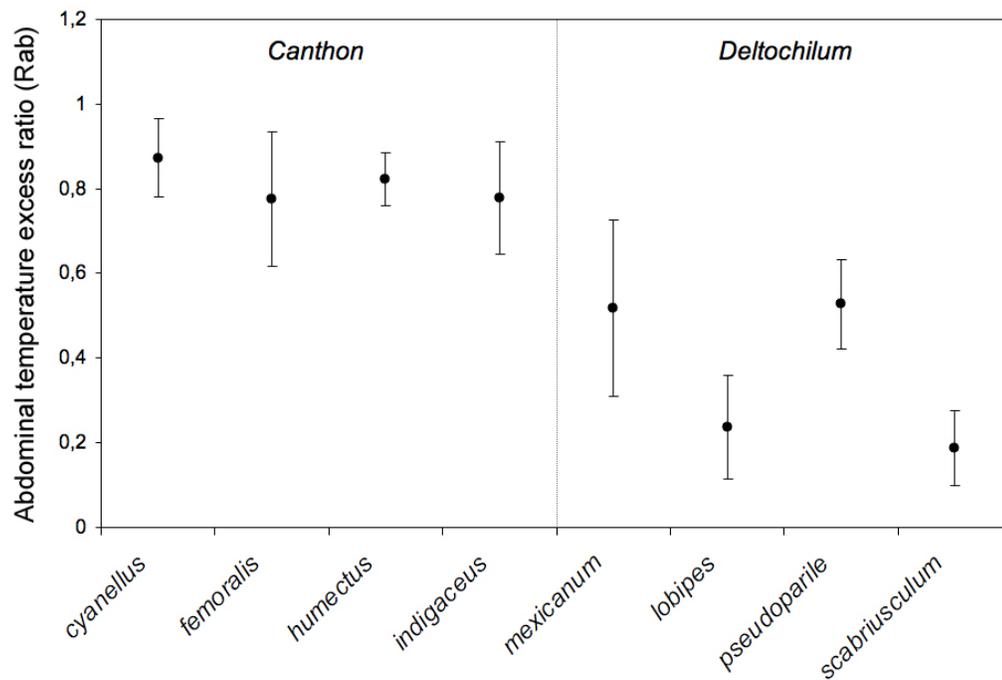
From the endothermic point of view, the fact that the ranges of  $T_a$  where a species can carry out its activities (especially flight) are relatively precise explains that groups of species of sympatric dung beetles present temporal segregation patterns, both daily and annual, which minimises the probability of encounters between individuals of different species that are potential competitors [10]. This phenomenon implies the existence of physiological limits (related to  $T_b$ ), amongst which each species finds its optimum, defining what we may call its thermal niche [11, 12]. Endothermic capacity of a species has implications for its temporal and spatial distribution. The difference between  $T_b$  and  $T_a$  (defined as temperature excess or endothermy) is a measurement that can explain the capacity of a species to be less dependent on ambient temperature for their flight or terrestrial activities also allowing the regulation of nest temperature in social insects [6]. On local scale, endothermic capacity and its regulation may define the thermal niche of a species and therefore the ambient range in which the species can be active during the day, during the seasons or the selection of different habitats. On a regional or geographical scale endothermy can also help to establish biogeographical and evolutionary patterns which are able to explain the current distribution of species from a point of view of their physiological limitations.

In this chapter we shall explore a series of points that will take us closer to an understanding of how thermoregulation, particularly in flight, plays a determining role in the ecology and spatial distribution of dung beetles, ~~whether on a local or geographical scale~~. Firstly all, we examine the diversity of types of flight and their implications in behaviour and thermoregulation. Subsequently, we revise the mechanism of heat production and dissipation among dung beetles to later describe the variation in these features among species, populations and individuals. Moreover, we will try to discuss the possible relevance of thermoregulation processes in explaining the geographical distribution of species, also providing some preliminary analysis. Finally, we assess whether the two main mechanisms related to body temperature control (heat production and heat dissipation) could be the consequence of evolutionary contingent adaptations related to the environmental conditions of the regions where the different lineages have evolved.

## Flight, behaviour and thermoregulation

The flight of a dung beetle determines the speed and efficiency with which it finds its food resources. Greater speed and skill during flight over the obstacles that may be found in its habitat can favour one species over another that does not have these qualities, mainly because dung beetles exploit ephemeral resources that will dehydrate or decompose quickly. In the Scarabaeidae species that are capable of endothermy, heat generated by the wing muscles passes by diffusion to the abdomen and excess heat is eliminated by the inner tegument or through the respiratory spiracles. This process can be regulated, depending on the degree of opening of the elytra during flight. In Canthonini, for example, we find a species that flies with its elytra closed (e.g. *Canthon*), regulating heat excess according to the degree of separation between these and the abdomen, whereas in other species (e.g. *Deltochilum*), the elytra remain completely open during flight, which enables diffusion of the excess heat generated. Obviously, the type of flight requires special morphological adaptations. For example, in the Canthonini species that flies with its elytra closed individuals can fly in or out of forests with great skill. Heliophylic species require great speed in flight adopting a shape that is much more aerodynamic and therefore achieving a greater flight speed. Personal unpublished observations allowed us to state that *Canthon humectus* Say, 1832 speeds over 30 km/h having a type of flight that is very regular and ~~on occasion~~ acrobatic, which permits easy avoidance of obstacles. Forest *Canthon* species as *C. cyanellus* LeConte, 1859 fly slowly adopting a zig-zag pattern which reflects a flight searching for forage that may lie hidden under fallen leaves, avoiding a great number of ~~obstacles~~. By contrast, those species that fly with their elytra open, such as the case of the genus *Deltochilum*, have a type of flight characterised by being extremely slow (unpublished data). All these flight types are reflected by thermoregulation patterns, since, as has already been mentioned, the shape adopted during flight may explain the degree of heat diffusion to the exterior through the abdomen. This rate of heat transfer from the thorax to the abdomen ( $R_{ab}$ ) is inferred by the quotient of the heat excess temperatures of the thorax ( $T_{th}$ ) and abdomen ( $T_{ab}$ ) regarding to ambient temperature ( $T_a$ ) [13-16]:  $R_{ab} = (T_{ab} - T_a) / (T_{th} - T_a)$ .

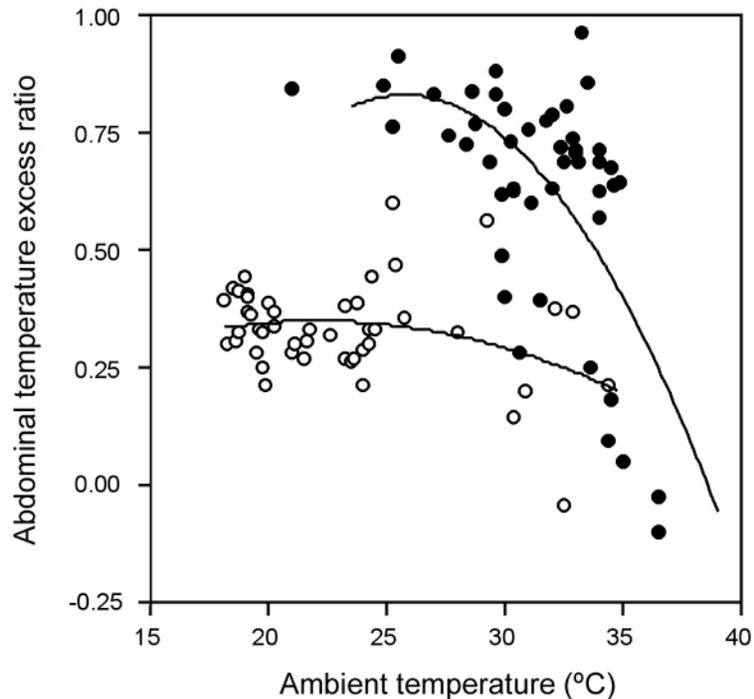
We have measured the body temperature of the species of two different Canthonini genera (*Canthon* and *Deltochilum*) along an altitudinal gradient in Veracruz (Mexico). According to the obtained results we could clearly distinguish two different patterns of heat excess loss that are related to flight habits of the two genera. The *Canthon* diurnal species present  $R_{ab}$  rates that are higher than the *Deltochilum* species that fly during the night or twilight (Fig. 1, unpublished data). In this case the capacity to fly with open elytra is not directly related to greater heat dissipation.



**Figure 1.** Abdominal temperature excess ratio ( $R_{ab}$ ) obtained in *Canthon* and *Deltochilum* genera across an altitudinal gradient from Veracruz (Mexico). We use Ni-Cr (+) / Ni-Al (-) Type K thermocouples (Thermocoax™, Suresnes, France) threaded into hypodermic needles (0.25 mm in diameter). Temperatures were read using MMS3000-T4™ Multi Measurement System™ (Commtest Instruments Ltd, Knoxville, TN, USA), with an accuracy of 0.5 °C. To obtain body temperature, the thermocouple was inserted into the metathorax to contact with the flight muscles and the abdomen. All temperatures ( $T_{th}$ ,  $T_{ab}$  and  $T_a$ ) were recorded within 1 to 3 seconds of capture and latex dissection gloves were used to protect the beetles from heat transfer.

If we study  $R_{ab}$  behaviour along the  $T_a$  range in which species can fly, we can define different thermoregulation patterns from a point of view of heat elimination mechanisms. An example can be found in Doñana National Park (Southern Spain) where two large-sized roller species coexist, *Scarabaeus sacer* Linnaeus, 1758 and *S. cicatricosus* Lucas, 1849. Both species compete for resources during a short period of the day but due to their different heat elimination patterns they have the possibility of segregating and flying preferably in periods that minimise this temporal overlap [10]. In this case, *S. sacer* is not capable of efficiently eliminating excess heat generated by the thorax during flight, which encourages this species to fly during the cooler hours of the day; this translates into independence between  $R_{ab}$  and  $T_a$ . On the contrary, *S. cicatricosus* can fly during the hotter hours of the day thanks to a high  $R_{ab}$  that decreases significantly as  $T_a$  increases, which explains the existence of a heat elimination mechanism that is more efficient than in the

case of *S. sacer* (Fig. 2). In this case, the thermoregulation strategy of *S. sacer* affords it a great capacity for thermoregulation of the thorax but it lacks a mechanism ~~that is~~ able to eliminate ~~excess heat~~ in an active way through the abdomen, which acts as a passive thermal window.

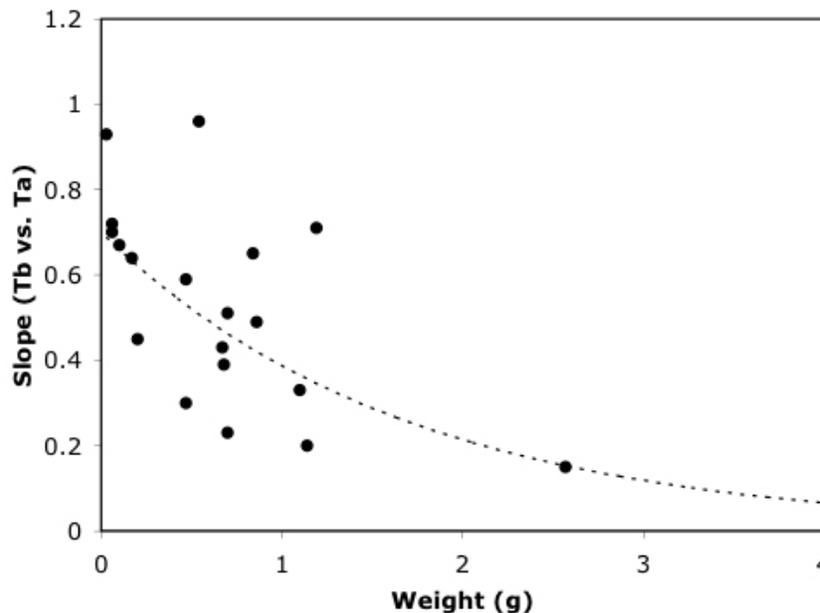


**Figure 2.** Abdominal temperature excess ratio ( $R_{ab}$ ) as a function of ambient temperature in *Scarabaeus sacer* (open circles) and *Scarabaeus cicatricosus* (filled circles) in the Doñana National Park (Southern Spain). Source: Reprinted with permission from Verdú et al., 2004. *Physiological Entomology* 29, 32-38. © 2004 with permission from Blackwell Publishing.

The existence of heat retention in the thorax has been observed in many insects typical of cold environments; in beetles, in particular it has been described in species of *Pleocomma* (Scarabaeoidea Pleocomidae). These ~~rain~~ beetles show impressive endothermy [17]. In the case of *S. sacer*, no thoracic ‘fur’ exists, but heat retention in the thorax is evident. In the case of *S. cicatricosus*, however this enables it to eliminate heat excess more actively, which may be related to an increase in turbulence due to the extended posterior legs during flight [10]. This mechanism of thermoregulation of the abdomen has been observed in other groups of insects typical of extremely hot environments, such as the case of the cicada *Diceroprocta apache* (Davis, 1921) (Homoptera: Tibicinidae), which eliminates excess heat through specialised pores [18].

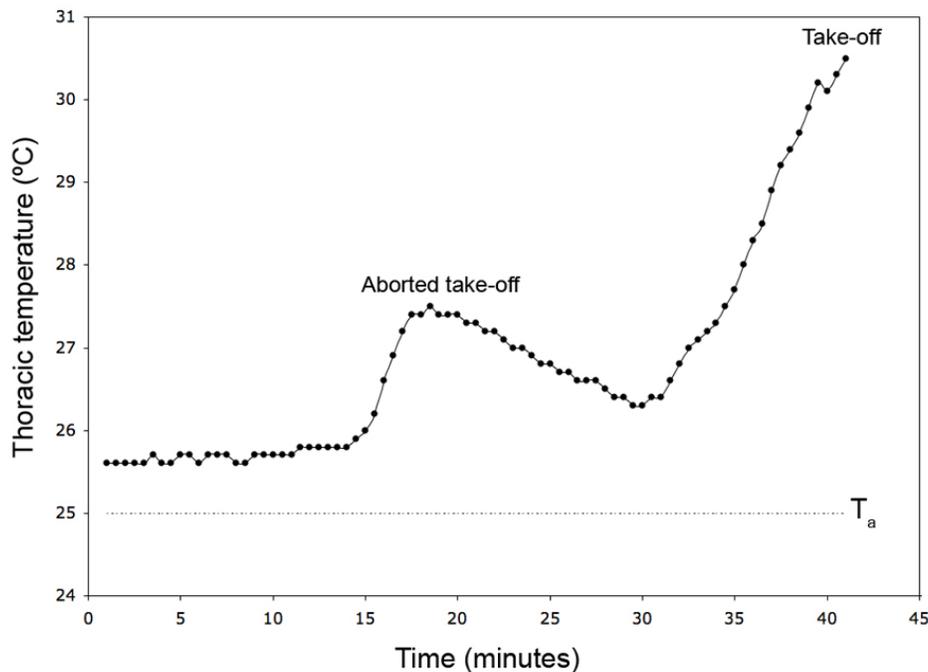
## Heat production and heat dissipation

As we have already seen, endothermy gives some species the capacity to carry out its flight activity at  $T_a$  that are relatively low. Whether it be on a daily or seasonal (annual) scale, this mechanism implies an evolutionary advantage which facilitates space-temporal segregation of potentially competitive species or, as we shall see further on, a probably greater capacity for geographical dispersion due to an increase in the range of thermal niche. Nevertheless, the acquisition of endothermy in itself requires pre-flight mechanisms that on occasion may put the individual's survival at risk. Before taking-off, an endotherm has to reach a minimum temperature that is independent of  $T_a$  [19]. During this warm-up process, the individual may be at risk from predators. Moreover, this warm-up has a high energy cost as the increase in the thoracic temperature is linearly related to metabolic rate [19]. This implies that body size is a determining factor in the thermoregulation patterns of organisms. There are two main patterns that separate dung beetle species whose weight is under 2 g, which present relative dependence on ambient temperature during flight, whereas species whose weight is over 2 g are capable of thermoregulation throughout the  $T_a$  flight range [7, 20]. This phenomenon is reflected by the existence of a negative relation between body weight and the slope of the  $T_b$  vs.  $T_a$  relationship, which will be lower in those species with a higher thermoregulation capacity (Fig. 3).



**Figure 3.** Relationship between slope of  $T_b$  vs.  $T_a$  and weight (g) obtained in *Canthonini* species across an altitudinal gradient from Veracruz (Mexico). Source: Reprinted with permission from Verdú et al., 2006. *Journal of Insect Physiology* 52, 854-860. © 2006 with permission from Elsevier.

Some species make their wing muscles vibrate (wing-shivering) in order to reach this minimum temperature. Dung beetles, in particular, also carry out muscle flexing exercises with their forelegs, by moving their head and ~~on occasion~~ ~~accompanied~~ by abdominal pumping movements which, as occurs in other insects (e.g. moths), ventilates the wing muscles and supplies them with the oxygen they require [21]. This sometimes implies failed attempts at take-off, when the temperature reached is not sufficient to ensure the maintenance of continuous flight (see the example of *Scarabaeus sacer* in Figure 4; *Geotrupes stercorarius* (Linnaeus, 1758) in Krogh and Zeuthen [5]).

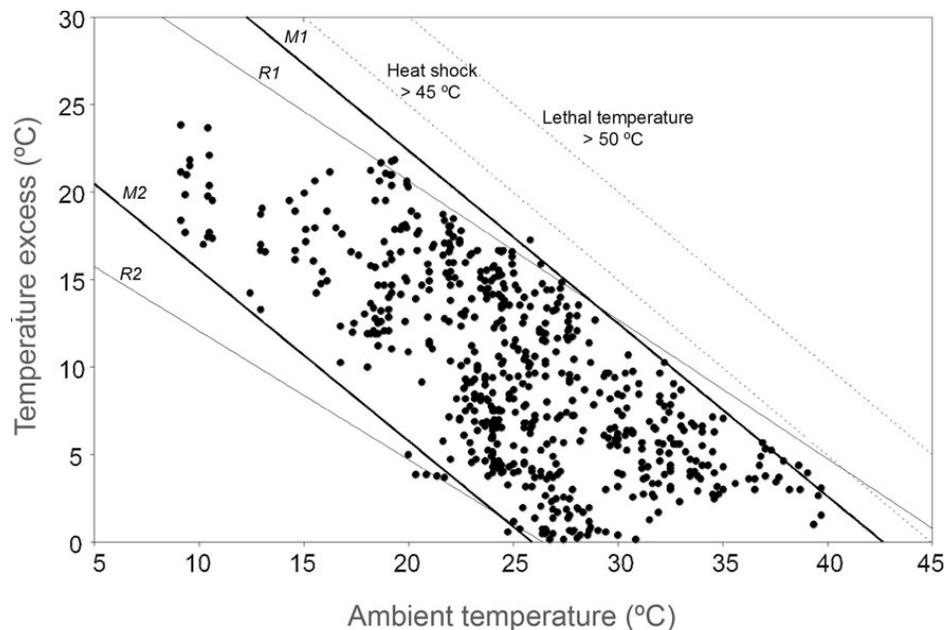


**Figure 4.** Thoracic temperature during pre-flight warm-up in *Scarabaeus sacer*. Note the time that this dung beetle needs to reach the minimum temperature of flight.  $T_a$  is the environmental temperature. Temperature recording was made using a Ni-Cr (+) / Ni-Al (-) Type K thermocouple (Thermocoax™, Suresnes, France) 0.25 mm in diameter. Temperatures were read using a data logger MMS3000-T4™ Multi Measurement System™ (Commtest Instruments Ltd, Knoxville, TN, USA), with an accuracy of 0.5 °C. To record body temperature, the thermocouple was inserted into the pronotum.

The majority of insects cannot take off if their thoracic temperature is below 25 or 30 °C and maintenance of flight requires temperatures of around 40 °C [22, 23]. Endothermic dung beetles need a  $T_{th}$  of at least 25 °C for successful take-off [20]. This temperature coincides with the 25-30 °C range observed for other groups of insects [6, 11, 19, 24]. From a physiological point of view, the neuromuscular system of wings requires a minimum temperature in order to

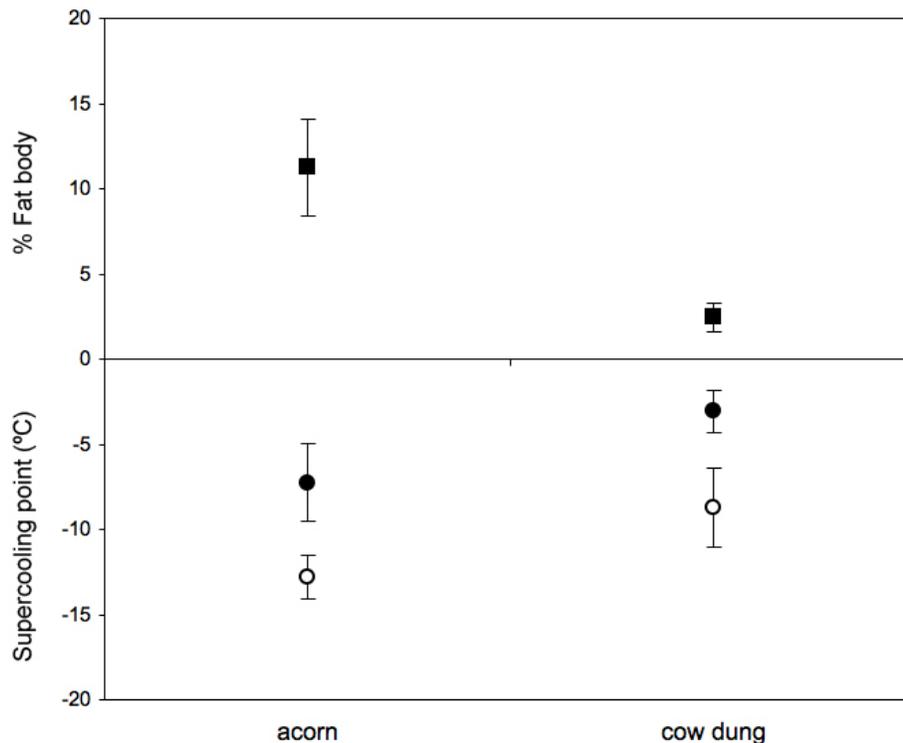
function efficiently. Nevertheless, the existence of a minimum temperature of around 25 °C for neuromuscular functioning does not necessarily imply that all endothermic dung beetles have the same take-off temperature. As in dragonflies [19], there is a positive relation between take-off temperature and body weight [7; unpublished data]. Specifically, in some tropical dung beetle species, oxygen consumption increases with body weight, which explains why larger-sized species present a higher metabolic rate and are able to colonise habitats at a higher altitude (or with lower ambient temperatures) [25].

In this way, pre-flight warm-up ensures that take-off be independent of  $T_a$  [19]. Nevertheless, in high ambient temperatures, species with high endothermic capacity run the risk of overheating if they do not have efficient mechanisms to dissipate any excess heat produced. In general, heat shock temperature is around 45-47°C in flying insects [6, 19, 24], and the temperature considered to be lethal is around 50-53°C [26, 27]. In dung beetles the maximum temperature during flight is approximately 42°C (Fig. 5), very close to heat shock temperature [20].



**Figure 5.** The relationship between environmental temperature ( $T_a$ ) and body temperature excess ( $T_{ex}$ ). The upper and lower boundaries for different models are 42 °C and 25 °C. Least-squares regression technique was used to estimate the slopes of the upper and lower boundaries. We defined ‘R’ models from a least-squares regression technique pairing the maximum and minimum  $T_{ex}$  values into classes with equal increments of  $T_a$ . We defined ‘M’ models from the same regression technique considering in this case the maximum and minimum values suggested in the literature [6, 19]. Source: Reprinted with permission from Verdú et al., 2006. *Journal of Insect Physiology* 52, 854-860. © 2006 with permission from Elsevier.

Generally speaking, endothermy in scarabs is associated with heat produced by wing muscles. As has already been mentioned, although other muscles such as the walking legs may help to reach the minimum temperature for flight in dung beetles, if wing muscle activity is absent, endothermy is not significant. The behaviour of some dung beetle species that have evolved and lost their capacity for flight and therefore muscles able to generate endothermy is proof of this. An example can be found in the species *Circellium bacchus* (Fabricius 1781). This large-sized species (around 8 g) is micropterous and lacks endothermy in all of its activities (walking, dung-ball making and rolling) [28]. Other examples of secondarily acquired ectothermy in ~~medium-sized~~ beetles are to be found in some species of the micropterous genera *Thorectes* and *Jekelius*. For example, in *Jekelius nitidus* (Jekel, 1866), body temperature ( $T_{th}$  and  $T_{ab}$ ) registered during its walking activity is dependent on ambient temperature, especially on ground temperature (unpublished data). However, some of these medium or large-sized ectothermic species seem to have chosen an astonishing strategy to remain active during periods of the day that are too cold for an ectotherm. The Iberian endemic *Thorectes lusitanicus* (Jekel, 1866), generally coprophagous, alters the metabolism changing its alimentary diet



**Figure 6.** The effect of food and acclimatization on fat body mass and supercooling point of the haemolymph for *Thorectes lusitanicus*. Values are mean  $\pm$  SD. Acclimatization at 20 °C (filled circles) and 10 °C (open circles) ( $n = 10$ , in both treatments).

which enables it to maintain its activities at environmental temperatures that are relatively low. In autumn and winter, individuals of *Thorectes lusitanicus* actively search for acorns from *Quercus suber* L. and *Q. canariensis* Willd to feed on. In the field and the laboratory, it has been demonstrated that *T. lusitanicus* prefer acorns instead of other more habitual trophic sources such as cattle or rabbit excrement [29, 30]. The nutrients supplied in acorns, rich in unsaturated fatty acids, proteins and carbohydrates [31, 32] make the insect's body fat significantly higher in weight than if it were to follow a diet based on cattle excrement (11% vs 2.5% respectively; see Fig. 6; J.R. Verdú, unpublished data).

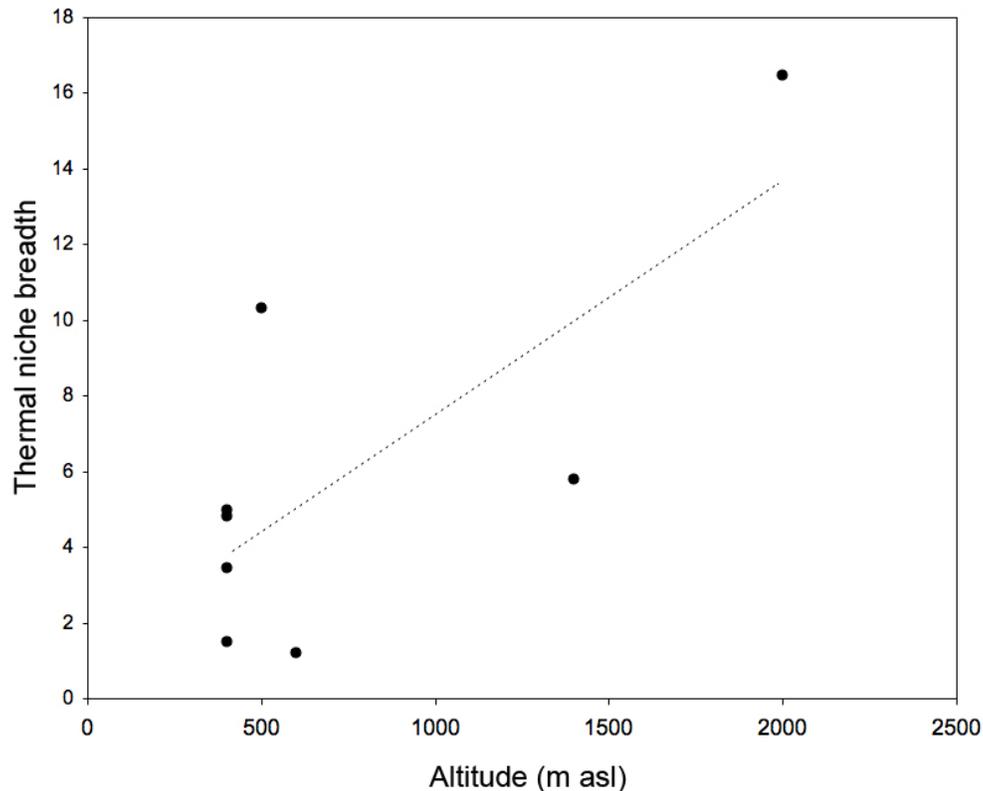
From an ecophysiological point of view, the body fat accumulated by individuals that feed on acorns provides the haemolymph with a greater concentration of proteins. This greater concentration of proteins in the haemolymph causes a notable decrease in the super-cooling point (SCP), from  $-9^{\circ}\text{C}$  in individuals fed on cattle excrement, up to  $-13^{\circ}\text{C}$  in individuals fed on acorns (acclimatization, at  $10^{\circ}\text{C}$ ). It has been possible to show that these proteins have hysteresis activity by using Differential Scanning Calorimetry, and to classify them within the antifreeze proteins (AFPs) (~~Verdú *et al.*, in preparation~~).

## Ecophysiology of thermoregulation

### Variability among species

Resource partitioning and possible competition have contributed to the evolution of breeding, and the thermoregulation strategies that favour coexistence among sympatric species of dung beetles [10, 33, 34]. Food relocation is a key characteristic of adult behaviour in these species and is accomplished by packing pieces of dung into a tunnel dug by the beetle both away from the source and then burying it (rollers) [35]. In rollers, endothermy is an important factor for the making, possession and transportation of dung balls because the individuals with higher  $T_b$  are the winners in terms of competition [8]. As both daily activity and seasonality are strongly related to the thermal biology of dung beetles, the coexistence in dung beetle assemblages is favoured ~~by existence~~ of different thermal strategies [33, 36-38]. On a temporal scale, some *Onitis* species separate their flight activity according to light intensity, avoiding possible interaction among species [33]. On a spatial scale, a group of Canthonini studied on an altitudinal gradient separate their distribution according to their temperature excess ( $T_{ex}$ ) capacity (Fig. 7).

The variability of the excess heat generated together with the range of ambient temperatures at which each species flies determines its thermal niche. In the case of sympatric species it has been demonstrated that different strategies exist which avoid possible competition to a great extent; what is



**Figure 7.** Relationship between thermal niche breadth (calculated by means of the ellipse formed by the standard deviation of the  $T_a$  during flight and the standard deviation of  $T_{ex}$ ) and altitude in *Canthonina* species along an altitudinal gradient in Veracruz (Mexico) ( $R^2 = 0.70$ ;  $p < 0.05$ ).

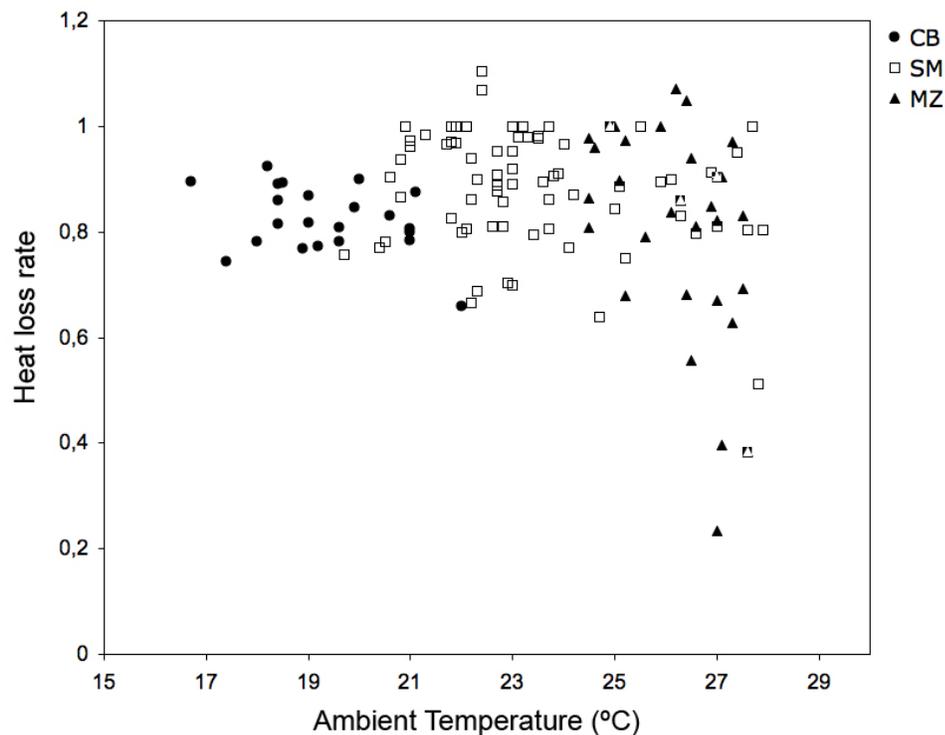
more frequent is that when two species share their thermal niche, they present alimentary preferences that are very different [12]. On other occasions, as in the case of *Scarabaeus sacer* and *S. cicatricosus*, they have very different thermoregulation mechanisms, thus avoiding any overlap between the two species [10].

### Variability within a species

This is one of the points that has least been studied, yet it is one of the most important from the point of view of how species adapt to changes in their distribution area, daily activities or phenology. It is true that little is known about the plasticity of species from a thermal point of view but in the few studies that have been carried out, it has been possible to demonstrate that different populations of the same species present thermoregulation mechanisms that are closely adapted to the concrete ambient conditions of its environment. For example, in *Canthon humectus* the ambient temperature flight range is between 16 °C and almost 29 °C. Nevertheless, if we consider the different populations

studied separately, these temperature ranges are reduced drastically to a few degrees. Much more interesting is the fact that each population presents different thermoregulation strategies according to the climate conditions where they live (Fig. 8, unpublished data). In the case of the population situated at a higher altitude (2200 m asl) the rate of abdominal heat loss ( $R_{ab}$ ) is independent of  $T_a$ , so that the strategy observed is that of avoiding loss of the heat produced by the wing muscles in order to avoid fast cooling-off due to the low ambient temperatures at which individuals fly (16-21°C). However, in the population that is further south and also located at a lower altitude (1200 m asl), a mechanism for the elimination of excess heat generated by wing muscles and the high ambient temperatures registered throughout their entire flight range (24-28°C) is evident. In the “intermediate” population located at an altitude of 1800 m asl, the  $T_a$  range in which *C. humectus* flies is much wider (20-28 °C), which explains why both mechanisms commented previously are seen.

In some cases, the changes can be observed in the flight period of the day. For example, in studies carried out in Brazil *Ateuchus apicatus* Harold, 1867 show evening flight habits [39]; however, in Uruguay, flight is recorded



**Figure 8.** Abdominal heat loss rate of with regard to environmental temperature for three different populations of *Canthon humectus* in Mexico. CB: Cruz Blanca (Veracruz), at Lat: 19°31'59"N, 2200 m asl; MZ: Barranca de Metztitlán (Hidalgo), at Lat: 20°35'10"N, 1800 m asl; SM: Sierra de Motozintla (Chiapas), at Lat: 15°21'49"N, 1500 m asl.

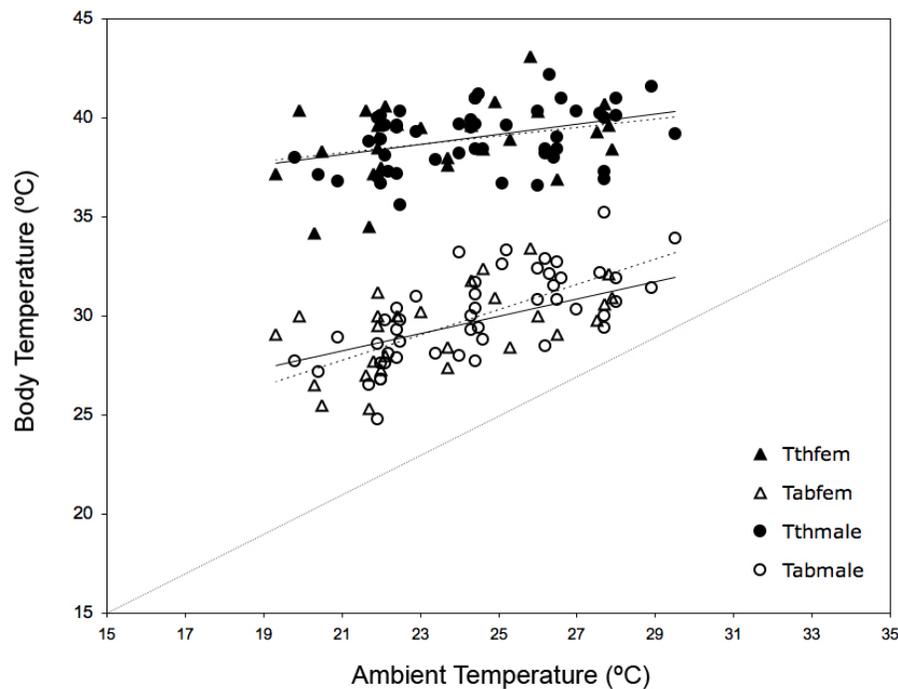
at midday (J.R.V. personal observations). This ~~has been explained~~ as a result of climatic differences between the regions. Changes ~~in~~ species flight period in different geographical areas have been observed for other dung beetle species (e.g. *Megathoposoma candezei* (Harold, 1873)) [40].

## Variability among individuals

We may even find a great variety of ~~behaviour~~ from a thermoregulation point of view within the same population. As has already been seen, body mass is directly related to the generation of internal heat. This explains the fact that variability exists within the same species, which is partially due to the variability in body mass, coloration, external morphology, etc. within the same population. From a thermal niche viewpoint, we suggest the existence of different constraints on individual niche breadth, most explained by physiological variability among individuals. According to the ‘niche variation hypothesis’, we would expect that generalist populations of endothermic dung beetles may tend to be more ecologically (and physiologically) variable as occurs with other animal groups [41].

Some examples also exist that are specially related to sexual dimorphism and different mechanisms can be observed between males and females. In the genus *Pleocoma*, more extreme divergence is observed, with the females being apterous whereas the males are good fliers with great endothermic capacity [17]. However, this behaviour is not frequent as generally almost perfect synchrony in the thermoregulation patterns between both sexes is found. This is even the case in some species that present marked sexual dimorphism, such as the case of *Phanaeus amethystinus* Harold 1863, where, despite the sexual structure of the male (head horn and angles of pronotum), both sexes present identical thermoregulation patterns over their entire flight range (Fig. 9, unpublished data). This is crucial for species that need to synchronise their flight period to facilitate both sexes meeting, as in the case of many Scarabaeidae species.

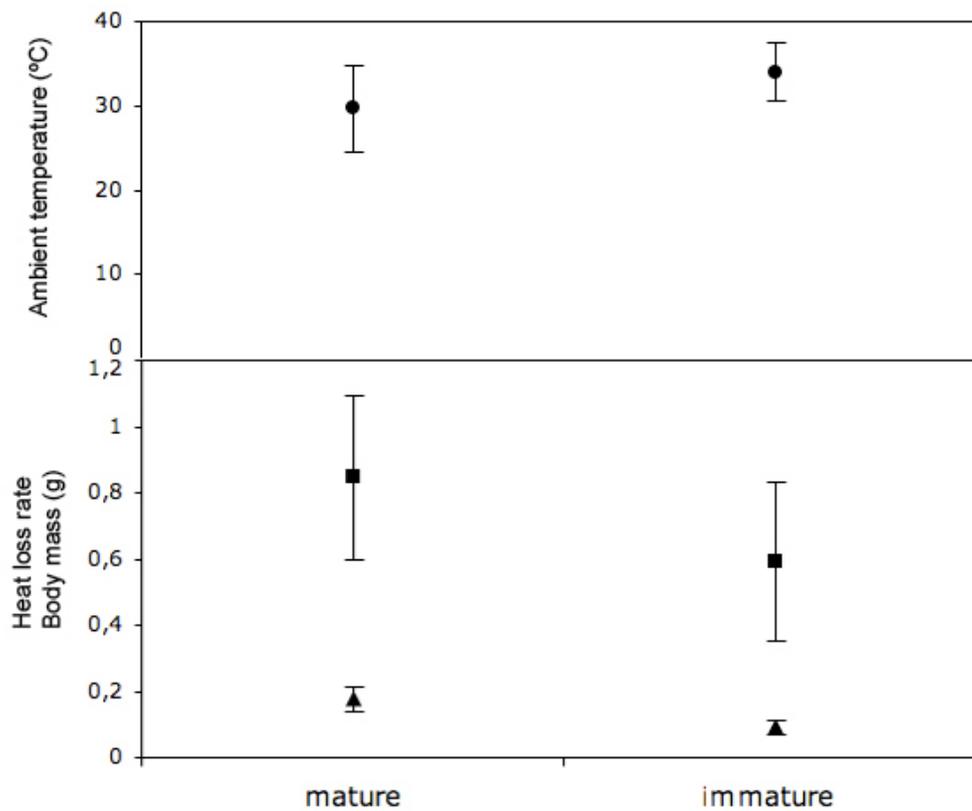
Differences in thermoregulation can be also found between individuals of the same size and sex due to the stage of maturity of an individual. This can be observed especially if we compare mature individuals with individuals that have recently emerged and whose cuticle is therefore still fragile due to less sclerotization. For example, in *Gymnopleurus flagellatus* (Fabricius, 1787), differences exist between the body mass of mature and immature individuals due to the lack of full development of their structures. This fact explains why immature individuals fly during the hotter hours of the day as they are unable to fly with  $T_a$  below 35 °C, whereas mature individuals not only fly at  $T_a$  below 28 °C but also present higher rates of loss of abdominal heat, which enables them to fly at  $T_a$  that are above 42 °C (Fig. 10, unpublished data).



**Figure 9.** Relations of thoracic temperature (filled circles and triangles) and abdominal temperature (open circles and triangles) at flight to ambient temperature in *Phanaeus amethystinus* Harold 1863 males (circles), and females (triangles). The fitted lines indicate regression lines. The dashed line is the isothermal line. Equations:  $T_{th}$  male (in dashed line):  $y = 0.22x + 33.71$  ( $R^2 = 0.12$ );  $T_{th}$  female:  $y = 0.26x + 32.81$  ( $R^2 = 0.12$ );  $T_{ab}$  male (in dashed line):  $y = 0.64x + 14.32$  ( $R^2 = 0.49$ );  $T_{ab}$  female:  $y = 0.43x + 19.13$  ( $R^2 = 0.29$ ).

## The spatial consequences of endothermy

Temperature is a fundamental factor that regulates the kinetic and metabolism of organisms [42], being recently proposed that higher environmental temperatures speed up the metabolism of individuals and, consequently, increase the probability of maintain higher populations and also facilitate the occurrence of genetic changes [43]. The existence of endothermy implies the regulation of body temperature by generating heat by behavioural, physiological and biochemical mechanisms. Full or partial endothermy has evolved independently in different animal groups (sharks, tunas, reptiles, birds, mammals and some insects), probably as a response to exploit expanded thermal niches after past climatic changes [44]. Larger animals need comparatively more energy than smaller animals [45] also being able to maintain their body temperature within a more limited range by inertia, a valuable physiological property. Thus, the capacity of generating heat unavoidably requires an increase in body size, mainly in those taxonomical

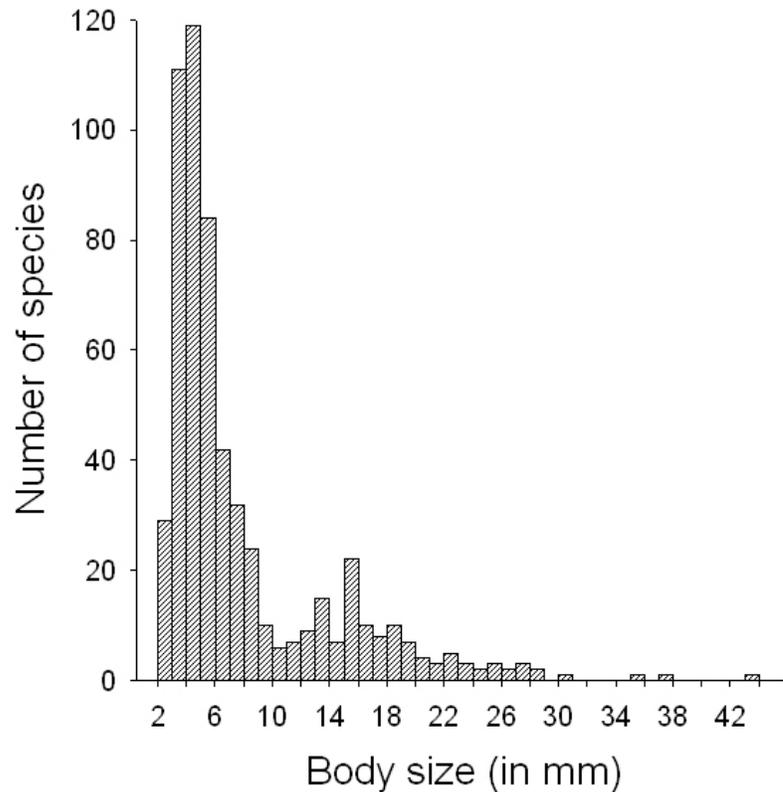


**Figure 10.** Behavioural and physiological differences between mature and immature individuals of *Gymnopleurus flagellatus* (in the Cabañeros National Park, Central Spain). Abdominal heat loss rate (squares) and ambient temperature of flight (circles) only show tendencies, while body mass difference between mature and immature individuals (triangles) was statistically significant. Values are mean  $\pm$  SD.

groups that are comparatively small bodied such as insects. Body size has been related to many different life histories and ecological traits, also influencing abundance as well as the evolution of organisms [46-50]. Species would increase their body size across the evolutionary time in response to changes in climatic conditions [51] and this evolutionary trajectory could unavoidably generate both a low speciation rate and a low population abundance.

The daily, seasonal and spatial distribution of a poikilotherm animal should be favoured by the existence of favourable climatic conditions. However, in the former pages we have shown that some dung beetle species have mechanisms of heat production and dissipation which imply the existence of a partial thermoregulation process. This endothermy enables the independence of species from the climatic conditions; large endothermic dung beetles are competitive advantageous, can have wide seasonal and daily activity periods, and also can probably inhabit a wider range of different

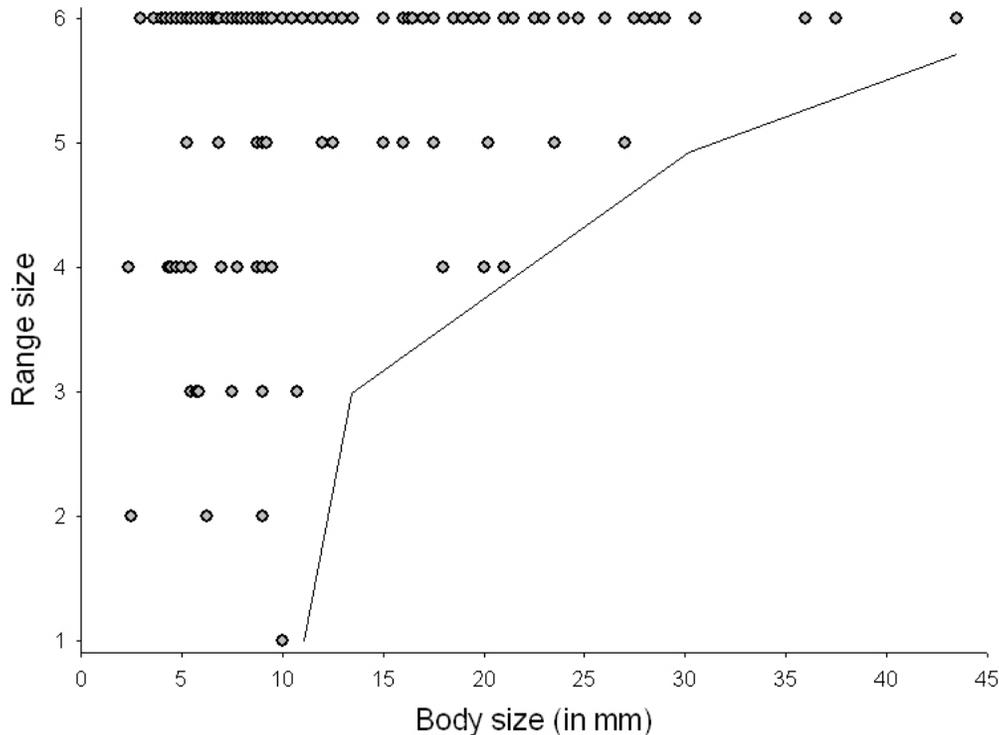
habitats than strictly ectothermic dung beetle species. As endothermy permits the exploitation of cooler environmental conditions, we should expect that those endothermic dung beetles have wider distribution ranges in temperate regions. In the western Palaearctic region there are many more small-bodied than large-bodied species, and a marked bimodal pattern exists; most of the species have a body length smaller than 1 cm with a second small peak of species around 1.3 and 1.8 cm in length (Fig. 11).



**Figure 11.** Body size distribution of western Palaearctic Scarabaeoidea dung beetles (in classes of 1 mm). Data from the same sources referred in Lumaret and Lobo [68].

This pattern must be viewed as the consequence of the interplay among speciation, dispersal and extinction forces across evolutionary times [52], favouring two opposite evolutionary routes, one of which is directed towards an increase in body size and temperature control. Although the number of lineages that have followed this tendency of body size increment seems to be smaller, these species are those that have developed specialized and energetically costly dung relocation behaviours [53], and are also the main and most effective dung consumers [54]. Geographical range size and body size are also related in the western Palaearctic dung beetles; there is no species with more than 1 cm in length that possesses a restricted distribution (less than

500.000 km<sup>2</sup>), and all the bigger species are widely distributed (Fig. 12). The same pattern can be observed in the Afrotropical dung beetles [55] and in many other animals [56], although there are also exceptions [57, 58] and few poikilotherm data have been analysed.



**Figure 12.** Relationship between body size and range size for the western Palaearctic dung beetles. Range size was estimated by considering six classes based on the percentage of the total western Palaearctic region area ( $12 \times 10^6$  km<sup>2</sup>) occupied by each species [68]. The line tries to represent the boundary constraint of this relationship.

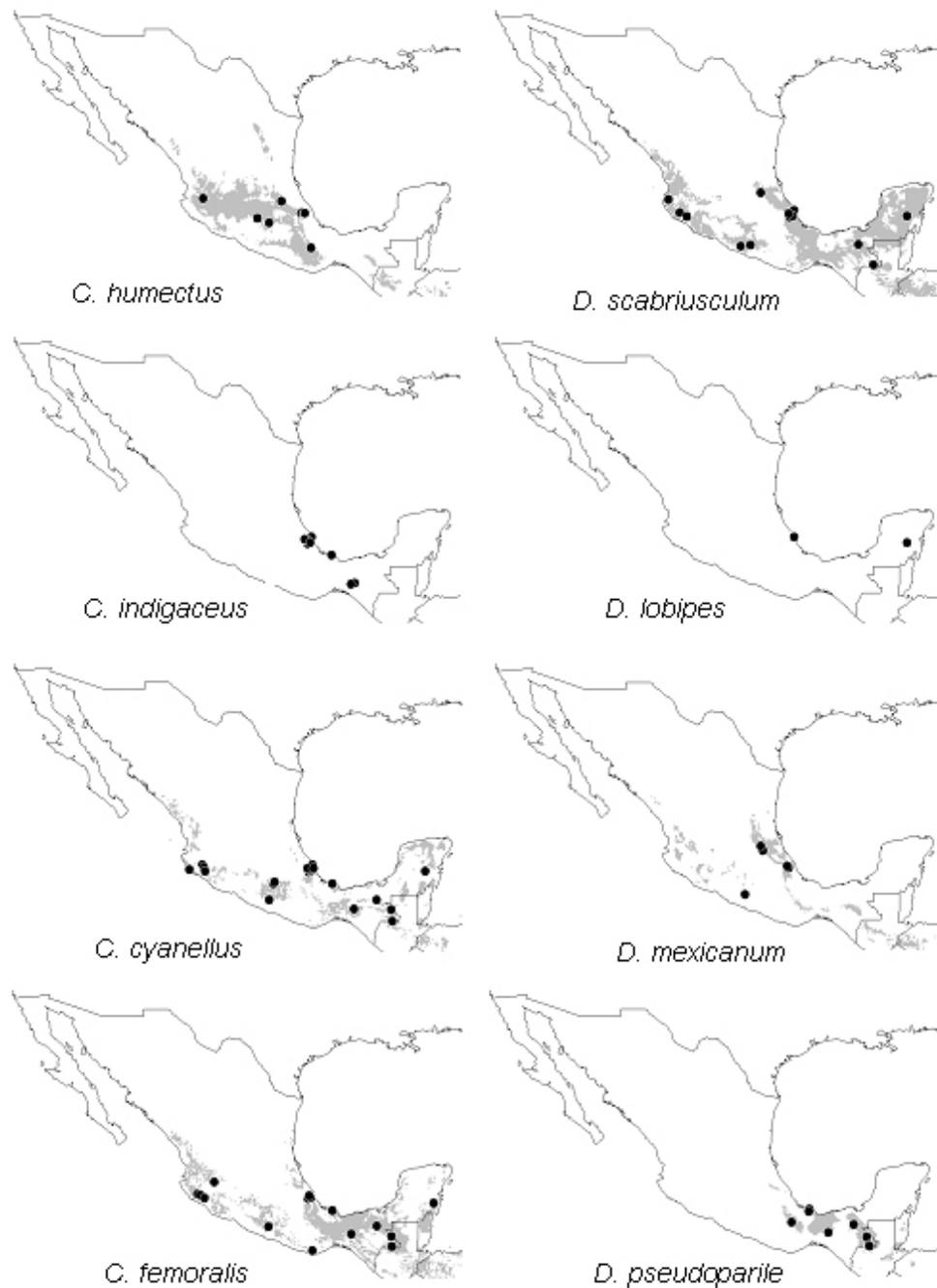
The available data on *Canthon* and *Deltochilum* species allow us to examine preliminarily whether range size is related to the degree of endothermy. These two Gondwanian genera, commonly present in the Neotropical dung beetle assemblages, differ in their body size (around 10 mm in *Canthon* species and 24 mm in *Deltochilum* species) as well as in their daily activity (*Canthon* species are generally diurnal while *Deltochilum* are mainly nocturnal). We use the endothermy information of four *Canthon* and four *Deltochilum* species together with the distributional information of these species to firstly examine whether temperature derived variables in the Mexican distribution range are correlated with the endothermic capacity of the species. As endothermy is especially advantageous under cold conditions we shall check if those species with a higher endothermic capacity are able to inhabit under cold conditions and over a wider

gradient of temperatures. In the same way, as heat generation is especially dangerous when maximum environmental conditions are higher, we shall test whether more endothermic species are geographically constrained by the existence of higher summer temperatures.

The ~~potential~~ distribution of species was estimated using predictive modelling techniques, the available presence information of the species, and the nineteen bioclimatic variables provided by Worldclim [59]: annual mean temperature, mean diurnal range, isothermality, temperature seasonality, maximum temperature of warmest month, minimum temperature of coldest month, temperature annual range, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, mean temperature of coldest quarter, annual precipitation, precipitation of wettest month, precipitation of driest month, precipitation seasonality, precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter and precipitation of coldest quarter. We used a maximum entropy approach (MaxEnt) to estimate predictive distribution models [60] because it is considered one of the best techniques for presence-only data [61]. This machine learning method uses an environmental vector to estimate potential distributions so that they will be similar to empirical (observed) distributions. Since both distributions will never be exactly equal, MaxEnt try to minimize this difference by assigning a different weight to the environmental variables combination with a *lambda* factor for every point in the spatial gradient. Besides linear terms, quadratic terms of environmental variables were also selected to enable more flexible curvilinear responses of dependent variable. The MaxEnt output is a continuous variable varying from 0 to 100, which indicates the ‘favourability’ of presence or ‘habitat suitability’ for every species. All models were run with Maximum Entropy Species Distribution Modeling v. 2.3 [62].

Once the ~~potential~~ distributions of each one of the eight species were estimated (Fig. 13) we calculate the total predicted area as well as the mean and range (maximum-minimum) scores of the different temperature variables considered for these areas (Table 1).

Although we examined the Spearman rank correlation coefficients ( $r_s$ ) for all the WordClim previously mentioned temperature variables, only the maximum temperature of the warmest month (MTWM) shows significant correlations. Both the mean scores of this variable and its range across the ~~potential~~ distribution of species are negatively correlated with endothermy scores ( $r_s = -0.707$ ,  $p = 0.05$  and  $r_s = -0.714$ ,  $p = 0.047$ ). The  $p$ -value of the following more correlated temperature variable is 0.17. Thus, those species with higher endothermic capacities seem to be unable to inhabit localities with high maximum summer temperatures, whereas those species with a moderate or low endothermic capacity will support the temperature stress motivated by



**Figure 13.** Potential distribution of four *Canthon* and four *Deltochilum* Mexican dung beetle species (in grey) and observed distribution points.

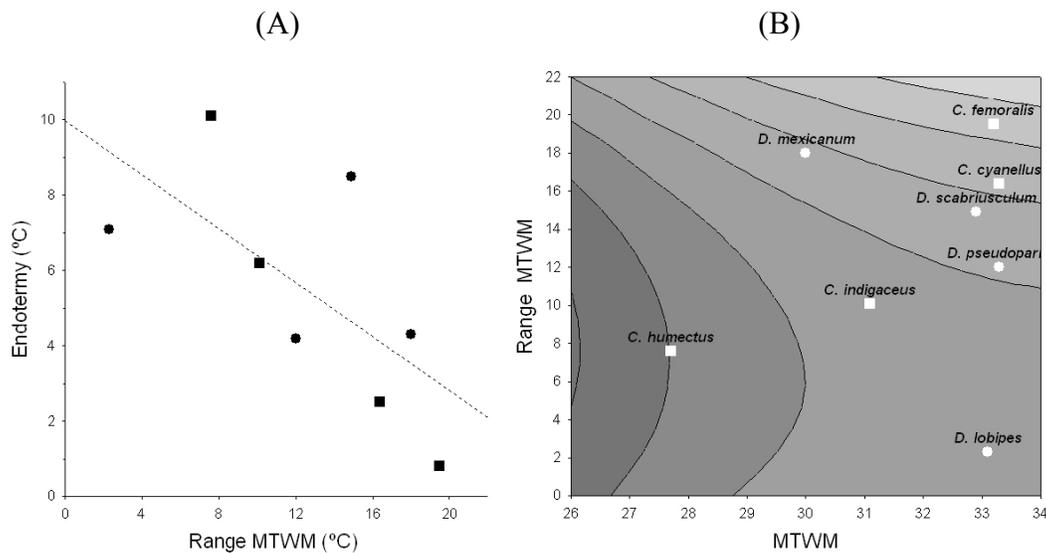
the existence of higher summer temperatures (Fig. 14A). Furthermore, this geographical limitation of endothermic species occur mainly within the diurnal *Canthon* species whereas nocturnal *Deltochilum* species would be able to inhabit the hottest summer sites probably due to their capacity to eliminate

more efficiently the excess of heat generated by thorax during flight (see Fig. 1). In a regression model MTWM accounts for 19% of total variability in endothermy scores and the range of MTWM explains 35%. Interestingly, the interaction between these two variables is able to explain almost 42% of variability in endothermy showing that although the majority of the species can live in places that are hot in summer, these sites are avoided by the *Canthon* species with a higher endothermic capacity (Fig. 14B).

Although preliminary, these results highlight that the heat generation in these insects can be an obstacle for colonisation of those regions with high summer temperatures unless the species has nocturnal habits. Our results do not support that those species with a moderate endothermic capacity are capable of colonising cold regions, although the species with the highest endothermic capacity (*Canthon humectus*) can potentially inhabit localities

**Table 1.** Number of database records used to derive potential distributions (Fig. 13), number of 0.08° cells in which each species is present and mean ( $\pm$  95% confidence interval) an range (maximum-minimum) data of three temperature variables across the whole potential distribution of each species. AMT = annual mean temperature; MTWM = maximum temperature of the warmest month; mTCM = minimum temperature of the coldest month. Endothermy is the averaged difference between  $T_b$  and  $T_a$  for environmental temperatures higher 25°C and lower than 45 °C. The maximum and minimum flight temperatures represent the approximate body temperatures at which each species flight. The scores of these variables are not significantly correlated with anyone of the examined temperature variables. All body temperature measurements are similar to those described in the Fig. 1.

	<i>Canthon humectus</i> Say, 1832	<i>Canthon indigaceus</i> LeConte, 1866	<i>Canthon cyanellus</i> LeConte, 1859	<i>Canthon femoralis</i> Chevrolat 1834	<i>Deltochilum scabritusculum</i> Bates, 1887	<i>Deltochilum lobipes</i> Bates, 1887	<i>Deltochilum mexicanum</i> Burmeister, 1848	<i>Deltochilum pseudoparile</i> Paulian, 1938
used records	36	60	124	96	68	40	34	44
observed cells	7	9	21	16	16	3	7	9
predicted cells	2606	107	1685	2645	4375	6	871	815
AMT	16.9 $\pm$ 0.1	23.1 $\pm$ 0.4	24.0 $\pm$ 0.1	23.9 $\pm$ 0.1	23.6 $\pm$ 0.1	25.8 $\pm$ 0.4	19.9 $\pm$ 0.2	24.7 $\pm$ 0.1
MTWM	27.7 $\pm$ 0.1	31.1 $\pm$ 0.4	33.3 $\pm$ 0.1	33.2 $\pm$ 0.1	32.9 $\pm$ 0.1	33.1 $\pm$ 1.1	30.0 $\pm$ 0.2	33.3 $\pm$ 0.1
mTCM	5.5 $\pm$ 0.1	14.7 $\pm$ 0.5	14.2 $\pm$ 0.1	14.3 $\pm$ 0.1	14.0 $\pm$ 0.1	17.6 $\pm$ 1.4	9.2 $\pm$ 0.2	16.3 $\pm$ 0.2
Range AMT	16.1	10.7	11.8	17.2	14.2	1.0	17.1	11.6
Range MTWM	7.6	10.1	16.4	19.5	14.9	2.3	18.0	12.0
Range mTCM	26.6	11.8	12.7	18.9	16.8	2.8	17.1	12.5
endothermy	10.1	6.2	2.5	0.8	8.5	7.1	4.3	4.2
maximum flight temperature	23	34	30	31	27	27	26	28
minimum flight temperature	17	29	26	25	23	23	21	24



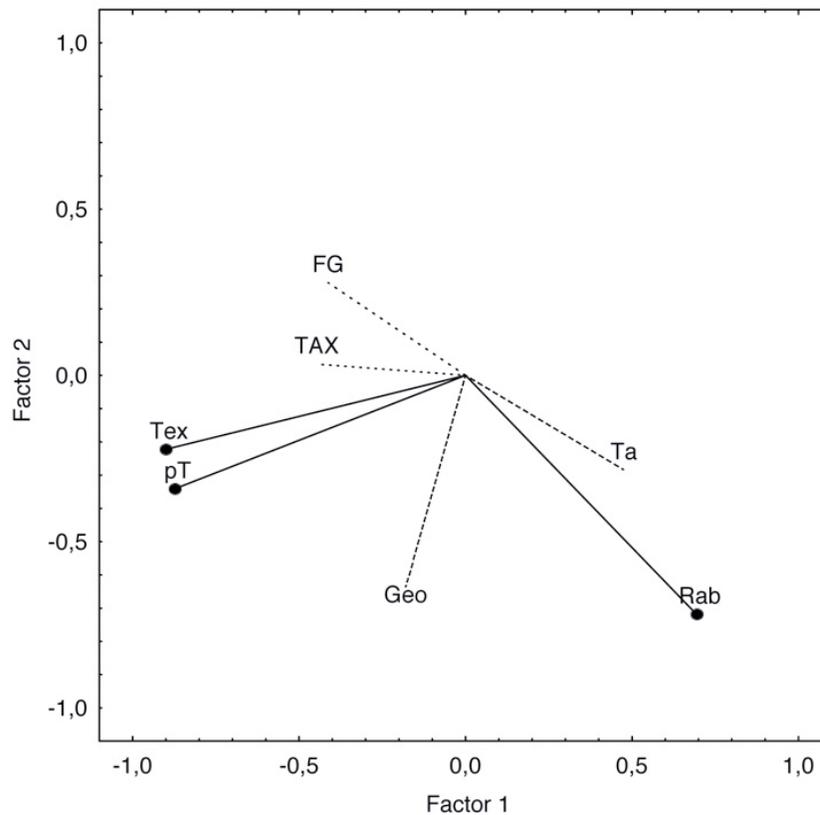
**Figure 14.** (A) Relationship between endothermy ( $T_{th}-T_a$ ) and the range of the maximum temperature of the warmest month (MTWM) occurred in the potential range of distribution of *Canthon* (■) and *Deltochilum* (●) species (see Fig. 13). The broken line is the lineal regression. (B) Surface plot between endothermy, the mean scores of MTWM and their range across the potential distribution of each species. Dark grey tones correspond to higher endothermic scores.

with the lower minimum temperatures of the coldest month (see Table 1). More data is needed to examine the ability of tropical endothermic species to exploit cold environments.

## Towards a biogeographical viewpoint of thermoregulation processes

The variables related to thermoregulation can depend on the environment or can be related to the ecology, behaviour and taxonomy (or phylogeny) of species. In order to simplify the relationships between this complex group of variables (biotic and abiotic), we made a Factorial Correspondence Analysis (using the Statistica software package [63]) using data from 15 dung beetle species inhabiting the Neotropical and Palaeartic regions. According our results, the abdominal heat loss rate ( $R_{ab}$ ) in dung beetle species highly depends on the environment conditions because this variable can be considered as an adaptation to heat stress in warm sites, being independent of the taxonomic group and the body size (see Fig. 15). However, this adaptation to extreme temperature conditions may be influenced by the geographic region at which the species inhabit. On the contrary, the heat excess temperature ( $T_{ex}$ ) seems to depend on the size of a species and even the functional or taxonomic group since they are related to the muscle mass

on which flight depends (Fig. 15). In other words, body mass, taxonomy and the functional group to which a species belongs influence the endothermic heat generation as well as the difference between this and  $T_a$  ( $T_{ex}$ ). Conversely, adaptation to thermoregulation of excess heat, measured by the rate of abdominal heat loss ( $R_{ab}$ ), depends directly on the environment and secondly on geographic region in which the species lives. In order to obtain a more concise perspective, we next explore these relationships ~~between variables~~ using ~~the~~ variance partitioning ~~techniques~~.



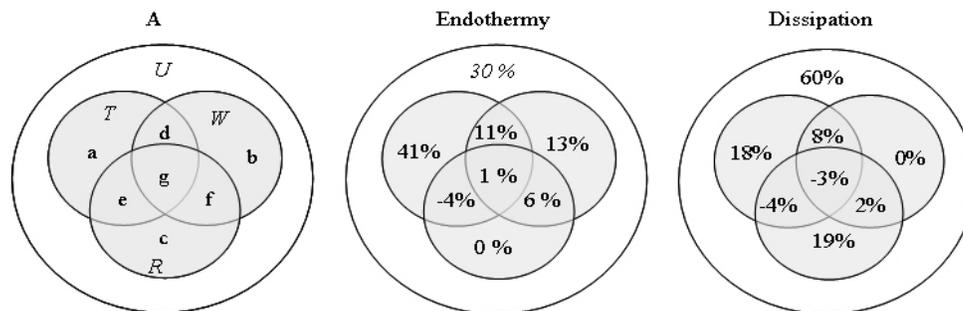
**Figure 15.** Factorial Correspondence Analysis showing relationships between biotic variables (pT: body mass; Tth: thoracic temperature; Tex: body excess temperature; and Rab: abdominal temperature excess ratio) and several non biotic factors (Geo: Geographical region (Neotropical and Palaeartic); FG: functional groups (Telecoprids, paracoprids and endocoprids; TAX: taxonomy at subfamily level; and Ta: ambient temperature during flight). Results obtained from data of 15 species (11 are Neotropical and 4 are Palaeartic ones). The first two factors accounted for 91.3% of the variance.

The competition for an ephemeral resource in poikilotherm dung beetles could have favoured: i) the tendency to fly as soon as possible diminishing the temperature threshold at which be active, and ii) mechanisms to avoid the overheating. The first adaptation would be associated with an increment in

body size and their ecological advantages become visible both in cold-adapted lineages of Laurasian origin and in warm-adapted Gondwanian ones. On the contrary, the second type of morphological and physiological adaptations should be more frequent in warm-adapted lineages because the climatic conditions impose the evolution of dissipation mechanisms.

We examine the comparative relevance of environmental temperature, body size and the biogeographic region in which each species inhabit on the  $T_{ex}$  (endothermy) and on abdominal heat loss rate ( $R_{ab}$ ), a measure of the existence of heat dissipation mechanisms. For that we study by variance partitioning techniques [64, 65] the scores of these two thermoregulation variables in eleven Neotropical species and eight Palaearctic dung beetle species. The mean number of individuals analyzed for each species is  $31 \pm 14$  (mean  $\pm$  95% confidence interval; minimum = 7, maximum = 107).

Our results (Fig. 16) clearly show that the pure effect of the biogeographic region does not have any influence on the endothermic scores of species. The heat production of the species depends on the body size but mainly of the environmental temperature found in each occasion. Contrariwise, the capacity of heat dissipation clearly depends on the environmental temperature but importantly on the biogeographic region:  $3.1 \pm 1.3$  °C for the Palaearctic species and  $5.5 \pm 2.5$  °C for Neotropical ones (mean  $\pm$  95% confidence interval;  $F_{(1, 580)} = 105.5$ ;  $p < 0.0001$ ), being the effect of body weight negligible (Fig. 16).



**Figure 16.** Variance partitioning results between three correlated explanatory variables: body weight (W), environmental temperature (T), and biogeographic region (R; Neotropical or Palaearctic) on heat production (temperature excess,  $T_{ex}$ ) and heat dissipation (abdominal temperature excess ratio,  $R_{ab}$ ). The figure A represent the different percentages of variability calculated by partial regression analysis (see [64, 65]). Negative joint effects (in d, e, g and f fractions) indicate that a variable acts in opposition or as suppressors of other variable. Both environmental and body temperatures were measured using digital thermometers and K thermocouples (accuracy of 0.5 °C). All the considered species are only distributed in the Neotropical or in the Palaearctic regions, not existing any species present at the same time in both biogeographic regions.

Hence, as we anticipated, these results support the proposal that the thermoregulation mechanisms devoted to avoid the overheating have been an evolutionary adaptation appeared under warm conditions, while those implied in the body heat production would be universal and dedicated to increase the competition ability of species. According to these results we hypothesize that the evolution of physiological dissipation mechanisms would have increased the competitive advantage of warm-adapted Gondwanian lineages in the warmest areas of temperate zones such as those of the Mediterranean region. The latitudinal variation in the qualitative composition of Nearctic dung beetle assemblages is due to the predominance of warm-adapted Scarabaeidae species in the southern and more diverse communities [66, 67]. As these species generally come from highly diversified Afrotropical and Neotropical genera, we suspect that the more complete thermoregulation processes evolved in these lineages, which imply the existence of heat production and heat dissipation mechanisms, can be one of the first factors able to explain the current distribution and dominance of these species in European environments.

## Concluding remarks

In summary, thermoregulation plays an important role in the ecology and spatial distribution of dung beetles, whether on a local, regional or geographical scale. In some places, physiological diversity explains some cases of coexistence without competition in terms of thermoregulation patterns, especially in *Scarabaeus* species in which interspecific interactions are important for establishing reproductive pairs. Moreover, the existence of different flight patterns has implications for behaviour and niche partitioning. The existence of a ‘free running clock’ that could restrict the daily or seasonal activity of species is a possible factor for understanding niche partitioning on a spatial and temporal scale. Hence, we suggest that studies on niche separation in dung beetles along habitat, daily or seasonal dimensions should be reanalysed in order to examine whether the formerly stated relevance of environmental variables to explain temporal and spatial separations between co-occurring species, is in fact causally due to the variation in physiological thermal adaptations. Moreover, as preliminary evidence suggests that populations and individuals have a wide physiological plasticity, it will be necessary to assess whether those species with a higher range of endothermic responses to the environmental conditions are also able to inhabit a higher variety of climatic conditions, both on a regional and geographical scale. Another interesting line of research could be the comparison of the thermal niches between invaders and non-invader dung beetles, as well as between those species that seem to respond quickly or slowly to climatic changes. We also need to follow the occurrence of these

thermal adaptations across the phylogeny, to examine the degree of variation of these variables between phylogenetically related species, and to estimate their difference between ancient separated high-level taxa currently inhabiting disconnected biogeographic regions. The distribution and abundance of organisms have been related to many environmental variables and it has always been difficult to establish reliable causal links from correlative analysis. We advocate that the estimation of physiological variables able to measure the production of heat and the capacity of heat dissipation can be a more promising avenue to explain the ecology and biogeography of poikilotherm animals such as dung beetles.

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