AN ABSTRACT OF THE THESIS OF

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Title: <u>The Roles of Environmental Constraints and</u>

<u>Aggression on Male-Female Pairing in the Coral-Reef Fish</u>

<u>*Gobiosoma evelynae*</u>

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Early theoretical models for the evolution of male-female

pairing were based largely on studies of birds. These models

assumed that biparental care of eggs and young was an

essential component of pairing. However, male-female pairing

is also a relatively common social system in coral-reef

fishes, and biparental care of young is extremely rare in

this group. Although pairing has been documented in at least

13 families of reef fish, surprisingly little is known about

the environmental and social factors that may maintain

heterosexual pairs as the basic social units. I tested two

hypotheses for pairing in a common Caribbean fish, the

cleaning goby *Gobiosoma evelynae*, a territorial species which

inhabits living coral heads. According to the Environmental

Constraints Hypothesis, pairing in *G. evelynae* is simply a

consequence of three related environmental parameters--low male mobility, low female density, and a uniform distribution of resources required by females. On reefs off St. Thomas, U.S. Virgin Islands, I found positive size-assortative pairing, frequent male movement between territories, rapid re-pairing by both males and females after experimental removal of a partner, and random distributions of apparently suitable coral heads required by females for territory space. These patterns are inconsistent with the Environmental Constraints Hypothesis for pairing.

Mate Guarding is an alternative hypothesis for pairing and is based on social interactions. This hypothesis, which states that paired gobies maintain exclusive access to their partners by expelling all potential sexual rivals, predicts sex- and size-specific aggression toward conspecifics. I released large and small male and female gobies directly onto the territories of pairs, and recorded the behavioral responses of the resident fish. As predicted, residents exhibited the greatest aggression toward large intruders of the same sex, and the least aggression toward large intruders of the opposite sex. Unpaired territorial females also responded aggressively to experimentally added females, and ignored added males. These results indicate that male-female pairs are maintained by mutual intrasexual aggression in this species, and that females (and possibly males) defend both partners and other resources associated with their territories.

The Roles of Environmental Constraints and

Aggression on Male-Female Pairing in the

Coral-Reef Fish *Gobiosoma evelynae*

by

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INTRODUCTION

Understanding the evolutionary forces producing
different social and mating systems is a major goal of
behavioral ecology. As the most speciose assemblage of
vertebrates, coral-reef fishes display a remarkable range
of social systems, from lone transients (e.g., some
barracuda; Thresher 1984) to highly integrated, territorial
harems (e.g., some wrasses; Warner and Hoffman 1980).

Heterosexual pairing has been reported in at least 13
families of coral-reef fishes (Barlow 1984, Thresher 1984),
and there is a growing number of studies of this social
system (Fricke 1973, 1976; Reese 1975, Lassig 1976,
Robertson *et al.* 1979, Pressley 1981, Gronell 1984, Barlow
1987, Driscoll and Driscoll 1988, Colin 1989, Donaldson
1989, Clark and Pohle 1992). Even when spawning cannot be
accurately monitored, observations of social groups

consisting of long-lasting male-female pairs are usually interpreted as evidence of monogamy. Although this interpretation may not be justified in some cases, social pairing itself remains an important phenomenon that has not been satisfactorily explained for any reef fish. The roles of environmental and social factors in promoting and maintaining pairs as the predominant social unit remain untested and largely speculative (but see Fricke 1986, Hourigan 1989).

Hypotheses for monogamy in fishes

At least eight hypotheses have been suggested to explain male-female pairing and monogamy in fishes. Three of these fall under the heading of cooperation (Barlow 1984) or "shared duty" (Wickler and Seibt 1981). According to the Biparental Care Hypothesis, monogamy should occur when male parental care is both nonshareable and indispensable to female reproductive success, such that desertion by either parent results in total brood failure (Wittenberger and Tilson 1980). Although this hypothesis applies well to some monogamous freshwater fishes (e.g., cichlids; Barlow 1974), there is only one reef fish with biparental care of eggs and young (*Acanthochromis polyacanthus*; Robertson 1973). This hypothesis therefore is generally not relevant to coral reef fishes. Of more relevance is the Resource Defense Hypothesis, which states

that pairing is favored if two individuals are required to jointly defend a necessary resource which they share between them (Wilson 1975). This hypothesis has been proposed to account for monogamy in butterflyfishes (Fricke 1986, Hourigan 1989). *By itself*, resource defense is not an adequate explanation for monogamy because it does not answer the important question "Why, if two are better that one, are not three better than two?" (Wickler and Seibt 1981). The need for territory defense could just as easily favor the formation of larger cooperative groups (as seen in some parrotfishes; Clifton 1990). Coordinated foraging between mated individuals has likewise been suggested to favor the formation of monogamous pairs. Pressley (1981) proposed this Cooperative Hunting Hypothesis to account for pairing in a coral reef fish, the hermaphroditic sea bass *Serranus tigrinus*. By itself, this explanation is insufficient for the same reason as above: it does not explain why a pair should form instead of a larger cooperative group.

Two additional hypotheses are relevant to reef fishes but are not directly testable unless polygyny can be induced in the same population for experimental comparison. The Increased Reproductive Efficiency Hypothesis asserts that monogamy should occur if males are more successful with one mate than with two or more. This can happen if the presence of a second female substantially reduces the success of a male's first mate by increasing competition or

increasing her conspicuousness to predators (Wittenberger
and Tilson 1980), or if monogamy insures the minimum
possible "recovery" time between spawnings for both sexes,
resulting in maximum fecundity over the spawning season
(Gronell 1984). Alternatively, the <u>Hybridization Avoidance
Hypothesis</u> asserts that monogamy is an adaptation to reduce
the chances of heterospecific mating (i.e., wasting
gametes). Fricke (1973) suggested this hypothesis to
account for pairing in the species-rich Chaetodontidae. It
can be rejected for several reasons, principally because
there is no correlation between local within-family species
richness and number of monogamous species (Thresher 1984,
Roberts and Ormond 1992).

Only three remaining hypotheses for heterosexual
pairing and monogamy are both relevant to coral reef fishes
and testable without experimentally inducing polygyny.
According to the <u>Mate-Guarding Hypothesis,</u> aggression by
paired females toward female conspecifics may prevent males
from acquiring additional mates (Wittenberger and Tilson
1980, Wickler and Seibt 1981, Barlow 1984). I examine this
hypothesis elsewhere (see Chapter 2). The last two
hypotheses involve constraints on group size imposed by the
density and mobility of individuals and by environmental
factors such as resource distribution. This chapter
addresses these hypotheses.

According to the <u>Low-Density/Low-Mobility Hypothesis,</u>
if conspecifics are relatively rare (low density) and/or

highly site-attached (low mobility), an individual should stay permanently paired with the first member of the opposite sex that it encounters and mate monogamously (Ghiselin 1969, Ralls 1977, Gronell 1984, Thresher 1984). This hypothesis requires low encounter rates between the sexes and assumes that the cost of searching for additional mates (such as lost opportunities to mate with a single partner, missed chances to feed, or increased risk of predation) outweigh the benefits of finding additional mates. Low mobility has been invoked to account for heterosexual pairing in several small, site-attached reef fishes, including some gobies (*Paragobiodon* spp., Lassig 1976), and hawkfishes (*Neocirrhites armatus* and *Oxycirrhites typus*, Donaldson 1989), but neither of these studies included experimental tests of the hypothesis.

According to the <u>Resource-Distribution Hypothesis</u>, if some resource needed by females is distributed uniformly in space and time, and is of sufficiently low quality that only one female can be supported locally, then females will also be distributed uniformly. If the distance between females is too great for a male to sequester more than one female at a time, then permanent pairing and monogamy will result. This hypothesis stems from models for the evolution of polygyny in birds (Verner and Willson 1966, Orians 1969, Emlen and Oring 1977); it describes environmental conditions at the opposite end of the spectrum from those which promote "resource-defense

polygyny" (Emlen and Oring 1977). The link between resource distribution, resource quality, and monogamous mating systems has been stressed by Slobodchikoff (1984) in general and by Barlow (1984, 1986, 1987, 1988) for coral-reef fishes in particular.

Such a resource-based hypothesis for pairing assumes that males, despite polygynous tendencies, are constrained by the environment to mate monogamously (i.e., "facultative monogamy" of Kleiman 1977; "circumstantial monogamy" of Wickler and Seibt 1981). For example, in the anemonefish *Amphiprion xanthurus*, most individuals live in permanent monogamous pairs, but monogamy is a condition imposed by the size of the anemone; unusually large anemones contained polygamous groups (Moyer and Sawyers 1973). In an experimental study, Fricke (1980) manipulated the size of artificial patch reefs constructed of coral, and found that the social and mating system of damselfish *Dascyllus marginatus* was directly affected by available space, with solitary males on the smallest reefs, monogamous pairs on intermediate sized reefs, and harems on the largest reefs. In both of these examples, the authors examined the effects of the *size* of habitat (resource) patches on the social and mating system. To my knowledge, no study has yet examined the effects of spatial *distribution* of resources (i.e., clumped vs. uniform) on the social and mating system of reef fishes.

In a review of monogamy in freshwater and coral-reef fishes, Barlow (1984) suggested that the Low-Density/Low-Mobility Hypothesis and the Resource-Distribution Hypothesis are sometimes difficult to separate, although he describes these two as alternatives. In fact, these hypotheses are virtually identical in their predictions and cannot be readily separated. Nalepa and Jones (1991) proposed an "Ecological Constraints Hypothesis" that combines the mobility of individuals and the spatial distribution of their critical resource (in their study, termites utilizing dead wood). As suggested by the following model for reef fishes, this composite hypothesis (hereafter called the "Environmental Constraints" Hypothesis) seems more appropriate than two distinct hypotheses because the spatial scale at which resource distribution becomes important depends entirely on the mobility of the animals using the resource. Essentially, there are three related parameters—male mobility, female density, and the spatial pattern of resources—that may impose severe constraints on the encounter rate between males and females and thus have a strong effect on the type of social and mating system that results.

Environmental Constraints Hypothesis for heterosexual pairing

Suppose that the resource in question is suitable space for a territory, such as a patch of living coral. Numerous small, site-attached fishes including blennies, gobies, and hawkfishes rely on such patches for home sites (Thresher 1984), so it is reasonable to assume that the distribution of suitable coral heads affects the distribution of these fishes. A simple conceptual model shows the effect of male mobility (i.e., territory area) and female density on the social system of such a reef fish. Assume that each female territory includes a single coral head, whereas each male defends the largest area possible so as to maximize the number of female territories included (see Hixon 1987). Assume also that there is at most one female per coral head, and therefore no substantial female-female interactions. Holding the distribution and density of coral heads constant, when male mobility (i.e., territory area) and/or female density is sufficiently low, males are unable to locate more than one female and heterosexual pairs result (Fig. 1.1, cases A, B, and C). When male mobility is sufficiently high relative to female density, males are able to sequester more than one female within their territory and polygynous groups result (Fig. 1.1, case D; this is equivalent to the "resource-defense polygyny" model of Emlen and Oring 1977).

It is clear that mobility and density cannot be considered separately. In reference to a social or mating system, the mobility of one sex can only be described relative to the density of the other sex, and *vice-versa*.

An analogous model for resource distribution illustrates the effect of varying the spatial pattern of coral heads on the social system of the same fish. Holding male mobility, female density, and coral density constant, when corals are arranged uniformly and the minimum distance between adjacent coral heads is greater than the maximum male territory diameter, males are unable to sequester more than one female, and pairs result (Fig. 1.1, case E). However, when corals are sufficiently clumped, such that more than one female-occupied head is within a male's territory, males are able to sequester two or more females within their territories (Fig. 1.1, case F), another example of resource-defense polygyny.

Note that, although the scenarios presented in figure 1 are derived by changing independently three different parameters, cases D and F are virtually the same scenario and both result in polygynous groups. Similarly, cases A, B, C, and E are virtually the same and all result in monogamous pairs. This model thus demonstrates that the Low-Density/Low-Mobility Hypothesis and the Resource-Distribution Hypothesis are actually subsets of a more general Environmental Constraints Hypothesis.

If coral reef fish form male-female pairs, is it possible to identify which, if any, of these proximate constraints is involved? In order to examine separately the effects of male mobility, female density, and resource distribution, it would be necessary to manipulate each parameter independently, as in the preceding model. Unfortunately, elevating fish density and moving large corals underwater is very difficult, and fish mobility cannot be effectively altered. However, even without performing these manipulations, four specific predictions from the composite hypothesis can still be tested. Since individuals constrained by low mobility and density would seldom have the opportunity to choose from among several potential partners (i.e., opportunities for mate-choice are rare), one can predict that (1) pairing should be random by size, not assortative. Furthermore, if low male mobility relative to female density causes heterosexual pairing and monogamy, then (2) there should be little or no movement of males and females between territories, and consequently (3) fish of either sex that lose their mates should be unable to re-pair quickly. Finally, if there is a cause-and-effect relationship between the spatial pattern of resources and social pairing, then (4) suitable coral heads should be distributed uniformly on a spatial scale relevant to the mobility of individuals, such that more than one suitable coral head does not occur within the confines of a single male's territory. Moreover, a uniform pattern of

suitable coral heads should produce a uniform pattern of female territories and heterosexual pairs.

Gobiosoma evelynae is a relatively common Caribbean goby that resides singly and in male-female pairs on living coral heads (Colin 1975). In an attempt to explain why this species forms heterosexual pairs, I tested the above four predictions of the Environmental Constraints Hypothesis by: (1) measuring the size of paired male and female *G. evelynae*; (2) monitoring the location and movement of individually marked males and females; (3) removing males and females from mated pairs; and, (4) analyzing spatial distributions of living coral heads and goby territories. My observations of *G. evelynae* were consistent with one assumption of the hypothesis: male territories were smaller than the distance between adjacent females, and therefore did not contain more than one female-occupied coral head. However, my results suggested that neither low mobility/low density nor the pattern of coral distribution is sufficient to explain heterosexual pairing in this species.

MATERIALS and METHODS

Study Site

This study was conducted off the southwestern shore of
St. Thomas, U.S. Virgin Islands, from June to September,
1991 and 1992. All work was performed using SCUBA on
shallow (4-12 m) fringing reefs surrounding two small
islets, Saba and Flat Cay, located near the University of
the Virgin Islands.

Study Species

Gobiosoma evelynae is a relatively common fish on
Caribbean reefs that forms pairs, and is presumed to be
monogamous (Colin, 1975). It is a cleaning goby which
resides on living coral heads and rock ledges, gleaning
ectoparasites off larger fish that pass its territory.
Males guard demersal eggs which are laid inside small holes
and crevices, where they are well hidden. *Gobiosoma* are
small, site attached, and very tolerant to the presence of
divers (if approached slowly, they often "clean" a diver's
hand), making them ideal fish for *in situ* behavioral
studies.

Capture and Marking

To identify individual fish, I captured gobies with a
dilute quinaldine/ethanol solution and an aquarium net, and
marked them in one of two ways: (1) by subcutaneous
injection of Liquatex brand colored acrylic latex paint;
or, (2) by nicking the yellow and white lateral stripe
posterior to each eye with the tip of a needle. The second
method left a small scar or set of scars unique to each
individual. I measured each goby to the nearest 0.1 mm
(total length, TL) and returned it to its coral head; the
entire procedure was done underwater and required 2-3 min
per fish. After release, I watched each fish until the
anesthetic effects of the quinaldine had worn off (about 5
min). There appeared to be no immediate adverse effects of
capture. Many gobies sought refuge in crevices soon after
being released, which resulted in the serendipitous
discovery of several nest holes.

To test for injury or mortality caused by capture and
marking, I placed 10 newly-marked *G. evelynae* in a weighted
glass aquarium *in situ* and checked their condition after 24
and 48 h.

To determine or confirm the sex of individuals, I
collected 55 single and 25 pairs of *G. evelynae* over the
course of the study. These were fixed in 10% formalin for
48 h, rinsed, and preserved in 10% ethanol. With the aid
of a dissecting microscope, the sex of preserved specimens

was determined by the appearance of the gonads and the shape of the urogenital papillae (papillae of females are blunt with a visible orifice; papillae of males are pointed with no visible orifice).

Survey Grids and Census Data

In 1991, I established two fixed rectangular survey areas, one at each site, and divided them into 5 x 5 m grids with string and metal stakes. The dimensions of the survey grids were 20 x 50 m at Saba and 10 x 40 m at Flat Cay; different total areas were used because the density of *G. evelynae* was >50% less at Saba than at Flat Cay. In 1992, the survey grid at Flat Cay was enlarged to 20 x 40 m. Both grids were located at a depth of 5-10 m and both contained pairs of *G. evelynae* and a congener, *G. prochilos*. One of the long sides of each grid was bordered by sand, which is not inhabited by these gobies. I marked and measured all medium and large (>20 mm TL) *G. evelynae* within the two survey grids (excluding a few individuals that were discovered late in the study).

To assess fidelity of male and female *G. evelynae* to partners and sites, I censused the Flat Cay survey grid every other day from August 1 to September 14, 1991 (23 censuses), and the Saba grid every 3-4 days from July 29 to September 13, 1991 (14 censuses). In 1992, I censused the Flat Cay grid every 2-5 days from June 15 to September 14

(35 censuses), and the Saba grid once per week from July 2 to September 10 (11 censuses). Due to the large size of each area, I could not conduct a thorough search of the entire grid at each visit. Instead, I checked known territories and attempted to locate all marked gobies. For an analysis of pair stability, I defined a pair as any two marked gobies seen together on at least two consecutive censuses. Marked fish that were seen together on only one occasion and never thereafter were not considered a pair for purposes of this analysis.

Female Reproductive Cycle

Gobiosoma evelynae are sexually monomorphic. However, for 2-3 days prior to spawning, females can be identified by their egg-distended abdomens, and eggs can usually be seen through the female's semi-transparent abdominal wall. During each census, I inspected each fish for visible eggs, and was eventually able to identify the female in most pairs. On each census, each female was categorized as: (1) abdomen distended, eggs visible; (2) abdomen distended, eggs not visible; or, (3) abdomen not distended, eggs not visible.

Spawning frequency in *Gobiosoma* could be inferred from a continuous record of female condition (gravid or not gravid). From July 24 to September 14, 1991, I monitored a group of marked female *G. evelynae* at Flat Cay and

estimated the number of clutches produced by each, and the time interval between clutches.

Removal Experiment

In 1991, I conducted an experiment in which male and female *G. evelynae* were captured and removed from their mates. A total of 32 gobies were removed, 14 at Saba and 18 at Flat Cay. All pairs included in the experiment met three criteria: (1) both fish in the pair were marked; (2) the same two marked fish had been together, at one location, for at least 8 days; and (3) the pair was not the nearest-neighbor of another pair involved in the experiment.

After establishing which pairs could be used on a particular day, I removed one fish at random from each pair, subject to the constraint that approximately equal numbers of males and females were eventually removed. Fifteen pairs had not been sexed by the time of removal; from these, I removed one fish at random and preserved it. The sex of the remaining seventeen fish was known prior to removal. These I simply moved to a new location (>200 m away) and released. After mate-removal, I monitored the location (present on original coral head, moved to new coral head, or absent) and status (paired or unpaired) of the remaining solitary fish. If a new pair formed, I measured the new partner and checked the reproductive

condition (gravid or not gravid) of the female. To
determine if local density affected the subsequent movement
and pairing of the solitary gobies, I counted all
conspecifics (>20 mm TL) within a 6 m radius of the
solitary fish on or soon after the day its mate was
removed. Thirteen marked pairs served as unmanipulated
controls for the removals.

Spatial Maps and Distribution Patterns

I drew detailed maps of the substratum of each survey
grid, showing in 2-dimensions (as seen from above while
hovering in the water) the outline of all living corals
with an area $\geq$ 0.02 m^2, identified by species. Since adult
G. evelynae were rarely observed on corals smaller than
this, the maps contained virtually all of the coral heads
large enough to be potential homesites. I also recorded
the locations and species of all coral heads occupied by
adult *G. evelynae* within the survey grids.

In the field, I measured the maximum length and width
of 104 coral heads (as if the coral were a 2-dimensional
ellipse as seen from above). These corals were all
occupied by pairs of *G. evelynae* and selected haphazardly
from reef areas within and adjacent to the survey grid at
Flat Cay. From these measurements, I computed areas (based
on a 2-dimensional ellipse) for each of the 7 common
species of corals occupied by pairs of gobies.

I used image-analysis software (Image 1.41--N.I.H.) to compute planar areas and generate xy-coordinates for all the living coral heads on the survey grid maps (n = 817 coral heads at Flat Cay and 955 at Saba). These maps contained many coral heads that were probably too small to be inhabited by pairs of *G. evelynae*. Therefore, for each species of coral, I omitted from the maps all heads smaller than those on which pairs of gobies were actually observed. I also omitted those species of coral upon which *G. evelynae* did not perch (i.e., highly branched corals such as *Acropora* spp. and *Porites* spp., "fuzzy" corals such as *Dendrogyra cylindrus*, and fire coral, *Millepora* spp.) This procedure resulted in 487 "inhabitable" coral heads at Flat Cay and 595 at Saba. The spatial distributions of these coral heads were analyzed using the Clark and Evans method of nearest-neighbor analysis corrected for lack of a border strip on the three sides of the survey grids not touching sand (Krebs 1989). The spatial distribution of all female-occupied coral heads within these two areas was also analyzed by the Clark and Evans method.

When they are not actively cleaning other fish or tending a nest, *G. evelynae* are found perched on non-obstructed patches of living coral. Although both sexes swim to other parts of their own and neighboring coral heads (for instance, when males visit their nest hole), such movement happens infrequently, making it impractical to measure male territory areas in the usual manner (i.e.,

by mapping the location of an individual at numerous times). Instead, I estimated male territory size based on two observations. First, male nest crevices were usually located in patches of dead coral less than 1.0 meter from the male's usual perching spot (mean distance $\pm$ SD from perch to nest crevice: 0.38 $\pm$ 0.37 m for n = 24 males). Second, although acts of territorial aggression were observed infrequently, when intrusions by conspecifics did occur, resident gobies vigorously gave chase, but did not pursue intruders further than 0.5-1.0 m. This suggests that territories do not extend beyond about 0.5-1.0 m from the starting point of the chase.

RESULTS

Pair Stability and Spawning Frequency

I monitored a total of 15 and 52 marked pairs of *G. evelynae* at Flat Cay and 8 and 6 marked pairs at Saba in 1991 and 1992, respectively. Marking did not appear to cause injury or mortality of gobies. All ten of the newly-marked fish confined to an aquarium *in situ* appeared to be uninjured after 24 and 48 h, and field recaptures showed no signs of infection at the sites where marks were applied.

Examination of gonads and urogenital papillae confirmed that pairs of *G. evelynae* always consisted of a male and a female. In the field, pairs remained together for periods ranging from three days to at least 92 days (Figs. 1.2, 1.3). The average amount of time ($\pm$ SD) that all marked pairs were together with certainty was 26 days ($\pm$ 15 days) out of 48 days of observation in 1991 and 38 days ($\pm$ 27 days) out of 92 days of observation in 1992 (Saba and Flat Cay pooled). These data underestimate the true amount of time that pairs stayed together, which was not known in most cases because the pair was found together when first marked and/or was still together on the last census. Therefore, *G. evelynae* indeed forms long-term male-female pairs, probably lasting at least a month.

Pairs appeared to spawn repeatedly and regularly. I monitored marked female *G. evelynae* at Flat Cay in 1991 to

determine spawning frequency and interspawning interval. Many of the same females were monitored throughout the summer, but the sample size grew from 13 to 34 fish as additional fish were sampled. Based on the relative frequency of females in each of three reproductive conditions over time, there appeared to be a fairly regular spawning cycle, punctuated by a transition from visibly gravid to not gravid every 6-8 days on average (Fig. 1.4). This transition was a sign that the female had spawned, so the amount of time between successive transitions was the interspawning interval. I observed 28 females complete 68 brood cycles. The maximum number of cycles observed per fish was six, completed by three different females. Two of these females were paired with the same two males throughout; the third was paired with an unmarked male. There was no apparent synchrony or periodicity in spawning (Fig. 1.5); on average, 34% of the females monitored were visibly gravid on any particular census.

Prediction 1:   Size-Assortative Pairing

There was a significant positive relationship between the size of males and females in pairs of *G. evelynae* in both years (n = 116 pairs, R^2 = 0.55, *P*< 0.001, sites and years pooled; Fig. 1.6). The prediction that pairing should be random by size was clearly rejected. Overall, paired males were slightly but significantly longer than

their partners (male mean TL = 28.9 mm, female mean TL = 28.3 mm; paired t = 2.55, P = 0.012), but this size dimorphism was not significant in either year analyzed separately. *Gobiosoma evelynae* less than approximately 20 mm did not form pairs.

Prediction 2: Patterns of Movement

Fifty-nine marked pairs separated naturally during the course of the study. Pair break-ups resulted from the movement or disappearance of males, females, or both simultaneously (Table 1.1). Males left their partners and moved to new territories significantly more often than did females (binomial test, P = 0.002). Males also disappeared more often that females, but not significantly more so (binomial test, 0.50 > P > 0.20). Presumably, many of the fish that disappeared had simply moved to new coral heads outside of the study area, where they were not resighted, although predation or other mortality sources could not be discounted. In any case, the prediction of little or no movement was not supported by these data.

Prediction 3: Mate-Removal and Re-Pairing

Fifteen solitary females and 17 solitary males were created by experimentally removing their mates (Table 1.2). Ten of these 15 females remained on their original coral

heads and had acquired new males by the end of the study (mean $\pm$ SD: 8 ± 5 days to re-pair). Two females remained on their original coral heads but did not form pairs, two others moved and joined formerly solitary males, and one disappeared.

Among the seventeen solitary males, eleven stayed on their original coral head and were joined there by new females (mean $\pm$ SD: 7 ± 7 days to re-pair). Three males stayed but did not form pairs, one moved and joined a solitary female, and two disappeared. These data do not support the prediction that fish of either sex that lose partners will remain unpaired for extended periods.

The rates of movement and disappearance of the 32 solitary fish in the removal study were no different from the rates of movement and disappearance among the 13 control pairs in the same time period. The number of adult conspecific neighbors within a 6 m radius ranged from 0 to 7 ($\overline{X}$ = 2.7 neighbors), and was also not different from the controls. Neighbor density was not correlated with the ability of *G. evelynae* to form new pairs, nor with the amount of time required to re-pair.

On average, the new males acquired by solitary females were significantly smaller than the original males which I removed (n = 12, paired $t = 2.80$, $P = 0.017$; Fig. 1.7a). Likewise, new females acquired by solitary males were significantly smaller than the original females (n = 12, paired $t = 3.79$, $P = 0.003$; Fig. 1.7b). The pattern of

positive size-assortative pairing was still significant between females and second males (R^2 = 0.48, P = 0.013), but not between males and second females (R^2 = 0.02, P = 0.63).

Prediction 4: Distribution of Females among Coral Heads

The vast majority of coral heads of all species within the two study grids were unoccupied by *G. evelynae* (Table 1.3). I pooled the 7 most commonly occupied coral species and computed their spatial distribution, after omitting from the analysis those coral heads that were smaller than the minimum size occupied by gobies. The distribution of these "inhabitable" coral heads was random within the survey grids at both sites (Saba: n = 595 coral heads, R (Index of Aggregation) = 0.99, z = -0.49, P > 0.05; Flat Cay: n = 487 coral heads, R = 1.05, z = 1.84, P > 0.05). The mean distance between neighboring corals ($\overline{r}_A$) was 0.65 m at Saba and 0.68 m at Flat Cay. Overall, 75% of female territories were located on three species of coral: *Montastraea annularis*, *M. cavernosa*, and *Siderastrea siderea*. These three species of coral were also the most common and together accounted for 92% and 75% of the live coral cover within the grids at Saba and Flat Cay, respectively. The prediction of uniformly spaced coral heads was rejected.

Based on the scaled maps, the spatial distribution of "inhabitable" coral heads occupied by females was random within the 1000 m^2 survey grid at Saba in both years (1991: n = 11 female-occupied corals; $\overline{r}_A$ = 5.49 m, R = 1.12, z = 0.63, P > 0.05; 1992: n = 14 female-occupied corals; $\overline{r}_A$ = 5.68 m, R = 1.31, z = 1.89, P > 0.05; Fig. 1.8a). The spatial distribution of female-occupied coral heads at Flat Cay was random in 1991 within the 400 m^2 survey grid (n = 19 female-occupied corals, $\overline{r}_A$ = 3.06 m, R = 1.23, z = 1.77, P > 0.05), but marginally uniform in 1992 when the grid was enlarged to 800 m^2 and more occupied coral heads were included (n = 25 female-occupied corals, $\overline{r}_A$ = 3.72 m, R = 1.23, z = 2.05, P < 0.05; Fig. 1.8b), even though the same Index of Aggregation (R) was obtained in both years. Note that R can vary from a minimum of zero (perfectly clumped) to a maximum of 2.15 (perfectly uniform); an R of 1.0 indicates a perfectly random pattern. Spatial distribution is significantly different from random if |z| > 1.96 (Krebs 1989). Essentially, the pattern of female distribution did not change at Flat Cay between years, but the larger sample obtained in 1992 increased the sensitivity of the test and a marginally uniform pattern was detected. Thus, the prediction of uniformly distributed females among coral heads was supported in only one of four cases. The density of G. evelynae of both sexes combined was over two times higher at Flat Cay than at Saba in both years (.098 and .063 fish/m^2 at Flat Cay

and .029 and .030 fish/m^2 at Saba in 1991 and 1992, respectively).

If one assumes that the average male territory is roughly circular in shape with a radius of at most 1.0 m centered on the male's resting spot (see Methods), then no male territory within the survey grids overlapped with more than one female-occupied coral head (Fig. 1.8a,b). Unlike most other results, this pattern was consistent with the Environmental Constraints Hypothesis.

DISCUSSION

The social system of adult *Gobiosoma evelynae* consisted of pairs of similarly-sized males and females, some of which remain together for at least three months. Since spawning occurs inside holes and crevices where it cannot be observed, it is impossible to know the extent of pair fidelity in this species. However, most fish did stay with one partner long enough to mate repeatedly, and some females went through six spawning cycles in the company of the same male. Because of variability in the length of time that pairs remained together, the mating system of this species may be serial monogamy. In any case, stable groups of three or more *G. evelynae* were never seen on the reefs where this study was conducted.

What prevents a pair from becoming a group of three or more? I tested a hypothesis that pairing is (1) a consequence of three closely related factors--low male mobility (small territory size), low female density, and a uniform distribution of resources (in this case, living coral heads)--which (2) constrain males by low encounter rates to remain with one female for an extended period of time. The mean distance between neighboring females (> 3 m) relative to my estimate of the maximum male territory diameter ($\leq$ 2 m) was consistent with this hypothesis. Indeed, the mapped distributions of coral heads and gobies in the two survey grids (Fig. 1.8a,b) resemble the

scenarios for low male mobility and/or low female density in the Environmental Constraints Hypothesis (Fig. 1.1, cases A, B, C). The maximum extent of male movement within a territory did appear to be less than the distance between adjacent females (or conversely, the density of females was low relative to the estimated size of male territories). Furthermore, a uniform distribution of female-occupied coral heads occurred at one site in one year (but was random in three other cases). Based on these data alone, the Environmental Constraints Hypothesis cannot be rejected. However, these patterns are necessary but not sufficient evidence. The predictions derived from this hypothesis also require a low encounter rate between males and females, and this is clearly not the case. If there is no barrier to movement between territories, and if encounter rates are reasonably high, then mobility, density, and resource distribution cannot be invoked to explain long-term pairing and monogamy.

I reject the Environmental Constraints Hypothesis for pairing in *Gobiosoma evelynae* for the following four reasons. First, the observed positive correlation between the sizes of females and their partners could only be caused by intrasexual competition and/or active mate choice by one or both sexes (McKaye 1986). This pattern would not result if *G. evelynae* simply paired off with the first potential mate encountered. The pairing of dissimilarly

sized fish after the intentional removal of females from pairs was most likely a temporary result of disturbance.

Second, movement of males to new territories was fairly common, and was a frequent cause of pair break-up (although movement *within* a territory did appear to be limited, relative to the distance between neighboring females, as predicted by the hypothesis).

Third, gobies of both sexes that lost their partners in the mate-removal experiment were able to acquire new partners within a few days. This is the strongest evidence against the Environmental Constraints Hypothesis for pairing. There appears to be a pool of smaller adults or subadults that is mobile and ready to fill openings as they arise. Because this experiment was conducted outside the fixed census areas, where the majority of gobies were not marked, I do not know if immigrant fishes were paired before they moved, or if they were previously unpaired floaters. If they were paired, the move may represent a change to a larger partner.

It is interesting that, following the removal experiment, the pattern of size-assortative mating was still present between females and second males, but not between males and second females. This result suggests that active mate choice was still operating in the first case, but not in the second, perhaps because only one sex (i.e., females) is choosy. A monogamous male would clearly benefit from pairing with a large mate, since female size

and fecundity are positively correlated in most fishes (Potts and Wootton 1984). Potential advantages for a female to pair with a large male are increased territory defense, egg defense and nest maintenance. In *Gobiosoma evelynae*, the advantage to a female of having a large male seems less obvious, since the male is not essential for territory defense as it is in some species of pair-forming butterflyfishes (Fricke 1986; Hourigan 1989).

Finally, there does not appear to be a direct relationship between the distribution of at least one important resource—suitably large, living coral heads—and the distribution of female gobies and pairs. The distribution of "inhabitable" coral heads was random at both Saba and Flat Cay, not uniform as predicted by the hypothesis. The distribution of females among coral heads was uniform in only one of four cases (Flat Cay in 1992); in both years less than 6% of the available coral heads at both sites were actually inhabited by *G. evelynae*. Even if "inhabitable" coral heads were uniformly spaced, it is hard to imagine that the distribution of a resource that is so heavily undersaturated by *G. evelynae* could be directly affecting the distribution of female gobies. If there is a large surplus of suitable living space, and females are still distributed uniformly, then either (a) some other process must be affecting the spatial pattern of females (e.g., social interactions between females or non-resource related limitations of goby abundance), or; (b) the

critical resource affecting female distribution has been misidentified.

Food is obviously one resource that may influence the distribution of females. *Gobiosoma evelynae* is a cleaner fish, so its food supply is the ectoparasites on other fishes (Randall 1967, Colin 1975). Opportunities for *G. evelynae* to feed appear to be temporally unpredictable and depend on the chance passing of a host within a meter or so of the goby's coral head. However, some cleaning stations were located near loose, semi-permanent aggregations of planktivorous damselfishes (*Chromis* spp.), which are frequently cleaned by *G. evelynae*. A similar phenomenon has been reported for the cleaner wrasse *Labroides dimidiatus* in the tropical Pacific (Robertson and Hoffman 1977). Among *Labroides*, the best cleaning stations are located above large, prominent coral heads, and hosts aggregate at these sites. *Labroides* females also tend to cluster at these limited sites, which allows dominant males to monopolize several females and mate polygynously (Robertson and Hoffman 1977). In contrast, *G. evelynae* territories with predictably high numbers of hosts were not occupied by more than one pair of gobies (see Appendix); in fact, many apparently suitable coral heads near *Chromis* aggregations were vacant. This suggests that food was not a limiting resource for *G. evelynae* and/or that host-fish aggregations cannot be successfully monopolized by males in this system.

Spawning periodicity also does not explain pairing in
G. evelynae. Computer simulations have shown that
synchronous spawning among local groups of females can act
to maintain stable pairing and monogamy (Knowlton 1979).
Presumably, female synchrony deprives males of the
opportunity to find additional receptive females, and
therefore males in such populations are less likely to
abandon their mates. Female *G. evelynae* appear to have a
cycle of 6-8 days between successive clutches, but there
was no overall periodicity or synchrony in spawning.

Under certain conditions, male parental care may
result in pairing. Parental care of demersal eggs imposes
an obvious constraint on the mobility of males. For
several days after spawning, male *G. evelynae* are not free
to seek additional females and must remain with the
developing embryos, which do not survive if care is not
provided (Colin 1975). The interspawning interval was
about the same as the interval between laying and hatching
(i.e., 7-9 days; Colin 1975, Harding, unpublished), during
which the male is occupied tending eggs. This may be more
than coincidence: males that are kept constantly busy
tending eggs have fewer opportunities to seek additional
females. In the monogamous coral reef pipefish
Corythoichthys intestinalis, females require the same
amount of time (about 10 days) to mature a clutch of eggs
as males require to brood a clutch until hatching (Gronell

1984).   Gronell suggests that this time constraint may bias the species toward monogamy.

The possibility that male parental care causes long-term pairing in *Gobiosoma evelynae* seems unlikely for two reasons. First, male *G.evelynae* could probably care for the broods of two or more females simultaneously (although male pipefish *C. intestinalis* apparently cannot; Gronell 1984). Brooding of multiple clutches by males is the norm among small, territorial, demersally spawning reef fishes (i.e.,*Stegastes (Eupomacentrus) partitus*: Schmale 1981; *Ophioblennius atlanticus*: Marraro and Nursall 1981; *Axoclinus carminalis*: Petersen 1989; *Trimma okinawae*: Sunobe and Nakazono 1990). Second, female *G. evelynae* do not participate in parental care; unlike males, their movement after spawning is not constrained. Female mobility between male territories was demonstrated in the mate-removal experiment, since males that lost their partners were joined by immigrant females within a few days.

What prevents two or more females from joining one male? The Environmental Constraints Hypothesis assumes that social interactions between females do not occur, but this is not a reasonable assumption. In fact, the aggression that I occasionally observed between paired *G. evelynae* and intruders during this study suggests another, more parsimonious hypothesis for the maintenance of pairs in this species: mutual mate-guarding. In the

butterflyfish *Chaetodon chrysurus*, strong aggression by each pair member against intruders of the same sex maintained stable heterosexual pairs, and unpaired butterflyfish could not hold territories (Fricke 1986). If male and female *G. evelynae* also attack primarily members of the same sex, then pairing could be maintained in the absence of other factors, such as a uniform distribution of resources, low mobility of males, or low density of females. In fact, intrasexual territoriality (or any territorial aggression between conspecifics) could, by itself, lead to a uniform distribution of fish, especially if densities are high. Intrasexual aggression in *G. evelynae* could be tested by releasing single males and females directly onto the territories of pairs and singles, and quantifying the reactions of the male and female residents to these intruders (see Chapter 2).

Table 1.1. Causes for separation of 57 pairs at Saba and Flat Cay in 1991 and 1992 combined. Male movement away from the pair's territory caused significantly more pair separation than female movement.

Cause of Separation	Male	Female	Both
Disappeared Permanently	19	12	9
Moved to a New Territory	16	1	0
Total	35	13	9

Table 1.2. Summary of mate-removal experiment at Flat Cay and Saba in 1991. In the male-removal treatment, focals = females; in the female-removal treatment, focals = males. In the control treatment, focals = both pair members.

| Treatment | Site | Number of Pairs | Response of Focal Individual | | | | Days to Re-Pair ($\overline{X} \pm$ SD) | Neighbors in 6 m Radius ($\overline{X} \pm$ SD) |
			Stayed and Re-Paired	Moved and Re-Paired	Stayed and Remained Single	Disappeared-- Status unknown		
Male Removal	Flat	9	5 (56%)	1 (11%)	2 (22%)	1 (11%)	8±3	3±2
	Saba	6	5 (83%)	1 (17%)	0	0	8±6	2±2
	Total	15	10 (67%)	2 (13%)	2 (13%)	1 (7%)	8±5	2±2
Female Removal	Flat	9	6 (67%)	1 (11%)	1 (11%)	1 (11%)	4±3	3±2
	Saba	8	5 (63%)	0	2 (25%)	1 (13%)	10±9	3±2
	Total	17	11 (65%)	1 (6%)	3 (18%)	2 (12%)	7±7	3±2
Control*	Flat	9	1 (11%)	0	5 (56%)	3 (33%)	12±0	5±1
	Saba	4	0	0	4 (100%)	0	---	2±0
	Total	13	1 (8%)	0	9 (69%)	3 (23%)	12±0	4±2

* Controls are 13 unmanipulated pairs within the survey grids; these pairs were stable for at least 8 days before the removal experiment began on 8-17-91 (see Fig. 1.2).

Table 1.3. Seven species of coral most frequently occupied by pairs of *G. evelynae*. For each species of coral, the "critical size" is the smallest size of coral head on which a pair of gobies was observed. Only 2% and 5% of the "inhabitable" coral heads were occupied by *G. evelynae* at Saba and Flat Cay, respectively.

| Coral Species | Critical Size (m^2) | Total Inhabitable Coral Heads | | Coral Heads Occupied by Females and Pairs | | | |
| | | | | Flat Cay | | Saba | |
		Flat Cay	Saba	1991	1992	1991	1992
Montastraea annularis	0.03	222	200	2	1	7	5
Montastraea cavernosa	0.03	89	267	5	8	2	4
Siderastrea siderea	0.09	89	82	7	6	2	3
Meandrina meandrites	0.09	34	0	0	0	0	0
Diploria labyrinthiformis	0.05	28	11	2	2	0	1
Colpophyllia natans	0.19	9	0	3	4	0	0
Diploria strigosa	0.05	10	35	0	0	0	1
Other	NA	6	0	0	4	0	0
TOTAL		487	595	19	25	11	14

Figure 1.1. **A-D**: Effect of varying female density and male mobility on the social system of a coral-dwelling reef fish. **(A, B,** and **C)** Low male mobility and/or female density results in male-female pairs. **(D)** Sufficiently high male mobility relative to female density results in polygynous groups. Note that the sex-ratio of the fish and the density and distribution of coral heads can all be constant among cases, as illustrated. **E-F**: Effect of varying coral-head distribution on the same reef fish. **(E)** Pairs are obtained when corals are uniformly distributed and the distance between adjacent suitable heads is greater than the maximum male territory diameter. **(F)** When corals are clumped relative to male territory size, polygynous groups are obtained. Note that coral-head density, female and male density, and male mobility (i.e., territory area) can all be constant in both cases, as illustrated.

Fig. 1.1.

FEMALE DENSITY

LOW   HIGH

MALE MOBILITY

LOW

HIGH

UNIFORM   CLUMPED

CORAL DISTRIBUTION

○ coral head, no female present

● female-occupied coral head

⟨ ⟩ male territory
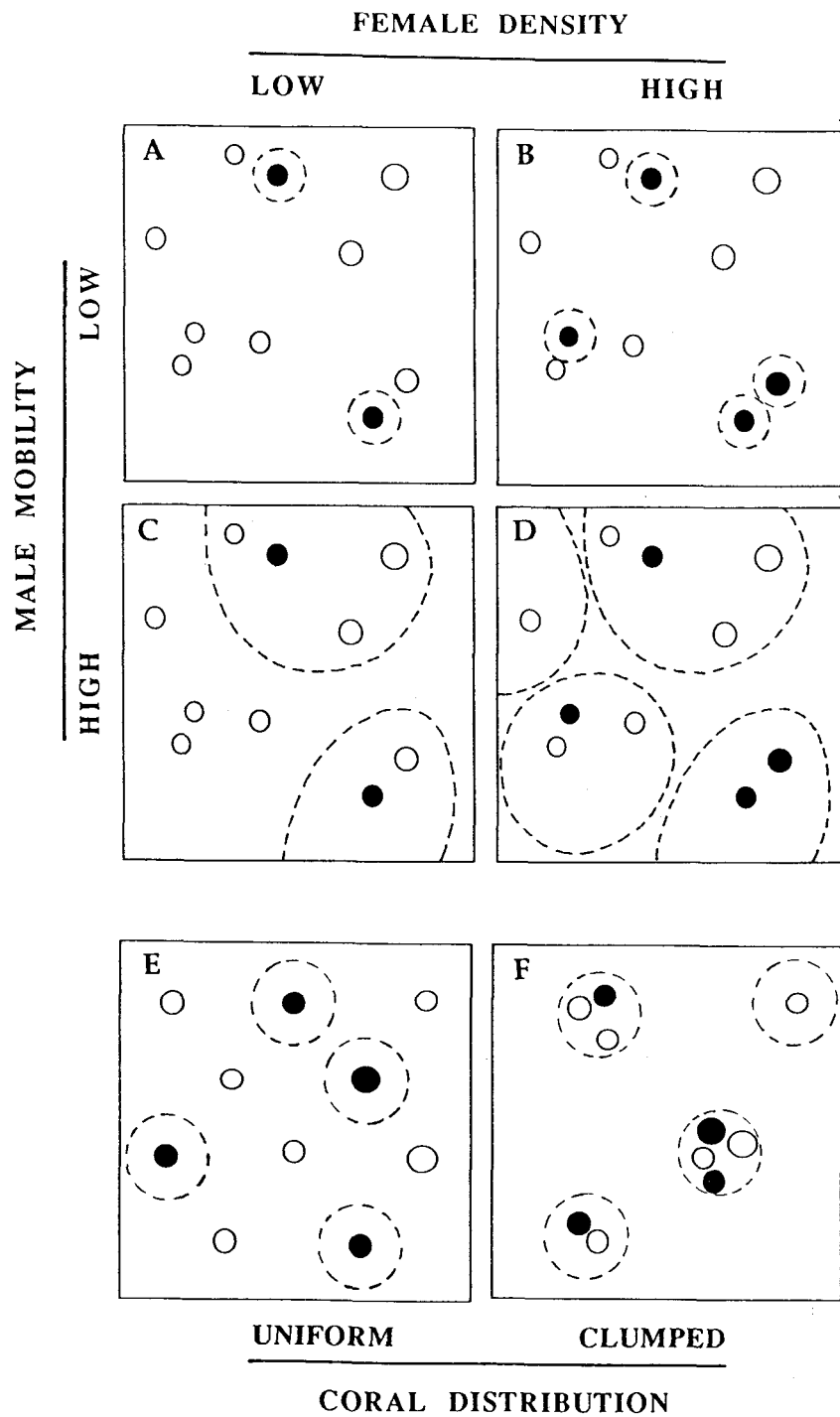
Figure 1.2. Amount of time 23 pairs of *G. evelynae* were seen together continuously in 1991 (n = 8 pairs at Saba and 15 pairs at Flat Cay). Fine lines are periods during which pairing was not certain (i.e., one or both fish not yet marked). Heavy lines are periods during which pairing was certain (i.e., both fish marked and present together at one location). Heavy lines thus represent the minimum possible time that pairs remained together, which ranged from 3 to 47 days. *Category A*: pairs that were found together when first marked, and were still together on the last census. *Category B*: pairs that were found together when first marked, but separated at known times. *Category C*: pairs that formed and separated at known times. The heavy lines with dots are 13 unmanipulated control pairs for the removal experiment that began on 8-17-91 (see text).

Fig. 1.2.
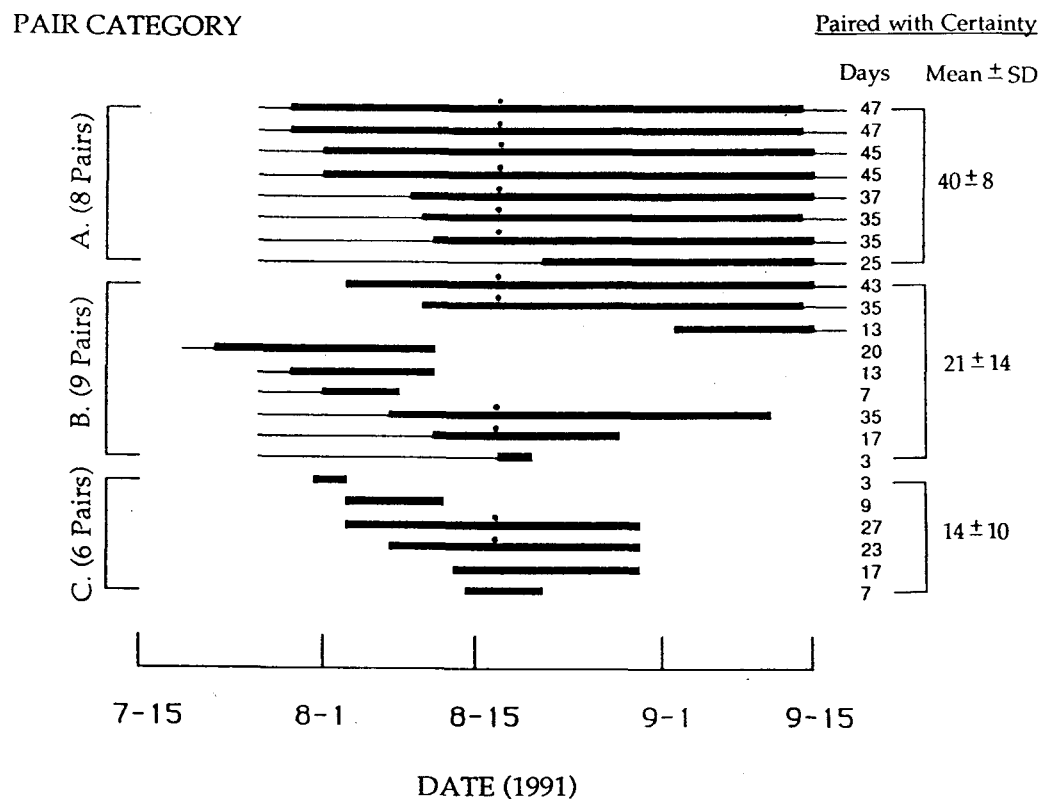
Figure 1.3. Amount of time 58 pairs of *G. evelynae* were seen together continuously in 1992 (n = 6 pairs at Saba and 52 pairs at Flat Cay). Fine lines, heavy lines, and Categories A-C are as described in Fig. 1.2. The minimum time that pairs remained together with certainty ranged from 3 to 92 days.

Fig. 1.3.
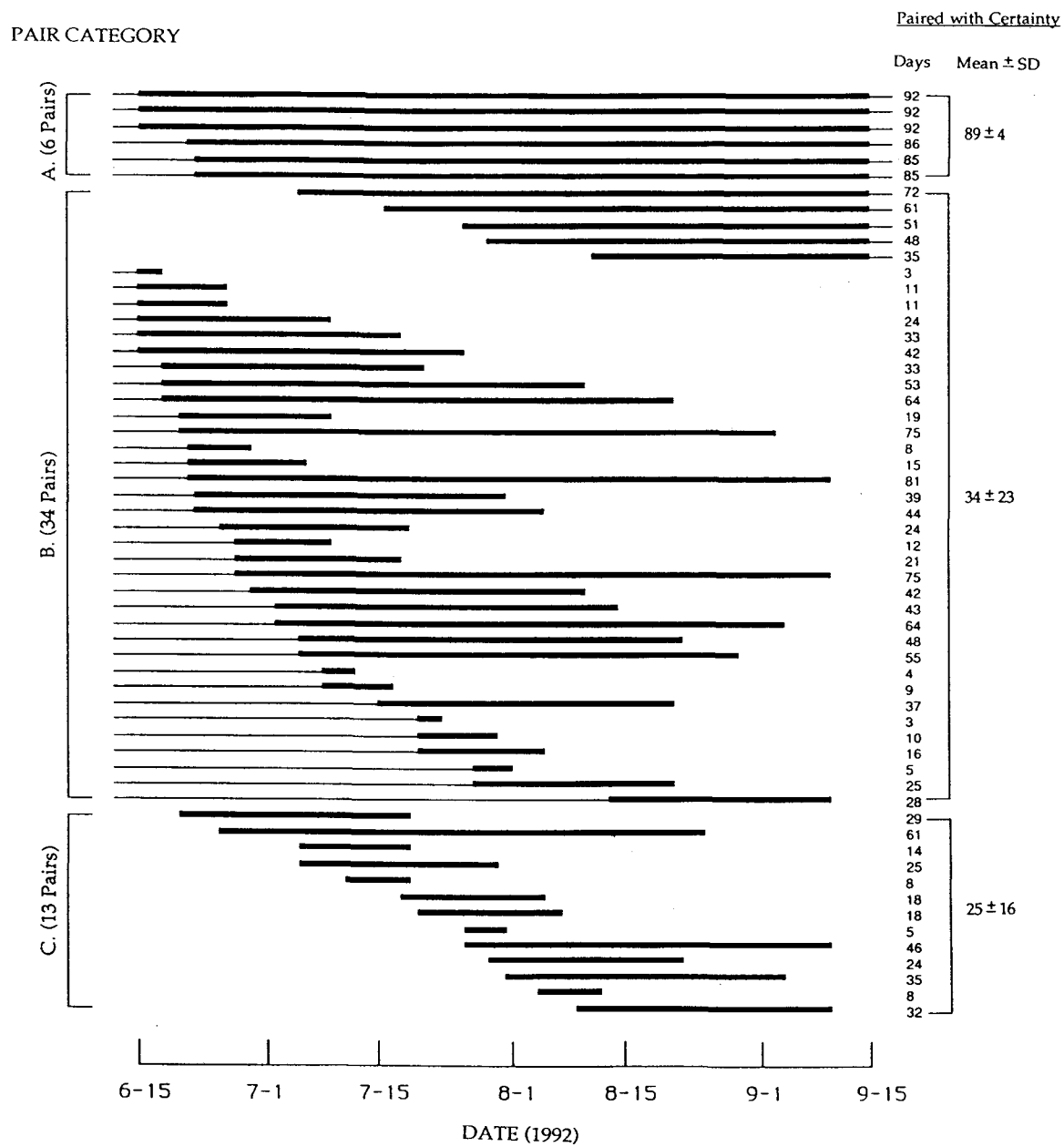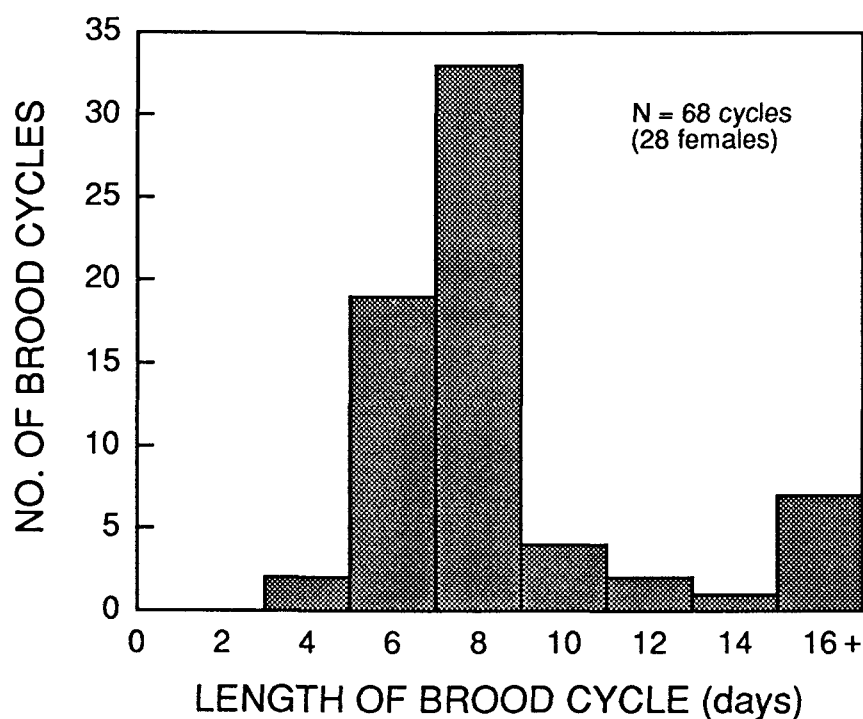
Figure 1.4. Frequency distribution of brood cycle durations among 28 *G. evelynae* females at Flat Cay in 1991. The duration of each cycle was the amount of time required for a transition from visibly gravid to not gravid to visibly gravid, which presumably corresponded to the interspawning interval. Because censuses were conducted every other day, there is a $\pm$ 2 day uncertainty for each brood cycle.
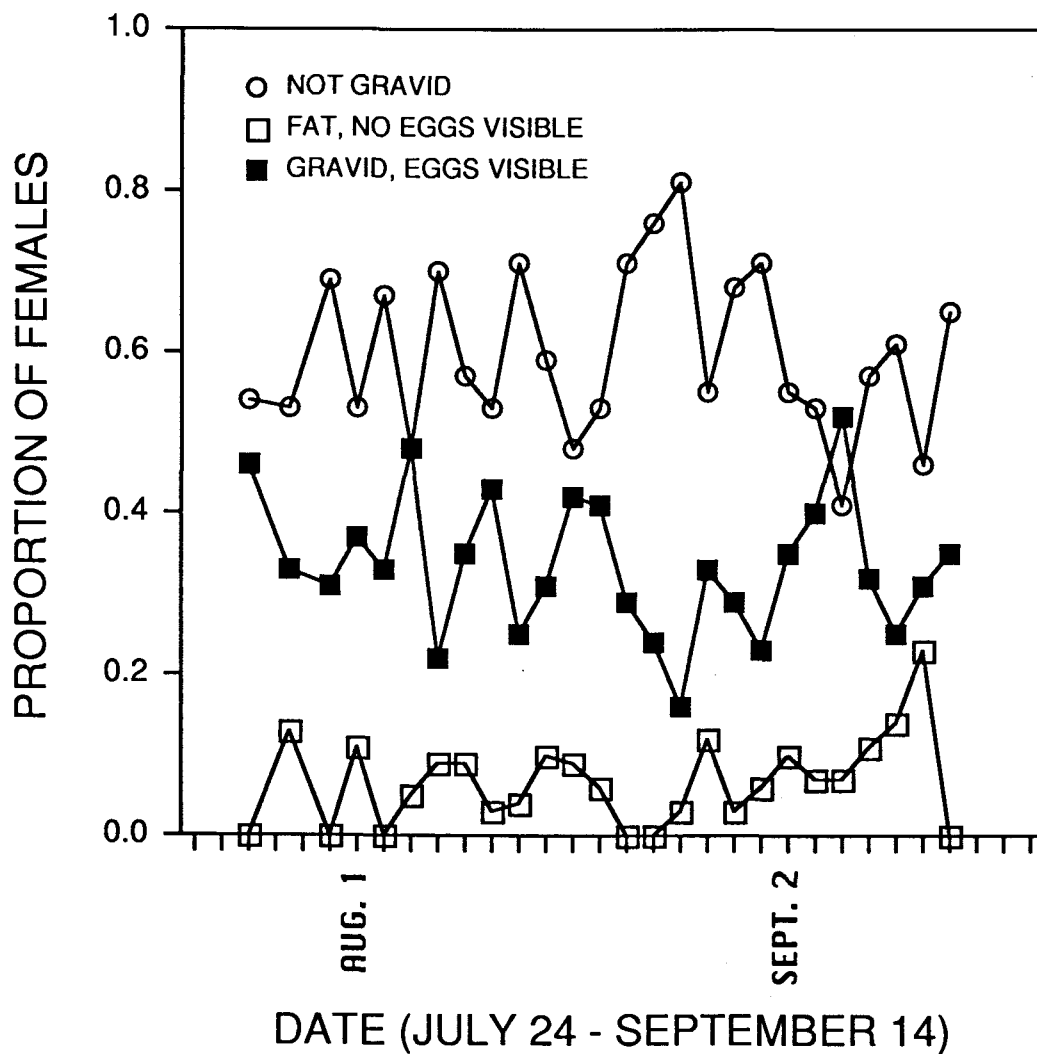
Figure 1.5. Relative frequency of females in three visually different reproductive states during the period from July 24 to September 14, 1991. Sample size ranged from 13 to 34 marked females.
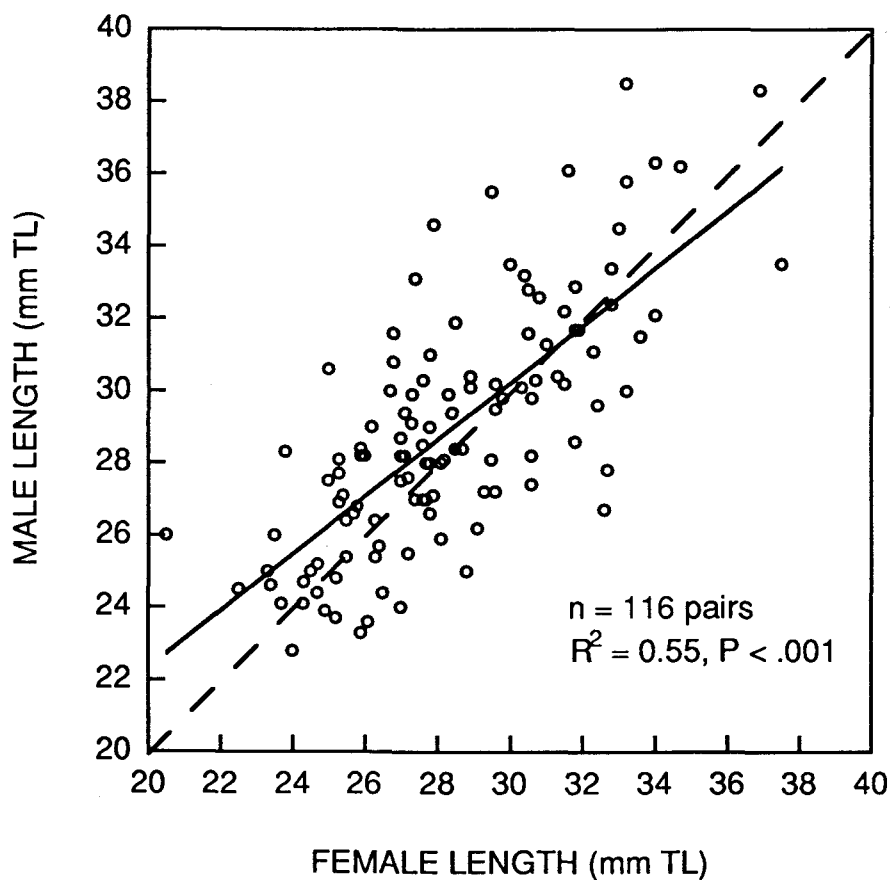
Figure 1.6. Relationship between total length of paired female and male *Gobiosoma evelynae*. Each point represents one pair. The slope of the regression (0.79) differs significantly from both zero (t = 11.7, P < 0.001) and 1.0 (t = -3.09, P < 0.005). Overall, males were slightly longer than females, as indicated by the majority of points lying above the dashed line of equality.

Figure 1.7. **A.** Relationship between the size (mm TL) of 12 solitary female *G. evelynae* and their first and second partners. The first partners were experimentally removed, the second partners are new males (replacements) that subsequently joined the female. Second males (filled circles) are significantly smaller than first males (open circles), and there is a positive relationship between the size of females and second males. **B.** Relationship between the size (mm TL) of 12 solitary male *G. evelynae* and their first and second partners. The first partners were experimentally removed, the second partners (replacements) are new females that subsequently joined the male. Second females (filled circles) are significantly smaller than first females (open circles), and there is no relationship between the size of males and second females.

Fig. 1.7.

A

(MALE LENGTH (mm TL) vs FEMALE LENGTH (mm TL))
○ male removed
● male replacement

B

(FEMALE LENGTH (mm TL) vs MALE LENGTH (mm TL))
○ female removed
● female replacement
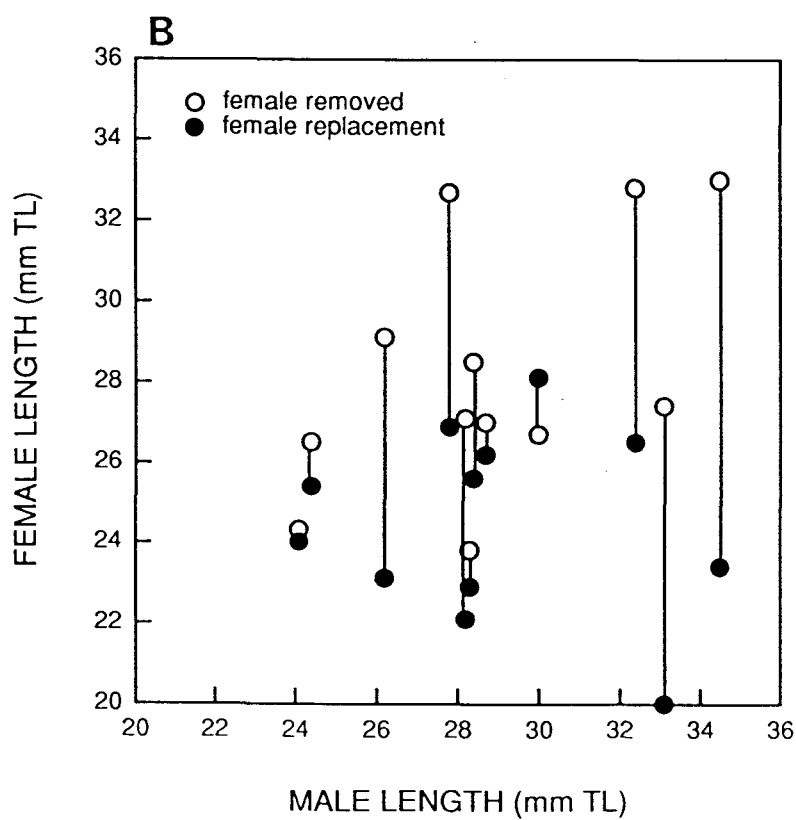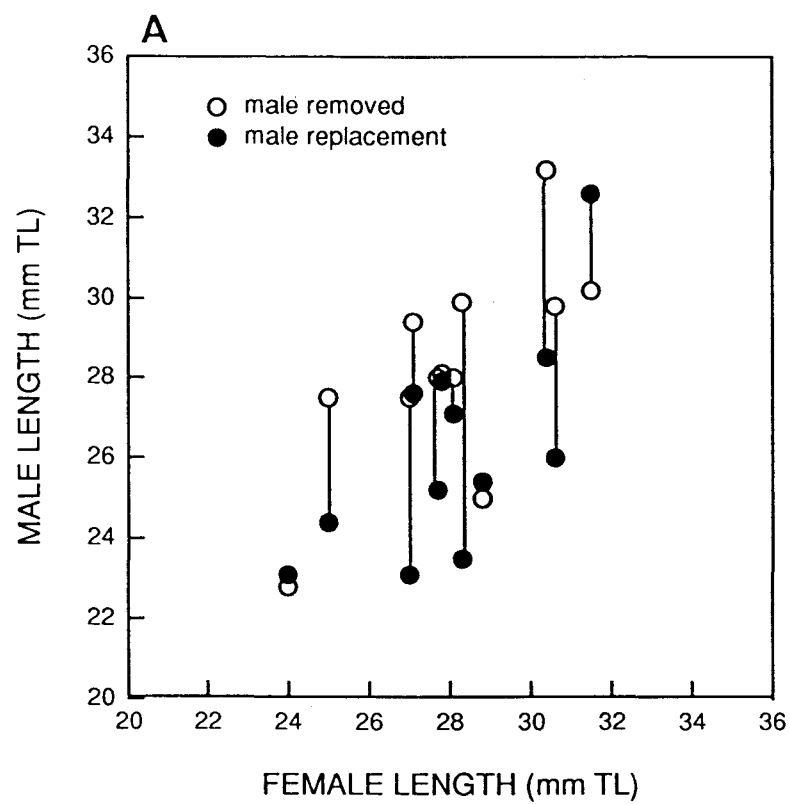
Figure 1.8. **A**. Scaled map of all "inhabitable" coral heads (n = 595) and all coral heads occupied by *G. evelynae* (n = 14) within the 1,000 m^2 survey grid at Saba in September, 1992. All occupied coral heads shown on the map contained pairs of gobies (i.e., one male and one female) at the time the map was drawn. The spatial distribution of "inhabitable" coral heads and coral heads with female gobies was random. **B**. Scaled map of all "inhabitable" coral heads (n = 487) and all coral heads occupied by *G. evelynae* (n = 25) within the 800 m^2 survey grid at Flat Cay in September, 1992. Three occupied coral heads shown on the map contained only female gobies at the time the map was drawn; the remaining 22 occupied coral heads contained pairs. The spatial distribution of the 487 "inhabitable" coral heads was random, but the spatial distribution of the 25 coral heads containing females was marginally uniform. In both maps, male territories were estimated to be uniformly circular planar areas no greater than 2.0 m in diameter. Note that each male territory contained only one female-occupied coral head and from zero to seven unoccupied but "inhabitable" coral heads, and that adjacent territories did not overlap.

Fig. 1.8.

A. Saba

· CORAL HEAD

⊙ FEMALE-OCCUPIED CORAL HEAD

◯ MALE TERRITORY

B. Flat Cay

DISTANCE (m)

DISTANCE (m)
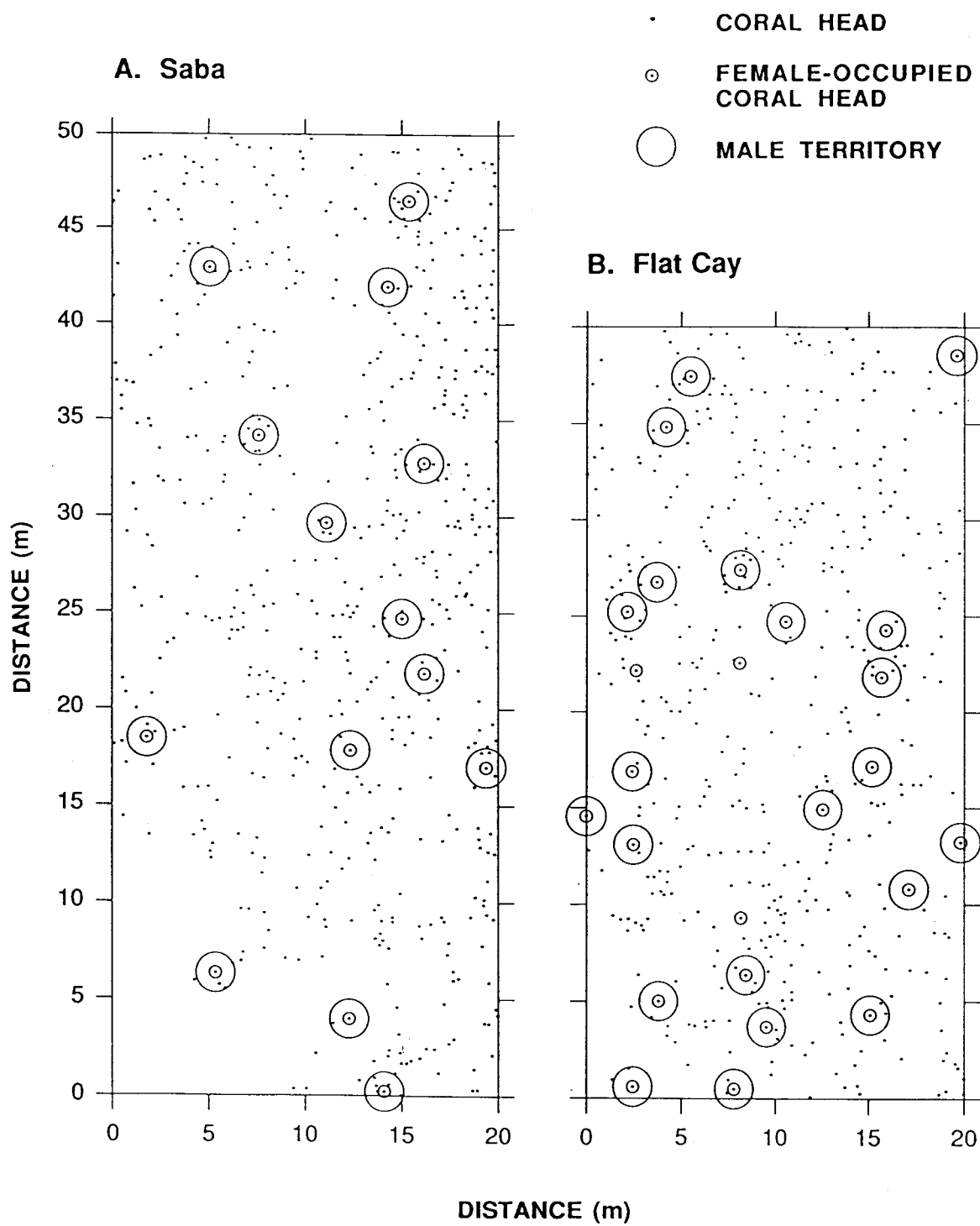
Chapter 2

Mate guarding and heterosexual pairing in the Caribbean goby *Gobiosoma evelynae*

INTRODUCTION

Early models for the evolution of monogamy were developed largely from studies of birds, the only vertebrate group in which this mating system predominates (Lack 1968). These models were based on the assumption that biparental care of eggs and young was essential. However, heterosexual pairing and monogamy also occur in groups such as coral-reef fishes (Barlow 1984, Thresher 1984), where biparental care of eggs and young is extremely uncommon. Monogamy in coral-reef fishes and similar groups therefore requires another explanation.

Several hypotheses have been proposed to account for heterosexual pairing and monogamy in reef fishes, and evidence from field studies suggests a variety of factors may be important. For instance, pairing may decrease time invested in repeated mate-assessment and courtship (Gronell 1984), or allow cooperation in territory defense (Fricke 1986, Hourigan 1989) or cooperative foraging (Pressley 1981). Despite many recent papers on monogamous reef fish, little consensus exists among researchers regarding the

mechanisms involved, even for the most extensively studied pair-forming species (chaetodontid butterflyfishes; Roberts and Ormond 1992). Furthermore, some of the hypotheses are untestable unless polygyny can be induced for experimental comparison (e.g., Increased Reproductive Efficiency Hypothesis and Hybridization-Avoidance Hypothesis; see Chapter 1). Others do not explain why a pair should form instead of a larger group, or why a heterosexual pair should form in preference to a homosexual one (e.g., Cooperative Foraging Hypothesis and Cooperative Resource Defense Hypothesis; see Chapter 1).

There are two hypotheses for heterosexual pairing that are both relevant to reef fish and testable without having to induce polygyny: the Environmental Constraints Hypothesis and the Mate-Guarding Hypothesis. The first of these is actually a more general composite of two hypotheses that were originally proposed separately: Low Mobility/Low Density (Gronell 1984, Thresher 1984) and Resource-Distribution (Barlow 1984, 1986, 1988). According to this composite hypothesis, three related factors--low male mobility, low female density, and a uniform distribution of resources required by females--decrease encounter rates between the sexes to such an extent that long-term pairing and monogamy is the best reproductive strategy available.

In Chapter 1, I described tests of the Environmental Constraints Hypothesis for male-female pairing in *G.*

evelynae. I found that some pairs remained intact for at least three months, a strong pattern of non-random pairing by size, frequent male movement between female territories, rapid re-pairing by males and females after loss of mate, random spatial distributions of apparently suitable, unoccupied coral heads, and mostly random distributions of female territories among coral heads. These results are inconsistent with the Environmental Constraints Hypothesis, which assumes that social interactions between females do not influence female distribution. Moreover, during my study I noted occasional territorial aggression in *G. evelynae,* which suggested a different explanation for heterosexual pairing in this species.

The Mate-Guarding Hypothesis (Wittenberger and Tilson 1980) is the simplest explanation for the occurrence of lasting heterosexual pairs in *G. evelynae.* This hypothesis states that aggression by paired females toward female conspecifics prevents males from acquiring additional mates. This phenomenon, also called "enforced monogamy" (Wickler and Seibt 1981) and "unilateral manipulated monogamy" (Barlow 1984), appears to be common in monogamous reef fishes (although not universal; Gronell 1984, Clark and Pohle 1992). Territorial aggression that is primarily or exclusively intrasexual has recently been reported in several families, including filefishes (Barlow 1987), hawkfishes (Donaldson 1989), damselfishes (Ochi 1989), and

butterflyfishes (Fricke 1986, Hourigan 1989). Additional
reports are reviewed by Barlow (1984).

In monogamous species in which mates share a common,
multipurpose territory, the occurrence of female aggression
is not, by itself, sufficient evidence for accepting the
Mate-Guarding Hypothesis. This is because female
aggression may be in defense of some other resource
associated with the territory (i.e., food, shelter, nest
sites, etc.) independent of the female's mate (Wagner
1992). An alternative explanation for female territorial
aggression, the Resource-Guarding Hypothesis, does not
consider mates to be one of the guarded resources.
Resource guarding, even if it is a cooperative male-female
venture, is not a valid hypothesis for monogamy because a
resource could just as easily be defended by a group of
three or more individuals.

Since there is likely to be a continuum between "pure"
mate guarding and "pure" resource guarding, mates are
probably only one of several resources that are guarded by
female territorial aggression in monogamous species.
Determining how much aggression is allocated to the defense
of each resource on the territory may be impossible.
However, if the result of female aggression is to sequester
the male, such that his only option for spawning with
additional females is to leave his present mate and
territory, then mate guarding is still a valid explanation
for pairing.

The Mate-Guarding Hypothesis thus requires that territorial females paired with males react most aggressively to female intruders. Intuitively, the hypothesis also requires that males guard their female partners as well (i.e., that mate guarding is mutual), because if they did not, multi-male groups and polyandry could conceivably result. If a strong pattern of positive size-assortative pairing occurs (as in *G. evelynae*), then it is also reasonable to assume that at least one sex forms pairs preferentially with large rather than small partners. Given these assumptions, the Mate-Guarding Hypothesis predicts both sex-specific and size-specific aggressive responses of paired residents to conspecific intruders. The specific predictions depend on whether or not resources in addition to the mate are also guarded. If they are not, then there is one set of predictions (Table 2.1, corollary 1a: Defense of Mate Only); if they are, then there is a slightly different set of predictions (Table 2.1, corollary 1b: Defense of Mate and Other Resources). Under corollary 1a, intruders of the opposite sex should never be attacked because they are not sexual rivals. Under corollary 1b, small intruders of the opposite sex should be attacked, because they are potential resource competitors, and are unfavored mates because of their small size. The resident's response to large intruders of the opposite sex is unpredictable, because they are simultaneously potential resource competitors and potentially favored mates. Note

that the predicted response of residents to intruders of the same sex is the same in both corollaries, namely: very aggressive if the intruder is large (because it is a sexual rival), and aggressive if the intruder is small (because it is also a sexual rival, but presumably less of an immediate threat because of its small size).

The alternative hypothesis, resource guarding, predicts aggression toward conspecific intruders of any sex and size, because all are potential resource competitors. Note that specific predicted responses may vary depending on whether large intruders are greater resource competitors than small intruders. In any case, the resident's response to males and females should be the same if the intruders are of equal size, assuming both sexes are equal threats to the defended resource(s).

I tested the predictions of the Mate-Guarding and Resource-Guarding Hypotheses (Table 2.1) in *G. evelynae* by placing large and small male and female gobies on the territories of pairs, thereby inducing measurable behavioral responses from resident male and female gobies. I compared the rates at which specific aggressive behaviors were performed by residents of each sex when confronted with the four types of intruders. I also released large males and females on the territories of unpaired females to determine whether aggression occurred in the absence of a mate. The observed patterns of aggression were most consistent with the male and female responses predicted by

Hypothesis 1, corollary 1b (Table 2.1), suggesting that *G. evelynae* defend both a mate and other resources. This study is the first of which I am aware to experimentally induce and compare rates of sex- and size-specific aggression in the field for any pair-forming reef fish.

MATERIALS and METHODS

Study System

This study was conducted from July to September, 1992,
on a shallow (4-12 m) fringing reef at Flat Cay, a small
islet on the southern side of St. Thomas, U.S. Virgin
Islands. All work was performed while SCUBA diving.

Gobiosoma evelynae is a relatively common Caribbean
reef fish that forms male-female pairs and is assumed to be
monogamous (Colin 1975). At St. Thomas, it occurs both
singly and in pairs, and holds territories on living coral
heads. Because it is small (<40 mm total length, TL),
site-attached, and very tolerant to the presence of divers,
G. evelynae is an ideal fish for *in situ* behavioral
studies.

Fish Tagging

I captured *G. evelynae* with a dilute
quinaldine/ethanol solution and an aquarium net, and
measured each fish to the nearest 0.1 mm TL. To track
known individuals, some fish were individually marked; this
was done by nicking the yellow stripe posterior to each eye
with the tip of a needle, as described in Chapter 1.
Marked gobies were immediately returned to their coral
heads; the entire procedure was done underwater and

appeared to have no adverse effects on the fish. Although
G. evelynae are sexually monomorphic, the female of a pair
can be identified in the field by her egg-distended
abdomen, which is visible for 2-3 days prior to spawning.
Preserved specimens can be sexed with a dissecting
microscope, based on the shape of the urogenital papillae.

Fish Addition Experiments

Additions to pairs

To test the predictions of the Mate-Guarding and
Resource-Guarding Hypotheses, I measured the behavioral
response of 12 paired males and females to conspecific
intruders placed on the territory occupied by each pair.
Given that the predictions of both hypotheses are based on
the sex and size of the intruder, each resident pair was
"challenged" with four types of intruders: a male smaller
than the resident male, a male larger than the resident
male, a female smaller than the resident female, and a
female larger than the resident female. All 24 of the
gobies in the 12 resident pairs were individually marked
prior to the experiment, and the identity of the female in
each pair was known. The 48 fish used as "intruders" were
measured, but were not marked, and their sex was unknown at
the time they were captured and used. (Intruders were
sexed after each trial, as described below.) All intruders
were used on the same day they were captured. Pairs were

challenged with one or two intruders per day. If a pair received two intruders on the same day, the additions were made at least 2 hours apart, on separate dives. The order of fish additions to territories was random by size and blind by sex.

Among the 12 resident pairs of *G. evelynae* whose behaviors were measured, the size of males (mean $\pm$ SD) was 28.7 $\pm$ 3.0 mm TL, and the size of their female partners was 28.1 $\pm$ 2.0 mm TL. In this experiment, "large" intruders were about 4 mm larger than resident fishes (12 large males: 32.7 $\pm$ 2.3 mm TL; 12 large females: 32.3 $\pm$ 2.7 mm TL), and "small" intruders were about 3 mm smaller than resident fishes (12 small males: 25.8 $\pm$ 1.8 mm TL; 12 small females: 25.0 $\pm$ 2.6 mm TL). Since *G. evelynae* begin to form pairs and spawn at about 20-22 mm, all intruders in this experiment were large enough to be sexually mature and form pairs.

Preliminary tests using intruders confined in clear glass bottles did not elicit responses from territory residents. Therefore, I released intruders directly onto the coral head occupied by the resident pair. The initial response of most newly-released intruders was not to flee, but simply to rest upon the coral substrate where I released them, which was as close to the resident pair as possible.

Resident gobies quickly approached intruders. Using a stopwatch, I began timing a trial as soon as one of the

residents was within a body length of the intruder, at which point the intruder obviously had been detected. During each trial, I recorded three distinct types of clearly aggressive behaviors displayed by residents, in the order that they occurred (see Results). Trials lasted from 8 to 30 minutes (mean duration $\pm$ SD: 15 min 30 s $\pm$ 6 min, n = 48 trials), depending on the intensity of the resident's response and the intruder's propensity to flee. Trials ended sooner when residents showed immediate and persistent aggression, because I was unable to keep the intruder in the territory. If an intruder was expelled by the aggressive behavior of one resident, I stopped the clock, recaptured the intruder, returned it to a point in the territory where it was again visible to both residents, and resumed timing. Each trial continued for several minutes, until both the male and the female resident had seen and approached the intruder one or more times. Thus, both residents were given approximately equal opportunity to respond during each trial. Most intruders were recaptured and returned to the focal territory at least once.

After a trial, intruders were recaptured, killed with quinaldine, preserved, and later examined under a dissecting microscope to determine their sex. Because the intruder's sex was unknown at the time of the addition, it was usually necessary to add more than four gobies to each pair to complete all four desired treatments.

Since trials did not last for a standard length of time, I computed behavior rates for each male and female resident (behavior rate = total number of times each behavior was performed/total time of trial). For each of the three behaviors, I compared the mean response rate of the 12 residents of each sex to each of the four intruder types, using a nonparametric ANOVA (Friedman 2-Way ANOVA, $df = 3$), which gives the test statistic χ^2_r. If the multisample null hypothesis of equal mean response to all four intruders (treatments) was rejected (i.e., if the ANOVA was significant), I used a nonparametric multiple comparison ("Tukey-type" test, Zar 1984) to identify specific differences between treatments a-posteriori.

Additions to single females

To further test the Mate-Guarding and Resource-Guarding Hypotheses, I challenged six unpaired female G. evelynae with both a male and a female intruder at different times. In this experiment, all six male intruders (29.8 ± 1.7 mm TL) and all six female intruders (30.0 ± 2.4 mm TL) were larger than the six resident territorial females that received them (26.6 ± 2.4 mm TL). The order of addition was blind, since the sex of the 12 intruders was unknown until after each trial. All six of the unpaired females were seen with males at other times during the study, hence their single status during this experiment was most likely a temporary condition.

Nevertheless, at the time they were tested there was no male present on the territory, and therefore any territorial aggression displayed by these females at that time was not interpreted as mate guarding. Trials lasted for 4 - 10 minutes (mean $\pm$ SD: 7 $\pm$ 2 min, n = 12 trials), after which the intruders were recaptured, preserved, and sexed. I used the Wilcoxon signed-rank test to compare the behavioral response of unpaired females to male and female intruders.

RESULTS

Fish Additions to Territorial Pairs

Paired male and female *G. evelynae* often greeted each other with a distinct wiggling display that apparently signaled mate recognition, and may have been associated with courtship. However, resident territorial gobies rarely gave this display to experimentally added fish, which were not actively courted by either sex. Usually, large intruders of the opposite sex were approached, inspected, and thereafter ignored.

The attack rates of male and female residents depended strongly on the sex and size of the intruder, as predicted by the Mate-Guarding Hypothesis. Residents attacked intruders of the same sex at higher rates than intruders of the opposite sex. In general, large gobies of the same sex were most vigorously attacked, and they often fought back, resulting in battles of several seconds that involved mutual biting to the head and body. In a few cases, large intruders were not expelled from the territory during the observation period, even after repeated displaying and biting by a resident. Large intruders of the opposite sex were rarely attacked. Small intruders were usually chased and expelled by both residents, regardless of their sex, and did not respond aggressively when attacked. Detailed results for three distinct behaviors are as follows:

(a) Biting

Biting was the most obviously aggressive behavior observed in *G. evelynae* interactions. Bite rates of resident males and females both differed significantly between intruder types (male residents: χ^2_r = 13.6 , P = 0.004; female residents: χ^2_r = 15.3, P = 0.002; Fig. 2.1). Among male residents, the *a-posteriori* multiple comparisons showed that male intruders (both large and small) were bitten at significantly higher rates than female intruders (both large and small) (Fig. 2.1a). Among female residents, bite rates varied more evenly between treatments (i.e., intruder sex and size contributed about equally to differences in bite rates) (Fig. 2.1b). However, there was a clear trend opposite that of the male residents, such that males bit mostly males and females bit mostly females. All twelve resident males bit large male intruders at least once per trial, but only one male bit a large female intruder. Eleven of twelve female residents bit large female intruders, but only four females bit large males.

(b) Threat Displays

During threat displays, residents held their bodies very stiff, and with fins flared and head pointing slightly down, slowly circled the intruding fish. Threat-display rates of resident gobies to large and small male and female intruders (Fig. 2.2) were similar to the patterns observed for bite rates, bolstering the interpretation that threat

displays were aggressive. Since threat displays often preceded biting, these behaviors were not performed independently of one another. Like bite rates, threat-display rates were not equal among treatments for either male or female residents (male residents: $\chi^2_r = 11.9$, $P = 0.008$; female residents: $\chi^2_r = 17.7$, $P = 0.001$). Among male residents, multiple comparisons showed that large male intruders elicited threat displays at significantly higher rates than female intruders (both large and small). Small male intruders elicited intermediate rates of threat displays (Fig 2.2a). Among female residents, large female intruders elicited significantly higher rates of threat displays than all other types of intruders (Fig. 2.2b).

(c) Chases

Chases were rapid pursuits that did not involve contact between fish, but usually led to the expulsion of the intruder from the territory, or caused the intruder to seek shelter in a hole or crevice within the territory. Chases often followed biting and threat displays, and were therefore not independent of these other aggressive behaviors. Interestingly, small intruders were chased at higher rates than large intruders (Fig. 2.3), apparently because small fish were more likely than large ones to flee immediately when approached. Thus, chase rates also varied significantly according to the sex and size of the intruder (male residents: $\chi^2_r = 14.9$, $P = 0.002$; female residents:

$\chi^2_r = 23.5$, $P < 0.001$). Male residents chased small males and small females at significantly higher rates than large females, and chased large males at intermediate rates (Fig. 2.3a). Female residents chased small females at significantly higher rates than all other types of intruders, and chased large males at very low rates (Fig. 2.3b).

Fish Additions to Single Females

The response of unpaired female *G. evelynae* to larger males and females was similar to the response of paired females, namely, female intruders were attacked and male intruders were not (Fig. 2.4). Specifically, all six resident females attacked (with bites and threat displays) added female intruders, but only one resident female attacked an added male. Bite rates differed significantly between male and female intruders (Wilcoxon test: $P < 0.05$). The sample size was too small to detect significant sex-specific differences in threat displays and chases (Wilcoxon test, $P > 0.05$), although the trend is clearly one of intrasexual aggression.

DISCUSSION

Overall, attack rates (primarily bite rates and threat-display rates) varied between treatments with a pattern that most closely followed the predictions of corollary 1b of the Mate-Guarding Hypothesis, that is, defense of mate and other resources (Table 2.1). Small intruders of the opposite sex were attacked at a higher rate than predicted by "pure" mate guarding, and the strong sex-specific response to large intruders was not consistent with the alternative hypothesis of resource guarding. Since the response of resident male and female gobies were almost mirror-images, based on the intruder's sex, mate guarding appeared to be mutual. Like paired females, unpaired females vigorously attacked female intruders but tended to ignore added males. Since any aggressive behavior from an unpaired fish is inconsistent with "pure" mate guarding, these results also support the conclusion that females guard resources on their territories in addition to mates.

What resources are guarded by female *G. evelynae*? For many reef fish, resources associated with the territory other than a mate include food and crevices for egg-laying and shelter. Crevices did not appear to be actively defended except when males defended clutches of eggs. Considering food, unlike territorial fishes that eat algae or benthic invertebrates, the diet of cleaning gobies is

primarily ectoparasitic gnathiid isopods on other, larger
fish (Randall 1967), which cannot be directly monopolized
or guarded. This situation occurs because host fishes
generally swim freely through the territories of several
cleaning gobies, which appear to clean opportunistically as
potential hosts pass (personal observation). Although I
seldom saw host fishes "lining up" to await the services of
cleaning gobies, as reported in some popular Caribbean
fish-identification books (e.g., Stokes 1984), some
territories did seem to be in better locations for cleaning
than others. In fact, time-budgets of cleaning activity
showed significant differences between goby territories in
both the number of hosts cleaned and total time spent
cleaning (see Appendix). These differences were apparently
due to an uneven distribution of host fishes on the reef.
For example, several time-budgeted territories were located
close to large, semi-permanent aggregations of chromis
(*Chromis multilineata* and *C. cyanea*); together, these two
species of planktivorous damselfishes accounted for over
80% of all cleaning acts observed in 20 hours of
observation at Flat Cay. I hypothesize that consistently
food-rich cleaning stations, such as those near large
schools of hosts, are one resource that females may have
defended in addition to a mate.

Most previous studies of monogamous coral-reef fish
have not examined territoriality in sufficient detail to
test the Mate-Guarding Hypothesis. This is either because

the sex of the interacting fish was unknown (e.g., Lassig
1976, Driscoll and Driscoll 1988), or because the response
of territory residents to conspecific intruders was not
directly measured, even when preliminary observations
showed that aggression was primarily intrasexual (e.g.,
Barlow 1987, Donaldson 1989, Ochi 1989). In the most
thorough study yet of territoriality in a monogamous reef
fish, Fricke (1986) induced intrasexual aggression in the
butterflyfish *Chaetodon chrysurus* using caged "intruders"
of known sex. Based on these experimental additions and on
observations of territorial disputes between tagged
individuals, he concluded that sex-specific fighting leads
to mutual mate-monopolization in this species. Since both
sexes use the same tactic, and share a common territory,
the group size of *C. chrysurus*, like that of *G. evelynae*,
is automatically reduced to one heterosexual pair.
However, Fricke also concluded that partner guarding was
largely independent of reproduction (since juvenile and
homosexual pairs were occasionally seen), and that pairing
occurs because two fish are always necessary for territory
defense in *C. chrysurus*. This situation is not true of *G.
evelynae*, among which juveniles did not form pairs, and
adults that lost their partners, either naturally or as a
result of experimental manipulation, were able to keep
their territories while temporarily single (see Chapter 1).
Thus, partner guarding in *G. evelynae* does appear to be
primarily for reproductive purposes.

In birds, the Mate-Guarding Hypothesis has received considerable recent attention, and several papers have emphasized female-female aggression as an important proximate mechanism preventing males from mating polygynously (e.g., Veiga 1992 and references therein). Such female aggression may account for male polyterritoriality, and if bigamy does occur, female aggression may also account for a greater than expected distance between the nests of first and second females (Slagsvold et al. 1992). This pattern of nest spacing and male polyterritoriality resulting from female behavior is unlikely to occur among reef fishes, however, since nests are built and tended primarily or exclusively by males, if at all. Furthermore, since female-female aggression in both birds and coral-reef fishes usually occurs within a multipurpose territory used for feeding, mating, egg-laying, and shelter, it has usually not been possible to determine precisely which resource(s) are being defended by females in either system. This problem was neatly resolved in a study of razorbills (*Alca torda*), a monogamous seabird in which female-female aggression occurs in mating arenas outside the breeding colony, away from territories and nests. Mated females whose mates are present in the arena attack other females, apparently in defense of the pair-bond itself (Wagner 1992). This kind of aggressive behavior is different from pre- and post-copulatory mate guarding of females by males to assure paternity (e.g.,

Birkhead et al. 1987, Van Rhijn 1991), which has a clear and direct genetic benefit for the male. Since cuckoldry is not possible in externally fertilizing species, paternity assurance cannot account for mate guarding in *G. evelynae*. Instead, both female and male *G. evelynae* appear to treat their partners as nonsharable reproductive resources, which are guarded from sexual rivals accordingly.

It is tempting to view joint male-female territory defense in pair-forming animals as a cooperative division of labor which is mutually beneficial to both partners. However, such a partnership need not be the best possible reproductive strategy for both individuals. If paired males and females exhibit a qualitatively different response to conspecifics, and if the difference is based largely on the sex of the conspecific, as in *G. evelynae*, then this suggests a potential conflict of interest between the sexes. Males, unable to move freely among females because of the constraints imposed by nest-tending, and deprived of the opportunity to form harems at the nestsite by the behavior of a resident female, are likely to be the manipulated sex if such a conflict exists in *G. evelynae*.

Table 2.1. Predicted responses of paired territory occupants to intruders of different sexes and sizes based on two alternative hypotheses.

| | | Response of Resident Male or Resident Female | | |
| | | Hypothesis 1: Mate-Guarding | | |
Intruder's Sex,	Size*	Corollary 1a: Defense of Mate Only	Corollary 1b: Defense of Mate and Other Resources	Hypothesis 2: Resource-Guarding
Same Sex	Large	Very Aggressive	Very Aggressive	Aggressive‡
Same Sex	Small	Aggressive	Aggressive	Aggressive‡
Opposite Sex	Small	None (or Court)§	Aggressive	Aggressive‡
Opposite Sex	Large	None (or Court)§	Unpredictable†	Aggressive‡

* Sex of intruder is relative to the resident. Size of intruder is relative to resident if intruder is same sex as resident, and relative to resident's mate if intruder is opposite sex of resident.

† Because intruder presents the conflict of being both a potential resource competitor and a potential mate, the specific response is unpredictable.

‡ Specific response may vary according to the intruder's size, but not according to the intruder's sex.

§ Intruder is not a threat to resources, but is a potential mate.

Figure 2.1. Aggressive bite rates ($\overline{X} \pm$ SE) of 12 paired *G. evelynae* males (**a**) and females (**b**) exposed to four types of conspecific intruders experimentally placed in the pair's territory. The horizontal lines beneath the abscissa connect treatments that did not differ at the 5% probability level.

Fig. 2.1

a. resident males

b. resident females

BITE RATE (bites/min)

LARGE
MALE

SMALL
MALE

SMALL
FEMALE

LARGE
FEMALE

SIZE AND SEX OF INTRUDER

Figure 2.2. Threat-display rates ($\overline{X} \pm$ SD) of 12 paired
G. evelynae males **(a)** and females **(b)** exposed to four
types of conspecific intruders experimentally placed in the
pair's territory. Horizontal lines beneath the abscissa
connect treatments that did not differ at the 5%
probability level.

Fig. 2.2.

a. resident males

b. resident females

THREAT-DISPLAY RATE (displays/min)

LARGE
MALE

SMALL
MALE

SMALL
FEMALE

LARGE
FEMALE

SIZE AND SEX OF INTRUDER

Figure 2.3. Chase rates ($\overline{X} \pm$ SD) of 12 paired *G. evelynae* males **(a)** and females **(b)** exposed to four types of conspecific intruders experimentally placed in the pair's territory. Horizontal lines beneath the abscissa connect t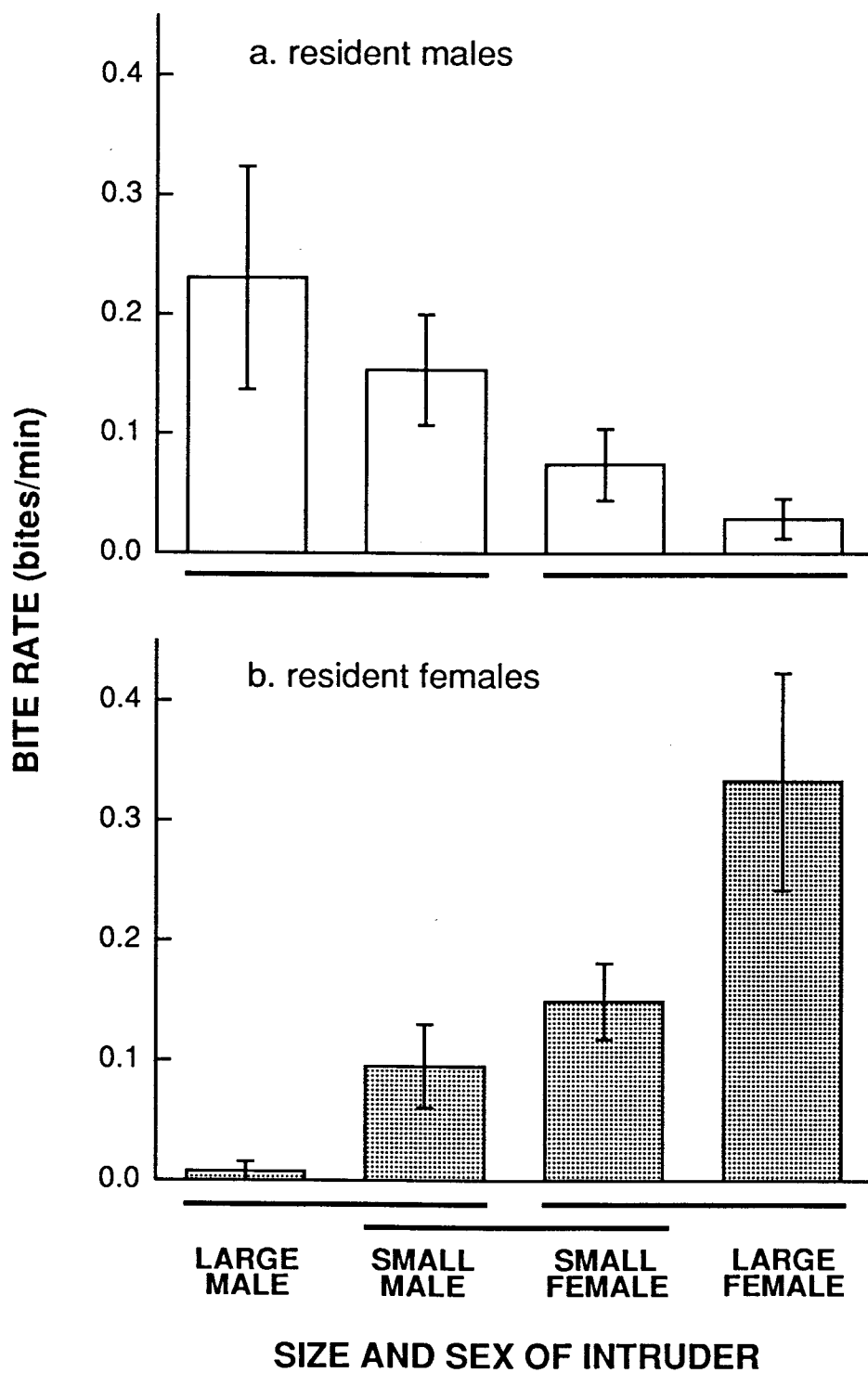reatments that did not differ at the 5% probability level. In both **(a)** and **(b)**, two treatments marked by crosses also did not differ significantly from each other.
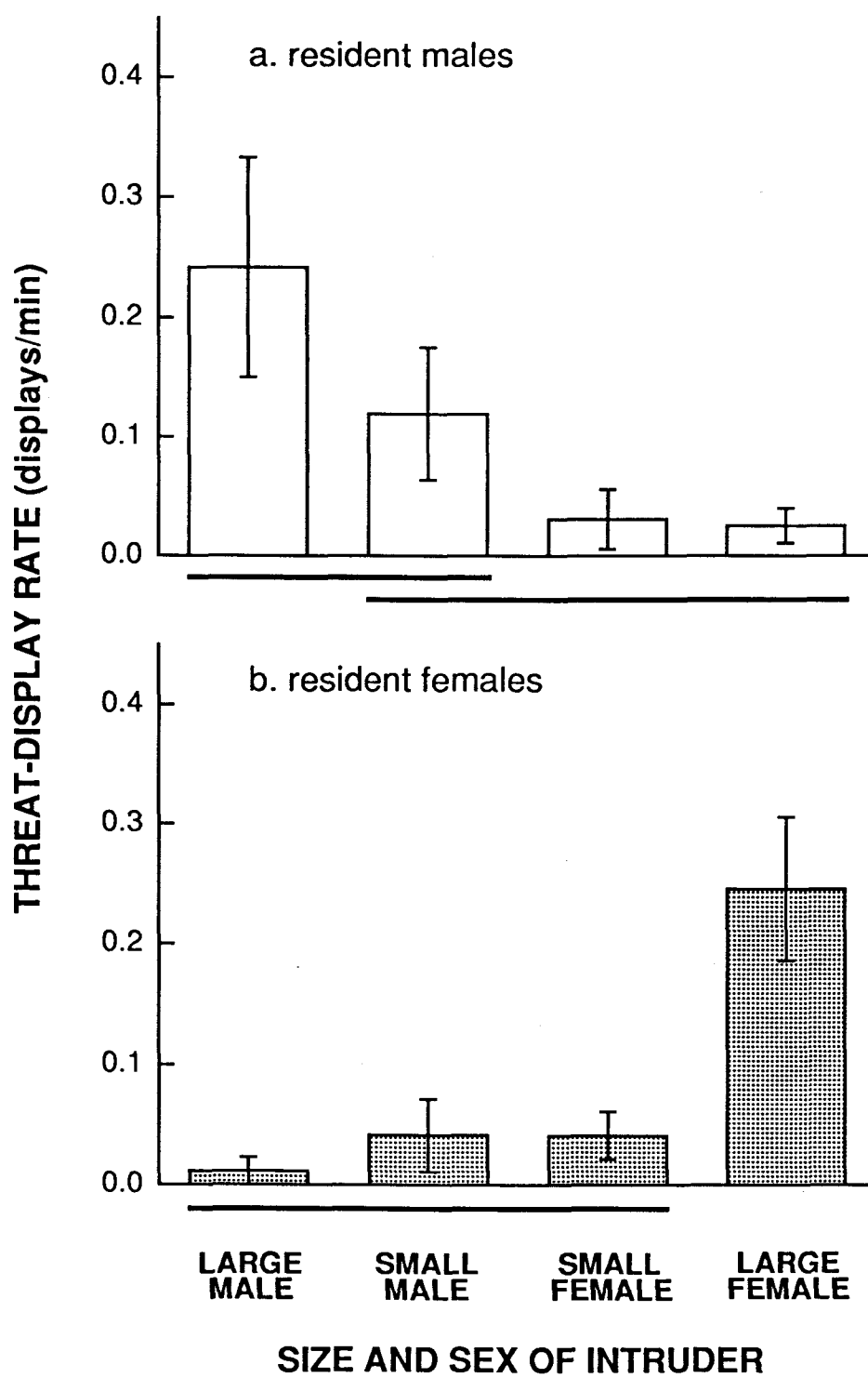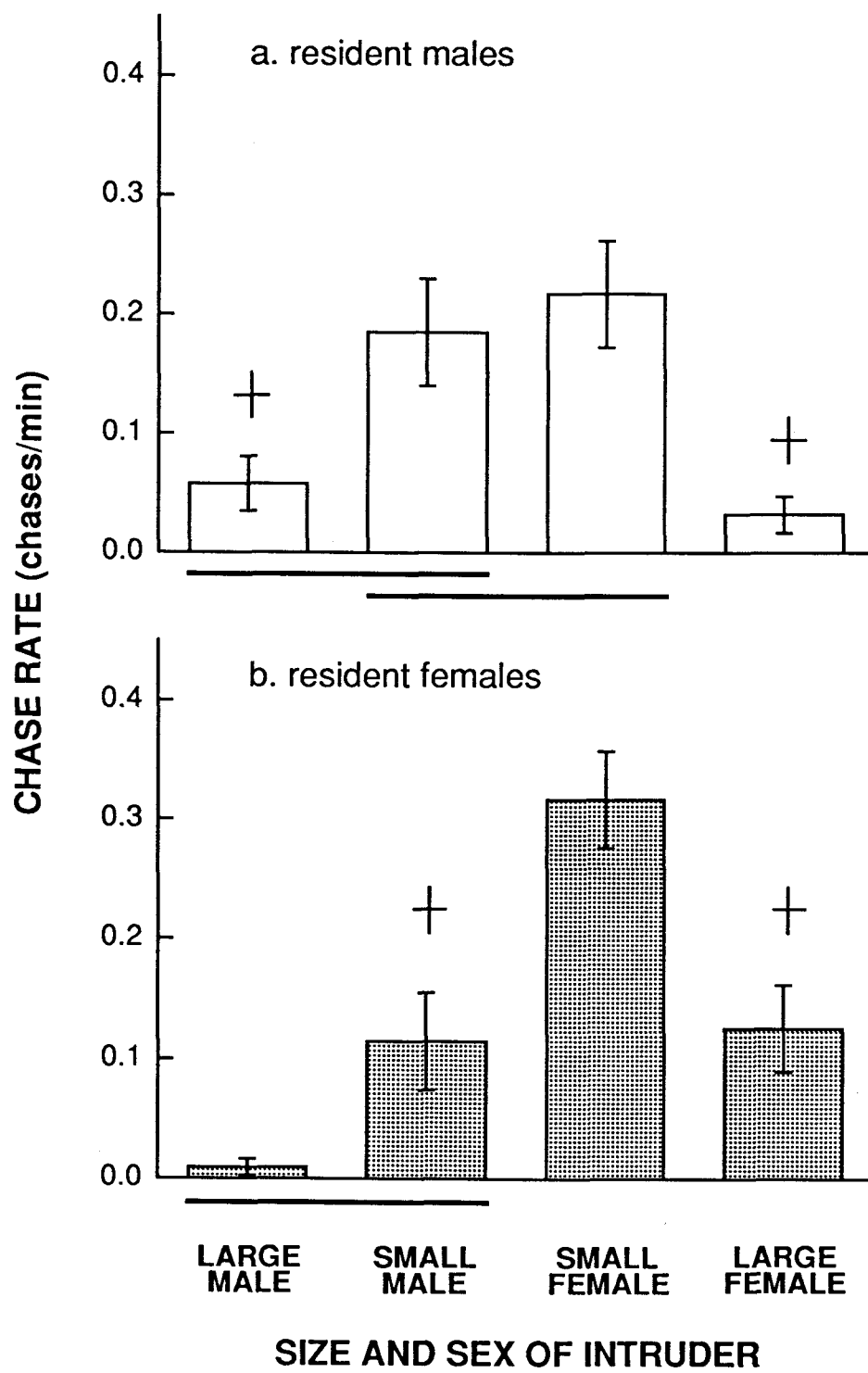
Fig. 2.3.

CHASE RATE (chases/min)

a. resident males

b. resident females

LARGE MALE　SMALL MALE　SMALL FEMALE　LARGE FEMALE
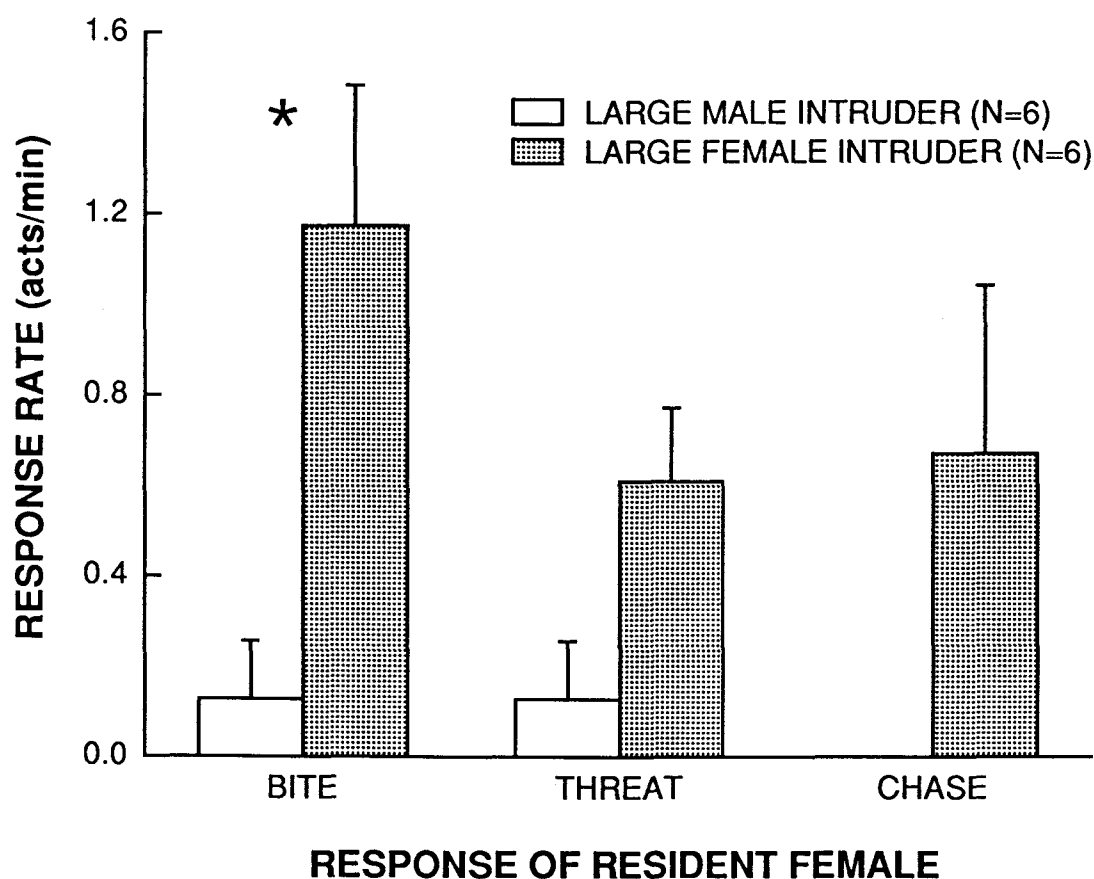
SIZE AND SEX OF INTRUDER

Figure 2.4. Aggressive response rates ($\overline{X}$ + SD) of 6 unpaired female *G. evelynae* to larger male and female conspecifics placed on the female's territory. Aggressive bite rates elicited by female intruders were significantly higher than bite rates elicited by male intruders (Wilcoxon test, P < 0.05, indicated by asterisk).

Literature Cited

Barlow, G.W. 1988. Monogamy in relation to resources. pp. 55-79 in: C.N. Slobodchikoff (ed.). The ecology of social behavior. San Diego: Academic Press.

Barlow, G.W. 1987. Spawning, eggs and larvae of the longnose filefish *Oxymonacanthus longirostris*, a monogamous coralivore. Env. Biol. Fish. 20:183-194.

Barlow, G.W. 1986. A comparison of monogamy among freshwater and coral-reef fishes. Proc. 2nd Internat. Conf. Indo-Pac. Fish., Tokyo. pp. 767-775.

Barlow, G.W. 1984. Patterns of monogamy among teleost fishes. Arch. FischWiss. 35:75-123.

Barlow, G.W. 1974. Contrasts in social behavior between Central American cichlid fishes and coral-reef surgeon fishes. Am. Zool. 14:9-34.

Birkhead, T.R., L. Atkin, and A.P. Moller. 1987. Copulation behaviour of birds. Behaviour 101:101-138.

Clark, E and J.F. Pohle. 1992. Monogamy in Tilefish. Nat. Geo. Res. Exp. 8:276-295.

Clifton, K.E. 1990. The costs and benefits of territory sharing for the Caribbean coral reef fish, *Scarus iserti*. Behav. Ecol. Sociobiol. 26:139-147.

Colin, P.L. 1989. Aspects of the spawning of western Atlantic butterflyfishes (Pisces: Chaetodontidae). Env. Biol. Fish. 25:131-141.

Colin, P.L. 1975. Neon gobies. T.F.H. Publications, Neptune City, N.J.

Donaldson, T.J. 1989. Facultative monogamy in obligate coral-dwelling hawkfishes (Cirrhitidae). Env. Biol. Fish. 26:295-302.

Driscoll, J.W. and J.L. Driscoll. 1988. Pair behavior and spacing in butterflyfishes (Chaetodontidae). Env. Biol. Fish. 22:29-37.

Emlen, S.T. and L.W. Oring. 1977. Ecology, sexual selection and the evolution of mating systems. Science 197:215-223.

Fricke, H.W. 1986. Pair swimming and mutual partner guarding in monogamous butterflyfish (Pisces, Chaetodontidae): a joint advertisement for territory. Ethology 73:307-333.

Fricke, H.W. 1980. Control of different mating systems in a coral reef fish by one environmental factor. Anim Behav. 28:561-569.

Fricke, H.W. 1976. Bericht aus dem Riff. Piper Verlag, Munchen.

Fricke, H.W. 1973. Behaviour as part of the ecological adaptation: *in situ* studies in the coral reef. Helgolander Wiss. Meeresunters. 24:120-144.

Ghiselin, M.T. 1969. The evolution of hermaphroditism among animals. Quart. Rev. Biol. 44:189-208.

Gronell, A.M. 1984. Courtship, spawning, and social organization of the pipefish, *Corythoichthys intestinalis* (Pisces: Syngnathidae) with notes on two congeneric species. Z. Tierpsychol. 65:1-24.

Hixon, M.A. 1987. Territory area as a determinant of mating systems. Amer. Zool. 27:229-247.

Hourigan, T.F. 1989. Environmental determinants of butterflyfish social systems. Env. Biol. Fish. 25:61-78.

Johnson, W.S. and Ruben, P. 1988. Cleaning behavior of *Bodianus rufus*, *Thalassoma bifasciatum*, *Gobiosoma evelynae*, and *Periclimenes pedersoni* along a depth gradient at Salt River Submarine Canyon, St. Croix. Env. Biol. Fish. 23:225-232.

Kleiman, D.G. 1977. Monogamy in mammals. Quart. Rev. Biol. 52:39-69.

Knowlton, N. 1979. Reproductive synchrony, parental investment, and the evolutionary dynamics of sexual selection. Anim. Behav. 27:1022-1033.

Krebs, C.J. 1989. Ecological methodology. Harper and Row, N.Y.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

Lassig, B. 1976. Field observations on the reproductive behavior of *Paragobiodon* spp. (Osteichthyes: Gobiidae) at Heron Island Great Barrier Reef. Mar. Behav. Physiol. 3:283-293.

Marraro, C.H. and J.R. Nursall. 1981. The reproductive periodicity and behaviour of *Ophioblennius atlanticus* (Pisces: Blenniidae) at Barbados. Can. J. Zool. 61:317-325.

McKaye, K.R. 1986. Mate choice and size assortative pairing by the cichlid fishes of Lake Jiloa, Nicaragua. J. Fish Biol. (Supplement A) 29:135-150.

Moyer, J.T. and C.E. Sawyers. 1973. Territorial behavior of the anemonefish *Amphriprion xanthurus* with notes on the life history. Japan. J. Ichthyol. 20:85-93.

Nalepa, C.A. and S.C. Jones. 1991. Evolution of monogamy in termites. Biol. Rev. Phil. Soc. Camb. 66:83-97.

Ochi, H. 1989. Mating behavior and sex change of the anemonefish, *Amphiprion clarkii*, in the temperate waters of southern Japan. Env. Biol. Fish. 26:257-275.

Orians, G.H. 1969. On the evolution of mating systems in birds and mammals. Am. Nat. 103:589-603.

Petersen, C.W. 1989. Females prefer mating males in the carmine triplefin, *Axoclinus carminalis*, a paternal brood-guarder. Env. Biol. Fish. 26:213-221.

Potts, G. and R. Wootton. 1984. Fish reproduction: strategies and tactics. Academic Press, N.Y.

Pressley, P.H. 1981. Pair formation and joint territoriality in a simultaneous hermaphrodite: the coral reef fish *Serranus tigrinus*. Z. tierpsychol. 56:33-46.

Ralls, K. 1977. Sexual dimorphism in mammals: avian models and unanswered questions. Am. Nat. 111:917-938.

Randall, J.E. 1967. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanogr. 5:665-847.

Reese, E.S. 1975. A comparative field study of the social behavior and related ecology of reef fishes of the family Chaetodontidae. Z. Tierpsychol. 37:37-61.

Roberts, C.M. and R.F.G. Ormond. 1992. Butterflyfish social behaviour, with special reference to the incidence of territoriality: a review. Env. Biol. Fish. 34:79-93.

Robertson, D.R. 1973. Field observations on the reproductive behaviour of a pomacentrid fish, *Acanthochromis polyacanthus*. Z. Tierpsychol. 32:319-324.

Robertson, D.R. and Hoffman, S.G. 1977. The roles of female mate choice and predation in the mating systems of some tropical labroid fishes. Z. Tierpsychol. 45:298-320.

Robertson, D.R., N.V.C. Polunin and K. Leighton. 1979. The behavioral ecology of three Indian Ocean surgeonfishes (*Acanthurus lineatus, A. leucosternon* and *Zebrasoma scopas*): their feeding strategies, and social and mating systems. Env. Biol. Fish. 4:125-170.

Schmale, M.C. 1981. Sexual selection and reproductive success in males of the bicolor damselfish, *Eupomacentrus partitus* (Pisces: Pomacentridae). Anim. Behav. 29:1172-1184.

Slagsvold, T., T. Amundsen, S. Dale, and H. Lampe. 1992. Female-female aggression explains polyterritoriality in male pied flycatchers. Anim. Behav. 43:397-407.

Slobodchikoff, C.N. 1984. Resources and the evolution of social behavior. pp. 227-251 in: P.W. Price, C.N. Slobodchikoff, and W.S. Gaud (eds.). A new ecology: novel approaches to interactive systems. Wiley, N.Y.

Stokes, F.J. 1984. Diver's and snorkeler's guide to the fishes and sea life of the Caribbean, Florida, Bahamas, and Bermuda. The Academy of Natural Sciences of Philadelphia Press.

Sunobe, T. and A. Nakazono. 1990. Polygynous mating system of *Trimma okinawae* (Pisces: Gobiidae) at Kagoshima, Japan, with a note on sex change. Ethology 84:133-143.

Thresher, R.E. 1984. Reproduction in reef fishes. T.F.H. Press, Neptune City, N.J.

Van Rhijn, J.G. 1991. Mate guarding as a key factor in the evolution of parental care in birds. Anim. Behav. 41:963-970.

Veiga, J.P. 1992. Why are house sparrows predominantly monogamous? A test of hypotheses. Anim. Behav. 43:361-370.

Verner, J. and M.L. Willson. 1966. The influence of habitats on mating systems of North American passerine birds. Ecology 47:143-147.

Wagner, R.H. 1992. Mate guarding by monogamous female razorbills. Anim. Behav. 44:533-538.

Warner, R.R. and S.G. Hoffman. 1980. Local population size as a determinant of mating system and sexual composition in two tropical marine fishes (*Thalassoma* spp.). Evolution 34:508-518.

Wickler, W. and U. Seibt. 1981. Monogamy in crustacea and man. Z. Tierpsychol. 57:215-234.

Wilson, E.O. 1975. Sociobiology: the new synthesis. Belknap, Cambridge, Mass. 697 pp.

Wittenberger, J.F. and R.L. Tilson. 1980. The evolution of monogamy: hypotheses and evidence. Ann. Rev. Ecol. Syst. 11:197-232.

Zar, J.H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, N.J.

Appendix

Appendix: Local variation in cleaning activity of female
G. evelynae

Aim: To determine if cleaning activity (i.e., number of
hosts cleaned and total cleaning time) of female *G. evelynae*
differs between female territories.

Methods: Nine *G. evelynae* territories were chosen
haphazardly from a 5 x 100 m strip along the sand-coral
border at the deep (8-12 m) margin of the reef at Flat Cay.
Six of these territories were occupied by male-female pairs,
and the remaining three by single females. Between 11 and 28
August, 1992, I measured the cleaning activity of these
resident gobies. Observations were stratified by time
between 1000 and 1600 hrs, a period when *G. evelynae*
cleaning activity has been shown to be relatively high and
constant (Johnson and Ruben 1988). The territory of each
female or pair was watched twice for 20 min in each of three
2-hr time periods (1000-1200 hrs, 1200-1400 hrs, and 1400-
1600 hrs) so that a total of six 20-min observations was
recorded for each territory. Observation times were
randomly assigned to territories each day, and each
territory was watched no more than once per day. During
observations, I counted (1) the number of host fishes
cleaned by female *G. evelynae*, and; (2) the total amount of
time that each female foraged (i.e., the amount of time
spent in physical contact with all hosts).

Because territories consisted of either single or paired (male-female) females, I first tested for differences in cleaning activity (number of hosts and total foraging time) between single and paired females with a nonparametric two-sample test (Mann-Whitney test). Because cleaning activity might vary over the diel period, I also tested for differences between times of the day with a nonparametric (Kruskal-Wallis) ANOVA. Since cleaning activity did not differ between single and paired females (Mann-Whitney test, number of hosts cleaned: U=277, P=0.39; total foraging time: U=282, P=0.44), nor between times of day (ANOVA, number of hosts cleaned: df=2, H=1.52, P=0.47; total foraging time: df=2, H=1.11, P=0.57), I pooled all females and times to test for differences in cleaning activity between individual territories, also using Kruskal-Wallis ANOVA. Lastly, to see if total time spent cleaning increased with the number of cleaning acts performed, I used Spearman rank correlation to measure the relationship between number of hosts and total foraging time.

Results:

Female Territory (status)	n	Hosts Cleaned* mean ± SD (min,max)	Total Foraging Time† mean ± SD (min,max)
18 (paired)	6	22.0 ± 17.9 (10,58)	223 ± 112 (89,370)
93 (single)	6	20.0 ± 14.4 (1,31)	189 ± 102 (19,306)
31 (paired)	6	12.5 ± 4.8 (5,17)	98 ± 38 (43,144)
53 (paired)	6	12.0 ± 1.9 (10,15)	137 ± 38 (81,181)
82 (single)	6	11.7 ± 11.2 (0,29)	86 ± 92 (0,247)
74 (paired)	6	6.7 ± 4.3 (3,15)	71 ± 54 (20,160)
34 (paired)	6	6.2 ± 4.2 (2,13)	42 ± 20 (18,67)
19 (paired)	6	2.8 ± 2.7 (0,6)	23 ± 22 (0,54)
20 (single)	6	1.5 ± 1.5 (0,4)	14 ± 11 (0,25)

*Number of hosts cleaned per 20 min observation period. Data are in descending order from highest to lowest rate of cleaning.
†Total time cleaning, in seconds, per 20 min observation period.

There were significant differences between individual female territories in both number of hosts cleaned (ANOVA, $df=8$, $H=25.1$, $P=0.001$) and total time spent foraging (ANOVA, $df=8$, $H=31.4$, $P<0.001$). There was also a significant positive relationship between the number of hosts cleaned and total foraging time ($n=54$, $r_s=0.84$, $P<0.001$).

Conclusion:

Some goby territories appear to be richer cleaning stations than others. The observed variation in total foraging time suggests that territories differ in the number of hosts that visit them. This is supported by the positive relationship between total foraging time and number of hosts cleaned. Moreover, *G. evelynae* females usually attempt to clean any suitable hosts that pass within reach. Although I did not directly measure local host density, the observed differences between females in foraging activity probably reflect differences in local host abundance, and not simply differences in female behavior.