

## COMPETITIVE INTERACTIONS AND THE AVAILABILITY OF SLEEPING SITES FOR A DIURNAL CORAL REEF FISH

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**Abstract:** A field study was made to test whether the population size of a diurnal reef fish, the wrasse *Thalassoma bifasciatum* (Bloch), was limited by inter- or intraspecific competition for sleeping shelter. *T. bifasciatum* is often attacked at dusk by two small territorial damselfishes, *Eupomacentrus dorsopunicans* (Poey) and *E. planifrons* (Cuvier). Although these three species sleep in the same general habitats, there are qualitative differences in the types of holes they use and how they use them. Wrasse holes are usually in these damselfishes' territories, but damselfish attacks do not prevent wrasses entering holes. Wrasses infrequently defend their holes intraspecifically. They regularly change their holes, with little intra- or interspecific aggressive interaction. When its hole is removed, a wrasse is late in retiring but finds a hole near its old one with little aggressive interaction, and does not have a higher mortality rate. Empty wrasse holes are rarely refilled, and then only by conspecifics. Wrasses added to reefs find unoccupied holes and do not usurp other fishes' holes. Damselfish defend their eggs and food against the wrasse, but not their sleeping shelter, nor living space per se. Sleeping sites are not limiting the wrasse, but are present in a surplus. Intraspecific hole defense by a wrasse prevents a delay in its retiring that would increase the risk of crepuscular predation on it.

### INTRODUCTION

Intraspecific and interspecific competition for living space has come to be considered of great importance in coral reef fish communities (Smith & Tyler, 1972, 1973a; Sale, 1974, 1975, 1976a, b, 1977; Smith, 1977). Such space provides fishes with food, spawning sites, nest sites, and shelter, including shelter in which diurnal fishes spend their nights. Although competition for shelter is often thought to be a significant cause of aggressive interactions that are observed during the day and at dusk on reefs (Hobson, 1972; Reinboth, 1973; Domm & Domm, 1973; Myrberg & Thresher, 1974; Thresher, 1976; Smith, 1977), there is a lack of experimental testing of whether diurnal reef fishes are competing for shelter and, more importantly, whether their populations are limited by such competition. Here we describe observations and experiments made to test if one Caribbean reef fish, the bluehead wrasse, *Thalassoma bifasciatum* (Bloch), is limited by either inter- or intraspecific competition (sense I of Birch, 1957) for sleeping shelter.

We chose *T. bifasciatum* for a variety of reasons. It is an abundant and conspicuous diurnal member of Caribbean reef fish communities (Feddern, 1965; Starck & Davis, 1966) that Reinboth (1973) suggested was involved in intraspecific competition for sleeping sites. It is also regularly attacked by other diurnal fishes as it seeks shelter

at dusk. There is no evidence that fish of either of this specie's two color phases (initial and terminal, see Feddern, 1965; Randall, 1968) defend permanent, exclusive, general purpose territories, although larger terminal phase males (blueheads) hold temporary territories during spawning periods (Reinboth, 1973; Warner *et al.*, 1975). Each adult has a large home range that lacks a discrete shelter near which it remains and uses throughout the day; thus the species is not a shelter specialist.

Here we also consider whether *T. bifasciatum* is involved in such competition with two common reef pomacentrids, *Eupomacentrus dorsopunicans* (Poey) and *E. planifrons* (Cuvier). These two fishes aggressively dominate many Caribbean reef fishes (Itzkowitz, 1974; Myrberg & Thresher, 1974; Robertson *et al.*, 1976; Thresher, 1976) and exert control over much more than half the hard substratum on certain reefs in our study area (our unpubl. data). Attacks by these two species represent almost all of the interspecific aggressive interactions that *Thalassoma bifasciatum* has at dusk, and nearly all the damselfish territories in which *T. bifasciatum* sleeps belong to them (see p. 291).

If the wrasse is competing for and limited by sleeping shelter, one might expect the following.

- 1) There should be overlap in the types of sites used by different species; or more particularly in how they use their sites, because one species might have competitively excluded another from a class of sites.
- 2) Each individual should defend and regularly use the same site.
- 3) A natural change of site should be accompanied by increased aggressive activity, the changing fish usurping a more subordinate fish's site.
- 4) The removal of an occupied site should result in increased aggressive activity as its owner seeks a new site, the usurpation of a more subordinate fish's site by that animal, and the premature death of the destroyed site's owner, or a subordinate fish.
- 5) The removal of a fish should lead to its site being taken over by another one.
- 6) The addition of a fish to a reef should result in heightened aggressive activity as it seeks a site, and either it being unable to find a site, or displacing a resident fish from its site.
- 7) The addition of sites to a reef could result in an increase in the size of the species' population.
- 8) The removal of a competitively more dominant species should lead to increased usage of its sites by the subordinate species.

We collected data aimed at points 1-6.

#### MATERIALS AND METHODS

The study was made between September 1976 and September 1977 on the reefs of San Blas Point, on the Caribbean coast of Panama.

Most of our observations and all the experiments were made on blueheads. This

was done for the following reasons. 1) The structure of the bluehead color pattern enabled us to recognize individuals without tagging them. 2) Such fish are the closest in size to the adult damselfishes by which the wrasse was most often attacked, and using them should therefore give the best chance of detecting interspecific overlap in sleeping site requirements. 3) One might expect blueheads to control usage of the most preferred sites if they are limiting, because they are aggressively the most dominant members of that species. Although one might expect competition to be more likely to occur among more recent immigrants (initial phase fish) than older residents, this could just as easily not be the case. Blueheads and initial phase fish evidently have different shelter requirements. Small initial phase fish use smaller holes than do the larger blueheads, because both tend to use tight-fitting holes, and individuals of the two color phases tend to sleep in different types of substratum. In addition, initial phase fish do not take over vacant bluehead holes (see pp. 288, 293).

#### OBSERVATIONS

We made two sets of observations on possible overlap in the types of sleeping sites used by blueheads and the two damselfishes. (Here "damselfishes" and "pomacentrids" refers to both *Eupomacentrus dorsopunicans* and *E. planifrons*, unless otherwise specified.) First, the physical characteristics of sleeping sites used by damselfishes in a series of substratum types in which blueheads often slept were determined, by watching individuals for about one hour around dusk and noting where each retired relative to the area in which it fed during the observation period. Secondly, we surveyed tubular sponges on a number of patch reefs 1.5–2.5 h after sunset. The insides of tubular sponges, in which blueheads commonly sleep, represent the only type of sleeping site that could be thoroughly surveyed for use by both blueheads and damselfishes.

#### EXPERIMENTS

*Hole removals.* We determined which hole each experimental animal was using regularly, then destroyed that hole about one hour before the fish would normally have retired. On that same night the fish was observed until it finally entered another hole and no other conspecifics were still active. This timing of hole removals gave the fish little time to find a new hole and thus maximized our chance of seeing competitive interactions. Subsequently, the presence of experimental fish on these reefs was intermittently checked.

*Bluehead removals.* On the first day of each experiment, a fish whose hole we knew was speared about one hour before it normally would have retired. Its hole was then observed until all conspecifics had taken to their holes. Such holes were checked intermittently on subsequent nights for new occupants. A series of naturally vacated sites was also monitored.

*Bluehead transplants.* Fish collected in a lift net (see Roede, 1972) were tail-clipped to facilitate their identification, taken to a different patch reef 1-2 km away, and released. Later that day each animal was observed from about one hour before its normal retiring time until it had entered a hole and all conspecifics in the vicinity had also done so. To determine if those fish remained on their new reefs, and to facilitate observations in failing light, the transplants were made onto small, shallow patch reefs (< 50 m diameter, in < 5 m water).

As a control, other fish on different patch reefs were handled and tail-clipped, then released on their home reefs. They were observed that same evening and their presence on the reefs checked on the following day.

We did not attempt to add sleeping sites to reefs, because of the difficulty of objectively defining and placing them. Damselfishes were not removed to see if their sleeping sites would be taken over by blueheads because damselfish populations can be quite dense (e.g. Robertson *et al.*, 1976), and vacated territories are often taken over within a few minutes by conspecifics (our unpubl. data).

## RESULTS

### OVERLAP IN SITE USAGE BY *THALASSOMA BIFASCIATUM* AND DAMSELFISHES

*Characteristics of T. bifasciatum's sleeping sites.* Fish of both color phases slept in a wide variety of substrate types, but principally live coral (Table I). Blueheads' holes were concentrated in different substrate types to those of initial phase fish (Table I). All of these fish slept on the reef on which they spent their days, rather than in ad-

TABLE I

Types of substrata in which sleeping sites used by *T. bifasciatum* were found: using raw data,  $\chi^2 = 39.6$ , d.f. = 6,  $P < 0.001$ .

Substratum type	Percentage of sites present in each substratum type	
	Blueheads' sites ( <i>N</i> = 117)	Initial phase fishes' sites ( <i>N</i> = 49)
Leaf coral patches ( <i>Agaricia</i> )	27	17
Solid, hemispherical coral heads (e.g., <i>Siderastrea</i> , <i>Porites astreoides</i> , <i>Montastrea</i> , <i>Diploria</i> )	20	14
Tubular sponges	18	8
Coralline rock of reef base	13	18
Finger coral patches ( <i>Porites</i> )	11	27
Fire coral ( <i>Millepora</i> )	8	10
Macroscopic algae masses (e.g., <i>Halimeda</i> )	3	6

jacent sand areas or sea grass beds. Although there was variability in the physical construction of the wrasses' holes, they usually were more or less tubular, fairly tight fitting to the fish, and made it relatively invisible from the surface (Table II).

TABLE II

Physical characteristics of sleeping holes used by *T. bifasciatum*: A, shape: tubular = elongate, cylindrical, 1-2 entrances; non-tubular = any other shape; B, fit: tight =  $\approx 1$  body depth wide; loose = 1-2 body depths wide; very loose =  $> 2$  body depths wide; C, visibility: invisible = visible only with difficulty, using a flashlight; semi-visible =  $\approx 1/4$  of body visible near surface of substratum; all visible = virtually all of the fish clearly visible close to surface of substratum.

Characteristic	Percentage of holes with each characteristic	
	Blueheads' holes ( <i>N</i> = 117)	Initial phase fishes' holes ( <i>N</i> = 49)
A. Shape of hole		
Tubular	60	41
Non-tubular	40	59
B. Fit of fish in hole		
Tight	52	64
Loose	31	25
Very loose	17	11
C. Visibility of fish in hole		
Invisible	68	80
Semi-visible	11	4
All visible	21	16

*Characteristics of the damselfishes' sleeping sites.* We observed 80 *Eupomacentrus dorsopunicans* and 57 *E. planifrons* whose territories were on substratum types in which over 75% of the *Thalassoma bifasciatum* sleeping sites were found: leaf coral, solid coral heads, fire coral, finger coral, and basal reef rock.

The sleeping sites used by adult damselfishes were different in construction from those used by the wrasse. Typically, damselfish sites were large chambers, 88% of them being two or more body lengths in largest dimension and not less than one body length in smallest dimension. These chambers usually opened widely at the top or one side, so that 68% of the fishes were completely and clearly visible to the observer, and only 5% were difficult to see. They were characteristically much larger than chambers used by blueheads, only 2% of them being as small as the largest type of hole used by blueheads. Such large open holes were used by only 8% of the blueheads.

Large juvenile damselfishes' holes were closer in size to blueheads' holes than adult damselfishes' holes were; 34% of such damsels' holes were as small as the large, open type of wrasse hole referred to above.

*Nocturnal use of tubular sponges.* Very few tubular sponges contained any resting diurnal fishes. All of these were wrasses, almost all of them *T. bifasciatum* (Table III).

TABLE III

Nocturnal occupation of tubular sponges by diurnal fishes: small = accommodating small damselfishes ( $\leq 40$  mm S.L.), and initial phase *T. bifasciatum*, but not blueheads; medium = accommodating all size classes of *T. bifasciatum* and small- to medium-sized damselfishes (40–70 mm S.L.); large = accommodating blueheads and damselfishes of all sizes.

Size class of sponge tube	Number of tubes searched <sup>1</sup>	Number of tubes occupied by the following diurnal fishes		
		<i>T. bifasciatum</i>	Damselfishes	Other species <sup>2</sup>
Small	2261	38	0	1
Medium	538	27	0	2
Large	127	0	0	0
Total	2926	65	0	3

<sup>1</sup> These tubes were in 464 sponge colonies observed on 7 patch reefs; 39 of these colonies contained resting diurnal fishes.

<sup>2</sup> *Bodianus rufus* (L.) (2 individuals) and *Halichoeres bivittatus* (1 individual), both wrasses.

*Method of use of sites.* Resting wrasses had their fins closed and lay motionless, in close contact with the substratum. They were either lying suspended in the framework of tight holes or against the floor and one side of larger ones. They were not oriented in any particular direction. The wrasses invariably rested singly in their holes ( $n > 300$  observations).

The damselfishes used their sites in a different manner to *T. bifasciatum*. They hovered in a normal swimming position above the bottom near the center of the chamber, maintaining position there by occasional rapid fluttering movements of their fins. Their median fins were kept continuously erect. We never saw two damselfishes sharing a hole on the same night.

#### REGULARITY OF USE AND DEFENSE OF SITES

##### *Regularity of use*

We made 189 nights of observations of 52 blueheads living on 12 reefs over periods of up to nearly 5 months. All fish were observed  $\geq 2$  nights, while 34 were observed on  $\geq 3$  nights, 19 on  $\geq 4$  nights and 12 on 5–12 nights. The degree to which blueheads used more than one hole varied from one fish being seen in the same site on six occasions over a 52-day period, to another using three sites on six occasions over a 36-day period. Twenty-one of those 52 blueheads changed sites during the observation period, and eight of 42 used one site on the first night they were

observed, and a different one on the night immediately following. Most hole changes seemed to be long-term changes. We checked on the location of 12 fish that used two holes on 2–10 occasions after they had changed holes. Only two reverted to their original hole. Those two were also the only two of 12 fish checked on  $\geq 5$  times that showed any tendency to switch back and forth between (two) regularly used holes. One of these and one other fish observed five times were the only two observed in  $> 2$  holes.

Members of both damselfish species were evidently not restricted to the use of a single, well-defined sleeping site in each territory. Five of 24 adult *Eupomacentrus dorsopunicans* and four of 16 adult *E. planifrons* apparently changed their positions in their territories from one night to the following night (observations were made on untagged and individually unrecognizable fishes). Also, three adult *E. dorsopunicans* left their own territories and moved into and slept in the territories of neighboring conspecifics after those neighbors had moved into shelter.

#### *Defense of sites*

Reinboth (1973) described a situation in which large blueheads resting in their holes attacked smaller conspecifics that followed and peered in at them. We observed the same situation infrequently. Small blueheads followed larger ones on 16% of the evenings, and were attacked on 56% of those ( $n = 191$  evenings, 81 blueheads). Initial phase fish followed blueheads on 15% of 191 evenings, and were attacked on 18% of those on which they followed. Aggressive interactions between initial phase fish that appeared connected with hole usage were observed infrequently (on five of 53 observation periods). Blueheads did not follow initial phase fish.

Most of the *Thalassoma bifasciatum* sleeping sites were in damselfish territories; 77 of 98 bluehead sites and 29 of 35 initial phase fish sites were. Almost all (99 of 106) wrasse sites that were in damselfish territories were in the territories of *Eupomacentrus planifrons* and *E. dorsopunicans*. Attacks by *E. dorsopunicans* and *E. planifrons* also constituted nearly all the interspecific aggressive interactions *Thalassoma bifasciatum* had at dusk; 56% and 38%, respectively, of 2605 agonistic interactions that 81 blueheads had during 191 observation periods. Attacks by other species of damselfishes were rare; 4% of the interactions represented attacks by *Eupomacentrus partitus* Poey (half of them were on one bluehead), and  $\leq 1\%$  by *Microspathodon chrysurus* (Cuvier), *Eupomacentrus variabilis* Castelnau and *E. leucostictus* Müller & Troschel.

Both sexes of both damselfishes attacked the wrasse; eight of 17 adult *E. dorsopunicans* and five of 16 *E. planifrons* that we shot after they had chased wrasses were females, and the remainder males.

Although damselfishes in whose territories the wrasse had sleeping sites did attack *Thalassoma bifasciatum* that approached and entered holes, we saw such attacks during only 30% of the crepuscular observation periods we made on blueheads ( $n =$

146 observation periods, 64 fish, 73 holes), and 4% of the observation periods on initial phase fish ( $n = 47$  periods, 47 fish, 47 holes). Most (93%) of the damselfish attacks occurred as the wrasse quietly moved about near its hole rather than as it was trying to enter it. When repeatedly attacked a wrasse would merely wait a short distance away until the damsel's attention turned elsewhere (which happened quickly), then dart rapidly to its hole. *T. bifasciatum* did not return attacks by adult damselfish, although blueheads chased attacking juvenile damselfishes ( $< 30$  mm S.L.). Once inside its sleeping site, a *T. bifasciatum* was no longer molested by a damselfish.

Agonistic interactions between *T. bifasciatum* and non-damselfishes were rare during crepuscular periods, 0.3% of the 2605 interactions referred to above were with the wrasse *Halichoeres bivittatus* (Bloch) and 0.2% and 0.1% with the parrotfishes *Scarus croicensis* Bloch and *Sparisoma chrysopterum* (Bloch & Schneider) respectively. Other than in experimental situations, we never saw interactions between blueheads and fishes other than damselfishes that were associated in any way with sleeping sites. We saw only one interspecific interaction that involved an initial phase fish. It displaced a smaller juvenile parrotfish (*S. viride* (Bonaterre)) from a sleeping site and used it.

#### BEHAVIOR DURING NATURAL SLEEPING SITE CHANGES

Seven blueheads changed from one site to another on two consecutive nights. Each was evidently familiar with the second site, as on the night on which they changed holes, none made a preliminary entry into the second site before its final entry, and only one inspected the new site before entering it. During the crepuscular period of the site-change night, none had any agonistic interactions that we could associate with the use of either of its sites.

#### EFFECTS OF REMOVING BLUEHEADS' SITES

We removed the holes of 14 fish living on six reefs. On the night on which its hole was removed, each fish repeatedly 'searched' around the location of the removed site. Before they finally entered new holes, these fish engaged in hole-seeking activity at a greater rate than on previous nights. The median frequencies of hole inspections and preliminary hole entries increased to 2.3/15 min from 1.1/15 min (on the night preceding hole-removal) and to 0.8/15 min from 0/15 min, respectively (Wilcoxon Sign Rank Test,  $P < 0.05$  and  $P < 0.01$  respectively,  $n = 13$  fish, 17-57 min/observation period).

On the experimental night the experimental animals also finally entered holes later than usual ( $\bar{x} = 6.5 \pm 4.3$ , 95% C.L. min later than on the previous evening,  $n = 13$  fish, 13 observations). Unmanipulated fish retired at the same time on two consecutive nights ( $\bar{x} = 0.2 \pm 2.4$  min earlier on the second night,  $n = 35$  fish, 70 observations).

The experimental fishes' new holes were close to their old ones; all 13 were within

10 m of the removed site, while nine were within 5 m and five within 1 m of it. Six of 12 fish that we checked used their first new site more than once, and one was seen in it intermittently over a five-week period. The other six changed sites several times (one using four sites in a 17-day period) and also switched back and forth between several sites.

On nights on which their holes were removed, none of the blueheads chased conspecifics from near their new holes before they entered them, although one resting fish did chase a smaller bluehead that peered in. Another of them went into a larger bluehead's hole and was subsequently ejected by that fish. While seeking new holes on the hole-removal evening, the experimental animals were attacked by damselfish more frequently than on the previous evening (median no. attacks/15 min were 5.9 and 3.9 respectively;  $P < 0.05$ , Wilcoxon Sign Rank Test). Eleven of the 13 new holes used by blueheads on the hole-removal night were in damselfish territories. One of the 13 fish chased a smaller parrotfish (*Scarus croicensis*) out of a hole and used it.

None of the 14 blueheads whose holes were removed disappeared from its home reef immediately after the experiment started. Ten were known to be present for 1–2.5 months after their holes were removed. There were no obvious differences in the mortality rates of experimental and control fish. Two of the experimental fish whose presence was checked for more than one week after their holes were removed, disappeared, one between 31 and 35 days and the other between 76 and 98 days after their holes were removed. Three of 23 unmanipulated blueheads whose presence in an area was checked for more than one week disappeared; between five and 20, six and 19, and 26 and 59 days after observations commenced, respectively.

#### USE OF VACATED BLUEHEAD SLEEPING SITES

We collected data on 41 vacated sites, 16 whose owners changed to other sites, nine whose owners had disappeared (died?) and 16 whose owners were speared.

In 11 of the 16 experimental removals we watched the sleeping site from the time its owner was shot until all conspecifics had retired. Only once did a conspecific even inspect the vacated hole. None of the 16 sites was taken over by other fish on that first night. The 41 sites were examined 274 times over periods of up to almost seven months, with 20 being observed over more than three months. Diurnal fishes were found in them on only 7.3% of those occasions. Only one of those sites was taken over by a bluehead on a regular basis, and only five were occupied on the last night on which they were checked. Thus, vacant bluehead sites were only very infrequently taken over by conspecifics (all of them blueheads). Only one of those sites was used by another diurnal fish (a small juvenile *Eupomacentrus dorsopunicans* on one night.)

## EFFECT OF ADDITION OF BLUEHEADS TO STRANGE REEFS

In these experiments four fishes were transplanted onto each of four patch reefs. Eleven fish on three reefs were used as controls.

All of the control fish remained on their reefs, while nine experimental fish disappeared from the reefs during the day on which they were placed there. We saw four of those nine moving off the reefs into surrounding sea-grass beds.

The experimental animals swam rapidly and continuously about on their new reefs. Their sleeping-site-seeking activity was much greater than that of the controls, the mean frequencies (with 95% confidence intervals) of hole inspections and preliminary hole entries were  $10.1 \pm 6.3/15$  min and  $3.4 \pm 1.3/15$  min, respectively, for the experimental fish ( $n = 7$ ) and  $1.4 \pm 1.6/15$  min and  $0/15$  min, respectively, for the control fish ( $n = 8$ ). The experimental fish made their final entry into holes about 20 min earlier than the resident blueheads did.

The holes used by six of the seven transplanted animals that remained on their new reefs on that first night were all in the main mass of the reef. Five of the six holes were in damselfish territories. The hole-seeking experimental animals were frequently harrassed by damselfishes as they coursed about peering into and briefly entering holes. Transplanted fish were also vigorously and persistently attacked by resident blueheads of the same or greater size. Only two of the sets of such interactions we saw could we associate with sleeping site usage. There were no indications that any of the transplanted fish attempted to usurp a resident bluehead's hole.

## DISCUSSION

## COMPETITION BETWEEN THE WRASSE AND THE TWO DAMSELFISHES

Although damselfishes defend their territories against the wrasse it usually sleeps in such territories, and is tolerated once it is in its shelter in such a territory. Further, adult wrasses use different types and sizes of holes from adult damselfishes; these two types of fishes use their holes in different ways, and vacant wrasse holes are almost never used by damselfishes. Thus there is very little overlap in use of this type of resource between adult wrasses and those damselfishes capable of aggressively dominating them, and wrasses are not using holes required by damselfishes.

Although some damselfish aggression against *Thalassoma bifasciatum* serves for the defense of damselfish eggs, males alone guard eggs (e.g. Williams, 1978; pers. obs.) and female damselfishes also attack wrasses.

Defense of food is the most likely general function of damselfish attacks on the wrasse. The wrasse is a predatory carnivore on plankton and small, motile, benthic animals, principally crustaceans (Randall, 1967). Both *Eupomacentrus* spp. are benthic feeding omnivores that eat mainly algae, but also sessile and motile animals of the general type eaten by *Thalassoma bifasciatum* (Randall, 1967; Emery, 1973)

(for these authors, *Eupomacentrus fuscus* = *E. dorsopunicans*, see Greenfield & Woods, 1974). Also, we regularly saw both damselfishes chase the wrasse from animal material and eat it, and the wrasse snatch animal material from the mouths of damselfishes.

Interestingly, the data that we collected on sleeping site use by the two *Eupomacentrus* also indicate that there is a surplus of sites for those species, and that a fish does not have to have its sleeping site in its territory. *E. rectifraenum* moves about its territories at night in the Gulf of California, rather than remaining in one fixed site (S. Tanaka, pers. comm.). A similar situation might prevail with the two species we studied. According to Emery (1973), *E. dorsopunicans* (= *fuscus*) is active enough at night to feed then.

#### COMPETITION BETWEEN *THALASSOMA BIFASCIATUM* AND SPECIES OTHER THAN DAMSELFISHES

There is almost no evidence of such competition, from either the observations on hole use and defense or the three sets of experiments.

#### INTRASPECIFIC COMPETITION

A few data could indicate the existence of such competition. Sleeping sites are defended, and most fish continue to use the same site over extended periods of time. Also, transplanted blueheads are harrassed by resident blueheads, and many leave their "new" reefs. Some fish, however, evidently have more than one site they use regularly, most tubular sponges are unoccupied, and vacated sites are only infrequently taken over by conspecifics. Furthermore, both fish deprived of holes and those transplants that remain on their new reefs find new sites without fighting over holes or usurping conspecifics' holes. Also, the former fish do not appear to die prematurely. Thus, most data do not support this hypothesis, and indicate that there is a surplus of sleeping sites.

Defense of holes brings about a one-fish-per-hole pattern of dispersion which could reduce both the risk of the hole owner being detected chemosensorally by nocturnal predators (e.g. moray eels, see Hiatt & Strasburg, 1960; Starck & Davis, 1966; Hobson, 1975); and the risk of transmission of parasites (see Hinde, 1956; Carrick, 1963). Hole defense could develop in the presence of a surplus of holes if it was "cheaper" or less risky for a fish to defend one than to allow another that happened to be first into its hole to keep it for the night. It would seem to require less energy to displace subordinate conspecifics than to spend time in searching for a new site. More importantly, dusk is a time of great piscivore activity (Hobson, 1965, 1972, 1975), when predatory fishes are at a visual advantage over their prey during rapidly falling light levels (Munz & McFarland, 1973). A significant delay in entering a hole at such a time, which hole preemption could produce, could easily increase a fish's chances of being eaten. Such a hypothesis requires that fish are

usually restricted to long-term use of one site. Our data on site usage and the behavior of animals deprived of sites indicate that such is the case, although a few fish regularly switch between two familiar sites.

Agonistic interactions between blueheads affect individual blueheads' spawning success (Warner *et al.*, 1975), and determine priority of access to food (Robertson & Hoffman, 1977). Attacks on transplanted fish by resident blueheads probably represent their attempts to displace strangers that constitute a threat to their spawning success. This, and the trauma of being transplanted, could result in some experimental fish leaving their new reefs and in the others seeking shelter early. The unnaturalness of transplantation probably also accounts for the differences in the times of entry into holes of transplanted fish and fish deprived of holes on their home reefs.

We conclude that neither intra- nor interspecific competition for nocturnal resting shelter is limiting *T. bifasciatum*'s population in our study area. Further, it seems unlikely that *T. bifasciatum* is limited by competition for shelter of any type, because it is not a diurnal shelter specialist, but roams widely, and because sleeping sites are the only type of shelter it defends.

#### FACTORS DETERMINING REEF FISHES' SHELTER REQUIREMENTS

In a general hypothesis proposed by Smith & Tyler (1972, 1973b, 1975) and Smith (1977) about shelter sharing among reef fishes, the size of shelter that a fish needs is considered to be directly and primarily related to its body size. Interspecific size differences, and therefore shelter size requirements, are considered to be the main mechanism by which interspecific competition for shelter among reef fishes is reduced. We suggest that where and how *T. bifasciatum* and the damselfishes spend the night represent different types of nocturnal sheltering strategies used by fishes of similar size. In the *T. bifasciatum* type, an elongate supple fish uses a tight fitting, elongate hole, and relies on avoiding being detected by a predator and probably the hole being too small for many predators to enter. Perhaps it is more difficult for a damselfish, with its discoid, more rigid body, to enter and manoeuvre in holes of that type. Differences in the abilities and limitations of wrasses and damselfishes could mean that damselfishes' movements would be too restricted within the cramped quarters of tubular sponges. Disadvantages a damselfish might accrue by resting instead in a more exposed situation might be offset by a combination of morphology and behavior. The damselfishes are relatively more heavily armoured than the wrasse, with tougher scales and more spiny fins, which they keep erect at night. Also, by being alert and mobile, damselfishes may be better able to detect and respond to the approach of predators.

The *T. bifasciatum* and damselfish types of behavior are two of many that we think will become evident as the nocturnal behavior of diurnal reef fishes is examined in greater detail. Not only size but the availability of behavioral, morphological and

chemical defenses, and the type of general habitat used for nocturnal resting areas (coral areas, sand or benthic plant beds) will affect the types of strategies used. The literature already contains indications of distinct differences in the nocturnal resting behavior of closely related species of fishes, and even of different age-classes of the same species (e.g., see Winn & Bardach, 1959; Casimir, 1971). Smith & Tyler's proposition thus represents an overstatement, because many other factors besides size determine fishes' shelter requirements.

#### ACKNOWLEDGEMENTS

Funding and facilities were provided by the Smithsonian Tropical Research Institute. Occasional help in data collection was rendered by J. Green, S. Hoffman, P. Lobel, C. Peterson, and D. Sides. The Government of the Republic of Panama and the Kuna Indians of the Comarca de San Blas facilitated work in the field. We thank J. Cubit, S. Hoffman, R. Warner, and an anonymous reviewer for their constructive comments on the manuscript.

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