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Research Article

Freshwater crabs as predators and prey: the case of *Ptychophallus uncinatus* Campos & Lemaitre, 1999 (Brachyura, Pseudothelphusidae) from Costa Rica, Central America

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ABSTRACT. Primary freshwater crabs are an important component of the food web in aquatic ecosystems, but our knowledge about the role of these decapods as predators and as prey is far from complete. Here we report observations of the feeding habits of the pseudothelphusid crab *Ptychophallus uncinatus* Campos & Lemaitre, 1999, made in 2013 during exploratory observations after sunset in the dusk and darkness of the early evening within the Veragua Rainforest Research & Adventure Park, Limón Province, in the Atlantic drainage of Costa Rica. We observed a case of cannibalism where an adult *P. uncinatus* was feeding on a smaller crab. Furthermore, *P. uncinatus* was observed to prey on an insect larva, a frog, and a lizard on three separate occasions. Additionally, a spider of the family Ctenidae was discovered feeding on a specimen of *P. uncinatus*. These observations revealed novel information about the role of *P. uncinatus* as both a predator and as an item of prey in a Neotropical freshwater ecosystem.

Keywords: *Ptychophallus uncinatus*; pseudothelphusid; ecosystems; Costa Rica

INTRODUCTION

Primary freshwater crabs are brachyurans that live exclusively in tropical and subtropical freshwater habitats worldwide for their entire life cycle, and that reproduce by direct development without any free-living larval stages (Cumberlidge & Ng, 2009; Wehrtmann *et al.*, 2010; Vogt, 2012). There are currently over 1,400 species of primary freshwater crabs assigned to five families: Trichodactylidae (48 species), Pseudothelphusidae (271 species), Potamonautidae (152 species), Potamidae (551 species), and Gecarcinucidae (372 species) (Cumberlidge, 2016). The freshwater crab fauna of the Neotropical region consists exclusively of pseudothelphusids and trichodactylids, and the latest estimates list a total of at least 319 species (Cumberlidge *et al*., 2014; Cumberlidge, 2016). Costa Rica is home to 15 species of pseudothelphusids, eight of which belong to the genus *Ptychophallus*, and no species of trichodactylids (Magalhães *et al*., 2015).

Current knowledge of the primary freshwater crabs includes taxonomic, systematic, zoogeographic, phylogenetic, and conservation studies (Yeo *et al*., 2008; Cumberlidge & Ng, 2009; Cumberlidge *et al*., 2009, 2014; Daniels *et al*., 2015; Poettinger *et al*., 2016), but there have been relatively few studies of freshwater crab ecology (Cumberlidge & Sachs, 1991; Dobson *et al.*, 2002; Wehrtmann *et al.*, 2010, 2016; Vogt, 2012; Xue *et al*., 2013). Rodríguez & Magalhães (2005) updated the biology of Neotropical freshwater crabs of the family Pseudothelphusidae and concluded that there was a need for more detailed ecological studies in order to develop a better understanding of the role of these decapods in freshwater habitats.

Primary freshwater crabs are an important component of food webs in aquatic ecosystems (Williner *et al.*, 2014, and references cited therein). Most species of

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freshwater crabs are omnivores that eat vegetable matter, live invertebrates, and even small vertebrates (Ng, 1988; Cumberlidge *et al*., 2009; Rosa *et al*., 2014). Although our understanding of the trophic ecology of freshwater crabs is far from complete, there have been several recent studies of the feeding ecology of trichodactylids in South America [*Bottiella niceforei* (Schmitt & Pretzmann, 1968) (cf. Pirela & Rincón, 2013); *Dilocarcinus pagei* Stimpson, 1861 (cf. Williner & Collins, 2002); *Trichodactylus borellianus* (Nobili, 1896) (cf. Carvalho *et al.*, 2013a,b); *T. kensleyi* Rodríguez, 1992 (cf. Williner & Collins, 2013; Williner *et al.*, 2014); *T. panoplus* (Von Martens, 1869) (cf. Burress *et al*., 2013), and *Zilchiopsis collastinensis* Pretzmann, 1968 (cf. Torres *et al*., 2012)]. The consumption of allochthonous plant debris reported in the above studies emphasizes the importance of freshwater crabs as shredders in tropical and subtropical streams (Dobson *et al*., 2002; Pirela & Rincón, 2013; Williner *et al*., 2014). These studies also revealed that *T. panoplus* was a strict herbivore and detritivore (Burress *et al*., 2013) while most of the other species were omnivores. One of these omnivorous species, *T. kensleyi*, was found to consume vegetal remains and algae as well as oligochaetes and chironomid larvae (Williner *et al*., 2014). The consumption of food by trichodactylid freshwater crabs varies throughout the day, but food items of animal origin are more often recorded at night when crabs are most active (Williner & Collins, 2002, 2013; Collins *et al*., 2007; Pirela & Rincón, 2013; Williner *et al*., 2014). In contrast, there is very little information available about the feeding ecology of pseudothelphusid crabs in the neotropics, although these crabs are more species-rich and more widely distributed than are trichodactylids (Crane, 1949; Maitland, 2003; Port-Carvalho *et al*., 2004; Fraiola, 2006).

Freshwater crabs are themselves important prey items for aquatic and terrestrial animals which makes these decapods an important link between aquatic and terrestrial ecosystems (Cumberlidge & Sachs, 1991; Rodríguez & Magalhães, 2005; Collins *et al*., 2007; Cumberlidge *et al*., 2009; Williner *et al*., 2014). For example, a study by Rowe-Rowe (1977) of the feeding ecology of the African clawless otter *Aonyx capensis* (Schinz, 1821) and the spotted-necked otter *Lutra maculicollis* (Lichtenstein, 1835) in South Africa revealed that *A. capensis* lived almost exclusively on frogs and freshwater crabs (*Potamonautes* sp.), while *L. maculicollis* fed on fish, frogs, and the freshwater crab *P. depressus* (Krauss, 1843). That study also showed that freshwater crabs (*Potamonautes* sp.) were the most important food item of the water mongoose *Atilax paludinosus* (Cuvier, 1829).

Here we present for the first time a summary of nighttime observations of the feeding behavior of *Ptychophallus uncinatus* Campos & Lemaitre, 1999, a species found in both Costa Rica (both Atlantic and Pacific drainages) and Panamá (Atlantic drainage) (Campos & Lemaitre, 1999; Magalhães *et al*., 2015).

MATERIALS AND METHODS

Study area

Observations of the feeding behavior in *P. uncinatus* were made in the Veragua Rainforest Research & Adventure Park (420 m a.s.l.), Province Limón, in the Atlantic drainage of Costa Rica (Fig. 1) as part of a study of the population dynamics of the freshwater crabs found there. This private reserve covers an area of 1,376 ha (http://www.veraguarainforest.com).

Observations

Nighttime exploratory walking surveys were carried out in the Veragua Rainforest Research & Adventure Park in Costa Rica as part of a monthly daytime sampling program (January 2013 through March 2014) to study population dynamics of freshwater crabs. The nighttime observations in the darkness of the early evening were made by DHD to encounter nocturnally active crabs that had left their aquatic habitats to feed on land. None of these specimens were collected. The daytime population study produced a total of 916 specimens of freshwater crabs, most of which (99%) belonged to *P. uncinatus* (the rest belonged to *Potamocarcinus magnus* (Rathbun, 1896)). Freshwater crab specimens collected during the population study were identified using the keys of Magalhães *et al.* (2015). It is safe to assume that the crabs observed (but not collected) during these nighttime walking surveys were also specimens of *P. uncinatus*, which is much smaller and more abundant in this area than *P. magnus*. Photographs were taken with a Fujifilm FinePix S1800 camera.

RESULTS

Cannibalism in *P. uncinatus*

At 23:02 h on 18 January 2013 turning over rocks in the stream at Quebrada Campamento (Fig. 1) resulted in the discovery of an adult freshwater crab (*P. uncinatus*) holding a juvenile of the same species in its chelipeds, and feeding on the smaller crab (Fig. 2, Table 1).

Predation by *Ptychophallus uncinatus*

At 22:10 h on 14 March 2013 turning over rocks in the stream at Quebrada Campamento resulted in the discovery of an adult freshwater crab (*P. uncinatus*)

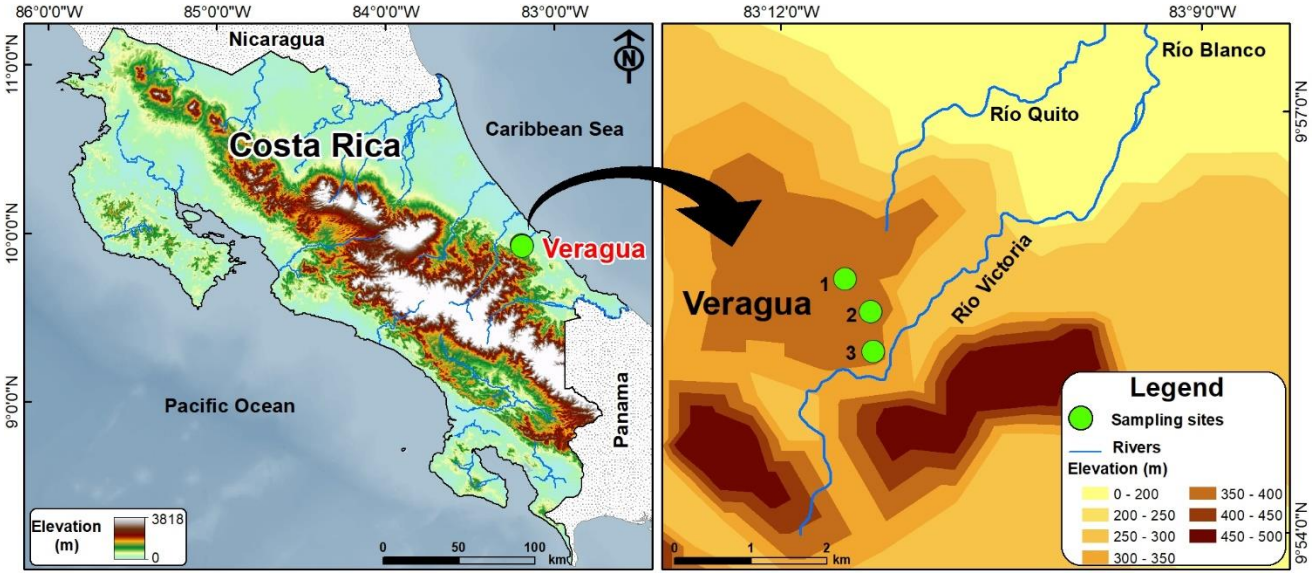

Figure 1. Location of the sampling sites in the Veragua Rainforest Research & Adventure Park in Costa Rica. 1: Quebrada Cicada, 2: Quebrada Campamento, 3: Quebrada Sukia.

Figure 2. *Ptychophallus uncinatus* observed at night predating a smaller juvenile crab (possibly of the same species) near a stream in Quebrada Campamento in Veragua Rainforest Research & Adventure Park in Costa Rica.

feeding on an insect larva (Diptera; probably of the family Muscidae), which is held in its chelipeds (Fig. 3a, Table 1).

At 22:45 h on 28 July 2013 turning over rocks in the stream at Quebrada Ciccaba (Fig. 1) resulted in the discovery of an adult freshwater crab (*P. uncinatus*) in a small pool hidden under a rock, holding a lizard (*Norops lemurinus*) in its major (right) cheliped (Fig. 3b, Table 1). Although the crab was eating the lizard, it was not clear to us whether the crab had killed the lizard or whether it had encountered a dead or dying specimen.

Table 1. Summary of observations of the freshwater crab *Ptychophallus uncinatus* as a predator and as a prey item in the Veragua Rainforest Research & Adventure Park, in Limón Province, Costa Rica.

Date	Time	Locality	Observation	Trophic role
18-Jan-13	After dark, 23:02 h	Under rocks in the stream at Quebrada Campamento	Large *P. uncinatus* predating smaller juvenile of same species (cannibalism) (Fig. 2).	Crab as intraspecific predator (cannibal)
14-Mar-13	After dark, 22:10 h	Under rocks in the stream at Quebrada Campamento	A large *P. uncinatus* feeding on an insect larva (Diptera; probably family Muscidae) (Fig. 3a)	Crab as predator
28-Jul-13	Daytime, 10:45 h	Small pool under rock stream in Quebrada Ciccaba	A large *P. uncinatus* holding a lizard (*Norops lemurinus*) in its right (major) cheliped (Fig. 3b). It is not known whether the crab killed the lizard.	Crab either as a predator or scavenger
29-Nov-13	After dark, exact time not available	A small water pool (50 cm diameter) collected in the trunk of a 4-meter long fallen tree where frogs (*Cruziohyhla calcarifer*) were depositing their eggs	A large *P. uncinatus* holding the head of a frog in its cheliped above the water surface (Fig. 4).	Crab as a predator
27-Apr-13	After dark, 21:35 h	On a small tree branch, Quebrada Sukia	Spider (family Ctenidae) holding a small crab (*P. uncinatus*) in both chelicerae and apparently feeding on the crab. It is not known whether the spider killed the crab (Fig. 5).	Crab either as prey or scavenged material

Another observation of predation by *P. uncinatus* was made in the evening of 29 November 2013, in a small pool of water (50 cm diameter) that had collected in the trunk of a 4 m long fallen tree where frogs (*Cruziohyhla calcarifer*) were depositing their eggs. A large *P. uncinatus* was observed holding the head of a frog in its cheliped above the water surface and then feeding on it (Fig. 4, Table 1). A second frog was observed sitting on the tree trunk outside the puddle and did not move.

Ptychophallus uncinatus as prey

At 21:35 h on 28 July 2013 at Quebrada Sukia (Fig. 1) a spider (family Ctenidae) was observed on a small tree holding a freshwater crab (*P. uncinatus*) in its chelicerae and feeding on it (Fig. 5, Table 1). It is not clear whether the spider had killed the crab or whether it had encountered a dead or dying specimen.

DISCUSSION

Our knowledge of freshwater crabs as predators and as prey is far from complete. Several studies on these decapods have demonstrated a wide range of feeding habits (Dudgeon & Cheung, 1990; Maitland, 2003; Rosa *et al*., 2014), while some authors have demonstrated the importance of freshwater crabs as prey for other animals (*e.g.*, Teran *et al.*, 1995; Dobson, 2004 and references cited therein). The present observations broaden our preliminary knowledge of freshwater crabs in food webs and provide novel information about the role of these decapods in the trophic networks of tropical aquatic ecosystems.

Cannibalism (intraspecific predation) is a widespread phenomenon among decapods (Koga *et al*., 1995; Lovrich & Sainte-Marie, 1997; Januario & Navarrete, 2013) that is regarded by some authors as an energy loop that maintains calories within a population (Polis,

Figure 3. *Ptychophallus uncinatus* feeding at night: a) on a dipteran larva and b) on a lizard (*Norops lemurinus*) at Quebrada Campamento and Quebrada Ciccaba, respectively, Veragua Rainforest Research & Adventure Park in Limón Province, Costa Rica.

Figure 4. *Ptychophallus uncinatus* holding the head of a frog (*Cruziohyhla calcarifer*) in its cheliped in Veragua Rainforest Research & Adventure Park in Limón Province, Costa Rica (Photo: José Andrés Salazar).

Figure 5. A spider (family Ctenidae) (black color) observed at night with a freshwater crab (*Ptychophallus uncinatus*) (light colored) held in its chelicerae in Veragua Rainforest Research & Adventure Park in Limón Province, Costa Rica.

1981). Although Yeo *et al.* (2008) stated (as an unpublished observation) that cannibalism is not uncommon among freshwater crabs, descriptions on this behavior in freshwater crabs are scarce (Ng & Ng, 1987; Maitland, 2003). Our observations (Fig. 1) demonstrated that intraspecific predation occurs in *P. uncinatus*. Additional studies, however, are required to assess the importance of this behavior in the feeding habits of this freshwater crab.

The observation that *P. uncinatus* is a predator of frogs (Fig. 4) is in agreement with reports by Willink *et al.* (2014) that demonstrated that other species of pseudothelphusids in Costa Rica were one of three classes of predators of poison-dart frogs. In that study, crabs attacked clay models of frogs and dragged them under rocks, under logs, or into their underground burrows (Willink *et al.*, 2014). The clay models of frogs attacked by the crabs either had deep cuts or were wholly torn apart (Fig. 6). Affonso & Signorelli (2011) reported predation by the trichodactylid freshwater crab *Dilocarcinus pagei* on the frog *Leptodactylus latrans* (Steffen, 1815) in Brazil, where they observed an adult crab feeding on it, and found the mutilated remains of other frogs nearby. Moreover, in laboratory experiments, *D. pagei* killed two out of six frogs and ate parts

Figure 6. A red clay model of a frog set in the Veragua Rainforest Research & Adventure Park, Limón Province, in the Atlantic drainage of Costa Rica showing the marks after having been attacked by a freshwater crab (Photo: Beatriz Willink).

of their bodies (Affonso & Signorelli, 2011). Freshwater crabs from different continents have been observed to feed on juvenile and adult anurans, and there are several records of freshwater crabs feeding on the eggs and tadpoles of amphibians (Toledo, 2005; Gutsche & Elepfandt, 2007; Caldart *et al*., 2011; Andrade *et al*., 2012; Pyke *et al*., 2013; Rosa *et al*., 2014; Nogueira-Costa *et al.*, 2016). Despite the scarcity of information available, it is clear that freshwater crabs do indeed attack and feed on anurans and their egg clutches. However, further field and experimental studies are needed to foster our understanding of the interactions between pseudothelphusid crabs and anurans.

Reports of crabs preying on reptiles are extremely rare. Although we are not sure about the cause of death of the lizard eaten by *P. uncinatus* (Fig. 3b), it cannot be ruled out that the crab attacked and killed the lizard. Maitland (2003) recorded several incidences of the semi-terrestrial pseudothelphusid freshwater crab *Eudaniela garmani* (Rathbun, 1898) eating different species of snakes in the rainforests of the Caribbean island of Tobago, and concluded that snakes might form a significant part of the diet of this freshwater crab. Additional field and experimental studies are necessary to evaluate the importance of reptiles in the diet of *P. uncinatus*.

Although the cause of death of the lizard eaten by *P. uncinatus* (Fig. 3b) remains unknown, it cannot be ruled out that the crab was consuming the flesh of an already dead lizard. Segadilha & Silva-Soares (2015) reported the case of the nocturnal freshwater crab *Trichodactylus fluviatilis* feeding on a dead adult female toad *Rhinella ornata* (Anura: Bufonidae) in the Atlantic rainforest mountains of southeastern Brazil. These observations suggest that Neotropical freshwater crabs may act as opportunistic scavengers.

Information of freshwater crabs preying on insect larvae is scarce. Fraiola (2006) and references cited therein, mentioned that larvae of aquatic insects formed part of the diet of the pseudothelphusid crab *Epilobocera sinuatifrons* in Puerto Rico. Some scattered reports on trichodactylid crabs (*Trichodactylus borellianus* and *T. kensleyi*) revealed that chironomid larvae (Order Diptera) were consumed by these crabs (Williner & Collins, 2013; Williner *et al.*, 2014). Considering our observation (Fig. 3a) as well as those reported in the literature, it seems reasonable to assume that insect larvae form part of the diet of Neotropical freshwater crabs. However, the importance of these invertebrate larvae in the diet of freshwater crabs still needs to be assessed. Future studies that evaluate the stomach contents of these crabs would add important data on the diet of these crabs.

Freshwater crabs are known to form part of the diet of some animals, including otters, trout, birds, snakes, crocodiles, and amphibians (Turnbull-Kemp, 1960; Rowe-Rowe, 1977; Purves *et al.*, 1994; Butler & Du Toit, 1995; Butler & Marshall, 1996). There exist several reports from the Neotropics of freshwater crabs as prey. Teran *et al.* (1995) studied the food habits of five species of turtles from Brazil and found the remains of pseudothelphusids in 10.8% of the stomachs analyzed. Port-Carvalho *et al.* (2004) observed a group of tufted capuchin monkeys (*Cebus apella* Linneaus, 1758) feeding on unidentified pseudothelphusid crabs. Caiman species in the Brazilian Amazon are also known to feed on freshwater crabs (Magnusson *et al.*, 1987; Da Silveira & Magnusson, 1999; Quadros & Monteiro-Filho, 2001). Fish stomach contents from species collected in the Rio Negro, Amazon, Brazil, revealed the presence of four trichodactylid crab species (Goulding *et al.*, 1988); the authors concluded that there was no evidence for specialized crab-eating fish species, and larger crustaceans formed part of broader diets. Slender-billed kites (*Helicolestes hamatus*) and snail kites (*Rostrhamus sociabilis*) have a specialized diet of freshwater snails. However, Beissinger *et al.* (1988) showed in a study carried out in Venezuela that these birds also prey on freshwater crabs. Schlüter & Salas (1991) mentioned that tadpoles of two microhylid species (Amphibia: Microhylidae) from Peru were caught by freshwater crabs (*Dilocarcinus* sp. and *Goyazana* sp.). Finally, the crab-eating fox (*Cerdocyon thous*) is another predator widely distributed in South America that has been observed to eat freshwater crabs during the dry season (Brady, 1979). Our observation of a spider eating a freshwater crab seems to be unique because we were unable to find similar reports in the literature.

Our preliminary (admittedly limited) observations on *P. uncinatus* revealed interesting and novel information about the role of this pseudothelphusid crab as both a predator and as an item of prey in a Neotropical freshwater ecosystem in Costa Rica. Since freshwater crabs are more active at night (Yeo *et al*., 2008) it is difficult to obtain a complete picture of the foraging activities of these decapods. It is clear that more studies are needed for a better understanding of the interactions between freshwater crabs and their potential prey and predators (Rodríguez & Magalhães, 2005).

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