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Courting females: ecological constraints affect sex roles in a natural population of the blenniid fish *Salaria pavo*

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In most animal species females are the sex with the limiting reproductive rate, which promotes the predominance of male intra-sexual competition, active courtship and more developed epigamic characters in males (Trivers 1985). In some species, however, sex-role reversal occurs, and the females actively court and compete for mates (insects: Gwynne 1981; Svensson & Petersson 1987; stomatopods: Hatziolos & Caldwell 1983; poison-arrow frog: Wells 1978; birds: Petrie 1983; Reynolds et al. 1986; Colwell & Oring 1988; pipefish: Berglund et al. 1989; Berglund & Rosenqvist 1990, 1993; Rosenqvist 1990). In these cases the operational sex ratio is biased towards females so that the reproductive rate is higher in females, often because of special features of male reproductive biology (e.g. pipefish; Berglund et al. 1989). In this paper we present evidence for ecological modulation of sex roles in a natural population of the blenniid fish *Salaria pavo* (Risso).

While in other known populations of this species parental males defend nesting territories where they actively court females (Fishelson 1963; Patzner et al. 1986), in the population studied, where nest sites are very scarce, courtship is almost entirely initiated by females, and both male and female intra-sexual competition occurs.

Males of *S. pavo* establish nests in natural cavities where they guard the eggs. Several females may visit a single nest and each female may spawn successively with different males during the breeding season (Patzner et al. 1986). The courtship in this species is usually initiated by the male (lateral jerking, zig-zag swimming and figure-8 swimming) and receptive females respond with a specific display (nuptial coloration, rapid respiratory movements, pectoral fin fanning and exposure of the ventral region to the male; Patzner et al. 1986).

The population we studied occurs in a lagoon (Ria Formosa, southern Portugal), where the only available cavities are in bricks used by clam-culturists to delimit their fields. Only those brick holes that have one of the openings obstructed serve as potential nest sites, and some bricks have several such holes. In such bricks guarding males form dense nest aggregations and do not defend a territory around the nest site. There is an excess of mature males that cannot establish nests and nesting males are significantly larger than non-nesting males. A detailed description of this population and its ecology is provided in Almada et al. (1994).

Behavioural observations on 97 nests were conducted by snorkelling in the breeding seasons of 1989 and 1994 (total observation time = 28 h, 54 min; each observation lasted from 15 to 90 min with an average of 25 min). In each observation we recorded the following variables: number of nests in the brick; number of visits and sex of the visitor; number of agonistic interactions and the identity (parental, floater or female) of the participants, and number of courtship episodes and the sex of the initiator.

There was a high level of competition for nest sites among the males. Intruding males were often observed to threaten and sometimes bite the protruding head of the guarding males, and most agonistic interactions between guarding and intruding males were initiated by the latter (chi-squared goodness-of-fit test assuming equal frequencies: $\chi^2 = 20{\cdot}6$, $df = 1$, $P < 0{\cdot}001$). Removal experiments confirmed the intense male competition for nests. In 15 nests in which the parental male was removed, 10 had been reoccupied by another male by the following day. This reoccupation rate is much higher than that found in a natural population of another intertidal blenny

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(*Lipophrys pholis* (L.)) nesting in a rocky shore habitat with no nest site limitations (Almada et al. 1992).

Courtship was initiated almost exclusively by females which often actively displayed to a succession of neighbouring males without the latter showing any courtship. In 598 courtship episodes observed the male actively courted in only one case. This is not due to a lack of courtship repertoire in the males since in aquaria males from this population actively courted females (unpublished data), exhibiting the behavioural patterns described by Fishelson (1963) and Patzner et al. (1986) for the males of other populations of this species.

The males were highly selective in which females they admitted to their nests (success of female courtship=3·69%, $N=597$) and were aggressive towards courting females (partial correlation between agonistic interactions directed by the guarding males towards visiting females and female courtship, controlling for the number of female visits: $r=0{\cdot}77$, $df=63$, $P<0{\cdot}001$). The observed nests had on average 89·1% of their inner surface covered by eggs (SD=17·5%, maximum 100%, minimum 40%, $N=53$).

Females preferentially attacked other females rather than guarding males and floaters (frequency of agonistic interactions (number of interactions/number of visits by the sex that initiated the interaction): females–females: $\bar{X}\pm\text{SD}=0{\cdot}127\pm0{\cdot}259$, $N=62$; females–males: $0{\cdot}06\pm0{\cdot}152$, $N=56$; Mann–Whitney U-test: $z=-2{\cdot}12$, $P<0{\cdot}05$) but male–male aggression was more frequent than female–female aggression (frequency of agonistic interactions (number of interactions/number of visits by the sex that initiated the interaction): males–males: $\bar{X}\pm\text{SD}=0{\cdot}786\pm1{\cdot}08$, $N=40$; females–females: $0{\cdot}127\pm0{\cdot}259$, $N=62$; Mann–Whitney U-test: $z=-5{\cdot}30$, $P<0{\cdot}001$; only aggression between floaters and between floaters and guarding males was included in the test as there were only two interactions between guarding males in 63 focal observations). There is a significant partial correlation between the frequency of courtship episodes by females and the frequency of agonistic interactions between females in each nest, after controlling for the number of visiting females ($r=0{\cdot}74$, $df=63$, $P<0{\cdot}001$). This finding, together with the qualitative observations on active interference by females in courtship episodes, suggest the existence of female–female competition for males in this population.

When considering cases of sex-role reversal in species with male parental care it is assumed that females are both the most active sex in courtship and the sex in which competition is strongest (Rosenqvist 1990; Berglund 1991). This link is logical when the number of offspring that may be cared for by a male is limited by physical constraints (e.g. size of ventral brooding area in male syngnathids), although it may not be true in all cases (e.g. *Hippocampus fuscus*; Vincent 1994). However, the operational sex ratio may be biased not only by physical limitations of one sex but, among other factors, also by the availability of nest sites in species in which males guard the offspring in a nest. In this case there is no theoretical reason for a link between a more active sex role and greater inter-sexual competition in females, since the males must also compete for nest sites. The present data indicate that in this population nest site availability is an ecological factor that limits the number of males that can guard eggs, which in turn limits spawning opportunities for the females. In this context female courtship is associated with high levels of both inter-male and inter-female competition. It is interesting to note that in aquarium studies of a closely related species, *Salaria basilisca* (Valenciennes), Heymer (1987) found that courtship is also initiated only by females. This species lives in *Posidonia oceanica* (L.) beds in which hard substrates for nests are probably very scarce.

Suppression of male courtship behaviour may be explained by acute competition for nest sites among males, associated with the females' high levels of readiness to spawn. If a male left a nest to court, there would be a high risk that an intruding male would take over the nest or enter the nest to ejaculate (in this species the sperm must be released in the water before the female spawns; Patzner 1984). This may also explain the suppression of territorial behaviour in this population. The females' role in courtship is possible because of the pre-existence of a female display in the species' behavioural repertoire, and because of the strong pressure on females to find spawning opportunities.

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REFERENCES

Almada, V. C., Gonçalves, E. J., de Oliveira, R. F. & Barata, E. N. 1992. Some features of the territories in the breeding males of the intertidal blenny *Lipophrys pholis* (Pisces: Blenniidae). *J. mar. biol. Ass. U.K.*, **72,** 187–197.

Almada, V. C., Gonçalves, E. J., Santos, A. J. & Baptista, M. C. 1994. Breeding ecology and nest aggregations in a population of *Salaria pavo* (Pisces: Blenniidae) in an area where nest sites are very scarce. *J. Fish Biol.*, **45,** 819–830.

Berglund, A. 1991. Egg competition in a sex-role reversed pipefish: subdominant females trade reproduction for growth. *Evolution*, **45,** 770–774.

Berglund, A. & Rosenqvist, G. 1990. Male limitation of female reproductive success in a pipefish: effects of body size differences. *Behav. Ecol. Sociobiol.*, **27,** 129–133.

Berglund, A. & Rosenqvist, G. 1993. Selective males and ardent females in pipefishes. *Behav. Ecol. Sociobiol.*, **32,** 331–336.

Berglund, A., Rosenqvist, G. & Svensson, I. 1989. Reproductive success of females limited by males in two pipefish species. *Am. Nat.*, **133,** 506–516.

Colwell, M. A. & Oring, L. W. 1988. Sex ratios and intrasexual competition for mates in a sex-role reversed shorebird, Wilson's phalarope (*Phalaropus tricolor*). *Behav. Ecol. Sociobiol.*, **22,** 165–173.

Fishelson, L. 1963. Observations on littoral fishes of Israel. I. Behaviour of *Blennius pavo* Risso (Teleostei, Blenniidae). *Israel J. Zool.*, **12,** 67–80.

Gwynne, D. T. 1981. Sexual difference theory: Mormon crickets show role reversal in mate choice. *Science*, **213,** 779–780.

Hatziolos, M. E. & Caldwell, R. L. 1983. Role reversal in courtship in the stomatopod *Pseudoguilla ciliate* (Crustacea). *Anim. Behav.*, **31,** 1077–1087.

Heymer, A. 1987. Comportment agonistique, stratégies reproductrices et investment parental chez *Blennius basiliscus* (Teleostei, Blenniidae). *Revue fr. Aquariol.*, **14,** 89–108.

Patzner, R. A. 1984. The reproduction of *Blennius pavo* (Teleostei, Blenniidae) II. Surface structures of the ripe egg. *Zool. Anz.*, **213,** 44–50.

Patzner, R. A., Seiwald, M., Adlgasser, M. & Kaurin, G. 1986. The reproduction of *Blennius pavo* (Teleostei, Blenniidae) V. Reproductive behavior in natural environment. *Zool. Anz.*, **216,** 338–350.

Petrie, M. 1983. Female moorhens compete for small fat males. *Science*, **220,** 413–415.

Reynolds, J. D., Colwell, M. A. & Cooke, F. 1986. Sexual selection and spring arrival times of red-necked and Wilson's phalaropes. *Behav. Ecol. Sociobiol.*, **18,** 303–310.

Rosenqvist, G. 1990. Male mate choice and female–female competition for mates in the pipefish *Nerophis ophidion. Anim. Behav.*, **39,** 1110–1115.

Svensson, B. G. & Petersson, E. 1987. Sex-role reversal courtship behaviour, sexual dimorphism and nuptial gifts in the dance fly *Empis borealis* (L.). *Ann. Zool. Fenn.*, **24,** 323–334.

Trivers, R. 1985. *Social Evolution.* Menlo Park, California: Benjamin Cummings.

Vincent, A. C. J. 1994. Seahorses exhibit conventional sex roles in mating competition, despite male pregnancy. *Behaviour*, **128,** 135–151.

Wells, K. D. 1978. Courtship and parental behavior in a panamanian poison-arrow frog (*Dendrobates auratus*). *Herpetologica*, **34,** 148–155.