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Cannibalism of an endemic island lizard (genus *Gallotia*)

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ABSTRACT

Cannibalism is not rare among animals, and particularly in reptiles it is favored by a strong ontogenetic shift in body size and generalized carnivore habits. We looked for evidence of this behavior in a medium-sized lizard, endemic of oceanic islands (Canary Islands), with a high prevalence of a parasite transmitted by cannibalism. Conspecific predation appeared in this lizard, with a rather low incidence (0.76% of fecal pellets included conspecifics), although the analysis of a very large sample ($n = 11{,}651$ pellets) indicated ontogenetic, sexual, and seasonal patterns of such predation. Only the largest individuals were cannibal, invariably males, which only depredated immature individuals, almost exclusively during the post-hatching period (summer and autumn). Together with other natural-history traits already known for the species (e.g., high density, low breeding output, large offspring), cannibalism adds further evidence that this lizard fits the island syndrome.

Cannibalism, the process of eating conspecific individuals at any stage of their life cycles, is not a rare phenomenon in the animal kingdom (Elgar and Crespi, 1992; Polis, 1981), and may play an important role influencing demographic processes (Fox, 1975). In reptiles, cannibalism can appear as consequence of important ontogenetic shift in body size and generalized carnivore habits, while cannibalism is not an uncommon feeding habit in lizards (Mitchell, 1986; Polis and Myers, 1985). Reptiles constitute a substantial component of island faunas (Losos et al., 1998), and island lizards also tend to follow the island syndrome, which predicts changes in body size, anti-predator behavior, and larger offspring, with respect to mainland relatives (Adler and Levins, 1994). In a global meta-analysis on island lizards, Novosolov et al. (2013) has hypothesized that large offspring are favored on islands because of increased intraspecific predation by adults in such environments.

Lehrs' Lizard, *Gallotia caesaris* (Lehrs, 1914), an endemic species from the islands of La Gomera and El Hierro (Canary Islands), exhibits a high prevalence of the coccidian parasite *Sacorcystis*, transmitted mainly by cannibalism (Matuschka and Bannert, 1989), suggesting that intraspecific predation must be significant; this suggestion extends to other *Gallotia* Boulenger, 1916 species (Matuschka and Bannert, 1987). However, previous dietary studies have shown that *G. caesaris* is mainly herbivorous (consuming leaves and seeds), a general trend in island lizards (Cooper and Vitt, 2002; Pérez-Mellado and Corti, 1993), secondarily consuming insects (beetles, ants, and flies), vertebrates being minor prey, with no record of predation on conspecifics (Barahona, 1998; Martin et al., 2005). Yet, the presence of conspecifics in prey remains is frequently found at a low rate, because cannibalism tends to be constrained to the largest individuals (Polis, 1988), to only one sex (e.g., females; Mociño-Deloya et al., 2009), or to short periods of the year (Fox, 1975). Large sample sizes spanning all periods of the activity cycle of the organism are hence required to detect such usually hidden behavior (Engeman et al., 1996).

We examined a very broad sample of pellets from *G. caesaris* in looking for the appearance of cannibalism, discussing on the importance of large samples in order to unveil this occasional but evolutionarily significant feeding behavior. The large sample also afforded the analysis of the intraspecific predation based on body size as well as sexual and seasonal cues. Lastly, we discuss if our results match the island syndrome applied to lizards.

The study area was a plot of around 5 ha in Orijamas (La Gomera, Canary Islands; 28°05′53″N–17°19′57″W; 70–100 masl), with a mean annual temperature of 22.0 °C and mean annual rainfall of 292 mm (data from the La Gomera Airport Meteorological Station, 215 m asl and 13 km southeast from the study area). The landscape was dominated by dense shrubs (*Euphorbia berthelotti*, *E. balsamifera*, *Kleinia neriifolia*, *Plocama pendula*) 80 cm high on average, irrigated gardens mostly with the same shrub species, and scattered rocky outcrops. *G. caesaris* density in the study area ranged between 1353 and 1912 ind/ha according to the season (unpublished data of

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the authors, compiled by a capture-recapture procedure and analyzed by the Schumacher–Eschmeyer estimator), much higher than in other areas of the species' range (García-Márquez et al., 1999).

We randomly collected pellets of *G. caesaris* through all months of the year, for a five-year period (years 2004–2008), trying to balance the sample size among months and years (Table 1). Two other lizards used the study plot, *Tarentola gomerensis* Joger and Bischoff, 1983 and *Chalcides coeruleopunctatus* Salvador, 1975, generating fecal pellets that could potentially be confused with those from *G. caesaris*. However, *T. gomerensis*, a nocturnal gecko, produced fecal pellets with a rougher surface, a diameter below the thinnest of fecal pellets of *G. caesaris*, and mostly adhering to vertical surfaces; *Ch. coeruleopunctatus*, a shy, thigmothermic skink, also produced smaller fecal pellets than *G. caesaris*, never deposited on rocks or open areas, the opposite being true for *Gallotia*. Given the great *G. caesaris* population density, long study period, and ample study plot, we assumed no pseudo-replication of the data.

In lizards, pellet size depends on lizard body size, particularly within the *Gallotia* genus (García-Márquez et al., 1999). To infer lizard body size from pellet size, we randomly captured 80 lizards of all body sizes that were measured (snout-vent length, SVL, to the nearest mm), sexed (according to coloration; Salvador (2007)), and kept individually in captivity until defecation. Fecal pellets were dried in the open air for 24 h, prior to being measured (maximum diameter, with a caliper, to the nearest 0.1 mm). We regressed lizard size (SVL) and pellet size (diameter) in this sample to estimate the lizard body size that produced fecal pellets collected in the wild.

In the lab, pellets were crumbled apart under magnification (20×), separating the different prey. We counted the number of prey items in a subsample of pellets of medium to large size, in order to have a proxy for the significance of the focal prey, conspecifics, in terms of prey frequency, although only vertebrate prey were identified for this study, following Barahona et al. (1998, 2000). Vertebrate prey were identified by scale and bone remains; scales from *T. gomerensis*, *C. coeruleopunctatus* and *G.caesaris*, are quite different among them (Salvador and Pleguezuelos, 2013), and the same applies to the jaw, skull and vertebrae of the three potential reptile prey (Barahona et al., 2000). We estimated the body size of *G. caesaris* prey specimens by comparing prey remains with a collection of skeleton vouchers of this species at the Department of Biology of the Universidad de Las Palmas de Gran Canaria (García-Márquez et al., 1999). Vertebrate prey were deposited as vouchers in the Centro de Recuperación del Lagarto Gigante de la Gomera.

We collected and analyzed 11,651 fecal pellets of *G. caesaris* (Table 1), the sample size of fecal pellets being consistent among months (approx. 200 items per month; Kruskal–Wallis test, H (11, 60) = 18.835, p = 0064) and years (approx. 2400 items per year; Kruskal–Wallis test, H (4, 60) = 5.792, p = 0.221). The frequency of pellets with remains of conspecifics was also quite consistent among years ($\text{chi}^2 = 0.16$, $p < 0.99$), and subsequently we pooled the data from all the years. A total of 94 of the fecal pellets contained vertebrate remains (0.81%): one *Ch. coeruleopunctatus* (0.008%), two *T. gomerensis* (0.016%), 89 *G. caesaris* (0.76%), and two saurian unidentified (0.016%). The average number of prey items per pellet was 10.6 ± 3. 7 (range 4–16, n = 32), and thus we estimated that conspecifics represented only 0.072% of the prey in the diet of *G. caesaris*. The number of pellets with conspecific prey was not consistent among months (K–W test, H (11, 60) = 42.03, $p < 0.0001$); multiple paired comparisons found differences between September and March, between May, June, and July, and between October and June (always $p < 0.03$). Conspecific predation was higher in the period September–December, and as much as 44.9% of the pellets with conspecific remains appeared in only two months, September and October (Table 1). Conspecific remains in the fecal pellets consistently corresponded to young individuals, 33–59 mm SVL.

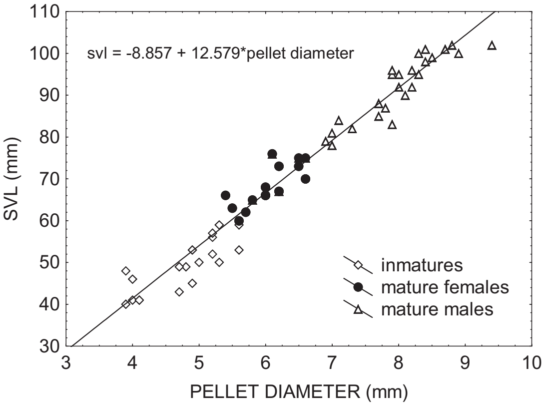

Fig. 1. Relationship between lizard body size (SVL) and maximum diameter of pellets of *Gallotia caesaris* specimens from La Gomera, Canary Islands, according to maturity and sex. Line represents slope of the equation.

Mean maximum diameter of all fecal pellets was 6.42 mm ± 1.85 (mean ± standard deviation; range 2.3–9.8 mm, n = 11,651). In the subsample of lizards in captivity, we failed to find sexual differences in the maximum diameter of fecal pellets when body size was taken into account (ANCOVA, with SVL as covariate and sex as factor; $F(1,58) = 1.056$, $p = 0.308$; slopes homogeneity, $F = 2.279$, $p = 0.136$). When juveniles and both sexes were considered, lizard body size (SVL) was correlated lineally and significantly with maximum diameter of fecal pellets ($r = 0.976$, $p < 0.0001$, $n = 80$). Within this subsample, mean juvenile SVL was 41.3 ± 3.5 mm (range 36.0–57.0 mm; n = 19), mean adult female SVL was 67.6 ± 4.0 mm (range 60.0–78.4 mm, n = 31) and adult male SVL was 76.5 ± 5.3 mm (range 62.1–102.0 mm; n = 30). When the entire sample was considered, *G. caesaris* fecal pellets containing remains of conspecific were in all cases wider that 7.0 mm in diameter, thus corresponding to predator individuals larger than 80 mm SVL (inferring lizard body size from fecal-pellet diameter by the regression equation in Fig. 1), that is, above the maximum juvenile (both sexes) and adult female body sizes.

Cannibalism detection in the feeding habits of organisms requires the analysis of large sample sizes of prey remains or field studies lasting many hours (Wilson, 1975; Engeman et al., 1996). A previous study based on the analysis of the gut content of 196 adult specimens of *G. caesaris* failed to detect the existence of cannibalism (Martin et al., 2005). However, the current study, based on a very large sample of fecal pellets did enable such detection, even identifying patterns of cannibalism linked to body size, sex, and season. We can also argue that the detection of cannibalism in our study area would be facilitated by the high density of this populations (García-Márquez et al., 1999), as intraspecific predation is often a function of density (Fox, 1975; Polis, 1981). *Gallotia* lizards also harbor the richest internal parasitic community reported for lacertids (Roca, 1999) and, observing the high prevalence of a parasitic coccidian, *Sarcocystis* Miescher, 1843, transmitted mainly by cannibalism in *G. caesaris*, Matuschka and Bannert (1989) suggested the existence of intraspecific predation, a prediction that we have confirmed. Prior suggestion also extends to other *Gallotia* species (Matuschka and Bannert, 1987), as cannibalism is frequent in insular species or populations (Pafilis et al., 2009; Raia et al., 2010). Hitherto, cannibalism has failed to be detected in most Canary Island lizards, even in the giant species (information compiled in www.vertebradosibericos.org). However, we suggest that detecting cannibalism in these lizards is simply matter of sample size in studying their diet, and a recent study supported by a rather great sample size in *G. atlantica* (Peters and Doria, 1882) (2155 prey) also detected cannibalism (Carretero et al., 2014).

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Table 1
Number of collected pellets (pell.) of *Gallotia caesaris* from La Gomera, Canary Islands, and number of pellets that contained conspecific remains (consp.), according to month and year (2004–2008 period).

Year		January	February	March	April	May	June	July	August	September	October	November	December	Total
2004	pell.	168	170	178	184	199	198	185	187	220	184	184	179	2236
	consp.	0	0	0	1	0	0	0	1	6	4	3	2	17
2005	pell.	179	208	195	211	179	182	198	204	211	202	198	202	2369
	consp.	3	1	0	0	0	0	0	0	2	6	3	2	17
2006	pell.	179	178	199	205	179	179	205	207	204	196	190	217	2338
	consp.	2	0	1	0	1	0	0	3	4	2	2	3	18
2007	pell.	165	185	181	198	197	205	195	195	212	185	185	185	2288
	consp.	1	3	0	0	0	0	1	2	4	3	2	2	18
2008	pell.	184	189	202	212	186	176	211	208	160	201	269	222	2420
	consp.	1	1	0	2	0	0	0	1	6	3	1	4	19
Total	pell.	875	930	955	1010	940	940	994	1001	1007	968	1026	1005	11651
	consp.	7	5	1	3	1	0	1	7	22	18	11	13	89

The incidence of cannibalism in *G. caesaris* was very low. However, this predation mode can have a significant effect on the energetic intake of cannibalistic lizards, as conspecific were their largest prey (from the data of the authors), and their importance as biomass consumed must be much greater. Notwithstanding, conspecific prey are usually among the heaviest prey of cannibals (Polis, 1981). Moreover, cannibalism, even at low rates, can have a demographic effect on some populations. In *Alligator mississippiensis* (Daudin, 1802) for example, cannibalism accounted for only 2.13% of the adult's diet in terms of prey frequency, but accounted for 63.7% of mortality among specimens in their first year of life (Rootes and Chabreck, 1993).

A general rule in cannibalistic feeding habits is that larger individuals prey upon smaller ones (Hutton, 1989; Pizzatto and Shine, 2008). In that asymmetrical interaction, cannibal organisms also benefit from lower risk during the predatory attack on their victims (Polis, 1981). Among the vertebrate prey of *G. caesaris*, the heterospecific prey are rather abundant in the study plot and smaller (*C. coeruleopunctatus*) or much smaller (*T. gomerensis*); as these prey appeared much less frequently than did conspecifics in the *G. caesaris* diet, we suggest that in this species cannibalism is not simply the consequence of its euriphagous feeding habits, but that conspecifics are actively depredated. To share a habitat also triggers the appearance of cannibalism (Fox, 1975) and indeed, considering the three reptile species in the study plot, the gecko occupies much more vertical surfaces and the skink is much more sciaphilic than the lizard.

We also found a seasonal pattern in the incidence of cannibalism in *G. caesaris*, most cases occurring during summer and fall, few of them during winter, and almost no cases during spring. Intraspecific predation usually corresponds to changes in the availability of conspecific prey (Pizzatto and Shine, 2008), which in *G. caesaris* shifts seasonally according its reproductive cycle. In this species, hatching occurs mostly during July, so that hatchlings (33.3 mm SVL on average; García-Márquez et al., 1999) and juveniles are available during the rest of summer and fall; by contrast, during winter, most juveniles reach body sizes that exceed maximum size depredated by adults (59 mm SVL; this study). During spring this circumstance becomes even more pronounced (García-Márquez et al., 1999), explaining the very low incidence of cannibalism during that season. Although we have no quantitative data on food availability, the seasons with the most incidence of cannibalism by *G. caesaris* were those with the highest food abundance (both plant and animal), in our study area, favored by the existence of some running water from nearby irrigated plots; thus, we rule out the possibility of food scarcity triggering the incidence of cannibalism. Most of the sample for the study of Martin et al. (2005) on the diet of *G. caesaris* was gathered during spring, this time frame explaining their failure to detect cannibalism.

Only *G. caesaris* males preyed on conspecifics. Castilla and Van Damme (1996) also found males to be more cannibalistic than females in *Podarcis liolepis* (Boulenger, 1905) in the Columbrete Islands. Generally linked to species with sexual dimorphism in body size, cannibalism is exerted by the larger sex (Packer et al., 1990; Polis, 1981). *G. caesaris* fits this rule, as our population was sexually dimorphic, males being larger (Salvador, 2007 this study) and the only cannibal. Notably, the maximum body size cannibalized by *G. caesaris* males is just below the minimum size of mature females (60 mm SVL; García-Márquez et al., 1999), and the season with the least incidence of cannibalism coincides with the species' mating period (spring; from pers. obs. of the authors, 2004–2008). Indeed, to consume mature sexual partners may decrease the reproductive success of the population and would be selected against (Fox, 1975). This sexual and seasonal constraint on cannibalism incidence in *G. caesaris*, although it must depend directly on adult male gape size, deserves further research.

Although cannibalism in general seems to be genetically based, it also appears to be induced by environmental cues (Hoffman and Pfennig, 1999; Polis, 1981), and an important environmental cue for the species here considered is insularity. *G. caesaris* is an insular endemic lizard, and we suggest that it follows the island syndrome, which predicts changes in population dynamics, life history, and anti-predatory behavior, among other traits (Buckley and Jetz, 2007; Novosolov et al., 2013; Raia et al., 2010). In favorable habitats *G. caesaris* can reach very high density (close to 2000 ind/ha). Its diet is broader than that of similar-sized lizards from the nearby mainland, and although mainly herbivorous (Martin et al., 2005), intraspecific prey are not neglected (this study). It lays once per year, the clutch size being rather low but offspring relatively large (2.7 offspring per brood, 33.3 mm SVL on average; García-Márquez et al., 1999), which rapidly grow to adult size (60 mm SVL, reached in about 8 months; García-Márquez et al., 1999). Large *G. caesaris* offspring are favored probably because of cannibalism by males. Reptile populations on islands with few heterospecific predators may lead to increased intra-specific competition and select for larger hatchlings, which perform better physiologically (Olsson et al., 2002) and more successfully avoid cannibalism (Novosolov et al., 2013; Pafilis et al., 2009); although we must not forget that cannibalism is also shown by some continental lizards (e.g., Amat et al., 2008; Busack and Jaksic, 1982). At last, because of Canarian lizards exhibit a similar adaptation in terms of ecomorphs (*sensu* Losos et al., 1998) in five of the islands, we predict cannibalism in

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another *Gallotia* species from that archipelago; that prediction has been supported by the recent finding of that behavior in *G. atlantica* (Carretero et al., 2014).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.jcz.2015.07.003.

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