

Evidence of cannibalism in a population of western Galápagos racers *Pseudalsophis occidentalis* (Serpentes: Colubridae)

LUIS ORTIZ-CATEDRAL^{1*}, HARRISON SOLLIS¹, EUAN MONCREIFFE², JOHANNES RAMIREZ³,
DANNY RUEDA³, CHRISTIAN SEVILLA³ & RICHARD WOLLOCOMBE⁴

¹The Snake Pit – Island Vertebrates Lab, School of Natural and Computational Sciences, Massey University, Private Bag 102-904 North Shore Mail Centre, Auckland, New Zealand

²Galápagos Conservation Trust, Charles Darwin Suite, 28 Portland Place, London, W1B 1LY, UK

³Dirección de Ecosistemas, Dirección del Parque Nacional Galápagos, Av. Charles Darwin, S/N Puerto Ayora, Santa Cruz, Islas Galápagos, Ecuador

⁴25 St Thomas Street, Winchester, Hampshire, SO23 9HJ, UK

*Corresponding author e-mail: l.ortiz-catedral@massey.ac.nz; luisortizatedral@gmail.com

ABSTRACT - Cannibalism is a common behaviour among snakes, but it has not yet been verified for any of the nine species of Galápagos racer (*Pseudalsophis* spp.), a group endemic to the Galápagos archipelago, Ecuador. Galápagos racers are opportunistic generalists feeding on a variety of vertebrate prey. There are a few anecdotal and suspected attempts of cannibalism among Galápagos racers, but it is unclear whether this behaviour occurs and if so, how frequent it is. We analysed 61 faecal samples from western Galápagos racers (*Pseudalsophis occidentalis*). In addition to the remains of well-known prey items such as lizards, we found snake teeth and skin fragments in 11 samples. Combined with previous observations of attempted cannibalism between western Galápagos racers, our results represent evidence that this species consumes other racers as prey. Our study contributes to a growing knowledge of the natural history of Galápagos racers and highlights the role of these reptiles in complex trophic interactions in the Galápagos islands.

INTRODUCTION

Cannibalism, the consumption conspecific prey, including eggs or hatchlings, is widespread among reptiles, with numerous examples from snakes. There are two broad categories of cannibalism: filial cannibalism (consumption of close genetic relatives) and heterocannibalism (consumption of unrelated conspecifics) (Thomas & Manica, 2003; Ibáñez & Keyl, 2010). As examples of filial cannibalism, Colombian rainbow boas (*Epicrates maurus*) and emaciated post-parturient Mexican lance-headed rattlesnakes (*Crotalus polystictus*) consume undeveloped eggs and non-viable offspring as a behavioural tactic to recoup energy losses (Lourdais et al., 2005; Mociño-Deloya et al., 2009). Examples of heterocannibalism are numerous, both for captive and wild snakes: Mitchell (1986) reviewed reports of cannibalism for 101 species of snakes from 1894 to 1985. Since this review is outdated, and numerous new studies and reports have been published since, it is reasonable to assume that cannibalism occurs in many more species.

Occasional consumption of unrelated conspecifics tends to be regarded as rare, but it is unclear to what extent this reflects the difficulty of studying snake diets in the wild. For instance, only two cases of cannibalism in smooth snakes (*Coronella austriaca*) were confirmed in a 9-year study in southern England (Jofré & Reading, 2020). Similarly, populations of Florida cottonmouths (*Agkistrodon conanti*) in the Cedar Keys, Florida, have been studied since the late 1930s to the present (Lillywhite et al., 2002; Lillywhite et al., 2015) and although snake prey (salt marsh snakes,

Nerodia clarkii) had been reported in their diet, attempts of conspecific cannibalism have only been observed as recently as 2015, possibly as a behavioural adjustment to a decrease in fish carrion that previously had been abundant (Sheehy III et al., 2017).

The Galápagos terrestrial snakes, or 'racers' are a monophyletic group of nine species (Zaher et al., 2019) that are widely distributed from sea level (Merlen & Thomas, 2013) to 1400 m a.s.l. (Arteaga & Guayasamín, 2020) and inhabit arid shrublands and deciduous forests (Christian, 2017). As a group, Galápagos terrestrial snakes remain poorly studied, chiefly due to the apparent low density of individuals across their geographic range, and the remoteness and inaccessibility of large populations. As a result, several aspects of their biology remain unknown.

Galápagos racers are regarded as opportunistic generalists that ingest prey head-first, feeding predominantly on small vertebrates such as lava lizards (*Microlophus* spp.), geckos (*Phyllodactylus* spp.), marine iguana hatchlings (*Amblyrhynchus cristatus*) (Ortiz-Catedral et al., 2019), and even small coastal fishes (Merlen & Thomas, 2013). In June 2015, R.W. observed three attempts of heterocannibalism in western Galápagos racers *Pseudalsophis occidentalis* (Van Denburgh, 1912) at Cabo Douglas, Fernandina Island. In two instances, the cannibal managed to subdue its prey but neither event resulted in full ingestion or death of the prey. In one instance (Fig. 1), the prey was subdued by its head, but it managed to free itself. In the other instance, the prey was ingested approximately half of its length, but the cannibal regurgitated the live snake. Regurgitation of live snake prey



Figure 1. An attempt of heterocannibalism among western Galápagos racers (*Pseudalsophis occidentalis*). The cannibal subdued a conspecific at Cabo Douglas, Fernandina Island, June 2015.

before full ingestion has been documented in California kingsnakes (*Lampropeltis californiae*) (Jackson et al., 2004) and black whip snakes (*Dolichophis jugularis*) (Göçmen et al., 2008). Christian (2017) reported snake teeth in the faeces of eastern Galápagos racers (*P. biserialis*) on Gardner-by-Floreana, but at the time these were regarded as the racer's own teeth, possibly ingested in the process of swallowing prey, or as part of the tooth replacement observed in snakes as suggested for other snake species (Abuys, 1987; Van Wyk, 1988).

As part of an ongoing large-scale study on the natural history and diversity of Galápagos racers, led by the Directorate of the Galápagos National Park, we analysed faecal samples of western Galápagos racers to better characterise the diversity of prey items consumed and to investigate whether remains of snake prey could be encountered. Faecal analyses have been used alone to study diet (Rudolph et al., 2002; Weatherhead et al., 2009) or to supplement stomach content studies in several snake species (Fitch, 1963; Slip & Shine, 1988; Agrimi & Luiselli, 1992; Daltry et al., 1998; Akani et al., 2001; Hill et al., 2001; Saviozzi & Zuffi, 2007; Cochran et al., 2021), and to document cannibalism in smooth snakes (*Coronella austriaca*) (Jofré & Reading, 2020) and false smooth snakes (*Macroprotodon cucullatus*) (Faraone et al., 2020). Here we present evidence of cannibalism in western Galápagos racers based on an analysis of faecal samples.

MATERIALS & METHODS

We captured western Galápagos racers on Fernandina Island, at Cape Douglas (0° 18' 17" S, 91° 39' 13" W) from 5th to 10th July 2018. The study site in Cape Douglas is a coastal area 17 ha in size, covered in arid scrub, 0-2 m a.s.l., with a vegetation community dominated by palo santo (*Bursera graveolens*), candelabro (*Jasminocereus thouarsi*) and thickets of monte salado (*Cryptocarpus pyriformis*).

We captured Galápagos racers by hand early in the morning or just before dusk as described in Ortiz-Catedral et al. (2019). We weighed each individual inside a cotton bag to the nearest 0.5 g, using a portable Pesola® scale, and measured the snout-vent length (SVL) to the nearest mm using string and a vinyl sewing tape. Individuals were sexed in the field by manual probing. This method consists of the slow introduction of a blunt, metal probe into the cloaca: in males, the probe enters deeper into the tail than in females (Gnudi et al., 2009). This method has been used successfully in various field studies (Blouin-Demers & Weatherhead, 2001; Willson et al., 2006; Evans et al., 2019). After sexing, the probe was sterilised with 96 % ethanol. To identify adult western Galápagos racers (total length > 59 cm) individually and as part of a mark-recapture study, a passive integrated transponder (PIT) (ID100 mini, TROVAN®) was inserted subcutaneously along the posterior third of the venter anterior to the cloaca on snakes with a total length greater than 50 cm. Each snake was released at the site of capture approximately 35-60 min after faecal samples and measurements were obtained, or if snakes were captured after dusk, they were kept overnight in individual cotton bags and released before dawn the following day. Faecal samples (one sample per individual) were obtained using the palpation technique (Daltry et al., 1996; Williams et al., 2016), stored in either 2 ml or 5 ml micro-centrifuge tubes, and fixed in 1.5 – 2.5 ml of 96 % ethanol until examination for contents. This technique has been used previously in another study on the diet of Galápagos racers (Ortiz-Catedral et al., 2019), and other snake species (e.g., Reading & Jofré, 2013). Faecal samples were examined visually using a 5 MP USB digital microscope (Celestron Handheld Digital Pro, Celestron, Torrance CA.) at the Invertebrate Collection Lab of the Charles Darwin Research Station in Puerto Ayora, Santa Cruz, Ecuador.

We recorded the presence of prey remains and classified

these into broad categories: scales, invertebrate remains, feathers, hairs, bones and other undigested materials. Reference voucher specimens at the vertebrate collection at the Charles Darwin Research Station (darwinfoundation.org/en/datazone) were used to verify the identity of prey species or broader taxonomic categories, by comparing scales, hairs, claws, skin and feathers of voucher specimens. Snake faecal samples often contain material that is too digested to allow for accurate identification (see Ortiz-Catedral et al., 2019). Whenever such material was observed, it was classified as ‘unidentified organic matter’. Whenever snake teeth were unambiguously identified, we made an attempt to count every tooth found in the faecal sample.

We compared morphological measurements and presence/absence of prey groups in samples using Welch’s test, and conducted regression analyses on SVL/mass relationships between males and females. Minitab (Minitab 17 Statistical software, 2010) was used for all statistical analyses and values are presented as mean ± standard deviation.

RESULTS

We captured a total of 93 western Galápagos racers at Cape Douglas, Fernandina Island: 61 females (SVL range: 49.60 – 100 cm) and 32 males (SVL range: 40.50 – 95 cm). We successfully obtained faecal samples from 61 individuals (66 % of total), of which 21 contained identifiable prey remains. Of these, four samples contained small bone fragments that could not be identified to a taxonomic group (Table 1). Prey remains, other than snakes, included Isabela lava lizard (*Microlophus albermalensis*) scales; Galápagos leaf-toed gecko (*Phyllodactylus galapagensis*) scales; marine iguana (*Amblyrhynchus cristatus*) hatchling claws and scales; an unidentified feather and rodent hairs (Table 1). The number of prey types that could be identified per sample was one (n=16), two (n=4), or five (n=1). The remaining 40 faecal samples contained digested material without identifiable remains.

We encountered snake remains (teeth, scales and skin fragments) in 11 samples (Table 1). Two females, with the IDs, 215A (SVL = 75.50 cm, mass = 78 g) and B28E (SVL = 76.30

Table 1. Prey species encountered in 21 faecal samples of western Galápagos racers (more than one prey type could be found per sample)

Class	Family	n	Prey species	Type
Reptilia	Tropiduridae	6	<i>Microlophus albermalensis</i>	S, C
	Phyllodactylidae	2	<i>Phyllodactylus galapagensis</i>	S
	Iguanidae	2	<i>Amblyrhynchus cristatus</i>	S, C
	Dipsadidae	11	<i>Pseudalsophis</i> spp.	T, S
Mammalia	Rodentia	1	Unidentified rodent hairs	H
Aves		1	Unidentified feather	F
Undetermined		4	Unidentified vertebrate	B

B = bone; C = claws; F = feather; H = hair; S = scales or skin; T = teeth

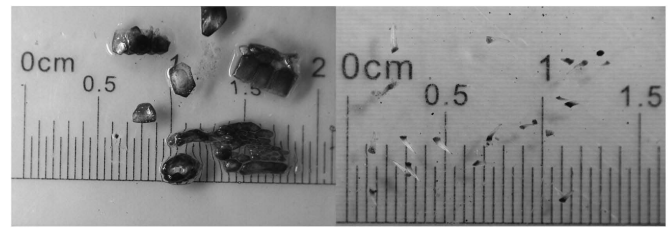


Figure 2. Snake remains in faecal samples of western Galápagos racers (*Pseudalsophis occidentalis*) - **Left:** snake skin fragments, individual B28E, **Right:** snake teeth, individual 215A

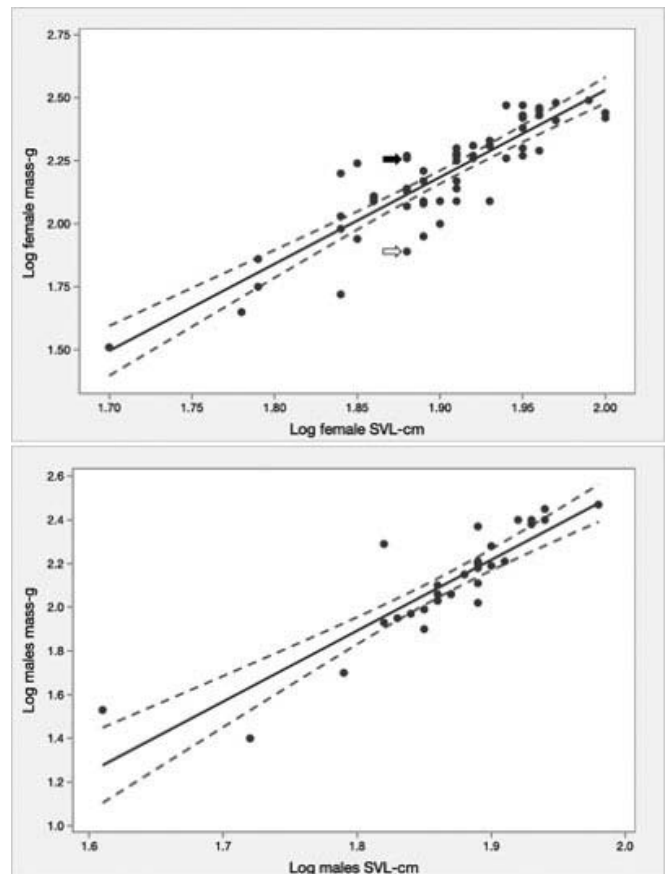


Figure 3. Regression analysis of western Galápagos racer (*Pseudalsophis occidentalis*) female (top) and male (bottom), \log_{10} mass-g vs \log_{10} SVL-cm with 95 % confidence intervals (dashed lines). **Female:** \log_{10} mass-g = $-4.36 + 3.44 \log_{10}$ SVL cm; $r^2 = 78.70$ %; $P < 0.001$; $n = 61$; **Male:** \log_{10} mass-g = $-3.75 + 3.14 \log_{10}$ SVL cm; $r^2 = 79.03$ %; $P < 0.001$; $n = 32$. Top panel: solid arrow- individual B28E; open arrow- individual 215A

cm, mass = 180 g), contained 28 snake teeth, and 31 snake teeth respectively, plus snake skin fragments, respectively (Fig. 2). The average number of snake teeth in faecal samples of the other nine samples was five (range: 1-13). The body condition of females 215A and B28E, were outside (below and above respectively) of the 95 % confidence interval the regression of SVL on mass for females (Fig. 3). We did not detect significant differences in SVL between females with no prey remains in faeces (SVL = 81.20 ± 8.91 cm) and females with identifiable prey remains in faeces (SVL = 79.90 ± 12.40 cm; Welch’s $t = 0.408$, $p = 0.68$, d.f. 20.8). Similarly, the SVL of males with no prey remains in faeces (SVL = 74.70 ± 11.10

cm) and males with visible prey remains in faeces (SVL = 68.50 ± 10.00 cm) did not differ significantly (Welch's $t = 1.24$, $p = 0.26$, d.f. 5.99).

DISCUSSION

Overall, the prey species listed here is similar to earlier studies that described the diet of Galápagos racers as including lava lizards, geckos, birds, and marine iguanas (Altamirano, 1996; Merlen & Thomas, 2013; Ortiz-Catedral et al., 2019), but with the noticeable addition of rodents. Native and introduced rodents have long been considered potential prey for Galápagos racers, but to the best of our knowledge our observations represent the first confirmed record in faecal samples of Galápagos racers. Our study site, Cabo Douglas on Fernandina Island, is free of introduced rodents (*Rattus* spp. and *Mus musculus*), but has populations of native rodents, known as "rice rats": *Nesoryzomys fernandinae* and *Nesoryzomys narboroughi* (Dowler et al., 2009), although which of these species had been consumed could not be determined from the available prey remains. Close relatives of *Pseudalsophis*, such as the West Indian racers in the genus *Alsophis*, are morphologically and ecologically similar to Galápagos racers and occasionally prey on small rodents such as *M. musculus* and juvenile *R. rattus* (Henderson & Powell, 2009; Questel, 2012), so although novel, this finding is not especially unexpected.

Our analysis revealed snake teeth in 11 samples, with a large number (≥ 28) in samples from two females. We cannot determine which proportion of the teeth encountered in our faecal samples represent the snake's own, resulting from breakage of teeth while swallowing prey (see Weatherhead et al., 2003) or as part of the natural teeth replacement (see Van Wyk, 1988). However, in two cases we encountered a large number of teeth, one alongside snake skin fragments, which clearly indicates ingestion of snake prey. Previous examination of eastern Galápagos racer faeces revealed the presence of variable numbers of teeth in faeces (Christian, 2017), some potentially lost as part of the normal process of tooth replacement or breaking off during prey ingestion, as described by other authors (Abuys, 1987; Van Wyk, 1988; Weatherhead et al., 2003). We do not know how many teeth can be lost at any one time as part of tooth replacement or prey handling in *Pseudalsophis*, but we suspect it is a small number rather than entire rows of teeth being lost at once. Based on museum specimens, Thomas (1997) conducted the most comprehensive morphological revision of the genus and reported dentition ranges from 10-15 maxillary teeth and 15-20 dentary teeth, with no mention of tooth loss in the specimens reviewed. Similarly, Maglio (1970) examined 200 skulls representing 33 diposadine species in the West Indies and reported only small inter-specimen variation (± 2 teeth) in dental series, but no major instances of tooth loss. We suggest that if breaking-off of numerous teeth at a time were a common occurrence among *Pseudalsophis* and allies, this would have been noticed in museum specimens (i.e., empty sockets). During our own examinations of live and preserved specimens of Darwin's racer (*Pseudalsophis darwini*), painted racer (*Pseudalsophis steindachneri*), central Galápagos racer (*Pseudalsophis dorsalis*) and eastern Galápagos racer

(*Pseudalsophis biserialis*), we have not detected significant tooth loss (Ortiz-Catedral, pers. obs.). Similarly, previous analyses of faecal samples in *Pseudalsophis* (Ortiz-Catedral et al., 2019; Christian, 2017) have not reported large numbers of teeth in the samples examined. To the best of our knowledge, no study has attempted to quantify tooth loss after prey handling in wild or captive snakes, therefore we are uncertain about the number of teeth that an individual snake could lose while ingesting prey.

Remains of snake skin associated with a case of cannibalism have been reported for a false smooth snake (*Macroprotodon cucullatus*) on Lampedusa Island (Faraone et al., 2020). We reject the possibility that the skin remains are indicative of a case of dermatophagy (shed-skin eating) (Weldon et al., 1993) because the skin fragments are pigmented, whereas western Galápagos racer shed skins, like those of most snakes, are pale and translucent. Coupled with earlier observations of attempted cannibalism at Cape Douglas (Fig. 1), we propose that our results represent evidence of cases of cannibalism in western Galápagos racers. Besides western Galápagos racers, another terrestrial snake inhabits Cape Douglas, the elusive Darwin's racer (*Pseudalsophis darwini*), a recently described small species (ca. 50 cm in length) (Zaher et al., 2018). Darwin's racers are uncommon, with only five individuals encountered in previous visits to Cape Douglas (Ortiz-Catedral & Ramirez, pers. obs.). In our study, we could not determine whether western Galápagos racers prey on *P. darwini* or whether the teeth and skin fragments encountered belong to *P. occidentalis* or *P. darwini*. The only observed instances of attempted cannibalism at this study site (Fig. 1) involved two *P. occidentalis*.

It is possible that the snake remains in individual 215A represent a case of scavenging on a dead snake, or cannibalistic carrion ingestion (sensu Lillywhite, 1982) rather than hunting of a live individual. Western Galápagos racers have been observed scavenging marine iguana hatchlings (Ortiz-Catedral et al., 2019). Thus, it is possible that western Galápagos racers consume snake carrion as part of a broader suite of prey, which is relatively common in snakes (DeVault & Krochmal, 2002). As direct observation of cannibalistic events is difficult to study in the wild, and observations of snakes hunting and subduing prey are infrequent (Cadena-Ortiz et al., 2017; Christian, 2017; Ortiz-Catedral et al., 2019), we suggest two alternative approaches could be used to determine the extent and temporal variability of their cannibalistic behaviour in Galápagos racers: induced regurgitation of prey by palpation (López & Giraud, 2003) or remote videography (Glaudas et al., 2017). Galápagos racers seasonally aggregate to forage on hatchling marine iguanas on Fernandina Island (R. Wollocombe, pers. obs.) which represents an opportunity to use videography to assess hunting strategies and prey diversity. Other techniques used to study snake diet, such as stable isotopes and faecal eDNA, are unlikely to be capable of detecting cannibalism (Hobson & Welch, 1995; Brown et al., 2013).

Cannibalism among snakes has been explained as a random opportunistic occurrence or as a response to low body condition and starvation stress (Sandfoss et al., 2017; Sheehy, 2017). It is unclear whether individuals that ingested snakes in our study did so as a response to decreased body condition,

as part of routine active hunting, or by scavenging. Similarly, it is difficult to establish whether they consumed adults or other age-classes of their own species or Darwin's racers. Our study is limited as it only encompasses a single event sampling (i.e., one sample per individual taken over just six days), therefore we did not determine intra-annual variability in patterns of snake consumption. There are several small island populations of Galápagos racers that could be the focus of more detailed studies and that will help us understand cannibalistic behaviour among these snakes and help us understand the extent and variability of cannibalistic behaviour in this group of reptiles. Our study contributes important information about the trophic relationships of Galápagos racers, especially considering the limited information on the biology of this group, and the growing need to manage endangered species in the Galápagos archipelago.

ACKNOWLEDGEMENTS

We would like to thank Roberto "Robby" Pepolas, Alfredo Abad, Novarino Castillo and his team of porters. Also, thanks to Simon Villamar, Tui de Roy, Toby Nowlan and Sam Steward (Silverback Productions, UK) for sharing observations on sightings of Galápagos racers in Fernandina Island. We would like to thank Gustavo Jiménez-Uzcátegui for facilitating access to voucher specimens at the Vertebrate Collection Charles Darwin Research Station, Puerto Ayora. Support for fieldwork was kindly provided by Massey University, Silverback Films, Mohamed bin Zayed Species Conservation Fund and Galápagos Conservation Trust. We also thank Mr. Eduardo "Vico" Rosero, captain on the boat Queen Mabel, for assistance accessing field sites. We also thank two anonymous reviewers, and Dr. J. Daltry for valuable constructive criticism that greatly improved an earlier draft of this paper. Finally, we thank the Directorate of the Galápagos National Park for providing permission to access all locations and for the capture and handling of snakes according to protocols approved in permits PC 74-17 and PC 08-19.

REFERENCES

- Abuys, A. (1987). The snakes of Surinam part XIX: Family Viperidae subfamily Crotalinae (genus *Crotalus*). *Litteratura Serpentina* 7: 282-296.
- Agrimi, U. & Luiselli, L. (1992). Feeding strategies of the viper *Vipera ursinii ursinii* (Reptilia: Viperidae) in the Apennine. *The Herpetological Journal* 2:37-42.
- Akani, G.C., Capizzi, D. & Luiselli, L. (2001). *Mehelya crossi* (West African File Snake). Diet. *Herpetological Review* 32:49-50.
- Altamirano, M.A. (1996). Potential Influences of Biotic and Abiotic Factors on Patterns of Activity in Galápagos Snakes: Locomotory Performance or Prey Abundance? Unpublished MSc thesis, University of Albuquerque, Albuquerque, USA. 26 pp.
- Arteaga, A., Bustamante, L., Vieira, J. & Guayasamin, J.M. (2020). Reptiles of Ecuador: Life in the middle of the world. Universidad Tecnológica IndoAmerica, Quito, Ecuador. 257 pp. DOI: 10.47051/MNHT9360
- Blouin-Demers, G. & Weatherhead, P.J. (2001). Habitat use by Black rat snakes (*Elaphe obsoleta obsoleta*) in fragmented forests. *Ecology* 82: 2882-2896.
- Brown, D.S., Ebenezer, K.L. & Symondson, W.O.C. (2013). Molecular analysis of the diets of snakes: changes in prey exploitation during development of the rare smooth snake *Coronella austriaca*. *Molecular Ecology* 23:3734-3743.
- Cadena-Ortiz, H., Barahona, A., Bahamonde-Vinueza, D. & Brito, J.M. (2017). Anecdotal predation events of some snakes in Ecuador. *Herpetozoa* 30: 93-96.
- Christian, E. (2017). Demography and conservation of the Floreana racer (*Pseudalsophis biserialis biserialis*) on Gardner-by-Floreana and Champion islets, Galápagos Islands, Ecuador. Unpublished MSc thesis, Massey University, Auckland, New Zealand. 186 pp.
- Cochran, C.K.L., Edwards, Z.D., Travis, L.R., Pompe, & Hayes, W. K. (2021). Diet and feeding frequency in the Southwestern Speckled Rattlesnake (*Crotalus pyrrhus*): ontogenetic, sexual, geographic, and seasonal Variation. *Journal of Herpetology* 55:77-87.
- Daltry, J.C., Wüster, W. & Thorpe, R.S. (1996). Diet and snake venom evolution. *Nature* 379: 537-540.
- Daltry, J.C., Wüster, W. & Thorpe, R.S. (1998). Intraspecific variation in the feeding ecology of the crotaline snake *Calloselasma rhodostoma* in Southeast Asia. *Journal of Herpetology* 32:198-205.
- DeVault, T.L. & Krochmal, A.R. (2002). Scavenging by snakes: An examination of the literature. *Herpetologica* 58:429-436.
- Dowler, R.C., Carroll, D.S. & Edwards, C.W. (2000). Rediscovery of rodents (Genus *Nesoryzomys*) considered extinct in the Galápagos Islands. *Oryx* 34: 109-117.
- Evans, A.M., Choiniere, J.N. & Alexander, G.J. (2019). The cutting-edge morphology of the mole snake's dental apparatus. *PeerJ* 7: e6943
- Faraone, F.P., Di Nicola, M.R. & Lo Valvo, M. (2020). A case of cannibalism in the false smooth snake *Macroprotodon cucullatus* on the island of Lampedusa. *The Herpetological Bulletin* 151: 43-44.
- Fitch, H.S. (1963). Natural history of the black rat snake (*Elaphe o. obsoleta*) in Kansas. *Copeia* 1963:649-658.
- Glaudas, X, Kearney, T.C., & Alexander, G.J. (2017). Museum specimen bias measures of snake diet: a case study using the ambush-foraging puff adder (*Bitis arietans*). *Herpetologica* 73: 121-128.
- Gnudi, G., Volta, A., Di Ianni, F., Bonazzi, M., Manfredi, S. & Bertoni, G. (2009). Use of ultrasonography and contrast radiography for snake gender determination. *Radiology & Ultrasound* 50: 309-311.
- Göçmen, B., Werner, Y.L. & Elbeyli, B. (2008). Cannibalism in *Dolichophis jugularis* (Serpentes: Colubridae): more than random? *Current Herpetology* 27: 1-7.
- Henderson, R.W., & Powell, R. (2009). *Natural History of West Indian Reptiles and Amphibians*. Gainesville: University Press of Florida. 495 pp.
- Hill, M.M.A., Powell, G.L. & Russell, A.P. (2001). Diet of the prairie rattlesnake, *Crotalus viridis viridis*, in southeastern Alberta. *Canadian Field-Naturalist* 115:241-246.
- Hobson, K.A. & Welch, H.E. (1995). Cannibalism and trophic structure in a high Arctic lake: insights from stable-isotope analysis. *Canadian Journal of Fisheries and Aquatic*

- Sciences* 52:1195-1201.
- Ibáñez, C.M. & Keyl, F. (2010). Cannibalism in cephalopods. *Reviews in Fish Biology and Fisheries* 20: 123-136.
- Jackson, K., Kley, N. J. & Brainerd, E. L. (2004). How snakes eat snakes: the biomechanical challenges of ophiophagy for the California kingsnake, *Lampropeltis getula californiae* (Serpentes: Colubridae). *Zoology* 107: 191-200.
- Jofré, G.M. & Reading, C.J. (2020). Cannibalism in smooth snakes, *Coronella austriaca*. *Herpetological Journal* 30: 168-172.
- Lillywhite, H.B. (1982). Cannibalistic carrion ingestion by the Rattlesnake, *Crotalus viridis*. *Journal of Herpetology* 16: 95.
- Lillywhite, H.B., Sheehy III, C.M. & McCue, M.D. (2002). Scavenging behaviors of cottonmouth snakes at island bird rookeries. *Herpetological Review* 33: 259-261.
- López, M.S. & Giraudo, A.R. (2003). Diet of the large water snake *Hydrodynastes gigas* (Colubridae) from northeast Argentina. *Amphibia-reptilia* 25: 178-184.
- Lourdais, O., Brischoux, F., Shine, R & Bonnet, X. (2005). Adaptive maternal cannibalism in snakes (*Epicrates cenchria maurus*, Boidae). *Biological Journal of the Linnean Society* 84: 767-774.
- Maglio, V. J. (1970). West Indian Xenodontine colubrid snakes: the probable origin, phylogeny, and zoogeography. *Bulletin of the Museum of Comparative Zoology at Harvard College* 141: 1-54.
- Merlen, G., & Thomas, R.A. (2013): A Galápagos ectothermic terrestrial snake gambles a potential chilly bath for a protein-rich dish of fish. *Herpetological Review* 44: 415-417.
- Minitab 17 Statistical Software. (2010). Computer Software. State College, PA. Minitab, Inc. minitab.com
- Mitchell, J. C. (1986). Cannibalism in reptiles: a worldwide review. *Herpetological Circular* 15: 37 pp.
- Mociño-Deloya, E., Setser, K., Pleguezuelos, J.A., Kardon, A. & Lazcano, D. (2009). Cannibalism of nonviable offspring by postparturient Mexican lance-headed rattlesnakes, *Crotalus polystictus*. *Animal Behaviour* 77: 145-150.
- Ortiz-Catedral, L., Christian, E., Skirrow, M.J.A., Rueda, D., Sevilla, C., Kumar, K., Reyes, E.M.R.R. & Daltry, J. (2019). Diet of six species of Galápagos terrestrial snakes (*Pseudalsophis* spp.) inferred from faecal samples. *Herpetology Notes* 12: 701-704.
- Questel, K. (2012). Contribution à la connaissance d'Alsophis rijgersmaei (Squamata, Dipsadidae, Xenodontinae) Sur l'île de Saint-Barthélemy. Réserve Naturelle de Saint-Barthélemy & *Alsophis*, 24 pp.
- Reading, C. & Jofré, G. (2013). Diet composition changes correlated with body size in the Smooth snake, *Coronella austriaca*, inhabiting lowland heath in southern England. *Amphibia-Reptilia* 34: 463-470.
- Rodrigues da Silva Banci, K., Torello-Viera, N.F., Freitas, A.C. & Marques, O.A.V. (2017). Feeding on elongate prey: additional data for the coral snake *Micrurus corallinus* (Merrem, 1820) (Elapidae) and comments on aposematism. *Herpetology Notes* 10: 335-338.
- Rudolph, D.C., Burgdorf, S.J., Conner, R.N., Collins, D., Saenz, S.C., Schaefer, R.R., Trees, T., Duran, C.M., Ealy, M. & Himes, J.G. (2002). Prey handling and diet of Louisiana Pinesnakes (*Pituophis ruthveni*) and Black Pinesnakes (*P. melanoleucus lodingi*), with comparisons to other selected colubrid snakes. *Herpetological Natural History* 9:57-62.
- Sandfoss, M.R., Sheehy, C.M. III, & Lillywhite, H.B. (2017). Collapse of a unique insular bird-snake relationship. *Journal of Zoology* 304: 276-283.
- Sheehy C.M. III, Sandfoss, M.R. & Lillywhite, H.B. (2017). Cannibalism and changing food resources in insular cottonmouth snakes. *Herpetological Review* 48: 310-312.
- Saviozzi, P. & Zuffi, M.A.L. (1997). An integrated approach to the study of the diet of *Vipera aspis*. *Herpetological Review* 28: 23-24.
- Slip, D.J. & Shine, R. (1988). Feeding habits of the diamond python, *Morelia s. spilota*: ambush predation by a boid snake. *Journal of Herpetology* 22:323-330.
- Thomas, R.A. (1997). Galápagos Terrestrial Snakes: Biogeography and Systematics. *Herpetological Natural History* 5: 19-40.
- Thomas, L.K. & Manica, A. (2003). Filial cannibalism in an assassin bug. *Animal Behaviour* 66: 205-210.
- Weatherhead, P.J., Blouin-Demers, G. & Cavey, K.M. (2003). Seasonal and prey-seize dietary patterns of Black ratsnakes (*Elaphe obsoleta obsoleta*). *The American Midland Naturalist* 150: 275-281.
- Weatherhead, P.J., Knox, J.M., Harvey, D.S., Wynn, D., Chiucchi, J. & Gibbs, H.L. (2009). Diet of *Sistrurus catenatus* in Ontario and Ohio: Effects of body size and habitat. *Journal of Herpetology* 43: 693-697.
- Weldon, P.T., Demeter, B.J. & Rosscoe, R. (1993). A survey of shed skin-eating (dermatophagy) in amphibians and reptiles. *Journal of Herpetology* 27: 219-228.
- Williams, R.J., Ross, T.N., Morton, M.N., Daltry, J.C., & Isidore, L. (2016): Update on the natural history and conservation status of the Saint Lucia racer, *Erythrolamprus ornatus* Garman, 1887 (Squamata: Dipsadidae). *Herpetology Notes* 9: 157-162.
- Willson, J.D., Winne, C. T., Dorcas, M. E. & Gibbons, J. W. (2006). Post-drought responses of semi-aquatic snakes inhabiting an insolated wetland: insights on different strategies for persistence in a dynamic habitat. *Wetlands* 26: 1071-1078.
- Wiseman, K.D., Greene, H. W., Koo, M.S. & Long, D.J. (2019). Feeding ecology of a generalist predator, the California Kingsnake (*Lampropeltis californiae*): why rare prey matter. *Herpetological Conservation and Biology* 14: 1-30.
- Van Wyk, J. H. (1988). The diet of the rhombic skaapsteker, *Psammophylax rhombeatus rhombeatus* (Serpentes: Colubridae). *Navorsing Van Die Nasionale Museum Bloemfontein* 5: 455-471.
- Zaher, H., Yáñez-Muñoz, M.H., Rodrigues, M.T., Graboski, R., Machado, F.A., Altamirano-Benavides, M., Bonatto, S.L., & Graziotin, F.G. (2018). Origin and hidden diversity within the poorly known Galápagos snake radiation (Serpentes: Dipsadidae). *Systematics and Biodiversity* 16: 614-642.

Accepted:11 May 2021