

# Mate competition and resource competition are inter-related in sexual selection

S. WACKER & T. AMUNDSEN

Department of Biology, Norwegian University of Science and Technology, Trondheim, Norway

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## Abstract

Sexual selection can be affected by the competition for limited breeding resources and/or the competition for limited mates. Although there is ample evidence for each type of competition by itself, little is known about their relative importance and interaction. To address these questions, we established 48 experimental breeding populations of the two-spotted goby (*Gobi-*uscus flaves**), a substrate-breeding fish with paternal care. In three experimental treatments, males were limited in the access to either nest sites or mates or were provided with both nests and mates in excess. We quantified male competition behaviour (agonistic and courtship), the opportunity for selection and selection on male body size. Limited access to nests and mates produced similar opportunities for selection, but only limited access to mates increased male competitive behaviours and caused positive selection on male body size. Selection on body size in the mate-limited treatment was due both to larger males being more likely to take up nests and to larger males being more likely to mate once they had a nest. These findings demonstrate that resource and mate limitation can differ in their effects on sexual selection. The results also reveal that resource and mating competition can be highly inter-related and not always separated in time, implying that methods to disentangle the two processes must be chosen with care. Future research should consider experimental and analytical approaches similar to those of the present study in attempts to elucidate the interaction of resource and mating competition in animals.

## Introduction

Sexual selection occurs when variation in mating success among individuals is related to variation in phenotypic traits (Darwin, 1871; Trivers, 1972). Variation in mating success often arises when matings are limited and animals compete for the access to matings by courtship and intrasexual aggression. In many species, variation in mating success is also related to the competition for limited breeding resources, such as territories or nest sites (Emlen & Oring, 1977; Ahnesjö *et al.*, 2001; Shuster & Wade, 2003). Those two types of competition are termed 'mating competition' and 'resource competition', respectively (Andersson, 1994). Resource-based mating systems occur in species across a wide

range of animal taxa, including arthropods (Baker, 1983; Thornhill & Alcock, 1983), amphibians (Wells, 2007), reptiles (Shine, 1988), birds (Bennett & Owens, 2002), fish (Breder & Rosen, 1966) and mammals (Ostfeld, 1990). The competition for access to limited breeding resources can be intense and may in some species explain a large part of total variation in mating success and thereby sexual selection (Emlen & Oring, 1977; Shuster & Wade, 2003).

Understanding the individual roles and the interaction of resource competition and mating competition is important for the understanding of sexual selection as a whole and its dynamics. For example, changes in the physical and social environment can affect the strength of sexual selection (Emlen & Oring, 1977; Shuster & Wade, 2003), but the effects may differ between resource competition and mating competition. Although for example nest site availability is expected to primarily affect resource competition (Forsgren *et al.*,

Correspondence: Sebastian Wacker, Department of Biology, Realfagbygget, NTNU, 7491 Trondheim, Norway.  
Tel.: +47 73596257; fax: +47 73596100; e-mail: wacker@bio.ntnu.no

1996; Jacot *et al.*, 2009), the operational sex ratio (OSR; the ratio of ready-to-mate males and females) is expected to primarily affect mating competition (Ahnesjö *et al.*, 2001; Weir *et al.*, 2011). The relative importance of resource competition and mating competition in a given species, and their interaction, should thus determine how changes in the environment are expected to affect sexual selection.

Empirical studies on sexual selection have typically either focussed on one type of competition or have been unable to disentangle the effects of mating competition and resource competition (Shuster & Wade, 2003; Klug *et al.*, 2010b). In many studies, the term mating competition is used in a broad sense, including the competition for resources. Studying the relative importance of resource and mating competition is complicated by the inter-relatedness of the two processes. In a simplistic scenario, all males would first compete for access to breeding resources and only successful males would later compete for matings (Ahnesjö *et al.*, 2001; Klug *et al.*, 2010b). However, resource competition and mating competition are not always clearly distinguishable. For example, female mate choice may be based partly on the quality of the breeding resource (Kelly, 2008 and references therein) and male–male resource competition would thereby affect mating competition. Likewise, mating competition may affect resource competition if certain males do not engage in resource competition because of their low expected success in mating competition (Trivers, 1972; Gross, 1996). The latter scenario predicts that, with an increasing strength of mating competition, more males would refrain from resource competition, thereby relaxing the competition for breeding resources. Finally, the two processes may not always be separated in time, but may occur partly or wholly simultaneously (Hunt *et al.*, 2009; Wacker *et al.*, 2012).

In the present study, we test the effects of mating competition and resource competition on sexual selection for male body size in a small marine fish, the two-spotted goby (*Gobiusculus flavescens*). The two-spotted goby has a resource-based mating system, with males defending nest sites during the breeding season. Males have previously been found to compete for matings (Forsgren *et al.*, 2004; Myhre *et al.*, 2012; Wacker *et al.*, 2013) and nest sites (Forsgren *et al.*, 2004; Mück *et al.*, 2013), making it a suitable model for such a test. In order to disentangle the effects of mating competition and resource competition on sexual selection, we established experimental treatments with limited access to either matings (i.e. females) or nests, providing the other resource in excess. In a third treatment, both resources were provided in excess. Notably, the question of the relative importance of resource and mating competition is related to the question of the importance of inter- and intrasexual selection in sexual selection, without the questions being interchangeable. Whereas

resource competition is resolved by same sex interactions (intrasexual), mating competition is resolved both by intrasexual interactions and (intersexual) courtship. The relationship between inter- and intrasexual selection has received considerable empirical and theoretical attention (e.g. Bradbury & Davies, 1987; Berglund *et al.*, 1996; Hunt *et al.*, 2009). By contrast, the relationship between resource and mating competition, which is the focus of the present study, is little explored.

The term mating competition is commonly used to describe phenomena at two different levels of explanation (Kokko *et al.*, 2012). First, it may describe a competitive situation in which the access to matings is limited; that is, an underlying resource conflict. Second, it may describe the competitive behaviour in itself; that is, the resolution, or observable manifestation, of that conflict. Our treatments represented resource and mating competition in the sense of competitive situations, and we then observed the behavioural resolution of these conflicts and the selective consequences. Thus, in our treatments, males could compete behaviourally over nests both when these were limited, and when mates were limited. Likewise, they could compete behaviourally over mates both when these were in short supply, and when nests were in short supply.

We calculated selection on body size, which is the most commonly studied trait in the context of sexual selection in males (Andersson, 1994; Blanckenhorn, 2005). Larger males have been found to be superior in both resource competition and mating competition across a wide range of taxa (Andersson, 1994; Blanckenhorn, 2005). We expected variation in mating success to be higher in both the mate-limited and the nest-limited treatments than in the nonlimited treatment (in which both mates and nests were present in excess). We also expected more male–male competition in the mate- and nest-limited treatments, but had no specific prediction for differences in the strength of sexual selection on male body size between the mate- and the nest-limited treatments.

## Materials and methods

The study was conducted during 16 May to 11 June 2011 at the Sven Lovén Centre for Marine Sciences, Kristineberg, on the Swedish west coast (58° 15'N, 11° 27'E).

### Model species

Two-spotted gobies are common along the rocky shorelines of Western Europe (Miller, 1986). During the breeding season (May–July), males take up nests in shallow waters (typically < 5 m depth). Nests typically consist of macroalgae (e.g. *Saccharina latissima* and *Laminaria digitata*) or empty mussels (mostly *Mytilus edulis*) (Gordon, 1983; Mobley *et al.*, 2009). Both males and

females may initiate courtship and males attract females to their nests by lead swims (Amundsen & Forsgren, 2001; Forsgren *et al.*, 2004). Several females typically spawn into a single nest (Gordon, 1983; Mobley *et al.*, 2009). Agonistic male–male encounters are frequent among nest-holding males, both in the presence and in the absence of females (Forsgren *et al.*, 2004; de Jong *et al.*, 2009). Previous work on gobies including the two-spotted goby has shown that size matters in behavioural interactions and nest acquisition in this group of fish (Lindström, 1988, 1992; Magnhagen, 1994; Forsgren *et al.*, 1996; Borg *et al.*, 2002; Wacker *et al.*, 2012). After female spawning, males provide parental care in the form of guarding, cleaning and fanning of the eggs until hatching (Gordon, 1983; Skolbekken & Utne-Palm, 2001; Bjelvenmark & Forsgren, 2003). Sneaking behaviour has been found to occur at a very low rate, with a negligible effect on sexual selection (Mobley *et al.*, 2009). Both sexes can reproduce repeatedly over the breeding season (de Jong, 2011) and normally live for only 1 year (Johnsen, 1945). Two-spotted gobies experience a strong seasonal change in the OSR, from male-biased early in the season to female-biased late in the season (Forsgren *et al.*, 2004). This change is mainly caused by a decrease in male density (Forsgren *et al.*, 2004; Myhre *et al.*, 2012).

### Experimental design

The study was aimed to test how resource competition (for nests) and mating competition (for females) affect sexual selection on male body size. In order to achieve this, we compared three treatments: (i) nest limitation, (ii) mate limitation and (iii) no limitation (nests and females in excess). All treatments involved four males. Nest limitation was established by providing only two nests, and mate limitation was established by providing only four females. Four females represented limited access to matings as the eggs of about four females fill one nest of the size used (Wacker *et al.*, 2013), so that all females could in theory be monopolized by only one of the males. We used 17 females to produce an excess of mating options, as clutches from about 16 are needed to fill the nests of all four males. Twelve nests represented an excess of nests, as males are not known to guard eggs in more than one nest at the same time (Mück *et al.*, 2013; Wacker *et al.*, 2013). In the mate-limited treatment, access to females was limited, but nests were provided in excess (four males, four females, 12 nests). In the nest-limited treatment, access to nests was limited, whereas females were provided in excess (four males, 17 females, two nests). Both resources were provided in excess in the nonlimited treatment (four males, 17 females, 12 nests). Notably, a full factorial experimental design would also have involved a treatment limiting the access to both nests and females. As such a treatment was not crucial to our analyses,

we chose to maximize the number of replicates rather than including a fourth treatment.

The experiment was conducted indoors in grey fibreglass tanks, measuring  $100 \times 100 \times 50$  cm (length  $\times$  width  $\times$  depth). Each tank had a separate flow of seawater, following natural temperature and salinity. Artificial light was set to a day:night rhythm of 16 : 8 h. Grey PVC tubes (inner diameter: 14 mm, length: 80 mm) attached to small rocks were provided as nesting substrates. For the treatment with two nests, these were placed in two neighbouring corners (with approximately 15 cm distance to the walls), resulting in a internest distance of approximately 70 cm. For the treatments with 12 nests, one nest was placed in each corner, and two nests along each of the sidewalls, with even distances among nests (ca. 23 cm) and at about 15 cm distance to the wall. In all tanks, four artificial algae were provided as shelter. Treatments were first assigned randomly to the tanks and then circulated with respect to the position of tanks in the room for each new set of replicates. A trial started with the introduction of males and females to the tank and lasted approximately 70 h.

In the first four replicates, four females in an enclosure were presented to the males for 24 h before the start of the actual experiment. The females and the enclosure were then removed and new females introduced when the trial was started. This procedure was intended to stimulate male competition for nests. However, males showed little interest in nest sites when they could not physically interact with females, and we therefore did not include this procedure from replicate five onwards.

### General procedures

Males were collected at the same day a replicate was started. We caught males using hand-held dip nets while snorkelling, at various sites close to the research station (ca. 0.1–3 km). Males were immediately transferred to single sex containers. We measured total length to the nearest 0.5 mm using a grid and weighed males to an accuracy of 0.01 g using a Mettler balance, after carefully removing excess water with a wet tissue. For each set of simultaneously initiated trials (two of each of the three treatments), we collected approximately 30 males. Twenty-four of these were assigned to the treatments, excluding exceptionally large ( $> 51$  mm) and very small ( $< 37$  mm) males. We established a marked within-trial size-span, based on a separation of the males into four size classes (Table 1). The average difference in total length between the largest and the smallest males within a trial was 9.1 mm (range: 6.0–11.5 mm). Details on the distributions of male total length and weight are given in Table 1. There was no difference in mean male total length among treatments ( $F_{2,45} = 0.33$ ,  $P = 0.72$ ). Neither did

**Table 1** Size classes of males used in a study of resource and mating competition in two-spotted gobies: distribution of male total length (TL; mm) and weight (mg) within trials, and size differences among size classes.

	Smallest	Small	Large	Largest
<i>n</i>	48	48	48	48
Total length (mm)				
Range	37.0–40.0	40.0–43.5	42.5–46.5	45.0–50.5
Mean	38.8	41.6	44.2	47.9
CV	0.023	0.020	0.022	0.033
Difference range	1–5	1.5–4	1.5–7	
Difference mean	2.8	2.7	3.7	
Difference CV	0.24	0.22	0.31	
Weight (mg)				
Range	350–558	450–671	490–853	662–1072
Mean	466	576	687	865
CV	0.11	0.09	0.11	0.11

the contrast in total length between the smallest and largest male within a trial differ among treatments ( $F_{2,45} = 0.82$ ,  $P = 0.45$ ). Mean total length of males in the experiment slightly increased over the season ( $F_{1,14} = 9.4$ ,  $P = 0.009$ ), with an estimated increase of 1.7 mm (4% of mean total length) from the first to the last replicate.

Females were collected the day before release into experimental tanks. Females were caught in the breeding habitat and transported to the laboratory in single sex containers, in which they were stored over night. To ensure that all females were ready-to-mate, we only used clearly gravid (round-bellied) females (Pélabon *et al.*, 2003; Forsgren *et al.*, 2004; de Jong *et al.*, 2009). To have treatments include females of approximately the same roundness, we first selected the females with the roundest bellies (approximately 25–40 females) and randomly distributed these to the six simultaneously initiated trials before randomly distributing the remaining females to the trials.

Males were marked for individual recognition using visible implant elastomer (VIE; Northwest Marine Technology; see de Jong *et al.*, 2009 for marking protocol). In previous laboratory and field studies on the species that employed VIE tags, fish behaved normally shortly after marking (de Jong *et al.*, 2009; Myhre *et al.*, 2012, 2013; Mück *et al.*, 2013; Wacker *et al.*, 2013). We used two colours (green and orange) and two positions (left and right of the dorsal fin) for marking. Colour and position were varied with respect to male size class to avoid potential confounding effects of colour marks even if no indications of such effects have previously been observed.

### Observational procedures

We recorded which males were mated (had eggs in their nests) after approximately 24, 48 and 64 h. Nests were inspected for eggs using a small mirror attached to

a pole. After inspecting the nests for eggs, we observed each tank for approximately 5 min and noted which males entered the nests that contained eggs. These males were recorded as nest holders of the according nests. This procedure was unambiguous, as we never recorded another nest holder at subsequent nest checks of nests with eggs. In four instances, males guarded eggs outside the provided artificial nest sites (at the sidewall of the tank). All four instances occurred in the nest-limited treatment and resulted in more than two mated males in those trials, despite only two nests being provided.

In order to record male mating competition behaviour, nest inspection and nest possession, we observed each tank for 20 min approximately 20, 44 and 66 h after releasing the fish. We observed all males within a tank simultaneously in order to increase observation time per male. This was unproblematic in almost all cases. However, during a few observations, male activity was very high and we may have missed some events of behaviour. As this was only the case in observations with very high frequencies of behaviour, this should be conservative with respect to treatment effects. We analysed behaviour not only as frequencies, but also as presence/absence data, that is, occurrence per male. This measure was unproblematic for all observations.

We recorded the following behaviours: (i) nest entries (entire fish enters a nest tube); (ii) agonistic fin displays (male erects dorsal fin in proximity to another male); (iii) agonistic chases (male darts towards another male); (iv) courtship fin displays (male erects dorsal fin in proximity to female); (v) quivers (male quivers entire body in proximity to female); (vi) lead swims (male swims to nest tube with undulating movements). In addition, we scan sampled position of the fish every minute, as being (i) inside nest (entire male in nest), (ii) in proximity to nest (male stays < 1 fish length away from nest tube) or (iii) elsewhere (all other positions).



We defined nest-holding males as males that, during a 20-min behavioural observation, either (i) entered a nest five or more times, (ii) stayed inside a nest in at least 25% of the scan samplings, (iii) stayed in proximity to a nest in at least 50% of the scan samplings or (iv) that were mated (i.e. had eggs in their nests). This definition did not preclude that more than one males were defined as nest holders of the same nest. As a result, in one trial of the nest-limited treatment, three males were classified as nest holders despite only two nests being provided.

### Measures of sexual selection

As outlined above, we studied the effects of resource and mating competition by limiting access to either breeding resources or mates and thus the underlying resource conflict. An alternative approach is to distinguish resource competition and mating competition by studying conflict resolution within a treatment. This is usually done by statistically separating selection associated with the acquisition of nests and selection (among nest holders) associated with the acquisition of matings (e.g. Magnhagen & Kvarnemo, 1989; Forsgren *et al.*, 1996; Klug *et al.*, 2010b). In this study, we combined this statistical approach with the experimental treatments, calculating selection associated with acquisition of nests and matings within each treatment; a comprehensive approach that, to our knowledge, has never been adopted before. This was done to test whether nest limitation resulted in selection related to nest acquisition, and mate limitation in selection related to mate acquisition, or whether the behavioural resolution of the underlying conflict was more complex, involving an interaction of resource and mating competition. Thus, our approach is aimed to reveal how a competitive situation (limited access to nests or mates) translates into competitive behaviours and consequent sexual selection.

The opportunity for selection ( $I$ ) is a measure of variance in reproductive success, indicating the upper limit of selection on any trait (Wade & Arnold, 1980; Shuster & Wade, 2003). In order to separate variation in reproductive success related to nest acquisition and to mate acquisition, we calculated  $I$  in three different ways (see Klug *et al.*, 2010b). The total opportunity for selection,  $I_{\text{total}}$ , was calculated as the variance in mating success (0 for unmated, 1 for mated males) divided by the square mean mating success. The opportunity for selection associated with nest acquisition,  $I_{\text{nest}}$ , was calculated as the variance in nesting success (0 for non-nest-holding and 1 for nest-holding males) divided by the square mean nesting success. The opportunity for selection associated with mate acquisition,  $I_{\text{mating}}$ , was calculated as the variance in mating success among nest-holding males (0 for unmated, 1 for mated males) divided by the square mean mating success among

nest holders. All measures of  $I$  were calculated within trials.

We calculated sexual selection on male body size as standardized selection differentials ( $s'$ ; Lande & Arnold, 1983) within trials. Total length was standardized to have a mean of zero and a standard deviation of one (Lande & Arnold, 1983) within trials. As for measures of  $I$ , we calculated selection on body size in three ways. Total selection was calculated as the difference in mean (standardized) total length between mated males and all males. Selection associated with nest acquisition was calculated as the difference in mean (standardized) total length between nest-holding males and all males. Selection associated with mate acquisition was calculated as the difference in mean (standardized) total length between mated nest holders and all nest holders.

We also calculated selection on male condition. Condition was calculated as the residuals from a linear regression of body weight (mg) on total length (mm). However, we did not detect significant selection on male condition calculated as total selection or associated with nest acquisition or mate acquisition (all  $P > 0.18$ ). We therefore only present the results for selection on male total length.

### Statistical analysis

In order to test for treatment effects on the proportion of males that showed a certain behaviour, we first calculated proportions within trials and then entered these proportions as response variables in generalized linear models (GLM). This was done for the analyses of nest holdership, mating, courtship and agonistic behaviour. All GLMs were fitted with a binomial error structure, as response variables were proportions. We used generalized linear mixed models (GLMM) to analyse the effect of body size on the likelihood of mating competition behaviour, as the observations were not independent. The GLMMs were fitted with a binomial error structure as the response variables were binary, and trial was included as random factor.

We analysed the behaviour pooled across the three observations and did not test for treatment differences for each observation period (24, 48 and 64 h) separately. This was done both for simplicity and as we were interested in the overall level of competition. Also for reasons of simplicity, we pooled the different courtship and agonistic behaviours. Analyses on frequencies of behaviour were carried out on the sum of the recorded behaviours in courtship and agonistic behaviour per individual, respectively.

We compared the opportunity for selection among trials with either an ANOVA or a Kruskal–Wallis test. For  $I_{\text{total}}$  and  $I_{\text{nest}}$  the residuals were reasonably normally distributed, but this was not the case for  $I_{\text{mating}}$  and we used a Kruskal–Wallis test for the latter. All statistical

analyses were carried out in R, version 2.13.1 (R Development Core Team., 2011).

## Results

### Male competition behaviour

Limited access to mates, but not limited access to nests, led to increased male–male competition. In the mate-limited treatment, a higher proportion of males showed agonistic behaviour ( $Z = 3.1$ ,  $P = 0.002$ ) and courtship ( $Z = 2.2$ ,  $P = 0.032$ ) than in the nonlimited treatment, and the rates of such behaviours were also higher (agonistic:  $t = 3.2$ ,  $P = 0.003$ ; courtship:  $t = 2.3$ ,  $P = 0.025$ ) (Fig. 1). In contrast, neither the proportion of males displaying agonistic behaviour ( $Z = -1.4$ ,  $P = 0.15$ ) or courtship ( $Z = -1.5$ ,  $P = 0.14$ ) nor the rates of such behaviours (agonistic:  $t = -1.4$ ,  $P = 0.17$ ; courtship:  $t = -0.8$ ,  $P = 0.45$ ) differed between the nest-limited treatment and the nonlimited treatment (Fig. 1).

The likelihood that a male behaved agonistically increased significantly with body length in the nest-limited treatment (GLMM:  $Z = 2.0$ ,  $P = 0.049$ ; Fig. 2b) and in the nonlimited treatment (GLMM:  $Z = 2.9$ ,  $P = 0.004$ ; Fig. 2c), but not in the mate-limited treatment (GLMM:  $Z = 1.4$ ,  $P = 0.17$ ; Fig. 2a), in which the likelihood of agonistic behaviour was very high across the range of male length. The likelihood of male courtship increased with male length in the nonlimited treatment (GLMM:  $Z = 2.0$ ,  $P = 0.046$ ; Fig. 2f), but not in the mate-limited treatment (GLMM:  $Z = 1.6$ ,  $P = 0.12$ ; Fig. 2d) or the nest-limited treatment (GLMM:  $Z = 0.7$ ,  $P = 0.49$ ; Fig. 2e).

### Nest occupation and mating

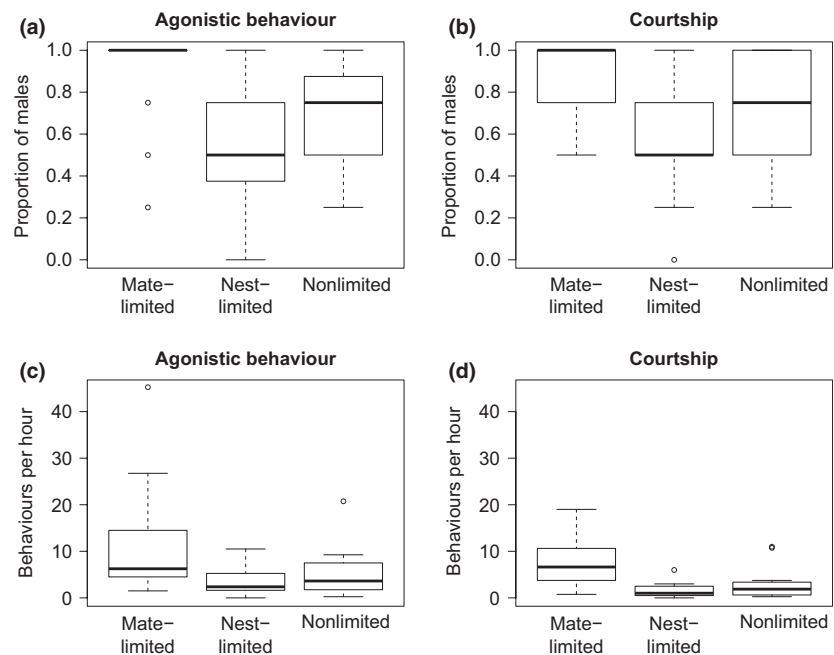
A high proportion of males held a nest and mated in the nonlimited treatment at the end of the experiment, as intended by the experimental setup (Fig. 3). The proportion of males that held a nest was significantly lower in the nest-limited ( $Z = -3.3$ ,  $P < 0.001$ ) and mate-limited ( $Z = -2.7$ ,  $P = 0.007$ ) treatments, even though nests were provided in excess in the latter treatment (Fig. 3). That on average, more than two males occupied nests in the nest-limited treatment (only two nests provided; Fig. 3) resulted from cases of males guarding eggs outside the provided nests (see methods). Also the proportion of males that mated was significantly lower in the mate-limited ( $Z = -4.4$ ,  $P < 0.001$ ) and in the nest-limited ( $Z = -3.3$ ,  $P = 0.001$ ) than in the nonlimited treatment (Fig. 3). Males never guarded eggs in more than one nest. Results for nest occupation and mating after 24 and 48 h are provided in Fig. S1.

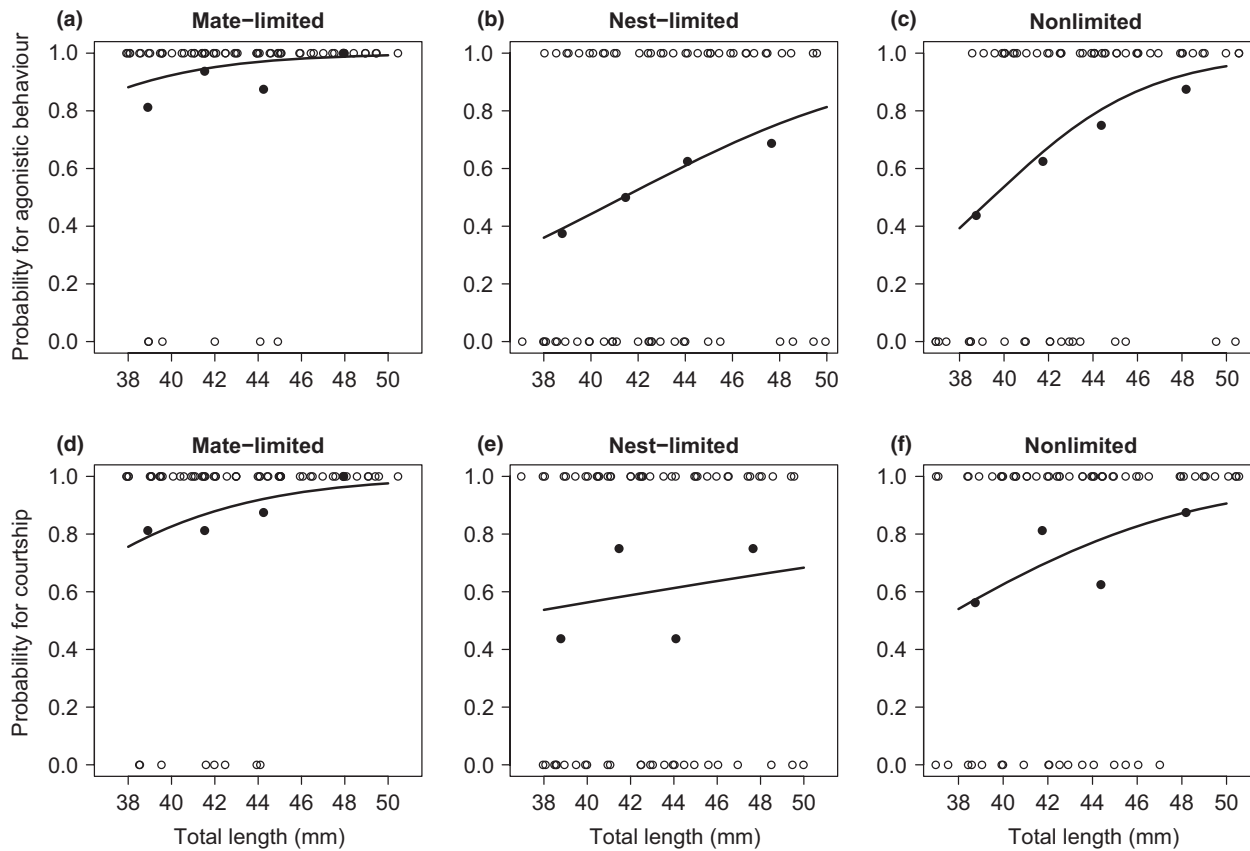
### Opportunity for selection

Within each treatment, we separately calculated the opportunity for selection associated with nest occupation and with mate acquisition, as well as the total opportunity for selection (see methods). Here, we present the results for the opportunity for selection and selection on body size at the end of the experiment (64 h). Results after 24 and 48 h are shown in Fig. S2.

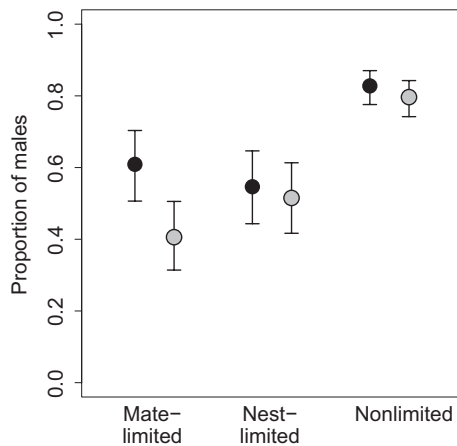
A high proportion of males holding a nest in the nonlimited treatment resulted in a low  $I_{\text{nest}}$  ( $I$  associated with nest acquisition), whereas  $I_{\text{nest}}$  was significantly higher in the mate- and nest-limited treatments

**Fig. 1** Male two-spotted goby (*Gobiulus flavescens*) agonistic and courtship behaviour in experimental treatments limiting access to mates or nest sites or providing both resources in excess. Proportions of males behaving (a) agonistically and (b) courting during at least one of three behavioural observation of 20 min each, and the number of (c) agonistic and (d) courtship behaviours per male during a total observation time of 60 min resulting from three observations of 20 min each (after 24, 48 and 66 h). Box plots show medians, upper/lower quartiles, and minima and maxima.





**Fig. 2** Sexual selection in male two-spotted gobies (*Gobiusculus flavescens*). The effect of total length on male two-spotted goby agonistic behaviour (a–c) and courtship (d–f) in experimental treatments limiting access to mates (a, d) or nest sites (b, e), or providing both resources in excess (c, f). Open circles represent individual males, solid circles represent means of each of the four male size classes and lines show the relationships between total length and probability of behaviour as estimated by generalized linear mixed models.

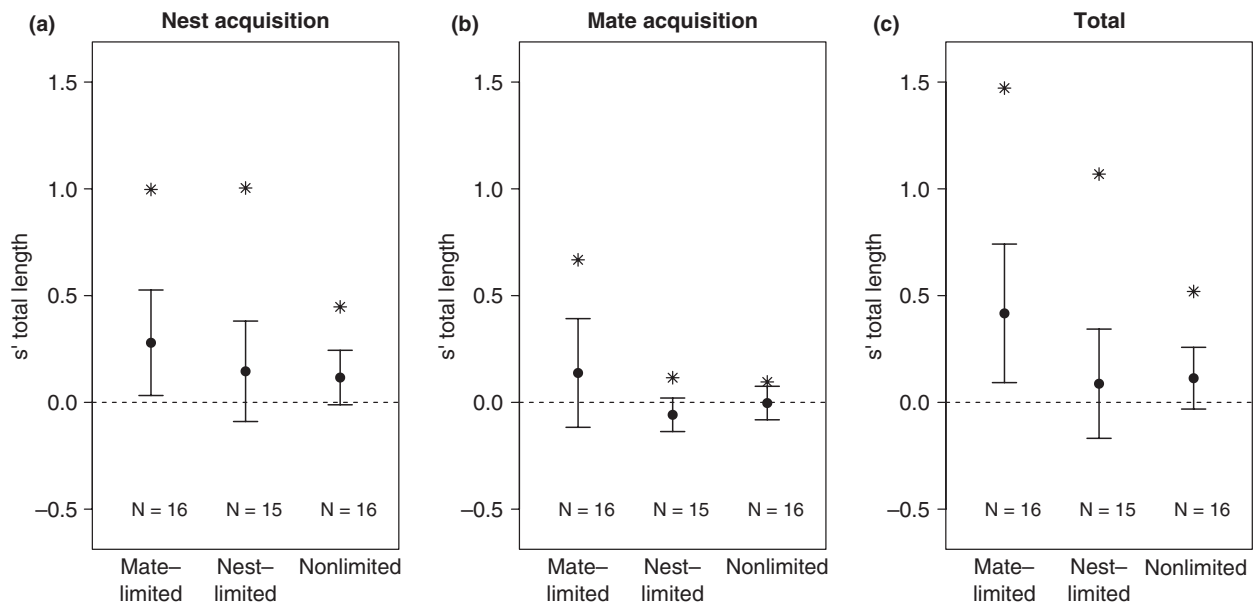


**Fig. 3** Proportions of two-spotted goby (*Gobiusculus flavescens*) males within trials that held a nest (black circles) and mated (grey circles) in experimental treatments limiting access to mates or nest sites or providing both resources in excess. Circles represent means and bars 95% confidence intervals as estimated by generalized linear models.

( $F_{2,44} = 7.3$ ,  $P = 0.002$ ; Fig. 4a). A low proportion of unmated nest holders in the nonlimited and nest-limited treatments resulted in a low  $I_{\text{mating}}$  ( $I$  associated with mate acquisition) in those treatments, whereas  $I_{\text{mating}}$  was substantial in the mate-limited treatment (Kruskal–Wallis test;  $\chi^2 = 11.4$ ,  $P = 0.003$ ; Fig. 4b). Finally, a high proportion of mated males in the non-limited treatment resulted in a low  $I_{\text{total}}$ , whereas  $I_{\text{total}}$  was higher in the mate- and nest-limited treatments ( $F_{2,44} = 21.6$ ,  $P < 0.001$ ; Fig. 4c).

### Selection on body size

We also separately calculated selection on body size related to nest occupation and to mate acquisition, as well as total selection. In the mate-limited treatment, we found significant positive selection on length associated with nest occupation ( $t = 2.2$ ,  $P = 0.04$ ; Fig. 4a). This is noticeable, as nests were present in excess in this treatment. By contrast, and contrary to expectation, we did not detect any selection on length related to nest acquisition in the nest-limited treatment



**Fig. 4** Standardized selection differentials on male total length (solid circles) and their 95% CI in experimental treatments limiting access to either mates or nest sites or providing both resources in excess in two-spotted gobies (*Gobiusculus flavescens*). Selection is presented for the processes of nest acquisition (a) and mate acquisition (b) separately and as total selection (c). The asterisks indicate the upper limit of the strength of selection (the square root opportunity for selection), and sample sizes are given per treatment.

( $t = 1.2$ ,  $P = 0.25$ ; Fig. 4a). We also found no significant positive selection on length associated with nest occupation in the nonlimited treatment ( $t = 1.8$ ,  $P = 0.09$ ; Fig. 4a), which was as expected.

We did not detect statistically significant selection on length associated with the acquisition of matings among nest-holding males in any of the treatments (all  $P > 0.1$ ; Fig. 4b).

Calculated on mating success at the end of the experiment, we found positive total selection on male length in the mate-limited treatment ( $t = 2.5$ ,  $P = 0.02$ ), but not in the nonlimited ( $t = 1.5$ ,  $P = 0.15$ ) or nest-limited ( $t = 0.7$ ,  $P = 0.51$ ) treatments (Fig. 4c). Notably, there was a large male advantage in mating in the nonlimited treatment at an early stage of the experiment (24 h; Fig. S2).

#### Seasonal change in the strength of sexual selection

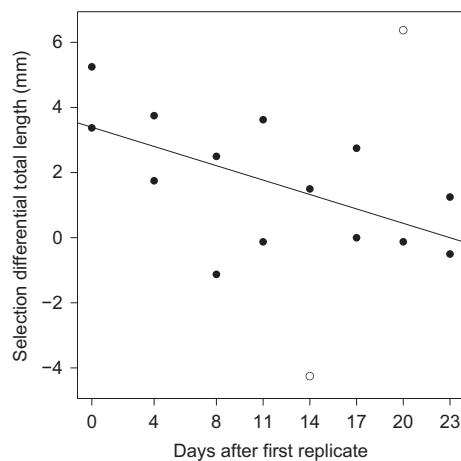
We tested whether the strength of selection on length changed over the breeding season, using linear regressions. As male–male competition is less extensive late in the season (Forsgren *et al.*, 2004), we might expect diminishing selection as the season progresses. The inspection of Cook's distances revealed two outliers with high leverage effects in the mate-limited treatment (Fig. 5). When removing these, the strength of selection on male length decreased significantly over the course of the season (measured as days after the start of the first replicate) in the mate-limited treatment (slope:  $-0.15 \pm 0.06$  mm\*day $^{-1}$ ;  $r^2 = 0.37$ ,  $F_{1,12} = 7.0$ ,

$P = 0.02$ ; Fig. 5). Including the two outliers, the seasonal effect was nonsignificant ( $-0.11 \pm 0.09$  mm\*day $^{-1}$ ;  $r^2 = 0.10$ ,  $F_{1,14} = 1.5$ ,  $P = 0.25$ ). Time in season did not affect the strength of selection in the nest-limited ( $r^2 = 0.00$ ,  $F_{1,13} = 0.0$ ,  $P = 0.96$ ) or in the nonlimited ( $r^2 = 0.01$ ,  $F_{1,12} = 0.1$ ,  $P = 0.72$ ) treatment.

#### Discussion

We found that limited access to mates increased male–male competition by means of agonistic interactions and courtship and led to selection on male body size, whereas the nonlimited treatment resulted in less competition and a high proportion of males that occupied nests and mated. Positive selection on male body size in the mate-limited treatment was an effect of larger males more often being nest owners and of larger males more often mating when holding a nest. The former finding is noticeable, because nests were present in excess in this treatment. By contrast, limited access to nests, a resource required to breed in the species, did not lead to increased male–male competition or significant selection on male body size. These effects were absent in the nest-limited treatment despite that larger males were more likely to be involved in agonistic interactions than smaller ones, and despite that the opportunity for selection was similarly high as in the mate-limited treatment. Taken together, the results demonstrate that limited access to resources required to mate, and to mates as such, can differ in their effects





**Fig. 5** Selection differentials for male total length (mm) in relation to breeding season (days after the start of the first replicate) in an experimental treatment limiting male access to mates in the two-spotted goby (*Gobiussculus flavescens*). The line shows the estimated relationship from a linear regression after the removal of two influential outliers (open circles; see text).

on sexual selection on male size, a trait of major ecological importance. They also show that competition for resources and for mates can be inter-related, as selection on body size in the mate-limited treatment was partly caused by a large male advantage in nest acquisition. These results question whether the processes of resource competition and mating competition are really distinct processes that can be separated theoretically and empirically.

### The effects of resource and mating competition on sexual selection

Our results suggest that mate availability but not nest availability affects sexual selection on male size in two-spotted gobies. That mate availability matters is in line with previous work on two-spotted gobies, which has demonstrated that variation in the operational sex ratio is a major determinant of sexual selection in the species (Forsgren *et al.*, 2004; Myhre *et al.*, 2012; Wacker *et al.*, 2013). However, the finding that limited access to nest sites did not increase male–male competition or selection on male body size is in contrast to findings in many other species with resource-based mating systems (Andersson, 1994; Blanckenhorn, 2005), including closely related gobies (sand goby: Lindström, 1988, 1992; Forsgren *et al.*, 1996; common goby, *Pomatoschistus microps*: Magnhagen, 1994; Borg *et al.*, 2002). In both the nest-limited and the nonlimited treatments of our experiment, the level of agonistic acts was moderate, but larger males performed more agonistic behaviours than smaller males (as previously found in the species; Wacker *et al.*, 2012). In the early

phase of the experiment, this led to an advantage of larger males in the monopolization of mates in the non-limited treatment, but not in the nest-limited treatment (Fig. S2). These results suggest that nest site shortage prevented large males from monopolizing matings. Nest possession may not primarily be regulated by aggressive behaviour in this species, at least not when mates are not limited. As a consequence, small and large males were equally successful in taking up nests in the nest-limited treatment. Small nest-holding males would then have been able to acquire matings, which were not limited in that treatment.

A small proportion of males did not take up nests in the nonlimited treatment, when nests and mates were provided in excess. This may have been because some individuals were not fully acclimated to the experimental conditions, or not quite ready-to-mate. It may, however, also reflect a low level of male–male competition for territorial space even when nests are plentiful. Whatever explanation is valid, the fact that some males remained unmated is unproblematic to our experimental design, as the proportions of nest-holding and mated males were much higher in the nonlimited than in the two limited treatments. Thus, the experiment succeeded in establishing the intended strong contrast in the level of competition.

Knowledge on the relative importance of resource and mate competition is crucial for predicting how ecological factors affect sexual selection, a key question in sexual selection research (Shuster & Wade, 2003). Our results suggest that mate availability, but not nest availability, affects sexual selection in the two-spotted goby. Those two ecological factors are considered to be of general importance in the regulation of sexual selection across animal taxa (Emlen & Oring, 1977; Shuster & Wade, 2003). However, their relative importance has rarely been addressed by empirical studies. Our results emphasize the importance of considering all types of competition in studies of sexual selection (Ahnesjö *et al.*, 2001; Shuster & Wade, 2003; Klug *et al.*, 2010b). Studying one type of competition in isolation can be relevant in the context of certain research questions, but does not necessarily reflect sexual selection as a whole (Hunt *et al.*, 2009; Klug *et al.*, 2010b). Although this conclusion seems trivial, it is rarely acknowledged and often ignored in empirical works (but see Klug *et al.*, 2010b).

Whereas sexual selection acted on male size only in the mate-limited treatment, the opportunity for selection was similar for the nest and the mate-limited treatments. This leads to two conclusions. First, one cannot infer ongoing selection from the variance in mating success. This point has been made in several theoretical (Arnold & Wade, 1984; Shuster & Wade, 2003; Jones, 2009; Klug *et al.*, 2010a) and empirical works (Klemme *et al.*, 2007; Fitze & Le Galliard, 2011; Wacker *et al.*, 2013), but is not always acknowledged (Klug *et al.*,

2010a). Second, resource and mate competition may differ in their effects on sexual selection not only when they generate different levels of variation in mating success (Klug *et al.*, 2010b), but also when variation in mating success is similar, but related to phenotypic traits only for one type of competition. Thus, the evolutionary consequences of nest and mate competition, respectively, cannot be explored on the basis of variation in mating success alone.

### The inter-relatedness of resource and mating competition

An important insight from our study is that the behavioural processes of resource and mating competition may not always be clearly distinguishable, but may instead be tightly inter-related. This was evident from sexual selection in the mate-limited treatment partly being the result of a large male advantage in nest acquisition. This finding has implications both theoretically and for empirical work. For example, the OSR (i.e. mate availability) is generally expected to affect mating competition, but not resource competition (Ahnesjö *et al.*, 2001). In contrast, our results suggest that large males monopolize mates by controlling the access to nests when mates are limited, representing an effect of mate availability on resource competition. As a consequence, treating resource and mating competition as independent and temporally separate processes in models of sexual selection may result in misleading conclusions.

That resource and mating competition are potentially inter-related stresses the importance of considering both processes also in empirical studies of sexual selection. This is often not the case. For instance, many field studies quantify sexual selection without considering non-resource-holding individuals, often because of practical limitations in sampling those individuals (Shuster & Wade, 2003; Klug *et al.*, 2010b). However, such studies not only miss any effects of resource competition (Shuster & Wade, 2003; Klug *et al.*, 2010b), but may also fail to capture important effects of mating competition that show up in interactions over breeding resources.

Our findings have implications for the quantification of resource and mating competition in empirical work. The results show that it can be misleading to distinguish between resource and mating competition on the basis of nest ownership and mating success among nest owners, as is often done (e.g. Magnhagen & Kvarnemo, 1989; Forsgren *et al.*, 1996; Klug *et al.*, 2010b). In studies adopting that approach, selection differentials calculated by comparing resource holders with the population average are typically attributed to resource competition, and selection differentials calculated by comparing mated resource holders with all resource holders are typically attributed to mating

competition. The application of this approach within experimental treatments of the present study shows that such inference can be too simplistic and miss important aspects of sexual competition. Within the mate-limited treatment, such calculations indicated that both resource competition and mating competition affected sexual selection on male body size. This result is counterintuitive, as matings, but not nests, were limited in this treatment and as we detected no selection on body size when nests were limited. Below, we propose two behavioural mechanisms (scenarios) that may have produced the large male advantage in nest ownership in the mate-limited treatment, involving behaviours attributable to either resource or mating competition.

First, large males may have agonistically prevented smaller males from holding a nest, thereby preventing them from courting (limited) females. Such behaviour would be defined as nest competition. Second, large males may have physically prevented smaller males from courting (e.g. by courtship interference), causing such males not to take up nests. Then, the observed behaviour would be defined as mating competition. These scenarios illustrate the importance of distinguishing between resource and mating competition defined as competitive situations and defined as realized behaviour (Kokko *et al.*, 2012). In the first scenario, the observed behavioural process is nest competition, even though it is ultimately aimed to secure limited matings, reflecting the competitive situation. Thus, the alternative meanings of 'mating competition' are not interchangeable and both theoretical and empirical works should be explicit in which meaning of the term is adopted (Kokko *et al.*, 2012).

We are not claiming that the processes of resource competition and mating competition interact, or overlap in time, in all species. In some species, resource competition may precede mating competition, with the two processes being completely separated (Ahnesjö *et al.*, 2001; Klug *et al.*, 2010b). However, it is largely unknown how widespread the scenario of an inter-relatedness of mating and resource competition is in nature. Therefore, there is an urgent need for empirical studies addressing the relative importance and inter-relatedness of mating and resource competition across animal taxa. Notably, the need for such studies has been acknowledged for the closely related question of the importance of male–male competition versus female choice in sexual selection, which has led to a better understanding of sexual selection (Bradbury & Davies, 1987; Berglund *et al.*, 1996; Hunt *et al.*, 2009). We could not have detected the inter-relatedness of resource and mating competition in our model species without the experimental design of comparing the effects of mate and nest limitation. Thus, we believe that the novel experimental approach of this study has the potential to significantly improve our understand-

ing of how resource and mating competition relate in the animal kingdom.

### Seasonal change in the strength of sexual selection

The strength of sexual selection in the mate-limited treatment decreased over the breeding season. This is in line with a previous finding that female choice for male body size decreases over the breeding season (Borg *et al.*, 2006). Thus, female choice likely explained the seasonal effect on sexual selection that we found, or at least part of it. A seasonal change in the strength of sexual selection in male two-spotted gobies is expected from the seasonal change in the OSR from male- to female-biased (Forsgren *et al.*, 2004). Male agonistic and courtship behaviour has been found to decrease over the season in the wild (Forsgren *et al.*, 2004; Myhre *et al.*, 2012), and recent experimental evidence has documented that the OSR causally affects male mating competition and sexual selection in the species (Wacker *et al.*, 2013). Within-season changes in the strength of sexual selection may have important evolutionary consequences, but have been little studied (Kasumovic *et al.*, 2008).

### Conclusions

Our study represents a novel experimental approach to the analysis of resource and mating competition, and their interaction, focusing on the underlying resource conflict and its consequences. We found that a shortage of mates was manifested in competition related to nest acquisition and in selection for large male size, whereas a shortage of nests did not result in the same competition for nests nor in selection for large males. These partly counterintuitive results reveal the complex interrelatedness of mate and resource competition. We suggest that these two 'episodes of selection' may not be temporally separate in many species and may in some cases be indistinguishable processes. This may have implications for sexual selection theory as well as for the interpretation of empirical results in studies of competition. We recommend that future studies aiming to analyse selection effects of mating and resource competition, and their potential interrelatedness, adopt protocols that experimentally manipulate the underlying resource conflict.

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## Supporting information

Additional Supporting Information may be found in the online version of this article:

**Figure S1** Proportions of two-spotted goby (*Gobiusculus flavescens*) males within trials that held a nest (black circles) and mated (grey circles) after (a) 24 h, (b) 48 h and (c) 64 h in experimental treatments limiting access to mates or nest sites or providing both resources in excess.

**Figure S2** Standardized selection differentials on male total length (solid circles) and their 95% CI in experimental treatments limiting access to either mates (mate-limited) or nest sites (nest-limited) or providing both resources in excess (nonlimited).

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