

## Effect of egg predator on nest choice and nest construction in sand gobies



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Nest defence is a particularly costly component of parental care. The costs of nest-related behaviours are affected by the nest's location, size and architecture; yet surprisingly little is known about how choice of a nesting site or nest characteristics are adjusted as a response to the threat of future nest predation. To address this topic, we investigated whether egg predation threat influenced nest choice and nest construction in the sand goby, *Pomatoschistus minutus*, a small marine fish with exclusive paternal egg care. We found that exposure to sand shrimp, *Crangon crangon*, a predator of sand goby eggs, did not affect male preferences for large nesting resources or the onset of nest-building activity. Small and large males did, however, respond differently to the presence of shrimp during the nest-building phase. In particular, large males used more sand to cover their nests in the shrimps' presence. By contrast, neither the presence of egg predators nor male size class affected the size of the nest entrance. Together, our results show that while the risk of future egg predation may not necessarily influence a male's decision to nest, during the nest construction phase it can nevertheless induce responses that strongly depend on builder phenotype.

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Looking after young is often costly in terms of survival rate or lost mating opportunities (Gross & Sargent 1985; Clutton-Brock 1991; Smith & Wootton 1995). The costs of parental activities are especially acute when it comes to defending a nest against would-be predators (Ghalambor & Martin 2001). In birds, for instance, parents incur higher costs from defence of chicks than from nest building or incubation (Owens & Bennett 1994). Similarly, in an egg-guarding fish, the smallmouth bass, *Micropterus dolomieu*, a higher abundance of nest predators was associated with markedly increased metabolic costs during egg guarding (Steinhart et al. 2005). In this respect, nest characteristics may, at least in some species, influence both the level of protection afforded to developing eggs or juveniles and the costs incurred by parents (Canali et al. 1991; Hoi et al. 1994; Bult & Lynch 1997; Jones & Reynolds 1999a; Petit et al. 2002; but see also Burhans & Thompson 1998). For instance, northern flicker, *Colaptes auratus*, nests that were

higher up above the ground and more concealed by vegetation around the nest cavity entrance were better protected against predation (Fisher & Wiebe 2006). Likewise, in hole-nesting bees and wasps, nest density, nest position and nesting behaviour can all affect the vulnerability of nests to parasites (Rosenheim 1989; Coster-Longman et al. 2002; Polidori et al. 2010). In fish, nest architecture can also affect the dissolved oxygen levels inside the nest and, in so doing, influence the cost of male egg care (Takegaki & Nakazono 2000). Nevertheless, despite the importance of nest location and nest architecture on offspring survival, surprisingly little is known about how the choice of nest site by parents or, indeed, adjustment of nest characteristics, is influenced by the future threat of nest predation.

The sand goby, *Pomatoschistus minutus*, is an excellent model organism for investigating the effects of predators on nesting behaviours because nesting decisions are an important determinant of offspring survival as well as female mate choice (e.g. Lindström & Ranta 1992; Svensson & Kvarnemo 2003, 2005; Lehtonen et al. 2010). Males of this small, benthic marine fish build nests under empty shells or flat rocks by piling sand on top of, and excavating under, the resource, leaving a single narrow nest opening. Males

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court females in close proximity to their nests (Lehtonen 2012) and, after spawning, are the exclusive caretakers of the eggs. Acquiring a suitable nest site and constructing an appropriate nest have important implications for goby males: smaller nest entrances (Lissåker & Kvarnemo 2006) and larger piles of sand (Lindström & Ranta 1992) can improve nest defence and facilitate female attraction (Svensson & Kvarnemo 2005; Lehtonen & Lindström 2009; Lehtonen et al. 2010). However, not all nesting decisions are without trade-offs or constraints. For example, while larger nests are desirable because they hold more eggs (Lindström 1988, 1992a), they are also more susceptible to nest take-overs (Lindström 1992b) and potentially more costly to defend against egg predators (Kvarnemo 1995). Similarly, while it is likely to be easier and less costly for larger males to construct well-covered nests, larger males are also more likely to be discriminated against by females if they occupy small nesting resources (Lehtonen et al. 2007).

We investigated whether nesting behaviours in sand goby males were affected by the presence of sand shrimp, *Crangon crangon*, a nocturnal predator of fish eggs and larvae (Oh et al. 2001) known to prey on sand goby eggs (Chin-Baarstad et al. 2009). Specifically, we tested whether the presence versus absence of shrimp had an effect on (1) male preferences for different-sized nesting resources, (2) the time males took to commence nest building, and (3) nest construction (i.e. nest entrance size and amount of sand piled on top of the nest) by males. If male gobies respond in a risk-sensitive manner to egg predators (see e.g. Steinhart et al. 2005; Chin-Baarstad et al. 2009), we predicted that the threat of future nest predation should influence a male's choice of nesting resource, his eagerness to build a nest and the quality of nest construction. Because the costs and benefits of maintaining and defending certain nest types can vary depending on the size of the care-giving male (Kvarnemo 1995; Lehtonen et al. 2007; Björk & Kvarnemo 2012), and because male size varies extensively within and between years (Lehtonen et al. 2010), our experiment was conducted using both small and large males (see below for details).

## METHODS

The study was carried out in 2010 at the Tvärminne Zoological Station (59°50.7'N; 23°15.0'E). To ensure that we had sexually active sand goby males for the study, we placed artificial nesting resources (tiles; 10 × 10 cm) in a shallow bay and waited for males to colonize the nests. The nesting males were then caught, using dip nets, and immediately transported back to the field station (maximum 30 min boat trip) in 50-litre coolers at a density of approximately 50 fish per cooler. At the station, the males were housed in stock tanks (ca. 100 litres), at a density of approximately 10–30 fish per tank. Before the experiments, fish were fed twice a day with either live mysid shrimp or (when live shrimp were not available) frozen chironomid larvae. Sand shrimp were trawled from the vicinity of sand goby nests where they occur in high numbers (but do not compete with sand gobies for nesting resources). Sand shrimp used in the study came from a group of 63 individuals (mean length ± SD: 45 ± 7 mm; weight: 0.73 ± 0.42 g). These were housed in stock tanks identical (but separate) to those used for housing gobies, and were fed on a mixed diet of frozen chironomid larvae and sand goby eggs retrieved from the artificial nests where male gobies were caught. All aquaria were kept under natural light conditions and supplied with a continuous through-flow of sea water. After the study, fish were either retained for use in unrelated behavioural research or, along with the sand shrimp, released back to the sea.

All animal experimentation in this study complies with the laws of Finland. The study procedures meet the standards of 'ELLA – the

National Animal Experiment Board' for noninvasive animal experiments.

### Choice of Nesting Resource

To investigate how the presence of potential egg predators and male size influences the choice of nesting resources, each male sand goby ( $N = 101$ ) was placed into a tank (50 × 30 cm and 30 cm high) with a 4 cm layer of fine sand on the bottom as substrate. We had, a priori, opted to use males from two size classes based on body length: (1) males that were smaller than average ( $N = 52$ ; mean total length ± SD: 48 ± 3.4 mm, range 38.5–53.5 mm; weight: 0.81 ± 0.17 g, range 0.45–1.14 g; hereafter referred to as 'small'), and (2) males that were larger than average ( $N = 49$ ; total length: 59 ± 2.0 mm, range 54.5–63.5 mm; weight: 1.48 ± 0.16 g, range 1.14–1.86 g; hereafter referred to as 'large'). Here, the average length refers to the total sample of males we caught during the breeding season (June) in 2010 ( $N = 205$ ; mean length: 53.7 mm, range 38.5–63.5 mm). Note that the size distribution of male sand gobies varies markedly between years (Lehtonen et al. 2010) and, in 2010, males were larger than in many other years (see Lehtonen et al. 2010).

Each male was allowed to choose between a small (5 × 5 cm) and a large (10 × 10 cm) ceramic tile, placed 20 cm apart on the surface of the substrate, as a potential nesting resource. Such tiles are similar in size to flat rocks that sand gobies commonly use for their nests in the wild and are also readily accepted by males under both laboratory and natural conditions (Lindström 1992a; Lehtonen & Lindström 2004; Wong et al. 2008). Males were assigned randomly to one of two treatments. In the predation treatment, five sand shrimp were haphazardly picked from the stock tanks and added to the experimental tanks of small ( $N = 25$ ) and large ( $N = 23$ ) males. We used five shrimp in our predator trials to simulate the high density of sand shrimp commonly observed around the nests of sand gobies in the wild (personal observations). After completion of the replicate, the shrimp were returned to the stock pool for use in subsequent trials. In the control treatment, trials with small ( $N = 27$ ) and large ( $N = 26$ ) males were conducted without addition of any shrimp. A male was deemed to have chosen a tile as his nesting site when he had started to pile sand on top of it while retaining an opening to the nest (Wong et al. 2008). If a male did not start to build a nest within 48 h, the replicate was terminated. Furthermore, in five replicates we were not able to determine or record unambiguously which of the two tiles was chosen. Hence, for assessing choice of nesting resource, we successfully tested 64 males.

### Time to Nest Building

To assess whether the presence of potential egg predators or male body size class affected the onset of nest building (as a proxy of the nest-builder's motivation to build his nest), we checked all tanks every 8 h (at 0600, 1400 and 2200 hours) for signs of nest building (determined by the presence of sand piled on top of the tile; sensu Wong et al. 2008; Japoshvili et al. 2012). By 'right censoring' the replicates in which a nest was not built within 48 h, we were able to use all 48 predation and 53 control replicates. We assumed that the probability of nest building would be constant over time and, hence, used an exponential model.

### Nest Characteristics

To assess the effects of predation and male size on nest characteristics, we used two ecologically relevant and commonly used measures of nest construction in sand gobies (see Japoshvili et al. 2012): (1) the amount of sand males pile on the nesting resource

(i.e. the tile), and (2) the width of the entrance to their nest (or 'nest opening' sensu Svensson & Kvarnemo 2003). After the first signs of nest-building activity were observed, the male was given 24 h to finish building the nest (typically nest building takes <1 day). We investigated potential differences in nest characteristics for replicates in which the male had (1) started to build a nest within 48 h, (2) choice of nesting resource size was unambiguously determined, and (3) a large nesting resource was chosen (because only a very small number of small nests, which are very likely to require a different nest-building effort, were chosen). We measured the amount of sand the male piled on top of the tile by drying the sand in an oven (36 h in 60 °C) and then weighing the dried sand (Lehtonen & Wong 2009). The width of the nest entrance, in turn, was measured using a ruler. In three cases, the male built his nest entrance facing the back of the tank and, as a result, we were not able to measure the nest entrance. Hence, our sample sizes were 56 and 53 for sand coverage and nest-opening measurements, respectively.

Statistical tests were conducted using Systat 12.0 (Systat Software Inc., Chicago, IL, U.S.A.) software. Parametric methods were only applied when their criteria were met.

## RESULTS

### Choice of Nesting Resource

Across treatments, when offered the choice between a large and a small tile, the male chose the larger tile in 56 of the 64 replicates (binomial test:  $P < 0.001$ ). Neither the presence of shrimp (29 of 32 males chose the large tile versus 27 of 32 in the control) nor male size class (30 of 34 large males chose the large tile versus 26 of 30 small males) had a significant effect on nest size choice (logistic regression, predation effect: estimate  $\pm$  SE =  $0.154 \pm 1.08$ ,  $Z = 0.143$ ,  $P = 0.89$ ; male size class effect: estimate =  $1.04 \pm 1.28$ ,  $Z = 0.813$ ,  $P = 0.42$ ; predation\*size class: estimate =  $-1.52 \pm 1.62$ ,  $Z = 0.935$ ,  $P = 0.35$ ).

### Time to Nest Building

Males started to build a nest within 48 h in 35 of 48 and 34 of 53 cases in the predation and control treatments, respectively, whereas 31 of 49 large males and 38 of 52 small males built a nest. Thus, there was no significant difference in the proportion of males that built a nest with respect to either predator presence or male size (logistic regression, predation treatment effect: estimate  $\pm$  SE =  $-0.159 \pm 0.595$ ,  $Z = 0.267$ ,  $P = 0.79$ ; male size class effect: estimate =  $0.758 \pm 0.665$ ,  $Z = 1.14$ ,  $P = 0.25$ ; predation\*size class: estimate =  $-0.535 \pm 0.878$ ,  $Z = 0.609$ ,  $P = 0.54$ ). Because the building effort of a small nest would be very different from that required for a large nest, we first conducted an analysis focusing on those males that chose to build their nests using the large tile ( $N = 56$ ). We found that the time it took to begin building a large nest was not affected by male size class (survival analysis using an exponential model, male size class effect: estimate =  $0.003 \pm 0.023$ ,  $Z = 0.124$ ,  $P = 0.90$ ) or by the presence versus absence of shrimp (predation treatment effect: estimate =  $0.376 \pm 0.299$ ,  $Z = 1.26$ ,  $P = 0.21$ ). However, when we also included males that built a small nest, we found that large males took longer to start nest building (male size class: estimate =  $0.015 \pm 0.002$ ,  $Z = 6.59$ ,  $P < 0.001$ ), whereas predation did not have a significant effect on the onset of nest building (predation treatment: estimate =  $0.420 \pm 0.377$ ,  $Z = 1.11$ ,  $P = 0.27$ ).

### Nest Characteristics

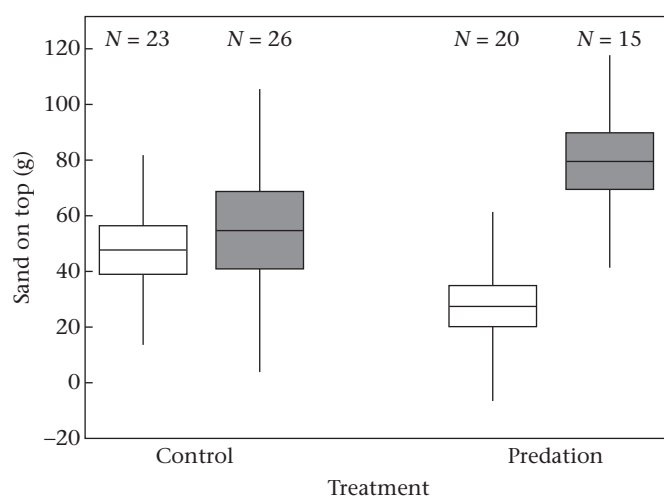
Large males placed more sand on top of their nests in the predation treatment than in the absence of egg predators, whereas the

opposite was true for small males (ANOVA on log-transformed sand weight, predation\*male size class:  $F_{1,52} = 8.01$ ,  $P = 0.007$ ; Fig. 1). Nest opening width, in turn, did not depend on the predation treatment or male size class (ANOVA on log-transformed nest opening width, predation effect:  $F_{1,49} = 0.935$ ,  $P = 0.34$ ; male size class effect:  $F_{1,49} = 0.904$ ,  $P = 0.35$ ; predation\*male size class:  $F_{1,49} = 0.002$ ,  $P = 0.96$ ).

## DISCUSSION

We investigated whether nesting behaviour in the sand goby was influenced by the presence of sand shrimp, a known predator of sand goby eggs. Based on earlier studies showing that reproductive decisions in a wide range of taxa can be highly sensitive to the risk of predation (including in sand gobies: Lissåker & Kvarnemo 2006; Chin-Baarstad et al. 2009), we predicted that the presence of egg predators should affect a male sand goby's choice of nesting resource, his eagerness to build a nest and the quality of nest construction. Moreover, given that the costs and benefits of maintaining and defending different-sized nests can vary depending on male size (Kvarnemo 1995; Lindström & Pampoulie 2005; Lehtonen et al. 2007; Björk & Kvarnemo 2012), we also expected small and large males to respond differently to the presence of shrimp. However, our results show that male sand gobies' preference for large nesting resources (Lindström 1988; Wong et al. 2008) did not depend on their own body size or on the presence of egg predators. Similarly, the decision to build a nest appeared to be unaffected by the presence of predators, with shrimp-exposed males constructing their nest as quickly as those that were allowed to build a nest in the absence of shrimp. In other words, the threat of future egg predation did not induce shifts in nesting resource choice or onset of nest building. These findings raise the question why the presence of shrimp had no effect on nest size choice or onset of nest construction.

In nest-building fish with exclusive paternal care, the size of a male's nest often influences male reproductive success (e.g. Hastings 1988; Bisazza & Marconato 1988; Marconato et al. 1989). This is also true in sand gobies: larger nests hold more eggs, and, as a result, the size of the nesting resource acts as a physical limit to the number of clutches a male is able to receive (Lindström 1988, 1992a). Hence, even if larger nests are more difficult to maintain and defend against



**Figure 1.** The amount of sand males piled on their nests in the two treatments. Small males are indicated with white boxes and large males with grey boxes. Central horizontal lines within the boxes indicate means, margins of the boxes are SEs and whiskers indicate SDs.



egg predators (Kvarnemo 1995), the higher egg capacity of large nests may be a more important factor in male nesting decisions than any nest size- or body size-dependent cost of nest defence. Moreover, for large males, nesting resource size can also play an additional role in female attraction, for example, if females discriminate against larger males occupying small nests (Lehtonen et al. 2007). Hence, at least for large males, female preferences may overrule the costs related to occupying a large nesting resource in a high predation risk environment. It is important to acknowledge the possibility that using large tiles to collect fish for this study may have resulted in a sample of males that were larger than average or males with a particular disposition towards choice of larger than average nesting resources. However, it is worth pointing out that an overall preference for large nesting resources has previously been found both in the field (Lindström 1988) and in the laboratory when fish had been collected using other methods (e.g. hand trawling; Wong et al. 2008). Moreover, we were interested in testing whether the threat of future nest predation induces a change in the preference for the size of the nesting resource, rather than the overall level of preference for larger nesting resources per se. Nevertheless, the possibility that individuals with weaker preferences for larger nests have lower thresholds for adjusting their preferences warrants further investigation.

In terms of sand coverage of the nest, we found that although large and small males piled comparable amounts of sand on top of their nests in the absence of shrimp, large males actually used much more sand to cover their nests than small males in the shrimps' presence. Hence, only large males increased their investment in nest concealment under predation threat. This is consistent with earlier studies, which suggest that male body size and nest elaboration are not always correlated (Svensson & Kvarnemo 2005; Lehtonen & Lindström 2009). The difference in sand coverage between large and small males is intriguing because well-concealed nests are often less vulnerable to predation, as has been shown, for example, in passerine birds (see Weidinger 2002; Fisher & Wiebe 2006). Hence, we might have expected both small and large males to increase nest concealment (here the amount of sand on top of the nest) under predation threat. Why was this not the case?

One possibility is that small males are more cost adverse and, as a consequence, have a different strategy from large males for optimizing their reproductive success under egg predation threat. The credibility of such an argument is supported by an interspecific study of birds suggesting that the size of nest-holders may influence the kinds of nest defence strategies that are used, with larger species expected to engage in more vigorous or efficient defence than their smaller counterparts (Weidinger 2002). More generally, the costs of presence of egg predators could also depend on parent size if, for example, predators differentially target large versus small nest-holders (Blanckenhorn 2000). Finally, it is also possible that males of different sizes differ in their ability to recognize the threat posed by sand shrimp. For example, prior experience and learning can affect readiness to recognize or deal with predators (reviewed in Montgomerie & Weatherhead 1988; Ferrari et al. 2007), with small and large males potentially differing in their experience levels or learning abilities.

It is currently not known whether nest concealment (in terms of the amount of sand on top or size of nest entrance) could actually serve as an effective defence against sand shrimp. Indeed, we found that the size of the nest entrances of shrimp-exposed males did not differ from that of nonexposed males. This contrasts with the earlier findings of Lissåker & Kvarnemo (2006), who found that the presence of a predatory crab caused goby males to reduce the size of their nest opening (but see Jones & Reynolds 1999b). Lissåker & Kvarnemo (2006) argued that a smaller nest entrance would make

it harder for egg predators to gain access to the nest. However, in that study, male gobies were already guarding eggs and were therefore confronted with a more imminent threat. In regard to the current study, we cannot rule out the possibility that nest entrance sizes might differ after egg laying, especially if males have the capacity to adjust the opening of their nest entrances relatively quickly, as seems to be the case in the sand goby (Japoshvili et al. 2012), and has been shown, for instance, in another fish, the three-spined stickleback, *Gasterosteus aculeatus* (Rushbrook et al. 2010; Wong et al. 2012). Hence, nesting individuals could be adjusting only a subset of nest characteristics to immediate environmental conditions, with further adjustments being made after eggs have been laid.

In conclusion, although the presence of egg-eating shrimp did not appear to affect the nesting decisions of male sand gobies, it did induce differences between large and small males in aspects of nest architecture that are presumably related to the costs and benefits of nest defence. It is well established that both nest-builder behaviour and the location and structure of the nest itself can influence offspring survival in a wide range of species (e.g. Eggers et al. 2006; Byrne & Keogh 2009). Far less attention, by contrast, has been given to understanding the influence of the threat of future nest predation on current parental strategies. The results of our study suggest that such threats can be important, and can affect nesting behaviours and nest architecture even before eggs are laid in the nest.

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