Snail susceptibility to crab predation: A case study of co-evolution from Lake Tanganyika, East Africa

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Introduction

Co-evolution has been invoked as an explanation for Lake Tanganyika's unusual endemic fauna. The crabs *Platytelphusa armata* and *Potamonautes platynotus* are molluscivores, found in the same habitats as the gastropods *Lavigeria coronata*, *L. grandis*, and *L. nassa* (West & Cohen 1994). As these are the largest gastropods in the *Lavigeria* species flock, and often the most exposed, we are determining whether shell size and sculpture provides protection from predation. We are also attempting to reveal the effectiveness of chela morphology among crab predators. The fine details of the predator-prey relationships will link the ecological processes with their potential evolutionary patterns.

Methods

Specimen collection was performed at two sites: Jakobsen's Bay (4º 54.64' S, 29º 35.92' E) and Hilltop (4º 53.20' S, 29º 36.75' E), in the vicinity of Kigoma Bay, Tanzania. Snails were collected from the rocky littoral zone on the coast south of Jakobsen's Beach by snorkel from 1-6 m. Crab traps baited with raw fish were used to catch crabs between 2-10 m depth from Jakobsen's Bay as well as Hilltop. Snails and crabs were kept in aerated tanks filled with water collected from 1km off shore in Kigoma Bay. Crabs were acclimated and starved for 24-48 hours to increase their motivation to feed.

Before the trials snail shells were scrubbed clean of algae to reveal scars and measured for shell height (maximum height measured from the apex of the basal inflection of the aperture), shell width (maximum width measured perpendicular to shell height), lip thickness (apertural lip thickness measured at the widest point of the lower and outer apertural inflection, with calipers inserted 2mm from the lip and between horizontal ribs), aperture-apex (pre-apertural height measured from the upper intersection of the last whorl at the aperture to the apex), and scar number and measurement (pre-apertural height of the individual at the time of scarring) (Cohen 1989). Snails with more than three scars or any damage to the lip of the shell were not used in the trials. The species *L. coronata*, *L. grandis*, and *L. nassa* were used at six size classes, evenly spaced, based on shell height. *L. coronata* ranged from 12-36 mm, *L. grandis* from 12-30 mm, and *L. nassa* from 12-24 mm. The size classes spanned the range from the maximum determined by the 1998 snail population data taken from Jakobsen's Beach to the minimum based on Socci's 2001 crab predation trials.

The relative susceptibility of six different size classes of snails to predation by *P. armata* and *P. platynotus* was tested in a series of laboratory experiments. Only adult crabs with both major and minor chela fully intact were used. Crabs were measured based on the methods of Cumberlidge et al. (1999) and Socci (2001). Carapace width (widest point behind the posterior anterolateral spine) and carapace length (distance between the center of the anterior interorbital margin and the center of the posterior margin) were measured as well as major and minor chela diagonal (maximum diagonal distance between the lower propodus-carpus articulation and the dactyl pivot point articulation), chela length (maximum distance between the lower propodus-carpus articulation and the tip of the pollex), and chela height (maximum height of the propodus measured perpendicular to the chela length) (Fig. 1 & 2).

The dentition of the major chela is divided into three classes based on wear patterns at the base of the dactylus and propodus: 1) lacking pronounced molariform teeth; 2) partially worn molariform teeth; and 3) fully differentiated, not worn down molariform dentition (Fig. 3 &4). Categorical data was also recorded for the sex of the crab, side of major chela, missing legs, and superficial carapace traits such as fungus and/or scars. Carapaces were tagged with numbered flags glued to the carapace to avoid reusing crabs after their release. Crabs were measured and tagged after the trials were completed to minimize stress to the individuals. All snail and crab measurements were made by a single person with the same digital calipers to reduce variability.

Three experiments were conducted between July 18th and August 4th 2002:
1) *L. coronata* and *L. grandis* exposed to *P. platynotus*
2) *L. coronata* and *L. grandis* exposed to *P. armata*
3) *L. nassa* exposed to *P. platynotus* and *P. armata*

The goal of Experiment 1 was to test the resistance across size classes to predation and make comparisons between *L. coronata* and *L. grandis* exposed by *P. platynotus*. Experiment 2 was identical to Experiment 1 except the predator was *P. armata*. Experiment 3 tested the resistance of *L. nassa* across a range of size classes and compared the predators *P. platynotus* and *P. armata*.

In experiments #1 and #2, representatives from each of the six size classes of *L. coronata* and *L. grandis* were exposed to a predatory crab. Experiment #3 had twelve individuals of *L. nassa*, 2 individuals from each size class; 1 full size class of *L. nassa* was paired with *P. armata* and one full size class was paired with *P. platynotus*.

Experiments consisted of four blocks of trials run on separate days. Each trial consisted of 12 containers, 12 individual *Lavigeria*, and 12 individual crabs. Snail and crab individuals were randomly assigned to chambers and held together in 2.2 L clear cylindrical lidded containers with 1.5L of fresh, aerated lake water. One square terra cotta tile was placed on the bottom of each container for substrate and visual barriers were erected between the containers. Trials were run for 18 hours, 13 dark and 5 light based on the photoperiods used by Socci in 2001. At the completion of each block of trials, snails were removed and recorded as dead, damaged, or not damaged. The category "snail death" was defined as successful predation by crushing the shell. "Snail damage" was defined as lip peeling or aperture crushing, but survival of the snail. Snails that were "not damaged" were found alive without shell chips.

Each experiment was analyzed separately using logistic regression. Container, crab sex and capture location, the starvation time of the crabs, snail shell height, shell lip thickness and species identity were included in preliminary models of survival and shell damage among survivors (SAS version 8.0, Proc Genmod).

Results

<u>*L. coronata* and *L. grandis* exposed to *P. platynotus*</u>
In Experiment 1 (*P. platynotus*, *L. coronata*, and *L. grandis*), smaller snails were more susceptible to crabs. All death occurred in the smallest size classes (Fig. 5A & C), although sample size was too small for statistical significance in this trial (Chi^2=2.0, D.F.=1, p=0.1561). Smaller snails were damaged significantly more frequently among surviving individuals (Chi^2=6.02, D.F.=1, p=0.0142). Snail species also had a significant effect on shell damage among surviving individuals (Chi^2=6.23, D.F.=1, p=0.0125) with *L. coronata* having a much higher probability of being damaged than *L. grandis*. *L. grandis* had higher mortality than *L. coronata* under the predation pressures of *P. platynotus* (Fig. 5A & C), although sample size was too small for statistical significance in this trial (Chi^2=1.3, D.F.=1, p=0.2540).

<u>*L. coronata* and *L. grandis* exposed to *P. armata*</u>
With the presence of predator *P. armata* in Experiment 2 (*P. armata*, *L. coronata*, and *L. grandis*), size had a significant effect on mortality of *L. coronata* and *L. grandis* (Chi^2=10.17, D.F.=1, p=0.0014) - smaller shells were more susceptible to being crushed. In the first two size classes *L. coronata* had very high mortality rates, but no mortality in size classes 3 and 4. *L. grandis* had lower mortality rates at the lowest two size classes, but were still susceptible to being crushed in size classes 3 and 4 (Fig. 5B &D). Lip thickness had a slight, but not significant effect on mortality. Damage to survivors was not significantly related to size or lip thickness.

<u>*L. nassa* exposed to *P. platynotus* and *P. armata*</u>

In Experiment 3, *L. nassa* size had a significant effect on mortality (Chi^2=5.44, D.F.=1, p=0.0197) and had a marginally significant relationship with shell damage among surviving individuals (Chi^2=3.65, D.F.=1, p=0.0560) (Fig. 5E & F).

P. platynotus and *P. armata* differed significantly in their abilities to kill *L. nassa* (Chi^2=4.20, D.F.=1, p=0.0405), and in their abilities to damage surviving individuals (Chi^2=3.87, D.F.=1, p=0.0491). *P. armata* was much better at predation of *L. nassa* as well as inflicting shell damages than *P. platynotus*.

Qualitative comparisons of experiments

In all cases *P. platynotus* was less successful at predation and more successful at damaging shells than *P. armata*. The smallest size classes always had higher mortality rates and the largest size classes were least likely to be damaged or killed (Fig. 5). Previous repaired shell scars did not show any significant effect on the ability of crabs to crush or damage shells.

Discussion

Our results indicate that *P. armata*, the more derived of the two crabs, is a more effective predator than *P. platynotus*. *L. coronata,* the more sculptured snail, was less frequently killed but more frequently damaged than *L. grandis*. Gastropods were most likely to be killed in the smallest 3 size classes, damaged in the middle classes, and resistant to shell crushing in the largest class. Although the smaller snail size classes were more susceptible to damage or death in controlled experiments, they may have adaptations in life history and/or behavior to make up for their structural vulnerability.

We suggest that the specialized traits possessed by these species provide different kinds of resistance to crushing predation. Protective shell features such as *L. coronata*'s heavily calcified rigid shell and *L. nassa*'s dense thick shells provide refuge from successful predation - handling damages are present but usually survived. Shell repair is an effective way to restore shell strength (Hinkley *et al*. 2001), and is commonly seen among these species (Phifer *et al.* 2001). *L. grandis* is relatively susceptible to predation at larger sizes than the other two gastropods. However, it is found in shallow water (dominantly 2-4m) thus may have protection by wave activity from crabs. *P. armata* was more common in deeper water, and was more deadly to *L. grandis*.

From the crab's perspective, heavily armored chelae with large molariform teeth were better adapted to shell crushing. Our data showed that *P. platynotus*, with their smaller chelae, are less successful at consuming molluscs than *P. armata*, which are strikingly well armed (Cumberlidge *et al.* 1999, West & Cohen 1994, West *et al.* 1991). Since chelae have uses other than feeding, a linear correlation between form and feeding abilities may be confounded. Shell peeling was very prevalent among both crab species. One *P. armata* pulled the largest size class of *L. coronata* out of its shell leaving the shell undamaged. This alternative predation technique is a great example of possible behavioral adaptations of the crabs. Lip damage can be interpreted as an inability to crush the remainder of the shell, or insufficient handling time and energy for shell peeling. The structural characteristics of these snails and crabs facilitate the perpetual coexistence and coevolution of strong predator-prey relationships. Our results strongly support the idea of an ongoing evolutionary arms race in the endemic fauna of this lake.

Recommendations

With time and material constraints it was impossible to run both species of crabs and the three species of *Lavigeria* in six size classes at once. Ideally all 5 species should be run together to eliminate temporal variables. I think that more replicates of each experiment as well as observations of handling time would provide insight to the predation abilities of each crab species. Since only shells with limited scars were used in these experiments it would be interesting to see if shell strength is weakened by an extensive history of repaired damages. Likewise it would be valuable to know the strength of the crab's chelae as well as the effect the side of the major chela has on predation success. In marine crabs the right major chela is predicted to have evolved in response to the predominantly dextral coiling of marine gastropods (West *et al.* 1991). Although *P. platynotus* and *P. armata* typically have right major chela, it would be of interest to examine how major side affects crushing abilities. It would also be fascinating to calculate prey value by looking at the yield of flesh (the pay off) per unit of effort or handling time. In addition to the structural adaptations observed in the laboratory, field observations should be made on the ecological variables that affect these predator-prey relationships.

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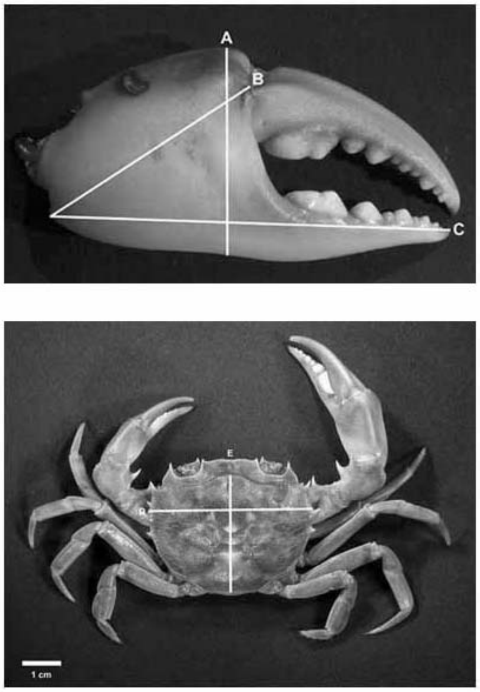

FIG. 1. *P. armata* measurements. A) Chela height. B) Chela diagonal. C) Chela length. D) Carapace width. E) Carapace length.

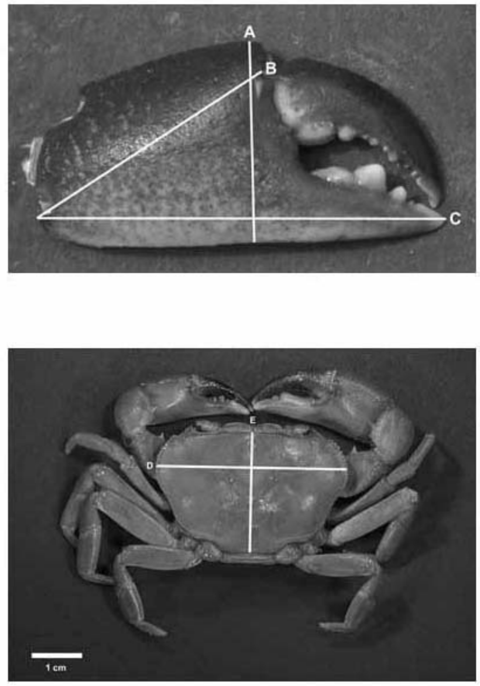

FIG. 2. *P. platynotus* measurements. A) Chela height. B) Chela diagonal. C) Chela length. D) Carapace width. E) Carapace length.

A. Lacking pronounced molariform teeth.

B. Partially worn molariform teeth.

C. Fully differentiated, not worn down molariform dentition.

FIG. 3. Three classes of major chela dentition for *P. armata*.

A. Lacking pronounced molariform teeth.

B. Partially worn molariform teeth.

C. Fully differentiated, not worn down molariform dentition.

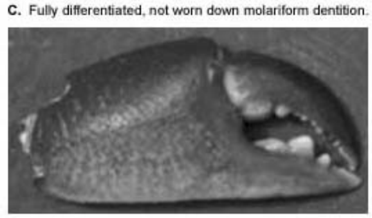

FIG. 3. Three classes of major chela dentition for *P. platynoti*