

Male parental care and female choice in the bicolor damselfish, *Stegastes partitus*: bigger is not always better

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Abstract. Female mate choice and patterns of clutch loss were investigated in a natural population of the bicolor damselfish, *Stegastes partitus*, in an attempt to link criteria used by females in mate choice with male or territory characteristics that enhance egg survival. Previous studies of mate choice in fish species with paternal care have demonstrated the importance of male size and the brood size defended by males in determining female choice. In the present study, neither male size nor brood size influenced male mating success. Of the measured male and territory characteristics, females chose males solely on the basis of their courtship rate. The lack of a female preference for large males and for males with relatively larger broods appeared to result from the patterns of clutch loss. Egg-hatching success was unrelated to either male size or brood size. Future work will determine whether males with high courtship rates provide superior parental care.

Mate choice has long been of interest to evolutionary and behavioural ecologists and has recently received a tremendous amount of theoretical and empirical support (see reviews by Halliday 1978; Bateson 1983). Since the reproductive success of females is generally limited by the number of eggs they can produce, while male reproductive success is limited only by the number of females with whom they mate, females should usually be the more discriminating sex (Williams 1966; Trivers 1972). When males provide some or all of the parental care to offspring, females should choose mates who will maximize offspring survival and female fitness (Trivers 1972), either by mating with males of high parental quality or males who defend high quality resources needed by offspring.

Many species of teleost fish are characterized by males who defend breeding sites and provide exclusive parental care of eggs. Studies of mate choice in such species have shown correlations between male mating success and male phenotypic characteristics (e.g. Downhower & Brown 1980; Gronell 1989; Knapp & Sargent 1989), nest characteristics (e.g. Sikkell 1988; Unger & Sargent 1988; Bisazza et al. 1989) and territory characteristics (Sargent 1982; Thompson 1986). However, while researchers have suggested which characteristics may be important to females in distinguishing between potential mates, they have rarely

attempted to demonstrate the consequences of female choice to offspring survival and female fitness. In addition, very few have conducted research of this sort in the field, where eggs are exposed to the assortment of natural biotic and abiotic variables that might influence offspring survival. Field studies that explore the fitness consequences of female mate choice in species with male parental care should permit a much more detailed understanding of sexual selection.

Several male and nest characteristics are known to have important consequences for female mate choice and offspring survival. Female mottled sculpins, *Cottus bairdi* (Downhower & Brown 1980) and redlip blennies, *Ophioblennius atlanticus* (Côte & Hunte 1989) in the field and river bullheads, *Cottus gobio* (Bisazza & Marconato 1988) in the laboratory prefer to mate with large males, and male size and egg-hatching success are positively correlated. In the laboratory, female fathead minnows, *Pimephales promelas*, prefer males whose nests contain eggs over males whose nests are empty (Unger & Sargent 1988) and egg survival is positively correlated with the number of eggs in the nest (Sargent 1988).

We investigated female mate choice in a natural population of the bicolor damselfish, *Stegastes partitus*, in St Croix, U.S. Virgin Islands. Our aim was to identify the criteria used by females to

distinguish between potential mates and determine the consequences of female choice to offspring survival.

METHODS

Study Organism

Stegastes partitus is a sexually monomorphic planktivorous pomacentrid common on coral reef habitats throughout the Caribbean (Randall 1968). Males and females defend permanent feeding territories from which males court females throughout the day (Myrberg 1972; Schmale 1981). Reproduction follows a lunar cycle, with spawning activity beginning a few days before the full moon and ending a few days after the new moon (Schmale 1981; Robertson et al. 1988). Spawning is restricted to a 1-h period starting at dawn. During this time, females travel to male territories and lay eggs on pieces of dead coral in the centre of a male's territory. Eggs are demersal and each clutch is laid in a discrete monolayer. Nests often contain clutches in various stages of development since males are sequentially polygynous. Males guard eggs until the eggs hatch as planktonic larvae, 3–5 days after laying (Robertson et al. 1988; personal observation; cf. Schmale 1981).

Study Population

Our study was conducted over three reproductive cycles between May and August 1989, on the Teague Bay forereef, St Croix, U.S. Virgin Islands. The 680-m² study site was delineated by the territories of 24 nesting males and 30 females and ranged in depth from 4 to 10 m. All data collection was done while using SCUBA and required approximately 3 h per day during the course of the study (315 h total).

All individuals were captured using a 5% solution of quinaldine in ethanol. Fish were individually marked in situ using dilute acrylic paint or tattooing ink injected subcutaneously (Thresher & Gronell 1978). Approximately 20% of the tags faded after 2 months; these fish were recaptured and remarked. Fish were sexed behaviourally by noting the presence of male courtship displays and the response of individuals toward whom the displays were directed (Schmale 1981). All males were given artificial nests since clutches laid in natural nests were often difficult to measure because of substrate heterogeneity.

These artificial nests were small clay flower-pots 13 cm in diameter laid on their sides and attached to the substrate near each male's natural nest. Natural spawning substrates were often similar in shape to the artificial nests and all males switched their activities to the artificial nests within 1–2 days (see also Gronell 1989). The use of artificial nests did not appear to alter female mate choice since the spawning patterns of several females monitored before and after the addition of artificial spawning substrates remained unchanged. In addition, several females from within the study area occasionally spawned on natural substrates with males from outside the study area.

The locations of territories within the study site were mapped by measuring, for all territories, the distance between the centre of a territory and the centres of all nearby territories. The centre of male territories was considered to be the nest (see Schmale 1981). Since females generally defended an area around a central piece of coral that was used for cover, the centre of female territories was considered to be the area to which females swam when disturbed. Spatial relationships between territories were established by triangulation.

Male Mating and Egg-hatching Success

Male mating and egg-hatching success were measured daily between 0900 and 1200 hours for 24 males over three reproductive cycles (May–August). The number, age, position and area of clutches in all nests was recorded. Age of eggs was determined on the basis of age-specific pigmentation: newly laid eggs were white, 1-day-old eggs were dull yellow, 2-day-old eggs were pink and 3-day-old eggs were dark purple (personal observation). Clutch areas were measured by tracing clutch perimeters onto transparent acetate sheets with a grease pencil and later measuring the areas using a digitizing pad. Tracing error was approximately 5% ($N=7$, range: 1.1–6.9%) and digitizing error was less than 1%. We assessed egg-hatching success by monitoring individual clutches over their 4-day developmental period. Male mating success was defined as the total clutch area received over a spawning cycle and male egg-hatching success as the total clutch area hatched/total clutch area received.

We determined the causes of egg-hatching failure by watching nests for any evidence of predation. Because clutches often disappear soon after spawning in other Caribbean damselfish species (Petersen

Table I. Mean, coefficient of variation (%) and range of potential correlates of male mating success

Parameter	Mean	Coefficient of variation	Range
Male size (SL, mm)	48.9	5.8	44.0–57.0
Courtship rate (no. of dips/10 min)	5.4	64.2	0.9–11.4
Courtship rate (no. of dips/bout)	1.4	47.7	0.2–2.4
Interspecific attacks (no. of attacks/10 min)	2.9	61.8	0.3–6.0
Female density (no./3-m radius)	2.6	43.1	1.0–5.0
Male density (no./3-m radius)	1.9	72.3	0.0–4.0
Average female size in vicinity (SL, mm)	45.5	4.9	41.0–50.5
Nest depth (m)	7.8	24.0	4.0–10.2

1990), we checked all newly laid clutches ($N = 461$) approximately every 10 min for 30 min after females finished spawning. In addition, nests were observed during behavioural focal samples (see below).

We identified spawning females on each day of all three reproductive cycles by checking nests every 10–15 min during the spawning period (0530–0700 hours). This sampling interval was sufficient to identify all individuals spawning on a particular day (see Results). Observations of female and male behaviour as females approached nests to spawn were recorded opportunistically.

Correlates of Male Mating and Egg-hatching Success

Several potential correlates of male mating and egg-hatching success were measured over the three reproductive cycles (Table I). Male standard length was measured to the nearest millimetre during tagging. Male courtship rate and aggressiveness were measured daily during cycle 3 for 11 of the 24 males in the study site. All observations were conducted between 0900 and 1200 hours.

Rates of courtship and aggression were measured during 10-min focal samples. A 10-min duration gave consistent measures of courtship rate when consecutive samples were taken for the same male. Male courtship consisted of distinct bouts (Schmale 1981; personal observation), during which males swam towards females while 'dipping'

(sensu Myrberg 1972). Courtship bouts were considered to be terminated when the male turned away from the female and swam rapidly back to his territory. Courtship levels were measured as the number of dips per focal sample and as the average number of dips per courtship bout. Interspecific attacks were recorded whenever the focal male attacked a heterospecific intruder, usually bluehead wrasses, *Thalassoma bifasciatum*, or juvenile striped parrotfish, *Scarus iserti*. Intraspecific attacks occurred infrequently and were not recorded. The total number of focal samples per male ranged from 6 to 15 ($\bar{X} \pm SE = 11.6 \pm 1.1$).

Measured territory characteristics included nest depth (measured with a capillary depth gauge) and, within a 3-m radius of a nest, the number of conspecific females, average size of conspecific females and number of conspecific males. A 3-m radius was chosen because this was the average distance travelled by females from their territories to male territories to spawn ($N = 166$, range = 0.5–9.2 m, $\bar{X} \pm SE = 3.0 \pm 0.8$). The latter three characteristics were measured because of their potentially confounding effect on male mating success.

In addition, to determine whether the quality of male parental care changed with brood size (brood size = total area of all clutches in nest), we measured the quality of parental care for 11 males during cycles 1 and 2. All observations were conducted between 0900 and 1200 hours. The amount of parental care given to eggs by males was quantified by estimating the distance between a male and his nest

every 10 s during a 5-min focal sample. Distances were recorded as falling into one of five categories: 0 (male in nest), >0-0.5, >0.5-1, >1-2, and >2 m. Each category was given an arbitrary value of 4, 3, 2, 1 and 0, respectively, and a parental care score for each focal sample was calculated by summing the values. The number of focal samples per male ranged from 1 to 8 ($\bar{X} \pm SE = 3.7 \pm 0.8$).

Data Analysis

Potential correlates of male mating success were analysed using multiple regression procedures. Stepwise multiple regression was used because this technique allows for the assessment of independent effects when variables are collinear. If parameter values include extreme measures and non-linearities however, multiple regression may give misleading results. Therefore, we examined the residuals of all parameter values and found no outliers or curvilinearity.

In the first analysis, the male and territory characteristics of 24 males for each of three reproductive cycles were used in the model, with cycle as a classification variable. The clutch area received by a male was treated as the dependent variable and independent variables included male standard length, nest depth, conspecific female density, average conspecific female size and conspecific male density.

A second analysis used the data on courtship and aggressive behaviour collected during cycle 3. In this stepwise multiple regression analysis, the number of dips per focal sample, number of dips per courtship bout and number of heterospecific attacks per focal sample were averaged over all focal samples for each male and were included as independent variables, in addition to those mentioned above.

RESULTS

Mating System

All spawning occurred between 0530 and 0700 hours. Before dawn, males and females were quiescent and males did not defend egg clutches. At dawn, females left their territories and swam directly toward a particular nest, often swimming past the nests of several other males. Females usually required 30-60 min to complete a clutch. In only four cases was a clutch found in a nest where we had not observed spawning. Of 461 spawnings

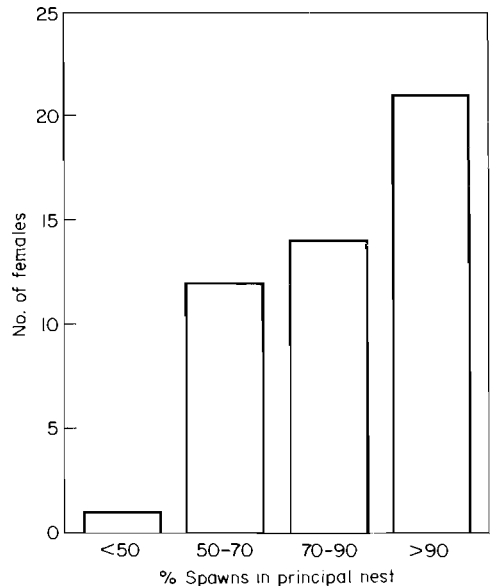


Figure 1. Frequency histogram for the percentage of spawns in the principal nest per reproductive cycle. The principal nest is the nest to which a female returned most often during a reproductive cycle.

observed, males mated with a single female per morning in 309 (67%), with two females in 134 (29%), with three females in 18 (4%), and in one case, with four females. When two or more females spawned in the same nest, all eggs were laid into a single clutch and were indistinguishable. Females spawned every 2 days and averaged 7.2 ± 0.3 spawns per cycle ($N=29$, range=4-11). Females showed high mate fidelity within a reproductive cycle, laying a majority of their eggs in a single nest (Fig. 1).

Females were seen 'visiting' males during the day on numerous occasions (see Schmale 1981; Gronell 1989). Visiting females left their territories, swam directly towards a particular nest, and usually spent approximately 30 s in and around the nest. Males dipped vigorously during female visits. Females usually entered the nest of only a single male per visit, but occasionally entered several nests during a single visiting bout. Twenty-four of 26 observed visits (92%) took place on the day before the visiting females spawned. Twelve of the 24 females (50%) spawned with the male that they were observed visiting on the previous day while the remaining 12 females spawned with a different male.

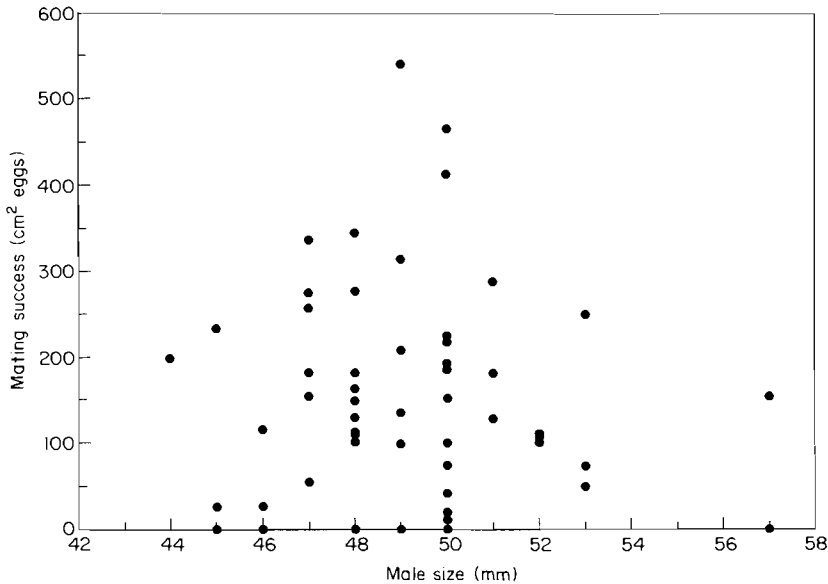


Figure 2. Male mating success (cm^2 eggs received per cycle) versus male size (standard length in mm) over three reproductive cycles in *S. partitus*. Mating success and male size are not significantly correlated ($N=61$, $r=0.09$, $P>0.40$).

Male Mating Success

Male mating success during each of the three reproductive cycles ranged from 0 to 539.4 cm^2 ($\bar{X}=139.4 \pm 16.4 \text{ cm}^2$). In the regression analysis using the data from all three cycles, the overall model was not significant ($N=61$, $F_{7,53}=2.10$, $P>0.05$), indicating that none of the measured male or territory characteristics, including male size (Fig. 2), influenced male mating success. In the analysis of data from cycle 3, however, the average number of dips per focal sample and female size both entered the model. Courtship rate had a strong positive effect on mating success ($N=11$, $F_{2,8}=32.4$, $P<0.001$) and explained 68% of the variance (Fig. 3). Female size had a marginally significant negative effect on mating success ($F_{2,8}=5.1$, $R^2=0.12$, $P=0.054$).

The brood size defended by males also did not appear to influence female mate choice. If females preferred to spawn in nests containing larger broods, female *S. partitus* who switched nests should have switched to nests containing larger broods than the nests they had previously favoured. This was not supported. In fact, when females switched nests, the nests to which they switched contained a significantly smaller brood than the previously favoured nest ($\bar{X}=20.7 \pm 4.1$ and $46.3 \pm 4.3 \text{ cm}^2$ respectively; $N=36$, $t=4.05$, $df=35$, $P<0.001$). The pres-

ence or absence of eggs in nests also did not appear to influence female mate choice, since in 12 of 36 nest switches, females spawned in empty nests despite the fact that the previous nest still contained eggs.

Patterns of Clutch Loss and Parental Care

Male parental care was limited primarily to egg defence, although guarding males occasionally removed sand and organic material from around the eggs. Males vigorously defended eggs against all potential predators ($N=125$, $\bar{X}=2.9 \pm 0.4$ attacks/10 min) and heterospecific fish species were observed removing eggs from nests on only two occasions (see below). Eggs were readily eaten by bluehead wrasses when the guarding male was temporarily removed, however.

We observed egg predation on six occasions during daily nest observations (total nest observation time = 72 h; 0630–0700 hours: 45 h; 0900–1200 hours: 27 h). Four of these were the result of cannibalism by the guarding male and always took place immediately after spawning. In three of the four cases, the nest contained two or more clutches and the guarding male ate only the most recently deposited clutch while continuing to guard older clutches. In the fourth case, the guarding male ate

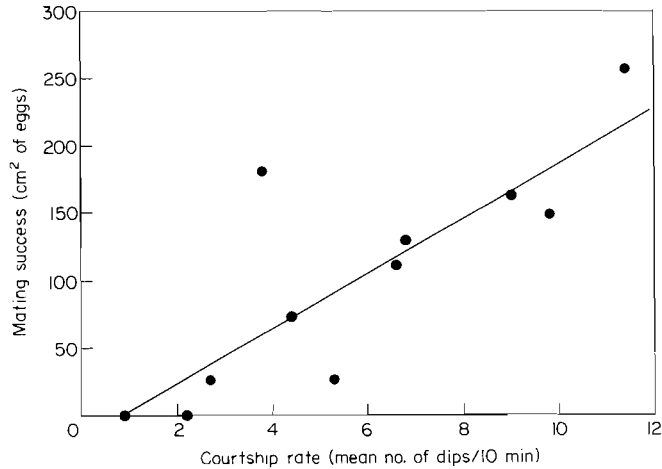


Figure 3. Male mating success (cm^2 eggs received during cycle 3) versus courtship rate in *S. partitus* ($Y = -16.3 + 20.7 X$).

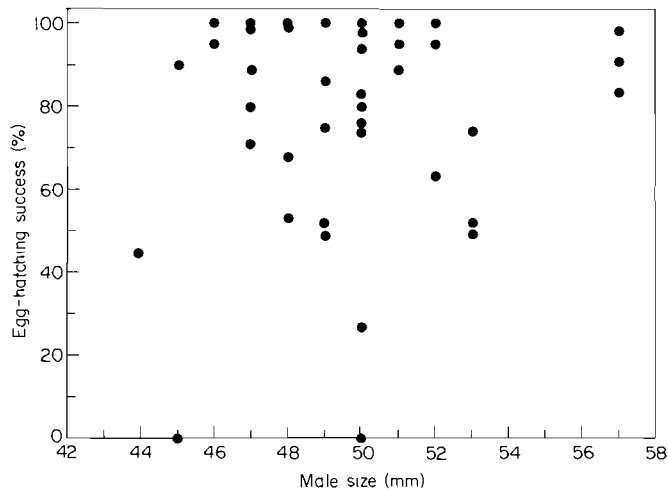


Figure 4. Egg-hatching success (% hatched/cycle) versus male size (standard length in mm) in *S. partitus*. Clutch survival and male size are not significantly correlated ($N = 48$, $r = 0.09$, $P > 0.50$).

the only clutch in the nest. The remaining two cases of predation were the result of a larger cocoa damselfish, *Stegastes variabilis*, taking over an *S. partitus* nest and eating all the eggs. In both cases, the cocoa damselfish continued to defend the nest for several days.

Despite the extremely infrequent observation of egg predation, 72 of 377 clutches (19%) disappeared before hatching. Eleven (15%) of these clutch losses occurred between 0530 and 1200 hours and, except for the two nest take-overs by cocoa damselfish, always involved only the loss of a single clutch.

Since no cocoa damselfish were seen in the vicinity of the five nests from which clutches disappeared unobserved, these clutch losses were probably also the result of filial cannibalism. The majority of clutch losses (85%), however, occurred between 1200 and 0530 hours the following morning. Of the 29 nests that suffered clutch losses between 1200 and 0530 hours, 15 contained multiple clutches at the time of clutch loss and of these, 13 (87%) lost the entire brood from the nest. The infrequent observation of egg predation and differences between the patterns of clutch losses during the

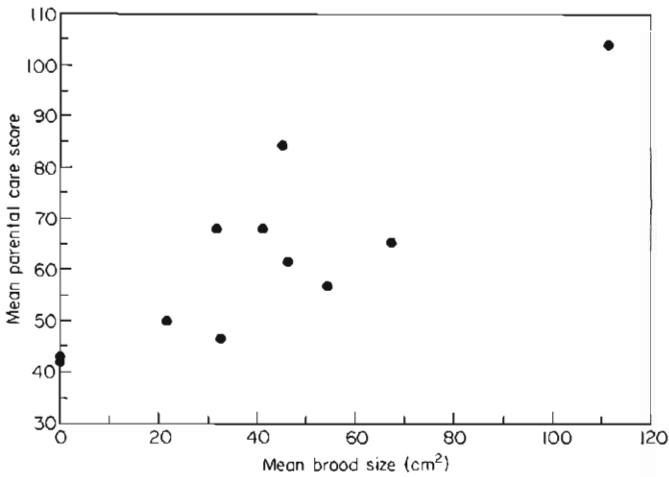


Figure 5. Mean parental care score versus mean brood size defended (cm²) for 11 male *S. partitus*. Points represent the parental care score and brood size averaged over all focal samples for a given male. See text for a description of the parental care score calculations. Parental care score and brood size are significantly correlated (Spearman rank correlation (one-tailed), $N = 11$, $r_s = 0.58$, $P < 0.05$).

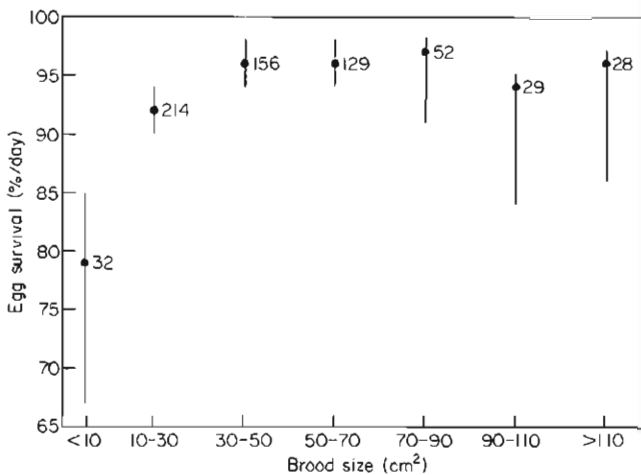


Figure 6. Mean (\pm SE) egg survival (%/day) versus brood size (cm²) in *S. partitus*. Sample sizes are given to the right of each mean.

two periods suggests that these 'catastrophic' losses occurred at night and were not the result of filial cannibalism (see also Petersen 1990).

Male size was not correlated with egg-hatching success (Fig. 4). In addition, male attendance at nests increased with increasing brood size (Fig. 5), but except for the relatively low survival of broods smaller than 10 cm², this increased nest attendance did not result in higher egg survival from broods of increasing size (Fig. 6). Broods smaller than 10 cm² survived at a significantly lower rate than broods larger than 10 cm² (broods smaller than 10 cm²:

$N = 32$; broods larger than 10 cm²: $N = 608$; $Z = 4.13$, $P < 0.001$), but made up only 5% of all broods. Broods in this category were significantly smaller than the average clutch size laid by even the smallest female ($\bar{X} = 6.9 \pm 0.3$ and 11.6 ± 0.7 cm² respectively, $t = 11.45$, $df = 41$, $P < 0.001$) and were often the result of spawnings terminated by females before completion of the clutch.

Courtship rate was positively correlated with egg-hatching success, but this relationship was not significant ($N = 8$, $df = 6$, $r = 0.33$, $P > 0.10$). However, the sample size is quite small and thus the test

lacks power. It remains a distinct possibility that males with high courtship rates also provide higher quality parental care.

DISCUSSION

Patterns of Clutch Loss

Nineteen per cent of clutches monitored during this study disappeared before hatching. This rate of clutch loss lies between the rates reported for two other Caribbean damselfish: 11.1% (Pressley 1980) and 14.8% (Petersen 1990) for the yellowtail damselfish, *Microspathodon chrysurus*, and 41% for the dusky damselfish, *Stegastes dorsopunicans* (Petersen 1990). Eleven of these 72 clutch disappearances occurred between 0530 and 1200 hours. Similarities between the patterns of clutch loss resulting from observed filial cannibalism and those clutch losses that were unobserved suggests that the majority of clutch losses occurring during this time were the result of filial cannibalism.

Eighty-five per cent of clutch losses, however, occurred between 1200 and 0530 hours the following morning and of these, 87% were 'catastrophic' losses in which all clutches from nests containing multiple clutches disappeared. These catastrophic losses were apparently the result of a nocturnal egg predator that was able to remove large numbers of eggs from nests (male *S. partitus* do not defend their eggs at night: Schmale 1981; personal observation).

A strikingly similar pattern of clutch loss was reported for a closely related Caribbean damselfish, *S. dorsopunicans*, by Petersen (1990). Of the clutches that disappeared before hatching, 21% disappeared during the day and were attributed to filial cannibalism and the remaining 79% disappeared at night. Studies of another Caribbean damselfish, *Stegastes leucostictus*, have also shown that clutches disappear much more often at night than during the day and several lines of evidence suggest that the brittlestar, *Ophiocoma echinata*, is the predator responsible for egg losses at night in this species (Itzkowitz, personal communication). Brittlestars were extremely abundant throughout the study site and may be responsible for the nocturnal egg losses observed in this study.

Female Mate Choice

Female *S. partitus* did not mate preferentially with larger males (Fig. 2) and male size was not correlated with egg-hatching success (Fig. 4). The

lack of a female preference for large male size in the beaugregory damselfish, *S. leucostictus* (Itzkowitz & Makie 1986) and the garibaldi, *Hypsypops rubicundus* (Sikkel 1988) may also result from the inability of larger males to hatch a greater proportion of their eggs than small males. This result is in marked contrast to the results of numerous studies that have found a female preference for large males (e.g. Hastings 1988a, b; Gronell 1989) and a positive correlation between male size and egg survival (Downhower & Brown 1980; Bisazza & Marconato 1988; Côte & Hunte 1989). Two explanations may account for the lack of a female preference for large males in *S. partitus*. Large male size may be advantageous primarily in defending nests against conspecifics (Downhower & Brown 1980; Bisazza & Marconato 1988). Such an advantage may not be present in *S. partitus*, however, since we never witnessed any nest intrusions by conspecifics. Alternatively, large male size may not confer benefits in egg survival because most of the egg losses in *S. partitus* apparently occur at night when males are not defending eggs.

The lack of a correlation between male size and mating success appears to contradict the results of Schmale (1981), who found a positive correlation between male size and mating success in this same species. However, the correlation in his study was based on the low mating success of three very small males, leading to his conclusion that 'spawning success varied greatly within any given size range and the length-success relationship was not significant for males over 77 mm' (Schmale 1981, page 1177; the three small males were less than 77 mm in total length). In addition, Myrberg et al. (1986) suggested that female *S. partitus* were differentially attracted to playbacks of courtship sounds (produced during dipping) of large males relative to those of small males. However, since only a single pair of recordings were used, it is difficult to assess the importance of male size from their experiments (Kroodsma 1989).

Female mate choice in *S. partitus* was apparently not influenced by the brood size defended by males or the presence or absence of eggs in nests. Despite increasing male parental care with brood size (Fig. 5), egg survival remained unchanged over the normal range of brood sizes defended by males (Fig. 6). This is contrary to the results of several other studies that have found a female preference for males whose nests contain eggs (Marconato & Bisazza 1986; Unger & Sargent 1988; Gronell 1989)

and a positive correlation between the number of eggs defended by a male and egg survival (Sargent 1988). As with the lack of a female preference for large males, the lack of a female preference for males defending larger broods in *S. partitus* may result from the patterns of egg loss. Females may not receive any benefits in terms of increased parental care to eggs by laying in nests containing large broods because eggs usually disappeared at night when nests were undefended.

Female choice of mates in *S. partitus* appeared to be based solely on male courtship rate. Courtship rate, averaged over one cycle, had a strong positive effect on male mating success (Fig. 3). Schmale (1981) also found courtship to be the most important influence on male mating success in *S. partitus*. In addition, in the present study courtship rate was positively correlated with egg-hatching success, but this relationship was based on a very small sample size and was not significant.

Several other studies of mate choice in fish species with paternal care have reported a correlation between male courtship rate and male mating success. In the blackeye goby, *Coryphopterus nicholsi* (Cole 1982), orange-tailed blue damselfish, *Chrysiptera cyanea* (Gronell 1989), and three-spined stickleback, *Gasterosteus aculeatus* (Jamieson & Colgan 1989), males who courted more had higher mating success, but in the browncheek blenny, *Acanthemblemaria crockeri*, male courtship rate and mating success were negatively correlated (Hastings 1988a). However, none of these studies attempted to determine what benefits, if any, females receive by choosing mates on the basis of courtship rate.

Since females are expected to make adaptive mate choices in species where males provide parental care, and since female *S. partitus* appear to distinguish among potential mates solely on the basis of courtship rate, it becomes important to determine what benefits, if any, females receive by choosing vigorously courting males. There are two possibilities. If females are unable to assess the future survival probabilities of their eggs in male-defended nests, courtship in *S. partitus* may have arisen by female choice for an arbitrary male character (Arnold 1983). Alternatively, courtship may be an indicator of male parental quality. However, the parental quality of individual males may be intrinsic and therefore relatively invariant or may change over the breeding season (e.g. as a result of changing fat reserves; Unger 1983). Our

preliminary observations show that courtship rates of individual male *S. partitus* can change markedly between reproductive cycles; this suggests that if courtship rate is correlated with parental quality in this species, it is more likely to indicate changeable male parental quality than a fixed intrinsic quality.

The possibility that characteristics chosen by females (e.g. courtship) may change over relatively short time periods and that these characteristics may indicate to females the current parental quality of potential mates has been relatively ignored in past empirical studies of mate choice, but is supported by recent theoretical work. Using a haploid genetic model, Hoelzer (1989) showed that male epigamic characters could evolve if they clarified the differences in non-heritable male parental quality among potential mates. Future research on *S. partitus* will investigate the possibility that females use male courtship to assess changing male parental quality.

In conclusion, male size and the brood size defended by males both appear unimportant in determining female mate choices in *S. partitus*, and neither male size nor brood size were correlated with egg survival. However, courtship rate had a strong positive effect on male mating success and appears to be the only criterion used by females to distinguish between potential mates. Although the basis for this female preference for vigorously courting males remains unclear, this study lays the groundwork for future research into male courtship and female choice in *S. partitus*.

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