# Activity and body orientation of *Gallotia galloti* in different habitats and daily times

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Abstract. In lizards, site selection is related to the acquisition of resources such as refuges, mates or prey, but also to the exploitation of sites suitable for thermoregulation. The latter process may be affected by lizard posture and body axis orientation in relation to the sun as a way to optimize heat exchange throughout the day. Specific postures and body orientations could also contribute to more efficient signal transmission in social contexts. In this paper we analyze activity and body axis orientation of adult males and females of the lacertid *Gallotia galloti* in two localities of Tenerife with different structural habitats. We performed transects at both sampling localities in the morning and at midday during May and June of three years (2002-2004). The numbers of lizards detected per unit time during transects at both localities were similar; however, significantly more males than females were detected. Moreover, more lizards were found oriented parallel or perpendicular to the sun, neither in the morning nor at midday, and there was no significant relationship between air temperature and lizard body orientation. This suggests that lizard body orientation is not constrained by thermoregulatory requirements. We discuss alternative hypotheses and conclude that body axis orientation in *G. galloti* lizards may reflect a compromise between the conflicting demands imposed by thermoregulation and social communication.

Keywords: communication, detection rates, Lacertidae, lateral signals, lizards.

#### Introduction

The interplay between habitat characteristics, behavioral patterns and thermoregulation has received much attention in studies of lizard behavior and ecology (Adolph and Porter, 1993; Tracy, 1982). The location of ectotherms in specific sites inside their home ranges has often been interpreted in terms of opportunities for thermoregulation, as it has important consequences for body temperature regulation (Pearson, 1977; Huey, 1982, 1991; Huey et al., 1984; Adolph, 1990; Schäuble and Grigg, 1998; Melville and Schulte, 2001; Scheers and Van Damme, 2002). Posture and body axis orientation can also affect heating/cooling rates and body temperature in many reptiles (Bartholomew, 1982; Bauwens et al., 1996;

Díaz et al., 1996; Ayers and Shine, 1997; Seebacher, 1999; Sartorius et al., 2002).

Site selection, posture and body axis orientation are also important for finding food, mates, hiding from predators, and social interactions (Díaz, 1992; Whiting et al., 1993; Bauwens et al., 1996; Baird et al., 2001). Conspicuousness has been shown both empirically and theoretically to be important for intraspecific communication in many vertebrate species (Endler and Théry, 1996; Fleishman, 2000). Males of many species, for example, perform lateral displays during which their flanks are maximally exposed to potential receivers (Chiszar, 1978). In lizards, lateral displays often reveal conspicuous lateral and ventrolateral color patches that are not clearly visible during routine activities (Cooper and Greenberg, 1992; Molina-Borja et al., 1998, 2006). A lizard's location, orientation, and posture at any given time determine how the available light sources illuminate its body surface and therefore affect the effectiveness of its visual signals (Rosenthal, 2006). For diurnal lizards, body axis orientation in relation to sunlight could be particularly important for com-

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munication; depending on the lizard's orientation relative to the sun at different times of the day, parts of its body could be differentially illuminated, making the animal more or less conspicuous to potential receivers.

Gallotia lizards (fam. Lacertidae) are endemic from the Canary Islands (Arnold, 1973). They are typical heliothermic lizards that depend on exposure to the sun to warm themselves and perform their daily activities. G. galloti galloti is distributed in the southern and central parts of Tenerife Island, from the sea shore up to altitudes of >2000 m a.s.l. in Teide National Park. They occupy ecologically diverse habitats which differ in vegetation, type of substrate, and temperature regimes. Lizard seasonal activity begins in April and peaks in May, June and July, with decreasing levels of activity during the hottest summer months and in winter; however, active animals may also be seen on warm winter days (unpublished observations). During the day they are mostly active in the early morning, reduce activity in the hottest hours of the midday, and may resume it in the late afternoon (Díaz, 1994; own unpublished observations). However, it is not known if males and females are equally active and if the number of individuals of each sex differs both within and between different habitat types.

In this work we present the results of a study of male and female lizard activity and body orientation in two habitats from Tenerife with different ecological characteristics and representing different thermal environments. We took advantage of differences in type of substrate, vegetation, and solar radiation intensity between the two sites in order to explore possible differences in activity and body orientation of G. galloti lizards. The main aim of the study was to look for sex-related differences in activity and specific body orientations relative to sunlight in two different daily periods and in the two habitats. Activity was analyzed in two ways: as the number of lizards that can be located outside their refuges and as the type of behavior they exhibited when first observed in the field (still or moving).

We hypothesized 1) that the number of active animals should be lower in Teide National Park (more severe weather conditions) in comparison to Güimar (near sea level, with much less drastic daily and seasonal weather variation); 2) that males should be more active - therefore, more easily detected - than females in both sites due to their active role with regards to reproduction (i.e. males tend to be more active and wideranging than females, particularly during the reproductive season); 3) that more lizards should be detected in the morning (when temperatures are lower) than at midday; 4) given that males are more often than females exposed and involved in intraspecific interactions, we expected to find a different distribution of body orientations in males and females; 5) on the other hand, if body orientation is important for thermoregulation we also should expect perpendicular orientations to be more frequently displayed in the morning than at midday.

#### Materials and methods

#### Study areas and species

We selected two different habitats in Tenerife, one at Malpaís de Güimar (28°18'N, 16°22'W, referred to as Güimar in the remainder of the text), a natural protected area in the SE of the island close to sea level, and the other in the periphery of Teide National Park (28°18'N, 16°33'W, hereafter referred to as Teide) in the centre of the island, around 2000 m a.s.l. Although they are relatively close (ca. 20 km apart), the two study sites have different ecological characteristics due to the altitudinal difference between them. The site at Güimar is a protected natural space with darkbrown to black lava fields that provide many rough surfaces and crevices, and with dispersed xeric plants including Euphorbia canariensis, Plocama pendula, Euphorbia balsamífera, and Periploca laevigata, The habitat at Teide is high montane scrubland and the main plants are Spartocytisus supranubius, Descourainia bourgeana, Adenocarpus viscosus, Nepeta teydea, Erysimum scoparium, and Pterocephalus lasiospermus. The substrate at this site is composed of granulated pumice with dispersed rock piles. Thermal regimes at the two sites are also very different, Teide having cold winter months with temperatures sometimes decreasing below 0°C. However, during most of the year the clouds stay below 1900 m a.s.l., so that the entire National Park always gets sunny days. In Güimar, temperatures never fall below 14°C. Ultraviolet (UV) radiation at ground level is more intense in Teide than in Güimar. (http:// www.aemet.es/es/eltiempo/observacion/radiacionuv/).

The lizard G. galloti galloti (Bischoff, 1982), one of two subspecies inhabiting the island, occurs at high densities in both study areas. It is a medium-sized lizard with mean snout-to-vent length 107.3 mm and 87.4 mm for males and females, respectively (Molina-Borja and Rodríguez-Domínguez, 2004). The species shows sexual dimorphism in body size and coloration (Molina-Borja et al., 1997, 2006), and during the breeding period (April to June) males can be seen wandering over their home ranges where they find females, food, and refuges (Molina-Borja, 1985). Males are more colorful than females, and both sexes have lateral and ventro-lateral blue patches that also show reflectance in the near UV range (Molina-Borja et al., 2006). Male coloration appears more vivid during the breeding season when males patrol their home ranges. These home ranges may overlap and, when two males meet, threat displays, fights and/or chases may occur (Molina-Borja, 1985). During agonistic interactions, as part of their displays, the contestants depress the gular area and compress the body laterally, thus making more visible the rows of blue/UV patches located laterally and ventro-laterally on both sides of their trunks (Molina-Borja, 1981, 1985; Molina-Borja et al., 1997).

#### Data collection

Observations were conducted during 80-100 m long transects that took around 30 min to walk. Transects were haphazardly oriented and located in different parts of the habitat in order to avoid re-sampling individuals. Each transect was run only once to further minimize the risk of lizard re-sampling and pseudo-replication. We selected two daily times to do transects, one in the morning (1000-1030 h, local time) and another at midday (1230-1300 h) in May and June of 2002-2004. For estimations of lizard activity, counts were made of all the lizards found within 2.5 m of the transect line and results expressed as detection rate (i.e. number of lizards detected per minute) and as total number of lizards/transect. Sex, age class and time when each specimen was initially detected were noted. We recorded the orientation of the longitudinal body axis of each specimen in relation to sunlight in three categories: perpendicular (shadow cast by the lizard to one side), parallel (shadow ahead or behind the lizard's body), and oblique (any angle intermediate between parallel and perpendicular). The first two categories have been referred to as "positive" and "negative" orientation, respectively (Heath, 1965, cited in Pough et al., 2003). We also noted the behavior pattern (from the published ethogram for the species, Molina-Borja, 1981, 1987) exhibited by each individual when first detected, if it was located in a sunny, sun-shaded or shaded location, and any other individuals found in its vicinity (within 1 m of the focal animal). Lizard observations were made through binoculars at a distance of at least 10 m to avoid possible disturbance to the animals. A total of 69 transects were performed, 39 in Güimar (19 in the morning and 20 at midday) and 30 in Teide (15 at each sampling time).

Lizard body temperature could not be recorded as the lizards are very wary and cannot be approached in the field at a distance where noosing or capturing by hand would be feasible.

To estimate operative temperatures and assess the effect of body axis orientation we recorded temperature changes inside a copper tube the size of a medium-sized lizard (Bakken and Gates, 1975; Hertz et al., 1993) placed on a roughly flat stone on the ground and with either parallel or perpendicular orientations relative to sunlight. The copper model (around 13 cm long) had a small hole that allowed the insertion of the sensing tip of a thermometer (thermocouple probe) attached to a Hobo data logger. We checked temperatures inside the copper tube 5 min after putting it on the ground. The use of more realistic (in morphology and color pattern) models has been shown to exert little influence on operative temperatures for small lizards (Shine and Kearney, 2001). Moreover, a high correlation (r = 0.99) between temperatures in a copper model very similar to ours and those of lizard carcasses was found for G. galloti by Díaz (1994) in a southern Tenerife population.

Air temperature was measured using a H8 Hobo data logger (0.1°C precision) provided with an external sensor placed at ground level (1 cm above a flat stone), both at the beginning and at the end of each transect, and both in a sunny and a shaded patch as a way to sample the two most extreme microenvironments. Weather and wind intensity were also recorded using the following categories: sunny (1), partly cloudy (2) and completely overcast (3), and no wind (0), soft breeze (1), mildly windy (2) and windy (3).

#### Statistical analyses

As we detected a low number of juvenile and newborn specimens during transects, their data were not included in the statistical analyses. Mean air temperature was analyzed with ANOVAs taking sampling sites and daily times as fixed factors. Due to data departure from parametric test assumptions, comparisons of temperatures inside copper tubes parallel or perpendicular to sunlight were performed with Mann-Whitney U tests.

To test for differences in the number of lizards detected per minute (arcsin square root transformed) at both sampling daily times, analysis of covariance was used taking sampling site and sampling time as fixed factors and air temperature as a covariate. Lizard activity was further analyzed by summarizing our behavioral observations during transects and assigning individuals to two broad categories of "Moving" or "Still" when first detected. The significance of the association between these two behavioral categories and sex was tested by G-tests of independence (Sokal and Rohlf, 1995). We also used goodness-of-fit G tests to compare observed and expected numbers of lizards in each of the three body orientation categories (parallel, perpendicular, and oblique). Expected values were calculated assuming equiprobability of the three body axis orientations. As there are potentially more oblique than parallel or perpendicular orientations, this provides a very conservative estimate of the relative use of parallel and perpendicular body axis orientations. In some cases, to increase the power of statistical tests we pooled data from separate contingency tables but only after a heterogeneity test (Zar, 1999) confirmed that

**Table 1.** Total number of males and females detected during transects (numbers in parentheses) performed at both sampling locations.

Location	Sampling time	Males	Females	
Güimar	Morning (19)	57	40	
	Midday (20)	44	37	
Teide	Morning (15)	83	31	
	Midday (15)	46	15	

contingency tables could be safely assumed to have come from the same statistical population. For all statistical calculations we used two-tailed tests and a significance level of  $\alpha = 0.05$ .

#### Results

# Temperature, lizard detection rates and weather conditions

Air temperatures at sunny patches ranged 22.3-49.8°C in Güimar and 31.9-54°C in Teide. Air temperatures at shaded patches ranged 26.3-33.2°C and 23.2-28.0°C, respectively in Güimar and Teide. Mean values were significantly higher at midday than in the morning transects ( $F_{1.44} = 36.64, P < 0.00001$  for sunny patches;  $F_{1,35} = 8.52$ , P = 0.006 for shaded patches), and there was a significant effect of locality, with higher mean temperatures in Teide  $(F_{1,44} = 8.64, P = 0.005 \text{ for sunny patches};$  $F_{1,35} = 18.14, P = 0.00018$  for shaded patches); however, the interaction between site and sampling time was not significant ( $F_{1,44} =$ 0.0001, P = 0.99 for sunny patches;  $F_{1,35} =$ 2.86, P = 0.1 for shaded patches.

Total numbers of individuals from each sex detected during transects are shown in table 1. As there were very few sampling dates with cloudy or partially cloudy weather at Güimar, we could not quantify the effect of cloud cover on the number of detected lizards. All recording days were sunny at Teide. There was no significant effect of wind conditions on the rate of detected lizards during transects in the two sampling localities (Güimar:  $F_{3,35} = 0.66$ , P = 0.58; Teide:  $F_{1,29} = 0.0001$ , P = 0.99).

Mean number of lizards detected taking air temperature as covariate did not differ between sites ( $F_{1,46} = 0.01$ , P = 0.92), nor between sampling times ( $F_{1,46} = 2.18$ , P = 0.14). The interaction between site and sampling time was likewise not significant ( $F_{1,46} = 1.62$ , P = 0.21). The effect of the covariate was in turn non-significant ( $F_{1,46} = 0.07$ , P = 0.79). Males were detected at a higher rate than females both in Güimar (t = 2.83, df = 25, P = 0.009) and Teide (t = 5.54, df = 18, P = 0.0003, fig. 1), and also in both daily sampling times within each site (data not shown).

#### Lizard behavior and location

When first sighted the lizards were more frequently performing the behaviour patterns "still" and "walking" (table 2). Lizards were observed more frequently in sunny patches during the morning and in partially or completely shaded locations during midday transects both at Güimar (*G* test of independence,  $G_{adj} =$ 7.059, df = 1, *P* < 0.01) and at Teide ( $G_{adj} =$ 11.76, df = 1, *P* < 0.001). Very rarely were other lizards detected within 1 m of the focal lizard. Of all individuals detected in the morning or at midday, only three males and three females had another lizard in their vicinity at each of the two sampling sites.

Most individuals detected were "Still" rather than "Moving" at both sites and sampling times (fig. 2). There was no significant relationship between sex and activity (*G* test of independence,  $G_{adj} = 1.484$ , df = 1, 0.50 < *P* < 0.10;  $G_{adj} = 0.01$ , df = 1, *P* > 0.70; and  $G_{adj} = 1.359$ , df = 1, 0.50 < *P* < 0.10, respectively for Güimar morning samples and Teide morning and midday samples). The only exception was for midday transects at Güimar where more males were found still than moving ( $G_{adj} = 9.284$ , df = 1, 0.01 < *P* < 0.001).

#### Body orientation

The relative frequency with which lizards adopted the three body orientations did not differ

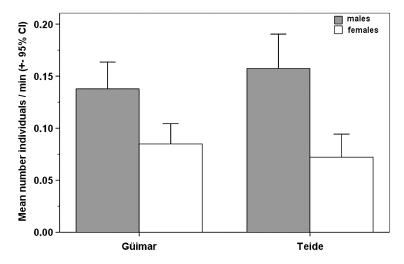


Figure 1. Mean ( $\pm$  95% CI) detection rates of males and females at both study sites.

Table 2. Percentages of lizards performing several behaviour patterns during transects at both sampling sites and times.

		Basking	Still	Walking	Foot-waving	Display	Running	Eating	Courting
Morning	Güimar Teide	1.25 0.65	70.62 73.51	24.37 21.45	2.50 0.65	0.00 0.65	1.26 1.25	0.00 1.91	0.00 0.00
Midday	Güimar Teide	$0.00 \\ 0.00$	67.75 58.85	22.84 25.54	0.86 0.00	$0.00 \\ 0.00$	7.66 15.55	$0.00 \\ 0.00$	$\begin{array}{c} 0.88\\ 0.00\end{array}$

among separate contingency tables for each sex, site or time when the transect was conducted (heterogeneity chi-square = 4.264, P > 0.5). A contingency table analysis of pooled data from all individuals at the two sampling sites showed that lizards exhibit a significant preference for parallel and perpendicular orientations (goodness-of-fit *G* test,  $G_{adj} = 29.561$ , df = 2, P < 0.001; fig. 3).

There was no statistically significant association between sex and body orientation for any locality or sampling time (*G* tests of independence, P > 0.1 in all cases), suggesting that males and females do not differ in the frequency with which they adopt the different body orientations. However, a separate analysis considering only those individuals that occupied sunny patches when first detected revealed a significant association between sex and body orientation in the data from morning transects at Güimar ( $G_{adj} = 6.851$ , df = 2, 0.05 < P < 0.02). In this case, a majority (65%) of males were found oriented parallel to the sun rays, whereas the frequencies with which females adopted parallel and perpendicular orientations were very similar (12 and 11, respectively, out of a total of 29 females).

Mean operative temperatures were 36.8 and 43.5°C respectively for morning and midday sampling times at Güimar and 37.9 and 45.8°C for those at Teide. Moreover, operative temperatures were not significantly different for copper tubes oriented perpendicular or parallel to the sun, neither in morning (Mann-Whitney *U* test, Z = -0.48, P > 0.05) or midday hours (Z = -0.69, P > 0.05).

#### Discussion

# *Lizard activity in relationship to environmental temperature*

Mean air temperatures were significantly higher in Teide than in Güimar and also at midday in



Figure 2. Frequency of males and females found "Moving" or "Still" at both sampling sites and daily times.

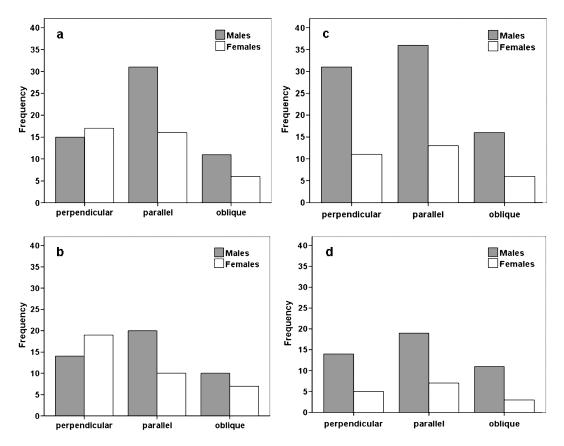


Figure 3. Frequency of males and females showing the three body axis orientations during the morning (top figures) and midday (bottom figures) sampling periods of Güimar (a and b) and Teide (c and d).

comparison with morning transects. This result is not unexpected given the absence of wind and the higher insolation rate – especially at midday, with peaks reaching 800-1000 watts/m<sup>2</sup> – in Teide National Park (Astrophysics Institute of Canary Islands, http://www.iac.es/weather/otdata/) in comparison with the lava fields of Güimar, close to sea level (550-600 w/m<sup>2</sup>, Solar Map, Technological Institute of Canary Islands).

Although fewer individuals were found during the morning in Güimar than in Teide, and more in the morning than at midday in Teide, the differences did not reach statistical significance; likewise, detection rates were not significantly different in the two sites at any of the sampling times studied. The small number of individuals detected at midday in Teide is likely due to lizards avoiding the high temperatures (up to 54°C) at sunny patches during that time. Individuals of G. galloti from another population were also shown to avoid sunny patches at midday (Díaz, 1994). It is widely documented that lizards adjust their activity to environmental temperatures allowing body optima for different physiological functions (Anguilletta et al., 2002) and behavior patterns (Huey, 1982; Van Damme et al., 1991). For example, Podarcis hispanica lizards control their body temperature by adjusting their activity differentially in relation to daily time: they move less in the morning and shuttle between sunny places and shaded ones in the hottest midday hours (Bauwens et al., 1996).

In Teide National Park, mean annual temperatures are much lower than at Güimar and conditions are adequate for lizard feeding and reproductive activities for a shorter time during the year. However, we detected a similar density of lizards in Teide than in Güimar. Therefore, it seems that weather constraints are not the main factor affecting *Gallotia galloti* lizard distribution and population densities at high elevations. Other factors such as food availability and/or lower predation levels at higher altitudes may play an important role. Densities of kestrels (probably one of the most important lizard predators in the island) are lower at high altitudes than near the shore, close to sea level (Carrascal & Palomino, 2005), and percentages of lizard remains in kestrel pellets are also significantly lower at high altitudes (J. Carrillo, personal communication).

## Lizard detection rates: Effects of sex

We detected significantly more males than females (per unit time) at both sampling sites. Previous observations have shown that during the reproductive season G. galloti males move through their home ranges to find females (Molina-Borja, 1985), a behavior also reported in other lizard species (Hews, 1990; Ruby, 1981; Trivers, 1976). The differences in detection rate between the sexes could be due to the higher activity levels of males and the comparatively reduced conspicuousness and/or exposure of females in open sites (Nicholson and Spellerberg, 1989; Stamps, 1983). For example, a reduction in locomotor activity has been detected for pregnant females of some species (Cooper et al., 1990). Alternatively, it could be that there are more males than females in the two populations studied. Complete census data for individuals of each sex are not currently available for our study sites. However, figures of can-trapped individuals in other studies conducted at the same sites show that the proportion of males is between 53.2 and 63.3% of total adult individuals captured (our own unpublished data); these figures are similar to the ones obtained during the transects performed in the current study (ranges of 48.1-59.2% and 53.8-62.9% of males at Güimar and Teide, respectively). More studies are clearly needed to determine whether males are more active - and therefore easier to detect - than females or the sex ratio in this population is male-biased.

### Body axis orientation

The preferential use of parallel and perpendicular body orientations by individuals of *G. galloti* at both sampling sites and daily times is intriguing. Waldschmidt (1980) also found parallel and perpendicular orientations to be the most frequent in Uta stanburiana and Sceloporus undulatus and interpreted them as behavioural responses to the thermal environment. Perpendicular body orientation in relation to sunlight increases the proportion of the animal's surface receiving solar radiation (i.e. its 'view factor') and represents an efficient way of increasing body temperature, at least in the early morning hours (low solar azimuth). Parallel orientation, on the other hand, minimizes the body surface exposed to the sun and therefore reduces radiant heat absorbance during the hottest part of the day. However, our data suggest that body axis orientation in G. galloti is not functional in relation to body temperature regulation, as operative temperatures were not significantly different for tubes with parallel or perpendicular orientations (see also Shine and Kearney, 2001). This agrees with the results of an experimental study showing that heating rates were not related to body orientation in Lacerta monticola (Martín et al., 1995). Similarly, computer simulations using data from the lizard Callisaurus dacronoides showed that body orientation did not influence body temperature (Muth, 1977).

There are several possible alternative - not mutually exclusive - explanations for the preferential use of specific body axis orientations. As the eyes of lizards are located laterally on the head, the intensity and spectral characteristics of the light reaching both eyes would be more similar for a lizard oriented parallel to sunlight than for a lizard adopting other body orientations; this could be important to obtain adequate visual information from conspecifics or predators, particularly in those contexts in which binocular cues may be important. Also, functional specialization of the cerebral hemispheres results in preferential use of one or the other eye for specific tasks and may impose further constraints on body axis orientation. Many lizards show a left-eye preference for viewing potential rivals and a right-eye preference for viewing prey (Deckel and Jevitts, 1997; Hews and Worthington, 2001; Bonati et al., 2008).

These biases in visual perception could be responsible for a preference for parallel and perpendicular orientations.

Site selection, body orientation, and posture are also important factors in visual communication and signal transmission (Rosenthal, 2006). Lizards with their body parallel to sun rays could get both sides of their trunk equally illuminated, while in a perpendicular orientation one side would be lit and the other in the shadow, at least during early morning and late afternoon hours. With both body sides illuminated the lizards would be conspicuous to conspecifics located to their left and to their right. Blue patches of G. galloti are located on the sides of the body and signal male fighting ability during contests (Molina-Borja et al., 1998; Huyghe et al., 2005; our own unpublished results), and therefore, making these patches more conspicuous to potential intraspecific receivers should be advantageous, at least for adult males during the reproductive season. Parallel orientation in particular seems well suited to making a male's coloration visible to a potentially large audience. In fact, our results show that parallel was the most frequent body orientation in males from both sites (fig. 5). Conspicuousness has obvious drawbacks as it may make lizards more attractive for predators (e.g. Stuart-Fox et al., 2003), but this cost should be negligible in G. galloti, at least for aerial predators (there are no snake predators in Tenerife) such as kestrels and buzzards, for which the lateral coloration should be almost undetectable when lizards are seen from above. Cloudsley-Thompson (1994) reported that some lizards adopt a negative orientation (body parallel to sun rays) as an antipredator strategy that minimizes the lizard's body shadow making it more cryptic to visual predators. However, this strategy would not be very effective in G. galloti, at least those moving on the black colored substrate of the lava fields at Güimar.

Both parallel and perpendicular body orientations were more common than oblique. This indicates that *G. galloti* lizards could use these body orientations to get better cost/benefit ratios for specific functions. Thus, for example, if the social system rewards certain individuals for being exposed at sunny patches (e.g. to advertise territory ownership), a parallel body orientation should be expected in order to communicate more efficiently with others while not getting too hot. A similar explanation was put forward for Galapagos iguanas, individuals adopting a negative orientation during the hottest daily hours in order to avoid overheating (Bartholomew, 1966). Future experimental work will help to clarify the selective trade-off that is responsible for the preference of G. galloti galloti lizards for parallel and perpendicular body orientations.

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