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Preliminary Investigations of Burrow Defense and Intraspecific Aggression in the Sea Urchin, *Strongylocentrotus purpuratus*[1]

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ABSTRACT: Intraspecific aggressive burrow defense behavior of the sea urchin *Strongylocentrotus purpuratus* was observed. An urchin occupying a burrow defends its position against intruders by moving out from the burrow and pushing the intruder away. Only spines are used in this behavior. When the intruder begins to retreat, usually within minutes, the occupant returns to the burrow. The burrow defense behavior of *S. purpuratus* was compared to that of the tropical urchin *Echinometra lucunter*.

ALONG THE EXPOSED ROCKY AREAS of the west coast of the United States, the sea urchin *Strongylocentrotus purpuratus* forms dense aggregations in the lower intertidal and shallow subtidal areas where wave and current action are strong (Hedgpeth 1968). Many individuals of *S. purpuratus* live in burrows dug into the rock and remain in those burrows much of the time (Hedgpeth 1968, Dayton 1975). Urchins excavate their burrows using spines and teeth (Otter 1932). *Strongylocentrotus purpuratus* individuals probably rely extensively on drift algae as food (Ebert 1968). Members of the genus *Echinometra* also apparently burrow and feed in a similar manner (Russo 1977).

Recently Grünbaum et al. (1978) reported aggressive behavior in *Echinometra lucunter*, an urchin that also lives in rock burrows in lower intertidal, shallow subtidal areas in tropical waters. An *E. lucunter* in a burrow will push away or bite an intruder. This behavior usually results in eviction of the intruder (Grünbaum et al. 1978). In this study we consider a similar aggressive territorial behavior of *Strongylocentrotus purpuratus* and compare this behavior to the aggressive behavior of *E. lucunter*.

MATERIALS AND METHODS

This study was conducted during low tides at Bodega Head, Bodega Bay, California, between August 1981 and January 1983. The study site was a rocky intertidal pool that contained many urchins in crevices and burrows. Preliminary observations were made of urchin behavior when urchins used as intruders were taken from various sites in the tidepool and placed adjacent to urchins in burrows. To characterize the aggression response seven urchins in well-defined burrows were selected as defenders. A large (6.4 cm test diameter), medium (4.7 cm) and small (3.3 cm) urchin were used as intruders and each was tested against all seven defenders. In an additional experiment urchins were removed from their burrows and replaced by different urchins. The new defenders were allowed to occupy the vacated burrows for 5 min. Then the former inhabitant (now the intruder) was placed next to the burrow opening and responses were recorded. These methods were similar to those used by Grünbaum et al. (1978) to test agonistic behavior in *Echinometra lucunter*. In addition, the distribution of the urchins within the tidepool was observed. The behavior of urchins in burrows when presented with other animals or plants was also observed.

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TABLE 1

DURATION AND DISTANCE MOVED IN THE AGGRESSIVE RESPONSE OF INDIVIDUALS OF *Strongylocentrotus purpuratus* IN BURROW DEFENSE

DEFENDER NUMBER	DEFENDER TEST DIAMETER (cm)	INTRUDER I (6.4 cm test diameter) T1*	T2†	D‡	INTRUDER II (4.7 cm test diameter) T1	T2	D	INTRUDER III (3.3 cm test diameter) T1	T2	D
1	6.5	5	4	0.5	>10	No reaction		3	2	2.0
2	5.4	1	8	3.5	>10	No reaction		1	3	1.0
3	5.2	1.5	8	3.0	5	2	3.0	2	2	2.0
4	3.6	2	3	3.0	1.5	2	3.0	2	2	1.0
5	3.5	2	2	1.0	2	0.5	0.5	1	2	3
6	3.1	1.25	5	3.6	2	3	3.5	1	2	1.5
7	3.1	2	6	1.0	1	3	2.2	2	2	2.0

* T1 = time (min) before defense reaction occurred.
† T2 = time (min) spent in contact and in pushing intruder away.
‡ D = distance (cm) intruder was pushed away.

RESULTS

In our study site, urchins in their burrows were spaced such that the spines of one urchin were not in contact with those of another. Generally, the urchins we observed rarely waved tube feet or moved their spines, and spines were not oriented in any particular direction. If two urchins were closely spaced, the tube feet of each would periodically wave in the direction of the other, but the spines did not move. When an urchin (intruder) was placed in contact with an urchin in a burrow (defender) the following behaviors were observed: the intruder usually moved closer to the defender; in areas of contact spines of both individuals were directed toward the opponent; in noncontact areas spines often became erect and formed easily distinguishable rows; tube feet became active over the entire aboral surface of both individuals; no pedicellarial activity was observed in any instance of aggression; after a variable time period, usually a few minutes, the defender moved a few centimeters out of its burrow, pushing the intruder away; and when the intruder started moving away on its own and contact was broken, the defender moved directly back into its burrow. The entire behavioral sequence took only a few minutes.

The aggression response experiment showed that in 19 of 21 trials defenders exhibited the described aggressive response to intruders. Regardless of size differences between defender and intruders, the defender retained control of its burrow in all trials (Table 1). Larger defenders tended to react more slowly than smaller defenders. The average time of contact before the aggression response started (disregarding the two no-reaction trials) was 2 min (s.d. = 1.18). The average time duration of the aggression response was 3.2 min (s.d. = 2.1), and the average distance an intruder was pushed away from the burrow was 2.1 cm (s.d. = 1.1) (Table 1).

In the experiment in which the original burrow occupant was replaced by a different urchin and then used as the intruder, the new occupant invariably retained possession of the burrow (Table 2). In most trials the intruder and occupant were of approximately equal size. The observed aggressive responses were essentially the same as initially observed (Table 2), except that responses were not as strong (average distance traveled was 0.86 cm instead of 2.1 cm). In one trial the new defender was approximately one-half the size of the intruder (no. 3, Table 2). After 40 min the small urchin still retained control of a small corner of the burrow while the larger intruder occupied the remainder of the burrow.

Urchins presented with plant material immediately grasped the plants with tube feet and hauled them in close to or under the body. Spines were not used, and urchins did not emerge from their burrows. When presented

TABLE 2

BURROW DEFENSE BY NEW BURROW OCCUPANT AGAINST ORIGINAL OCCUPANT

TRIAL NUMBER	TEST DIAMETER OF NEW OCCUPANT	TEST DIAMETER OF ORIGINAL OCCUPANT (cm)	T2 (min)	D (cm)
1	4.5	4.9	3	1.5–2
2	2.0	3.3	7	1.5
3	2.5	4.7	40	0*
4	3.5	3.2	3	1
5	4.0	4.4	2.5	1
6	3.4	3.6	1	0.5
7	3.1	4.0	1	0
8	3.0	2.5	2	0.5
		Mean	2.8	0.86
		S.d.	2.0	0.56
		(except trial 3)		

NOTE: T2 = minutes spent in aggressive activity; D = distance in centimeters intruder was pushed.
* In trial 3 new occupant was unable to push intruder out of burrow. Both urchins occupied the burrow for the duration of the observation.

with *Tegula funebralis* or *Pachygrapsus crassipes*, urchins in burrows showed no response other than waving of a few tube feet.

DISCUSSION

Continued occupancy of a burrow by individual *Strongylocentrotus purpuratus* should be important to the urchin for several reasons. First, excavating the burrow requires energy, and an animal who made a burrow might be reluctant to give it up. Second, *S. purpuratus* lives in areas of strong waves and currents, and burrows are an effective means of protection from being swept away by water movements. Dayton (1975) has observed that when *S. purpuratus* individuals do leave their burrows they often fail to return. Finally, burrows can afford protection from many types of urchin predators, including fish (Nelson and Vance 1979), sea otters, sea stars, birds, and so forth (Moore 1966).

Major predators of *Strongylocentrotus purpuratus* include the sea star *Pycnopodia helianthoides* (Dayton 1975), sea otters (Lowry and Pearse 1973), gulls and other birds, especially in high intertidal areas (R. Pierotti, pers. comm.), and man (Tegner and Dayton 1977). Different species of urchins show various alarm or escape responses to the presence of predators (Moitoza and Phillips 1979). Individuals of *S. purpuratus* flatten their spines exposing the pedicellariae and sometimes move away from their burrows in the presence of *P. helianthoides* (Moitoza and Phillips 1979, Dayton 1975). An individual usually uses its pedicellariae for defense first and will not leave its burrow unless the sea star is within 5 to 10 cm (Dayton 1975). The observed aggressive behavior of *S. purpuratus* is obviously a different type of reaction than the escape response to predators. In our observations, pedicellariae were never used, and spines were directed toward the intruder.

In response to food, the urchins attached tube feet to algae and drew it to the body. This was a different behavior than the one elicited by contact with other urchins. The difference in urchin behavior, as described in this study, from that of urchins toward predators or food, lends support to the hypothesis that the present behavior is agonistic and caused by the need to defend the burrow.

In the case of *Strongylocentrotus purpuratus* burrow defense should occur in nature fairly frequently. Not all individuals in a given area have burrows. We observed many individuals in crevices and nestled among *Mytilus californianus*, and these individuals could act as natural "intruders." In addition, after "stampede" episodes following the presence of *Pycnopodia helianthoides* in an urchin bed (Dayton 1975), there should be an increase in homeless urchins looking for places to hide.

Although *Strongylocentrotus purpuratus* forms dense aggregations, our observations showed that individuals rarely touch each other. Rather, they stay far enough away so only tube feet make occasional contact.

The only other reports we know of, of aggressive territorial defense behaviors in urchins, are of *Echinometra lucunter* (Grünbaum et al. 1978). Specimens of *E. lucunter* also occur in rock burrows in areas of heavy surf. The territorial defense behavior of *Strongylocentrotus purpuratus* individuals shows similarities and differences to the agonistic behavior described for *E. lucunter*. *Echinometra lucunter* was often observed to use its Aristotle's lantern to bite intruders (Grünbaum et al. 1978). We never observed biting behavior in *S. purpuratus*. Rather, the occupant moved out of its burrow and simply pushed the intruder away. By moving out of the burrow and pushing against the intruder, the normal occupant of the burrow consistently maintained its burrow in our experiments. The burrows of *S. purpuratus* usually fit closely around the inhabitant, so much larger intruders cannot usually occupy the burrow of a small individual, even if the occupant were evicted. Smaller urchins, however, also appeared to be more aggressive than larger individuals, and large intruders were consistently driven away by them.

In experiments with *Echinometra lucunter*, Grünbaum et al. (1978) reported that original occupants were able to reclaim burrows after new occupants had been introduced to the burrows. The results from our similar experiments with *Strongylocentrotus purpuratus* showed that with this species the new occupant was, in most cases, able to retain control of the burrow against the original occupant. We do not yet know if the observed aggressive burrow defense behavior of *S. purpuratus* is only intraspecific or if it is also interspecific. In intertidal, rocky, wave swept areas *S. purpuratus* is not likely to come in contact with urchins of other species, except an occasional *S. fransiscanus*. *Strongylocentrotus fransiscanus* is not typically a burrow dweller (Tegner and Dayton 1981), and adults are much larger than adults of *S. purpuratus*. Although *S. fransiscanus* can push the shorter-spined *S. purpuratus* away when contact is made (Schroeter 1978), there is no reason to expect frequent interspecific burrow defense conflicts in nature.

Strongylocentrotus purpuratus is an abundant member of subtidal kelp forest communities (Tegner and Dayton 1981). We do not yet know if the defense behavior we observed is also characteristic of these subtidal populations of *S. purpuratus*. If it is characteristic of both intertidal and subtidal groups, the importance of maintaining a burrow may be related primarily to protection from predation, as in the case of *Centrostephanus coronatus* (Nelson and Vance 1979). If the burrow defense behavior is characteristic primarily of intertidal individuals, the behavior would suggest a strong protective response to physical stress resulting from wave action.

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