Escape Response of the Sea-Anemone *Anthopleura nigrescens* (Verrill) to its Predatory Eolid Nudibranch *Herviella* Baba spec. nov.

BY

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INTRODUCTION

Eolid nudibranchs are generally associated with various coelenterates on whom they feed, and whose non-everted nematocysts they store. The eolids have evolved many different adaptations to their coelenterate prey (Hyman, 1967). But coelenterates are not always a passive prey in the association.

Swimming in the anemones *Stomphia coccinea* Müller and *Actinostola* spec. nov. (Actinostolidae) in contact with *Aeolidia papillosa* (Linnaeus, 1761) (Aeolidiidae) has been reported as a possible escape response (Robson, 1966). A similar response is also elicited in these anemones through electrical stimulation, contact with certain sea stars, and in *Actinostola* spec. nov. through contact with *S. coccinea,* but not vice versa (Yentsch & Pierce, 1955; Sund, 1958; Ross & Sutton, 1964a, 1964b, 1967; Ward, 1965; Robson, 1966; Ross, 1967). Substances of a different chemical nature, extractable from the sea star and the eolid, cause swimming in the anemones, but no chemical could be demonstrated in the response of one species of anemone to the other.

The significance of the various swimming responses of these anemones is not known. These actinostolids are deep-sea species, at present not accessible to field work; therefore no information is available on their predator-prey relationships in nature. The sea stars apparently do not prey on these anemones. Robson (1966) considers the anemones' response to the eolid an escape response because the geographic distribution of both is broadly related, and in the aquarium *Aeolidia papillosa* will bite into these anemones. Ross (1967) states that the eolid and the anemones are not frequently found living close together in the field. *Aeolidia papillosa,* however, is not restricted as to depth. It is common in the intertidal area and information is readily available on its feeding habits there, where it is known to feed on a variety of anemones and even hydroids (Stehouwer, 1952; Braams & Geelen, 1953; Miller, 1961). That is, it is not at all monophagous. The fact that it is not frequently found near the actinostolids in the field may be due to escape of the anemones from the vicinity of the eolid. At the same time, the fact that the eolid will bite into the actinostolids in the aquarium may be an attempt of a polyphagous predator to feed on prey with which it has no contact in nature.

The present is a report on the anemone *Anthopleura nigrescens* (Verrill, 1928) (Actinidae) and the eolid *Herviella* Baba spec. nov. (Favorinidae). It is hoped that it will shed further light also on the previous case.

ANIMALS and HABITAT

Herviella spec. nov. mimics *Anthopleura nigrescens* and can be mistaken for the anemone. Both species were found in the same habitat in the intertidal area on a narrow strip of beach near Kewalo Basin, Honolulu, Hawaii. The anemones were abundant on loose rocks which lie on a bottom of mixed sand and gravel, often exposed during low tide. The column is equipped with suckers which attach an "armor" of gravel and other foreign material. When above water, the anemones close and contract, and are thus completely shielded by the "armor".

The eolids were found between February and August, 1966, mostly in pairs or larger groups, on the underside of rocks with or without anemones. During a brief inspection in the field at night eolids were also observed crawling above the rocks, and an eolid was encountered in the midst of preying on a specimen of *Anthopleura nigrescens* which had its pedal disk detached from the rock.

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Provisions for extensive field work at night could not be made at the time. Eolids were not observed to feed in the field during the day. Like the anemones, eolids were often found above water level. They reproduced throughout the period noted above. A few tiny specimens, as small as 7 mm long compared to up to 40 mm in adults, were collected in June, indicating that occurrence in the intertidal area is not restricted to the reproductive phase. Neither species was found on the fringing reef away from shore, or the sand between reef and shore.

LABORATORY OBSERVATIONS

In the aquarium eolids crawled up to water level whenever the air-pump was stopped; they descended however to feed on anemones attached to the floor of the aquarium. They fed on the column and tentacles of *Anthopleura nigrescens,* at night as well as during the day, but would not feed on the only other unidentified anemone available in the eolids' natural habitat. The eolids approach *A. nigrescens,* touch it repeatedly with the tentacles, bite and attach with the jaws.

Anemones collected in the field and allowed to attach to the aquarium floor were found to be detached from the substratum when being preyed upon by the eolids. But when it was noticed that (a) detachment of the anemone occurred too rapidly to be attributable to destruction of the attachment apparatus; (b) a preying eolid does not remain constantly attached to its prey, but separates from the anemone every few minutes, and then reattaches to it; (c) an anemone which detached from the substratum due to eolid predation, reattaches readily when removed from its predator; and when this sequence of events was visualized under natural conditions, the possible significance became apparent.

Therefore anemones were brought into the aquarium still attached to the original rocks on which they had been found in the field, and eolids were allowed to feed on them. It was found that when an eolid attaches to an anemone, the anemone responds by gradually shedding the "armor" and detaching the pedal disc, all in a few minutes. The eolid may lift the front part of its body and carry the detached anemone upwards with it. For some reason, eolid and anemone eventually separate. The released anemone rolls or drops off the rock to the floor of the aquarium, where it remains lying on the column. The fall is often interrupted by the falling anemone attaching its tentacles to the rock, and sometimes even settling on the pedal disk, or crawling on the column, then detaching and resuming the downfall.

Anemones which dropped off the rock, right themselves and attach to the floor of the aquarium in a few minutes to half an hour at the most. The eolid on its part very soon turns to feed on another anemone in its vicinity. Thus, the intermittent feeding of an eolid on a single anemone, which occurs with anemones attached to the flat horizontal floor of the aquarium, inevitably transforms into successive feeding on several different anemones when these are attached to their natural, irregularly shaped substratum.

Cases of partial detachment of the pedal disk, where the anemone reattached on the same spot, without detaching all of the pedal disk, as well as cases of delayed detachment only after separation from the predator, also occurred. A single case was observed where an anemone crawled on the pedal disk up the rock and away from the eolid before it detached. Out of 67 recorded observations on anemones bitten by an eolid, 66 detached within minutes. In the one case which did not, the eolid fed for over an hour on the tips of the tentacles only, and the anemone shed part of its "armor".

The exact mechanism of detachment could not be determined by simple observations. However, in a few cases, carefully observed, it was found that detachment began by contraction of the pedal disk and column and shedding of "armor" on the side attacked by the eolid, and uplifting of the pedal disk on the opposite side, with the anemone eventually tilting and falling away from the eolid.

It is not known yet what is the direct stimulus for shedding the "armor" and detachment of the pedal disk of *Anthopleura nigrescens* preyed upon by *Herviella* spec. nov. The anemones do not detach to simple mechanical injury caused by prodding stainless-steel needles through the column.

To lend further support to an interpretation of the response of *Anthopleura nigrescens* to *Herviella* spec. nov. as an escape response, it was important to assess the survival value of the response. Therefore, a simple test was conducted: three groups of 10 anemones each (a), (b), (c) were obtained and placed in three small, separate, equal aquaria respectively. Groups (a) and (b) were obtained by mechanically scraping anemones off a rock, taking care not to include specimens with injured pedal disk due to scraping. Group (c) was obtained by allowing eolids to feed on anemones attached to the rock, and collecting anemones which escaped. Subsequently, 10 eolids were added to group (a) to assess maximum possible damage due to predation when ultimate escape is not possible. Group (b) was kept as controls, which had not been, and were not subsequently, subject to eolid attack at all. Group (c) was kept to assess possible longterm effects induced by eolids prior to escape. The answer to these simple questions is not apparent *a priori,* because no one had studied them in these species. The test was terminated at the end of 17 days.

It was found that in group (a) the eolids gradually devoured and completely destroyed the anemones in 7 days; in groups (b) and (c) all anemones survived in seemingly perfectly good condition.

This simple test shows that predation without escape may proceed to the extent of total destruction of the anemones, whereas anemones which escape are as perfectly viable as controls which had not been attacked at all.

DISCUSSION

A natural predator-prey bond between the anemone *Anthopleura nigrescens* and the eolid *Herviella* spec. nov. is indirectly indicated by: 1. occurrence of both in a very limited area in the same habitat; 2. a remarkable mimicry between the two; 3. the occurrence of young specimens of the eolid in the same habitat; 4. the fact that in the aquarium *Herviella* spec. nov. feeds on *A. nigrescens* to complete destruction of the anemone; it does not feed on, or mimic, the only other anemone available in the same restricted area; and eolids driven to the surface by cutting off the air supply will descend to feed on *A. nigrescens* attached to the aquarium floor. Also a specimen of *Herviella* spec. nov. was actually encountered in the field at night, with its mouth attached to a specimen of *A. nigrescens.*

The detachment of the anemone to predation by the eolid is considered an escape response in view of the survival value of the response in the laboratory under conditions simulating those in the field. The *Anthopleura nigrescens* which was preyed upon by *Herviella* spec. nov. in the field also had its pedal disk detached from the rock.

The separation of predator and prey, which is an essential link in the sequence of events which result in escape of the anemone, is possibly due to slow writhing on the part of the anemone, or to the eolid's manner of feeding.

Anthopleura nigrescens which detaches from its rock in nature cannot attach to the loose bottom sand, and water movement, not involved in the aquarium, is bound to play a role in the intertidal area. In fact, a detached *A. nigrescens* was encountered in the field, lying on the sand above water level at night, as well as one being carried by surf during the day. This is not to suggest that their detachment was necessarily due to eolid predation. Nor is it being suggested that escape from its predatory eolid, *Herviella* spec. nov., is the sole function of the ability of *A. nigrescens* to shed foreign material attached to its suckers, and detach the pedal disk.

The variety of adaptations of eolids to their coelenterate prey suggests a very ancient association between these two groups. The response of *Anthopleura nigrescens* to *Herviella* exhibits certain similarities to the response of the Actinostolidae to *A. papillosa.* It is perhaps too early to say whether these similarities are superficial only, or not. The eolids belong to two different families, whereas the Actiniidae belong to the subtribus Endomyaria, and the Actinostolidae to the Mesomyaria. This raises the question whether these are two isolated cases. It may be worthwhile noting that TARDY (1962, 1965), who was interested in eolids but paid little attention to the behavior of their coelenterate prey, notes that anemones preyed upon by several eolids he was studying, finally detached.

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