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Female sand gobies gain direct benefits by choosing males with eggs in their nests

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Abstract In some fish species with paternal care, females prefer to spawn with males whose nests already contain eggs. Several hypotheses have been put forward to explain this behaviour, such as reduced risk of predation or cannibalism (the dilution effect), increased parental investment, and mate copying. This experimental study focuses on female mate choice in the sand goby, *Pomatoschistus minutus*. Females were found to choose males with eggs in their nests. In addition, hatching success increased with clutch size, mainly because males with larger clutches showed less filial cannibalism. Increased egg survival in large clutches may thus be explained by a combination of the dilution effect and higher parental investment. In another experiment, females did not seem to copy the observed mate choice of other females. In conclusion, female preference for males with eggs in their nests is adaptive, and can be explained by direct benefits, as more surviving offspring are produced.

Key words Mate choice · Paternal care · Filial cannibalism · *Pomatoschistus minutus* · Gobiidae

Introduction

Natural selection should favour females that lay their eggs so as to maximize the survival of the offspring. In some species of fish with exclusive paternal care, females prefer to spawn with males whose nests already contain eggs (Ridley and Rechten 1981; Marconato and Bisazza 1986; Unger and Sargent 1988; Gronell 1989; Knapp and Sargent 1989; Sikkel 1989; Goldschmidt et al. 1993; Kraak and Groothuis 1994). Four, not mutually exclusive, hypotheses have been put forward to explain the evolution of this preference:

1. By laying eggs among other eggs the risk of predation or cannibalism will be diluted, which is termed the "dilution effect" (Rohwer 1978; Ridley and Rechten 1981; Unger and Sargent 1988). This is the case if the proportional egg consumption is lower for larger egg masses; thus, as more clutches are laid in the same nest, the risk of a particular female's eggs being eaten decreases; the "selfish herd", *sensu* Hamilton (1971).
2. The parental investment hypothesis predicts that males should invest more paternal care in larger and therefore more valuable clutches (Coleman et al. 1985; Sargent 1988; Petersen and Marchetti 1989).
3. By copying the mate choice of others, females avoid the costs of assessing mates themselves and are able to mate with males that have been attractive to other females (as indicated by the presence of eggs in this case), supposedly leading to the production of attractive sons if those desirable traits are heritable (Ridley 1978; Losey et al. 1986; Gibson and Höglund 1992; Pruett-Jones 1992; Dugatkin 1992; Dugatkin and Godin 1992).
4 The presence of eggs in a male's nest could function as a direct signal to the females, showing that the male is a successful parent (Ridley 1978; Sargent 1988; Kraak and van den Berghe 1992).

On the other hand, there may be other reasons for females preferring to mate monogamously (spawn in empty nests), or preferring the number of clutches in the nest to be below some upper limit. In aquatic animals, embryonic oxygen consumption increases with the number of eggs in a nest (Reebs et al. 1984), and the male must compensate for this by increasing its egg fanning behaviour, as documented in bluegill sunfish,

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Lepomis macrochirus (Coleman and Fischer 1991), and the goby *Padogobius martensi* (Torricelli et al. 1985). Maybe not all males are able to increase fanning as clutches are added. Higher offspring numbers may also, through density-dependent effects, negatively affect offspring growth rate and survival, as found in a dart-poison frog (Summers 1990) and a pipefish (Ahnesjö 1992). Furthermore, males may be more likely to eat eggs from later received clutches than from earlier ones, because of the different reproductive values of young and old eggs (Salfert and Moodie 1985; Petersen and Marchetti 1989). Females should therefore avoid being the last to lay eggs in a particular nest.

Parents may sometimes consume their progeny, i.e. filial cannibalism (Rohwer 1978). This behaviour has been documented in several taxa (Polis 1981), and is especially prevalent in fishes (Dominey and Blumer 1984). It may involve the whole clutch or part of it. Following Rohwer (1978), filial cannibalism in fishes with paternal care is nowadays viewed as an adaptive behaviour that maximizes the parent's lifetime reproductive success, rather than an abnormal behaviour (reviewed in FitzGerald 1992). Guarding and fanning eggs is energetically expensive and may also reduce foraging opportunities (Magnhagen 1986; De Martini 1987), often leading to a decline in the male's physical condition (DeMartini 1987; Coleman and Fischer 1991; Lindström and Hellström 1993). Brood-caring males may, by cannibalizing part of their progeny, remain in sufficiently good physical condition to care for additional clutches (Rohwer 1978), or avoid dying of starvation before the eggs hatch (Marconato and Bisazza 1988; Marconato et al. 1993). Males may also eat their entire broods, especially when the brood is smaller than usual and its reproductive value so low that it is outweighed by the costs of parental care (Petersen and Marchetti 1989). Filial cannibalism will certainly generate conflicts of interest between the sexes, and adds another factor which females should take into account when choosing a mate.

The aim of this study was to test experimentally whether female sand gobies, *Pomatoschistus minutus*, prefer males whose nests contain eggs to males whose nests are empty, and, if this was found to be the case, to look for adaptive mechanisms explaining this preference.

Methods

The sand goby is a marine fish that is abundant on shallow, sandy bottoms along the coasts of Europe. It usually reproduces during one season only (Healey 1971). The breeding season in our study area lasts from early May to July. There is no sexual dimorphism in body size, but males develop breeding coloration with blue-black fins that is absent in females. The male builds a nest underneath an empty mussel or clam shell by covering it with sand and excavating it underneath. He then attracts females to his nest by a specific courtship behaviour, which involves erecting all fins and standing motionless on the pelvic fin, followed by short swimming bouts close to the female, and a leading display back to the nest. When spawning, the female attaches the eggs in a single layer to the ceiling of the nest (Fonds 1973; Hesthagen 1977). After spawning, the female leaves the nest, and the male guards the eggs until hatching (Hesthagen 1977), which takes 1–3 weeks, depending on water temperature (Fonds 1973; Kvarnemo 1994). During this time the male fans the eggs, thereby increasing the water circulation and improving oxygenation, and removes debris, as well as dead eggs. Immediately after hatching, the juveniles start an independent pelagic life. The sand goby is promiscuous; both males and females may spawn repeatedly with different partners during the breeding season (Healey 1971). A single male can care for egg clutches from several females at the same time.

The study was carried out in May–July 1993 at Klubban Biological Station, Fiskebäckskil, on the west coast of Sweden (58°15′N, 11°28′E). Sand gobies were caught with a hand-trawl in a shallow sand-bottom bay and taken to the laboratory. They were kept, sexes separate, in storage tanks (120–140 l) and fed fresh mussel meat once a day. Both storage tanks and experimental aquaria were provided with continuously renewed water from the sea. All experiments were carried out indoors, but under a natural light regime controlled by a timer, with a period of dusk and dawn one hour before and after the dark period, respectively. Experimental aquaria had a 3-cm layer of sand on the bottom and were provided with clay flower pots (diameter 6 cm, depth 6 cm), cut in half, as nest substrate. At the end of the study, all fishes were returned to the sea.

Female choice between males with and without eggs

We divided 40-l aquaria (length 75, depth 21, height 25 cm) into two compartments using transparent plexiglass screens. One male and one female were introduced into each compartment and provided with a nest site. The males on each side of the screen were matched for the same size and breeding colour. The fish were then left alone until they had built nests and spawned, usually within 1–3 days. After spawning, the females were removed. When both males in an aquarium had obtained eggs, both pots were briefly removed and one of them, randomly chosen, was substituted by an empty clay pot. The other male was allowed to keep his eggs by returning his clay pot. Males allowed to keep their eggs (mean male body length ± SD; 52.6 ± 5.5 mm) did not differ in size from those deprived of their eggs (52.8 ± 4.8 mm) (paired $t = 0.28$, $df = 13$, $P = 0.78$). When both males had rebuilt their nests the screen was removed, and a new ripe female was placed in the aquarium and allowed to choose between the two males ($n = 15$). Choice of mate was defined as where the female spawned. The courting behaviour of each male was observed for 10 min during each half hour until spawning started, to look for a possible treatment effect on courtship (see Jamieson and Colgan 1989). A courtship index was calculated by noting the following behaviours; swimming towards or near the female, display posture, leading display to the nest, and fanning/defense display in the nest (which they often do even if the nest is empty). Swimming and display posture each scored one point, whereas leading display and nest display scored two points, as the last two behaviours were usually more vigorous. Behaviours were scored for each occurence. Average courtship indices were calculated (over all observations) for each male and tested pairwise.

Visual copying of another female's mate choice

The experiment was carried out in the same kind of aquarium as described above. Two matched males and two nest sites were placed in each aquarium, one to the left and the other to the right. A female was placed in a net cage in the aquarium to encourage male nest building. When both males had built their nests, the female in the net cage was removed and the aquarium was divided in three compartments with transparent plexiglass screens. Thereafter, two new females matched to be of approximately the same size and roundness (indicating ripe eggs) were added. The first female was placed in the empty middle compartment of the aquarium, thereby able to see everything that occurred, while the second female was put into one of the randomly chosen outer compartments of the aquarium, together with that male. When the second female had spawned, she was taken away and both males had their nests substituted with new empty pots. The males were allowed to rebuild before the screens were removed and the first female was released (*n* = 16). We then noted in which nest she spawned.

Brood size and egg survival

Each male was allowed to build a nest in an aquarium (19 l) and was randomly given one (*n* = 16), two (*n* = 13), or three females (*n* = 17) to spawn with, resulting in a broad range of brood sizes (area of eggs = 3.2–34.2 cm^2). All females were ripe but were randomly chosen with respect to size. The females were removed after spawning, the nest was briefly taken away and the area covered with eggs outlined with a pencil, and part of it was photographed with a camera mounted on a dissecting microscope. This procedure was repeated just before hatching. On the photos we counted the number of eggs on a section of the egg mass to estimate egg density. Between spawning and hatching the males were left undisturbed, apart from being fed once a day.

We estimated hatching success by comparing the egg area just after spawning (area 1) with the area just before hatching (area 2). The relative success of broods of different sizes was then compared. The risk of a female's eggs being cannibalized would be reduced if males ate a lower proportion of eggs in larger broods, i.e. a dilution effect would result. The egg loss also give information on parental investment. If males increase their parental investment with increasing brood size, males with large broods should refrain from eating eggs while males with small broods might consume their broods if the reproductive value do not outweigh the costs of caring.

In a similar manner, egg density immediately after spawning was compared with density just before hatching (excluding clutches with no eggs left). Comparing the decrease in egg density between males with different brood sizes may yield information on potential disadvantages connected with larger broods. If density decreases more in large broods than in small, this may imply that large broods suffer, for example, from a shortage of oxygen and that males do not compensate for the increased needs. We did not, however, try to measure directly any costs of care.

Results

Female choice between males with and without eggs

There was no difference in courtship between males deprived of their eggs and males allowed to keep theirs (mean courtship index ± SD; males without eggs: 1.0 ± 2.1; males with eggs: 0.7 ± 1.5; Wilcoxon matched-pair sign-rank test; $P = 0.92$, $n = 15$).

In 13 of the 15 replicates the female spawned with the male whose nest contained eggs, and only in two cases with the male deprived of his eggs (binomial test; $P < 0.01$). Thus, female sand gobies prefer to spawn with males whose nests contain eggs.

Female copying

The test female spawned with the same male as the previous female in only 8 out of 16 replicates (binomial test; $P = 1.0$). Hence, females did not appear to copy the observed mate choice of another female.

Brood size and egg survival

The typical pattern of egg loss observed was that all eggs in a particular area of the nest disappeared, or whole clutches disappeared, often within the first days. Hatching success (area 2/area 1) increased with larger initial egg area (Spearman rank correlation; $r_S = 0.62$, $n = 46$, $P < 0.001$, Fig. 1). The absolute size of the egg area that disappeared (egg area 1 − area 2) was on average 4.2 cm^2 (SD 4.8), or 30% of the initial area, and it decreased with increasing brood size ($r_S = -0.36$, $n = 46$, $P < 0.05$). Thus, males with larger initial broods consumed fewer eggs than males with smaller broods (even though they had access to more eggs, and potentially could have eaten more eggs). Similarly, nests whose eggs were all consumed had a smaller initial brood size (mean ± SD; 10.2 ± 3.6 cm^2, $n = 9$) than nests where the whole brood survived to hatching (22.9 ± 3.6 cm^2, $n = 8$) ($t = 5.4$, $P < 0.001$).

In the analysis of egg density, sample size was lower due to a failure with the film, and because several broods disappeared completely. Egg densities was higher after spawning (mean ± SD eggs/cm^2) 99 ± 17 ($n = 26$), compared to just before hatching 89 ± 20 ($n = 20$) (paired $t = 3.11$, $P < 0.01$, $df = 19$). The decrease in egg density (density 1 − density 2) was 9 ± 14 eggs/cm^2 ($n = 20$), or 9%, and was not associated with initial egg density, or with initial area (Table 1).

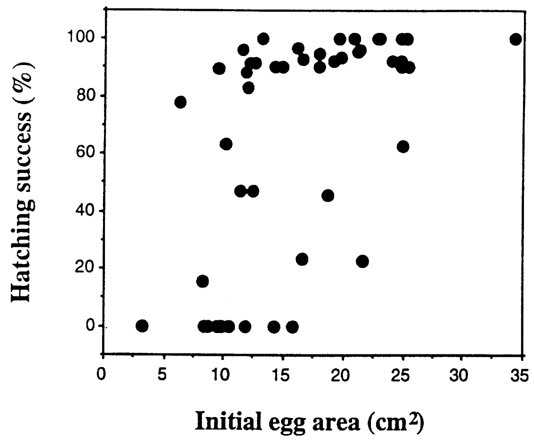

Fig. 1 Hatching success in the sand goby in relation to initial brood size, measured as area (cm^2) of the nest covered by eggs

Table 1 Multiple regression between initial egg density and initial brood area as independent variables and decrease in egg density as dependent variable ($F_{2,17} = 0.5$; $P = 0.62$; $n = 20$)

Variable	Coefficient	SE	t	P
Density	0.2	0.2	1	0.35
Area	−0.02	0.5	0.05	0.96

Discussion

Our first experiment clearly showed that female sand gobies preferred males whose nests contained eggs over males whose nests were empty. This did not seem to be caused by any differences in courtship between the males. Thus, the presence of the eggs seems to be the important cue to the choosing females, as has been demonstrated in the blenny *Aidablennius sphynx* (Kraak and Groothius 1994). Even though females prefer to spawn with males whose nests contain eggs, they may not always be able to do so, for example, if the nest is completely full of eggs. Whether female sand gobies avoid nests with much older eggs, as documented in other species of fish (Petersen and Marchetti 1989; Sikkel 1989), is unknown. Also, males may not accept new eggs after their eggs have reached a certain age and the male has turned into an exclusively parental phase (van Iersel 1953).

The visual copying experiment indicated that the observation of another female consorting with a male does not seem to be important in directing female choice (hypothesis 3), in contrast to what has been found in the guppy *Poecilia reticulata* (Dugatkin 1992; Dugatkin and Godin 1992). In fact, the second female spawned as often with the "unattractive" male (seen without female) as with the previously "attractive" one (seen with a female). A possible alternative interpretation could be that a female, observing another female spawning in a nest and upon investigating this nest finding it empty, may reject the owner of the nest as a poor parent. However, if this was the case, females in the copying experiment should have shown a preference for the non-spawning male, which was not the case. Further experiments may investigate this in more detail to fully exclude copying as being important in this species. Apparently copying did not take place, and since none of the males possessed eggs at the time of the choice, female choice was probably based on some other variable not measured in the experiment. Other factors, such as male size and coloration (Forsgren 1992) and courtship intensity (Forsgren, in press), have also been shown to influence female choice. Females might base their mate choice on egg presence only when other characters are more or less equal. Alternatively, choice could be based on several cues, taking each into account according to some priority or weighting system (Wittenberger 1983).

In the third experiment, several factors should have influenced hatching success, including filial cannibalism and aeration. We assume that a decrease in egg area in this experiment was caused mainly by filial cannibalism. A decrease in egg density, as revealed by the photos, on the other hand, should be caused mainly by the selective removal of individual eggs by the male, probably as a result of poor egg development, e.g. due to oxygen deficiency, low fertilization success or disease. Indeed, the distribution of undeveloped eggs is not patchy but randomly spread over the egg area (personal observation).

Hatching success increased with increased initial brood size (Fig. 1), because males did not increase their egg consumption in proportion to increased numbers of eggs in the nest; actually, males with large broods consumed fewer eggs. Thus, a dilution effect was apparent (hypothesis 1), which has also been found in the painted greenling *Oxylebius pictus* (DeMartini 1987), for example. Moreover, our results suggest that males were more willing to invest in large broods, as they did not cannibalize their eggs to the same extent as males with smaller broods (hypothesis 2). Since a large brood has greater reproductive value than a small brood, males should invest more, in terms of parental effort, in large broods. Increased paternal care and egg survival with increasing brood size has been demonstrated in the fathead minnow, *Pimephales promelas* (Sargent 1988). In our study, many males with large broods did not eat any eggs at all, whereas many males with small broods ate all their eggs. This is in accordance with earlier studies (Petersen and Marchetti 1989) which showed that whole clutch cannibalism may occur when the reproductive value of the brood is so low that it does not outweigh the cost of parental care. Another potential benefit of increased parental investment, not dealt with in this paper, concerns brood defence against egg predators. Males may take higher risks when guarding larger broods and defend them more vigorously, as has been documented in a number of fish species (Pressley 1981; Coleman et al. 1985; Ridgway 1989; Magnhagen and Vestergaard 1993).

The finding that hatching success increased with initial brood size supports the idea that decrease in egg area was caused by filial cannibalism. If this pattern of egg loss had been caused by poor egg development, the opposite result would be expected (i.e. higher hatching success for smaller broods). For example, if egg mortality was caused by poor fertilization success, this should have been more severe in the larger broods where the male had to spawn repeatedly and fertilize more eggs. Similarly, if egg mortality was caused by fungi or disease, this should have occurred more frequently in larger broods, which involved more females. The same would be true if the decrease in egg area had been caused by oxygen deficiency, which should have been more common in larger broods (Reebs et al. 1984).

The decrease in egg density explained a much smaller proportion of total egg mortality than that associated with the large decreases in egg area. Egg density did not decrease more in large broods than in small ones. Thus, we did not find any detrimental effects (due to, for instance, oxygen deficiency) on egg survival in large broods. However, this obviously does not mean that there is no upper limit on brood size. The clay pots used in this experiment correspond well in size to natural nest sites (Kvarnemo 1994), and broods found in nature should therefore rarely be larger than those in the experiment. Thus, spawning in a nest already containing eggs seems to have no disadvantages, given the range of nest sizes commonly found in our population.

Consequently, laying eggs in nests that already contain eggs is adaptive because more eggs will survive to hatching. This is because males with large egg masses consume fewer of the eggs in their nest. Our results fit nicely with the proposition of Jamieson (1995) that female choice for males with eggs in the nests may be explained more often by increased egg survival than by mate choice copying. Whether female sand gobies in the field also use the presence of eggs in the nest as a direct indication of the parental quality of the guarding male (hypothesis 4) cannot be ascertained from the present study, as brood sizes were experimentally manipulated by us in a random fashion.

To conclude, our experiments clearly show that female sand gobies prefer to spawn with males whose nest contains eggs, and this does not seem to be an effect of copying. This preference can be explained by an increased hatching success of larger broods. The presence of other eggs dilutes the risk of a given female's eggs being eaten. Moreover, males with large broods presumably increase their parental investment by not cannibalizing their eggs. No detrimental effect of large brood size was found. Thus, by choosing males whose nests already contain eggs, females gain direct benefits through the production of more offspring.

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