

# Should females prefer males with elaborate nests?

Topi K. Lehtonen and Bob B.M. Wong

School of Biological Sciences, Monash University, Vic 3800, Australia, and Department of Biological and Environmental Sciences, PO Box 65, Viikinkaari 1, FI-00014, University of Helsinki, Finland

It is widely assumed that when males alone are responsible for nest building, nest characteristics should reflect the quality of its owner and that the nest itself should be an important cue in female choice. This, however, does not always have to be the case if, for example, nest attributes are an unreliable reflection of male quality. Here, we investigate whether females should prefer nest characteristics in a small marine fish, the sand goby, *Pomatoschistus minutus*. Previous findings suggest that female sand gobies prefer males that possess well-built nests (based on the amount of sand piled on top). It was unclear, however, whether females chose males based on the quality of the nest per se or some other, correlated quality of the builder. In the current study, we found conflicting evidence of whether males in good condition are able to bring a greater percentage of eggs to the hatching stage. In a field investigation, we also found that the relationship between body condition and the degree of nest construction was temporally unstable. Furthermore, when we experimentally disentangled nest quality from other male traits, we showed that females did not prefer to spawn with males that had the most elaborate nests. Together, these results suggest that females do not necessarily prefer males based on nest characteristics and may, instead, rely on multiple cues when choosing mates, the relative importance of which should vary depending on context. *Key words*: body condition, multiple cues, nest construction, nest takeovers, *Pomatoschistus minutus*, sexual selection. [*Behav Ecol* 20:1015–1019 (2009)]

Animals often deposit their eggs, or rear their offspring, in purpose-built nests. The level of protection provided by the nest and, hence, the survival prospects of the developing young are likely to be influenced by both the location of the nest (Byrne and Keogh 2009) and the quality of its construction (Hoi et al. 1994; Bult and Lynch 1997). In some species, males alone are responsible for nest building. In such taxa, the nest itself may also reveal important information about the quality of its builder if nest characteristics reliably reflect the physical condition of the male or important aspects of his intrinsic (i.e., genetic) quality. This would make nests analogous to other traits that have traditionally been viewed as extensions of male phenotype (Borgia 1995; Vahed 1998; Schaedelin and Taborsky 2006). In passerine birds, for example, the volume of nest material collected by males is correlated positively with male immune response (Soler et al. 2007). Hence, by assessing a male's nest and the quality of its construction, females may benefit either directly, by selecting a suitor who can maximize the survival of her offspring, or indirectly, through the inheritance of good genes that increase offspring viability or attractiveness (e.g., Soler, Möller, and Soler 1998).

Given the potential benefits involved, it may be tempting to assume that the nest, itself, should play a pivotal role in mate attraction and that females should pay close attention to nest quality when selecting a mate. Numerous studies have shown that females often prefer males that build nests with particular characteristics (Kodric-Brown 1990; Hoi et al. 1994; Östlund-Nilsson and Holmlund 2003; Quader 2006). Only a handful, however, have provided direct evidence of nests functioning as reliable sexual signals. Indeed, few have actually tried to determine whether females are choosing males based on the quality of the nest per se or some other characteristic of the builder

that happens to be correlated with the quality of nest construction. For example, in the small tree finch, *Camarhynchus parvulus*, male phenotype and nest quality, although correlated, were found to have independent effects on female choice (Kleindorfer 2007). More broadly, there is no a priori reason to assume that the quality of a nest should necessarily reflect the quality of its owner. Choosy females, depending on context, may sometimes have to make a direct assessment of both the nest and its owner due to differences in the relative importance (and reliability) of each trait (Hastings 1988; Candolin and Reynolds 2001). Furthermore, nest inspection may not always yield accurate information about the owner if, for example, the current condition of the builder has changed since constructing the nest or if the current occupier is a different individual to the one who built the nest. The latter can arise if suitable nesting resources are scarce and takeovers are common, as has been reported in taxa as diverse as fiddler crabs (Jennions and Backwell 1996), fish (Bisazza and Marconato 1988; Takahashi et al. 2001), and birds (Wiebe 2003).

The sand goby, *Pomatoschistus minutus*, is a small benthic fish found in sandy coastal habitats across Europe (Miller 1986). Males typically build nests under empty mussel shells or rocks by piling sand on top of—and excavating under—the substrate, leaving a single narrow opening. Males use vigorous courtship displays to attract females to the nest. During the breeding season, males may receive eggs from several females and look after multiple clutches simultaneously by actively fanning the eggs and defending them against potential predators (Lindström 1988; 1992a). Female sand gobies prefer males that exhibit superior parental attributes (Lindström et al. 2006) and are able to deliver higher egg-hatching success (Forsgren 1997; Lehtonen and Lindström 2007). Studies have shown that preferred sand goby males also construct well-covered nests (Svensson and Kvarnemo 2005; Lehtonen and Lindström 2009). In a closely related species, the common goby, *Pomatoschistus microps*, males manipulated to be in poor physical condition built scantily covered nests (Kvarnemo et al. 1998). Such males also experienced lower egg-hatching

Address correspondence to B.B.M. Wong. E-mail: bob.wong@sci.monash.edu.au

Received 12 November 2008; revised 30 April 2009; accepted 31 May 2009.

success, suggesting that the amount of sand piled on top of the nest may function as a sexual trait that reliably signals male condition (Kvarnemo et al. 1998). Moreover, like common gobies, the amount of sand found on top of the nest of sand gobies can also be quite substantial (personal observations). As a result, it has recently been suggested that nest quality may also be an honest signal of male condition in sand gobies (Olsson et al. 2009). However, whether female choice in sand gobies is based on nest coverage per se, or some correlated aspect(s) of the nest builder, remains unclear. In the field, high rates of nest takeovers (Lindström 1992b; Lindström and Pampoulie 2005) could potentially undermine the value (if any) that females may obtain from trying to relate the quality of nest construction with the quality of its occupier.

The aim of the current study was to investigate whether female sand gobies should use nest construction (i.e., quantity of sand piled on top of the nest) as a mate choice cue. This was achieved through a series of complimentary laboratory and field-based experiments. First, we examined whether male body condition is correlated with his parental qualities. This was achieved in the laboratory by comparing egg-hatching success when males, naturally differing in condition, were each given the opportunity to tend a clutch. We then explored whether nest construction reliably reflects the condition, size, or expected reproductive success (in terms of eggs guarded) of its occupier. This was assessed in a natural population characterized by a chronic shortage of nest sites and high rates of nest takeovers (Lindström 1992b; Lindström and Pampoulie 2005). Here, we predicted that any relationship between nest construction and the condition of the occupier could potentially fade over time as males deplete their energy reserves or are replaced with intruders following nest takeovers. Finally, we test whether females are likely to be choosing males based on the actual quality of the nest itself (i.e., nest coverage). This was achieved in a controlled laboratory experiment designed to disentangle nest quality with other, potentially correlated, aspects of male quality by deliberately manipulating nest architecture after males had constructed their nests (Jones and Reynolds 1999).

## METHODS

### Does egg-hatching success reflect male condition?

We carried out laboratory experiments during the sand goby breeding season, between May and July, in 2003 and 2006 to investigate how male parental abilities might be related to body condition. Fish in both years were collected using a combination of dip netting and hand trawling near the Tvärminne Zoological Station in southern Finland. These were then transported back to the Station where they were maintained in several separate-sex aquaria. All tanks used for stocking or experiments were housed under natural light conditions and supplied with a continuous through flow of fresh seawater. Fish subsisted on a diet of live *Neomysis integer* shrimps and frozen chironomid larvae prior to experimentation. Males were fed 2–3 chironomid larvae per day during the parental phase of each trial (see below).

Trials were performed in individual aquaria provided with a 4-cm layer of sand as substrate and a halved clay flowerpot (diameter 6 cm) as a nesting resource for the male. The ceiling of the flowerpot was lined with a piece of transparent acetate film onto which the female could attach her eggs during spawning. The use of the transparency allowed us to remove and photograph the egg mass with minimal disturbance to the male (Lehtonen and Lindström 2007) who quickly resumed care of his clutch after it was returned to the nest.

All fish used in the study were weighed and measured (total length) immediately before the experiment. For each trial,

a male was introduced into the aquarium and given 24 h to construct a nest. Completed nests were easily distinguished by the presence of sand piled on top of, and around, the flowerpot, leaving a single opening at the front (Svensson and Kvarnemo 2003). Males that had successfully built a nest were then provided with a gravid female and given 48 h to spawn. During this time, we checked the nest every few hours for the presence of eggs. In 2003, 40 males (total length:  $48 \pm 3.3$  mm [mean  $\pm$  standard deviation, SD]; weight:  $0.78 \pm 0.16$  g) spawned within the given time frame. The 2006 sample included 12 males (total length:  $54 \pm 3.8$  mm; weight:  $1.12 \pm 0.26$  g). Once spawning had taken place, we removed the female, carefully slid the piece of transparency out of the nest, and photographed the clutch. After photography, the clutch was returned to the male who was then allowed to care for his brood. Immediately prior to hatching (i.e., 8 days after spawning), we photographed the clutch again so that we could count the embryos and compare this with the size of the initial spawning and, in so doing, calculate the percentage of eggs that had survived (e.g., Forsgren 1997). As a measure of male body condition, we used residuals of the length–weight regression based on log-transformed data to determine whether a male was heavy or light relative to his body length. In order to increase the accuracy of the regression baseline, we calculated the residuals using all of the measured males that we had stocked in the laboratory (2003:  $n = 65$ ; 2006:  $n = 97$ ).

### Is nest appearance correlated with male condition?

In order to investigate whether the quality of nest building (i.e., amount of sand covering the nest) was related to the condition of nest occupiers, we conducted a field study in an area of shallow water situated within a sand-covered cove near the field station in June 2006. We introduced ceramic tiles ( $10 \times 10$  cm) to the study area as potential nesting resources for the sand gobies. The size of the tiles chosen falls within the natural range of nesting resources exploited by male sand gobies in this population (Wong et al. 2008). Each tile was positioned at least 1 m apart from the next, along a line demarcated by a length of twine anchored at both ends into the substrate. We conducted 3 separate treatments, quantifying nest quality and male condition 8, 24, and 168 h (1 week) after tiles ( $n = 50$  per treatment) were introduced into the field. Each treatment consisted of a separate line and the lines were located close to each other within the study area. We chose 1 week as the maximum time period for monitoring males in the study because, in June, with water temperatures between 11 and 16 °C, sand goby eggs take approximately 8 days to hatch (personal observation).

For each nest, we attempted to catch the resident male with a dip net. We also collected the sand piled on top of each occupied nest by carefully lifting the nest off the substrate and into a shallow tray. Despite our best efforts, however, some males managed to evade capture, and several nest samples were lost during lifting due to wave action. Nevertheless, in most cases, we successfully caught the male and collected the sand, which was later transferred into individually numbered zip-lock plastic bags corresponding to the identity of the male occupying the nest. The underside of each tile was photographed next to a strip of grid paper (for scale) using an Olympus C-5060 digital camera. The area of any egg masses was then measured back in the laboratory using image analysis software (SigmaScan Pro 5.0; SPSS Inc.). Males were individually weighed and measured (total length) and the amount of sand piled on top of the nest was dried and weighed. To quantify body condition, we used 2 different measures. As in the previous experiment, we used residuals of  $\log(\text{length}) - \log(\text{weight})$  regression over all males caught in the field

( $n = 94$ ). As an additional measure of male condition, we used body lipids. The difference in dry weight of males before and after lipid extraction relative to the original dry weight gave us an estimate of the proportionate body fat content. The procedure used for lipid extraction followed that of Lehtonen and Lindström (2007), except that, instead of ethylene petrol, diethyl ether ( $C_2H_5OC_2H_5$ ) was used as the reagent.

#### Do females prefer males with well-covered nests?

Although studies have previously found that female sand gobies prefer males with well-covered nests (Svensson and Kvarnemo 2005; Lehtonen and Lindström 2009), it is unclear whether the target of female choice was the actual nest itself or some other, correlated, attribute of the nest builder. As a result, we conducted an experiment (adapted from Jones and Reynolds 1999) to try to disentangle female preferences based on nest architecture from other, potentially confounding, attributes of the builder.

Fish used in this experiment were collected and housed under identical conditions as those outlined in the laboratory study described earlier. Experimental trials in the current study were carried out in 2006 in individual tanks filled with a 4-cm layer of sand as substrate. Each tank was initially divided lengthwise down the middle into 2 separate, equal-sized compartments using an opaque Perspex sheet. A halved flowerpot (diameter 6 cm) was placed into each of the 2 compartments. Each pot was placed at the same end of the aquarium with the opening of both facing the other end of the tank. A male was then randomly assigned to each compartment. Both males were size matched to within 1 mm of total length. Males were given 24 h to construct their nest. If one or both males had not constructed a nest within the allocated time, the trial was discarded. If, however, both males had constructed a nest, we carefully inspected the nest of both males to determine which of the males had built the more elaborate nest (as determined visually by the amount of sand piled on the top of each nest). We then manipulated the 2 males' nests, removing sand from the nest of the male that had initially constructed the more elaborate nest and piling sand on top of the more modest nest (Jones and Reynolds 1999). In so doing, the male that had initially piled more sand on his nest now had a less well-built nest and vice versa. This was done to control for the possibility that females may be selecting males based on other traits associated with nest building (Jones and Reynolds 1999). After manipulating the nest, we removed the Perspex divider separating the 2 compartments and replaced it with a smaller divider that extended only part way across the length of the tank. This was positioned between the 2 nests to prevent visual contact and physical interference between the 2 males, but allowed a female to inspect and move between the 2 males. A gravid female was then introduced to the opposite end of the aquarium and given 24 h to inspect both males and spawn. After this time, we checked the inside of both nests to determine with whom the female had spawned. We carried out 32 trials, 2 of which had to be discarded: In one, the male who had initially built the bigger nest restored it to its former size; in another, the female spawned with both males. Thus, a total of 30 trials (involving 60 males:  $53 \pm 3.6$  mm,  $1.07 \pm 0.22$  g, and 30 females:  $47 \pm 5.7$  mm,  $0.84 \pm 0.28$  g) were successfully completed.

## RESULTS

#### Does egg-hatching success reflect male condition?

We found that heavier males relative to their length (indicating a good condition) were able to bring a greater percentage of

eggs to the hatching stage in 2006 (Spearman rank correlation,  $r_s = 0.648$ ,  $df = 10$ ,  $P = 0.023$ ) but this was not the case in 2003 ( $r_s = -0.207$ ,  $df = 38$ ,  $P = 0.20$ ).

#### Is nest quality correlated with male condition?

Nest building appeared to be positively associated with male body condition early on after colonization but became less so over time: males that were heavy relative to their length had well-covered nests 8 and 24 h after the nests had been placed in the field and male body fat percentage was positively associated with nest coverage at 24 h (Table 1). Both of these patterns, however, disappeared after 168 h (i.e., 1 week) (Table 1). Furthermore, after 24 h, the amount of sand on top of the nest was positively correlated with the area of eggs in the nest, and at 168 h, the amount of sand was negatively correlated with the length of the nest owner (Table 1). The total length (mean  $\pm$  SD) of males occupying the nests was  $51.3 \pm 0.6$ ,  $52.0 \pm 0.9$ , and  $52.4 \pm 0.8$  mm, at 8, 24, and 168 h, respectively. Thus, there were no size differences in males between the 3 treatments (Model II ANOVA,  $F_{2,91} = 0.427$ ,  $P = 0.65$ ).

After 1 week (168 h), 46 nests had eggs in them. Of these, 21 nests contained at least some eggs that had clearly visible eyespots, indicating that these eggs were within 2 days of hatching and had therefore survived since the initial wave of colonization. Eighteen of these 21 nests also contained much newer eggs (judging by their coloration and lack of eyespots), indicating that the males had kept attracting new females when guarding the eggs they already had.

#### Do females prefer males with well-covered nests?

When decoupling male phenotype from nest height, we found no evidence of females preferring the male in possession of the more elaborate nest (i.e., with more sand piled on top). Specifically, 11 of 30 females spawned with the male that had been manipulated to possess the more elaborate nest but had originally built the less elaborate one. The rest spawned with the other male (binomial test;  $P = 0.20$ ).

## DISCUSSION

A multitude of studies have reported female preferences for males that construct nests with particular characteristics (Kodric-Brown 1990; Hoi et al. 1994; Östlund-Nilsson 2001; Östlund-Nilsson and Holmlund 2003; Quader 2006). Although evidence suggests that the quality of nest construction can, in some instances, function as reliable signals of male

**Table 1**  
Correlates (Spearman rank correlation) of the weight of sand piled on top of sand goby nests

Treatment	Correlate							
	Total length		Residual weight		Lipid content		Egg area	
	$r_s$	$n$	$r_s$	$n$	$r_s$	$n$	$r_s$	$n$
8 h	-0.275	26	0.445*	26	0.219	26	0.141	26
24 h	0.279	29	0.367*	29	0.391*	29	0.503*	29
168 h (week)	-0.427*	36	0.093	36	0.098	36	-0.025	36

Treatment indicates the time elapsed since introducing the artificial nest sites to the field. Significant correlations ( $P \leq 0.05$ ) are indicated with an asterisk.

quality (e.g., Soler, Cuervo, et al. 1998; Soler, Möller, and Soler 1998; Barber et al. 2001), this may not always be the case. Different male traits may be correlated within the same individual (Candolin 2003), making it difficult to determine whether females are actually choosing males based on the quality of the nest per se or relying on other cues associated with the quality of the builder. In sand gobies, preferred males build well-covered nests with large volumes of sand piled on top (Svensson and Kvarnemo 2005; Lehtonen and Lindström 2009). Recently, in a laboratory-based study, Olsson et al. (2009) reported a positive link between manipulated male condition and the level of nest construction. Based on these results, the authors suggested that nest cover is an honest signal of male condition and that females should use the quality of nest construction as a cue in selecting their mates (Olsson et al. 2009). In the current study, however, when we experimentally decoupled nest quality from other traits that may be correlated with nest building (sensu Jones and Reynolds 1999), we found that female sand gobies did not necessarily prefer males that occupied the most elaborately covered nests. Why?

In sand gobies, females prefer males that are good fathers and are able to bring more of her eggs to the hatching stage (Forsgren 1997; Lehtonen and Lindström 2007). The value of making a proper assessment of male condition could therefore be important if the condition of a male affects his parental qualities. For example, in the closely related common goby, *P. microps*, males manipulated to have poor physical condition were also more likely to cannibalize their clutch (Kvarnemo et al. 1998). Results in sand gobies, however, are less clear. We found a positive association between male body condition and hatching success in 2006 but not in 2003. In addition, earlier work on sand gobies have failed to find any direct evidence linking male condition and hatching success (Forsgren 1997). Thus, the relationship between male body condition and his parental quality is at best temporally unstable, varying, for example, over different environmental conditions or periods of the breeding season.

Even if condition was, indeed, related to parental quality in sand gobies, evidence from our field study suggests that nest quality may not always be a reliable signal of condition under natural (i.e., competitive) situations. Although the amount of sand piled on top of the nest was initially associated with body condition, this association was no longer apparent after a week. There are a number of reasons why this might be the case. One possibility is that nesting males may be losing condition over time due to energetically costly investment in nest defense, mate attraction and paternal care. Thus, although nest building reliably reflected male condition early on during nest occupation, it is likely to become less reliable with time as male condition declines. Another possibility is that intruders may have displaced original nest builders so that, in time, the quality of nest construction no longer reflects the quality of its occupier. In our study population, suitable nest sites (i.e., shells and rocks) are in limited supply leading to intense levels of male–male competition for available nests (Forsgren et al. 1996). As a result, nest takeovers are common, with larger and more aggressive males enjoying a competitive advantage (Lindström 1992b; Lindström and Pampoulie 2005). To some extent, invading males may be able to adjust the appearance of the nest but any mismatch between the intruder and the nest would still diminish the value of the nest as a direct cue in mate choice. Thirdly, aggressive males that have managed to displace previous owners may invest poorly in parental care activities, such as nest building, relative to their body condition (Qvarnström and Forsgren 1998). Interestingly, we found a negative relationship between nest quality and male body size a week after the introduction of tiles to the study area.

Given the temporally unstable nature of the relationship between nest appearance and male characteristics, such as condition, females are likely to be using cues other than, or in addition to, nest quality when assessing mates. Doing so could be advantageous if the use of such cues provides additional, or more reliable, information about the quality of prospective suitors (Candolin 2003). Such a situation has been found, for example, in the European bitterling, *Rhodeus amarus* (Candolin and Reynolds 2001). In that species, female spawning decisions are guided by assessment of male courtship and coloration, as well as direct inspection of the nesting resource (mussels). Male traits, in this regard, are believed to reveal important information about male reproductive status and genetic quality, whereas nest attributes provide valuable insights into the survival probability of the female's offspring (Candolin and Reynolds 2001).

According to recent evidence, female sand gobies attend to multiple mate choice cues (Lehtonen et al. 2007). Moreover, the relative importance of different cues can vary, depending on context (Lehtonen and Lindström 2009). Presumably, within the context of the current study, the relative value of different cues could vary temporally from the time that nest sites are first occupied by males. This, in turn, may explain why nests with the most elaborate constructions received the most eggs when surveyed 24 h after tiles were introduced into the field but not at any of the other sampled times, when the attributes of the nest and male were less likely to match each other. This mismatch of different cues could also offer an additional explanation for why females in our laboratory experiment did not prefer mediocre nest builders that had been manipulated to have a high nest cover (see also Lehtonen et al. 2007).

In conclusion, the results of our study suggest that sand goby nests are not reliable extensions of male phenotype and, therefore, female gobies cannot necessarily rely on nest appearance as a cue in mate choice. It remains unclear if female sand gobies are choosing males based on condition because research, to date, has yielded conflicting results with regard to whether male body condition correlates with parental qualities in sand gobies. In any case, the relationship between nest and male condition is one that appears to be unstable over time, possibly due to a decline in the condition of original nest builders, nest takeovers, or both. Thus, for male constructions to function as reliable extensions of male phenotype, females need to be certain that the male they are assessing is actually responsible for the construction of the structure and that the structure itself is an accurate, current reflection of the quality that it is purporting to signal.

## FUNDING

Academy of Finland (T.K.L.: 124796; BMW: 108228; salary from Kai Lindström to T.K.L.: 26721), Finnish Cultural Foundation (T.K.L.), and Australian Research Council (B.B.M.W.: DP0771070).

We thank Kai Lindström for his mentorship, the anonymous reviewers for their helpful comments, and the Tvärminne Zoological Station for access to facilities, equipment, and logistical support. Our study complies with all the relevant laws of Finland and Australia.

## REFERENCES

- Barber I, Nairn D, Huntingford FA. 2001. Nests as ornaments: revealing construction by male sticklebacks. *Behav Ecol*. 12:390–396.
- Bisazza A, Marconato A. 1988. Female mate choice, male-male competition and parental care in the river bullhead, *Cottus gobio* L. (Pisces, Cottidae). *Anim Behav*. 36:1352–1360.

- Borgia G. 1995. Why do bowerbirds build bowers? *Am Sci.* 83:542–547.
- Bult A, Lynch CB. 1997. Nesting and fitness: lifetime reproductive success in house mice bidirectionally selected for thermoregulatory nest-building behavior. *Behav Genet.* 27:231–240.
- Byrne PG, Keogh JS. 2009. Extreme sequential polyandry insures against nest failure in a frog. *Proc R Soc Lond B Biol Sci.* 276:115–120.
- Candolin U. 2003. The use of multiple cues in mate choice. *Biol Rev.* 78:575–595.
- Candolin U, Reynolds JD. 2001. Sexual signaling in the European bitterling: females learn the truth by direct inspection of the resource. *Behav Ecol.* 12:407–411.
- Forsgren E. 1997. Female sand gobies prefer good fathers over dominant males. *Proc R Soc Lond B Biol Sci.* 264:1283–1286.
- Forsgren E, Kvarnemo C, Lindström K. 1996. Mode of sexual selection determined by resource abundance in two sand goby populations. *Evolution.* 50:646–654.
- Hastings PA. 1988. Female choice and male reproductive success in the angel blenny, *Coralliozetus angelica* (Teleostei: Chaenopsidae). *Anim Behav.* 36:115–124.
- Hoi H, Schleicher B, Valera F. 1994. Female mate choice and nest desertion in penduline tits, *Remiz pendulinus*: the importance of nest quality. *Anim Behav.* 48:743–746.
- Jennions MD, Backwell PRY. 1996. Residency and size affect fight duration and outcome in the fiddler crab *Uca annulipes*. *Biol J Linn Soc.* 57:293–306.
- Jones JC, Reynolds JD. 1999. The influence of oxygen stress on female choice for male nest structure in the common goby. *Anim Behav.* 57:189–196.
- Kleindorfer S. 2007. Nesting success in Darwin's small tree finch, *Camarhynchus parvulus*: evidence of female preference for older males and more concealed nests. *Anim Behav.* 74:795–804.
- Kodric-Brown A. 1990. Mechanisms of sexual selection: insights from fishes. *Ann Zool Fenn.* 27:87–100.
- Kvarnemo C, Svensson O, Forsgren E. 1998. Parental behaviour in relation to food availability in the common goby. *Anim Behav.* 56:1285–1290.
- Lehtonen TK, Lindström K. 2007. Mate compatibility, parental allocation and fitness consequences of mate choice in *Pomatoschistus minutus*. *Behav Ecol Sociobiol.* 61:1581–1588.
- Lehtonen TK, Lindström K. 2009. Females decide whether size matters: plastic mate preferences tuned to the intensity of male–male competition. *Behav Ecol.* 20:195–199.
- Lehtonen TK, Rintakoski S, Lindström K. 2007. Mate preference for multiple cues: interplay between male and nest size in the sand goby, *Pomatoschistus minutus*. *Behav Ecol.* 18:696–700.
- 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*. *Mar Biol.* 113:475–480.
- 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. *Behav Ecol Sociobiol.* 30:53–58.
- Lindström K, Pampoulie C. 2005. Effects of resource holding potential and resource value on tenure at nest sites in sand gobies. *Behav Ecol.* 16:70–74.
- Lindström K, St. Mary CM, Pampoulie C. 2006. Sexual selection for male parental care in the sand goby, *Pomatoschistus minutus*. *Behav Ecol Sociobiol.* 60:46–51.
- Miller PJ. 1986. Gobiidae. In: Whitehead PJP, Bauchot M-L, Huureau J-C, Nielsen J, Tortonese E, editors. *Fishes of the North-Eastern Atlantic and the Mediterranean.* Vol. 3. Paris (France): UNESCO. p. 1019–1085.
- Olsson KH, Kvarnemo C, Svensson O. 2009. Relative costs of courtship behaviours in nest-building sand gobies. *Anim Behav.* 77:541–546.
- 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. *Behav Ecol Sociobiol.* 50:263–269.
- Östlund-Nilsson S, Holmlund M. 2003. The artistic three-spined stickleback (*Gasterosteus aculeatus*). *Behav Ecol Sociobiol.* 53:214–220.
- Quader S. 2006. What makes a good nest? Benefits of nest choice to female Baya weavers (*Ploceus philippinus*). *Auk.* 123:475–486.
- Qvarnström A, Forsgren E. 1998. Should females prefer dominant males? *Trends Ecol Evol.* 13:498–501.
- Schaedelin FC, Taborsky M. 2006. Mating craters of *Cyathopharynx furcifer* (Cichlidae) are individually specific, extended phenotypes. *Anim Behav.* 72:753–761.
- Soler JJ, Cuervo JJ, Møller AP, de Lope F. 1998. Nest building is a sexually selected behaviour in the barn swallow. *Anim Behav.* 56:1435–1442.
- Soler JJ, Møller AP, Soler M. 1998. Nest building, sexual selection and parental investment. *Evol Ecol.* 12:427–441.
- Soler JJ, Martín-Vivaldi M, Haussy C, Møller AP. 2007. Intra- and interspecific relationships between nest size and immunity. *Behav Ecol.* 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. *J Evol Biol.* 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*. *Behav Ecol.* 16:1042–1048.
- 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. Ichthyol Res.* 48:91–95.
- Vahed K. 1998. The function of nuptial feeding in insects: a review of empirical studies. *Biol Rev.* 73:43–78.
- Wiebe KL. 2003. Delayed timing as a strategy to avoid nest-site competition: testing a model using data from starlings and flickers. *Oikos.* 100:291–298.
- Wong BBM, Lehtonen TK, Lindström K. 2008. Male nest choice in sand gobies, *Pomatoschistus minutus*. *Ethology.* 114:575–581.