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NOTE

The feeding behavior of Costa Rican velvet worms: food hiding, parental feeding investment and ontogenetic diet shift (Onychophora: Peripatidae)

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Abstract: We report, for the first time in onychophorans, food hiding, parental feeding investment and an ontogenetic diet shift, from adhesive to prey, after their first two weeks of life.

Key words: feeding behavior, Peripatidae, invertebrate behavior, undescribed Costa Rican onychophorans, parental investment.

The basic feeding behavior of onychophorans has been known for over a century: they capture with a powerful adhesive, and ingest the partially digested tissues (Moseley, 1874; Bouvier, 1905; Manton, 1937; Manton & Heatley, 1937; Lavallard & Campiglia, 1971; Ruhberg &Storch 1977; Read & Hughes 1987; Baer & Mayer 2012). The adhesive is metabolically valuable and remains adhering to the prey are re-ingested (Read & Hughes, 1987). In the species *Euperipatoides rowelli*, prey are hunted collectively and consumed in hierarchical order according to size (Reinhard & Rowell, 2005). Nevertheless, feeding behavior has only been studied in few of over 200 named species (Read & Hughes, 1987; Mayer et al. 2015), and new behaviors could still be unrecorded. Here we report, for the first time in the phylum Onychophora, food hiding behavior, parental feeding investment and an ontogenetic change in diet from adhesive slime expelled by the adults to prey.

From December 2016 to January 2018, we kept individuals from eight unidentified species of onychophorans from the family Peripatidae in separated terraria (collection permit codes: SINAC-SE-CUSBSE-PI-R-133-2016 and SINAC-SE-CUSBSE-PI-R-015-2017). Once a week we fed them live or freshly killed insects and took notes on their behavior. Terraria were plastic containers (33 x 20 x 12 cm) with 2 cm dirt, mosses, twigs and bark. The terraria received natural light and humidity was constantly 99%; temperature was 25-27°C in daytime and 22-23°C at night (Inkbird Thermometer & Hygrometer ITH-10). The Gandoca onychophoran had a larger terrarium (45 x 29 x 39 cm) and 3 cms of dirt.
In all cases the main author observed feeding behavior from 7 PM (when food was introduced) to 8 PM, and when the animals fed, helped himself with a red light that he turned on and off every 30 s to reduce disturbance to the onychophorans. Food that was not used by 8 PM was left there for 12 hours, and untouched food as removed 12 hours later to prevent contamination. The full names and geographic origin of species are detailed in Barquero-González et al. (2016a) and Sosa et al. (2018).

All animals followed the known sequence to capture and consume food described by Read & Hughes 1987 and Mayer et al. 2015 (Fig. 1A). However, two new behaviors were recorded: food hiding and ontogenetic diet shift.

Some animals dragged small prey, or carried pieces of larger prey in the mouth, and hid them in burrows and under moss or objects (San Carlos (N=3), Drake (N=5) and Fortuna species (N=2), Fig. 1B, C). Nevertheless, at the start of the feeding process, adults could also feed on different prey parts without aggression (Fig. 1D).

Members of all species in our terraria would sometimes start feeding by the prey thorax, but some also started by the head (Batán, Quesada, Sarapiquí, Gandoca and Fortuna species, as well as *Epiperipatus*

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biolleyi and *Peripatus solorzanoi*); or by the abdomen (Agujas and San Vito species; Fig. 2). Our subjective impression is that when the prey was relatively large in relation to the onychophoran body, the head was eaten first.

Our animals were collected together in the field and, thus, probably genetically related (Monge-Nájera, 1995), which would explain why they shared prey. Food hiding has evolved independently in some invertebrates, including Silphid beetles (Lawrence, J. F. & Newton, A. F., Jr. 1995), and in vertebrates (e.g. lions, see Estes, 1991). Hiding unfinished prey must allow onychophorans, which hunt only a few times per month and are slow to process food (Read & Hughes, 1987), to protect this resource from scavengers and predators.

Parental feeding investment and ontogenetic diet shift: during their first two weeks of life, the young only fed on the adhesive threads used to capture prey by the mother, rather than on the prey itself; and after those two weeks, adult females shared the prey with their offspring, or the young captured prey by themselves (N=3; Gandoca species).

The consumption of the slime from their mother is a clear case of parental feeding investment, given that solitary adult onychophorans consume their own slime after catching and feeding on a prey (Read & Hughes, 1987) and can be aggressive at feeding in group (Reinhard & Rowell, 2005). Therefore, indirect fitness could have played a role at shaping this trait in onychophoran evolutionary history.

An ontological diet shift is present in a variety of organisms; from zooplankton to butterflies and turtles. The shift can be either continuous as in scorpions (Polis, 1984) or discrete as in butterflies and reptiles (Werner & Gilliam, 1984). In the case of onychophorans, by weight their slime consists of 90 % water and 10 % proteins, carbohydrates and lipids (Corrales-Ureña et al., 2017), which can be enough for the dietary requirements of a newborn onychophoran.

We suggest two nonexclusive hypotheses for the emergence of the diet shift: (1) feeding on the slime might be an adaptation to an immature digestive system. The digestive enzymes may not be developed enough to digest prey in a practical time, or more moultings could be needed for mandibles to become strong enough to cut the prey's cuticle. (2) Energetically, the maternal adhesive might be a better option than the prey itself, if its peptides are recycled. This might be similar to web consumption in orb-weaver spiders (Opell, 1998).

Equivalent observations in peripatopsids should help understand the evolutionary origin of this ontogenetic diet shift in Onychophora.

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Fig. 1. The feeding sequence includes the use of adhesive to secure prey (A: adult female inspecting a dead cricked that we placed in the terrarium; before eating, she applied adhesive nonetheless), and hiding unfinished prey (she used her mandibles to drag it under a piece of wood, B-C). Adults can feed simultaneously, without aggression, on different prey parts (D).

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Fig. 2. Some onychophorans start feeding by removing the head (e.g. *P. solorzanoi*, A), others by opening the abdomen (San Vito Onychophoran, B), and others by separating the thorax (Fortuna Onychophoran, C).