Courtship as an honest indicator of male parental quality in the bicolor damselfish, Stegastes partitus

Previous work on the bicolor damselfish, a species with exclusive male parental care of eggs, suggested that female mate choice was based on male characteristics. The aims of this study were to determine whether females discriminate among potential mates on the basis of courtship and, if so, to determine whether courtship serves as an indicator of male parental quality. Observations made over two reproductive cycles showed that courtship rates and mating success of individual males are positively correlated and that males begin courting several days before females begin laying eggs. Experimental manipulations showed that a male’s courtship rate is indicative of the subsequent egg survival from his nest. We suggest that observed differences between males in their courtship rates and parental ability may be a result of differences in their energy reserves. These results demonstrate the operation of honest advertising and lend support to adaptive models of sexual selection. [Behav Ecol 1991;2:295–300]

Males of many animal species have elaborated secondary sexual characters that appear to be detrimental to their survival (see Darwin, 1871). Increasing evidence suggests that these ornaments often arise as a result of sexual selection via female choice (see Bate son, 1983; Bradbury and Andersson, 1987 for recent reviews). However, the mechanisms by which female choice results in the evolution of elaborate male characters are still a matter of considerable debate (Bradbury and Andersson, 1987; Partridge and Harvey, 1986).

Sexual selection theory suggests two very different mechanisms for the evolution of elaborate ornaments in males. “Arbitrary trait” models are based on the ideas of Fisher (1930) and propose that the male characters chosen by females are arbitrary and that the coevolution of female preference and male trait causes a runaway exaggeration of the trait. The theoretical plausibility of such a runaway “Fisher process” has since been confirmed (Kirkpatrick, 1982; Lande, 1981; O’Donald, 1980). Empirical support for such a process, however, is virtually nonexistent and may be extremely difficult to obtain.

Alternatively, “adaptive” or “signaling” models of sexual selection propose that female choice is nonarbitrary. These models propose that females choose mates on the basis of characters that signal male quality, and matings with high-quality males result in direct fitness benefits to females. These benefits may result from increased offspring viability (Andersson, 1986; Hamilton and Zuk, 1982; Pomiankowski, 1988; Zahavi, 1975), female fecundity (Grafen, 1990b), or offspring survival (Maynard Smith, 1985). Male quality may be a function of a male’s genotype (Andersson, 1986; Hamilton and Zuk, 1982; Pomiankowski, 1988; Zahavi, 1975) or phenotype (Grafen, 1990b) and is advertised by the degree of ornament elaboration.

A critical aspect of these adaptive models is that male advertisement must be honest. Although it remains debatable whether signals can be immune from cheating (Dawkins and Krebs, 1978; Krebs and Dawkins, 1984; Zahavi, 1975), recent population genetic (Grafen, 1990b) and evolutionarily stable strategy (ESS) models (Grafen, 1990a) suggest that honest signals are theoretically possible. In these models, low-quality males do not “cheat” by increasing their level of advertisement to match that of high-quality males because a given level of advertisement is assumed to be more costly (e.g., in terms of survivorship) for males of low quality than for males of high quality. Therefore, although low-quality males are capable of increasing their level of advertisement, they do not do so because this increase would not result in higher lifetime reproductive success.

Although several studies of mate choice have suggested that signals serve as honest indicators of male quality (see below), few (e.g.,

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Knapp and Kovach • Courtship and male parental quality 295
Møller, 1990) provide the direct evidence necessary to conclude that offspring benefit from the female preference for elaborate male characters. In guppies and house finches, females choose males with the greatest amount of orange carotenoid pigmentation (Endler, 1980; Hill, 1990; Kodric-Brown, 1989). Because carotenoids cannot be synthesized and must be acquired through food, these authors suggested that the degree of a male's orange pigmentation may be an indicator of his feeding ability. However, whether or not male feeding ability can have consequences for offspring fitness remains to be shown. In addition, several researchers investigating mate choice in birds have suggested that some secondary sexual characters (courtship, conspicuous plumage) may advertise male parental ability (Eckert and Weatherhead, 1987; Norris, 1990b). However, because these studies provided only correlational evidence (e.g., males with high courtship rates fed their offspring at higher rates; Eckert and Weatherhead, 1987), it is difficult to eliminate the possibility that intrinsic differences in brood quality gave rise to the observed differences in male parental care quality. For example, if females vary in the quality of offspring they produce (e.g., size of offspring at hatching), male provisioning rates may be a function of offspring quality and not intrinsic male quality. In the present study we remove this potentially confounding factor by randomizing eggs among nests and show that differences in egg survival are due to intrinsic differences in male parental quality.

In the bicolor damselfish, Stegastes partitus, males provide exclusive parental care of eggs. Previous research on this species showed that male size and the clutch area in nests are unimportant in female mate choice and egg survival (Knapp and Warner, 1991). Other researchers have also found no correlation between male size and mating success (Itzkowitz and Makie, 1986; Sikkel, 1988) or between male size and egg survival (Petersen, 1990). These results are in marked contrast to numerous other studies of female mate choice in fishes with paternal care (e.g., Bisazza and Marconato, 1988; Côte and Hunte, 1989; Downhower and Brown, 1980; Gronell, 1989; Knapp and Sargent, 1989; Sargent, 1988). Male size may not influence egg survival in the bicolor damselfish because nest takeovers by larger conspecific males, a frequent source of egg mortality in other fishes with paternal care (e.g., Bisazza and Marconato, 1988; Gronell, 1989), are extremely uncommon. Egg survival may not be affected by the clutch area in nests because most egg losses occur at night when males are not defending eggs.

Only male courtship rate explained a significant amount of the variance in male mating success, and courtship rate and mating success were positively correlated (Knapp and Warner, 1991). This is in agreement with the results of an earlier study of female mate choice in the bicolor damselfish (Schmale, 1981). It remains unclear from these results, however, whether females receive any fitness benefits by mating with high-courtting males.

The objective of the present study, therefore, was to determine whether courtship rate serves as an indicator of male parental quality. We sought first to confirm the positive correlation between male courtship rate and mating success and to determine whether males begin courting before the start of a reproductive cycle (i.e., before females begin laying eggs). If male courtship precedes the start of a reproductive cycle instead of beginning concurrently or afterward, females may be able to use courtship to distinguish among potential mates before starting to lay eggs.

Having confirmed that courtship rate and male mating success are positively correlated and that males begin courting before females begin laying eggs, we used an experiment to test the prediction that courtship displays performed by males before the start of a reproductive cycle accurately reflect male parental quality, i.e., that male courtship rate and subsequent egg survival are positively correlated.

**METHODS**

**Study species**

Bicolor damselfish are a common, sexually monomorphic Caribbean reef fish (Randall, 1968) in which both males and females defend permanent territories (Myrberg, 1972; Schmale, 1981). Reproduction follows a lunar cycle with spawning beginning a few days before the full moon and ending a few days after the new moon (Knapp RA, unpublished data; Robertson et al., 1988). During a reproductive cycle, females spawn every 2 days and show high mate fidelity (Knapp and Warner, 1991). Spawning occurs during a 1-h period starting at dawn during which females travel to and lay eggs in male territories. Males have never been seen to use alternative mating tactics (e.g., sneaking) during more than 250 h of spawning observations (Knapp RA, personal observation). Eggs are demersal and are laid in a discrete monolayer. Nests often contain clutches in various stages of development because males are sequentially polygynous. Males guard eggs until the eggs hatch as planktonic larvae, 3.5 days after laying (Knapp RA, personal observations; Robertson et al., 1988). In addition to defending eggs, males produce...
vigorous courtship displays throughout the day. During courtship, a male leaves his territory and swims toward a female while performing a series of rapid vertical dives termed "dips" (Myrberg, 1972).

**Study methods**

We conducted the study over four reproductive cycles between May and August, 1990, on the Teague Bay forereef, St. Croix, U.S. Virgin Islands (17°45' N, 64°35' W). The 680-m² study site was delineated by the territories of approximately 25 males and 30 females. Before the first reproductive cycle, we replaced natural nests of all males with small clay flowerpots. The replacement of natural nests with artificial nests does not appear to influence female mate choice in this species (see Knapp and Warner, 1991). All fish were individually marked with subcutaneous injections of acryl paint (Thresher and Gronell, 1978). To determine whether courtship rate and mating success were correlated, we monitored the courtship rates and mating success of 24 males during the first and second reproductive cycles. We measured courtship rates daily for males chosen at random by counting the number of dips performed per 10-min period. We measured mating success daily by tracing the perimeter of any new egg clutches onto transparent acetate sheets and later digitizing the clutch areas (see Knapp and Warner, 1991, for details). We calculated the mating success of individual males by summing the areas of all clutches received during a reproductive cycle. The courtship rate of individual males was calculated by averaging the number of dips per 10 min over all focal samples per reproductive cycle. Within a reproductive cycle, the number of focal samples per male ranged from 5 to 19 (x ± SE = 11.5 ± 0.67).

To determine whether females could assess males on the basis of courtship rate before the start of a reproductive cycle, we compared the temporal sequence of courtship with that of egg laying over the first and second reproductive cycles. If males begin courting several days before females begin laying eggs, females would have the opportunity to distinguish among potential mates on the basis of courtship.

To determine whether courtship rates of males were indicative of subsequent egg survival in their nests, we performed an experiment in which males with differing courtship rates were given standard presentations of eggs to defend. This experiment consisted of two manipulations, one at the beginning of the third and one at the beginning of the fourth reproductive cycle. For each manipulation, we first measured the courtship rates of 16 males by counting the number of dips performed per 10-min period on each of 2 days before the start of each reproductive cycle (N_total = 32). Nine of these 16 males were then chosen for each manipulation to represent the range of available courtship rates (N_total = 18).

Measuring courtship rates before the onset of a reproductive cycle allowed us not only to determine whether females might be able to assess male parental quality before laying eggs, but also eliminated the possibility that courtship rates were influenced by the presence or absence of eggs in nests, as occurs in the three-spined stickleback, *Gasterosteus aculeatus* (Jameson and Colgan, 1989).

On the second day of each cycle and just after spawning ceased (0730 h), we obtained nine nests from nonexperimental males, each containing one newly laid clutch of eggs, which we then substituted for those of the nine experimental males. Because eggs adhere tightly to the nest surface immediately after being laid, we could pick up and move nests among males without disturbing the eggs. In addition, preliminary manipulations showed that males readily defended unrelated eggs. Because egg survival in this species is not influenced by clutch size when clutches are >10 cm² (Knapp and Warner, 1991), males were given clutches measuring >10 cm². Because egg losses from foster clutches occurred only from around the clutch perimeters, we measured egg losses by tracing clutch perimeters daily until the eggs hatched. Any new clutches laid into the 18 nests during the experiment were removed immediately after the spawning period. If courtship serves as an indicator of a male's parental ability, courtship rate and egg survival should be positively correlated.

Of the 18 males used in the experiment, we used two males in both manipulations. Both males were observed courting during one reproductive cycle and not during the other. This provided an opportunity to determine the degree to which courtship served as an indicator of the parental quality of the same males over time. One male was never observed to court during cycle 3 but courted during cycle 4, and the second male courted during cycle 3 but failed to court during cycle 4.

By randomizing clutches among males, we ensured that any observed pattern of egg loss did not result from differences in brood quality giving rise to differences in the quality of male parental care. However, at the time of the nest replacements, 12 of 13 courting males were defending eggs, whereas 0 of 5 noncourting males were defending eggs. This could potentially bias the results if egg survival were influenced by differences in parental motivation between males that initially had and did not have eggs. This did not appear to be
RESULTS

Male courtship rates and mating success were significantly positively correlated during both reproductive cycles (Figure 1; cycle 1: N = 24, F_{1,22} = 81.5, R^2 = .78, p < .0001; cycle 2: N = 24, F_{1,22} = 19.9, R^2 = .45, p < .0002; both cycles combined: N = 48, F_{1,46} = 128.2, R^2 = .73, p < .0001; data for cycle 1 and for combined cycles were square-root transformed). This relationship remained highly significant when noncourting males were excluded from the analysis (cycle 1: N = 20, F_{1,18} = 40.1, R^2 = .67, p < .0001; cycle 2: N = 22, F_{1,20} = 10.9, R^2 = .32, p < .004; both cycles combined: N = 42, F_{1,40} = 59.8, R^2 = .59, p < .0001; data for cycle 1 and for combined cycles were square-root transformed). These results suggest that females mate preferentially with males with high courtship rates.

During both cycles, males began courting 4 to 6 days before females began spawning (Figure 2). Courtship rates measured for males before the start of a reproductive cycle were significantly positively correlated with male courtship rates measured over the first 5 days of that reproductive cycle (N = 18, r = .82, p < .001). Therefore, females could use male courtship rate to discriminate among potential mates before the onset of a reproductive cycle (i.e., before females begin laying eggs).

In the nest replacement experiments, all males began defending their foster clutches immediately after the manipulation. Male courtship rate and egg survival were positively related (Figure 3). This relationship was highly significant regardless of whether the noncourting males were included in the analysis (one-tailed Spearman rank test; all males: N = 18, r = .92, p < .0005; courting males only: N = 13, r = .78, p < .005). Five of 7 males courting at rates above 4 dips/10 min hatched 100% of their foster eggs, but none of the males courting at lower rates succeeded in hatching more than 85%. The two males used in both manipulations hatched similar proportions of their clutches to other males courting at comparable rates (Figure 3). The size of clutches given to males did not influence egg survival (cycle 3: N = 9, r = -.52, p > .1; cycle 4: N = 9, r = -.01, p > .1; both cycles combined: N = 18, r = -.15, p > .1). These results strongly suggest that by mating with males with higher courtship rates, females could increase the survivorship of their offspring.

DISCUSSION

The results of this study show that females mate preferentially with high-courting males and that high-courting males hatch a greater proportion of their eggs than males courting at low rates. Therefore, a male's courtship rate appears to serve as an honest advertisement of his parental ability. This is in accordance with the predictions of the "strategic handicap" model (Grafen, 1990b) in which males use ornaments to voluntarily convey information to females, and advertising level is a continuous and increasing function of male quality.

Several other empirical studies of mate choice lend support to the idea that advertisement may signal male quality. Female great tits (Parus major) mate preferentially with males with more conspicuous plumage (Norris, 1990a). Males with conspicuous plumage were more likely to defend their broods, and matings with these males resulted in heavier fledglings, apparently because conspicuous males delivered food at higher rates or of higher...
quality to nestlings (Norris, 1990b). A similar situation may exist in red-winged blackbirds (Agelaius phoenicus), in which males with high courtship rates provision nestlings at higher rates (Eckert and Weatherhead, 1987).

However, with the exception of the present study, the only study of honest advertisement we have found that eliminated any potential female contribution to brood quality was that by Möller (1990) in which he conducted partial cross-fostering experiments in barn swallows (Hirundo rustica). By exchanging a randomly chosen half of the offspring in one nest with a randomly chosen half of the offspring in another nest, Möller was able to determine the male and female contribution to offspring fitness. His experiments showed that male tail length is negatively correlated with the intensity of infection by hematophagous mites, that resistance to mites is at least partially heritable, and that matings with long-tailed males produce offspring with higher mite resistance (Moller, 1990). Therefore, tail length appears to be an honest indicator of a male’s genetic quality, and females use tail length to discriminate among potential mates (Moller, 1988).

Although the results of the present study show that male bicolour damselfish use courtship to advertise their quality, it is important to determine the proximate basis for the observed differences in parental ability between low- and high-courting males. Male parental care in teleost fishes is often energetically expensive (DeMartini, 1987; Pedersen, 1979, cited in Dominey and Blumer, 1984; Unger, 1983), and males with low energy reserves may be unable to provide high-quality parental care to eggs (Unger and Sargent, 1988). The possibility that the parental quality of male bicolour damselfish is a function of energy reserves is suggested by the patterns of clutch loss in the nest replacement experiment. Foster clutches that suffered partial egg losses during the experiment always lost eggs only from around the clutch perimeter (clutches in natural nests are also much more likely to lose eggs from the perimeter than from within the clutch; Knapp RA, unpublished data). Although these egg losses may be attributable to the guarding male, small heterospecific fishes also occasionally eat S. partitus eggs (Knapp and Warner, 1991). However, in contrast to the observed pattern of clutch loss from experimental nests, predation by heterospecifics generally results in the haphazard removal of several clumps of eggs from inside the clutch periphery (Knapp RA, personal observation). This difference suggests that partial egg losses from experimental nests are the result of guarding males selectively eating portions of their clutches. In addition, two of the five foster clutches given to noncourtng males were cannibalized by the guarding male within 6 h of the manipulation (the other three clutches were eaten by neighboring S. diancaeus, against whom the much smaller S. partitus were unable to defend their nests). Therefore, females may discriminate against noncourtng and low-courtng males because these males have low energy reserves and augment their food intake by eating eggs.

The possibility that male parental quality is a function of energy reserves is further supported by preliminary results obtained from fat extraction of males with known courtship rates. Despite a small sample size, male fat content and courtship rate were strongly and positively correlated (N=5, r=.97, p<.01; fat extractions were carried out by R. C. Sargent at the University of Kentucky who had no prior knowledge of the courtship rates of each fish). Future experiments in which male fat content is increased by supplemental feeding will aid in elucidating the role of energy reserves in determining male parental quality. These experiments may also provide insights into what prevents low-courtng males from cheating and increasing their rates of advertisement.

From our study, we conclude that male bicolour damselfish accurately signal their parental quality by the vigor of their courtship displays. Females mate preferentially with vigorously courtng males, and such males have higher offspring survival from their nests. In addition, the observed variation among males in parental quality may be a result of differences in their energy reserves. Our results demonstrate the operation of honest advertisement and lend support to adaptive models of sexual selection.

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