



## Repeatability of nest size choice and nest building in sand gobies

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To be useful as mate choice cues, behavioural traits have to be performed consistently within individuals. This may also be true for nest construction, which, in addition to influencing offspring survival, can also function as an extended phenotype of the builder. We tested whether choice of a nesting resource and subsequent nest-building performance are repeatable traits in the sand goby, *Pomatoschistus minutus*, a small marine fish with paternal egg care and female mating preferences that are influenced by male nest-building behaviour. When given a choice between three different-sized nesting resources (flowerpots), males, on average, preferred medium-sized nesting resources, with larger males preferring larger nests than smaller individuals. At the individual level, the choice of nesting resources was so variable between consecutive trials that choice behaviour was not repeatable. Furthermore, nest building, measured as the amount of sand piled on top of the nesting resource, was highly repeatable when males were free to choose their nest, but had only a low repeatability when males had just a single option. In neither case was the size of the nest entrance repeatable between consecutive rounds of nest building. These results highlight the context-dependent signal value of extended phenotypes. In particular, reliability of nest-building behaviour as a signal seems to be influenced by the male's opportunity to choose the object it uses for nesting.

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Many species build nests to provide protection for developing eggs or juveniles (Hansell 2005). Nest characteristics (such as its location, size or general quality) can have important consequences for the reproductive success of parents (Canali et al. 1991; Lukas & Orth 1995; Petit et al. 2002; Gill et al. 2005). For example, well-constructed nests may decrease the risk of predation (Lindström & Ranta 1992) or make conditions more conducive to offspring development (Hostache & Mol 1998; Jones & Reynolds 1999; Takegaki & Nakazono 2000). Furthermore, in some taxa, the appearance of the nest itself may function as a mate choice cue by revealing important information about the quality (e.g. condition) of the builder (Kodric-Brown 1990; Hoi et al. 1994; Östlund-Nilsson & Holmlund 2003; Quader 2006). For example, in some passerines, the volume of nesting material collected by males is positively correlated with immune response (Soler et al. 2007). Likewise, in magpies, *Pica pica*, nest-building effort is known to function as a sexually selected trait that reveals important information regarding male parental quality (Soler et al. 2001).

If nest construction is important for egg or offspring survival, one might expect individuals to be relatively consistent in their nest-building effort. Similarly, if a nest's attributes reliably reflect the quality of its builder, we should expect consistent between-individual variation in nest-building behaviour. Surprisingly, however, only a handful of studies have explored within-individual consistency of nesting behaviours (Rushbrook et al. 2008; Olsson et al. 2009; Walsh et al. 2010). Notwithstanding this general lack of studies, a powerful approach for assessing the potential for genetic variation in such behaviour is to measure the consistency of nest building across successive nesting attempts under fixed environmental conditions. Data on the appearance of the nest structure can then be used to calculate the 'repeatability' ( $r$ ) of the behaviour (Boake 1989; Bell et al. 2009). Repeatability sets the upper limit of heritability and has been widely used to understand evolutionary processes. High repeatability values indicate that there are consistent differences between individuals (Falconer & Mackay 1996; Bell et al. 2009). When nest building can be regarded as an extended phenotype, it is often repeatedly expressed within a limited breeding season, providing opportunities for assessment of repeatability and, hence, potential for heritable variation (Rushbrook et al. 2008).

The sand goby, *Pomatoschistus minutus*, is a species in which males regularly build multiple nests within a single breeding season.

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To build a nest, a male needs to find and choose a suitable nesting resource, such as an empty mussel shell or flat rock (Lehtonen & Lindström 2004; Wong et al. 2008). There is extensive variation between different habitats and locations in terms of available nesting resources and, hence, opportunities for nest site choice without having to evict prior residents (Forsgren et al. 1996; Lehtonen & Lindström 2004). After acquiring a suitable nesting resource, the male piles sand on top of it and excavates under it, leaving a single narrow opening. After nest construction, the male uses intense courtship displays to attract females to spawn in the nest (Lehtonen 2012). Here, the acquisition of a nest of suitable size is likely to be important for male reproductive success (Lindström & Pampoulie 2005; Lindström et al. 2006; Lehtonen et al. 2007), as nest size determines the maximum number of clutches the male can receive (Lindström 1992a) and has also been shown to influence his attractiveness to females (Lehtonen et al. 2007). Similarly, the amount of sand the male piles on top of his nest may play an important role in female choice (Svensson & Kvarnemo 2005; Lehtonen & Lindström 2008), although whether nest quality is an honest signal of male condition in sand gobies remains contentious (Lehtonen & Wong 2009; Olsson et al. 2009). Indeed, to date, very little is known about the consistency of nest-building behaviour (i.e. nest choice, nest covering and nest construction) within males relative to the variation that is widely assumed to exist between individuals.

In this study, we experimentally investigated choice of nesting resources and nest construction, as well as the repeatability of these behaviours, in male sand gobies. If nest building is to be a potentially useful indicator of male quality for females (Olsson et al. 2009), we predicted that nest-building effort should be consistent within individuals but vary between males. We assessed both the amount of sand piled on the nest and the area of the nest opening, as both may influence the male's mating success (Kvarnemo et al. 1998; Svensson & Kvarnemo 2005; Lehtonen & Wong 2009; Olsson et al. 2009).

## METHODS

### *Fish Collection and Housing*

Our study was carried out during the sand goby breeding season between June and July 2010 at the Tvärminne Zoological Station in southern Finland (59°50'N, 23°15'E). Sand gobies were collected using dip nets and transported back to the field station. During the short (maximum 30 min) transport to the station, fish were kept in insulated 50-litre plastic tubs (coolers), filled with water to a depth of 30 cm. At the station, they were housed in several separate-sex aquaria (ca. 100 litres), each of which contained 10–30 individuals at a time. All aquaria were kept under natural light conditions and supplied with a continuous through flow of sea water. During housing, fish were fed twice a day with live mysid shrimp and frozen chironomid larvae ad libitum. All fish were released back to the sea at the completion of the study.

All animal experimentation in this study complies with the laws of Finland. The study procedures met the standards of 'ELLA—the National Animal Experiment Board' for noninvasive animal experiments.

### *Choice of Nesting Resource and its Repeatability*

To investigate male nest choice and the repeatability of nest construction, we offered male sand gobies a repeated choice between three different-sized flowerpots as a potential nesting resource. Males were randomly placed into individual aquaria measuring 68 × 25 cm and 30 cm high. The bottom of each tank was covered with a 4 cm layer of sand and contained the halved clay flowerpots

(4 cm, 6 cm and 10 cm diameter representing small, medium and large nesting resources). The three pots were randomly assigned to the left, right and centre of each tank, with their entrances facing the front of the aquarium. We checked tanks three times a day for signs of nest construction (the male excavating under, and piling sand on top of, a nest). Twenty-four hours after noting the start of nest-building activity, we recorded which of the pots the male was occupying and measured a number of nest attributes (see 'Repeatability of Nest Characteristics' below). In some replicates, more than one pot showed signs of nest-building activity. In such cases, we used the male's location inside the pot to determine which of the nesting resources he had ended up choosing. We then removed all three flowerpots from the aquarium, levelled the sand on the bottom of each tank and then reinstated the flowerpots (once again, randomly assigning each pot to the left, right and centre of the tank with their entrances facing the front). We then repeated the same procedure to measure the repeatability of male choice for the size of nesting resource and the quality of construction (see below). After the experiment, the males were measured using a ruler and an electronic balance. In total, 40 males (mean total length ± SD = 54.5 ± 4.5 mm, weight 1.22 ± 0.31 g) were each tested twice. Of these, 31 males built a nest in both rounds and were used in subsequent analyses. Here, the choice situation did not allow calculation of actual repeatability values *sensu* Becker (1984). Instead, we assessed whether the choices were significantly more repeatable than what would be expected if the choice behaviour was random.

### *Repeatability of Nest Characteristics*

Twenty-four hours after noting the start of nesting activity (see above), we measured the height of sand piled on top of the nest and the width of the nest entrance using a ruler. We also took a digital photograph of each nest entrance using a Canon PowerShot G5 digital camera, with a ruler placed next to the nest entrance as a scale. The scale was later used for calibrating the nest entrance area measurements in the image analysis software Image J (<http://rsbweb.nih.gov/ij/>).

To control for the possibility that a male's opportunity to choose between different-sized nesting resources influences nest-building effort, we also conducted a second experiment in which the size of the nesting resource was kept constant. The procedures were similar to that of the above experiment except that we now provided each tank with only one medium-sized halved clay flowerpot (diameter: 6 cm) in the middle of the tank. This experiment was successfully replicated with 23 fish (total length 52.4 ± 4.3 mm, weight 1.11 ± 0.24 g). However, nest measurements from both rounds (to calculate repeatability of nest characteristics) are available only for 21 individuals.

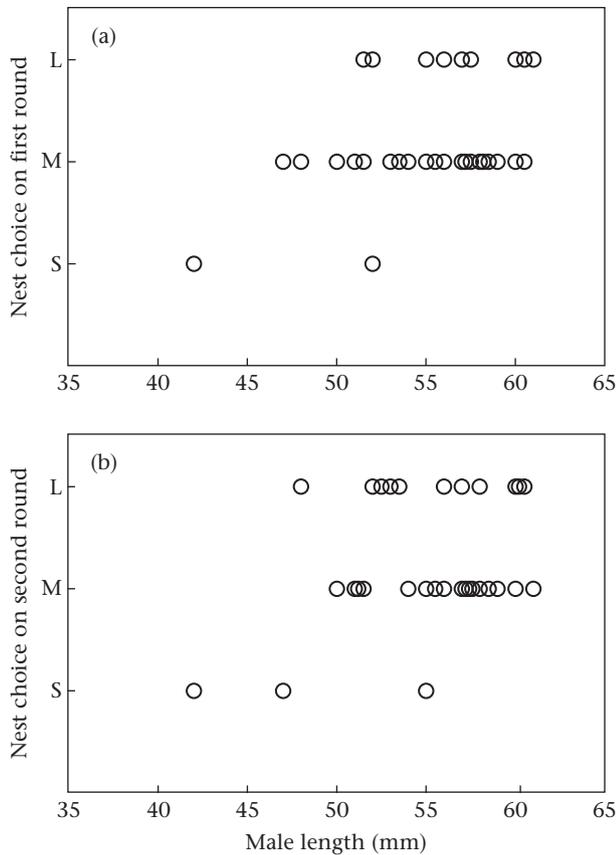
Here, we were able to calculate repeatability values (and their SEs and 95% confidence intervals) by using one-way ANOVAs to partition the total variance in nest building into the variance between and within males. In this regard, the ratio of the variance between males to the total observed variance gives an estimate of repeatability, as detailed in Becker (1984).

## RESULTS

### *Choice of Nesting Resource and its Repeatability*

Male size predicted the first nest size choice: bigger males chose, on average, bigger nests (multinomial logistic regression:  $\chi^2_2 = 7.43$ ,  $P = 0.024$ ; Fig. 1). Similarly, when choosing the second nest, bigger males chose bigger nests ( $\chi^2_2 = 7.56$ ,  $P = 0.023$ ; Fig. 1).

The nest size choices of the 31 goby males that built a nest on both rounds deviated from random on the first round (log-



**Figure 1.** The size distribution of males that chose small, S, medium-sized, M, and large, L, flowerpots in the experiment in which males were given a choice of nesting resource. (a) Nest choice during the first choice trial, and (b) nest choice during the second trial.

likelihood test:  $G_2^2 = 17.4$ ,  $P < 0.001$ ), with only two males choosing to build the small nest (indicating avoidance: binomial distribution:  $P = 0.001$ ), 20 males choosing the medium-sized nest (indicating preference: binomial distribution:  $P < 0.001$ ) and nine males building the large nest (indicating no deviation from random choice regarding this nest size: binomial distribution:  $P = 0.77$ ). The pattern of nest size choices of these males was similar also in the second round (log-likelihood test:  $G_2^2 = 10.9$ ,  $P = 0.004$ ) with three, 17 and 11 males choosing to build the small (binomial distribution:  $P = 0.005$ ), medium (binomial distribution:  $P = 0.022$ ) and large (binomial distribution:  $P = 0.93$ ) nest, respectively. On both rounds, the males chose randomly between the nests placed in the corners and middle of the tank (round 1: 23 nests in the corners and eight nests in the middle, binomial distribution assuming 1/3 as the expected probability for choosing the nest in the middle:  $P = 0.49$ ; round 2: 21 nests in the corners and 10 nests in the middle, binomial distribution:  $P = 1.0$ ). Finally, of these 31 males, 15 chose the same nest size on both rounds, whereas 16 chose a different nest size each time. This implies that there was no significant concordance ('repeatability') in nest size choice (assuming 1/3 as the probability for choosing the same nest size on both rounds if the second choice was independent of the first one, binomial distribution:  $P = 0.12$ ).

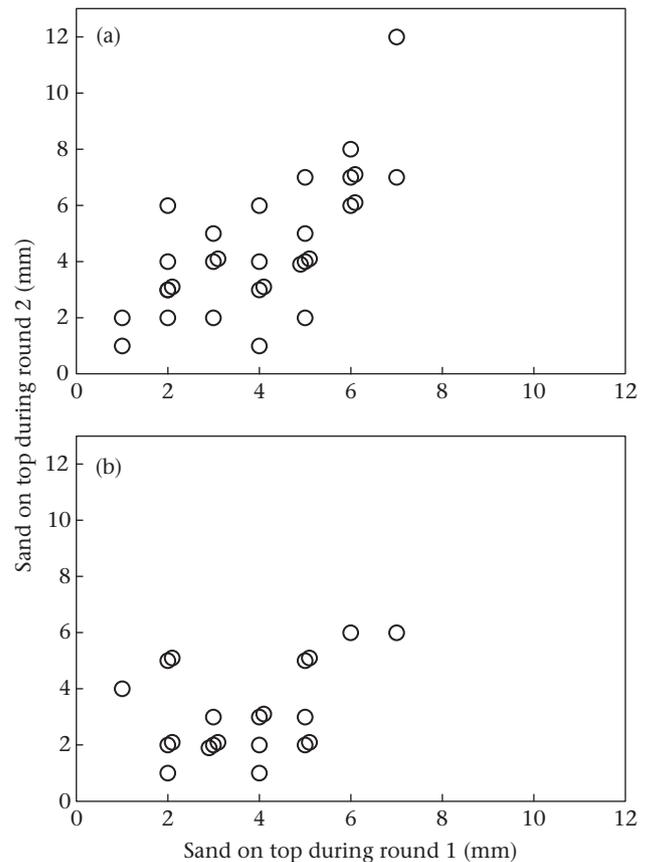
#### Repeatability of Nest Characteristics

The amount of sand the males piled on their nest had a high repeatability (the associated  $F = 4.73$ , repeatability  $r = 0.65$ ,  $SE = 0.11$ , 95% confidence interval = 0.39–0.82) in the first

experiment (i.e. the experiment in which they were free to choose between different-sized nests), and a repeatability of  $r = 0.35$  (the associated  $F = 2.06$ ,  $SE = 0.20$ , 95% confidence interval =  $-0.082$ – $0.67$ ) in the second experiment (Fig. 2). The width and area of the nest entrance showed no repeatability in the first (nest entrance width: the associated  $F = 1.11$ , repeatability  $r = 0.053$ ,  $SE = 0.19$ , 95% confidence interval =  $-0.30$ – $0.40$ ; nest entrance area: the associated  $F = 1.14$ , repeatability  $r = 0.065$ ,  $SE = 0.18$ , 95% confidence interval =  $-0.29$ – $0.41$ ) or the second experiment (width: the associated  $F = 1.01$ , repeatability  $r = 0.007$ ,  $SE = 0.22$ , 95% confidence interval =  $-0.41$ – $0.43$ ; area: the associated  $F = 1.14$ , repeatability  $r = 0.064$ ,  $SE = 0.23$ , 95% confidence interval =  $-0.37$ – $0.48$ ).

#### DISCUSSION

Theory predicts a relationship between body size and the quality (e.g. size) of the resource being defended (Dill 1978; Adams 2001). It has also been suggested that, at least in gobies, size-dependent costs and benefits of nest defence and maintenance should determine the size of the nest a male of a certain size should choose (Kvarnemo 1995; Björk & Kvarnemo 2012). In the current study, we found that, at the population level, male sand gobies preferred medium-sized nesting resources and larger males had a higher probability of choosing a larger resource. This is concordant with previous studies, which showed that body size can influence the choice of breeding site (Natsumeda 1998; Hendry et al. 2001), and male gobies, in particular, avoid smaller nesting



**Figure 2.** The depth of sand piled on the nest (halved clay pot) during the two rounds of nest building. (a) Results from the first experiment in which males were allowed to choose between pots of three different sizes. (b) Results from the second experiment in which only one medium-sized pot was provided.

resources in favour of either medium (Kvarnemo 1995; Wong et al. 2009) or larger nests (Lindström 1988). However, a lack of repeatability of choices within individuals suggests that there is considerable variation in choice of nesting resources. Currently, we do not have enough data to judge why exactly this is the case. We offer two hypotheses that could be tested in future studies.

The first factor that could help to explain the observed pattern is the intense competition for nest sites that commonly occurs in the study population. Indeed, when nest sites become available in the field, they are quickly colonized (Forsgren et al. 1996). The initial colonization is random with respect to male size, that is, there is no correlation between male size and nest size (Lindström 1988), but later on, a positive correlation appears between male and nest size because nest take-overs by larger intruder males occur more frequently in large than small nests (Lindström 1988, 1992b). Therefore, repeatability in the choice of nesting resources may be low when males have evolved to make their choice quickly, even in the face of a risk of frequent suboptimal choices. Second, it is possible that the first nesting attempt, which we made unsuccessful by levelling the sand, affected motivation or energy levels of the males, biasing their choices on the second round. Specifically, nest building is likely to be energetically demanding (Kvarnemo et al. 1998; but see Olsson et al. 2009), and changes in male condition or motivation can therefore influence their investment in any given nesting attempt (Lindström 1998; Olsson et al. 2009). Indeed, the high within-individual variation in nest choice appears consistent with the results of Lehtonen & Wong (2009). In that study, a positive relationship between the quality of field-constructed nests and the condition of the nest holders disappeared soon after initial nest colonization. Similarly, under laboratory conditions, nest appearance and male condition are not always correlated (Lehtonen & Wong 2009).

The costs and benefits associated with maintaining nests of different sizes (Kvarnemo 1995; Natsumeda 1998; Björk & Kvarnemo 2012) might also affect how a male invests in building the nest. A low-quality nest may be worth only a low investment and nest-building effort. In the experiment in which we gave males flowerpots of only one size, body size and/or nest maintenance ability of the focal male was more likely to be mismatched with the size of the nesting resource. This, in turn, could have contributed to a more variable, that is, less repeatable, nest-building effort. In contrast, when we gave males a choice of nest sizes, it is likely that they were in a better position to choose a size that best matched their current state, and therefore they also built in a highly repeatable manner.

Over our two experiments, repeatability for the amount of sand piled on top of the nest was 0.35–0.65, whereas the size of nest entrance was not repeatable ( $r = 0.007$ – $0.065$ ). These values are similar to those measured in a U.K. population of three-spined sticklebacks, *Gasterosteus aculeatus* ( $r = 0.066$ – $0.505$ , depending on how nest building was measured; Rushbrook et al. 2008). By comparison, the repeatability dimensions of male-built nests in African weaver birds varied between  $r = 0.06$  (NS) and  $r = 0.21$  (significantly repeatable) depending on species (Walsh et al. 2010). The repeatable aspects of nest-building effort (in our case, the amount of sand piled on the nest) suggest that a well-built nest may not only indicate direct benefits (see e.g. Lindström & Ranta 1992), but also has potential to signal benefits to females, by being a repeatable, extended feature of the male's phenotype (see e.g. Borgia 1995; Vahed 1998; Schaedelin & Taborsky 2006). Indeed, many studies have reported female preferences for males that construct nests with particular characteristics (Östlund-Nilsson 2001; Östlund-Nilsson & Holmlund 2003; Quader 2006). Similarly, there is evidence that nest cover could, at least under some circumstances (see Lehtonen & Wong 2009), be an honest signal of

male condition in sand gobies (Olsson et al. 2009), with males that top large volumes of sand on the nest being preferred by females (Svensson & Kvarnemo 2005; Lehtonen & Lindström 2009; Lehtonen et al. 2010).

In the sand goby, the repeatability of female preference varies between 0.503 and 0.756 depending on how it is measured (Lehtonen & Lindström 2008). Taken together with the current findings, these values suggest that, at least in sand gobies, both nest building in males and preferences in females could show an evolutionary response to selection. We offer two mechanisms that could explain why this variation has not been erased from the population by selection. First, traits that are subject to mate choice, such as nest construction, can be subject to environmental peculiarities (for example Cotton et al. 2006) and show considerable fluctuations between years (Lehtonen et al. 2010). Such variations in sexual selection could be related to, for example, population density (Kokko & Rankin 2006). Like other small fishes, the sand goby may be sensitive to low temperatures (Kamler 1992), and variations in the harshness of winters have been observed to cause large fluctuations in sand goby densities (Parmanne & Lindström 2003). Second, the importance of potential mate cues, such as nest characteristics, can be unstable even within a shorter time-scale. Indeed, although sand goby females usually prefer males with high nest-building investment (see above), Lehtonen & Wong (2009) showed that when nest-building skills and nest appearance are decoupled (for example as a consequence of a nest take-over), females do not prefer to spawn with males that had the largest amount of sand on their nests.

We found no consistency within males in the way they constructed the nest entrance. Previous studies have shown that males respond to environmental factors by adjusting nest entrance size. In the presence of sneaker males, nest-holding males construct smaller nest openings, probably to hamper the ability of sneakers to enter the nest and deposit sperm (Svensson & Kvarnemo 2003). Likewise, at low oxygen levels males maintain bigger nest openings to facilitate water exchange in the nest (Lissåker et al. 2003). Therefore it seems that there are several reasons why males should dynamically adjust nest entrance size, and thus a 'snapshot' of this trait cannot reflect male qualities directly or indirectly.

In conclusion, although larger sand goby males preferred larger nesting resources, within-individual variation was so extensive that nest choices of individual males did not indicate significant consistency in choice. An aspect of nest-building effort, the amount of sand on the top of the nest, had a high repeatability only when the males had been able to choose between nesting resources of different sizes. These results indicate that at least some aspects of nest building have a potential signal value, for example within the framework of mate choice. However, our results suggest that reliability of the signal may be context dependent, as we found significant consistency only when males had the opportunity to choose themselves a nesting resource suitable for them. Another important aspect of nest building, the size of the nest entrance, showed no repeatability. The reason could be that the nest entrance needs to be adjusted continually with respect to a number of external factors and therefore it will not provide reliable information about the builder.

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## References

- Adams, E. S. 2001. Approaches to the study of territory size and shape. *Annual Review of Ecology and Systematics*, **32**, 277–303, <http://dx.doi.org/10.1146/annurev.ecolsys.32.081501.114034>.
- Becker, W. A. 1984. *Manual of Quantitative Genetics*. 4th edn. Pullman, Washington: Academic Enterprises.
- Bell, A. M., Hankison, S. J. & Laskowski, K. L. 2009. The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, **77**, 771–783, <http://dx.doi.org/10.1016/j.anbehav.2008.12.022>.
- Björk, J. R. & Kvarnemo, C. 2012. Mechanisms behind size-assortative nest choice by sand goby males in the absence of intrasexual competition. *Animal Behaviour*, **83**, 55–62, <http://dx.doi.org/10.1016/j.anbehav.2011.09.033>.
- Boake, C. R. B. 1989. Repeatability: its role in evolutionary studies of mating behaviour. *Evolutionary Ecology*, **3**, 173–182, <http://dx.doi.org/10.1007/BF02270919>.
- Borgia, G. 1995. Why do bowerbirds build bowers? *American Scientist*, **83**, 542–547.
- Canali, E., Ferrante, V., Todeschini, R., Verga, M. & Carenzi, C. 1991. Rabbit nest construction and its relationship with litter development. *Applied Animal Behaviour Science*, **31**, 259–266, [http://dx.doi.org/10.1016/0168-1591\(91\)90010-U](http://dx.doi.org/10.1016/0168-1591(91)90010-U).
- Cotton, S., Small, J. & Pomiankowski, A. 2006. Sexual selection and condition-dependent mate preferences. *Current Biology*, **16**, R755–R765, <http://dx.doi.org/10.1016/j.cub.2006.08.022>.
- Dill, L. M. 1978. An energy-based model of optimal feeding-territory size. *Theoretical Population Biology*, **14**, 396–429, [http://dx.doi.org/10.1016/0040-5809\(78\)90016-3](http://dx.doi.org/10.1016/0040-5809(78)90016-3).
- Falconer, D. S. & Mackay, T. F. C. 1996. *Introduction to Quantitative Genetics*. 4th edn. Essex: Longman.
- Forsgren, E., Kvarnemo, C. & Lindström, K. 1996. Mode of sexual selection determined by resource abundance in two sand goby populations. *Evolution*, **50**, 646–654.
- Gill, S. A., Stutchbury, B. J. M. & Murphy, M. T. 2005. Nest building is an indicator of parental quality in the monogamous neotropical buff-breasted wren (*Thryothorus leucotis*). *The Auk*, **122**, 1169–1181, [http://dx.doi.org/10.1642/0004-8038\(2005\)122\[1169:NBIAIO\]2.0.CO;2](http://dx.doi.org/10.1642/0004-8038(2005)122[1169:NBIAIO]2.0.CO;2).
- Hansell, M. H. 2005. *Animal Architecture*. New York: Oxford University Press.
- Hendry, A. P., Berg, O. K. & Quinn, T. P. 2001. Breeding location choice in salmon: causes (habitat, competition, body size, energy stores) and consequences (life span, energy stores). *Oikos*, **93**, 407–418, <http://dx.doi.org/10.1034/j.1600-0706.2001.930306.x>.
- 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, <http://dx.doi.org/10.1006/anbe.1994.1296>.
- Hostache, G. & Mol, J. H. 1998. Reproductive biology of the neotropical armoured catfish *Hoplosternum littorale* (Siluriformes: Callichthyidae): a synthesis stressing the role of the floating bubble nest. *Aquatic Living Resources*, **11**, 173–185, [http://dx.doi.org/10.1016/S0990-7440\(98\)80114-9](http://dx.doi.org/10.1016/S0990-7440(98)80114-9).
- Jones, J. C. & Reynolds, J. D. 1999. The influence of oxygen stress on female choice for male nest structure in the common goby. *Animal Behaviour*, **57**, 189–196, <http://dx.doi.org/10.1006/anbe.1998.0940>.
- Kamler, E. 1992. *Early Life History of Fish: an Energetics Approach*. London: Chapman & Hall.
- Kodric-Brown, A. 1990. Mechanisms of sexual selection: insights from fishes. *Annales Zoologici Fennici*, **27**, 87–100.
- Kokko, H. & Rankin, D. J. 2006. Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Proceedings of the Royal Society B*, **361**, 319–334, <http://dx.doi.org/10.1098/rstb.2005.1784>.
- 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, <http://dx.doi.org/10.1007/BF00005855>.
- Kvarnemo, C., Svensson, O. & Forsgren, E. 1998. Parental behaviour in relation to food availability in the common goby. *Animal Behaviour*, **56**, 1285–1290, <http://dx.doi.org/10.1006/anbe.1998.0899>.
- Lehtonen, T. K. 2012. Signal value of male courtship effort in a fish with paternal care. *Animal Behaviour*, **83**, 1153–1161, <http://dx.doi.org/10.1016/j.anbehav.2012.01.040>.
- Lehtonen, T. & Lindström, K. 2004. Changes in sexual selection resulting from novel habitat use in the sand goby. *Oikos*, **104**, 327–335, <http://dx.doi.org/10.1111/j.0030-1299.2004.12489.x>.
- Lehtonen, T. K. & Lindström, K. 2008. Repeatability of mating preferences in the sand goby. *Animal Behaviour*, **75**, 55–61, <http://dx.doi.org/10.1016/j.anbehav.2007.04.011>.
- Lehtonen, T. K. & Lindström, K. 2009. Females decide whether size matters: plastic mate preferences tuned to the intensity of male–male competition. *Behavioral Ecology*, **20**, 195–199, <http://dx.doi.org/10.1093/beheco/arn134>.
- Lehtonen, T. K. & Wong, B. B. M. 2009. Should females prefer males with elaborate nests? *Behavioral Ecology*, **20**, 1015–1019, <http://dx.doi.org/10.1093/beheco/arp091>.
- 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, <http://dx.doi.org/10.1093/beheco/arm03>.
- Lehtonen, T. K., Wong, B. B. M. & Lindström, K. 2010. Fluctuating mate preferences in a marine fish. *Biology Letters*, **6**, 21–23, <http://dx.doi.org/10.1098/rsbl.2009.0558>.
- Lindström, K. 1988. Male–male competition for nest sites in the sand goby, *Pomatoschistus minutus*. *Oikos*, **53**, 67–73.
- Lindström, K. 1992a. Female spawning patterns and male mating success in the sand goby *Pomatoschistus minutus*. *Marine Biology*, **113**, 475–480, <http://dx.doi.org/10.1007/BF00349174>.
- Lindström, K. 1992b. 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, <http://dx.doi.org/10.1007/BF00168594>.
- Lindström, K. 1998. Energetic constraints on mating performance in the sand goby. *Behavioral Ecology*, **9**, 273–276, <http://dx.doi.org/10.1093/beheco/9.3.297>.
- 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, <http://dx.doi.org/10.1093/beheco/arlh132>.
- Lindström, K. & Ranta, E. 1992. Predation by birds affects structure of breeding population in male sand gobies, *Pomatoschistus minutus*. *Oikos*, **64**, 527–532.
- Lindström, K., St Mary, C. M. & Pampoulie, C. 2006. Sexual selection for male parental care in the sand goby, *Pomatoschistus minutus*. *Behavioral Ecology and Sociobiology*, **60**, 46–51, <http://dx.doi.org/10.1007/s00265-005-0138-0>.
- Lissåker, M., Kvarnemo, C. & Svensson, O. 2003. Effects of a low oxygen environment on parental effort and filial cannibalism in the male sand goby, *Pomatoschistus minutus*. *Behavioral Ecology*, **14**, 374–381, <http://dx.doi.org/10.1093/beheco/14.3.374>.
- Lukas, J. A. & Orth, D. J. 1995. Factors affecting nesting success of smallmouth bass in a regulated Virginia stream. *Transactions of the American Fisheries Society*, **124**, 726–735, [http://dx.doi.org/10.1577/1548-8659\(1995\)124<0726:FANSOS>2.3.CO;2](http://dx.doi.org/10.1577/1548-8659(1995)124<0726:FANSOS>2.3.CO;2).
- Natsumeda, T. 1998. Size-assortative nest choice by the Japanese fluvial sculpin in the presence of male–male competition. *Journal of Fish Biology*, **53**, 33–38, <http://dx.doi.org/10.1111/j.1095-8649.1998.tb00106.x>.
- Olsson, K. H., Kvarnemo, C. & Svensson, O. 2009. Relative costs of courtship behaviours in nest-building sand gobies. *Animal Behaviour*, **77**, 541–546, <http://dx.doi.org/10.1016/j.anbehav.2008.10.021>.
- 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, <http://dx.doi.org/10.1007/s002650100350>.
- Östlund-Nilsson, S. & Holmlund, M. 2003. The artistic three-spined stickleback (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology*, **53**, 214–220, <http://dx.doi.org/10.1007/s00265-002-0574-z>.
- Parmanne, R. & Lindström, K. 2003. Annual variation in goby larvae abundance in the Northern Baltic. *Journal of Fish Biology*, **62**, 413–426, <http://dx.doi.org/10.1046/j.1095-8649.2003.00037.x>.
- Petit, C., Hossaert-Mckey, M., Perret, P., Blondel, J. & Lambrechts, M. M. 2002. Blue tits use selected plants and olfaction to maintain an aromatic environment for nestlings. *Ecology Letters*, **5**, 585–589, <http://dx.doi.org/10.1046/j.1461-0248.2002.00361.x>.
- Quader, S. 2006. What makes a good nest? Benefits of mate choice to female Baya weavers *Ploceus philippinus*. *The Auk*, **123**, 475–486, [http://dx.doi.org/10.1642/0004-8038\(2006\)123\[475:WMAGNB\]2.0.CO;2](http://dx.doi.org/10.1642/0004-8038(2006)123[475:WMAGNB]2.0.CO;2).
- Rushbrook, B. J., Dingemans, N. J. & Barber, I. 2008. Repeatability in nest construction by male three-spined sticklebacks. *Animal Behaviour*, **75**, 547–553, <http://dx.doi.org/10.1016/j.anbehav.2007.06.011>.
- Schädelin, F. C. & Taborsky, M. 2006. Mating craters of *Cyathopharynx furcifer* (Cichlidae) are individually specific, extended phenotypes. *Animal Behaviour*, **72**, 753–761.
- Soler, J. J., de Neve, L., Martinez, J. G. & Soler, M. 2001. Nest size affects clutch size and the start of incubation in magpies: an experimental study. *Behavioral Ecology*, **12**, 301–307, <http://dx.doi.org/10.1093/beheco/12.3.301>.
- Soler, J. J., Martin-Vivaldi, M., Haussy, C. & Möller, A. P. 2007. Intra- and inter-specific relationships between nest size and immunity. *Behavioral Ecology*, **18**, 781–791, <http://dx.doi.org/10.1093/beheco/arm045>.
- 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, <http://dx.doi.org/10.1046/j.1420-9101.2003.00591.x>.
- 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, <http://dx.doi.org/10.1093/beheco/ari085>.
- Takegaki, T. & Nakazono, A. 2000. The role of mounds in promoting water-exchange in the egg-tending burrows of monogamous goby, *Valenciennesa longipinnis* (Lay et Bennett). *Journal of Experimental Marine Biology and Ecology*, **253**, 149–163, [http://dx.doi.org/10.1016/S0022-0981\(00\)00251-3](http://dx.doi.org/10.1016/S0022-0981(00)00251-3).
- Vahed, K. 1998. The function of nuptial feeding in insects: a review of empirical studies. *Biological Reviews*, **73**, 43–78, <http://dx.doi.org/10.1111/j.1469-185X.1997.tb00025.x>.
- Walsh, P. T., Hansell, M., Borello, W. D. & Healy, S. D. 2010. Repeatability of nest morphology in African weaver birds. *Biology Letters*, **6**, 149–151, <http://dx.doi.org/10.1098/rsbl.2009.0664>.
- Wong, B. B. M., Lehtonen, T. K. & Lindström, K. 2008. Male nest choice in sand gobies, *Pomatoschistus minutus*. *Ethology*, **114**, 575–581, <http://dx.doi.org/10.1111/j.1439-0310.2008.01500.x>.
- Wong, B. B. M., Järvenpää, M. & Lindström, K. 2009. Risk-sensitive mating decisions in a visually compromised environment. *Biology Letters*, **5**, 600–602, <http://dx.doi.org/10.1098/rsbl.2009.0350>.