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Invertebrate Predators of *Anolis* Lizards: A New Observation and a Summary of Published Reports

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Many reptiles are important predators of invertebrates and can have measurable impacts on the composition and dynamics of invertebrate communities (Reagan 1996; Schoener et al. 2002). However, this predator-prey interaction is sometimes reversed, as reptiles are often prey for a variety of arthropods (McCormick and Polis 1982; von May et al. 2019; Reyes-Olivares et al. 2020). Most reptiles that succumb to predation by arthropods are relatively small species or are at young, vulnerable life stages (McCormick and Polis 1982; Chalcraft and Andrews 1999). Anoles (*Anolis* spp.) are excellent examples, as many species are relatively small (<10 cm snout-vent length), have high population densities, and occur in regions (Neotropics) with a high diversity of predatory invertebrates; consequently, anoles are potentially an important energy source for higher trophic levels (Reagan 1996; Losos et al. 2009), as well as predatory invertebrates (e.g., spiders, Reyes-Olivares et al. 2020). Nevertheless, despite the potential importance of anoles as prey of invertebrates, these types of interactions are haphazardly documented and probably observed far less frequently than these predation events actually happen, especially given the large number of reports of other small terrestrial vertebrates as prey for arthropods (McCormick and Polis 1982; Toledo 2005; Reyes-Olivares et al. 2020). Herein we describe a new observation of an invertebrate predator on an anole and provide a summary of published reports of anoles as prey of invertebrates. This brief summary aims to highlight invertebrates as an important predator guild for this ecologically important group of lizards.

At 2323 h on 13 August 2019, we observed remnants of an anole in close proximity (~5 cm) to a Tropical Shield Mantis (*Choeradodis rhombicollis*) at La Selva Biological Station, Puerto Viejo de Sarapiquí, Costa Rica (Fig. 1). The

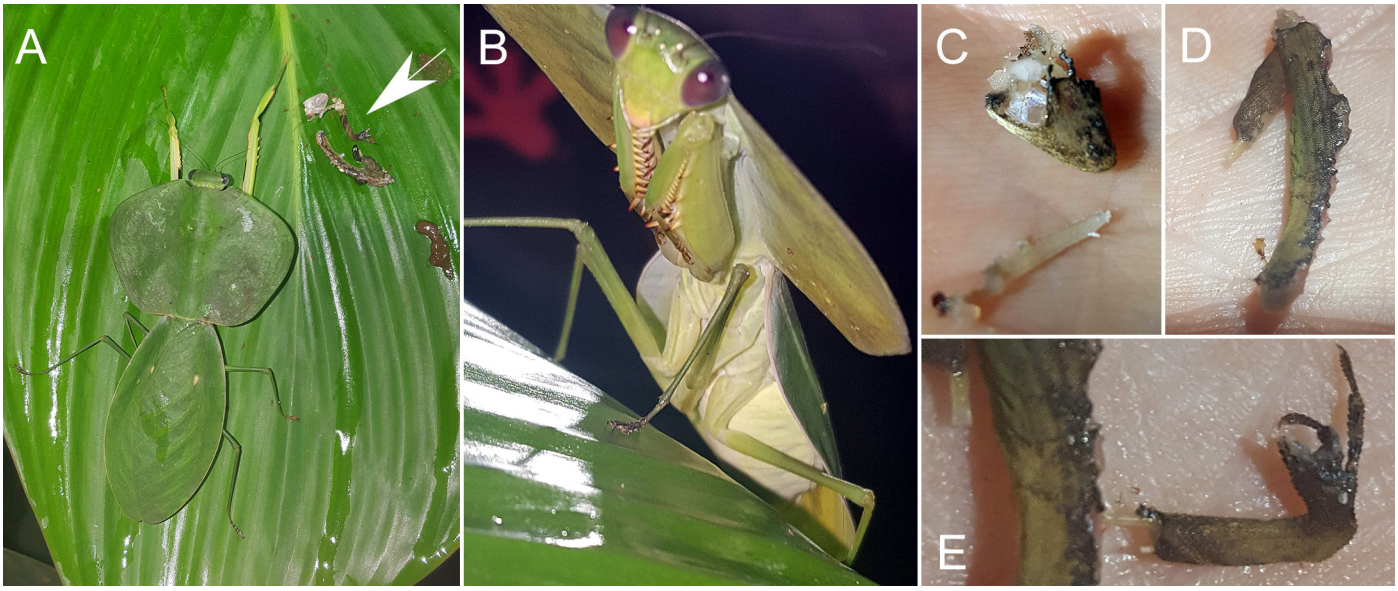

Figure 1. Anole predation by a Tropical Shield Mantis (*Choeradodis rhombicollis*) (A–B). The mantis was observed in close proximity to remnants of an anole (arrow in A) that included a skull (C), parts of hindlimbs and tail (D–E), and an unidentified bone. The skull and right hindlimb provided diagnostic characteristics of *Anolis*, and the skin color, size, and habitat suggest that this species was either *A. limifrons* or *A. lemurinus*. Photographs by David Laurencio.

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Table 1. Published reports of invertebrate predators of *Anolis* lizards. Because many reports of anoles as prey of invertebrates are anecdotal and buried within the literature, we may have missed some published observations. Observations that were reported online or via iNaturalist are not included.

Prey	Predators	Localities	References
A. agassizi	Land crab (*Gecarcinus malpilensis*)	Malpelo Island, Columbia	Rand et al. 1975; Wolda 1975
A. allisoni	Scorpion (*Heteroctenus junceus*)	Cuba	Rodriguez-Cabrera et al. 2021
A. carolinensis	White-banded Fishing Spider (*Dolomedes albineus*)	Texas, USA	Eversole 2022
A. carolinensis	Wolf Spider (*Lycosa ammophila*)	Florida, USA	Corey 1988
A. carolinensis	Jumping Spider (*Phidippus regius*)	Florida, USA	Nyffeler et al. 2017
A. carolinensis	Sarcophagid fly (*Lepidodexia blakeae*)[1]	Louisiana, USA	Irschick et al. 2006
A. chrysolepis	Spider (*Ctenus* sp.)	French Guiana	de Massary 1999
A. cusuco	Mantis (unidentified species)	Cusuco National Park, Honduras	Lonsdale and Brown 2019
A. fuscoauratus	Whip scorpion (*Heterophrynus* sp.)	Sani Reserve, Ecuador	Thomas 2020
A. fuscoauratus	Ctenid spider (*Ctenus* sp.)	Columbia	Medina-Rangel 2013
A. fuscoauratus	Cockroach (*Amazonica* or *Cariblatta* sp.)[2]	Ecuador	van den Burg and González de Rueda 2021
A. homolechis	Katydid (*Erechthis gundlachi*)	Cuba	Yong 2017
A. humilis	Ctenid spider (unknown species)	Costa Rica	Guyer 1988
A. humilis	Ctenid spider (*Ctenus curvipes*)	Costa Rica	Folt and Lapinski 2017
A. humilis	Ctenid spider (*Cupiennius* sp.)	Costa Rica	Folt and Lapinski 2017
A. gundlachi	Spider (*Oligoctenus ottleyi*)	Puerto Rico	Clark and Gillingham 1990
A. limifrons	Wandering Spider (*Cupiennius getazi*)	La Selva Biological Station, Costa Rica	Losos 2009[6]
A. limifrons	Cone-headed Katydid (*Copiphora cultricornis*)	Costa Rica	Nuñez Escalante et al. 2021
A. limifrons	Ctenid spider (*Cupiennius* sp.)	Panama	Bock and Quintero 1987
A. limifrons	Ants (*Solenopsis* sp.)[3]	Barro Colorado Island, Panama	Andrews 1982; Chalcraft and Andrews 1999
A. limifrons	Snail (*Salasiella browni*)[3]	Barro Colorado Island, Panama	Andrews 1982
A. polylepis	Wandering Spider (*Cupiennius cossineus*)	Costa Rica	Nuñez Escalante et al. 2021
A. polylepis	Flame-bellied Orbweaver (*Eriophora fuliginea*)	Costa Rica	Nuñez Escalante et al. 2021
A. porcatus	Orbweaver spider (*Argiope trifasciata*)	Cuba	Armas and Alayón 1987
A. porcatus	Scorpion (*Centruroides gracilis*)	Cuba	Armas 2001
A. porcatus	Orbweaver spider (*Cyrtophora citricola*)	Brazil	Antonio et al. 2020
A. rodriguezii	Sparassid spider	Mexico	García-Balderas et al. 2016
A. ophiolepis	Scorpion (*Heteroctenus junceus*)	Cuba	Rodríguez-Cabrera et al. 2021
A. osa	Wandering Spider (*Kiekie curvipes*)	Costa Rica	Cubas-Rodríguez and Teruel 2022
A. sagrei	Marsh Crab (*Armases cinereum*)[3]	Florida, USA	Cates et al. 2014; DeSana et al. 2020
A. sagrei	Ctenid spider (*Cupiennius cubae*)	Cuba	Hernández and Rodríguez-Cabrera 2014
A. sagrei	Orbweaver spider (*Argiope trifasciata*)	Puerto Rico	Armas and Alayón 1987; Armas 2001
A. sagrei	Scorpion (*Centruroides gracilis*)	Mexico	Cubas-Rodríguez and Teruel 2022
A. sagrei	Scorpion (*Heteroctenus junceus*)	Cuba	Rodríguez-Cabrera et al. 2021
A. sagrei	Jumping spider (*Phidippus regius*)	Florida, USA	Nyffeler et al. 2017
Anolis sp.	Jumping spider (*Phidippus bidentatus*)	Costa Rica	Nyffeler et al. 2017
Anolis sp.	Whip scorpion (*Phrynus longipes*)	Hispaniola	Armas 2001
Anolis sp.[4]	Tarantula (*Avicularia laeta*)	El Verde, Puerto Rico	Reagan 1996
Anolis sp.[4]	Tailless whip scorpion (*Phrynus longipes*)	El Verde, Puerto Rico	Reagan 1996
Anolis sp.[4]	Centipede (*Scolopendra alternans*)	El Verde, Puerto Rico	Reagan 1996
Anolis sp.[5]	Tropical shield mantis (*Choeradodis rhombicollis*)	La Selva Biological Station, Costa Rica	Present report

[1]This fly is more appropriately considered a parasite than a predator, but it can kill anoles.
[2]This is an observation of a cockroach feeding on the tears (lachryphagy) of *A. fuscoauratus* while it was sleeping.
[3]Predation was reported on anole eggs, rather than on free-ranging lizards.
[4]The *Anolis* species was not identified, but likely was *A. cuvieri*, *A. gundlachi*, *A. evermanni*, or *A. stratulus*.
[5]The *Anolis* species could not be confidently identified, but likely was *A. limifrons* or *A. lemurinus*.
[6]The species of predatory spider in the photograph in Losos et al. (2009) was verified by Folt and Lapinski (2017).

mantis and anole remnants were ~1 m above the ground on a leaf. We did not observe the mantis actively consuming the anole, but the proximity of the anole remnants provided evidence of predation by the mantis. Indeed, most vertebrate predators of anoles would swallow the prey whole (snakes) or move the individual to another location for consumption (birds), whereas mantids capture and manipulate prey with their forelimbs before subsequently chewing it (Reid et al. 2010), potentially leaving remnants as observed here. The lizard remnants included the head and parts of the left and right hindlimbs. The shape of the head and presence of toepads and claws on the right hindlimb were indicative of *Anolis*. Based on the color and size of the body parts and the habitat (open area within the biological station's campus), we were able to eliminate several potential species, and are confident that this was either a Slender Anole (*A. limifrons*) or Canopy Anole (*A. lemurinus*). *Anolis limifrons* is the most commonly observed species at this site (Perez-Martinez et al. 2021) and is often found on leaves in habitats similar to that observed here. However, while the skin coloration is consistent with that of *A. limifrons*, the short snout and markings on the legs also seem to resemble those of *A. lemurinus*. Photos of this individual were accessioned in the Auburn University Museum of Natural History (AHAP-D 2835).

Predation of anoles and other lizards by other mantid species has been reported previously (Jehle et al. 1996; Lonsdale and Brown 2019; see also internet photos/videos), but to our knowledge, this is the first report of this predatory interaction with *C. rhombicollis*. Like other mantids, members of the genus *Choeradodis* presumably prey on other invertebrates as well as vertebrates (e.g., salamanders, Buttenhoff 1995). The cryptic morphology (i.e., leaf mimic) and diurnal sit-and-wait predatory strategy of *Choeradodis* mantids (Lücking et al. 2010) indicate that these predators respond to moving prey during the day. Thus, the lizard might quite possibly have been captured during the day when it was active, and our encounter was when the mantid was finishing its meal, leaving only a few unconsumed body parts some time later. Alternatively, this predator may have captured the anole while sleeping on the leaf at night (Clark and Gillingham 1990) and consumed most of it prior to our observation.

Invertebrate predation on vertebrate animals is relatively poorly studied and therefore underestimated (Nordberg et al. 2018; Nyffeler and Altig 2020), but an accumulation of anecdotal reports and some focused research suggest that invertebrate predators may play a larger role in shaping vertebrate populations than has been historically appreciated (McCormick and Polis 1982; von May et al. 2019; Reyes-Olivares et al. 2020). The growing number of observations of anole predation by invertebrates (Table 1) suggests that these predator-prey interactions are not trivial. Indeed, given the high abundance and diversity of predatory invertebrates and species of *Anolis* throughout the Caribbean and mainland Neotropical regions, these types of predatory encounters likely occur far more often than what is reported. The list of reports in Table 1 indicates that specialized predators (e.g., ctenid spiders) capture juvenile or adult individuals most frequently, whereas opportunistic scavengers (e.g., crabs, snails, ants) prey on anole eggs. While most reports of anole predation by invertebrates are anecdotal observations by researchers, focused experimental studies demonstrate that invertebrate predators of anole eggs can influence population demographics (Andrews 1988) and may impose selective pressures on nesting behaviors of females (DeSana et al. 2020). Although predation rates are difficult to quantify (due to low rates of observation), experimental studies that measure and/or manipulate invertebrate predator densities (i.e., using field enclosures or exclosures) and measure the effects on survival rates will provide important insights into the role of invertebrates in shaping key aspects of anole biology (e.g., anti-predator behaviors, phenotypic selection, population dynamics). Natural history observations, such as those listed in Table 1, are critical in forming the foundation for these types of experimental studies.

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