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A reliable indicator of female fecundity: the case of the yellow belly in *Knipowitschia panizzae* (Teleostei: Gobiidae)

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Abstract A large body of research has developed on male ornaments and their role in sexual selection while female ornaments have been less investigated. This study focused on the presence, function, and possible role of a sexually dimorphic nuptial trait as an indicator of female quality in a fish species presenting “conventional” sex roles: the yellow patch on the belly of *Knipowitschia panizzae* females. Aquarium spawning experiments demonstrated that this ornament is due to dermal pigments, is displayed only when the female is ready to spawn, and is switched off within minutes from the end of egg deposition. This sexual trait is variable in size among females and indicates female fecundity relative to her own body size. As a consequence, female yellow belly appears to be a reliable indicator of female quality as measured by current fecundity. Field data on natural nests highlights that males usually perform parental care on only one egg batch at a time. The modality of egg deposition suggests that males may be limited in their potential reproductive rates by environmental factors. Male limitations in egg care could favour male choosiness and the evolution of female nuptial displays.

Introduction

In several animal taxa, the role of arbitrary male secondary sexual traits and the information they convey to females have been widely investigated (Andersson 1994). Male ornaments, and in particular bright colouration,

have been demonstrated to indicate male quality such as ability in parental care (Candolin 2000; Keyser and Hill 2000), number of sperm delivered (Pilastro et al. 2002), and health status in relation to parasitic load (Milinski and Bakker 1990; Houde and Torio 1992; Hôrak et al. 2001).

Female ornaments are usually less common and less developed than those of males and are often explained through genetic correlation of the trait between males and females (Andersson 1994). In some cases, however, it has been suggested that female ornaments could be sexually selected, through female–female competition or male mate choice (Andersson 1994; Amundsen 2000). In particular, male preference for more ornamented females has been demonstrated in birds (see for review Amundsen 2000), primates (Domb and Pagel 2001), and fish (Berglund et al. 1986; Rowland et al. 1991; McLennan 1995; Amundsen and Forsgren 2001; Berglund and Rosenquist 2001).

Sexually selected female ornaments are expected to be present in sex role reversed species (e.g. Berglund et al. 1997), that is, those species in which the potential reproductive rate is higher in females than in males and females actively compete for mates (Vincent et al. 1992; Andersson 1994; Amundsen 2000), such as species in which males perform parental care and are limited in the number of clutches they can care for simultaneously. However, female ornaments are present also in species with more “conventional” sex roles, species where males show breeding colouration, perform courtship behaviours, and engage in intrasexual contests (Rowland et al. 1991; McLennan 1995; Swenson 1997; Amundsen 2000; Amundsen and Forsgren 2001).

In birds and primates, female ornaments have been recognised to indicate female quality in terms of health condition, ability of parental care, and reproductive success (Amundsen 2000; Domb and Pagel 2001). In contrast, in fish the possible function of female ornaments as indicator of quality still remains to be investigated.

The family Gobiidae represents a good model to study the sexual selection of male and female secondary

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sex traits. Indeed among gobiids, species with male and/or female ornaments, different types of mating systems, and a plastic adoption of sex roles according to resource availability are present (Breder and Rosen 1966; Miller 1984; Thresher 1984; Swenson 1997; Amundsen and Forsgren 2001; Borg et al. 2002). In particular in the lagoon goby *Knipowitschia panizzae* (Verga, 1841), a species with conventional sex roles and dimorphic breeding colouration, during the breeding season females display a conspicuous bright yellow-orange colouration on the belly (Gandolfi et al. 1991). This trait is among the few cases of a female ornament described in fish species with conventional sex roles (Rowland et al. 1991; McLennan 1995; Swenson 1997; Amundsen and Forsgren 2001).

In this study we evaluated the possible role of the yellow belly colouration as an indicator of individual quality in the lagoon goby. In particular we (1) described the anatomical features of the female yellow colouration on the belly (pigment location), (2) recorded the timing of its display, (3) measured its intrasexual variability in colour and size during the breeding season, and (4) analysed its relationship with number and quality (size, yolk content, and larval size at hatching) of laid eggs. In addition, to investigate possible factors favouring the presence of this female ornament, we studied the male mating system by evaluating, in a field survey, (1) number of eggs per nest, (2) number of clutches per nest, (3) nest size, and (4) pattern of egg deposition.

Materials and methods

Study species and animal collection

The lagoon goby is a small species (maximum size: 45 mm) with a short life span (1 year), inhabiting muddy-bottom inside lagoons and estuaries along the northern Adriatic Sea (Whitehead et al. 1986). During the breeding season, extending from February to May (De Girolamo 1994), males display dark bars along their sides, dark fins, and a blue spot on the first dorsal fin; they defend a nest, usually constituted by empty bivalve shells, court females, and perform parental care on eggs until hatching (Gandolfi et al. 1991). Observations of mating behaviour and qualitative analyses of reproductive apparatus development appear to exclude the presence of alternative male mating tactics in this species (C. Mazzoldi, unpublished data). This study was performed from March 2000 to May 2001. Specimens were collected in a shallow muddy area in the southern Venetian Lagoon by SCUBA divers using hand nets.

Female ornaments

Individuals were sexed by the shape of the genital papilla (Gandolfi et al. 1991) and/or by the breeding colouration for males. A subset of individuals was dissected for

anatomical analysis of the yellow belly patch (see below), while the others were used in spawning experiments in which yellow patch size, colour intensity, timing of display, and relationship with egg number and quality were investigated.

Ten females, five collected during and five collected outside the breeding season, were sacrificed with an excess of anaesthetic (MS222) and dissected under a stereomicroscope. We recorded the presence/absence of yellow pigments in the skin, coelomic wall, and developing eggs. The same procedure was applied to ten males, five during and five outside the breeding season.

For spawning experiments males and females were kept separated in stock tanks provided with sandy bottom and artificial shelters. Seawater was renewed daily, and the temperature range was kept at 18 to 22°C. Light regime followed natural conditions, and fishes were fed once a day with brine shrimps (*Artemia*). Males, ranging in size from 34 to 42.5 mm total length (TL), were kept individually in 36-l aquaria with an artificial nest made from half of a piece of PVC pipe (inner surface: 7–14 cm²). Each nest ceiling was provided with an acetate sheet that could be easily removed to collect eggs. After at least 2 days of acclimatisation, a ripe “yellow bellied” female was added to each aquarium. For each spawning the following data were recorded: (1) male and female body size (TL in millimetres); (2) yellow colouration intensity (by comparing it with a colour Pantone scale on live female in the tank); (3) yellow patch area (estimated, before egg deposition, by tracing the borders of the yellow-coloured area on a transparent nylon sheet adhered to the female belly and computing the area using Image-Nt software, in square millimetres); (4) time of disappearance of the yellow colouration on female belly (the female was left undisturbed in the aquarium for at least 1 h after the spawning and every 10 min we recorded the presence of the patch); (5) total number of laid eggs (eggs were counted under the stereomicroscope); (6) egg size (for a sample of 20 to 40 eggs per batch; because eggs present an elongate shape, major and minor diameters were measured under a stereomicroscope, using a calibrated eyepiece; precision: 0.026 mm); (7) percentage of yolk ($100 \times \text{yolk diameter} \times \text{egg minor diameter}^{-1}$); (8) larval size (for 17 batches, after yolk absorption larvae were anaesthetized with MS222 and their standard length, SL, was measured under a stereomicroscope, using a calibrated eyepiece; precision: 0.093 mm. After measurement, larvae were released in the field).

Yellow colouration intensity and patch area were estimated before spawning. Only data obtained from females that spawned the same day of the measurement have been included in the analyses. Change in colour intensity or patch area during fish handling was never observed. To evaluate the number of egg clutches found in natural nests in the field we recorded embryo developmental stages according to the method assessed for other lagoon gobies (Mazzoldi et al. 2000, 2002).

Mating system

During two breeding seasons (2000 and 2001), field observations were performed, in a shallow muddy area in the southern Venetian Lagoon, to collect information on nests, nesting male characteristics, egg number, number of egg batches, and pattern of egg deposition in the nest. Nests and nesting males were collected simultaneously by SCUBA divers using hand nets. A total of 35 nests were brought to the laboratory to measure (1) nesting male size (TL, in millimetres; $n=29$); (2) nest inner surface and egg area (estimated by drawing on a transparent nylon sheet the nest inner surface and the area occupied by the eggs and computing the area using Image-Nt software, in square centimetres); (3) percentage of nest area occupied by eggs ($100 \times \text{egg area} \times \text{nest area}^{-1}$); (4) number of eggs (see laboratory data); (5) egg density (number of eggs \times egg area $^{-1}$); (6) number of egg clutches (see laboratory data). Eggs were reared in tanks and, after hatching, larvae were released in the field.

Statistical analyses

When not otherwise noted, means \pm standard error (SE) are given. The number of samples used in the analysis is denoted by n . Data were checked for normality using a Shapiro–Wilk test, and, if not normally distributed, they were log or square root transformed. Percentage data were converted to proportions and arcsin transformed (Sokal and Rohlf 1997). Where transformation did not attain normality, non-parametric tests were applied. Data were analysed using STATISTICA 5.1.

Results

Female ornaments

Female bellies showed, at the stereomicroscope analysis, yellow-pigmented cells in the dermis both during and outside the breeding season. Yellow-pigmented cells were present anterior to the genital papilla and on the ventral part of body sides. The coelomic wall was blackish due to the presence of chromatophores, while the ovarian wall, oocytes, and laid eggs were always transparent-whitish. Males lacked yellow-pigmented cells in their integument. Females showed bright yellow colouration only during the breeding season.

A total of 26 spawnings occurred in aquaria (Table 1). Usually the female started the courtship by displaying her yellow belly to the male. Males responded by becoming darker and moving back and forth between the female and the nest. When males were reluctant to mate (three cases) females repeatedly displayed their yellow belly. The spawning colour pattern became evident in all females only when they were ready to spawn (as indicated by their round belly or swollen genital

Table 1 *Knipowitschia panizae*. Data on aquarium spawnings. TL total length; SL standard length

| | Mean \pm SE | Range | No. in sample |
|--------------------------------------|-----------------|-----------|---------------|
| Male TL (mm) | 39.6 \pm 0.57 | 34.0–42.5 | 18 |
| Female TL (mm) | 38.9 \pm 0.36 | 35.0–42.0 | 26 |
| Yellow patch area (mm ²) | 134 \pm 5 | 63–195 | 26 |
| No. eggs | 235 \pm 14 | 107–371 | 26 |
| Major egg diameter (mm) | 2.34 \pm 0.06 | 1.56–2.92 | 26 |
| Minor egg diameter (mm) | 0.93 \pm 0.01 | 0.85–0.98 | 26 |
| Yolk diameter (mm) | 0.79 \pm 0.01 | 0.74–0.85 | 26 |
| Larval SL (mm) | 4.21 \pm 0.05 | 3.86–4.61 | 17 |

papilla) and vanished in a maximum time of 20 min after the end of egg deposition.

The yellow colouration presented well-defined margins. The area of the yellow colouration on the female belly was highly variable among females (Table 1, Fig. 1), while its colour intensity, always matching the tone E-X000 (100% yellow) of the Pantone colour scale, was not. The yellow patch area positively correlated with the number of laid eggs ($r=0.48$, $P<0.05$, $n=26$) but not with female TL ($r=0.06$, $p>0.05$, $n=26$; Fig. 1). Considering that the number of released eggs highly correlated with female size ($r=0.67$, $P<0.001$, $n=26$), we statistically controlled for this by performing a multiple regression analysis with egg number as the dependent variable and female TL and yellow patch area as predictors ($F_{2,23}=20.73$, $P<0.001$; female TL: $t=5.15$, $P<0.001$, partial $r^2=0.46$; yellow patch's size: $t=3.57$, $P<0.01$, partial $r^2=0.20$; Fig. 2). The area of the yellow colouration did not correlate with any of the other egg and larvae characteristics investigated: minor diameter ($r=0.18$, $P>0.05$, $n=26$), major diameter ($r=0.20$, $P>0.05$, $n=26$), percentage of yolk ($r=-0.30$, $P>0.05$, $n=25$), larval size (Spearman's correlation coefficient: $r_s=-0.2$, $P>0.05$, $n=17$). Larvae from eggs developed in aquaria hatched in 6 to 7 days, depending on rearing temperature (20–24°C) and regardless of their size.

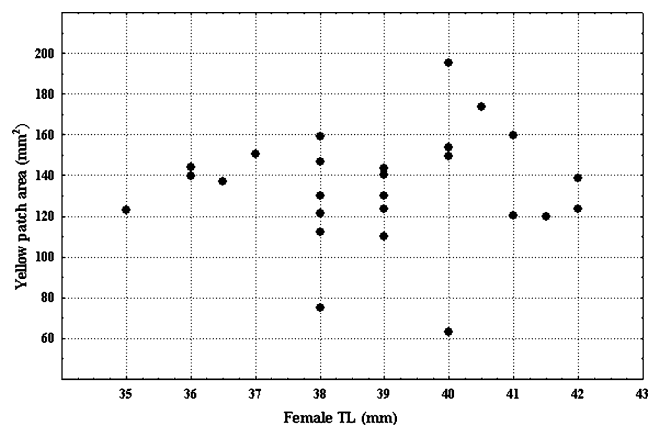


Fig. 1 Relationship between yellow patch area and female size. TL Total length

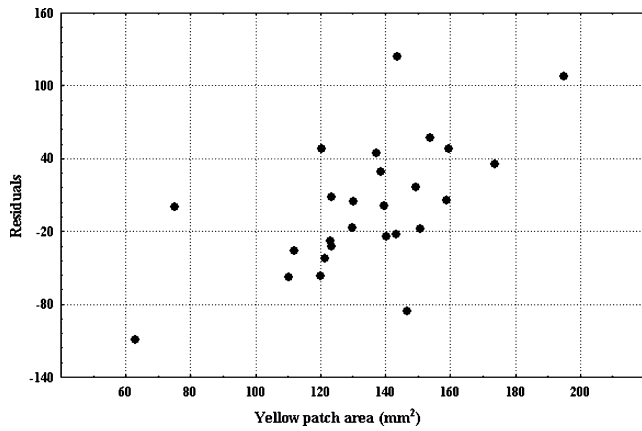


Fig. 2 Relationship between residuals of the regression egg number/female TL and yellow patch area

Mating system

Descriptive statistics from nests are reported in Table 2. Inside the nest the eggs were laid in one layer only in the central part of the ceiling, covering the nest surface only partially (Fig. 3). There was a weak positive correlation between male and nest size ($r=0.38$, $P<0.05$, $n=29$). Larger nests contained a larger egg area ($r=0.60$, $P<0.001$, $n=35$), while there was a weak correlation between nest area and egg number ($r=0.34$, $P<0.05$, $n=35$). Eggs were spaced out more in larger nests, as highlighted by a negative correlation between egg density and nest size ($r=-0.48$, $P<0.01$, $n=35$). There was no correlation between male size and egg number ($r=0.02$, $P>0.05$, $n=29$). In only four cases we recorded more than one egg clutch simultaneously.

Discussion

This study demonstrates that the yellow belly colouration showed by lagoon goby females (1) is due to dermal pigments, (2) indicates female readiness to spawn, (3) is variable in size among females, and (4) constitutes a reliable indicator of a female quality in terms of quantity of released eggs relative to her own size as well as absolutely. Females show the yellow colouration on

Table 2 *K. panizzae*. Data on nests in the field

| | Mean \pm SE | Range | No. in sample |
|---|-----------------|-----------------|---------------|
| Male TL (mm) | 35.3 \pm 0.51 | 29.0–41.5 | 29 |
| Nest area (cm ²) | 7.18 \pm 0.43 | 3.2–13.0 | 35 |
| Egg area (cm ²) | 2.42 \pm 0.15 | 1.3–5.0 | 35 |
| Percentage of nest occupied by eggs | 35.3 \pm 1.73 | 15.3 \pm 62.9 | 35 |
| No. eggs | 233 \pm 12 | 91–381 | 35 |
| Egg density (no. eggs \times cm ⁻²) | 100.4 \pm 4.4 | 48.6–168.5 | 35 |
| Egg developmental stages | 1.1 \pm 0.1 | 1–2 | 34 |

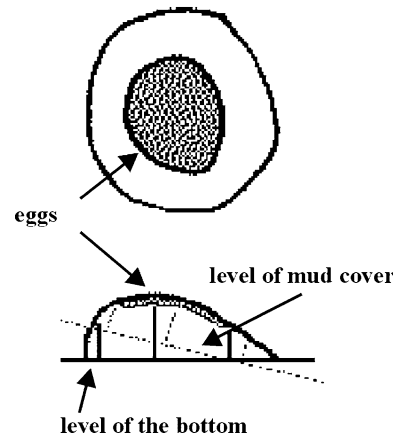


Fig. 3 Schematic drawing of egg deposition in a nest

their belly only before spawning, rapidly switching off the colour after egg deposition. Female nuptial colouration is highly conspicuous in the field (M. Massironi and C. Mazzoldi, personal observation) and therefore could be costly in terms of predation risks. The association between nuptial colouration and readiness to spawn has been attributed to advantages to males in recognising receptive females with respect to energy expenditure in courtship displays and avoidance of female cannibalism on eggs already present in the nest (Rowland et al. 1991; Swenson 1997). However, the variability presented by the yellow colouration on the belly of lagoon goby females suggests a possible additional role of this trait as an indicator of female quality. Intrasexual variability in the nuptial colouration has been observed in other species and can include variability in colouration (Amundsen and Forsgren 2001), contrast (Berglund et al. 1997), and size (Berglund et al. 1986; Amundsen and Forsgren 2001). In the lagoon goby, the yellow patch on the female belly did not present any visible variability in colour intensity, even if we cannot exclude that males could perceive variations that are undetectable to the human eye. However, a wide variability was instead present in the size of the yellow patch. In other fish species, the size of the female belly colouration has been found to vary in relation to body size (Berglund et al. 1986; Amundsen and Forsgren 2001). Through the relation between female size and fecundity (Bagenal 1966), this ornament acts as an amplifier of female size (Berglund 2000), reinforcing male choosiness for larger females (Kodric-Brown 1990). In contrast, in the lagoon goby the size of the yellow patch showed variability regardless of female size, indicating female fecundity relatively to her own body size. Therefore this sexual trait appears to be an honest signal that, integrating the information about fecundity that female size usually conveys to males, may increase the accuracy of male choice.

In other fish species (Baird 1988; Amundsen and Forsgren 2001), the orange-yellow colouration is mainly due to the pigmentation of developing eggs visible through the thin belly skin. In contrast, in the

lagoon goby eggs are unpigmented and dermal pigments are entirely responsible for the colouration of the belly in females. Yellow-orange pigments have been found to indicate quality in terms of parasitic load in different species (Milinski and Bakker 1990; Houde and Torio 1992; Hōrak et al. 2001). The nature of belly pigments in the lagoon goby and the possible relation between yellow patch size and parasitic load deserve further investigation.

In the lagoon goby aggressive interactions among females have never been observed in the lab or in the field (M. Massironi, personal observation), but we cannot exclude that interactions among females may occur when male availability is limited (Borg et al. 2002) or may involve communication mechanisms undetected by the human eye. However the lack of evidence of direct female–female competition and the relation between the yellow belly and female fecundity suggest that the nuptial colouration of lagoon goby females may be related to male mate choice, as reported for other fish species with ornamented females (Berglund et al. 1986; Rowland et al. 1991; McLennan 1995; Amundsen and Forsgren 2001; Berglund and Rosenqvist 2001). Despite preliminary experiments suggesting a similar male response in lagoon goby (Massironi et al., unpublished observations), male mate choice in relation to female yellow belly variability needs to be addressed by further specific investigations.

Male choosiness is expected in species in which males are limited in their potential reproductive rate (Clutton-Brock and Vincent 1991; Kvarnemo and Ahnesjö 1996). While in other goby species, nests are usually completely covered by eggs (Mazzoldi et al. 2002; Mazzoldi and Rasotto 2002), in the lagoon goby the nest ceiling was only partially covered by eggs. In particular, eggs were laid only in the central part of the inner surface of the nest, suggesting that nest borders could represent an unsuitable environment for egg deposition or development. Indeed nest borders are in direct contact with the muddy bottom that, especially during the warm season, often becomes anoxic (Fenchel and Riedl 1970). Oxygen limitation could constraint the number of clutches a male can care for, as has been hypothesised for another goby species, *Eucyclogobius newberry*, in which females also show nuptial colouration (Swenson 1997). The observation that in the lagoon goby eggs are less dense in larger nests further supports the possible influence of oxygen availability on the pattern of egg deposition. The similarities between these two species suggest that environmental factors, such as oxygen availability, may depress male potential reproductive rates in species with “conventional” sex roles, such as gobies that usually present a highly polygynous mating system (Cole 1982; Thresher 1984; Lindström 1992; Magnhagen and Kvarnemo 1989; Mazzoldi et al. 2000; Mazzoldi and Rasotto 2002), consequently limiting mate availability and thus favouring male choosiness and the rise of female nuptial displays. Limitation in

male reproductive rates may skew the operation sex ratio towards females in *K. panizzae*, a species that, in the Venetian Lagoon, presents a female-biased sex ratio (Gandolfi et al. 1991; De Girolamo 1994).

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