

INFLUENCE OF ENERGY RESERVES ON THE
EXPRESSION OF A SECONDARY SEXUAL TRAIT IN
MALE BICOLOR DAMSELFISH, *STEGASTES PARTITUS*

Roland A. Knapp

ABSTRACT

Recent theoretical investigations suggest that male energy reserves may often play a central role in sexual selection because of their influence on male secondary sexual characteristics. However, the importance of male energy reserves to mating systems is at present difficult to evaluate because of the paucity of studies in which energy reserves are experimentally manipulated. Previous research on the bicolor damselfish, a marine species with exclusive male parental care of eggs, showed that courtship is an indicator of male parental quality and that females use courtship to distinguish among potential mates. In addition, preliminary results suggested that courtship rate and parental quality may both be a function of male energy reserves. The objective of this study was to experimentally manipulate male energy reserves in a natural population of bicolor damselfish by diet augmentation, and thereby determine the effects of energy reserves on courtship rates. The diet augmentation experiment strongly influenced male courtship rates. As predicted, fed males courted at higher rates than unfed males, and courtship was an increasing function of body fat. Contrary to the prediction that the courtship rates of unfed males would remain the same before and after the diet augmentation experiment, however, courtship rates of unfed males decreased significantly. This may indicate that in addition to the strong effect of the diet augmentation experiment on courtship rate, other factors such as changes in the availability of natural food and social interactions among males also influenced courtship rates. Although male energy reserves are known to influence the expression of secondary sexual characters in birds, amphibians, and freshwater fishes, the results of this study demonstrate that similar processes can also operate in marine fishes.

The evolution of elaborate secondary sexual characters in males of many animal species remains one of the most difficult and controversial problems in evolutionary biology (reviewed by Partridge and Harvey, 1986). Since these characters often appear detrimental to the survival of the bearer, Darwin (1871) proposed that such traits did not evolve under natural selection, but instead evolved via sexual selection because of the advantage they conferred in obtaining mates. He suggested that this advantage might often be the result of a female preference for males with more exaggerated secondary sexual characters (e.g., ornaments, displays). The evolution of secondary sexual characters and female preferences is subject to two very different interpretations. According to one view, elaborate male secondary sexual characters have evolved as a result of female preferences for male traits that are currently unrelated to male quality, with females benefiting only indirectly through the increased attractiveness of their sons (Fisher, 1930; O'Donald, 1980; Kirkpatrick, 1982). The importance of this "Fisher process" remains unclear, since empirical support is difficult to obtain. The alternative view maintains that elaborate ornaments or displays have evolved because they accurately signal male quality (Zahavi, 1975; Grafen, 1990), and by choosing mates on the basis of such characters, females obtain direct fitness benefits as a result either of offspring inheriting the genes for high viability from their fathers (Hamilton and Zuk, 1982; Andersson, 1986; Pomiankowski, 1988), or of increased offspring survival as a consequence of high quality paternal care (Maynard Smith, 1985; Hoelzer, 1989; Price et al., 1993). The results of several empirical studies

support the view that the degree of male character elaboration can serve as an indicator of either male viability (Watt et al., 1986; Göransson et al., 1990; Møller, 1991) or parental quality (Hill, 1991; Knapp and Kovach, 1991).

Several recent theoretical investigations suggest that the degree of male character elaboration and benefits obtained by females as a result of their choice of mate may often be mediated through overall male condition (Andersson, 1986; Grafen, 1990; Price et al., 1993). For example, in species in which males provide parental care and develop elaborate secondary sexual characters, the quality of paternal care and the degree of character development may both be a function of male energy reserves, since both are often energetically costly (Coleman and Fischer, 1991; Höglund et al., 1992). In such species, females choosing elaborately adorned or vigorously displaying males will be choosing males in good condition who may be more able to provide high quality parental care. Although a few studies have shown that male condition does influence the expression of secondary sexual characters (Evans, 1991; Milinski and Bakker, 1990; Andersson, 1992), I do not know of any studies showing a relationship between male condition (e.g., energy reserves) and character expression in a marine fish.

As is typical of pomacentrids, male bicolor damselfish (*Stegastes partitus*) provide sole care to eggs. Females mate preferentially with vigorously courting males (Schmale, 1981; Knapp and Warner, 1991), and male egg-hatching success is an increasing function of courtship rate (Knapp and Kovach, 1991). Therefore, as a result of their preference for vigorously courting males, females choose mates who provide high-quality parental care. In addition, preliminary data suggest that male condition is highly variable among males, and that courtship rate and male energy reserves are positively correlated (Knapp and Kovach, 1991). These results raise the possibility that males are food-limited, and that courtship rate serves as an indicator of male condition, which may in turn influence the quality of parental care. Therefore, the objective of the present study was to experimentally manipulate male energy reserves in the field and determine the effect of this manipulation on male courtship vigor. I predicted that fed males would have higher courtship rates than unfed males, and that courtship rate would be an increasing function of male energy reserves.

Study Species.—Bicolor damselfish are a sexually monomorphic Caribbean reef fish (Randall, 1968). Males and females defend permanent territories from which they feed on current-borne plankton (Emery, 1973). Reproduction is lunar cyclic, with spawning beginning just before the full moon and ending just after the new moon (Robertson et al., 1988; Fig. 1). Spawning occurs during a 1-h period starting at dawn during which females travel to and lay eggs in male territories (Myrberg, 1972). Eggs are defended by males until the eggs hatch as planktonic larvae, 3.5 days after laying (Robertson et al., 1988). Beginning after the dawn spawning period and continuing throughout the day, males produce vigorous courtship displays in which a male leaves his territory and swims toward a female while performing a series of rapid vertical dives termed "dips" (Myrberg, 1972). Courtship rates among males are highly variable (Knapp and Warner, 1991).

MATERIALS AND METHODS

I conducted this study over three reproductive cycles from April–June 1991 on the Teague Bay forereef, St. Croix, U.S. Virgin Islands (17°45'N, 64°35'W). The 700-m² experimental site encompassed the territories of 22 nesting male bicolor damselfish and approximately 40 female bicolor damselfish. At the beginning of the first reproductive cycle, I replaced the natural nests of all males with artificial nests (small clay flowerpots; see Knapp and Warner, 1991, for details). All males were

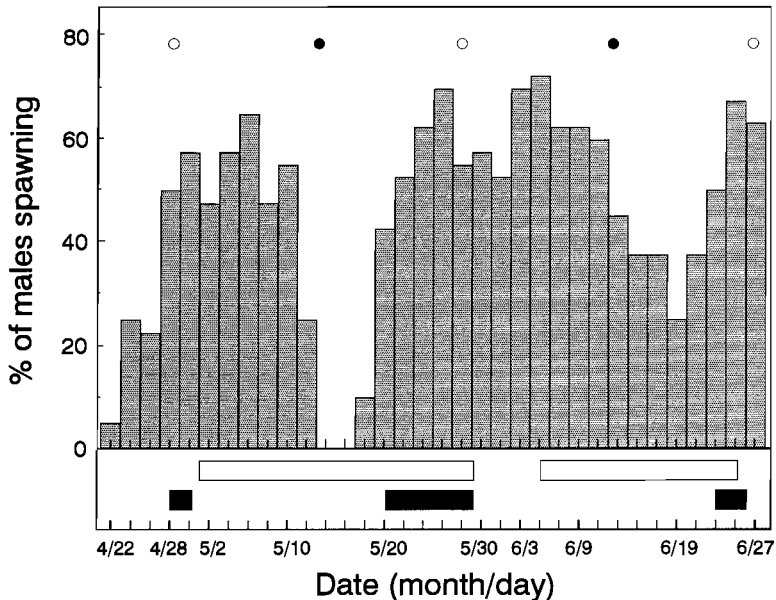


Figure 1. Histogram of reproductive activity (% of males spawning/day) in *Stegastes partitus* over the duration of the diet augmentation experiment. Open circles represent full moons and solid circles represent new moons. The timeline shows when courtship measurements (■) and diet augmentations (□) were conducted.

identifiable on the basis of size, territory location, and prominent scars or tags (subcutaneous injections of acrylic paint; Thresher and Gronell, 1978).

At the beginning of the first reproductive cycle, the 22 males on the study site were divided into two groups: "fed" and "unfed." To ensure that fed and unfed males were interspersed and that females would be surrounded by males in both treatments, I assigned males to each of these treatments systematically. Male territories occurred in a narrow band (approximately 10 m wide) along the base of the reef. Since the reef runs in an east-west direction, I classified males by moving a rope from east to west over the band of territories (and perpendicular to the base of the reef) and assigned the male in each successive territory encountered by the rope as "fed" or "unfed" in an alternating manner.

Timing of Reproductive Cycles.—During the diet augmentation experiment, I monitored spawning activity at an unmanipulated site to allow me to follow the progression of each reproductive cycle. This was necessary to ensure that courtship measurements for the diet augmentation experiment were started at the same stage of each cycle (Fig. 1). The spawning activity monitoring site was approximately 30 m away from the experimental site, and bicolor damselfish from the two sites were never seen interacting during the experiment. I monitored daily spawning activity by noting the presence of new clutches in the nests of 20 males over the duration of the diet augmentation experiment. Since even widely separated populations of bicolor damselfish show identical lunar patterns of reproduction (Knapp, unpubl. data), the spawning activity at the unmanipulated site was representative of that at the experimental site.

Measurement of Male Courtship.—I measured the courtship rates of fed and unfed males at the beginning of each of three reproductive cycles (Fig. 1). I measured courtship rates by counting the number of dips performed by individual males during 10 min focal observations (Knapp and Warner, 1991, for details). During courtship measurement periods (April 28–30, May 20–29, June 23–26), focal observations were taken daily for all 22 males. I calculated average courtship rates of males during each period by dividing the sum of daily courtship rates for each male by the number of days in the period. When courtship measurement periods overlapped with the feeding period (May 20–29, June 23–26), I fed males after completing courtship measurements.

Diet Augmentation.—I conducted diet augmentations during three reproductive cycles (Fig. 1). I augmented the diets of males in the "fed" category by feeding these males small pieces of beef fat (\bar{x} = 0.002 g/piece) once daily from May 1–29 and June 5–25 (Fig. 1). I delivered known amounts of food

directly to individual males by using a large syringe, and fed males until they began refusing delivered food. Any uneaten pieces were immediately sucked back into the syringe to prevent "unfed" males from eating them, and to reduce the likelihood of attracting heterospecific fishes.

Measurement of Male Energy Reserves.—After the June 23–26 measurement of courtship rates, I sacrificed all fed and unfed males for fat extraction. I measured males for standard length and weighed them after removing any material contained in digestive tracts. I estimated male energy reserves by extracting nonpolar lipids. Such lipids are the major source of energy for reproduction in fishes (Reznick and Braun, 1987; Coleman and Fischer, 1991), and should therefore provide an accurate measure of the amount of energy available to male bicolor damselfish. Prior to fat extraction, fish were dried at 50°C for 10 days to a constant weight, and then ground into a fine homogenate using a mortar and pestle. The entire homogenate from each fish was refluxed in petroleum ether for 12 h in a Goldfish Fat Extraction Apparatus (Dobush et al., 1985). The percent body fat of individual males was calculated by dividing the total weight of extracted nonpolar lipids by the pre-extraction weight of the fish homogenate.

Condition factors are commonly used to produce a measure of fish robustness that is independent of size (Bolger and Connolly, 1989), and are often used to estimate male energy reserves (Milinski and Bakker, 1990). The validity of using male condition as an estimate of energy reserves is uncertain, however, since there is some evidence that fish replace utilized lipids with water (Unger, 1983; Fitzgerald et al., 1989). To compare the results of the diet augmentation experiment obtained using male energy reserves versus male condition, I calculated condition factors of individual males in addition to measuring percent body fat. Although condition factors are often calculated simply as (weight/length³), the exponent that produces the best linear relationship between weight and length may often differ among fish species (Bolger and Connolly, 1989). Therefore, I calculated condition factors from equations generated using the NLIN procedure of SAS software (SAS, 1988). Condition factors based on wet weight (wet condition) and dry weight (dry condition) were calculated from the following equations:

$$\text{Wet condition} = 10^4 \times \text{wet weight (g)/length (mm)}^{2.505}$$

$$\text{Dry condition} = 10^4 \times \text{dry weight (g)/length (mm)}^{3.040}$$

Data Analysis.—One fed male and one unfed male disappeared during the course of the experiment, and I excluded both males from all analyses. I tested all variables for normality before analysis with parametric statistics. Any variables that were distributed in a non-normal fashion I first transformed to fit a normal distribution. If unable to do so, I subjected them only to non-parametric analyses.

Courtship rates of males measured during the second and third reproductive cycles (i.e., after the start of diet augmentation; Fig. 1) were significantly correlated ($N = 20$, $r = 0.63$, $P < 0.003$). Therefore, I calculated "post-feeding" courtship rates for fed and unfed males by averaging the number of dips performed during all 14 focal samples taken for each male (20–29 May, 23–26 June).

RESULTS

Diet augmentation strongly influenced courtship rates of male bicolor damselfish. Courtship rates of fed and unfed males did not differ before diet augmentation (Fig. 2; one-tailed Mann-Whitney U -test: $Z = -0.26$, $P > 0.5$), but fed males courted at significantly higher rates after diet augmentation (Fig. 2; one-tailed Mann-Whitney U -test: $Z = 2.12$, $P < 0.02$). Furthermore, after diet augmentation, fed males courted at higher rates than unfed males on 13 of 14 days (one-tailed binomial test, $P < 0.001$).

The higher courtship rates of fed males relative to unfed males appear to result primarily from a decrease in the courtship rates of unfed males. While the courtship rates of unfed males measured after the period of diet augmentation were significantly lower than those measured before diet augmentation (Fig. 2; Wilcoxon Rank Sum Test (one-tailed); $N = 10$, $T^- = 46$, $P = 0.03$), courtship rates measured during the two periods for fed males were not significantly different (Fig. 2; Wilcoxon Rank Sum Test (one-tailed); $N = 10$, $T^+ = 42$, $P = 0.08$). However, the lack of a significant increase in the courtship rates of fed males should be interpreted with caution since the result is only marginally non-significant and the small sample size decreases the likelihood of detecting significant differences.

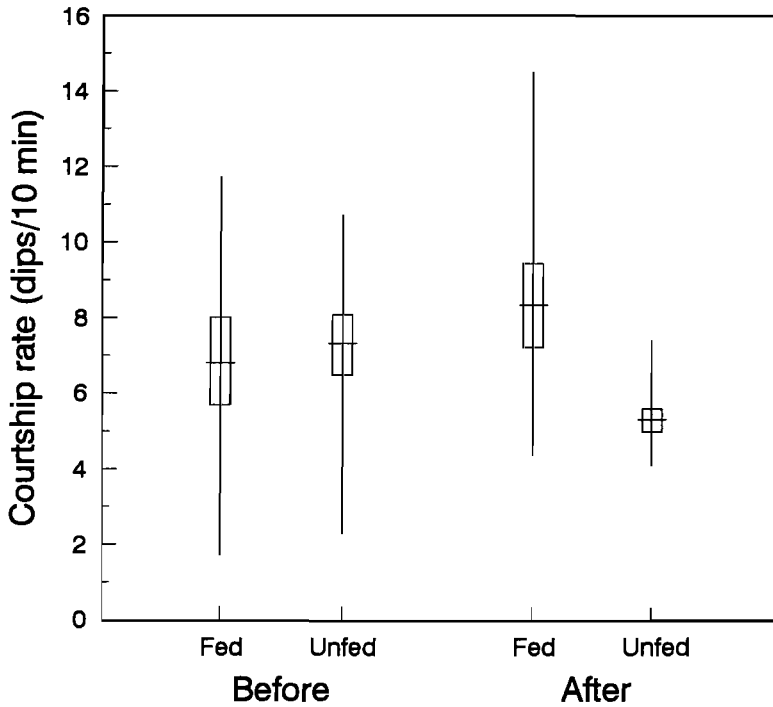


Figure 2. Courtship rates of fed and unfed males before and after diet augmentation in *S. partitus*. Values are means (horizontal lines), standard errors (vertical bars), and ranges (vertical lines). Sample sizes are 10 for each group. Courtship rates were not different before diet augmentation, but after diet augmentation fed males courted at significantly higher rates than unfed males.

The variance in courtship rates of unfed males also decreased significantly after the period of diet augmentation (Fig. 2; $S^2_{\text{before}} = 5.94$, $S^2_{\text{after}} = 1.14$; $F_{9,9} = 5.21$, $P < 0.05$) while the variance in courtship rates of fed males remained unchanged ($S^2_{\text{before}} = 13.39$, $S^2_{\text{after}} = 11.50$; $F_{9,9} = 1.16$, $P > 0.5$).

After the period of diet augmentation, fed males had significantly higher levels of body fat than unfed males (Table 1). Fed and unfed males did not differ in size, wet condition, or dry condition (Table 1). Males in the "fed" category showed consistent differences in their willingness to consume food delivered to them (range = 0.6–40.6 pieces/male/day; $\bar{x} = 16.8$ pieces/male/day). Although it is unclear what caused these differences in feeding rates among males, the number

Table 1. Results of diet augmentation experiment

Male characteristic	Fed males	Unfed males	Test statistic	P
	\bar{x} (1 SE)	\bar{x} (1 SE)		
Body fat (%)	14.7 (1.9)	7.5 (1.2)	10.43	0.002*
Wet condition (weight/length ^{2.505})	3.3 (0.1)	3.2 (0.1)	0.37	0.55†
Dry condition (weight/length ^{3.040})	1.3 (0.0)	1.3 (0.0)	1.56	0.23†
Standard length (mm)	53.2 (1.1)	52.4 (0.7)	0.45	0.51†

* One-way analysis of variance (one-tailed).

† One-way analysis of variance (two-tailed).

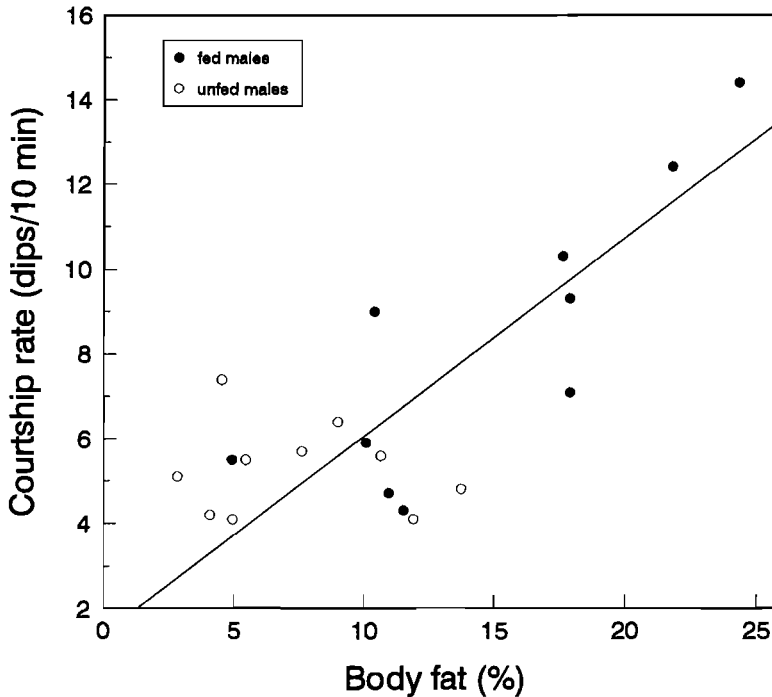


Figure 3. Courtship rate (mean number of dips·10 min⁻¹) versus percent body fat in male *S. partitus*. Courtship rate and percent body fat are significantly correlated for fed males and fed + unfed males, but uncorrelated for unfed males alone.

of pieces of food eaten by a male was significantly positively correlated with his % body fat ($N = 10$, $r = 0.85$, $P = 0.002$) and with his courtship rate ($N = 10$, $r = 0.84$, $P < 0.003$), both measured at the end of the diet augmentation experiment. Furthermore, courtship rate increased significantly with male body fat among fed males (Fig. 3; $N = 10$, $F_{1,8} = 18.47$, $R^2 = 0.66$, $P < 0.003$). These results indicate that males who ate more of the delivered food had higher energy reserves, and support the hypothesis that male courtship rates are an increasing function of energy reserves.

Although I expected that the courtship rates of unfed males would show the same positive correlation with % body fat as that shown by the courtship rates of fed males, courtship rate and % body fat of unfed males were uncorrelated (Fig. 3; $N = 10$, $r = -0.13$, $P > 0.4$). This lack of a relationship may have resulted from the narrow range of courtship rates observed for unfed males after the period of diet augmentation (Fig. 2). In fact, courtship rates of unfed males may lie along the same regression line as those of fed males, since when fed and unfed males are included in the same analysis, the relationship between courtship rate and body fat remains highly significant (Fig. 3; $N = 20$, $F_{1,18} = 25.73$, $R^2 = 0.57$, $P < 0.0001$).

Courtship rates were uncorrelated with either wet condition (fed males: $N = 10$, $r = 0.04$, $P > 0.9$; unfed males: $N = 10$, $r = 0.25$, $P > 0.4$; all males: $N = 20$, $r = 0.14$, $P > 0.5$) or dry condition (fed males: $N = 10$, $r = 0.33$, $P > 0.3$; unfed males: $N = 10$, $r = 0.18$, $P > 0.6$; all males: $N = 20$, $r = 0.38$, $P > 0.09$). Male body fat was also uncorrelated with wet condition (fed males: $N = 10$, $r =$

0.27, $P > 0.4$; unfed males: $N = 10$, $r = 0.09$, $P > 0.8$; all males: $N = 20$, $r = 0.25$, $P > 0.2$). Body fat and dry condition were uncorrelated for both fed and unfed males (fed males: $N = 10$, $r = 0.56$, $P > 0.09$; unfed males: $N = 10$, $r = 0.22$, $P > 0.5$), but significantly positively correlated for all males combined ($N = 20$, $r = 0.52$, $P < 0.02$).

DISCUSSION

The results of the diet augmentation experiment show that male courtship rate is correlated with the amount of food eaten by individual males and with male percent body fat. These results strongly suggest that energy reserves influence male courtship rates in the bicolor damselfish. Two alternative explanations for the relationship between male energy reserves and courtship rate are possible, however. These are (1) that intrinsic differences among males in their willingness to consume food resulted in the relationship between body fat and male courtship rate; and (2) that the positive relationship between body fat and male courtship rate is a consequence of vigorously courting males requiring more food instead of more food resulting in higher courtship.

The observed correlations between the number of pieces of food eaten and both % body fat and courtship rate may be caused not by the diet augmentation experiment, but instead by intrinsic differences between "fussy" males (i.e., those males who ate only a small percentage of delivered food in the diet augmentation experiment) and "non-fussy" males. For example, if fussy males have a naturally lower food intake than non-fussy males, then fussy males may also have lower energy reserves and courtship rates than non-fussy males, even in unmanipulated populations. Under these conditions, the pre-feeding and post-feeding courtship rates of fed males should be positively correlated. The fact that pre-feeding and post-feeding courtship rates of individual males are uncorrelated ($N = 10$, $r = 0.01$, $P > 0.9$) lends support to the idea that the diet augmentation experiment, not intrinsic male "fussiness", caused the relationships between the amount of food eaten and both % body fat and courtship rate.

The lack of a correlation between pre-feeding and post-feeding courtship rates also minimizes the possibility that the number of pieces of food eaten is the result, instead of the cause, of the measured courtship rates. If the positive correlation between courtship rate and the number of pieces of food eaten was a result of vigorously-courting males needing a higher food intake, then pre-feeding and post-feeding courtship rates would also be positively correlated. Because they are uncorrelated, the differences among fed males in their energy reserves and courtship rates are likely to be a consequence of among-male differences in the amount of food eaten during the diet augmentation experiment.

Despite the strong correlation between male courtship rate and % body fat, courtship rate was uncorrelated with condition as calculated from either wet or dry weight. In addition, there was no consistent relationship between % body fat and either wet or dry condition, suggesting that neither wet nor dry condition can be used to estimate male energy reserves in the bicolor damselfish. A lack of relationship between condition and energy reserves has also been reported in the fathead minnow, *Pimephales promelas* (Unger, 1983), and the three-spined stickleback, *Gasterosteus aculeatus* (Fitzgerald et al., 1989). Therefore, despite being widely used in fisheries research to estimate male energy reserves (Bolger and Connelly, 1989), condition factors may often be of limited utility.

The results of the diet augmentation experiment and the results of other studies suggest that the energy-limited expression of male secondary sexual characters

(e.g., ornaments, courtship displays) may be relatively common in fishes. For example, an observational study of the three-spined stickleback, *Gasterosteus aculeatus*, showed that the expression of male breeding coloration was correlated with condition (Milinski and Bakker, 1990). In an experimental study of the guppy, *Poecilia reticulata*, Kodric-Brown (1989) demonstrated that the expression of male orange coloration preferred by females is largely dependent upon diet. Although sticklebacks and guppies are both freshwater species, the current study extends these findings to a marine fish.

Although the diet augmentation experiment suggests that energy reserves are the primary factor influencing male courtship, several results suggest that factors other than diet augmentation, such as changes in natural food levels and social interactions among males may also have influenced male courtship rates. First, although I expected any difference in post-feeding courtship rates to result from an increase in the courtship rates of fed males, the observed difference between the courtship rates of fed and unfed males after the period of diet augmentation resulted primarily from a decrease in the courtship rates of unfed males. Second, the variance in courtship rates of unfed males decreased significantly between before and after the period of diet augmentation, while the variance in courtship rates of fed males remained unchanged. Third, although the courtship rates of fed males measured after the period of diet augmentation are positively correlated with % body fat, no correlation exists between courtship rate and % body fat for unfed males.

One explanation for the unexpected decreases in both the mean and variance of courtship rates of unfed males is that the availability of natural food may have decreased during the experiment. Under these conditions, diet augmentation could have provided sufficient energy to allow fed males to maintain their courtship rates while declining energy reserves of unfed males may have forced them to reduce their courtship rates.

An alternative explanation for the unexpected changes in the courtship rates of unfed males is that the unfed males adjusted their courtship rates based on the courtship rates of nearby fed males. By such a mechanism, the decrease in the mean and variance of courtship rates and the observed lack of a correlation between courtship rate and male body fat among unfed males could have resulted from unfed males being unable to match the courtship rates of nearby fed males, and subsequently reducing their courtship rates to conserve energy reserves. Although the diet augmentation experiment demonstrated the significant effect of energy reserves on male courtship rates, further experiments will be necessary to investigate whether social factors also influence male courtship rates.

In conclusion, previous research on mate choice in the bicolor damselfish, *Stegastes partitus*, demonstrated that females discriminate among potential mates on the basis of courtship rate (Schmale, 1981; Knapp and Warner, 1991), and that the female preference for the most vigorously courting males resulted in females mating with males of high parental quality (Knapp and Kovach, 1991). The results of the present experimental study show that courtship rate is influenced primarily by male energy reserves. Therefore, although male energy reserves are known to influence the expression of secondary sexual characters in birds, amphibians, and freshwater fishes, the results of this study demonstrate that similar processes can also operate in marine fishes.

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ADDRESS: *Sierra Nevada Aquatic Research Laboratory, University of California, Star Route 1, Box 198, Mammoth Lakes, California 93546*; MAILING ADDRESS: *Marine Science Institute, University of California, Santa Barbara, California 93106*.