

On the incidences of cannibalism in the lizard genus *Sceloporus*: updates, hypotheses, and the first case of siblicide

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Abstract. Although cannibalism is not unusual in amphibians, it is rare in reptiles. The working hypotheses on the occurrence of cannibalism in reptiles assume that it occurs as an opportunistic feeding event, but these hypotheses have not been formally described. Here we report a cannibalistic event in the Eastern Fence Lizard, *Sceloporus undulatus undulatus*. DNA tests were used to confirm that the lizard was consumed by a sibling, and thus our report is of the first case of siblicide in the genus *Sceloporus*. We also present an updated list of cannibalistic events, as reported in the literature, for the genus *Sceloporus*, and describe testable hypotheses regarding the rare occurrence of cannibalism based on juvenile and adult densities, food availability, and distance to nesting grounds.

Keywords. Size disparity, juvenile density, adult density, oviposition site, food availability, rates of cannibalism, nesting grounds

We report here on a case of cannibalism in *Sceloporus undulatus undulatus* (Bosc and Daudin in Sonnini and Latreille, 1801; as cited in Harper, 1940) and attempt to put it in perspective within the genus *Sceloporus*. We compiled the published reports of cannibalism in the genus *Sceloporus* to achieve an updated list (since Polis and Myers, 1985), and take this opportunity to readjust the momentum of a few miscitations in earlier publications before they accumulate in the literature via their otherwise inevitable trajectories. We conclude by suggesting testable hypotheses on the rare occurrence of cannibalism in *Sceloporus*.

We have included five more incidences to the list in Polis and Myers (1985) that were either not included or happened since (Table 1). Two are examples of cannibalism in *S. magister* (Cardwell, 1994; Moll and Koenig, 2003), one an example in *S. graciosus* (Knowlton, 1934), and two are new species added

to the list, *S. undulatus undulatus* (this study) and *S. variabilis variabilis* (Mendoza Quijano et al., 1991). Based on taxonomic recommendations of Leache and Reeder (2002), *S. undulatus undulatus* from Alabama (this study) is part of an eastern clade, now species *S. undulatus* and *S. undulatus hyacinthinus* from Texas (as in Groves, 1971; Table 1) is part of the central clade, now species *S. consobrinus*.

Our reported incidence is the first of cannibalism in *S. undulatus undulatus* (now *S. undulatus* according to Leache and Reeder 2002), and also the first recording of siblicide in *Sceloporus*. Siblicide has, in fact, only been documented in lizards one other time that we could find (Geczy, 2009). Our incidence occurred in laboratory housing (an enclosure of 56 x 40 x 30 cm, L x W x D), consisting of a paper towel substrate, refuge, water dish, and a 60 watt heat bulb on one end. At the time of the cannibalistic event the enclosure contained 5 lizards, 3 from one mother and 2 from another, all of which were 33 weeks of age but varied substantially in size (estimated SVLs 53 mm to 37 mm based on each individual's linear growth trajectories; Table 2). We noticed a lizard (parents were from Geneva State Forest, Geneva County, AL) missing from this enclosure on 26 March 2013. Its tail, however, was still present. Four days later, 30 March 2013, we found the fecal pellet that was obviously lizard remains (Fig. 1).

We extracted DNA with the DNeasy Animal Tissue Kit (Qiagen, Valencia, CA USA) from the fecal pellet

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Table 1. A listing of published incidences of cannibalism in the genus *Sceloporus*. Updated since Polis and Myers (1985).

<i>Sceloporus</i> Species	Predator data	Prey data	Incidences	Lab/field	Tail/body	References
1 <i>S. chrysostictus</i>	Adult	Juvenile ¹	1 of unknown	Field	Body	Smith and Fritts 1969
2 <i>S. graciosus</i>	-	-	1 of 39	Field	Body	Rose 1976
3 <i>S. graciosus graciosus</i>	Adult	Juvenile	1 of 1332	Field	Body	Knowlton 1934
4 <i>S. magister</i>	Adult	Juvenile	1 of 21	Field	Body	Tanner and Krogh 1973
5 <i>S. magister</i>	Adult	Juvenile	1 of unknown	Field	Body	Caldwell 1994
6 <i>S. magister</i>	Adult	Sub-adult	1 of unknown ²	Field	Body	Moll and Koenig 2003
7 <i>S. occidentalis</i>	-	-	1 of 92 ³	Field	Body	Rose 1976
8 <i>S. occidentalis occidentalis</i>	Adult	Juvenile	3 of 210	Field	Body	Johnson 1965
9 <i>S. orcutti</i>	Sub-adult	Juvenile	1 of 367	Field	Body	Mayhew 1963, 1968
10 <i>S. torquatus torquatus</i>	Adult	Juvenile	1 of 9 ⁴	Field	Body	Staton and Conzelmann 1975
11 <i>S. undulatus hyacinthinus</i>	Adult	Juvenile	1 of unknown	Captivity	Body	Groves 1971
12 <i>S. undulatus undulatus</i>	Sub-adult	Juvenile ⁵	1 of 286	Captivity	Body	This study
13 <i>S. variabilis variabilis</i>	Adult	Juvenile	1 of unknown	Field	Body	Mendoza Quijano <i>et al.</i> 1991
14 <i>S. woodi</i>	Adult	Juvenile	1 of 438	Field	Body	Bowie 1973

¹Prey not completely swallowed when adult was shot. ²This occasion was witnessed, but 6 fecal pellets were checked with none obtaining a conspecific. ³45 individuals allopatric and 47 sympatric with *S. graciosus*. ⁴Adult stomachs. Seven juveniles were also caught and had not eaten a conspecific. ⁵Lizards were siblings of the same age, but different size. Both were born and reared in the lab under conditions similar to the other 284 lizards. We included whether it was tail or body because some reported cases of cannibalism are partial, often of the tail (e.g. Rudolf and Antonovics, 2007; de Sales *et al.*, 2011).

and from tissue samples (tail clips) from all four lizards that resided in the enclosure with the cannibalized lizard. We took two DNA samples from the consumed lizard (ID #2215; Table 2). The first was extracted from material on the outer surface of the body (i.e. sloughed off DNA from the consumer) in effort to identify the cannibal. The second was taken from the center of the fecal pellet to identify the genotype of the cannibalized individual. We amplified six microsatellite loci: SW614-A1, SW614-A4, SW614-A7, SW614-B1, SW614-B6, and SW614-B10 (Ernst *et al.*, 2004). We followed similar protocols as Heath *et al.* (2012), except resultant PCR products were sent to the University of Georgia Genomics Facility for fragment analysis. We used the microsatellite data for two objectives; 1) to confirm the expected relatedness among individuals in the enclosure, and 2) to identify the culprit cannibal via matching the external DNA sample with an individual.

The microsatellite loci supported the relationships among individuals. Within each of the two previously identified sibling groups (ID #s 2215, 2220, and 2313; ID #s 2222 and 2231) at least one allele was shared at each locus (except locus SW614-B1 for ID #s 2222 and

2231) and each group was associated with some unique (group specific) alleles (Table 2). Results confirmed also that the cannibalized individual (ID # 2215, male) was consumed by a sibling (ID # 2313, female; Table 2). The cannibalized lizard was an estimated 37 mm SVL (the smallest of the group), and the cannibal 47 mm SVL. The outer and inner DNA sample from the fecal pellet was identical at five of the six loci, but multiple bands were observed at locus SW614-A7. These bands were consistent with combining the genotype of the cannibalized individual (ID # 2215) and its sibling (ID # 2313). This test was not definitive because a perfect match to one individual was not resolved and the outer DNA sample contained mostly DNA from the consumed lizard. However, the extra allele found on the consumed individual (the fecal pellet) was unique to its sibling (Table 2).

We took this opportunity to compile a list of cannibalistic events reported in the literature that were within the genus *Sceloporus* (Table 1). We felt the number of additions and updates justified a current review. While reviewing the literature we noticed a few inconsistencies in regard to cited examples of

Table 2. Observed microsatellite genotypes (number of base pairs as alleles) and expected relationship among individuals at six loci (SW614-A1, SW614-A4, SW614-A7, SW614-B1, SW614-B6, and SW614-B10). SVL estimations (in mm) are for time at cannibalistic event and based on each individual's linear growth trajectory. The alleles in bold denote the confirmation of combined genotypes in the outer slough of the fecal pellet.

ID	SVL	Mom	A1	A4	A7	B1	B6	B10
2215 outer DNA	-	unknown	391 401	377 407	242 246 254	323 331	297 297	185 197
2215 inner DNA	37	002/51	391 401	377 407	242 246	323 331	297 297	185 197
2220	53	002/51	401 401	381 407	244 246	323 331	297 297	183 197
2313	47	002/51	401 405	377 407	246 254	323 331	297 297	183 197
2222	48	4002	393 401	377 379	244 248	331 333	297 297	197 197
2231	42	4002	387 401	379 379	244 250	327 347	297 297	183 197

cannibalism in *Sceloporus magister*, some of which were accumulating through the “domino” effect. We feel that explicitly addressing them may correct the course of accumulation. Knowlton and Thomas (1934) have been cited as an example of cannibalism in *S. magister* (Groves, 1971), however their record is of *S. magister* consuming *Cnemidophorus tessallatus* (Cardwell, 1994; and Moll and Koenig, 2003 cite it correctly). Polis and Myers (1985) used Groves (1971) as a reference for the example of cannibalism in *S. magister*, which is incorrect by domino effect. Cannibalism in *S. magister* had been documented at that point, however, by Tanner and Krogh (1973). Vitt and Ohmart (1974) have been cited also

as an example of cannibalism in *S. magister* (Mendoza Quijano et al., 1991), however their record is of *S. magister* consuming *Cnemidophorus tigris* (Cardwell, 1994 cites this correctly). There are now three examples of cannibalism in *S. magister* that include its finding in one of 21 stomachs (Tanner and Krogh, 1973), one of an unknown number of stomachs (Cardwell, 1994), and one chance witnessing of a cannibalistic event (Moll and Koenig, 2003; includes picture of the event), after which 6 fecal pellets around the area were checked but had no sign of vertebrate remains (Table 1).

Cannibalism in reptiles is a relatively rare occurrence, but that it happens at all is of interest (Polis and Myers,



Figure 1. The cannibalized *Sceloporus undulatus* lizard (fecal pellet) and its sibling. The pictured sibling was the largest lizard (53 mm SVL) in the enclosure, thus we assumed originally it was the cannibal. The cannibal confirmed by DNA tests, however, was a different sibling (47 mm SVL), which was still considerably larger than the cannibalized lizard (37 mm SVL). The colored paint markings were used in an ongoing experiment to identify individual lizards without handling to assess toe clips.

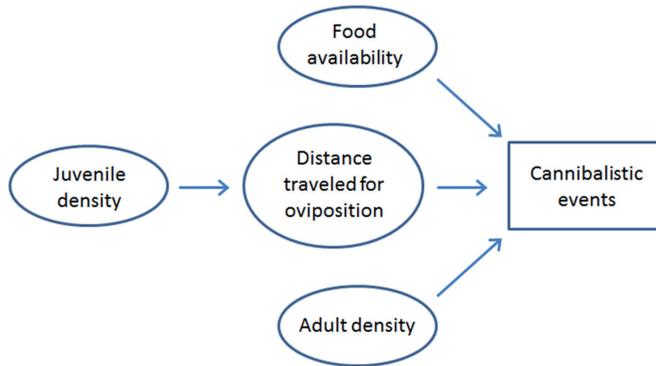


Figure 2. General model describing ecological factors that likely influence the rate of cannibalistic events in opportunistic feeders such as *Sceloporus* lizard species.

1985). It has been argued that cannibalism is not an evolutionarily stable strategy because the danger of retaliation is too large among organisms as similar as conspecifics (Dawkins, 1989) and because average energetic cost of reproduction is higher than energetic gain from consumption of offspring (Garn and Block, 1970; Garn, 1979). In populations of some non-reptilian species, however, cannibalism is a common occurrence (e.g. Fox, 1975; Polis, 1981; Polis and Myers, 1985). Where cannibalism is a viable strategy, the ecological signatures present themselves as production of divergent cannibalistic ecomorphs (e.g. Polis, 1981; Pomeroy, 1981; Crump, 1983; Pfennig, 1992), intra-population

cycles among polymorphisms (e.g. Persson *et al.*, 2003; Persson *et al.*, 2004), and/or reproductive strategies in which cannibalism serves to satisfy energy needs during periods of high demand (e.g. Thornhill, 1976; Pizzatto and Shine, 2008). These processes are not mutually exclusive and cannibalism does not ubiquitously explain their existence, especially in complex ecological systems (e.g. Wikan and Eide, 2004). Some amphibian populations do exhibit cannibalism as well as the associated ecological signatures (e.g. Pomeroy, 1981; Crump, 1983; Pfennig, 1992). However, reptile populations, and those of *Sceloporus* in particular, do not appear to implement viable cannibalistic strategies because we do not observe high rates of cannibalism even in a cyclical fashion, nor do we observe divergent cannibalistic polymorphisms.

In cases where cannibalism occurs but occurs rarely, such as in *Sceloporus* populations and most lizards in general, it is reasoned that cannibalism occurs as part of normal feeding behavior because the species are opportunistic feeders (Polis and Myers, 1985). Certainly most, if not all, *Sceloporus* species are opportunistic feeders (e.g. Jackson, 1973; Vitt and Ohmart, 1974; Toliver and Jennings, 1975; Ballinger and Ballinger, 1979; Barbault, Ortega and Maury, 1985). Other factors that may influence cannibalistic tendencies are environmental and/or nutritional stress, and high conspecific densities (Fox, 1975; Kaplan and Sherman, 1980; Polis, 1981; Polis and Myers, 1985). In general only smaller conspecifics are cannibalized because of the size disparity (Polis, 1981; Polis and Myers, 1985, this study), which suggests that the size disparity is essential for lizard populations to exhibit cannibalistic tendencies.

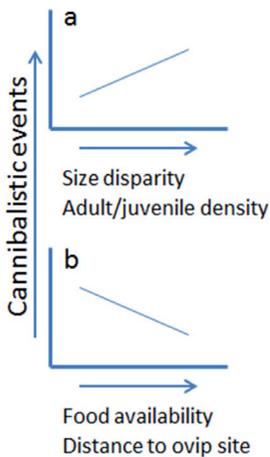


Figure 3. Proposed relationships between ecological traits associated with populations and occurrence of cannibalistic events in opportunistic feeders. Positive relationships (a) and negative relationships (b). Ovip is oviposition abbreviated.

With these ideas in mind we propose a model that could be used to test the ecological causes of cannibalism in *Sceloporus* (possibly other taxonomic groups). Our model provides hypotheses that are yet to be explicitly tested. The model suggests relationships among relative adult and juvenile densities, food availability, and the average distance between the general population and nesting areas (Figs. 2 & 3). Because *Sceloporus* lizards are opportunistic feeders cannibalistic events perpetrated by adults should increase as opportunity and demand increase. An increase in juvenile density would increase opportunity via encounter rates and a decrease in food availability would increase demand. A factor that likely affects juvenile density in areas of adult lizards is the distance between the general population and nesting areas. Some *Sceloporus* species will travel over 100 m to oviposition sites (Angilletta, Sears and Pringle, 2009). The further hatchlings are from adults, the more time it will take for hatchlings to migrate into areas of high adult density. That time will allow hatchlings to grow larger, which should affect intraspecific predation rates because of the influence of size disparity, and allow greater normal mortality, which would decrease the number of hatchlings/juveniles successfully reaching the general population and thus decrease encounter rates between conspecifics of disparate sizes. This model results in multiple specific hypotheses. If cannibalism occurs merely opportunistically, cannibalistic events should 1) increase as size disparity increases (Fig. 3a), 2) increase as the ratio of adult to juvenile density increases (Fig. 3a), 3) decrease as food availability increases (Fig. 3b), and 4) decrease as the distance traveled for oviposition increases (Fig. 3b). These hypotheses should be testable as more data become available on cannibalistic events and population ecology for specific *Sceloporus* populations and/or species.

Our reported case of cannibalism occurred in captivity, a scenario which may facilitate cannibalistic events. Currently, however, this hypothesis lacks support given that our rate of cannibalism was within the range of rates observed in the field, and of the fourteen reported incidences only two were among lizards in captivity (Table 1). More data is necessary to make assessments beyond these. Although we report a case of siblicide by cannibalism in the laboratory, it is likely extremely rare in wild populations of *Sceloporus*. Siblicide and cannibalism each are rare in lizards (Polis and Myers 1985) and the rarity of cannibalism in wild populations of *Sceloporus* implies the extreme rarity of the special case of siblicide by cannibalism. Even if siblicide by

cannibalism was a common form of cannibalism, confirming it would require DNA tests, which themselves rarely occur in such cases. Furthermore, siblicide by cannibalism would require siblings to remain in proximity, differential growth rates between siblings, and survival long enough for the growth rates to result in size disparity. None of these scenarios are likely in the wild, especially with the necessary concurrence. Siblicide could occur between siblings from clutches occurring months apart, but this would still require proximity and a rare cannibalistic event.

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