

# Shell damage in salt marsh periwinkles (*Littoraria irrorata* [Say, 1822]) and resistance to future attacks by blue crabs (*Callinectes sapidus* [Rathbun, 1896])

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**Abstract:** Unsuccessful predation by the blue crab (*Callinectes sapidus* [Rathbun, 1896]) on salt marsh periwinkle snails (*Littoraria irrorata* [Say, 1822]) could result in shell damage and the subsequent development of a visible shell scar. We experimentally determined whether scarred *L. irrorata* are more or less resistant to blue crab predation than unscarred individuals. We simultaneously presented equal numbers of similar-sized scarred and unscarred snails to individual blue crabs and recorded the number of each type of snail consumed. We also compared shell attributes of scarred and unscarred snails from two marsh sites on Sapelo Island, Georgia, U. S. A. Crabs consumed significantly more unscarred than scarred snails, suggesting that unscarred snails are more easily accessed. This pattern was more pronounced when the snails were close to the maximum edible size. Measurements indicated that the shells of scarred snails had significantly thicker lips than those of unscarred snails. These results demonstrate that shell scars correlate with greater predation resistance in *L. irrorata*.

**Key Words:** predation, *Littoraria*, *Callinectes*, shell repair, salt marsh

Animals have evolved a variety of defensive morphological traits that confound the capture and handling efforts of their predators. Morphological adaptations can derive from natural selection for a particular structure or trait, or from plastic morphological responses to encounters with risk (Vermeij *et al.*, 1981; Dodson, 1989). Although not extensive, most research on plastic morphological responses focuses on how organisms adapt after sensing chemical cues that signal the presence of a predator (Appleton and Palmer, 1988; Dodson *et al.*, 1994; Lewis and Magnuson, 1999; Trussell and Smith, 2000). In this paper, we examine another mechanism by which the morphology of prey might respond to predation risk. We investigate whether prey morphology is distinct between prey that have had injurious, nonlethal encounters with a predator versus prey that have not been previously injured. In the case of repair following an injury, the defensive capacity of any damaged structures may be compromised or improved.

Snails display a wide range of behavioral and morphological antipredatory adaptations (Appleton and Palmer, 1988; Covich *et al.*, 1994; Lewis and Magnuson, 1999;

Turner *et al.*, 1999). Morphological adaptations that increase handling time may ultimately reduce predation risk. In environments with high predation risk, natural selection has resulted in some snail species developing thick shells, narrow apertures, and reduced spires. These traits increase handling difficulty for crushing predators such as crabs (Vermeij and Covich, 1978; Palmer, 1979; Bertness and Cunningham, 1981). At time scales much shorter than that of natural selection, individual snails may develop stronger shells in response to chemical cues released by the feeding activities of decapods (Appleton and Palmer, 1988; Trussell and Smith, 2000), although this process is not universal (Lewis and Magnuson, 1999).

For marsh periwinkles (*Littoraria irrorata* [Say, 1822]), behavioral adaptations reduce predator encounter rates (Hamilton, 1976; Warren, 1985; Dix and Hamilton, 1993). Morphological antipredatory adaptations, however, have not been demonstrated for *L. irrorata*. For example, Blundon and Vermeij (1983) compared the shell strength of *L. irrorata* that had survived previous attempts at predation by blue crabs (*Callinectes sapidus* [Rathbun, 1896]), as indicated by scars on the shell (Vermeij, 1978), with snails lacking any indication of ever encountering a predator. Pressing the ultimate body whorl with an Instron testing device, they found no difference in shell strength between the two classes of snail. Crabs employ many forms of

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attack when foraging on snails (Hamilton, 1976; Bertness and Cunningham, 1981; Vermeij, 1982a). For example, *C. sapidus* prey on relatively large snails by progressively chipping away at the aperture lip, rather than applying force to the ultimate body whorl (Schindler *et al.*, 1994). We investigate here whether the presence of a scar correlates with snail vulnerability to crab predation.

Predation pressure by crabs on snails and injury rates of snails are greater at lower elevation sites within a given marsh (Schindler *et al.*, 1994), and this difference may have consequences for shell morphometry. Larger crabs, which have higher predation success rates for a given sized snail, may occur at lower elevation marshes (Schindler *et al.*, 1994). To evaluate the general effect of scarring on morphometry across disparate sites, we examined the effect of scar presence on morphometry at both a low and a high elevation site. To evaluate the effect of scarring on predation success across a range of predator strengths, we examined predator success across a wide range of crab and snail sizes.

Blue crabs display size preferences and will discard snails that are too large to handle (Hamilton, 1976; Schindler *et al.*, 1994). As the crab carapace width / snail shell length ratio (crab / snail size ratio) increases above 6.4, most snails are crushed and consumed by crabs. Below this ratio (i.e., when a snail is relatively large for a given crab) there is a linear decrease in the likelihood of a shell being crushed (Schindler *et al.*, 1994). We predict that if the presence of a scar influences the vulnerability of snails to predation, this effect would be manifest below crab / snail size ratios of 6.4. Below this ratio, subtle differences in morphology will have discernable effects on vulnerability to successful attack. Above this ratio all snails would be extremely vulnerable, independent of scarring status.

We conducted laboratory tests and morphometric measurements to determine whether the presence of a scar in the shells of *Littoraria irrorata* correlates with differential predation success by *Callinectes sapidus*. To test the null hypothesis that scarring does not correlate with crab predation success, we investigated whether blue crabs consumed significantly more scarred or unscarred snails of similar size. To determine if relative consumption rate was related to crab size, snail size, or crab/snail size ratio, we investigated whether differences were more apparent for specific subsets of the experimental populations. Finally, we measured aperture and lip characteristics of scarred and unscarred *L. irrorata* to identify differences in shell traits between scarred and unscarred snails.

## METHODS

### Consumption comparison

We conducted an experiment to test whether blue

crabs more readily consumed scarred or unscarred snails. We collected all experimental *Littoraria irrorata* from a 180 m<sup>2</sup> region of Dean Creek Marsh, Sapelo Island, Georgia, USA. We measured snail shell length to the nearest millimeter with calipers, and examined snails for the presence of a scar (a jagged line associated with a visible indentation in the shell). The snails used in feeding experiments ranged in size from 14 to 22 mm. We collected crabs from South End Creek Marsh and from the coastal beach southeast of Dean Creek. We transferred crabs to a large flow-through holding tank and conditioned them to the laboratory environment for at least 48 hr, during which time they were not fed. After the acclimation period, individual crabs were transferred to separate flow-through glass aquaria.

We conducted 33 feeding experiments using 13 crabs (1 to 6 experiments per crab; Table 1). In each experiment, we simultaneously presented an individual crab with 10 snails of equal length, 5 that had shell scars and 5 that did not. We continued an individual feeding experiment until the crab had consumed at least 3 snails or had ceased feeding for at least 15 min. After completion of an experiment, we recorded the number of remaining scarred and unscarred snails. A number of experiments using separate crabs in separate aquaria were conducted simultaneously. We did not reuse snails for any experiment and we removed from our analysis experiments in which crabs did not consume any snails.

To determine whether scarring status influenced the number of snails consumed, we ran a G-test on the pooled data from the 33 experiments (Sokal and Rohlf, 1995). Because crabs were presented with 10 snails in each experi-

**Table 1.** Blue crab carapace width (mm), snail shell length (mm), and total number of snails presented to each crab. In each experiment, five scarred and five unscarred snails were presented. When more than one experiment was performed at a given size, the number of experiments is listed in parentheses.

Carapace Width (mm)	Snail Sizes (mm) (Number of Experiments)	Total Number of Snails Presented
82.2	16	10
86.7	14, 15, 16(2)	40
102.2	14(2), 16(2), 17(2)	60
106.8	17, 18	20
113.5	17, 18(2)	30
118.3	19, 20	20
119.2	17(2), 18(2)	40
121	18, 21	20
124.2	17, 18	20
129.7	19	10
132.4	20, 21	20
133	15, 20	20
134.6	20, 22	20

ment, for the G-test we define each individual snail as an observation, generating a total sample size of 330 observations. We compared the total number of scarred and unscarred snails eaten with the null hypothesis that equal numbers of each would be consumed. We used heterogeneity G-tests to evaluate whether consumption of snails by individual crabs deviated significantly from the experimental crab population, or whether the consumption of snails by individual crabs varied among experiments (Sokal and Rohlf, 1995).

We recognized that scarring status might not affect crab predation success for very small, easily crushed snails. Thus, we intentionally conducted multiple experiments above and below a critical crab / snail size ratio (6.4), determined experimentally by Schindler *et al.* (1994). We also intentionally used a broad range of crab and snail sizes in order to separately examine the effect of crab and snail size. In total, we conducted 15 experiments above and 18 experiments below the critical size ratio. We also examined the results for statistical significance when data were separately pooled by median snail or crab size. The median sizes (18 mm for snails and 115 mm for crabs) are sizes at which predation success by *Callinectes sapidus* on *L. irrorata* changes significantly (e.g., see table 3 in West and Williams [1986] and fig. 9 in Schindler *et al.* [1994]).

### Shell morphometry

We compared shell characteristics of 257 unscarred and 48 scarred snails collected from a site with high predation risk and a site with low predation risk. All snails were collected in late October, 1999. The site with high predation risk, Lighthouse Marsh, is located along the shore of Doboy Sound, a source of crabs for these intertidal marshes. By contrast, predation risk is reduced at North End Marsh, a higher elevation site located at the headwaters of Dean Creek about 3 km from Doboy Sound (Schindler *et al.*, 1994). We captured and measured 113 unscarred snails and 27 scarred snails from Lighthouse Marsh and 144 unscarred and 21 scarred snails from North End Marsh. We measured shell traits to the nearest 0.01 mm using a dial caliper. The attributes measured were shell length, aperture length, aperture width, and lip thickness (see axis orientations in figure 1 of Janson and Sundberg [1983]). Aperture length and width were the distances between the inner surfaces of the aperture along these axes. For lip thickness, measurements were collected at least three times on separate randomly selected locations 1 mm inside the lip edge and the minimum value was recorded. Particular traits were occasionally, and inadvertently, not measured for a few snails, resulting in a sample size of between 297 and 305 measured snails per trait. In addition, we estimated the shape of the aperture as an ellipse, and calculated aperture area from the measurements of aperture length and width.

We used general linear models to determine the relative importance of collection site and scarring status on aperture length, aperture width, aperture area, and lip thickness (Draper and Smith, 1998). These morphological traits scale with overall shell length (see Results section). Therefore, we first de-trended the data for the effect of length by fitting a linear regression of each trait vs. shell length and then taking the residuals. For each trait, these residuals were checked for normality and then analyzed as a function of site, scarring status, and the site x scarring status interaction.

## RESULTS

### Consumption comparison

In all experiments combined, 165 scarred and 165 unscarred snails were presented to the blue crabs. Of these, the crabs ate 76 scarred and 98 unscarred snails, a significant difference ( $p < 0.025$ ; Table 2). When the crab or snail population was examined by size, crabs ate more unscarred than scarred snails, but the pattern was only significant for small ( $< 18$  mm) snails (Table 2). No heterogeneity was observed between individual crabs and the entire experimental population. Furthermore, no heterogeneity was found between trials, indicating that crab behavior was consistent among trials.

Crabs consumed fewer scarred snails in trials when the crab to snail size ratio was small (Fig. 1). Individual G tests indicated significance for the low size ratio but not for the high size ratio crabs (Table 2). In trials characterized by high body size ratios (i.e. relatively small snails), predation rates were uniformly high at around 60%, with only an 8% decrease for scarred snails.

### Shell morphometry

Aperture length, aperture width, aperture area, and

**Table 2.** Consumption percent differences (percent of unscarred snails consumed minus the percent of scarred snails consumed) and G-test results for all trials and for subsets of the sample categorized according to snail shell length (large  $\geq 18$  mm > small), crab carapace width (large  $\geq 115$  mm > small), and crab / snail size ratio.

Sample Type (N)	Consumption Percent Difference (Unscarred - Scarred)	G
All Trials (330)	13	5.90*
Large Snails (160)	10	1.60
Small Snails (170)	18	5.37*
Large Crabs (170)	13	2.87
Small Crabs (160)	15	3.62
Crab / Snail Size Ratio $< 6.4$ (180)	19	6.46*
Crab / Snail Size Ratio $> 6.4$ (150)	8	0.98

\* indicates significance at  $\alpha = 0.025$

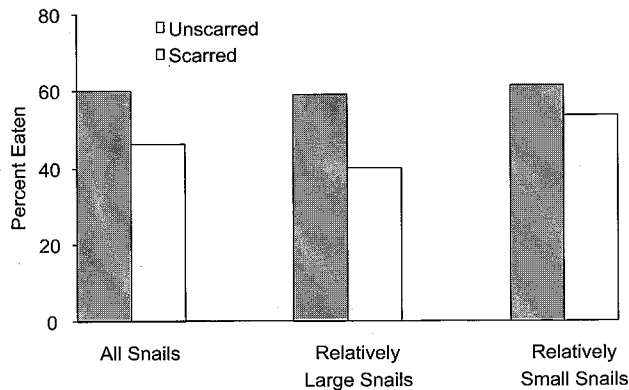


Fig. 1. The percentage of all snails eaten ( $N = 330$ ), and the percentage of relatively large ( $N = 180$ ) and relatively small ( $N = 150$ ) snails eaten. The relatively large snails have a crab / snail size ratio below 6.4 and the relatively small snails have a crab / snail size ratio above 6.4.

lip thickness all scaled positively with shell length ( $R^2 = 0.87, 0.79, 0.85, \text{ and } 0.67$ , respectively; linear regression  $p < 0.001$  in all cases). Probability plots indicated that all four sets of residuals followed a normal distribution. After removing the effect of shell length, we determined the interactive effect of site (high vs. low predation risk) and scarring status on each of these three shell traits. Aperture length was reduced in snails collected from Lighthouse Marsh ( $p < 0.001$ ), the site with high predation risk; and was reduced in snails bearing a scar ( $p = 0.039$ ; Fig. 2A). The interactive effect of site and scarring status was not significant at  $p = 0.05$ .

There was an interactive effect of site and scarring status on aperture width ( $p = 0.017$ ). On scarred snails, aperture width was increased at Lighthouse Marsh, where predation risk was allegedly higher. By contrast, the aperture width of scarred snails was reduced at the site with low predation risk, North End Marsh (Fig. 2B).

Variability in aperture area was not explained by site, scarring status, or their interaction ( $p > 0.05$ ; Fig. 2C).

Finally, lip thickness was greater at the site with high predation risk ( $p = 0.016$ ), and was greater on snails bearing a scar ( $p = 0.023$ ; Fig. 2D). There was no interactive effect on lip thickness.

## DISCUSSION

The blue crabs used in this experiment ate significantly more unscarred than scarred snails. Additionally, scarred snails had thicker lips and differently shaped apertures than unscarred snails. Integration of these results suggests two hypotheses: first, following an attack, repair results in a shell with an improved defensive capacity; second, lip thickness is inversely related to vulnerability. In the

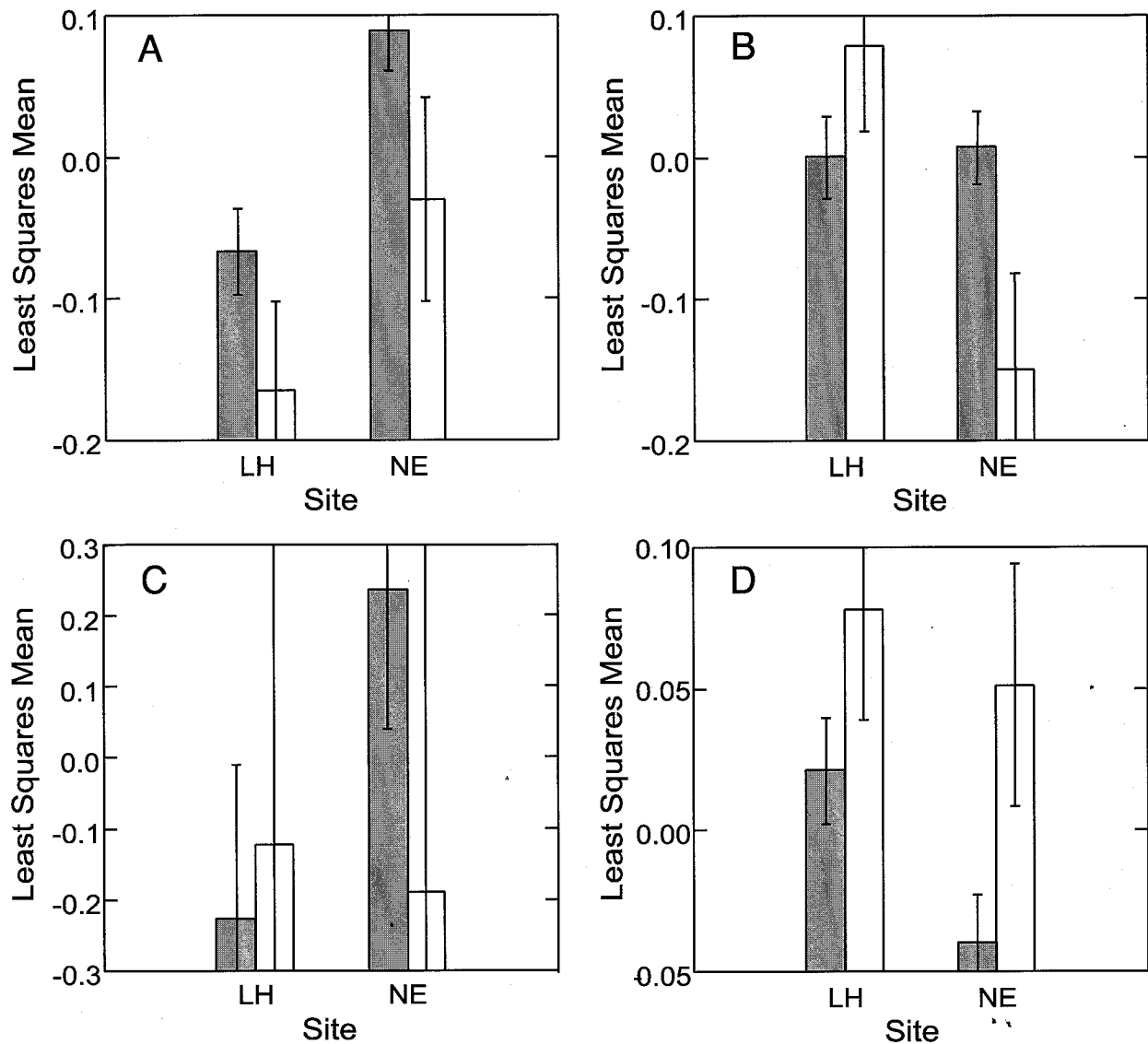
following discussion, we further evaluate these hypotheses.

Our data suggest that snails that have experienced predation attempts have shells with an improved capacity for defense. This improvement probably lies in the increase in lip thickness, but does not derive from any changes in aperture shape. Apertures were shorter on scarred snails. In some cases, however, apertures were also wider. These changes in aperture shape result in no net change in aperture area. Consequently, scarring status likely has little effect on a crab's ability to insert its chelae into the aperture in attempts to chip the shell. Chelae insertion is more frequently used by crabs to access large snails (Schindler *et al.*, 1994). Therefore, the more significant difference in predation success between scarred and unscarred snails below 18 mm than above 18 mm supports the hypothesis that chelae insertion success does not depend on scarring status.

Increase in the thickness of the aperture lip, however, would influence a crab's ability to chip a snail shell. Our data provide evidence for the hypothesis that thicker lips endow snails with greater resistance to predation. In the field, snails with scars had thicker lips, and in our experiment, snails with scars were eaten less frequently. Furthermore, Blundon and Vermeij (1983) demonstrate that overall strength of the shell's body whorl does not significantly differ between scarred and unscarred snails, implicating a more isolated morphological mechanism, such as differences in lip thickness.

The increased lip thickness of scarred snails could result from at least two mechanisms. First, scarred snails may have inherited greater resistance, regardless of scarring status, as evidenced by their survival of a previous predation attempt. In other words, the scarred population represents the skewed result of natural selection due to removal of weak shelled individuals from the entire population (Vermeij, 1982b; Johannesson and Johannesson, 1996). Second, morphological responses may be induced by unsuccessful attacks. A scarring event may lead to the development of antipredatory morphology in individual snails (Appleton and Palmer, 1988). This hypothesis is supported by the work of Trussell and Smith (2000), who demonstrate shell thickening of *Littorina obtusata* in response to predator effluent across a wide geographic range. Regardless of the mechanism, because *Littoraria irrorata* exhibit a planktonic larval stage (Bingham, 1972), spatial variation in lip thickness would only be maintained by adult exposure to predation gradients after settlement.

Our data also suggest that snail shell attributes are influenced by predation risk regardless of whether an individual snail is attacked. Snails collected from Lighthouse Marsh, where predation risk is high, had shorter apertures and thicker lips than snails collected from the less risky North End Marsh site. Both scarred and unscarred snails demonstrated this pattern. Snails may have differed



**Fig. 2.** Relationships of traits of snail shells with site (Lighthouse Marsh, LH - high predation risk; North End Marsh, NE - low predation risk) and scarring status (open bar - scarred; dark bar - unscarred). A site with high predation risk (Lighthouse Marsh, LH) and a low predation risk site (North End Marsh, NE) were sampled for scarred and unscarred snails. Shell traits include (A) aperture length (number of snails,  $N = 305$ ), (B) aperture width ( $N = 300$ ), (C) aperture area ( $N = 300$ ), and (D) lip thickness ( $N = 297$ ). Bars indicate the least-squares means of an ANOVA of shell trait as an interactive function of site and scarring status. Error bars = 1 SE. Data are the residuals from a linear regression of shell trait vs. shell length.

between sites in these morphological traits for two reasons. First, selective pressures would be greater at Lighthouse Marsh. Second, snails may respond to chemical cues indicative of risk that are released by crabs (Trussell and Smith, 2000). We only have one site apiece characterized by high and low predation risk. Thus, we submit only as a suggestion that periwinkle morphology responds to predation risk in the absence of an actual scar-inducing encounter. Nevertheless, natural selection for improved defensive capacity is a pervasive, widespread process in gastropod-decapod systems (e.g., Kitching and Lockwood, 1974).

Differences in the vulnerability of scarred and unscarred snails were particularly evident when snails were close to the maximum edible size (i.e. when the crab / snail size ratio was less than 6.4). This is consistent with Elner and Hughes' (1978) demonstration that for crabs, the cost of handling prey changes more rapidly at high prey sizes. In the context of optimal foraging theory (Pyke *et al.*, 1977), our results suggest that the difference in overall energetic gain between scarred and unscarred snails is most pronounced at the maximum edible snail size. At this size ratio, the subtle morphometric differences associated with

scarring have the greatest effect.

There are several possible consequences of shell damage for *Littoraria irrorata*. First, as noted above, scarred snails have thicker lips than unscarred snails. This increased lip thickness may be a barrier to efficient consumption by blue crabs. Second, snails may suffer a trade-off between repairing the shell and various physiological processes. For instance, the energetic cost of repair may compromise reproductive output and growth. Stahl and Lodge (1990), however, found no such trade-off in one freshwater species, and inferred that population growth was not compromised by nonlethal injuries. Third, it is possible that increases in lip thickness associated with scarring may reduce soft tissue mass, causing a reduction in the energetic value of snails for crabs.

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