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Author(s): Robert R. Warner and Eric T. Schultz

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SEXUAL SELECTION AND MALE CHARACTERISTICS IN THE BLUEHEAD WRASSE, *THALASSOMA BIFASCIATUM*: MATING SITE ACQUISITION, MATING SITE DEFENSE, AND FEMALE CHOICE

ROBERT R. WARNER AND ERIC T. SCHULTZ¹

Department of Biological Sciences and Marine Science Institute, University of California,
Santa Barbara, CA 93106 USA

Abstract.—Through a series of replacement experiments with the bluehead wrasse, *Thalassoma bifasciatum*, we have identified male morphological characteristics that appear to be under phenotypic sexual selection. We were particularly interested in whether the various sources of sexual selection (male–male competition for unoccupied mating sites, defense of mating sites against small males, and female choice of males) were (1) independently associated with different phenotypic characteristics; (2) jointly affected the same characteristic in the same way; or (3) jointly affected the same characteristic in an antagonistic fashion. We replaced the resident large, brightly colored Terminal Phase (TP) males on a reef with the same number of TP males from other reefs. When transplanted, these males contest with each other to take over mating sites. The transplanted group of males were then scored for three components of fitness: (1) the quality of the site obtained through competition with other large males; (2) the male's ability to defend arriving females from small intruding males; and (3) changes in female visits to the site once the new male takes over. The first and second components are part of intrasexual selection; the third represents intersexual selection. We measured the opportunity for selection by partitioning variance in mating success, and measured the direct effects of sexual selection by estimating the covariance between morphology and fitness components. *Opportunities for selection:* Because females generally remain faithful to particular mating sites, most (54%) of the explainable variation in male mating success is due to the acquisition of a particular mating territory, which is the outcome of competition among TP males. There was less variation in mating success due to shifts in site use by females and defense of females against the intrusions of smaller males, but all components were significant. *Effects of selection:* Success in male–male competition among TP males, estimated by the quality of the territory acquired, was positively associated with body length and the relative length of the pectoral fin. Success in territorial defense against small males was primarily related to body length, with lesser contributions from body depth and the area of a white band on the flank. Contribution to fitness through female choice of males was positively associated with white band area. In the two instances where a character was associated with two fitness components, the direction of selection was the same. While body length was positively associated with winning intrasexual contests, it was not correlated to any behavioral measures of aggression. Similarly, the white band associated with attractiveness was not correlated with any aspect of courtship or aggression. Parasite load was uncorrelated with other morphological characters, and did not appear to affect any aspect of sexual selection. There was no evidence for stabilizing selection or significant additional contributions from second-order effects to the fitness surfaces. Fitness functions calculated using cubic splines were generally linear except for body length, which appeared sigmoid in its effect on site acquisition ability; this same feature tended to plateau in its effect on site defense. Analyses of the interactions of selection gradients with reef or experiment indicated that the effect of particular male characters on estimates of fitness was generally homogeneous in both time and space.

Key words.—Bluehead wrasse, coral reef fish, intersexual competition, mate choice, sexual dimorphism, sexual selection, *Thalassoma bifasciatum*.

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This paper addresses questions of central interest to behavioral ecologists working on sexual selection and the evolution of mating systems. In a particular mating system, what are the relative roles of competition between males (intrasexual selection) versus

direct choice by females (intersexual selection) in determining the mating success of males? Do these two sources of phenotypic selection work in concert or in conflict on sexually dimorphic traits found in males, or are they independently associated with different traits?

Sexual selection theory attempts to explain sexual dimorphism and the elaboration of secondary sexual characteristics. Both

¹ Present address: Marine Science Research Center, State University of New York, Stony Brook, NY 11794-5000 USA.

intra- and intersexual selection can simultaneously operate within a species (Darwin, 1871; Borgia, 1979; Burley, 1981; Bradbury and Davies, 1987; Arcese, 1989; Moore, 1990), and we can gain a deeper understanding of the evolutionary dynamics involved by studying all potential sources of selection. As Moore (1990) pointed out, the fact that both mechanisms often occur simultaneously does not in any way imply that they are acting on the same characters. Unfortunately, the two types of sexual selection are most often considered separately in empirical and theoretical investigations (Bradbury and Davies, 1987), with most recent work concentrated on intersexual selection (e.g., Lande, 1981; Kirkpatrick, 1982; Curt-singer and Heisler, 1988; but see Kirkpatrick, 1987). The evolution of a particular trait under intersexual selection can be strongly affected by other sources of selection on the trait (Kirkpatrick, 1987), and thus it is important to know the extent to which selection for characteristics that aid male-male competition augments or conflicts with selection for characteristics chosen directly by females.

In addition to differences resulting from inter- and intrasexual selection, many mating systems may impose more than one type of intrasexual selection on dimorphic characters. In species with alternative male mating behaviors, the characteristics that affect the ability of larger males to win contests with other large males may not be the same as those that affect the ability to defend a female against the intrusions of smaller males. The impact of males with alternative tactics can constitute an important source of selection. For example, in the Mediterranean nearshore fish *Symphodus tinca*, mating rates of dominant males increased four-to-sevenfold when smaller "sneaker" males were removed (van den Berghe et al., 1989). While there has been considerable discussion about how intense male-male competition might give rise to alternative mating tactics in the first place (Gadgil, 1972; Dominey, 1984; Gross, 1992), there has been no development of the idea that such tactics are in themselves a source of sexual selection.

In this study, we use a field experimental approach to analyze phenotypic sexual se-

lection on male traits in the bluehead wrasse, *Thalassoma bifasciatum*, a common coral reef fish of the Western Atlantic. By replacing whole groups of resident males with experimentally transplanted groups, we were able to monitor the performance of males in (1) winning a mating site in competition against other large males, (2) attracting females to the site, and (3) defending the site against the intrusions of smaller males. Past work has suggested that there is a great deal of opportunity for selection in each of these episodes (Warner et al., 1975; Warner and Hoffman, 1980a; Warner, 1984a, 1986, 1987; Schildhauer, 1991). We quantify this by determining the contributions of each of these episodes of sexual selection to variance in male mating success. We then ask what male characteristics appear to be associated with the three sources of selection, and whether these sources act independently on different characteristics. If they act on the same characteristics, do they act congruently or in conflict?

Natural History

Adult bluehead wrasse remain on their home reefs, with no emigration or immigration (Warner and Hoffman, 1980a, 1980b). Eggs are pelagic with no parental care. During the larval period of about 50 days it is likely that the young are mixed and widely dispersed among reefs (Victor, 1986).

Mating takes place daily, usually in mid-afternoon, at specific sites that remain in use for generations (Warner et al., 1975; Warner and Robertson, 1978; Warner, 1988). The spawning period is discrete, averaging 110 min in duration (Warner and Hoffman, 1980a). Mating itself consists of an upward rush of about 1 m, with release of gametes at the apex. Most mating sites are occupied by large, brightly colored Terminal Phase (TP) males who defend a territory around a site and mate singly (pair-spawn) with females. On larger reefs (those with more than about 200 individuals) the most active mating sites are occupied by aggregations of smaller Initial Phase (IP) males, who closely resemble females and mate in groups with single females (group-spawning; Warner et al., 1975; Warner and Hoffman, 1980a; van den Berghe and War-

ner, 1989). These smaller males also attempt to intrude actively on the mating activity of TP males by entering unobtrusively and attempting to pair-spawn with females when the TP male is occupied elsewhere (sneaking), or by joining the TP male at the apex of a spawning rush (streaking). Alternatively, groups of IP males may enter a territory en masse, overwhelm the defenses of the TP male, and group-spawn with the arriving females. Experiments have shown that IP males can substantially lower the mating success of TP males (Warner and Hoffman, 1980*b*). Accordingly, TP males spend most of their time in defense against small males, averaging nearly three aggressive acts per minute on larger reefs (Warner and Hoffman, 1980*a*).

Past work has shown that most females tend to remain faithful to a mating site, and daily mating success can differ by as much as an order of magnitude among sites (Warner, 1986, 1987). Females generally feed at upcurrent areas of the reef and then travel to specific sites to mate. These sites are usually located in positions that potentially reduce predation on the mating adults and drifting eggs (Randall and Randall, 1963; Robertson and Hoffman, 1977), and may also increase fertilization rate (Petersen et al., 1992). Thus site characteristics can be important to females, and female site fidelity represents a mating resource to TP males.

Despite female site fidelity, mating success associated with a site can nearly double or be halved when a new male assumes ownership. Large changes in site-associated mating success occur only when a new male takes up occupancy; thus changes in mating success appear to reflect female responses to the appearance and behavior of the new site owner. Females arrive at a territorial mating site unaccompanied by TP males, and are always courted by the resident male. However, females may leave without mating, and between 5 and 10% of a female's spawns occur at other sites (Warner, 1986). It therefore appears that females are able to evaluate males and choose among them.

On any reef, there are two to three times as many TP males as there are territories, and the largest of these nonterritorial TP males contend for occupancy of a site when one becomes available (Hoffman et al., 1985;

TABLE 1. Schedule and sample sizes of the transplant experiments.

| Year | Reef | Number of sites | Number of experiments | Total number of males used |
|------|------|-----------------|-----------------------|----------------------------|
| 1988 | 16C | 5 | 3 | 11 |
| 1988 | 18 | 3 | 2 | 5 |
| 1989 | 8 | 4 | 5 | 20 |
| 1989 | 11 | 5 | 4 | 19 |
| 1990 | 11 | 5 | 3 | 13 |
| 1990 | 13 | 5 | 3 | 11 |

Schildhauer, 1991). Contests between TP males over vacant territories are usually settled in less than two days (Warner, 1986; Schildhauer, 1991). In 17 years of observation of this species, we have never witnessed a usurpation of an occupied territory on an undisturbed reef. Thus once a male acquires a territory, he can retain it until death; average tenure on a site is about 90 days (Warner, 1984*a*).

As is common in many reef fishes (Warner, 1984*b*), TP males can result from sex change and color change of large females as well as from color change of large IP males (Warner and Swearer, 1991). TP males derived from females are identical in size range, coloration, behavior, and mating success to those derived from males (Warner and Robertson, 1978; Warner, 1984*a*).

MATERIALS AND METHODS

The Experiments

All observations and manipulations were carried out on five patch reefs (reefs 8, 11, 13, 18, and 16C; Gladfelter and Gladfelter, 1978, provide a map of this area) located in Tague Bay, St. Croix, U.S. Virgin Islands, near the West Indies Laboratory (Table 1). Reefs 11, 13, and 16C each had sites permanently occupied by group-spawning aggregations of IP males. On all reefs, however, there were roving groups of IP males that often attempted to intrude upon the mating activities of territorial TP males.

Individuals, groups, or whole populations can be transplanted to other reefs with no ill effects (Warner and Hoffman, 1980*b*; Warner, 1988, 1990*a*, 1990*b*). Previous work (Warner 1990*b*) showed that when all territorial and nonterritorial TP males are

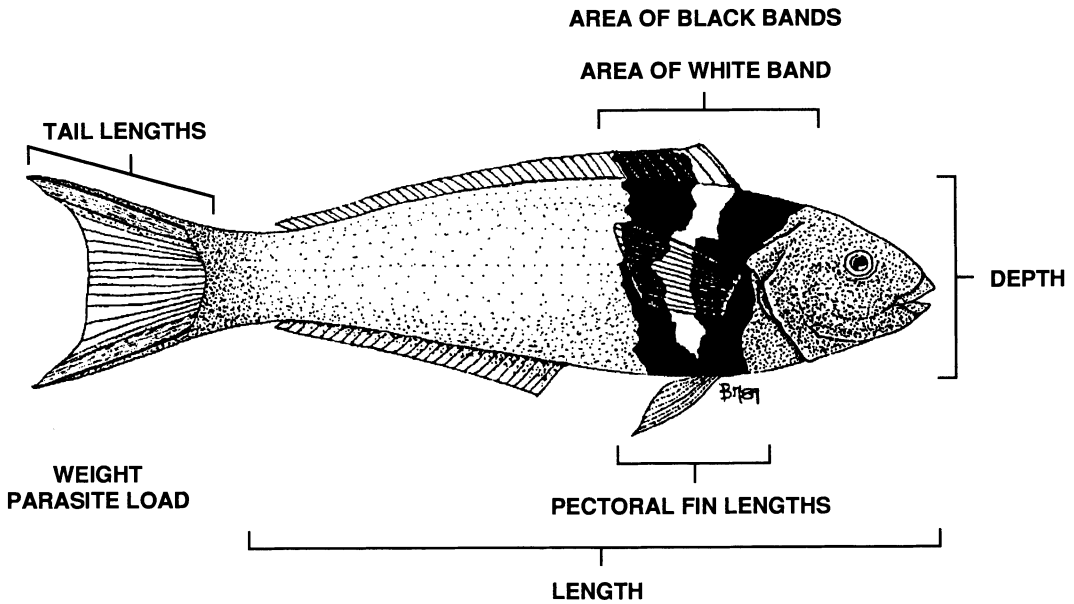


FIG. 1. An outline of the major morphological features of a terminal color phase bluehead wrasse, *Thalassoma bifasciatum*, showing the characters that were included as independent variables in the multiple regression analyses of fitness components associated with sexual selection.

removed from a reef and replaced by a new group, the same spawning sites remain in use. The experiments reported here consisted of three phases. First, we measured the daily mating success associated with each mating site on the target reef. Second, we removed all TP males (both territorial and nonterritorial) from the target reef and replaced them with a group of territorial males that had not been on the target reef previously. Finally, one week after new males established themselves at the mating sites, we returned to the reef and resumed our observations. By that time, all of the mating sites were occupied by transplanted males. We recorded territorial male mating behavior and mating success for a minimum of four days. The territorial males could then be scored for three components of fitness: (1) the quality of the site obtained through competition with other large TP males; (2) the degree to which the male can defend arriving females from the actions of small intruding IP males; and (3) the degree to which females leave or recruit to the site once the new TP male takes over. The first and second components are episodes of intrasexual selection; the third represents intersexual selection. We did not have enough

observers to monitor the activity of the transplanted TP males who failed to secure a territory, and thus they are not included in the overall analysis. These nonterritorial TP males have very low rates of mating success (Warner et al., 1975; Warner, 1984a; Hoffman et al., 1985).

The replacement experiment was repeated on the same reef several times to evaluate the effects of different males within a particular site. We report here on 20 experiments performed on five different reefs (Table 1).

Field Measurements.—Observers were positioned at each mating site on the reef for the entire duration of a spawning period. In 1988 and 1989, the following data were recorded:

Mating: The total number of matings that occurred on the site, and whether these matings were (1) with the TP male alone, (2) with the TP male plus a streaker IP male, (3) with a male other than the TP owner, or (4) with a group of IP males. In case (2), the TP male was assigned half of a mating.

Courtship: The number and duration of each TP courtship bout. Courtship

consists of swimming in tight circles above the mating site while vibrating the pectoral fins. We also recorded the frequency of another courtship element, looping, which consists of a rapid upward and then downward movement.

Aggression: The number and duration of aggressive bouts (direct chases of another individual), and whether this aggregation was directed toward a TP or an IP individual.

Residence: The number and duration of times spent off the territory, out of sight of the observer. Overall rates of courtship and aggression were calculated from time actually spent on the territory.

In 1990, observers would often monitor two mating sites simultaneously. For this reason, in that year we recorded only the number and nature of the matings taking place.

Laboratory Measurements.—At the termination of the observation period, all transplanted males were recaptured. We measured the Standard Length (SL) of males that had failed to acquire a territory, and then released them on reefs distant from those used in the experiments. For the territorial males, we measured a suite of characters (see Fig. 1) that reflect (1) characters that may convey general fitness (body size measures and pectoral fin length); (2) secondary sexual characteristics (coloration, and the elongated tail fins); and (3) parasite burden. Details are as follows:

Morphology: We measured the SL of each male, body depth, the length of the tail fins, the length of the pectoral fins, and wet body weight. Weight was not measured in the 1988 series.

Coloration: Photographs were taken in the laboratory of each fish. Using these, we quantified features of TP coloration by measuring the areas of the anterior and posterior black bars and the area of the intervening white bar. Color hue and intensity can be altered nearly instantaneously by the male so these were not measured.

Parasites: In 1989 and 1990 each male was assayed for parasite load through complete dissection. No external or gill parasites were found, but internal para-

sites were common. We examined gut, liver, gonad, coelomic cavity, brain, and the entire musculature. By far the most common parasites were large nematodes in the gut and encysted pseudophyllid cestodes in the dorsal musculature (B. Hoffman, pers. comm.), and it is these parasites that are used in further analyses.

Analysis

The first step in our analysis of sexual selection investigated sources of variation (opportunities for selection) in territorial TP male mating success. We identify the contributions from the mating site itself and from differences among males in losses of matings to IP males and attractiveness to females. In the second step, we attempt to identify the effect of sexual selection by asking what male characteristics were associated with success in each of three selection episodes.

Opportunities for Selection: Sources of Variation in Mating Success among Territorial Males

The series of experiments allows an analysis of the relative contributions to variance in mating success due to differences among mating sites and among males. We stress that this analysis does not measure the intensities of sexual selection; rather, the relative contributions to variance set an upper limit on the degree to which selection can operate (Arnold and Wade, 1984a). It is also limited to the circumstances under which the experiments occurred, which do not precisely mimic the natural, unmanipulated situation (see Discussion).

We first separated the effects of site and male in an analysis of variance of the daily number of matings accruing to TP males at their mating sites. Because a series of males occupied the same mating sites over the course of the experiments, the main effects were site, male, and date, with males nested within sites. Because of this nesting, site variation in the model includes that due to males as well. We estimated the actual variance associated with male and site by using formulae for the expected values of mean squares in each analysis of variance (Sokal and Rohlf, 1981).

The site effect is a measure of the opportunity for one form of intrasexual selection, because TP males contend for occupancy of these sites. The male effect (nested within sites) represents contributions to variance in mating success due to two factors: (1) Territorial TP males may vary in their ability to mate with arriving females by preventing the intrusions of IP males (another source of intrasexual selection). We expressed this as the proportion of spawns occurring at a male's site that actually accrued to him. (2) Females may abandon or recruit to a new male at a particular site (intersexual selection). We expressed this as the proportion of total spawns occurring on the reef that took place at his site.

Because we have multiple observations for each male, and because we observed a succession of males at each site, the contribution to variance in each component of mating success from these sources was estimated by a separate two-way analysis of variance, including both site and male effects, the latter again nested within site. This controls for potential differences among sites in difficulty of defense or overall popularity with females.

The Effect of Sexual Selection on Male Characteristics

Three episodes of selection (site acquisition, site defense, and attractiveness to females) were analyzed in separate multiple regression analyses (see Lande and Arnold, 1983; Arnold, 1983; Arnold and Wade, 1984a, 1984b; Endler, 1986; Mitchell-Olds and Shaw, 1987; and Mitchell-Olds and Bergelson, 1990, for an exposition of the use of multiple regression in the analysis of selection). Standardized partial regression coefficients (or directional selection gradients, β) were used to compare the effect of significant predictors within and between analyses. The original regression slopes were divided by SD_y/SD_x , where SD_y is the standard deviation of the response variable and SD_x is the standard deviation of the predictor. The standardized coefficient expresses the slope as the change in standard deviations of y to changes in x , also in terms of standard deviations. The multiple regressions were run as analyses of covariance, with experimental block included as a classification

variable. This was done to adjust for differences in mating rates and IP male activity between reefs or over the course of an experiment.

We also calculated reduced models for each regression to ensure that the effects of important predictors were not obscured by collinearity, using the all-subsets method for model selection (Hocking, 1976). In this method, a group of models is selected from all possible sets by evaluating, in turn, all models with one predictor, then those with two predictors, etc. Among the models in each group, we chose the one with the largest coefficient of determination (r^2). Finally, from the models in the selected set, we took as the preferred model that which minimized the S_p statistic (an estimator of total discrepancy; see Hocking, 1976; Draper and Smith, 1981; Linhart and Zucchini, 1986). Variables included as covariates to adjust for site differences in the response variables (see below) were forced to remain in all models.

The standard errors for regression coefficients were estimated using a weighted, delete-one jackknife of least squares estimates (Mitchell-Olds and Shaw, 1987; Mitchell-Olds, 1989). Significance was estimated from jackknife t -tests (Wu, 1986; Mitchell-Olds, 1986) using programs provided by T. Mitchell-Olds (FreeStat; see Mitchell-Olds, 1989). In addition, we examined the shape of the fitness function for the residuals of each significant variable using the nonparametric cubic spline regression method (Schluter, 1988; GLMS version 9/15/89 kindly provided by D. Schluter).

Because weight and parasite load were not measured in 1988, we performed separate analyses for 1988–1990 and for 1989–1990. Note that these are not independent sets of data, because the former data set includes the latter.

We investigated potential curvature of the fitness surface for each model by testing for the overall significance of the aggregate of all second-order terms (see Mitchell-Olds and Bergelson, 1990). For each selection episode, we used the following formula to calculate F -values for testing the hypothesis that there were no significant additional contributions of second-order effects to the regression models (Sokal and Rohlf, 1981):

$$F_{(k_2-k_1), (k_e)} = [(SS_2 - SS_1)/(k_2 - k_1)] \div [SS_e/k_e]$$

where k_1 and SS_1 = model degrees of freedom and sum of squares in the linear model, and k_2 , SS_2 , SS_e , and k_e = model degrees of freedom, sum of squares, error sum of squares, and error degrees of freedom in the second-order model. Note that this approach does not ask whether specific second-order terms are significant, but rather whether the addition of all second-order terms significantly improves the regression model. The possibility of nonlinearity in specific terms was investigated using the cubic spline technique (see above).

For observations spanning 1988–1990, we tested second-order models that included both quadratic and crossed (interaction) variables. For the 1988–1990 data, which had two more linear variables and fewer observations, we were able to test only models that included all quadratic terms.

Male Characteristics.—The morphological and coloration characteristics, as well as the parasite data, form the independent variables for the selection analyses (Fig. 1). Prior to the analyses all variables were transformed to reduce collinearity (see below). Each variable was then expressed as the deviation from the mean value. The transformations performed were as follows:

Morphometric variables were expressed as the individual's residual in a linear regression of the character against SL (Reist, 1985). Thus individuals with longer-than-average pectoral fins, for example, would have a large positive residual value. We used the average length of paired structures (pectoral fins and tail lobes). *Weight* was expressed as the individual's residual in a regression of the cube root of weight versus SL.

Coloration was entered as two variables. The first estimated the relative size of the overall black-and-white patch on the flank of the male (Fig. 1) as the residual of the square root of the total patch area regressed against length. The second variable expressed the relative area of white in the patch as the residual of the square root of the white area regressed against the square root of the black area.

Parasite load entered as two terms, re-

flecting total number of parasites in the gut and musculature, respectively.

While behaviors were measured for each territorial male in 1988 and 1989, these were not used as independent variables in the regressions. This is because behavior can be as much of a response to the situation in which a male finds himself as it is a description of the characteristics of a particular male. It is not at all clear how much of any behavior is causally related to the fitness components, and how much results from the particular reproductive success that a male is experiencing. Instead, we discuss intercorrelations between fitness measures, significant morphological variables and various measures of behavior.

Fitness Components.—The response variables reflect a fitness component appropriate to a specific episode of selection (competition between TP males to acquire a territory, competition between a territorial TP male and smaller IP males for matings at a site, or the degree of attractiveness of a TP male at a site). These variables were devised to be independent and to quantify separate components of overall male success. The appropriate fitness component and adjustments for each analysis will be discussed in turn:

Quality of site acquired: Success in territory acquisition (due to competition between TP males) was quantified as the quality of the site acquired, based on past spawning activity there. The specific response variable was the mean total number of matings occurring per day during the residency of the *prior* occupant of the site. This reflects the number of females that were faithful to a particular site before the actions of a target male had the opportunity to affect that fidelity. Females continue to arrive at the site during the contention period, and physical characteristics are not a reliable guide to the spawning activity occurring at a site (Warner, 1988, 1990a). Thus the transplanted males are likely to use female arrivals to estimate site quality. Some mating sites on reefs are occupied by groups of IP males, and most of the matings that occur there are unavailable to TP males (Warner and Hoffman, 1980a, 1980b). Such sites were not included in this analysis.

Site defense: Success in contending with

intruding IP males was quantified as the probability that a female mating at a site does so with the territory owner instead of an intruder. Specifically, the response variable was the arcsine transformation of the proportion of the total number of females mating at a site that spawn with the resident TP male. A complicating factor is that sites differ in their proximity to the group-spawning aggregation of IP males, and thus different sites may offer more or fewer challenges from intruding IP males (Warner and Hoffman, 1980a, 1980b). We adjusted for this by including the (arc-sine transformed) proportion of the daily total matings that the prior owner accrued as a covariate (*ARSPRIOR*).

Female choice: Finally, success in attracting females to the site was quantified as the number of females currently arriving at the site, adjusted for prior spawning activity. The response variable was based on the number of matings occurring per day on the target male's site, regardless of whether the male participated in them or not. We included the prior daily total mating rate among the predictor set as a covariate (*PREVSPWN*). By adjusting in this way the fitness component reflects changes in the number of females arriving when a new male takes over, independent from fitness arising from site acquisition. Because it is unclear just what is the basis of female choice at sites that are dominated by group-spawning, those sites were excluded from this analysis.

Spatial and Temporal Variation in Selection

The possibility that there might be reef- or experiment-specific variation in selection gradients was investigated with specific analyses of covariance for each source of sexual selection, using the morphological variables indicated by the reduced regression models. The analysis used the same observations and dependent variables as the regression models that estimated the selection gradients. To analyze spatial and temporal variation in the regression slopes (selection gradients) we used tests for interactions between the morphological variables and (1) the reef in which the experiments were conducted and (2) the ex-

periment itself (nested within reef). A significant interaction indicates that selection gradients differ across reefs or between experiments (see Mitchell-Olds and Bergelson, 1990, for a similar approach).

RESULTS

Territorial Acquisition

Of the 264 TP males collected at the termination of the 20 experimental sequences, 84 (32%) had acquired a mating territory. This corresponds closely to the proportion of TP males that were territorial on unmanipulated reefs (26 of 76, or 34.2%). Because virtually all mating takes place on specific sites on the reef, the acquisition of such a site by a male is a major determinant of mating success. Various studies carried out in different years in the San Blas Islands of Panama indicated that TP males without permanent territories have a mating success averaging only 0.28 to 3.7 matings per day (mean = 1.7 matings per day; Warner et al., 1975; Warner, 1984a; Hoffman et al., 1985). The average mating success of territorial TP males in our St. Croix sample is 14.8 ± 1.1 matings per day ($\bar{X} \pm 1$ SE, $N = 88$). If the mating rates of nonterritorial TP males in St. Croix are similar to that occurring in Panama, acquisition of a territory represents an eight-fold increase in mating success, on average, for a TP male. Mating rates of nonterritorial TP males in St. Croix are likely to be as low or lower than occurred in Panama, because we very rarely saw one of these males engage in spawning, even though several were usually in sight during our observation periods.

Within the transplanted groups, the longest TP males tended to be those that acquired mating territories (Fig. 2). The average length of nonterritorial TP males was 74.90 ± 0.52 mm, while territorial TP males averaged 82.21 ± 0.86 mm ($\bar{X} \pm 1$ SE, $t = 7.9$, $P < 0.001$). While territory acquisition is important to mating success, the losers in a particular contest for a territory are likely to have several subsequent opportunities, and these nonterritorial TP males continue to grow rapidly (Warner, 1984a; Hoffman et al., 1985). Thus the passage from nonterritorial to territorial TP male is an ontogenetic transition dependent on size. In

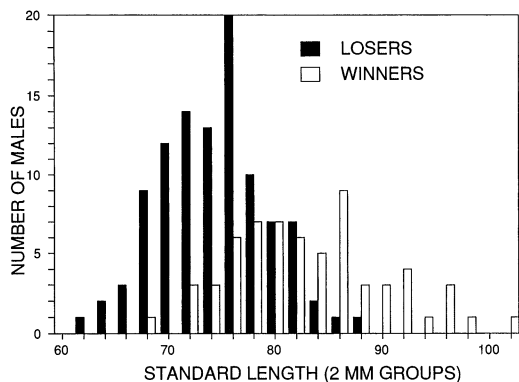


FIG. 2. Size distributions for TP males (by 2 mm groups) involved in the transplant experiments. Males that were successful in acquiring a mating territory (“winners”) are shown as white bars.

contrast, once a male acquires a territory he is unlikely to change sites (Schildhauer, 1991), and this study concentrates on the factors contributing to fitness in this critical period.

*Opportunities for Selection:
Sources of Variation in Mating
Success among Territorial Males*

Variation in mating success among territorial males may arise from three sources, which correspond to the following fitness components:

A. *Possession of sites of differing quality.* Because most females remain faithful to sites when a new male takes over, and sites differ in the number of associated females (Warner, 1987), sites represent mating resources of differing basic quality. They vary from poor sites with fewer than 3 female mating visits per day, up to extremely successful sites with an average of over 50 females a day. An ANOVA indicates that 54% of the total explainable variance in the daily matings accruing to territorial males is accounted for by differences in site quality (Table 2A).

Another 45% of the explainable variance in mating success was accounted for by differences among the males themselves, independent of site. Two fitness components contribute to this variance:

B. *Defense of females arriving at a site.* Losses to intruding IP males can be severe; during the course of the experiment, 28% of all matings were lost in this way. Males

TABLE 2. Analyses of contributions to variance in territorial TP male mating success in the experiments.

A. Relative contribution to variance in daily spawning rate (log-transformed) accruing to territorial males due to site, male (nested within site), and date. Data are from 1989–90. $N = 225$, $r^2 = 0.84$.

| | <i>df</i> | <i>MS</i> | <i>F</i> | <i>P</i> |
|-------------|-----------|-----------|----------|----------|
| Site | 13 | 8.07 | 4.5 | <0.001 |
| Male (site) | 33 | 1.81 | 5.3 | <0.001 |
| Date | 40 | 0.31 | 0.9 | 0.66 |
| Error | 124 | 0.34 | | |

B. Analysis of variance in male success due to differences among males in their ability to defend a mating site against the intrusions of IP males. The response variable is the (arc-sine transformed) proportion of matings occurring at a site that actually accrued to the resident male. $N = 57$ males, 16 sites, average of 3.9 days per male. $r^2 = 0.72$.

| | <i>df</i> | <i>MS</i> | <i>F</i> | <i>P</i> |
|-------------|-----------|-----------|----------|----------|
| Site | 15 | 1.43 | 3.9 | <0.001 |
| Male (site) | 45 | 0.36 | 3.9 | <0.001 |
| Error | 163 | 0.09 | | |

C. Analysis of variance in TP male success due to differences among males in their ability to affect the number of females mating at a site once a new male assumes ownership. The response variable is the proportion of matings on the reef that occurred at a particular male's mating site. $N = 57$ males, 16 sites, average of 3.9 days per male. $r^2 = 0.88$.

| | <i>df</i> | <i>MS</i> | <i>F</i> | <i>P</i> |
|-------------|-----------|-----------|----------|----------|
| Site | 15 | 0.36 | 8.6 | <0.001 |
| Male (site) | 45 | 0.04 | 6.7 | <0.001 |
| Error | 164 | 0.01 | | |

vary in their ability to defend their territories. In extreme cases, the male is forced to abandon mating at his site for the bulk of the mating period, while other males lose none of their matings to interlopers. The analysis of variance in the proportion of matings accruing to resident males indicated that sites differed in the degree to which they were intruded upon by IP males, and that within a site males differed substantially in their defensive ability (Table 2B).

C. *Changes in the number of females associated with a site.* Once experiment-wide changes in spawning rate were accounted for, sites changed an average of 45% in their associated mating rate (calculated as the absolute percentage change from previous values, either up or down; $N = 59$, $SD = 42\%$). The analysis of variance indicates that sites differed in the number of females associated with them, and that differences in male attractiveness also have a significant effect on the overall daily variation in female visitation rate (Table 2C).

The magnitude of the contribution to

TABLE 3. Values for untransformed morphological features of Terminal Phase males used in the experiments. See Figure 1.

| Feature | N | Minimum | Maximum | Mean | SD |
|--|----|---------|---------|-------|------|
| Standard length (mm) | 79 | 68.0 | 100.2 | 81.1 | 7.1 |
| Body depth (mm) | 79 | 16.0 | 26.0 | 20.8 | 2.4 |
| Tail length (mm) | 79 | 10.5 | 36.5 | 22.3 | 5.2 |
| Pectoral fin length (mm) | 79 | 13.4 | 23.7 | 17.7 | 2.3 |
| Area of black + white (mm ²) | 78 | 142.1 | 512.7 | 312.6 | 83.0 |
| Area of white (mm ²) | 78 | 35.8 | 144.3 | 72.7 | 23.9 |
| Weight (g) | 63 | 5.8 | 19.5 | 11.2 | 2.9 |
| Gut parasites | 63 | 0 | 3 | 0.5 | 0.8 |
| Muscle parasites | 63 | 0 | 14 | 2.3 | 3.1 |

variance from differences in defensive ability is greater than that from differences in attractiveness, but both are highly significant. They also appear to act independently, because the two response variables are uncorrelated ($r = 0.004$). Although the contribution to mating success variance is larger from intrasexual sources (the combination of quality of site acquired and defense of that site) than it is from female choice, this does not necessarily imply that phenotypic selection on characteristics for male-male competition is more intense than that due to female choice. There may, for example, be a large stochastic component that enters into TP male accession to territories, but female choice of male characteristics may be highly predictable. It is also possible that some of the mating success variance attributed to site is due to the consistent acquisition of certain sites by males with particularly attractive characteristics. Thus it is necessary to associate variance in fitness components with specific characteristics, which is taken up in the next sections.

The Effect of Sexual Selection on Male Characteristics

The Characters Themselves.—The raw values of the male characteristics are shown in Table 3. Morphometric characters (length, depth, mean tail length, and mean pectoral fin length), coloration characters, and body weight were highly intercorrelated (Table 4). Once the morphometrics, overall color area, and weight were expressed as residuals in regressions with length, few intercorrelations remained (Table 4). There were positive correlations between the residuals of pectoral length and tail length, and also be-

tween body depth and weight; thus these characters appear to develop together independently of length.

In general, coloration tended to vary independently of other characters once they were transformed, with the exception that longer individuals tended to have a greater proportional area of white within the flank black-and-white patch (Table 4). Parasite loads also tended to be uncorrelated with any other morphological characteristic, either raw or relative to standard length. The only exception to this was a negative correlation between muscle parasite load and tail length.

Associations of Male Characteristics and Fitness Components.—The three analyses, each representing a separate episode of sexual selection, will be presented in turn.

Quality of site acquired: We first asked what characteristics of males are associated with gaining high-quality mating sites as a result of competition with other TP males. In the experiments, the fitness component (site quality) ranged between values of 0.7 and 61.0 matings per day (grand mean = 19.6, SD = 14.8, $N = 70$). For both the 1988–90 and 1989–90 observations, success due to quality of site acquired was positively related to body length and pectoral length (expressed as the residual in a regression with length; Table 5). No other variable had any significant effect on winning a quality mating site. Reduced models had the same results as the full models: the best fits were achieved with the inclusion of body length and pectoral length. Tests for additional contributions from second-order effects were not significant in either set of

TABLE 4. Correlation matrix of original (below the diagonal) and transformed (above the diagonal) morphological variables for the experimental TP males. The transformed variables entered into the models shown in Tables 5 through 7. Square roots of color areas and cube root of weight were used in the calculation of the correlation values. Transformed morphometric variables are residuals in regressions against length. White area was expressed as the residual in a regression against black area. See text for details. Sample sizes are shown in parentheses. Significance levels: * $P < 0.1$; ** $P < 0.05$; *** $P < 0.01$; **** $P < 0.001$.

| | Body length | Body depth | Tail length | Pectoral fin length | Black + white area | White area | Body weight | Gut parasite load | Muscle parasite load |
|----------------------|-----------------|-----------------|-----------------|---------------------|--------------------|-----------------|-----------------|-------------------|----------------------|
| Body length | — | −0.10 (79) | 0.07 (79) | 0.07 (79) | −0.02 (78) | 0.23* (78) | 0.01 (63) | 0.20 (63) | −0.07 (63) |
| Body depth | 0.90*** (79) | — | 0.12 (79) | 0.10 (79) | 0.05 (78) | 0.04 (78) | 0.65*** (63) | −0.20 (63) | −0.09 (63) |
| ail length | 0.72*** (79) | 0.69*** (79) | — | 0.39*** (79) | 0.21+ (78) | 0.18 (78) | 0.03 (63) | −0.19 (63) | −0.38** (63) |
| Pectoral fin length | 0.85*** (79) | 0.78*** (79) | 0.76*** (79) | — | 0.13 (78) | 0.09 (78) | 0.13 (63) | 0.00 (63) | −0.03 (63) |
| Black + white area | 0.82*** (78) | 0.75*** (78) | 0.67*** (78) | 0.73*** (78) | — | 0.04 (78) | 0.16 (63) | −0.14 (63) | 0.09 (63) |
| White area | 0.61*** (78) | 0.58*** (78) | 0.57*** (78) | 0.54*** (78) | 0.71*** (78) | — | 0.01 (63) | 0.10 (63) | −0.09 (63) |
| Body weight | 0.97*** (63) | 0.93*** (63) | 0.69*** (63) | 0.84*** (63) | 0.83*** (63) | 0.58*** (63) | — | 0.01 (63) | 0.12 (63) |
| Gut parasite load | 0.20 (63) | 0.11 (63) | −0.01 (63) | 0.17 (63) | 0.10 (63) | 0.13 (63) | 0.20 (63) | — | −0.04 (63) |
| Muscle parasite load | −0.07 (63) | −0.11 (63) | −0.31* (63) | −0.07 (63) | −0.01 (63) | −0.07 (63) | −0.05 (63) | −0.04 (63) | — |

TABLE 5. Linear effects (directional selection gradients, β) of TP male morphological characters on the fitness component reflecting the quality of mating sites acquired through contests with other TP males. Shown are the full and reduced regression models for 1988–90, which did not include parasite or weight information, and for 1989–90, which included all measurements listed. The following symbols are used in this and subsequent tables: $^+P < 0.1$; $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

| Variable | 1988–90 | | | | 1989–90 | | | |
|---------------------|---------|--------|---------|--------|---------|--------|---------|--------|
| | Full | | Reduced | | Full | | Reduced | |
| | β | t | β | t | β | t | β | t |
| Standard length | 0.35 | 2.93** | 0.33 | 3.12** | 0.64 | 2.79** | 0.55 | 3.06** |
| Body depth | 0.09 | 0.91 | | | 0.13 | 0.90 | | |
| Tail length | 0.08 | 0.60 | | | 0.14 | 0.52 | | |
| Pectoral fin length | 0.26 | 2.21* | 0.31 | 3.06** | 0.46 | 2.66* | 0.40 | 3.05** |
| Black + white area | 0.05 | 0.60 | | | 0.07 | 0.38 | | |
| Relative white area | −0.04 | −0.30 | | | −0.27 | −0.98 | | |
| Body weight | — | — | — | — | −0.10 | −0.67 | | |
| Gut parasites | — | — | — | — | −0.07 | −0.50 | | |
| Muscle parasites | — | — | — | — | −0.06 | −0.34 | | |

1988–90: $N = 70$, $r^2 = 0.53$ (full), $r^2 = 0.51$ (reduced).
1989–90: $N = 55$, $r^2 = 0.57$ (full), $r^2 = 0.53$ (reduced).

data (1988–1990: $F_{6,38} = 1.02$, $P = 0.43$; 1989–90: $F_{9,22} = 1.3$, $P = 0.29$).

When we used Schluter’s (1988) cubic spline technique to investigate the form of selection for each significant character, the only nonlinear relationship was that of body length to the fitness component (Fig. 3). There was no evidence for a fitness component maximum at intermediate lengths; instead, the relationship between the component and length appears sigmoid.

A survey of the behavioral correlates of quality site acquisition revealed the following: males that acquired good sites chased IP males at a lower rate ($r = -0.43$, $N = 47$, $P = 0.02$), and they made more frequent forays off their territory ($r = 0.52$, $N = 46$, $P < 0.01$). All other correlations were not significant.

Site defense: In contrast to site acquisition, defense against small IP males continues on a daily basis. The fitness component ranged between 0 (all spawns lost) and 1.0 (none lost), with a mean of 0.73 (SD = 0.27, $N = 67$). The average number of aggressions against small males was 73.5 per spawning period in 1989, and could be as high as 265. As in acquisition of quality sites, successful site defense was strongly and positively associated with body length (Table 6), regardless of the years used. In the 1989–1990 models, the effect of the relative size of the white band on the side of the male was significant ($P = 0.02$), and in 1988–1990 body depth also tended ($P = 0.08$) to be associated

with successful defense. In the reduced models, body length retained its importance (all years, $P < 0.01$), as did the white coloration variable (1988–1990: $P = 0.02$; 1989–1990: $P = 0.03$). Body depth was important only in 1989–1990 ($P = 0.03$). Runs including quadratic and crossed terms indicated no significant additional contribution of second-order effects (1988–1990: $F_{6,42} = 0.98$, $P = 0.45$; 1989–1990: $F_{9,17} =$

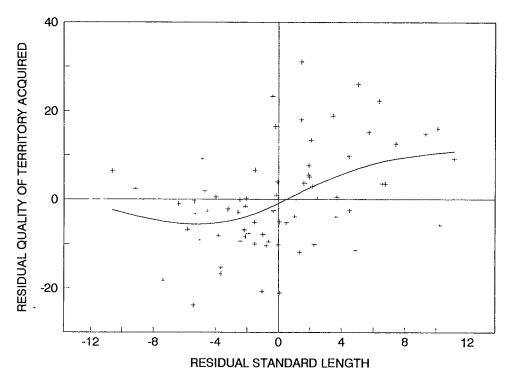


FIG. 3. Relationship between body length and contributions to reproductive success arising from the acquisition of a particular mating territory. The fitness component in this case is expressed as the residual of prior mating success of the territory in a regression of success against all significant characters except length. Length is expressed as the residual of length in a regression against all other significant characters. Note that this plot displays the same relationship between success and length as that analyzed by the reduced model in Table 5. The fitness function was calculated using cubic splines, based on 1988–1990 data; the outer lines are one SE, calculated by bootstrap methods.

TABLE 6. Linear effects of male morphological characters on the fitness component reflecting ability to defend mating sites against intruding IP males. Details are as in Table 5.

| Variable | 1988–90 | | | | 1989–90 | | | |
|---------------------|---------|-------------------|---------|--------|---------|-------------------|---------|--------------------|
| | Full | | Reduced | | Full | | Reduced | |
| | β | t | β | t | β | t | β | t |
| ARSPRIOR | 0.20 | 1.70 ⁺ | 0.21 | 2.09* | 0.22 | 1.87 ⁺ | 0.21 | 1.86 ⁺ |
| Standard length | 0.32 | 2.86** | 0.31 | 2.83** | 0.47 | 2.60* | 0.52 | 3.53** |
| Body depth | 0.07 | 0.79 | | | 0.23 | 1.83 ⁺ | 0.26 | 2.34* |
| Tail length | 0.09 | 0.68 | | | -0.06 | -0.20 | | |
| Pectoral fin length | -0.04 | -0.45 | | | -0.09 | -0.72 | | |
| Black + white area | 0.02 | 0.16 | | | 0.02 | 0.09 | | |
| Relative white area | 0.18 | 1.81 ⁺ | 0.20 | 2.33* | 0.39 | 2.47* | 0.29 | 2.24* |
| Body weight | — | — | — | — | -0.29 | -1.52 | -0.33 | -1.83 ⁺ |
| Gut parasites | — | — | — | — | -0.02 | -0.14 | | |
| Muscle parasites | — | — | — | — | -0.07 | -0.40 | | |

1988–90: $N = 67$, $r^2 = 0.60$ (full), $r^2 = 0.59$ (reduced).
 1989–90: $N = 55$, $r^2 = 0.64$ (full), $r^2 = 0.64$ (reduced).

1.42, $P = 0.24$). When the cubic spline technique was applied, only body length had a nonlinear fitness function. Its effect on defensive ability appears to plateau in the greater size ranges (Fig. 4).

In terms of behavior, males successful in defense tended to have a lower aggression rate to IP males ($r = -0.31$, $N = 50$, $P = 0.03$), took more forays per unit time off their territory ($r = 0.48$, $N = 49$, $P < 0.01$), but spent less total time off the site ($r = -0.46$, $N = 50$, $P < 0.01$). There were no other significant correlations.

Female choice: Mean number of matings per day for new owners ranged between 1.5 and 54 matings per day (grand mean = 19.24, SD = 12.1, $N = 63$). The relative area of the lateral white patch was a significant predictor of increases in mating success in the full 1988–1990 model and in both reduced data sets as well (Table 7). The 1989–1990 full model indicated a tendency toward a negative association between female choice and males that were disproportionately heavy ($P = 0.07$); however, the effect of body weight disappeared in the reduced model. As in the other analyses, an F -test of the full models including second-order terms indicated no additional significant overall effects (1988–1990: $F_{6,31} = 1.45$, $P = 0.23$; 1989–90: $F_{9,17} = 1.6$, $P = 0.19$). Cubic-spline analyses indicated that the white coloration variable had linear relationship with the fitness component.

Males who were successful in attracting and retaining females tended to court fewer times per spawning female ($r = -0.35$, $N =$

45, $P = 0.02$), and there was a trend for these males to have longer courtship bouts ($r = 0.26$, $N = 45$, $P = 0.08$).

Spatial and Temporal Variation in Selection

There were no significant interactions between selection gradients and experiment, indicating that the effect on a fitness component of a particular male characteristic did not differ temporally within a reef from

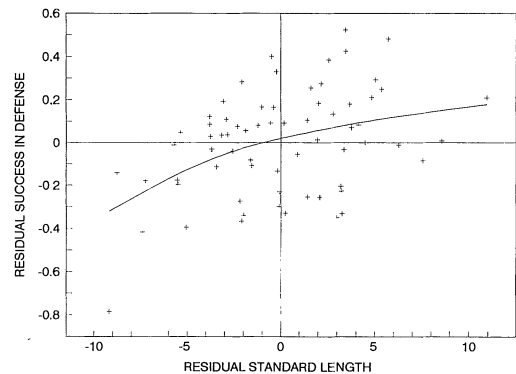


FIG. 4. Relationship between body length and the component of fitness arising from successful defense of a mating territory. The fitness component in this case is expressed as the residual of the arcsine transformed proportion of the total spawnings accrued by the resident male in a regression of this proportion against all significant characters except length. Length is expressed as the residual of length in a regression against all other significant characters. Note that this plot displays the same relationship between success and length as that analyzed by the reduced model in Table 6. The fitness function was calculated using cubic splines, based on 1988–1990 data; the outer lines are one SE, calculated by bootstrap methods.

TABLE 7. Linear effects of male morphological characters on the fitness component reflecting the ability to attract and retain females at mating sites. Details are as in Table 5.

| Variable | 1988-90 | | | | 1989-90 | | | |
|---------------------|---------|---------|---------|---------|---------|---------|---------|---------|
| | Full | | Reduced | | Full | | Reduced | |
| | β | t | β | t | β | t | β | t |
| PREVSPWN | 0.37 | 4.62*** | 0.42 | 5.59*** | 0.56 | 3.89*** | 0.54 | 4.50*** |
| Standard length | 0.12 | 1.10 | | | 0.04 | 0.23 | | |
| Body depth | -0.03 | -0.31 | | | 0.06 | 0.47 | | |
| Tail length | -0.06 | -0.65 | | | 0.04 | 0.23 | | |
| Pectoral fin length | 0.11 | 1.37 | | | 0.12 | 0.95 | | |
| Black + white area | 0.07 | 0.92 | | | 0.00 | 0.00 | | |
| Relative white area | 0.19 | 2.11* | 0.23 | 2.94** | 0.28 | 1.53 | 0.44 | 3.87*** |
| Body weight | — | — | — | — | -0.20 | -1.89+ | | |
| Gut parasites | — | — | — | — | -0.11 | -1.03 | -0.13 | -1.20 |
| Muscle parasites | — | — | — | — | 0.05 | 0.41 | | |

1988-90: $N = 63$, $r^2 = 0.80$ (full), $r^2 = 0.78$ (reduced).
1989-90: $N = 51$, $r^2 = 0.84$ (full), $r^2 = 0.82$ (reduced).

experiment to experiment (results not shown). This was also generally true for interactions between character effects and reef; thus selection gradients were generally uniform across spatial scales as well. The only exceptions to this were significant interactions between reef and the effect of pectoral fin length in the quality of sites acquired, and between reef and the effect of body length in site defense (Table 8).
These analyses also indicated a reef main effect on the distribution of response variables for all episodes of selection in all years; thus reefs varied in the total amount of mating activity occurring on them. Within a reef, response variables were not affected by experiment for either aspect of intrasexual selection, but there were significant experiment main effects in the analysis of female choice (results not shown). This indicates

that it was proper to include experimental block as a classification variable in the original multiple regression analyses.

DISCUSSION

There have been two general approaches taken in recent studies on the effects of phenotypic sexual selection on male traits. The first approach sorts through a series of characters potentially important to sexual selection, using multiple regression techniques similar to the approach that we have used here for the bluehead wrasse (e.g., Gibson and Bradbury, 1985; Höglund and Lundberg, 1987; Andersson, 1989; Hews, 1990; Moore, 1990; Zuk et al., 1990). This allows an estimate of the association of a particular character with some fitness component, holding the effects of other traits constant. The standardized partial regression coeffi-

TABLE 8. Tests for spatial and temporal heterogeneity in the action of sexual selection. Shown are the significant F -ratios for the interactions of reef and morphological characteristics, from models including reef, experiment (nested within reef), and the significant morphological variables from the multiple regressions (Tables 5-7). There were no significant interactions of morphological characteristics and experiment.

| Interactions with reef: | Character | F -ratio | df | P |
|--------------------------|---------------------|------------|-------|------|
| Quality of site acquired | | | | |
| 1988-90 | Pectoral fin length | 2.31 | 4, 41 | 0.07 |
| 1989-90 | Pectoral fin length | 3.41 | 2, 34 | 0.05 |
| Site defense | | | | |
| 1988-90 | Body length | 4.27 | 3, 39 | 0.01 |
| 1989-90 | none | | | |
| Female choice | | | | |
| 1988-90 | none | | | |
| 1989-90 | none | | | |

cients (or selection gradients) allow an estimate of the degree of importance among traits, as well as the direction of phenotypic selection on the trait (Lande and Arnold, 1983; Endler, 1986; Mitchell-Olds and Shaw, 1987). While these studies are extremely useful in identifying potentially important characteristics, multivariate analyses of more than one source of sexual selection have been carried out only for a fungus beetle (Conner, 1988), a dragonfly (Moore, 1990), a lizard (Hews, 1990), and red jungle fowl (Zuk et al., 1990; Ligon et al., 1990).

The second approach identifies a potentially important characteristic more or less arbitrarily, and then proceeds directly to investigations of phenotypic selection on that character. These sorts of investigations have taken two forms. In some studies, changes in the distribution of the characteristic have been followed through successive episodes of selection (e.g., van den Berghe and Gross, 1989). Alternatively, the characteristic has been directly manipulated to measure its effect on some fitness component (e.g., Semler, 1971; Andersson, 1982; Arak, 1983; Ryan, 1985; Kodric-Brown, 1985; Bischoff et al., 1985; Møller, 1988; Höglund et al., 1990). These approaches are valuable in specifying the dynamics of selection on a particular trait. Their only deficiency is that the character was often chosen a priori, and other uninvestigated characteristics may also be of importance.

Here we treat three different sources of sexual selection simultaneously, and investigate interactions among these sources on male characteristics. In addition, we have used a multiple regression approach to identify potentially important characteristics among a suite of initial possibilities, thereby reducing the arbitrariness of an a priori choice.

Opportunities for Selection and the Mating System of the Bluehead Wrasse

The mating system of *Thalassoma bifasciatum* is particularly well known, and several of its features can be related to important features of sexual selection.

Intrasexual selection: The mating system of the bluehead wrasse superficially resem-

bles an "exploded lek" system in that mating sites are fixed but somewhat dispersed (Payne and Payne, 1977; Borgia et al., 1985). However, a female tends to be quite faithful to a particular mating site, even when a new male takes possession of it (Warner, 1987). Each mating makes up a very small proportion of a female's lifetime reproductive success, and thus survival over many reproductive bouts is much more critical to female fitness than an increase in the return from any particular bout. The survival benefits of continuing to mate at a known site may be much more important than any gains to be made through mate assessment and subsequent switching (Warner, 1986, 1987). Because of this, sites are a dependable and measurable mating resource for males, and this forms the basis for intrasexual competition between TP males. Even highly unattractive males may be able to gain mating success simply by acquiring certain sites (Table 2A). This is in contrast to some other studies of phenotypic sexual selection (e.g., Andersson, 1989; Moore, 1990), where differences in success among territorial males appear to be largely due to female choice rather than the quality of the site they have won.

On the other hand, IP males have testes that are three to four times larger than TP males (Warner and Robertson, 1978), and they can substantially reduce the mating success of large males (Warner and Hoffman, 1980a, 1980b). Thus it is no surprise that defensive ability can contribute significantly to TP male success (Table 2B). It should be noted, however, that the effectiveness of an individual TP male in site defense appears to improve over time: while TP males lost over 25% of their matings to IP males in the week after manipulation, less than 3% of matings are lost in this way by males who have been in residence for a number of weeks ($N = 12$ native males; see also Hoffman et al., 1985).

Intersexual selection: Competition between males has a greater effect on variance in mating success than does female choice (Table 2). Recently it has been suggested that in some cases intrasexual competition could essentially overwhelm the role of female choice in the evolution of sexually selected traits (Beehler and Foster, 1988), es-

pecially where female movements are limited (e.g., Hews, 1990). While intrasexual competition is certainly strong in the bluehead wrasse, a significant amount of variation in mating success among males can still be ascribed to female choice (Table 2C). This is because they are not coerced to mate at particular sites and can move freely among potential mates.

Correlates and Interactions of Male Characters Potentially Important in Sexual Selection

Body Length and Depth.—Length was important in both winning a quality site and the defense of that site; relative body depth also was associated with site defense in 1989–1990. In general, longer and deeper males had higher success. Size has been implicated in all phases of sexual selection in a wide variety of organisms (e.g., Le Boeuf, 1974; Perrone, 1978; Howard, 1978; Clutton-Brock et al., 1982; Bateson, 1983; Côté and Hunte, 1989; Hews, 1990; Moore, 1990), and it is not surprising that it conveys success in competition between males. Detailed studies of territorial contention conducted by Mark Schildhauer (1991 and pers. comm.) indicate that contests between males consist of parallel swims and alternating chases over the territory, in which the leader and follower repeatedly exchange roles. The former behavior may act to assess relative size, and the latter may test swimming speed, which within a species is a function of individual body length (reviewed by Videler and Wardle, 1992).

All morphometric characters are correlated with length, of course, and the apparent importance of length per se could be a reflection of our decision to use it as the referent for other variables. However, multiple regressions with unscaled variables (not shown here) showed length explained more variance than any other correlated variable, in terms of both site acquisition and site defense.

Body length was the only male characteristic that appeared to have anything other than a linear relationship with fitness components. In the contests between TP males for mating site acquisition, the advantage of additional length is greatest in the middle range (Fig. 3). This situation can arise if all

smaller TP males are relegated to poor sites and larger TP males nearly always get successful sites. The result for site defense against IP males has a similar interpretation: at the largest TP male sizes, further increases in size convey little increased benefit (Fig. 4). In neither case was there any evidence for stabilizing selection: that is, no maxima occurred at intermediate trait values. This illustrates the usefulness of the cubic spline technique for investigating fitness surfaces: while in both these cases a length² term would be significant in a full model, the cubic spline regression shows that selection is directional (see Schluter, 1988). Note that the residuals used in the cubic spline plots have corrected for correlations with other independent variables in the same fashion as the multiple regression models.

In general, body length was uncorrelated to any of the behaviors that we measured. The only exception to this was a strong negative relationship with courtship frequency per spawning female ($r = -0.52$, $N = 51$, $P < 0.001$). Thus longer males appear to spend less time in courtship per female in the highly successful sites they have acquired.

Coloration. The relative size of the lateral white band appeared to be important in female choice and in defense against smaller males. This term was expressed for each male as the residual in the regression of area of white against the combined area of the adjoining black bands (see Fig. 1); thus individuals with relatively conspicuous white bands appear to be favored by females in mating, and are more successful in defending those females against the intrusions of IP males.

Because the eggs are pelagic and there is no parental care, male bluehead wrasses provide no obvious direct benefit to the female or the young. This is similar to many lekking species, and the evolution of female preferences for male characteristics in such species remains a matter of debate (see Balmford, 1991, and Kirkpatrick and Ryan, 1991, for recent reviews). The white band encompasses the thickest part of the body, covering both the swimming muscles (wrasses use pectoral sculling to swim) and the gut; thus it may reveal the robustness and feeding ability of a particular male (Zahavi, 1977; Andersson, 1986; Grafen, 1990).

Alternatively, the band is also by far the most conspicuous feature on the body, and its effect on females may simply be a result of selection on males to exploit the existing visual system of females (Endler, 1989; Ryan, 1990). Conspicuousness could also aid in site defense through longer-distance deterrence of intruding males. It remains to be shown whether there is variation among females in preference for the white band, and whether there are any associated direct or indirect costs and benefits (see Reynolds and Gross, 1990).

While this coloration variable remains positively correlated with length (indicating that longer individuals tend to have relatively larger white bands, Table 4), length itself was unimportant to female choice. The coloration character did not correlate with any measure of aggression or courtship.

Parasites.—In general, parasites appeared to have little or no effect on sexual selection. This lack of effect of parasites is especially intriguing given the suggestion that some male secondary sexual characters may serve as indicators to females of parasite load (Hamilton and Zuk, 1982). Tail length (both in raw form or scaled to length) was the only male morphological characteristic that we measured that was correlated with parasite load (Table 4). Individuals with more muscle parasites tended to have relatively shorter tails. However, tail length was not associated with any of the fitness components measured. Given the Hamilton-Zuk hypothesis, one might expect that the white band on the flank, which did appear to affect female choice, would be negatively correlated with parasite load. No such relationships are apparent (Table 4).

Relative Pectoral Fin Length.—This was important in securing a quality territory in competition with other TP males. A relatively large fin should result in faster swimming speeds (J. Videler, pers. comm.). Because contests between TP males consist of alternating chases (see above), faster swimming may convey an advantage in these contests. Relative pectoral length did not correlate with any behavioral measure, but it should be noted that all behavioral data were taken after male-male competition for site acquisition was completed.

Weight.—In the full 1989–90 model for

intersexual selection, disproportionately heavy individuals tended to be less successful in attracting females (Table 7). Body weight per se may be inconsequential in many fishes, because most have physiological means to make themselves weightless in water (Schmidt-Nielsen, 1972). However, fishes that are disproportionately heavy should displace more volume and have greater mass, and this could reduce their speed and agility in the tight turns characteristic of courtship. The alternative interpretation is that attractive males lost more weight over the course of the experiment, perhaps because of increased allocations of energy towards reproduction (e.g., Sargent, 1985).

Spatial and Temporal Heterogeneity in Selection

There were remarkably few significant differences in selection gradients among reefs, and none among experiments (Table 8). Thus the effect of male characteristics on fitness components was generally uniform across reefs and experiments.

The significant interaction between reef and the effect of body length on defensive ability (Table 8) may reflect spatial variability in the intensity of IP male activity (Warner, 1984a, 1984b). A higher proportion of spawns were lost on larger reefs with active group spawning aggregations (reefs 13 and 11), and the selection gradients for the effect of size on defensive ability tended to be higher on these reefs (unpubl. obs.). Similarly, the relationship between pectoral fin length and the ability to acquire a quality site varied significantly between reefs; selection gradients tended to be higher on larger reefs, where TP males must swim farther distances during contention for territories.

In these analyses of spatial and temporal effects, the significant main effect of reef suggests that reefs differed in the distribution of response variables. In other words, there were reef-to-reef differences in the range of mating site qualities, in the degree to which IP males posed problems for territory owners, and the degree to which females tended to switch sites when new males took occupancy. This is not surprising, considering the extreme diversity of shape and size

TABLE 9. Intercorrelations among the fitness components. Values for site defense and female choice were entered as residuals in a regression against the appropriate adjuster for site differences (*ARSPRIOR* or *PREVSPWN*). * $P < 0.05$.

| | Site defense | Female choice |
|--------------------------|-----------------|----------------|
| Quality of site acquired | 0.13 (61) | -0.31* (59) |
| Site defense | | 0.22 (60) |

among patch reefs (Warner and Hoffman, 1980a). For example, a reef with a broad downcurrent edge has more potential mating sites compared to a reef with a narrow downcurrent point (see Warner, 1988), and thus variance in mating success among territorial males may be relatively lower on broader reefs. The proportion of the population made up of IP males also varies strongly with reef size (Warner and Hoffman, 1980a). Reefs with higher proportions of IP males have heightened IP male activity (Warner, 1984a), which would increase the intensity of defensive activity in TP males.

Within a reef, intrasexual selection gradients did not change over the course of a series of experiments on a reef, but intersexual gradients did. This temporal effect indicates that the tendency of females to switch sites may have changed from experiment to experiment.

Comparisons with Other Systems

Overall, there was no evidence of directional phenotypic selection arising from different sources acting antagonistically on any morphological trait. The possession of a longer body and relatively larger white bands conveyed higher success in both selection episodes in which they were significant. This is similar to the findings of Moore (1990) for a coloration character in a dragonfly, and Zuk et al. (1990) and Ligon et al. (1990) for comb size in red jungle fowl, where these characters showed congruent directional selection from both intrasexual and intersexual sources. The only study that suggests antagonistic selection arising from intra- versus intersexual sources is that of Boake (1989) for a picture-winged fly. She found

that body size is under positive selection in male-male contests, but tended ($P = 0.07$) to be under negative selection for courtship success.

Interestingly, as in some previous studies (Moore, 1990; Zuk et al., 1990), female bluehead wrasses showed no response to male size per se, but responded instead to coloration characters. In his study of a fungus beetle, Conner (1988) also found no evidence for female responses to male size; coloration was not investigated. In contrast, Johnson (1988) suggested that coloration may be important in female-female competition in pinyon jays, but heavier females were more attractive to males.

A survey of the behavioral correlates of fitness components in this study justifies the decision not to include behavior among the male traits in the regression analyses. Courtship rates were *negatively* correlated with success in attracting females, and aggression rates toward small males were *negatively* correlated with site acquisition and defense. This indicates that courtship and defense, like many other behaviors, may be more a response to the situation in which a male finds himself rather than an intrinsic quality of the individual. In this interpretation, males court at a higher rate in response to being unsuccessful, and must be more aggressive in areas with high concentrations of small males. In a study with red jungle fowl, Zuk et al. (1990) also found few correlations with courtship behavior and reproductive success, and no correlations between morphology and courtship behavior. Studies which treat both morphology and behavior as intrinsic male characteristics (e.g., Andersson, 1989) should be viewed with some caution unless it can be demonstrated that the males are constrained in their ability to alter their behavior.

Possible Spurious Correlations

There is the possibility that a character shown to be important for one aspect of sexual selection appears important elsewhere because the outcome of one episode of selection has indirect effects on another. In this study, indirect effects are possible if two fitness components are correlated, and if they share a significant male characteristic. The only two components that are cor-

related are quality of site acquired and female choice (Table 9): territories that were highly successful prior to a manipulation tended to decline in mating success after, and vice versa. There were no significant male characters shared by these two components (Tables 5 and 7).

Comparison with the Unmanipulated System

The experiments in this study used transplantations of entire groups of males to reefs upon which all prior-resident males had been removed. This greatly facilitated the investigation of the male characters under phenotypic sexual selection because sample sizes were large, and the group of males in contention could be easily identified.

Under normal circumstances, however, all mating sites on a reef do not become available at once, and simultaneous replacements could have a disruptive effect on the reef as a whole. To investigate the magnitude of this effect, we performed a series of single-male removals in 1988; in these removals, all other males on the reef are natives, and no other sites are disrupted. As with the larger experiments, we estimated changes in the number of females associated with a site as the absolute percentage change in the daily total of matings from previous values, either up or down, and adjusted for overall changes in spawning rate derived from simultaneous observations of unmanipulated sites. These single-removal sites changed an average of 48% in their associated mating rate ($N = 11$, $SD = 29\%$), nearly identical to the value for the multiple-removal males (45%). Similarly, average losses to IP males at sites were virtually the same after single removals (28%) as after multiple removals (27%).

Thus our estimates of contributions to natural variance in male mating success from these two components do not appear to be inflated because of our experimental procedures. However, there is a possibility that the amount of variance in mating success explainable by male differences may be less than indicated in Table 2A. Under normal circumstances, the contending group of males for a particular site does not include all of the TP males on the reef, but instead only the largest nonterritorial TP males and

nearby territorial males (Schildhauer, 1991). The largest male within the contending group tends to win, but there are often other larger males who do not enter into the competition. Some of these larger males would stand to gain in mating success, but possession of even a moderately successful territory effectively removes a male from contention because he cannot simultaneously maintain his own site and assess another. Thus, as Schildhauer (1991) has shown, a very large male might win a moderately successful site on one day, but then be out of the competition for a more successful site soon after. While male length correlates strongly with mating success over all TP males, the correlation is weaker among the most successful males.

Concluding Remarks

An ideal study of sexual selection should go beyond simple phenotypic selection, measuring heritability of the characteristics and the genetic variance/covariance matrix to predict the actual evolutionary response to selection. The long pelagic larval period of the bluehead wrasse makes it much less amenable to studies of the heritability of traits. While it is possible that features under phenotypic selection may not have any evolutionary consequences (Price et al., 1988), even if they are heritable (Alatolo et al., 1990), sexual selection theory makes many assumptions about the action of phenotypic selection. These assumptions strongly affect the predicted evolutionary outcome (Arnold, 1983; Heisler et al., 1987). Thus there is a continuing need for studies that document the actual workings of phenotypic sexual selection on male traits.

The multiple regression techniques used in this work are extremely useful for identifying potentially important characteristics among a pool of candidates, but they do not establish causation or eliminate problems arising from correlations among measured characteristics or other unmeasured variables. The next step is to conduct experiments on the causes for and the mechanisms of sexual selection, particularly in reference to consistency and consequences of female preferences. Manipulative experiments in the field are one of the most convincing ways to test hypotheses, and we now know the

proper characteristics to investigate and the context in which to manipulate them.

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