Will he stay or will he go? Features of nest-guarding common gobies affecting response to predation risk

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Individuals of the same species often show consistent differences in behaviour, categorized as personalities. For an animal with parental care, reproductive success may be affected by the behaviour of the parent. When reanalysing a previously published field study, I found that nest-guarding male common gobies, *Pomatoschistus microps*, showed individual differences in behavioural response to disturbance during simulated predation risk. There was also a difference in nesting success with some nests being abandoned prematurely. The males were tested over a nesting cycle with respect to individual behaviour patterns. Two behaviours were quantified, in the presence of a live eelpout, *Zoarces viviparus*, behind glass: (1) time away from nest after being evicted by the approach of a finger, and (2) the distance between the finger and the nest when the male escaped from the nest. Of 24 males studied, only half remained in their nest for the whole nesting cycle, while the other nests were abandoned earlier, failing in the current reproductive event. No direct effects of behaviour were found in males that abandoned early or remained at the nest for the full nesting cycle. However, larger males stayed away from the nest for longer and more often abandoned their nests prematurely than smaller males. This may be explained by a better competitive ability to renest for a larger male. Behaviour, but not nesting success, was also connected with brood size. Males with smaller broods stayed away from the nest for longer. Nesting success thus seemed to result from a combination of size and male personality.

In fish with parental care, reproductive success may be affected by individual behavioural traits of the parent, in combination with environmental characteristics, such as the availability of nest sites and/or the amount of predation risk. A well-studied trade-off is that between investing in the current offspring and future possibilities of reproduction (Clutton-Brock, 1991; Sargent, 1986; Sargent & Gross, 1985; Stearns, 1992). Parents sometimes face a trade-off between reproductive efforts and survival (Cole & Quinn, 2014) and lifetime reproductive success may increase if current parental care decreases (Ward et al., 2009). Individuals within populations may trade current and future reproduction in different ways (Wolf et al., 2007). For example, individuals have been found to differ consistently in parental care, as a result of differences in personality (Burtka & Grindstaff, 2013; Stein & Bell, 2015). There may, however, be several reasons for a parent's decision to invest in or to abandon the current brood, such as predation risk (Deal et al., 2017; Magnhagen, 2008). Risk of predation can also change reproductive behaviour (Magnhagen, 1991), as well as increase competition for

safe nest sites (Lindström & Ranta, 1992). Further, variation in resource acquisition ability may affect the relationship between individual behaviour patterns and investment in current reproduction (Laskowski et al., 2021; Haave-Audet et al., 2022).

Consistent individual differences in behaviour (termed personality, temperament or behavioural syndromes) have been demonstrated in a variety of taxa (Gosling, 2001; Reale et al., 2007; Sih et al., 2004). Personality may be defined by behavioural correlations within or across situations, or by consistent behavioural differences between individuals over time (e.g. Reale et al., 2007; Sih et al., 2004). One aspect of personality is the bold/shy continuum (Wilson et al., 1993), and the degree of boldness may influence the individual's reproductive success (Ballew et al., 2017; Reale et al., 2009). The maintenance of behavioural differences within populations has been explained by fluctuations in the environment that lead to temporal variation in the fitness of individuals with different personalities (Dingemanse et al., 2004; Magnhagen et al., 2014). Studies on the effect of personality and behaviour on fitness and reproductive success have considered mate preference (de Oliveira et al., 2021; Godin & Dugatkin, 1996; Kalb et al., 2016; Kniel & Godin, 2020; Patrick et al., 2012; Teyssier et al., 2014), nest

acquisition (Kalb et al., 2016; Seltmann et al., 2014; Zhao et al., 2016) and survival of the offspring (Dingemanse et al., 2004; Boon et al., 2007; Wetzel, 2017). Here, I investigated whether the behaviour of male common gobies, *Pomatoschistus microps*, under simulated predation risk varies consistently between individuals. If so, could these differences lead to variation in nest-guarding success, in terms of who stays with the nest during a whole nesting cycle or who abandons it prematurely?

The common goby is a small marine fish living in shallow soft-bottom areas along the coasts of Europe. It is short-lived and reproduces repeatedly during one season only (May—August; Miller, 1975). The males use mainly bivalve shells as nest material, which they cover with sand, excavating underneath the shell. The females place their eggs in a layer in the ceiling of the nest, and the males guard and fan the eggs until hatching. Caring effort has been found to increase with time spent guarding and with brood size (Magnhagen & Vestergaard, 1991, 1993). The species has been used in earlier studies dealing with trade-offs between reproductive investments and risk avoidance (Magnhagen & Vestergaard, 1991, 1993), alternative reproductive tactics (Magnhagen, 1992, 1994, 1998), sexual selection (Heubel, 2018) and personality (Kalb et al., 2016; Vallon et al., 2016). Competition for nest sites can also affect the reproductive behaviour of male gobies (Borg et al., 2002).

The data used in the current article are taken from an earlier field study on risk taking in connection with current reproductive investments and probabilities of future reproductive opportunities (Magnhagen & Vestergaard, 1991). We simulated a situation in which there was a potential trade-off between a male's own survival and offspring survival. We showed that male common gobies took higher risks with increasing time spent guarding a brood, that is, with time after spawning. This was explained by the increasing probability of the offspring to survive to hatching. The males also showed higher risk taking later in the season, with a decrease in probability of future reproduction (Magnhagen & Vestergaard, 1991). In the original article we found that the presence of the predator made the male stay away longer compared to in its absence (Magnhagen & Vestergaard, 1991). We also found that an increased boldness with time since spawning was not related to habituation to the treatment (Magnhagen & Vestergaard, 1991).

Here, I looked at behavioural variation between males, which was not considered earlier. If behaviour differs consistently between individuals, the question is whether these differences are also reflected in the nest holders' reproductive success. The hypothesis is that bolder individuals, taking higher risks to guard their nests, are more successful in keeping their nest for the whole nesting cycle, from spawning to hatching of the offspring.

METHODS

The field study was carried out in May 1989 (Magnhagen & Vestergaard, 1991), at the Isefjord Laboratory, Vellerup Vig (Zealand, Denmark, 55°44′N, 11°52′E). The common goby was very abundant in the shallow soft-bottom bay in the vicinity of the laboratory. Clay flowerpots (width 4.5 cm, depth 4 cm), cut in half, were used as nest material. The pots are within the size range of the mussel shells usually used for nests in this species, and commonly used in studies of goby reproduction. The pots were placed on the bottom at 30—50 cm depth, about 1.5 m apart, and their locations were marked with sticks. After 1 day, 56 nests had been built from in total 60 pots. Of these nests nine had received eggs, and after 2 days there were another 15 nests with eggs. The nest-holding males were captured with dip-nets, and their body length measured (average total body length $\pm$ SD, 44.0 ± 2.1 mm, $N = 24$). Nest area covered with eggs was measured as length $\times$ width (average area 6.6 ± 2.3 cm^2, $N = 19$). To check that the same fish occupied the

nest throughout the observation period, the males were individually marked by cutting a small piece of the tail fin with a fine pair of scissors. The marked fish were identified on day 6 by catching them from the nest by dip-net and studying them in a small transparent box with water (8×6 cm and 5 cm deep), before putting them back in front of the nest opening. The male always returned to the nest after it was put back in its original position. The remaining males ($N = 16$) were the same as on day 1.

We used eelpout, *Zoarces viviparus* (body length around 20 cm) to simulate predation risk. They were caught with a fyke-net in the vicinity of the field station, kept in a net pen between tests, and released at the end of the study. During the tests one eelpout was put in a glass jar (20×8 cm and 18 cm deep) with a glass lid. The water was exchanged several times during this period, when going from one nest to another, and each session lasted about 2 h.

To study the response of parental male gobies to predators, the jar with the eelpout was placed approximately 15 cm from the nest (Fig. 1). As the nest-guarding male was lying with the head outside the nest opening, the observer slowly moved a hand, with an outstretched finger, through the water towards the nest opening until the male left the nest. Two variables were measured: the distance of the finger from the head of the fish when the fish left the nest (escape distance) and the time from leaving until returning to the nest (time away from nest). Distance was estimated with a ruler after the fish left. Maximum time measured was 180 s; longer times away were calculated as 180 s. Short escape distances and short times away from the nest were interpreted as taking high risks of being caught by the predator, thus showing a high degree of boldness. The risk of nest predation would increase with an increase in the time the male stayed away from the nest. On day 1 we also performed the same test without the presence of a predator, to get an indication of whether the predator was perceived as a threat to the goby. We made three consecutive tests with each fish each day until the nest was abandoned (4—8 days, i.e. 12—24 tests per fish with a predator present), starting the day after the male had received eggs in his nest. The water temperature varied during the study from 14.5 °C at the beginning of the nesting cycle to 28 °C (an exceptionally warm day at the end of the nesting cycle, day 6—7), with an average of 19.3 °C. At this temperature the hatching time for the embryos in the nest would be approximately 8 days (Magnhagen & Vestergaard, 1993).

Statistical Analyses

The behavioural measures for the first 4 days after spawning were used in the analyses here, to compare males with different nest-guarding success (since some males had already abandoned the nest after 4 days). In most analyses the median values for each individual and day were used, to avoid pseudoreplication. All the estimates were used only in the mixed-effects models using individual as a random effect (see below).

Males remaining in their nest for different numbers of days (indicating nest-guarding success) were assigned to three 'success' groups (remaining for 8 days, leaving after 6—7 days or leaving after 4—5 days). To test whether these groups showed different behaviour patterns, repeated-measures ANOVAs were performed. The individual daily median values of time away from nest and escape distance, repeated over the first 4 days, were used as response variables. The day and nesting success were set as between-subject effects and tested fish individual as a within-subject effect. Tukey's post hoc test was used to identify differences between groups where the ANOVA showed significance.

Mixed-effects models (GLMM) were used to assess the proportion of the total variation in behaviour explained by differences between individuals. The two measured behaviours, time away

Figure 1. Experimental set-up with simulated predation risk in the form of an eelpout, enclosed in a glass jar, in front of the goby nest to the left (only the rim of the pot is visible at the opening). A common goby is seen leaving the area in the bottom of the photograph. Photo: Carin Magnhagen.

from nest and escape distance, were used as response variables, and day from spawning (1–4) as a fixed continuous variable. Individual, and the three daily repeats, nested in individual, were added as random effects. Variance components analysis of the random effects was carried out to decompose the variation explained by the within-individual and between-individual effects (Pinheiro & Bates, 2000; Börger et al., 2006).

To test for a correlation between the two quantified behaviours, time away and escape distance, the average measure of the 4 days was used for each individual in Pearson correlation tests.

Consistency between situations, comparing behaviour with and without a predator, measured on day 1, were tested with Spearman rank correlations, using the median value of the three tests per individual. The effects of predator treatment (presence/absence) on behaviour were tested with Wilcoxon matched-pair comparisons.

The differences in body length and brood size of males in the three 'nest success' groups were tested with one-way ANOVA. To test the effect of body size and brood size on behaviour, the individual average measures over the 4 days, of time away from nest and escape distance, were used in Pearson correlation tests.

Analyses were performed with Statistica (v. 13, TIBCO Software Inc. 2018), except for the GLMMs where R version 4.0.3 (2020), library (nlme) was used. Values that exert extreme influence on the regression fit were identified using 'Cook's distance' which measures the impact of the respective value on the regression equation (Fox, 2002). Data sets that did not conform to the requirements for parametric testing were analysed with nonparametric tests (Spearman rank, Wilcoxon matched-pair comparison).

Ethical Note

Fish were handled carefully, to avoid affecting their natural behaviour. The fish were studied in their natural environment and none died during the study. When catching the fish for measuring and marking, we quickly placed them in a small Plexiglas box with water to avoid exposing them to air and to minimize handling of the fish. At the time of the data collection there were no requirements for an ethical permit for field studies. However, the methods used in this study comply with the ASAB/ABS guidelines.

RESULTS

Twelve of the males remained at their nest for 8 days and were probably successful in the hatching of their offspring. Eight males abandoned the nest after 4–5 days. These nests were found with the pot standing upright in the sand, with no eggs remaining. The remaining four nests were abandoned after 6–7 days, but the cause is uncertain. The males were thus divided into three groups with respect to days spent guarding the nest (nest-guarding success score, 1–3). The repeated-measures ANOVA showed that both time away from nest and escape distance differed between days, with the highest values at the beginning of the test period, but there was no effect of nesting success (Table 1, Fig. 2).

The GLMMs indicated that day had a significant effect on both time away from nest and escape distance (Table 2). The variance components showed that differences between individuals explained 32–35% of the total variation in behaviour, while differences within individuals (controlled for day) were negligible (Table 2).

Individual averages of time away from nest and escape distance across the first 4 days were positively correlated (Pearson correlation test: $t_{22} = 2.89$, $R^2 = 0.28$, $P = 0.008$; Fig. 3). Also, averages between tests with and without predator presence on day 1 were positively correlated (Spearman rank correlation: time away: $t = 3.11$, $r_s = 0.55$, $P = 0.005$; escape distance: $t = 5.48$, $r_s = 0.76$, $N = 24$, $P < 0.001$; Fig. 4). Time away from nest was longer in the presence of a predator than in its absence (Wilcoxon matched-pair comparison: $z = 3.15$, $N = 24$, $P = 0.002$), and escape distance was shorter in the presence of a predator ($z = 2.30$, $N = 24$, $P = 0.021$).

Table 1
Repeated measures ANOVA on the effects of day (1–4) and nesting success (three groups) on the behaviour of nest-guarding male common gobies after being chased away in the presence of a predator

	Time from nest				Escape distance			
	F	df	P	Tukey	F	df	P	Tukey
Day	12.58	3, 54	**<0.001**	1 > 2–4, 2 > 4	5.31	3, 54	**0.002**	4 < 1, 2
Nesting success	0.22	2, 18	0.80		0.37	2, 18	0.70	
Day∗success	1.94	6, 54	0.091		0.32	6, 54	0.81	

The day (repeated measure) and nesting success are between-subject effects; individual is a within-subject effect. Significant P values are in bold. Tukey post hoc test shows significant differences between days.

Body length differed between males from the three nest-guarding success groups. The males that abandoned the nest after 4–5 days were larger (mean ± SD = 45.6 ± 1.7 mm) than those that remained for 6–7 days (43.0 ± 1.4 mm) or 8 days (43.1 ± 1.9 mm; ANOVA: $F_{2, 21} = 5.68$, $P = 0.011$, Tukey post hoc: size at 4–5 days > size at 8 days; Fig. 5). No differences in brood size were found between the groups ($F_{2, 16} = 0.06$, $P = 0.94$).

An individual average across all 4 days showed a positive correlation between time away from nest and body length (Pearson correlation test: $t_{22} = 2.17$, $R^2 = 0.27$, $P = 0.041$), and a negative correlation between time away and egg area ($t_{16} = -2.62$, $R^2 = 0.30$, $P = 0.019$). One outlier was removed for the analysis on the effect of egg area because of the bias this case made on the estimation of the regression coefficients (correlation without removal: $t_{17} = -1.67$, $R^2 = 0.14$, $P = 0.11$; Cook's distance = 0.52; Fig. 6). This fish abandoned the nest early, but still had a short time away and a short escape distance, in contrast to the others in its 'success group'.
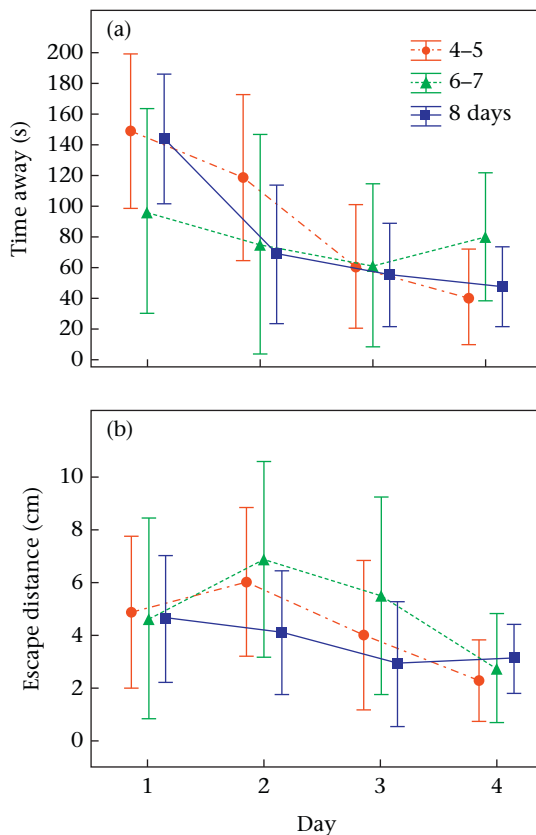
There were no correlations between escape distance and body length ($t_{22} = 0.04$, $R^2 = 0.00$, $P = 0.99$) or egg area ($t_{17} = 0.85$, $R^2 = 0.02$, $P = 0.85$).

DISCUSSION

The individual males responded differently when being chased from their nests in the presence of a predator, even though the average measurements of escape distance and time away from the nest showed a general decrease with day after spawning (see also Magnhagen & Vestergaard, 1991). About a third of the total variation in behaviour was explained by differences between males (controlled for day). In a field study like this, there are, of course, factors in the surroundings that cannot be controlled for during the tests. This may be the cause of the high residual variance components. However, the two measured behaviours were positively

Table 2
Statistical results for the behaviours tested in GLMMs, including Wald statistics and variance components

	Time away			Escape distance		
	F	df	P	F	df	P
Day	99.1	1, 200	**<0.001**	32.9	1, 200	**<0.001**
Variation explained						
Within individual (%)	<0.1			<0.1		
Among individuals (%)	32.1			35.1		
Residual (%)	67.9			64.9		

Day, i.e. day after spawning, is the fixed effect, tested for time away from nest and escape distance. Significant P values are in bold. The table also gives the percentage of the total variation of behaviour explained by the nesting factors within an individual, among individuals and the residual variance of the random effects of the mixed-effect model.
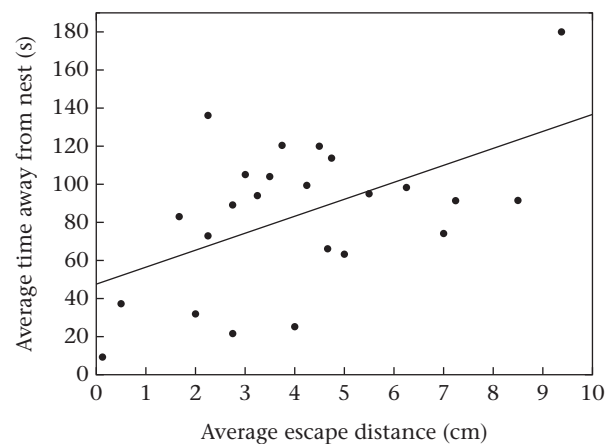

Figure 2. (a) Time away from nest and (b) escape distance (from the approaching finger), for male common gobies chased from their nest, 4 days from the day after spawning. The males are divided up in three groups according to their 'nesting success', i.e. number of days remaining by their nest. Data points show means ± 95% confidence interval.

Figure 3. Correlation between time away from nest and escape distance (from the approaching finger), for individual male common gobies chased from their nest. Data points show individual mean values of the first 4 days of testing, and the line shows the result from a Pearson correlation test ($P < 0.01$).
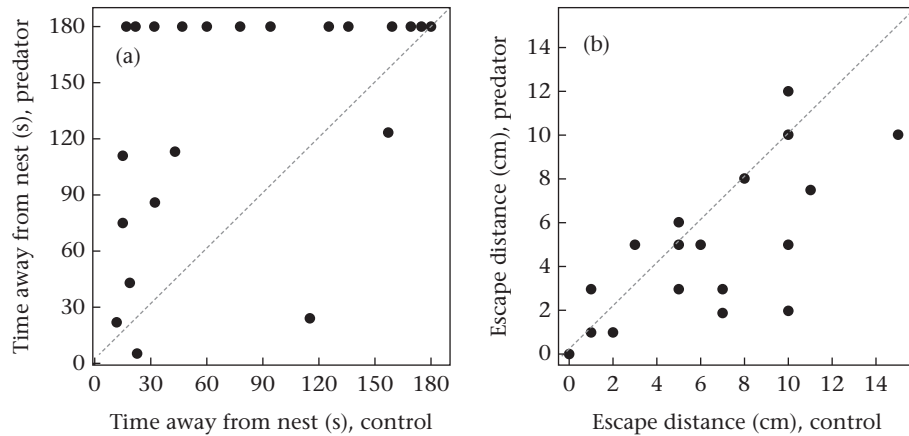
Figure 4. Correlations between (a) time away from nest and (b) escape distance (from the approaching finger), in the presence and absence (control) of a predator on day 1 of the breeding cycle. Data points show individual median values of the three tests per treatment. Dotted lines show the expected relation if no difference between treatments were found.

correlated, suggesting an occurrence of consistent differences in boldness between males. Further, the correlations between behavioural measures with and without a predator present indicates differences between individuals. These comparisons also show that the presence of the predator was considered as a threat. Consistent differences in activity (Vallon et al., 2016) and exploration tendencies (Kalb et al., 2016) have also been found in this species.

In the current study, none of the behaviours connected to boldness could be directly associated with nesting success, that is, number of days spent guarding the nest before it was abandoned. Several other studies have shown that individual reproductive success can be associated with behavioural variation in boldness and aggressiveness. A meta-analysis across taxa found that bolder individuals, especially males, had a higher reproductive success than shyer ones (Smith & Blumstein, 2008). In the common goby the acquisition of a nest site is essential for reproduction, and male personality may have an effect on nest monopolization (Kalb et al., 2016). Furthermore, in zebrafish, *Danio rerio*, spawning in the open water, bold males fertilized more eggs than other males (Ariyomo &

Watt, 2012). In largemouth bass, *Micropterus salmoides*, bolder males had greater reproductive success, in terms of number of offspring, compared to shyer males (Ballew et al., 2017). The influence of boldness on reproductive success may, however, depend on age (Reale et al., 2009), size (Ballew et al., 2017) or environmental factors (Dingemanse et al., 2004).

Instead, goby male size seemed to affect nest-guarding persistence. Surprisingly, larger males often failed with the current brood, more frequently getting their nest destroyed after 4–5 days, compared to smaller ones. There was also an effect of size on time away from nest, with larger males on average staying away for longer. Although there was no direct effect of behaviour on nesting success, these two results indicated that larger males may fail because they showed less bold behaviour than smaller ones. There could be several reasons why larger males failed to stay on their nest for the whole nesting cycle. The abandoned nests were disarranged and seemingly raided by egg predators. For example, the shore crab, *Carcinus maenas*, and the netted dogwhelk, *Tritia reticulata*, have both been found to prey on eggs in goby nests (Kvarnemo, 1995; Olsson et al., 2016; although the dogwhelk may not be able to move the clay pot). Egg predation could depend on the males not guarding the nests efficiently, indicated by the longer times away from the nest of the larger males in our tests. However, the occurrence of filial cannibalism has also been found in the common goby (Svensson et al., 1998; Vallon et al., 2016) and the closely related sand goby, *Pomatoschistus minutus* (Lissåker & Svensson, 2008), and cannot be ruled out here. In that case, the male itself would have instigated the desertion of the nest.

There is often a trade-off between investment in the current offspring and future reproductive events (Sargent & Gross, 1985), and size may be one factor affecting the ability of male common gobies to get access to nest sites and mates. Larger common gobies can evict smaller males from their nests (Magnhagen, 1998). In the closely related sand goby large males occupied nest sites more often than small ones, when presented to the nest simultaneously (Magnhagen & Kvarnemo, 1989). Female preference is not necessarily determined by size in gobies but may be based on complex interactions between nest construction (Svensson & Kvarnemo, 2005; Kalb et al., 2016), visual and acoustic courtship intensity (Amorim et al., 2013; Forsgren, 1997b) and parental ability (Forsgren, 1997a; Takahashi & Kohda, 2004). However, in the common goby, females preferred larger males with elaborate nests, and did not choose mates according to personality (Kalb et al., 2016). Size preference in female common gobies may, though, depend on social context (Heubel, 2018).
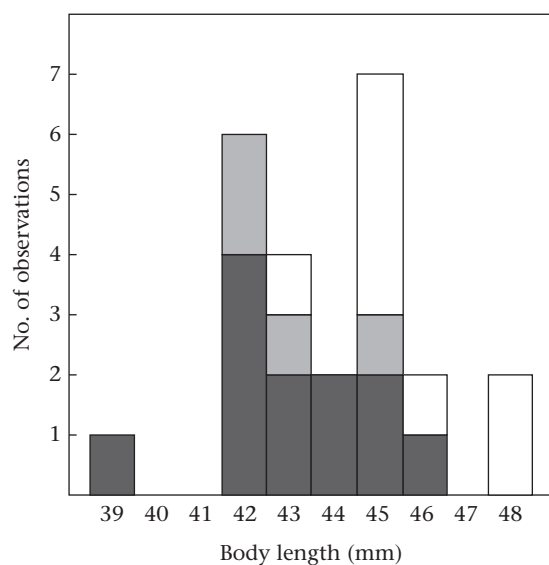

Figure 5. Size distribution of male common gobies used in the study. White bars denote males that abandoned their nests after 4–5 days, light grey bars those that were gone after 6–7 days and dark grey bars show males that was still by the nest after 8 days.
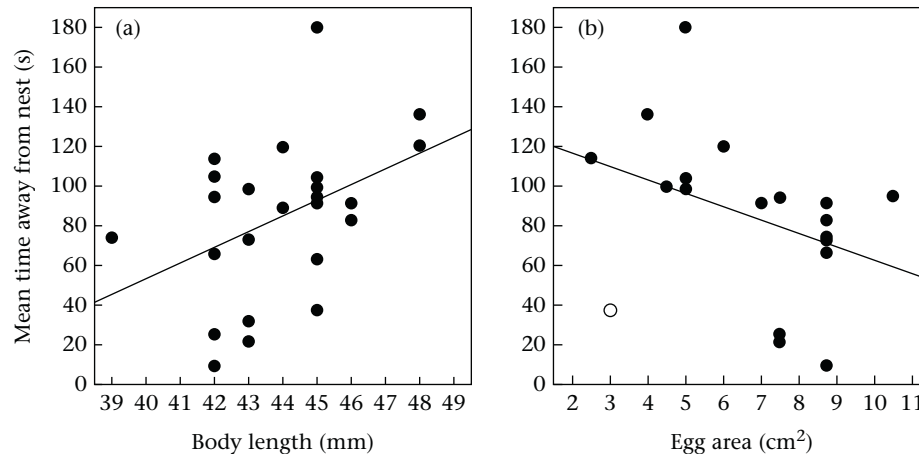
Figure 6. Correlations between time away from nest and (a) body length and (b) area of the nest covered with eggs. Data points show individual mean values of the first 4 days of testing, and the lines show the results from Pearson correlation tests ($P < 0.05$). In (b), one outlier, shown as an open circle, was removed from the analysis according to Cook's distance.

Larger males would have a higher probability of occupying a new nest compared to smaller males in a competitive situation (Magnhagen, 1998; Magnhagen & Kvarnemo, 1989). In the field study, 56 of 60 flowerpots were occupied the day after we placed them in our field study area, indicating that competition for natural nest material was high. If smaller males are less competitive regarding nest occupation, they would have a higher motivation to invest in the current brood in spite of the daily disturbances. Our results could then be in accordance with the suggestion that acquisition ability is affecting the relation between reproductive allocation and personality (Laskowski et al., 2021; Haave-Audet et al., 2022).

The behaviour of the males differed not only with male size but also with brood size, measured as the area of the nest covered with eggs. With a larger brood size, the male returned faster to his nest. This makes sense as brood defence should be greater for larger broods, since a large brood would have a higher reproductive value than a small one (Sargent, 1986). In the common goby, nest-guarding males spent more time fanning a larger brood (Vallon & Heubel, 2017), and defended their nests more aggressively when their broods were larger (Magnhagen & Vestergaard, 1993). Also in smallmouth bass, *Micropterus dolomieui*, males increased their defence with brood size (Ridgway, 1989; but see Steinhart et al., 2008).

Conclusions

The nest-guarding males showed consistent individual differences in the quantified behaviours. No direct effect of male behaviour was found on nest-guarding success. However, an indirect result, with larger males staying away for longer from the nest and more often failing to complete the nesting cycle, implies that behaviour may play a role in reproductive success. Whether this can be explained by a higher ability of larger males to acquire a new nest should be investigated further. However, other confounding factors, such as density and location of nest predators would also affect the nesting success of the parental males.

Author Contributions

The field study that this paper is based on was performed in 1989, and there is one publication on the data already (Magnhagen & Vestergaard, 1991). My collaborator Klaus Vestergaard sadly died about 20 years ago, and in the current paper I have reanalysed some of the data using a new perspective. All these analyses were made by me alone, but I do acknowledge my former collaborator.

Data Availability

Data are available at Mendeley https://doi.org/10.17632/r38h47tyd6.1. See Magnhagen (2023).

Declaration of Interest

I declare that I have no conflict of interest.

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