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Daily Activity Patterns and Thermal Tolerance of Three Sympatric Dung Beetle Species (Scarabaeidae: Scarabaeinae: Eucraniini) from the Monte Desert, Argentina

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Abstract
Tolerance to extreme temperatures, thermal limits, and the mechanisms of thermoregulation are related to internal functions of insects and partly define their ecological niche. We study the association between daily activity of dung beetles from the Monte Desert in Argentina and their tolerance to high temperatures. Results indicate that for all three sympatric species studied, *Eucranium belenae* Ocampo, *Anomiopsoides cavifrons* (Burmeister), and *Anomiopsoides fedemariai* Ocampo, daily activity is associated to ground temperature. *Eucranium belenae* is active when ground temperature is relatively low and it is less tolerant to long periods of activity at high temperatures in the lab, while *A. cavifrons* and *A. fedemariai* are active when ground temperatures are higher, and they tolerate high temperatures for longer periods of time than *E. belenae* in the lab. These species coexist and use similar food sources, and this ecophysiological study may help to explain how they differentiate under the same environmental conditions. The Monte Desert is considered an extreme environment, and studies on thermal tolerance offer testable predictions to understand how species would respond to climate change.

Introduction

Tolerance to high and low temperatures, thermal limits, the endo or exothermic capacity of a species, and the mechanisms of thermoregulation and respiration are related to internal functions of insects (May 1979) and partly define their ecological niche. Tolerance to high temperatures and the thermal range of an insect are particularly important for species that inhabit extreme environments such as deserts. Temperature tolerance defines periods and hours of activity which, in turn, may affect the species capacity to compete for resources (Heinrich 1976, Ybarrondo & Heinrich 1996). In environments where resources are scarce and competition is high (Acebes *et al* 2012), differential use of the microenvironment where a species develops its activity, or the time of day when the species is active, might define a partition of the limited resources and, consequently, allow the coexistence of species that are ecologically similar (Tokeshi 1999, Feer & Pincebourde 2005).

The thermal tolerance range of a species is defined as the value of maximum critical temperature (CTmax) and minimum critical temperature (CTmin) that the species can tolerate (Huey & Stevenson 1979, Hill *et al* 2006). An indirect method to estimate these critical temperatures is studying how long a species can tolerate temperatures that were previously considered the maximum and minimum limits for a species or group of species (Sheldon & Tewksbury 2014). This thermal tolerance range defines in part the ecological niche

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of a species in a given community (Charle 1927). Among the multidimensional axes that define the niche of a species is the time and space where it is active, and both are constrained by the resources used and the physiological characteristics of the species. The niche of dung beetle species is defined across several ecological axes that include the following: resource size, trophic preferences, time to colonization of food source, seasonality, daily activity, foraging strategy, nesting strategy, endothermic capacity, and mechanisms of thermoregulation (Hanski & Camberfort 1991, Lumaret & Iborra 1996, Ocampo & Philips 2005, Verdú *et al* 2006, 2007, Chao *et al* 2013). Each dung beetle species has specific hours of activity and they can be divided into diurnal, nocturnal, or crepuscular (Fincher *et al.* 1971, Krell-Westerwalbesloh *et al* 2004, Feer & Pincebourde 2005). In turn, it is also known that daily activity of dung beetles is related to certain physiological characteristics, such us mechanisms of thermoregulation, tolerance to maximum and minimum temperatures, and thermal range (Verdú *et al* 2006, Verdú *et al* 2007).

Studies on physiological mechanisms, such as those mentioned above, are very useful to understand the mechanisms of species diversity and the changes that might result as a consequence of global warming (Sheldon & Tewksbury 2014). It is known that, as a consequence of global warming, some species might face changes in distribution, and even extinction (Erasmus *et al* 2002, Brook *et al* 2008). Studies on their eco-physiology, particularly thermal tolerance, might help to understand the potential response of a species and prevent the consequences (Sheldon & Tewksbury 2014).

Daily activity patterns of dung beetles are highly variable, and taxa that have diversified in the desert are no exception (Monteresino & Zunino 2003, Ocampo 2004, Ocampo & Philips 2005). The daily activity pattern could be tightly associated to thermal tolerance of an individual. Our goal is to evaluate the relation between tolerance to high temperatures and daily activity of three sympatric species of dung beetles of the tribe Eucraniini: *Eucranium belenae* Ocampo, *Anomiopsoides cavifrons* (Burmeister), and *A. fedemariai* Ocampo. They coexist and use similar food sources in the Monte Desert in Mendoza, Argentina, a region that is characterized by extreme high temperatures during the summer (Ocampo 2007, 2010a, b). This is the first study on eco-physiology of dung beetles in extreme habitats.

Under the hypothesis that greater tolerance to high temperatures allows longer activity at higher ground temperatures, we predict that species that tolerate longer periods of time at high temperatures in the lab will show greater activity at higher ground temperatures than those that are less tolerant, i.e., those that are immobilized faster when exposed to the same high temperatures.

Materials and Methods

Study area and species

We conducted this study between October 2012 and February 2013, that is, during southern hemisphere spring and summer seasons, in the Monte biogeographic province, in Mendoza, Argentina. In this area, the weather is arid and semi-arid, with mean annual precipitation of 210 mm. We recorded a mean maximum temperature of 38.6°C during the study period, whereas the mean minimum temperature was 24.25°C.

During our study, the minimum ground temperature recorded at daylight was 20°C at 9:00 h, and the maximum temperature was 77°C at 14:00 h (V. C. Giménez Gómez pers. obs). The study area was located in Lavalle (32°15′12″S, 67°49′13 with O / 32°35′38″S, 68°17′27″O), part of the desert in Mendoza province. Three species of dung beetles of the tribe Eucraniini were selected for this study: *E. belenae*, *A. cavifrons*, and *A. fedemariai*. These species were chosen because they coexist in the study area and share and compete for similar food sources (Ocampo 2007, 2009). All three species feed on dry dung, as the majority of Eucraniini species do, and of small pieces of dry plant material (Ocampo & Philips 2005, Ocampo 2007, 2009, 2010a). Eucraniini species are easy to find and identify while they are active, as they are diurnal and flightless, and have a characteristic morphology.

Daily activity

To estimate daily activity patterns of the studied species, we defined transects of 50 × 4 m, that were walked within 4–6 min while recording all individuals of the three species that fell in each transect and that were walking or foraging. Before walking each transect, soil temperature was recorded with a digital thermometer (appropriate for − 50 to + 150°C). A total of 154 transects were completed during 5 days, of which 94 transects were done between 8:00–13:30 h and 60 transects between 16:00–20:00 h. Our first transects included the time between 13:30–16:00 h, but because after 12 transects no individuals were observed during this period of time, we assumed that activity was null and no further effort was dedicated to that period.

Tolerance to high temperatures

To measure tolerance to high temperatures, 15 adult individuals of each of the three species were collected, transported to the lab, and conditioned at 22°C for 22–26 h for acclimation in a terrarium setup with soil collected in their natural habitat. By following that procedure, we ensured that all individuals started the high temperature tolerance test from the same basal ambient temperature. Because body weight is directly related to thermal tolerance in dung beetles (Verdú *et al* 2006, Verdú & Lobo 2008), all individuals were weighted before running the test using a digital scale, with a precision of 0.001 g. Body weight was used as a co-variable for statistical analysis.

A static method was used to run the thermal tolerance test (Merrick & Smith 2004, Sheldon & Tewksbury 2014), where each individual was exposed to a constant temperature of 48°C until it lost control of its movements. The static temperature of 48°C was selected because previous studies (F.C Ocampo & K. Sheldon unpublished) indicate that it approximates well the maximum temperature that these beetles can tolerate in their environment. We used a thermal bath, consisting of a metallic container in which water temperature is controlled using a Fisher Scientific Type-Kentre digital thermometer with 0.1-°C precision (Lutterschmidt & Hutchinson 1997, Sunday *et al* 2011). Inside this container, 50-ml plastic cups were introduced and left half submerged in the water. The inside of the cup remained dry and held one individual dung beetle. Plastic cups were covered with a glass so that the temperature and humidity of the beetles remained constant during the test. Four individual beetles were subject to the test at one time. We recorded the time when the individual flipped on its back and could no longer flip back over on its legs, as we considered that as a sign that the individual had reached its limit of thermal tolerance

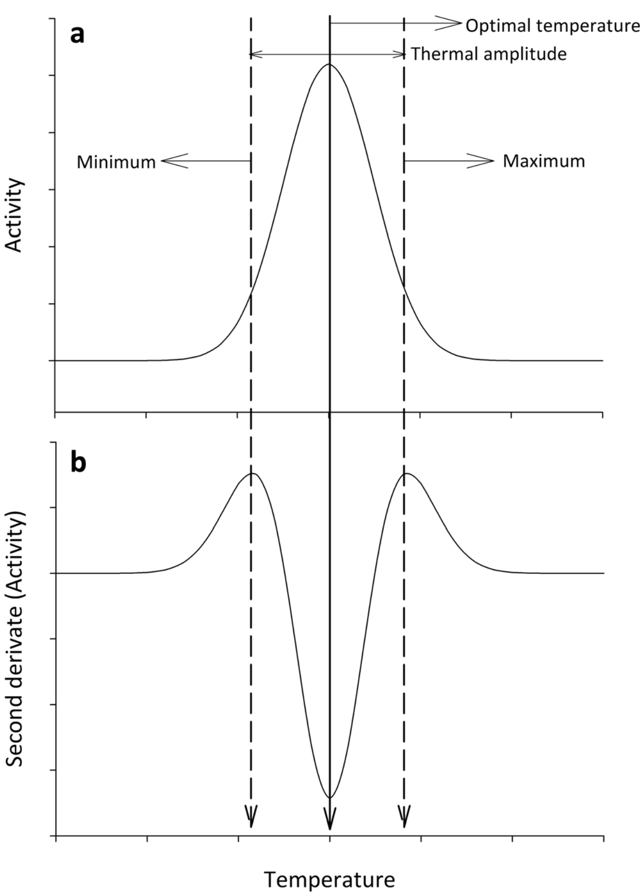

Fig 1 Model of uni-modal response of activity as a function of temperature. The model (a) assumes an optimal activity temperature (Gaussian function) and a thermal tolerance determined by a minimum and a maximum temperature of activity, calculated based on the second derivative of the Gaussian function (b).

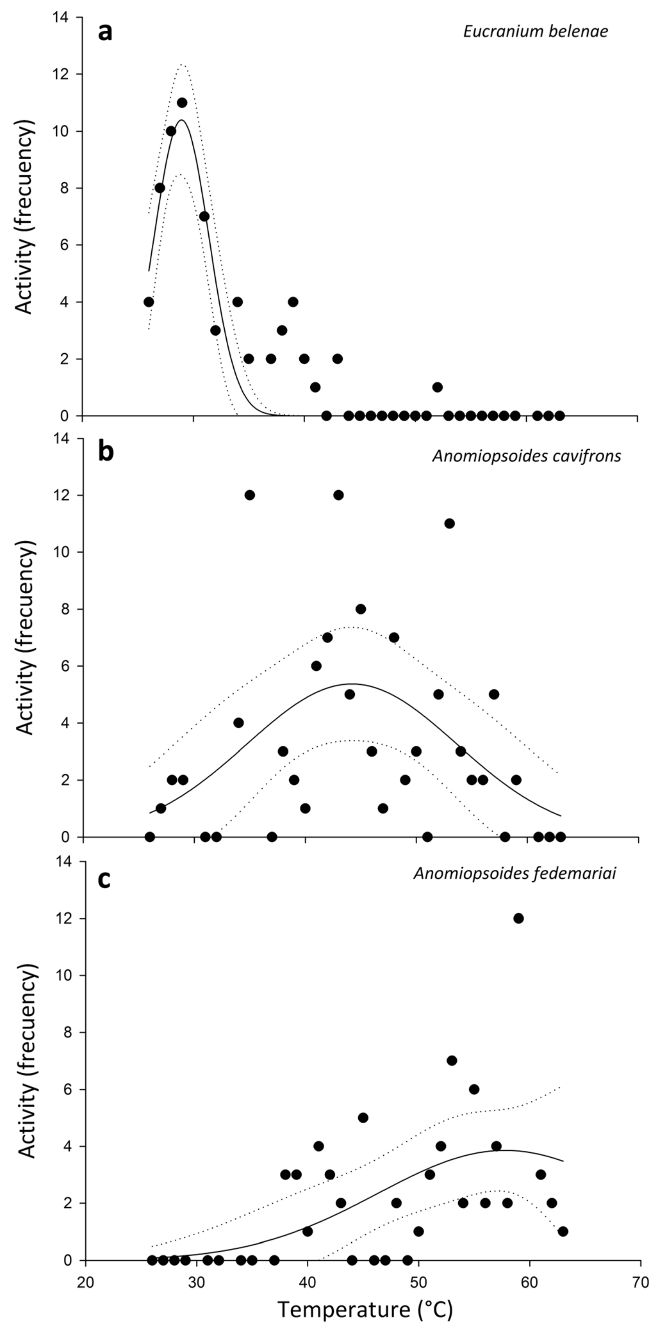

Fig 2 Patterns of daily activity for *Eucranium belenae* (**a**), *Anomiopsoides cavifrons* (**b**), and *Anomiopsoides fedemariai* (**c**) as a function of ground temperature (°C) throughout the day. The continuous line represents activity and the dotted line the confidence interval of activity.

(Roberts *et al* 1991, Klok & Chown 1997). That was taken as its maximum tolerance time.

Statistical analysis

To estimate activity patterns as a function of ground temperature and time of day, we calculated the mean number of individuals per species observed per transect, at each recorded temperature and time of day (independent variables). To relate activity with temperature, we used a uni-modal response model (Gaussian) (Fig 1); optimal temperature and thermal amplitude (minimum and maximum) were calculated from this model. To represent the response pattern, we used a Gaussian model, considering temperature as the independent variable and activity as the dependent variable:

$$Activity = a * \exp\left(-0.5 * ((temperature - x0)/b)^2\right)$$

where $x0$ represents the position of the activity peak on the X axis and a and b modulate the amplitude of the curve.

Optimal temperature was calculated based on the minimum of the second derivate of the Gaussian function (Fig 1 (a)) and compared among species based on their confidence intervals. To calculate thermal amplitude, we used the maximum values of the second derivative, which represent the inflection point of the Gaussian function (Fig 1 (b)).

To analyze daily activity pattern of species as a function of time of day, we adjusted a multi-modal function (modified sine) because species could show more than one activity peak during the day. We calculated optimal activity times based on the maximum values of the function and compared these maximum values between species based on a confidence interval:

$$Activity = y0 + a * e^{(-x/d)} * \sin\left(2 * \mathrm{pi} * x/b + c\right)$$

where $y0$ and a determine mainly the amplitude of the response (lower and upper limits of the peaks), d and b determine the number of peaks (frequency), and c determines the distance between peaks.

Finally, to study tolerance to high temperature of the three species (tolerance experiment), we compared tolerance time at 48°C using an ANCOVA, with body weight as a co-variable for each species. Also, we performed a post hoc comparison through the Tukey test to compare between pairs of species.

Results

The three species studied significantly adjusted to a Gaussian model, showing a uni-modal pattern of activity as a function of temperature (Fig 2, Table 1). *Eucranium belenae* ($R^2 = 0.41$, $p < 0.01$) showed its activity peak (optimal temperature) at a temperature significantly lower than that for *A. cavifrons* ($R^2 = 0.23$, $p = 0.01$) and *A. fedemariai* ($R^2 = 0.22$, $p < 0.01$) (Table 1), while the latter, congener species, showed an intermediate optimal temperature. The results of the multimodal function (activity as a function of time) showed that the three species had a significant activity pattern as a function of time of day, with one or two peaks of activity throughout the day (Fig 3), depending on the species. *Eucranium belenae* ($R^2 = 0.77$, $p < 0.01$) showed just one peak of activity and was active preferentially early in the morning. *Anomiopsoides cavifrons* ($R^2 = 0.65$, $p < 0.01$) and *A. fedemariai* ($R^2 = 0.56$, $p < 0.01$) showed two well-defined activity peaks, although the peak at noon was higher in both cases (Fig 3b, c). Finally, the thermal tolerance analysis showed that a difference exists in tolerance time at 48°C among the three species (ANCOVA, $F = 3.89$, *d.f.* = 3, $p = 0.028$, and *post-hoc* comparisons). *Eucranium belenae* showed less tolerance time to high temperatures, *A. cavifrons* showed an intermediate value, and *A. fedemariai* showed the greatest tolerance time (Table 1). The co-variable (body weight) did not have a significant effect ($F = 1.23$, $p = 0.2731$).

Discussion

According to our hypothesis, the daily activity pattern of the species studied differed with temperature and time of day, and we argue that it is associated to the thermal tolerance of each species. The least tolerant species, *E. belenae*, shows its

Table 1 Daily patterns of activity of three dung beetle species in a Monte Desert area in central-western Argentina. Mean (5–95% CI).

	Eucranium belenae	*Anomiopsoides cavifrons*	*Anomiopsoides fedemariai*
Body weight (mean)	1.35	0.14	0.48
Optimal temperature (°C)	28.9 (27.5–30.4)	44.2 (34.8–52.8)	57.8 (47.2–NS)
Primary peak of activity	9:12 (8:38–9:52)	10:50 (9:47–11:49)	11:46 (10:52–12:37)
Secondary peak of activity	NA	18:29 (16:54–NS)	17:21 (16:22–18:28)
Tolerance period (48°C) (s)	409 ± 642[a]	1786 ± 517[b]	2516 ± 327[b]

Different letters indicate significant differences.

NA not applicable, *NS* not calculated.

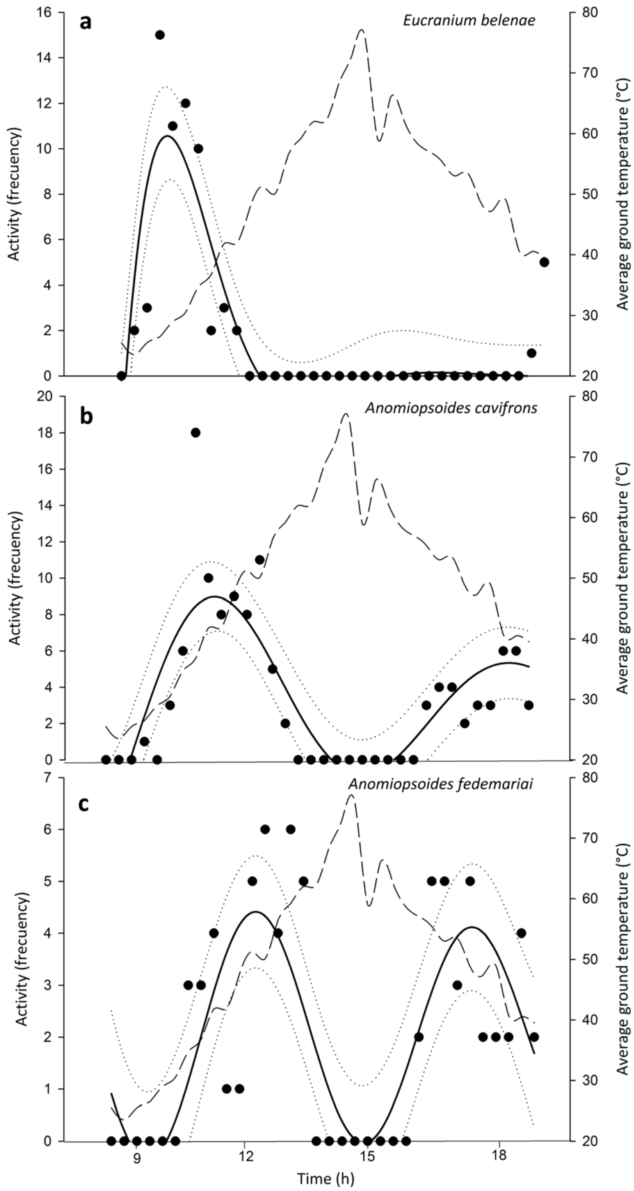

Fig 3 Patterns of daily activity of *Eucranium belenae* (**a**), *Anomiopsoides cavifrons* (**b**), and *Anomiopsoides fedemariai* (**c**) as a function of time of day. The dashed line represents average ground temperature, the continuous line represents activity, and the dotted line represents the confidence interval of activity.

activity peak at lower temperatures corresponding to the morning, while the more tolerant species, of the genus *Anomiopsoides*, had their activity peak at higher temperatures, at noon. The uni-modal activity pattern of *E. belenae* may be due to the limited time period measured. It is possible that this species has a second activity peak at dusk, when the temperature is lower. This relation between activity and thermal tolerance coincides with studies showing that activity patterns are related to physiological properties, such as thermoregulation, in dung beetles (Verdú *et al* 2004, 2012) and other invertebrates and vertebrates (Hastings & Toolson 1991, Scheers & Van Damme 2002), and also to endothermy in dung beetles (Bartholomew & Casey 1977, Bartholomew & Heinrich 1978, Caveney *et al* 1995).

It has been demonstrated that mechanisms of thermoregulation explain, at least partly, daily activity patterns in each species of endothermic dung beetles (Verdú *et al* 2012). Therefore, species that have active mechanisms of thermoregulation may be active during times of the day when temperature is high, because they can eliminate excess body heat and prevent dying of overheating. In the case of ectothermic species, such as these beetles from extreme environments, they show the same characteristic, a behavioral mechanism that allows them to prevent overheating (F.C Ocampo and K. Sheldom obs. pers). Therefore, the activity pattern shown by the species under study may be explained by that behavioral mechanism. Although *A. fedemariai* and *A. cavifrons* have similar activity patterns, *A. fedemariai* has a higher tolerance time which allows individuals of this species to cover longer distances while seeking for food. Individuals of *A. cavifrons*, instead, only cover short distances avoiding overheating and returning promptly to their burrows (F.C. Ocampo, in prep).

The fact that species of the genus *Anomiopsoides* are active at a time of the day when temperature is high (although not as high as between 13:00 and 17:00 h, when we did not detect activity) suggests that they have an active thermoregulation mechanism that allows them to dissipate excess body heat. This may offer a competitive advantage to *A. fedemariai* and *A. cavifrons* over *E. belenae*, as they can remain active at a time of day when the latter species cannot. Also, active thermoregulation may explain the daily activity pattern observed, because, since all species feed on similar resources, thermoregulation may allow them to divide their activity throughout the day and, concomitantly, coexist in the same habitat. Although the three species feed on dehydrated dung (Ocampo & Philips 2005, Ocampo 2007, 2010a), it has been observed that species of the genus *Anomiopsoides* tend to use different resources when they are in sympatry. *Anomiopsoides fedemariai* continues to use dry dung, but *A. cavifrons* turns, almost exclusively, to plant material (Ocampo 2007). This division of resources may offer an explanation of how species with such similar habits may coexist and be active at the same time of day (Ocampo & Hawks 2006).

Ours is the first study on eco-physiology of dung beetles in the Monte Desert. Although we partly explain daily activity of the three species studied as a function of their thermal tolerance, more studies are needed to complement ours. Studies on thermoregulation and water loss (respirometry) for species that live in an extreme environment may give greater understanding about their daily behavior. Moreover, the search for physiological and ecological mechanisms that explain the distribution of desert species, particularly those mechanisms related to thermal tolerance, is especially important in times of rapid climate change driven by humans (Sunday *et al* 2011).

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