

Scarring and sculptured shells: Crab impacts on morphology of *Lavigeria* in Lake Tanganyika

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Abstract

The morphological similarity between marine gastropods and the gastropods of Lake Tanganyika has recently been attributed in part to a coevolutionary relationship with the lake's durophagous crabs. It is possible that the diversity of the gastropods, especially in the genus *Lavigeria* is related to this predation pressure. If crabs induce morphological defenses in the snails then natural selection acts to encourage not fixed characters, but morphological plasticity. I surveyed three sites to understand the differences in scarring frequency and shell morphological characters between depth, species, and site. Sites were found to have different scarring frequencies. I found depth to have an effect on scarring frequency. I also found that *L. grandis* across two sites had lower scar frequencies than other species at the same site. Either reduced vulnerability to crab predation or increased mortality from attack could explain this trend. Future analysis of morphological characters will attempt to correlate morphological characters to scarring frequency to test for evidence of inducible defenses in *Lavigeria*.

Introduction

The sculptured morphology of Lake Tanganyika gastropod shells has long interested biologists (Fryer 2000; Coulter 1991). Recent work has attributed the armored morphology of several groups of gastropods in the lake to selection pressure from the lake's durophagous crab species (West, *et al.* 1991). The most diverse group of sculptured gastropods is the genus *Lavigeria*, which is now believed to include up to thirty endemic species (Michel & Todd in prep).

It is possible that crab predation differentially affects different *Lavigeria* species, thus contributing to endemic divergence. Predation pressure may vary across sites, or within sites, among gastropod species, among microhabitats or with depth. Additionally, diversity may be in part explained by the interaction of natural selection and inducible defenses. If a non-fatal attack by a crab induces morphological changes in a snail's shell, then future selection pressure acts not just on fixed characters but also on the capacity for morphological plasticity.

I had three goals. My first goal was to establish a baseline of comparison of variation in shell morphology within and between species at different depths and locations. To this end I collected morphometric data on the shells. My second goal was to better understand the extent of selection pressure exerted by crabs on *Lavigeria*. Snail shells bear scars as evidence of past crab attacks that the snail survived. Therefore I determined the scarring frequency of *Lavigeria* populations at different depths and locations. My final goal was to determine if *Lavigeria* respond to crab predation attempts with a change in shell morphology, i.e. do they exhibit inducible defenses.

Methods

I chose three sites near Kigoma, Tanzania characterized by rocky substrate: Jakobsen's Beach, Kalalangabo, and Mitumba a site in Gombe Stream National Park. At each site I collected available *Lavigeria* species (*L. nassa*, *L. grandis*, *L. coronata*, *L. sp. W.* (commonly known as "mondo coarse ribbed")) from a stretch of approximately twenty meters lateral distance at two meters depth (Table 1). At Jakobsen's and Kalalangabo I collected *Lavigeria nassa* from ten meters as well. Animals at two meters were collected using a combination of SCUBA and snorkeling, those at ten meters by SCUBA alone. I brought the animals to shore and scrubbed them to remove algae cover. After examination of each animal, I sorted them into two groups, scarred and unscarred and determined the total number of snails in each group. I then divided each group into three size categories and selected eighteen from each category at random. Balanced sampling design and large sample sizes are critical in this kind of study where statistical

Table 1. Species collected at different sites and depths in

	depth (m)	JKB	MIT	KLG
<i>L. nassa</i>	2	X	X	X
<i>L. nassa</i>	10	X		X
<i>L. grandis</i>	2	X		X
<i>L. coronata</i>	2	X		
<i>L. sp. W</i>	2			X

Table 2. Scarring frequency of *Lavigeria* species at different

Site	Species	Depth	N	Percent scarred
Jakobsen's	<i>L. nassa</i>	2	145	40.69
Beach	<i>L. nassa</i>	10	105	56.19
	<i>L. grandis</i>	2	433	32.10
	<i>L. coronata</i>	2	136	39.71
Mitumbe	<i>L. nassa</i>	2	184	37.50
Kalalangabo	<i>L. nassa</i>	2	129	34.11
	<i>L. nassa</i>	10	266	42.86
	<i>L. grandis</i>	2	162	19.14
	<i>L. sp. W</i>	2	171	32.16

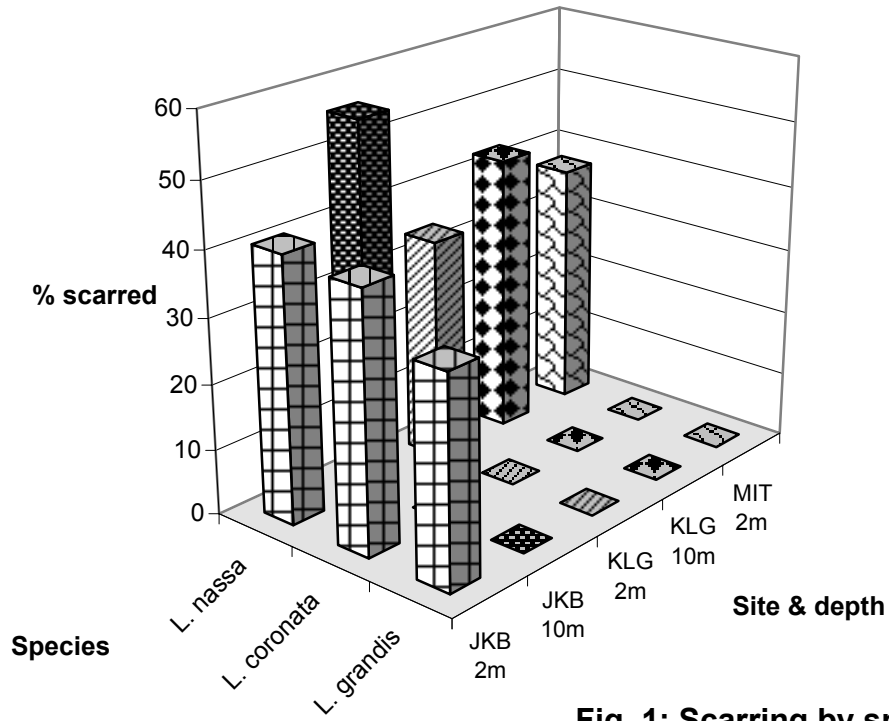


Fig. 1: Scarring by species site & depth

power is at a premium (Underwood 1997). I returned those remaining to the collection site or preserved them for other analyses (e.g. DNA sequencing, cytology, brood and embryo sizes). Morphometric data was collected using digital calipers (ETC Industrial) for fifty individuals of each type - scarred and unscarred - of each species at each depth collected. Morphometric data included total height measured on the vertical axis from the apex of the shell to the anterior edge of the aperture and total width measured perpendicular to height at the widest point on the shell. I also determined aperture height (maximum long orientation) and width (maximum perpendicular to aperture height), lip thickness, and number of ribs per whorl. In addition, I also measured the distance along the spire from the top of the aperture to the apex and, on scarred specimens, the comparable distance from the scar to the shell apex on scarred individuals. This can then give a measure of relative size when the crab was attacked, allowing a plot of ontogenetic predation risk. I then crushed the shells using a vice, removed the body carefully, and dried the shell fragments at fifty degrees Celsius. After removal, I determined the mass of the shell fragments to test for changing shell mass as a predation response.

Results

Scar frequency was highest at Jakobsen's beach (Fig. 1, Table 2). Scar frequency was also found to be greater at ten meters than at two meters (Fig. 1, Table 2). At both Jakobsen's and at Kalalangabo, *L. grandis* was found to be scarred the least. Analysis of the morphometric data is not complete at this time.

Discussion

I estimated the predation pressure on several *Lavigeria* species by determining scar frequency. The high scarring frequency at Jakobsen's could be due to higher crab densities, more gastropod attacks per crab, or greater snail survivorship of crab attacks. A survey of crab densities at the sites would test the relationship between crab population size and scarring frequency. Gut content or isotope studies of the crabs could address the question of trophic preference by crabs. Gastropod survivorship could be tested experimentally with damaged shells returned to the field.

Similarly, the increased scarring frequency at greater depth could also be attributed to increased crab density. However, it is also possible that life history factors are responsible, if older, and thus potentially more scarred individuals prefer greater depths. This will be tested in the analysis of the probability of scarring with respect to size.

L. grandis was found to have the lowest scarring frequencies as two sites. The species could be less vulnerable to crab attack due to size or habitat preference, as it is found on the surfaces of large boulders in the wave washed shallow littoral zone, which presumably is difficult terrain for crabs. It is also possible that *L. grandis* experiences higher mortality, such that attacked snails do not survive to produce scarred adults. Predator choice between *L. grandis* and its sympatric species remains to be determined and may be a venue for future research. When scars were present, they were often quite subtle - it is possible that because of its smoother growth form and finer ribs, scarring is less detectable in this species relative to the others, where scars are heavy and unequivocal.

The analysis of the shell morphological data with respect to scarring will be the first test of inducible defense in *Lavigeria*. This will clarify the dynamics of the coevolutionary relationship between shell - breaking crabs and their sculptured gastropod prey in Lake Tanganyika.

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