

JEM 00847

## Stereotypy, ontogeny, and heritability of drill site selection in thaidid gastropods

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(Received 11 August 1986; revision received 1 December 1986; accepted 9 December 1986)

**Abstract:** Laboratory observations on the feeding behavior of four species of thaidid gastropods (Muricacea), when fed on the intertidal barnacle *Balanus glandula* (Darwin), revealed two interesting patterns. First, large individuals of *Thais* (or *Nucella*) *emarginata* (Deshayes) (> 15 mm shell length) exhibited remarkably little variation in the locations at which they drilled barnacles, either among individual snails, among populations along a wave exposure gradient ( $\approx 5$  km), or among populations along the Pacific coast of North America ( $\approx 3000$  km). The results of laboratory crosses suggested that the small differences which did exist between populations from southeast Alaska (U.S.A.) and Vancouver Island, British Columbia (Canada) were genetically determined.

A second pattern of interest was an ontogenetic shift in the preferred location of drilling in all four species of *Thais* examined (*T. canaliculata* (Duclos), *T. emarginata*, *T. lamellosa* (Gmelin), and *T. lima* (Gmelin)): larger snails drilled much more frequently in the opercular region and, concomitantly, more frequently at the occludent margins of the scutal plates. The ontogenetic shift in these snails appeared to be primarily genetically predetermined rather than learned, since individuals of *T. emarginata* grown from one size class to the next on mussels (*Mytilus edulis* L.) did not differ greatly in their selection of drilling locations on *Balanus glandula* from those grown similarly on barnacles.

**Key words:** Muricacea; Feeding behavior; Development; Barnacle; Variation; Predation

### INTRODUCTION

Behavioral traits are generally assumed to be more labile evolutionarily than physiological or morphological ones. One would thus expect behavioral traits to exhibit measurable differences among distant populations in species with large geographic ranges and little gene flow due either to chance or to differences in selection regime on these large (> 1000 km) geographic scales. In addition, because of the frequently observed changes in feeding behavior with increased experience in predatory marine invertebrates (Willows, 1973; Berg, 1976, 1978; Hughes, 1980), learning would seem to be the most likely explanation for ontogenetic changes in feeding behavior on a single species of prey. We present evidence from laboratory observations which suggest that

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neither of the above expectations is borne out for the selection of attack locations on barnacle shells by thaidid gastropods.

Thaidid gastropods are common predators of rocky intertidal and shallow subtidal barnacles and mussels along the northern Pacific coast of North America (Ricketts *et al.*, 1968; Carefoot, 1977). They attack prey principally by drilling through the shell. Carriker & van Zandt (1972) have thoroughly described the drilling process, which involves the repeated, cyclical application of the accessory boring organ to dissolve away the organic matrix of the prey shell, and the radula to remove exposed calcium carbonate crystals, until the shell is penetrated. As emphasized elsewhere (Palmer, 1982), both the long duration of this process (as long as several days for very large prey), and the fine positional precision needed to drill through as little shell material as possible, may place a high premium on the ability to select the least time consuming drill location.

Locations of drill sites have been examined for fossil (Reyment, 1967; Carriker & Yochelson, 1968, Sohl, 1969; Adegoke & Tevesz, 1974; Berg & Nishenko, 1975; Dudley & Vermeij, 1978) and recent (Tanaka, 1950; Radwin & Wells, 1968; Berg & Porter, 1974; Menge, 1974; Carefoot, 1977; Barnett, 1979; Vermeij, 1980; Boggs *et al.*, 1984) gastropods on a variety of prey types. In an earlier study (Palmer, 1982), *Thais* were found to drill preferentially at the margins of parietal (lateral) skeletal plates on barnacles, where there is a region of overlap between the thin ala and radius of adjacent plates. Because thaidids produce a neurotoxic salivary secretion (Huang, 1972), they may only need to penetrate to the space between these overlapping plates, and then feed through the gaping opercular plates once the toxin has taken effect, thus substantially accelerating the feeding process.

Kohn (1983, p. 51) has noted that all studies to date had indicated that juvenile gastropods "are competent to feed on the same types of food and in the same manner as adults". Many gastropods are also capable of learning both how to distinguish among and how to attack prey (Willows, 1973). Learning in thaidid prosobranchs was first suggested by Fischer-Piette (1935), who observed that *Purpura* (= *Thais*) *lapillus*, when confronted with an unfamiliar prey – a bed of mussels in an area where they had not formerly occurred – could sometimes be found drilling empty, gaping mussel shells, even from the inside out. The incidence of these 'mistakes' declined over time as snails supposedly learned to drill only living mussels. Morgan (1972) showed that *Thais lapillus* were able to reduce handling time as they gained experience attacking mussels (*Mytilus edulis*). Palmer (1982) suggested that *Thais* species might also learn to attack barnacles at the sutures between skeletal plates.

## METHODS

We collected data on the locations of attack for four species of *Thais* (or *Nucella*) occurring on the northern Pacific coast of North America, *T. canaliculata* (Duclos),

*T. emarginata* (Deshayes), *T. lamellosa* (Gmelin), and *T. lima* (Gmelin), feeding on the acorn barnacle *Balanus glandula* (Darwin). *Thais lima* were collected at Torch Bay, Alaska (58° 15' N: 136° 50' W). All *T. canaliculata* and *T. lamellosa* were collected intertidally near the Bamfield Marine Station on Barkley Sound, Vancouver Island (48° 50' N: 125° 10' W). *Thais emarginata* were collected from Santa Barbara, California (34° 25' N: 119° 50' W); San Juan Island, Washington (48° 35' N: 123° 05' W); Torch Bay; and from a number of locations along an exposure gradient in Barkley Sound, including (from exposed to protected) Execution Rock (48° 49' 30" N: 125° 09' 30" W), Nudibranch Point (48° 49' 10" N: 125° 09' 50" W), Wizard Island (48° 51' 40" N: 125° 09' 10" W), the leeward side of Ohiat Island (48° 51' 30" N: 125° 10' 40" W), the leeward side of Kirby Point (48° 50' 55" N: 125° 12' 00" W), and the Ross Islets (48° 52' 30" N: 125° 09' 20" W). Except for *T. canaliculata* and those *T. emarginata* collected directly from the field along the exposure gradient in Barkley Sound, and, in contrast to Palmer (1982), all snails from which feeding observations were taken had been raised from egg capsules in the laboratory.

*Thais* were held in cages (usually 5 to a cage, with two exceptions: 'small' snails of all species, and large *T. emarginata* held as individuals) which were continuously immersed in flow-through sea-water aquaria. Snail shell length, from apex to tip of siphonal canal, was measured to the nearest 0.1 mm with Vernier calipers. For analysis, snails were grouped into three size categories: small (4.0–7.9 mm), medium (8.0–14.9 mm), and large (> 14.9 mm).

*Balanus glandula*, provided on small stones in the cages, were removed at various intervals and examined for evidence of drilling. Drill marks left by snails were often complete holes through plates, but more commonly they were ovoid gaps between plates. Attacks by small snails on small barnacles were often observed as shallow circular depressions in the shell. No distinction was made between complete holes through which the snail might have fed, and holes which seemed barely to penetrate to tissue, though the latter seemed to be more common. For each drill mark, its exact location on the barnacle shell was noted, and the antero-posterior opercular diameter of the barnacle was measured to the nearest 0.1 mm (using Vernier calipers or an ocular micrometer).

To determine if small apparent differences in location of attack between two geographically distant populations were genetically determined, six breeding pairs of *Thais emarginata* were established with one parent from Torch Bay AK and the other from Wizard Island BC (see Palmer (1984b) for details of the breeding protocol). The attack frequencies of two size classes of the resulting hybrid offspring were compared against those from comparable size classes of offspring from within-population crosses.

To test the effect of prior feeding experience on drill site selection, two discrete size classes of *Thais emarginata* were deprived of barnacle prey and fed small mussels (*Mytilus edulis* L., 15–25 mm shell length) for a period of 14 wk. A total of 41 snails were used, 35 'small' and six 'medium'; mortality over the course of the experiment reduced these groups to 13 and five individuals, respectively. After the 14 wk of mussel diet, both

groups had grown into the next larger size class ('medium' and 'large', respectively). Barnacles were then reintroduced into the cages, and attack locations were observed.

To estimate the change in barnacle shell thickness with size, 53 *Balanus glandula* ranging in size from 1.3 to 6.4 mm opercular diameter were killed and their shell plates disarticulated in a dilute solution of sodium hypochlorite. The thickness of lateral wall plates and scutal plates was measured in the center of each plate. Since tergal plates were rarely observed to be attacked (probably because they are held against the inner surface of the carinal and carinolateral plates), their thicknesses were not measured. All measures were made using dial calipers to 0.01 mm.

Frequencies of attack at various sites on the barnacle skeleton were categorized in a manner similar to Palmer (1982) by assigning attacks to one of two attack regions (opercular or parietal (= lateral)) and one of two attack sites within each region (sutural or through). Attacks within the 'opercular region' (on any of the tergal or scutal plates) were divided into 'suture' attacks (on the margin of one plate, or between two plates) and attacks 'through' the middle of a plate. Attacks within the 'parietal region' (associated with the carinal, carinolateral, lateral, or rostral plates) were also divided into 'suture' attacks (including attacks at the junction of any plate and the basis) and attacks 'through' plates. Examples of actual attack locations for *T. emarginata* are illustrated in Fig. 1.

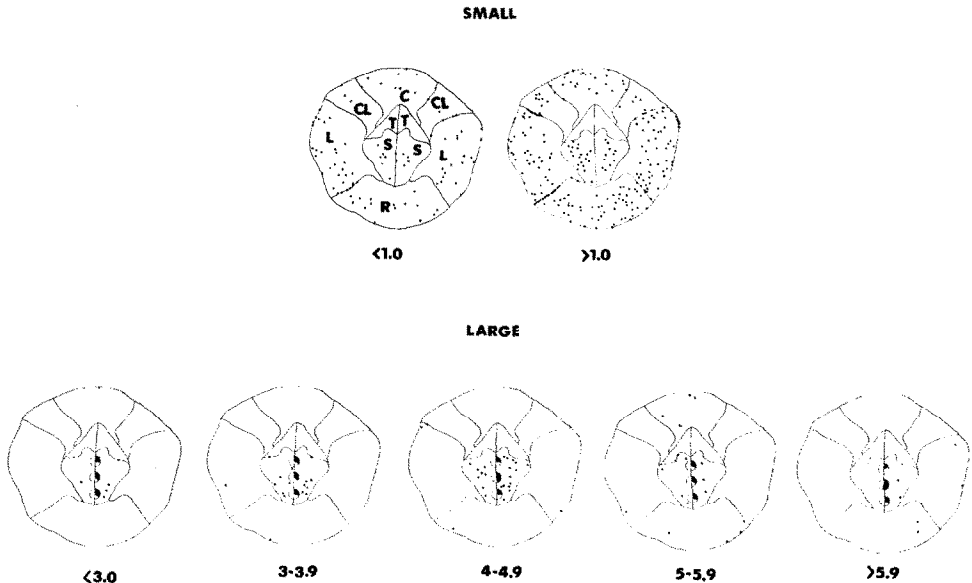


Fig. 1. Examples of attack locations for small (4.0–7.9 mm) and large (> 14.9 mm) *Thais emarginata* from Bamfield, British Columbia (sample sizes and actual proportions given in Fig. 6), plotted on hypothetical barnacle shells. Barnacle opercular diameter (in mm) is given below each plot. Where many attacks occurred along the median opercular suture, pie diagrams indicate the proportion of all attacks for any one plot which occurred along the anterior, middle, or posterior portion of the suture. C, carinal plate; CL, carinolateral plates; L, lateral plates; R, rostral plate; S, scutal plates; T, tergal plates.

Patterns of attack were analyzed by fitting a log-linear hierarchical model to a multi-way frequency table for particular subsets of observations (BMDP 4F; Dixon, 1983). This analysis describes relationships among factors of the table (e.g. snail size, barnacle size, region and site of attack, etc.), and determines which factors, as well as which interactions among these factors, contribute significantly to variation among the observed cell frequencies of the table (similar to an analysis of variance). To avoid large numbers of empty cells in the multi-way contingency tables, it was frequently necessary to pool observations across some barnacle sizes.

The analysis uses two Chi-square tests – of partial and marginal association – to screen out the effects of interest. Tests of partial association test the significance of the difference between a model including all effects of order  $k$  (main effects,  $k = 1$ ; 2-way interactions,  $k = 2$ ; etc.), and the model which includes all effects of order  $k$  except the effect being tested. Tests of marginal association test the significance of the difference between a model which includes a single effect of order  $k$ , and the model which includes all effects of order  $k-1$  implicit in the single effect. The two tests are equivalent for first-order effects (main effects). All those effects for which both tests suggest significant differences between the observed and expected values in the multi-way contingency table are grouped into a preliminary model (the two tests do not always yield identical results). The remaining effects are then screened and added to the preliminary model in a stepwise fashion to determine which combination of effects (the “best model”) can account most parsimoniously (with the fewest terms) for the observed cell frequencies.

As in analysis of variance, when interactions of order  $k$  are statistically significant, the statistical significance of all main effects or interactions of lower order wholly included within that interaction are generally not of interest; they are also not indicated below as components of the ‘best model’. For example, if the three-way interaction SRL (attack site  $\times$  attack region  $\times$  snail length) is statistically significant, then any conclusion about the biological significance of the two-way interaction SR (attack site  $\times$  attack region) would have to be qualified by the value of  $L$  (snail length).

Another feature of such analyses is that some effects in the ‘best models’, though they contribute to the fit of the models, are not relevant to the discussion of attack behavior. For example, in many of the analyses below the interaction term BL (barnacle size  $\times$  snail size) is included in the ‘best model’. However, we were only interested in examining those factors influencing attack site (S) or attack region (R). Hence the fact that small snails attacked smaller barnacles more frequently than larger ones while the reverse was true for large snails, although of interest in terms of the biology of feeding in these snails, is not relevant to a discussion of choices of attack location. See Brown (1976) for a more detailed discussion of multi-way contingency table analyses.

Patterns of variation in barnacle skeletal plate thickness as a function of opercular diameter were analyzed by analysis of covariance (ANCOVA) (BMDP 1V; Dixon, 1983).

## RESULTS

To facilitate presentation, we use the following abbreviations for 'effects' in the multi-way contingency tables; their interpretations if statistically significant would be (interaction effects included here only for those that were significant and relevant):

*Main effects*: frequencies of attack varied among:

S: attack sites (suture vs. through);

R: attack regions (opercular vs. parietal);

B: barnacle sizes;

L: snail sizes (shell length);

I: individual snails;

C: collection sites along a wave exposure gradient;

G: geographic regions along the Pacific coast;

P: offspring from different parents (pure vs. hybrid); or

T: experimental treatments (grown on mussels or grown on barnacles).

*Two-way interaction effects*: observed frequencies at an attack site (S) or attack region (R) depended on:

SR: each other;

SB, RB: barnacle size;

SL, RL: snail size;

SG, RG: geographic region along Pacific coast;

SP, RP: history of parents; or

ST, RT: experimental treatment

*Three-way interaction effects*: the dependence of attack site frequency on attack region (SR) or the dependence of attack region on barnacle size (RB) varied with:

SRB: barnacle size;

SRL, RBL: snail size; or

SRG: geographic region along Pacific coast.

#### VARIATION AMONG INDIVIDUALS, LOCAL POPULATIONS, AND DISTANT POPULATIONS

For all 17 large *Thais emarginata* on which individual observations were made, the only statistically significant pattern of variation was a dependence of attack site on attack region (SR; Table Ia, Fig. 2): the proportion of sutural attacks on *Balanus glandula* was consistently higher in the opercular region than the parietal region. This same dependence was also observed to be significant for groups of large individuals both from along a wave exposure gradient (SR; Table Ib, Fig. 3) and from different geographic regions along the Pacific coast (SR; Table Ic, Fig. 4), although the extent of this dependence varied along the coast (SRG; Table Ic). In addition, when considering all

TABLE I

Variation in frequencies of attack by large (> 15 mm) *Thais emarginata* at various locations on the shell of *Balanus glandula*: (a) among individual snails, (b) among snails from six sites along a wave exposure gradient, (c) among snails from different populations along the Pacific coast of North America (Torch Bay, Alaska; Bamfield, British Columbia; San Juan Island, Washington; Santa Barbara, California).

Statistical significance of effect	Comparison					
	(a) Among individuals		(b) Along wave-exposure gradient		(c) Along Pacific coast	
	Partial	Marginal	Partial	Marginal	Partial	Marginal
$P < 0.05$					RG	SRG
$P < 0.01$	B				RB	BG
$P < 0.001$	S, R, SR	SR	S, R, B, C, SR	SR	S, R, B, G, SR, SG, BG	SR, SG, RB
Best model:	SR*, B		SR*, B, C		SRG*, RB*, BG	

Table entries are codes for effects (either main effects or interactions from a multiway contingency table analysis); they are categorized by type of Chi-square test (partial, marginal) and by probability that a particular effect is statistically significant. Effects not included in the table were not significant at the 0.05 level. Significance levels are derived from fitting a hierarchical log-linear model to frequencies of attack. Factors examined: attack site (S), attack region (R), barnacle size (B), snail shell length (L), individual snail (I), collection site along wave exposure gradient (C), and geographic location along the Pacific Coast (G). Data are from Figs. 2-4. Effects without asterisks in the best model are not relevant. See text for an explanation of the analysis and for an interpretation of specific interaction terms.

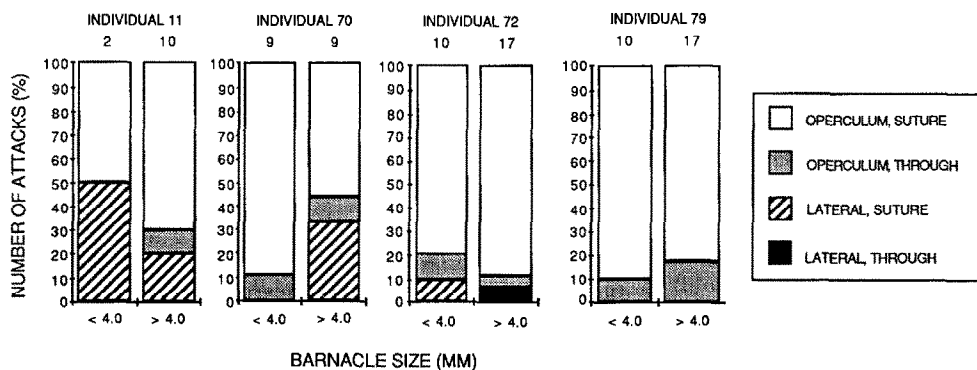


Fig. 2. Percent of attacks at different locations on the shell of *Balanus glandula* by different individual adult *Thais emarginata*. Each column represents a different size class of barnacles. 'Opercular' attacks refer to any attacks associated with the opercular plates and 'lateral' attacks refer to attacks at the parietal plates. Attacks within either of these regions were either at sutures or through the skeletal plates. Numbers above each column indicate the number of observations from which the percentages were calculated. Only the data for four individuals are presented; data for 17 individuals were collected and analyzed.

populations along the Pacific coast, the frequency of attack in a particular region depended on barnacle size (RB; Table Ic): larger snails attacked large *B. glandula* more frequently in the parietal region (most noticeable in Fig. 4b).

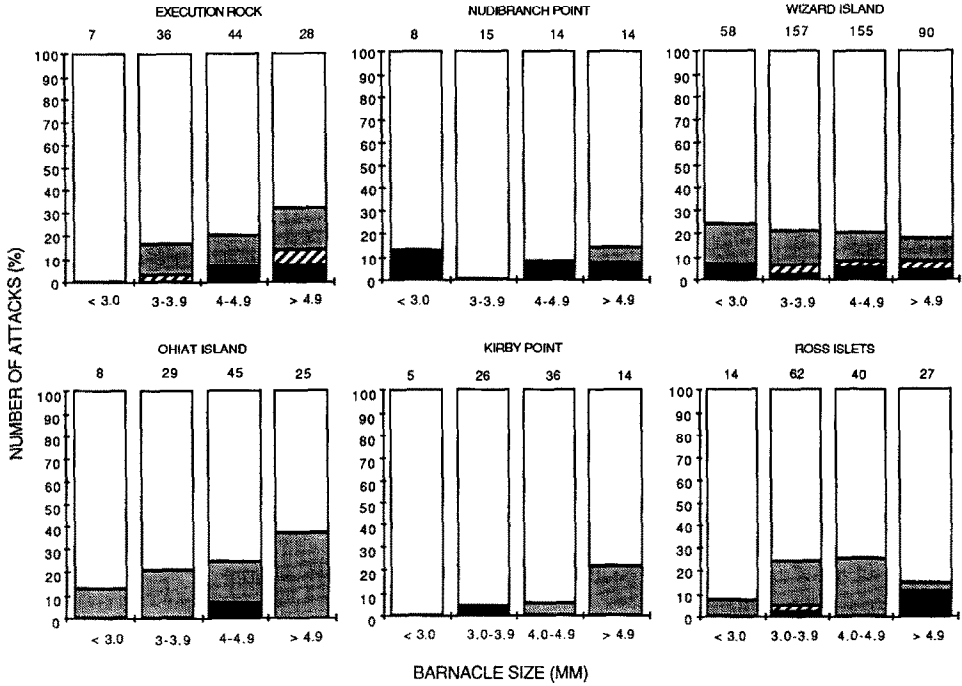


Fig. 3. Percent of attacks at different locations on the shell of *Balanus glandula* by adult *Thais emarginata* from different populations along a wave exposure gradient (from most exposed, Execution Rock, to most protected, Ross Islets) in Barkley Sound, Vancouver Island, Canada. Representations and shading of bars as in Fig. 2.

Large *Thais emarginata* did not differ significantly in attack behavior among different local populations from Barkley Sound (SC, RC, SRC not significant; Table Ib, Fig. 3). In addition, a limited comparison of medium-sized and large snails from two Barkley Sound populations (Nudibranch Point and Wizard Island) revealed no differences in attack behavior between the two size categories (not presented). The attack site differences among adult snails did not vary directly with the degree of wave exposure. The lowest frequency of opercular attacks at suture (0.776) was observed in a group from a moderately exposed shore (Ohiat Island), while snails from the most protected shore (Ross Islets) had an intermediate frequency of attacks at suture (0.790). The highest frequencies of such attacks (0.926, 0.902) were observed in groups from protected (Kirby Point) and moderately exposed (Nudibranch Point) shores, respectively.

A rather striking feature of these data was the relative lack of variation among large

individuals at any scale examined. None of the interactions of attack site or attack region with individual snails (SI, RI, SRI), or with collection site along a wave exposure gradient (SC, RC, SRC), were significant (Tables Ia and b). Virtually all individuals or

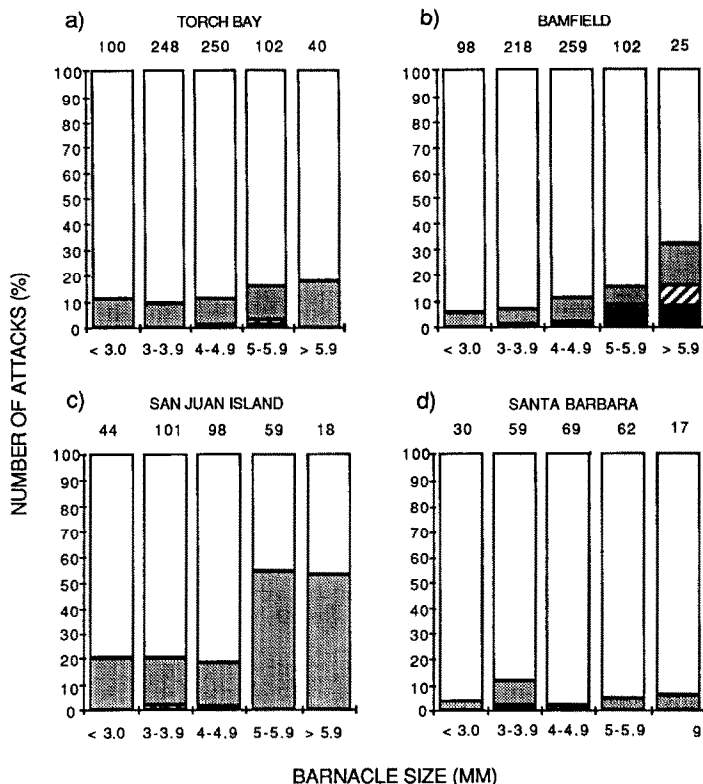


Fig. 4. Percent of attacks at different locations on the shell of *Balanus glandula* by adult *Thais emarginata* from different populations along the northern Pacific coast of North America. (a) Torch Bay, Alaska; (b) Bamfield, British Columbia; (c) San Juan Island, Washington; (d) Santa Barbara, California. Representations and shading of bars as in Fig. 2.

populations exhibited  $> 75\%$  attacks at the suture between the scutal plates (open portions of bars, Figs. 2 and 3). Only on a large geographic scale did significant variation in attack site or region appear (SRG; Table Ic): animals from the vicinity of Bamfield, BC exhibited an elevated frequency of drilling in the parietal region (Fig. 4b) while those from Santa Barbara, CA [which may be a separate species (ARP, unpubl. data)] exhibited virtually no parietal attacks (Fig. 4d). Even though significant variation existed, however, attacks at suture between the scutal plates still generally exceeded  $75\%$ , except for the largest barnacles ( $> 5$  mm opercular diameter).

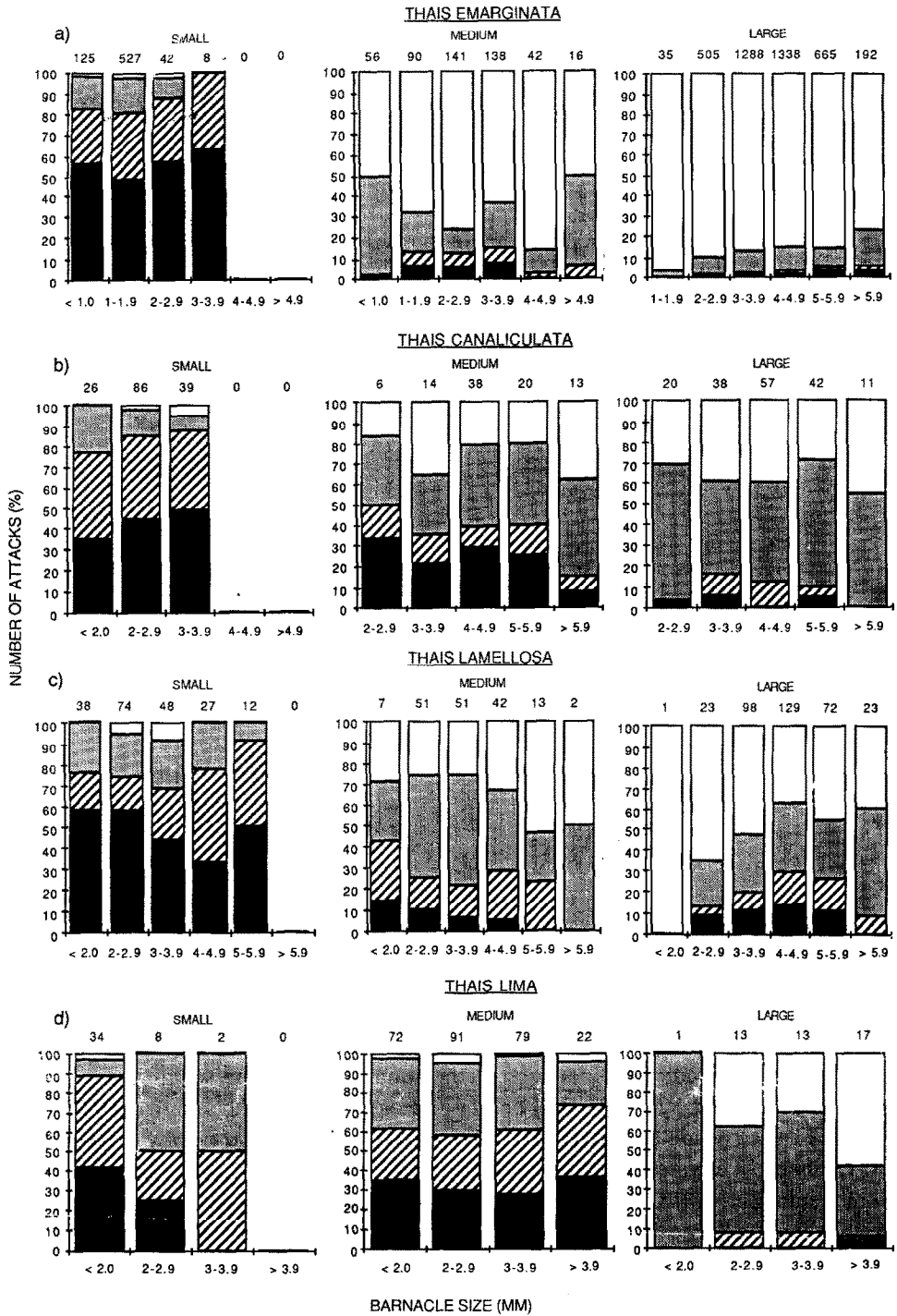


Fig. 5. Percent of attacks at different locations on the shell of *Balanus glandula* by three different size classes of each of four species of *Thais*. Size classes of snails were: 4.0–7.9 mm (small), 8.0–14.9 mm (medium), and > 14.9 mm (large). (a) *T. emarginata*; (b) *T. canaliculata*; (c) *T. lamellosa*; (d) *T. lima*. Representations and shading of bars as in Fig. 2.

VARIATION AMONG SPECIES OF *THAIS*

As reported previously (Palmer, 1982), the dependence of frequency of attack on attack site, attack region, barnacle size, and snail size varied among all four *Thais* species, even though snails in the present study were raised from egg capsules entirely in the laboratory (Fig. 5a–d, Table IIa–d). The most consistent pattern observed across all species was the dependence of attack behavior on snail size (SL, RL, SRL): large snails tended to concentrate their attacks in the opercular region, usually at the suture between scutal plates, while smaller snails attacked with less specific preferences for attack sites and regions (Fig. 5).

Rather curiously, the four species were not uniform in their attack behavior. *Thais emarginata* concentrated their attacks more on the sutures between opercular plates (Fig. 5a). *Thais lamellosa*, *T. canaliculata*, and *T. lima*, on the other hand, drilled a large proportion of holes wholly through the opercular plates, even as adults (Fig. 5b–d). For all species, however, the frequency of opercular attacks increased with increasing snail size as did the proportion of sutural attacks within the opercular region.

## HERITABILITY OF VARIATION IN ATTACK BEHAVIOR

Although many small differences in attack location frequencies were observed between Alaskan and Vancouver Island snails (Fig. 6), only two were significant statistically ( $2 \times 2$  contingency table analysis of individual size categories of barnacles with Yates' correction for small sample sizes where appropriate, Sokal & Rohlf (1981)). First, small Alaskan snails conducted more total sutural attacks (lateral plus opercular) on barnacles,  $> 1.0$  mm than small Vancouver Island snails (43% vs. 29%,  $P = 0.036$ , Fig. 6a; note also the significant dependence of attack site on origin of parents for small snails (SP, Table III)). Second, large Alaskan snails attacked the opercular region as a whole (both at sutures and through) on the largest barnacles ( $> 5.9$  mm) more frequently than large snails from Vancouver Island (100% vs. 84%,  $P = 0.038$ ; Fig. 6b; note also the significant dependence of attack region on origin of parents for large snails (RP, Table III)). In both of these cases, the frequencies of attacks by hybrids were intermediate to those of the two pure groups (37 and 95%, respectively, Fig. 6). Parallel patterns of hybrid intermediacy were observed for adjacent size categories of eaten barnacles in both cases ( $< 1.0$  mm for small snails and 5.0–5.9 mm for large snails, Fig. 6), suggesting that these results were not statistical artifacts.

In one instance, hybrids appeared to behave differently from both parental populations, even though the parental populations themselves did not differ. Small hybrids attacked both size categories of barnacles more frequently in the opercular region than small snails from either parental population (Fig. 6a; note the significant dependence of attack region on origin of parents by small snails (RP, Table III)).

TABLE II  
 Variation in frequencies of attack by four species of *Thais* at various locations on the shell of *Balanus glandula*: (a) *Thais emarginata*, (b) *T. canaliculata*, (c) *T. lamellosa*, (d) *T. lima*. Factors examined: attack site (S), attack region (R), barnacle size (B), and snail shell length (L). Data are from Fig. 5. Table entries and interpretations as in Table I.

Statistical significance of effect	Predator species							
	(a) <i>Thais emarginata</i>		(b) <i>Thais canaliculata</i>		(c) <i>Thais lamellosa</i>		(d) <i>Thais lima</i>	
	Partial	Marginal	Partial	Marginal	Partial	Marginal	Partial	Marginal
$P < 0.05$		SBL	R, SR		R	RB, SRB	SR	
$P < 0.01$	RBL	RBL						SRL
$P < 0.001$	S, R, B, L, SR, SB, SL, SL, RL, BL, SRL	SR, SB, SL, RB, RL, BL, SRL	S, B, L, RL, BL	RB, RL, BL	S, B, L, SR, SL, RL, BL	SR, RL, BL	R, B, L, SL, RL, BL, SRL	SB, SL, RL, RB, BL
Best model:	SRB*, SRL*, RBL*		RL*, RB*, BL		SR*, SL*, RL*, BL		SRL*, SB*, RB*, BL	

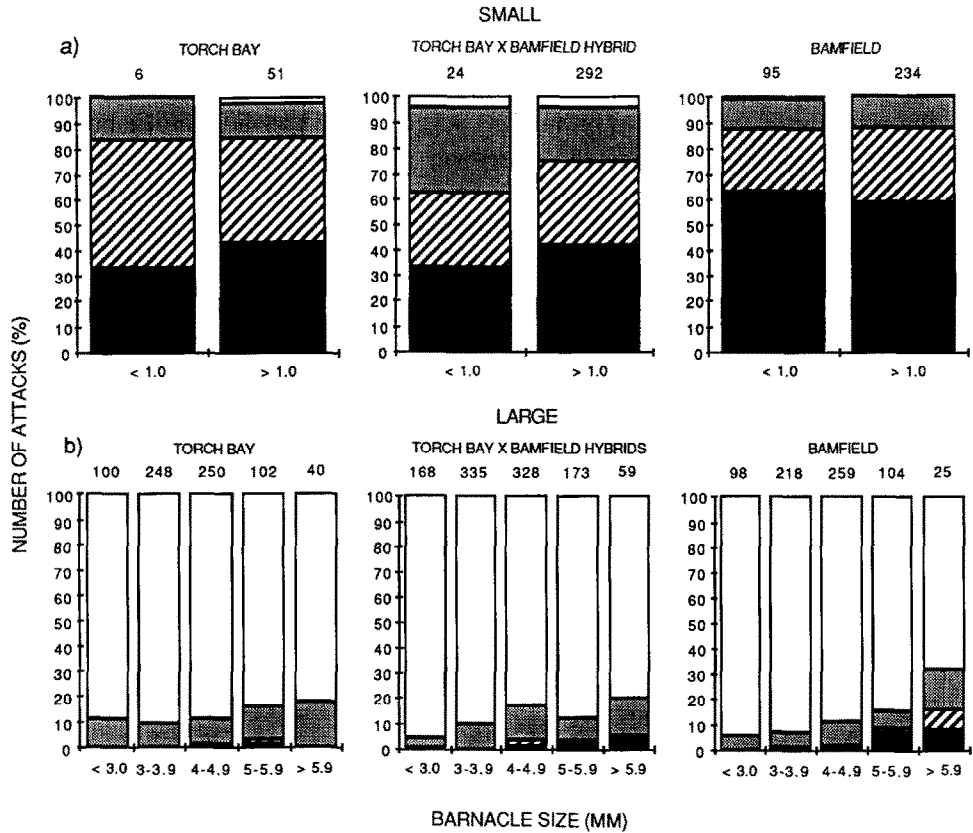


Fig. 6. Percent of attacks at different locations on the shell of *Balanus glandula* by small (4.0–7.9 mm) and large (> 14.9 mm) *Thais emarginata* from within- and between-population crosses. (a) Offspring from pure Torch Bay, Alaska crosses; (b) hybrid offspring from crosses between Torch Bay and Bamfield snails; (c) offspring from pure Bamfield, British Columbia crosses. Representations and shading of bars as in Fig. 2.

TABLE III

Inheritance of attack behavior differences for two different size classes of *Thais emarginata*. Factors examined: attack site (S), attack region (R), barnacle size (B), snail shell length (L) and history of parents (P; pure Torch Bay, Alaska, pure Bamfield, British Columbia, Torch Bay × Bamfield hybrids). Data are from Fig. 6. Table entries and interpretation as in Table I.

Statistical significance of effect	Size class of <i>Thais emarginata</i>			
	Small		Large	
	Partial	Marginal	Partial	Marginal
$P < 0.05$		SP	RP	RP
$P < 0.01$	SP		SB	
$P < 0.001$	S, R, B, P, SR, RB, BP	SR, RP, BP	S, R, B, P, SR, RB	SR, SB, RB
Best model:	SR*, SP*, RP*, BP		SR*, SB*, RB*, RP*	

## EFFECT OF FEEDING HISTORY ON ONTOGENY OF DRILL-SITE SELECTION

The behavior of snails grown on mussels suggests that very little of the observed ontogenetic shift towards increased stereotypy in *Thais emarginata* was learned. Although snails (of both size classes) grown on mussels did attack the opercular region less frequently than those grown on barnacles (Fig. 7; effect RT, Table IV), this

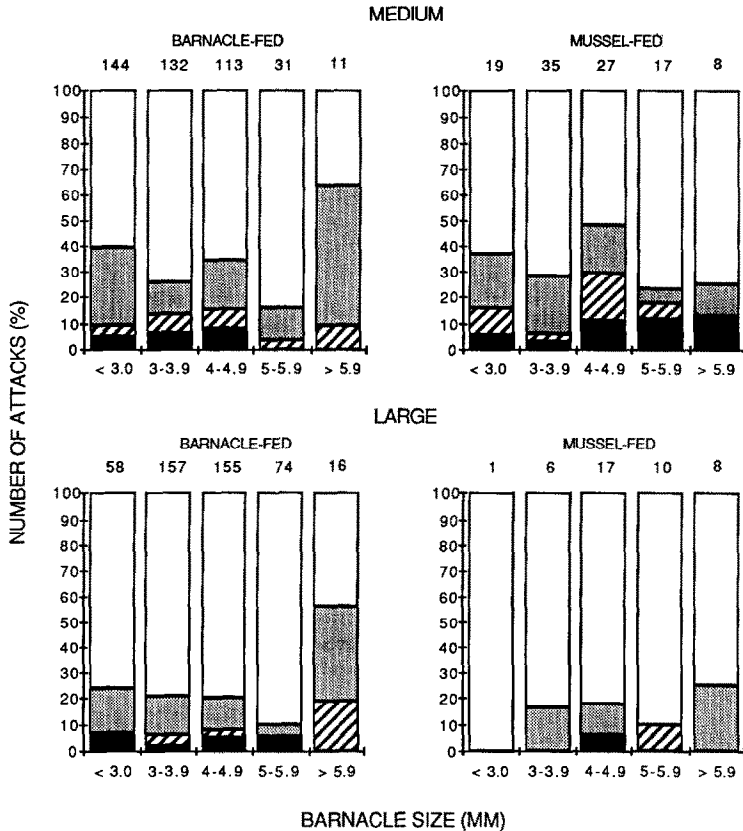


Fig. 7. Percent of attacks at different locations on the shell of *Balanus glandula* by medium (8.0–14.9 mm) and large (> 14.9 mm) *Thais emarginata* grown on different diets. Representations and shading of bars as in Fig. 2.

difference was small (0.862 vs. 0.918 for mussel-fed and barnacle-fed groups, respectively) and not highly significant ( $P = 0.031$ ). In addition, the growth on mussels had no effect on choice of attack site (ST) or on the dependence of attack site on attack region (SRT, Table IV). Most importantly, had the barnacle attack-behavior remained unchanged while the snails were growing on mussels, as would be expected if learning were important, the difference between mussel- and barnacle-fed snails following the 14 wk diet on mussels should have been much greater (0.187 vs. 0.888, comparing small and medium snails in Fig. 5a).

TABLE IV

Effect of sustained mussel diet on attack locations on shells of *Balanus glandula* by two size classes of *Thais emarginata*. Factors examined: attack site (S), attack region (R), barnacle size (B), snail shell length (L) and experimental treatment (T; grown on barnacles or grown on mussels). Data are from Fig. 7. Table entries and interpretation as in Table I.

Statistical significance of effect	Partial	Marginal
$P < 0.05$	SL, RL	RT, SRB
$P < 0.01$		RL
$P < 0.001$	S, R, B, T, SR, SB, BL, BT, LT	SR, SB, SL, BL, BT, LT
Best model:	RT*, SR*, SB*, SL*, RL*, BL, BT, LT	

CHANGES IN BARNACLE MORPHOLOGY WITH SIZE

The thickness of all barnacle shell plates increased significantly with barnacle size (Fig. 8), although less rapidly for opercular than lateral plates. The rate of increase of lateral plate thickness with barnacle size was not uniform among plate types ( $P = 0.0237$ , ANCOVA). The source of these differences were the carinolateral plates; the carinal, lateral, and rostral plates formed a homogeneous group (regression lines were not significantly different from each other,  $P = 0.3455$ ). When these plates were combined, their thickness increased significantly more rapidly than that for scutal plates ( $P = 0.0007$ ). Thus, as barnacles increased in size, the relative thickness of scutal plates decreased.

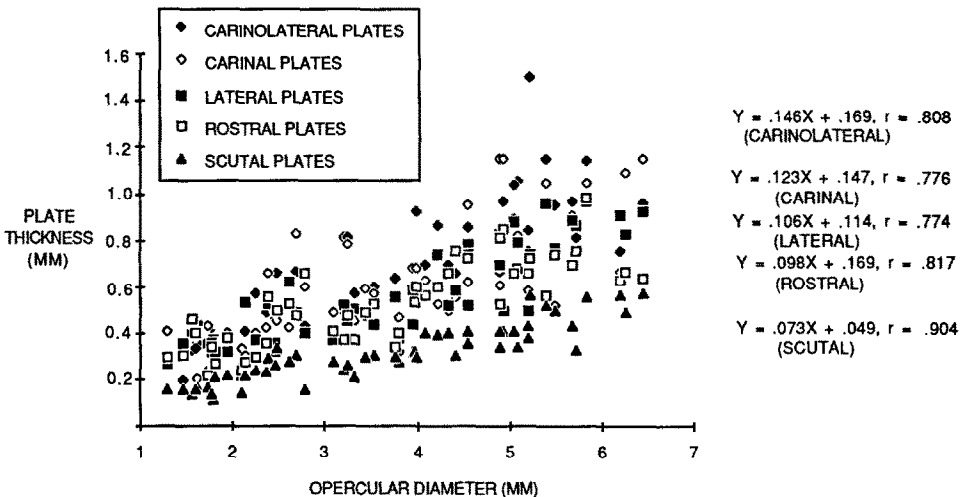


Fig. 8. Barnacle shell plate thickness plotted against opercular diameter for 53 *Balanus glandula* ranging in size from 1.3 to 6.4 mm. Least-squares linear regression equations and correlation coefficients are shown for each plate type.

## DISCUSSION

VARIATION AMONG ADULT *THAIS EMARGINATA*

Perhaps the most surprising result of our study was the relative lack of variation in attack behavior among adult *T. emarginata* on any scale from among individual snails to among populations along the northern Pacific coast of North America (Figs. 2–4). We found no significant behavioral differences among individual *T. emarginata* (Fig. 2), nor among *T. emarginata* sampled from sites along a wave exposure gradient in Barkley Sound (Fig. 3). A statistically significant difference did exist among widely-isolated populations along the Pacific northwest coast (Fig. 4), but this variation was small compared to differences among snail size classes (see below). This stereotypy in attack behavior is remarkable, given that other aspects of the feeding behavior of *Thais* may vary markedly among similar individuals living on the same short (10–20 m) stretch of shoreline (West, 1986). Given that the stereotypy of drilling behavior varies substantially with snail size, implying abundant opportunity for selection to alter the behavior through heterochrony, the relative lack of variation even among rather distant populations for a gastropod with very limited dispersal capabilities (Palmer, 1984b) suggests very strong stabilizing selection for the observed pattern of stereotypy.

## HERITABILITY OF VARIATION IN ATTACK BEHAVIOR

Although the differences in the frequencies of attack at particular locations on barnacles were small between Alaskan and Vancouver Island snails, we feel it is more than coincidence that in the only two instances where statistically significant differences did exist, the frequencies of attack by hybrids were intermediate between the two groups of pure snails (total sutural attacks by small snails and total opercular attacks by large snails on larger barnacles; Fig. 6). The intermediate behavior of hybrids suggests a polygenic basis to these differences, as noted for other complex behaviors (Ehrman & Parsons, 1981). The greater frequency of opercular attacks by small hybrids than by small snails from either of the groups of pure snails (Fig. 6a) is more difficult to interpret, but the consistency of this difference in behavior by hybrids on both size categories of barnacles also suggests a genetic basis. Additional breeding studies are needed to determine the strength of these conclusions.

## ONTOGENETIC VARIATION IN ATTACK BEHAVIOR

Three trends in the attack behavior of *Thais* are apparent from Fig. 5: as snails increased in size, they tended to attack larger barnacles, they attacked the opercular plates more frequently, and they tended to concentrate their attacks at the suture between the scutal plates. We initially interpreted the observed changes in drilling behavior with increased snail size as evidence of learning. Many aspects of the feeding behavior of gastropods in general (Willows, 1973) and thaidis in particular (Morgan,

1972) may be acquired through experience. *Thais* might learn with experience to attack barnacle prey at the opercular sutures, and attack all barnacles the same way regardless of size. However, prior feeding experience had very little effect on location of attack by *Thais emarginata* (Fig. 7). Snails fed a pure diet of mussels for a significant portion of their juvenile lives developed preferences for attack locations on barnacles which were very similar to the preferences of snails fed continuously on barnacles. The ontogeny of attack behavior in *Thais* seems to be controlled by developmental processes independent of environmental influences.

#### EFFECT OF BARNACLE SIZE

One possible advantage to the increased frequency of opercular attacks by *Thais* is an allometric change in skeletal plate thickness of barnacles: larger barnacles have relatively thicker lateral wall plates than do smaller ones (Fig. 8). Snails preying on small barnacles may be less selective in choosing drill sites because plate thicknesses do not differ much in these barnacles. Snails which tend to prey on large barnacles may be able to decrease drilling time substantially by attacking the opercular plates. Although we present no data on the thickness of shell plate margins, snails may be able to reduce drilling time further by attacking the suture between scutal plates.

The dependence of attack behavior on barnacle size, however, may potentially have confounded our conclusion that *T. emarginata* did not learn to drill more frequently at the margins of the scutal plates as they increased in size. All four *Thais* species exhibited both a change in drill site selection behavior with increasing snail size, and an increased tendency to attack larger barnacles. Although we made no effort to control the range of barnacle sizes offered to different snail size classes, other evidence suggests that where prey have no 'escape in size' (Paine, 1976), larger thaidids prefer to attack larger barnacles (Palmer, 1983, 1984a). Given these parallel changes, it might be tempting to conclude that the *Thais* responded mechanically to prey size by attacking small barnacles in a non-selective manner, and attacking large barnacles selectively at the opercular suture. However, the data indicate otherwise.

Barnacle size had no significant effect on attack locations by size classes of *T. canaliculata*, *T. lamellosa*, or *T. lima* (Fig. 5). In addition, the best single data set, for large *T. emarginata* (which included the largest number of observations across the widest range of barnacle sizes), strongly suggests that these snails did not respond facultatively to different barnacle sizes: the frequency of sutural attacks in the opercular region was uniformly high across all barnacle sizes. If there was any pattern at all, larger barnacles were attacked less frequently at the suture between the scutal plates than small barnacles (Fig. 5a).

The significant effect of barnacle size on choice of attack region by size classes of *Thais emarginata* (effect RBL, Table IIa) was probably due to the variable handling of barnacle sizes by medium-sized snails (Fig. 5a). This result is difficult to interpret, but it is inconsistent with the suggestion that drill site selectivity varies directly with prey

size. The best evidence certainly suggests that barnacle size does not have an overriding influence on the location of attacks by *Thais*.

If, as we suggest above, larger barnacles are more easily attacked at the opercular plates than smaller barnacles because these plates are relatively thinner in larger barnacles (Fig. 8), then the lack of any observed effect of barnacle size on degree of stereotypy would seem at first glance contradictory. In other words, why are large snails not more stereotyped when attacking large compared to small barnacles? One possible explanation for this apparent anomaly relates to the precision with which snails can assess barnacle size. Presumably, since larger snails consume larger barnacles on average, they will be under stronger selection than smaller snails to attack the opercular plates of all sizes of barnacles as long as there is little or no disadvantage to opercular attacks on smaller barnacles. A barnacle-size-dependent stereotypy would require that the snails obtain more information to be successful, and since snails probably cannot assess barnacle size without error, such a size dependence might result in more frequent 'mistakes' when drilling larger barnacles. Alternatively, genuine scaling limitations may exist whereby a large snail with a large accessory boring organ and radula may be much less efficient at nonsutural attacks on any sized barnacle than a small snail. The real question seems to us to be why individuals of *Thais* of all sizes are not more stereotyped.

#### VARIATION AMONG *THAIS* SPECIES

Given that the ontogenetic changes in drilling behavior in *Thais emarginata* are largely genetically programmed and are under strong stabilizing selection on a large geographic scale, as suggested above, we find it surprising that such large differences exist among the four species of *Thais* examined. All four species do show a similar ontogenetic progression in attack behavior (Fig. 6), implying that there is a 'best way' to attack barnacles, but considerable variation among species still exists. Ecological differences among these species, in either their intertidal distribution or their diets (Palmer, 1980), may have resulted in selection for different modes of attack (Lively, 1986). However, as discussed elsewhere (Palmer, 1982), the adaptive value of differences among species remains enigmatic.

#### ACKNOWLEDGEMENTS

This study was supported in part by Natural Sciences and Engineering Research Council of Canada and University of Alberta scholarships and a Dalhousie University Graduate Fellowship to Michael Hart, and by NSERC operating grant A7245 to A. R. Palmer. The director and staff at the Bamfield Marine Station provided logistical support, for which we are grateful. G. J. Vermeij and an anonymous reviewer provided useful comments on the manuscript.

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