Diet of six species of Galapagos terrestrial snakes (*Pseudalsophis* spp.) inferred from faecal samples

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The Galapagos terrestrial snakes, or ‘Galapagos racers’ (*Pseudalsophis* spp.) are a monophyletic group of nine species within Dipsadidae, exclusively found in the Galapagos Islands (Zaher et al., 2018). A single continental species, *P. elegans*, is the closest relative of these island species (Zaher et al., 2018), and is found from Ecuador to Chile (Armendáriz, 1991; Carrillo de Espinoza and Icochea, 1995; Thomas, 1977). The group has been the subject of various taxonomic reviews since the early 1900s (Thomas, 1997). Although there have been significant advances in understanding the evolutionary history of the group and their phylogenetic affinities (Grazziotin et al., 2012; Zaher et al., 2018), basic aspects of their biology have remained largely undocumented, in particular the diversity of prey consumed by the different species across the Galapagos archipelago and mainland South America. For instance, in the 106 years since VanDenburg’s (1912) first account of food items in the stomach contents of Galapagos racers, there have only been five studies that describe prey species for these snakes, which report: lava lizards (*Microlophus* spp.) (Altamirano, 1996; Merlen and Thomas, 2013; Cadena-Ortiz et al., 2017); marine iguana (*Amblyrhynchus cristatus*) hatchlings (Laurie and Brown, 1990; Merlen and Thomas, 2013); land iguana (*Conolophus subcristatus*) hatchlings (Werner, 1983); and coastal fishes (*Bolinichthys longipes*, *Dialommus fuscus* and *Labrisomus dendriticus*) (Merlen and Thomas, 2013). There are also unpublished reports of Galapagos racers ingesting large painted locusts (*Schistocerca melanocera*) (Jackson, 1993), and three observers (park rangers from the Galapagos National Park) have witnessed *P. dorsalis* ingesting eggs of Galapagos doves (*Zenaida galapagoensis*) on Santa Fe Island (G. Quezada, M. Gavilanes and C. Gaona pers. comm.). There is even an unconfirmed report of a terrestrial snake ingesting the fruit pulp of bitter melon (*Mormodica charantia*) on Santa Cruz Island (Olesen et al., 2018), but it is unknown whether the snake ate the bitter melon deliberately or by accident (e.g. while preying on a small vertebrate associated with the fruit). To contribute to the knowledge of the feeding ecology of Galapagos racers, and to shed light on the biology of these poorly studied reptiles, we conducted a field study on the prey diversity of six species at nine localities in the Galapagos Islands from 2015 to 2018. We examined 79 faecal samples opportunistically collected in the field during our ongoing studies on the morphological variability of Galapagos racers and, in particular, the demographics of Floreana racers (*P. biserialis biserialis*). Furthermore, we report eight predation events observed in the field at two locations for two species.

We captured racers and conducted field observations, on the following islands: Seymour Norte (0° 23’ 30” S, 90° 17’ 0” W); Santa Fe (0° 49’ 0” S, 90° 3’ 30” W); Fernandina (0° 22’ 0” S, 91° 31’ 20” W); Rabida (0° 24’ 35”, 90° 42’ 30” W); Santiago (0° 15’ 30” S, 90° 43’ 30” W) and Pinzon (0° 36’ 30” S, 90° 39’ 57” W), and the following islets: Champion (1° 14’ 7” S, 90° 23’ 8” W); Gardner-by-Floreana (“Gardner”) (1° 19’ 52” S, 90° 17’ 20” W); and Tortuga Islet (1° 1’ 21.5” S, 90° 52’ 11.5” W). Galapagos racers typically have a bi-modal pattern of peak activity occurring between approximately 05:30 h to 10:00 h and 16:00 h to 19:00 h (Altamirano, 1996; Christian, 2017). We searched for
races during these peak activity periods and captured them by hand. Every captured racer was placed in a cloth bag, measured, weighed, photographed and faecal samples obtained. The total processing time per snake from capture to last measurement took approximately one hour.

We obtained faecal samples using a palpation technique. This method is minimally invasive and has been successfully used to yield useful dietary information in closely related snakes (Daltry et al., 1996; Williams et al., 2016). To extract faecal samples, individual Galapagos racers were held firmly in one hand around the mid-body. Gentle pressure was then applied slowly to palpate the intestinal tract, three quarters of the way down the body until faecal matter was extruded. Due to the delicate nature of this procedure, training in the field was provided by J. C. Daltry (see also Daltry et al. 1995; Williams et al., 2016). Faecal samples were collected in 2 ml micro-centrifuge tubes and fixed in 0.5-1.5 ml of 96 % ethanol until examination for contents. An alternative method to identify prey items is forced regurgitation (Drummond and Garcia, 1989; Manjarrez et al., 2013), but this method is more invasive and requires finding snakes in the process of ingesting or recently ingested prey, which only applied to 7 % of our encounters with racers on the Galapagos Islands.

Faecal samples were examined using dissection microscopes at the Invertebrate Collection Lab of the Charles Darwin Research Station in Puerto Ayora, Santa Cruz, Ecuador. We recorded the presence of scales, invertebrate remains, feathers, bones and other undigested materials. We also examined under the same microscopes reference voucher specimens of potential prey items from the vertebrate collection at the Charles Darwin Research Station (darwinfoundation.org/en/datazone). The prey remains in faecal samples were often large enough to be identified at the species level, but due to the fragmented nature of most of the material, we were unable to estimate prey size or age. Of the 79 faecal samples collected via the palpation technique, only 54 samples (from eight localities) had identifiable material (Table 1). The remaining 25 samples (from Champion and Gardner Islets) had material too digested to allow identification under a microscope. After examination, samples were returned to plastic tubes and deposited at the Directorate of the Galápagos National Park.

Table 1 summarises the variety of prey items identified in faecal samples of six species of Galapagos racers. The most frequently identified prey in our samples were lava lizards (*Microlophus* spp.) (28 samples), recorded in five of the six snake species. The second most common prey type identified from faecal samples were leaf-toed geckos (*Phyllocladus* spp.), recorded from three snake species. The remains of small invertebrates (beetles, ants and centipedes) were also identified in 24 samples, but it is unclear if these represent secondary ingestion (e.g. invertebrates predated on by lizards). We also identified small feathers in 12 samples from a single species and population (*P. biserialis* on Gardner). Lastly, remains of avian eggshells were found in two samples from two populations. In addition to these samples, we observed eight predation events and one scavenging event. The predation events consisted of five instances of predation on hatchling marine iguanas (*A. cristatus*) on the coast of Cape Douglas (Fernandina Island), and one adult female lava lizard (*Microlophus albemarlenis*) by *P. occidentalis* at “La Cumbre”, near the summit of Fernandina. The other two predation events were on lava lizards (*M. indefatigabilis*) on Seymour Norte by *Pseudalsophis dorsalis*. At Cape Douglas, Fernandina Island, we also observed the only instance of scavenging in this study: on the morning of July 5th 2018, we accidentally disturbed a large *P. occidentalis* in the process of ingesting a marine iguana hatchling. We captured the snake to obtain faecal samples and morphometric data. Two hours after, as we approached the site to release the snake, we observed a smaller racer ingesting the same partially digested marine iguana hatchling. We observed this snake ingest the whole hatchling and decided not to disturb the racer. Scavenging in the field has been documented for at least 43 snake species (DeVault and Krochmal, 2002). To the best of our knowledge, this is the first instance of scavenging reported for Galapagos racers.

Our study contributes to the knowledge on the basic biology of Galapagos racers and indicates that these terrestrial snakes are generalist predators across the archipelago, primarily ingesting reptiles (lava lizards and geckos). Our study also reports the first instances of birds and bird eggs as prey items for two racer species. Although the eggshells and feathers could not be identified to species level, we speculate these could belong to Darwin’s finches (*Geospiza* spp., *Certhidea* spp. and/or *Camarhynchus* spp.), which are common on Gardner and Santa Fe where the faecal samples containing feather remains were collected. Regarding predation of avian prey, the closely related and similar-sized mainland species *Philodryas chamissonis* has been reported ingesting nestlings of two bird species (Greene and Kaksic, 1992; Escobar and Vukasovic, 2003; Torres, 2017). Combined with previous reports
Table 1. Prey identified in faecal samples of Galapagos racers (n = 54 including samples with no identifiable remains) at eight localities. Column numbers indicate the number of faecal samples containing prey per locality.  

<table>
<thead>
<tr>
<th>Racer species</th>
<th>Locality</th>
<th>n</th>
<th>Lava lizard</th>
<th>Gecko</th>
<th>Invertebrate</th>
<th>Feather</th>
<th>Avian egg shell</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pseudalsophis biserialis</td>
<td>Champion</td>
<td>13</td>
<td>2⁴</td>
<td>4⁵</td>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Gardner</td>
<td>41</td>
<td>11⁴</td>
<td>6⁶</td>
<td>14</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>P. dorsalis</td>
<td>Santa Fe</td>
<td>4</td>
<td>2⁵</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P. occidentalis</td>
<td>Fernandina</td>
<td>7</td>
<td>3⁶</td>
<td>2⁸</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P. thomasi</td>
<td>Rabida</td>
<td>3</td>
<td>2⁴</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Santiago</td>
<td>3</td>
<td>2⁴</td>
<td>3⁵</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>P. occidentalis</td>
<td>Tortuga</td>
<td>6</td>
<td>4⁸</td>
<td>5⁸</td>
<td>5</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>P. slevini</td>
<td>Pinzon</td>
<td>2</td>
<td>2⁸</td>
<td>2⁸</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

of P. biserialis inspecting active nests of finches and mockingbirds (Mimus spp.) (Ortiz-Catedral, et al., 2017), this suggests that nestlings could be common prey for Galapagos racers, but this aspect, along with the potential consumption of avian eggs, requires further investigation.

No evidence of mammalian hair, teeth or claws were found in the faecal samples, but most samples were collected from racers on islands that lack terrestrial mammals. We cannot rule out the possibility that Galapagos racers would opportunistically prey on small native or non-native rodents. West Indian racers in the genus Alsophis, for example, show many morphological and ecologically similarities to the genus Pseudalsophis and, while most species feed primarily on lizards, other prey including birds, frogs, fishes and small rodents such as Mus musculus and juvenile Rattus rattus have also been reported (Henderson & Powell, 2009; Questel, 2012). We did not encounter seeds in our collection of faecal samples on eight islands, therefore cannot confirm whether Pseudalsophis spp. consumes fruit pulp on other islands.

Our study reports five previously undocumented prey species: Microlophus grayii and Phyllodactylus baurii for P. biserialis on Champion and Gardner Islets; P. galapagensis for P. occidentalis on Tortuga Islet; M. duncanensis for P. slevini on Pinzon Island; and M. indefatigabilis for P. dorsalis on Santa Fe and Seymour Norte Islands. Our study shows that the palpation technique can reliably yield material for field studies on the diet of Galapagos racers. We recommend examining whether Galapagos racers consume fruit pulp if presented with it in a captive setting, to verify whether these items represent a relevant component of their diet. We hope this study promotes further studies on the feeding ecology of Galapagos racers and their mainland relatives, to advance our knowledge of the niche breadth and potential dietary shifts associated with the colonisation of the Galapagos Islands. These studies will positively impact our ability to conserve this diverse, yet neglected component of the Galapagos fauna.

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References


