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Ecological modulation of reproductive behaviour in the peacock blenny: a mini-review

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Abstract The inter-populational variation in the reproductive behaviour of the peacock blenny *Salaria pavo* (Risso 1810), particularly the influence of the ecologic environment, was reviewed in the present work. Two populations of this species inhabiting contrasting environments were studied: the Ria Formosa population, a coastal lagoon with sandy/muddy substrate located in the south of Portugal, and the Gulf of Trieste, an area presenting rocky substrate located in the northern Adriatic sea. The remarkable differences in the mating system and reproductive behaviour between the two populations (namely sex-role reversal and high frequency of alternative reproductive tactics (ARTs) at the Ria Formosa *vs* typical sex roles and low frequency of ARTs at the Gulf of Trieste) are interpreted as a plastic behavioural and physiological response to contrasting ecological conditions. Androgens, namely 11-ketotestosterone, seem to act as mediators of this response. The expression and activity of the enzyme aromatase in the brain also seems to play a key role in fine-tuning the behavioural output in all male morphs as well as females.

Keywords Blenny · Behaviour · Plasticity · Androgens

Introduction

Theoretical models have demonstrated that mating systems are the outcome of the dynamics between both female and male strategies: males and females can express adaptively flexible, choosy and indiscriminate behaviour so that they may change their behaviour—from moment to moment—to fit dynamically changing circumstances (Gowaty and Hubbell 2005). Flexible sex roles have been widely demonstrated in fish. For example, Forsgren et al. (2004) showed that along the spawning season of a population of the two spotted goby *Gobiusculus flavescens* (Fabricius 1779), the operational sex ratio (OSR: the ratio of males in condition to reproduce to fertilisable females) shifts towards females, and fish progressively change sex roles with male courtship being predominant at the beginning of the breeding season and female courtship being predominant towards its end. In the present paper, we present a mini-review of the evidence for ecological modulation of reproductive behaviour in the peacock blenny *Salaria pavo* (Perciformes, Bleniidae).

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This fish presents high sexual dimorphism: males are larger than females and exhibit conspicuous secondary sex characters, like a head crest and anal gland, which consists of modified rays of the anal fin (Patzner et al. 1986; Papaconstantinou 1979). These characters develop mainly in the breeding season (Fig. 1). The mating system is promiscuous, with exclusive male parental care. In rocky shore populations, males nest in crevices or holes in the rock and defend a courting territory around the entrance of the nest where they perform elaborate courtship displays, assuming a bourgeois reproductive tactic. Females usually have a passive role in courtship, responding with changes in colouration and a few displays before they enter the nest to spawn (Patzner et al. 1986).

The Ria Formosa population, however, presents severe changes to this pattern. In this coastal lagoon, nesting substrates are scarce, and the only adequate sites to establish nests are bricks located in artificial reefs, used by clam culturists to delimit their fields. During the breeding season, nests are highly aggregated, rendering the maintenance of the typical bourgeois territory impossible (Almada et al. 1994; Saraiva et al. 2012). Sex-role reversal has been described for this population, with females displaying intense and elaborate courtship and males assuming an almost passive role in courtship (Almada et al. 1995; Saraiva et al. 2012). In the Ria Formosa, there is also a high proportion of small parasitic males that mimic female morphology and courtship behaviour (Fig. 1). These males rely on their female-like appearance and try to achieve parasitic fertilizations by entering the nest during spawning episodes (Gonçalves et al. 1996, 2003b). These alternative reproductive tactics are sequential: males that assumed a parasitic tactic in one breeding season usually acquire a nest in the next season.

In the present review, we address essential questions regarding the emergence of these behavioural differences between populations. The main hypothesis is that the variations in the mating system should be due to high behavioural plasticity under the influence of the ecological environment, namely the abundance and dispersion of nesting sites (Saraiva et al. 2012). More precisely, the following questions are addressed:

1. Are the sex roles dynamic in this species and can they be modulated through experimental manipulation of nest-site aggregation?
2. How does the mating system work in populations inhabiting sites with different nest availability and dispersion? Are there alternative reproductive tactics in populations where nest sites are abundant?
3. Are there morphological changes in females and different male morphs between populations? What are the endocrine correlates of such differences?
4. What are the differences in the neuroendocrine regulation of reproductive behaviour between the two populations?

Methods

An integrative approach was used to address these questions: transects to quantify abundance and dispersion of nest sites (Saraiva et al. 2012), behavioural

Fig. 1 Photograph of a mature male (**a**), a female (**b**) and a parasitic male (**c**) during the breeding season. *1* Head crest; *2* fully developed anal gland

observations in the field and in the laboratory to assess behavioural differences between populations and the ecological factors responsible for them (Saraiva et al. 2009, 2012, in press), morphometry to identify correlates of sexual preference and condition-dependent traits (Saraiva et al. 2010), radio-immuno assays and quantitative RT-PCRs to identify the underlying physiological factors (endocrine and neuroendocrine) in control of reproductive behaviour (Saraiva et al. 2010; Gonçalves et al. 2010).

Results and discussion

The results point to a high behavioural plasticity in this species, with a strong influence of nest-site abundance and dispersal in modulating the mating system and reproductive behaviour (Saraiva et al. 2009; Oliveira et al. 1999). In fact, the aggregation and scarcity of nest sites in Ria Formosa apparently promote a strong competition for access to nests sites, favouring larger males and probably promoting the development of more pronounced secondary sex characters as intra- and inter-sexual signalling (Saraiva et al. 2010). As only the largest males acquire nests in this population, the operational sex ratio (number of mature females/ number of males qualified to mate) should be biased towards females, limiting their reproductive potential and causing sex-role reversal (Saraiva et al. 2012). On the other hand, a large proportion of sexually mature males cannot breed and the smallest adopt alternative reproductive tactics (Gonçalves et al. 2003a, b). These

Table 1 Inter-populational comparison in morphological and hormonal variables

	Nest holders		Parasitic males		Females		Planned comparisons (RF *vs* GT)		
	RF	GT	RF	GT	RF	GT	Nest holders (*t*, *P*)	Parasitic males (*t*, *P*)	Females (*t*, *P*)
SL (cm)									
Mean	9.44	8.21	5.53	5.78	6.54	6.70	5.37, 0.000*	−0.77, 0.442	−0.71, 0.478
SE	0.21	0.13	0.13	0.24	0.17	0.09			
N	33	111	30	23	31	158			
Crest size									
Mean	1.29	1.12	0.99	0.96	1.00	0.89	5.91, 0.000*	0.899, 0.369	4.24, 0.000*
SE	0.02	0.02	0.01	0.01	0.04	0.01			
N	33	63	30	23	31	111			
Relative anal gland area									
Mean	1.94	1.27					5.69, 0.000*		
SE	0.10	0.08							
N	33	46							
GSI									
Mean	1.19	1.64	3.57	5.48			2.08, 0.039*	6.26, 0.000*	
SE	0.06	0.11	0.24	0.49					
N	24	47	21	13					
T (ng/ml)									
Mean	1.96	2.08	0.41	0.70	0.60	1.74	0.266, 0.791	−0.41, 0.686	−2.32, 0.024*
SE	0.46	0.45	0.20		0.13	0.42			
N	12	9	9	1	10	9			
11KT (ng/ml)									
Mean	4.09	1.46	0.75	0.04	0.52	0.60	−2.90, 0.005*	0.22, 0.825	0.26, 0.798
SE	1.26	0.37	0.20		0.06	0.26			
N	12	9	9	1	10	9			

GSI gonado-somatic index, *SL* standard length, *RF* Ria Formosa, *GT* Gulf of Trieste

Test differences at $P < 0.05$ are marked with *. Modified from Saraiva et al. (2010), see original article for details

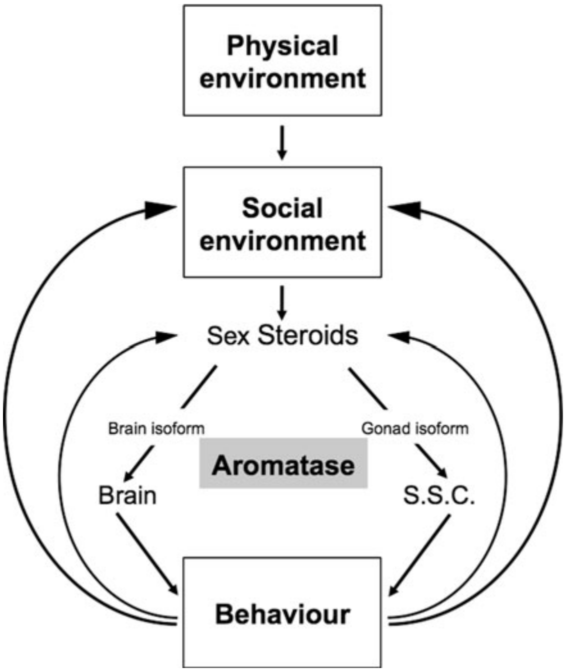

Fig. 2 Integrative perspective of the mechanisms underlying behavioural plasticity in *S. pavo*. The physical environment (e.g. nest availability and aggregation) influences the social environment (e.g. ratio of females and males that are qualified to mate, as well as type of males and competition within each sex). The social environment acts on individual behaviour mediated internally by sex steroids, which in turn are regulated through the enzyme aromatase that converts androgens into estrogens. The two isoforms of aromatase can adjust behavioural patterns through independent local action in the brain (e.g. influencing androgen-dependent behavioural displays) or in the gonad (e.g. regulating systemic levels of steroids and the development of secondary sex characters (S.S.C.)). Closing the loop, each individual's behaviour has a direct effect on surrounding conspecifics as well on its own internal state

parasitic males occur in much lower frequency in the Gulf of Trieste (Saraiva et al. 2010; Saraiva et al. 2012), but their actual mating tactic remains unknown since they seem not to mimic female courting behaviour as their Ria Formosa counterparts (Saraiva et al. 2011).

Although bourgeois males in the Gulf of Trieste are smaller and have less developed secondary sex characters than in Ria Formosa, they present relatively larger gonads (Saraiva et al. 2010). It is probable that sperm competition is higher in the Gulf of Trieste. This can be explained by the longer periods outside of the nest that bourgeois males from this population spend, increasing the chance for nest takeovers or stealing fertilizations by rivals; and as parasitic males do not have an active female courtship to mimic, there is much higher unpredictability in reproductive opportunities (Oliveira et al. 2009; Saraiva et al. 2010, 2012).

Bourgeois males from Ria Formosa have higher circulating levels of 11-keto-testosterone and more developed crests and anal glands (Saraiva et al. 2010; Table 1), suggesting that a) there is a correspondence between this hormone and the development of secondary sex characters and b) androgens are highly sensitive to the social environment (Oliveira and Gonçalves 2008; Saraiva et al. 2010). Concerning aromatase, an enzyme that converts androgens into estrogens and thus is probably involved in the regulation of courtship and androgen-dependent aggressive behaviours, there is a higher expression of the *cyp19b* gene (encoding the brain isoform of aromatase gene) in the brains of bourgeois males from Ria Formosa. A higher local testosterone–estradiol conversion rate may be down-regulating the aggressiveness and courtship in these males, allowing them to cohabitate with neighbours (Gonçalves et al. 2010). In addition, aromatase activity both at a gonadal and brain level seems to be an important regulatory mechanism underlying the expression of male alternative reproductive tactics. The transition to the nesting male tactic is apparently accompanied both by a higher conversion of androgens into estrogens in the brain and by an increase in testicular androgen production. At a gonadal level, aromatase activity thus regulates not only sexual differentiation but also the investment in reproduction both ontogenetically and seasonally (Gonçalves et al. 2008).

Conclusions

The peacock blenny is a very good candidate to study both proximate and adaptive mechanisms of behavioural plasticity. The available data allow an integrated understanding of some of the mechanisms that regulate behavioural plasticity in *S. pavo*, whose expression of reproductive behaviours seems to be closely related to ecological factors. Constraints in availability and dispersion of nest sites apparently unleash a cascade of social and behavioural adjustments that, via hormonal mediation, allow a plastic response to a changing environment (Fig. 2).

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