The Temporal Structure of Behavioral Interactions in *Hermissenda crassicornis*

(Opisthobranchia)

BY

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(2 Text figures)

INDIVIDUALS OF THE EOLID NUDIBRANCH, *Hermissenda crassicornis* (Eschscholtz, 1831) engage in aggressive interactions with conspecifics. ZACK (1975) described the sequential structure of these interactions in detail but provided little information on their temporal structure other than overall durations. The purpose of this report is to present additional, more detailed temporal information on these interactions to add to the description of them. These interactions take on several forms that may be placed in a series graded according to the behavior patterns displayed by the participants (ZACK, 1975). At the lowest level (Zack's level Ia) two animals meet, contact one another briefly, and then move apart. In the most intense and lengthy interactions (Zack's level IIIb), two animals meet in a head-to-head orientation, engage in repeated and reciprocal tentacular contact ("flagellation"), move into a right-side-to-right-side position ("sidling"), and then lunge and bite at one another before they move apart. In this study, three types of interactions are analysed: 1) those with sidling (which in all cases was preceded by flagellation), 2) those without sidling but with flagellation, and 3) those with neither sidling nor flagellation.

The animals observed in this study were obtained at low tide from the rocks around the U.S. Highway 1 bridge abutment at Elkhorn Slough (Moss Landing, California). The animals were collected in June, 1979, and taken to the Long Coastal Marine Laboratory (Santa Cruz, California) for observation. In the laboratory, the animals were individually housed in small plastic cups approximately 6 cm in diameter and 7 cm deep. Each cup had its own supply of fresh, running sea water from a holding tank on the station property. The nudibranchs were fed fresh mussel (*Mytilus californianus*) every other day at which time material remaining from the previous feeding was removed.

To observe their interactions, pairs of animals were placed in 1 to 2 cm of sea water in a 5 to 6 cm diameter watch glass. The ensuing interactions were recorded in writing or with a SONY Videorover (AV-3400 and AVC-3400) for detailed temporal analysis. For purposes of temporal analysis, the onset of an interaction was taken as the first physical contact between the animals and the end when the animals were separated by 1 cm or more.

The temporal structure of interactions with sidling is shown in Figure 1. The longest part of these interactions

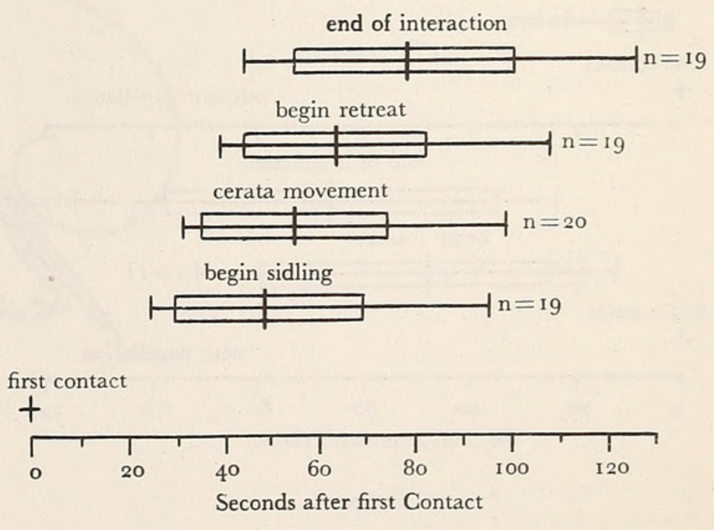

Figure 1

The temporal structure of head-to-head interactions with sidling. The mean time of occurrence, standard deviation (open bar), range, and sample size (n) are shown for each event is from initial contact to the beginning of sidling, that is, when the animals engage in flagellation and slowly advance toward one another. The beginning of sidling is defined as the time when the animals' bodies first begin to overlap at the head, right-side-to-right-side. Forward movement stops when each animal has his head positioned approximately over the other animal's gonopore on the right side. At this point there is typically a brief pause just before both animals erect and elongate their cerata (Zack's "cerata movement"). One or both animals then begin biting and lunging at the other. One animal then turns away from the other and begins to move away, marking the beginning of retreat. The other animal typically follows briefly while lunging once or twice before the retreating animal moves out of range. Although the animals are poised in copulation-like posture during sidling, it seems clear, as Zack suggested, that these interactions are not copulatory since the time between initiation of sidling and cerata movement is on the average less than 10 sec. In opisthobranchs, copulatory durations are characteristically a matter of many minutes or hours rather than seconds (*e.g.* BEEMAN, 1970; KUPFERMANN & CAREW, 1974).

Interactions leading to sidling most frequently followed initial head-to-head contact (ZACK, 1975). Only 6% of the 18 interactions on the videotapes that did not begin head-to-head lead to sidling. On the other hand, not all head-to-head interactions (46% of 39 on videotape) lead to sidling. These interactions were of two types, those with flagellation and those without, and these were temporally analysed for comparison with those head-to-head interactions that lead to sidling (Figure 2). Those interactions without sidling but with flagellation were not significantly different in overall duration from those with sidling and flagellation ($t = 1.148$, 27 df, $p > 0.10$). Also, the time from first contact until sidling began or one animal began retreat was not significantly different between the two types of interactions ($t = 0.36$, 30 df, $p > 0.36$) which indicates that when flagellation occurs it has some typical duration. Flagellation was usually terminated when one animal began lunging and biting at the other. The time from the beginning of retreat to the end of the interaction did not differ significantly between the two types of interactions with flagellation ($t = 0.42$, 27 df, $p > 0.33$).

Interactions without flagellation were significantly shorter than those with sidling and flagellation ($t = 8.02$, 32 df, $p < 0.0001$) and those with flagellation but no sidling ($t = 4.62$, 23 df, $p < 0.0001$). These encounters were characterized by one animal beginning to lunge at the other immediately after initial contact, hence the time from initial contact to the beginning of retreat was only a matter of a few seconds. The time from beginning of retreat to the end of the interaction was not significantly different from that for interactions with flagellation but without sidling ($t = 0.203$, 23 df, $p > 0.42$) or that for interactions with sidling and flagellation ($t = 0.777$, 32 df, $p > 0.22$).

These results are in general agreement with those of ZACK (1975) and show that those interactions involving sidling and, in particular, flagellation are substantially longer than those without these behavior patterns. It appears particularly likely that flagellation reflects efforts on the part of each participant to assess the aggressive motivation and possibly size of the other individual. Zack has shown large size to be an important variable determining success in these interactions. In addition, although these encounters have never been observed to end in copulation by Zack or this author, their form suggests that given the appropriate context and motivation on the part of the participants they may lead to copulation. Flagellation and sidling may also be means of assessing willingness to mate. Clearly, more detailed observations of these interactions are needed both in the field and under controlled laboratory conditions before reasonable proximate and ultimate explanations for their occurrence and form can be proposed.

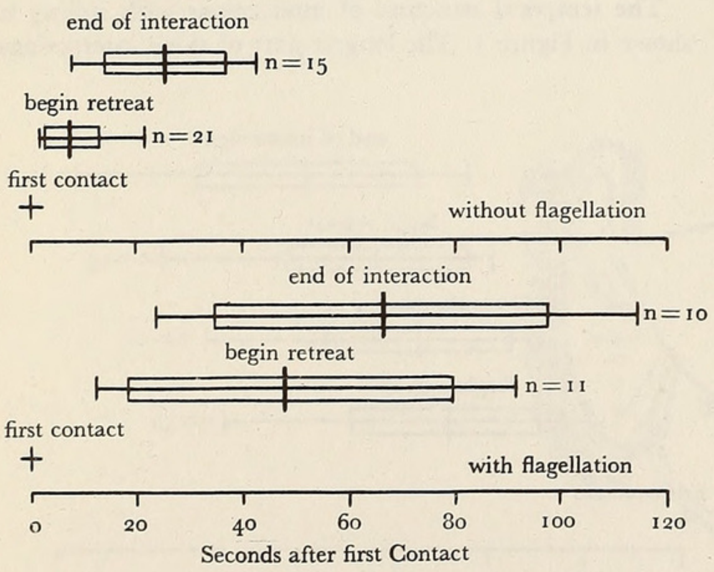

Figure 2

The temporal structure of head-to-head interactions without sidling. Above, interactions without flagellation; below, interactions with flagellation. The mean time of occurrence, standard deviation (open bar), range, and sample size (n) are shown for each event

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