Sexually selected nest-building – *Pomatoschistus minutus* males build smaller nest-openings in the presence of sneaker males

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condition;
cuckoldry;
extra-pair paternity;
Gobiidae;
ornament;
Pisces;
sperm competition;
Teleostei.

**Abstract**

Both natural selection and sexual selection may act on nest-building. We tested experimentally how different regimes of egg-predation and male–male competition influence nest-building before mating, using the marine fish sand goby, *Pomatoschistus minutus*. Males with sneaker males present built the smallest nest-openings, smaller than males held alone or with *Pomatoschistus microps* males (which may predate eggs and compete over nest-sites but not compete over fertilizations). Males with visual access to other nest-building males tended also to build smaller openings than males held alone or with *P. microps*. Males with egg-predators present built nests with openings not differing significantly from any other treatment. Our results indicate that the small nest-openings found in the sneaker male treatment are sexually selected through protection against sneaking or by female choice. Across treatments, time span before a male started to build his nest also explained variation in nest-opening width; males starting late built larger nest-openings.

**Introduction**

Many species of animals build nests (Hansell, 2000). The nest may protect the offspring from adverse environmental conditions such as extreme temperatures, wind or water (e.g. Hostache & Mol, 1998; Hansell, 2000). Another important effect is the protection against predators. The nest can protect the offspring as well as the parents from being discovered and predated upon (Lindström & Ranta, 1992; Jones & Reynolds, 1999; Hansell, 2000). A second protective mechanism may be that the nest *per se* makes it easier for a parent to defend itself and the offspring, as in *Reticulitermes speratus* termites (Matsuura, 2002) and nest sealing in Bucerotidae hornbills (Kemp, 1995).

In birds, the evidence for an influence of predation on the choice of nest-sites is extensive (Hansell, 2000). For example, female *Ficedula albicollis* (pied flycatcher) prefers males with nest boxes high up in the trees, which are the nest boxes that suffer from less predation (Alatalo et al., 1988). Female preference for safe nest-sites has also been found in fishes (Sargent & Gebler, 1980; Lavery, 1991; Kraak et al., 1999; Östlund-Nilsson, 2000).

Males may invest in constructions that are exclusively display sites. Those are ornaments that indicate the physical or genetical quality of the male (Hamilton & Zuk, 1982), and are completely independent of the care of eggs and young. Examples are Ptilonorhynchidae (bowerbirds) (Hansell, 2000) and many Lake Malawi Cichlidae (McKaye, 1991; Taylor et al., 1998).

In species with paternal care the nest may provide the female with information on the quality of the care the male is going to provide (Hoelzer, 1989). In birds, nest-building behaviour is often used in the courtship and the nest has been shown to correlate with paternal care (Moreno et al., 1994; Møller et al., 1995; Soler et al., 1995). Furthermore, similar to bowers, the nest may also function as an ornament (Soler et al., 1998; Jones & Reynolds, 1999). In fish, nest-building has been shown to correlate negatively with immune stress (Barber et al., 2001) and positively with experimentally manipulated...
body condition (Kvarnemo et al., 1998; Jackson et al., 2002). Therefore, the nests of fishes should provide the female with information on male quality.

Finally, a well-built nest may be easier to protect against nest take-overs and sneaker male intrusions, and might thus be sexually selected through male–male competition. Defence against nest take-overs may actually be the primary function of nest sealing in the hornbill Bycanistes subcilindricus (Kalina, 1989). However, the importance of a nest as a physical defence to prevent conspecific males from stealing fertilizations is virtually unexplored. Furthermore, a sneaker male or a male without a nest-site may also find it harder to discover a cryptic nest, as suggested for Gasterosteus aculeatus (threespined stickleback) (Sargent & Gebler, 1980). Consequently, nest constructions can be sexually selected, in addition to being naturally selected. The mode of selection is also likely to vary over time, with stronger sexual selection before egg laying shifting to natural selection after egg laying.

The aim of this study was to investigate to what extent egg-predators, competing males and sneaker males influence Pomatoschistus minutus (sand goby) males during nest-building before mating, to modify the appearance of their nests. Therefore, P. minutus males were allowed to build nest with either P. minutus sneakers (smaller males), smaller Pomatoschistus microps (common goby) males, or invertebrate egg-predators in their aquaria, or with visual access to other nest-building P. minutus males. As a control, one group of males built their nests alone. If (A) the shape of the nest before mating is primarily naturally selected to protect against future egg-predation, we predicted that (i) the nest-openings in the egg-predators treatment should be small; (ii) there should be no difference between the two treatments where sneakers or P. microps males were present, as both may predate the nest and; (iii) the largest nest-opening should be found in the predator free alone treatment. In contrast, (B) if the nest before mating is also sexually selected by female choice, we predicted that: (i) the nest-openings should be smaller in the treatment with visual access to other nest-building P. minutus males (i.e. potential competitors for females) compared with the P. microps male treatment and; (ii) the largest nest-openings should be found in the alone treatment. (C) If the nest-building before mating is mainly selected by competition over nest-sites and by nest take-overs, (i) then the smallest nest-openings should be found in the sneaker male treatment as well as the P. microps male treatment as both treatments involve a competition over nest-sites. Finally, (D) if the sexual selection is mediated through protection against sneaker males rather than competition between nest holding males over females, (i) the smallest nest-openings would be expected in the sneaker males treatment. Neither of these predictions is mutually exclusive as a small nest-opening is likely to be beneficial in several ways at the same time. However, the results of this study showed that the focal males perceived the sneaker males as the most serious threat, which gives the strongest support to the last prediction.

Methods

The species

Pomatoschistus minutus (Pallas) (sand goby) is a small short-lived marine and brackish fish. They are found in coastal areas of Europe and breed in shallow sand bottom areas (Miller, 1986). The male builds a nest, often using an empty mussel shell that he excavates and covers with sand. Nest-building males develop a breeding colouration with black and blue colour on the anal and first dorsal fins. The male courts a female, who after approving of both him and his nest attaches her eggs to the shell in a single layer. After spawning, the male alone tends the eggs until hatching by guarding and fanning them as well as removing dead or diseased eggs. During one brood cycle the male may receive eggs from several females. After the eggs hatch the male can receive several new broods and similarly, females may spawn several times during the season (reviewed in Forsgren, 1999).

In this species sneak fertilizations are common, both in the field (Jones et al., 2001a; Jones et al., 2001b) and under laboratory conditions (O. Svensson & C. Kvarnemo, unpublished data). Smaller males, that are less likely to defend a nest and attract a female, sneak or even force themselves through the narrow opening of the nest, fertilize some eggs, and leave. The nest holding male defends the nest-opening vigorously against such smaller males. In this paper we will refer to such small males, that typically carry very pale breeding colouration, sneaker males.

Pomatoschistus microps (Krøyer) (common goby) and P. minutus breed sympatrically in the study area. They are behaviourally and morphologically very similar (Miller, 1975; Magnhagen, 1999). In the field, they presumably predate on each other’s eggs as well as compete over the same nest-sites periodically. Carcinus maenas L (shore crab) and Hinia reticulata (L) (netted dogwhelk) are also known egg-predators of Pomatoschistus spp. (Kvarnemo, 1995).

General methods

The experiment was carried out at Tjärnö Marin Biological Laboratory on the west coast of Sweden (58°52’N, 11°10’E) in the early summer of 2000 and 2001. The fish were caught in a nearby bay with a hand trawl and kept in 130-L storage aquaria for at least 36 h before the trial. In the experiment, 20-L aquaria with a 3 cm layer of fine sand were used. One-third from the back, a mussel shell (mean ± SD; year 2000: width, 50 ± 2.9 mm; length,
86 ± 4.8 mm; year 2001: width, 57 ± 2.1 mm; length, 92 ± 3.5 mm) was put into the sand at an angle, making the height of the initial nest-opening 3 cm. All males were randomly divided into their treatments. To encourage nest-building, a female in a net cage (the 2000 trial) or in a clear plastic vial (the 2001 trial) was put into each aquarium. The vial was provided with sand, a net over the opening and holes on the sides to enable water circulation. All fish in the storage aquaria were fed with chopped mussel meat (Mytilus edulis) and shrimps (Crangon crangon). In addition, mussel meat was provided in all experimental aquaria on the first day of the nest-building trial. All aquaria were provided with through-flowing natural seawater with a salinity of 35% and a temperature of 10–12 °C.

The year 2000 experiment

As a pilot study, we performed a nest-building experiment where 20 males were allowed to build nests alone, and 21 males to build their nests with two sneaker males present in order to increase the risk of sneaking (nest-building males, 57–71 mm total length (TL); sneaker males, 39–53 mm TL). All aquaria were provided with through-flowing seawater with a salinity of 35% and a temperature of 10–12 °C.

In 2000 we extended the study with three new treatments, resulting in a total of five treatments. The size of the focal males ranged between 48–93 mm TL. The males were divided into five different treatments: 1. Sneaker males: two smaller and, therefore, potential sneaker males were present to increase the perceived risk of sneaking (42–52 mm TL).
2. Nest-building males: the nest-building male had visual contact with two other nest-building males (48–75 mm TL) in the adjoining aquaria on both sides to increase the impression of male–male competition. The males seemed to consider the males behind the glass as an opponent, as they showed aggressive colourations, displayed vigorously and performed tail beats towards each other.
3. Egg-predators: one C. maenas (carapace width 12–15 mm) and one H. reticulata (length 21–24 mm) were present to increase the perceived risk of future egg-predation.
4. P. microps males: two P. microps males (length 35–37 mm) were present as a control to the possibility that nest holders see the sneaker males as egg-predators or nest-site competitors.
5. Alone: the male was allowed to build his nest alone to have a situation with no risk of sneaking. Nest-site competition, competition over females or egg-predation.

The experiment was started late in the evening. Every 12 h during 48 h, we noted if there were any visible traces of nest-building. Nest-opening width was measured two times for each replicate: 48 h after the start of the experiment across all treatments and 24 h after the first traces of nest-building in each particular replicate (which on average was 60 h after the start of the experiment).

The entire experimental set-up was repeated five times (starting 31/5, 3/6, 7/6, 11/6, 16/6) using 30–40 experimental aquaria each time. If the male had moved some sand, even very little, it was considered to be a built nest. If a nest was not considered to be built or the replicate was removed from the study (number of successful replicates/number of started replicates: sneaker males 16/21, alone 11/20, Pearson χ² = 1.76, d.f. = 1, P = n.s.). A nonsignificant difference in nest-opening width (mean ± SD, alone 24 ± 1.3 mm, sneak 15 ± 0.8 mm, F₁,₂₅ = 2.55, P = 0.12, Fig. 1) was considered to make it worthwhile to perform an extended study.

The interaction term was always removed from the model after being checked for nonsignificance and the

![Fig. 1 Nest opening width of the sneaker males and the alone treatments 48 h into the experiment for years 2000 and 2001. The figure shows mean ± SE.](image-url)
statistics are hence presented for the remaining terms. Duncan’s test was used for all post hoc comparisons. STATISTICA 5.5 software was used for all statistical calculations except for the partial correlation analysis where we used StatView. After the experiment, all fish were released or used in other experiments. Our licence was provided from the Swedish National Board for Laboratory Animals (Dnr. 114-2000).

**Results**

**Sneaker male treatment vs. alone treatment, years 2000 and 2001**

Comparing the width of the nest-openings of males that were allowed to build alone to males housed together with sneaker males, there were no significant differences within the treatments between the years concerning nest-opening width 48 h into the experiment, nor was there a significant interaction between treatment and year. However, the treatment had a highly significant effect on the width of the nest-opening, with smaller widths when the nest was built in the presence of sneaker males than alone (factorial ANOVA, treatment $F_{1,54} = 13.38$, $P < 0.001$, year $F_{1,54} = 0.349$, n.s., interaction year $\times$ treatment $F_{1,54} = 2.25$, n.s.; Fig. 1).

**Five treatments, year 2001**

There was a strong correlation between time to nest-building and nest-opening width in the year 2001 data 48 h into the experiment (Table 1). Thus, the five treatments were compared with time to nest-building as covariate. The treatments had a significant effect on nest-opening width at 48 h (ANCOVA, treatment $F_{4,80} = 2.84$, $P < 0.05$; covariate $F_{4,80} = 9.61$, $P < 0.01$; interaction treatment $\times$ covariate $F_{4,76} = 0.417$, n.s.). In the post hoc test the nest holders in the sneaker male treatment had significantly smaller nest-openings compared with males held alone and *P. microps* treatments. In addition, the nest-building males treatment showed a trend to differ from both the alone treatment and the *P. microps* treatment (Fig. 2).

![Fig. 2 Nest opening width in five treatments in year 2001, measured 48 h into the experiment, with time to nest building as a covariate (ANCOVA). The figure shows mean ± SE. Duncan’s post hoc test, **$P < 0.01$, o $P < 0.10$.](image)

### Table 1  $R$-values of the partial correlation with nest opening measured 48 h into the experiment. Sixty-one observations were used in this computation

<table>
<thead>
<tr>
<th></th>
<th>Male length</th>
<th>Shell width</th>
<th>Time to nest building</th>
<th>Nest opening width</th>
</tr>
</thead>
<tbody>
<tr>
<td>Start date</td>
<td>-0.090</td>
<td>-0.050</td>
<td>0.069</td>
<td>0.164</td>
</tr>
<tr>
<td>Male length</td>
<td>0.111</td>
<td>0.120</td>
<td>0.127</td>
<td></td>
</tr>
<tr>
<td>Shell width</td>
<td>-0.007</td>
<td>0.094</td>
<td></td>
<td>0.413***</td>
</tr>
<tr>
<td>Time to nest building</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Significant $r$-values $***P < 0.001$.

### Table 2  $R$-values of the partial correlation with nest opening measured 24 h after the first traces of nest-building (which on average was 60 h after the start of the experiment). Sixty-one observations were used in this computation

<table>
<thead>
<tr>
<th></th>
<th>Male length</th>
<th>Shell width</th>
<th>Time to nest building</th>
<th>Nest opening width</th>
</tr>
</thead>
<tbody>
<tr>
<td>Start date</td>
<td>0.052</td>
<td>-0.114</td>
<td>-0.106</td>
<td>0.110</td>
</tr>
<tr>
<td>Male length</td>
<td>0.154</td>
<td>0.144</td>
<td>0.179</td>
<td></td>
</tr>
<tr>
<td>Shell width</td>
<td>-0.029</td>
<td>0.168</td>
<td></td>
<td>0.455***</td>
</tr>
<tr>
<td>Time to nest building</td>
<td></td>
<td></td>
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</tbody>
</table>

Significant $r$-values $***P < 0.001$. 
Discussion

There is no doubt that the main function of the *P. minutus* nest is protection against egg-predators. In the field an exposed egg mass would be predated upon immediately. However, in this experiment, we did not investigate the adaptive significance of the nest *per se*, but the variation in the width of the narrow nest-opening before mating.

Forty-eight hours into the experiment, *P. minutus* males with sneaker males present during nest-building, built smaller nest-openings before mating compared to males that were held alone. This result suggests that nest holding males reduced the size of their already small nest-openings, because they perceived the sneaker males as a threat.

Feasibly, the nest-holding males may have reduced the size of the nest-openings because they perceived the smaller sneaker males as a threat not only as cuckolders, but also as competitors for females, for nest-sites or as future egg predators. However, the results from our five-treatment study of 2001 indicate that the nest holders did not primarily regard these sneakers to be egg predators or nest-site competitors, because they did not react by reducing the nest-opening in the presence of a potential egg predator and nest-site competitor, namely *P. microps* males. It is likely that the benefit of a small nest-opening before mating would be low in terms of reducing the risk of future egg-predation, both because egg-predation cannot occur when there are no eggs in the nest, and because males often have to rebuild the narrow opening after spawning anyway. Consequently, assuming that small *P. minutus* are not much more sever egg-predators than *P. microps*, it is improbable that the reason for building the extra-small nest-openings in the presence of small *P. minutus*, is to reduce the risk of egg-predation. Similarly, *P. microps* is probably a more severe nest-site competitor than small *P. minutus* that are known to be poor nest-site competitors (Magnhagen & Kvarnemo, 1989). Therefore, because the nest-holders did not even reduce their nest-openings in the presence of *P. microps*, it is unlikely that they reduced their nest-openings to prevent the smaller *P. minutus* males from taking over their nests.

In contrast to egg predation, a small nest opening may be beneficial in protecting against sneaking already before mating, because most sneak attempts do occur shortly before or around the start of spawning (O. Svensson, C. Kvarnemo & W. Manson, unpublished data). The longevity of *P. minutus* sperm exceeds the duration of the spawning (O. Svensson & H. Elofsson, unpublished data), which may explain why sneakers are most persistent at this time. In addition, female choice will also occur before spawning, and if indeed females do prefer small nest-openings then reducing the width might be a way for *P. minutus* to attract matings in competition with other males. In fact, our data show that males with visual access to other nest-building males had a similar (but nonsignificant) effect as sneaker males had. As the difference between the treatments of the sneaker males and the nest-building males is far from significant, it is not possible to exclude the possibility that this behaviour has been sexually selected for, not only to reduce sperm competition from sneaker males, but also by female choice for small nest-openings. In *P. microps*, for example, females are known to base their mate choice on nest appearance (Jones & Reynolds, 1999). Other, not mutually exclusive, explanations include the possibility that other nest-building males might sneak as well, or perhaps that the sight of other nest-building males is indicative of high male density and hence that there will be many sneaker around.

The nest-openings in the egg predator treatment (*C. maenas* and *H. reticulata*) were intermediate in size to all other treatments and differed from no other treatment. This result is difficult to interpret. Males should have good reasons to reduce the size of the nest-opening in the presence of egg-predators compared with when reared alone, as *C. maenas* have been shown to discover *P. microps* nests more easily with large than small nest-openings (Jones & Reynolds, 1999). However, *P. microps* males did not adjust their nests either, when a caged *C. maenas* was introduced after spawning (Jones & Reynolds, 1999).

In 2001, there was a strong positive correlation between the time span before nest-building started and the width of the nest-opening (the corresponding data does not exist from year 2000). The correlation is still highly significant when controlling for males that started early and had been improving their nest for a longer time (that is when the nest-opening width was measured 24 h after the first traces of nest-building in each particular replicate) indicating that late builders are poor builders. Similarly, in *P. microps* a large nest-opening before spawning has been shown to be associated with lower future hatching success (Kvarnemo et al., 1998). Barber et al. (2001) also found that in *G. aculeatus*, variation in nest appearance was correlated with the time to nest-building, as well as immunological traits and secondary sexual characters. Barber et al. (2001) suggested this pattern occurs either because of previous investment by the field caught males, or because low quality males or sneaker males built nests in the competition-free laboratory, and that these males needed longer time to prepare physically for nest-building. Furthermore, in an experiment, Jamieson & Colgan (1992) found that the males that were last to complete nest-building, and consequently last to spawn in their own nest, were sneaking more frequently. In *P. minutus*, smaller males are more likely to act as sneaker (O. Svensson & C. Kvarnemo, unpublished data), which is also true for *P. microps* (Magnhagen, 1992). Yet, despite a large variation in male body length among focal males, we found no correlation between male size and time to nest-building.

Natural and sexual selection are often likely to have similar selection pressures on nest building and their...
relative importance are hard to distinguish. If a nest protects against intrusion, it presumably protects against predators as well as conspecific males. The same is true for camouflage. As mentioned in the introduction, the bucerotid hornbill female seals herself into the nest together with her eggs. Presumably, in this case the nest is not only a camouflage but also a physical defence (Kemp, 1995), in particular against nest take-overs (Kalina, 1989). In the present study on P. minutus, males exposed to male–male competition, built nests with extra small nest openings before mating. Most likely, protection against sneaker male intrusion is the primary reason for this reduced size of the nest openings, although increased competition over the choice of the female is also possible. Still, the main function of the nest is no doubt protection against egg predation. In general terms, it is possible that the importance of sexual selection on nest building has been obscured by evolutionary advantages caused by natural selection. Such selective forces are likely to be even more entangled if females choose nests, or nest building behaviour, based on predation risk. This is the case in P. microps, where it is shown both that a small nest opening protects against egg predators and that females prefer to spawn in high built nests with small nest openings (Jones & Reynolds, 1999). In addition, passerine bird nests seem to be both naturally and sexually selected (Soler et al., 1998). Furthermore, the condition of the male and the time span before a male starts to build his nest have been found to affect nest building (the present study, Kvarnemo et al., 1998; Barber et al., 2001; Jackson et al., 2002), which females may use in their choice.

Without costs of constructing and maintaining a ‘perfect’ nest, there should be no variation in nest appearance. In birds, such costs can be increased predation risk and costs of carrying nest material (reviewed in Soler et al., 1998). In fish, most likely there are energetic costs associated both with nest-building per se and with fanning of oxygen-rich water to the developing eggs to compensate for the reduced water exchange around them (Kvarnemo et al., 1998; Jackson et al., 2002; Lissakér et al., 2003). It is very probable that nest-guarding males have to trade-off the benefits from a small nest-opening against the increased fanning costs, and that such a trade-off is particularly important for energetically limited males. Therefore, the benefit of further reducing the narrow nest-opening may outweigh the costs only when the reduced risk of sperm competition or increased attraction to females is added to the reduced risk of predation. Such additive effects of natural and sexual selection pressures call for further research.

To conclude, whilst female choice for well-built nests has been studied to some extent before, to our knowledge, this is the first study showing males to modify their nests as a response to male-male competition.

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**References**


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