Short Communication

Ecological interactions between arthropods and small vertebrates in a lowland Amazon rainforest

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Abstract.—Ecological interactions such as those involving arthropod predators and parasitoids and their prey or hosts provide evidence for selective pressures influencing small vertebrate populations, and are key to understanding the many connections that shape food webs in tropical rainforests. Here, we document 15 predator-prey interactions involving different types of arthropod predators and vertebrate prey including frogs, lizards, snakes, and a mammal. Documented also are three cases of fly myiasis in frogs, and provide further evidence of a commensal relationship involving a tarantula and a narrow-mouthed frog in lowland Amazonian Peru.

Many groups of arthropods are predators of vertebrates and play a critical role in the structure and functioning of food webs (McCormick and Polis 1982). Spiders are among the most diverse predaceous arthropods in the tropics and exhibit high levels of both family and species richness in this climatic region (Cardoso et al. 2011). Reports of spider predation on vertebrates include prey from all major vertebrate taxonomic groups including fishes, amphibians, reptiles, birds, and mammals (McCormick and Polis 1982; Greene 1988; Das et al. 2012; Nyffeler and Knörnschild 2013; Nyffeler and Pusey 2014). In addition to spiders, other predaceous arthropods common in terrestrial environments include scorpions, centipedes, ants, and beetles, while those in aquatic environments include water bugs, dragonfly larvae, diving beetles, and other invertebrates (Corey 1988; Toledo 2005; Wells 2007; von May 2009a; Biggi and Tomasinelli 2017). Most predaceous arthropods rely on specialized trophic structures and venom to capture and paralyze vertebrate prey (McCormick and Polis 1982). Morphological adaptations include modified jaws, enlarged beaks, and massive chelicerae. Some taxa have evolved dozens of venom proteins that are injected at once during prey capture. For example, the venom of some species of giant water bugs (Belostomatidae) contains a powerful mix of nearly 130 venom proteins, including cytolytic toxins, antimicrobial peptides, and enzymes, that they inject in their fish prey (Walker et al. 2018).

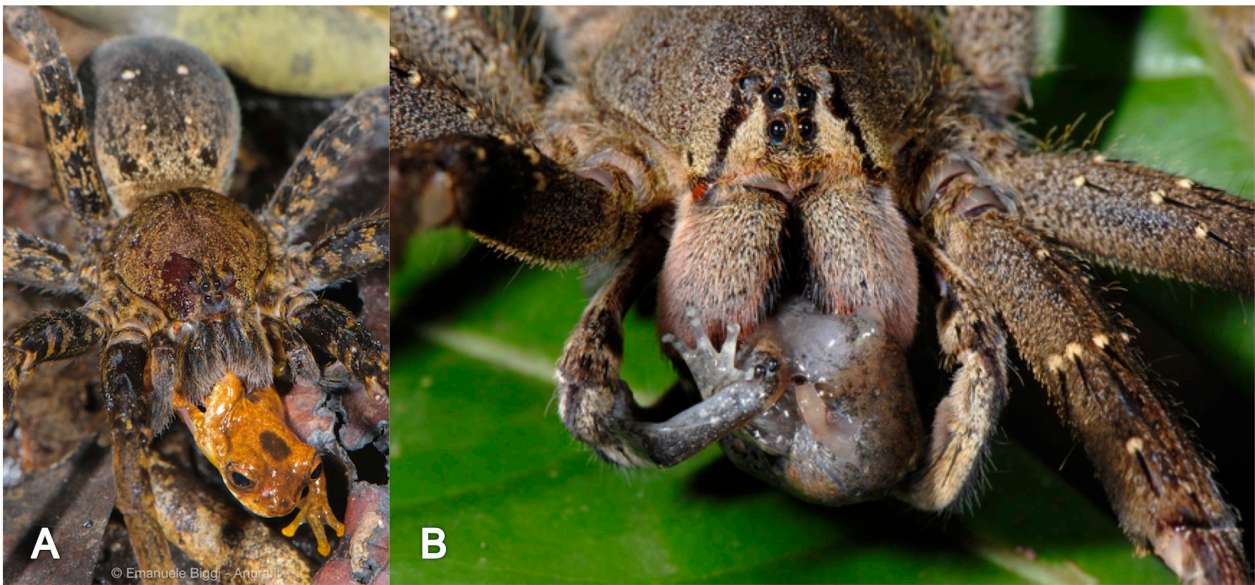**Correspondence.** [1]*rvonmay@umich.edu*

Fig. 1. (A) The spider *Ancylometes* sp. (Ctenidae) preying upon an adult *Dendropsophus leali*; **(B)** the spider *Phoneutria* sp. (Ctenidae) preying on a sub-adult *Hamptophryne boliviana. Photos by Emanuele Biggi (A) and Francesco Tomasinelli (B).*

Predation of small vertebrates by arthropods has been documented in several lowland rainforest sites (e.g., Corey 1988; Menin et al. 2005; Toledo 2005; Das et al. 2012; Nyffeler and Knörnschild 2013; Nyffeler and Pusey 2014), yet our knowledge of these interactions remains limited, especially given the diversity of vertebrate prey and potential arthropod predators in species-rich tropical communities. It is valuable to document these predator-prey interactions in the field, because they provide a snapshot of the many connections that shape food webs and provide evidence for selective pressures influencing small vertebrate populations. This is especially important in tropical rainforests, given their exceptional levels of biodiversity. Documenting predation by spiders and other arthropods in these ecosystems is essential even if many predaceous arthropods remain undescribed and are mostly classified as morphospecies (Cardoso et al. 2011), because they provide insights into an important source of vertebrate mortality that appears to be less common in extra-tropical communities.

Here, documented are 15 predator-prey interactions involving different types of arthropod predators and vertebrate prey including frogs, lizards, snakes, and a mammal. Also documented are three cases of fly myiasis (live parasitic infestation by maggots) in frogs, and provide further evidence of a commensal relationship involving a tarantula and a narrow-mouthed frog in lowland Amazonian Peru.

Our main study site, Los Amigos Biological Station (12°34'07"S, 70°05'57"W, 250 m elev.), is located in Madre de Dios region, southeastern Peru. A general overview of the amphibian and reptile fauna, the habitats, and the local climate at this site was provided by von May et al. (2006, 2009b, 2010a,b), and Whitworth et al. (2016) provided a preliminary list of the reptile taxa recorded at this site. Additionally, we report two predator-prey observations from Villa Carmen Biological Station (12°53'43.8"S, 71°24'13.7"W, 520 m elev.), also located in Madre de Dios region, and one parasitoid observation from Madre Selva Research Station, Loreto region, northern Peru (3°37'39.1"S, 72°14'24.4"W, 105 m elev.). The predator-prey observations are presented in chronological order and involve prey in different life stages including eggs, larvae, juveniles, and adults. In most cases, the prey specimens were not collected because they were consumed by the predators. Identification of prey was primarily done in the field and was subsequently confirmed based on photographs presented herein. The observations on parasitoid infections and commensalism are also presented in chronological order.

Predator-prey Interactions

On 20 February 2008, at 1947 h, we observed a spider of the genus *Ancylometes* (Ctenidae) preying upon an adult *Dendropsophus leali* (Hylidae; Figure 1A). The spider held its prey tightly by the back. This observation took place in the floodplain forest, at a site located approximately 2 km from the station.

On 22 February 2008, at 2056 h, we observed a spider of the genus *Phoneutria* (Ctenidae) preying on a sub-adult *Hamptophryne boliviana* (Microhylidae; Figure 1B). The spider held its prey tightly by the body and the frog did not display any movement. This observation took place in the floodplain forest, at a site located 1.5 km from the station.

On 23 February 2008, around 2110 h, we observed a fishing spider of the genus *Thaumasia* (Pisauridae) preying upon a tadpole (unidentified) at a temporary pond located in terra firme forest (Figure 2A). The pond is located near

Fig. 2. (A) The fishing spider *Thaumasia* sp. (Pisauridae) preying upon a tadpole (unidentified) at a temporary pond located in terra firme forest; **(B)** a ctenid spider (genus undetermined; Ctenidae) preying upon a subadult *Boana* sp. G. *Photos by Emanuele Biggi (A) and Francesco Tomasinelli (B).*

(~50 m) the station laboratories and is used by at least a dozen amphibian species during the wet season (R. von May, pers. obs.).

On 25 February 2008, at 2122 h, we observed a ctenid spider (genus undetermined; Ctenidae) preying upon a subadult *Boana* sp. G (Hylidae; Figure 2B). The spider was on top and the frog did not display any movement. This observation took place in the terra firme forest, at a site located approximately 1 km from the station.

On 25 February 2008, around 2200 h, we observed a theraphosid spider (Theraphosidae), possibly in the genus *Pamphobeteus*, preying upon an adult *Hamptophryne boliviana* (Microhylidae; Figure 3A). Both individuals were found in the leaf litter, and the spider was holding the frog by the posterior section of the body. This obser-

vation took place in the floodplain forest, at a site located approximately 1.5 km from the station.

On 11 March 2016, during a night survey, we observed a wandering spider (Ctenidae) preying upon an individual of *Leptodactylus didymus* (Leptodactylidae). Both individuals were found on a leaf, and the spider was holding the frog by the back (Figure 3B). We encountered both individuals in the terra firme forest approximately 1 km from the station.

On 17 March 2016, at 2130 h, during a leaf-litter plot survey, we observed a spider of the genus *Ctenus* (Ctenidae) holding an individual of *Cercosaura eigenmanni* (Gymnophthalmidae) by the middle of its body (Fig. 4). Upon capture, the spider held its prey tight; the lizard tail kept moving for several minutes after capture. At the time of

Fig. 3. (A) A theraphosid spider, cf. *Pamphobeteus* sp. (Theraphosidae), preying upon *Hamptophryne boliviana*; (B) a ctenid spider (Ctenidae) preying upon *Leptodactylus didymus*. *Photos by Emanuele Biggi (A) and Pascal Title (C).*

Fig. 4. The spider *Ctenus* sp. (Ctenidae) preying upon a subadult *Cercosaura eigenmani*. Photo by Mark Cowan.

preservation of both individuals, the spider had released its prey, which was already dead. This observation took place in the terra firme forest, at a site located 3.5 km from the station.

On 24 October 2016, at ~2100 h we disturbed a scolopendrid centipede (Chilopoda, Scolopendridae) that was consuming a live juvenile snake, *Dipsas catesbyi* (Colubridae), in the leaf litter near Villa Carmen Biological Station. A precise identification of the predator is not possible because it abandoned its prey and quickly retreated into the leaf litter before we had time to take a photograph. The snake had a gaping wound in its right side, where the scolopendrid had eaten through the skin and muscle of the body wall (Fig 5A). Due to the sever-

ity of its injuries, the snake was humanely euthanized, preserved as a voucher specimen, and deposited in the herpetological collection at the Museum of Natural History, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM 37084). It had an SVL of 245 mm and a tail length of 84 mm.

On the morning of 7 November 2016, we found a juvenile snake, *Micrurus obscurus* (Elapidae) deceased in a funnel trap, being consumed by a scolopendrid centipede (Chilopoda, Scolopendridae). By the time we removed the predator from the trap, it had decapitated the snake and removed the skin and muscle from ~20 mm of the vertebral column (Fig 5B). This observation took place in a forest with short and narrow stemmed trees with
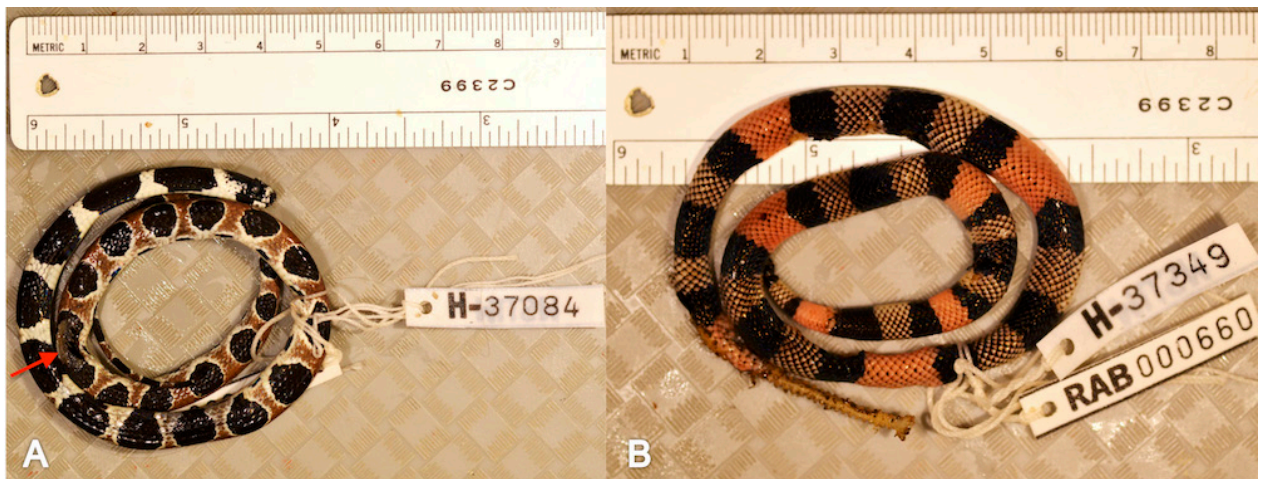

Fig. 5. (A) Juvenile snake *Dipsas catesbyi* with lesion caused by scolopendrid centipede (red arrow); **(B)** juvenile snake *Micrurus obscurus*, missing head and soft tissues on most anterior part of body as a result of predation by scolopendrid centipede. *Photos by Joanna Larson (A–B).*

Fig. 6. (A) Theraphosid spider *Pamphobeteus* sp. (Theraphosidae) preying upon the mouse opossum *Marmosops* cf. *noctivagus*; **(B)** The same individual of *Pamphobeteus* sp. dragging the mouse opossum on the leaf litter. *Photos by Maggie Grundler (A–B).*

little understory and rocky soil near Villa Carmen Biological Station. The snake had an SVL of >248 mm and a tail length of 16 mm. The snake specimen was deposited in the herpetological collection at the Museum of Natural History, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM 37349).

On 18 November 2016, at 2313 h during a night survey, we observed a theraphosid spider, *Pamphobeteus* sp. (Theraphosidae) preying upon a mouse opossum, *Marmosops* cf. *noctivagus* (Didelphidae). The spider was on the ground in the leaf litter holding the opossum by the neck region (Fig. 6); a video of the interaction is archived in the University of Michigan Deep Blue Data repository (doi.org/10.7302/Z2862DP1). When we first encountered the pair, the opossum was still responsive and kicking weakly. We observed the interaction for approximately 5 minutes after which time the opossum ceased all movement and the spider dragged it away around a tree root. This observation took place in the floodplain

forest, approximately 2 km from the station. It is worth noting that this appears to be the first documentation of a large mygalomorph spider (infraorder Mygalomorphae) preying upon opossums (R. Voss, pers. comm.). Opossum species in the genus *Marmosops* are primarily found on the forest floor, are active at night, and live in different habitats including old growth forest, secondary forest, and open areas (Emmons and Feer 1997). In the lowlands of southeastern Peru, *Marmosops noctivagus* is the only local species with clear-white underparts, and the grayish dorsal pelage of the individual preyed upon by the spider (Fig. 6) suggests that it was a juvenile or subadult (R. Voss, pers. comm.).

On 22 November 2017, at 2254 h during a standardized night survey, we observed a wandering spider (Ctenidae) preying upon an individual of *Hamptophryne boliviana* (Microhylidae). Both individuals were found in the leaf litter, and the spider was holding by the rear right leg (Fig. 7A). We observed as the spider manipulated the
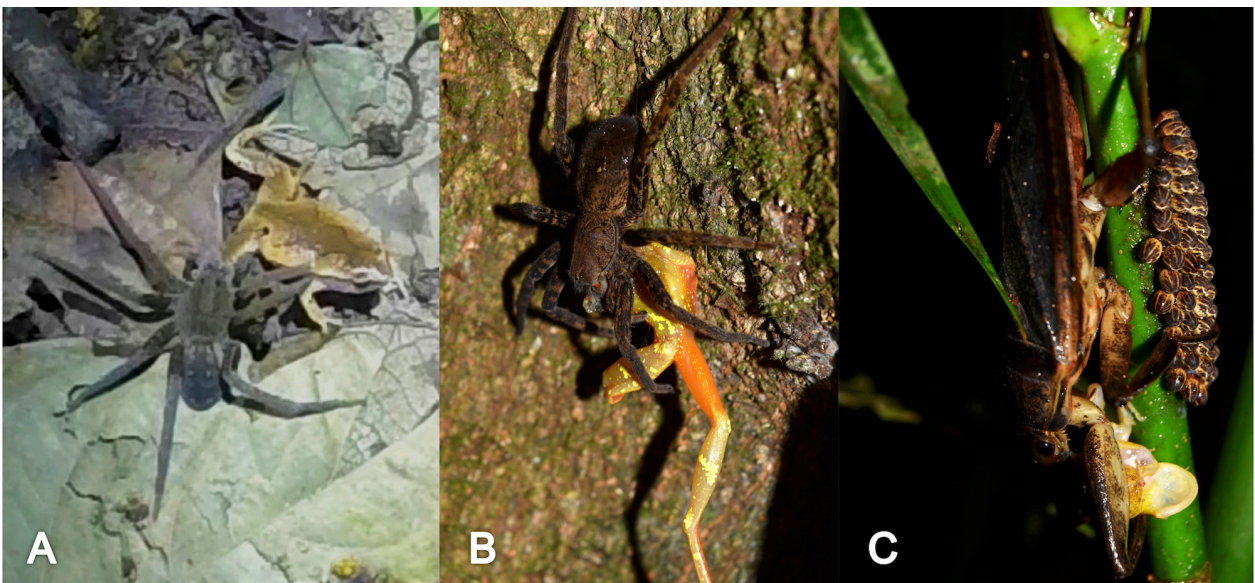

Fig. 7. (A) A wandering spider (Ctenidae) preying upon *Hamptophryne boliviana*; **(B)** the spider *Ancylometes* sp. (Ctenidae) preying upon an adult *Dendropsophus sarayacuensis*; **(C)** giant water bug (Belostomatidae) preying upon an adult *Dendropsophus minutus*; the belostomatid was guarding a clutch of eggs (likely its own clutch). *Photos by Erin Westeen (A) and María Isabel Díaz (B–C).*

Fig. 8. (A) Stingless bees in the genus *Trigona* (Apidae) preying upon a clutch of tree frog eggs (Hylidae) at a temporary pond located in terra firme forest; **(B)** the spider *Phoneutria* sp. (Ctenidae) preying upon an adult *Dendropsophus kamagarini*. *Photos by Rudolf von May (A) and Roy Santa-Cruz (B).*

frog and maintained a hold of its leg for 20 minutes before continuing with the survey. Both individuals were encountered in the leaf litter in the terra firme forest, approximately 400 m from the station. The spider superficially resembles those in the genus *Ancylometes* (Ctenidae); however, the genus assignment is tentative because no voucher specimen is available.

On 26 November 2017, at 2313 h, during a survey of frog breeding activity in a temporary pond, we observed a spider of the genus *Ancylometes* (Ctenidae) holding an individual of *Dendropsophus sarayacuensis* (Hylidae) by the head and the anterior part of the body (Fig. 7B). Both individuals were on the trunk of a tree located in an inundated area near the pond's edge, 0.35 m above the water surface. This observation took place in the terra firme forest, at a site located approximately 600 m from the station.

On 27 November 2017, at 2219 h, we observed a giant water bug (Belostomatidae) holding an individual of *Dendropsophus minutus* (Hylidae) by the body (Fig. 7C). The belostomatid was perched on the stem of a small plant and was guarding a clutch of eggs (likely its own clutch), ca. 0.2 m above the water surface. This observation took place in the terra firme forest, at a site located approximately 600 m from the station.

On 29 November 2017, at 1410 h, we observed stingless bees of the genus *Trigona* (Apidae) preying upon a clutch of tree frog eggs (Hylidae) at a temporary pond located in terra firme forest (Fig. 8A). The pond is located approximately 600 m from the station. The egg clutch was attached to a small tree branch, ca. 1.0 m above the water surface, and was in partial shade. Prior to this observation, several species of tree frogs of the genus *Dendropsophus* (Hylidae) were observed breeding at this pond

over several nights (H. Cárdenas and M.I. Diaz, pers. obs.).

On 29 November 2017, at 2110 h, we observed a spider of the genus *Phoneutria* (Ctenidae) preying upon an adult *Dendropsophus kamagarini* (Hylidae). Though the only photo available of this event (Fig. 8B) does not show the spider holding onto the frog, the actual predation event appeared to have had taken place moments prior to finding the spider and frog in the field (as suggested by the frog posture in the image). After taking the photo, the frog did not display any movement and the spider started eating it (no additional image is available). This observation took place in the terra firme forest, at a site located approximately 100 m from the station.

Most predation events documented here involve spiders that belong to different families and those in the family Ctenidae were the most frequently seen predators (Appendix 1). Ctenid spiders, also known as wandering spiders, are ubiquitous across Neotropical rainforests and forage in different microhabitats including the leaf-litter, tree trunks, and the canopy (Gasnier et al. 1995; Pétillon et al. 2018). Ctenid spiders are typically sit-and-wait predators, which choose a leaf or a branch for their nightly hunt and are very sensitive to air and ground vibrations, but also their eyes seem to play a role in prey and motion detection (Neuhofer et al. 2009). They use specialized hairs (also known as trichobothria; Barth et al. 1993) on the legs and pedipalps to detect air vibration and the direction of prey. The principal eyes are responsible for object discrimination (Schmid 1998) and the secondary eyes are responsible for motion detection (Neuhofer et al. 2009). Depending on the species, they tend to hunt terrestrially (e.g., many *Ctenus* species) or arboreally (e.g., *Phoneutria* and *Cupiennius*). However, these strategies are not strict and we found these spiders
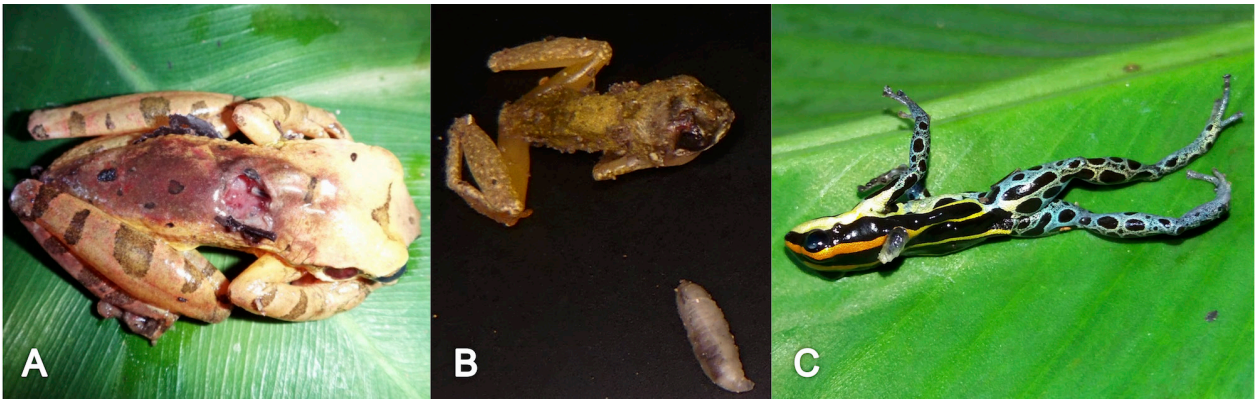
Fig. 9. (A) *Osteocephalus* cf. *leprieurii* infected by several fly larvae; part of the skin of the infected area was removed to show cavity with degraded tissue and one fly larva (on right); **(B)** *Dendropsophus leali* and fly larvae (Diptera) that emerged through the frog's mouth; **(C)** *Ranitomeya uakarii* infected by a maggot that emerged from a small round lesion on its back. *Photos by Rudolf von May (A), Daniel Rabosky (B), and Valia Herrera (C).*

almost everywhere from the ground up to the canopy (E. Biggi and F. Tomasinelli, pers. obs.).

Parasitoid Infections

Though technically distinct from predators, parasitoids may also represent an important source of mortality in small Amazonian vertebrates. Several studies have documented lethal cases of flesh fly myiasis affecting small frogs (Crump and Pounds 1985; Hagman et al. 2005; Eizemberg et al. 2008). Below, we document three cases of fly myiasis in lowland Amazonian frogs.

On 12 January 2012, around 2210 h, we found a juvenile *Osteocephalus* cf. *leprieurii* infected by several fly larvae. The frog was captured during a visual encounter survey in the floodplain forest, approximately 1 km from the station. The frog was placed in a perforated plastic container and observed over the following day. At mid-afternoon, the frog had died and we removed three fly larvae; the cutaneous lesions on its back were conspicuous (Fig. 9A). On 20 November 2016, we captured an adult *Dendropsophus leali* (Hylidae) at approximately 0930 h, sheltering under leaf litter that had been placed atop a funnel trap in floodplain forest; the animal was placed in a plastic bag and retained for processing. The frog was observed alive at 0830 h the following day, but had died with mouth agape by 1130 h. Upon removing the frog from the container, a large dipteran larva exited the mouth of the frog; the larva was approximately 8 mm long (versus 20 mm SVL for the frog). Efforts were made to rear the larva; however, the adult escaped following pupation. Immediately following the exit of the larva, the skin around the thoracic and abdominal region of the frog appeared to be shrunken, as though significant visceral loss had occurred (Fig. 9B). The frog was preserved as a specimen and deposited in the University of Michigan Museum of Zoology (UMMZ 246153). This case is notable relative to other myiases reported for frogs, because no external or cutaneous lesions were noted, as is charac-

teristic for many flesh fly infections, and because of the large size of the larva relative to the frog. In addition to these two tree frogs, we observed one case of fly myiasis in the poison frog *Ranitomeya uakarii* (Dendrobatidae). On 20 January 2017, at 1230 h, we observed an individual of *R. uakarii* hopping on the leaf litter; we captured it and placed it in a plastic bag, and took it to the lab to process it later the same day. When we returned from fieldwork around 1630 h, the frog was dead and we noticed a maggot that periodically emerged from a small lesion on its back (Fig. 9C); a video of the interaction is archived in the University of Michigan Deep Blue Data repository (doi.org/10.7302/Z2862DP1). This observation took place in terra firme forest near Madre Selva Biological Station (3°37'14.8"S, 72°14'48.5"W), Loreto region, northern Peru. The host exhibited a small round wound on the back, similar to those observed in other poison frogs (Hagman et al. 2005).

Commensalism between Spiders and Frogs

In addition to the predation and parasitoid infection events described above, and countless more that take place every day in the rainforest, a more congenial relationship between spiders and frogs exists in southwestern Amazonia. This relationship involves a tarantula and a narrow-mouthed frog that uses the same retreat site used by the spider. The spider was originally identified as *Xenesthis immanis* (Theraphosidae) and the frog as *Chiasmocleis ventrimaculata* (Microhylidae), respectively (Cocroft and Hambler 1989). Field observations and experiments showed that the spider is able to capture and eat several other frog species, while it rejects *C. ventrimaculata* (Cocroft and Hambler 1989; Csakany 2002). Here we update the identification of both participants in this interaction, based on our observations at Los Amigos Biological Station. The spider belongs to the genus *Pamphobeteus* (Theraphosidae; Fig. 10) and the frog is *Chiasmocleis royi* (Microhylidae; Fig. 10), a species described recently (Peloso et al. 2014). If an individual of

Fig. 10. A more congenial relationship: the spider *Pamphobeteus* sp. (Theraphosidae) and *Chiasmocleis royi*. *Photo by Emanuele Biggi.*

C. royi approached or was presented to young or adult individuals of *Pamphobeteus*, the spiders always felt the air movement and tried to grasp the frog as it was a prey, but they always released it without even trying to bite the frog (Cocroft and Hambler 1989; Biggi and Tomasinelli, pers. obs.).

In one evening in early March 2008, right after dusk set, we observed the emergence of three *C. royi* from a single burrow (first ones to emerge), followed by the emergence of more than 10 spiderlings (second group), and, lastly, an adult female *Pamphobeteus*. The frogs dispersed through an area surrounding the burrow (≤ 2 m²) while all spiders stayed closer to the burrow (E. Biggi and F. Tomasinelli, pers. obs.). The female *Pamphobeteus* appeared to react to minimum air movement more rapidly than the spiderlings. In addition, we saw multiple individuals of *C. royi* near other spider burrows. This observation took place in the floodplain forest, at a site located approximately 1.5 km from the station. Furthermore, on 8 March 2008, we found five individuals of *C. royi* next to a spider burrow with multiple entrances; the first and second individual of *C. royi* were <2 cm from two separate entrances, and a third individual of *C. royi* was ca. 15 cm from a third entrance. This third entrance led to a section of the burrow occupied by at least two *Pamphobeteus* spiderlings. We captured and measured one adult and three juvenile *C. royi* (SVL in mm were as follows: 19.9, 13.3, 13.2, 15.2). This observation also took place in the floodplain forest, at a site located approximately 1.5 km from the station. In the same evening, we found seven juvenile individuals

of *C. royi* around a different spider burrow occupied by 6–8 spiderlings. The frogs were 5–50 cm from the entrance of the burrow. We captured and measured six of these juvenile *C. royi* (SVL in mm were as follows: 14.6, 15.7, 14.6, 14.6, 16.2, 14.9).

Similar associations between spiders and frogs have been documented in North America, India, and Sri Lanka. In North America, Blair (1936) described the association involving another species of narrow-mouthed frog, *Gastrophryne olivacea* (Microhylidae), and the spider *Aphonopelma hentzi* (Theraphosidae). Field observations showed that one or more frogs may occupy a spider burrow and the resident spiders did not prey upon the frogs (Blair 1936). Subsequent studies of *G. olivacea* showed that the frogs also occupy burrows used by rodents, and researchers hypothesized that the underground microhabitats probably protect the frogs from desiccation in xeric environments (Fitch 1956; Hunt 1980). Another association involves the Túngara Frog *Engystomops pustulosus* (Leptodactylidae) and a theraphosid spider (Powell et al. 1984). As in the previous case, researchers found multiple frogs inside spider burrows and observed that the spiders did not prey upon the frogs. Powell et al. (1984) hypothesized that skin secretions probably deter the spiders from predating the frogs. In India, the narrow-mouthed frog *Uperodon taprobanicus* (Microhylidae) has been observed in tree holes used by the theraphosid spider *Poecilotheria hanumavilasumica* (Siliwal and Ravichandran 2008). On multiple night surveys conducted in Rameshwaram Island, the researchers never

Fig. 11. Juvenile *Pamphobeteus* sp. infested by fly larvae. *Photo by Emanuele Biggi.*

observed *P. hanumavilasumica* preying upon the frogs (Siliwal and Ravichandran 2008). In Sri Lanka, a closely related frog species, *Uperodon nagaoi* (Microhylidae), has been observed in tree holes used by two species of theraphosid spiders, *Poecilotheria ornata* and *Poecilotheria* cf. *subfusca* (Karunarathna and Amarasinghe 2009). These researchers observed the frogs and the spiders sharing the same tree holes on multiple occasions, yet no predation events were recorded.

In their study, Cocroft and Hambler (1989) proposed the hypothesis that chemical defenses in the skin of *C. royi* prevent spider predation and suggested that the frog might be a commensal because it obtains protection against predators. In this study, we observed that some spiderlings had fly larvae attached to their bodies (Fig. 11; E. Biggi and F. Tomasinelli, pers. obs.). These observations prompted some questions. Is the frog's presence in the burrow beneficial to the spiders? Are the frogs keeping the number of pests inside the nest in check? If the frog had chemical defenses, are these defenses secreted by skin glands (e.g., skin alkaloids), or do they have a dietary origin, or are they produced by the microbiome on the frog's skin? All of these hypotheses remain untested.

Conclusion

The collection and dissemination of natural history data are critical for understanding how invertebrate predators and parasitoids impact small vertebrates communities in tropical rainforests. Future studies aimed at quantifying the frequency of ecological interactions (e.g., predation, commensalism) involving arthropods and small vertebrates across tropical and temperate forest habitats will shed light on patterns of commonness and rarity of these organisms among regions, and their effect on the structuring and functioning of food webs.

Literature Cited

Barth FG, Wastl U, Humphrey JAC, Devarakonda R. 1993. Dynamics of arthropod filiform hairs. II. Mechanical properties of spider trichobothria (*Cupiennius salei* Keys.). *Philosophical Transactions of The Royal Society B Biological Sciences* 340: 1294.

Biggi E, Tomasinelli F. 2017. *Predatori del microcosmo. La Lotta per la Sopravvivenza di Insetti, Ragni Rettili e Anfibi.* Daniele Marson Editore, Italy. 224 p.

Blair WF. 1936. A note on the ecology of *Microhyla olivacea. Copeia* 2: 115.

Cardoso P, Pekár S, Jocqué R, Coddington JA. 2011. Global patterns of guild composition and functional diversity of spiders. *PLoS ONE* 6: e21710.

Cocroft RB, Hambler K. 1989. Observations on a commensal relationship of the microhylid frog *Chiasmocleis ventrimaculata* and the burrowing theraphosid spider *Xenesthis immanis* in southeastern Peru. *Biotropica* 21: 2–8.

Corey DT. 1988. Comments on a wolf spider feeding on a green anole lizard. *Journal of Arachnology* 16: 391–392.

Crump ML, Pounds JA. 1985. Lethal parasitism of an aposematic anuran (*Atelopus varius*) by *Notochaeta bufonivora* (Diptera: Sarcophagidae). *The Journal of Parasitology* 71(5): 588–591.

Csakany J. 2002. Study on the chemical communication between the microhylid frog, *Chiasmocleis ventrimaculatata*, and a theraphosid spider involved in a commensal relationship. Unpublished report, State University of New York, New York, USA. 13 p.

Das KSA, Sreekala LK, Abdurahiman O. 2012. Predation on the Kelaart's Pipistrelle Bat, *Pipistrellus ceylonicus* Kelaart (Chiroptera: Vespertilionidae), by the Reddish Parachute Tarantula, *Poecilotheria rufilata* Pocock (Araneae: Theraphosidae), in Chinnar Wildlife Sanctuary, Kerala, India. *Tropical Natural History* 12(2): 257–260.

Eizemberg R, Sabagh LT, da Silva Mello R. 2008. First record of myiasis in *Aplastodiscus arildae* (Anura: Hylidae) by *Notochaeta bufonivora* (Diptera: Sarcophagidae) in the Neotropical area. *Parasitological Research* 102: 329–331.

Emmons LH, Feer F. 1997. *Neotropical Rainforest Mammals: A field guide.* Second Edition. University of Chicago Press, Chicago, Illinois, USA. 307 p.

Fitch HS. 1956. A field study of the Kansas ant-eating frog, *Gastrophryne olivacea. University of Kansas Publications, Museum of Natural History* 8(4): 275–307.

Gasnier TR, Höfer H, Brescovit AD. 1995. Factors affecting the activity density of spiders on tree trunks in an Amazonian rainforest. *Ecotropica* 1: 69–77.

Greene HW. 1988. Antipredator mechanisms in reptiles. Pp. 1–152 In: *Biology of the Reptilia: Volume 16. Ecology B. Defense And Life History.* Editors, Gans C, Huey RB. Allan R. Liss, New York, New York, USA. 659 p.

Hagman M, Pape T, Schulte R. 2005. Flesh fly myiasis (Diptera, Sarcophagidae) in Peruvian poison frogs genus *Epipedobates* (Anura, Dendrobatidae). *Phyllomedusa* 4(1): 69–73.

Hunt RH. 1980. Toad sanctuary in a tarantula burrow. *Natural History* 89(3): 48–53.

Karunarathna DMSS, Amarasinghe AAT. 2009. Mutualism in *Ramanella nagaoi* Manamendra-Arachchi & Pethiyagoda, 2001 (Amphibia: Microhylidae) and *Poecilotheria* species (Aracnida [sic]: Thereposidae [sic]) from Sri Lanka. *Taprobanica* 1: 16–18.

Menin M, Rodrigues DJ, Azevedo CS. 2005. Predation on amphibians by spiders (Arachnida, Araneae) in the Neotropical region. *Phyllomedusa* 4(1): 39–47.

Myers CW, Rand AS. 1969. Checklist of the amphibians and reptiles of Barro Colorado Island, Panama, with comments faunal change and sampling. *Smithsonian Contributions in Zoology* 10: 1–11.

Neuhofer D, Machan R, Schmid A. 2009. Visual perception of motion in a hunting spider. *Journal of Experimental Biology* 212: 2,819–2,823.

Nyffeler M, Knörnschild M. 2013. Bat predation by spiders. *PLoS ONE* 8(3): e58120.

Nyffeler M, Pusey BJ. 2014. Fish predation by semi-aquatic spiders: a global pattern. *PLoS ONE* 9(6): e99459.

Pétillon J, Leroy B, Djoudi EA, Vedel V. 2018. Small and large spatial scale coexistence of ctenid spiders in a neotropical forest (French Guiana). *Tropical Zoology* 31(2): 85–98.

Peloso PLV, Sturaro MJ, Forlani MC, Gaucher P, Motta AP, Wheeler WC. 2014. Phylogeny, taxonomic revision, and character evolution of the genera *Chiasmocleis* and *Syncope* (Anura, Microhylidae) in Amazonia, with descriptions of three new species. *Bulletin of the American Museum of Natural History* 386: 1–96.

Powell R, Little LW, Smith DD. 1984. Eine Wohngemeinschaft von *Physalaemus pustulosus* (Cope, 1864) (Salientia: Leptodactylidae) mit einer bodenbewohnenden Vogelspinne. *Salamandra* 20: 273–274.

Schmid A. 1998. Different functions of different eye types in the spider *Cupiennius salei. Journal of Experimental Biology* 201: 221–225.

Siliwal M, Ravichandran B. 2008. Commensalism in microhylid frogs and mygalomorph spiders. *Zoos' Print* 23(8): 13.

Toledo LF. 2005. Predation of juvenile and adult anurans by invertebrates: current knowledge and perspectives. *Herpetological Review* 36(4): 395–400.

von May R, Emmons LH, Knell G, Jacobs JM, Rodríguez LO. 2006. *Reptiles del Centro Río Los Amigos, Manu y Tambopata, Perú.* The Field Museum, Chicago, Illinios, USA. Rapid Color Guide # 194, 8 pl.

von May R, Reider KE, Summers K. 2009a. Effect of body size on intraguild predation between tadpoles of bamboo-breeding poison frogs and predaceous mosquito larvae. *Journal of Freshwater Ecology* 24(3): 431–435.

von May R, Siu-Ting K, Jacobs JM, Medina-Müller M, Gagliardi G, Rodríguez LO, Donnelly MA. 2009b. Species diversity and conservation status of amphibians in Madre de Dios, Peru. *Herpetological Conservation and Biology* 4: 14–29.

von May R, Jacobs JM, Santa-Cruz R, Valdivia J, Huamán J, Donnelly MA. 2010a. Amphibian community structure as a function of forest type in Amazonian Peru. *Journal of Tropical Ecology* 26: 509–519.

von May R, Jacobs JM, Jennings RD, Catenazzi A, Rodríguez LO. 2010b. *Anfibios de Los Amigos, Manu y Tambopata, Perú.* The Field Museum, Chicago, Illinios, USA. Rapid Color Guide # 236, 12 pl.

Walker AA, Hernández-Vargas MJ, Corzo G, Fry BG, King GF. 2018. Giant fish-killing water bug reveals ancient and dynamic venom evolution in Heteroptera. *Cellular and Molecular Life Sciences* 75(17): 3,215–3,229.

Wells KD. 2007. *The Ecology and Behavior of Amphibians.* University of Chicago Press, Chicago, Illinios, USA. 1,400 p.

Whitworth A, Downie R, von May R, Villacampa J, McLeod R. 2016. How much potential biodiversity and conservation value can a regenerating rainforest provide? A "best-case scenario" approach from the Peruvian Amazon. *Tropical Conservation Science* 9(1): 224–245.

Appendix 1. Summary of predator-prey interactions reported in this study.

Arthropod Predator		Vertebrate Prey		
Genus / species / (or common name)	Family	Genus / species / (or common name)	Family	Figure number
Ancylometes sp.	Ctenidae	*Dendropsophus leali*	Hylidae	1A
Phoneutria sp.	Ctenidae	*Hamptophryne boliviana*	Microhylidae	1B
Thaumasia sp.	Pisauridae	Tadpole	N/A (Anura)	2A
Ctenid spider sp.	Ctenidae	*Boana* sp. G	Hylidae	2B
Theraphosid spider	Theraphosidae	*Hamptophryne boliviana*	Microhylidae	3A
Ctenid spider	Ctenidae	*Leptodactylus didymus*	Leptodactylidae	3B
Ctenus sp.	Ctenidae	*Cercosaura eigenmanni*	Gymnophthalmidae	4
Centipede	Scolopendridae	*Dipsas catesbyi*	Colubridae	5A
Centipede	Scolopendridae	*Micrurus obscurus*	Elapidae	5B
Pamphobeteus sp.	Theraphosidae	*Marmosops* cf. *noctivagus*	Didelphidae	6
Ctenid spider	Ctenidae	*Hamptophryne boliviana*	Microhylidae	7A
Ancylometes sp.	Ctenidae	*Dendropsophus sarayacuensis*	Hylidae	7B
Water bug	Belostomatidae	*Dendropsophus minutus*	Hylidae	7C
Trigona sp.	Apidae	Frog eggs	Hylidae	8A
Phoneutria sp.	Ctenidae	*Dendropsophus kamagarini*	Hylidae	8B

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