Patterns of Copulation in the Simultaneous Hermaphrodite *Aplysia dactylomela* (Gastropoda: opisthobranchia)[1]

by

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ABSTRACT

The numbers of observations of Aplysia dactylomela found alone or in contact did not differ during the morning or afternoon, or with group size. Significantly more observations of copulation occurred in the morning, than in the afternoon. These results were confirmed in a subsequent longitudinal study. Most aplysia copulated between 3 and 7 times. Four sea hares were predominantly sperm recipients and five were predominantly donors; 17 were neither. Frequency of copulation was positively correlated with the number of different partners; sperm donors had fewer partners than sperm recipients. The significance of these findings for species adaptation is discussed.

Index terms: Aplysia dactylomela; social behavior; sex role; diel factors; copulation

Aplysia have been used extensively in neurophysiological and biochemical studies in the laboratory Thompson (1976), Fentress (1970), and Kandel and Kupfermann (1970), and behavioral investigations (Aspey and Blankenship (1976), Audesirk (1975), Carew and Kupfermann (1974), Frings and Frings (1965), Hamilton and Ambrose (1975), Jacklet (1972), Johan-Parwar (1972), Kupfermann (1968, 1974), Kupfermann and Carew (1974), Lederhendler et al. (1975), Lee (1969)) are increasing in number. Although hermaphroditism is found in several species, simultaneous hermaphrodites with internal fertilization are rare. As this species is a simultaneous hermaphrodite, it offers a unique opportunity to investigate underlying mechanisms for assumption of one or more sex roles. This study is based on laboratory data obtained during field trips to Bimini, The Bahamas in May 1964, and June-July 1970.

Animals were collected in the lagoon of Bimini and returned to 1000 liter concrete tanks in the Lerner Marine Laboratory. These tanks were supplied with sea water pumped from the ocean. The behavior of groups of animals was observed during half-hourly spotchecks from 5:30 to 11:30 AM and 12 and 11:30 PM. Observations were made of individually tagged animals as to their social activity: alone, in contact, or copulating. The sex role, either as sperm donor or sperm recipient was noted when copulation occurred. (See Lederhendler et al. (1975) for further procedural details).

Aplysia may copulate in pairs, in triplets, or in chains (Eales 1921). In the last two cases, an individual can both give and receive sperm at the same time, and thus perform a dual role. Reciprocal copulation by a pair

has not been reported in the literature, but recently Lederhendler (1976) has reported that these do occur sufficiently frequently to be noted.

In earlier field work, (Lederhendler et al. 1975), it was found that the time of day was related to whether animals were found together or alone. This temporal pattern was confirmed (Table 1). Group size did not influence the number of observations in which animals were found alone; the numbers of such observations in the morning and afternoon did not differ ($X^2 = 0.6$, $P > .05$). Similarly, there was no effect of group size or time period on observations in which animals were in contact ($X^2 = 1.6, P > .05$). However, in cases where copulation was observed, there were significantly more such observations in the morning than in the afternoon ($X^2 = 4.20, P < .05$). Group size was not a relevant factor.

The above data were derived from cross-sectional observations. A subsequent field trip in June and July 1970 confirmed them in longitudinal data of groups of 5-10 animals during a three week period. Of 11 animals that were both in contact and copulating, 10 showed more of both behavior items during morning observations than afternoon observation. Further, of 7 animals that were observed in contact only, and not observed copulating, there was no difference between morning and afternoon frequencies (4 in the morning, 3 in the afternoon). Of 20 animals which were observed copulating, 19 were seen engaged in such activity more frequently in the morning, than in the afternoon. When the entire sample of 37 animals was combined, 33 showed one or both of these activities more frequently in the morning, than in the afternoon (binomial test, $P < .001$)

During the 1964 research, we found that most aplysia were observed copulating between 3 and 7 time (Fig. 1). In order to make statistical

comparisons of sex roles, only animals that copulated a minimum of 5 times were included in the analysis. Thus, if an animal assumed sperm donor or recipient role consistently, it would be significant at least at the P = .109 level, in the instance of only 5 observations of copulation. Using this criterion, 4 animals were recipients more often than donors, 5 were donors more often than recipients, and 17 were not consistent. Thus, most of the animals showed no difference in sex role, as might be expected of a simultaneous hermaphrodite. The distribution of number of times animals were observed copulating suggested that there might be a relationship between that variable and adoption of a sex role.

The frequency of copulation was found to be positively correlated with the number of different partners (Spearman RHO= 0.86, P = .01). Sperm recipients copulated with a greater number of different animals than did the sperm donor. When the relationship was plotted (Figure 2), the animals which assumed consistent sex roles were in a different part of the distribution than were animals that were not consistent. The group median for number of different partners (3.5 partners) and the group median for a number of copulations observed (5.5 copulations) segregated 7 of the 9 consistent sex role animals in the upper right quadrant of the graph. In other words, 4 of the consistent sperm recipients and 3 of the 5 consistent sperm donors copulated frequently and with many different partners. A further comparison of the 5 consistent sperm donors and 4 sperm recipients showed that sperm recipients had statistically more partners than did the sperm donors (Mann-Whitney U=3, P =.056).

The finding that sperm recipients receive sperm from many different animals, while sperm donors are more likely to give sperm to a small number of animals suggests a selective reproductive process that may be of adaptive significance (Parker, 1970). This behavior may increase genetic variability in the least "expensive" way. If the sperm recipient is also the egg-laying animal, its energy is needed for that process. The sperm donor spends its energy in searching for sperm recipients. Thus, energy is used efficiently by the donor in searching out partners and by recipients laying eggs, and genetic variability is increased. It is possible that the amount of sperm a sea hare receives or donates might provide an hormonal feedback in a system regulating frequency of copulation, sex role and egg-laying. Lederhendler (1976) has found that the interval between egg-laying in the laboratory by sea hares maintained individually is 3 days. The longer animals remain alone, the greater the interval range becomes.

These observations and those reported in this study suggest that the storage of sperm from many donors may create a pool from which sperm may respond to the maturation of eggs prior to their being laid or to some hormonal concommitants of these processes by roving out of the storage chamber and fertilizing the eggs before they are laid. The movement of the sperm may stimulate the laying of the eggs. When the sperm have been stored a long time, although they may still be able to fertilize the eggs the time required for the entire process may become prolonged.

These observations do not explicate the processes underlying the assumption of sperm donor or recipient roles. However, they do indicate the possibility of a relationship between fertilization, egg-laying and the copulatory role assumed.

TABLE 1

SOCIAL BEHAVIOR OF Aplysia dactylomela IN THE LABORATORY (BIMINI, 1964)

GROUP SIZE	NUMBER OF OBSERVATIONS	OBSERVATIONS IN WHICH SEA HARES FOUND		
		ALONE	CONTACT	COPULATING
			AM	
4	4	2	1	3
5	22	19	13	18
6	6	6	3	6
7	11	9	7	7
8	3	3	0	3
			PM	
5	9	7	6	5
6	16	16	7	9
7	7	7	3	4

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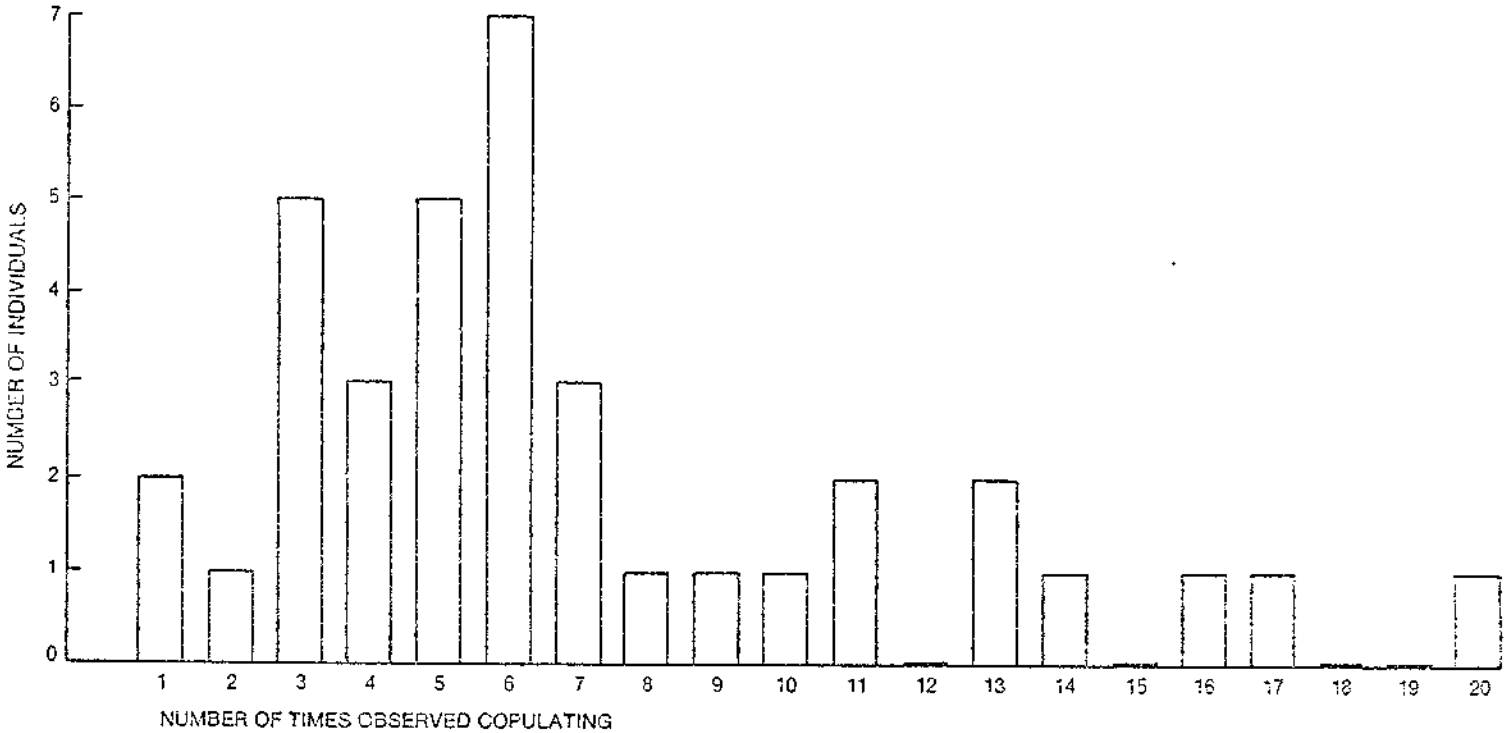
NUMBER OF OBSERVED COPULATIONS BY INDIVIDUAL SEA HARES (*Aplysia dactylomela*)
(MAY, 1964; N=37)



RELATIONSHIP BETWEEN
FREQUENCY OF OBSERVED COPULATION AND NUMBER OF PARTNERS
IN *Aplysia dactylomela* (MAY, 1964)