Animal Behaviour 166 (2020) 289–296

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Male phenotype and resource type influence nesting behaviour in a fish

Topi K. Lehtonen [a, b, c, *], Bob B. M. Wong [b, c]

[a] Ecology and Genetics Research Unit, Faculty of Science, University of Oulu, Oulu, Finland
[b] School of Biological Sciences, Monash University, Victoria, Australia
[c] Tvärminne Zoological Station, University of Helsinki, Hanko, Finland

ARTICLE INFO

Article history:
Received 5 January 2020
Initial acceptance 22 January 2020
Final acceptance 24 April 2020
Available online 9 July 2020
MS. number: 20-00009R

Keywords:
binary choice
body size
context dependence
extended phenotype
male–male competition
nest architecture
nesting behaviour
parental care
resource
sand goby

In many brood-rearing species, suitable nesting resources are needed for nest construction. Here, we used males of a small marine fish, the sand goby, *Pomatoschistus minutus*, to study the associations between the nest owner's phenotype (i.e. body size), the characteristics of the nesting resource used for nest construction (i.e. resource size and shape) and nest-building behaviour (i.e. eagerness to build a nest and extent of nest elaboration). We found that male body size was associated with nesting resource size and resource architecture in the field, with the smallest males occupying small flat resources and the biggest males occupying large arched resources. In the laboratory, the type of resource occupied in the field had a limited effect on the level of nest elaboration, but not on other nesting behaviours. Large body size, in turn, was associated with preference for larger resources and, in some circumstances, also the level of nest elaboration. Body size did not affect the eagerness to initiate nest building. Furthermore, males chose arched nesting resources more often than those that were flat, and this preference was also reflected under a 'no-choice' scenario, based on the time taken for males to initiate nest building. Overall, the results indicate that the importance of male size in nest building is context dependent, while nesting behaviours can also be affected by resource size, resource architecture and, under some circumstances, the nest builder's experience with resource use.

Many animals rear their offspring in purpose-built nests, the characteristics of which affect their reproductive success (Barber, 2013; Guillette & Healy, 2015). Larger nests, for example, may provide better thermal insulation for the developing brood (Hoi, Earley, & Wolf, 1994), conspicuous nests may improve a nest owner's encounter rate with potential mates (Genner, Young, Haesler, & Joyce, 2008), while nest concealment may reduce the risk of brood predation (Cresswell, 1997; Fisher & Wiebe, 2006; Weidinger, 2002). Indeed, both the choice of nesting location and nest architecture can affect offspring survival in a range of taxa, including fish (Raventos, 2006; Takegaki & Nakazono, 2000), amphibians (Byrne & Keogh, 2009), birds (Burton, 2006; Quader, 2006) and mammals (Bult & Lynch, 1997). Regarding nest characteristics, individuals may need to trade between multiple factors to optimize their reproductive output. For example, optimal thermoregulation of eggs in the nest may have to be traded against the need for nest crypticity against would-be predators, as in piping plovers, *Charadrius melodus* (Mayer et al., 2009). Similarly, while possession of a high-quality nest can improve mating opportunities for nest holders, it may also increase their likelihood of being challenged and usurped by superior competitors, as in Mediterranean wrasse, *Symphodus ocellatus* (Alonzo, 2004).

The characteristics of the ready-built nest, such as its size and elaboration, may also function as an extended phenotype (Schaedelin & Taborsky, 2009) and play a critical role in mate attraction (Danylchuk & Fox, 1996; Eckerle & Thompson, 2006; Hastings, 1988; Johnson & Searcy, 1993; Östlund-Nilsson, 2001; Takahashi & Kohda, 2002). For this to be the case, one should expect nest structures and their owners to show consistent covariation. For example, in barn swallows, *Hirundo rustica*, the volume of nest material is positively related to immune response (Soler, Martín-Vivaldi, Haussy, & Møller, 2007), while in common gobies, *Pomatoschistus microps*, the amount of sand piled on top of a male's nest is correlated with his body condition (Kvarnemo, Svensson, & Forsgren, 1998). However, the appearance of the constructed nest is not the only important aspect of nest-building

* Correspondence: T. K. Lehtonen, Ecology and Genetics Research Unit, Faculty of Science, University of Oulu, Post Box 3000, Oulu, 90014, Finland.
E-mail address: topi.lehtonen@oulu.fi (T. K. Lehtonen).

https://doi.org/10.1016/j.anbehav.2020.06.001

behaviour that might correlate with builder phenotype. In some taxa (including many species of nest-guarding fish), before nest construction can even take place, individuals must first acquire one or more suitable resources with which to build their nest (Barber, 2013). Yet, in contrast to the attention given to the relationship between builder phenotype and characteristics of the ready-built nest, much less is known about how a nest builder's phenotype might influence its choice of nesting resource.

The sand goby, *Pomatoschistus minutus*, is an excellent model species for studying the relationship between the nest builder's phenotype and nest-related behaviours. High success in nesting attempts is important because the species typically has only a single, extended breeding season (Healey, 1971). After finding an empty mussel shell or a flat stone (hereafter referred to as 'nesting resource'), a sand goby male builds a nesting chamber underneath the resource and piles sand on top of it (Lehtonen, Wong, & Kvarnemo, 2016; Lindström, 1988; Svensson & Kvarnemo, 2003). The characteristics of the nesting resource, as well as the completed nest, can have a direct impact on male mating success. In particular, nest characteristics (e.g. size and architecture) can physically limit the maximum number of eggs a male is able to acquire (Lindström, 1988) and affect his investment in brood care (Järvi-Laturi, Lehtonen, Pampoulie, & Lindström, 2008), the susceptibility of eggs to predation (Lehtonen, Vesakoski, Yli-Rosti, Saarinen, & Lindström, 2018; Lindström & Ranta, 1992) or the intensity of intraspecific competition (Lindström, 1992; Svensson & Kvarnemo, 2003). Hence, males should be highly selective when choosing nesting resources, with their phenotype, especially body size, potentially being important (Japoshvili, Lehtonen, Wong, & Lindström, 2012; Kvarnemo, 1995; Lehtonen et al., 2016). In this respect, breeding sites occupied by sand gobies vary in terms of availability of nesting resources and, hence, available opportunities for resource choice without first having to evict the current resident (Forsgren, Kvarnemo, & Lindström, 1996; Lehtonen & Lindström, 2004). Female sand gobies in our study population, in turn, do not always prefer large males, but rather males that are matched in size with their nesting resource (Lehtonen, Rintakoski, & Lindström, 2007).

Here, our aim was to use the sand goby to study the associations between the nest owner, the nesting resource and nest-building behaviour. In particular, we assessed whether male nesting resource choice and nest-building behaviours are linked to the male's body size, prior resource use experience or the characteristics of nesting resources available to him. To do this, we first conducted a field experiment to test whether males of different phenotype (i.e. body size) occupy nesting resources of different architecture (arched and flat) or size (smaller or larger). We then carried out two laboratory experiments to test whether a male's size or his earlier nesting resource use relates to his nesting resource choice under controlled laboratory conditions. In this context, we also investigated how nest-building behaviours (eagerness to build a nest and the extent of nest elaboration) may be affected by male size, prior experience (i.e. the nesting resource that the male was using in the field at the time of capture) and type of nesting resources offered in the laboratory. We hypothesized that male size is positively associated with the size of his chosen resource, his nest-building effort and his probability of preferring the more conspicuous arched nesting resource type (Fig. 1). We also expected that males occupying larger resources in the field might, under laboratory conditions, show a similar preference or be more diligent nest builders.

METHODS

Both the field and laboratory components (see below) of this study were conducted during the sand goby breeding season, between late May and late June, in 2016, at the Tvärminne Zoological Station of the University of Helsinki (59°50.7′N, 23°14.9′E; see map in the Supplementary Material). The field site (Vargskär: 59°49.4′N, 23°08.7′E) has a large area of sandy substrate covered by shallow water (≤1.5 m). Suitable nesting resources (such as mussel shells and flat stones) at this site are scarce, resulting in male–male competition over nesting resources and high rates of nest occupancy of the resources that are available (Lehtonen and Lindström, 2004; Lindström, 1988).

Field Experiment: Distribution of Male Phenotypes

To test the relationship between nesting resources and their holders in the wild, we placed unglazed ceramic nesting resources that were either arched (halved terracotta flowerpots) or flat (tiles) across the study site at Vargskär. For both architecture types, arched and flat, two different sizes were deployed. Smaller arched nesting resources had a maximum mouth diameter of 4.5 cm and length of 4.2 cm, while the same measures for larger arched nesting resources were 8.3 cm and 8.1 cm, respectively (Fig. 1). The two flat nesting resource sizes were 5.0 × 5.0 cm and 9.9 × 9.9 cm. Importantly, both the smaller and larger nesting resources of the two types had matching surface areas. Arched (i.e. halved flowerpots) and flat (tiles) nesting resources are similar to the natural nesting resources found in the area (i.e. mussel shells and flat stones) and are readily accepted by nesting sand goby males both in the field (arched nesting resources: Forsgren et al., 1996; Lindström & Pampoulie, 2005; flat nesting resources: Lindström, 1988; Wong, Lehtonen, & Lindström, 2018) and under laboratory conditions (arched nesting resources: Japoshvili et al., 2012; Lehtonen et al., 2016; flat nesting resources: Flink & Svensson, 2015; Lehtonen, Lindström, & Wong, 2013).

The nesting resources of all types (with respect to architecture and size) were placed in the study area either singly or (due to logistic restrictions) in pairs of the same type, with their locations identified by marks on weighted rope lines that ran along the sandy substrate, each line anchored into the substrate at both ends. When in pairs, the minimum distance between the two nesting resources was 40 cm, while the minimum distance between pairs, as well as nesting resources without a pair, was 2 m. A similar number (ca. 20) of each type of nesting resource was placed in the field site at a time. For logistic reasons, ca. 6–10 nesting resources closest to each other were of the same type (i.e. arched or flat and of a certain size). The nesting resources were sampled on 10 different occasions across the field site during the peak breeding season (late May–late June), with 3–5 days between each sampling effort. To control for

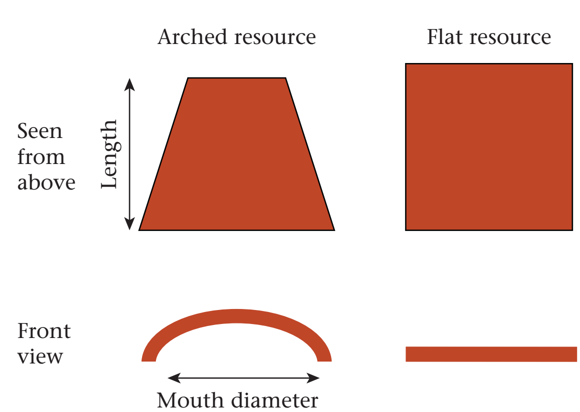

Figure 1. Diagram of the two nesting resource architecture types used in this study, arched and flat.

any microhabitat variation, after every other sampling occasion, the locations of the marker lines, and hence nesting resources, were changed, without reusing any previous locations. Nest occupation level was high for all resource types.

The nesting resources were sampled with the aid of a mask and snorkel, on each occasion using a hand net to catch males that had built a nest (with catching success of ca. 75–95% for all resource types, depending on the weather and water conditions during, and the time available for, catching the fish). We then recorded the type of resource the male had been occupying. The males were transported in containers back to the field station, where they were weighed to the nearest 0.01 g on an electronic balance, and their total lengths measured to the nearest 0.5 mm on a measuring board with a grid scale. We measured total lengths of males from 143 smaller arched, 135 smaller flat, 144 larger arched and 137 larger flat nesting resources. Most of these males (see below for sample sizes) were later used for the laboratory experiments, as detailed below.

Laboratory Experiment 1: Nest Architecture

Back at the field station, males were first kept, typically for a couple of days and always less than a week, in holding aquaria of ca. 100 litres (with a substrate of fine sand and maximum of 20 individuals in each tank). During that time, the males were fed with live opossum shrimp, *Neomysis integer*, ad libitum. The holding and experimental tanks (see below) were in a noninsulated greenhouse and supplied with a continuous through-flow of sea water, pumped from a nearby bay. This ensured natural water conditions that were typical for the study site at the time of year (temperature: 10–15 °C; salinity: ca. 5.5 ppt; Merkouriadi & Leppäranta, 2015) and day/night cycle (ca. 18.5/5.5 h at the time of the experiments) throughout the study.

In the first laboratory experiment, we investigated whether males have a preference for an arched or flat nesting resource (in the absence of rivals), and whether any such preference is related to the type of nesting resource the male was occupying in the field. We also assessed whether eagerness to nest (time to initiate nest building) and the extent of nest elaboration (amount of sand piled on the nest) were affected by these factors. The trials were run in tanks (68 × 25 cm and 22 cm water depth) with a 4 cm layer of fine sand as substrate. Before the onset of a trial, two nesting resources (see below for details) were placed randomly to the left, centre or right position within the experimental tank (see Lehtonen et al., 2016). Hence, one of the three possible positions where the resource could have been placed within the aquarium was left empty in a randomized fashion. All randomization for the study was done using random numbers that were generated at https://www.random.org/.

Each focal male was given the option of choosing between an arched and a flat nesting resource. The sizes of the nesting resources were chosen so that the effective area for egg deposition was, as closely as possible, the same for the two types. The two resource types were also similar in coloration, although an earlier study has shown that sand goby males do not discriminate between nesting resources of different colours (Wong, Lehtonen, & Lindström, 2008). We had three different categories of replicates, with males given the option of the following choices: (1) two small nesting resources (arched: maximum diameter at the mouth 4.2 cm and length 4 cm; flat: 4.3 × 4.3 cm); (2) two medium-sized resources (arched: 6.5 cm and 6 cm; flat: 6.7 × 6.7 cm); and (3) two large resources (arched: 10.3 cm and 10.0 cm; flat: 11.7 × 11.7 cm). The entrance of the arched nesting resource faced one of the longer sides of the tank. The tanks were positioned behind blinds to minimize disturbance.

Gobies were allocated to the different treatments in a randomized fashion so that, as far as possible, the same number of individuals occupying each nesting resource type in the field was used in each treatment. A replicate was initiated by placing a sand goby male into the experimental arena (haphazard location with respect to the nesting resources). The male was then given up to 48 h to initiate nest building. During this time, the experimental tanks were checked about seven times a day, with the checks distributed as evenly as possible between 0800 and 2300. At each check, we recorded male location and any signs of nest building. A male was considered to have initiated nest building when he had started to pile sand on top of, and excavate under, the nesting resource, leaving a single narrow entrance to the nest. In such cases, the time to initiate nest building was recorded as the midway point in time between when the onset of nest building was first observed and when the tank was last checked without any such signs (Lindström & Lehtonen, 2013). After the male was observed to have initiated nest building, he was left in the tank for at least 12 (but no more than 24) h to finish building a nest, which usually took 1 h or less, with additional nest elaboration sometimes taking place within the following few hours. In some of these replicates (ca. 10% over the data set), both nesting resources showed signs of the male having initiated a nest. In such cases, we employed a criterion used in previous studies (Japoshvili et al., 2012; Lehtonen et al., 2016), which is to tally the times that the male was observed using the nests he had built up and determine the ‘chosen’ option as the nesting resource with which the male had most frequently associated. Although this does not differentiate between males that were more decisive (i.e. only built up one nest) versus those that were less decisive (built two nests but settled in one), we do not consider this potential source of noise in the data set to be an issue, given our sample sizes. Our approach also avoids having to define choice using more subjective criteria that would require the exclusion of data. In all cases, time to the onset of nest building was defined by the first signs of nest building.

After completion of the replicate, we measured the level of nest elaboration as the amount of sand on top of the chosen nesting resource (sensu Lehtonen & Wong, 2009). This was done by carefully lifting the nesting resource onto a tray, which collected the sand that the goby had piled on top of his nest. Owing to the shape of the arched resources (Fig. 1), only the sand placed directly on the ridge of the resource (halved pot) was collected. The weight of this fraction is a good indicator of the total amount of sand that the male had placed on the nest (Lehtonen et al., 2016). For both nest types, the collected sand was later dried in an oven for 36 h at 60 °C, and then weighed on an electric balance (Lehtonen & Wong, 2009; Lehtonen et al., 2016).

In total, nest type preferences of 112 males were assessed (mean ± SE total length = 51.0 ± 0.6 mm, weight = 1.05 ± 0.04 g). Of these, 99 initiated nest building within 48 h. Each male was used in only one of the two laboratory experiments.

Laboratory Experiment 2: Nest Size

Experiment 2 used replicates that were also included in a complementary study that assessed whether sand gobies make comparative versus absolute resource choice decisions (Lehtonen & Wong, 2020). Experiment 2 had the same procedures as experiment 1, except that focal males were given the opportunity to choose between nesting resources that were of the same type but differed in size. In particular, 273 males (total length = 50.4 ± 0.4 mm, weight = 0.99 ± 0.02 g, size data missing for three males) were used to investigate the following choice scenarios: (1) small (S) versus medium-sized (M) nesting resource

($N_{arched} = 39$, $N_{flat} = 71$); (2) small (S) versus large (L) resource ($N_{arched} = 38$, $N_{flat} = 43$); and (3) medium (M) versus large (L) resource ($N_{arched} = 36$, $N_{flat} = 46$). These replicates resulted in 199 choices, as detailed in the Results.

Statistical Analyses

All analyses were run using R 3.3.2 software (The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org). To assess whether different types of nesting resources attracted males of different sizes in the field, we ran an ANOVA with the total length (square-root transformed) as the response variable and the nest type in the field (small arched/small flat/large arched/large flat) as the explanatory variable. Here, Tukey HSD was used for assessing significance of pairwise differences.

To assess, in experiment 1, whether male size or the nesting resource type the male had occupied in the field was associated with his choice of nesting resource architecture in the laboratory, we applied a generalized linear model with a binomial distribution, with the choice (arched/flat) as the response variable and the nesting resource occupied in the field (small arched/small flat/large arched/large flat), the size of the two available nesting resources (small/medium/large) and male body size (total length) as explanatory variables. For the simplicity of interpretation, we only assessed the main effects.

To assess males' choice between two nesting resources of the same type but different size (i.e. laboratory experiment 2), we applied a generalized linear model with a binomial distribution with the choice (smaller/larger of the two nesting resources) as the response variable and the nest type occupied in the field (smaller arched/smaller flat/larger arched/larger flat), the available size options in the different treatments (S versus M/S versus L/M versus L) and male body size (total length) as explanatory variables.

For both laboratory experiments 1 and 2, we also tested whether the time it took for males to start nest building (as a proxy of their eagerness to build a nest) differed depending on the type of nesting resource occupied in the field. For both data sets (experiments 1 and 2), we applied a Cox proportional hazards analysis that included the nesting resource type occupied in the field (smaller arched/smaller flat/larger arched/larger flat) and male total length as variables. In the analysis of experiment 1, the model also included the size of the two available nesting resources (S/M/L) as another explanatory variable. The analysis of experiment 2, in turn, included the three nesting resource size choice scenarios (S versus M/S versus L/M versus L) and the type of resource (arched/flat) as additional explanatory variables. Males that did not commence nest building within the allocated 48 h period were 'right censored' (Lagakos, 1979) in these analyses.

Finally, in both laboratory experiments, we assessed the relationship between the type of nesting resource occupied in the field and the extent of nest elaboration (i.e. the weight of sand collected from the top of the nest, when necessary square-root or log transformed for improved normality). For the data sets of both experiments, the analyses were conducted separately for the arched (only sand directly on the ridge collected) and flat (all sand piled on top of the object collected) nesting resources. In each case, we used a linear model with the type of nesting resource occupied in the field (smaller arched/smaller flat/larger arched/larger flat) and male total lengths as explanatory variables. In experiment 1, the size of the nesting resources available in the replicate and, in experiment 2, the size of the nesting resource used by the male for nest building were included as additional explanatory variables.

Ethical Note

The field survey and laboratory experiments were noninvasive and designed to investigate nesting decisions and behaviours that sand gobies would exhibit in the wild. All animals, upon completion of their replicates, were returned to the sea. The study was approved by the Finnish Animal Experiment Board (ESAVI/3915/04.10.07/2016).

RESULTS

Field Experiment: Distribution of Male Phenotypes

In the field, different types of nesting resources attracted males of different body sizes (ANOVA: $F_{3,555} = 25.27$, $P < 0.001$). In particular, the larger arched and flat nesting resources were occupied by the largest males (Fig. 2). Compared to these two resource types, males occupying smaller arched nesting resources were significantly smaller, while males occupying smaller flat resources were the smallest (Fig. 2).

Laboratory Experiment 1: Nest Architecture

In laboratory experiment 1, when males chose between two nesting resources of the same surface area but of different architecture (arched versus flat), neither the type of the resource the focal male had occupied in the field (generalized linear model: $\chi^2_3 = 0.053$, $P = 1.0$) nor the male's body size ($\chi^2_1 = 0.725$, $P = 0.39$) had a significant effect on the choice outcome. However, the nesting resource size treatment did have an effect ($\chi^2_2 = 34.5$, $P < 0.001$). In particular, while males overall chose the arched nesting resource more often (83 times out of 99), the flat option was chosen more often with increasing size of the available resources: small resource: 0/34 replicates; medium-sized resource: 1/33; large resource: 15/32.

Laboratory Experiment 2: Nest Size

In laboratory experiment 2, when males were allowed to choose between two resources of the same architecture (either arched or flat) but of different sizes, the nesting resource they had occupied in the field did not have a significant effect on whether the larger option was chosen (generalized linear model: $\chi^2_3 = 4.924$, $P = 0.18$). The sizes of available choice options did have an effect ($\chi^2_2 = 12.93$,

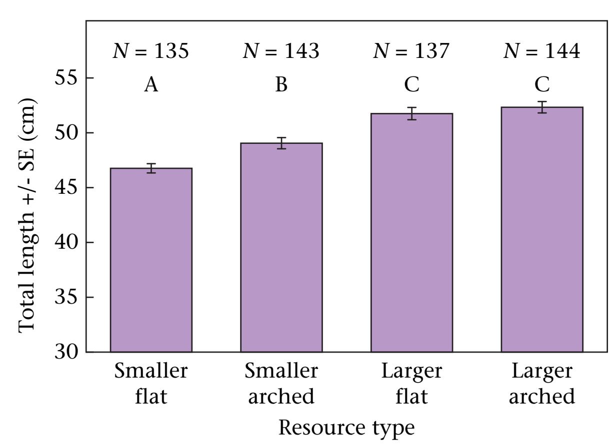

Figure 2. Mean (±SE) total length of males occupying different types of nesting resources in the field. Resource types without a letter in common are significantly different (Tukey HSD test, $\alpha = 0.05$).

$P = 0.002$), with the larger of the two resources chosen as follows: S versus M option: 59/65; S versus L: 59/66; M versus L: 47/68. In addition, the probability of the larger resource option being chosen increased with male body size ($\chi^2_1 = 5.550$, $P = 0.018$).

Eagerness to Build a Nest in the Laboratory

In experiment 1, in which the focal males chose between an arched and a flat nesting resource of the same size, neither the nesting resource occupied in the field (Cox proportional hazards test: $\chi^2_3 = 2.884$, $P = 0.41$) nor male total length ($\chi^2_1 = 0.1903$, $P = 0.66$) significantly affected the time taken by males to begin nest building. However, the focal male took longer to initiate nest building when the two nesting resources were small ($\chi^2_2 = 15.97$, $P < 0.001$; Fig. 3).

Similarly, in experiment 2, the nesting resource the male had occupied in the field ($\chi^2_3 = 3.412$, $P = 0.33$) and male total length ($\chi^2_1 = 2.663$, $P = 0.10$) did not significantly affect the time it took for him to initiate nest building. Males took longer to begin building their nests when they were offered small and medium-sized nesting resources than when a large resource option was available ($\chi^2_2 = 19.61$, $P < 0.001$; Fig. 4). Nest building was also initiated quicker when the male had two arched nesting resources to choose from than when flat nesting resources were offered ($\chi^2_1 = 20.83$, $P < 0.001$; Fig. 5).

Extent of Nest Elaboration in the Laboratory

When males chose to build a nest using an arched nesting resource in experiment 1 ($N = 83$ replicates), its size had an effect on the amount of sand the male piled on it (linear model: $F_{2,76} = 21.01$, $P < 0.001$), with more sand being piled on larger nests. By contrast, the type of resource occupied in the field ($F_{3,76} = 1.660$, $P = 0.18$) and male total length ($F_{1,76} = 0.0004$, $P = 0.98$) did not have an effect. When a flat nesting resource was chosen in experiment 1 ($N = 16$), none of these factors had a significant effect on the amount of sand piled on the nest (medium-sized versus large nest: $F_{1,10} = 0.2208$, $P = 0.65$; nest type in the field: $F_{3,10} = 0.5660$, $P = 0.65$; male total length: $F_{1,10} = 0.2539$, $P = 0.63$).

Regarding the replicates of experiment 2 in which the focal male chose between two arched nesting resources ($N = 100$ choices made), the range of available nesting resource sizes had a significant effect on the amount of sand piled on the nest by the focal male (linear model: $F_{2,91} = 4.971$, $P = 0.009$), with 5.48 ± 0.48 g ($N = 33$), 12.34 ± 1.57 g ($N = 33$) and 8.50 ± 1.06 g ($N = 34$) of sand piled on the nest ridge when choosing between S versus M, S versus L and M versus L resources, respectively. In addition, male size ($F_{1,91} = 13.33$, $P < 0.001$) and the type of nesting resource the male had occupied in the field ($F_{3,91} = 2.881$, $P = 0.040$) had an effect on the amount of sand piled on the nest ridge. In particular, large males piled on more sand, as did males that had occupied a larger arched nesting resource in the field: 8.55 ± 0.90 g ($N = 24$), 7.02 ± 1.40 g ($N = 26$), 11.5 ± 1.71 g ($N = 25$) and 8.07 ± 1.36 g ($N = 25$) of sand were piled on the nest ridge by males that had occupied a smaller arched, smaller flat, larger arched and larger flat resource, respectively. When focal males in experiment 2 chose between two flat nesting resources ($N = 99$ choices made), the range of available nesting resources ($F_{2,92} = 0.6217$, $P = 0.54$) and the type of nesting resource the male had occupied in the field ($F_{3,92} = 0.2955$, $P = 0.83$) did not have a significant effect on the amount of sand piled on the nest. However, the amount of sand piled on a male's nest was positively associated with his total length ($F_{1,92} = 5.047$, $P = 0.027$).

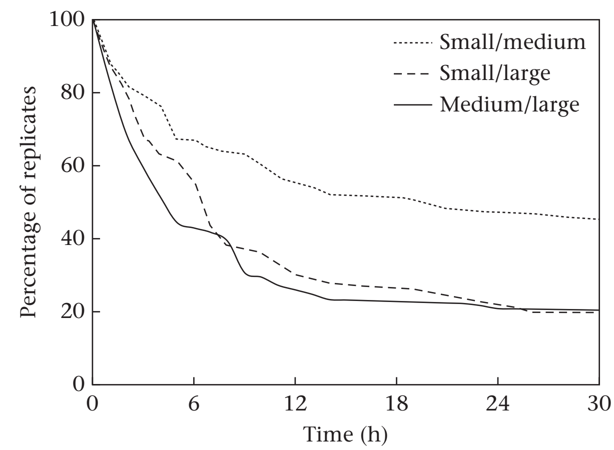

Figure 4. Percentage of replicates in which the focal male had not initiated nest building in laboratory experiment 2 with different nesting resource size options. Replicates with arched and flat resources are combined. The sample sizes are 110, 81, 82 for the combinations of small/medium, small/large and medium/large nesting resources, respectively.

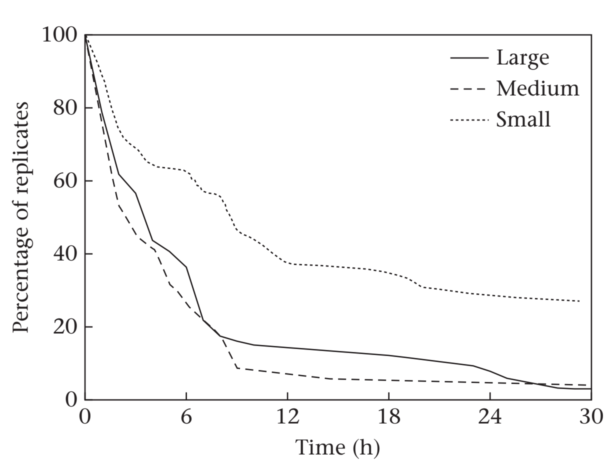

Figure 3. Percentage of replicates in which the focal male had not initiated nest building (laboratory experiment 1, progress during the first 30 h of 48 h is shown). Sample sizes were 45, 34, 33 for replicates with small, medium and large nesting resources (either arched or flat), respectively.

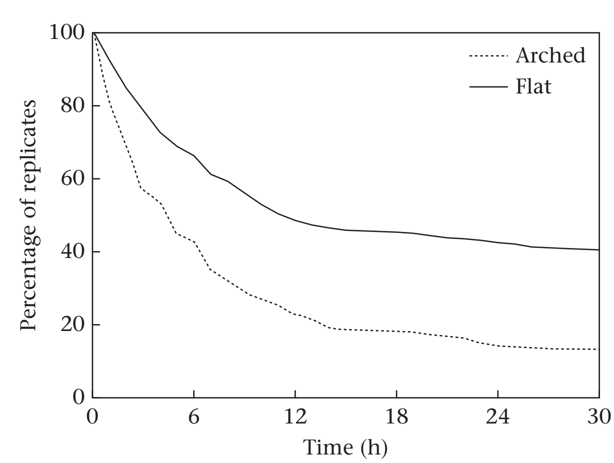

Figure 5. Percentage of replicates in which the focal male had not initiated nest building in laboratory experiment 2 with regard to the two types of nest architecture. Different size choice options were combined. Sample sizes were 112 and 158 for arched and flat nesting resources, respectively.

DISCUSSION

We found a relationship between nesting resource type and male body size in the field. In particular, the largest sand goby males were occupying nesting resources that were larger (of the two size categories) and arched (rather than flat). This relationship between resource type and male phenotype is likely to result from males of different sizes differing not only in their nesting resource preferences (Kvarnemo, 1995; Lehtonen et al., 2016) but also their resource-holding potential (Lindström & Pampoulie, 2005), with a male of a certain size more likely to be replaced by a larger rival when it is occupying a resource type that is under more intense competition. This is consistent with findings reported in other taxa, including other species of nest-building fish, in which male resource-holding potential correlates positively with the value of the male's resource (e.g. Kelly, 2008; Takahashi, Kohda, & Yanagisawa, 2001).

Regarding resource choice and nest-related behaviours under laboratory conditions, one of our main goals was to investigate whether the choices and nesting behaviours of sand goby males are related to resource size and type, male phenotype or the male's prior experience in occupying a nesting resource of a certain type in the field. For nesting resource size, we found that the probability of the larger option being chosen in a laboratory setting increased with male body size. Similar findings have been reported in multiple species of nest-building fish (Bisazza, Marconato, & Marin, 1989; Takahashi et al., 2001; Uglem & Rosenqvist, 2002), including the sand goby (Japoshvili et al., 2012; Kvarnemo, 1995; Lehtonen et al., 2016). Such size-assortative choice is most probably due to large males being better able to meet the energetic and ecological demands of owning a large nesting resource. These demands are associated with, for instance, covering the resource with more sand, circulating larger volumes of water when aerating eggs in the nest, or defending the nest and eggs against usurpation, parasitic egg fertilizations or would-be egg predators (Kvarnemo, 1995; Lehtonen et al., 2018; Lindström & Pampoulie, 2005; Olsson, Kvarnemo, & Svensson, 2009). In addition, sand goby females are known to prefer males whose body size matches nesting resource size (Lehtonen et al., 2007). In the current study, a male's eagerness to initiate nest building was not associated with his body size. However, male size was positively associated with the level of nest elaboration (i.e. the amount of sand piled on top of the nest) when males were given the opportunity to choose between two resources of different sizes (but of the same architecture; experiment 2) but not when males were given the choice between two nesting resources differing in architecture but not size (experiment 1). Similarly, while some previous studies have found a positive correlation between male size and the extent of nest elaboration (Lehtonen et al., 2016), others have not (Svensson & Kvarnemo, 2005). Earlier findings also suggest that the association between male size and the level of nest elaboration may depend on ecological factors, such as water clarity (Lehtonen, Lindström, & Wong, 2015). Hence, together with these earlier findings, the current results suggest that the importance of male body size in nest-related behaviours is context dependent. More generally, small and large individuals may adopt different strategies when trying to maximize their reproductive payoffs (Blanckenhorn, 2000; Gross, 1996).

Nest architecture also matters: males more often chose an arched nesting resource than a flat resource of the same surface area. Interestingly, the popularity of the two resource types depended on nesting resource, but not male, size, with the flat option becoming more attractive with increasing resource size. We consider three mutually nonexclusive, ecologically relevant hypotheses for why sand goby males prefer arched resources. First, because the rim of an arched nesting resource extends higher above the substrate (Fig. 1), it may be more conspicuous (before being covered with sand) and act as a stronger stimulus to the male than a flat resource. However, a potential argument against this hypothesis is the finding that the popularity of the arched option decreased with resource size. A second potential reason why males prefer arched resources is that the arched shape may allow males to expend less time and energy in the initial phases of nest building. Third, as a marine species, sand gobies have evolved with access to arched mussel shells as nesting resources, whereas the use of flat stones in nesting is probably rare for populations of marine gobies, such as the sand goby, living outside the brackish Baltic Sea.

Notably, our conclusions were the same independent of whether we assessed popularity of an option as an actual choice (binary choice scenario) or as the time it took for a male to initiate nest building (no-choice scenario). Regarding the latter, when two nesting resources of the same type were offered, males initiated nest building quicker when the two resources were arched than when they were flat. Similarly, males not only chose the larger nesting resource of the two more often, but it also took less time for the focal male to initiate nest building (in experiment 2) when at least one large nesting resource was available. Moreover, males also took less time to initiate nest building (in experiment 1) when offered choices between larger nesting resources of the same size (i.e. they were quicker under M versus M and L versus L scenarios than under S versus S). Hence, the results suggest that, regarding nesting behaviour, binary choice and no-choice scenarios yielded consistent results. Thus, our findings highlight the utility of both methods in the study of choice decisions (see also e.g. Dougherty & Shuker, 2015; Kacelnik & Marsh, 2002).

We found limited evidence that the type of nesting resource occupied in the field affects subsequent nesting behaviour in the laboratory. In particular, prior nesting resource experience did not affect resource choice or eagerness to initiate nest building. We cannot rule out the possibility that the result was driven by the level of competition among males being different under laboratory and field conditions. In the field, each male claimed a nesting resource under a competitive situation and in the absence of a different resource option nearby, whereas in the laboratory, each male was alone in the choice arena. Nevertheless, when males chose between two arched nesting resources in the laboratory, those that had occupied a larger arched nesting resource in the field piled more sand on their nests (even when accounting for body size) than those that had occupied other types of nesting resources. In some species, prior experience has been found to affect key behaviours, such as aggression and mate choice (Hsu, Earley, & Wolf, 2006; Rosenqvist & Houde, 1997). Our results suggest that this may also be the case in the context of nest elaboration in sand gobies. It is also conceivable that, independent of prior experience, males that were able to invest more in nest elaboration (by displacing, and piling up, larger amounts of sand) were also more likely than other males to occupy a larger arched nesting resource in the field.

In conclusion, this study highlights the important relationship between male phenotype and nesting behaviour. Interestingly, the importance of male size was found to be context dependent, varying with respect to the available resources and the specific nesting behaviour being assessed. Indeed, besides uncovering the role of nest architecture, our findings provide methodological insights relevant to studies of resource choice and nesting behaviours, with no-choice and binary resource choice scenarios yielding consistent results regarding male preferences for resource size and architecture. This was underscored, for instance, by males not only choosing an arched over a flat nesting resource when both types were available, but also initiating nest building quicker when they had access to an arched resource. Overall, our findings show how key reproductive behaviours, resource choice and nesting behaviour, can be affected by the attributes of both the nest builder (body size) and the resource (size and architecture).

Declaration of Interest

The authors declare no competing interests.

Acknowledgments

We thank the staff of Tvärminne Zoological Station for logistic assistance, the School of Biological Sciences at Monash University for financial support and two anonymous referees for their helpful comments.

Supplementary Material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.anbehav.2020.06.001.

References

Alonzo, S. H. (2004). Uncertainty in territory quality affects the benefits of usurpation in a Mediterranean wrasse. *Behavioral Ecology, 15*, 278–285.

Barber, I. (2013). The evolutionary ecology of nest construction: Insight from recent fish studies. *Avian Biology Research, 6*, 83–98.

Bisazza, A., Marconato, A., & Marin, G. (1989). Male competition and female choice in *Padogobius martensi* (Pisces, Gobiidae). *Animal Behaviour, 38*, 406–413.

Blanckenhorn, W. U. (2000). The evolution of body size: What keeps organisms small? *The Quarterly Review of Biology, 75*, 385–407.

Bult, A., & Lynch, C. B. (1997). Nesting and fitness: Lifetime reproductive success in house mice bidirectionally selected for thermoregulatory nest-building behavior. *Behavior Genetics, 2*, 231–240.

Burton, N. H. K. (2006). Nest orientation and hatching success in the tree pipit *Anthus trivialis*. *Journal of Avian Biology, 37*, 312–317.

Byrne, P. G., & Keogh, J. S. (2009). Extreme sequential polyandry insures against nest failure in a frog. *Proceedings of the Royal Society B: Biological Sciences, 276*, 115–120.

Cresswell, W. (1997). Nest predation rates and nest detectability in different stages of breeding in blackbirds *Turdus merula*. *Journal of Avian Biology, 28*, 296–302.

Danylchuk, A. J., & Fox, M. G. (1996). Size- and age-related variation in the seasonal timing of nesting activity, nest characteristics, and female choice of parental male pumpkinseed sunfish (*Lepomis gibbosus*). *Canadian Journal of Zoology, 74*, 1834–1840.

Dougherty, L. R., & Shuker, D. M. (2015). The effect of experimental design on the measurement of mate choice: A meta-analysis. *Behavioral Ecology, 26*, 311–319.

Eckerle, K. P., & Thompson, C. F. (2006). Mate choice in house wrens: Nest cavities trump male characteristics. *Behaviour, 143*, 253–271.

Fisher, R. J., & Wiebe, K. L. (2006). Nest site attributes and temporal patterns of northern flicker nest loss: Effects of predation and competition. *Oecologia, 147*, 744–753.

Flink, H., & Svensson, P. A. (2015). Nest size preferences and aggression in sand gobies (*Pomatoschistus minutus*). *Behavioral Ecology and Sociobiology, 69*, 1519–1525.

Forsgren, E., Kvarnemo, C., & Lindström, K. (1996). Mode of sexual selection determined by resource abundance in two sand goby populations. *Evolution, 50*, 646–654.

Genner, M. J., Young, K. A., Haesler, M. P., & Joyce, D. A. (2008). Indirect mate choice, direct mate choice and species recognition in a bower-building cichlid fish lek. *Journal of Evolutionary Biology, 21*, 1387–1396.

Gross, M. R. (1996). Alternative reproductive strategies and tactics: Diversity within sexes. *Trends in Ecology & Evolution, 11*, 92–98.

Guillette, L. M., & Healy, S. D. (2015). Nest building, the forgotten behaviour. *Current Opinion in Behavioral Sciences, 6*, 90–96.

Hastings, P. A. (1988). Female choice and male reproductive success in the angel blenny, *Coralliozetus angelica* (Teleostei: Chaenopsidae). *Animal Behaviour, 36*, 115–124.

Healey, M. C. (1971). Gonad development and fecundity of the sand goby, *Gobius minutus* Pallas. *Transactions of the American Fisheries Society, 100*, 520–526.

Hoi, H., Schleicher, B., & Valera, F. (1994). Female mate choice and nest desertion in penduline tits, *Remiz pendulinus*: The importance of nest quality. *Animal Behaviour, 48*, 743–746.

Hsu, Y., Earley, R. L., & Wolf, L. L. (2006). Modulation of aggressive behaviour by fighting experience: Mechanisms and contest outcomes. *Biological Reviews, 81*, 33–74.

Järvi-Laturi, M., Lehtonen, T. K., Pampoulie, C., & Lindström, K. (2008). Parental care behaviour of sand gobies is determined by habitat related nest structure. *Behaviour, 145*, 39–50.

Japoshvili, B., Lehtonen, T. K., Wong, B. B. M., & Lindström, K. (2012). Repeatability of nest size choice and nest building in sand gobies. *Animal Behaviour, 84*, 913–917.

Johnson, L. S., & Searcy, W. A. (1993). Nest site quality, female mate choice, and polygyny in the house wren *Troglodytes aedon*. *Ethology, 95*, 265–277.

Kacelnik, A., & Marsh, B. (2002). Cost can increase preference in starlings. *Animal Behaviour, 63*, 245–250.

Kelly, C. D. (2008). The interrelationships between resource-holding potential, resource-value and reproductive success in territorial males: How much variation can we explain? *Behavioral Ecology and Sociobiology, 62*, 855–871.

Kvarnemo, C. (1995). Size-assortative nest choice in the absence of competition in males of the sand goby, *Pomatoschistus minutus*. *Environmental Biology of Fishes, 43*, 233–239.

Kvarnemo, C., Svensson, O., & Forsgren, E. (1998). Parental behaviour in relation to food availability in the common goby. *Animal Behaviour, 56*, 1285–1290.

Lagakos, S. W. (1979). General right censoring and its impact on the analysis of survival data. *Biometrics, 35*, 139–156.

Lehtonen, T., & Lindström, K. (2004). Changes in sexual selection resulting from novel habitat use in the sand goby. *Oikos, 104*, 327–335.

Lehtonen, T. K., Lindström, K., & Wong, B. B. M. (2013). Effects of egg predator on nest choice and nest construction in sand gobies. *Animal Behaviour, 86*, 867–871.

Lehtonen, T. K., Lindström, K., & Wong, B. B. M. (2015). Body size mediates social and environmental effects on nest building behaviour in a fish with paternal care. *Oecologia, 178*, 699–706.

Lehtonen, T. K., Rintakoski, S., & Lindström, K. (2007). Mate preference for multiple cues: Interplay between male and nest size in the sand goby, *Pomatoschistus minutus*. *Behavioral Ecology, 18*, 696–700.

Lehtonen, T. K., Vesakoski, O., Yli-Rosti, J., Saarinen, A., & Lindström, K. (2018). The impact of an invasive mud crab on brood success of nest-building fish in the Northern Baltic Sea. *Biological Invasions, 20*, 981–993.

Lehtonen, T. K., & Wong, B. B. M. (2009). Should females prefer males with elaborate nests? *Behavioral Ecology, 20*, 1015–1019.

Lehtonen, T. K., & Wong, B. B. M. (2020). Context-dependent resource choice in a nest-building fish. *Animal Behaviour, 166*, 297–303.

Lehtonen, T. K., Wong, B. B. M., & Kvarnemo, C. (2016). Effects of salinity on nest-building behaviour in a marine fish. *BMC Ecology, 16*, 7.

Lindström, K. (1988). Male-male competition for nest sites in the sand goby, *Pomatoschistus minutus*. *Oikos, 53*, 67–73.

Lindström, K. (1992). The effect of resource holding potential, nest size and information about resource quality on the outcome of intruder-owner conflicts in the sand goby. *Behavioral Ecology and Sociobiology, 30*, 53–58.

Lindström, K., & Lehtonen, T. K. (2013). Mate sampling and choosiness in the sand goby. *Proceedings of the Royal Society B: Biological Sciences, 280*, 20130983.

Lindström, K., & Pampoulie, C. (2005). Effects of resource holding potential and resource value on tenure at nest sites in sand gobies. *Behavioral Ecology, 16*, 70–74.

Lindström, K., & Ranta, E. (1992). Predation by birds affects structure of breeding population in male sand gobies, *Pomatoschistus minutus*. *Oikos, 64*, 527–532.

Mayer, P. M., Smith, L. M., Ford, R. G., Watterson, D. C., McCutchen, M. D., & Ryan, M. R. (2009). Nest construction by a ground-nesting bird represents a potential trade-off between egg crypticity and thermoregulation. *Oecologia, 159*, 893–901.

Merkouriadi, I., & Leppäranta, M. (2015). Influence of sea ice on the seasonal variability of hydrography and heat content in Tvärminne, Gulf of Finland. *Annals of Glaciology, 56*, 274–284.

Östlund, & Nilsson, S. (2001). Fifteen-spined stickleback (*Spinachia spinachia*) females prefer males with more secretional threads in their nests: An honest-condition display by males. *Behavioral Ecology and Sociobiology, 50*, 263–269.

Olsson, K. H., Kvarnemo, C., & Svensson, O. (2009). Relative costs of courtship behaviours in nest-building sand gobies. *Animal Behaviour, 77*, 541–546.

Quader, S. (2006). What makes a good nest? Benefits of nest choice to female Baya weavers (*Ploceus philippinus*). *The Auk: Ornithological Advances, 123*, 475–486.

Raventos, N. (2006). Nest site characteristics and nesting success of the five-spotted wrasse *Symphodus roissali* in the north-western Mediterranean Sea. *Journal of Fish Biology, 68*, 305–309.

Rosenqvist, G., & Houde, A. (1997). Prior exposure to male phenotypes influences mate choice in the guppy, *Poecilia reticulata*. *Behavioral Ecology, 8*, 194–198.

Schaedelin, F. C., & Taborsky, M. (2009). Extended phenotypes as signals. *Biological Reviews, 84*, 293–313.

Soler, J. J., Martín-Vivaldi, M., Haussy, C., & Møller, A. P. (2007). Intra- and interspecific relationships between nest size and immunity. *Behavioral Ecology, 18*, 781–791.

Svensson, O., & Kvarnemo, C. (2003). Sexually selected nest-building–*Pomatoschistus minutus* males build smaller nest openings in the presence of sneaker males. *Journal of Evolutionary Biology, 16*, 896–902.

Svensson, O., & Kvarnemo, C. (2005). The importance of sperm competition risk and nest appearance for male behavior and female choice in the sand goby, *Pomatoschistus minutus*. *Behavioral Ecology, 16*, 1042–1048.

Takahashi, D., & Kohda, M. (2002). Female preference for nest size in the stream goby *Rhinogobius* sp DA. *Zoological Science, 19*, 1241–1244.

Takahashi, D., Kohda, M., & Yanagisawa, Y. (2001). Male–male competition for large nests as a determinant of male mating success in a Japanese stream goby, *Rhinogobius* sp. DA. *Ichthyological Research, 48*, 91–95.
Takegaki, T., & Nakazono, A. (2000). The role of mounds in promoting water-exchange in the eggtending burrows of monogamous goby, *Valenciennea longipinnis* (Lay et Bennett). *Journal of Experimental Marine Biology and Ecology, 253*, 149–163.
Uglem, I., & Rosenqvist, G. (2002). Nest building and mating in relation to male size in corkwing wrasse, *Symphodus melops*. *Environmental Biology of Fishes, 63*, 17–25.
Weidinger, K. (2002). Interactive effects of concealment, parental behaviour and predators on the survival of open passerine nests. *Journal of Animal Ecology, 71*, 424–437.
Wong, B. B. M., Lehtonen, T. K., & Lindström, K. (2008). Male nest choice in sand gobies, *Pomatoschistus minutus*. *Ethology, 114*, 575–581.
Wong, B. B. M., Lehtonen, T. K., & Lindström, K. (2018). Spatial and temporal patterns of nest distribution influence sexual selection in a marine fish. *Oikos, 127*, 1104–1112.