Male Nest Choice in Sand Gobies, *Pomatoschistus minutus*

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Abstract

Although material resources can have a direct bearing on the fitness of *both* sexes, few studies have actually examined resource-based preferences from a male choice perspective. In sand gobies, *Pomatoschistus minutus*, the size of a male's nest influences his attractiveness to females and also dictates the number of eggs he can receive. Thus, one might expect males to prefer larger nests. However, an earlier study of marine sand gobies from a population with a surplus of nest sites and high nest predation found that males exhibited size-assortative nest preferences. Here, we investigated male nest preferences from a brackish population characterised by a chronic nest shortage but lower predation risk. A survey of naturally settled nests in the field (shells and rocks) showed a pattern of size-assortative nest occupancy consistent with the previously studied population, with larger males occupying larger (i.e. rock) nests. However, when offered a choice of potential nests in the absence of male competition, we found that all male gobies in our population, irrespective of their own body size, actually preferred larger nests. Moreover, a predilection towards large nests superseded any preferences based on nest colour. Our results not only indicate the existence of male preferences for material resources but, considered in the light of previous work, also suggest that such preferences may vary among populations and, importantly, may not necessarily be realised in a competitive setting.

Introduction

Material resources can have a direct impact on male mating success. Females, for instance, may often select males based on the quality of resources on offer, as shown, for example, in gift-giving dance flies (LeBas et al. 2004) and resource-defending antelopes (Balmford et al. 1992). In many species of nest-guarding fish, the size of a male's nest has also been shown to directly affect the number of clutches he is able to receive, thus acting as a physical limit to the number of mating opportunities a male can obtain (Hastings 1988; Bisazza et al. 1989; Lindström 1992a). It is not surprising then, given the obvious impact that resource quality can have on male

fitness, that males often compete vehemently for access to resources that are required for breeding (Gustafsson 1988).

Despite their apparent importance in determining male reproductive success, however, few studies have actually considered whether males are choosy about the quality of material resources. The fact that some resources are contested more vigorously than others implies that such preferences exist. On the other hand, males could be less discerning than females if, for example, the value of attracting females to a lower quality resource exceeds the value of seeking a better, higher quality, alternative (Candolin & Reynolds 2001). More generally, one might expect the availability of resources to also

differ among populations and this, along with other environmental variables (such as the relative cost and benefits of resource acquisition and defence), might be predicted to drive differences among populations in male preferences (cf. geographic variation in female preferences, Endler & Houde 1995; Wong et al. 2004).

The sand goby *Pomatoschistus minutus* is a small benthic fish common to shallow sandy habitats across coastal Europe (Miller 1986). Males build nests under empty mussel shells or rocks by piling sand on top of, and excavating under, the substrate, leaving a single narrow opening. Male gobies use colourful courtship displays to attract females to the nest. If successful in his efforts, the female will enter the male's nest and attach her eggs in a single layer on the ceiling of the nest. Males then fan the eggs and guard them against potential egg predators. Sand gobies generally survive only a single breeding season (Healey 1971). During this time, females may spawn repeatedly with multiple partners, and males may receive eggs from several females, guarding multiple clutches simultaneously (Lindström 1988, 1992a). The size of a male's nest determines the number of clutches he can receive (Lindström 1988) and, more recently, has also been shown to influence his attractiveness to females (Lehtonen et al. 2007). Consequently, one might expect males to benefit from choosing larger nests. However, in all sand goby populations studied thus far, males exhibit a size-assortative pattern of nest occupancy in the field, with larger males occupying the largest nests (Lindström 1992b; Forsgren et al. 1996). Is this pattern due to variation in male preferences or, alternatively, the outcome of intrasexual competition relegating smaller males to inferior resources? Evidence from a marine population of sand gobies from the Gullmar Fjord suggests the former (Kvarnemo 1995). In that population, potential nesting resources occur in surplus (Forsgren et al. 1996) but due to the presence of egg predators, smaller males likely incur higher costs maintaining and successfully defending larger nests, resulting in males choosing nests that were proportionate to their own body size (Kvarnemo 1995). Both the availability of nests and the costs associated with nest defence, however, are known to vary among sand goby populations (Forsgren et al. 1996). Thus, both the ecological conditions and the mechanisms responsible for driving patterns of nest occupancy could, quite conceivably, differ among populations even if the patterns, themselves, do not (Lindström 1992b; Forsgren et al. 1996).

Accordingly, in the current study we set out to examine male nest preferences in a brackish population of sand gobies from the Finnish Baltic. This population, in contrast to that of the Gullmar Fjord, inhabits an environment that lacks any formidable egg predators (i.e. whelks and crabs). The Baltic population, however, is marred by a chronic shortage of suitable nest sites, resulting in higher rates of nest occupancy, and more intense male-male competition (Forsgren et al. 1996). In light of these factors, should males in the Baltic population prefer nests that are proportionate to their own body size or should they prefer larger nests? Given variation in nest quality (i.e. nest size) and the higher risk of competition over larger nests in this population (Lindström & Pampoulie 2005), one might expect size-based differences in resource-holding potential to favour the former (*sensu* Härdling & Kokko 2005). On the other hand, due to the absence of formidable egg predators in the Finnish Baltic, the lower cost of having to defend a large nest against potential egg predators could mean that males, irrespective of their own body size, should, when given a choice, prefer larger nests.

This study comprises two parts. First, we conducted a field survey to examine natural patterns of nest occupancy in the Finnish Baltic population of sand gobies. Second, to control for the potentially confounding effects of male–male competition, we carried out a series of experiments in the laboratory using gobies from the Finnish population to test the preferences of males when offered the choice between potential nests differing in two key nest attributes, size and colour. Why? As far as we are aware, previous studies of male nest choice in fishes have only ever considered nest size. In the field, however, nest size and colour could be confounded if, for example, small and large nests differ in colour (e.g. light-coloured mussel shells vs. dark-coloured rocks). Thus, our experiments allow us to disentangle any preferences based on nest size from those based on colour.

Methods

Field Survey

We measured the size of naturally occupied sand goby nests that contained eggs. This was achieved by snorkelling and scuba diving along a shallow sandy beach located near the Tvärminne Zoological Station in southern Finland. The water depth of the selected study area ranged from 30 to 120 cm. When a nest was located (n = 58), we recorded whether it was

excavated under mussel shell or rock. We then caught the male and measured his total length (TL) using a ruler (to the nearest mm). The outline of the nest was then traced onto overhead transparency for a subset of the samples (n = 43), photographed, and the area bordered by the outlines measured using image analysis software (Sigma Scan Pro 5.0; SPSS Inc., Chicago, IL, USA).

Nest Choice Experiments

We conducted three separate choice experiments in the laboratory to assess the preference of males for two nest attributes, size and colour. Fish for experimental work were collected using hand trawls near the Tvärminne Zoological Station. Males were maintained in separate-sex aquaria measuring 80 × 80 × 30 cm (length × width × height) at a stocking density of approximately 50 fish per tank. Aquaria were housed under natural light conditions and supplied with a continuous through flow of fresh seawater. Fish subsisted on a diet of live opossum shrimp *Neomysis integer* and frozen chironomid larvae. Fish were not fed during trials (which lasted less than 48 h). All three experiments were conducted using aquaria measuring 50 × 30 × 30 cm (length × width × height) filled to a depth of 25 cm with fresh seawater. A 4-cm layer of sand was placed on the bottom of each test aquarium. Two square ceramic tiles (colour and dimensions below) were placed on top of the sand, 20 cm apart, as potential nests. Sand gobies readily nest and spawn under ceramic tiles which are an effective means for experimentally manipulating nest size and colour (Lindström 1992a). After the tiles were put in place, a male was netted from the stock tank and gently introduced into the choice aquaria. All males were tested individually (to avoid any potentially confounding effect of male–male competition) and were assigned randomly to treatment. A male was deemed to have chosen a nest site when he piled sand on top of one of the tiles and excavated under the tile, with his head resting at the entrance of the nest site. We recorded which tile the male chose. We then measured the length (mm) and wet weight (g) of each male. After fish were measured and weighed, they were returned to a separate set of stock tanks for use in unrelated experiments (i.e. focal males were only ever tested once in the current study). The nest built by the male in each trial was then carefully levelled and the position of tiles in each tank was then switched between replicates to avoid possible side bias.

Experiment 1: nest size

In the first experiment, we were interested in testing whether males had preferences for the size of potential nest sites. Here 50 males were offered the choice between two tiles matched for colour (either all white or all brown tiles were used in any given trial) but differing in size (i.e. a 5 × 5 cm tile vs. a 10 × 10 cm tile). There was no significant difference in either weight (Mann–Whitney U-test: U = 336.5, p = 0.64, $n_1 = n_2 = 25$) or length (Mann–Whitney U-test: U = 358, p = 0.38, $n_1 = n_2 = 25$) of males offered white tiles compared with those offered brown tiles (weight of males offered brown tiles: 0.69 ± 0.048 g; length: 46.2 ± 0.90 mm. Weight of males offered white: 0.66 ± 0.056 g; length: 45.1 ± 1.13 mm).

Experiment 2: nest colour

Experiment 2 was designed to test whether males had nest preferences based on colour. Males were offered the choice between two size-matched tiles, one that was white and one that was dark brown. Since sand gobies have similar tristiumulus colour vision to that of humans (Jokela-Määtta et al. 2007), tiles were chosen by human observers to visually match, the colour of the two objects normally used as nest sites by males in the study population: the white shells of mussels, *Mya arenaria*, and dark-coloured rocks. The experiment was replicated with 136 males. Half of these (i.e. n = 68) were tested using small tiles (5 × 5 cm) and the rest were tested using large tiles (10 × 10 cm). There was no significant difference in either the weight (Mann–Whitney U-test: U = 2115.5, p = 0.39, $n_1 = n_2 = 68$) or length (Mann–Whitney U-test: U = 2072, p = 0.30, $n_1 = n_2 = 68$) of males offered all small tiles vs. those offered all large tiles (weight of males offered small tiles: 0.79 ± 0.038 g; length: 48.21 ± 0.73 mm. Weight of males offered large tiles: 0.74 ± 0.036 g; length: 47.18 ± 0.66 mm).

Experiment 3: nest size vs. nest colour

As size and colour of potential nests may be confounded in the field (i.e. if light-coloured shells are generally smaller than dark-coloured rocks), our final experiment was designed to disentangle male preference (if any) based on nest size from male preference (if any) based on nest colour. We did this by mismatching the size and colour of potential nest sites, offering 50 males the choice between either a

large white tile vs. a small brown tile or a large brown tile vs. a small white tile. Once again, there was no significant difference in either weight (Mann–Whitney U-test: U = 307.5, p = 0.92, n_1 = n_2 = 25) or length (Mann–Whitney U-test: U = 309.5, p = 0.95, n_1 = n_2 = 25) of males between treatments (weight of males offered large brown tile vs. small white tile: 0.70 ± 0.040 g; length: 46.1 ± 0.84 mm. Weight of males offered large white tile vs. small brown tile: 0.71 ± 0.057 g; length: 46.3 ± 1.10 mm).

Results

Field Survey

Overall, there was a positive relationship between male length and the size of his nest (Spearman's rank correlation: r_s = 0.757, p < 0.001, n = 43). However, considering rocks and shells separately, we found that this relationship was significant only for males nesting under rocks (rock: r = 0.446, p = 0.049, n = 20; shell: r = 0.316, p = 0.14, n = 23; Fig. 1) More generally, rocks had a larger surface area than shells (Mann–Whitney U-test: U = 0, p < 0.001, n_{rock} = 20, n_{shell} = 23; Fig. 1), and males occupying the former were larger than those that occupied the latter (mean length of males occupying rock: 51.2 ± 0.95, shell: 42.2 ± 1.02, Mann–Whitney U-test: U = 107, p < 0.001, n_{rock} = 32, n_{shell} = 26).

Nest Choice Experiments

Experiment 1: nest size
We found that males preferred large over small tiles (39 out of 50 chose large; binomial test: p < 0.001). The response of males to large vs. small tiles did not differ depending on whether they were offered all brown or all white tiles (white tiles: 21 out of 25 chose large, brown tiles: 18 out of 25 chose large; Fisher's Exact test: p = 0.50). There was no difference in the size of males that chose large tiles vs. those that chose small tiles (weight of males that chose large: 0.67 ± 0.044 g, small: 0.69 ± 0.062 g, Mann–Whitney U-test: U = 193, p = 0.61, n_{large} = 39, n_{small} = 11; length of males that chose large: 45.5 ± 0.86 mm, small: 46.0 ± 1.29 mm, Mann–Whitney U-test: U = 198.5, p = 0.71, n_{large} = 39, n_{small} = 11).

Experiment 2: nest colour

The response of males to tile colour differed depending on whether they were offered all small tiles or
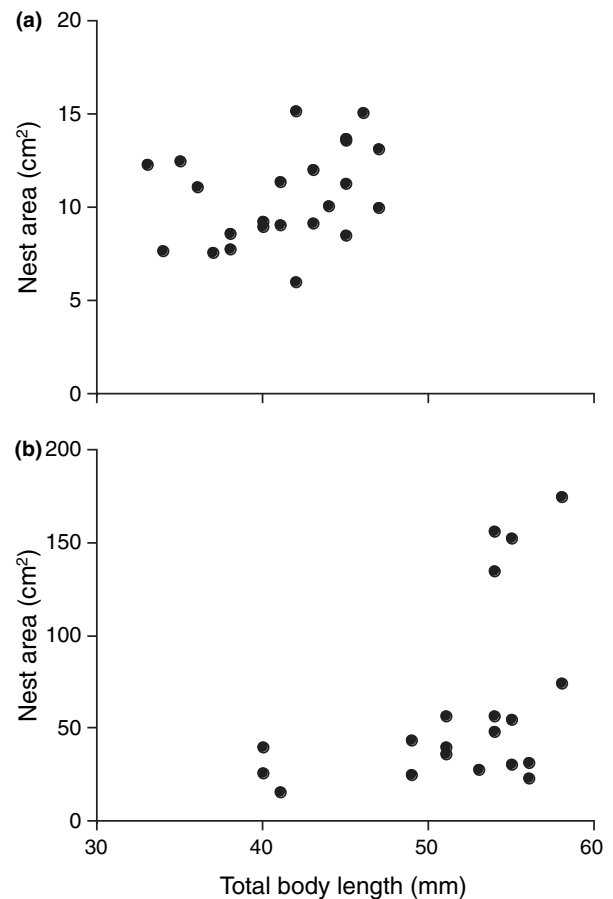
Fig. 1: Relationship between male body length and nest area for males nesting under (a) shells and (b) rocks.

all large tiles (Fisher's Exact test: p = 0.014). Males offered a small white tile vs. a small brown tile did not show a preference for one over the other: 33 of 68 built their nest under the white tile (binomial test: p = 0.90). By contrast, 48 out of the 68 males offered a choice between a large white tile vs. a large brown tile preferred to build their nests under the former (binomial test: p = 0.001). There was no difference in the size of males that chose white tiles vs. those that chose brown tiles. This was true for males offered all large tiles (weight of males that chose white: 0.74 ± 0.04 g, brown: 0.76 ± 0.06 g, Mann–Whitney U-test: U = 524.5, p = 0.55, n_{white} = 48, n_{brown} = 20; length of males that chose white: 46.86 ± 0.77 mm, brown: 47.9 ± 1.25 mm, Mann–Whitney U-test: U = 535.5, p = 0.45, n_{white} = 48, n_{brown} = 20) as well as males offered all small tiles (weight of males that chose white: 0.76 ± 0.048 g, brown: 0.82 ± 0.058 g, Mann–Whitney U-test: U = 524.5, p = 0.55, n_{white} = 48, n_{brown} = 20; length of males that chose white: 47.67 ± 0.95 mm, brown:

48.7 ± 1.1 mm, Mann–Whitney U-test: $U = 535.5$, $p = 0.45$, $n_{white} = 48$, $n_{brown} = 20$).

Experiment 3: nest colour vs. nest size

Males in experiment three also preferred large over small tiles (36 out of 50 chose large; binomial test: $p = 0.003$). The response of males to large vs. small tiles did not differ depending on whether the large tile was brown or white (18 out of 25 chose large white tile over small brown tile; 18 out of 25 chose large brown tile over small white tile; Fisher's Exact test: $p = 1$). There was no difference in the size of males that chose large tiles vs. those that chose small tiles (weight of males that chose large: 0.70 ± 0.041 g, small: 0.71 ± 0.067 g, Mann–Whitney U-test: $U = 267$, $p = 0.75$, $n_{large} = 36$, $n_{small} = 14$; length of males that chose large: 46.2 ± 0.82 mm, small: 46.2 ± 1.27 mm, Mann–Whitney U-test: $U = 255$, $p = 0.95$, $n_{large} = 36$, $n_{small} = 14$).

Discussion

We found that, irrespective of their own size, male sand gobies from the Finnish Baltic preferred large nests. Moreover, size preference appeared to supersede any preferences based on colour. This result differs from that obtained in an earlier study of nest preferences in marine sand gobies from the Gullmar Fjord (Kvarnemo 1995). In that population, males exhibited size-assortative nest preferences. So, why might male sand gobies in our population prefer large nests irrespective of their own body size? One obvious benefit of owning a large nest is that it is able to hold more eggs (Lindström 1988). Larger nests may also be more attractive to females (Lehtonen et al. 2007). Hence, in common with other species of nest-guarding fish with paternal care, the size of a male's nest is likely to have a direct bearing on his reproductive success (Côté & Hunte 1989; Marconato et al. 1989; Magnhagen & Vestergaard 1993). Of course, large nests may also impose greater energetic demands on males in terms of egg-fanning behaviour (Lindström & Hellstrom 1993). Excavating a bigger nest opening can, to some extent, ameliorate this problem but this may also expose males to an increase in the cost of nest defence (Kvarnemo 1995).

The relative cost of nest defence against egg predators, however, appears to vary dramatically among sand goby populations. Male gobies from the Gullmar Fjord population are confronted with formidable egg predators in the form of dog whelks *Hinia reticulata* and shore crabs *Caracinus maenas* (Kvarnemo 1995). The high cost of defending nests against these predators has been posited as one reason why small gobies from that population avoid larger nests (Kvarnemo 1995). Specifically, in that study, it was argued that smaller males with larger nests would have to have bigger nest openings to offset the energetic demands of ventilating their nests and this, in turn, could make them more vulnerable to nest incursions by would-be predators. Notably, however, such predators are absent from the brackish environment of the Finnish Baltic, suggesting that the cost of nest defence may be lower in the current study population. Thus, the absence of these egg predators might possibly explain why, in our population, males prefer large nests irrespective of their own size.

In common with earlier studies, however, nest occupancy in the field shows a pattern of 'size-assortment', with larger males occupying larger rock nests and smaller individuals occupying smaller shell nests. Moreover, for males occupying rock nests, we also found a positive relationship between male length and the size of his nest. Such a pattern, considered in the light of our laboratory results, suggests that size-assortative nest occupancy in the Finnish Baltic is likely due to male-male competition: large males out compete smaller males for the biggest nests which, in turn, are relegated to competing amongst themselves for less desirable (small) nests. Such results underscore the fact that male preferences for material resources may not always be realised in a competitive setting. It is important to bear in mind; however, that male competition does not always dictate patterns of nest occupancy. If males prefer nests that are proportionate to their own body size, and if nests occur in surplus, the same patterns of size-assortative nest occupancy can also be due to male choice, as reported in the Gullmar Fjord population (Kvarnemo 1995). Importantly, evidence in sand gobies suggests that nest occupancy in the field, even among populations of the same species, could be the outcome of entirely different mechanisms (i.e. male choice in the Gullmar Fjord population vs. male competition in the Finnish Baltic).

The colour preference revealed in this study is intriguing. Males were indifferent to colour when offered small tiles but showed a strong preference for nesting under large, white tiles. Why? We rule out low statistical power in trials where males were offered small tiles, since the power to detect an effect

of a size comparable to that obtained for large tiles (where g = 0.4) is greater than 99%. One possibility, instead, is that males may have been attracted to a supernormal stimulus (Kilner et al. 1999; Schiestl 2004); although the colour of the preferred tiles (at least to the human observer) were similar to the mussel shells typically used by sand gobies as nest sites, the surface area of the large tiles far exceeds the surface area of natural shells occurring in our study area. Another possibility is that males might have preferred the large white coloured tiles because they were drawn to novel stimuli (Burley et al. 1982; Östlund-Nilsson & Holmlund 2003). In sand gobies, an ability to respond favourably towards, and exploit, novel nest sites is likely to be adaptive, especially in a population faced with a shortage of nesting resources. A proclivity to exploit novel resources is demonstrated by the fact that male sand gobies in this population have recently been documented invading rocky (i.e. novel) habitats to take advantage of the greater availability of potential nest sites (rocks) in those habitats (Lehtonen & Lindström 2004).

In conclusion, we show that male sand gobies exhibit clear preferences for material resources. Considered in the light of earlier studies, however, evidence suggests that these preferences can vary among populations and, depending on resource availability, might not be realised in a competitive setting. More generally, an understanding of male preferences for the quality of material resources lags far behind what is known from the female choice perspective. This is despite the fact that, in many taxa, the quality of resources held by males can have an important impact on the fitness of both sexes. To date, most studies of resource ownership have tended to focus on how males compete and hold onto resources that are needed for breeding. Rewarding insights will no doubt follow from future studies expanding this research focus by asking if, and how, such resources might be selected in the first place.

Acknowledgements

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