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Cannibalistic Propensities in the Lizard *Podarcis hispanica atrata*

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To understand the population dynamics and life-history evolution of animals, it is crucial to study factors that influence survival of eggs and juveniles (Dunham et al., 1988). In short-lived animals such as small lizards, population dynamics appear to be particularly sensitive to fluctuations in annual recruitment and survival of eggs and juveniles (references in Overall, 1994). In some species, cannibalism on immature conspecifics (i.e., infanticide) seems to be a significant source of juvenile mortality and can influence many aspects of the life history and structure of populations (Polis, 1981; Elgar and Crespi, 1992).

Podarcis hispanica atrata is an endangered subspecies endemic to 20 ha of the Mediterranean islands of Columbretes. It is an heliothermic lizard that maintains high, constant body temperatures during the day, while moving frequently between rocks, ground, and vegetation to thermoregulate, feed, and socially interact (Bauwens et al., 1996). Lizards are active most of the year, depending upon weather conditions. Lizards show clear sexual dimorphism in body and head size and body mass, males being bigger than females (Castilla and Bauwens, 1991b). Adults of both sexes share the same microhabitat and defend small areas within their territory as basking or resting sites. During the summer, mean home-range size of adult males is aproximately twice (132.3 m^2) that of adult females (86.5 m^2) (Swallow and Castilla, 1996). Bushes, burrows, rocks, bricks, and rock crevices serve the lizards as nocturnal retreats and diurnal refugia from avian predators. Females attain sexual maturity at 51–53 mm SVL. Cop-

TABLE 1. SIZE CHARACTERISTICS (SVL AND MASS) OF CANNIBAL AND NONCANNIBAL INDIVIDUALS OF BOTH SEXES AND OF JUVENILES OFFERED TO THE ADULT LIZARDS. Indicated are the mean (± 1 SE) SVL and mass, with sample size in parentheses.

	Males		Females	
	Cannibal (13)	Noncannibal (9)	Cannibal (2)	Noncannibal (10)
SVL (mm)	66.8 ± 1.0	66.2 ± 0.2	64.8 ± 1.3	62.4 ± 0.8
Mass (g)	7.4 ± 0.4	8.2 ± 0.5	5.3 ± 0.1	4.6 ± 0.4
Juvenile SVL (mm)	32.5 ± 0.7	33.0 ± 1.6	33.1 ± 3.2	31.2 ± 0.5
Juvenile Mass (g)	0.70 ± 0.1	0.73 ± 0.1	0.75 ± 0.2	0.60 ± 0.04
	(5)	(3)	(2)	(4)

ulations occur from March to July. Some females lay at least three clutches per year (mean clutch size is 2.9 eggs) from May to July, and some use communal nests (Castilla and Swallow, 1995; Castilla and Bauwens, 1996). Hatchlings emerge between the end of June and Sept. with a mean SVL of 28.1 mm and mean body mass of 0.51 g (Castilla and Swallow, 1996).

In the Columbretes Islands (Mediterranean Sea, 39°54′N, 0°41′E, Castellón, Spain), many adult *P. h. atrata* were observed consuming conspecific eggs and hatchlings over several years under natural conditions (Castilla, 1995a). In addition, 37 of 108 hatchlings (34%) captured from July to Oct. exhibited broken or regenerate tails (Castilla and Bauwens, 1996). This suggests prior agonistic interactions with conspecifics or contact with predators (Rand, 1954; Pianka, 1970, but see Jacksic and Greene, 1984). During the summer, *P. h. atrata* and seabirds are the only vertebrates inhabiting the island (Castilla and Bauwens 1991b). Together these observations suggest that conspecific adults may be the most important predators for juveniles, although scorpions also eat hatchling *P. h. atrata* (Castilla, 1995b). Thus, the prevalence of infanticide could be very high in this population. However, the diet of *P. h. atrata* consists largely of arthropods (i.e., coleoptera, diptera, miriapoda, arachnida, and gasteropoda) and also of some plant material, fruits, and human discards (Castilla et al. 1987), and no vertebrate remains have been found in stomach contents and fecal pellets prior to our study. Similarly, analyses of the stomach contents in a large number of the mainland *P. h. hispanica* have revealed no conspecific or vertebrate remains (Pérez-Mellado, 1983). Our aims in this study are to quantify the propensity of adult male and female lizards (*P. h. atrata*) to infanticidal behavior and to compare morphological characteristics of cannibal lizards with those of noncannibals.

Material and methods.—The study was conducted from 1–17 Oct. 1994 on the island Columbrete Grande (13 ha) under ambient conditions. Temperature ranged from 17.0–24.0 C and humidity from 71–94%. Experiments were performed between 1200 and 1800 h (Mean European Time) in an area of 500 m^2 with high density of lizards (> 800/ha) where lizards are habituated to human activity (Castilla and Bauwens, 1991b).

Nine field-captured juveniles (Table 1) were used (some of them twice) to test the infanticidal propensity of 34 adults. Each adult was presented with one juvenile lizard tethered to a 1 m long nylon thread tied to the end of a 2 m long pole. We first held the juvenile (stimulus) 15 cm from the adult and moved it slightly while standing approximately 1.5 m from the lizards. We recorded the reaction of the adult immediately after stimulus presentation. After a positive response of the adult (i.e., the adult moved toward the juvenile), the stimulus was moved approximately 1 m (distance determined from knowledge of the foraging behavior of this species). The juvenile was moved at sufficient speed to keep it near the adult, while preventing capture. If adult lizards did not react to the initial stimulus presentation, to establish whether the adult was motivated to eat at the time of the experiment, we held the juvenile near the adult for three minutes, and then we exchanged the juvenile lizard for a meal-worm (25 mm in length) and presented it to the adult using the same technique described for the juvenile stimulus presentation.

We restricted the definition of cannibalism to those cases in which the lizard attempted to capture one live juvenile for the total distance of 110 cm. A lizard was considered noncannibalistic when the juvenile was ignored but the meal-worm was consumed and when initial response to the juvenile was positive but the pursuit distance was less than 100 cm and the mealworm was consumed. All tested adult lizards were captured immediately after the experiment with a baited noose (Castilla et al., 1994) and marked with color codes to ensure that they were tested for cannibalism only once. Juveniles were kept in a terrarium with food and cover for at least 5 h between presentations. To examine for morphological differences between cannibalistic and noncannibalistic lizards, we measured (SVL) and weighed them, and the dorsal and ventral color pattern was recorded (Table 1).

Results.—In our experiment, 13 of 22 (59%) males tested and two of the 12 (17%) females tested exhibited cannibalistic propensity. In males, the proportion of cannibalistic individuals was significantly higher than in females (G-test: $G = 6.08$, $df = 1$, $P = 0.01$). Within each sex, mean body size (SVL and mass) of cannibals did not differ from noncannibals (ANOVA, $P > 0.30$ in both cases). However, only a small range of body sizes was available for testing. All cannibal and noncannibal males had black-brownish reticulate dorsal pattern and white-yellowish to bright orange ventral color. However, no significant differences were found in the dorsal or ventral color patterns of cannibal and noncannibal males (G-test, $P > 0.90$). Small sample size prevented a similar comparison for the females.

Discussion.—Our study combined with direct observations of adults preying on juveniles under natural conditions (Castilla, 1995a), strongly suggests that cannibalism is a common behavior in the Columbretes population. Although sample size was small, adult males appeared to be more cannibalistic than females.

Cannibalism in many reptiles was considered to be purely opportunistic predation, with starvation as the most important factor promoting such behavior (Polis and Myers, 1985). For the lizard *Leiocephalus schreibersi*, where 27% males and 43% females show cannibalistic propensities, Jenssen et al. (1989) concluded that infanticide in that species serves as an exploitative food, a means to eliminate juveniles as competitors or as a density dependent mechanism of population regulation (for these and other possible causes of cannibalism, see Polis, 1981).

Adult *P. hispanica atrata* large enough to be cannibalistic are present in the study area throughout the year, and juveniles small enough to be vulnerable to cannibalism (at least smaller than 40 mm SVL) are present from June to Dec. Thus, the pressure of cannibalism on juveniles in this population must be not only high, but also prolonged within a year. Under these circumstances, one can expect high mortality in juveniles and therefore intense selection for large hatchling size and fast juvenile growth rate (see Polis, 1981). In fact, when comparing *P. h. atrata* with other *P. hispanica* populations in the mainland, data indicate that *P. h. atrata* reach sexual maturity with larger body size, show a higher growth rate during their first year of life, and lay fewer and larger eggs (Castilla and Bauwens, 1996). However, these data could also reflect the tendency for insular populations to produce individuals larger than their corresponding mainland populations with no selection pressures due to infanticide.

High intraspecific predation pressure in *P. h. atrata* may explain why juveniles seem to avoid contact with adults. Juveniles and adults exhibit statistical differences in microhabitat choice; juveniles spend less time than adults at exposed basking sites; and juveniles are generally less conspicuous in the field than adults (Castilla and Bauwens, 1991a). In addition, body temperatures in the field and preferred temperatures in a thermogradient are on average 1 C lower in juveniles than in adults (Castilla and Bauwens, 1991a). This difference in body temperature could be related to a difference in surface/volume ratio (Porter and Tracy, 1983). However, the high level of cannibalism in this population suggests an alternative, evolutionary interpretation for age differences in preferred body temperature. To avoid predation by adults, juveniles may have been forced to occupy thermally less favorable habitats and also to maintain lower body temperatures than adults. This difference may have constituted a selection pressure favoring the evolution of lower preferred temperatures in juveniles to match body temperatures in the field (for a similar example with scorpions, see Polis, 1980). Thus, thermoregulatory behavior, and the spatial and temporal patterns of surface activity of juveniles, could have evolved in concordance to avoid predation by adults (see Polis, 1980, 1981). Even when cannibalism accounts for a small proportion of a species' diet, it may still account for most juvenile mortality (Fox, 1975) and may significantly reduce population size. This must have a great impact on species with small populations such as *Podarcis* on Columbrete Grande (surface area of 13 ha) and an even greater impact on populations with less than 100 individuals living on smaller (< 2 ha), neighboring islets. It is therefore important to discover whether there are differences in the frequency of cannibalism among different populations within the archipelago and between other populations.

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