

Interspecific Aggression and its Relevance to the Concept of Territoriality in Reef Fishes

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SYNOPSIS. Territorial behavior is a conspicuous determinant of social organization in many reef fishes. Field observations have indicated that an accurate description of a given organization must consider not only conspecific encounters but also those involving members of the other species which make up the behavioral community. Data, relevant to the above consideration, were gathered on the reef for the three-spot damselfish, *Eupomacentrus planifrons*, at intervals throughout the year.

Experiments determined (i) the greatest distance from its residence ("maximum distance of attack") that a territorial male would initiate attacks on given individuals of various species, and (ii) number of nips that such a male directed at "intruders" when the latter were placed adjacent to its residence.

The "maximum distance of attack" was found to be characteristic for each "intruding" species: conspecifics—farthest from, congenetics—slightly closer to, and the remaining species—closest to the residence. Territorial males appeared to ignore any given fish until it had reached its respective boundary. Over a broad range, size within a given species appeared unimportant. The number of attacks directed at "intruders" adjacent to the residence was, however, less clearly species-specific. Both parameters varied seasonally in a parallel fashion, this seasonality reflecting closely the annual reproductive cycle of *E. planifrons*. General observations on populations of *E. planifrons* and other damselfishes were carried out by SCUBA and the use of underwater television.

Results demonstrated that territorial males of *E. planifrons* not only recognize different species of reef fishes, but also that they possess serial territories whose areas of defense vary depending on the particular species of intruder present at the time. Random observations on other species of reef fishes indicate that this important feature of interspecific aggression is not unique to the single species tested here.

INTRODUCTION

Among the several cornerstones underlying social organization, two, in particular, stand out—intraspecific aggression and territoriality (i.e., defense of area) (Noble, 1939; Nice, 1941; Tinbergen, 1957). The numerous monographs, books, and major reviews, devoted wholly or largely to one or both of these factors, which have appeared within the past few years testify to the importance ascribed to them. Their often close relationship has resulted in the

suggestion that intraspecific aggression, itself, be included in any definition of territoriality (e.g., Armstrong, 1947). Field evidence of the inappropriateness of such a suggestion has come forth largely through studies on various species of birds. Howard (1920), for example, pointed out many cases of interspecific territoriality, primarily among non-related species which have similar nest requirements. More recently, authors have described numerous cases of interspecific territoriality among various species of birds (Fuggles-Couchman, 1943; Simmons, 1951; Lanyon, 1957; Selander and Giller, 1959; Johnson, 1963, 1966; Willson and Orians, 1963), and several reviews of the subject have appeared (Fisher, 1964; Orians and Willson, 1964; Murray, 1971).

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Thus, the concept of interspecific territoriality has existed within the bird literature for more than 50 years. Yet, since most of the cases involved only sibling species, its importance consistently remained in question. Despite Howard's work, it was felt that such activity was simply the result of mistaken identity (e.g., Tinbergen, 1935, 1936; Armstrong, 1947; Lanyon, 1957; Selander and Giller, 1959; Murray, 1971) and that it would disappear as species diverged. Orians and Willson (1964) argued, however, that many cases *appeared* (our italics) to involve stable systems of sustained aggression which they found difficult to dismiss as misidentification.

Cases of interspecific territoriality and aggression were also reported in another group of vertebrates—the fishes. Until recently, however, they have been few in number (Gerking, 1959). Winn (1958) had shown that certain species of darters (Percidae) defended territories in aquaria not only against members of their own species, but also members of several other species of darters. Both Newman (1956) and Stringer and Hoar (1955) noted that several species of trout (Salmonidae) demonstrated among themselves high levels of interspecific aggression. More cases of interspecific territoriality operating in the field have only recently come to light (Fricke, 1966; Rasa, 1969; Clarke, 1970; Low, 1971; Myrberg, 1972a). Low (1971) also provided a review of the subject as it applies to fishes. This review has been of special value as various authors have implied that aggression and territoriality in reef fishes are primarily, if not exclusively, intraspecific in nature (Lorenz, 1962, 1966; Zumpe, 1965; Fricke, 1966).

The possible importance of interspecific aggression came to our attention some years ago when one of us (AAM) initiated various field programs, centering on the behavior of selected reef fishes found off the coast of Bimini, Bahamas, and South Florida. During the course of these studies, it became readily apparent that numerous species of fishes not only held territories (defined as above) in the face of conspecifics, but also against fishes of numerous other species, widely divergent in

form, size, and color pattern. Long term observations suggested that such interspecific territoriality not only involved stable systems of sustained aggression over long periods of time, but also that large expenditures of energy were obviously required to maintain such systems. This indicated that territorial exclusion was based upon some selective advantage to the behavior (note Orians and Willson, 1964). Since then, several studies have been carried out on various subjects which only peripherally dealt with the problem at hand. Most only mentioned the interesting interspecific relationships that commonly existed between members of the subject species and members of numerous other species of fishes common to the coral reef community (Cummings, 1968; Colin, 1970, 1971; Myrberg, 1972b, 1973). Recently, we had the opportunity to carry out a preliminary field description of interspecific territoriality in one of the common damselfishes found in the shallow reef areas off South Florida. We wanted to examine what appeared to be a stable system of sustained aggression which served to characterize interspecific territoriality in the subject species. This report centers on the findings of that particular study and relates them to previous discussions of this recognized, but little understood phenomenon.

MATERIALS AND METHODS

Subjects were territorial males of the threespot damselfish, *Eupomacentrus planifrons* (Cuvier). This species was chosen because of its availability, its maintenance of territory throughout the year, and its interest to us. Based on limited aquarium facilities for providing field-sized territories to members of the species, the entire study was, of necessity and by design, carried out in the field.

The site chosen for study was a large, rocky outcrop (12 × 4 × 2.5 m) located at a depth of 13 m, approximately 8 km east of Elliott Key in the charted area of Triumph Reef, Florida Keys. The outcrop was typical of the area—heavily overgrown

with vegetation, soft and hard coral, sponge and other encrusting organisms. Threespot damselfishes were prevalent in one area of the site where small caves and

crevices were in abundance. This particular area was subsequently termed the Subject Rock (Fig. 1). Preliminary observations had shown that these damselfishes seldom

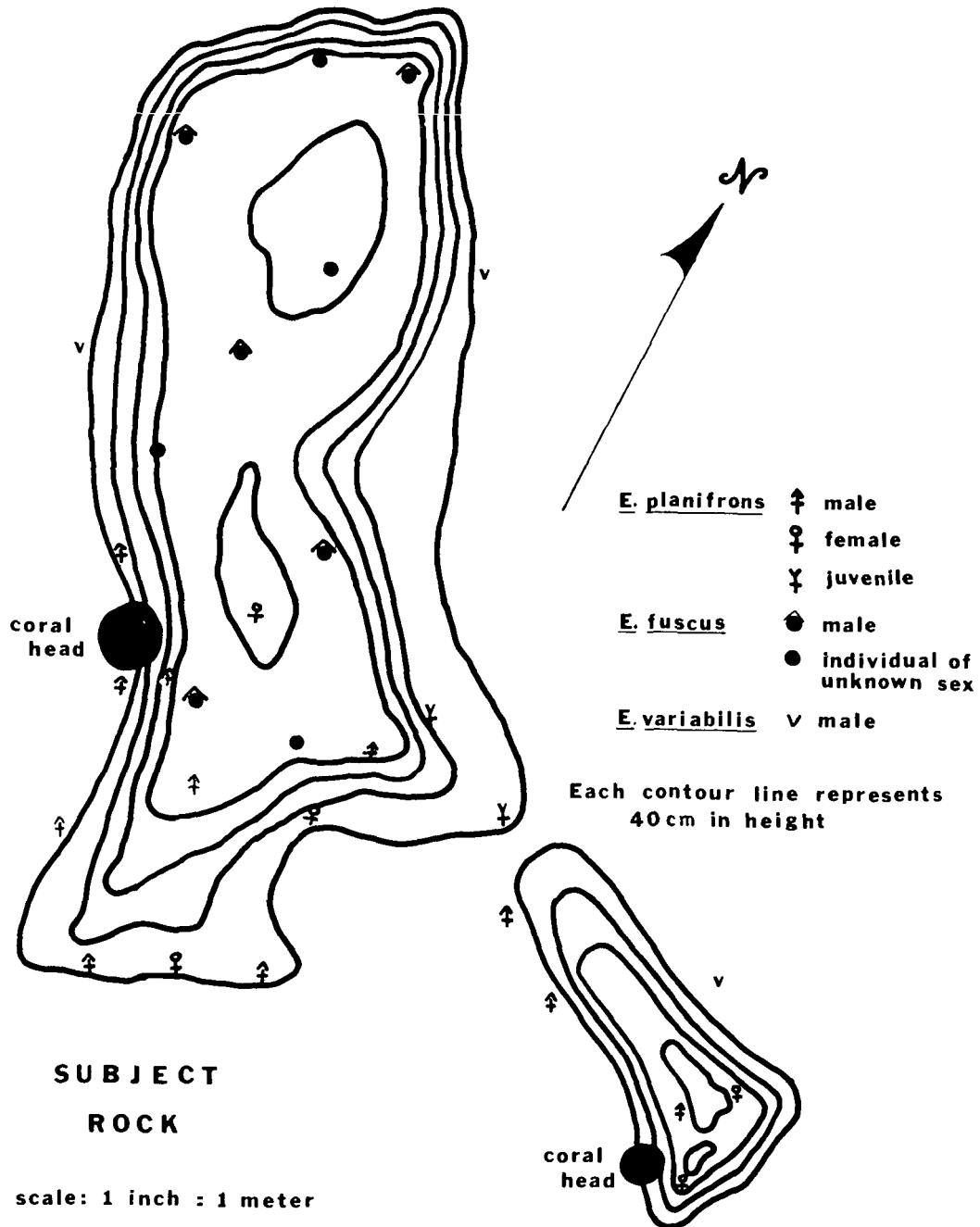


FIG. 1. Diagram of the Subject Rock, showing areas of residence of various damselfishes found thereon.

The most peripheral of contour lines represents a distance of 40 cm above the sandy substrate.

moved over large areas of the outcrop. Rather, each spent most time within a restricted region of the substrate and, from which, it drove away most intruding fishes. It was also apparent that some species were attacked far from the residence, while others were allowed to approach more closely before being driven away. Finally, though these respective differences appeared consistent for a given territory-holder, they varied in absolute terms among the various territory-holders since the sizes of defended areas (less than 2 m to over 3 m in diam) were clearly related to bottom topography, as well as to the size of the damselfish itself. Due to the wealth of confounding variables, no absolute measure could be applied commonly among the various territory-holders and relative measures were of little value since we did not know which relevant standard to use in comparing such measures. To obviate these difficulties at this early stage in our work, we felt it best to limit our measurement to males that were defending large areas and to confine such measurements largely, but not exclusively, to one individual whose behavior, we believe, typified, in principle, that shown by other members of its species at the Subject Rock. Clear dangers associated with such an approach, fortunately, did not materialize, based on many hours of qualitative observations at the site, as well as a quantitative extension of the present work to other members of the same colony, to be reported elsewhere.

The primary male selected for study held a residence at the base of the Subject Rock. Its area of defense against conspecifics extended from that residence for a distance of about 4 m over a broad expanse of relatively open ground to the south and southwest. This arrangement permitted a diver to measure accurately distances (by a measured rod) from the residence, as well as to present test subjects in the area with assurance that the resident male would note rapidly any such intrusion. This was, indeed, the case in every test. A second male was also used in testing certain factors having to do with one phase of the study.

This particular male was located on the far side of the Subject Rock and it defended an area similar in size to that of the primary male.

Members of 12 species of common reef fishes were originally considered to act as territorial intruders in our tests. Unfortunately, the vicissitudes of diving and collecting resulted in only nine species being tested in most series. Results cover only these latter species. Selection was based on close taxonomic relationships (adult males of *E. planifrons*, *E. fuscus*, *E. variabilis*, and *E. partitus*), as well as food habits (see Randall, 1967; Emery, 1968). *Eupomacentrus planifrons*, *E. fuscus* and *E. variabilis* feed primarily on benthic algae; *E. partitus* and *Chromis cyanea* (a pelagic damsel) feed primarily on plankton; *Halichoeres garnoti* (a wrasse) is an adventitious feeder; *Hypoplectrus gemma* and *Serranus tigrinus* (both small basses) feed primarily on small invertebrates and occasionally on fishes; and finally, *Holacanthus tricolor*, the rock beauty, feeds primarily on sponges. Since only one of the above species was clearly sexually dimorphic, i.e., the wrasse, both sexes were intentionally tested only in this case.

Prior to a given test series, one (for the wrasse, two) individual of each of the above mentioned species was captured by net elsewhere on the reef complex. Then, each fish was placed into a separate glass jar (4-liter volume). These so-called "model-bottles" were then set aside for about 1/2 hr to allow the fishes time to overcome the effects of capture. All individuals were of a size that provided ease in movement within the bottle. While there was some variation due to characteristic sizes of the different species, most animals tended to be comparable in size—in part by design. In contrast, their body shapes and colors varied considerably (Fig. 2).

After the appropriate waiting period, the model-bottle, holding the first fish to be presented, was placed at least 4 m from the residence of the primary male. The latter usually moved in the direction of the intruder, but stopped before reaching it, and then resumed other activities. A wait-

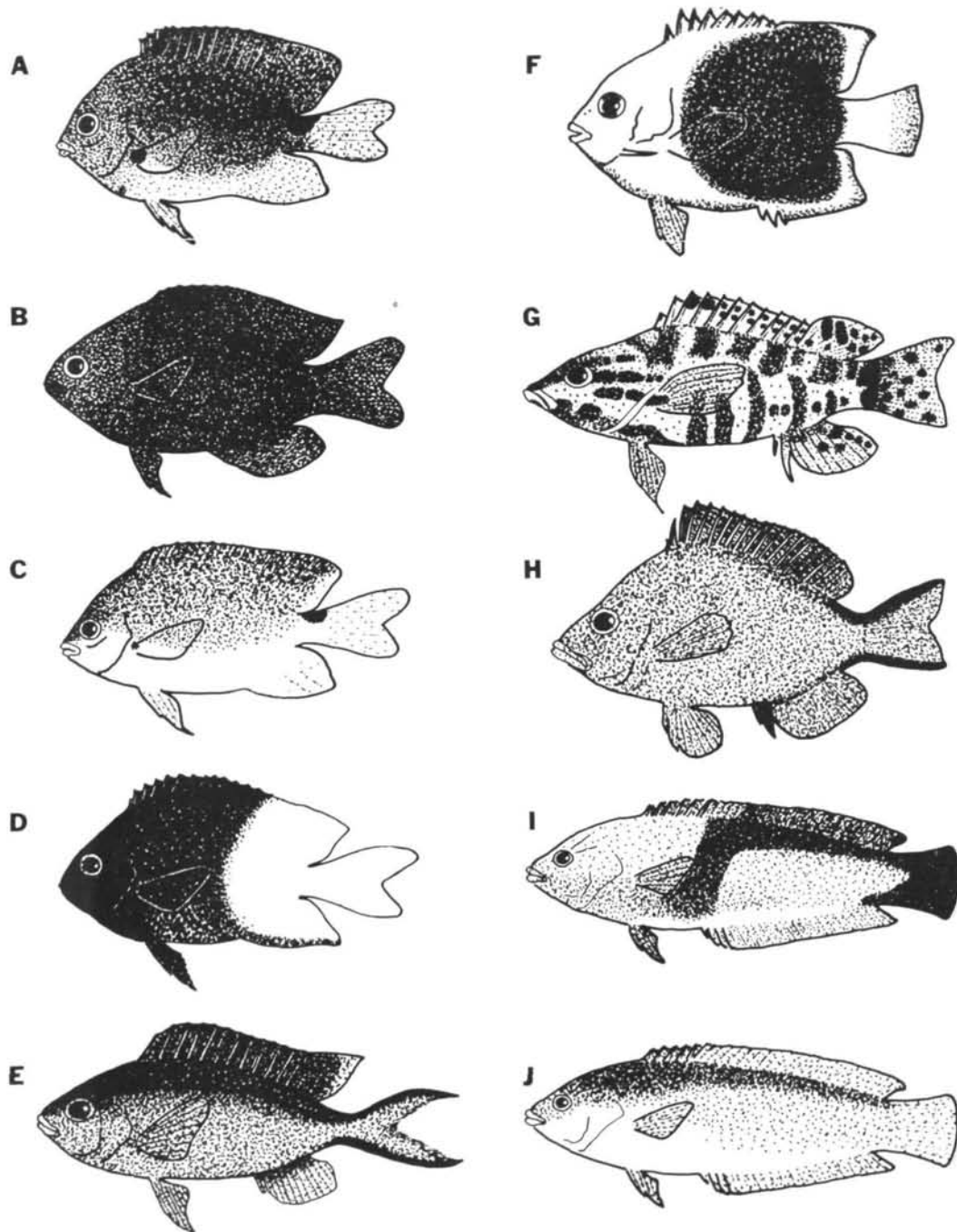


FIG. 2. Diagrams of those species of intruders used in the study. *A*, *Eupomacentrus planifrons* (brown and tan); *B*, *E. fuscus* (dark brown to almost black); *C*, *E. variabilis* (drab, bluish-yellow); *D*, *E. partitus* (black, anteriorly; white posteriorly); *E*, *Chromis cyanea* (bright blue with black edges of caudal fin); *F*, *Holacanthus tricolor* (orange with black spot);

G, *Serranus tigrinus* (white with black markings); *H*, *Hypoplectrus gemma* (blue with black edges of caudal fin); *I*, male *Halichoeres garnoti* (yellowish-green with black vertical and horizontal band on body and black caudal fin); *J*, female *Halichoeres garnoti* (varying shades of brown). (Drawn from Böhlke and Chaplin, 1968.)

ing period of approximately 30 sec then followed. After this short period, the model-bottle was moved by hand, a short distance toward the residence. This distance was dictated largely by the prior actions of the resident male. If, during the initial presentation, the resident stopped its forward movement reasonably far from the model-bottle, the latter was moved as much as 50 cm toward the residence. On the other hand, if the resident closely approached the bottle, but did not quite reach it, the increment of movement toward the resident was only about 10 cm; again a 30 sec wait, and so on. By this means we were able to determine the farthest distance from the residence that the male would attack the intruder (attack being defined as butting or nipping that part of the bottle closest to the captive fish). This point was verified immediately thereafter by returning the bottle to a slightly more distant point and then advancing it once again toward the resident. After this was done three or four times and the point remained consistent, within a few cm, this was considered the "maximum distance of attack" by the resident onto the individual tested in the bottle.

Subsequent to determining that point, we carefully moved the intruder to the residence. Upon reaching that point, the model-bottle was rapidly placed down, the diver retreated some meters away and for the next 3 min, he counted the number of nips (= butting) that the resident male now directed at the intruder. After this was completed, the captive fish was released elsewhere on the reef complex and the resident male was not disturbed by us for a few minutes. Then testing resumed. Although this break was admittedly brief, from the standpoint of possible habituation effects upon later testing, no evidence was obtained that a longer break, e.g., 10 to 15 min, would have appreciably changed the data. Also, we had to take into account that other fishes in the immediate vicinity could not be restricted without seriously jeopardizing the natural situation, and thus, these fishes continually entered and

were chased from the resident's territory.

The second test involved one of the nine remaining intruders in its respective model-bottle. The same procedure for presentation was followed; this continued until all 10 intruders had been tested on the resident male. This constituted one series.

The order of testing was largely random during any given series, except that congenics tended to be tested early, though not in all cases. These fishes were often difficult to capture and so initial collecting was directed at them. Although few series constituted this preliminary study, no order effects were apparent. This has, since, been substantiated by a further study to be reported elsewhere (RET).

Additional tests were also carried out to determine whether the maximum distance of attack was affected by size-differences among intruders of the same species. These tests were carried out over three days during a brief period when no other testing was being conducted at the Subject Rock. Six different-sized individuals of *H. tricolor* and five of *E. variabilis* were collected and these presented, on separate days, 17 to 21 times apiece to the resident following the procedures outlined above. Maximum distances of attack were subsequently determined for each of these fishes onto the two resident threespot damselfishes, mentioned above. Time between tests was 5 min in each particular series, with tests alternating between the two resident males for about 2.5 hr/day (not including time for breaks in diving).

To determine possible changes in the parameters chosen for study, a single series of experiments was attempted during each of 8 months during 1971. Each series was run about the same time each month. Unfortunately, a complete, or near complete, series was obtained during only five of these eight series, i.e., January, March, April, May, September. Only these five series are referred to in the text.

General observations on populations of *E. planifrons* and other damselfishes were carried out by SCUBA and the use of underwater television.

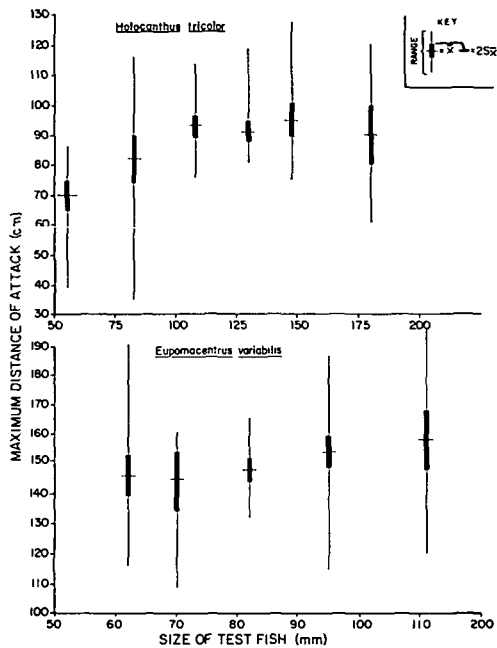


FIG. 3. Graphical analyses (Hubbs and Hubbs, 1953) of the effect of size of two intruding species upon the maximum distance of attack by two *E. planifrons* at the Subject Rock. For further information see text.

RESULTS

Effects of size of intruder upon the responses of a territory-holder

Within the range for the species tested, size largely did not affect the maximum distance of attack (Fig. 3). Graphical analysis, based upon the overlap of two standard errors on either side of the mean (see Hubbs and Hubbs, 1953), showed a lack of significance ($P > 0.05$) across the five different sizes of *E. variabilis*, tested ($n = 99$). With one exception, this was also true for the second species, *H. tricolor* ($n = 109$). The exception, the smallest individual tested, was allowed to approach the residence significantly closer ($P < 0.05$) than the remaining size groups.

No measures were made of the possible effects of size on the number of nips per 3-min test period at the residence.

Maximum distance of attack

The levels of this response clearly varied, in most cases, depending upon the species of intruder presented to the territory-holder. To provide ease in comparison, these response differentials are depicted in Figure 4 (*E. planifrons* and congeners) and Figure 5 (remaining species). It was clearly apparent that the maximum distance of attack, when compared within and among series, provided a quite characteristic rank for a given species, relative to all others.

As a group, members of the genus, *Eupomacentrus*, were not allowed to approach the residence of the territory-holder as closely as the remaining species tested. Conspecifics were always attacked farthest from, and *E. partitus* closest to, the residence. Systematic affinity, *per se*, did not appear to be the only reason, however, for exclusion reasonably far from the residence since *E. partitus* was allowed to approach the residence even closer than several non-congeners. Among this latter group, the maximum distance of attack was always greatest for *H. tricolor* and least for *S. tigrinus*. In three of the four series in which it was tested, *H. gemma* ranked next to *S. tigrinus*. The remaining species varied over a mid range. It is noteworthy here that the male and female of *H. garnoti* were treated similarly, even though they

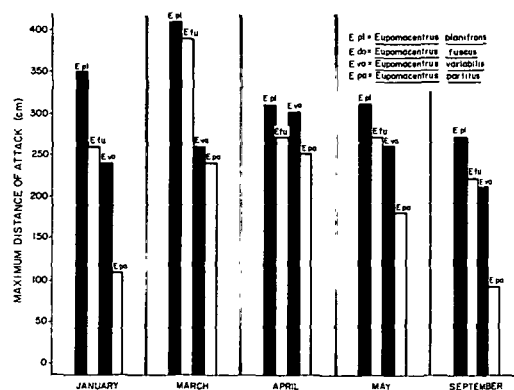


FIG. 4. Summary of data on the maximum distances of attack by the territorial *E. planifrons* against intruding male conspecifics and males of congeners during five test series. Distance of attack measured from anterior face of residence.

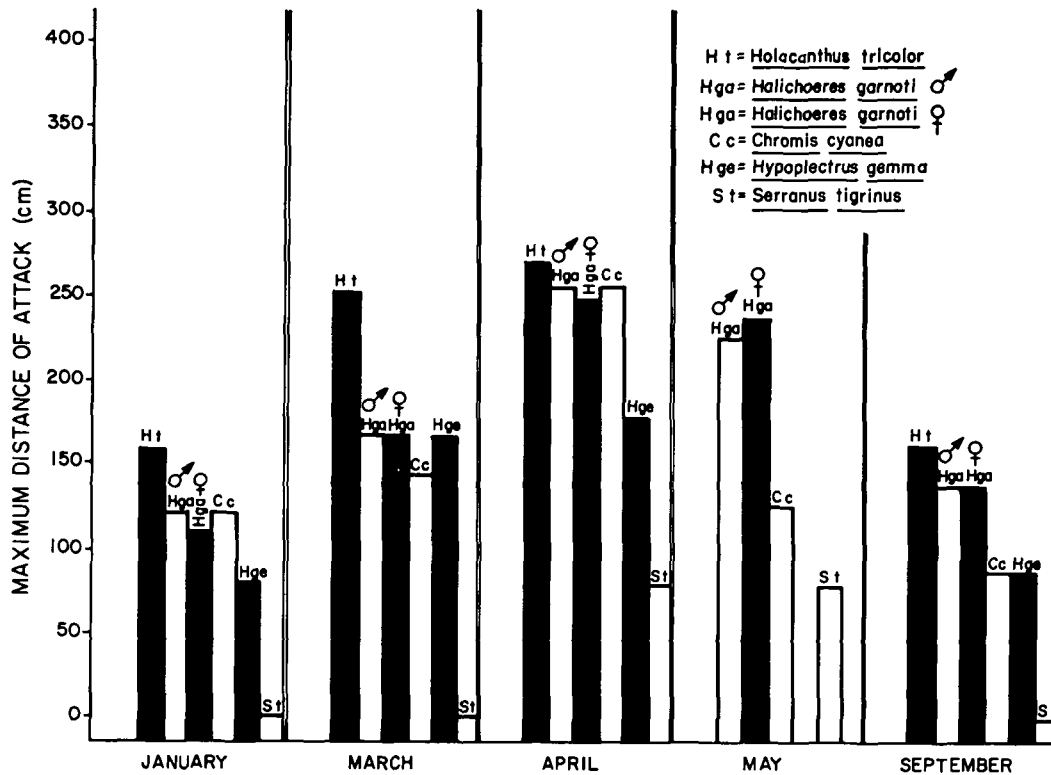


FIG. 5. Summary of data on the maximum distances of attack by the territorial *E. planifrons* against several species of intruding non-congeners during

five test series. Distances of attack measured from anterior face of residence.

are consistently somewhat different in size and greatly different in color pattern.

To determine whether actual values correlated with our apparent ranking, we applied a Spearman Rank Test (Wyatt and Bridges, 1966) to the data (Table 1). Unfortunately, only four series were included since we lacked data on two species in May.

Actual rank for each series was determined by the cline that existed among the actual distances measured for each species, while apparent rank was based on the cline that existed among the mean maximum distances of attack for all species over the four series. The high coefficients ($r_s = 0.91$; $P < 0.01$) reflected the consistency of the spe-

TABLE 1. Summary of data on maximum distance of attack by territorial male *E. planifrons* onto different species of intruders during four test series (for further information see text) (distance in meters).

Variable	Apparent rank										Rank correlation	
	E pl	E fu	E va	H t	E pa	H ga ♂	H ga ♀	C c	H ge	S t	r_s	P
1. January	3.5	2.6	2.4	1.6	1.1	1.1	1.1	1.1	0.8	0.0	0.90	<0.01
2. March	4.1	3.9	2.6	2.5	2.4	1.7	1.7	1.4	1.7	0.0	0.96	<0.01
3. April	3.1	2.7	3.0	2.7	2.5	2.6	2.5	2.6	1.8	0.8	0.85	<0.01
4. September	2.7	2.2	2.1	1.7	0.9	1.4	1.4	0.9	0.9	0.0	0.92	<0.01
\bar{x}	3.3	2.8	2.5	2.2	1.7	1.7	1.6	1.5	1.3	0.2		

E pl = *Eupomacentrus planifrons*; E fu = *E. fuscus*; E va = *E. variabilis*; H t = *Holacanthus tricolor*; E pa = *E. partitus*; H ga ♂ = male *Halichoeres garnoti*; H ga ♀ = female *Halichoeres garnoti*; C c = *Chromis cyanea*; H ge = *Hypoplectrus gemma*; S t = *Serranus tigrinus*.

cies relationships to the responses of the resident, *E. planifrons*. These same data were also subjected to an analysis of variance (Wyatt and Bridges, 1966). This was done not only to analyze once again for species differences, but also to determine possible seasonal influences upon response differentials. In both, differences were significant at greater than 0.01 level (i.e., species— $F_{9, 27} = 19.51$, and seasonal— $F_{3, 27} = 15.58$).

Thus, beyond corroborating the distinctiveness of the resident's responses to the various species of intruders, these results also signified a seasonal pattern within the data (see Figs. 4, 5). With the exception of conspecifics and *E. fuscus*, these figures reveal that the maximum distance of attack rose from a low value in January to a peak in April, followed by a decrease in September. A comparison of the January and April data (Fig. 6) shows an increase in the maximum distance of attack for eight of the nine species tested, while all species show a clear reversal of this pattern in the April and September data (Fig. 7). Figure 8, providing a direct comparison of these two patterns, demonstrates that the response directed to a given species by the territory-holder remained quite constant relative to the responses directed to the other species (note the reasonably parallel

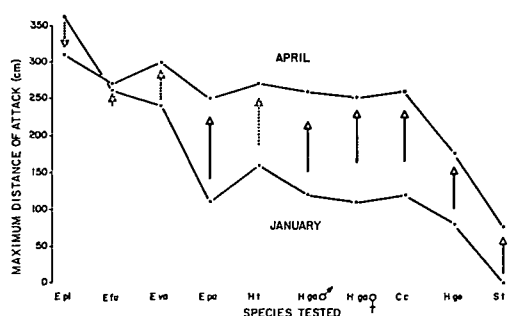


FIG. 6. Comparison of the maximum distances of attack that the territorial *E. planifrons* directed at the various species of intruders during the January and April series. Greater distance of attack implies expansion of area of defense. Arrows with solid shafts indicate significance levels of 0.05, or greater; arrows with dotted shafts indicate no significance; arrow with thin shaft indicates insufficient data for analysis. See Figures 4 and 5 for species designations.

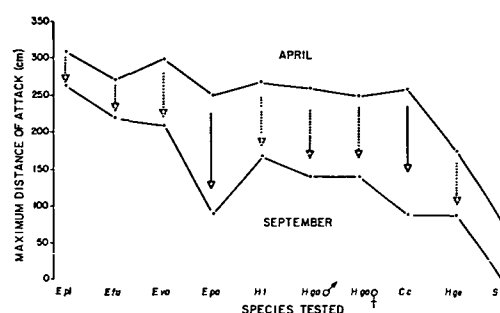


FIG. 7. Comparison of the maximum distances of attack that the territorial *E. planifrons* directed at the various species of intruders during the April and September series. Reduced distance of attack implies compression of area of defense. Arrows with solid shafts indicate significance levels of 0.05, or greater; arrows with dotted shafts indicate no significance; arrow with thin shaft indicates insufficient data for analysis. See Figures 4 and 5 for species designations.

lines).

The above analyses suggest the presence of a stable, year-round pattern of response by the territory-holder which agreed closely with the seasonal cycle of reproduction (i.e., courtship and spawning) for its species (Myrberg and Thresher, unpublished). Reproduction is certainly peaking in April, while it is at its lowest ebb in January. Some courtship (no eggs) is, however, still seen in September, thus explaining perhaps the slight dissimilarity in the January and September patterns. This apparent correlation of the onset, peak and end of the reproductive period with the expansion and compression of territories suggests a link, either direct or indirect, between the two (see Discussion).

The similarity of these patterns also verified the validity of the experimental technique, in face of the different individuals representing a given species during the various series, the manner of their presentation, and finally, differences in the specific environmental conditions present at the time of testing (e.g., surge action, water clarity, and temperature).

As noted earlier, conspecifics and *E. fuscus* varied from the seasonal pattern discussed above. Both peaked earlier than the other species, in March rather than in April. This result was predictable. If the

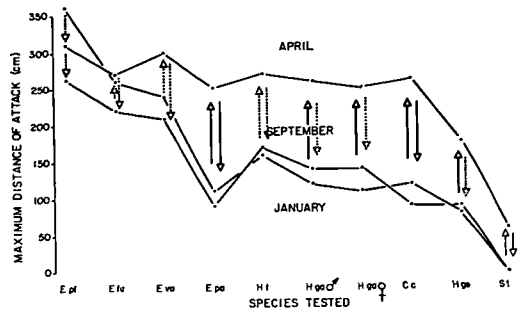


FIG. 8. Direct comparison of January-April and April-September data on maximum distances of attack by the territorial *E. planifrons*. The figure, superimposing Figure 6 upon Figure 7, shows the similarity of distances involved in the expansion and compression of the areas of defense directed against the respective intruders. See Figures 4 and 5 for species designations.

territorial increases were related to the reproductive period, it follows that early in the season dominance hierarchies and territories would need to be reaffirmed. Such might well be directed primarily against conspecifics and closely related *E. fuscus*, both of which were abundant on the Subject Rock and which held contiguous territories. The remaining congeners were either less similar in appearance to the resident or did not hold contiguous territories with it. Following this "socially turbulent" period, these relationships would stabilize and increased energy could be used to defend an area

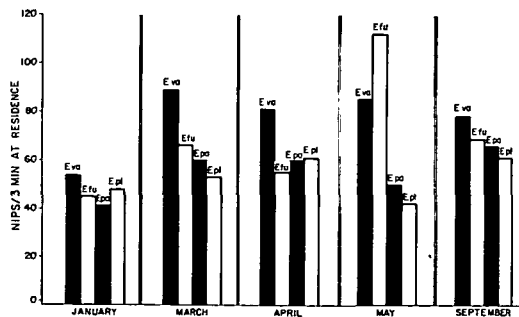


FIG. 9. Summary of data on the number of nips/3 min that the territorial *E. planifrons* directed at male conspecifics and males of several congeners, after they had been placed, individually, directly in front of its residence. Results from five series are shown. See Figure 4 for species designations.

against other intruders. This pattern is clearly realized in the above data.

Number of nips per 3-min period at the residence

Analysis of the nip data paralleled that carried out for the maximum distance of attack. Species differences in the responses of the resident were, however, less clear for these data (Figs. 9, 10), but a pattern nevertheless was apparent. In contrast to the results of the preceding section, congeners, as a group, were attacked about the same levels as the other species; conspecifics ranked seventh of the ten individuals tested and they were generally attacked

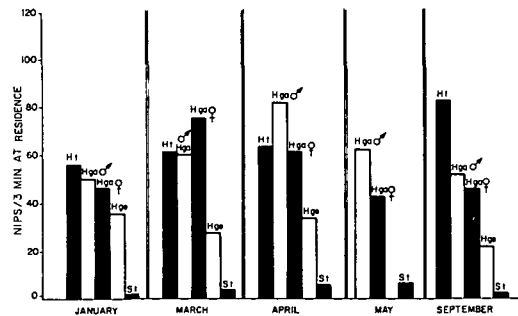


FIG. 10. Summary of data on the number of nips/3 min that the territorial *E. planifrons* directed at the several species of non-congeners, after they had been placed, individually, directly in front of its residence. Results from five series are shown. See Figure 5 for species designations.

less than any other congeneric. For four of the five series, *E. variabilis* generated the greatest number of nips during test periods, and for all series, *S. tigrinus* and *H. gemma* generated, respectively, the lowest and next lowest number. Among other non-congeners, *H. tricolor* consistently provoked a relatively large number of nips.

Reflecting the above, Spearman Rank Coefficients for these data (Table 2) were generally lower than those reported for the maximum distance of attack ($r_s = 0.81$). However, the correlations were all significant at the 0.05 level, and four of the five at the 0.01 level. The results of the analysis of variance among species were also signifi-

TABLE 2. Summary of data on number of nips/3-min period directed by territorial male of *E. planifrons* at various species of intruders during four test series (for further information see text).

Variable	Apparent rank										Rank correlation	
	E va	C c	H t	H ga ♂	E fu	H ga ♀	E pa	E pl	H ge	S t	r_s	P
1. January	54	51	56	50	45	46	41	48	35	0	0.88	<0.01
2. March	89	53	61	60	66	75	60	53	27	1	0.66	<0.05
3. April	81	66	63	81	55	61	60	61	33	3	0.86	<0.01
4. September	78	120	91	51	69	45	66	61	21	0	0.83	<0.01
\bar{x}	76	73	65	60	59	57	57	56	29	1		

E va = *Eupomacentrus variabilis*; C c = *Chromis cyanea*; H t = *Holacanthus tricolor*; H ga ♂ = male *Halichoeres garnoti*; E fu = *E. fuscus*; H ga ♀ = female *Halichoeres garnoti*; E pa = *E. partitus*; E pl = *E. planifrons*; H ge = *Hypoplectrus gemma*; S t = *Serranus tigrinus*.

cant at the 0.01 level ($F_{9, 27} = 11.18$), while among series (i.e., seasonal differences), the level reached 0.05 ($F_{3, 27} = 3.02$).

From the data illustrated in Figures 9 and 10, it is apparent that a seasonal pattern is present though it is weaker than that shown by the previous measure of response. Although our comparison of the January and April data for all species (Fig. 11) shows a general increase in the number of nips per test period between the two series, no general reversal occurred in the comparison of the April and September data (Fig. 12). Thus, though not as clear as the previous parameter, patterning was again shown across species and also across series.

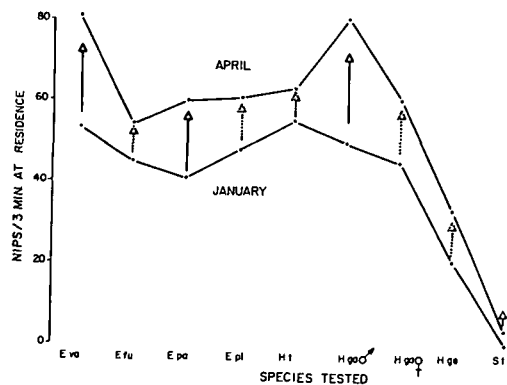


FIG. 11. Comparison of the number of nips/3 min that the territorial *E. planifrons* directed at the various species tested in front of its residence during the January and April series. Greater number of nips implies more intense defense. Arrows with solid shafts indicate significance levels of 0.05, or greater; arrows with dotted shafts indicate no significance; arrow with thin shaft indicates insufficient data for analysis. See Figures 4 and 5 for species designations.

Summary of results

Though both responses of the territory-holder—maximum distance of attack and number of nips per 3-min period at the residence—varied significantly with the species tested, the greatest and most stable differences occurred in the former parameter. Conspecifics were always attacked farther from the residence than any other species tested. Further, the territory-holder, in general, did not allow congenetics to approach the residence as closely as non-congenetics. This was not the case, however, for the nip data, as both were attacked at approximately the same levels. Rank analysis and analysis of variance indicated significant patterning of both responses of the territory-holder to the various species. Thus, it appeared as if this resident possessed a territory, the size of which was dependent upon the particular species of intruder.

Controls showed that within the range tested, size of intruder largely did not affect the maximum distance of attack. Only the smallest individual of one species generated a significantly lower result.

There were seasonal variations in the levels of both parameters. For conspecifics and *E. fuscus*, the maximum distance of attack increased from a low January level to a peak in March and subsequently a decrease in September. The remaining species showed a similar pattern, except that the peak occurred later—in the April series. The number of nips per 3-min test period at the residence also showed a significant seasonal pattern, but it was cer-

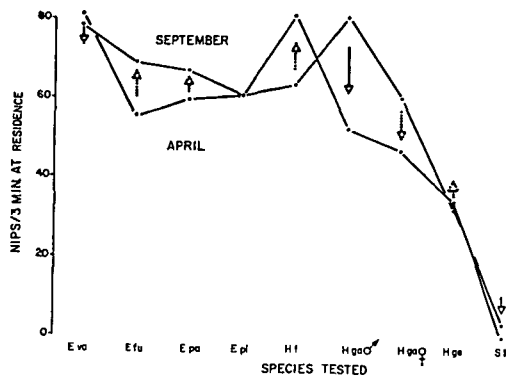


FIG. 12. Comparison of the number of nips/3 min that the territorial *E. planifrons* directed at the various species tested in front of its residence during the April and September series. Fewer number of nips implies less intense defense. Arrow with solid shaft indicates significance level of 0.05, or greater; arrows with dotted shafts indicate no significance; arrow with thin shaft indicates insufficient data for analysis. See Figures 4 and 5 for species designations.

tainly less clear than the former parameter. This seasonality appeared related, either directly or indirectly, to the annual reproductive cycle of *E. planifrons*.

DISCUSSION

Although the data from this preliminary study are limited, rather clear patterns have emerged. These, in turn, have allowed us to gain an ever-increasing appreciation of the intricacy of interaction that exists among the many species of fishes making up the coral reef community.

There can be little doubt that territorial, threespot damselfish defend their areas against intruders throughout the year. This is based, not only on the results of this study, but also on approximately 150 man-hr of additional field observations. The time and energy that is devoted to interspecific territoriality by this damselfish (and other damselfish—see Cummings, 1968; Clarke, 1970; Low, 1971; Myrberg, 1972a) points to a strong selective advantage(s) for such behavior. Before discussing this particular point, however, a few other points should be brought forth.

Throughout all series, the selected measures provided such consistent patterns of

territorial aggression that certain conclusions were, at once, apparent. Firstly, although different members of a given species were used for each series, the position of a given species, relative to all others, varied little or not at all throughout testing (at least, when maximum distances of attack were compared). Thus, during all series, our resident apparently perceived members of a given species as relative equals, but species, themselves, as being clearly (and consistently) different entities. Secondly, although the maximum distances of attack from the residence remained consistent for a given species during a given series of tests, each of these distances varied seasonally in a manner closely paralleling the reproductive season of the threespot damselfish in our area. Thus, the area of defense did not appear as a single bounded territory, expanding and contracting throughout the year, but rather as a serial territory—in the sense that at a given time, the size of the territory was dependent not only upon the season, but also upon the species of intruder, as well. A territorial damselfish, defending an area in March, for example, excludes a male conspecific 4 m from its residence, a male bicolor damselfish, *E. partitus*, or a rock beauty, *H. tricolor*, 2.5 m from its residence, a blue hamlet, *H. gemma*, 1.6 m from its residence, and so on. Accordingly, the territory appeared as a series of areas surrounding the residence, each area apparently reflecting the amount of space that secures a limited resource(s) from members of a particular species.

If this model is, indeed, correct, then certain predictions are in order. For example, if the entire area of defense is based upon a single limiting resource (e.g., a specific type of food, such as benthic algae), the important variable across species lines should, in most cases, be the amount each threatens that resource. If, in contrast, the different sized territories reflect the fact that various resources are being secured by the resident, then certain boundaries secure specific levels of one resource, while other boundaries secure specific levels of others. This is perhaps the more likely possibility. In any case, with periodic ex-

pansion and compression of territories, all boundaries within a serial territory need not expand nor compress to the same degree. For example, in the case of compression, those boundaries farthest out may slowly encroach upon those nearest the residence and as this continues, the outer rings join those located more centrally until either the compression ceases due to increased aggression by the territory-holder or the latter is driven away.

The above results show that our resident maintained various boundaries, differentiating among the various species tested. Yet, the number of such boundaries may actually be vast, considering the community represented and the ability of an individual to use its sensory modalities. The problems associated with such a proposal may not be as great as one might think, based upon the fine discriminatory abilities that various species of fishes have shown when confronted with tasks which bespeak the problem of species recognition (Göz, 1941; Teichmann, 1959; Kühme, 1963; Kuenzer, 1966; Myrberg, 1966, 1972b, 1973; Winn, 1967, 1972; Sutherland, 1968; Trevarthen, 1968; Yager, 1968; Kleerekoper, 1969; Brockmann, 1971; and Myrberg and Spires, 1973). Despite this, it is noteworthy that our resident male, with few exceptions, treated the males and females of *H. garnoti* in a most similar manner even though their color patterns are highly divergent (males are also slightly larger than females). This suggests that if vision is, indeed, playing a role here, and there is every reason to believe that it is, form rather than color pattern may be a major determinant in interspecies recognition. Additional evidence in favor of this suggestion will be reported elsewhere.

Although our work does not bear directly upon the problem, it does shed, perhaps, some light on the ideas and previous work associated with the concept of poster-coloration (Lorenz, 1962, 1966; Zumpe, 1965; Fricke, 1966). The threespot damsel could hardly be described as a poster-colored fish; rather, any description of it should appropriately include the term, drab. According to the concept of poster-

coloration, such bright colored fishes are invariably aggressive, if not exclusively then primarily, towards conspecifics and a few other species which have similar markings (i.e., possessing similar releasers). It also maintains that, in contrast, drab fishes of the same habitat are intraspecifically, largely non-aggressive (Lorenz, 1962). Yet, territory-holders of our drab species attacked not only conspecifics far from their residences (up to more than 4 m), but also members of several other species. Thus, the generalization that drab fishes are "peaceful" toward conspecifics simply does not hold for the threespot damselfish. In fact, the generalization does not appear true for many territorial fishes of our area, based on general field observations.

Another point, brought out by our findings and already alluded to by others (e.g., Orians and Willson, 1964), is that stable systems of sustained aggression over long periods of time do not support the idea that interspecific battles are based on mistaken identity or a surplus of drive which has reduced powers of discrimination. Such ideas actually ignore a more probable alternative, that ecologically similar species may have a variety of signals available to them which distinguish "friend from foe." Upon closer reading of studies carried out by proponents of poster-coloration (Zumpe, 1965, Fricke, 1966), one finds certain results unexplained. Perhaps such findings will become more canonical if interspecific aggression is no longer relegated to a mistake, but rather a means for allowing two or more species of similar ecologies to live in the same habitat and yet compete for and/or maintain sufficient amounts of one or more limited resources for purposes of survival and reproduction (see Cody, 1969).

This should not be construed, however, as an attempt to reduce the importance of intraspecific aggression on the reef, or anywhere else. This importance, itself, was clearly noted in our subjects who invariably defended their largest areas against conspecifics. It is noteworthy, however, that a number of other species brought forth greater attack at the residence than male conspecifics. These other species must

have been considered as greater threats at the residence, while just the opposite was apparent for the areas surrounding the residence. This indicates that there is a difference in functional significance of these two features.

The functional significance of intraspecific territoriality has been the subject of numerous reviews (Lack, 1934; Noble, 1939; Tinbergen, 1939, 1953, 1957; Collias, 1944; Bourlière, 1952; Carpenter, 1958; van den Assem, 1967), and from these, it is obvious that the major advantages of any such system rests with reproductive function and access to food resources.

When attempts have been made to assess the functional significance of interspecific territoriality, interest has centered largely on the latter function, i.e., assurance of an adequate food supply (e.g., Orians and Willson, 1964; Low, 1971). Although there can be little doubt that maintenance of a food supply has clear selective advantage for any species, the clear relationship that existed between the level of interspecific territoriality (based on distance of attack) and the level of reproductive activity (low in January and September, moderate in March and May, and high in April) in our subject species forces one not to dismiss reproductive functions so rapidly. It's possible that this relationship is tied also to food supply, based on increasing and decreasing energy requirements associated with reproduction. Other advantages of such territoriality, having to do with reproduction include, however, maintenance of a nest site and defense of eggs (Albrecht, 1969; Clarke, 1970; Fishelson, 1970). Several species tested by us could well use such a nest-site themselves or feed, instead, on the eggs. Defense of nest-site, even considered by Howard (1920) as one of the major causes for interspecific territoriality in birds, is clearly associated with such behavior in our subject species, based on the common observance that intensity of interspecific territoriality increases tremendously in damselfishes which are guarding eggs.

Yet, one cannot deny that species having food requirements similar to the threespot

damsel were clearly excluded from its territory. The trouble is that species having far different requirements were also consistently excluded, though from a smaller area.

These findings can only support the multi-functional concept of interspecific territoriality. That is, it must function not only to reserve a food supply, but also to protect spawn and/or to maintain an area around the residence for a purpose(s) other than that of a food resource. Such a purpose may well be to partition living space (see Smith and Tyler, 1972). Perhaps members of various species cannot even maintain residences or rest-sites without defending areas around them (Hobson, 1972). In any case, future studies will, no doubt, yield important information on this particular problem, as well as on other fascinating aspects of interspecific territoriality and community interaction.

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