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Defensive Behavior as an Escape Strategy in Four Species of *Gallotia* (Sauria, Lacertidae) from the Canary Islands (Spain)

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We studied the occurrence of threat display as a defensive behavior at different temperatures in two large-sized (*Gallotia simonyi* and *Gallotia stehlini*) and two small-sized (*Gallotia atlantica* and *Gallotia caesaris*) lacertids from the Canary Islands. Lizards were chased on a linear track at five temperatures (24, 28, 32, 36, and 40 C). Only adult individuals of the two large-sized species sporadically adopted the threat display, and *G. stehlini* used the display more often than did *G. simonyi*. Among these, there was no clear pattern of relationship between temperature and probability of display nor differences between sexes.

LIZARDS may use different tactics to escape from their predators (Brodie et al., 1991). Although many species rely on flight as their main escape tactic (Greene, 1988), some species adopt passive behaviors enhancing crypsis (Bauwens and Thoen, 1981; Greene, 1988); other species have natural defenses in their bodies or aposematic coloration that deters predators (Brodie et al., 1991); and yet other species adopt active aggressive defense behavior, such as threatening or attacking the predator (Greene, 1988; Hertz et al., 1982).

Temperature has a direct effect on the physiological processes of ectothermic vertebrates (e.g., Huey, 1982; Huey and Bennett, 1987) and, thus, affects antipredator behavior. In lizards of the family Lacertidae, the most common antipredator tactic is flight; the thermal dependence of this behavior has been studied extensively (Bauwens et al., 1995; Van Damme et al., 1989a, 1989b). Moreover, temperature also affects the probability of a lizard facing its predator with aggressive displays rather than fleeing in what has been termed "fight versus flight." Hertz et al. (1982) showed that *Agama savignyi* and *A. pallida* were more likely to face their predators at low body temperatures and were more likely to flee from them at high body temperatures.

The likelihood of success of an aggressive display is dependent on its effect on the predator. Apart from the existence of specialized organs such as brightly colored tongues or dewlaps, which may be exaggerated in defensive postures, or the reliance on postures that may mimic poisonous species such as snakes (Greene, 1988), an important element for the effectiveness of the display should be the potential damage the lizard could inflict on its predator, especially the effect of its bite. This is likely to be related to the overall size of the lizard. The genus *Gallotia* occurs solely on the Canary Islands (Spain) and includes some of the largest lacertids, comparable in size with some of the extinct species described for the archipelago (López-Jurado and Mateo, 1995; Mateo et al., 1999), with *Lacerta lepida* in Europe (Vicente, 1989; Mateo and Castroviejo, 1990), and with some African and European lacertids (Arnold and Burton, 1987; Bons and Geniez, 1996).

In this paper, we compare the thermal dependence of defensive behavior, that is, the probability of the lizards facing and threatening the source of fright (predator) instead of running, in two small and two large species of *Gallotia*. In the latter, we compare the results between adults and juveniles. *Gallotia stehlini* is the largest of the species (up to 280 mm SVL; Mateo and López-Jurado, 1992), and occurs on Gran Canaria Island. *Gallotia simonyi* is the second largest species (the largest known individual alive in captivity is 226 mm SVL, see for example Márquez et al., 1997), occurring in the smaller island of El Hierro. The natural population of *G. simonyi* is estimated to be below 200 individuals (Pérez-Mellado et al., 1999), and a captive breeding colony, kept as part of a recovery plan, barely exceeds this number (Pérez-Mellado et al., 1997), rendering this species one of the most threatened species of vertebrates in the world (IUCN, 1996). *Gallotia atlantica* is a substantially smaller species (maximal SVL of 70 mm, in Castroviejo et al., 1985) that occurs on the eastern islands of Lanzarote and Fuerteventura and in a small area on Gran Canaria (Barquin and Martin, 1982; Castroviejo et al., 1985). *Gallotia caesaris* is the other small species (maximal SVL of 81 mm, in Márquez et al., 1997) and is sympatric with *G. simonyi*.

MATERIALS AND METHODS

Experiments with *G. simonyi* and *G. caesaris* were performed at the captive breeding facility,

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Centro de Recuperación del Lagarto Gigante de El Hierro, located on the island of El Hierro (27°46′N, 17°59′W), between 21 April and 27 June 1996. Individuals of *G. simonyi* were obtained from the captive breeding colony where they live in open-air terraria, and the experiments were conducted in a laboratory adjacent to the facility. Individuals of *G. caesaris* were captured in the immediate vicinity of the facility.

Experiments with *G. stehlini* and *G. atlantica* were performed at the facilities of the Centro de Investigaciones Herpetológicas in Gran Canaria (28°9′N, 15°39′W), from 16–23 August 1996. Individuals of *G. stehlini* were captured inside and outside the open-air terraria of the exhibits of the reptile park where they live. These animals were therefore habituated to the presence of humans and to semicaptive conditions and therefore could be considered to live in comparable conditions as the captive population of *G. simonyi*. Individuals of *G. atlantica* were captured on Arinaga, East of Gran Canaria (27°50′N, 15°20′W), the only population known on this island. All captured individuals were kept in captivity for at least two weeks before testing.

Only individuals with complete tails were used for the tests, and all of them were fed ad libitum with crickets and tomatoes during the period of testing. Specimens captured from the wild were released at their original capture site upon the end of testing. Snout–vent length (to the nearest 1 mm) was recorded prior to testing for all individuals.

Defensive behavior was measured by placing each lizard on one end of a linear track long enough (4 m for large lizards and 2 m for smaller ones) to provide space for the lizard to escape. The choice of the lizards was then to escape to the end of the track or face the predator (the researcher was the surrogate predator). Prior to testing, all animals were held in a temperature-controlled chamber for 30–60 min. All lizards were tested following the same sequence of temperatures determined randomly at the beginning of the study (28, 24, 32, 40, and 36 C). Each individual was tested three times at every temperature, with an interval of at least one hour between tests (Bauwens et al., 1995). Immediately before each test, the cloacal temperature of each animal was measured with a Miller and Weber thermometer (accuracy, 0.2 C). Then the lizard was placed on one end of a track and was chased by hand until it showed one of the two behaviors. The occurrence of defensive behavior was then scored as in Hertz et al. (1982), that is, the animal faced the researcher and adopted a threat display (mouth open wide and hissing noise, characteristic of *Gallotia* species, see Cejudo et al., 1998), rather than running away. For each individual at each temperature the frequency of adopting a defensive posture was calculated. For example, an individual facing and threatening the predator in one of three tests at 32 C would be assigned a frequency of 0.33 for that temperature. Statistical comparisons were performed using JMP version 3.0.2. Juvenile *G. simonyi* were not tested at 40 C to avoid potential harm to individuals of this highly endangered species.

Results

A total of 14 adult *G. simonyi* were used for the tests (eight males and six females, mean SVL = 195.9 mm, SD = 18.9, range 170–226), and 23 two-year-old juveniles were also tested (mean SVL = 60.8 mm, SD = 4.5, range 54–72.5). A total of 15 adult *G. stehlini* were tested (seven males and eight females, mean SVL = 184.0 mm, SD = 32.4, range 129–241), and five juveniles of unknown age were also tested (mean SVL = 91.1 mm, SD = 17.3, range 65–112). In addition, 18 adult individuals of *G. caesaris* were included in the tests (10 males and eight females, mean SVL = 68.0 mm, SD = 5.9, range 57-79), and seven adult *G. atlantica* were tested (three males and four females, mean SVL = 58.3 mm, SD = 8.7, range 47–76).

Only adult individuals of the two large-sized species adopted the threat display (Table 1). *Gallotia stehlini* adopted the threat display more often (9.5% vs 0.5%) than *G. simonyi* (Mann-Whitney *U*-test: $Z = 9.44$, df = 1, $P = 0.002$).

There was no clear pattern of relationship between temperature and the probability of occurrence of the threat display in adult *G. stehlini*; actually, the variability between temperatures was not significantly higher than the variability within temperatures (Kruskal-Wallis ANOVA: *G. stehlini*, χ^2 7.15, df = 4, $P = 0.12$). In adult *G. simonyi*, the threat display only occurred in one test at the highest temperature (40 C). Curiously, this is the only temperature at which *G. stehlini* did not exhibit that behavior at all. Pooling the results of all trials at all temperatures, the frequency of threat display was not significantly different between males and females in adult *G. simonyi* (males, n = 8, mean frequency = 0.008; females, n = 6, mean frequency = 0.00; Mann-Whitney *U*-test: $Z = -0.721$, $P = 0.47$) nor in adult *G. stehlini* (males, n = 7, mean frequency = 0.07; females, n = 8, mean frequency = 0.13; Mann-Whitney *U*-test: $Z = -0.56$, $P = 0.57$). Similarly, the correlation between size (SVL) and frequency of threat display was not signifi-

TABLE 1. PROBABILITY OF OCCURRENCE OF THREAT DISPLAY AT DIFFERENT TEMPERATURES IN FOUR SPECIES OF *Gallotia*. N = number of lizards subjected to three races at each temperature; *P* = average of the individual probabilities that lizards exhibited the threat display; SD, standard deviation.

	p total	24 C				28 C				32 C				36 C				40 C			
		N	*P*	SD	Range	N	*P*	SD	Range	N	*P*	SD	Range	N	*P*	SD	Range	N	*P*	SD	Range
G. stehlini																					
adults	0.11	10	0.2	0.28	0–0.66	14	0.2	0.38	0–1	15	0.05	0.17	0–0.66	10	0.1	0.22	0–0.66	12	0	0	0
juveniles	0	5	0	0	0	5	0	0	0	5	0	0	0	5	0	0	0	5	0	0	0
G. simonyi																					
adults	0.01	14	0	0	0	14	0	0	0	14	0	0	0	14	0	0	0	14	0.03	0.09	0–0.33
juveniles	0	23	0	0	0	23	0	0	0	23	0	0	0	23	0	0	0	—	—	—	—
G. caesaris	0	18	0	0	0	18	0	0	0	18	0	0	0	18	0	0	0	18	0	0	0
G. atlantica	0	7	0	0	0	7	0	0	0	7	0	0	0	7	0	0	0	7	0	0	0

cant among adults in either of the two large species (*G. simonyi*, n = 14, $r = 0.07$, $P = 0.79$; *G. stehlini*, n = 15, $r = 0.06$, $P = 0.81$).

DISCUSSION

In all four species, flight was overwhelmingly more prevalent than fight as an antipredator behavior. Antipredator behavior through threat display occurs solely in adult individuals of the two large-sized species. Neither juveniles from the large-sized species nor adults from the two small species exhibited this behavior. Because juveniles do not rely on this behavior, threat displays may be of selective advantage only in individuals of large sizes. Considering that common kestrels (*Falco tinnunculus canariensis*) are the most common natural lizard predators at least on the island of El Hierro (Cejudo et al., 1999b), the relatively small difference in size between a predator and a large lizard means a bite from a lizard will be a serious deterrent to the kestrel. In *G. stehlini*, there was no difference in the probability of either sex using threat displays; in *G. simonyi*, only one male exhibited the threat display. Furthermore, and unlike in two species of *Agama* (Hertz et al., 1982), temperature had no effect on the likelihood of exhibiting this behavior. This is in agreement with the flat thermal-sensitivity function found for sprint speed in the two large species, which means that sprint performance does not change substantially over a relatively wide range of temperatures (D. Cejudo and R. Márquez, unpubl.). Because smaller lizards do not rely on the threat display, the display may be an "honest" one, advertising for the possibility of a dangerous bite from the powerful jaws of these large-sized lizards, rather than mimicking the threat display of a (potentially poisonous) snake (there are no snakes on the Canary Islands).

The interspecific comparison shows that *G. stehlini* tended to exhibit the threat display more often than *G. simonyi*. This result is not surprising because *G. stehlini* appears to be much more aggressive in interspecific encounters than *G. simonyi* (Cejudo et al., 1999a). This result cannot be solely explained by individuals of *G. simonyi* coming from a captive population, because the individuals of *G. stehlini* used for the tests were collected in open air terraria and were therefore also in semicaptive conditions. Furthermore, unlike other species of *Gallotia*, adult *G. simonyi* does not use aggressive displays in intraspecific encounters (Cejudo et al., 1998). The near lack of antipredator threat displays possibly may have played a role in the vulnerability to predation of *G. simonyi*, which has led to the near extinction of this species (López-Jurado and Mateo, 1999; Pérez-Mellado et al., 1997). The antipredator tactics of *G. simonyi* are not too effective against introduced cats (García et al., 1997, 1999; Rodríguez-Domínguez et al. 1997).

Although flight may be the most important element in the antipredator tactics of all four species, it appears that defensive threat display is sporadically used but solely by adult individuals of the large-sized species. This suggests that, as for many continental lacertids (Bauwens et al., 1995; Martín and López, 1995; Greene, 1988), escape (sprint speed) may be the main behavioral antipredator strategy in *Gallotia*.

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