CANNIBALISM IN THE SPANISH ALGYROIDES (*ALGYROIDES HIDALGOI*, LACERTIDAE): ECO-EVOLUTIONARY IMPLICATIONS?

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Abstract.—Cannibalism is a widespread behavior, although relatively less reported in reptiles than other taxa. Many studies indicate its importance in population regulation and life history of the species concerned, while others regard it as an opportunistic behavior. We present the first report of cannibalism in the Spanish Algyroides (*Algyroides hidalgoi*), a small and stenotopic lacertid lizard that occupies rocky shaded and humid localities in a reduced distribution area in the southeastern mountains of the Iberian Peninsula. Within an ongoing study of the species trophic ecology, we found tail-scales of this lizard within a fecal pellet. By studying the morphology and microornamentation of the scales, we identified the victim as an adult conspecific, and we discuss the implications of the event within the framework of the particularities of the species. While cannibalism by lizards has been associated mainly with high lizard population densities and unproductive and predator-scarce environments (mainly islands), the Spanish Algyroides shows nearly the opposite characteristics. The scales found represent a very small proportion of the studied ingested prey. Cannibalism seems not to have important demographic implications in this species. The case adds to other cannibalism reports that do not find adaptive value of this behavior in lizards, and contributes to the discussion found in the literature (opportunism vs adaptation) stressing the need of further research.

Key Words.—conspecific predation; feeding behavior; lacertids; lizards; scale microornamentation; Spanish Algyroides

Resumen.—El canibalismo es un comportamiento muy extendido, aunque relativamente menos descrito en los reptiles que en otros grupos zoológicos. Muchos trabajos señalan su importancia en la regulación de poblaciones y la estrategia vital de las especies implicadas, mientras que otros lo consideran un comportamiento oportunista. Presentamos el primer caso de canibalismo en la Lagartija de Valverde, *Algyroides hidalgoi*, un lacértido muy pequeño y estenotópico que ocupa localidades umbrías y húmedas en un área de distribución muy reducida en las sierras surorientales de la Península Ibérica. Durante un estudio en curso sobre la ecología trófica de la especie, encontramos escamas caudales de esta lagartija en uno de los excrementos. El estudio de la morfología y la microornamentación de las escamas, nos permitió identificar la víctima como un conspecífico adulto. Discutimos las implicaciones del evento en el contexto de las particularidades de la especie. Mientras que el canibalismo en los lagartos y lagartijas se ha asociado principalmente a densidades de población altas y medios poco productivos y con escasa presión de depredación (principalmente en islas), la Lagartija de Valverde parece mostrar características prácticamente opuestas. Las escamas encontradas representan una proporción muy baja en nuestra muestra de presas consumidas. El canibalismo no parece tener gran importancia en la demografía de esta especie. El caso se suma a otros registros de canibalismo que no encuentran valor adaptativo en este comportamiento en lagartos y lagartijas, y contribuye a la discusión existente en la literatura (oportunismo vs adaptación), enfatizando la necesidad de futuras investigaciones.

Palabras Clave.—comportamiento de alimentación; lacértidos; Lagartija de Valverde; lagartos y lagartijas; microornamentación de escamas; predación intraespecífica.

INTRODUCTION

Cannibalism is widespread in many zoological groups (Fox 1975; Polis 1981; Pfenning 1997), and it has been the subject of many field and laboratory studies. In reptiles, cannibalism has been reported in many species, albeit with relatively lower frequency and intensity, particularly in lizards, than in other groups, both vertebrates and invertebrates (Fox 1975; Polis 1981; Polis and Myers 1985; Pfenning 1997) and has received relatively less attention in an eco-evolutionary context (but see for instance Ohlberger et al. 2020 and references therein). Many studies on reptilian cannibalism consider this behavior (as in other animals) highly significant for the population dynamics and life history of the species concerned (e.g., Cushing 1992;

Dong and Polis 1992; Mateo and Pleguezuelos 2015; Dias et al. 2016; Ohlberger et al. 2020). In this sense, cannibalism is considered to have high adaptive value, even in cases with low intra-population cannibalism frequency (e.g., Fox 1975; Polis 1981; Cushing 1991). Some studies emphasize the implications of cannibalism in the energy budget at individual and population level (Rootes and Chabreck 1993). Lacertilian cannibalism has been mainly associated with situations of food shortage (Carretero et al. 2010; Cooper et al. 2015; Torres et al. 2019; but see Fox 1975), and frequently studied on islands with low predator pressure and high population densities of lizards (e.g., Castilla and Van Damme 1996; Carretero et al. 2010; Cooper et al. 2015). Other authors have simply seen opportunism in this behavior, related to the generalist trophic-strategy widely attributed to most species of lizards, and considering the low relative frequency of cannibalistic events found in lizards (e.g., Polis and Myers 1985; Amat et al. 2008; Carretero et al. 2010; Sales et al. 2011; Van Kleeck et al. 2018). Interspecific lizard saurophagy is also common (Alemán and Sunyer 2014; Van Kleeck et al. 2018; Andriopoulos and Pafilis 2019; Christopoulos et al. 2020), as well as keratophagy, the consumption of reptilian shed skin (Groves and Groves 1972; Mitchell et al. 2006; Vacheva 2018).

Here we report the first evidence of cannibalism in the Spanish Algyroides (*Algyroides hidalgoi*; Lacertidae). This lizard was formerly *Algyroides marchi* (see Sánchez-Vialas et al. 2019 for a taxonomical review). In the course of an ongoing study of the trophic ecology of *A. hidalgoi*, we found within a fecal pellet from an adult male with a snout-vent length (SVL) of 43.8 mm two contiguous partial whorls of scales of the tail of a lizard (sum of 19 scales; Fig. 1). The Spanish Algyroides is one of the smallest lacertid lizards (SVL < 50 mm), and it inhabits a small geographic distribution (Rubio 1997, 2002) occupying an area less than 5,000 km^2 in the southeastern mountains of the Iberian Peninsula (Prebetic ranges, *sensu* Sánchez 1982). The species is a stenotopic lizard, concentrating mostly in limited rocky, humid, and shady localities (Rubio and Carrascal 1994; Carretero et al. 2010; Rubio and Martín 2017). In many of these typical locations (but not in others; Fernández-Cardenete and García-Cardenete 2015; unpubl. data), the species tends not to share its habitat with other lizards (Rubio 1997; unpubl. data). Individuals of four sympatric lizard species (a geckonid lizard, the Moorish Gecko, *Tarentola mauritanica,* and three lacertid lizards, the Ocellated Lizard, *Timon lepidus,* the Large Psammodromus, *Psammodromus algirus*, and the Green Iberian Wall Lizard, *Podarcis virescens*), however, were found very close to (or occasionally just inside) some of typical locations of *A. hidalgoi,* locations usually exclusively occupied by *A. hidalgoi* (Palacios

et al. 1974; Sánchez-Videgaín and Rubio 1996). The objective of this study was to confidently identify lizard scales within a scat and to estimate its size/age class by studying the morphology and microoonamentation of the scales. We also discuss this case within the Opportunism versus Eco-evolutionary Framework considering the particularities of our predator.

Materials and Methods

Caudal scales of the Spanish lacertid lizards are easily distinguished morphologically from the rest of the body scales because they are typically elongated, more or less keeled, superimposed, and pointed backwards (Salvador 2014). This was true of the scales we found in a scat and of those of the sympatric lacertid lizards sharing the area with *A. hidalgoi*. We positively determined our sample as lacertid lizard caudal scales. Regarding the other candidate species, the gekkonid *T. mauritanica* can be eliminated as a possible victim due to its large wide, granular, caudal scales, which differ greatly from our focal scales. The scales of the lacertid *Psammodromus algirus* are also quite different, being wide, strongly keeled and pointed (Fig. 1). This left three remaining candidates. *Timon lepidus* is a large lizard (SVL: adults < 260 mm, hatchlings = 40 mm; Arnold and Ovenden 2002; Mateo 2017), but we included it in the study because it was possible that a piece of tail (perhaps from a juvenile) had been eaten. *Podarcis virescens* is a more comparable lizard in size and general morphology to *A. hidalgoi*.

For an interspecific comparison of the scale morphology, we considered the shape, symmetry, width (W, at the scale transversal midline) and length (L, from tip to the proximal scale base visible under the previous scale) of a scale, and we estimated the scales surface (L × W in mm^2) and elongation (L/W). For each lizard species (three specimens per species), we sampled one scale, dorsal and ventral, from every 10 caudal-scale whorls, from the tip to the proximal tail (where scales morphology change to body-scales). We numbered the scales from 10 to 60. All lizard specimens were previously preserved in 70% ethanol. The specimens are housed in the Spanish National Museum of Natural Sciences. We examined the scales under a stereomicroscope (40×) with micrometric eyepiece. For the interspecific comparisons of the scale dimensions, we used the Mann-Whitney *U*-test and Kruskal-Wallis at α = 0.05.

To confirm the prey identity, we compared the microoonamentation of caudal scales of the three candidate species with the fecal-pellet scales. We used a Scanning Electron Microscope (SEM; Hitachi S-3000N, Hitachi Hihg-Tech Corporation, Tokyo, Japan) at different magnifications (750–9,000×; see

Arnold [2002] for a review of scale microornamentation of lacertid lizards). We removed, with fine forceps, the β-layer of the scale epidermis. Our victim scales were constituted not only by the oberhautchen-βkeratin layers, but they retained small parts of inner tissues, indicating they were not part of a skin shed (see Alibardi 1999 or Alibardi et al. 2012, and references therein for scale-structure descriptions). As the main part of the fecal-pellet scales belonged to the ventral tail zone, we used ventral caudal scales from the candidate lizard species in the interspecific microornamentation comparisons.

RESULTS

The morphology of the caudal scales of the three species we studied varied along the tail length. They become progressively more keeled, pointed, and elongated from the proximal tail zone towards the tip, while the number of scales in a whorl of caudal scales increased. The ventral scales were slightly less keeled and longer than the dorsal tail scales although these differences tended to disappear towards the distal part of the tail. The interspecific comparison of the scale dimensions separate both *Podarcis virescens* and *Timon lepidus* from *Algyroides hidalgoi*; the scales of *A. hidalgoi* are significantly smaller (surface differences: $U > 40$, $P < 0.005$). Although *A. hidalgoi* scales tend to be more elongated, the interspecific differences in the mean elongation values were not significant ($H = 0.56$, df = 2; $P > 0.05$). The dimensions and morphological comparison of the scales from the fecal pellet show that they belonged to a scale whorl from the proximal ventral tail zone of an adult *A. hidalgoi* (Fig. 1, 2). The largest estimated surface area of *A. hidalgoi* was 0.66 mm^2; the estimated surface area of the fecal-pellet scale was 0.63 mm^2. The pattern of these scales comprised a central symmetric scale, which sub-parallel sides widened towards its base, and were surrounded laterally by narrower and more asymmetric pointed scales towards the dorsal side. The scales of *P. virescens* from the same tail zone are less pointed and clearly less keeled than *A. hidalgoi* scales, while those of *Timon lepidus* scales are also keeled but of a more rounded shape (Fig. 1).

The microornamentation patterns of the caudal scales of the three examined species and the fecal-pellet scales present narrow transversal strap-shaped cells (following Arnold 2002 nomenclature), which were more or less slightly curved. At 1000× magnification (Fig. 3), the scales of *A. hidalgoi* and those from the fecal-pellet show long cells (long transversal axis) with slightly denticulate borders, while *P. virescens* cells are clearly shorter with smooth margins and frequently exhibit very short distances between opposite cells-tips (indicated by white ellipses in Fig. 4). This feature is different from *A. hidalgoi*, the other candidate species, and the fecal-pellet
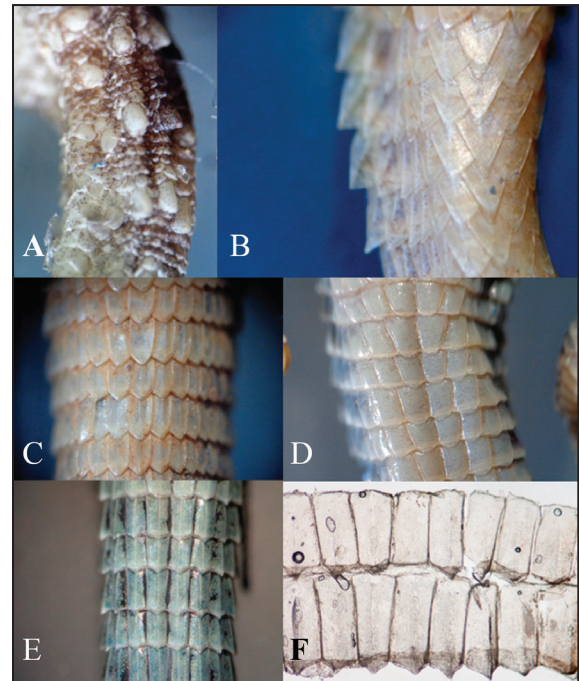

FIGURE 1. Ventral caudal scales of (A) the Moorish Gecko, *Tarentola mauritanica*, (B) the Large Psammodromus, *Psammodromus algirus*, (C) the Ocellated Lizard, *Timon lepidus*, (D) the Green Iberian Wall Lizard, *Podarcis virescens*, (E) the Spanish Algyroides, *Algyroides hidalgoi,* and (F) scales found on an *A. hidalgoi* fecal pellet. All photographs are at a similar tail ventral zone (proximal tail) and from lizards of relatively similar size (snout-vent length < 51 mm; not the same magnification). The scales from the scat fit the morphology of *A. hidalgoi*, with keeled and pointed scales, arranged with a symmetric central scale, with widen scale base (fourth scale from left, D, and third scale from left, E), surrounded by more asymmetric scales. (A, B, C, and D photographed by José Luis Rubio, and E and F photographed by Alejandro Alonso-Alumbreros).
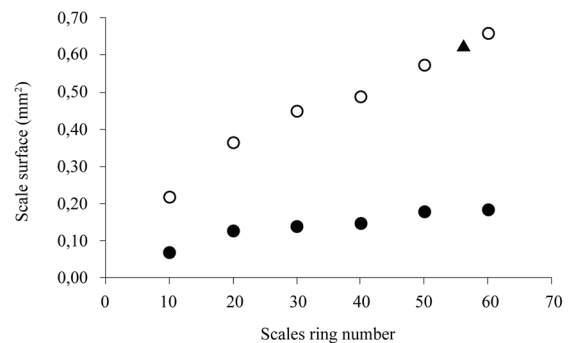

FIGURE 2. Surface area approximation (length × width) of the scales along the tail of a Spanish Algyroides (*Algyroides hidalgoi*) juvenile (open circles) and adult (closed circles), and the scales found in an *A. hidalgoi* fecal pellet (triangle), associated for its size to the largest scales of *A. hidalgoi*. The scales are numbered from tip, number 1, to near proximal tail zone, number 60.
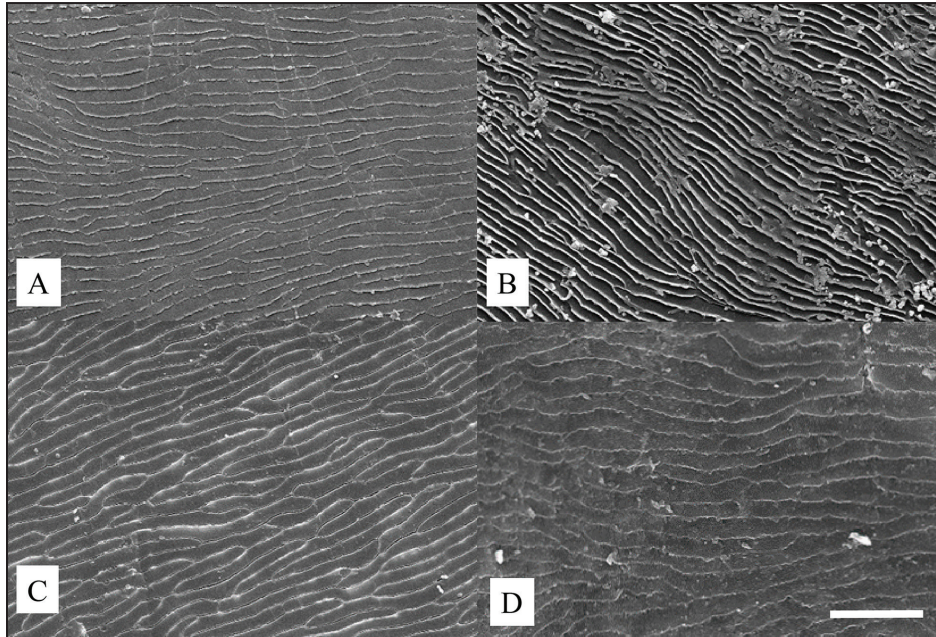
FIGURE 3. Microornamentation of the scales of three lacertid lizards, (A) the Spanish Algyroides, *Algyroides hidalgoi*, (C) the Green Wall Lizard, *Podarcis virescens*, (D) the Ocellated Lizard, *Timon lepidus,* and (B) scale found in a fecal pellet. All show transversal strap-shaped cells, but with different cells pattern, dimensions, margins, and surface texture. The similarities of A and B indicates the *A. hidalgoi* origin of the scales in the pellet. All scales detached from the ventral base-tail zone (1,000× magnification). Scale bar = 5 µm. (Photographed by José Luis Rubio).
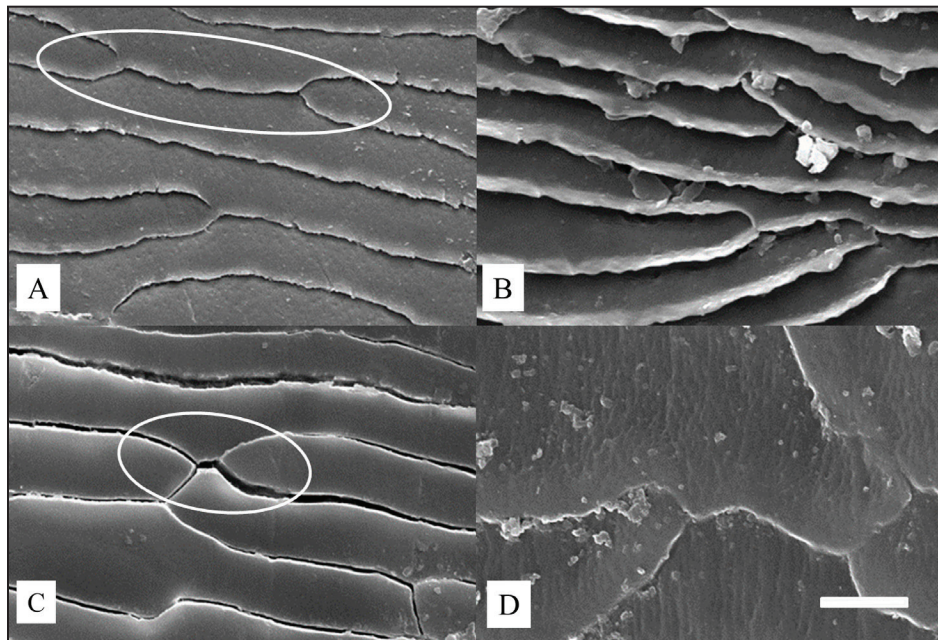
FIGURE 4. Microornamentation at 5,000× magnification of the scales displayed in Figure 3, showing in detail (A, B) a cell surface with subtle scattered pits in the scales of the Spanish Algyroides (*Algyroides hidalgoi*) and the scales found in a fecal pellet, (C) a smooth cell surface of the Green Wall Lizard (*Podarcis vierscens*), and (D) tiny longitudinal ridges in the Ocellated Lizard (*Timon Lepidus*). The ellipses show (A) different distance-patterns between transversally opposite cells typically found in *A. hidalgoi*, and (C) *Podarcis virescens*. Scale bar = 5 µm. (Photographed by José Luis Rubio).

scales (Fig. 3). The cells width (the anteroposterior axis length) in *A. hidalgoi*, *P. virescens*, and the fecal-pellet scales were similar, whereas *T. lepidus* demonstrates wider and longer cells, with irregular margins (Fig. 3). At higher magnification (5,000×; Fig. 4), the cells surface of the scales of *A. hidalgoi* and the fecal-pellet scales show subtle minute scattered pits, whereas *T. lepidus* cells have tiny longitudinal ridges and the surface of *P. virescens* cells is smooth. The SEM images show a light coloration of the cell margins in the fecal-pellet scales, apparently reflecting thinner and slightly raised edges, possibly due to some abrasion while in the gut of the lizard.

DISCUSSION

Unlike reported cases of tail autophagy (e.g., Clark 1971; Fernández and Arribas 2014; Iglesias-Carrasco and Cabido 2016; Thanou and Kornilios 2019), we captured the predator with its own tail unscathed. As we found no other part of the body of the prey except tail scales, we could not determine whether the predator ingested the whole tail or just a part of it (the remnant scales were found in a single fecal pellet). An attack by an adult lizard on a juvenile conspecific is the most frequent type of lizard cannibalism reported (Polis and Myers 1985; Rugiero 1994; Castilla and Van Damme 1996; Burke and Mercurio 2002; Grano et al. 2011). Given the large size of the scales eaten, we were certain we had a case of cannibalism by an adult *A. hidalgoi* on another adult individual rather than on a young individual. Considering the relatively small body size that *A. hidalgoi* adults achieve (< 50 mm SVL)**,** it is very unlikely that the predator could swallow an entire adult or even sub-adult conspecific. Although *A. hidalgoi* has a small adult/juvenile SVL ratio (one of the smallest among the Lacertidae; Rubio 1996), the intraspecific predation on juveniles is quite possible considering their small size (SVL < 29 mm; Rubio 1996). The ingestion of recent autotomized tails after an agonistic encounter between male lizards has been reported (Castilla and Van Damme 1996; Jennings and Thompson, 1999; Iglesias-Carrasco and Cabido 2016). We cannot be sure whether the tail in our case was freshly autotomized or if it was carrion, but the scales showed no signs of post-mortem deterioration that could suggest scavenging. We also cannot know either whether the predator attacked the victim or, though improbable, it scavenged a recently autotomized tail.

Opportunism versus adaptive behavior.—Within our study of the diet of *A. hidalgoi*, the ingested scales represent 0.22% of the total prey items (n = 460). From these data, cannibalism appears to be comparatively rare in this species (Rocha et al. 2000; Mateo and Pleguezuelos 2015; Pérez-Cembranos et al. 2016). This is consistent with the opportunistic character proposed for this behavior (Polis and Myers 1985; Amat et al. 2008; Capula and Aloise 2011; Simović and Marcović 2013). Conversely, other authors consider a significant influence of cannibalism on the population dynamics of lizards (Fox 1975; Jenssen et al. 1989; Cushing 1991; Castilla and Van Damme 1996; Žagar and Carretero 2012). The frequency of cannibalism in lizards is usually low (Henle 1988; Rugiero 1994; Burke and Mercurio 2002; Capula and Aloise 2011), although for some lizard species, there are numerous instances of cannibalism (Castilla and Van Damme 1996; Capula and Aloise 2011; Žagar and Carretero 2012; Simović and Marković 2013; Pérez-Cembranos et al. 2016). The diet of these species, though, typically includes other lizard species, and even mammals (Cattaneo 2005; Capula and Aloise 2011; Dias et al. 2016). Pérez-Cembranos et al. (2016), in spite of having reported repeated cannibalism events for the lacertid lizard Liliford's Wall Lizard (*P. lilfordi*) from the Balearic Islands (among a large prey sample and over many years of study), considered cannibalism sporadic, although important. Although *Algyroides hidalgoi* consumes a range of prey taxa, it also shows prey selection (taxa consumed vs taxa availability) for a few taxa that compose the main part of the species diet (Rubio 1996). Our piece of tail, like the rest of prey consumed by *A. hidalgoi* in low proportion, would be consistent with trophic opportunism.

Population density and food availability.— Cannibalism in lizards, and other animals, has been attributed to environments with scarce resources such as small islands with high population densities (e.g., Fox 1975; Cushing 1991; Pérez-Mellado and Corti 1993; Pérez-Cembranos et al. 2016), or mainland areas with strong seasonally or permanently low food availability (e.g., Mahendra 1936; Díaz and Carrascal 1993; Van Damme 1999; Amat et al. 2008). The Spanish Algyroides inhabits a mountain range surrounded by arid lowlands in the southeastern Iberian Peninsula, which restrict its distribution (Rubio 2002; Brakels et al. 2010; Rubio and Martín 2017). This area could be considered a continental island for the species, though apparently not for its prey (mainly spiders and other arthropods; Rubio 1996). The humid localities occupied by *A. hidalgoi* should not be considered impoverished, according to its productivity (unpubl. data). The population where the specimen was found had an estimated density of lizards of 212 individual/ha (Rubio and Carrascal 1994). This figure is much lower than the density typically found on islands (Buckley and Jetz 2007; Cooper et al. 2015; Pérez-Cembranos et al. 2016). The food availability in this locality would also decrease in summer (Diaz and Carrascal 1993), but to what extent the prey abundance in this type of localities occupied by *A. hidalgoi* can lead to food limitation needs further study.

Mountainous highlands are often considered poor environments (Amat et al. 2008), in which lizards at the end of the activity season could benefit from the food-intake increase from cannibalism when facing hibernation (Torres et al. 2019). Many cannibalism cases have been reported from different seasons and environmental conditions, mainly with high or warm temperatures (Pafilis et al. 2009; Capula and Aloise 2011; Grano et al. 2011; Simović and Marković 2013). Our findings took place in late July when environmental temperatures are high in the area (Agencia Estatal de Meteorología 2019).

Another source of possible intraspecific competition could be the availability of space as a resource, with competition being fostered by high densities. Our sample plot, which was typical of *A. hidalgoi* habitats, was comprised mainly of large rocks (0.7–5 m diameter) that provided a considerable surface area with crevices that are typically used by the species (Rubio and Carrascal 1994; Rubio 1996; Harris et al. 1999). This structure would reduce the density estimate above but would improve the food availability. So intraspecific competition, for space and food, should be not strong.

Concluding remarks.—Considering the low percentage that the ingested scales presented set against our total prey sample, and that the event seems to have little importance on the demography and population density of *A. hidalgoi*, the cannibalism case reported here does not appear to have important eco-evolutionary implications. Our study contributes to the current discussion on opportunism versus adaptation found in the literature considering the particularities of the species involved. It adds to the works of others that have not found an adaptive value of cannibalism in lizards. On the other hand, studies working with large samples (e.g., Mateo and Pleguezuelos, 2015; 11,651 pellets) found cannibalism patterns, apparently confirming the hypothesis of Wilson (1975) and Polis and Myers (1985) indicating that it may be necessary to study cannibalism over longer time periods and large sample size to find deeper meaning from reptilian cannibalism events, stressing the need of further research.

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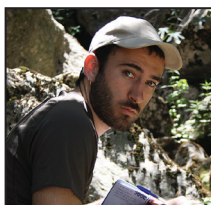
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