

The influence of egg survivorship on the subsequent nest fidelity of female bicour damselfish, *Stegastes partitus*

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Abstract. In many animal species, females lay eggs within male territories. Research on female choice in such species has shown that females often assess male or territory quality indirectly on the basis of male characters that are correlated with male or territory quality. Researchers have given much less attention to the possibility that females can assess male or territory quality directly based on the survival of previous broods. This study demonstrates that in the bicour damselfish, a species with exclusive male parental care of eggs, females use the survival of previously-laid eggs to avoid nests that have a low probability of offspring survival. Females mate repeatedly during a reproductive cycle and although they generally show high nest fidelity, this fidelity is broken when a nest loses an entire brood to nocturnally feeding brittlestars. Experimental removal of broods and addition of brittlestar odours to nests demonstrate that brittlestar odours are sufficient to cause females to avoid nests. Females may also respond to visual cues associated with brood loss. In addition, clutches laid in nests after nocturnal complete-brood losses are much less likely to survive than clutches laid in nests that have not suffered nocturnal complete-brood losses. Therefore, by avoiding nests from which brittlestars have recently removed eggs, females increase the probability of future egg survival.

During the breeding seasons of a wide array of animal taxa, males defend territories into which females lay eggs (e.g. insects: Zeh & Smith 1985; amphibians: Duellman & Treub 1986; fishes: Breder & Rosen 1966; birds: Welty & Baptista 1988). Eggs may subsequently receive no parental care, care from males alone, or biparental care (see Clutton-Brock 1991, for a recent review). If offspring survival varies among territories because of differences in territory quality or in male parental quality, females should assess the quality of available territories or males before choosing a nest site in which to lay eggs.

Females may be able to assess the probability of offspring survival indirectly on the basis of male characters that are correlated with male or territory quality. The results from recent empirical research on female choice suggest that such indirect assessment may be common in nature. For example, in the house finch, *Carpodacus mexicanus*, females prefer to mate with males with brighter red

coloration and such bright males feed offspring at higher rates than dull males (Hill 1991). In the red-winged blackbird, *Agelaius phoeniceus*, males with the highest display rates are chosen as mates (Weatherhead & Robertson 1977), and male parental quality is positively correlated with display rate (Searcy & Yasukawa 1981). Female pied flycatchers, *Ficedula hypoleuca*, mate preferentially with males with the highest song rates, and a male's song rate is a function of food availability on his territory (Gottlander 1987). In the mottled sculpin, *Cottus bairdi* (Downhower & Brown 1980), redlip blenny, *Ophioblennius atlanticus* (Côte & Hunte 1989), and river bullhead, *Cottus gobio* (Bisazza & Marconato 1988), females mate preferentially with the largest males and offspring survival is positively correlated with male size.

Alternatively, females may be able to assess territory quality or male parental quality directly by monitoring offspring survival. This possibility has been virtually ignored by behavioural ecologists interested in female choice, but should be possible under the following conditions: (1) offspring remain on territories for a period of sufficient

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duration to allow assessment by females; (2) territory quality or male parental quality does not change markedly between broods, thereby allowing females to assess the probability of future offspring survivorship from the survival of previous broods; and (3) females lay eggs over a relatively long period of time, thereby allowing later-laying females to base their site choice on the survival of broods deposited by early-laying females.

These conditions may often be met in teleost fishes. In many species of teleost fish, males defend breeding territories into which females lay demersal eggs (Breder & Rosen 1966). Eggs are usually guarded by the resident male at least until they hatch, several days after laying (Breder & Rosen 1966; Blumer 1982). In addition, because females often mate repeatedly during a breeding season and breeding seasons often last for several months, nests often contain eggs over a relatively long period of time.

In the bicolour damselfish, both males and females are permanently territorial and only males provide parental care to eggs. Females mate repeatedly during a reproductive cycle and show high nest fidelity, with the majority of females laying more than 70% of their eggs in a single nest (Knapp & Warner 1991). However, preliminary observations showed that although female nest fidelity is unaffected by partial brood losses, females switch nests when their favoured nest loses an entire brood (personal observation). Therefore, the objectives of this paper are to: (1) show that the nest fidelity of female bicolour damselfish is influenced by the survival of previously-laid broods; (2) present the results from a series of experiments that show that females use predator-specific olfactory cues and perhaps visual cues in assessing brood losses; and (3) show that female avoidance of nests that have suffered complete-brood losses increases the probability of future brood survival.

Study Species

Bicolour damselfish are a sexually monomorphic pomacentrid found on shallow coral reef habitats throughout the Caribbean (Randall 1968). Reproduction is lunar cyclic with most spawning occurring between the full and new moon (Robertson et al. 1988; unpublished data). During a reproductive cycle, females spawn every 2 days, laying their eggs

in discrete nests within male territories during a 1-h period starting at dawn (Knapp & Warner 1991). At the beginning of the spawning period, females leave their territories and swim directly to a particular nest, generally beginning to spawn with little or no courtship from the resident male. Eggs are laid in a compact monolayer and are tightly adhered to the nest surface. Eggs from all females spawning in a nest on a single day are laid in a discrete clutch. Males are polygynous and nests often contain a brood composed of several clutches in different developmental stages. Males guard eggs during the day, but not at night (Knapp & Warner 1991; see Discussion). Eggs hatch at dusk, 3-5 days after laying (Robertson et al. 1988; personal observation).

The majority of clutch losses in this species occur at night and characteristically involve the loss of all eggs from a nest (Knapp & Warner 1991). Two lines of evidence implicate the brittlestar, *Ophiocoma echinata*, as the predator responsible for these nocturnal complete-brood losses. First, Itzkowitz & Koch (1991) showed that *O. echinata* is a major nocturnal predator of eggs from nests of the beaugregory damselfish, *Stegastes leucostictus*, in Discovery Bay, Jamaica. *Ophiocoma echinata* were very abundant on my study site and I often observed them beneath *S. partitus* nests during daily clutch measurements and crawling near nests that contained eggs during night dives. Second, when I caged individual *O. echinata* overnight into nests that contained eggs, resulting patterns of egg loss were identical to natural nocturnal brood losses, i.e. the entire brood was eaten, leaving behind only the egg-attachment threads (unpublished data).

METHODS

This study was conducted over eight reproductive cycles between May and August, 1989-1991, on the Teague Bay forereef, St Croix, U.S. Virgin Islands (17°45'N, 64°35'W). At the beginning of each field season, I placed an artificial nest in the territories of approximately 30 males as part of an ongoing study of female mate choice in this species (Knapp & Kovach 1991; Knapp & Warner 1991). These artificial nests were small clay flowerpots (13-cm diameter) laid on their sides near each male's natural nest. Males and females switched their attention to the artificial nests within 1-2 days. I

could identify all individuals on the basis of size, territory location, and tags (subcutaneous injections of acrylic paint) or prominent scars. All observations and experiments were conducted while using SCUBA.

Egg Losses and Female Nest Fidelity

In this section, I describe the methods used to elucidate the patterns of complete-brood loss and the effects of such losses on female nest fidelity. I investigated the patterns of brood loss by measuring the brood area (brood area = total area of all clutches in a nest) in each of 24 nests daily over three reproductive cycles in 1989 and two reproductive cycles in 1990. I measured brood areas by tracing clutch perimeters onto transparent acetate sheets and later digitizing the clutch areas (see Knapp & Warner 1991, for details). Brood measurements were taken between 0900 and 1200 hours. Since individual clutches can be identified on the basis of age-specific pigmentation (see Knapp & Warner 1991), I determined whether or not clutches survived to hatch by recording their presence or absence daily over the 3-5-day developmental period of each clutch. In a previous study on *S. partitus*, Knapp & Warner (1991) showed that of the clutches that disappear before hatching, the vast majority (>97%) are lost either immediately after spawning as a result of cannibalism by the guarding male, or at night when males do not guard their eggs (see also Petersen 1990). Therefore, in the present study, clutches were assumed lost during the day if they disappeared between 0530 and 1200 hours and lost at night if they disappeared between 1200 and 0530 hours the following day.

To determine whether brood losses influence female spawning patterns, I identified all spawning females on each day of all five reproductive cycles by checking nests every 10-15 min during the spawning period (0530-0700 hours; see Knapp & Warner 1991, for details). Observations of male and female behaviour as females approached and entered nests were recorded opportunistically.

Nest Manipulations and Female Fidelity

The observations described above demonstrated that female nest fidelity is broken when the favoured

nest suffers a nocturnal complete-brood loss. Therefore, in this section, I describe two experiments designed to elucidate the cues female bicour damselfish use to avoid nests that recently lost a complete brood. The first experiment involved the removal of broods from nests during the day and just after dusk. I will refer to this experiment as the 'Egg Removal Experiment'. In the second experiment, I simultaneously manipulated the presence or absence of broods and brittlestar odours in nests just before dawn. I will refer to this experiment as the 'Egg Removal/Odour Addition Experiment'.

In the Egg Removal Experiment, I removed all eggs from 12 nests in an attempt to experimentally duplicate complete-brood losses and the effect of these losses on female fidelity. In 1989, I removed eggs from eight nests between 0900 and 1200 hours and, in 1990, from two nests between 0800 and 0900 hours and two nests between 1930 and 2030 hours. I used a small knife to scrape the eggs from the nest and ocean currents quickly carried eggs away from the nest site. On the morning following egg removal, I positioned myself 2-3 m from the manipulated nest before *S. partitus* became active (0510-0530 hours). When females arrived at the nest, I recorded their identities and behaviour, and the nest in which they spawned.

Since the Egg Removal Experiment failed to influence female nest fidelity, I conducted a preliminary experiment in 1990 in which I caged brittlestars in nests overnight and then monitored female responses at these nests the following morning (brittlestars were removed before *S. partitus* became active). This manipulation caused a marked reduction in female nest fidelity. The fact that females avoided experimental nests even when the caged brittlestar had not eaten any of the eggs suggested the potential importance of olfactory cues left in nests by brittlestars.

Therefore, I conducted the Egg Removal/Odour Addition Experiment to test the hypothesis that females were responding to olfactory cues left behind by brittlestars and to distinguish between effects due to brittlestar odours and those due to egg loss. To do this, I cut each of several 13-cm diameter flowerpots vertically into three equal-sized pieces ('tiles'). Four tiles were then placed in each of two 36 × 25 × 12 cm plastic containers, one that contained four to six *O. echinata* and the other that was empty. The goal was to permeate tiles in the brittlestar enclosure with brittlestar odours ('brittlestar tiles') while keeping the other tiles free

of such odours ('control tiles'). I drilled numerous small holes into each container to allow water exchange and anchored both near the study site. I substituted new brittlestars for the old ones approximately every 7 days.

Manipulations were conducted over three reproductive cycles during May–July, 1991. Nests containing a minimum of two clutches and in which at least one female was expected to spawn the following morning were assigned to one of four treatments: (1) eggs present (eggs not removed), control tile added; (2) eggs present, brittlestar tile added; (3) eggs removed, control tile added; and (4) eggs removed, brittlestar tile added. These treatments will be referred to as 'Eggs/Control Tile', 'Eggs/Brittlestar Tile', 'No Eggs/Control Tile', and 'No Eggs/Brittlestar Tile', respectively. Available nests were randomly assigned to a particular treatment. The Eggs/Control Tile treatment served as a baseline against which I compared the female fidelity to nests assigned to the other three treatments.

I manipulated one to four nests per morning. Manipulations were set up approximately 15 min before *S. partitus* became active. I removed tiles from holding boxes, placed them singly in sealable plastic bags, swam to the selected nests, and placed a single tile onto the bottom of each nest. The inserted tiles never covered any egg clutches, since clutches are adhered to the inner nest walls or ceiling instead of the sand-covered nest bottom. To ensure that any differences in female fidelity between treatments were not the result of differences in nest disturbance, I handled all nests to a similar degree. Therefore, nests differed only in whether eggs were removed and whether they contained brittlestar odours. I removed eggs by scraping them out of nests with a small knife. I subsequently observed nests from 2–3 m away for the duration of the daily spawning period (0520–0700 hours). During this period, I recorded the identity of females arriving at each manipulated nest, behaviour at the nest, and identity of females who spawned. I removed tiles from nests at the end of the spawning period.

Nests were often used more than once in this experiment (range = 1–5; $\bar{X} = 2.8$). This was necessary because of the large number of nests required, and time limitations that restricted the number of nests that could be monitored daily to no more than 30. However, once assigned to a particular treatment, individual nests were never assigned to that treatment again during the same reproductive

cycle, and were never assigned to the same treatment more than twice over the duration of the experiment.

Female Nest Avoidance and Future Egg Survival

The observations and experiments described so far showed that females avoid nests from which brittlestars have removed all eggs during the previous night (see Results). Therefore, in this section I describe an experiment designed to ascertain whether this female avoidance behaviour is a strategy to increase the survival of subsequent offspring. If nests that suffer nocturnal complete-brood losses are more likely to lose subsequent broods, for example, if brittlestars have a higher return rate to those nests from which they have eaten eggs in the recent past, then females would benefit by switching to another nest after a nocturnal complete-brood loss. Since 15 of 38 nests (39%) that suffered nocturnal complete-brood losses received eggs (i.e. the female spawned) within 2 days of the loss, I was able to test this hypothesis by comparing the survival of these clutches with the survival of clutches laid in nests from which complete broods were experimentally removed.

For each nest, I measured the survival of only the first clutch laid within 2 days after a nocturnal complete-brood loss or experimental brood removal. I considered a clutch to have survived if at least a portion of the clutch remained 3 days after being laid. Since broods were removed from nests in both groups prior to the measurement of clutch survival, any differences in clutch survival should be largely the result of the type of prior brood loss (natural complete-brood loss versus experimental removal). Although more females spawned subsequently in nests from which broods were experimentally removed than in nests that suffered nocturnal complete-brood losses ($\bar{X}_{\text{removal}} = 3.9 \pm 0.3$, $\bar{X}_{\text{loss}} = 2.3 \pm 0.3$; *t*-test: $t = 2.67$, $df = 20$, $P < 0.05$), the resulting difference in brood size should not have biased the results since egg survival is not influenced by brood size in *S. partitus* (Knapp & Warner 1991; this study). Only seven of the original 12 nests in the Egg Removal Experiment were included in the present analysis, since three nests did not receive any clutches during the 2-day period after brood removal and two nests were not monitored for the full 3-day period after clutch laying. I predicted that clutches laid into nests after nocturnal complete-brood losses would

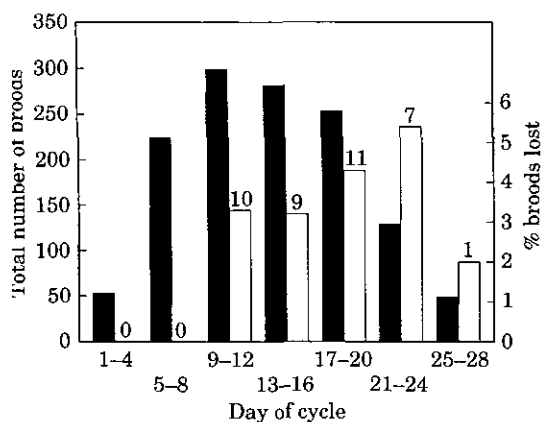


Figure 1. Total number of broods on the study site (■) and the percentage of broods lost (□) as a function of the day of the reproductive cycle in *S. partitus*. 'Number of broods' is the number of egg-containing nests on the study site on a given day. Data were collected over five reproductive cycles and since reproductive cycles varied from 26 to 28 days in length, cycles were standardized according to their median date. The actual number of broods lost in each category are given above the open bars.

have lower survival than those laid into nests from which broods were experimentally removed.

RESULTS

Egg Losses and Female Nest Fidelity

Of the 831 clutches laid during the five reproductive cycles, 146 (18%) disappeared before hatching. Thirty-two (22%) disappeared during the day and the remaining 114 (78%) disappeared at night. To determine whether complete-brood losses (i.e. loss of all clutches from a nest) occurred more often during the day or at night, I compared the patterns of loss from broods that contained multiple clutches at the time of clutch disappearance. Of the broods that suffered nocturnal clutch losses, 33 contained multiple clutches at the time of clutch loss and of these, 30 (91%) lost all clutches in a single night. Of the broods that lost clutches during the day, 17 contained multiple clutches at the time of clutch loss and of these, only 10 (59%) lost all clutches. Therefore, most clutch losses occur at night and unlike diurnal clutch losses, nearly always involve the loss of the entire brood from a nest.

The probability of nocturnal complete-brood loss increased significantly from the beginning to the end of a reproductive cycle (Fig. 1; chi-squared

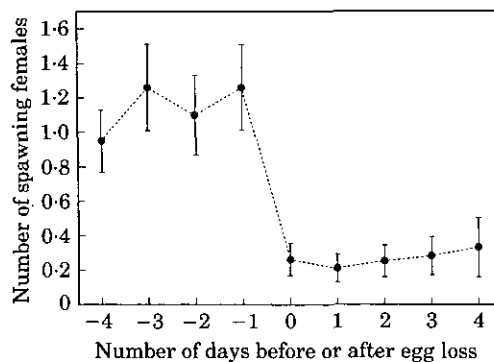


Figure 2. Mean number (\pm SE) of females spawning per nest before and after a complete-brood loss in *S. partitus*. Complete-brood losses occurred during the night before day 0. Data are based on female spawning patterns at 38 nests. The number of females spawning on days -2 and -1 were significantly different from the number spawning on days 0 and 1.

test for two independent samples: $\chi^2 = 11.34$, $df = 4$, $P < 0.05$). Although the average size of broods that were lost tended to be larger than the average size of broods present ($\bar{X}_{\text{lost}} = 47.1 \text{ cm}^2$, $\bar{X}_{\text{present}} = 37.6 \text{ cm}^2$), this difference was not statistically significant (Mann-Whitney *U*-test: $N_{\text{total}} = 1279$, $N_{\text{lost}} = 38$, $z = 1.49$, $P > 0.10$).

Nocturnal complete-brood losses had a very strong influence on female nest fidelity (Fig. 2), with the number of females spawning per nest declining five-fold between the period 2 days before and 2 days after the loss (number of females spawning 2 days before versus 2 days after loss: $\bar{X} \pm \text{SE} = 2.39 \pm 0.23$ versus 0.47 ± 0.11 ; paired *t*-test: $N = 38$, $t = 6.97$, $P < 0.0001$; although I observed a total of 50 nocturnal complete-brood losses, I had data only on the number of females spawning and the brood area laid for 38 of these losses). Observations of 23 females as they approached and entered nests that had suffered a complete-brood loss during the previous night showed that females approach such nests in the normal fashion, but instead of immediately entering the nest and beginning to spawn, they usually hesitate a few centimetres from the nest entrance for up to several minutes. Females then enter the nest for 0.25–5 min without laying eggs before returning to their territories. These females subsequently visit the nests of one to three other nearby males, but they often return to the nest that had suffered the complete-brood loss at least once more during the dawn spawning period. In only eight of the 38 complete-brood losses (21%) did

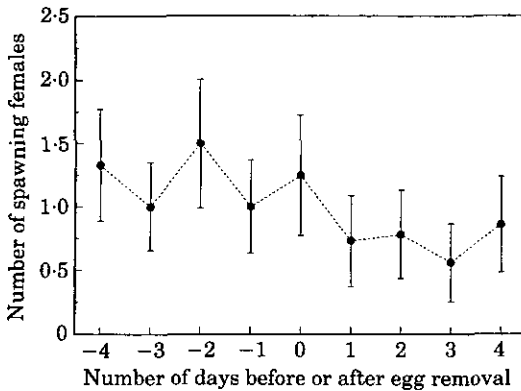


Figure 3. Mean number (\pm SE) of females spawning per nest before and after experimental egg removals in *S. partitus*. Removals were conducted during the day or night before day 0. Data are based on egg removals from 12 nests. Since day and night removals did not have different effects on female fidelity, the data were combined. The number of females spawning on days -2 and -1 were not significantly different from the number spawning on days 0 and 1.

females eventually spawn with the male whose nest they arrived at initially, instead of with a new male.

Nest Manipulations and Female Fidelity

Egg removal experiment

The Egg Removal Experiment showed that females did not respond differentially to day versus night brood removal. The probability of a female spawning (number of females spawning 2 days after the manipulation/number of females spawning 2 days before the manipulation) was not different between the two groups (day removal: 0.75 (18 of 24), night removal: 0.83 (5 of 6); Fisher's exact test, $P > 0.2$). Results of day and night brood removals were therefore combined for subsequent analyses. The number of females spawning per manipulated nest 2 days before the experimental removal of complete broods was not significantly different from the number of females spawning per nest 2 days after the removal (Fig. 3; $\bar{X}_{\text{before}} = 2.50 \pm 0.23$, $\bar{X}_{\text{after}} = 1.92 \pm 0.38$; paired t -test: $N = 12$, $t = 1.21$, $P > 0.25$). Therefore, in contrast to the strong effect of natural complete-brood losses on female fidelity (Fig. 2), the experimental removal of complete broods in the Egg Removal Experiment had little, if any, effect on female fidelity.

Egg removal/odour addition experiment

The Egg Removal/Odour Addition Experiment had strong negative effects on female fidelity (Fig.

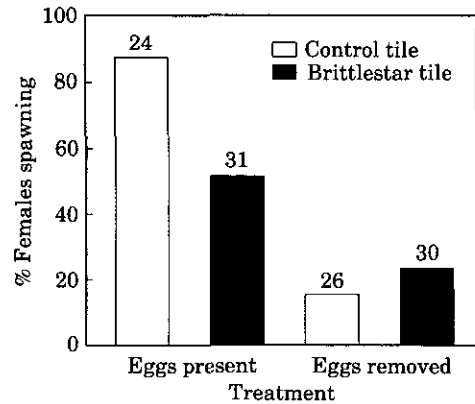


Figure 4. Percentage of females arriving at nests who spawned versus nest treatment in *S. partitus*. The number of females who arrived at nests in each treatment are given above each bar. The percentage of females spawning in each treatment were all significantly different from each other except the No Eggs/Control Tile and No Eggs/Brittlestar Tile treatments.

4). The insertion of control tiles into nests and the associated nest disturbance appeared to have little or no effect on female spawning patterns since 21 of 24 females arriving at control nests (Eggs/Control Tile treatment) spawned in those nests (88%). The Eggs/Brittlestar Tile treatment significantly decreased female fidelity relative to that observed for nests assigned to the Eggs/Control Tile treatment ($\chi^2 = 8.02$, $df = 1$, $P < 0.005$). This indicates that brittlestar odours have a strong effect on female spawning patterns, and that female fidelity is decreased to approximately 50% by the presence of brittlestar odours even if all eggs remain in the nest. The No Eggs/Control Tile and No Eggs/Brittlestar Tile treatments also strongly decreased female fidelity (No Eggs/Control Tile versus Eggs/Control Tile: $\chi^2 = 25.96$, $df = 1$, $P < 0.001$; No Eggs/Brittlestar Tile versus Eggs/Control Tile: $\chi^2 = 22.22$, $df = 1$, $P < 0.001$). The No Eggs/Control Tile and No Eggs/Brittlestar Tile treatments had significantly greater depressive effects on female fidelity than the Eggs/Brittlestar Tile treatment (No Eggs/Control Tile versus Eggs/Brittlestar Tile: $\chi^2 = 8.07$, $df = 1$, $P < 0.005$; No Eggs/Brittlestar Tile versus Eggs/Brittlestar Tile: $\chi^2 = 5.17$, $df = 1$, $P < 0.025$). The No Eggs/Control Tile and No Eggs/Brittlestar Tile treatments did not have significantly different effects on female fidelity ($\chi^2 = 0.55$, $df = 1$, $P > 0.30$). Therefore, although the addition of brittlestar odours alone (Eggs/Brittlestar Tile) had a strong negative effect on female fidelity, this effect was not

as strong as egg removal alone (No Eggs/Control Tile) or egg removal with the addition of brittlestar odours (No Eggs/Brittlestar Tile). The strong effect of pre-dawn egg removal in this experiment is in marked contrast to the lack of a significant effect of either day or night removals on female fidelity in the Egg Removal Experiment (Fig. 3), and suggests that the strength of female response is a function of the timing of egg removal.

Female Nest Avoidance and Future Egg Survival

The survival of clutches laid in nests after nocturnal complete-brood losses was markedly lower than that of clutches laid in nests after experimental brood removal. Of 15 clutches laid in nests after nocturnal complete-brood losses, only six (40%) survived for more than 3 days. In contrast, all seven clutches laid in nests from which I experimentally removed broods survived for more than 3 days. This difference was statistically significant (six of 15 clutches versus seven of seven clutches; Fisher's exact test, $P=0.01$). Of the nine clutches that disappeared after being laid in nests after nocturnal complete-brood losses, six disappeared at night and were apparently eaten by brittlestars. The remaining three clutches disappeared immediately after being laid and were apparently cannibalized by the guarding male. If the three cannibalized clutches are removed from the analysis to exclude the possibility that differential filial cannibalism is responsible for the observed differences in clutch survival, the outcome is unchanged. The survival of clutches laid in nests after nocturnal complete-brood loss remains significantly lower than the survival of clutches laid in nests after experimental brood removal (six of 12 clutches versus seven of seven clutches; Fisher's exact test, $P=0.03$). Therefore, the avoidance by female *S. partitus* of nests that recently suffered brood predation by brittlestars appears to be a strategy to increase the survival of subsequent offspring, since clutches laid in nests after brittlestar predation have a lower chance of surviving than clutches laid in nests that brittlestars have not yet discovered. This lower probability of survival appears to be largely the result of brittlestars being more likely to return to nests from which they had previously removed eggs. Whether males are more likely to cannibalize clutches laid in nests after nocturnal complete-brood losses, perhaps because such clutches have a high probability of being eaten by brittlestars, remains to be determined.

DISCUSSION

Patterns of Egg Loss

The majority of egg losses observed during this study occurred at night and involved the simultaneous loss of all clutches (i.e. the entire brood) from a nest (see also Knapp & Warner 1991). These nocturnal complete-brood losses occurred in a temporally non-random manner. Over a reproductive cycle, the probability of complete-brood loss is at a maximum approximately 12 days after the peak brood availability (Fig. 1), suggesting that the frequency of complete-brood loss is not simply a function of the number of broods present. This time lag is not the result of a decline in the quality of parental care over a reproductive cycle, since complete-brood losses occur at night when males are not defending their eggs (see below). Instead, it suggests the brittlestars require a certain amount of time to detect the presence of broods in nests.

Nocturnal complete-brood losses are also an important source of egg mortality in other Caribbean fish species with demersal eggs. Petersen (1990) reported that in the dusky damselfish, *Stegastes dorsopunicans*, 79% of the clutches that failed to hatch disappeared at night, and generally involved the simultaneous loss of all clutches from a nest. Similarly, in *S. leucostictus*, 69% of clutches that disappeared prematurely were lost at night (Itzkowitz & Koch 1991). The high frequency of nocturnal egg losses relative to day losses in these species may stem from the patterns of male parental care. Although males of these damselfish species vigorously defend their nests against all intruders during the day (Ebersole 1977; Petersen 1990; Knapp & Warner 1991), they provide no defence at night (Petersen 1990; Knapp & Warner 1991; personal observation) and are often found quiescent in shelter holes 0.2–1 m from the nest (personal observation). This lack of nocturnal nest defence presumably allows easy nest access to night-active egg predators such as brittlestars.

Egg Losses and Female Nest Fidelity

Nocturnal complete-brood losses have a strong negative effect on the spawning patterns of female *S. partitus*. Although females generally show high nest fidelity (Knapp & Warner 1991), females switch to other nests when their favoured nest suffers a complete-brood loss during the previous night (Fig. 2). Most females avoid such nests for

at least 5 days after the brood loss. The decrease in female fidelity does not appear to be simply a response to the loss of eggs, since when I removed eggs from nests during the day or at night (Egg Removal Experiment), female fidelity was not significantly changed (Fig. 3). This differential female response to brood loss also rules out the possibility that females avoid nests after complete-brood losses because they prefer nests with eggs over those that are empty (e.g. Unger & Sargent 1988; Gronell 1989). This is in agreement with previous research on *S. partitus* which showed that females do not appear to discriminate among potential spawning sites on the basis of the number of eggs in nests (Knapp & Warner 1991).

The Egg Removal/Odour Addition Experiment demonstrated that the female avoidance of nests that recently suffered a nocturnal complete-brood loss is at least in part a response to brittlestar odours. The addition of brittlestar odours to nests was sufficient to cause a significant decrease in female nest fidelity, even when nests still contained eggs (Eggs/Brittlestar Tile versus Eggs/Control Tile; Fig. 4). This result shows that the recent presence of brittlestars in nests can markedly decrease the likelihood that females will continue to spawn there, even if broods are left uneaten.

The experimental removal of eggs from nests just before the dawn spawning period also decreased female nest fidelity (No Eggs/Control Tile versus Eggs/Control Tile; Fig. 4). This result was completely unexpected, since the removal of eggs during the day or at night did not alter female fidelity (Egg Removal Experiment; Fig. 3). This difference in the willingness of females to spawn suggests that the female response depends on the time of brood loss. However, if females base their spawning decisions on whether the brood disappeared during the day or at night, then females (which are inactive from dusk to dawn) should be equally likely to spawn in nests from which I removed broods at night as in those from which I removed broods just before dawn. The fact that females avoided only nests from which I removed broods just before dawn suggests that the cue used by females is not the actual brood loss, but instead something related to the loss. The simplest explanation for this differential female response is that in addition to using brittlestar odours, females use odours given off by broken eggs to detect nocturnal complete-brood losses. If this is indeed the case, then egg removals conducted during the day or just after dark may

allow sufficient time for any odours of broken eggs to disperse, while removals conducted just before the dawn spawning period would subject females to the highest possible concentration of such odours. Future experiments in which the odours of broken eggs are introduced into nests at different times of the day will be necessary to test this possibility.

Although the Egg Removal/Odour Addition Experiment suggests that the decreased nest fidelity of female *S. partitus* after nocturnal complete-brood losses is a response to nest cues, changes in male behaviour after brood losses could also influence female fidelity. However, the only noticeable male behaviour that is directed at females during the spawning period is courtship, and males characteristically court at very low levels during this time. In fact, females often enter nests and begin spawning without male courtship (Knapp & Warner 1991). In addition, although I was only able to make qualitative observations of male behaviour during the Egg Removal/Odour Addition Experiment, the behaviour of males as females approached nests did not appear to differ between males assigned to the four treatments. However, further experiments need to be performed to properly assess the relative influence of nest cues and male behaviour on female nest fidelity.

The recent presence of brittlestars in nests may influence the spawning patterns of at least one other Caribbean damselfish. In *S. leucostictus*, the total number of new eggs in nests is negatively correlated with the number of days that a brittlestar remains in the nest vicinity (Itzkowitz & Koch 1991). However, since nests were checked only every 2 days and no observations of females arriving at nests were made, it is unclear if this relationship is the result of females actively avoiding those nests inhabited by brittlestars, or whether all nests received the same number of new eggs, but that nests with resident brittlestars had higher rates of egg predation.

Female Nest Avoidance and Future Egg Survival

Female *S. partitus* appear to avoid those nests that recently suffered nocturnal complete-brood losses because clutches laid into such nests have a higher chance of being lost than clutches laid into nests that have not suffered recent nocturnal complete-brood losses. This increased probability of egg loss suggests that once brittlestars discover a nest, they have a higher likelihood of returning to that nest than to undiscovered nests.

The results of at least one additional study also suggest that predators have a higher return rate to nests they have preyed upon earlier, and that this predictable predation risk influences nest-site preferences. In the Tengmalm's owl, *Aegolius funereus*, the probability of nest predation increases with the age of the nest hole and owls prefer to nest in new holes (Sonerud 1985). Sonerud (1989) demonstrated that the increasing predation risk was a result of long-term memory by the predator, since the predation rates in nestboxes he moved between breeding seasons were lower than in nestboxes that were not moved.

The present study provides one of the first experimental demonstrations that females can use the survival of previous clutches to directly assess the probability of future egg survival, and that mating decisions based on direct assessment increase the survival of subsequent offspring. However, numerous observational studies also suggest the operation of direct assessment by females. For example, in the blenny, *Aidablennius sphynx*, a species with exclusive male parental care of eggs, a recent study by Kraak & van den Berghe (1992) showed that when females spawn in empty nests, they often lay only small numbers of eggs. Such nests subsequently receive large numbers of eggs if these small clutches survive, but receive only a few eggs if the small clutches disappear. This observation led Kraak and van den Berghe to suggest that the small clutches are 'test eggs' which allow females to directly assess a male's parental ability.

In the goldeneye, *Bucephala clangula*, the probability of nest predation is higher for nests that were preyed upon in the previous year than for those where the previous nesting was successful (Dow & Fredga 1983), and females who lose a brood are more likely to switch nests the following year than females who bred successfully (Dow & Fredga 1983). Many seabirds and shorebirds have long-lasting pair bonds, with the same individuals remating year after year (Rowley 1983). Although 'divorce' in these species is generally uncommon, when it does occur it is frequently the result of low reproductive success during the previous year (e.g. kittiwake, *Rissa tridactyla*, Coulson 1966; silver gull, *Larus novaehollandiae scopulinus*, Mills 1973; Manx shearwater, *Puffinus puffinus*, Brooke 1978; ring-billed gull, *Larus delawarensis*, Southern & Southern 1982; oystercatcher, *Haematopus ostralegus*, Harris et al. 1987). Based on these results,

Diamond (1987) suggested that females use offspring survival to directly assess mate quality, and divorce those males who provide inadequate parental care. However, other researchers have argued that there is no direct causal link between reproductive failure and divorce. Instead, divorce may be a consequence of reproductive failure prematurely breaking the seasonal pair bond (Rowley 1983), or of the unpredictable return times of females the year following a reproductive failure (Coulson & Thomas 1983). Therefore, the mechanism underlying the phenomenon of divorce after reproductive failure may be easier to elucidate in bird species that raise two or more broods in a single reproductive season, since in such species any between-year confounding effects can be excluded. Although available evidence is scarce, data from eastern bluebirds, *Sialia sialis*, suggests that divorce is a direct consequence of low reproductive success. Eastern bluebirds raise two broods per year, and the probability that a female will obtain a new mate for her second brood increases with decreasing fledging success of the first brood (Pinkowski 1977; Gowaty in Rohwer 1986). Thus, the results of the above-mentioned studies and those of the present study suggest that direct assessment may be a relatively widespread phenomenon.

Conclusion

Previous research on female choice in *S. partitus* showed that before the start of a reproductive cycle (i.e. before eggs are present in nests) females use male courtship vigour to choose males of high parental quality (Knapp & Kovach 1991). Therefore, male courtship provides females an indirect method of assessing the probability of future egg survival. The present study provides evidence that after a reproductive cycle begins, females can determine the probability of future offspring survival directly by monitoring the survival of eggs in nests. Although females usually show high nest fidelity, they switch nests if their favoured nest suffers a complete-brood loss due to brittlestar predation. Females appear to use cues specific to brittlestars to avoid these nests because clutches laid in nests after brittlestars remove the entire brood are less likely to survive to hatch than clutches laid in nests that have not suffered brood losses. Therefore, female bicourous damselfish are capable of both directly and indirectly assessing expected future egg survival from nests, and females use this information

to make mating decisions that increase offspring survival.

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