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BEHAVIORAL ECOLOGY - ORIGINAL RESEARCH

Body size mediates social and environmental effects on nest building behaviour in a fish with paternal care

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Abstract Body size, social setting, and the physical environment can all influence reproductive behaviours, but their interactions are not well understood. Here, we investigated how male body size, male–male competition, and water turbidity influence nest-building behaviour in the sand goby (*Pomatoschistus minutus*), a marine fish with exclusive paternal care. We found that environmental and social factors affected the nest characteristics of small and large males differently. In particular, association between male size and the level of nest elaboration (i.e. the amount of sand piled on top of the nest) was positive only under clear water conditions. Similarly, male size and nest entrance size were positively associated only in the absence of competition. Such interactions may, in turn, help to explain the persistence of variation in reproductive behaviours, which—due to their importance in offspring survival—are otherwise expected to be under strong balancing selection.

Keywords Body size · Eutrophication · Interference competition · Nesting environment · Parental care

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Introduction

An individual's 'optimal' reproductive strategy is likely to depend on myriad social and environmental factors (Schaffer 1974; Gross 1996) which are expected to affect different individuals differently. Indeed, it is becoming increasingly apparent that variation in individual responses to the physical and social environment could be adaptive (Wolf et al. 2008; McNamara et al. 2009; Dingemanse et al. 2010; Dingemanse and Wolf 2013), with individuals adjusting their behaviours in different ways depending on environmental context. Environmental effects, in this regard, are also pertinent for species with parental care (Carlisle 1982), especially when eggs or young are reared in purpose-built nests (Eggers et al. 2006; Suski and Ridgway 2007; Byrne and Keogh 2009).

For males, proximity to rivals is a fundamental component of an individual's social environment. Intraspecific competition is closely linked to male reproductive success (Berglund et al. 1996), with evidence showing that variation in the competitive setting can affect the relative success of different types of males (Andersson 1994). Such effects can also be highly sensitive to the physical environment (including any changes that might take place). For instance, in three-spined sticklebacks (*Gasterosteus aculeatus*), male aggression has been found to be sensitive to water depth (Lachance and FitzGerald 1992)—and hence presumably water clarity—with decreased visibility from algal blooms compromising the reliability of sexual signals that are otherwise kept honest by male–male interactions (Wong et al. 2007).

By having profound effects on reproductive outcomes, male body size can play an especially important role in mediating the response of individuals to social and environmental conditions. Large body size commonly enhances male reproductive success in a wide range of taxa, from amphipods (Wellborn 1995) and butterflies (Wiklund and Kaitala 1995) to fishes (Sabat 1994; Johnson and Hixon 2011), snakes (Shine 2003) and mammals (Modig 1996). Although smaller males can, under certain conditions, have a reproductive advantage over larger rivals (Bisazza and Pilastro 1997; Blanckenhorn 2000), often they must resort to alternative behavioural strategies to maximise their chances of success (Gross 1996). For instance, in the European adder (*Vipera berus*), small males avoid aggressive encounters with larger males and court females only when larger males are absent (Madsen et al. 1993). Similarly, reproductive activity in fathead minnows (*Pimephales promelas*) is mediated by size-dependent social status, with small males holding territories—and spawning earlier—when large, dominant rivals were absent (Danylchuk and Tonn 2001). Yet, despite such examples, most of what we currently know about interactions between body size, social setting, and the physical environment has come from studies of species with size-based alternative reproductive phenotypes (e.g. Atlantic salmon, *Salmo salar*; Aubin-Horth and Dodson 2004). Less, by contrast, is known about the influence of these factors on species with more flexible, opportunistic male reproductive strategies.

The sand goby (*Pomatoschistus minutus*) is an ideal species for assessing variation in male nest-building behaviour in response to the immediate social and physical environment. Males of this sexually dimorphic fish species compete for access to empty mussel shells or flat rocks (Lehtonen and Lindström 2004; Wong et al. 2008). If successful, the male builds up a nest by piling sand on top of, and excavating under, the resource, leaving a single narrow nest-opening. After courting females in close proximity to his nest where spawning takes place, the male takes exclusive care of the eggs by cleaning and fanning the developing embryos and defending the brood against egg predators (Chin-Baarstad et al. 2009). Previous studies have shown that nest-holding males are sensitive to their surrounding environment and will adjust the architecture of their nests in response to, for example, the presence of sneaker males (Svensson and Kvarnemo 2003). Environmental factors have also been shown to influence the cost of male egg-care behaviour, with males modifying the amount of care they provide to offspring in response to habitat-related differences in nest structure (Järvi-Laturi et al. 2008) and differences in oxygen levels associated with algal blooms (Järvenpää and Lindström 2011). Finally, male body size is likely to be important to the success of any given strategy (Wong et al. 2009; Lehtonen et al. 2013). In this regard, sand gobies are known to exhibit considerable variation in male body size, both within and between years (Lehtonen et al. 2010). In terms of nest building, moving and piling large volumes of sand on top of the nest should be less costly for large males, which are also better at defending their nest from competitors (Lindström and Pampoulie 2005). Smaller males, by contrast, are more likely to (but do not always) engage in sneaker strategies (Svensson and Kvarnemo 2005).

In this study, we used the sand goby to assess (1) whether nest-building behaviour is sensitive to the presence of a competitor (social environment), algae-induced water turbidity (an important aspect of the physical environment), and their potential interactive effects; and (2) whether small and large males respond differently to these environmental effects. We predict that nest building behaviour of sand goby males should not only be sensitive to environmental and social factors but also that competitive and turbid conditions could be taxing to nest-building males, potentially decreasing male investment in nest-building effort. Moreover, if the effects of the social and physical environment differ depending on the size of individuals, we might expect to see this reflected in differences in the nest-building behaviour of small and large males.

Materials and methods

Collecting and housing

The experiment was conducted at the Tvärminne Zoological Station, southern Finland (59°50.7′N, 23°15.0′E), in late May–June, 2010. Male sand gobies were collected using dip nets and transported back to the station (max. 30-min boat trip) in 50-l coolers at a density of approximately 60 fish per cooler. At the station, the males were housed in stock tanks (ca. 100 l), at a density of approximately 10–30 fish per tank. Before the experiments, fish were fed twice a day with either live mysid shrimp or (when live shrimp were not available) frozen chironomid larvae. Males used in the study were all sexually-mature, ready-to-breed individuals (identified by the presence of coloured ventral fins).

Experimental procedure

Experimental replicates were carried out in tanks measuring (length × width) 50 × 30 cm, with a 4-cm layer of fine sand on the bottom. A ceramic tile measuring 10 × 10 cm was placed in the middle of the tank on top of the substrate as a nesting resource. Depending on treatment, tanks were filled to a depth of approximately 25 cm with either clear seawater (replicates: $n = 26$; tanks: $n = 66$) or water containing a non-toxic flagellate algae (*Isochrysis* sp.) (replicates: $n = 26$; tanks: $n = 64$). The latter is a naturally-occurring member of the local phytoplankton community (Heuschele et al. 2009) and was used to simulate an ecologically-relevant change to the physical environment caused by the frequent algal blooms that occur in the Baltic during

Table 1 Hierarchical model simplification procedure for the two response variables describing nest characteristics of the sand goby (*Pomatoschistus minutus*)

Predictor variable	Response variable							
	Sand on top (square-root transformed)				Nest entrance area			
	Order	X^2	*df*	*P*	Order	X^2	*df*	*P*
Competition:turbidity:weight	1	0.428	1	0.51	1	0.181	1	0.67
Competition:turbidity	2	0.383	1	0.53	2	0.021	1	0.88
Competition:weight	3	1.95	1	0.16	4	4.37	1	0.037
Turbidity:weight	4	4.02	1	0.045	3	1.69	1	0.19

the sand gobies' breeding season. For the turbidity treatment, the algae–seawater mixture was prepared according to previously published methods (e.g. Wong et al. 2007; Järvenpää and Lindström 2011). Turbidity levels, measured with a Hach 2100P portable nephelometer immediately before and after the start of each replicate, were significantly higher in tanks containing algae (median turbidity before the start of replicate: 6.29 NTU, range 2.71–9.29 NTU; after: 5.25 NTU, range 2.42–15.9) compared to those without (median turbidity before the start of replicate: 1.14 NTU, range 0.47–2.95 NTU; after: 1.07 NTU, range 0.34–3.01 NTU) (Mann–Whitney *U* test, before: $U_{66,64} = 4$, $P < 0.001$; after: $U_{66,64} = 1$, $P < 0.001$). These turbidity values are well within the range observed in the Baltic Sea (Granqvist and Mattila 2004).

Both in the presence and absence of algae, males (mean body mass ± SD 1.21 ± 0.13 g; range 0.69–1.53 g; $n = 104$) were given an opportunity to build a nest when they were on their own and when they were in the presence of a competitor. To achieve this, each male was haphazardly paired with another, so that size difference between the males in a pair was 1–3 mm (to help with identification). In half of the replicates ($n = 26$) both males in each pair were first tested on their own. Twenty-four hours after nest attributes of both males had been measured (see below), males were tested again in a separate experimental tank, this time in the presence of its rival. In the remaining replicates ($n = 26$), the order of testing was reversed (i.e. males were first tested in the presence of its rival, followed by a 24-h break, before being tested alone). Because only a single nesting resource (i.e. tile) was provided, when tested in each other's presence, males had to compete with each other before nest building could take place. Tanks were checked every 8 h (at 0600, 1400 and 2200 hours) for signs of nest building (i.e. sand piled on top of, and excavation under, the tile) (Japoshvili et al. 2012). After the first signs of nest building, males were left in the tank for another 24 h to complete their nests. After this time, we measured the size of the nest opening and quantified the level of nest elaboration by quantifying the amount of sand piled on top of the nesting resource (Japoshvili et al. 2012). To measure the size of the nest opening, we took a digital photo of the entrance, with a ruler placed next to the entrance for scale. The area of the nest opening was then measured using the image analysis software Image J, using the ruler in the image for calibration (Japoshvili et al. 2012). To measure the amount of sand the males had piled on top of their tile, we carefully collected the sand by lifting the tile into a tray, and then drying the sand that was collected from the top of the tile in an oven for 36 h at 60 °C. The dry weight of the sand was then measured. The males were either retained for use in other, unrelated behavioural experiments or returned back to the sea.

Design and statistical analyses

In accordance to the above, our experimental design included two treatment categories: (1) water quality with two treatment levels, clear and turbid water, and (2) nesting site competition with two treatment levels, no competition and competition. Because our purpose was to expose all males to both the no competition and competition treatment levels, we employed a paired design: only males that built a nest both in the absence and presence of a competitor were included ($n = 22$ clear and $n = 22$ turbid replicates). Three nest entrance areas (2 without competition, 1 with competition) could not be included in analyses due to missing values. The amount of sand piled on top of the nest and nest entrance area were analysed in two separate Linear Mixed Models using R software (R Development Core Team, Vienna, Austria), with male ID treated as a random factor to take into account the paired design (Crawley 2005). In both sets of models, competition treatment, turbidity treatment, and body mass (as a proxy of body size) were included as fixed explanatory variables. Both models were simplified by hierarchic removal of non-significant interaction terms (Table 1).

Results

Males piled 56 ± 40 g ($n = 88$) of sand on their nests, while entrances of the nests had an area of 1.28 ± 0.52 cm^2 ($n = 85$). When males were competing for the single nest

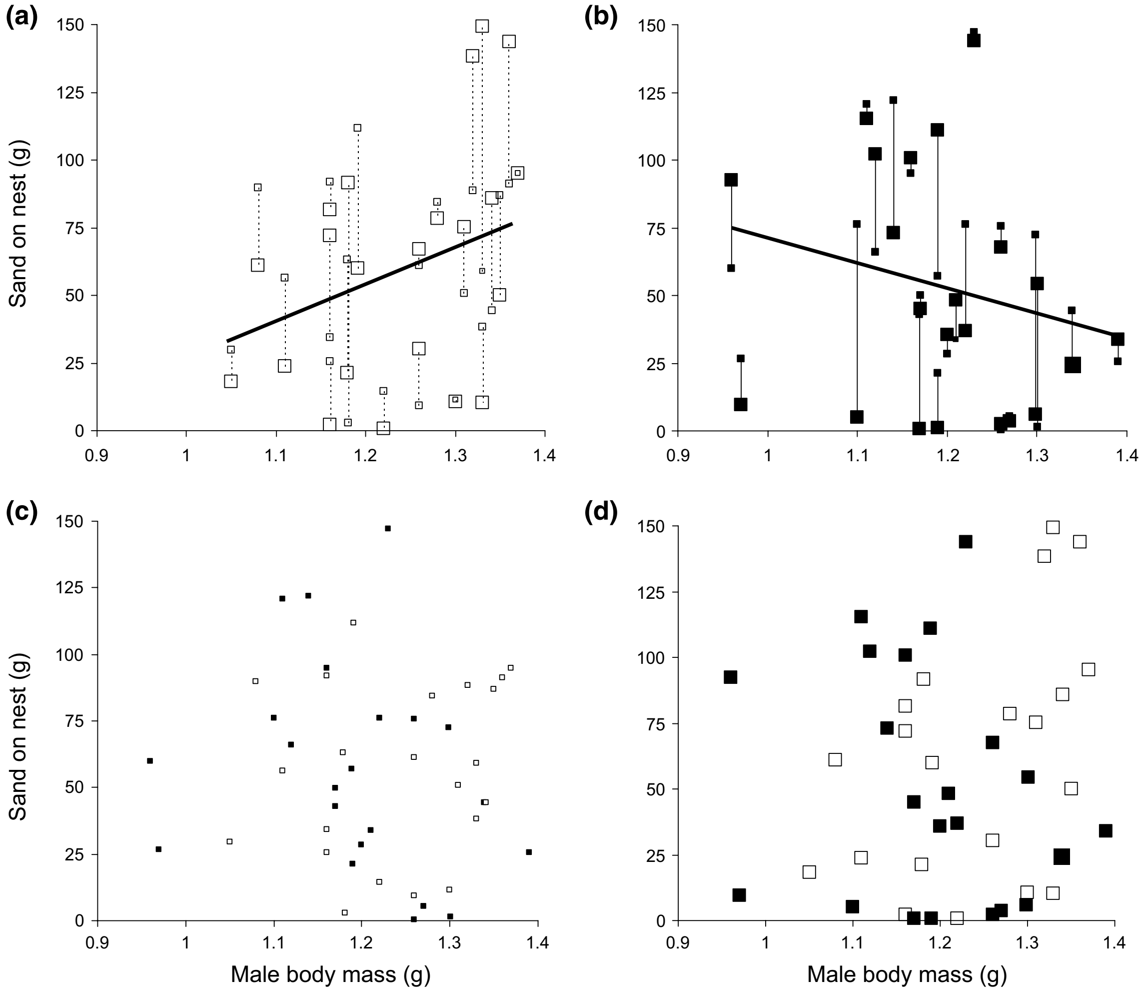

Fig. 1 The amount of sand piled on top of the nest of the sand goby (*Pomatoschistus minutus*) when the nest-builder was **a** in clear water ($n = 22$), **b** in turbid water ($n = 22$), **c** on his own ($n = 44$) and **d** in the presence of a competitor ($n = 44$). Observations for the same nest-builder are connected with a vertical line. *White box* clear water, *black box* turbid water, *small box* male on his own, *large box* male in the presence of a competitor. The *trend lines* illustrate a significant interaction between male body mass and turbidity treatment and have been calculated using the average of the two values for each nest-builder

site, the larger of the two males in a pair claimed the nest in 28 of 44 replicates (binomial test, $P = 0.096$).

There was a significant interaction between turbidity and male body mass on the amount of sand piled on top of the nest (Table 1). Male body mass tended to be positively correlated with the weight of sand piled on top of the nest in clear water (parametric correlation, $r_{20} = 0.382$, $P = 0.079$) (Fig. 1a), whereas the association was negative (albeit not significantly so) in turbid water (parametric correlation, $r_{20} = -0.252$, $P = 0.26$) (Fig. 1b). Competition did not have a significant effect on the amount of sand males piled on top of their nest (Linear mixed model, competition effect, $t_{43} = 0.668$, $P = 0.51$) (Fig. 1).

The area of the nest entrance was positively associated with male size when males were alone (no competition) (parametric correlation, $r_{40} = 0.361$, $P = 0.019$) (Fig. 2c), whereas this was not the case in the presence of a competitor (parametric correlation, $r_{41} = 0.017$, $P = 0.91$) (Table 1). Water turbidity did not have a significant effect on the size of the nest-opening (Linear mixed model, turbidity effect, $t_{41} = 0.798$, $P = 0.43$) (Fig. 2).

Discussion

We found support for our prediction that environmental and social factors influence nest-building behaviour in male sand gobies. Moreover, the presence of microalgae and a competitor had different effects on nest building by small and large males. Specifically, male size was positively associated with the amount of sand the males used for covering their nests in clear but not turbid water. Male size was also

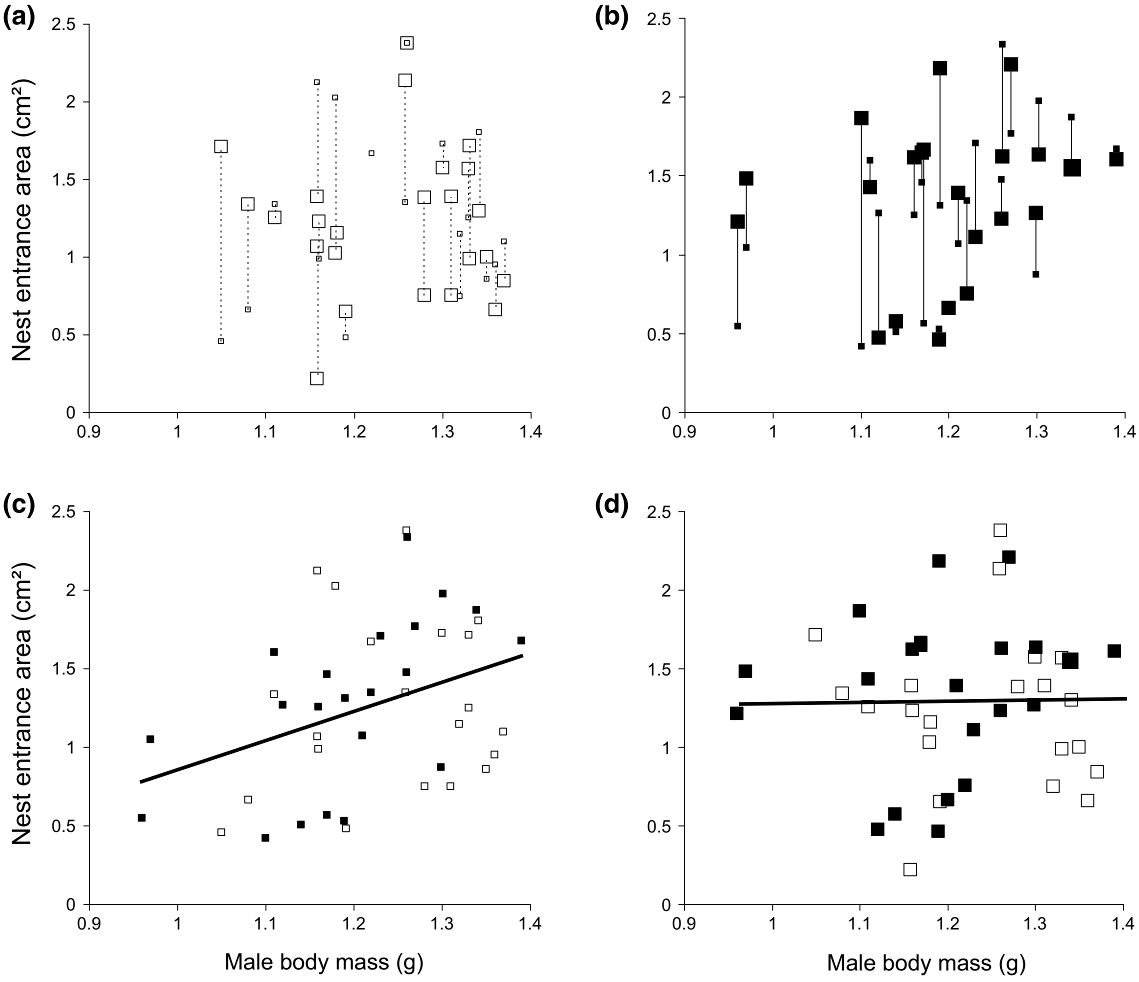

Fig. 2 The area of the nest entrance when the nest-builder was **a** in clear water ($n = 22$), **b** in turbid water ($n = 22$), **c** on his own ($n = 42$) and **d** in the presence of a competitor ($n = 43$). Observations for the same nest-builder are connected with a vertical line. *White box* clear water, *black box* turbid water, *small box* male on his own, *large box* male in the presence of a competitor. The *trend lines* illustrate a significant interaction between male body mass and competition treatment

positively associated with nest-entrance size when males built their nests alone, whereas this was not the case in the competitive environment. Such results are concordant with recent evidence suggesting that small and large males also respond differently to predation threat in a reproductive context: large males boost their nest-building effort relative to small males in response to egg-predators (Lehtonen et al. 2013), while predation risk on adult gobies shifts spawning latency in favour of larger males (Wong et al. 2009). Together, these findings suggest that environmental factors can have varied effects on reproductive behaviours depending on male size.

So why should selection favour differences in the tactics of small and large males in relation to the social and physical environment? One possibility is that costs associated with the presence of a competitor depend on the size of the nest holder. In fish, male parental expenditure and investment are sometimes size-dependent (Sabat 1994; Wiegmann and Baylis 1995), with large males often being better at defending their nests against aggressive nest-takeovers compared to smaller individuals (e.g. Bisazza and Marconato 1988). Sand gobies are no exception: in an experimental manipulation of resource holding potential in the field, Lindström and Pampoulie (2005) found that larger sand goby males are able to hold onto their nests for longer, whereas small nest owners are at greater risk of being displaced by larger intruders. In this regard, an increase in the number of visits in and out of the nest when interacting with the competitor (resulting in a wider nest entrance) could explain why smaller males had relatively wider nest entrances in the competition treatment. Such a higher investment in male–male interactions could also be coupled with a decreased time investment in keeping the nest entrance tidy. Large males, by contrast, may be less affected by a competitor's presence (Lindström and Pampoulie 2005) and, instead, rely upon the positional advantage gained by staying in the nest (see Jennions and Backwell 1996).

Another factor that could help explain our results is that body size may influence environmental optima for engaging in alternative reproductive tactics (i.e. sneaking). We know that large and small males differ in their overall proclivity to engage in sneaking behaviour, which, in turn, could have consequences for nest architecture (Svensson and Kvarnemo 2003). For instance, Svensson and Kvarnemo (2003) showed that sand goby males adjust their nest entrances in response to the presence of sneakers as an apparent defence against lost fertilisations. Importantly, recent evidence in another species of fish, the three-spined stickleback, demonstrated that the success of such a strategy can potentially vary with algae-induced water turbidity (Vlieger and Candolin 2009), which in the context of our study, may explain different responses of large and small males under clear versus turbid conditions. In particular, a greater shift by large males from nest maintenance to the sneaking strategy in turbid water could result in the decreased elaboration of their nests under turbid conditions. Furthermore, algal turbidity has been found to result in a decreased investment in at least some parental activities (Järvenpää and Lindström 2011). A stronger such pattern in large males (and possibly even a reversal in small ones) could result in the observed, turbidity-driven shifts in nest elaboration by large versus small males.

Finally, we cannot exclude a link between female mate preferences and differences in nest-building activity between large and small males. Nest characteristics are often believed to act as extended phenotypic signals that reveal important information about the quality of the builder (reviewed in Schaedelin and Taborsky 2009). Previous studies show that in sand gobies both nesting resources per se, as well as the way the nest has been built, can play an important role in female choice (Svensson and Kvarnemo 2005, Lehtonen et al. 2007). For instance, sand goby females discriminate against large males occupying small nesting resources (Lehtonen et al. 2007). Although all nesting resources in the current study were of the same size (10 × 10 cm), the attractiveness of small and large males may have been affected differently by the way the nests were built. Sensitivity of such size-dependent attractiveness differences in relation to the physical or social context (as suggested by our earlier work: Lehtonen and Lindström 2009; Lehtonen et al. 2010) could help to explain why nest architecture of small and large males responded differently to social and environmental context.

Interestingly, not all aspects of nest building were similarly sensitive to the same environmental conditions. Although sand coverage of the nest responded to water turbidity (with small and large males responding differently), nest entrance size did not. Meanwhile, nest entrance size—but not sand coverage—was adjusted to the competitive environment (in a body size-dependent fashion). The reason(s) for these differences are unknown and warrant further investigation. Nonetheless, the complexity of the responses by small and large males could underlie the persistence of high variation in reproduction-related behaviours, such as nest building, which are thought to be under strong balancing selection due to their importance to offspring survival (Rudolf and Rödel 2005; Jensen et al. 2009: Reedy et al. 2013). Similarly, the different responses by small and large males to changes in local physical or social conditions could offer at least a partial explanation for the temporal fluctuations in the relationship between male and nest characteristics, observed at the population level (Lehtonen and Wong 2009).

In conclusion, consistent with recent theoretical and empirical predictions suggesting that individuals within a population may exhibit adaptive variation in their responses to their environment (Wolf et al. 2008; McNamara et al. 2009; Dingemanse et al. 2010; Dingemanse and Wolf 2013), we have shown here that body size can be important in mediating the response of individuals to social and environmental conditions. In particular, we have revealed size-dependent responses in the context of nest building, a behaviour that is closely related to the fitness of offspring. Finally, the results show that not all aspects of nest-building are sensitive to the same environmental factors, helping to explain the persistence of variation in reproductive behaviours, which are otherwise expected to be under strong balancing selection due to their importance in offspring survival.

Author contribution statement BBMW, TKL and KL conceived the experiments. TKL and BBMW performed the experiments. TKL analyzed the data. TKL and BBMW wrote the manuscript with KL providing edits and advice.

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Conflict of interest The authors declare that they have no conflict of interest.

Ethical standard All applicable national guidelines for the care and use of animals were followed. The experimental procedures were approved by ELLA—the National Animal Experiment Board of Finland.

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