

Shell Strength of Mud Snails (*Ilyanassa obsoleta*) May Deter Foraging by Diamondback Terrapins (*Malaclemys terrapin*)

ABSTRACT.—Diamondback terrapins (*Malaclemys terrapin*) do not eat the common and abundant mud snail (*Ilyanassa obsoleta*) even though terrapin diets are dominated by similarly sized gastropods. To resolve this paradox, we tested a structural defense hypothesis as the potential deterrent against predation. We compared resistance to compressive force of *Ilyanassa* and three invertebrates (*Littorina irrorata*, *Uca* spp, and *Callinectes sapidus*) that terrapins commonly eat. *Ilyanassa* shells were 2–3 times more resistant to crushing than the other prey. High processing costs for mud snails (in terms of structural resistance to crushing) may deter predation by terrapins despite the low search costs and equivalent energetic returns relative to alternative prey items.

INTRODUCTION

Diamondback terrapins (*Malaclemys terrapin*) consume a variety of small shellfish, crustaceans and fish (Ernst *et al.*, 1994). In South Carolina salt marshes, 76–79% of the terrapin diet is composed of periwinkles (*Littorina irrorata*) from the *Spartina alterniflora* meadows of the upper intertidal zone (Tucker *et al.*, 1995). Terrapin activity is strongly synchronized with high tide (Muehlbauer, 1987) and when salt marsh meadows are inundated, terrapins swim to forage on *Littorina* that cling to *Spartina* stems (Tucker *et al.*, 1995). Given a tidal restriction on easy access to *Littorina*, it was puzzling that terrapins ignored a common and abundant gastropod of similar size, the mud snail (*Ilyanassa obsoleta*).

Ilyanassa graze on the exposed mudflats of the lower intertidal zone (Pace *et al.*, 1979) and are therefore more accessible than *Littorina* in the upper intertidal zone (Vaughn and Fisher, 1992). *Ilyanassa* and *Littorina* are found throughout the salt marsh with localized densities reaching 400–700 per m² (Odum and Smalley, 1959; Montague *et al.*, 1981). Size distributions of *Ilyanassa* and *Littorina* are similar (Hamilton, 1978) so gape limitation of terrapins does not preclude ingestion of *Ilyanassa*. Consequently, foraging terrapins could potentially shift from *Littorina* to *Ilyanassa* during ebbing tides as accessibility of each prey altered, and a converse shift would be predicted to accompany flooding tides. However, there was no evidence that *Ilyanassa* were eaten by terrapins (Tucker *et al.*, 1995).

Foraging theory suggests that if energetic returns do not offset the sum of searching and processing costs, predators are unlikely to include a given prey in the diet (Pyke, 1984). In the present case, why should turtles with a strong dietary dependence on gastropods bypass presumably suitable and abundant prey? Differing energetic profitability is unlikely because energetic values for molluscs are equivalent on a dry weight basis (Cummins and Wuycheck, 1971). Initial search costs by terrapins appear negligible as mud snails are abundant and highly visible. We identified three remaining possibilities: *Ilyanassa* might employ a behavioral response, a chemical deterrent, or a structural defence to escape predation by terrapins.

Regarding the first mechanism, experiments have shown that crushed mud snails release an alarm substance that induces nearby snails to bury in the substrate (Atema and Stenzler, 1977; Stenzler and Atema, 1977; Ashkenas and Atema, 1978). However, the response takes several minutes and remains highly localized so an alarm substance is unlikely to preclude predation by terrapins. A toxic or noxious substance seems unlikely since such phylogenetically dissimilar animals as crabs (Stenzler and Atema, 1977; Ashkenas and Atema, 1978), moon snails (Stenzler and Atema, 1978), and migratory birds (Recher, 1966) all feed readily on *Ilyanassa* (Stenzler and Atema, 1977; Ashkenas and Atema, 1978). This left the structural defense hypothesis as a logical premise to test. If the crushing resistance of a shell deters terrapins from opening gastropods in the first place, then concerns about escape behavior or secondary metabolites are misplaced.

MATERIALS AND METHODS

We collected prey samples from known terrapin habitat at Kiawah Island, South Carolina (Gibbons and Harrison, 1981). We sampled the entire spectrum of prey sizes to account for the terrapin's sexual dimorphism (Gibbons and Lovich, 1990) because large females consume significantly larger prey than the smaller males (Tucker *et al.*, 1995). We tested resistance to crushing in *Ilyanassa* and *Littorina* over

TABLE 1.—Average force (kg) required to crush mud snails in comparison to prey commonly eaten by diamondback terrapins. Predictive relationships for force to crush a prey of given size (mm) were calculated over the same size range (9–20 mm) of *Ilyanassa* and *Littorina*

Species (sample size)	Average force (± 1 sd) (range)	Predictive relationship	(r^2 value)
<i>Ilyanassa</i> (n = 46)	214.9 kg (± 123.5) (54.6–478.4)	mass = 11.81(10) ^{0.078} (prey size)	($r^2 = 0.85$)
<i>Littorina</i> (n = 100)	98.2 kg (± 58.7) (22.2–256.2)	mass = 7.16(10) ^{0.069} (prey size)	($r^2 = 0.81$)
<i>Uca</i> (n = 8)	67.9 kg (33.5) (29.5–123.2)	mass = -7.23 (prey size) + 180.85	($r^2 = 0.33$)
<i>Callinectes</i> (n = 3)	160.3 kg (32.0) (140.4–197.1)	mass = 1.15 (prey size) + 105.43	($r^2 = 0.77$)

the size range commonly eaten by terrapins (9–20 mm) and ignored both smaller and larger (to 26 mm) *Littorina* found at the Kiawah field site (see Fig. 4, Tucker *et al.*, 1995). We also tested fiddler crabs (*Uca* spp.) and small blue crabs (*Callinectes sapidus*) since these prey were taken by terrapins but at lower frequencies. We tested live snails or freshly thawed snail and crabs to avoid postmortem changes in structural properties of the shell (Currey, 1979; Labarbera and Merz, 1992). We measured each prey item with calipers to the nearest 0.1 mm for (1) apex to spire length of snails and (2) carapace width of crabs. Snail lengths were converted to shell widths by the following regression equations: *Ilyanassa* width = 0.43(length) - 0.14 (Dimock, 1985); *Littorina* width = 0.77(length) (Tucker *et al.*, 1995).

Terrapins feed by crushing prey between the ridged alveolar surfaces of the jaws. We attempted to measure compressive bite force of live terrapins directly but terrapins were reluctant to bite the measuring apparatus. Instead we imitated the feeding process by applying compressive force directly to prey items placed on a calibrated pressure load cell (Kistler 9001A, 7500N). As increasing pressure was applied, the electromotive force generated in the compressed load cell (± 0.01 V DC) was read directly from an attached multimeter until the prey item crushed. The force required to process prey of a given size and type was calculated from a calibration curve for the load cell. We described trends in shell strength for each prey type by fitting curves to the data by ordinary least squares regression.

RESULTS

The average shell strength of an *Ilyanassa* was twice that of *Littorina*, three times that of *Uca*, and 1.3 times that of *Callinectes* (Table 1). The force necessary to process *Ilyanassa* and *Littorina* increased exponentially with size, whereas the force necessary to process crabs showed linear trends (Fig. 1). For the small crabs (*Uca*), linear declines in crushing force with increasing size were found but the large crabs (*Callinectes*) required a linear increase in crushing force with increasing size (Fig. 1).

DISCUSSION

Terrapins that can process large *Littorina* should also be capable of crushing at least small *Ilyanassa* (Fig. 1). However, an absence of *Ilyanassa* in diet samples (Tucker *et al.*, 1995) suggests that it is more efficient to harvest large *Littorina* than small *Ilyanassa* for the same processing effort. *Littorina* are sufficiently abundant in South Carolina salt marshes that it is unlikely that terrapins would be forced to feed on *Ilyanassa* unless local *Littorina* populations were reduced. Terrapins forage efficiently, if not optimally (Pyke, 1984), considering the substantial increase in processing costs for *Ilyanassa* over *Littorina* when searching costs for the former are negligible and energetic benefits are equivalent. At least two additional tests are needed to determine whether terrapins are foraging optimally: (1) cafeteria experiments to determine if terrapins eat *Ilyanassa* when offered nothing else and (2) manipulation

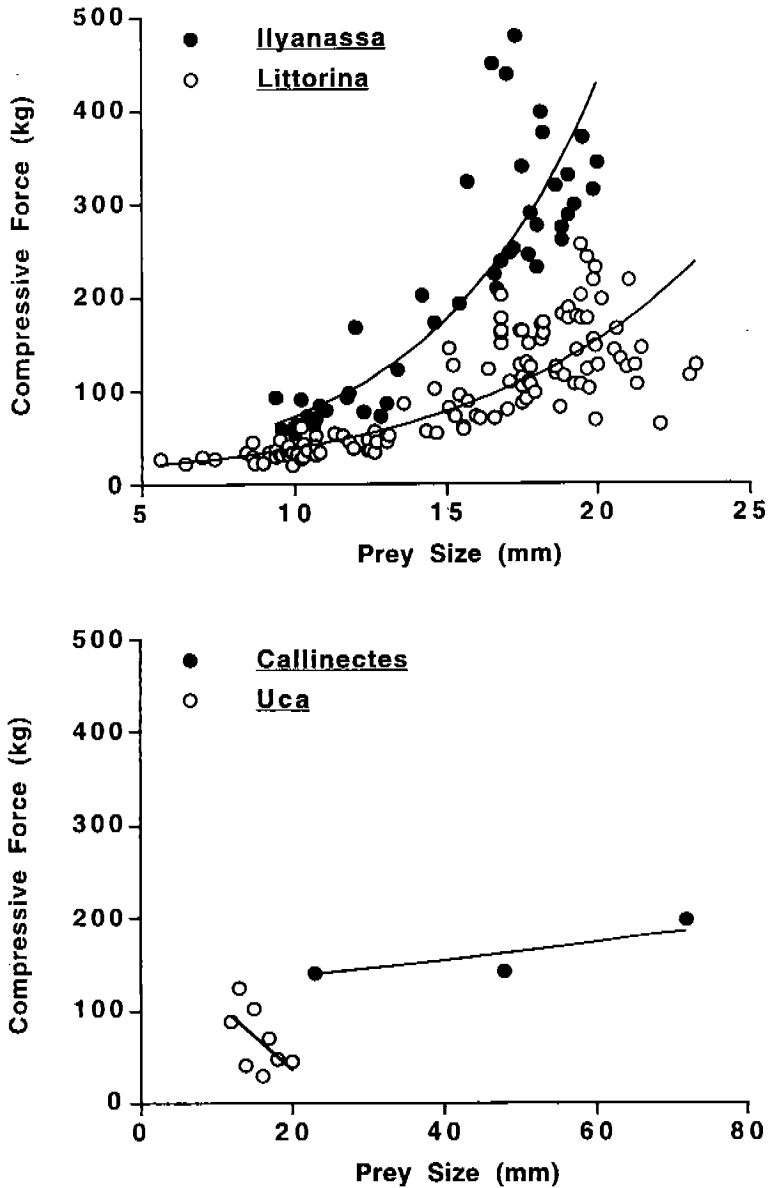


FIG. 1.—Compressive forces necessary to crush *Ilyanassa obsoleta* in comparison to common prey items in diets of terrapins in South Carolina

of abundance and sizes of *Littorina* and *Ilyanassa* to identify if a threshold exists for switching among prey.

It would be informative to test whether possible trade-offs between processing costs and energetic pay-offs influence terrapin diets in other regions. For example, northern populations of terrapins consume mussels (*Mytilus edulis*) (Hurd *et al.*, 1979) and the shell strength of mussels increases ex-

ponentially with size (Currey, 1979) yet terrapins in captive feeding trials consumed mussels larger than *Littorina* on average (Davenport *et al.*, 1992). However, it should be noted that the *Littorina littorea* used in the feeding trials (Davenport *et al.*, 1992) was not a species available to terrapins in their native habitat and no comparisons were made of relative shell strength. The same study noted different foraging tactics by terrapins for crabs of different sizes and interpreted the pattern as a trade-off between processing costs and pay-offs (Davenport *et al.*, 1992). However, the explanation of gape limitation was overlooked and such processing limitations would clearly be relevant when only small male terrapins were tested (Davenport *et al.*, 1992).

Our finding of an exponential increase in pressure necessary to crush *Littorina* is a biomechanical explanation for the observed difference in snail sizes consumed by small male and large female terrapins (Tucker *et al.*, 1995). Additional growth in cranial dimensions by female terrapins evidently provides additional crushing capacity.

Our results clearly indicate that a lack of sutures and low spire height in *Ilyanassa* creates a stronger shell architecture than found in *Littorina* of equal size. In general, gastropod shell strength is enhanced by reductions in suture length and the number and expression of growth lines (Blundon and Vermeij, 1983). A robust shell structure in gastropods offers increased resistance to predators (Ash, 1989; Bertness and Cunningham, 1981; Currey and Hughes, 1982; Hughes and Elner, 1979) and resistance to breaking in high energy surf areas (Currey and Hughes, 1982). Interspecific variations in gastropod shell architecture and strength occur (Lowell *et al.*, 1994), within a genus geographically (Bertness and Cunningham, 1981; Currey and Hughes, 1982), and even for color morphs within a species (Cook and Kenyon, 1993).

A potential influence on shell strength of snails is the high sensitivity of molluscs to elevated levels of tributyltin (TBT) compounds used in ship antifouling paints. Shell thickening is initiated at 10 ng l⁻¹ of TBT in oysters (Waldock *et al.*, 1987) and concentrations easily exceed this near large boat yards (Bryan *et al.*, 1989). It is unknown whether TBT levels in South Carolina salt marshes reach levels sufficient to elicit a change in shell structure of *Ilyanassa* but we doubt it for the Kiawah study site which has few boat docks.

Although robust shell architecture may provide some protection from terrapin predation, other predators of mud snails are present during low or high tides. Adult *Ilyanassa obsoleta* were immune from attack by native crabs but smaller individuals were easily opened by a larger introduced crab, *Carcinus maenas* (Brenchley, 1982). There are conflicting views on the importance of shorebird predators. For example, *I. obsoleta* were seldom present in diets of migrant shorebirds or fish in the Bay of Fundy (Hincklin and Smith, 1979; Crawford, 1988). In contrast, mud snails comprised 66% and 33% of the diets of black-bellied plovers (*Pluvialis squatarola*) and willets (*Catoptrophorus semipalmatus*) and at least 10% of the diet for several other shorebirds in California (Recher, 1966). Further study is needed to clarify the extent of predation on *Ilyanassa* in southeastern salt marshes.

Terrapins offer a valid model for further empirical tests of foraging theory in that they are mobile predators that ingest prey of variable size and energetic content (Tucker *et al.*, 1995). The present evidence suggests that processing costs for *Ilyanassa* may deter terrapins from consuming them despite a reduced search cost and equivalent energetic return in comparison to other prey.

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LITERATURE CITED

- ASH, V. B. 1989. Resistance to shell breaking in two intertidal snails. *Zool. J. Linn. Soc.*, **96**: 167–184.
- ASHKENAS, L. R. AND J. ATEMA. 1978. A salt marsh predator-prey relationship: attack behavior of *Carcinus maenas* (L.) and defences of *Ilyanassa obsoleta* (Say). *Biol. Bull. (Woods Hole)*, **155**: 426.

- ATEMA, J. AND D. STENZLER. 1977. Alarm substance of the marine mud snail, *Nassarius obsoletus*: biological characterization and possible evolution. *J. Chem. Ecol.*, **3**: 173-187.
- BERTNESS, M. D. AND C. CUNNINGHAM. 1981. Crab shell-crushing predation and gastropod architectural defence. *J. Exp. Mar. Biol. Ecol.*, **50**: 213-230.
- BLUNDON, J. A. AND G. J. VERMEIJ. 1983. Effect of shell repair on shell strength in the gastropod *Littorina irrorata*. *Mar. Biol.*, **76**: 41-45.
- BRENCHLEY, G. A. 1982. Predation on encapsulated larvae by adults: effects of introduced species on the gastropod *Ilyanassa obsoleta*. *Mar. Ecol. Progr. Ser.*, **9**: 255-262.
- BRYAN, G. W., P. E. GIBBS, R. J. HUGGETT, L. A. CURTIS, D. S. BAILEY, AND D. M. DAUER. 1989. Effects of tributyltin pollution on the mud snail, *Ilyanassa obsoleta*, from the York River and Sarah Creek, Chesapeake Bay. *Mar. Pollut. Bull.*, **20**: 458-462.
- COOK, L. M. AND G. KENYON. 1993. Shell strength of colour morphs of the mangrove snail *Littorina pallescens*. *J. Mollusc. Stud.*, **59**: 29-34.
- CRAWFORD, R. J. 1988. Behavioral and ecological importance of a mud snail (*Ilyanassa obsoleta*) population in a temperate macrotidal estuary. *Can. J. Zool.*, **66**: 459-466.
- CUMMINS, K. W. AND J. C. WUYCHECK. 1971. Caloric equivalents for investigations in ecological energetics. *Mitt. Int. Ver. Theor. Angew. Limnol.*, **18**: 1-158.
- CURREY, J. D. 1979. The effect of drying on the strength of mollusc shells. *J. Zool. Lond.*, **188**: 301-308.
- AND R. N. HUGHES. 1982. Strength of the dogwhelk *Nucella lapillus* and the winkle *Littorina littorea* from different habitats. *J. Anim. Ecol.*, **51**: 47-56.
- DAVENPORT, J. M., M. SPIKES, S. M. THORNTON AND B. O. KELLY. 1992. Crab-eating in the diamondback terrapin *Malaclemys terrapin*: dealing with dangerous prey. *J. Mar. Biol. Assoc. U.K.*, **72**: 825-848.
- DIMOCK, R. V., JR. 1985. Quantitative aspects of locomotion by the mud snail *Ilyanassa obsoleta*. *Malacologia*, **26**: 165-172.
- ERNST, C. H., J. E. LOVICH AND R. W. BARBOUR. 1994. Turtles of the United States and Canada. Smithsonian Institution, Washington, D.C. 578 p.
- GIBBONS, J. W. AND J. R. HARRISON III. 1981. Reptiles and amphibians of Kiawah and Capers Island, South Carolina. *Brimleyana*, **5**: 145-162.
- AND J. E. LOVICH. 1990. Sexual dimorphism in turtles with emphasis on the slider turtle (*Trachemys scripta*). *Herpetol. Monogr.*, **4**: 1-29.
- HAMILTON, P. V. 1978. Intertidal distribution and long-term movements of *Littorina irrorata* (Mollusca: Gastropoda). *Mar. Biol.*, **46**: 49-58.
- HINCKLIN, P. W. AND P. C. SMITH. 1979. The diets of five species of migrant shore-birds in the Bay of Fundy. *Proc N. S. Inst. Sci.*, **29**: 483-488.
- HUGHES, R. N. AND R. W. ELNER. 1979. Tactics of a predator, *Carcinus maenas*, and morphological responses of the prey, *Nucella lapillus*. *J. Anim. Ecol.*, **48**: 65-78.
- HURD L. E., G. W. SMEDES AND T. A. DEAN. 1979. An ecological study of a natural population of diamondback terrapins (*Malaclemys terrapin*) in a Delaware salt marsh. *Estuaries*, **2**: 228-33.
- LABARBERA, M. AND R. A. MERZ. 1992. Postmortem changes in strength of gastropod shells: evolutionary implications for hermit crabs, snails, and their mutual predators. *Paleobiology*, **18**: 367-377.
- LOWELL, R. B., C. R. FLETCHER, J. GRAHAME AND P. J. MILL. 1994. Ontogeny of shell morphology and shell strength of marine snails *Littorina obtusa* and *Littorina maria*: different defence strategies in a pair of sympatric sibling species. *J. Zool. Proc. Zool. Soc. Lond.* **234**: 149-164.
- MONTAGUE, C. L., S. M. BUNKER, E. B. HAINES, M. L. PACE AND R. L. WETZEL. 1981. Aquatic macroconsumers, p. 69-85. In: L. R. Pomeroy and R. G. Weigert (eds.). The ecology of a salt marsh. Springer-Verlag, New York.
- MUEHLBAUER, E. I. 1987. Field and laboratory studies of tidal activity in the turtle *Malaclemys terrapin terrapin*. Ph.D. Diss., New York University, New York. 60 p.
- ODUM, E. P. AND A. E. SMALLEY. 1959. Comparison of population energy flow of a herbivorous and a deposit-feeding invertebrate in a salt-marsh ecosystem. *Proc. Natl. Acad. Sci.*, **45**: 617-622.

- PAGE, M. L., S. SHIMMEL AND W. M. DARLEY. 1979. The effect of grazing by a gastropod, *Nassarius obsoletus*, on the benthic microbial community of a salt marsh mud flat. *Estuarine Coastal Mar. Res.*, 9: 121-134.
- PYKE, G. H. 1984. Optimal foraging theory: a critical review. *Annu. Rev. Ecol. Syst.*, 15: 523-575.
- RECHER, H. F. 1966. Some aspects of the ecology of migrant shorebirds. *Ecology*, 47: 393-407.
- STENZLER, D. AND J. ATEMA. 1977. Alarm response of the marine mud snail, *Nassarius obsoletus*: specificity and behavioral priority. *J. Chem. Ecol.*, 3: 159-171.
- TUCKER, A. D., N. FITZSIMMONS AND J. W. GIBBONS. 1995. Resource partitioning by the estuarine turtle *Malaclemys terrapin*: trophic, spatial, and temporal foraging constraints. *Herpetologica*, 51: 167-181.
- VAUGHN, C. C. AND F. M. FISHER. 1992. Dispersion of the salt-marsh periwinkle *Littorina irrorata*: effects of water level, size, and season. *Estuaries*, 15: 246-250.
- WALDOCK, M. J., J. E. THAIN AND M. E. WAITE. 1987. The distribution and potential toxic effects of TBT in UK estuaries during the 1980s. *Appl. Organometal Chem.*, 1: 287-301.

ANTON D. TUCKER, Department of Zoology, University of Queensland, Brisbane 4072 QLD, Australia, and S. REBECCA YEOMANS and J. WHITFIELD GIBBONS, Savannah River Ecology Laboratory, Drawer E, Aiken, South Carolina 29802, Submitted 3 June 1996; accepted 19 December 1996.

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