Plasticity in reproductive behaviour in two populations of the peacock blenny

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Summary

In the peacock blenny (*Salaria pavo)* the reproductive behaviour is described to vary between two populations that differ in nest availability. At the Gulf of Trieste (GT), Italy, where nest availability is high, conventional sex roles are present and males adopting an alternative parasitic reproductive tactic are rare. Conversely, at Ria Formosa (RF), Portugal, where nest site availability is low, females are the courting sex and a high percentage of parasitic males occur. Laboratory experiments were used to study the degree of plasticity of the reproductive behaviours used by females and by the two male morphs in both populations. Nesting males were sequentially presented with a female and a female-like parasitic male and the reproductive behaviours of all fish were quantified. Under similar laboratory conditions, nesting males from both populations did not differ in sexual or agonistic displays towards females or parasitic males, showing that males from the sex-reversed population are also able to express significant levels of courtship. In contrast, females followed the typical population pattern, with females from RF courting nesting males more and more readily than females from GT. We hypothesised that apparent differences in behavioural plasticity between nesting males and females were a consequence of the perception of the presence of eggs in the nest. Nesting males from both populations received an empty nest during test trials and, thus, had to court females in order to receive a first spawn. On the other hand, females were probably unaware of the presence or absence of eggs when presented to the nesting male and assumed the population typical courtship profile. Interestingly, the parasitic males' behaviour towards

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the nesting male closely followed the displays of females from their own population; parasitic males from RF courted the nesting male with a high frequency of female-like displays while parasitic males from GT failed to exhibit female-like courtship behaviour. Taken together, the results suggest that *S. pavo* presents high levels of plasticity in reproductive behaviours and that these may underlie the interpopulation differences in behaviour reported for the species. Additionally, the results also suggest that the parasitic male reproductive tactic at GT is not based on female-mimicry.

Keywords: behavioural plasticity, alternative reproductive tracts, courtship, *Salaria pavo*, blenniidae.

1. Introduction

Teleost fish are the vertebrate group presenting the most extreme examples of behavioural plasticity, particularly with regard to the expression of reproductive behaviours. The most striking examples are probably found among hermaphroditic species where the same animal may, according to environmental and internal cues, irreversibly switch from either male-to-female or female-to-male reproductive behaviours (sequential hermaphroditism, Warner, 1988) or switch back and forth between the male and female behavioural phenotypes (reversible hermaphroditism, Sunobe & Nakazono, 1993). Other examples of species with sequential alternative reproductive tactics include species where the same animal (usually males) may adopt a behavioural phenotype (e.g., a parasitic tactic) to reproduce under certain conditions and switch into another behavioural phenotype (e.g., a territorial tactic) in response to external and internal cues (Taborsky, 2001; Oliveira et al., 2005). Less dramatic examples illustrating behavioural phenotypic plasticity in teleosts can also be found. For example, males and females can adjust their sexual displays in a dynamic fashion throughout the same breeding season depending on the temporal variation of male and female potential reproductive rates, with sex roles switching between conventional (male courtship predominates) and reversed (female courtship predominates) (Forsgren et al., 2004; Shibata & Kohda, 2006). Thus, variation in behaviour between different populations of the same species may not necessarily reflect genetic differences but may be the outcome of variation in the behavioural response of similar genotypes to different environmental conditions. Phenotypic behavioural plasticity is now thought to have important evolutionary implications. On one hand, plasticity in the behavioural response to changing environmental conditions can be viewed as slowing down genetic evolution as the same genotype can originate different phenotypes, favouring individual adaption to local conditions (Pigliucci, 2005). On the other hand, when behavioural plasticity is costly and/or incomplete, it can originate directional selection of particular behavioural phenotypes under stable environmental conditions (DeWitt et al., 1998; Price et al., 2003). The study of phenotypic behavioural plasticity is, thus, essential for understanding the evolution of behaviours.

In the peacock blenny *Salaria pavo* Risso, inter-population variation in sex roles and in the expression of male alternative reproductive tactics has been described (Almada et al., 1995). This species is usually found in rocky shores of the Mediterranean and adjacent Atlantic areas, where males build nests in holes or crevices in the rock and defend courting territories around the entrance of the nest (Fishelson, 1963; Patzner et al., 1986; Zander, 1986). In these populations, nesting males are territorial and actively court females with conspicuous displays (coloration changes, 'figure-8 swimming') performed outside of the nest. Females respond to male courtship with changes in coloration and ultimately by entering the nest (Patzner et al., 1986). In a population found in a coastal lagoon at Ria Formosa (RF, southern Portugal), the reproductive behaviour is strikingly different, with females taking the leading role in courtship and males assuming a more passive role and hardly leaving the nest (Almada et al., 1994, 1995). These differences were hypothesized to be due to ecological constraints. At RF nesting substrate is very scarce and adequate sites are only found in artificial reefs built by clam culturists to delimit their fields (Almada et al., 1994). The scarcity and aggregation of nest sites has apparently promoted high competition for access to nests, thus excluding less competitive males from nesting. At the peak of the breeding season nests become filled with eggs and females compete for access to nesting males, thus resulting in the reversal of sex-roles in this population (Almada et al., 1995; Saraiva et al., 2009). A comparative study of the field behaviour exhibited by males and females of the RF population with the behaviour of animals from a population at the Gulf of Trieste (GT, Italy) that inhabit a rocky shore environment with abundance of nest sites, confirmed the reversal of sex-roles at RF and the conventional sex-roles at GT (Saraiva, 2009; Saraiva et al., in press). Another consequence of limited nesting sites in lagoon populations is the occurrence of a high proportion of alternative reproductive phenotypes among young males. Small, less competitive males that are unable to acquire a nest reproduce by mimicking female behaviour and morphology in order to enter nests and steal fertilizations from nest-holders (Ruchon et al., 1995; Gonçalves et al., 1996, 2003a). Inter-sexual copying by these parasitic males is not limited to behaviour and morphology but also involves copying female choice for nesting males (Gonçalves et al., 2003b), suggesting a strong social component of this behavioural tactic. The decision to reproduce as a parasitic male seems to be condition-dependent, as young males choosing to reproduce directly as nest holders or even to skip reproduction during their first breeding season also occur at RF. Additionally, both parasitic and immature males switch to the nest holder tactic from their second breeding season onwards, illustrating the flexibility of reproductive behaviours in this species (T. Fagundes, J. Saraiva, D. Gonçalves and R.F. Oliveira, unpublished). Interestingly, in the GT population a low proportion of males assuming a parasitic tactic have also been found but field observations failed to detect female-mimicking behaviour (Saraiva et al., in press). This suggests interpopulation variation both in the incidence of the parasitic tactic and in the behavioural expression of the tactic.

To investigate the degree of plasticity of reproductive behaviours in females and in the two male morphs from the RF and GT populations, we exposed nest-holder males, females and parasitic males from both populations to similar laboratory conditions and quantified the expression of reproductive behaviours. We predicted similar behavioural patterns if interpopulation differences are mainly a consequence of behavioural plasticity, and different behavioural profiles if differences between populations are inbuilt (i.e., are genetic or epigenetic).

2. Materials and methods

2.1. *Fish*

The experiments were carried out in the Marine Biology Laboratory of the University of Trieste, located in the GT in the Northern Adriatic Sea (Italy) and at Culatra Island, located in RF in the Algarve (Portugal). The RF population occurs in a mudflat area where natural substrate appropriate for nesting is absent. Fish reproduce in artificial materials (usually bricks) used to delimit clam culture fields and the availability of potential nesting sites is very low. In Trieste, the substrate is mainly constituted by limestone rocks and boulders that create an intricate labyrinth of crevices, holes and galleries of many shapes and sizes, thus providing appropriate nesting sites in abundance (Saraiva, 2009). Fish were captured with a food trap while snorkelling (GT) or during low tide in bricks (RF) and transported to the laboratory in aerated containers. Nest-holder males, females and parasitic males were housed separately in large tanks with abundant shelter (and available nests in the case of nesting males). Parasitic males were identified as small males that did not exhibit secondary sexual characters and from which sperm release could be elicited after gently pressing the abdominal cavity (Gonçalves et al., 1996).

2.2. Presentation tests

The experimental room was illuminated by natural light (GT) or by artificial light (RF) and in this case photoperiod was adjusted according to natural conditions. All fish were fed daily with mussels, *Mytilus edulis*.

Parental males were left to acclimate in 50-l individual test tanks either for 48 h (GT) or for 2 h (RF) prior to the onset of the experiment. Fish from GT were found to be more sensitive to captivity conditions, hence the longer habituation time. These individual tanks had the bottom covered with sand and contained one potential nest placed in the centre of the tank. In order to provide males with nests as familiar as possible to the ones found at their own natural location, the characteristics of the nests varied between the GT and the RF experimental set-up. In the GT, males nest in rock orifices, usually circular, with an internal volume ranging from 5 to 150 cm^3 (Saraiva et al., 2010) and, thus, PVC tubes measuring 15×3 cm diameter (106 cm^3) were used. At RF, males usually nest in brick holes (Almada et al., 1994; Oliveira et al., 1999) and opaque glass boxes of $21 \times 5 \times 5.5$ cm (577 cm^3) were used in this population. Both types of nests had one of the extremities covered with an opaque piece of plastic. This difference in nest shape and size is purposed to provide the parental male with a structure as similar as possible to its own conception of nest and avoid a potential confounding effect of nest unfamiliarity. Accordingly, all males typically adopted the nest during the first minutes of the habituation period and did not abandon the nest throughout most of the experimental period.

Each nesting male was sequentially presented with a ripe female (female presentation test) and a parasitic male (parasitic male presentation test) on the same day. The sequence of the female and parasitic male presentation was balanced to control for order effects. In some trials the female or the parasitic male remained hidden behind the male's nest for the whole observation period and these trials were removed from the analysis. Observations lasted 15 min (RF) or 20 min (GT); thus, the frequency of behaviours per minute was used in all analyses.

The RF experiments were carried out first. These observations were video recorded and behaviours quantified using the Observer PC software V3.0 (Noldus Information Technology, Wageningen, The Netherlands) in order to comprehensively assess the behavioural repertoire of males and females. The most conspicuous features of courtship and aggression displays identified from these observations and used in this study for parasitic males, females and nesting males were the frequency and latency of courtship displays and, for nesting males, also the frequency of attacks directed towards parasitic males or females (see Patzner et al., 1986 for details on these behaviours). At the GT these behavioural variables were directly observed and recorded in check sheets. Aggressiveness from nesting males towards females and parasitic males in relation to the total number of aggressive and sexual displays exhibited by the nesting male was determined according to the following index: frequency of attacks/(frequency of attacks + frequency of courtship). This index is used to assess the overall direction of the interactions of nesting males towards females and parasitic males (reproductive vs. agonistic).

The size of female and parasitic males used in the experiments did not differ between populations (mean ± SE: Females RF $= 7.06 \pm 0.12$ cm, GT $= 7.36 \pm 0.14$ cm, t-test: $t = -1.111$, $p = 0.271$, $N_{\text{GT}} = 8$, $N_{\text{RF}} = 11$; parasitic males RF $= 5.75 \pm 0.09$ cm, GT $= 5.53 \pm 0.23$ cm, $t = 1.166$, $p = 0.248$, $N_{\text{GT}} = 12$, $N_{\text{RF}} = 36$). Nest holders were larger in RF than in GT (mean ± SE: Males RF $= 10.28 \pm 0.17$ cm, GT $= 9.53 \pm 0.28$ cm, t-test: $t = 2.589$, $p = 0.016$, $N_{\text{GT}} = 12$, $N_{\text{RF}} = 36$). This follows the pattern found for *S. pavo* in these populations, where nest-holders are known to be larger in RF (Saraiva et al., 2010).

Statistical analyses were performed using the software Statsoft Statistica 8.0 for Windows. All tests were two-tailed and the significance level was set at 0.05. Non-parametric tests were used because data did not conform to parametric normality and homoscedasticity assumptions. Means ± SE are presented throughout.

3. Results

3.1. Female presentation test

In the RF female presentation test, females courted more frequently than males (Wilcoxon-matched paired test, $Z = 2.9$, $p = 0.003$, $N = 11$; Figure 1), initiated courtship more often than males (females = 91%, males = 9%, Z-test of proportions, $p < 0.001$, $N = 11$) and the latency to the first courtship was lower in females than in males (females = 69.1 ± 49.1 s, males = 341.8 ± 26.0 s, $Z = 2.8$, $p = 0.004$, $N = 11$). All females courted the nesting male while only 9% of the males courted females (z-test of proportions, $p < 0.001$, $N = 11$; Figure 2). Contrarily, in the GT female presentation test, males and females did not differ in the frequency of courtship displays ($Z = 0.3$, $p = 0.726$, $N = 8$; Figure 1), probability of

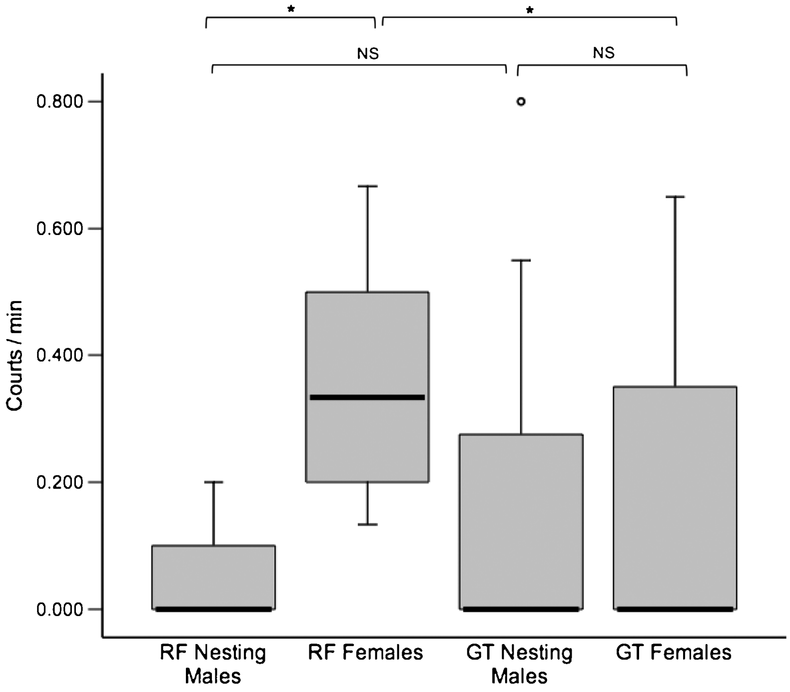

Figure 1. Frequency of courtship displays of males and females in the Female Presentation Test (FPT) (see text for details). The box-plot represents the median, interquartile range, maximum and minimum and outliers. * indicates significant differences at $p < 0.05$. NS, non-significant.

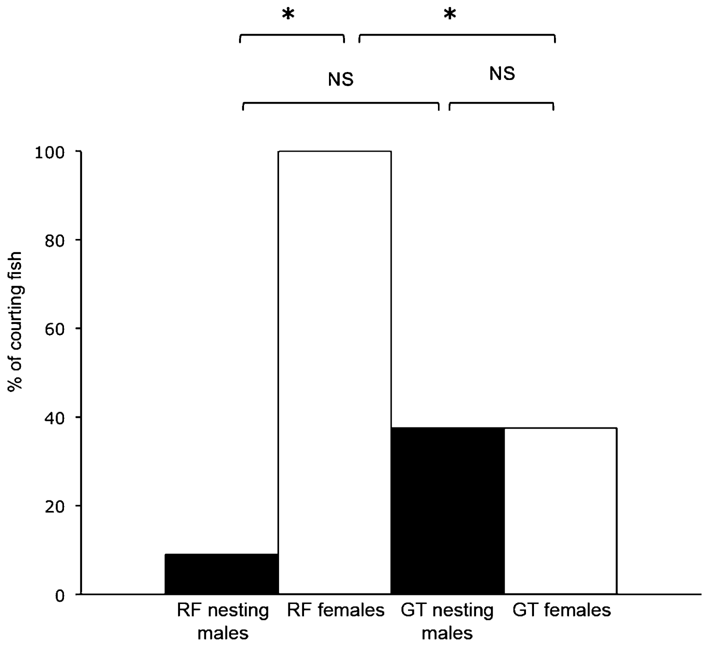

Figure 2. Percentage of individuals that displayed courtship behaviours in the Female Presentation Test (FPT) (see text for details). * indicates significant differences at $p < 0.05$. NS, non-significant.

initiating courtship (females = 50%, males = 50%, $N = 8$), latency to initiate courtship (females = 193 ± 111.7 s, males = 256.0 ± 113.8 s, $Z = 0.1$, $p = 0.916$, $N = 8$) nor in the proportion of animals exhibiting courtship displays (Z-test of proportions, $p = 1.0$, $N = 8$; Figure 2).

When comparing the results between populations, females from RF courted males with a higher frequency (Mann–Whitney U, $Z = 2.0$, $p = 0.049$, $N_{\mathrm{GT}} = 8$, $N_{\mathrm{RF}} = 11$; Figure 1), initiated courtship more often (RF = 91%, GT = 50%, z-test of proportions, $p = 0.045$, $N_{\mathrm{GT}} = 8$, $N_{\mathrm{RF}} = 11$), with a lower latency (RF = 69.1±26.0 s, GT = 658.5±123.6 s, $Z = 3.3$, $p = 0.001$, $N_{\mathrm{GT}} = 8$, $N_{\mathrm{RF}} = 11$) and in a higher percentage of trials (Z-test of proportions, $p = 0.002$, $N_{\mathrm{GT}} = 8$, $N_{\mathrm{RF}} = 11$; Figure 2) than females from GT. There was no difference between populations in the frequency of male courtship displays towards females ($Z = 0.1$, $p = 0.960$, $N_{\mathrm{GT}} = 8$, $N_{\mathrm{RF}} = 11$; Figure 1), in the latency of male courtship displays (RF = 697.0 ± 89.1 s, GT = 360.0 ± 127.6 s, $Z = 0.3$, $p = 0.774$, $N_{\mathrm{GT}} = 8$, $N_{\mathrm{RF}} = 11$) nor in the percentage of males that courted females

(Z-test of proportions, $p = 0.132$, Figure 2), although males from RF initiated courtship less often than males from GT (RF = 9%, GT = 50%, Z-test of proportions, $p = 0.045$). Males also did not differ between populations in aggressiveness towards females (aggressiveness index: RF $= 0.8 \pm 0.1$, GT $= 0.4 \pm 0.1$, $Z = 0.4$, $p = 0.687$, $N_{\mathrm{GT}} = 8$, $N_{\mathrm{RF}} = 11$).

3.2. Parasitic male presentation test

In the RF parasitic male presentation test, parasitic males courted nesting males more frequently than the reverse ($Z = 4.5$, $p < 0.001$, $N = 36$; Figure 3), initiated courtship more often (Parasitic males = 94%, Nesting males = 6%, Z-test of proportions, $p < 0.001$, $N = 36$) and with a lower latency (Parasitic males $= 212.4 \pm 53.3$ s, Nesting males $= 799.2 \pm 39.2$ s, $Z = 4.7$, $p < 0.001$, $N = 36$) and courted in a higher proportion of trials

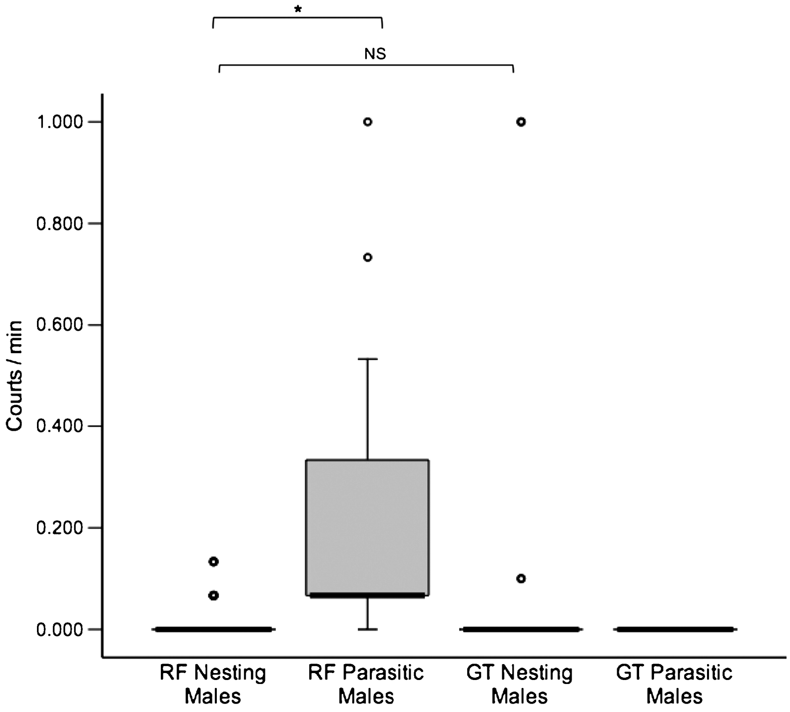

Figure 3. Frequency of courtship displays of nesting males and parasitic males in the Parasitic male Presentation Test (PPT) (see text for details). The box-plot represents the median, interquartile range, maximum and minimum and outliers. * indicates significant differences at $p < 0.05$. NS, non-significant.

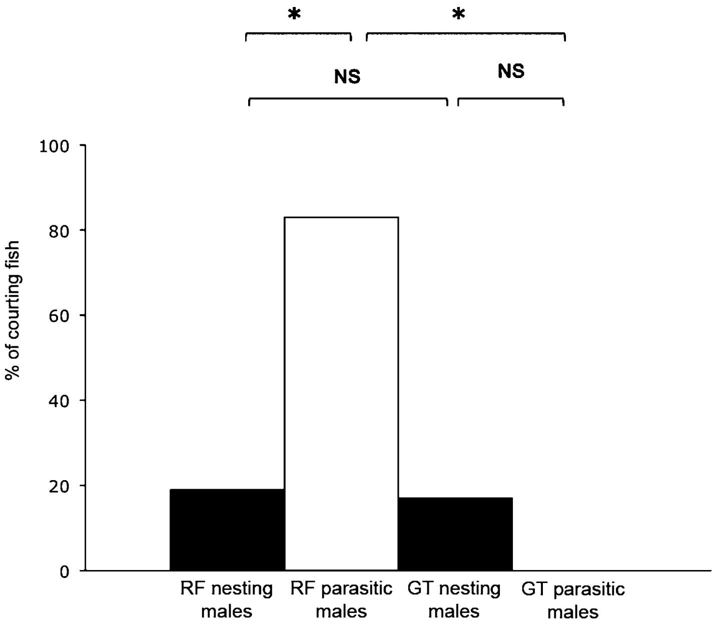

Figure 4. Percentage of individuals that displayed courtship behaviours in the Parasitic male Presentation Test (PPT) (see text for details). * indicates significant differences at $p < 0.05$. NS, non-significant.

than nesting males (Parasitic males = 83%, Nesting males = 19%, Z-test of proportions, $p < 0.001$, $N = 36$; Figure 4). In contrast, none of the tested parasitic males courted the nesting male at GT, although differences in the proportion of trials where courtship was expressed did not differ between nesting and parasitic males (Z-test of proportions, $p = 0.139$, $N = 12$; Figure 4).

There were no differences between populations regarding the frequency of courtship displays directed by nest holders towards parasitic males ($Z = 0.0$, $p = 0.990$, $N_{\mathrm{GT}} = 12$, $N_{\mathrm{RF}} = 36$; Figure 3) nor in the proportion of nest-holders courting parasitic males (z-test of proportions, $p = 0.832$, $N_{\mathrm{GT}} = 12$, $N_{\mathrm{RF}} = 36$; Figure 4). There was also no difference in the overall aggressiveness of nest-holders of the two populations towards parasitic males (aggressiveness index: RF $= 0.770 \pm 0.066$, $GT = 0.546 \pm 0.142$, $Z = 1.3$, $p = 0.196$, $N_{\mathrm{GT}} = 12$, $N_{\mathrm{RF}} = 36$). Contrarily, the parasitic male's behaviour was strikingly different between populations, with 83% of the parasitic males courting the nest-holder at RF and none at GT (Z-test of proportions, $p < 0.001$, $N_{\mathrm{GT}} = 12$, $N_{\mathrm{RF}} = 36$; Figure 4).

4. Discussion

The different behavioural profiles observed for the two populations could result from high phenotypic behavioural plasticity in *S. pavo*, i.e., from genetically similar animals being able to produce divergent behavioural phenotypes in response to different environmental conditions. In this scenario, differences in behaviour should be attenuated under similar environmental conditions. Initially, our results suggested that the nest-holder male morphotype is most flexible, as similar levels of courtship and agonistic behaviours were recorded for males of the two populations. Contrarily, females and parasitic males continued to express the behaviours of their original populations. However, certain ecological factors may account for these differences.

In a previous field study, nesting males at GT were found to express 10 fold higher courtship rates than males at RF (Saraiva, 2009; Saraiva et al., in press). Our lab experiments indicate that RF and GT nesting males express courtship behaviour at similar rates under similar lab conditions. These results may be explained by the presence of eggs in the nest. The field study was conducted at the peak of the breeding season and in this period males at RF typically have the nests filled with eggs (Oliveira et al., 1999) while males at GT have their nests much less filled with eggs (Saraiva, 2009; Saraiva et al., in press). In our experiments, nest-holder males were provided with an empty nest in the test tank at the beginning of the observations. Therefore, both RF and GT males had to court in order to attract females and get a first spawn. This interpretation is supported by data collected for another blenny, *Petroscirtes breviceps*, where nesting males decrease courtship rate as the nest gets filled with eggs, and increase courtship when it becomes empty (Shibata & Kohda, 2006). If a similar pattern is true for nesting males of *Salaria pavo*, this could explain the observed differences between field and lab observations. In the field, nests at RF contain more eggs, and males court less than those at GT. For our lab experiments, nest-holder males were caught from their nests in the field and kept for two days in all-male tanks with available empty nests before observations. Assuming egg density is a cue mediating male courtship displays, RF and GT males may have courted at similar levels in order to attract females and get a first spawn. If this is the case, the results suggest a high plasticity in nesting males' sexual displays in response to the presence of eggs in the nest. These results also predict that at the beginning of the breeding season, when nests are empty in both populations, male courtship displays should be similar. This hypothesis can be tested by future experiments manipulating the presence of eggs in the nest and quantifying the male courtship behaviour and by field observations in the two populations at different times of the breeding season.

Female courtship behaviour in the lab, however, reflected the differences observed in the field, with females from RF courting a nesting male more frequently and more readily than females from GT. This suggests a lower behavioural plasticity of females when compared to nesting males but alternative explanations are possible. Female courtship behaviour may be influenced by cues such as the presence of eggs in the male' nest or the frequency of male courtship. Females from RF come from a population where nest-holders are scarce and choosy and where females need to court more in order to be accepted into the nest (Almada et al., 1994; Oliveira et al., 1999); females from GT come from a population with abundant nesting-males and where males take the initiative in courtship (Saraiva, 2009; Saraiva et al., in press). But after capture, females in both populations were kept in all-female tanks before the male presentation. Thus, one possible explanation for the results is that females were unable to detect the absence of eggs in the males' nests and followed the information they had available from their home populations. If this hypothesis is correct, the stronger differences in behaviour between females of the two populations, as compared to nesting males under standardized laboratory conditions, does not reflect a less plastic behavioural response of females but a different perception of changes in conditions between females and nesting males, as males were exposed for two days to an empty nest while females were not exposed to nests or males before the test trials. If this is the case, females from both populations should exhibit similar levels of courtship after assessing egg density and/or experiencing similar levels of male courtship. Alternatively, females possibly detected the absence of eggs in the male's nest (e.g., through olfactory cues) but changes in behaviour may not be immediate. In the two-spotted goby *Gobiusculus flavescens*, the sex roles gradually change from conventional to reversed over the course of the breeding season that lasts for three months (Forsgren et al., 2004) and in the blenniid fish *Petroscirtes breviceps* sex-roles shift from typical to reversed and back during an 8-month breeding season (Shibata & Kohda, 2006). Changes in reproductive behaviour implies individuals are gathering information from the environment and adjusting the animals' internal state through hormonal processes that may produce a lag in the animals response (Forsgren et al., 2004). As females in our experiments were exposed to nesting males with empty nests for a short period, there was probably not enough time to adjust the behavioural response and, therefore, they adopted the standard pattern of courtship for their population. Males, on the other hand, were kept for two days in all-male stock tanks provided with empty nests before the experiment and, therefore, had more time to adjust their behaviour to this condition. Thus, our results are compatible with the view that changes in reproductive behaviour are slow and long-lasting probably involving a re-organization of the physiological mechanisms underlying reproduction. A third alternative hypothesis would be that differences in female behaviour between populations are a consequence of developmental plasticity. The exposure to different ecological conditions in the two populations could lead to a different development of female reproductive behaviours. If this is the case, a lower plasticity of sexual behaviours in females, as compared to nesting males, would be present in adults. These alternatives can be tested by exposing females from both populations for a longer period of time to males displaying similar levels of courtship. If female behaviour also shows a high degree of plasticity, displays from females of both populations should converge whether if differences are a consequence of developmental plasticity female displays should remain unlike.

Regarding parasitic males, more than 80% courted the nesting-male at RF with female-like displays but none of the GT parasitic males exhibited this behaviour or tried to sneak into the nest. The GT parasitic males have very high gonadosomatic indexes (Saraiva et al., 2010), typical of parasitic males (Taborsky, 1998), and readily release sperm after gentle pressure of the abdomen, strongly suggesting that they are actively enrolled in reproduction. The fact that female-like courtship displays were never observed for these males at GT, both in the lab (this study) and in the field (Saraiva, 2009; Saraiva et al., in press), strongly suggests an alternative reproduction mode. At RF the most distinctive feature of courtship events are the conspicuous female courtship displays towards nesting-males (Almada et al., 1995). Parasitic males in this population effectively imitate these displays in order to approach nests and steal fertilizations (Gonçalves et al., 2003b) and this study confirms that these are very common displays at RF. At GT the most distinctive feature of courtship episodes is the male ‘S courtship’ display that occurs outside the nest (Patzner et al., 1986) and females seldom court males (Saraiva, 2009; Saraiva et al., in press). Thus, at GT parasitic males presumably will rely on their female-like appearance either to be courted by males or to remain inconspicuous in order to approach nests and steal fertilizations. This would explain why parasitic males did not actively court the nesting-male at GT but did so at RF and suggests that parasitic males are able to adjust their behavioural phenotype to the average female behavioural phenotype of the population. Again, this generates an interesting and testable hypothesis as parasitic males from the two populations can be exposed to either courting or non-courting females and the impact of social copying in the parasitic male's sexual displays can be assessed (Gonçalves et al., 2003b).

Taken together, the results suggest a high degree of behavioural plasticity in *S. pavo* which may underlie the interpopulation behavioural differences reported for the species. Further experiments are necessary to confirm this for females and parasitic males. The results also suggest that parasitic males use alternative behaviours to female-mimicry to achieve fertilizations of eggs at populations where sex-roles are conventional. Interestingly, the sneaker's approach to their parasitic tactic seems to be not only dependent on ecological conditions (Taborsky, 2001; Oliveira et al., 2005), but also on the females' actual courtship behaviour. The males of *S. pavo* may rely on a high degree of developmental plasticity to use social information for choosing to (1) breed parasitically, eavesdropping on females and mimic their behaviour, or (2) develop directly into the bourgeois tactic, investing in growth and allocating energy to compete for resources to become a nest-holder.

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