

## MATE- AND OVIPOSITION-INFLUENCED HOST PREFERENCES IN THE CORAL-FEEDING SNAIL *CYPHOMA GIBBOSUM*<sup>1</sup>

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**Abstract.** Mate-searching has been hypothesized to influence the host preferences of small grazers, yet no previous field data have examined this idea. I examined the host preferences of *Cyphoma gibbosum*, a generalist gastropod that feeds on gorgonian corals, and tested if mate searching or oviposition preferences contributed to variation in host preferences. I constructed experimental reefs containing three species of gorgonian corals at uniform densities and placed snails on these reefs either alone or in groups of four. Half of the groups of snails were single-sexed while the other half contained two snails of each sex. I observed snail movements by conducting daily censuses of the reefs and constructed transition matrices describing the movements of snails in each treatment among the three species of coral.

Snails showed preferences for some hosts over others, and these preferences varied due to both mate searching and oviposition. Snails preferred to occupy *Briareum asbestinum* over *Plexaurella dichotoma* or *Pseudopterogorgia acerosa*, but these preferences were strongly influenced by previous experience. Moreover, females tended to move from *B. asbestinum* to *Plexaurella dichotoma* to oviposit, and back to *B. asbestinum* afterwards. Finally, both males and females moved frequently towards members of the opposite sex, in order to copulate, which influenced their distribution among hosts.

These data reveal that behaviors associated with mating can influence host preferences and need to be considered in understanding host utilization patterns.

**Key words:** aggregation; *Cyphoma gibbosum*; foraging ecology; gorgonian corals; grazing; habitat; host quality; mate-influenced host preferences; mating opportunities; movement patterns; multiple hypothesis testing; oviposition preference; sex-specific foraging behavior.

### INTRODUCTION

The host preferences of small grazers may be influenced by a variety of factors including food quality, risk of predation (defined generally to include parasitism), risk of physical disturbance, and social interactions because they must receive both suitable habitat and food from a host. While studies have emphasized the influences of food quality (Caswell and Reed 1976, Damman 1987, Hay et al. 1987), predation (Jaenike 1985, Damman 1987), and physical disturbance (Holdren and Ehrlich 1982) on host preferences, no field experiment has examined the influence of social interactions (Jaenike 1990). Tests of several influencing factors at the same time are equally rare, but are logical next steps in this ongoing debate (Quinn and Dunham 1983, Courtney 1988, Janzen 1988). These multiple-factor tests will be especially informative given that several factors are probably acting in most systems.

While much attention has been focused on the quality of hosts as food and, more recently, their quality as refuges against predators, the influence of social interactions on host preferences has been largely ignored. To date, only theoretical work by Colwell (1986a, b) has examined in detail the role of social interactions

in influencing host preferences. Colwell (1986a) developed a quantitative model that demonstrated that specialization can evolve in small grazers if it increases their chance of encountering mates. Since specialists have fewer potential hosts, they have a greater probability of sharing a host with a conspecific. Many small grazers have limited movement capabilities, and consequently their reproductive output may be limited by mating opportunities. Colwell (1986b) also produced evidence from hummingbird flower mites (Family Ascidae; Genera *Proctolaelaps* and *Rhinoseius*) that selection, through increased mate-finding, may have led to host specialization. This selection is frequency dependent, where the “best” host on which to specialize is that preferred by potential mates. Under this frequency dependence, grazers may be better off choosing a host that is poorer in food or refuge quality if that host is more likely to have potential mates in residence. Therefore, host recognition systems, drift, and other stochastic processes that created a preference for the “suboptimal” host may be maintained or even strengthened through social interactions. The experiment presented here is the first field test of the mate-influenced host preference hypothesis.

*Cyphoma gibbosum*, a generalist gastropod, was chosen to examine the influences of both social interactions and inherent host quality (attributes of the host,

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including its quality as a food and as a refuge against predation and physical stress, that are independent of the presence or absence of other grazers) on host preferences. This snail offers several advantages for testing the mate-influenced host preference and other host preference hypotheses. First, its shell is a suitable substrate for non-invasive individual marking. Second, it is relatively immobile, allowing long-term tracking of individuals. Finally, it is a generalist so that variation in host preference can be used to examine the effect of social interactions on those host preferences.

The host preferences of *C. gibbosum* have been measured at several sites around the Caribbean Sea and differ widely (Birkeland and Gregory 1975, Hazlett and Bach 1982, Harvell and Suchanek 1987, Lasker and Coffroth 1988, Lasker et al. 1988). These differences were not an artifact of variation in the host populations; each study accounted for host densities when calculating preferences, and similar host species were available. Lasker and Coffroth (1988) also demonstrated that there can be wide variability in host preferences of this snail among sites even within an area as small as the Caribbean coast of Panama. Moreover, they showed that the preferences at a given site can vary from year to year. They speculated that part of the variability may result from social interactions between *C. gibbosum* individuals. Like many other gastropods, these snails follow mucous trails left by conspecifics (Gerhart 1986) and aggregate (Birkeland and Gregory 1975, Gerhart 1986). While Gerhart (1986) concluded that aggregations are most likely to benefit snails by decreasing predation risk, he also speculated that individuals might aggregate in order to find mates. I was able to test the latter hypothesis using data gathered to answer the following main questions of this study:

- 1) do males and females differ in their host preferences?
- 2) do females have different preferences near oviposition than at other times?
- 3) what is the effect of the presence of conspecifics on host preferences? and
- 4) does this social effect depend on the sex of the conspecifics?

To make these comparisons more powerful, I controlled for inherent host qualities by: (1) using host species that differed widely in chemistry, colony structure, and color, and therefore probably differed in their host qualities; (2) controlling the host densities and diversities; and (3) statistically accounting for host preferences before analyzing the differences due to social environments.

## METHODS

### *Study organism*

*Cyphoma gibbosum*, the flamingo tongue, is an ovulid gastropod that lives sub-tidally and is common on many Caribbean and southern Atlantic coral reefs. This

snail is a generalist grazer of gorgonian corals (Order Scleractinia), accepting many, if not all, species of gorgonian (J. P. Nowlis, *personal observation*). Adults are dioecious and do not seem to change sex once full grown (*personal observation*). All adults live and feed on gorgonian corals, and females oviposit encapsulated eggs onto their surface. Oviposition occurs roughly on a lunar cycle, although individual females can lay several egg masses within a cycle (*personal observation*).

The eggs develop into veliger larvae while still encapsulated on the surface of the coral colony, and the encapsulation probably keeps them from interacting with the colony directly. Roughly a week and a half after oviposition the larvae hatch out of the capsules and spend an undetermined length of time feeding in the plankton (Bandel 1973). The larvae metamorphose into juveniles and gradually grow to adult form. Many tiny (<5 mm) juvenile *C. gibbosum* can be found on gorgonian coral colonies. They are rarely or never seen on any other substrate (J. P. Nowlis, *personal observation*), suggesting that larvae settle specifically onto gorgonian colonies. Juveniles tend to hide under branches of the coral colonies during the day and remain on the same colony for long periods (Harvell and Suchanek 1987, *personal observation*). In contrast, adults are visible during the day and move frequently between coral colonies. Accurate measurements of movement patterns among a limited set of host species is possible with adults because *C. gibbosum* are abundant and each individual moves frequently.

### *Study site*

I performed the following experiments at the now-defunct West Indies Laboratory, Saint Croix, U.S. Virgin Islands, during the summer of 1989. I collected *C. gibbosum* from the back reef of Teague Bay (0–5 m depth) and the fore reef of Salt River Canyon (8–15 m depth). Both areas have dense gorgonian assemblages with abundant *C. gibbosum* populations. I set up the experiment itself in the sand bed near the back reef of Teague Bay. Although I collected *C. gibbosum* from many species of gorgonian coral, I found the majority on *Briareum asbestinum*. *B. asbestinum* was quite common at both collection sites.

### *Experimental techniques*

I individually marked each snail in the laboratory by gluing a colored and numbered bee tag (from Chr. Graze K. G., Weinstadt, Endersbach, West Germany) to its shell using Elmer's Wonder Bond Plus (Borden, Columbus, Ohio, USA). I then placed each snail in a 5% by volume solution of methanol in sea water. After 10 min I was able to identify each snail's sex with only a gentle tug on its foot. Males and females have distinct copulatory organs: a penis and genital opening, respectively (Ghiselin and Wilson 1966). In the rare cases in which a snail was not relaxed after 10 min, I returned it to the running sea water system for 30 min to 1 h

before making a second attempt. Although methanol is a potentially toxic chemical, it is also commonly used as an anesthetic. Methanol did not seem to have long-term effects; few snails died of causes other than predation over the course of the summer, and snails returned to seemingly normal behavior almost immediately upon their return to the running sea water system.

### Experimental design

Since *C. gibbosum* will accept most species of gorgonian corals, it would be virtually impossible to measure their preferences for all possible hosts, especially because a snail's preferences can vary depending upon its previous host. Therefore, I constructed experimental reefs using constant densities of only three gorgonian coral species: *Briareum asbestinum* (Family Briareidae), *Plexaurella dichotoma* (Family Plexauridae), and *Pseudopterogorgia acerosa* (Family Gorgonidae). These species were distinct from each other in their color, structure, and chemistry (Gerhart 1983, W. Fenical, *personal communication*). Therefore I assumed they represented different inherent host qualities. I pooled the observations of snails on *P. acerosa* with those of snails on no host for some of the data analyses due to the rarity of both types of observations.

I constructed experimental reefs using either one or four concrete blocks (each 0.4 m × 0.2 m × 0.2 m), and attached a single 0.3 m tall branch from each of the species of gorgonian corals to each block. All corals transplanted well and most even survived a hurricane between the conclusion of this experiment and the next summer (J. P. Nowlis, *personal observation*). I attempted to array the corals so that a snail on any coral branch was equally near to branches of each of the three species of coral, including the species on which it resided at the time. Since this arrangement was not strictly possible, I randomly assigned one of three distribution patterns of host species to each reef. The reefs were placed in the sand a minimum of 10 m away from the natural reef (Fig. 1). Within each row I also spaced the reefs 5 m apart and alternated between the two sizes (one or four blocks), assuming that 5 m would be sufficient to keep snails on the reef to which they were assigned.

Reefs varied in two social factors: group size and sex ratio. I placed the snails on the reefs either alone (on one-block reefs) or in groups of four (on four-block reefs), the groups of four containing either a single-sexed group or a mixed-sexed group (two members of each sex). The sexes were evenly represented on reefs containing only one sex of snail, creating the following social environments (sample size): solitary males (8), solitary females (8), single-sexed group males (16), single-sexed group females (16), and mixed-sexed groups (16 males, 16 females). I used a randomized-block design to assign social environments to reefs in the first of two experimental runs. The positions of the all-male

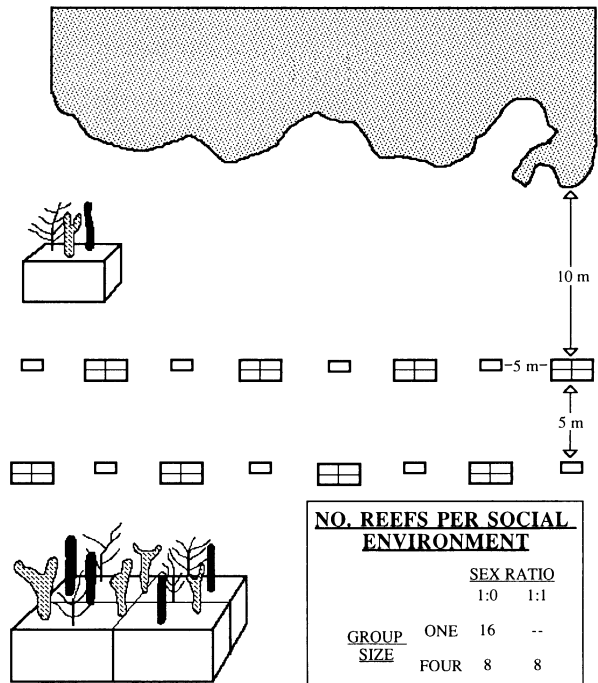


FIG. 1. Experimental reef array. Sixteen reefs were arrayed in two rows and each was used in two runs. The single-block reefs contained one of each of three species of gorgonian corals and one *Cyphoma gibbosum* snail, whereas the four-block reefs contained four of each species of gorgonian coral and four *C. gibbosum*.

and all-female reefs were switched in the second run to control maximally for sex differences. After the data were collected I separated female movement into two categories: oviposition movements, made during the two censuses before and after oviposition, and non-oviposition movements. I inferred that a certain female had produced an egg mass by its presence on a colony that she alone had occupied during the previous day. However, I could not determine the mother of some egg masses because of the presence of > 1 female on a colony during the time the egg mass was laid.

I recorded the position of each snail, the presence of egg masses on a coral colony, and the occurrence of behaviors including copulation and ongoing movement in daily censuses of the reefs during two experimental runs: 10–23 June 1989 and 15–22 July 1989. Copulation by *C. gibbosum* occurs in a stereotypical position with the male on the female's right side, and often lasts as long as 4 h (Ghiselin and Wilson 1966). Thus, I probably only observed one sixth of all copulations that occurred. Between runs I scrubbed the reefs and raked the surrounding sand bed to removed any impact of the previous inhabitants. I chose to end both runs after an unknown predator ate a large number (roughly half) of the experimental *C. gibbosum*, as evidenced by the shell fragments that remained—often with tags still attached. When < 5 snails were eaten or otherwise missing on a given census, I replaced them

the next day. I suspended wire-mesh roofs 0.45 m above the experimental reefs to minimize predation on snails during the second run.

Finally, to determine whether snails aggregate preferentially with members of the opposite sex in the field, I collected all snails found during two 30-min dives between 10 and 15 m in Salt River Canyon, placing each group of two or more in its own separate container. I determined the sex of each snail and compared the sex composition of groups to that of the snail population as a whole. The collection yielded 15 individuals, nine pairs, and one trio. The trio was excluded from analysis to increase statistical power. Nevertheless, its sex composition was consistent with the pattern observed from the pairs.

#### Data analysis

I analyzed the data using log-linear categorical modelling (for a detailed description of technique see Caswell [1989] or Searle et al. [1992]), comparing the movement patterns of snails in each treatment as represented by transition matrices. In this analysis I pooled the data from the replicate snails in each treatment. The data could have been summarized by calculating the frequencies at which snails occupied each host species (i.e., 60% on *B. asbestinum*, 20% on *Plexaurella dichotoma*, and 20% on *Pseudopterogorgia acerosa* or no host). However, these frequencies of occupation varied depending on the snail's host during the previous census. For example, if a snail was previously on *B. asbestinum*, it was observed on *B. asbestinum* on 85% of the next censuses, *Plexaurella dichotoma* on 9% of the next censuses, and *Pseudopterogorgia acerosa* or no host on 6% of the next censuses. A transition matrix takes these frequencies of occupation given *B. asbestinum* was the previous host and combines them with the frequencies of occupation given *P. dichotoma* and *P. acerosa* or no host were the previous hosts. Thus, a transition matrix serves as a summary of host preferences.

I considered the following factors in the first analysis: experimental run (first and second); sex (males and females); oviposition state (ovipositing and non-ovipositing females); sex ratio (single-sexed and mixed-sexed groups); and group size (one and four snails). I tested the importance of a factor by constructing two models from the observed data, one that treated each category within the factor separately and one that pooled these categories together. If the separation of the factor's categories significantly increased the fit of the model to the actual data, the snails in those categories differed in their movement patterns and thus, in their host preferences. Therefore results will be presented as the improvement of fit ( $\Delta\chi^2$ ), the extra parameters required for this improvement ( $\Delta df$ ), and the associated level of significance.

The data from the first analysis included multiple observations of single individuals, creating the poten-

tial for results biased by pseudoreplication. To account for pseudoreplication I preformed a second analysis that tested an additional parameter, individual variability (for technique see Cox and Snell [1989]). The tools to do such an analysis are not yet publicly available, but I was able to use a program developed and tested by C. McCulloch (Biometrics Unit, Cornell University, Ithaca, New York, USA). I had to split my data in two to meet the constraints of this program. As such, the results were complicated, and I will only report the aspects that have bearing on the interpretations of the first analysis.

A forager can show preferences by staying longer on preferred hosts (tenure) and/or by preferentially moving to preferred hosts when moving (new host preference) (Harvell and Suchanek 1987). To distinguish between these measures of preference, I divided the daily census data into two complementary sets: a tenure data set and a new-host preference data set. I then analyzed both data subsets using log-linear categorical modelling, but only tested factors that were shown to be significant from the analyses above. If I found that a factor, such as oviposition state, had a significant effect on one or both data subsets, I graphed the significant data subset(s) categorized by that factor (e.g., tenure measures for snails in each oviposition state on each coral species). In one case I found that a factor was significant in the analysis of the whole data set but not in the analyses of either subset, probably due to loss of power associated with the smaller sample sizes of the subset data. Since the factor had a significant effect on preference patterns overall and neither subset was ruled out, both subsets were examined.

#### RESULTS

The first analysis of the whole data set showed that snails preferred some hosts over others, both generally (as in frequency of observations on each host) and as a transition matrix (as in the same frequencies cross-classified by previous host) (Table 1). Furthermore, three factors contributed to the variation in preferences: run, sex ratio, and oviposition state (Table 1). None of the interactions between factors were significant, and a model lacking all factor interactions was not significantly different from a model containing all possible interactions (Table 1). This result is particularly important with respect to the difference between runs. Since run did not interact with sex ratio or oviposition state, these factors were consistent on both runs.

In the second analysis of the whole data set, the results were largely similar. The data were run in two separate analyses due to limitations in the analysis program: first, looking at arrivals or stays on *Briareum asbestinum* and *Plexaurella dichotoma* (*Bri-Pll* data set); and second, looking at arrivals or stays on *B. asbestinum* and *Pseudopterogorgia acerosa* or no host (*Bri-Ps* data set). Individual variation played a mar-

TABLE 1. Log-linear categorical modelling results.

Model	$\chi^2$	df
1) All factors and factor interactions	0	0
2) All factors but no interactions	27.94	72
3) All factors but run	45.48	78
4) All factors but general host preferences	133.43	74
5) All factors but transition matrix	149.57	76
6) All factors but sex	38.59	78
7) All factors but oviposition state	52.33	78
8) All factors but sex ratio	44.62	78
9) All factors but group size	35.55	78

Factor	Models compared	$\Delta\chi^2*$	$\Delta df^\dagger$	P
All factor interactions	2 vs. 1	27.94	72	<1
Run	3 vs. 2	17.54	6	<.01
General preferences	4 vs. 2	105.49	2	<.001
Transition matrix	5 vs. 2	121.63	4	<.001
Sex	6 vs. 2	10.65	6	<.1
Oviposition state	7 vs. 2	24.39	6	<.001
Sex ratio	8 vs. 2	16.68	6	<.025
Group size	9 vs. 2	7.61	6	<.5

\* The improvement of fit.

† The extra parameters needed for the improvement of fit.

ginal role in the *Bri-Pll* data (log-linear modelling,  $\Delta\chi^2 = 3.51$ ,  $\Delta df = 1$ ,  $P < .1$ ) and a significant one in the *Bri-Ps* data (log-linear modelling,  $\Delta\chi^2 = 54.04$ ,  $\Delta df = 1$ ,  $P < .001$ ). Taken alone, these results only specify that there were differences between individuals in their preference patterns that were not accounted for by the treatment effects.

When the individual variation factor was included in models used to test another factor, pseudoreplication was no longer a problem. In such analyses each of the two effects of interest, sex ratio and oviposition state, were still significant in at least one of the two data sets. Differences in sex ratio accounted for a significant amount of variation in the *Bri-Ps* data set (log-linear modelling:  $\Delta\chi^2 = 10.22$ ,  $\Delta df = 2$ ,  $P < .01$  for *Bri-Ps*;  $\Delta\chi^2 = 3.59$ ,  $\Delta df = 2$ ,  $P > .1$  for *Bri-Pll*) while differences in oviposition state accounted for a significant amount of variation in the *Bri-Pll* data set and only a marginally significant amount of variation in the *Bri-Ps* data set (log-linear modelling:  $\Delta\chi^2 = 9.72$ ,  $\Delta df = 2$ ,  $P < .01$  for *Bri-Pll*;  $\Delta\chi^2 = 5.30$ ,  $\Delta df = 2$ ,  $P < .1$  for *Bri-Ps*). Since both sex ratio and oviposition state made a significant difference in the preferences for at least two of the three host choices, they certainly had an overall effect on the movement patterns.

### Run

The transition matrices varied between the first and second run performed over the summer (Table 1). I tested the data in subsets to assess the relative importance of different types of preference. The tenure data, including only information about staying or leaving a colony, showed a significant effect of run (log-linear modelling,  $\Delta\chi^2 = 11.39$ ,  $\Delta df = 3$ ,  $P < .01$ ) while the new host preferences did not. Therefore, the difference between the two runs was due primarily to a difference in tenure lengths (Fig. 2), which were longer on all

species in the second run. The *Cyphoma gibbosum* from this run may have been disturbed less since they were covered with roofs. In any case, the difference between runs did not interact statistically with any of the other factors. Therefore, the patterns discussed below were consistent in both runs.

### Host species

I examined the effects of host species in two steps: first for general preferences and second for preferences based on previous host species (i.e., transition matrix). The general preferences showed the following order: *B.*

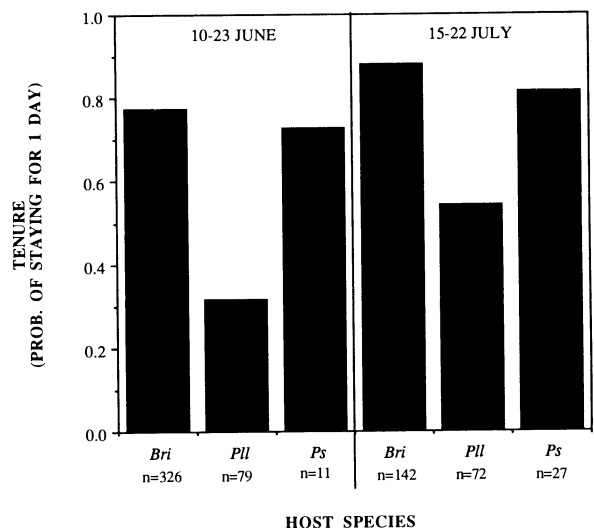


FIG. 2. Differences in tenure times between runs. Log-linear modelling (tenure data subset),  $\Delta\chi^2$  (the improvement of fit) = 11.39,  $\Delta df$  (the extra parameters required for the improvement) = 3,  $P < .01$ . For this and all subsequent figures, *Bri* = *Briareum asbestinum*, *Pll* = *Plexaurella dichotoma*, *Ps* = *Pseudopterogorgia acerosa*, and *Ps/Off* = *P. acerosa* or no host.

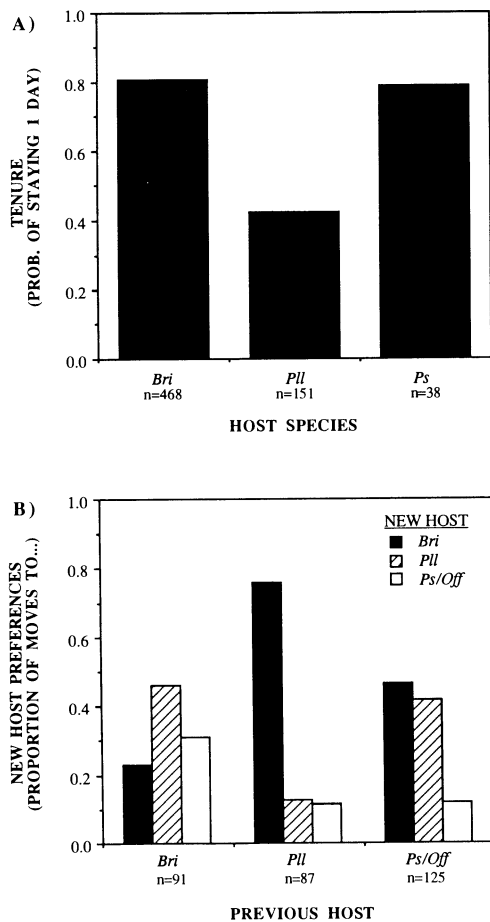


FIG. 3. Movement pattern differences based on host species. (A) Tenure times. Log-linear modelling (tenure data subset),  $\Delta\chi^2 = 57.97$ ,  $\Delta df = 2$ ,  $P < .001$ . (B) New host preferences. Log-linear modelling (new host preference data subset),  $\Delta\chi^2 = 16.42$ ,  $\Delta df = 4$ ,  $P < .001$ . See Fig. 2 for explanation of acronyms and symbols.

*asbestinum* over *Plexaurella dichotoma* over *Pseudopterogorgia acerosa* or no host, though a transition matrix was a better descriptor than a list of general preferences (see data below and Table 1).

I found that host species preferences played a role in both data subsets. There were preferences to stay longer on *B. asbestinum* and *P. acerosa* than on *Plexaurella dichotoma* (Fig. 3A). New host preferences were more complicated; snails moving from *B. asbestinum* preferred to move to *P. dichotoma*, those from *P. dichotoma* preferred *B. asbestinum*, and those from *Pseudopterogorgia acerosa* or no host had roughly equal preferences for *B. asbestinum* and *Plexaurella dichotoma* (Fig. 3B).

A transition matrix can be used to predict the stable distribution of a population (Kareiva 1982). If the transition matrix were the only effect on the distribution of *C. gibbosum* and did not vary due to social interactions or other factors, its projected population distribution would be likely to match the observed dis-

tributions on the host species. The projection of the transition matrix pooled over all treatments predicted a distribution as follows: 73.6% of the observations on *B. asbestinum*; 18.5% of the observations on *P. dichotoma*; and 7.9% of the observations on *Pseudopterogorgia acerosa* or no host. The actual proportions of observations in these categories, respectively 60.5%, 19.5%, and 20.0%, were similar, but still significantly different from the predicted proportions ( $G$  test,  $G = 60.195$ ,  $df = 2$ ,  $P < .001$ ). The differences may have been due to the influence of oviposition preferences and social interactions as detailed below.

#### Oviposition state

Females exhibited a unique movement pattern during the two censuses before and after oviposition (Table 1), leaving their host more often, particularly when

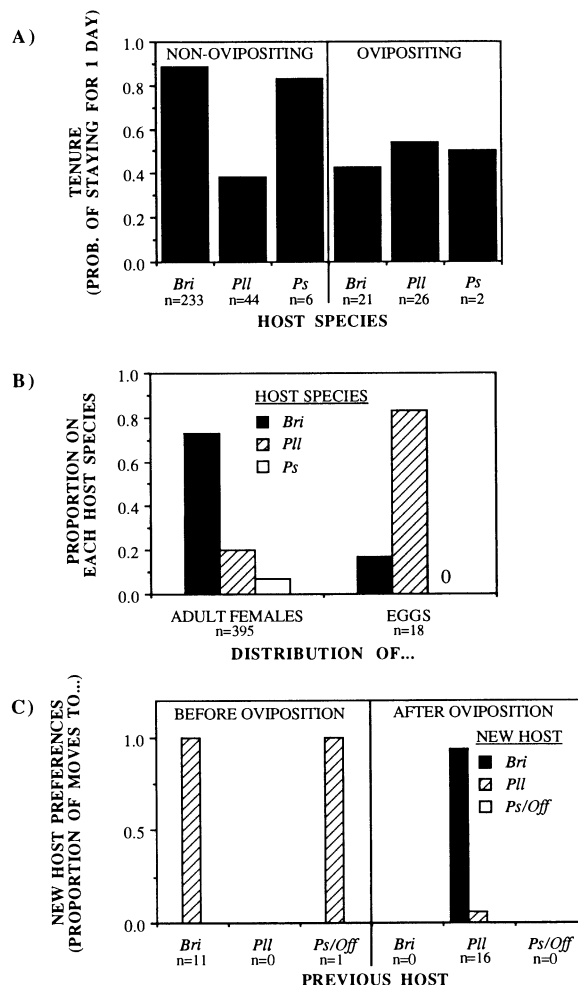


FIG. 4. Movement pattern differences based on oviposition state. (A) Tenure times. Log-linear modelling (tenure data subset),  $\Delta\chi^2 = 21.52$ ,  $\Delta df = 3$ ,  $P < .001$ . (B) Oviposition preferences—distributions of adult females and eggs.  $G$  test,  $G = 33.58$ ,  $df = 2$ ,  $P < .001$ . (C) New host preferences before and after oviposition. For explanation of acronyms and symbols, see Fig. 2.

their host was *B. asbestinum* (Fig. 4A). Although they did not differ significantly in new host preferences during oviposition, females oviposited almost exclusively on *Plexaurella dichotoma*, a rarely used host in general (Fig. 4B). The lack of a significant difference in new host preferences may have resulted from sparse data and the pooling of movements before and after oviposition. When new host preferences of females before oviposition were separated from those after oviposition, a striking pattern emerged—ovipositing females moved almost exclusively from *B. asbestinum* to *P. dichotoma* before ovipositing and back to *B. asbestinum* afterwards (Fig. 4C).

#### Sex ratio

Groups composed of both sexes had different movement patterns from those containing only males or females (Table 1). However, neither data subset showed a significant effect of sex ratio. Differences in tenure were minimal, the main difference being shorter tenure on *Pseudopterogorgia acerosa* in 1:1 male-to-female sex ratios (Fig. 5A). However, the tenure measurement on *P. acerosa* in 1:1 sex ratio groups was based on only two observations from a single individual. In contrast, sex ratio was at least marginally significant in the new host preference data (Log-linear modelling,  $\Delta\chi^2 = 10.32$ ,  $\Delta df = 6$ ,  $P \approx .1$ ), suggesting that new host preferences may be more important than tenure in describing sex ratio differences.

The difference in new host preferences between groups of 1:0 and 1:1 (male-to-female) sex ratios were fairly complex (Fig. 5B). Most significantly, preferences were more extreme in groups with a 1:1 sex ratio. These groups showed stronger preferences for the preferred hosts and weaker preferences for the least-preferred host category, *Pseudopterogorgia acerosa* or no host. Many of the observations in this least-preferred category were of snails on no host. However, while snails in groups of 1:0 sex ratio used *P. acerosa* occasionally, those in 1:1 sex ratio groups virtually ignored *P. acerosa* as a host. As evidence, note the sample sizes in Fig. 5A.

Individuals generally stayed on the reefs to which they were assigned but occasionally moved to a different reef in the array. These moves of 5 m or more were not distinguished in the above analyses but warranted further examination. The majority of these inter-reef moves were made by males (Fig. 6A). Furthermore, males were marginally more likely to make an inter-reef move if they were assigned to a reef that lacked females (Fig. 6B). Most striking of all, males had an uncanny ability to move to reefs that contained only females (Fig. 6C). Females also showed a tendency to move toward males, although there were too few inter-reef moves by females to test this pattern statistically.

If *C. gibbosum* do move toward members of the opposite sex, then I would predict that groups would

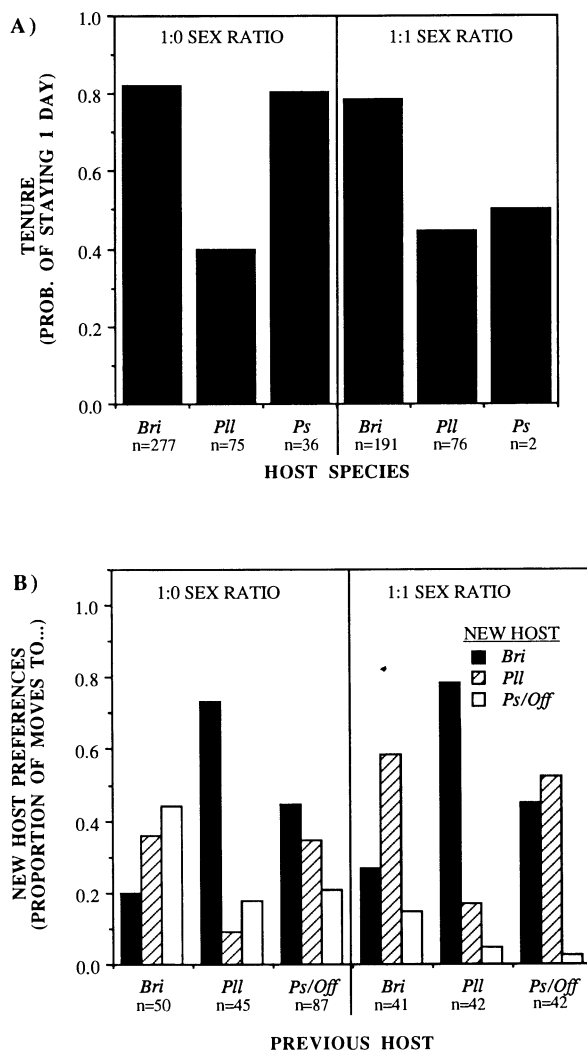


FIG. 5. Movement pattern differences based on group sex ratio. (A) Tenure times. Log-linear modelling (tenure data subset),  $\Delta\chi^2 = 2.42$ ,  $\Delta df = 3$ ,  $P < .5$ . (B) New host preferences. Log-linear modelling (new host preference data subset),  $\Delta\chi^2 = 10.32$ ,  $\Delta df = 6$ ,  $P \approx .1$ . For explanation of acronyms and symbols, see Fig. 2.

contain a roughly even sex ratio, both in this experiment and on natural reefs. First, I examined the sex composition of pairs that formed on colonies from reefs that contained both males and females. Pairs alone were used because there were only two males and two females on these reefs, so that any group larger than a pair would necessarily contain both males and females. The observed data showed mostly male-female pairs, while random pairing would have resulted in only a 50% frequency of mixed-sexed pairs (Fig. 7A). Observations made on a field population with a roughly even sex ratio (47% male, 53% female) supported this result. All nine field-collected pairs contained one female and one male, a higher proportion than expected by chance ( $P < .005$ , as calculated from a binomial distribution).

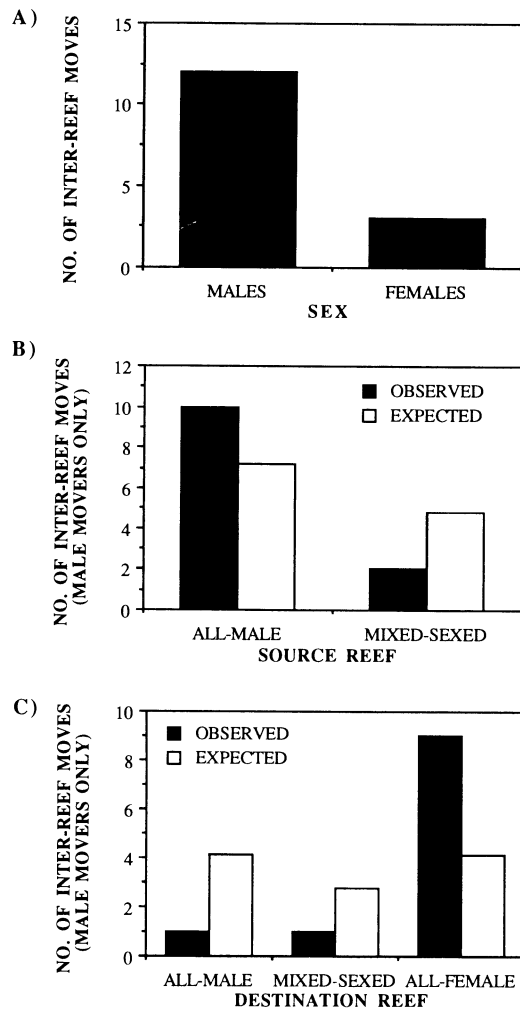


FIG. 6. Inter-reef moves = moves of  $\geq 5$  m. (A) Tendency of the sexes to make inter-reef moves.  $G$  test,  $G = 5.782$ ,  $df = 1$ ,  $P < .025$ . (B) Source reef, where the mover originated (males only).  $G$  test,  $G = 3.068$ ,  $df = 1$ ,  $P \approx .08$ . Expected values were generated by assuming that every male was equally likely to make an inter-reef move. Therefore, these values are proportional to the number of replicate males on each type of reef. (C) Destination reef, where the mover was found (males only).  $G$  test,  $G = 9.186$ ,  $df = 2$ ,  $P < .025$ . Expected values were generated by assuming that inter-reef-moving males were equally likely to be found on each type of reef. Therefore, these values are proportional to the frequency of each reef type.

Finally, I calculated the relative mating successes of snails following three movement categories—no movement, intra-reef movement, and inter-reef movement—for both males and females to see if movement and mating success were related. Mating success was calculated for a movement category by dividing the number of observed copulations following that movement type by the total number of those types of moves made over the summer. I found that both males and females were more likely to be found copulating the

more extensive their move during the previous day (Fig. 7B).

## DISCUSSION

### *Mate- and oviposition-influenced host preferences*

The movement patterns exhibited by *Cyphoma gibbosum* in this experiment support the mate-influenced host preferences hypothesis. Although the effect was stronger in males, both males and females showed a tendency to aggregate preferentially with members of the opposite sex. In fact, if one looks at all movements made during the course of the experiment, 54% of male and 34% of female movement brought them to either a reef or colony containing members of the opposite sex. These figures are particularly impressive considering that over half of the experimental snails were on reefs that lacked members of the opposite sex.

Since host preferences were strong in this experiment, social interactions and oviposition preferences could easily have been overlooked. Unlike many stud-

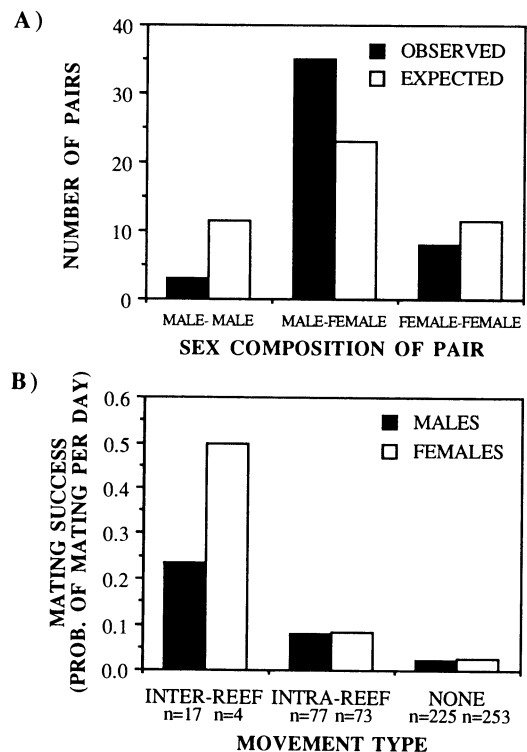


FIG. 7. Sex-specific aggregations for copulation. (A) Sex compositions of pairs found on reefs with a 1:1 (male-to-female) sex ratio.  $G$  test,  $G = 15.521$ ,  $df = 2$ ,  $P < .001$ . Random pairings with respect to sex would have resulted in the following sex composition frequencies:  $\frac{1}{2} \cdot \frac{1}{2}$  male-male;  $\frac{1}{2} \cdot \frac{1}{2}$  female-female; and  $2 \cdot \frac{1}{2} \cdot \frac{1}{2}$  male-female. The larger number of male-female pairs results from the dual possibility of having a male-female pair and a female-male pair. (B) Mating success after various movement types.  $G$  tests, males:  $G = 11.465$ ,  $df = 2$ ,  $P < .005$ ; females:  $G = 9.795$ ,  $df = 2$ ,  $P < .01$ . Both sexes had higher mating successes after more extensive moves.



ies on host preferences, however, this one examined multiple hypotheses simultaneously. In doing so, it was possible to gain greater insight into the host preferences of *C. gibbosum*.

Oviposition preferences by females may have kept this system dynamic, in that males often moved to hosts containing females, regardless of host species. Males may have visited *Plexaurella dichotoma* only to gain copulations with ovipositing females. If females had preferred to oviposit as well as live on *Briareum asbestinum* in this experiment, *C. gibbosum* would have appeared to be a specialist. In this hypothetical scenario, mate searching would have clearly narrowed host preferences. Instead, mate searching had a dual effect.

It was not clear from this experiment why females preferred to oviposit on *P. dichotoma*, but otherwise live on *B. asbestinum*. *B. asbestinum* contains highly deterrent compounds (C. D. Harvell, *personal communication*) that might have an adverse effect on the development and survival of *C. gibbosum* larvae. However, microscopic examination of the basement walls of capsules suggested that encapsulated larvae are at least partly protected from the chemistry of their coral hosts (J. P. Nowlis, *personal observation*). On the other hand, *P. dichotoma* has an induced structural response to damage by *C. gibbosum* that may deter adult snails (J. P. Nowlis, J. M. West, and S. May, *unpublished data*). Females typically oviposit over areas of the colony they have just grazed. If this grazing is sufficient to induce the colony response and the response deters some egg predator from searching that colony, then *P. dichotoma* may serve as a refuge against egg predation. Pilot data from following eight egg masses suggested that eggs may experience greater predation on *B. asbestinum* than on *P. dichotoma*, despite the deterrent chemistry of *B. asbestinum*. Further work is needed, however, to gain a better understanding of this oviposition pattern.

The oviposition-influenced host preferences of females interacted with the mate-influenced host preferences of both males and females to produce a complex host preference pattern. While oviposition preferences led to broader diets, mate finding had a dual effect. In searching for mates, both males and females virtually ignored *Pseudopterogorgia acerosa*, the least-preferred host. However, males may have visited *Plexaurella dichotoma* more often in the presence of females due to mate searching.

It is possible that the interaction between mate- and oviposition-influenced host preferences has produced the variation in host preferences of this snail across the Caribbean (Birkeland and Gregory 1975, Hazlett and Bach 1982, Harvell and Suchanek 1987, Lasker and Coffroth 1988, Lasker et al. 1988). These studies all examined more than three host species in fairly natural settings. If female oviposition patterns differed slightly between these studies, male movement towards females would have accentuated the differences. Or per-

haps stochastic variation in oviposition patterns, accentuated by movement towards mates, might have produced the differences in preferences between the studies. This latter hypothesis could even have produced differences in observed preferences in the absence of actual differences.

#### *Implications for the theories of aggregation and specialization*

Gregarious tendencies played an important role in the distribution of *C. gibbosum* in this study. Previous work has established that food quality (Raffa and Berryman 1983, Okamura 1986, Trowbridge 1991a), physical stress (Moran 1985), and predation risk (Hamilton 1971, Okamura 1986) may influence gregarious behavior. Aggregation may also increase mating success, particularly in sessile or relatively immobile organisms (Pennings 1991).

Gerhart (1986) examined several possible hypotheses as to how and why *C. gibbosum* aggregate in the field. He concluded that (1) aggregation is a result of mucous trail following; and (2) predation is the most likely selection factor favoring gregariousness, although he did suggest that mate finding may also play a role. He argued that the brightly colored mantle of *C. gibbosum* can serve as aposematic coloration. If so, a group is more likely to make an impression on a naive predator than is a single individual. Furthermore, an individual is less likely to be the victim of a naive predator's learning in a group than alone. One must be careful of this second conclusion, as it assumes that predators do not preferentially attack groups.

The data presented here broaden Gerhart's findings. First, snails moved distances >5 m in 1 d across previously uncrossed sand beds to get to reefs containing members of the opposite sex, suggesting that there are water-borne cues that serve as attracting pheromones. Over long distances these cues undoubtedly play an important role in producing aggregations. Since pheromone-following behavior was sex-specific, with males primarily seeking out females, it should come as no surprise that most pairs that were observed in both experimental and natural settings contained a female and a male, rather than two members of the same sex. These aggregations probably occurred as a result of mate searching. The aggregations also might have offered protection from predators; but if predation were the main selective pressure producing these aggregations, more single-sexed groups would have been observed. The extreme rarity of such single-sexed groups and the increase in mating success following movements support the hypothesis that mating opportunities can be both the proximate and ultimate cause of gregariousness in *C. gibbosum*.

*C. gibbosum* is not a specialist, even within the context of this experiment that offered only three potential hosts. Their pattern of host use must be considered carefully when testing Colwell's (1986a) theory of host

specialization in order to increase the chance of finding mates. *Plexaurella dichotoma* was included in the diet of female *C. gibbosum* because it was a preferred oviposition site, and in the diet of males because they followed females. Thus, *P. dichotoma* was used primarily because it is a good oviposition site, and only secondarily because of mate finding. Therefore, mate finding behavior did not broaden the diet of *C. gibbosum* since females would have used *P. dichotoma* even if males had not. Moreover, there is evidence that mate-finding behavior may have narrowed these snails' diet. The main difference in the host preferences of single-sexed and mixed-sexed groups was the use of *Pseudopterogorgia acerosa*—mixed-sexed groups virtually ignored this least-preferred host. Therefore, it seems that mate-finding behavior led to a reduction in the host breadth of *C. gibbosum*.

#### *Differences between marine gastropods and insects*

While the literature on the influences of marine gastropod host preferences is nowhere near as extensive as the literature on insects, some comparison can be made. The most widely tested hypotheses on insect host preferences have been examined with marine gastropods. Authors have shown that marine gastropods can benefit in more than one way from their host preferences. They can grow better (Jensen 1983, Pennings 1990a), reduce predation (Paul and Van Alstyne 1988, Pawlik et al. 1988, Paul and Pennings 1991), or both (Pennings 1990b). Like many insects, marine gastropods may only recognize a narrow range of hosts (Trowbridge 1991b). Also, marine gastropods—sea slugs in particular—have the ability to sequester defensive compounds (Karuso 1987), as do many insects (Duffey 1980). Unlike insects, however, mate-influenced host preferences have been demonstrated in both *C. gibbosum* and the sea slug *Doridella steinbergae* (J. P. Nowlis, unpublished data).

There are several possibilities as to why mate-influenced host preferences have been demonstrated in marine gastropods but not insects. First, two classic papers, by Dethier (1954) and Ehrlich and Raven (1964), have influenced which hypotheses on insect host preferences have been studied. These widely known and thought-provoking papers both examined butterfly host preferences but did not discuss the impact of mate-searching on those host preferences.

Second, most phytophagous, or plant-eating, insects are closer to the specialist end of the generalist–specialist continuum (Futuyma and Gould 1979, Cates 1980). It would be complicated to demonstrate mate-influenced host preferences in a specialist because they are constrained, by definition, in their ability to exhibit variation in host preferences. Without variation, it would be difficult to demonstrate shifts in host use based on mate searching. The only option would be to infer past history, which often results in which-came-first arguments. Yet generalist insects do exist, and

would be interesting to test for mate-influenced host preferences.

Finally, butterflies have received far greater attention than other insect groups in host preference studies. Butterflies, and some other phytophagous insects, have separate feeding and breeding sites (Shields 1967, Wiklund 1977, Scott 1983, Hendrichs et al. 1991). Though *C. gibbosum* also has distinct feeding and ovipositing preferences, its reduced mobility and adult food requirements force it to feed on its oviposition host. Thus, *Plexaurella dichotoma* is considered a host of *C. gibbosum* while the breeding sites of the above insects are not considered hosts. An examination of one of the many species of insects with hosts that serve both as feeding (or ovipositing, since the larvae often feed but do not move) and breeding sites might reveal mate-influenced host preferences. Some likely insect candidates include tephritid flies (Bush 1969), bark beetles (Raffa and Berryman 1983), and fig wasps (Wiebes 1979).

Any study that attempts to understand the host preferences of insects, marine gastropods, or any other grazer will need to examine multiple hypotheses simultaneously. The factors that are studied should include food quality, refuge quality, oviposition preferences (if applicable) and mate-influenced host preferences.

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