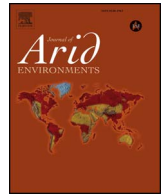




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Ecophysiological traits and activity patterns of coleopterans from Atacama Desert provide clues to the functional responses of small ectotherms to climate change

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ABSTRACT

There is an increasing contribution of ecophysiology in community ecology and climate change contexts. As such, functional patterns under extreme water and temperature restrictions in deserts can provide inference of the responses of small ectotherms to climate change. However disentangling the interactive effects between both factors requires experimental evidence. Here we took advantage of a *flowering desert* episode promoting a population bloom in *Gyriosomus* (Coleoptera: Tenebrionidae) beetles from Atacama Desert to test this interactive hypothesis. By systematically sampling two sympatric *Gyriosomus* species, we analyzed the differences in activity, body temperature and water loss rate. Body size regardless the species or sex was responsible for the observed behavioral and ecophysiological patterns. Large coleopterans (females > males, *G. kingi* > *G. planicollis*) lost less water and were active at higher temperatures making their bimodal diel activity less marked. Beyond the confirmation of the crucial role of water availability and inactivity in arid ecosystems, these results suggest that functional responses of small ectotherms to climate change will be size-dependent while advocate for integrating hydric and thermal data to better understand this transition.

1. Introduction

The inclusion of functional traits in the analysis of biodiversity is improving our understanding on how species and communities vary in time and space, how they interact and which conservation risks they face (McGill et al., 2006; Gilman et al., 2010). In particular, ecophysiological traits provide inference on the species' fundamental niche, overcoming the effects of biotic interactions and dispersal (Sillero, 2011). If fundamental niche of a given species can be consistently assessed, predicting its responses under novel environments will be more reliable (Kearney et al., 2010). Because of that, ecophysiological information is gaining relevance in macroecology and risk assessment, particularly for small ectotherms which are largely sedentary and directly exposed to local climate variations (Chown and Gaston, 2008; Žagar et al., 2017). In this context, the analysis of the ecophysiology in those species living under extreme environmental conditions in terms of

humidity and temperature may shed light on the expected responses by species from more mesic environments will face in the future if climate change scenarios, dominated by warming and aridification, are confirmed (Huey et al., 2012).

In arid environments water availability and extreme temperatures are crucial factors controlling biological processes of organisms, affecting their diversity and abundance (Whitford, 2002). However, disentangling their effects on a given species in practice reveals difficult since their variation in nature is generally associated and effects on organisms may be interactive. Hence, not only field surveys but also experimental evidence is needed. In this context desert coleopterans constitute excellent model organisms. This is highly successful group which combines several phenotypic adaptations to survive in this restrictive environment in terms of temperature and humidity (Cloudsley-Thompson, 2001). Remarkably, they can be locally abundant, especially during the rare humid episodes taking place in desert ecosystems

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Table 1

Number of specimens, body mass (m_b), body temperature (T_b), substrate temperature (T_s) and air temperature (T_a), and recorded per species and sex in the Llanos de Challe National Park (Atacama region of Chile). The values correspond to the mean, the standard deviation and maximum and minimum value.

Mean \pm SE Min – Max	<i>Gyriosomus kingi</i>		<i>Gyriosomus planicollis</i>	
	males (n = 95)	females (n = 93)	males (n = 27)	females (n = 33)
Mb (g)	0.51 \pm 0.01 0.3–0.7	1.07 \pm 0.02 0.8–1.6	0.42 \pm 0.02 0.2–0.6	0.84 \pm 0.03 0.7–1.3
Tb (°C)	31.88 \pm 0.48 20.40–39.52	33.02 \pm 0.50 21.96–40.66	32.88 \pm 0.73 25.49–39.52	33.90 \pm 0.64 23.62–39.00
Ts (°C)	36.18 \pm 0.85 21.23–54.79	36.65 \pm 0.81 22.89–54.27	36.67 \pm 1.20 27.3597–49.80	38.24 \pm 1.25 22.16–52.40
Ta (°C)	23.25 \pm 0.31 16.76–29.65	23.29 \pm 0.30 17.90–31.00	24.01 \pm 0.60 18.839–29.23	24.09 \pm 0.58 18.63–30.89

(Cloudsley-Thompson, 1991), then providing a unique opportunity for record both field and experimental data.

In the transitional coastal desert of Chile (latitude 25–32° S), the irregular precipitations above 150 mm combined with appropriate temperature and light conditions may cause an increase in primary production, mainly of short-lived geophytes (Gutiérrez, 2008). This event, which represents the humid phase of the coastal desert (flowering desert), causes a direct or indirect increase in the population size of numerous taxa by activating their halted biological cycles (latency, diapause), triggering reproductive events (Armesto et al., 1993), or causing population outbreaks (Cepeda-Pizarro et al., 2007; Pizarro-Araya et al., 2015). The epigeal tenebrionid beetles from the genus *Gyriosomus* (Cepeda-Pizarro et al., 2005a, 2005b) represent an endemic and eremic group from Chile with 38 species described to date. Approximately 90% of the genus diversity is distributed across coastal dunes and plains of the Atacama and Coquimbo regions (Pizarro-Araya and Jerez, 2004; Pizarro-Araya and Flores, 2004). *Gyriosomus* populations tend to increase during the humid phase of the coastal desert, contributing to plant resource fragmentation and nutrient cycles (Cepeda-Pizarro et al., 2005a, 2005b), and serving as a key trophic resource for reptiles and mammals (Castro et al., 1991; Pizarro-Araya, 2010; Valladares Faúndez et al., 2015).

Despite this pivotal role, studies on *Gyriosomus* have focused mainly on taxonomical (Mondaca, 2004; Pizarro-Araya and Flores, 2004), bionomical (Pizarro-Araya et al., 2005, 2007, 2011), biogeographical (Pizarro-Araya and Jerez, 2004), and general ecological aspects (Cepeda-Pizarro et al., 2005a, 2005b; Pizarro-Araya, 2010; Alfaro et al., 2009, 2016), whereas physiology and ethology (Vidal et al., 2011) have been largely neglected. However, both are relevant to interpret their temporal and -spatial abundance and distribution (Bozinovic, 2002). As other desert ectotherms adult *Gyriosomus* are directly exposed to the physical restrictions prevailing in such environments, namely strong thermal variations and the limited availability of free water (Cloudsley-Thompson, 2001). To maintain their water balance and body temperature within an optimum range, these organisms possess a combination physiological, behavioral, and morphological strategies (Cloudsley-Thompson, 1988).

In this context, we conducted an integrated analysis of the activity patterns and the thermal and hydric biology of two *Gyriosomus* species living sympatrically in a dune ecosystem of the coastal area of the Atacama region of Chile (Pizarro-Araya and Jerez, 2004; Cepeda-Pizarro et al., 2005a). These species can be considered representing the extreme of an environmental shift in global climate that is affecting most small terrestrial ectotherms. By understanding the physiological and behavioral mechanisms used by these species in arid conditions we intend to infer the responses, and vulnerabilities, of small ectotherms to climate change. As such, we examined the activity pattern, body temperatures and water loss rates considering species and sex while taking body size into account. Here we postulate that the water loss rate, traded off with body temperature and determined by body mass, would be the main factor restricting the diurnal activity. In this way small

ectotherms should restrict epigeal activity to those hours when thermal costs are lower, namely, reducing evaporative water loss at very high temperatures and, hence, maintaining a positive water balance.

2. Materials and methods

2.1. Study site

The study was conducted in the Llanos de Challe National Park (28°11'02.7" S; 71°09'18.9" W, 30 m.s.l.; Atacama region, Chile). This area is part of the plant formation of the coastal desert of Huasco (Gajardo, 1993), included in the transitional coastal desert of Chile (latitude 25–32° S) (Cepeda-Pizarro et al., 2005a, 2005b). The climate in the area is semiarid subtropical Mediterranean in the northern margin and marine subtropical Mediterranean in the southern margin (Novoa and Villaseca, 1989). The total precipitation recorded in the study area (Huasco Bajo Station 20°20'21" S; 71°11'35" W, 50 m.s.l) in 2015 was 50.5 mm and was concentrated in July (11 mm), August (37 mm), and October (2.5 mm) (DGA, 2016).

2.2. Study species

Gyriosomus kingi Reed, 1873, and *Gyriosomus planicollis* Gebien, 1944 are two tenebrionid species widely distributed along the Atacama region from Hacienda Castilla - Llanos de Challe National Park (27°53'-28°11' S) to Travesía - Freirina (27°32'-28°30' S). Both species live in sympatry and syntopy in dune ecosystems of the coastal area of the Atacama region of Chile (Pizarro-Araya and Jerez, 2004; Cepeda-Pizarro et al., 2005a). They are univoltine, have their last larval stage in diapause (Cepeda-Pizarro et al., 2005a) and emerge after rainfall episodes. Morphologically, both species differ in size (Cepeda-Pizarro et al., 1996), with *G. kingi* (mean length 17.86 mm) being larger than *G. planicollis* (mean length 16.72 mm). At intraspecific level they are both characterized by their notorious sexual dimorphism where females are larger than males (Cepeda-Pizarro et al., 1996; see also Table 1).

2.3. Censuses

A total of 188 specimens of *G. kingi* (95 males; 93 females) and 60 specimens of *G. planicollis* (27 males; 33 females) were captured in a random walking route during a single uninterrupted sampling effort conducted between 8.30 a.m. and 9.00 p.m. in the spring of 2015. The study site covered an area of 105 ha, which was traveled through 100-meter walking routes arranged in a parallel manner according to Vidal et al. (2011).

For each captured specimen we recorded the specimen's sex (based on sexual secondary characters) and body mass (Digital Scale, Model 1108-5; \pm 0,01 g) together with the time of the day. To prevent pseudoreplication all measured individuals were marked using an indelible pen.

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