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Cover Photo: Outcrop showing Pleistocene soil profile,
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SHELL REPAIR ON RECENT CERION FROM SAN SALVADOR ISLAND: DOES IT INDICATE HABITAT COMPLEXITY?

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ABSTRACT

Shell repair, as an indicator of unsuccessful predation, occurs in relatively high frequencies on *Cerion* from exposed, eastward facing coastal regions of San Salvador Island. *Cerion* from inland sites or from the leeside of the island have relatively little incidence of repaired shells. Repair is determined by either: (1) noting the number of major disruptions of the sculptural or whorl pattern, or, (2) jagged areas that have subsequently been repaired. Of the 14 localities examined, only two sites representing lake habitats had little if any repaired shells (e.g., Stouts Lake and South Barn Cay Ridge). Young *Cerion* and adults from most localities experienced the same frequency of shell repair. The results suggest that biotic factors (assuming that shell repair indicates unsuccessful predation) may be stronger on coastal, unprotected sites of San Salvador, whereas inland and lake sites may not have this level of habitat complexity.

INTRODUCTION

Shell repair is considered to be an important indicator of predation in modern and fossil gastropod communities from marine settings (Papp et al., 1947; Robba and Ostinelli, 1975; Vermeij et al., 1981; Vale and Rex, 1988). In the marine environment, shell repair may not be directly correlated with intensity of predation or predation rates (Schoener, 1979) nor are peeled apertures directly correlated to predation (Walker and Yamada, 1993). Rather, repaired scars can be used to infer predation in habitats where direct observation of predation may be difficult, such as in the deep sea (Vale and Rex, 1988, 1989; Walker and Voight, 1994). In the deep sea, the degree of shell repair is suggested to be correlated with increase in habitat complexity due to predation and/or increase in physical disturbance (Vale and Rex, 1988). Here we report on the incidence of shell repair on the terrestrial gastropod, *Cerion* from San Salvador Islands, Bahamas and suggest that the degree of shell repair may be correlated to habitat complexity in terrestrial ecosystems as well.

METHODS

Live *Cerion* and those from Recent death assemblages were collected from 14 localities from San Salvador Island, Bahamas (Fig. 1). All shells were measured for shell height and examined under a dissecting scope for the incidence of shell repair on all whorls. Whorls 1-4 (not including the protoconch) were considered "juvenile" and whorls 5-preterminal lip, were considered "adolescent." Adult *Cerion* are determined by the development of the terminal lip (Gould, 1993) and thus all whorls before this lip could be considered "preadult. " The distinction between juvenile and adolescent whorls was made based on size which could affect predation frequency. Repair is determined by either: (1) noting the number of major disruptions of the sculptural or whorl pattern, or, (2) jagged areas that have subsequently been repaired (Fig. 2).

Shell repair was measured by the

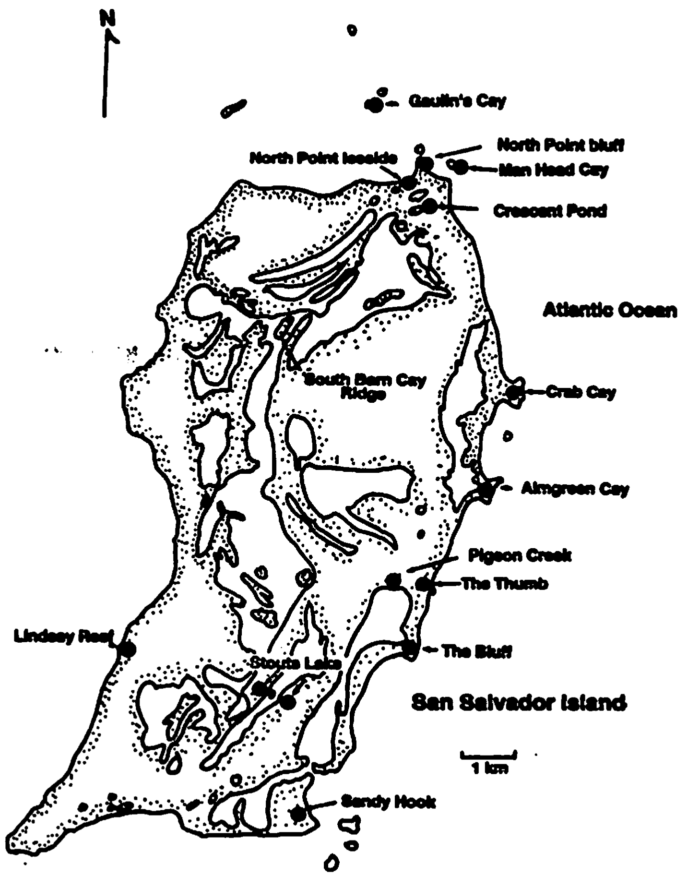

Figure 1. Map of San Salvador, Bahamas. Dots indicate sample localities.

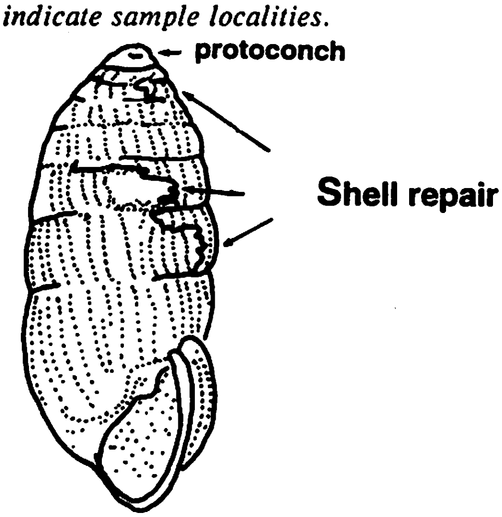

Figure 2. Line drawing of adult Cerion *shell.*

number of individuals with at least one repair divided by the total number of individuals in the sample (after Vale and Rex, 1988; Gellar 1983). Here, we differ from Vermeij, who has used another method, that of the average number of predation scars per individual (Vermeij, 1982; Vermeij et al., 1980). We used the latter as a more conservative measure of shell repair.

Habitat determinations were as follows: protected sites were inland habitats protected from the full force of the trade winds which blow from the east; unprotected sites are subject to the full force of the winds, withlive *Cerion* fully exposed to sun and wind; high vegetation refers to coastal plants 4 to 5 feet in height, consisting of coastal rock and coppice plants (e.g., Sea grape, *Coccoloba uvifera;* tall hardhead, *Phyllanthus epiphyllanthus).* Low vegetation for open terrain consisted of Bay Geranium, *Ambrosia hispida;* stunted Hardhead, *Phyllanthus epiphyllanthus;* low black torch, *Erithalis fruticosa;* and Common Ernodea, *Ernodea littoralis)* (Correll and Correll, 1982; Kass, 1991). Open terrain refers to areas with an open canopy of vegetation, rolling or flat terrain.

RESULTS

Shell repair was highest in coastal, exposed regions of San Salvador Island with the exception of two localities (The Bluff and The Thumb), and lowest in protected, inland sites (Table 1). Shell repair frequencies varied between 0.51 and 0.74 at the unprotected sites, while the protected sites varied between 0.01 and 0.29. The Bluff and The Thumb localities had frequencies similar to those of the protected sites, 0.19 and 0.26 respectively.

With relatively few exceptions, the frequency of repaired shells did not vary greatly between juvenile and adolescent *Cerion* (Table 1). For half of the localities, adolescent whorls had slightly more shell damage than the juvenile whorls. Damage, and subsequent repair of the terminal lip (aperture) rarely occurred in adult *Cerion.* Multiple events of shell repair (e.g., a shell with more than one major repair) was also rare except for the Man Head Cay locality, which also had the highest frequency ofrepaired shells.

Robust shells, that is thick, ribbed to fine-ribbed large shells (shell height >24.00 mm) sustained the most shell damage, while thin, small shells from the protected lake or pond sites sustained the least shell damage (Table 1).

TABLE 1. Shell repair on Recent Cerion from San Salvador Island, Bahamas. Key: Protected: protected from wind; unprotected: full force of easterly tradewinds.

Locality	Habitat Type	Cerion Type	Sample Size	Shell Height (mean in mm)	Shell Repair Whorls 1-4 (number of individuals/ frequency)	Shell Repair Whorls 5-pre-terminal whorl (number of individuals/ frequency)	Aperture Repair (number of individuals/ frequency)	Multiple Repair (number of individuals/ frequency)	Total Repaired Shells (frequency)
Almgreen Cay	High coastal vegetation; unprotected	White;slight axial ribbing	65	27.53	26/.40	20/.31	8/.12	5/.07	40/.62
Crab Cay	High coastal vegetation; unprotected	White; fine to strong ribbing	100	25.72	31/.31	22/.22	5/.05	15/.15	51/.51
Crescent Pond	Inland; protected	White to brown; fine ribs	80	21.94	2/.02	12/.15	4/.05	0/0.0	18/.22
Gaulin's Cay	Marginal vegetation; unprotected	White; faint ribbing pattern	30	31.61	10/.33	5/.16	4/.13	0/0.0	19/.63
Lindsay Reef	Open terrain; low growing coastal vegetation; protected; leeside	Brown (mottled), strong ribs	69	19.12	0/0.0	1/.01	5/.07	0/0.0	6/.08
Man Head Cay	Open terrain; low growing coastal vegetation; unprotected	White; slight ribbing	111	26.35	59/.53	77/.69	20/.18	42/.37	83/.74
North Point-Bluff	Live Cerion; Open terrain; high coastal bluff; low lying vegetation; unprotected	Brown (mottled); strong ribs	101	24.21	30/.30	39/.38	2/.02	11/.11	60/.59
North Point-Leeside	Live Cerion; high coastal vegetation; adjacent to leeside beach; protected	White; slightly speckled; strong ribs	105	24.08	13/.12	19/.18	6/.06	7/.06	31/.29
Pigeon Creek	Inland; low vegetation; most protected of all sites	Brown (mottled); strong ribs	21	24.23	1/.04	3/.14	2/.09	0/0.0	6/.28
Sandy Hook	Coastal; low vegetation with palmettos; somewhat protected	Brown (mottled); strong ribs	81	21.02	1/.01	2/.02	7/.08	0/0.0	11/.13
South Barn Cay Ridge	Margins of lake; low growing vegetation; protected	C. universa-like; White, speckled with brown; thin-shelled	66	18.36	0/0.0	1/.01	0/0.0	0/0.0	1/.01
Stouts Lake	Inland; high growing vegetation; protected	Brown to white; thin with fine ribs	55	17.43	3/.05	1/.02	1/.02	0/0.0	5/.09
The Bluff	High coastal vegetation; unprotected	White with some brown morphs; strong ribs	121	27.15	5/.04	12/.10	2/.01	2/.01	23/.19
The Thumb	Open terrain; low growing coastal vegetation; unprotected	White; fine ribs	34	24.82	3/.09	5/.14	1/.03	0/0.0	9/.26

DISCUSSION

High frequencies of shell damage to *Cerion* were characteristic of the unprotected sites from the northeastern coast of San Salvador, such as the bluffs associated with Almgreen, Crab, Gaulin's and Man Head Cay. In these localities, live *Cerion* experience the full force of the easterly trade winds and major shell damage may occur in these localities from physical factors, such as wind or hurricanes. However, it would take a very strong wind to dislodge the *Cerion* at San Salvador, as they are tightly fastened to their substrates with a thick epiphragm (Walker, pers. observ.). The ribby nature of the shell may also act to reduce drag forces due to differential wind velocities and may also prevent the snail from being dislodged (e.g., the dimpled golf ball example from Vogel, 1981). But *Cerion* aren't golf balls, and this biomechanical idea has yet to be tested for ribby versus non-ribby morphs of *Cerion*.

Not all exposed sites had high frequencies of repair, as two sites from the mid-to southeastern portion of the island had moderate frequencies of shell damage. Further, two protected sites (i.e., North Point leeside, and Pigeon Creek) had moderate frequencies of shell repair suggesting that physical factors may not account for all shell damage. Almost all shell damage takes place before the secretion of the terminal lip on *Cerion*, with a minor amount of damage to the lip itself. The last secreted whorl is thin and fragile before it makes its terminal lip (Walker, pers. observation). Juvenile and adolescent *Cerion* also possess fragile body whorls, which are easily broken. Repaired peel marks as known for marine crabs, were not observed (e.g., Papp et al., 1947; Vermeij, 1982). Rather the damage to the shell appeared to be repaired ripped or crushed last whorls during various growth phases of the pre-adult *Cerion* indicating the ease at which *Cerion* can be damaged.

Woodruff (1978) has suggested that land crabs (e.g., *Gecarcinus lateralis* from Abaco Island, Bahamas) take a number of *Cerion* to their burrows and break the shells into fragments; leaving a small shell midden. However, no middens have yet been observed near crab burrows on San Salvador. A live *Gecarcinus ruricola* from San Salvador was starved for one day, and then given a selection of various sizes of *Cerion*, but did not attack the shells after three days and was released. Live *Cerion* tethered with monofilament line and placed in front of active burrows of *Gecarcinus* on Lee Stocking Island, Exuma Cays, also have not experienced any predation after two years (Walker, 1994; Walker, in prep.). Live *Cerion* left tethered in front of *Cardisoma* burrows for a week on Lee Stocking Island also were not preyed upon. The crab species in question *(Cardisoma guanhumi* and *Gecarcinus ruricola)* may be vegetarians but their biology is poorly known. It is quite possible that their diets may differ depending on habitat and locality. Walker has observed the yellow crowned night heron *(Nyctanassa violacea)* attacking terrestrial hermit crabs housed in *Cerion* or marine shells, but has not observed predation on the living snail. Woodruff (1978) also suggests rats eat *Cerion* but this has not been observed on San Salvador Island.

The higher the frequency of repair, the greater is the likelihood that selection favors the traits that protect against lethal breakage (Vermeij, 1979; Vermeij et al., 1980) and consequently, gastropods that are subjected to lethal predation would be predicted to not have a high incidence of shell repair (Vermeij, 1979). Evidence of repair should be more frequent in gastropod species with anti-predator features, such as narrow apertures, thick shell, strong sculpture, low spires, the capacity to retract the soft parts far into the shell and a thickened outer lip (e.g., Vermeij, 1974; Vermeij, 1982; Zipser and Vermeij, 1980). *Cerion* possesses two of these characteristics: the ability to retract far within the shell and a thickened outer lip. The shell thickness is relative. While most *Cerion* look robust as adults, when growing their body whorls are fragile and will break with the slightest pressure. When observed from the adult growth stage, it appears that the thickened, terminal lip would protect *Cerion* from predation and the incidence of repair is low at this stage. However, this does not explain the high frequency of shell repair on pre-adult *Cerion* (i.e., on whorls previous to the secretion of the terminal lip) from the unprotected sites. Retraction of the soft-parts into the shell may account for this observed high frequency of repair if a predator is responsible for the damage.

At the protected sites, moderate frequencies of shell repair were observed, although the *Cerion* possessed similar characteristics as those from unprotected sites, ribby, large shells with terminal lips. At Stouts Lake and South Barn Cay Ridge, *Cerion* were small, thin and possessed fine ribs and exhibited very little repair. Do these findings suggest that *Cerion* are easy to crush at Stouts Lake or at South Barn Cay Ridge, and the incidence of predation is high leaving few survivors to repair their shells? Are there few predators at these sites? Or, are *Cerion* distasteful--they certainly are to most humans (Gould, 1993; but see Gould, 1971)? We speculate that the high incidence of repair may not be due to one causal factor but indicates the degree of physical and biological complexity of the habitat. At the unprotected sites, predation and physical factors (winds, storms) both may contribute to the high incidence of shell damage. Physical factors that affect shell breakage would be predicted to be negligible at protected localities, with the incidence of shell repair most likely attributed to biological factors. The incidence of shell repair can be traced in the fossil record of *Cerion* (Walker, 1994; Walker and Hearty, 1993), thus further refining paleoecological and taphonomic studies of *Cerion* from Quaternary deposits in the Bahamas.

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