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ESCAPE RESPONSES AND PREY AVAILABILITY IN A KELP FOREST
PREDATOR-PREY SYSTEM

Prey abundance and availability are key parameters in theoretical models of optimal foraging (Krebs 1977; Pyke et al. 1977). However, precise definitions of prey availability are elusive because they must take into account such phenomena as palatability, detectability, digestibility, and other traits (Menge 1972). Important among these other traits are defensive behavioral patterns of mobile prey triggered by the presence of specific predators. These behavioral patterns should reduce the availability of the prey to their predators and therefore influence food selection by the predators.

Marine molluscs have long been known to exhibit stereotyped defensive behavior in the presence of specific sea star predators (Bennett 1927; Bullock 1953; Clark 1958; Yarnall 1964; Feder 1963; Margolin 1964*a* 1964*b*, 1975; Montgomery 1967; Mauzey et al. 1968; Edwards 1969; Phillips 1976, 1977; Dayton et al. 1977). The spectacle of normally sluggish benthic molluscs running, jumping, swimming, or otherwise fleeing from an attacking predator impressively demonstrates the potential these behavior patterns have in reducing predatory mortality. Some investigators have, in fact, noted a correlation between the escape response shown by prey and a lower incidence of predation than would be expected on the basis of its relative abundance (Feder 1959, 1963; Margolin 1964*b*). Some studies have sought to assess the effectiveness of these responses in the laboratory (Margolin 1964*b*; Moitza and Phillips 1979) and in the field (Phillips 1976; Dayton et al. 1977). The question which remains to be answered quantitatively is just how important are behavioral defense mechanisms in reducing the availability of prey to their predators.

A 2-yr study of prey selection by a generalist asteroid predator in a kelp forest system was carried out in 1976–1978 (Harrold 1981). The results of this study suggested that behavioral defense responses to two gastropods, *Tegula pulligo* and *Calliostoma ligatum*, reduced their occurrence in the diet of the predatory sea star *Pisaster giganteus*. Furthermore, although *T. pulligo* occurred in the diet over three times more frequently than *C. ligatum*, I observed that actively foraging sea stars encountered *T. pulligo* much less frequently than *C. ligatum*. Either sea stars preferred *T. pulligo* over *C. ligatum*, or *T. pulligo* was less successful at escaping predation than *C. ligatum*, or both. I report here the results of a field experiment designed to test the null hypothesis that reduced prey availability stemming from prey defense behavior best explains the observations.

Both *T. pulligo* and *C. ligatum* show stereotyped escape behavior patterns when touched by a foraging *Pisaster giganteus*. Snails of both species begin repeated, violent 180° twists of the shell around the dorso-ventral axis the moment a tube foot contacts the snails' soft parts. If tube foot provocation continues, the snails release their grasp of the substrate and (usually) tumble away from the attacking sea star. This does not result in mortality because the snails can right

themselves very quickly. If at any time during an encounter the grasp of the tube foot is broken, the snails crawl away from the point of contact at top speed. In addition to this behavior pattern, *C. ligatum* uses the ventral side of the posterior part of its foot to maintain a thin slippery mucous layer over the dorsal surface of its shell. Apparently this layer makes it difficult for *Pisaster giganteus* to get a firm grasp of the snail's shell, thereby enhancing the grip-breaking effect of shell twisting. Furthermore, I observed that *C. ligatum* bite in response to contact with *Pisaster giganteus* in laboratory aquaria. Upon contact with sea star, the snail would raise its head and anterior portion of its foot off the substrate and come down on the surface of the sea star while making a quick biting motion with its radula. The star would respond by retracting the bitten ray and the snail would turn and move away from the star. While this response was observed on numerous occasions in the laboratory, I observed it only once in the field when a snail approached and touched an inactive sea star. *Tegula pulligo* does not maintain a mucous layer and has not been observed to bite.

To see whether predator preference or differential escape capability of the prey was responsible for the discrepancy between prey abundance and the presence of prey in the diet of sea stars, the escape behavior of individuals of both snail species was neutralized by placing them in isotonic $MgCl_2$ for 5 to 10 min. Snails which were not subjected to the narcotizing agent served as controls. Then the snails were taken into the field where actively foraging *Pisaster giganteus* were located. One control and one narcotized specimen of both snail species were placed directly in the path of the sea star, 5 to 10 cm in front of the leading ray. The identities of snails captured and eaten or those which escaped were recorded. Any snail which was not ingested, for whatever reason, was recorded as an escape. Because the granite outcrops on which the experiments were carried out provided few horizontal surfaces and wave surge was always present, narcotized snails could roll away as the sea star approached and were counted as having escaped. The stars were watched until the snails were captured or had successfully escaped. The positions of the four snails relative to the sea star were rotated for each trial. Similar sizes of both species of snails were used, and ranged from 16 to 20 mm basal diameter. Thirty-three trials were carried out over 4 days using SCUBA.

Did defensive behavior reduce the chances of being captured by foraging sea stars? The data in table 1 show that the answer is clearly yes. In both species, a higher percentage of the narcotized group was captured ($P < .01$ in both cases, chi-square test of independence). Control *C. ligatum* suffered significantly fewer captures than control *T. pulligo* ($P < .05$, chi-square test of independence) while both species suffered similar mortality when narcotized ($P > .05$, chi-square test of independence); apparently, the stars did not prefer one species over the other when the snails were narcotized. Field observations revealed that sea stars have difficulty holding onto the mucus-covered shell of *C. ligatum*, but not the shells of *T. pulligo*, providing an explanation for the less frequent capture of *C. ligatum*. Surprisingly, in none of the trials did I observe a biting response in control *C. ligatum*.

This field experiment shows that *C. ligatum* appears less frequently than *T.*

TABLE 1

CAPTURE FREQUENCY OF CONTROL AND EXPERIMENTAL *Tegula pulligo* AND *Calliostoma ligatum* EXPOSED TO FORAGING INDIVIDUALS OF *Pisaster giganteus*

	TREATMENT		CHI-SQUARE BETWEEN TREATMENTS
	Narcotized	Control	
<i>Tegula pulligo</i>	22 (66.7%)	13 (39.4%)	23.24 ($P < .01$)
<i>Calliostoma ligatum</i>	25 (75.8%)	5 (15.2%)	24.44 ($P < .01$)
Chi-square, between species67 (NS)	4.89 ($P < .05$)	

NOTE.—Each group comprised 33 individual snails.

pulligo in the diet of *Pisaster giganteus* because its defense mechanisms are more effective, not because it is less preferred. Moitoza and Phillips (1979) reached the same conclusion from laboratory experiments with the predatory asteroid *Pycnopodia helianthoides* and two species of its sea urchin prey, *Strongylocentrotus franciscanus* and *S. purpuratus*. There are few reports of field experiments showing that defensive behavior of prey reduces predatory mortality. Phillips (1977) observed that, in the field, the gastropod *Olivella biplicata* avoided being eaten by its predator *Pisaster brevispinus* by burying itself in sand. That more quantitative work in this area has not been done is somewhat surprising in view of the voluminous literature which deals with prey selection in generalized predators. Theoretical ecologists could benefit from a closer examination of predator-prey interactions under field conditions. This approach might not lead to a more precise definition of prey availability but would perhaps suggest ways to revise optimal foraging models to reflect more accurately conditions in nature.

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