FIELD ANALYSIS OF THE DOMINANCE HIERARCHY OF THE BICOLOR DAMSELFISH <u>STEGASTES</u> <u>PARTITUS</u> (POEY) (PISCES: POMACENTRIDAE)

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ABSTRACT

The dominance relations of the damselfish *Stegastes partitus* were examined in the field. The dominance hierarchy, based on aggressive interactions, was linear and size-dependent, with most aggression between individuals most similar in size and least between those most dissimilar in size. These results show both similarities to and differences from results obtained in a very similar earlier study on the same species but conducted entirely in the laboratory. The importance of field studies in assessing the degree of reliability of results obtained under artificial conditions is emphasized.

INTRODUCTION

Many species of animals display a dominance hierarchy among members of social units. A group of animals may be said to have a dominance hierarchy if the interactions between individuals allow some to have priority over others under certain circumstances. The most simple hierarchy is defined as follows: individual A dominates all members of a group; another animal B dominates all members except A, and so on to the last member, omega, which dominates no other individuals. If this relationship holds, then the hierarchy is said to be linear (Chase, 1974).

Considerable research has examined the dominance relations of a wide variety of animal species. However, the majority of studies have been conducted in the laboratory or under other artificial conditions. In studies carried out both in the field and in the laboratory on the same species, there often have been discrepancies in the conclusions. Thompson (1960) found that laboratory populations of house finches had a hierarchy dominated by females, but that field populations did not show this pattern. In some primates, a different form of social structure was evident between captive animals and the same species in the field (Rowell, 1967; Hinde, 1974). In the baboon, *Papio anubis*, interactions were about four times as frequent among captive animals as among individuals observed in the field (Rowell, 1967). Among the fishes, Myrberg (1972*a*) conducted a field and laboratory study of territoriality and social hierarchy in the bicolor damselfish (Pomacentridae), *Stegastes* (= *Eupomacentrus*)

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partitus. However, limitations of resolution in the underwater camera used for field observations precluded analyses as detailed as those obtained during the laboratory section of the work. Therefore, the two parts of the study were not strictly comparable.

Many damselfish are territorial, and the bicolor, like several other closely related species, defends a territory which it infrequently leaves. In the field, several or many such territories may be found in close proximity, forming colonies on suitable substrate. Reproduction usually occurs within colonies, which consist of both males and females. Colony members frequently interact with each other close to territory borders. In small colonies, all colony members may interact with one another, whereas in very large colonies many individuals rarely come into contact. Small colonies are, therefore, particularly useful for studies on intracolony social relationships.

The aims of the present study were: (a) to examine in detail the aggressive social interactions of small colonies of the bicolor damselfish in the field and (b) to compare the dominance system of these colonies with hierarchies found in the laboratory (Myrberg, 1972*a*).

METHODS

The study was conducted from October 9-16, 1980, from the NOAA underwater facility, HYDROLAB, situated in 50 feet of water off the north coast of St. Croix in the U.S. Virgin Islands.

Seven small damselfish colonies, each confined to a patch of coral rubble and separated from each other by clear areas of sand, were selected. The colonies were small enough to permit interactions between all colony members. Aggressive social interactions ("chases") were recorded between all individuals in each colony, where both the giver and receiver of each "chase" were noted. A chase is defined as a rapid swim towards a fish that is moving away or that starts to move away from the chaser (Myrberg, 1972*b*).

Each colony contained six to eight individuals, most of which were distinguishable on the basis of size. However, very small fish ("tinies") were difficult to identify individually. Consequently, in the colonies containing more than one "tiny," i.e., in colonies larger than six fish, the number of interactions per tiny was determined by dividing the sum of chases given or received by all tinies of a particular colony by the number of tinies in that colony. Therefore, in each colony larger than six individuals, the rank (see below) of six consisted of an average interaction rate per tiny.

Data were taken during both the morning and afternoon over a period of 3-6 days and until at least 65 interactions had been noted for each colony (average observation time per colony = 131 minutes; range = 85-240 minutes). Since colonies were monitored for varying lengths of time, the observations were standardized to give the number of chases per 100 minutes per colony so that the colonies could be compared directly.

Matrices were constructed for the chase data from each colony by assigning dominance ranks to every colony member. For example, rank 1 chased each other colony member more than any member chased it; rank 2 chased each colony member more than any other member chased it, except for rank 1.

For analysis, data on chases were ordered by rank, and all data for each rank were summed across all 7 groups. The data were then divided into three categories: (a) the number of chases received by each rank; (b) the number of chases given by each rank; and (c) the number of chases given by each rank to each other rank. Each of these categories was analyzed using the Kruskal-Wallis one-way ANOVA to determine whether or not there was a significant difference among ranks, i.e., an H-value giving $p < 0.05$. If so, then the data were subjected to a nonparametric version of the Newman-Keuls Multiple Range test (Zar, 1974) to determine how the distribution of chases varied among ranks (significance level, $p < 0.05$).

RESULTS

For each colony, a distinct size-dependent social hierarchy was apparent; it was highly linear with proportionally very few reversals (4.5%). A reversal is a chase directed at an individual higher in the hierarchy than the chaser.

Figure 1 shows the distribution of chases received by each rank (category a). This distribution is not homogeneous (Kruskal-Wallis, $p < 0.001$). The nonparametric Multiple Range test showed that ranks 3 and 4 received the most chases; ranks 2, 5, and 6 received less than 3 and 4 but more than rank 1 ($p < 0.05$ in each case).

Figure 2 shows the distribution of chases given by each rank (category b). This distribution is not homogeneous (Kruskal-Wallis, $p < 0.001$). The nonparametric Multiple Range test showed that ranks 1, 2, and 3 gave the most chases; rank 4 gave fewer chases but more than ranks 5 and 6 ($p < 0.05$ in each case).

Figure 3 shows the distribution of chases from each rank to each rank below it in the hierarchy (category c). The distribution is not homogeneous for ranks 1 to 4 (Kruskal-Wallis, $p < 0.01$). In most cases, each rank directed most chases to its closest ranking subordinate and least to the individual ranked farthest from itself. See figure 3 for the significant differences shown by the nonparametric Multiple Range test ($p < 0.05$ in each case).

CONCLUSIONS

The analyses of the distribution of chases given and received show that there is a distinct pattern to intracolony aggression:

(a) there is a strong size-dependent social hierarchy which is linear with few reversals;

(b) individuals chase those closest to and just below themselves in rank most frequently and those furthest in rank least frequently;

(c) the highest ranking individuals (1, 2, and 3) chase more than other ranks. Lower ranking individuals chase progressively less the lower their rank;

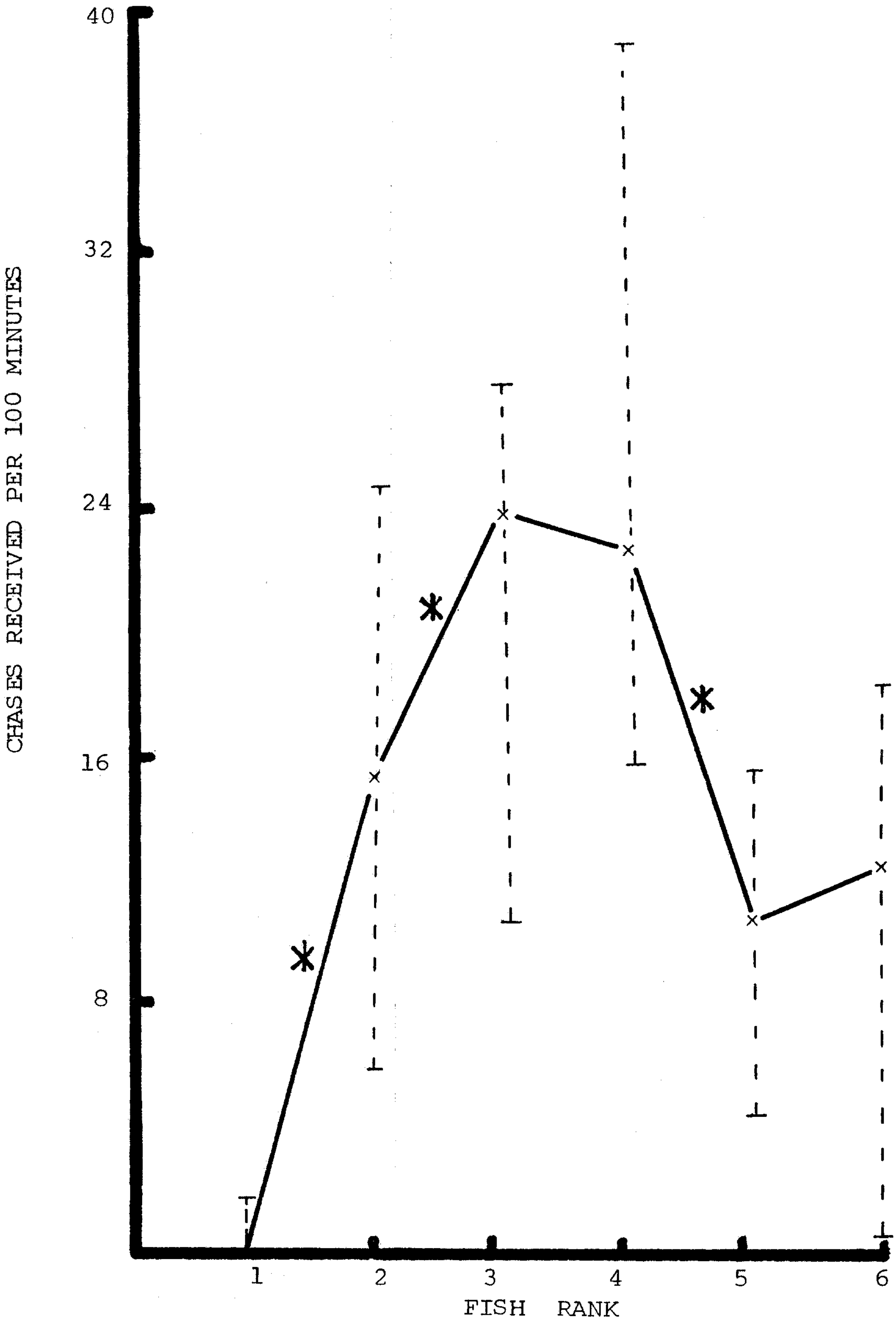

Figure 1.--Chases received by each rank plotted as medians and interquartile ranges. The asterisks denote significant differences between adjacent points ($p < 0.05$); e.g., rank 2 received more chases than rank 1.

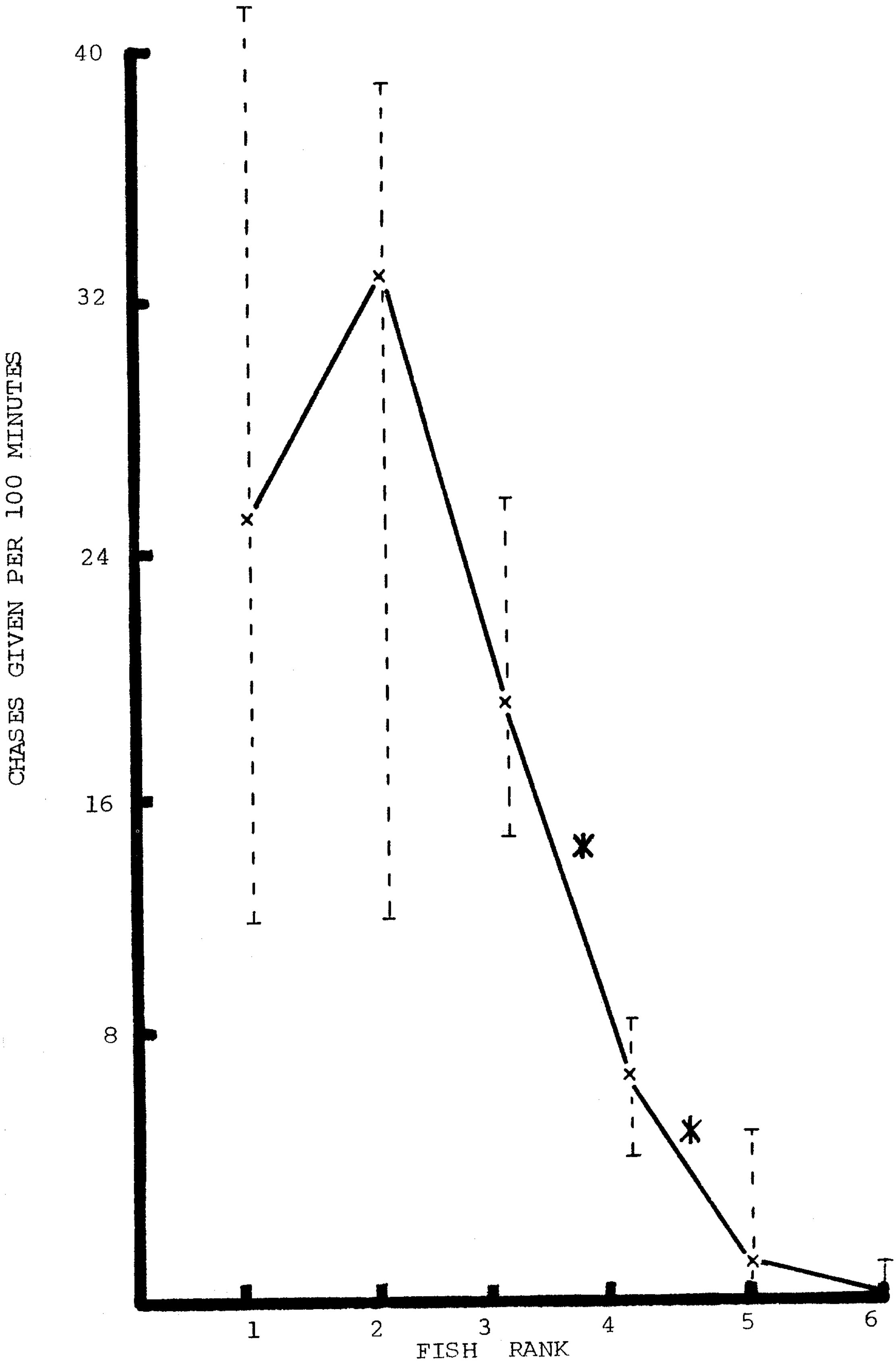

Figure 2.--Chases given by each rank plotted as medians and interquartile ranges. The asterisks denote significant differences between adjacent points ($p < 0.05$); e.g., rank 4 gives fewer chases than rank 3.

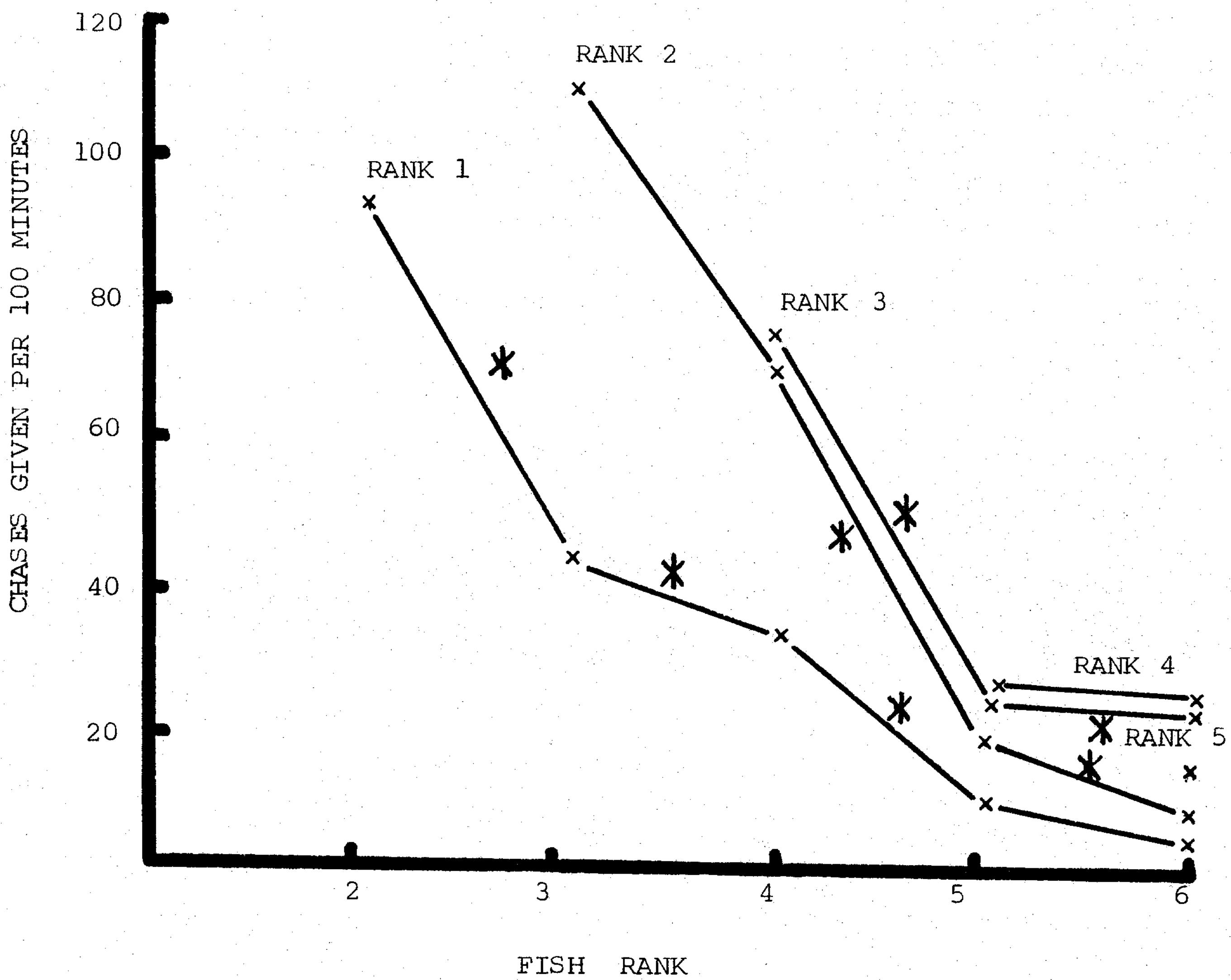

Figure 3.--Chases given by each rank to each rank below it. Data from all seven groups are summed. Each line represents the chases given by a particular rank to all ranks below it; e.g., rank 1 chased rank 2 a total of 96 times. The asterisks denote significant differences ($p < 0.05$) between adjacent points; e.g., rank 1 chased rank 2 significantly more than it did rank 3.

(d) ranks 2, 3, and 4 receive most chases and ranks 1, 5, and 6, the least.

It is clear that in the bicolor damselfish, size plays an important role in intraspecific aggression. As in many other species, dominance relations are strongly correlated with body size (beetles, Beebe, 1947; lobsters, Fielder, 1965; voles and deermice, Grant, 1970). Aggression is most intense between individuals of similar size and least intense between individuals most dissimilar in size (Noble, 1939; Collias, 1944; Miller, 1964; Coates, 1977).

The importance of size in the dominance relations of damselfish may result from size-dependent competition for certain resources. Individuals of different sizes may have different food or shelter requirements (Rasa, 1969; Emery, 1973). Several studies have reported that in pomacentrids, small individuals often share the territory of an adult conspecific (Clarke, 1970; Emery, 1973; Sale, et al., 1980), either because the adult tolerates them or because of "topological deception" (Sale, et al., 1980) whereby they can avoid the adult by using space in which they cannot be pursued. The low number of chases given and received by these small individuals implies that they are not attempting to compete aggressively with the larger fish for the space they share. Large size in male bicolors appears to be one of the factors associated with high reproductive success (Schmale, 1980). In order to establish the significance of size and how it relates to aggression in this species, detailed studies on the feeding, reproduction, and use of space and shelter are necessary. Account should be taken of fish size, stage of maturation (juvenile, adult; reproductive, nonreproductive), and sex.

The present study demonstrates both similarities and differences between field and laboratory results on the dominance relations of the bicolor damselfish. Previous work on this species (Myrberg, 1972a) focused on two distinct time periods: reproductive and nonreproductive. The distribution of aggression between colony members was found to differ markedly between these two periods in the laboratory phase of the study. The field phase of the study covered only the reproductive period and was much less detailed than the laboratory phase because of the inability of the underwater camera to record all aggressive interactions between colony members, especially those involving very small fish. The present study is considered equivalent to the nonreproductive period of the Myrberg study, since little courtship activity and no egg-guarding behavior by males were observed.

The present field analysis and Myrberg's laboratory results for the nonreproductive period show the following similarities: There is a strong size-dependent linear dominance hierarchy with a very low percentage of reversals; the highest ranking individuals did the most chasing and the lowest ranks the least; the middle ranks received the most chases and rank 1 and the lowest ranks the least.

However, there were two differences between the two studies. First, the rate of interactions was markedly higher in the laboratory study, in which a rate of 10 chases per individual per hour was recorded as opposed to the 1.5 chases per individual per hour in the present study. This is a common difference between field and laboratory studies and may be due to: (a) the inability of small individuals to escape those chasing them in an aquarium, (b) the lack of interspecific interactions in the laboratory, and/or (c) the lack of space available per individual in an aquarium, although both the present study and Myrberg's laboratory study had similar fish densities of 0.2 m^2 (Myrberg) and 0.1-0.2 m^2 (this study).

Second, the relative distribution of chases given by each rank to each other rank below it in the hierarchy differs between the two studies. In the laboratory (Myrberg, 1972a), the distribution of chases among individuals showed no clear pattern, except for one fish, YB, which directed successively fewer chases at individuals ranked progressively further away from itself. This 'YB' pattern of chasing was seen very clearly and consistently in all colony members of the present study.

It is of considerable interest that during the reproductive period of Myrberg's study, the pattern of intracolony aggression in the laboratory and possibly in the field differed from that recorded during the nonreproductive period, with more aggression being directed towards the lowest ranking individuals than towards those closest in rank. Field work similar to that of the present study needs to be conducted during the reproductive period to establish if this difference is significant and related to the phase of the reproductive cycle.

In conclusion, the dominance relations in the bicolor damselfish during the nonreproductive period show both similarities and differences when laboratory and field studies on colonies of similar size are compared. The nature of these differences implies that the laboratory may be used for detailed work impossible to carry out in the field, but that laboratory results must be interpreted with caution and should not be used as the sole source of information on the ecological significance of dominance relations. The importance of parallel field and laboratory studies is emphasized, since it is evident that many factors may influence intracolony aggression.

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