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Filial cannibalism in a nest-guarding fish: females prefer to spawn in nests with few eggs over many

Maria Norevik Andrén · Charlotta Kvarnemo

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Abstract In fish, fecundity correlates with female body size and egg-tending males often eat small broods. Therefore, small females may prefer to spawn in nests that already contain many eggs, to ensure the brood is as large as possible. In contrast, large females may prefer nests with few eggs, if high egg number or density has a negative effect on egg survival, or if there are drawbacks of spawning last in a nest. To test the hypothesis that female body size affects nest (and male mate) choice, using the sand goby (*Pomatoschistus minutus*), we allowed small and large females to choose between two males that were matched in size — one guarding a small clutch and the other a large clutch, respectively. We recorded where females spawned (measure of female preference), the combined brood size, male courtship, egg care and nest building. We also quantified the effect of brood size and egg density on egg survival in a separate data set. Although the combined broods did not exceed the small brood sizes that are at risk of being eaten, both small and large females preferred to spawn in nests with smaller clutch sizes. This preference could not be explained by more courtship or male parental effort, nor by reduced survival of larger or denser broods. Instead, our result might be explained by females avoiding the danger of cannibalism of young eggs by males or the risk of reduced egg health associated with being near the nest periphery.

Keywords Brood reduction · Clutch size · Courtship intensity · Female choice · Filial cannibalism · Gobidae · Mate choice · Reproductive success

Introduction

When individuals reproduce, they are expected to carefully consider the circumstances under which they mate, and which mate to choose, before investing time, effort and gametes into a breeding attempt (Clutton-Brock 1991; Andersson 1994; Stearns 1989; Kokko and Jennions 2008). In general, individuals are expected to choose a mate that maximizes the fitness benefits of mating, both directly and indirectly (Møller and Thornhill 1998). Choosiness is expected to be particularly important in animals whose reproductive success relies on one or both parents providing parental care. In fact, more or better parental care is one of the text book explanations for why animals are choosy (e.g., Bateson 1983; Andersson 1994; Alcock 2009).

The majority of teleost fishes do not provide parental care. However, in the families that do, which is ~20 % of families, it is most common that the male alone cares for the eggs (Gross and Sargent 1985; Reynolds et al. 2002. Among those fishes with male care, it is also very common that the male eats some or all of the eggs in his care. This is called filial cannibalism (Rohwer 1978). Although filial cannibalism may seem maladaptive at first sight, it need not be if it allows the cannibalizing male to increase his lifetime reproductive success (Rohwer 1978; Sargent 1992; Manica 2002a). For example, by eating some of the present brood (partial clutch cannibalism), a male may improve the chances of keeping the

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M. N. Andrén · C. Kvarnemo
Department of Zoology, Stockholm University, Stockholm, Sweden

C. Kvarnemo
e-mail: charlotta.kvarnemo@bioenv.gu.se

M. N. Andrén (✉) · C. Kvarnemo
Department of Biological and Environmental Sciences,
University of Gothenburg, Gothenburg, Sweden
e-mail: lissa2@hotmail.se

remaining offspring healthy or increasing his own ability to complete the current brood cycle. This would benefit both the male and the female(s) that have contributed to the brood (Sargent 1992). However, if filial cannibalism only increases the male's own success in future reproduction (which is especially likely for whole clutch cannibalism), any egg consumption by the male will clearly be detrimental to the egg-laying female(s), giving rise to a strong sexual conflict (Rohwer 1978; Lindström 2000; Wedell et al. 2006). From the female's point of view, it is therefore best to choose a male that provides care without cannibalizing any, or as few as possible, of her eggs. Although other factors, such as mate availability, paternity and nutritional status may also influence whether egg-guarding males show filial cannibalism (e.g., Mehlis et al. 2009, 2010; Myint et al. 2011), our main focus here is on the effects of brood size.

Several studies in fishes have reported that larger clutch sizes have higher survival (Sargent 1988; Lindström 1998; Koskela et al. 2000), and also, receive more parental care (van Iersel 1953; Coleman and Fischer 1991; Forsgren et al. 1996; Lindström 1998; Suk and Choe 2002; Manica 2003; Karino and Arai 2006) — whereas small clutches are more frequently reported to be fully cannibalized (Schwanck 1986; Petersen and Marchetti 1989; Petersen 1990; Lindström and Sargent 1997; Forsgren et al. 1996; Manica 2002b; Lissåker et al. 2003). Presumably, this may be because a large clutch has a higher reproductive value to the male compared to a small clutch, and because the benefit of continued care for a small clutch might not outweigh the cost of care (Rohwer 1978). Because small females lay smaller clutches than large females (Svärdson 1949; Healey 1971; Sargent and Gross 1986), small females' clutches are more vulnerable to whole clutch cannibalism by the parental male, which should affect their choice of spawning site and mate (Petersen and Marchetti 1989). In other words, it should be more important for a small female to choose a male that already has enough eggs in his nest to avoid the potential loss of reproductive success through filial cannibalism compared to a large female (Forsgren et al. 1996; Manica 2002b; Lissåker et al. 2003; Lissåker and Kvarnemo 2006). However, because large clutches receive more care, it is not unreasonable to assume that it would benefit females of all sizes to lay their eggs in nests where there are relatively many eggs, over nests with very few eggs, provided that there is space to deposit the eggs.

Earlier studies have shown a strong female preference for spawning with males that already have eggs in their nests over males with empty nests (e.g., Sargent 1989; Goldschmidt et al. 1993; Forsgren et al. 1996). This preference has been hypothesized primarily to reduce the risk of filial cannibalism (Rohwer 1978; Lindström 2000), and secondarily, as a means to shorten mate search time if females are simply copying the mate choice of other females (Losey et al. 1986; Crowley et al. 1991; Dugatkin 1992; Pruett-Jones 1992; Brown and Laland 2003). That is, the presence of eggs can provide a signal to females about the male's ability to care for eggs (Rohwer 1978; Sargent 1988; Forsgren et al. 1996), and a larger preexisting brood might create a more attractive signal. Moreover, the presence of eggs may also indicate that the nest is in a location that might be good for, e.g., decreased predation risk or better egg development. For example, bluefin killifish (*Lucania goodie*) females prefer to spawn in locations where eggs are present over empty spawning sites, even though there is no parental care in this species (Welsh and Fuller 2011).

On the other hand, there are also many reasons for females to avoid spawning in nests with many eggs already in them. Such avoidance has been found in e.g., three-spined stickleback (*Gasterosteus aculeatus*) (Belles-Isles et al. 1990; Goldschmidt et al. 1993) and 15-spined stickleback (*Spinachia spinachia*) (Östlund-Nilsson 2002). In species that actively oxygenate their eggs, the cost of care increases with brood size, since larger numbers of eggs require more oxygen (Coleman and Fischer 1991; Perrin 1995; Payne et al. 2002; Bakker et al. 2006). Thus, there may be an upper limit to the number of eggs, or to the egg density, that can be adequately oxygenated in a nest at one time (Vickery et al. 1988; Payne et al. 2004). Furthermore, Sargent (1992) and Kraak (1996) have suggested that filial cannibalism could be a means to control infections. If so, it is possible that large brood sizes or high egg density facilitates the spread of pathogens, such as fungus and bacteria. If this is the case, one would expect females to avoid spawning in nests with large or dense broods, possibly with a stronger aversion by large than small females, since larger female fish typically lay larger clutches (Svärdson 1949; Healey 1971; Sargent and Gross 1986). One may also expect females to avoid being the last to spawn in a nest, regardless of their own size, because, as predicted by Rohwer (1978), eggs laid last in a brood may be at a heightened risk of being eaten by the nest guarding male. If so, females should prefer to spawn in a nest with fewer eggs, since the likelihood of other females adding more eggs later should decrease as the nest becomes full. In addition, in species in which last eggs are laid along the periphery, it is also possible that this position is unfavourable for the eggs (Thomas and Manica 2003; Green et al. 2006; Kudo 2006).

Because small females are typically more exposed to whole clutch filial cannibalism due to their small clutch sizes (Manica 2002b; Lissåker et al. 2003), they may also need more information or persuasion before making a mate choice. If so, small females might be expected to take longer to choose a mate or require more male courtship before starting to spawn (cf. Forsgren 1997). On the other hand, large females may be more choosy, because they are preferred as mates by males (Kvarnemo and Forsgren 2000), and therefore can afford to be choosy. If this is the case, it would be reflected in a longer latency to spawn or more courtship required before large females start to spawn.

Thus, we had two opposing predictions: (A) Any female, but small females in particular, may prefer to spawn in nests that contain many eggs to few, to ensure the combined brood is as large as possible. (B) Any female, but large females in particular, may prefer nests with few eggs, if high egg number or density affects egg survival negatively, or if there are drawbacks of spawning last in a nest. We tested these predictions using the sand goby (*Pomatoschistus minutus*), a species that uses empty mussel shells as nest sites. Males provide egg care and exhibit filial cannibalism (Lindström 1998; Lissåker et al. 2003; Klug et al. 2006; Lissåker and Kvarnemo 2006). Several females typically spawn in the same nest (Jones et al. 2001), with the eggs attached individually in a single layer to the mussel shell that forms the ceiling of the nest. Average clutch size is about 2300 eggs, but clutch size is strongly correlated with female size (Kvarnemo 1994). In most cases, the female spawns her whole clutch with only one male, unless she is disturbed during spawning (Singer et al. 2006). The first female to spawn in a nest starts attaching her eggs in the centre of the shell and additional females attach their eggs among and around the previous eggs (MNA and CK, personal observation).

By allowing small or large females to choose between two males of similar size, but guarding a small and large clutch, respectively, we evaluated whether small and large females differ in their choosiness (measured by latency to spawn and courtship intensity prior to spawning) and preference for initial clutch size in the nest (large or small). We also investigated whether egg numbers, egg density or clutch area affect egg survival. With sand gobies having well-covered nests with very small nest entrances, oxygen limitations have been implicated in partial clutch cannibalism (Klug et al. 2006). If so, high egg density, or egg numbers, would be expected to have a negative effect on egg survival, predictions that we tested with a separate data set.

Methods

Study species

The sand goby is a small coastal species with a life span of 1–2 years. In the study area they are thought to have only one reproductive season, but both males and females breed repeatedly in multiple brood cycles during that single season. Both sexes breed promiscuously and show no sign of pair bonding. The male excavates a nest under an empty mussel shell, which he covers with sand, leaving only a small nest opening. Nest holding males develop a breeding coloration during the reproductive season, consisting of melanized dark fins, an iridescent blue stripe with a black edge on the anal fin and a blue, black and white spot on the first dorsal fin (Forsgren 1992; Kvarnemo et al. 2010). Males attract potential mates to their nests with courtship displays, and several females may spawn sequentially in one male's nest. Spawning females spawn their eggs to the ceiling of the nest in a single layer and then leave. The male provides all parental care by defending the nest from egg predators and cleaning the eggs, which likely reduces the spread of disease. He also oxygenates the eggs by fanning them with his pectoral fins or tail fin. For detailed references on the reproductive behavior of the sand goby, see Forsgren (1999).

Location, capture and storage

The female choice experiment was conducted at Kristineberg Marine Research Station on the Swedish west coast, May–June 2004 and 2005. The data on egg survival were collected from the same population of fish, but the experiment was carried out May–June 1990 and 1991 at Klubban Biological Station, situated nearby. For both studies, we caught sand gobies using a hand trawl in Bökevik bay, near the two research stations. We kept the fish in separate male and female storage aquaria (length 70 cm, width 50 cm, height 35 cm; filled with approx. 110 l) in the laboratory for at least 3 days to acclimatize. All storage and experimental aquaria had running, natural seawater and a 3- to 4-cm layer of sand in which to burrow and hide. During storage time the fish were fed chopped fresh mussel meat (*Mytilus edulis*) and frozen Alaska Pollock (*Theragra chalcogramma*) daily. In the female choice study, the fish were not fed during the experimental period (max. 4 days, in most cases less; see below). In the egg survival study, they were fed once a day or every fourth day, which we know did not influence whole or partial clutch cannibalism (Kvarnemo 1997 and below). In comparison, lack of feeding did influence filial cannibalism in the closely related common goby (*P. microps*), but only when the fish were kept unfed for considerably longer times than was the case in the current studies (Kvarnemo et al. 1998). Even so, low feeding only affected partial clutch cannibalism, but not whole clutch cannibalism, which is a main focus of the current study.

Female choice study

Experimental set-up

The female choice experiment was conducted in 17 aquaria (length 50 cm, width 36 cm, height 30 cm; filled with approx. 45 l), each with a glass lid. All aquaria were divided into two visually isolated male compartments by an opaque divider and each compartment was equipped with a halved clay flowerpot (6 cm in diameter) to serve as a standardized nest site (Fig. 1a). Before placing the nest sites in the aquaria, we attached a transparent, adhesive plastic film to the pot, with either a small (diameter 25.0 mm, area 5.2 cm^2) or a large (diameter

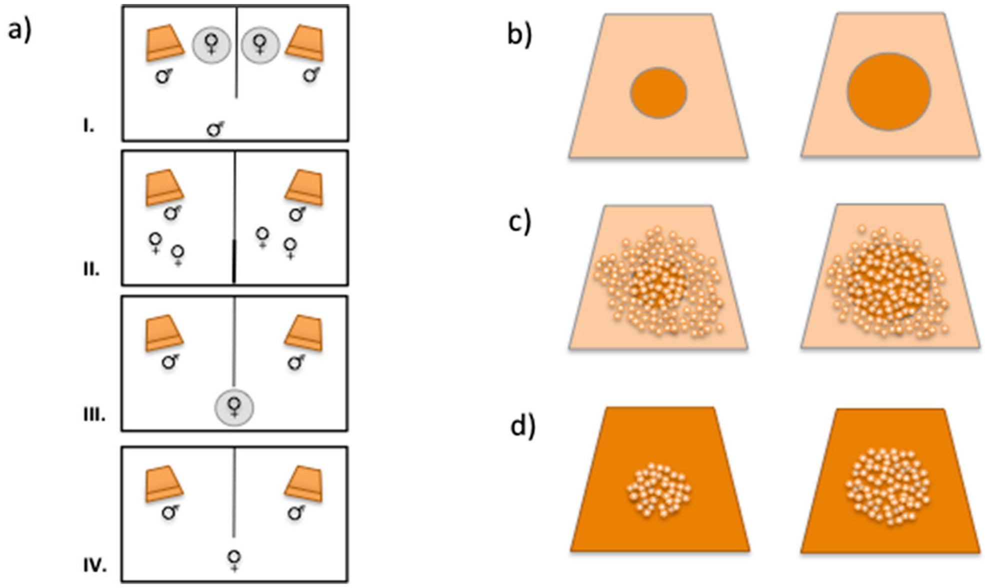

Fig. 1 In the female choice experiment, all tanks were divided into two parts, each with half a flowerpot as nest site (**a**-i). Adhesive plastic film covered the inside of the pots, with a small or a large hole cut out of the film (**b**), one of each in each tank. Three males competed for the two nest sites. Two gravid females in a plastic vial were placed next to each nest site during this phase. Once nests were built on both sides, the tank was sealed off with a second divider and two females were allowed to spawn on each side (**a**-ii) and attach their eggs inside the nest (**c**). The plastic film was then removed, leaving only the eggs that were attached to the flowerpot and not to the film, hence creating small or large "initial clutches" (**d**). After males had rebuilt their nests, the second divider was removed. A small or large "focal female" was initially placed in a plastic vial (**a**-iii) and later released into the tank. It was free to spawn with either the male having the small or the large brood in his nest (**a**-iv)

28.5 mm, area 15.9 cm^2) circular hole cut out of the film (Fig. 1b). We placed a nest with a small hole in the film in one of the compartments (randomly chosen) and one with a large hole in the other. The males could not see each other when they were in the nest but could swim freely to the other side of the aquarium and interact. Thus, the divider separated the two nest sites visually and physically, but still permitted interactions between the males (Fig. 1a-i). All experimental aquaria were visually isolated from each other, in order to prevent interactions with individuals in other aquaria.

Three males were placed in each aquarium. Based on our visual inspection, these males were matched as closely as possible for size, breeding coloration and body condition based on their general "chubbiness". The three males were then left to compete for the two nest sites, which led to the two stronger and more motivated males getting the nests. The third male was removed when the two other males had started to construct nests. We did not measure breeding coloration or body condition, but after the experiment we confirmed that the two males were of very similar size (see below). Similar methods to visually match males according to breeding coloration in sand gobies have been used many times before (Forsgren et al. 1996), and by first visually matching the males and then removing the least competitive of the three, our explicit aim was to minimize any difference between the remaining two in terms of body condition, strength, motivation, etc.

Two gravid females, kept in a perforated plastic vial, were placed next to each nest site during the nest-building phase, to serve as visual and olfactory stimuli to the males (Fig. 1a–i). If none or only one of the males built a nest overnight, we replaced the stimulus females with a new set of females, to incite nest-building, and expedite the start of a trial. As soon as both males had built nests, an additional divider was placed in the aquarium to seal off the two compartments completely (Fig. 1a-ii). Females were then released from the container and allowed to spawn with the nest holding male on their respective sides. We added one extra female to each side, in order to increase the likelihood that the brood was large enough to cover the entire hole in the adhesive film (Fig. 1c).

When spawning had occurred on both sides, the females were returned to the sea. The nests were picked up and the adhesive film was gently removed, leaving only the eggs that had been attached to the flowerpot and not to the film (Fig. 1d). These manipulated (from now on referred to as "initial") clutches were photographed, using a digital camera. The two sizes of holes in the plastic film allowed us to manipulate initial clutch size, without doing any damage to the remaining eggs and without leaving any remains of the removed eggs on the pot surface. This experimental approach also meant that both males were given a similar spawning history. The average size of all fully cannibalized clutches across several years of experimental work with sand gobies is approx. 12 cm^2 (MNA, unpublished data). The size of the small hole was about half that size, whereas the size of the large hole was approximately the mean size of a single-female clutch (approx. 14 cm^2; MNA, unpublished data). However, because the holes in the adhesive film did not always get completely covered with eggs, the initial clutch areas were slightly smaller than the sizes of the holes (mean±SE; initial small clutches: 4.2±0.1 cm^2, N=21, initial large clutches: 10.3±0.4 cm^2, N=21). As all previous nest constructions were destroyed when the pots were picked up, the males had to rebuild their nests after the pots were returned. In nature, rebuilding and nest reconstruction happen frequently, as the nests are often exposed to various degrees of destruction by wave movements and egg predators, such as shore crabs and netted dog whelks (Järvi-Laturi et al. 2011; CK, personal observation).

Individual males were only used once in the experimental set-up. Males that failed to build a nest within 3 days and females that failed to spawn were returned to the sea and replaced with new individuals. Gravid females that had been used to incite nest building, but had not yet spawned, were returned to a separate storage tank for rest and food before being re-used as stimulus and spawning females with other males 2–3 days later. In contrast, all females (henceforth referred to as "focal females") that were used in the actual female choice trials (see below) were only used once.

Female choice trials

In each trial, one gravid focal female of either small or large body size was allowed to choose between the two males with small or large initial clutch sizes in their nests. On average (±SE), small focal females were 47.3±1.0 mm (range 42–55 mm, N=16) and large focal females were 61.4±0.6 mm (range 56–70 mm, N=34) in total length.

The extra divider was removed at the start of each trial so that the two males were free to interact again, but they did so only to a limited extent due to the remaining divider (Fig. 1a-iii). The focal female was placed in a perforated plastic vial in the middle of the aquarium at a position that allowed her to see both nests and both males (Fig. 1a-iii). After 1 h, the female was released and all individuals were observed for 1 h (Fig. 1a-iv).

During the behavioral observations, we noted if the female started to spawn during the trial or not. We also measured the time spent by males in different activities and the frequency of these activities. All behaviors were noted during the observations but we focused our analyses on those most likely to influence female spawning decisions, such as male courtship and egg-tending behavior. We classified male displays (which included erect fins, bouncing and trembling of the body, and leading the female to the nest) as courtship behavior. Furthermore, we classified male nest building activity, fanning, egg inspection, cleaning and smearing mucus over the egg surface, as egg care. Male–male interactions, such as chasing each other, were rare (only seen in three trials) and not included in a separate analysis. Instead, since male–male interactions may influence female mate choice, their time and frequencies were included as male courtship. Female-initiated interactions included female courtship of the male, entering the nest and following the male to the nest. We also recorded the nest opening size (visually estimating width and height and later calculating the opening size as an oval: $A=\pi hw$; see Lissåker and Kvarnemo 2006) at the end of the observation period.

To determine if large and small females differed in their latency to spawn, we recorded the time until spawning during the observation period. For females that did not spawn during that time, we checked the aquaria for spawning pairs, or used indirect evidence of recent spawnings, such as newly spawned eggs and slim females, three times a day for 3 days after the observation. Because a single spawning event typically takes 1–2 h, this intensity of surveillance provides a good estimate of latency to spawning. Once spawning occurred, the combined brood area was documented using a digital camera. Clutch areas were then calculated using UTHSCSA Image Tool 3.00 software for Windows. These photographs were not originally intended for estimating egg densities. However, based on a subsample of images from ten trials with sufficiently good resolution, average egg density after the focal female had spawned was 204 eggs/cm^2, ranging 170–236 eggs/cm^2. These densities fall well within the ranges investigated in the egg survival study (below and Fig. 4). Similarly, the areas covered by eggs in the mate choice experiment (Fig. 3) fall safely within the range of egg areas investigated in the egg survival experiment (6.8–29.0 cm^2).

The choice tests were always run as soon as both males had received eggs. Furthermore, to reduce any potential effect of egg age on female mate choice, the age difference between the eggs in the two nests was never more than 1 day. Given these constraints, behavioral observations were completed for 50 trials (16 with a small focal female, 34 with a large focal female, with a total of 100 males). At the end of each trial, male total body length was measured to the nearest mm, after which the fish were released back into the wild. There was no significant difference in male body length between males with small and large clutches or between replicates with large or small focal females (repeated-measures analysis of variance [ANOVA]: initial clutch size: $F_{1,48}$=1.22, p=0.27; female size: $F_{1,48}$=0.85, p=0.36). On average (±SE), body length of males guarding small clutches was 55.7±1.1 mm and large clutches was 54.8±1.1 mm in the 16 trials with a small focal female, and 56.6±0.9 and 56.5±0.8 mm, respectively, in the 34 trials with a large focal female.

However, a fair number of these trials had to be excluded from the study (Table 1). There were 16 trials in which one or both of the initial clutches were cannibalized fully or partially before the female made a choice (19 clutches in total: 14 small

Table 1 Overview of replicate numbers for the small and large focal female treatment groups and reasons for losses

	Size of focal female Small	Large
Initial replicate numbers	16	34
Replicates lost, due to		
- One or both initial clutches eaten before choice was made	−1	−15
- Focal female spawned in both nests	−0	−2
- Focal female did not spawn within 3 days	−6	−5
Remaining replicate numbers	9	12
- Outlier clutch size	−0	−1
- Focal female's clutch eaten before being measured	−2	−1
Remaining replicate numbers for clutch size	7	10

and five large). In two trials, the focal female spawned in both nests, making her choice ambiguous. In addition, six small and five large focal females did not spawn within 3 days, excluding another 11 trials. This left us with nine small and 12 large focal female trials. One of the large females made a choice of where to lay her eggs, but the clutch was tiny (approx. one-fifth of the size of the clutches spawned by the other females in this group), and thus not representative of large female clutches. We therefore included this female in all analyses, except for the clutch size analyses and mean values of clutch sizes. In addition, two clutches spawned by small females and one by a large female were eaten completely before we could measure them (all three in small-clutch nests, suggesting that these nests are indeed more risky). This reduced the sample sizes on combined brood areas even further to seven for small and ten for large focal females. These females, as well as, the outlier female were still used in the choice analysis.

Egg survival study

To investigate whether a large number of eggs, a high density of eggs or a large area covered by eggs have negative effects on egg survival, we returned to a data set collected in 1990 and 1991. The results of this experimental study are published (Kvarnemo 1997), but not the aspects presented here. The study was carried out in 20 small experimental aquaria (length 38 cm, width 20 cm, height 25 cm; filled to approx. 17 l), equipped with sand, a halved flowerpot (6 cm in diameter) and a continuous flow of natural seawater. Each male ($N=54$) was allowed to spawn with a single female and then left to care for the eggs until just before hatching. Sand goby eggs are tiny and numerous and egg density is relatively uniform within a spawned clutch. Therefore, rather than counting each egg individually, the number of eggs in each nest was estimated by multiplying the total area covered by eggs by the density (number of eggs per cm^2) of eggs inside a small area, determined by photographing a marked area of 0.5 cm^2 using a camera mounted on a microscope. Clutch area was determined by marking the outline of the clutch with a pencil. After hatching, the outline was traced onto thin paper of known density, which was then cut out and weighed. This method has been used before by, among others, Svensson et al. (1998). Clutch area and egg density were determined once within 24 h of spawning and once 1–2 days before hatching. Egg survival was calculated as the proportion of initial egg numbers that were present on the second occasion.

Statistics

All data were tested for normality and homogeneity of variances, proportional data were arc-sin square root transformed and continuous data were square root or log-transformed when necessary. Two-tailed tests or F ratios with a significance level of 0.05 were used. The data were analysed using STATISTICA 7.1 (StatSoft Inc.) or JMP 7.0 (SAS institute Inc.) software.

Due to the paired nature of our female choice set-up, with two males responding to the same female, we used repeated measures ANOVAs with initial clutch size as the repeated measure and female size as factor. One-way ANOVAs were used for comparing clutch sizes spawned by large and small females, and clutch size after spawning in nests with initially large or small clutches. These comparisons were not paired because each female laid eggs only once and in only one of the nests. All non-significant interactions were removed from the models. Female latency to spawn and some male behavioral data that did not meet the assumptions of ANOVA (normality and homogeneity of variances) were analysed using non-parametric Mann–Whitney U-tests and Wilcoxon matched-pairs tests. For frequency data, such as female nest choice and whole clutch cannibalism, we used Chi-square analysis or a binomial test.

The effect of the number of eggs on egg survival (proportion of the initial clutch that survived to close to hatching) was analysed using linear regression, and the effects of the unmanipulated initial clutch area and initial egg density on egg survival were analysed using a multiple regression (method: forward stepwise with probability to enter=0.25). Because the adaptive significance of whole clutch cannibalism may differ from partial clutch cannibalism, we repeated the analyses using logistic regressions to evaluate if egg number, or egg density and clutch area affected the occurrence of whole clutch cannibalism. The egg survival data were extracted from a study in which the egg-tending males were fed every day or every fourth day (see Kvarnemo 1997, for further details). However, since feeding treatment did not affect any of the current results ($p>0.70$), this factor was removed from the analyses that are reported in the Results section.

Results

Female choice study

Female behavior

In the female choice study, seven out of nine small females chose to spawn in the small-clutch nest (i.e., the nest with the small initial clutch) while only two chose the large-clutch nest. Similarly, nine out of 12 large females chose the small-clutch nest and three chose the large-clutch nest for spawning (Fig. 2). Thus, preference was not influenced by female size (Chi-square: $\chi^2=0.14$, $df=1$, $N=21$, $p=0.71$), and across both female sizes, females showed a significant preference for spawning in nests with small initial clutches (binomial test: $N=21$, $p=0.03$).

The small initial clutches were significantly smaller compared to large initial clutches, also after the females had chosen to lay their eggs in one of the nests (one-way ANOVA: $F_{1,16}=18.79$, $p<0.001$; Fig. 3). As expected, small focal females laid smaller clutches than large focal females (one-way ANOVA: $F_{1,15}=5.94$, $p=0.03$; mean±SE: 5.2±0.7 and 7.5±0.6 cm^2, respectively). Small females achieved an average combined brood area of 9.6 cm^2 if they chose to spawn in the nest with the small initial clutch, compared to 18.0 cm^2 if they chose the nest with the large initial clutch, whereas large females achieved a combined brood area of 12.1 cm^2 if they chose the nest with the small initial clutch, compared to 15.2 cm^2 if they chose the nest with the large initial clutch (Fig. 3).

Both small and large females spent about the same time interacting with males with small and large initial clutches (repeated measures ANOVA: clutch size: $F_{1,19}=0.02$, $p=0.87$; female size: $F_{1,19}<0.01$, $p=0.97$; mean±SE: 525±184 s). The latency to spawning also did not differ between small and large focal females (Mann–Whitney *U*-test: $U=51.50$, $N_L=12$, $N_S=9$, $p=0.86$) or between initial clutch sizes of the chosen male (Mann–Whitney *U*-test: $U=35.00$, $N_L=5$, $N_S=16$, $p=0.68$) (median=23, interquartile range=4 h).

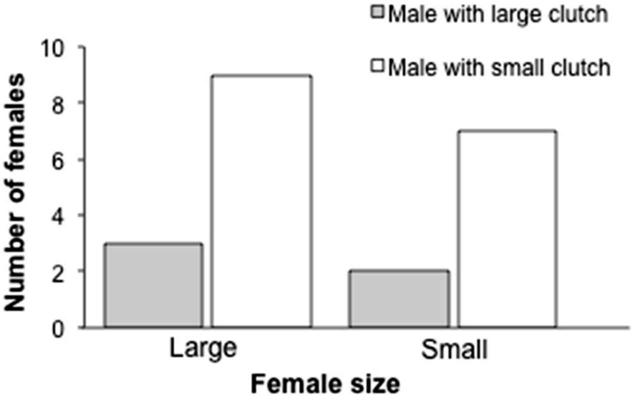

Fig. 2 Female choice result, measured as the number of large and small females that chose to spawn with a male with a small or a large initial clutch of eggs in his nest

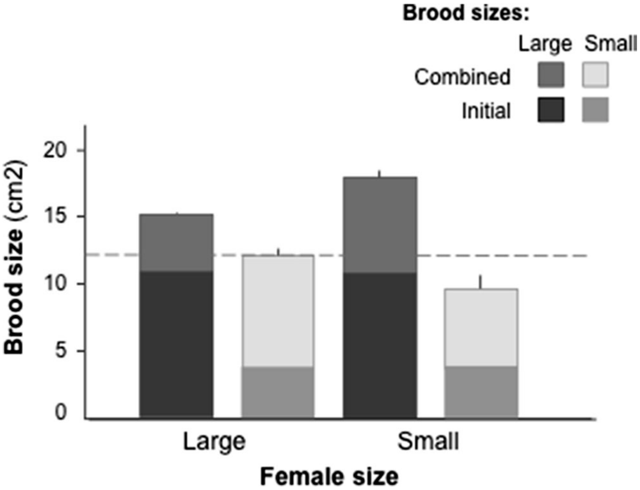

Fig. 3 Combined brood size (cm^2, mean±SE) after large and small females had chosen where to spawn (i.e., in nests of males with either a small or a large initial clutch in the nest). Sample sizes for the four groups (left to right) are 2, 8, 2 and 5. The dashed line shows the overall average clutch size that suffered whole clutch cannibalism

Male behavior

Before the female had chosen where to lay her eggs we tested whether male behavior differed between males that were guarding a small or a large clutch, and whether it was affected by female size. The time males spent on courtship was the same, regardless of initial clutch size and female size (repeated-measures ANOVA: clutch size: $F_{1,19}=0.23$, $p=0.63$; female size: $F_{1,19}=0.47$, $p=0.50$; mean±SE: 329±95 s). Likewise, there was no difference in courtship frequency between males with small and large clutches (Wilcoxon matched pairs test: $T=58.50$, $Z=0.08$, $N_L=21$, $N_S=21$, $p=0.93$; median=0, interquartile range=6 times) and no significant effect of female size (Kruskal–Wallis: $Z=1.41$, $N_L=12$, $N_S=9$, $p=0.16$). The time males spent on egg-care did not differ between males with small and large initial clutches, nor was it influenced by the size of the focal female (repeated-measures ANOVA: female size: $F_{1,19}=3.31$, $p=0.08$; clutch size: $F_{1,19}=0.13$, $p=0.72$; mean±SE: 476±115 s). Likewise, there was no difference in egg-care frequency between males with small and large clutches (Wilcoxon matched-pairs test: $T=61.50$, $Z=1.04$, $N_L=21$, $N_S=21$, $p=0.30$; median=1, interquartile range=8) and no effect of female size (Kruskal–Wallis: $Z=0.96$, $N_L=12$, $N_S=9$, $p=0.34$). Finally, the nest opening sizes were also the same, regardless of initial clutch size and female size (repeated-measures ANOVA: clutch size: $F_{1,19}$=1.53, p=0.23; female size: $F_{1,19}$=0.15, p=0.70; mean±SE: 4.7±0.8 cm^2).

Across the entire study, initial clutches that were small were completely consumed more often (14 of 50 nests) than clutches that were large (5 of 50 nests) (Chi-square: χ^2=4.16, df=1, N=100, p=0.04). In addition, we found that the size of the focal female influenced the likelihood that the initial clutch was eaten before she spawned. Such whole clutch cannibalism happened in 15 of the 34 replicates with a large focal female, while it only happened in one of the 16 replicates with a small focal female (Chi-square: χ^2=7.17, df=1, N=50, p=0.007; Table 1). Although this is reported here as a male behavior, we cannot exclude that also the focal female ate some of the eggs.

Egg survival study

To establish whether the females' preference for small-clutch nests (above) can be explained by any negative effect of large clutches, we tested how egg numbers, egg densities and size of the areas covered by eggs affect egg survival. The number of eggs in the clutch had no significant effect on the proportion of eggs that survived until near hatching (linear regression: $F_{1,52}$ <0.02, p=0.89). Similarly, the number of eggs in the clutch did not affect the occurrence of whole clutch cannibalism (logistic regression: whole model: χ^2=0.03, df=1, p=0.85). Since the number of eggs was estimated from egg density and clutch area, their separate effects on egg survival were also analysed. High egg density had a positive effect on egg survival (Fig. 4), contrary to our expectations based on the result from the female choice study, whereas clutch area had no significant effect (stepwise multiple regression: egg density: $F_{1,52}$=4.42, p=0.04; clutch area: $F_{1,52}$=0.82, p=0.37).

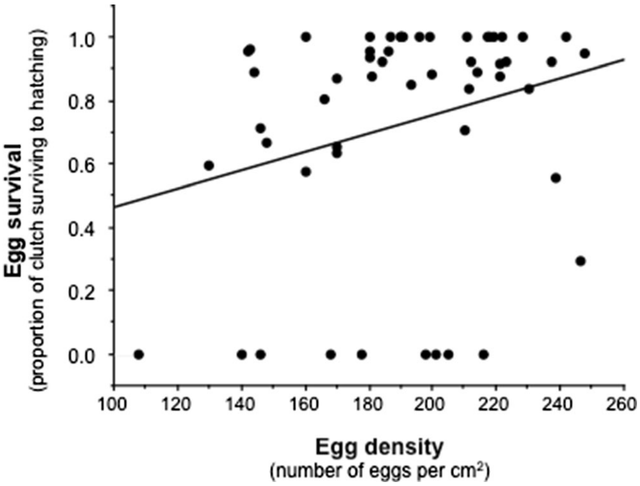

Fig. 4 Egg survival (proportion of spawned eggs surviving to hatching) in relation to egg density (number of eggs per cm^2) shown with regression line (y=0.03x+0.179)

Neither egg density nor clutch area affected the incidence of whole clutch cannibalism in this data set (logistic regression: whole model: χ^2=3.82, df=2, p=0.15; likelihood ratio test: egg density: χ^2=2.67, df=1, p=0.10; egg area: χ^2=0.63, df=1, p=0.43).

Discussion

Contrary to our prediction A, this study shows that both large and small sand goby females prefer to mate with males that have small clutches in their nests (Fig. 2). We also found no indication that small females are choosier than large females, or vice versa, in terms of latency to spawn, or in the amount of courtship before spawning. We found, however, strong support for prediction B, namely that females avoid spawning in nests with large initial clutches, possibly because there are costs associated with spawning close to the periphery or being one of the last females to spawn in a nest. We discuss each of these results below.

Small females showed a preference for nests with small initial clutches, even though the combined brood size after spawning did not exceed the small brood sizes that are at high risk of being totally cannibalized by males (Fig. 3). To some extent, this result is surprising since a large number of studies have found that small clutches are more likely than larger clutches to be fully cannibalized by the caring male – in sand gobies and other species (e.g., Schwanck 1986; Petersen and Marchetti 1989; Petersen 1990; Forsgren et al. 1996; Kvarnemo et al. 1998; Manica 2002b, 2004; Lissåker et al. 2003; Neff 2003; Lissåker and Kvarnemo 2006). In fact, even the large females did not achieve a combined brood size that was large enough to be "safe", when they chose to lay their eggs in the nest with the small initial clutch. In contrast, the few females that chose to lay their eggs with the male that had a large initial clutch achieved a combined brood size that was above the critical limit, regardless of their own body size.

Many male traits provide the female with information on direct or indirect benefits (Jennions and Petrie 2000; Candolin 2003; Lindström and St. Mary 2008). Thus, both physical and behavioral traits of the males may influence female spawning decisions. In sand gobies, females prefer large and more colorful males (which may indicate indirect benefits as well as direct) (Forsgren 1992; Lindström and Hellström 1993). However, in our study, males were matched for size, breeding coloration and condition. Therefore, female preference for nests with small clutch sizes cannot be explained by the male traits that we measured. Female sand gobies also prefer courting males (Forsgren 1997) and males providing more or better parental care (Forsgren 1997; Lindström et al. 2006). Fanning to ventilate the eggs is an important aspect of parental care, and several studies of sand gobies and other species of fish show female preference for males that fan more often (e.g., Tinbergen and van Iersel 1947; Pampoulie et al. 2004; Lindström et al. 2006). In the present study, however, there was no significant difference in time spent on courtship or egg-care between males that cared for large and small broods. Female sand gobies also include nest quality in mate choice (Lehtonen et al. 2007), but again, nest-opening size, as a measure of how well-built the nests were, did not differ between males with small or large initial clutches, or between trials with large or small focal females. A female preference to spawn in nests with fewer eggs has been found before in three-spined and 15-spined sticklebacks (Belles-Isles et al. 1990; Goldschmidt et al. 1993; Östlund-Nilsson 2002). Goldschmidt et al. (1993) found that females were more likely to enter nests with intermediate sized broods compared to nests with small or large broods, even though males that guarded the preferred broods did not court more than other males. Similarly, we found no difference in courtship or any other male behaviors that we measured. Therefore, it is unlikely that female spawning preference was influenced by male behavior in our study. Instead, our results suggest that females were responding to the eggs themselves.

One reason why females prefer to spawn in nests with small clutches is that small clutches consume less oxygen and produce less carbon dioxide (Coleman and Fischer 1991) and males might be able to ventilate small broods better, in line with Payne et al.'s (2004) model of oxygen mediated filial cannibalism. However, this explanation might be less likely to apply to species that lay their eggs in a single layer, like sand gobies, than to species that lay their eggs in clusters (Östlund-Nilsson 2002; Payne et al. 2002, 2004). A study of a brackish population of sand gobies found a negative effect of high egg density on egg survival, but similar to Lissåker et al. (2003), this effect could not be explained by oxygen deficiency (Klug et al. 2006). Our current results show no effects of egg number or area covered by eggs on egg survival, but in contrast to Klug et al. (2006), we did find a *positive* effect of high egg density on egg survival (Fig. 4). A possible explanation to these contradictory results might be the difference in salinity between our study areas. Klug et al.'s (2006) result might indicate that in brackish areas, densely attached eggs are more susceptible to fungal or other infections that thrive in low salinity waters (Schreier et al. 1996; St. Mary et al. 2004).

In the painted greenling (*Oxylebius pictus*), the percentage of surviving eggs increased with the number of clutches spawned in the same nest, except when the numbers of clutches exceeded eight (DeMartini 1987). Thus, it is possible that negative effects on egg survival could arise at higher abundances or densities of eggs than occurred in our study. Nevertheless, because the clutch sizes and egg densities in our egg survival study correspond well to those of the female choice study, reduced survival at very high density cannot easily explain the observed female preference for nests with smaller clutches of eggs. Furthermore, spawning in a small-clutch nest is no guarantee that egg density will stay low, since the male may attract eggs from other females later. In 20 field nests from the same population as the present study, for which parentage was genetically determined, two to six different females had spawned in each nest, with an average of 3.4 (Jones et al. 2001).

Rohwer (1978) predicted that if some eggs hatch later than others, males would at some point benefit from eating those eggs rather than continuing to guard them. Consistent with this prediction, and the fact that young eggs contain more nutrients, while being reproductively less valuable than more developed eggs, males have been found to eat more of young than old eggs (e.g., Salfert and Moodie 1985; Petersen and Marchetti 1989; but see Sikkel 1994; Takegaki et al. 2011), and females to show a preference for laying their eggs next to young eggs in the nest (Sikkel 1989; Afonso and Santos 2005). In the sand goby, Klug and Lindström (2008) found that when nest guarding males show partial clutch cannibalism, large eggs laid last in a brood are at the highest risk of being eaten. Some possible explanations for partial clutch cannibalism may be that both large and newly spawned eggs contain more nutrients, and by eating these eggs, the male may be able to synchronize hatching within the nest. Then, as a consequence, females that avoid nests with a large number of pre-existing eggs are less likely to be the last to spawn in that nest. In this context, it is important to add that there is no effect of female body size on egg size in our study population (CK, unpublished data), which therefore may explain why large and small females avoided this possibility equally.

Sand goby females will attach their eggs to the hard substrate that forms the ceiling of the nest, e.g., a mussel shell, stone, pot, or similar. Typically, the first female will lay her eggs as close as possible to the center of the nest and any subsequent females will then lay their eggs between and around the pre-existing clutch of eggs (MNA and CK, own observations). It appears as if they are actively avoiding areas that are close to the sand and near the edge of a nest. This spawning behavior may be adaptive if eggs that are placed in the center are ventilated more efficiently. It may also be easier for the male to keep eggs that are deposited in this position healthy, while cleaning them using his mouth or depositing anti-microbial mucus around them, like the grass goby (*Zosterisessor ophiocephalus*) does (Giacomello et al. 2008). It is also possible that eggs around the edges are more prone to damage or infections, e.g., due to silting or abrasion. These suggestions provide alternative, but so far untested, explanations for the female preference to spawn in small-clutch nests shown in this paper.

Finally, we found that filial cannibalism of the initial clutches occurred significantly more often when the focal female was large than when she was small (Table 1). One explanation for this could be that males paired with a large female perceived their future reproductive success as positive and thus valued the present brood less. This result is in line with Kondoh and Okuda's (2002) predictions that males should be more likely to cannibalize eggs if they have a good chance of obtaining new eggs to replace the eaten ones. In the sand goby, female body size generally affects the reproductive value of the clutch, as large sand goby females spawn larger clutches (Healey 1971). However, it is also possible that large female size signals indirect genetic benefits to the male (e.g., viability genes, since size increases with age). Regardless of which, our results could indicate that males valued their current (i.e., the initial) clutch more, by refraining from eating the clutch or by better defending it against cannibalism by the focal female when the focal female was small and the immediate prospect of spawning with a large female was low. Similarly, in two experimental studies of the freshwater lizard goby (*Rhinogobius flumineus*), nest-guarding males ate more eggs from clutches when there was a surplus of replacement eggs available (due to a female biased adult sex ratio, nest space limitation or high female fecundity) (Okuda et al. 2004; Takeyama et al. 2013). In accordance with these results, Myint et al. (2011) found that lizard goby females were reluctant to spawn with males that had another female close to the nest, possibly because high mate availability increases the risk of male filial cannibalism.

In summary, we found that females, regardless of body size, preferred to spawn in nests with small initial clutches. This preference cannot be explained by negative effects of high egg density or large clutch size, as we found higher survival in high density clutches, and no effect on egg survival related to total clutch size (egg numbers or area covered by eggs). Instead, the most likely explanation for our result is that females reduce their risk of filial cannibalism by avoiding being the last female to spawn in a nest. However, whether this is due to males targeting younger eggs to cannibalize, or because eggs close to the perimeter of the brood face greater hazards, still remains to be investigated.

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