

Selection for Prey Shell Thickness by the Naticid Gastropod *Euspira lewisii* (Naticidae) on the Bivalve *Protothaca staminea* (Veneridae)

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Abstract. Previous ecological and paleobiological studies of naticid gastropods have shown that naticids are energy maximizers, choosing prey with the lowest ratio of drilling time cost (determined by prey shell thickness) to energy return benefit (determined by prey internal volume). We tested if naticids select for prey shell thickness by offering two morphs of a common prey species and determining whether the thinner-shelled morphs were more likely to be drilled.

Laboratory choice experiments in which naticid predators *Euspira lewisii* Gould, 1847 were offered thick- and thin-shelled morphs of the bivalve *Protothaca staminea* Conrad, 1837 revealed that the thinner-shelled prey were drilled significantly more often than the thicker-shelled prey, resulting in positive selection differentials for shell thickness. Multivariate logistic regression showed that, out of the five prey shell variables measured, only prey shell thickness had a significant effect on survival. The mechanism for naticids to select for thickness in prey shells is not known and future laboratory and field work examining naticid prey selection may indicate how this occurs. Future work should also include similar experimentation with a wider variety of prey and a larger range of predator size-classes.

Our investigation has important implications for evolutionary and ecological studies involving this predator taxon and supports previous research showing that naticids follow the energy maximization principle.

INTRODUCTION

Naticids (family Naticidae) are sand-dwelling carnivorous snails that use a radula to drill into the shells of their prey. The uniquely beveled hole drilled by naticids allows for both behavioral and morphological studies on topics such as co-evolution (Kelley, 1992), escalation (Kelley & Hansen, 1996) and prey selection (e.g., Franz (1977); Kelley (1988, 1991); Kitchell et al. (1981)). Previous experimentation established that naticids are selective predators that follow the energy maximization principal, choosing prey with the lowest cost-to-benefit ratio (Kitchell et al., 1981). For most bivalve prey species, this ratio is directly proportional to the ratio of shell thickness-to-internal shell volume (Kelley, 1989).

Many studies have shown prey shell thickness to be a significant factor affecting predation (see Vermeij (1987) for a review). Kelley (1989) found that prey shells had thickened over evolutionary time while naticid predation rates had decreased; from this she

concluded that naticids affected the thickness of five prey species (but see Grey et al. (2006)). This conclusion is partially reliant on the untested assumption that naticids select for prey shell thickness. If naticids place significant selection pressure on one or more heritable prey characters (e.g., shell thickness), then naticids may affect the morphology of that prey species. Selection on shell thickness has been shown in other tactile predator species including crabs (Boulding, 1984) and lobsters (Griffiths & Seiderer, 1980).

Boggs et al. (1984) mechanically thinned the shells of *Mercenaria mercenaria* Linnaeus, 1758 and found that the naticid *Neverita (Polinices) duplicata* Say, 1822 did not preferentially choose the thinner- or thicker-shelled prey. This experiment indicated that naticids are not able to directly select for shell thickness when offered a novel prey type. Their study did not use a common prey species of naticids and the mechanical alteration of prey shells may have produced results unlikely to be reproduced in nature. For instance, small cracks may

have formed during alteration and weakened the shell structure.

We examined prey selection of naticid gastropods and aimed to determine if naticids are able to select for shell thickness. If so, they should follow the energy maximization principle of Kitchell et al. (1981) and would choose thinner-shelled over thicker-shelled prey, and thickness would be a significant factor to survival (i.e., thicker-shelled prey are less likely to be drilled). Measures of the intensity and direction of selection on traits, such as selection differentials and gradients, should be positive, indicating selection for thinner shells. Selection differentials and gradients are used to measure selection on quantitative traits and are explained further in the Methods.

METHODS

With SCUBA we collected six naticids – *Euspira lewisii* Gould, 1847 – with maximum shell dimensions ranging from 66 to 75 mm, from Trevor Channel near Bamfield Marine Science Centre in British Columbia. We collected native littleneck clams – *Protothaca staminea* Conrad, 1837 – ranging in length from 31.2 to 60.0 mm from the same region. We chose *P. staminea* as the prey species because they are a common prey item of *E. lewisii* and because there are naturally occurring thick-shelled and thin-shelled populations in the area. The thin-shelled population occurred in a lagoon-like setting where their smaller shell thickness-to-length ratios have been attributed to faster growth rates (Boulding, 1983). While shell thickness can be affected by growth rate, it is a heritable quantitative trait in other molluscs (Boulding & Hay, 1993) and is also likely heritable in bivalves.

The naticid predators and bivalve prey were maintained at Bamfield Marine Science Centre in flow-through, unfiltered seawater (10–11°C; 30–32 o/oo) for a period of two weeks prior to commencement of the selection experiment to ensure that they became accustomed to the laboratory habitat. Each snail was housed in a glass aquarium (tank) containing fine sand obtained from their natural habitat; the sand depth was 10 cm.

We measured length, width and inflation with digital calipers on *P. staminea* shells prior to feeding trials. A representative internal volume was calculated as the product of those three variables: previous work (Grey, 2001) showed significant correlation between this product and actual internal volume determined by filling the shells with fine sand. For each feeding trial, we placed two clams from the thin-shelled population and two from the thick-shelled population in random positions in the tank. Prey shell lengths within trials were similar, with standard deviations of less than 1 mm, to ensure that the snails were not selecting

for shell length as has been shown in previous studies (e.g., Broom, 1982; Kitchell et al., 1981; Peitso et al., 1994).

Each trial ended when half (two) of the supplied clams had been drilled. We stopped the trials without disturbing the predation behavior: after one week we determined the position of the snail in each tank through visual clues if possible or lightly by hand if not. Once the snail was located, we gently searched the sand around the snail for eaten clams; the location of the eaten clams was usually easy to determine because they were at least partly visible above the sand. If no eaten clams were found then we checked the tank again after a couple of days. If two eaten clams were found the trial was stopped. If only one eaten clam and two uneaten clams were found then we assumed the snail was in the process of drilling the other, which was taken from the snail and became the second selected individual. In all such cases this second clam had been completely drilled and was being eaten. Hence, any drilling was only disturbed once the snail had already made its first two choices. No incomplete boreholes were found in the trials, showing that no clams were abandoned by the snail.

After each trial, uneaten clams were emptied and the thickness at the umbo (the drill hole site for all eaten clams in our trials) was measured on all clams (eaten or not). There were three to five feeding trials for each naticid snail. All measurements were entered into a customized database using a data acquisition program written in FoxPro. An Analysis of Variance was performed to ascertain if there were significant differences between the thicknesses of the shells that were and were not drilled.

Standardized selection differentials and selection gradients indicate the direction and strength of selection: the magnitudes of these quantities correspond to the strengths whereas the signs of these quantities correspond to the directions (reviewed by Endler (1986)). A positive selection differential shows that bivalves with thicker shells are more likely to survive naticid predation than those with thinner shells. The selection differential is the difference between trait means before and after selection. We calculated selection differentials for each snail using

$$S = \frac{\mu_x - \mu_z}{\sigma_z}$$

where μ_x represents the average shell thickness of the two surviving bivalves after selection, μ_z is the average thickness of the four bivalves before selection and σ_z is the standard deviation of the shell thickness before selection (Endler, 1986).

A univariate linear selection gradient is the slope of a least-squares regression line with relative fitness as the dependent variable and the trait value as the in-

Table 1

Descriptive Statistics and Analysis of Variance comparing shell thickness in the thin and thick-shelled populations of *Protothaca staminea*.

Groups	<i>n</i>	Mean	Variance
Thin-shelled population	42	1.14	0.300
Thick-shelled population	42	1.27	0.316

Source of Variation	SS	df	MS	F	P-value
Between groups	0.36	1	0.36	3.96	0.05
Within groups	7.49	82	0.09		
Total	7.85	83			

dependent variable. In our study, fitness is either zero (eaten) or one (not eaten) so a linear regression is not the most appropriate statistical method. Furthermore, phenotypic correlations among traits are very common and natural selection often acts on many characters simultaneously (Lande & Arnold, 1983) and, hence, a multivariate analysis is used. A multivariate logistic regression calculates a multivariate selection gradient (Janzen & Stern, 1998), which is useful for determining which traits in a correlated group (in this case, thickness, length, width, inflation and volume) are the focus of selection. A multivariate logistic regression was performed to estimate the multivariate selection gradient for all trials combined; this method has been applied to naticid gastropod predation in a previous study (Grey et al., 2006). The model for logistic regression,

$$W(z) = \frac{e^{\alpha_0 + \alpha^T z}}{1 + e^{\alpha_0 + \alpha^T z}}$$

relates the survival probability (*W*) for an individual to that individual's trait values (*z*). The fitness data (*w*₁, *w*₂, ..., *w*_{*m*}) are the selection outcomes for each of *m* individuals (*w*_{*i*} = 1 for survival and *w*_{*i*} = 0 for death by drilling). *W*(*z*) is the survival probability for a set of *n* traits, *z* = (*z*₁, ..., *z*_{*n*}). $\alpha = (\alpha_1, \alpha_2, \dots, \alpha_n)$ contains the logistic regression coefficients for the *n* traits and α_0 is an intercept (Janzen & Stern, 1998). The prey trait

variables were thickness, length, width, inflation and volume. Logistic regression coefficients were converted into selection gradients, β_{avggrad} , using the methods described in Janzen & Stern (1998). The resulting values indicate the strength of selection for each trait. These calculations were performed using a logistic regression program, LogReg, written by P. Lelièvre in Matlab.

RESULTS AND DISCUSSION

An Analysis of Variance revealed significant thickness differences (*p* = 0.05; Table 1) between the thin- and thick-shelled morphs of *P. staminea*. Table 2 shows a summary of the choices made by the six naticids for each trial; the naticids displayed a preference for thinner-shelled prey: an Analysis of Variance indicated there were significant differences (*p* < 0.001; Table 3) between the thickness of shells that were eaten by naticids and those that were not. Boulding (1984) found a similar result for rock crabs – *Cancer productus* Randall, 1839 – preying on thin- and thick-shelled *P. staminea*.

With the exception of two trials, selection differentials were all positive and ranged from –0.39 to 0.83, with a mean of 0.54 for all trials (Figure 1). The multivariate logistic regression established that length, width, inflation and volume were not significant factors to prey survival; thickness was the only variable

Table 2

Bivalve prey drilled by *Euspira lewisii* in experimental feeding trials. The snails were offered 2 thin- and 2 thick-shelled morphs of *Protothaca staminea* and the trials ended when half of the prey had been eaten.

Naticid	Prey Choice for Each Trial					Total
	Trial 1	Trial 2	Trial 3	Trial 4	Trial 5	
1 (66 mm)	2 thin	1 thin, 1 thick	1 thin, 1 thick	1 thin, 1 thick	1 thin, 1 thick	6 thin, 4 thick
2 (67 mm)	1 thin, 1 thick	1 thin, 1 thick	2 thin	—	—	4 thin, 2 thick
3 (70 mm)	2 thin	2 thin	2 thin	—	—	6 thin, 0 thick
4 (71 mm)	2 thin	2 thin	2 thin	—	—	6 thin, 0 thick
5 (72 mm)	2 thin	2 thin	2 thin	2 thin	—	8 thin, 0 thick
6 (75 mm)	2 thin	2 thin	1 thin, 1 thick	—	—	5 thin, 1 thick
Total	11 thin, 1 thick	10 thin, 2 thick	10 thin, 2 thick	3 thin, 1 thick	1 thin, 1 thick	35 thin, 7 thick

Table 3

Analysis of Variance comparing *Protothaca staminea* shells that were drilled by *Euspira lewisii* versus those that were not drilled.

Groups	<i>n</i>	Mean	Variance
Drilled	42	1.07	0.224
Not drilled	42	1.35	0.316

Source of Variation	SS	df	MS	F	P-value
Between Groups	1.67	1	1.67	22.26	9.9×10^{-6}
Within Groups	6.18	82	0.08		
Total	7.85	83			

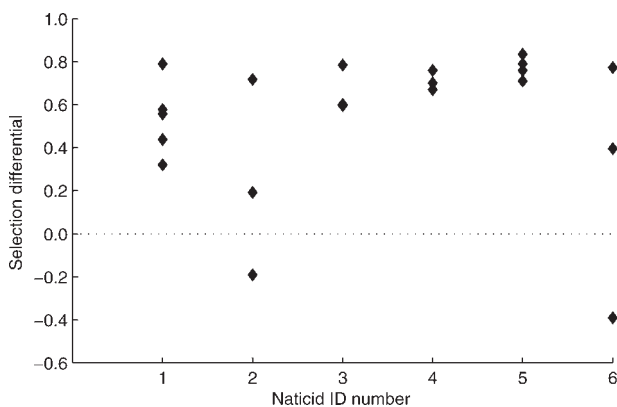


Figure 1. Selection differentials calculated for each trial ($n = 21$) plotted against predator identification number. The corresponding shell lengths are as follows: 1 = 66 mm; 2 = 67 mm; 3 = 70 mm; 4 = 71 mm; 5 = 72 mm; 6 = 75 mm.

with a significant effect on prey survival ($p < 0.001$; Table 4). The resulting selection gradient (β_{avggrad}) for thickness was large and positive while the selection gradients for all other traits were not significant (Table 4). These results are consistent with the findings of Kitchell et al. (1981) that naticids select prey on the basis of the ratio of thickness-to-internal volume (cost-to-benefit). Many studies following Kitchell et al. (1981) using fossil assemblages also empirically support this cost-to-benefit relationship (Kelley, 1988,

1989, 1991), implying that naticids select for thinner shells.

It is not surprising that prey shell length and its correlates (width, inflation and volume; Figure 2) were not significant in the model (using $\alpha = 0.05$; see Table 4) because we attempted to hold prey shell length constant within trials. In a natural setting with many prey choices we expect they might have a significant effect on survival, at least for immobile epifaunal prey. Infaunal or mobile prey may rely on behavioral strategies for avoiding predation (e.g., escape strategies or burying deeper in the sediment).

In this experiment the finer points of the naticids' feeding behavior were not easily observable and it was not possible to determine how they chose the thinner-shelled prey items or if they were aware of all choices before commencing drilling. The mechanism for which naticids are able to select prey with thin shells is still unclear. In the wild, it is possible that the increased handling time required to drill thicker shells makes it more probable that the naticids will abandon those shells due to some disturbance. There may also be a correlated trait other than those included in this study that acts as a tactile clue for prey shell thickness. For example, Boulding (1984) found that the valves of thin-shelled morphs of *P. staminea* connected at a smaller angle at the ventral margin compared to the thick-shelled morphs. Also, different hardnesses of the thick-

Table 4

Overall multivariate logistic regression results: β is the logistic regression output, β_{avggrad} is the transformed logistic regression coefficient and SE is the standard error; $n = 84$. Analyses used bivalve prey fitness (drilled versus undrilled) as the dependent variable and thickness, length, width, inflation and volume as the independent variables.

Variable	β	β_{avggrad}	SE	P-value
Thickness	13.2	1.70	3.43	0.00
Length	-0.80	-0.15	0.40	0.14
Width	0.55	0.04	3.89	0.69
Inflation	1.10	0.11	0.33	0.10
Volume	-0.00	-0.00	0.6	0.56

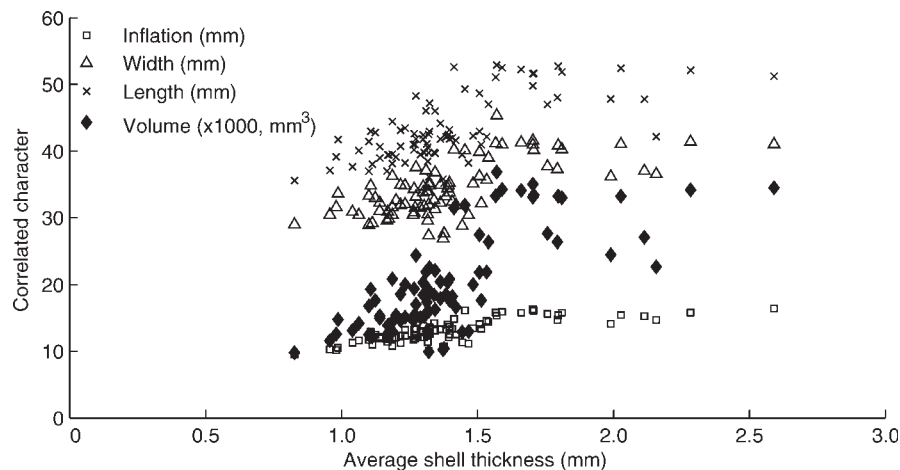


Figure 2. Relationships between prey shell thickness and inflation ($y = 4.39x + 6.95$; $R^2 = 0.59$; $p < 0.001$); width ($y = 8.79x + 22.04$; $R^2 = 0.44$; $p < 0.001$); length ($y = 10.98x + 27.8$; $R^2 = 0.45$; $p < 0.001$); and volume ($y = 17.77x - 4.69$; $R^2 = 0.54$; $p < 0.001$) for *P. staminea*. $N = 84$ for all correlations.

and thin-shelled clams may provide a tactile clue to naticid predators. Another possibility for the selection mechanism is a variation of prey behavior between the thick- and thin-shelled clams: for example, they may have had different feeding strategies and such behavior may have affected naticid prey choice.

We have shown that naticids show preference towards thinner shells over thicker ones in a controlled laboratory experiment with a common, unaltered prey species. This research has important implications for evolutionary and ecological studies involving naticids and on prey selection in general. Future experimentation with a larger variety of size classes, inclusion of more shell characters correlated to thickness (such as the angle at the ventral margin and live weight), and close observation of naticid predation behavior (a difficult task because they are infaunal) may reveal additional information on naticid prey selection. Furthermore, comparison of thicknesses for shells with incomplete boreholes versus those completely drilled may determine whether or not our results are reproducible in the wild.

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