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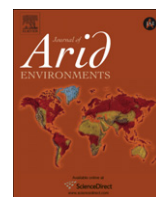
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## Daily activity and thermoregulation in predator–prey interaction during the Flowering Desert in Chile

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### ABSTRACT

We studied how features of thermal resources affect the patterns of activity of predator (*Callopistes maculatus*) and its prey (*Gyriosomus batesi* and *Gyriosomus subrugatus*) during the phenomenon of the Flowering Desert in Chile. We predict that restrictions or variations in temperature affect mainly the activity of insects, and that this variation in the activity of insects affects the patterns of activity of the predator. The daily activity of the three species was bimodal, but both prey species disappear when temperatures exceed 40 °C. According to our results, the prey are thermoconformers to air and substrate temperature, whereas the predator is a thermoregulator to environmental conditions by their independence of air and substrate temperature.

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### 1. Introduction

Temperature has profound effects on ectothermic animals (Cossins and Bowler, 1987). It controls nearly all physiological and biochemical processes, thus determining a considerable number of life-history traits (Finke, 2003). On a long-term scale (i.e., evolutionary), temperature has important consequences for ectotherms, determining patterns of daily activity (Alexander, 1999), movement (Gilbert and Raworth, 1996), body size (Sibly and Atkinson, 1994), reproduction (Madsen and Shine, 1999), and feeding (Blouin-Demers and Weatherhead, 2001), whereas on a short-term scale (i.e., seasonal changes), temperature modified some of these patterns (Labra et al., 2001).

In desert ecosystems, the pattern of productivity is regulated by short and infrequent pulses of rainfall (Whitford, 2002). Thus, productivity may be high, supporting rich but short-lived vertebrate and invertebrate assemblages (Cossins and Bowler, 1987). In this context, predator–prey interactions play a major role in the structure and function of desert assemblages (Closs and Lake, 1994)

influencing factors mediated by environmental conditions such as behavior (Peterson, 1987). Thus, the analysis and interpretation of predator–prey interactions in desert systems associated with thermal resources are important factors in the ecology of ectothermic organisms such as insects (Heinrich, 1995) and lizards (Spotila and Standora, 1985). As the cost of adjusting body temperature close to mean activity temperature in an arid environment may be considerable (Al-Johany and Al-Sadoon, 1996), it could be beneficial for an ectothermic animal in a habitat with a wide range of temperatures and low food availability not to maintain a narrow body temperature range (Peterson, 1987). Prey can influence predators, since prey abundance and quality affect the feeding rates, growth, and reproductive success of predators (Torres-Contreras et al., 1994). Also, temporal and spatial changes in prey availability and vulnerability may have an effect on the movement, and the spatial and temporal distributional patterns of predators (Meserve et al., 2003).

The Atacama Desert, located on the western coast of South America, is the driest desert in the world (Rundel et al., 2007). There are sites with no recorded rainfall where erosion occurs primarily from the wind. The "Desierto Florido" (Flowering desert) is a remarkable phenomenon which usually takes place when El Niño/Southern Oscillation causes the ocean currents to shift and direct storms towards the desert that promote a high biodiversity of

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plants, invertebrates, and vertebrates that increases the availability of resources for predators (Meserve et al., 2003; Pizarro-Araya, 2010).

*Callopiastes maculatus* (Molina, 1782) is a moderate-sized (81.5–173.0 mm SVL) teiid lizard that inhabits extended sand burrows in scrubland habitats of northern Chile (Donoso-Barros, 1966; Vidal, 2008). Information available on *C. maculatus* suggests that this species feeds mostly on plants, invertebrate animals, small rodents; *Abrothrix olivaceus* (Wartherhouse, 1837), and lizards (*Liolaemus*) (Castro et al., 1991), and cannibalism has been reported (Vidal and Ortiz, 2003). In the northern distribution of *C. maculatus*, its diet has been described as consisting of abundant invertebrates from the genus *Gyriosomus* Guérin Meneville, 1834. In this area, two *Gyriosomus* species (Tenebrionidae) coexist with this lizard (Pizarro-Araya and Jerez, 2004; Pizarro-Araya et al., 2008): *G. batesi* Fairmaire, 1876, and *G. subrugatus* Fairmaire, 1876. It has been described that *C. maculatus* feeds on these two species (Reyes, 1998), whose relative abundances fluctuate between a Flowering Desert year (i.e., ENSO year [El Niño–Southern Oscillation] or humid non-ENSO year) and a non-Flowering Desert year (i.e., dry non-ENSO year) (Pizarro-Araya, 2010). Both *Gyriosomus* species show sexual dimorphism where males are smaller than females. In addition, *G. batesi* are bigger than *G. subrugatus* (J. Pizarro-Araya pers. obs.).

We report how features of the environmental thermal resources affect the patterns of activity of the predator (*C. maculatus*) and its prey (*G. batesi* and *G. subrugatus*). We predict that the restrictions or variations in temperature affect mainly the activity of insects (*Gyriosomus* species) due to differences in body size (sexual dimorphism and differences between species) and their dependence on environmental conditions, and that this variation in activity modulates the patterns of activity of the predator.

## 2. Materials and methods

### 2.1. Study area

The study was performed during November 2002, in two desert localities from northern Chile: Chacrita (28°23'39.3"S, 70°42'49.4"W, 644 msl) and Algarrobal (28°07'45.6"S, 70°39'36.5"W, 428 msl), Vallenar, Huasco Province, Atacama Region, Chile (Fig. 1). The sites are located on the Algarrobal-

Carrizal basin, which has no permanent superficial water courses. However, sporadic and intense rains can originate superficial flows, in some cases torrentially, that flow down its slopes (Luzio and Alcayaga, 1992). The habitat is a scrubland dominated by the shrubs *Encelia canescens* Lamarck, 1786 (Asteraceae), and *Skytanthus acutus* Meyen, 1834 (Apocynaceae) (Squeo et al., 2008). In a typical year, the vegetation is limited to an association of *Euphorbia copiapina* Philippi, 1858, *Skytanthus acutus* Meyen, 1834, *Encelia tomentosa* Walpers, 1840 (Gajardo, 1993). During the Flowering Desert, an explosion of biodiversity promotes high lizard and arthropod abundances, mainly of coleopteran tenebrionids, as a result of the high productivity and availability of food resources in the environment (Pizarro-Araya et al., 2008).

### 2.2. Daily activity

Sites were continuously walked along parallel 100 m transect lines during the entire daily active period of lizards and insects (09:00 AM to 08:00 PM). The transects were walked in opposite directions to minimize the probability of repeatedly observing the same individual. Immediately after observation, the following data were recorded: time of the day, species, sex, air temperature (10 cm above the substrate,  $T_a$ ), and substrate temperature (in contact with the surface,  $T_s$ ) with a UNI-T M-890C thermometer ( $\pm 0.1$  °C). Sex in these individuals is easy to determine because in the case of lizards, males present a red-orange coloration in the chest that females do not have (Donoso-Barros, 1966; Vidal and Ortiz, 2003); in the case of tenebrionids, females are bigger than males (Aalbu et al., 2002). The species of *Gyriosomus* were determined using keys of the Kulzer (1959) and comparing the specimens with material preserved in the Museo Nacional de Historia Natural (MNNC, Chile).

### 2.3. Thermal physiology

A total of 66 lizards (*C. maculatus* 30 males, 36 females) and 204 tenebrionids (*G. subrugatus*: 85 males, 53 females; *G. batesi*: 31 males, 35 females) were captured. After capture, the following data were recorded: species, sex, body temperature ( $T_b$ ); cloacal temperature for lizards with a Cu-constantan thermocouple (Cole Parmer® thermometer,  $\pm 0.1$  °C) and subelytral cavity temperature for tenebrionids (with a UNI-T M-890C thermometer,  $\pm 0.1$  °C)

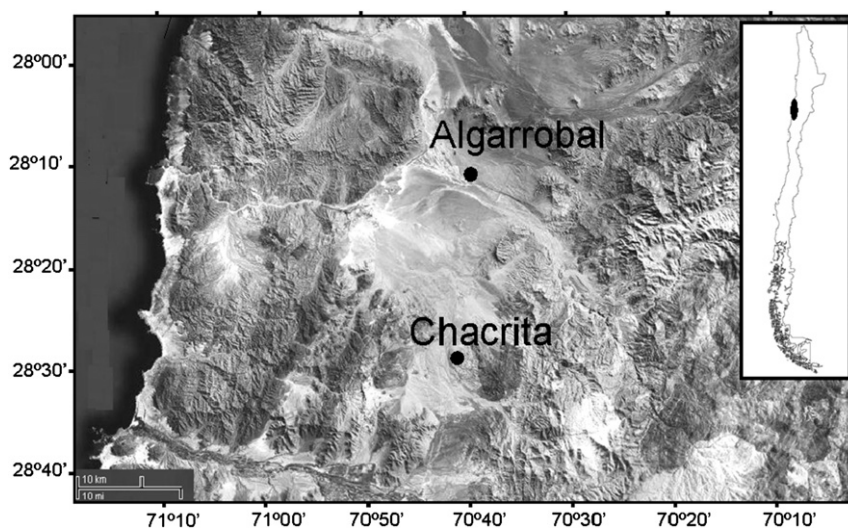


Fig. 1. Geographic location of the study sites. Insert: The main map corresponds to the dark area of the general map of Chile.

according to Duncan (2003), air temperature ( $T_a$ : 10 cm above the substrate), and substrate temperature (in contact with the surface,  $T_s$ ). Both thermometers were calibrated before taking the field measurements. Lizards were weighed (g) and body length (mm) was measured in each insect. Subsequently, the animals were released.

### 2.4. Statistical analyses

Prior to statistical analyses, all data were examined for assumptions of normality and homogeneity of variance, using Kolmogorov–Smirnov and Levene's tests, respectively. The analyses of the differences in weight (lizards) and body length (darkling beetles) between sexes were performed by means of a one-way analysis of variance (ANOVA). A one-way ANCOVA was used to determine differences in body temperature between sexes in relation to air and substrate temperatures, with weight (lizards) and body length (insects) as covariate (Sokal and Rohlf, 1995), followed by Tukey tests for differences between the species. The thermoregulatory ability was estimated from the variances of  $T_b$  and from the slopes of the linear regressions (Sokal and Rohlf, 1995) between  $T_b$  vs.  $T_a$ , and between  $T_b$  vs.  $T_s$  (Huey, 1982). A slope equal to one indicates that animals are completely thermoconformers (Cortés et al., 1992).

### 3. Results

A total of 66 lizards (30 males, 36 females) and 700 tenebrionids (*G. subrugatus*: 356 males, 141 females; *G. batesi*: 126 males, 77 females) were observed during sampling. The weight (for lizards), length (for insects), and temperature measurements of the different species and sexes are shown in Table 1. A one-way ANOVA considering sex as a factor (on weight and length) indicated that males of *C. maculatus* were significantly larger than females ( $F_{(1,64)} = 7.297$ ,  $P = 0.0088$ ) while among *Gyriosomus* species, females were significantly larger than males (*G. subrugatus*:  $F_{(1,136)} = 136.79$ ,  $P = 0.0001$ ; *G. batesi*:  $F_{(1,64)} = 119.28$ ,  $P = 0.0001$ ).

The daily activity of the three species is shown in Fig. 2. Although *C. maculatus* shows a bimodal activity, both prey species disappear when air temperatures exceed 40 °C, showing discontinued and bimodal activity. Significant differences in activity were recorded between the three species studied ( $F_{(2,106)} = 11.27$ ;  $p = 0.0003$ ). *Gyriosomus* species differ in starting activity time schedule ( $p < 0.001$ ), with *G. subrugatus* (smaller species) beginning its activity (10:00 AM) before *G. batesi* (larger species; 11:00 AM) and *C. maculatus* (11:00 AM). In the afternoon, the activity occurs in the opposite direction. When analyzing the sexes separately, significant differences in activity are found where insect males tend to be more abundant at the beginning and end of the day, while the lizards there is a contrary trend ( $P = 0.019$ ; Fig. 2).

The mean body temperature of *C. maculatus* was 39 °C, both sexes with similar temperatures ( $P = 0.296$ ), whereas that of *G. subrugatus* was 24 °C, without differences between sexes ( $P = 0.119$ ) and *G. batesi* was 27 °C ( $P = 0.292$ ). Body temperature

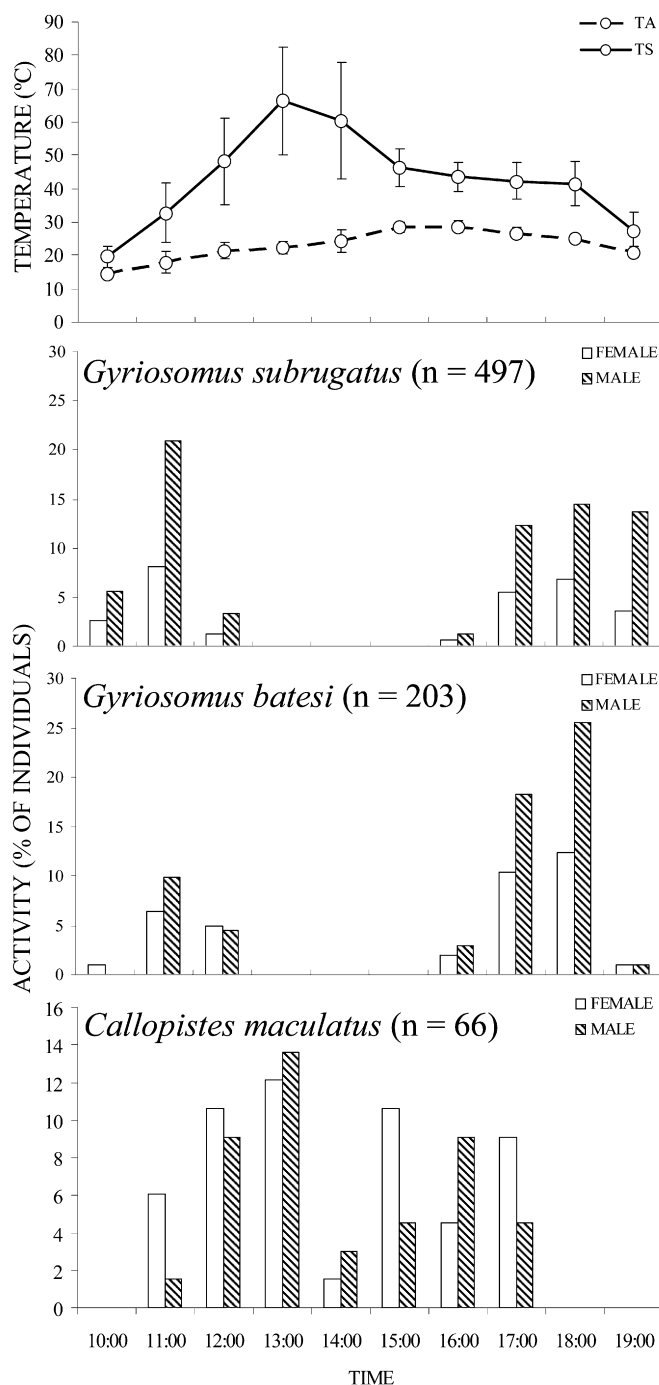


Fig. 2. Daily activity (for sexes) of the prey *Gyriosomus subrugatus* and *Gyriosomus batesi* and their predator, *Callopistes maculatus*. It indicates air (TA) and substrate temperature (TS) during daily activity.

Table 1 Mean ± standard error for weight (W, *Callopistes maculatus*), body length (BL, *Gyriosomus* species), body temperature ( $T_b$ ), air temperature ( $T_a$ ), and substrate temperature ( $T_s$ ) on three species from the Flowering desert. n: sample size, M: male, F: female.

Species	n		W(g)/BL(mm)		$T_b$		$T_a$		$T_s$	
	M	F	M	F	M	F	M	F	M	F
<i>C. maculatus</i>	30	36	37.25 ± 1.9	31.03 ± 1.4	38.28 ± 0.8	39.61 ± 0.9	25.03 ± 0.7	24.82 ± 0.7	50.28 ± 2.3	51.47 ± 2.8
<i>G. subrugatus</i>	85	53	13.25 ± 0.1	15.42 ± 0.1	25.25 ± 0.3	22.68 ± 0.5	24.30 ± 0.2	22.17 ± 0.4	27.09 ± 0.2	25.12 ± 0.4
<i>G. batesi</i>	31	35	13.98 ± 0.3	19.24 ± 0.3	27.20 ± 0.3	26.05 ± 0.6	27.9 ± 0.3	26.06 ± 0.6	31.15 ± 0.4	28.65 ± 0.7

showed similar ranges and standard deviations in both sexes in invertebrate species, as well as lizard species (Table 1). There were no significant differences between males and females in the relationship  $T_b$  versus  $T_a$  (*C. maculatus*:  $P = 0.195$ ; *G. subrugatus*:  $P = 0.219$ ; *G. batesi*:  $P = 0.221$ ) and  $T_b$  versus  $T_s$  (*C. maculatus*:  $P = 0.846$ ; *G. subrugatus*:  $P = 0.820$ ; *G. batesi*:  $P = 0.327$ ). The slopes of the regression lines of  $T_b$  versus  $T_a$  and  $T_b$  versus  $T_s$  were equal to zero for both sexes of *C. maculatus*, making it a thermoregulator (Fig. 3). *Gyriosomus* species instead showed slopes different from zero for both sexes because they are thermoconformers (Figs. 4 and 5).

#### 4. Discussion

Ecological theory postulates that energy availability affects population densities (Sutherland, 1983). However, energy acquisition may entail costs that differ in time and in space. In the past two decades a large volume of research has focused on foraging trade-offs, the interplay between the need to acquire energy by foraging and the costs incurred in this life-sustaining activity (e.g., Fedriani and Manzaneda, 2005). Few of the numerous studies on interspecific interactions address the patterns of resource availability and their possible role in community structure (e.g., Kneitel and Chase, 2004) or their behavior (Chown and Nicholson, 2004). Resource availability is a significant variable in ecological interaction, both as a lead force in population dynamics and indirectly through diel, seasonal, and spatial variations in habitat use. In the Atacama Desert we find potential relationship between availability of resource patterns and predator behavior, where prey

(thermoformer and restricted in their daily activity), could determine the behavior of a predator (thermoregulator) during their daily activities, although this study did not examine the direct relationship between the two behaviors. *Gyriosomus* species, as all endemic South American tenebrionids, have not been studied insofar as thermal behavior is concerned, so the information provided by this study is a first approximation to the understanding of their physiology in desert habitats.

Fluctuations in environmental temperatures between day and night, and seasonal temperatures in arid environments are wide; hence organisms have to deal with these changes so as to maximize their activity periods to cope with low prey density and survive in these harsh habitats (Al-Johany and Al-Sadoon, 1996). In the Chilean Desert, thermal changes between day and night are abrupt (Khodayar et al., 2008), which suggest that organisms could face restrictions for its maintenance in this desert. For *C. maculatus* (predator in this desert system), thermal restrictions may be irrelevant. In fact, despite showing a bimodal activity typical of lizards from temperate environments, it shows a high activity during the hours of greatest heat. In contrast, both *Gyriosomus* species (considered prey in this system) show a narrower activity during the hours of higher temperature (40 °C), although their activity ranges from 24 °C in *G. subrugatus*, to 27 °C in *G. batesi*. The key to the survival of Tenebrionidae and other beetles in dry environments consists in avoiding climatic extremes as far as possible through a combination of refuge against the most adverse conditions, morphological adaptations, behavior, and specialized physiology (Cloudsley-Thompson, 2001). On the other hand, insects are not the only prey of *C. maculatus*, since the lizards of the genus

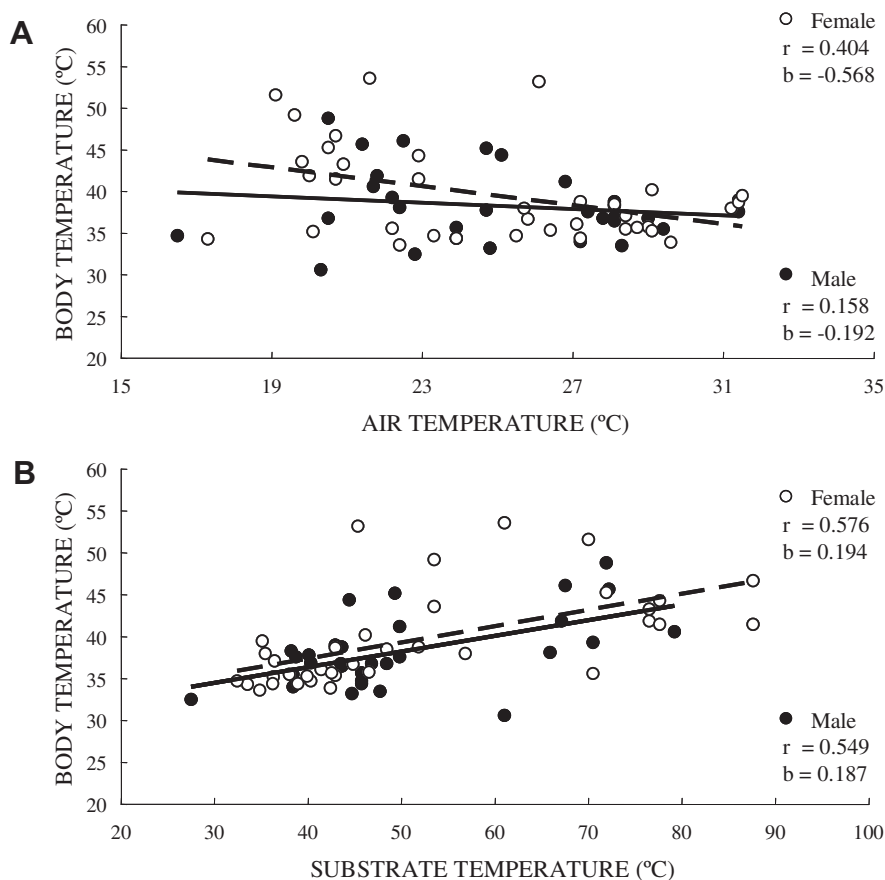


Fig. 3. Relationship between (A) body and air temperatures, and (B) body and substrate temperatures in males and females of *Callotistes maculatus*. The slopes ( $b$ ) and  $r$  values are indicated.

*Liolaemus*, which are blooming desert moments of great abundance, are also prey to the reptile (Vidal and Ortiz, 2003). In these cases, prey lizards have clear bimodality daily activity patterns, but also thermoregulatory (Cortés et al., 1992). This fact suggests that perhaps the alleged link between daily activities *Callopistes* with insect prey, are also related to the lizards' prey. However, it is important to note that, according to Cortés et al. (1992), *C. maculatus* is dependent thermally during the autumn-winter, unlike lizards of the genus *Liolaemus*, opening a new possibility to study to try to determine a direct relationship between prey and predator pattern.

Whereas thermal responses are primarily behavioral, adaptation responses to aridity are mostly physiological. In fact, desert beetles avoid desiccating environments in various ways, tolerate transient fluctuations in the ionic composition of their haemolymph, restrict water loss through a combination of ecological adaptations and physiological processes, and use moisture obtained opportunistically from a variety of sources (Cloudsley-Thompson, 2001; de los Santos and de Nicolas, 2008). Other desert beetles, such as *Gyriosomus* species in the Atacama Desert, avoid the heat of the sun by hiding in vegetation or under stones, or burying themselves deeply in the substrate (Ward and Seely, 1996). Other studies on tenebrionid populations frequently emphasize structural modifications such as the length and form of the legs (Krasnov et al., 1996) of the subelytral cavity (Duncan, 2003), and body size (Holland et al., 2005) as adaptations to microclimate and

edaphic factors. The typical morphological adaptations of desert Tenebrionidae were listed by Marcuzzi (1960) as follows: (1) increase in the volume of the subelytral cavity; (2) an unusually dark-colored integument; (3) fossorial legs in both larvae and adults; (4) large body size; (5) shortening and broadening of the bodies of the larvae. Also, heat may be gained or lost by conduction, convection, and radiation. In the case of surface-living desert beetles, heat exchange by conduction can largely be ignored because only very small areas of the tarsi are normally in contact with the substrate (Koch, 1961). In contrast, heat exchange by convection is very important (Turner and Lombard, 1990).

In this way, the daily activity of many beetle species has been described as thermally opportunistic (i.e., thermoconformer) because the insects show variable activity patterns associated with a range of air temperatures (Cooper, 1993) or climates (Scholtz and Caveney, 1992) which modulate other behaviors such as feeding during the morning, breeding, and dispersal in the afternoon. An important consideration should be made here. The fact that insect species (*G. batesi* and *G. subrugatus*) show bimodal daily activity could explain the behavior of *C. maculatus* (predator) in the sense that this could adjust its daily activity to that of the prey. Diel, lunar, and seasonal patterns in predation risk seem to affect foraging activity patterns and foraging microhabitat use to minimize risk (Mandelik et al., 2003). Reproductive success is probably more important for *Gyriosomus* than the risk of predation by *C. maculatus*.

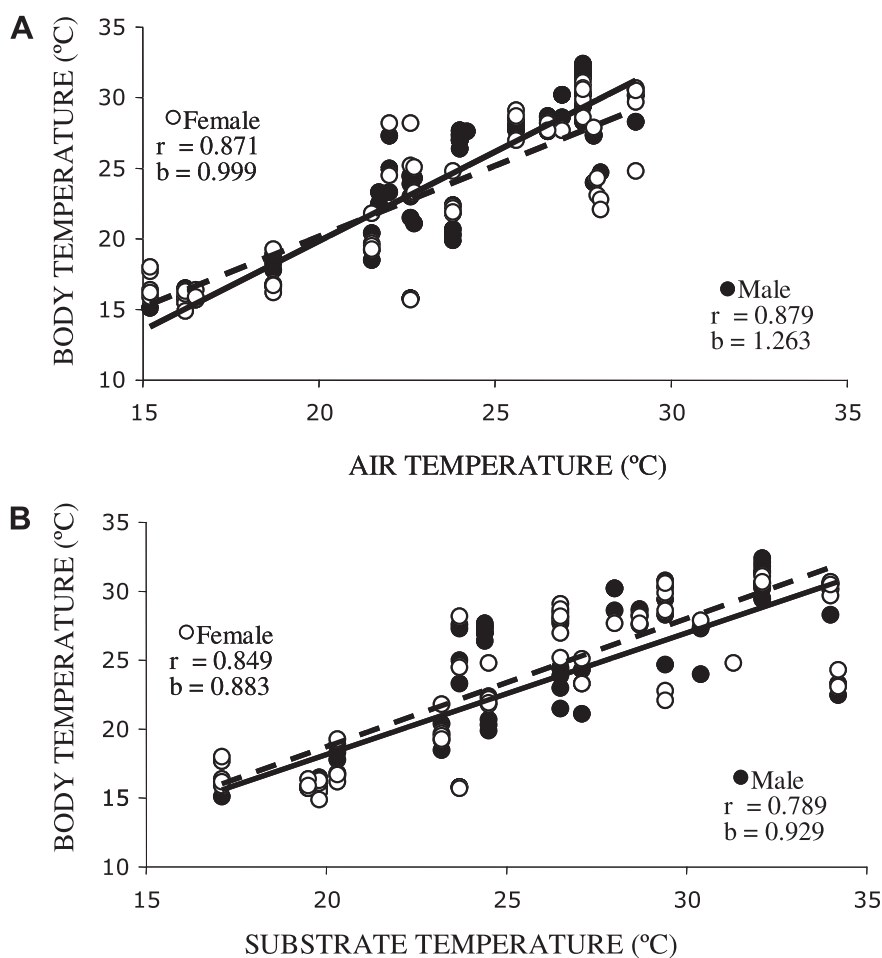


Fig. 4. Relationship between (A) body and air temperatures, and (B) body and substrate temperatures in males and females of *Gyriosomus subrugatus*. The slopes ( $b$ ) and  $r$  values are indicated.

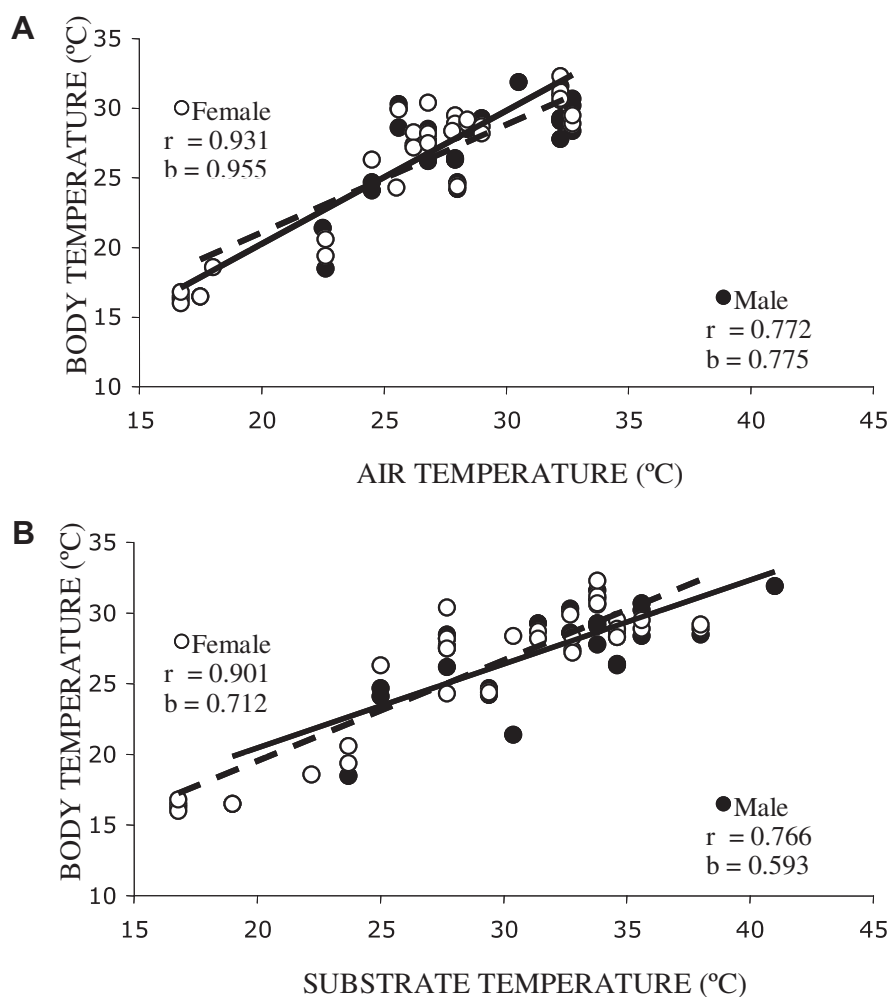


Fig. 5. Relationship between (A) body and air temperatures, and (B) body and substrate temperatures in males and females of *Gyriosomus batesi*. The slopes ( $b$ ) and  $r$  values are indicated.

## 5. Conclusions

According to Stevenson (1985), ectotherms use behavioral mechanisms to find appropriate thermal conditions within their environments because their metabolic rates and other physiological mechanisms are usually insufficient to control body temperature under a single set of environmental conditions. For *Gyriosomus* species, the inability to properly thermoregulate could have a deleterious effect, e.g., impaired development, compromised mobility, ineffective foraging, poor predator evasion, and unsuccessful mating, so behavioral thermoregulation is a highly effective method of maintaining preferred body temperatures. Although *C. maculatus* prey on these species because of their high abundance and low thermoregulatory capacity, *C. maculatus* could be considered an efficient predator.

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