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Spatial Dispersion and Nonmigratory Spawning in the Bluehead Wrasse (*Thalassoma bifasciatum*)

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Abstract

Earlier studies of the behavior of the bluehead wrasse *Thalassoma bifasciatum* have shown it to be a migratory spawner with large terminal-phase males defending temporary spawning territories. We describe a variant social structure where fish occupy permanent home ranges, spawn within or near these home ranges, and are not territorial. Movements of identified terminal-phase and intermediate males and females were mapped in the backreef areas of three coral reefs in Puerto Rico. Locations of spawns were then compared with these home-range maps. All fish used most or all of their morning home range during the afternoon spawning period. Both terminal-phase males and females spawned within or near their home ranges. Males were relatively tolerant of other males during the afternoon spawning period: only one in five encounters between large males resulted in aggressive chases. The location of chases bore no relation to spawning sites, areas of morning foraging, or to home-range borders. A Monte Carlo computer simulation was used to measure home-range dispersion of terminal-phase and intermediate males at our main site. If males were territorial, we should expect their home ranges to be significantly overdispersed within the cumulative area they occupied. During the first year male home ranges were overdispersed but during the second year they were randomly dispersed, even though the same number of terminal-phase males occupied the same study site both years. Differences in social behavior between backreef areas and other areas reported in the literature, and found in other portions of our reefs, may be related to differences in feeding ecology between populations and between different portions of the same reef.

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Introduction

The bluehead wrasse, *Thalassoma bifasciatum*, is one of the best studied coral-reef fishes. It has been used to test hypotheses concerning life-history strategies and the evolution of sex change (WARNER et al. 1975; WARNER & HOFFMAN 1980 a; WARNER 1984, 1985), the economics of territorial defense

(WARNER & HOFFMAN 1980 b), female mate choice (WARNER 1986, 1987), and the evolution of mating systems (ROBERTSON & HOFFMAN 1977; WARNER & ROBERTSON 1978). In all of these studies, done off the Caribbean coast of Panama, fish spent most of the day in upcurrent plankton-feeding groups and migrated during the daily spawning period to specific mating areas. Large males set up temporary territories at these areas, and smaller males spawned in groups or attempted to sneak matings.

The high concentrations of males and females at these spawning areas leads to an intensely competitive social system in which large males accrue a disproportionate share of mating (WARNER et al. 1975). The intensity of competition in and around the spawning territories seen in these early studies led to the suggestion that small males are disadvantaged reproductively in comparison with large males and small females. Consequently, individuals could improve their lifetime reproductive value by being females when small and males when large (WARNER et al. 1975). Thus, the selective advantage of protogynous hermaphroditism was intimately related to territorial competition among males for a restricted number of spawning sites during the mating portions of the day.

In backreef areas off Puerto Rico, the social structure of this species seemed to differ from these descriptions. Individuals appeared sedentary and the population was dispersed over wide areas, and no obvious spawning migrations or temporary male territoriality were observed. Because the generality of the above explanation for the evolution of protogyny in this fish should depend on the degree of ubiquity of the competitive, territorial mating system, we set out to describe the mating system in backreef areas. Specifically, we tested the hypotheses that fish migrate from their morning home ranges to downcurrent mating sites and that terminal-phase males defend temporary mating territories during the mid-day spawning period.

Materials and Methods

Subject Species and Study Site

T. bifasciatum is an extremely abundant wrasse that inhabits a wide variety of Caribbean reef habitats (FEDDERN 1965; KIMMEL 1985). It is a generalist feeder, taking zooplankton, a wide variety of benthic organisms, and ectoparasites from other fish (RANDALL 1967). Populations of *T. bifasciatum* generally contain two types of males (REINBOTH 1973). Initial-phase (IP) males are small, colored like females, and have matured directly as males. Terminal-phase (TP) males are larger and are either individuals that have changed sex and color from an earlier female stage or are initial-phase males that have changed color. TP males typically pair spawn with single females, while IP males can either pair spawn or spawn in large groups containing one female and a number of other males (WARNER et al. 1975).

Individuals were classified as IP males, IP females, TP males, or transitionals (WARNER & ROBERTSON 1978). Sex was determined for IP males and females by capturing individuals during the spawning period, gently milking the gonads and examining the gametes in plastic bags. An individual in transition between initial and terminal-phase color was called an intermediate (INT) if it maintained permanent vertical stripes along its flank. If all but the three post-opercular stripes had disappeared and the head was deep blue, the fish was classified as a TP. Because the great majority of all INTs in previous studies contained functioning testes (REINBOTH 1972; ROEDE 1975) and because all INTs observed spawning in our study spawned as males, all INTs were treated as males.

Observations in Panama revealed three types of TP and INT males: territorial individuals, associated satellites and floaters (WARNER, R. R., pers. comm.). We sought evidence for such a distinction, but found a full range of variation in degree of overlap and degree of association between males of differing sizes; we found no reliable criteria for singling out discrete degrees of association.

Home-range maps and spawning locations were plotted on portions of three fringing reefs, San Cristóbal (ROGERS 1979), La India and Corona de Atravesado on the southwest coast of Puerto Rico (Fig. 1). These reefs measured approximately 225, 200, and 100 m, respectively, along their seaward crests. Study sites on all three reefs were in sheltered, backreef areas in depths of 1.0–3.5 m, where the habitat consisted of coral heads and colonies of gorgonians scattered over coral rubble and calcareous sand. Data on home range dispersion and aggressive behavior were obtained in a 50 × 50-m grid made of steel rods and polypropylene rope, divided into 225 numbered quadrats 3.3 m on a side, located at our main study site on San Cristóbal. The male : female sex ratio of IPs at this site was 1 : 5.3; when 57 IPs were caught in baited traps and sexed, 48 (84 %) were female and nine were male.

Home Ranges and Spawning Locations

On San Cristóbal, we mapped the home ranges of 10 TP males, 10 INT males, and 9 females whose home ranges were centered in the central 81 quadrats of the grid in two different years. We then followed selected individuals during afternoon spawning periods to locate their spawning sites. Females and INT males were selected to represent the full range of body sizes in the grid, from small females to the largest males. Data were collected between May–Aug. 1984, and between Jan.–Apr. 1985. In both years the central area was occupied by five TP males and at least five INTs. TP and INT individuals were identified by unique variations in their color (REESE 1973; WILLIAMS 1978; WARNER & HOFFMAN 1980 a), specifically in the post-opercular stripes. Females were captured in baited traps, sexed, injected subcutaneously with acrylic paints in unique patterns (THRESHER & GRONELL 1978) and released at the point of capture. Females were held for about 5 min between the time of capture and release.

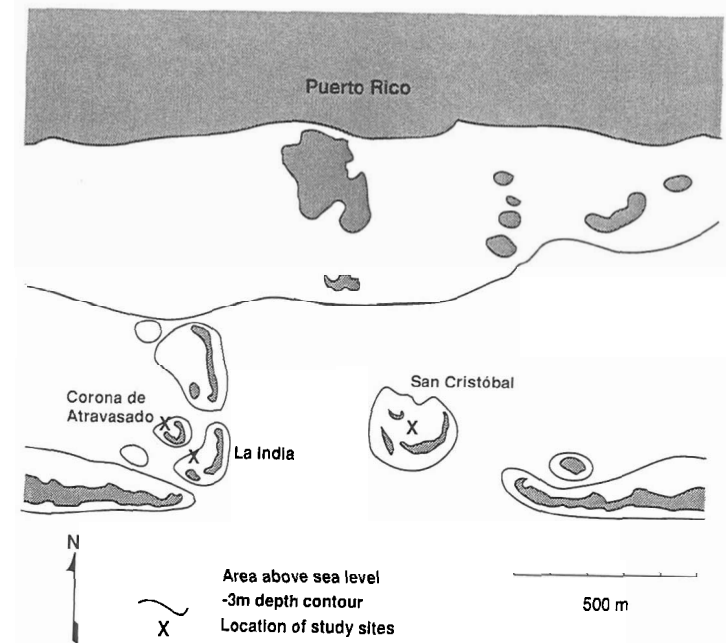


Fig. 1: Map showing reefs in southwestern Puerto Rico, including the three study reefs

Home range data during both years were taken between 08.19 and 12.30 h. Females were observed during five 30-min observation periods and males during 10 15-min periods. In each period, we followed the subject and recorded the number of seconds it spent in each quadrat. These values were then reduced to a list of all quadrats entered and the proportion of total observation time spent in each quadrat. From this list we calculated the smallest set of quadrats within which the fish spent 75 %, 90 %, and 100 % of its time (the 75 %, 90 % and 100 % home ranges). The 100 % home range included all quadrats in which the fish was ever seen during these morning observation periods.

Home range data on San Cristóbal were recorded during 239 observation periods totalling 70.5 h on 29 fish. Both 90 % and 100 % home range sizes approached asymptotic levels closely by the 90th min of observation in all females, INTs, and all but one TP male. Thus, our observation times were adequate to characterize home range size (BROWN 1975).

We recorded spawning data for a total of ten TPs, three INTs and six females. At San Cristóbal we recorded spawning locations for five males (two TPs and three INTs), in 1984 and six females in 1985. We observed each male continuously for approximately 2.5 h during the afternoon spawning period on six days, giving a total of 74.2 observation h for all five males. The location of each spawn or courtship was recorded. Courtship was defined as the performance of pectoral flutters or loops in the presence of females (REINBOTH 1973; ROBERTSON & HOFFMAN 1977). Spawning was defined as a rapid rush toward the surface by one male and one IP fish, regardless of whether or not a gamete cloud was seen (WARNER & HOFFMAN 1980 b).

Females spawn much less frequently than some males (WARNER et al. 1975; HOFFMAN et al. 1985); hence, methods were adjusted to increase the efficiency of observation. One of three females were marked and observed during the spawning period on the same day. The observer swam repeatedly over the grid looking for abdominal swelling, an indicator of readiness to spawn, in any marked female. Once a marked female with a swollen abdomen was detected, she was continuously followed wherever she went until she spawned. The spawning location was recorded. At the conclusion of spawning by this female, the search resumed for another spawning-ready fish. When the first-observed female spawned early, it was often possible to observe the spawning of a second or third female in the same spawning period. Female spawning behavior was observed a total 17.7 h on 10 days. Because only 1–3 females were observable on any given day, the maximum number of spawns that could have been observed with our techniques for the six marked females over the 10 observation periods, even assuming optimistically that each female spawned once daily (WARNER 1986), was 18. These spawnings were, in fact, seen, suggesting that few, if any, spawns were missed with these methods.

On La India and Corona de Atravesado reefs we used an abbreviated version of the methods given above, focusing on four large TP males at each site. Large males were selected because, in Panama, they are more likely to behave territorially than small males (WARNER et al. 1975). Data were collected in June, 1988. For each fish, we collected home range data during at least six 15-min observations during the morning feeding period and during at least six observations during the later spawning period by recording fish position every 15 s on detailed scale maps of the reef. The convex polygon method (BROWN 1975) was used to circumscribe home-range boundaries around these points, creating a separate home range map for the morning and the afternoon periods. Spawning locations were then superimposed on these maps.

Home Range Dispersion and Territorial Behavior

In the grid on San Cristóbal reef we recorded the frequency and location of courtship, spawning and aggressive encounters during the afternoon observation periods. We assumed that territoriality by males could be recognized by using any or all of the following features: (1) space used by males in the afternoon, which was virtually completely overlapping with morning home ranges for all individuals on all three reefs, would be statistically overdispersed. Thus, in the central portion of the grid, where the entire area falls within the home range of at least one male, male home ranges should be spaced apart to a greater extent than would be expected if their home ranges were placed randomly within the same area. If this assumption were not true, then males would have no exclusive area, i. e. no territory, other than that provided by random occupation of space. (2) Aggressive interactions should occur in relation to whatever area or location was being defended. If males defended entire home ranges, then aggression should occur on the periphery of the home range or primarily in the area of

overlap with neighboring males. If males defended courtship and spawning sites, then aggression should occur in relation to these sites. If aggression does not occur in relation to spatial features of the home range, there is no evidence to indicate whether part or all of the home range is being defended. (3) Males should display low tolerance for other males approaching them. Consequently, most encounters between males during the spawning period should result in an aggressive chase.

To quantify the degree of overlap in male home ranges we calculated Pianka's index of overlap (PIANKA 1975; WASER & WILEY 1979) for each possible pair of fish, based on the proportion of time each fish spent in each quadrat. This index theoretically varies from zero (no overlap) to one (both individuals spent identical amounts of time in the same quadrats). The nearest neighbor of a subject was defined as that individual with which the subject had the highest index.

To analyze spatial dispersion of male home ranges we used a Monte Carlo computer simulation (BINDER & STAUFFER 1987; SOKAL & ROHLF 1981). Each quadrat within the home range was characterized by the proportion of time spent in it by the male. The most used quadrat in a male's observed home range was placed at a randomly chosen location within a simulated grid. The home range was oriented randomly in one of four perpendicular directions, and all other used quadrats were then placed in the appropriate location with respect to the most used quadrat. This procedure was repeated for all ten males. Pianka's index of overlap was then calculated for each possible pair of fish, and one run of the simulation was complete. The simulation consisted of 5000 runs. We used the mean, over all fish, of Pianka's index of overlap between each fish and its nearest neighbor as our test statistic. The simulation generated a random probability distribution for this statistic. Since we wished to test whether males were territorial and their home ranges overdispersed, we employed a one-tailed test. The probability of observing an index of overlap as small or smaller than the actual value was found by comparing the observed value with the randomly generated probability distribution. If fewer than 5 % of the randomly generated values were less than the observed value, p was less than .05 for a one-tailed test and we concluded statistically significant overdispersion.

Computer simulations were run separately for all 10 males, for TP males only, and for INT males only, in each of the two years of observation. The simulations would thus reveal whether TP males had spatial dispersion patterns that were the same as or different from those of INT males or from all males taken together.

Behavioral interactions were recorded for five males (three INTs and two TPs) during their afternoon spawning periods in 1984. Each male was followed as a focal animal. Whenever the focal male came within 1 m of another male for more than 5 s, an interval that approximated the error of our timing accuracy, the instance was defined as an encounter. The duration and location of encounters were recorded. When one fish swam rapidly at another fish that swam away, the interaction was called a chase and was characterized as aggressive. The number and quadrat location of chases were recorded. Levels of aggression were estimated by calculating the number of chases per observation hour and the number of chases per encounter. For comparison, similar data were also recorded during the morning observation periods of ten males (five TP and five INT males) in 1985.

To obtain an estimate of the dispersion of IP individuals, most of which were females, we censused IP fish within the central grid (DREW 1986). An observer swam slowly over the grid, spending 45 s in each quadrat counting the number of fish. Censuses were taken between 09.00 and 14.00 h on 13 days. Dispersion of fish over the central grid was analyzed by computing the variance-to-mean ratio for the number of individuals per quadrat. The value expected if fish were randomly dispersed over the central grid is 1.0 (PIELOU 1977).

Results

Home Ranges and Spawning Location

The area used by males during the spawning period was almost the same as the morning home range for all 13 males on all three reefs. In the grid on San Cristóbal, home range sizes did not differ significantly between 1984 and 1985 for any color phase of fish for 75 %, 90 %, or 100 % estimates (Mann Whitney U-test, $p > 0.05$ for all comparisons). Consequently, data from both years were

Table 1: Median values and 95% confidence limits (in parentheses) for the area (m²) of 75%, 90% and 100% estimates of home range for initial-phase fish (IP), intermediate males (INT), and terminal-phase males (TP)

Fish class	n	Estimates of home range size (m ²)		
		75%	90%	100%
IP	9	20 (10–30)	30 (10–30)	60 (40–70)
INT	10	55 (40–80)	90 (70–120)	195 (150–220)
TP	10	80 (30–130)	135 (60–200)	275 (190–340)

Kruskal-Wallis ANOVA: $p < 0.001$ $p < 0.001$ $p < 0.001$

pooled. Home range size differed significantly among the three color phases of fish (Table 1), with females having smaller home ranges than INTs (Mann Whitney U-test, $p < 0.001$ for all estimates), and INTs having smaller home ranges than TP males (Mann Whitney U-test, $p = 0.06$ for 75% estimates, and $p < 0.05$ for 90% and 100% estimates). In the analyses which follow, 100% home range estimates are used.

The 100% home range sizes of males varied from 11 to 43 quadrats, i. e. from 122–478 m². Most home ranges were irregularly shaped, especially for INT and TP males, and covered substantial areas. When data for all fish were pooled, home range size correlated positively with body size (Spearman $r_s = 0.95$, $n = 29$, $p < 0.001$). Because data on home range size of the large males at La India and Corona de Atravesado were not strictly comparable to data

Table 2: Spawning locations of terminal-phase (TP) and intermediate (INT) male *T. bifasciatum* with respect to male home ranges (HR). "Max distance" is the maximum observed separation between a spawning location and the nearest home range border. TL = total length

Site	Fish #	Type	TL (cm)	Number of spawns		
				in HR	out of HR	Max distance
Main	M1	TP	11.8	60	0	
Main	M5	INT	10.3	8	0	
Main	M6	INT	9.8	5	0	
Main	M7	INT	9.8	9	0	
Main	M8	TP	11.5	37	2	12 m
Corona	C1	TP	10.6	61	12	1 m
Corona	C2	TP	10.7	3	22	5 m
Corona	C3	TP	10.2	20	0	
Corona	C4	TP	9.8	8	1	1 m
India	I1	TP	12.3	31	0	
India	I2	TP	12.2	12	0	
India	I3	TP	11.2	37	0	
India	I4	TP	12.1	24	0	
Total:				315	37	

from the main site, we have omitted data from these two sites from the analysis of home range size.

On all three reefs, spawning occurred within or close to the border of the morning home ranges of all fish. On San Cristóbal, all but one of the five males observed during afternoon spawning periods spawned exclusively within their morning home range (Table 2). The other male had 2 of his 37 spawns (5%) outside of his home range, one 3 m and the other 12 m from the nearest home range quadrat. Of a total of 121 male spawns observed at the main site, 98% were within morning home range boundaries.

At La Corona, 92 (72%) of 127 observed male spawns were inside the morning home range (Table 2). 32 spawns were within 1 m of the nearest home range border. The remaining 3 spawns were a maximum of 5 m from the nearest home range border. At La India, 100% of 104 observed male spawns were within the morning home range. Thus, of the 13 males and 352 spawns observed on all three study reefs, 9 males (accounting for 206 spawns) spawned entirely within their morning home range, and four males had a total of 37 spawns (11% of the total number of spawns) outside of their morning home range. These "outside" spawns were a mean distance of 1.68 m (max = 12 m) away from the nearest home range border.

Female spawnings were observed only at San Cristóbal. A total of six identified females were followed during the spawning period over 10 days. During this period 15 spawns by six females were observed. Each female spawned 1–4 (median 2) times. On most occasions (range 0–100%, median 88%), females spawned within their morning home ranges. When data from all females were pooled, 60% of spawns occurred within the females' home ranges. Six spawns were 3.3–13.3 m (median 6.6 m) outside of the subject female's home range. All were inside the study grid and were thus confined to a relatively small portion of the reef.

Our population differed substantially from descriptions in the literature in the number of sites at which a given male spawned. San Cristóbal males spawned in a minimum of 2 different quadrats (the male which spawned least) and in a maximum of 13 quadrats, whereas males in Panama had a maximum of 4 spawning sites (WARNER 1985). A given quadrat could contain up to three local spawning sites. We ranked spawning quadrats by the number of spawns observed within them. In total, spawns in a fish's first-ranking quadrat accounted for only 33.9% of total spawns (41 out of 121 total).

Dispersion of Home Ranges

Indices of overlap between nearest neighbor males on San Cristóbal varied widely (Table 3). Some males had home ranges that were largely exclusive of neighboring males, while others overlapped almost entirely with a neighboring male. Indices for 1984 and 1985 did not differ significantly (Mann-Whitney U-Test, $U = 35$, $p > 0.05$).

The results of the Monte Carlo simulations differed for the two study years (Table 4). In 1984, fish were significantly overdispersed ($p < .05$), regardless of

Table 3: Pianka's index of overlap with the nearest neighbor of each male *T. bifasciatum* during two successive years. (TP: terminal-phase male; INT: intermediate male)

1984		1985	
TP	Overlap	TP	Overlap
M1	0.439	M3	0.353
M2	0.278	M5	0.682
M4	0.414	M7	0.924
M8	0.533	M9	0.250
M10	0.183	M10	0.517
INT	Overlap	INT	Overlap
M3	0.151	M1	0.139
M5	0.439	M2	0.386
M6	0.278	M4	0.517
M7	0.119	M6	0.386
M9	0.533	M8	0.924

which subgroup of males (INTs only, TPs only, or all fish together) was examined. In contrast, no overdispersion was found in the 1985 data; males were randomly dispersed. Both in 1984 and in 1985, the dispersion of TPs was identical to the dispersion of INTs. Thus, even though TPs had greater reproductive success than INTs within a reef (Table 2), they dispersed themselves in identical patterns.

The mean density of IP fish (both males and females) on the central grid was 0.96 fish/quadrat or 0.88 fish/10 m². The variance-to-mean ratio for the number of IP fish per quadrat was 3.85. This ratio significantly exceeded unity, the ratio expected if fish were randomly dispersed ($\chi^2 = 308$, $df = 80$, $p < 0.001$). Therefore, the IP fish were aggregated in space on the central grid.

Behavioral Interactions

The main activity of all fish during the morning was benthic feeding. During the afternoon, males mixed mating behavior with feeding, and females continued

Table 4: Means and ranges for observed and simulated values of Pianka's index of overlap in home ranges of terminal-phase males (TPs), intermediate males (INTs) and of both male types pooled (All)

Category	n	\bar{X} observed	\bar{X} simulation	Range of simulation	p values
1984 All	10	0.337	0.586	.309—.786	0.0002
1984 TPs	5	0.220	0.453	.042—.790	0.032
1984 INTs	5	0.026	0.400	.009—.887	0.003
1985 All	10	0.508	0.505	.226—.779	0.512
1985 TPs	5	0.348	0.329	.016—.773	0.563
1985 INTs	5	0.166	0.343	.009—.764	0.108

to feed benthically with a brief pause for spawning. Of 3636 feeding bites counted ($n = 5$ fish), only 1 % were on planktonic food items.

Males encountered, i. e. moved to within 1 m of each other, a median of 8.4 and 10.8 times/h in the morning in 1985 and in the afternoon in 1984, respectively. They spent medians of 23 % and 13 % of the observation time in encounters during these two years. During the afternoon spawning period, the rate of chasing was 0.7—3.7 times/h, with median 2.6, and the number of chases per encounter ranged from 0.15—0.25; the median was 0.19. Thus, most encounters did not lead to aggressive chases; males were relatively tolerant of one another even during the spawning period.

The location of every aggressive act was plotted on the home range map of each male. Aggressive acts occurred in 0.25—0.64 (median 0.31) of male home-range quadrats and were not located with respect to any apparent special feature of the home range. For example, there was no consistently significant correlation, positive or negative, between quadrat usage for courtship and/or spawning and rate of aggression or between morning use for foraging and afternoon aggression (Table 5). Males behaved aggressively in central portions of their home range as well as along the periphery.

Table 5: Spearman correlation coefficients between afternoon aggression (Aggr) and courtships-and-spawnings (C/S) or morning usage (AM Use) for each of 5 males

Fish	M1 ^a	M5 ^b	M6 ^b	M7 ^b	M8 ^a
C/S vs. Aggr.	0.03	-0.65*	-0.35	-0.47	-0.39
AM Use vs. Aggr.	-0.52*	0.16	-0.77*	0.34	-0.18

^a: terminal-phase male, ^b: intermediate male, *: $p < 0.05$ one-tailed.

Discussion

On all three study reefs, females and both INT and TP males occupied permanent all-purpose home ranges. During the morning, individuals foraged on the substrate and interacted with individual neighbors behaviorally. In the afternoon, males spawned at multiple sites almost entirely within their morning home ranges. Females spawned within their home range or close to it. In contrast, fish in Panama have been described as occupying upcurrent plankton-feeding groups in the morning and then migrating, often substantial distances, to down-current areas where TP males and females each spawn at a small number of mating sites in the afternoon (WARNER 1984, 1986, 1987; ROBERTSON & HOFFMAN 1977).

We found no convincing evidence of male territoriality in this variant of the social system. INT and TP males were relatively tolerant of other males within their home ranges. Fewer than one in four male-male encounters during the spawning period resulted in an aggressive chase. The location of chases was not correlated spatially with spawning-site location or morning usage and bore no clear relation to home range borders.

Finally, the computer simulation yielded conflicting results for two data sets in different years at the same site. In 1984, male home ranges were overdispersed, as one would expect if home ranges were defended as territories. However, these males tolerated a minimum of three out of every four intrusions by other males within their home range without chasing them. These results suggest that overdispersion of home ranges in 1984 was not caused by male-male aggression. In 1985, on the same site with the same number of TP males occupying the center of the grid, home ranges were randomly dispersed. The difference between the two years cannot be attributed to different home range sizes, different sample sizes, different techniques or different numbers of males on the grid. The most likely cause of the different dispersion patterns is the difference in identity of individual males between the two years, i. e. that different sets of males use space differently. Since choice of mating sites by females is traditional, with the same sites in use for prolonged periods (WARNER 1988), the difference in male dispersion is not likely to stem from differences in female behavior between the two years.

Whatever the cause, the variation in home range dispersion, inconsistency in location of chases, and tolerance of males for each other do not constitute convincing evidence for a consistent or well-developed system of spawning territories in this portion of our reefs. In contrast, territorial males in the San Blas Islands displayed low tolerance to the approach of another male, chasing them at high frequencies, and a substantial proportion of their time was spent defending spawning sites (WARNER & HOFFMAN 1980 b).

The most striking difference between our study populations and those described in Panama is that our fish did not migrate to the downcurrent end of the reef before spawning. Although a few fish spawned a few meters from their morning home range, no migration was seen in the backreef study areas of any of the three study reefs. When dye was released at various sites around San Cristóbal to document the speed and direction of current, the most downcurrent end of the reef was at least 100 m of almost continuous coral cover from our grid (SHAPIRO et al. 1988). The intervening area was occupied by spawning conspecifics and no physical barrier prevented migration. When the grid at San Cristóbal was divided into upcurrent and downcurrent halves, a significantly larger number of spawns were located in the upcurrent half (SHAPIRO et al. 1988). Thus, it would appear that the fish in backreef areas do not select specific spawning sites with respect to their location in the current.

In other portions of our reefs, i. e. along the forereef and in areas of vertical reef face, males and females did migrate to spawning sites and their behavior appeared to be the same as that described in Panama, i. e. individuals fed on zooplankton during the morning and migrated to other sites in the afternoon where TP males defended temporary territories. Females either spawned in pairs within these territories or spawned in groups with IP males in nearby areas. Thus, the populations in our reefs are organized into at least two variants of social and mating structures. Similar variation in social and mating structure has been documented in another protogynous labrid, *Halichoeres maculipinna* (THRESHER 1979; ROBERTSON 1981).

If those features of the social system examined in this study have been selected to adapt to local resource distribution, as is often thought to be true in terrestrial animals (RUBENSTEIN & WRANGHAM 1986; SLOBODCHIKOFF 1988), then the migratory and nonmigratory variants on our reefs should match differences in resources. The clearest difference in resources between forereef and backreef areas is likely to be availability of food, with most of the zooplankton arriving at the reef front removed by planktivorous fishes before the water approaching the reef is swept over the reef flat or around the edges of the reef into the backreef area (HAMNER et al. 1988).

On our reefs, *T. bifasciatum* in forereef areas foraged pelagically on zooplankton, while those in backreef areas fed benthically on the substrate. Once the population is separated into different feeding types located on different parts of the reef, differences in water movement between forereef and backreef may influence the mating system. We suggest that backreef areas (where foraging occurs) lie in locations with respect to water movement and other reef structures that make them adequate areas for releasing pelagic eggs (RANDALL & RANDALL 1963; JONES 1968). Forereef areas, where *T. bifasciatum* feeds on plankton, may be unsuitable for pelagic spawning because surface water from these areas passes over the reef crest (SHAPIRO, HENSLEY & APPELDOORN, unpubl. data). Consequently, selection should produce the ability of individual fish to match their spawning areas with their feeding ecology. The result will be migration from forereef planktivorous areas to locations nearer the lateral edge of the reef, where water containing spawned eggs will not pass over the reef crest. If there is significant concentration of spawning in these areas, then specific sites would become economically defensible and large males would chase intruding males away.

In contrast, fish feeding benthically in backreef areas can remain in place to spawn. These backreef locations are spread over a relatively large area. If there are many possible specific sites for mating, spawning becomes spread over a diffuse area and the potential gains of temporary resource-defense polygyny, as seen in migratory populations, cease to outweigh the costs and territoriality will not develop (EMLEN & ORING 1977).

We do not believe that the proximate cause of migrating or remaining in morning home ranges to spawn is simply a function of current speed, despite the fact that average current velocities may be less in backreef than in forereef areas. If migration were induced simply by current attaining a particular value, then we would expect normally migratory populations not to migrate on days of low current, a result that has not been reported in the literature, and fish in backreef sites to migrate on days of strong current, a result we never observed even when storms resulted in vigorous currents over our sites.

The consequences of the more sedentary and less aggressive social structure in the backreef areas are likely to be theoretically important. *T. bifasciatum* is a protogynous hermaphrodite and has been used in the past to test hypotheses about sex change (WARNER et al. 1975) and mating systems (ROBERTSON & HOFFMAN 1977; WARNER & ROBERTSON 1978). In these papers, the mating system and sex change itself are assumed to have evolved under conditions of intense

competition for limited spawning sites. As a result of this heavy competition small differences in size are believed to have resulted in disproportionately large gains in male reproductive success, and this to have resulted in selection for protogynous hermaphroditism (WARNER 1975).

In the nonmigratory populations documented here, the relatively large number and wide dispersion of spawning sites and the absence of consistent defense of home ranges or spawning sites leads to reduced competition between males for mates. In this situation, size is probably a less important determinant of male mating success than other factors such as home range location. Since the above explanation for the evolution of protogyny in this species is based on the idea of a size advantage in competition for mates, its adequacy may depend on the relative proportion of reef populations that employ the migratory, territorial/group spawning system vs. the nonmigratory, all-purpose home range mating system documented here.

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