



**Competition, Comparative Life Histories, and Maintenance of Shell  
Dimorphism in a Barnacle**

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## COMPETITION, COMPARATIVE LIFE HISTORIES, AND MAINTENANCE OF SHELL DIMORPHISM IN A BARNACLE<sup>1</sup>

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**Abstract.** Two discrete shell morphs of the acorn barnacle *Chthamalus anisopoma* coexist on rocky intertidal shores in the northern Gulf of California. One morph (called “conic”) has the conical shape characteristic of acorn barnacles, while the other morph (called “bent”) has the rim of the barnacle’s aperture oriented perpendicular (rather than parallel) to its base. The results of a companion study show that development of the bent morph is induced by a carnivorous gastropod (*Acanthina angelica*), that bents are more resistant than conics to attack by this predator, and that the risk of predation is spatially heterogeneous. The purpose of the present study was to determine if bents are less fit than conics in the absence of predation by *Acanthina*, a necessary condition for the predator-induced developmental switch to bents to be resistant to invasion and replacement by the unconditional strategy “always grow bent over.” Four alternative hypotheses were tested: bents (1) are poorer competitors for space, (2) grow slower, (3) reproduce later, and (4) are less fecund than conics. The results of field experiments gave no evidence to suggest that bents are inferior competitors for primary space. Bents, however, were found to be both less fecund and slower growing than conics. Because of the multiplicative effect of growth and fecundity on fitness, the cost of being bent is expected to be high, and a necessary condition for maintenance of the barnacle dimorphism is met.

**Key words:** barnacle; canalization; *Chthamalus*; competition; conditional strategy; dimorphism; life histories; predation; trade-offs.

### INTRODUCTION

The results of theoretical population biology suggest that two (or more) genetically determined morphs of the same species can coexist without heterosis if (1) the environment is patchy, and (2) the relative fitnesses of the morphs are patch dependent in such a way that each morph has a fitness advantage in one of the patches (see Levine [1953], Levins [1968] and reviews by Roughgarden [1979] and Hedrick et al. [1976]). This result can easily be extended to the maintenance of environmentally determined morphs, with the additional proviso that the average probability of making the “right” choice be greater than one-half (Lively 1986a). The main conceptual difference between the two types of polymorphism is that genetically determined morphs represent multiple, unconditional (or canalized) developmental strategies, while environmentally induced morphs represent a single developmental strategy which is conditional on the environment. Both types of polymorphism, however, require a trade-off among morphs as a necessary condition for evolutionary stability (*sensu* Maynard Smith 1982). The purpose of the present study was to determine whether this condition of a trade-off is met in an intertidal barnacle which is dimorphic for shell shape.

The acorn barnacle *Chthamalus anisopoma* Pilsbry shows such a dimorphism in the northern Gulf of California (Lively 1984). The more common of the two

shell morphs has the conical, volcano shape characteristic of acorn barnacles (Darwin 1854), while the other morph appears bent over with the aperture oriented perpendicular to its base (Fig. 1). The results of a companion study (Lively 1986b) show that the bent condition is a developmental response to the presence of the carnivorous snail *Acanthina angelica*, and that “bents” are more resistant than “conics” to specialized attack by this predator. The results of that study also show that predation by *Acanthina* is spatially heterogeneous and is heaviest in the vicinity of crevices that it uses as refugia during periods of tidal inundation.

Given that the bent form is more resistant to attack by a common predator, it is reasonable to ask why the conditional strategy “grow bent in the presence of *Acanthina*” has not been replaced by the unconditional strategy “always grow bent over.” There are at least three possible answers to this question: (1) the unconditional strategy is not an option because of developmental constraints; (2) replacement of the conditional strategy by the unconditional strategy is presently in progress; and (3) the conditional strategy is evolutionarily stable. As argued above, the last hypothesis requires a trade-off such that the expected fitness of bents in the absence of predation by *Acanthina* is less than that of conics. In the present study, I evaluated some potential costs that may be associated with the bent-over condition. The specific null hypotheses addressed were: (1) survivorship of bents when crowded by conics is equal to that of conics when comparably crowded by conics; (2) the two morphs grow at equal rates; (3) they begin reproduction at the same age; and (4) they are equally fecund. The results were inconsistent with

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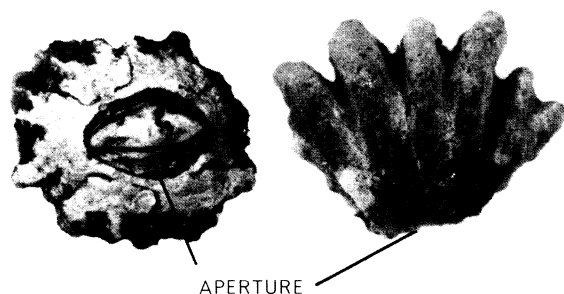


FIG. 1. Top view of the conic (left) and bent (right) morphs of *Chthamalus anisopoma*. Both individuals are lined up along the rostro-carinal axis with the carinal plate on the right-hand side. The aperture of the bent morph is in a plane perpendicular to the plane of the page and that of the conic morph. Rostro-carinal diameters are 3.6 mm and 3.9 mm for the conic and bent morphs, respectively.

two of these null hypotheses (bents grew slower and were less fecund than conics) and provided evidence for the trade-off necessary for selection to favor the conditional developmental strategy over an unconditional one.

#### METHODS AND MATERIALS

##### *Study site*

Field experiments were conducted at Punta Peñasco, a rocky point composed of large basalt boulders near the coastal town of Puerto Peñasco, Sonora, Mexico (31°20' N, 113°40' W) on the northern Gulf of California. The northern Gulf is well known for its large tidal amplitude ( $\approx 8$  m at Puerto Peñasco during spring tides) and seasonal extremes in air and sea-surface temperatures (see Brusca 1980). Wave action is generally mild, but the waves produced by occasional local storms can affect the composition of the sessile community.

##### *Intra- and intermorph competition for space*

Competition for space, both within and between the two morphs, was studied by comparing the survivorship of bents when crowded by conics (intermorph competition) with that of conics when comparably crowded by conics (intramorph competition). It is reasonable to suspect a priori that the bent form of *C. anisopoma* is more subject to mortality from crowding by conics due to undercutting (sensu Connell 1961) on the "short" side or by inhibition of its feeding due to blockage of the perpendicular aperture.

To determine the effect of crowding by the conic form on the survivorship of both morphs, I established 3–4 quadrats (approximate area: 100 cm<sup>2</sup>) on each of five large (desk-sized) basalt boulders between 21 November and 6 December 1983. The boulders were in the upper half of the *Chthamalus* zone (1–2 m above

MLW [mean low water]) and all quadrats ( $N = 18$ ) contained a mixture of both morph types in different proportions. The barnacles were 2–3 mo old judging by the size range (rostro-carinal diameters: 2.0–3.5 mm). Within each quadrat 10 individuals of each morph were selected which were "solitary" (not in direct contact with conspecifics) and "crowded" (adjoined by two or more conics), and the locations of these barnacles were mapped onto clear plexiglass plates (using different colors of permanent markers for each of the four treatments). Reference points for the maps were established on the rocks (using a marine epoxy) to ensure accurate replacement of the plexiglass plates. Individuals within 1 cm of "solitary" individuals were periodically removed (by scraping) for the duration of the experiment.

To prevent selective removal of the conic form by *Acanthina*, this gastropod was removed (at least once a month) from within 4 m of each of the experimental boulders. The quadrats were sampled periodically (about every 6 wk) until mean survivorship in at least one of the treatments dropped below 50%. The survivorship data were analyzed by a three-way analysis of variance. The a priori prediction was that crowded individuals would experience higher mortality than uncrowded individuals, and that crowded bents would have a higher mortality than crowded conics. This would surface as an interaction effect between morph type and crowding.

##### *Life histories*

*Growth rate and onset of reproduction.*—To determine the growth rates of the two morphs and their ages and sizes at first reproductive effort, *C. anisopoma* were "farmed" on three, 3.1 mm thick, clear plexiglass plates (12.5 × 12.5 cm). To facilitate larval settlement, 121 small pits were drilled on one side of the plates in an 11 × 11 grid pattern so that the distance between two adjacent pits in any row or column was 1 cm. The plates were attached side by side (on 12 June 1983) with brass screws to a fibreglassed wooden plank bolted to a large boulder at 1.3 m above MLW at Punta Peñasco. Individuals that settled between the pits were wiped away. In those cases where two or more individuals settled in a single pit, all but the largest individual were removed with a probe. In this way, both density and nearest neighbor distances were strictly regulated. In addition, the orderly arrangement of the pits allowed each individual to be identified and followed through time by a coordinate system.

During low tides on 17 June and daily during the period 20–28 June 1983, I added  $\approx 30$  *Acanthina* to each of the two outside plates. The snails were allowed to crawl off and were observed to crawl over the middle plate as well. This had the effect of producing a mixture of the two morph types on each plate. At  $\approx 10$ -d intervals (for 12 wk) the transparent plates were tem-

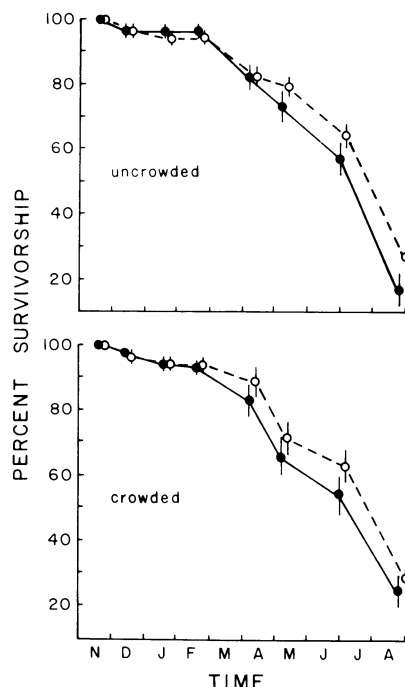


FIG. 2. Survivorships over time for the conic (●) and bent (○) morphs of *Chthamalus anisopoma* under crowded and uncrowded conditions in the competition experiment. Vertical bars are  $\pm 1$  standard error about the mean.

porarily removed, returned to the laboratory, and inspected through the bottom for the presence of ripe ovaries (operational definition: presence of discrete yellow egg masses at  $30\times$  under a stereomicroscope). Because this barnacle has a membranous base, the reproductive state of individual barnacles could be easily determined without destructive sampling. At the same time, the basal diameters along the rostro-carinal axis were measured using a lens micrometer. (Rostro-carinal diameter is shown below to be a reliable predictor of body size in both morphs.) Time to first reproduction was analyzed using a repeated measures ANOVA (see Winer 1971), and the rostro-carinal diameters of

the two morphs at the end of the experiment were compared using a two-way (morph  $\times$  block) ANOVA.

**Shell mass and fecundity.**—To compare the number of eggs and the masses of the shells for different-sized *Chthamalus* of both morphs, small basalt boulders having individuals of both morph types were collected during four successive spring-tide series beginning 21 November 1983. Individual barnacles were pried off the boulders and observed while still alive under a dissecting microscope. When individuals were found bearing nauplii, the nauplii were removed from the shell, fixed, and separated in Gibson's solution (see Bagenal 1967), and counted. The soma was then cut away from the shell, fixed as were the nauplii, and measured along a standardized axis (from the distal end of the body to the joints of the first appendages) using an ocular micrometer. Finally, the remaining fleshy material was cut away from the shells, and the shells were weighed after being placed in a drying oven for 12–15 h at  $60^{\circ}\text{C}$ .

## RESULTS

### Competition for space

The results of the competition experiment gave no evidence to suggest that the bent form is more susceptible than conics to mortality due to crowding (Fig. 2). The anticipated interaction effect between crowding and morphology was not observed in any of the samples (Table 1). Hence, intermorph competition (measured in terms of mortality) does not appear to be more intense than intramorph competition in this species, and it is unlikely to be an important factor in the maintenance of this *Chthamalus* dimorphism. This is not to say that competition does not affect growth and survivorship in these barnacles. Crowded individuals were much smaller than uncrowded individuals and seemed more likely to be removed in some sites due to wave action. Evidence for the latter comes from a significant crowding  $\times$  block interaction effect in the May sample, which was taken shortly after a storm (Table 1). However, the survivorship of crowded bents was not significantly less than that for crowded conics.

TABLE 1. Results of ANOVA on survivorship for the two shell morphs of *Chthamalus anisopoma* under crowded and uncrowded conditions. Values are mean squared terms from ANOVAs on each sample.

Source	df	Sample date			
		April	May	July	August
Main effects					
Morph	1	1.33	4.56	7.45	10.37*
Crowding	1	4.27	7.65	0.02	4.71
Site	4	15.27***	22.81***	35.01***	58.78***
Morph × Crowding	1	1.68	0.01	0.59	1.49
Morph × Site	4	0.45	1.35	0.32	2.64
Crowding × Site	1	5.19	7.38*	3.93	1.66
3-way interaction	4	1.37	1.07	1.64	0.64
Error	52	2.60	2.91	3.48	2.41

\*  $P \leq .05$ , \*\*\*  $P < .001$ .

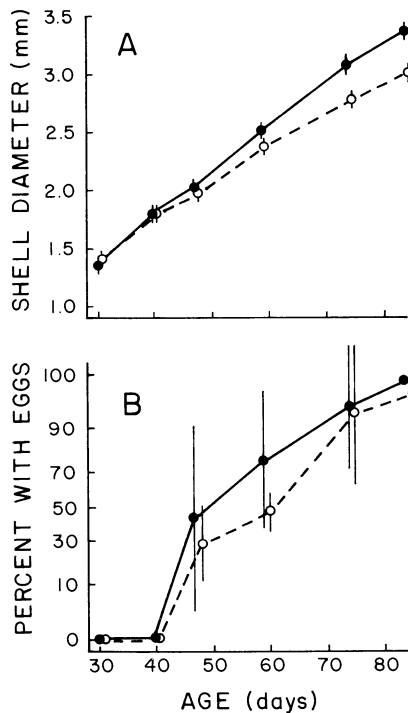


FIG. 3. Shell (rostro-carinal) diameter (A) and percent of individuals with eggs (B) as a function of age for the conic (●) and bent (○) morphs of *Chthamalus anisopoma*. Vertical bars are 95% confidence intervals of the means. Percentages were back-transformed from arcsine  $\sqrt{P}$ .

No overgrowth or undercutting by either morph was observed.

At the end of the experiment (in August 1984), the survivorship of bents was greater than that for conics (Fig. 2, Table 1). This was most likely due to selective predation by a low number of *Acanthina* that moved in between removals. Such predation might also have contributed to the highly significant block effects (Table 1), as some of the blocks were more likely to be reinvaded by *Acanthina* than others. It would not account, however, for the lack of asymmetric competition between the morphs; no cases were observed in which the conic competitors of a bent individual were removed.

#### Structural constraints and material costs

**Growth and onset of reproduction.**—The results of “farming” both morphs interspersed and under low-density conditions indicated a faster growth rate for the conic form. At 30 d, when the two morphological types could first be distinguished, there was no apparent difference between their mean sizes (Fig. 3A). At 84 d, however, conics were significantly longer along the rostro-carinal axis than bents (Table 2).

It is noteworthy that there was a significant plate (block) effect in the growth experiment (Table 2). This is surprising given the proximity of the plates and their

TABLE 2. Results of the ANOVA for final rostro-carinal diameter for the two *Chthamalus anisopoma* morphs in the growth experiment on plexiglass after 84 d (see Fig. 3A).

Source	df	MS	P
Main effects			
Morph	1	595.81	<.001
Plate	2	106.02	<.002
Morph $\times$ Plate	2	31.21	>.130
Error	107	15.10	

similar orientation. Microspatial differences which are not easily observable, therefore, may be of great consequence to barnacles and other intertidal species.

The differences between morphs with respect to changes in the frequencies of individuals of both morph types with ripe ovaries, over the course of the experiment (Fig. 3B) were not significant (Table 3). Both morphs were first observed with ripe ovaries at  $\approx 6$  wk of age, a result which is consistent with the work of Malusa (1983) concerning onset of reproduction in the conic form. Hence, there is no evidence to suggest that the faster growth by conics is at the expense of a delay in the timing of their first reproductive effort.

**Shell mass and fecundity.**—The results of the study to compare the shell masses and fecundities of the two morphs relative to their body sizes are presented in Fig. 4. The regressions of shell mass against body size (Fig. 4A) did not differ significantly between the two morphs (Table 4). There was also no significant difference between morphs in the regressions of rostro-carinal diameter against body size (Table 4). The latter result shows that use of rostro-carinal diameter as a measure of size in the growth experiment (above) is satisfactory.

The results do, however, indicate a significant difference in the fecundities of the two forms. The difference between elevations (intercepts) for the regressions of egg number against body size was significant (Table 4), with the elevation of the conic line being higher (Fig. 4B). The difference between the slopes of these lines, however, was not significant (Table 4).

#### DISCUSSION

The results of the present study show that the expected reproductive success of bents is less than that

TABLE 3. Repeated measures ANOVA for the percentages of the two *Chthamalus anisopoma* morphs with eggs over time (see Fig. 3B). Data were arcsine-transformed before statistical computations (see Zar 1974).

Source	df	MS	P
Morph	1	345.04	>.200
Error	4	164.29	
Time	3	3237.15	<.001
Morph $\times$ Time	3	59.49	>.250
Error	12	39.57	

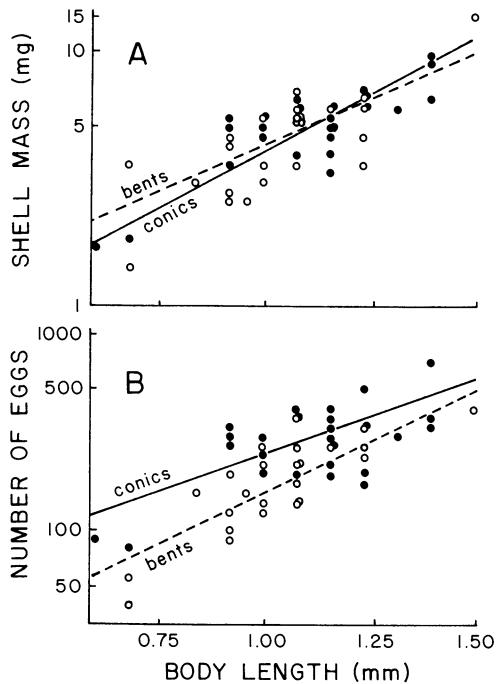


FIG. 4. Regressions of shell mass (A) and egg number (B) against body length for the conic (●) and bent (○) morphs of *Chthamalus anisopoma*. The vertical axes were back-transformed from  $\log(x)$ .

of conics where predation by *Acanthina* is low or absent. As was argued previously, such a "cost" to being bent is a necessary condition for the evolutionary stability of the conditional developmental strategy "grow bent in the presence of *Acanthina*." The cost of being

bent, however, appears to be independent of mortality due to intermorph competition, as there was no significant difference between the survivorships of bents and conics when comparably crowded by conics. This lack of asymmetric competition between the morphs differs from experimental studies on full species of barnacles in which competitively superior species exclude stress-tolerant species from the relatively benign lower intertidal (Connell 1961, Luckens 1975, Wethey 1983, Dungan 1985). The mechanism for such competitive exclusion normally involves either undercutting or overgrowth of the stress-tolerant species by the competitive dominants (see Connell 1961).

There is no precedent, however, for undercutting or overgrowth within barnacle species. Monospecific (and monomorphic) stands of acorn barnacles commonly grow up (instead of out) under crowded conditions. When settlement density is sufficiently high, this tendency results in mounds known as hummocks (Barnes and Powell 1950, Connell 1961). Both the conic and bent forms were observed in the present study to be present in hummocks and presumably grew up by adding shell material at the base in the manner suggested by Darwin (1854). In most cases the bent form retained its "hooded" shape in spite of the crowded conditions. The greater ease of detachment of barnacles in hummocks appeared to account for the greater mortality of both forms under crowded conditions following a storm during the competition experiment; nevertheless, crowding affected the mortality of both forms equally.

The results of the present study do, however, indicate a trade-off in two important life-history parameters;

TABLE 4. Analysis of covariance summary for the regressions of egg number, shell mass, and rostro-carinal diameter (dependent variables) against body length (independent variable) for the two shell morphs of *Chthamalus anisopoma* (see Zar 1974). All variables were log-transformed before statistical computations.

	Dependent variable		
	Egg number	Shell mass	Shell diameter
Slopes $\pm$ SE			
Bents	$2.48 \pm 0.37^{***}$	$2.07 \pm 0.34^{***}$	$0.71 \pm 0.16^{***}$
Conics	$1.81 \pm 0.33^{***}$	$1.74 \pm 0.24^{***}$	$0.56 \pm 0.11^{***}$
Intercepts $\pm$ SE			
Bents	$2.17 \pm 0.14$	$0.61 \pm 0.13$	$1.61 \pm 0.06$
Conics	$2.36 \pm 0.13$	$0.63 \pm 0.10$	$1.63 \pm 0.04$
Regression ss			
Bents (1 df)	0.85	0.59	0.07
Conics (1 df)	0.55	0.51	0.05
Residual ss			
Bents (24 df)	0.46	0.40	0.09
Conics (23 df)	0.41	0.22	0.06
Pooled (47 df)	0.87	0.62	0.13
Common (48 df)	0.90	0.63	0.13
Total (49 df)	1.25	0.63	0.14
Probability of equal:			
Slopes	$>.10$	$>.50$	$>.50$
Elevations	$<.001^{***}$	$>.50$	$>.10$

\*\*\*  $P < .001$ .

bents grew more slowly and were less fecund than conics. One possible explanation for this result is that bents require a greater material investment in their shells, thereby decreasing the energy available for both reproduction and body growth. If this were true, bent shells should have been heavier per unit body size than conics, but this was not the case. It is reasonable to suspect, therefore, that the reduced fecundity of bents results from a reduced internal volume for brooding, and that the reduced growth rate is caused either by impediments to the uptake of food or nonenergetic, structural constraints on growth.

Palmer (1981) gives an elegant example of how non-energetic constraints on growth affect fitness in thick- and thin-shelled morphs of a marine snail. Body growth in both morphs appears to be limited by a maximum rate of shell deposition such that (when prey are abundant) the two morphs add shell mass at nearly equal rates; but because of the thicker shell, the thick-shelled morph adds soft body tissue at a slower rate. A conceptually similar structural constraint might explain the slower growth of the bent form of *C. anisopoma*. Assuming that the barnacles are growing at the maximum possible rate, growth in the bent form might be reduced because shell material is added to only one side.

The reduced growth and fecundity of the bent morph is consistent with the trade-offs suggested for other conditional dimorphisms. In *Daphnia*, for example, crests that reduce the risk of predation by invertebrates are inducible by exposing juveniles to chemical cues released by the predators (Grant and Bayly 1981, Kruegar and Dodson 1981). Crested individuals were found to be less fecund than uncrested individuals of *D. carinata* (Grant and Bayly 1981; see also O'Brien and Vinyard 1978, Dodson 1984). Similarly, predators are known to induce the production of spines in both rotifers (Gilbert 1966, Gilbert and Stemberger 1984, Stemberger and Gilbert 1984) and bryozoans (Yoshioka 1982, Harvell 1984). The spines reduce the risk of predation by other rotifers and nudibranchs respectively, and in the case of bryozoans at least the production of spines are known to be coupled with a reduction in fecundity (Yoshioka 1982). Trade-offs in conditional dimorphisms independent of predator-prey interactions have also been shown. Perhaps the best known of these are the wing polymorphisms of insects. In general, long-winged forms are superior with respect to dispersal, but develop slower and are less fecund than short-winged or wingless morphs (see Vepsäläinen 1978, Harrison 1980, Zera 1984).

It is difficult, however, to determine whether such trade-offs are sufficient for the maintenance of polymorphisms. For the barnacle dimorphism discussed in the present study, the cost to being bent is expected to be large due to a multiplicative reduction in expected fitness resulting from constraints on both growth and fecundity. The evolutionary stability of conditional

strategies, however, is dependent on more than just the magnitude of the trade-off. The probabilities of making the "right" choices in the alternative patches and the frequencies of the patches figure predominantly (Lively 1986a). It cannot be concluded, therefore, that the barnacle dimorphism is stable, but a necessary condition for stability is met.

In summary, the bent morph of *C. anisopoma* is more resistant to attack by *Acanthina*. This resistance to predation gives bents a fitness advantage in the "harsh" or predation-stressed areas near crevices where predation by *Acanthina* is concentrated. The conic morph, by contrast, grows faster and is more fecund than bents, which gives it a fitness advantage in the "benign" or relatively predation-free patch away from such crevices. This trade-off between resistance to predation and the capacity for growth and reproduction (in an environment which is heterogeneous with respect to predation intensity) satisfies a necessary condition for the persistence of the conditional developmental strategy "grow bent in the presence of *Acanthina*."

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