ORIGINAL PAPER

Male lagoon gobies, *Knipowitschia panizzae*, prefer more ornamented to larger females

Matteo Pizzolon · Maria B. Rasotto · Carlotta Mazzoldi

Abstract Female ornamentation may be directly sexually selected, by male choice or female competition, or occurs as the result of a genetic correlation, arising from sexual selection on males. However, increasing evidence supports the former hypothesis, suggesting that males actively choose their partner preferring traits indicative of female quality. In the lagoon goby, *Knipowitschia panizzae*, a polygynous species whose males perform parental care to eggs, body length and the size of a sex-specific yellow patch on the belly are known to be reliable indicators of female fecundity. In this paper, we tested, using dummies, the male's mating preferences for female body and yellow belly patch sizes. The two experimental trials in which a single female trait was variable showed that males prefer a larger belly patch and a larger body size, indicating that both these characters are selected by male mate choice. However, when faced with dummies exhibiting an inverse combination of body and belly patch sizes (experiment 3), males significantly preferred the smaller ones with larger yellow belly patches. A calculation of dummy theoretical fecundity reveals that in the first two experiments, males would have received an immediate benefit from their choice in terms of egg number, whereas in the third one, males chose partners that would have provided them with fewer eggs. The male lagoon goby preference for females with larger belly patches, regardless of their size, suggests that this trait, in addition to indicating fecundity, conveys information about other aspects of female and/or egg quality.

M. Pizzolon · M. B. Rasotto · C. Mazzoldi (✉)
Department of Biology, University of Padova,
via U. Bassi 58/B,
Padova 35131, Italy
e-mail: carlotta.mazzoldi@unipd.it

Introduction

Lower investment in offspring and higher variance in reproductive success usually lead to sexually selected extravagant traits in males rather than in females (Darwin 1871; Andersson 1994). Numerous studies support this argument, documenting male competition and female mate choice (Andersson 1994). Female ornaments, in contrast, have traditionally been considered artefacts, through genetic correlation, of selection on male traits and as such have rarely been investigated (Lande 1980). This conception has recently been challenged, and the broader scenarios under which female ornaments might evolve have begun to be recognized (Amundsen 2000). Indeed, experimental evidence and comparative studies have demonstrated that both female intra-sexual agonistic interactions and male mate choice may be important in the evolution and maintenance of sex dimorphic traits in females (e.g. Amundsen 2000; Amundsen and Forsgren 2001; Bonduriansky 2001; Griggio et al. 2005; Torres and Velando 2005). In particular, ornamented females and choosy males have been documented not only in the so-called sex role-reversed species, as expected from theoretical predictions (Emlen and Oring 1977; Clutton-Brock and Vincent 1991; Clutton-Brock and Parker 1992; Vincent et al. 1992; Barlow 2005), but also in both monogamous and polygynous species with conventional sex roles (Amundsen 2000; Amundsen and Forsgren 2001; Griggio et al. 2005; Heinsohn et al. 2005; Torres and Velando 2005), being male choice of partners favoured in different social and environmental circumstances (Johnstone et al. 1996; Kvarnemo and Simmons

1999; Bonduriansky 2001; Kokko and Monaghan 2001; Simmons and Kvarnemo 2006).

If the female ornamental traits are adaptive, they are expected to be favoured in sexual selection games, and their expression should be indicative of individual quality (Hamilton and Zuk 1982; Fitzpatrick 1994; Amundsen 2000). Experimental evidence shows that the relationship between male preferences and female ornamentation may be positive (Beeching et al. 1998; Amundsen 2000), null (Wolf et al. 2004) or negative (Nordeide 2002; Nordeide et al. 2006). The merging pattern seems ambiguous; however, the association of female sexually dimorphic traits with aspects of phenotypic quality has been investigated only in a handful of species. In particular, female ornamentation can be indicative of body size and/or condition (Johnsen et al. 1996; Amundsen et al. 1997; Jawor et al. 2004), parasite load (Potti and Merino 1996; Roulin et al. 2001; Cordoba-Aguilar et al. 2003), ability to tolerate reproductive costs (Hanssen et al. 2006) and fecundity, in terms of egg number (Berglund et al. 1986; LeBas et al. 2003; Massironi et al. 2005), egg quality (Domb and Pagel 2001; Pizzari et al. 2003; McGraw et al. 2005; Cornwallis and Birkhead 2007) or number of broods per season (Domb and Pagel 2001). By contrast, female ornamentation does not signal female quality in an agamid lizard, *Ctenophorus ornatus* (LeBas and Marshall 2000), and in a goby fish, *Gobiusculus flavescens*, where the higher egg carotenoid content exhibited by more colourful females does not reflect egg or larval quality (Svensson et al. 2006). A better comprehension of the general principles guiding the evolution of such female traits requires additional studies testing female ornaments for potential function and male choice.

Male preference for more fecund females has been demonstrated in several fish species where males provide sole parental care of the eggs and fecundity is highly variable among females (Andersson 1994; Itzkowitz et al. 1998; Kvarnemo and Forsgren 2000). By undertaking parental care, a male may limit his own potential reproductive rate and could therefore benefit from discriminating among females of different reproductive potential (Clutton-Brock and Parker 1992). Indeed, males may gain immediate benefits by choosing a more fecund female, and the strength of this preference is expected to be inversely related to the opportunity of a single male to mate with several females. Body mass or size is the trait most commonly related to fecundity in fish, and male preference for this trait has been widely demonstrated (e.g. the pipefishes *Syngnathus typhle* and *Nerophis ophidon*, Berglund et al. 1986; *Gasterosteus aculeatus* and *Oncorhynchus kisutch*, Sargent et al. 1986; *Ophioblennius atlanticus*, Côte and Hunte 1989; *Poecilia latipinna*, Ptacek and Travis 1997; Gabor 1999; *Stegastes leucostictus*, Itzkowitz et al. 1998; *G. aculeatus*, Kraak and

Bakker 1998; *Pomatoschistus minutus*, Kvarnemo and Forsgren 2000, *G. flavescens*, Pélabon et al. 2003; *Poecilia reticulata*, Dosen and Montgomery 2004). However, in two species with male parental care and a short life cycle, the two-spotted goby, *G. flavescens*, and the lagoon goby, *Knipowitschia panizzae*, a female-specific yellow colouration on the belly has been documented to convey information on egg number or quality (Amundsen and Forsgren 2001; Massironi et al. 2005). In the two-spotted goby, more colourful females are strongly preferred by males and produce eggs richer in carotenoids; however, the content of these anti-oxidants does not appear to be related to egg and larval quality (Svensson et al. 2006). In the lagoon goby, *K. panizzae*, males typically care for only one clutch at a time, and thus female fecundity is the major determining factor of males' reproductive success. In this species, female fecundity is positively correlated to both body length and a conspicuous yellow patch displayed on the belly before spawning (Massironi et al. 2005). While no evident variation has been observed in the intensity of the yellow colouration, the size of this patch varies widely among females and is not related to female length (Massironi et al. 2005). The lack of aggressive interactions among females seems to exclude a possible involvement of the yellow belly patch in female–female competition (Massironi et al. 2005). However, no information is available on possible male preference for the two traits indicating female fecundity in this species. Our study was aimed to: (1) test if the female nuptial colouration is sexually selected by male mate choice, (2) test if males exert mate choice on the basis of female body size and (3) evaluate the relative importance of these two traits for male mate choice. In addition, with the goal to understand the possible benefit of male choice, a theoretical estimation of female fecundity in relation to the yellow belly patch size was performed using the field collected data of Massironi et al. (2005).

Materials and methods

Model species

The lagoon goby (*K. panizzae*, Verga 1841) is an euryhaline teleost species belonging to the family Gobiidae. It inhabits muddy bottoms of northern Adriatic lagoons and estuaries, usually at a depth lower than 2 m. This goby is relatively small sized (45 mm total length at maximum), has a short life span (up to 1 year; Whitehead et al. 1986) and its breeding season lasts from February to May (Massironi et al. 2005). Females lay demersal eggs in nests, mainly consisting of empty bivalve shells, and males perform all parental care of the eggs until hatching (Gandolfi et al.

1991). Males seldom take care of more than one egg clutch at time (Massironi et al. 2005). During the breeding season, the species presents sexual dimorphic colouration: males show dark bars along their sides, dark fins and a blue spot on the first dorsal fin, while females present a dark spot on the mentum, a dark first dorsal fin and an evident yellow belly colouration because of dermal pigments (Massironi et al. 2005).

General methods

The study was conducted at the Chioggia Hydrobiological Station (Venice, Italy) from February to May 2005 and 2006. Fish were caught in the southern part of the Venetian lagoon by scuba-divers using hand-held nets. Individuals were separated by sex by the shape of the dimorphic genital papilla and/or by breeding colouration (Gandolfi et al. 1991). A total of 45 males in 2005 and 22 males in 2006, ranging in size from 38 to 42 mm, were brought to the laboratory. In addition, in 2005, ten females and ten males were caught and used to observe courtship displays before the initiation of experimental trials. All fish were kept in stock tanks (36 l) until they were used for the experiments. The aquaria were provided with sandy bottoms and artificial shelters. Water was renewed daily. The temperature was maintained between 18 and 22°C, and the light regime followed natural conditions. Fish were fed daily with fresh chopped *Mytilus* sp. ad libitum. Observations of courtship displays were performed in aquaria provided with a Polyvinyl chloride (PVC) pipe as an artificial nest (length=6 cm; diameter=3 cm). One male and one female were placed in the tank, and their courtship and eventual spawning behaviour were recorded. According to these observations, males court females by spreading the first dorsal fin and leading the female to the nest by swimming back and forth between the female and the nest entrance.

Mate preference trials were conducted in experimental aquaria, and artificial female dummies were used. The dummies were made from fish-shaped lures of grey semi-transparent silicone. Considering that the colour intensity of the yellow belly patch has been found to be invariable among females and consistently matching the tone E-X000 of the Pantone colour scale (Massironi et al. 2005), a yellow patch was created on the dummy's belly using acrylic colour corresponding to the previous described colour tone (Acrylide yellow, Hue 7.74Y, Value 7.64, Chroma 12.59). To complete the imposture, two fins, a dorsal and a caudal, made of acetate paper, were added (Fig. 1). A total of 18 dummies were prepared, three for each of six types, differing in total length and/or yellow patch area (Table 1). The range of dummy size and yellow patch area was set according to the values measured in the Venetian lagoon goby population (Massironi et al. 2005).
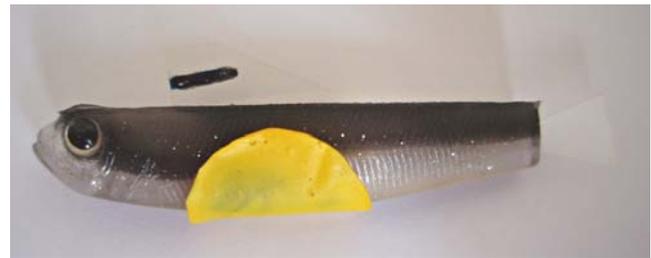
**Fig. 1** Picture of a dummy used in the experiments

Expected fecundity of the different dummies was estimated with a multiple regression model (see below).

The experimental tank (34×34×34 cm), provided with a sandy bottom, was subdivided in four parts (Fig. 2) with transparent Plexiglas partitions: A, a large section (34×25 cm) for the male was provided with an artificial nest in the middle consisting of a half PVC tube (length=6 cm; diameter=3 cm); B and C, two smaller sections (12×9 cm) for the dummies and D, a small section (9×9 cm) to separate B and C. A dark removable partition was placed between part A and the other sections.

Males were put in the aquarium to acclimatize for an average of 2 days before the experiment. A male was considered acclimatized when he covered the artificial nest with sand, preparing it for breeding (Massironi et al. 2005). Males that did not cover the nest within 4 days were removed. A dummy, randomly taken from the group specific to the trial underway, was placed in each of parts B and C for the experiment. Dummies were buoyant and kept at 3 cm from the bottom with a transparent nylon thread tied to a weight burrowed in the sandy bottom. In this position, dummies were mimicking the typical belly display that females exhibit during courtship. The dark partition was then gently removed, and the behaviour of the male was observed for 30 min. If the male responded to the dummies, he exited from the nest, performed courtship displays in front of the glass separating him from the dummy, and attempted to lead the dummy to the nest. Preference for a dummy was estimated as the time spent by

Table 1 Total length and yellow patch area of dummies used in the experiments

Dummies	Dummy total length (mm)	Yellow patch area (mm²)
MFSP: medium-size female, small patch	40	80
MFLP: medium-size female, large patch	40	180
SFMP: small female, medium patch	35	140
LFMP: large female, medium patch	42	140
SFLP: small female, large patch	35	180
LFSP: large female, small patch	42	80
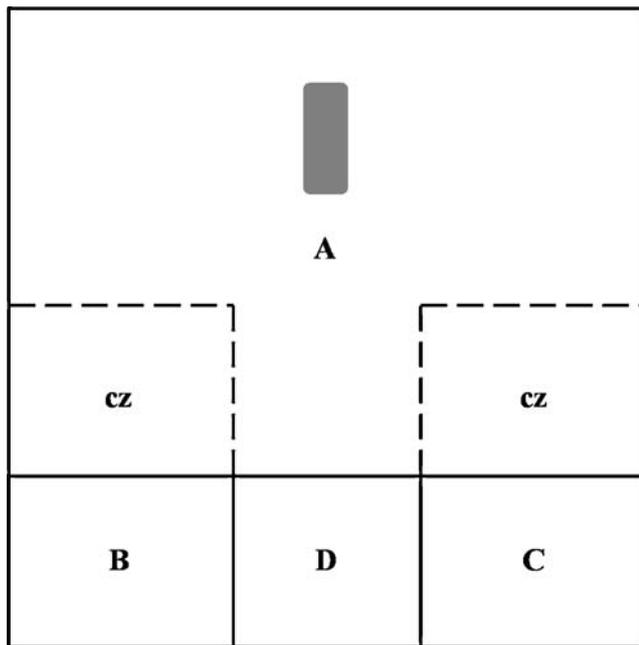
Fig. 2 Experimental aquarium: *A* male section, *B* and *C* dummy sections, *D* separation section, *cz* choice zones. The *grey box* represents the nest

the male in front of the dummy section, within a choice zone of less than or equal to 5 cm in front of the section. The time spent in front of part D or at the back of the aquaria was considered as no choice. If a male did not exit from the nest or did not perform any courtship display within the first 10 min, the experiment was interrupted and discarded.

The experimental set up was: (a) experiment 1 (25 trials): yellow patch area; two female dummies of the same

body size with different sized yellow patches: medium-size female, small patch vs medium-size female, large patch, (b) experiment 2 (17 trials): female size; two dummies with the same yellow patch size and different lengths: small female, medium patch vs large female, medium patch, (c) experiment 3 (14 trials): yellow patch area vs female size; two dummies differing inversely in size and yellow patch area: large female, small patch vs small female, large patch. All males were used for a single trial and were kept for 1 day after the experiment and fed ad libitum before being released. All the fish were released into their natural habitat after the experiments.

Data analyses

All data are reported as means±standard deviation. Differences between years in the willingness to court dummies were tested with the Fisher exact test. Differences in the proportion of time males spent in the choice and in the neutral zones were tested with a *t* test for paired data, after arcsine transformation. Male preference was calculated on the basis of the proportion of time each male spent in front of a given dummy relative to the total time spent in the choice zone. Preference (proportion of time) was tested against an expectation of no preference (proportion of time=0.5), with a one-sample test. Proportions were arcsine transformed. A multiple regression analysis was applied to estimate dummy fecundity. The model was calculated using the data of female total length (mm) and yellow patch area (mm^2), as independent variables, and fecundity (total number of laid eggs) as the dependent one. Data from Massironi et al. (2005) were used. The regression was

Fig. 3 Male preferences for (dummy) female traits in the three experiments. *Exp. 1* Yellow patch area, *Exp. 2*, female size, *Exp. 3* yellow patch area vs female size. Abbreviations: *MFSP* medium-size female, small patch, *MFLP* medium-size female, large patch, *SFMP* small female, medium patch, *LFMP* large female, medium patch; *SFLP* small female, large patch, *LFSP* large female, small patch
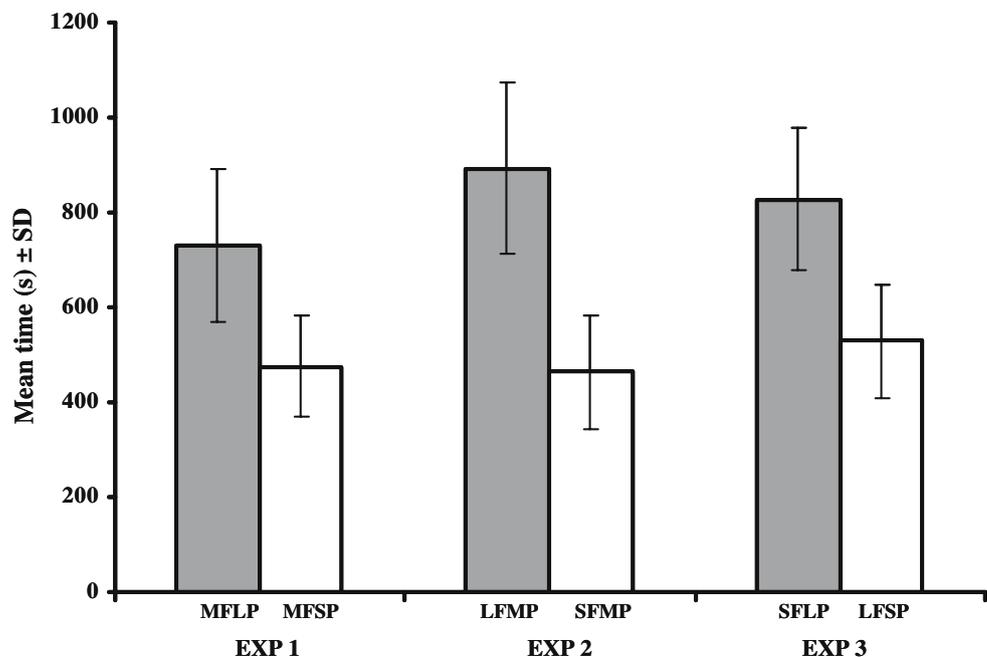
calculated with the raw data and after log transformation. Statistical analyses were performed using STATISTICA 7.1 for Windows.

Results

In 30 out of 39 trials in 2005 and 10 out of 17 in 2006, males showed an interest in the dummies, swimming in front of the dummies and trying to lead them to the nest. No statistical differences between years in the willingness to court dummies were found (Fisher exact test: $p=0.206$). The 16 experiments in which males did not show any interest in the dummies were excluded.

In all the experiments, males spent more time in the choice zone than in the neutral one (experiment 1: choice zone=1,205.1±235.6 s, neutral zone=594.4±235.6, $t=5.63$, $df=19$, $p<0.001$; experiment 2: choice zone=1,233.1± 158.1 s, neutral zone=566.9±158.1, $t=6.42$, $df=9$, $p<0.001$; experiment 3: choice zone=1,232.6±70.6 s, neutral zone=567.4±70.6, $t=14.22$, $df=9$, $p<0.001$). In experiment 1 (yellow patch area), in all 20 valid trials, males spent more time in front of the dummy presenting the larger yellow patch (Fig. 3), with a proportion of time significantly higher than 0.5 ($t=8.34$, $df=19$, $p<0.001$; Table 2). In experiment 2 (female size), in nine out of ten valid trials, males spent more time in front of the larger dummy (Fig. 3), with a proportion of time significantly higher than 0.5 ($t=4.14$, $df=19$, $p=0.002$; Table 2). In experiment 3 (yellow patch area vs female size), in nine out of ten valid trials, males spent more time in front of the smaller dummy presenting the larger yellow patch (Fig. 3), with a proportion of time significantly higher than 0.5 ($t=2.95$, $df=19$, $p=0.016$; Table 2).

Model to estimate fecundity

The linear model offered the best estimate of fecundity (fecundity $= -875.61 + 24.65 \times TL + 113.92 \times$ yellow patch; $F_{2,23}=20.73$, $p<0.001$; adjusted $r^2=0.612$), while in the model with log-transformed data, the determination coefficient had lower values. Both independent variables were significant in the regression (Female total length: $t=$

Table 2 Proportion of time males spent in front of the chosen dummy: experiment 1: dummy presenting the larger yellow patch; experiment 2: larger-sized dummy; experiment 3: smaller dummy presenting the larger yellow patch

Experiment	Mean±SD	Range
Exp. 1: yellow patch area	0.606±0.055	0.530–0.729
Exp. 2: female size	0.654±0.114	0.471–0.835
Exp. 3: yellow patch area vs. female size	0.608±0.115	0.350–0.744
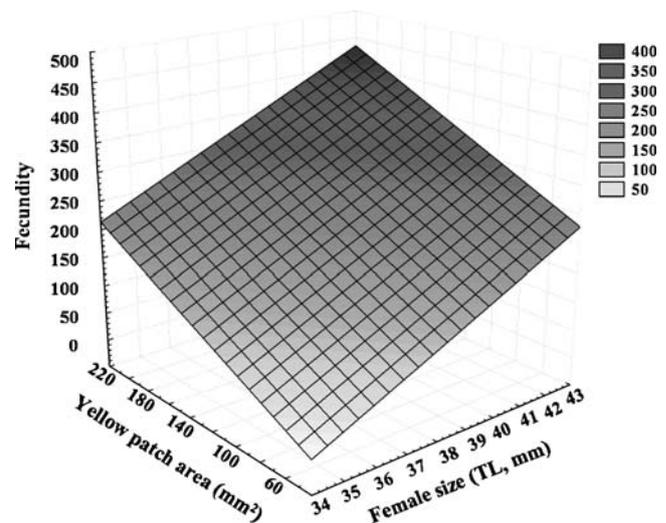
Fig. 4 A three-dimensional graph representing the variation in female fecundity in relation to size and yellow patch area, calculated with the linear regression model

5.15, $p<0.001$; yellow patch area: $t=3.57$, $p=0.002$), and females may attain the same estimated fecundity with different combinations of length and yellow patch area (Fig. 4). The estimated fecundity of the dummies is reported in Table 3.

Discussion

Our results provide evidence of a clear male preference towards the two considered female traits: body length and yellow patch size. The use of dummies, justified by a male response higher than 70%, further strengthens the results, as no confounding variables, such as female behaviour or readiness to spawn, may have influenced male preferences. When responding to the stimuli, males spent more than 66% of their time in the choice area, demonstrating a robust response to the experimental tests, even higher than that

Table 3 Estimated fecundity of the dummies used for the three experiments

Experiment	Dummy	Fecundity	Confidence limits
Exp. 1: yellow patch area	MFSP	198.2	155.1–241.3
	MFLP	292.6	265.3–319.8
Exp. 2: female size	SFMP	146.0	103.0–189.1
	LFMP	318.1	282.5–353.7
Exp. 3: yellow patch area vs. female size	LFSM	247.3	194.8–299.9
	SFLP	169.6	122.6–216.7

MFSP Medium-size female, small patch, *MFLP* medium-size female, large patch; *SFMP* small female, medium-patch, *LFMP* large female, medium patch, *SFLP* small female, large patch, *LFSP* large female, small patch

found in similar species using alive individuals (Amundsen and Forsgren 2001; Pélabon et al. 2003).

In the experiments where male preference for the two traits was tested separately, males spent more time associating with the dummies presenting the larger yellow patch and the greater body length, indicating that both these traits are actually sexually selected by male mate choice. While we did not test it in this study, the influence of intra-sexual competition on these traits appears unlikely given that agonistic behaviour among females has never been observed (Massironi et al. 2005). The observed male preference for larger females is not unexpected as, in fish, fecundity is usually positively related to female size (Bagenal 1966) and male choice based on female size has been demonstrated in several species (e.g. Berglund et al. 1986; Itzkowitz et al. 1998; Kraak and Bakker 1998; Kvarnemo and Forsgren 2000; Pélabon et al. 2003). In the lagoon goby, with body length and yellow patch size related to fecundity (Massironi et al. 2005), mate prefer-ences give males an immediate benefit in terms of egg number. This is confirmed by the estimation of dummy fecundity, with a reward for the male of 1.5 and 2.2 times the eggs he would have obtained spawning, respectively, with the dummy presenting a smaller yellow patch or of smaller size. In general, the strength of male preference is expected to be related to the variance in mate quality (Johnstone et al. 1996; Kvarnemo and Simmons 1999; Bonduriansky 2001), that is to say, in this case, to the variance in fecundity. In highly polygynous species, male preference for large females is not expected to be strong, given that males may obtain similar advantages mating randomly with several females instead of actively choosing only large females, wasting time and potential mates because of this choice (Itzkowitz et al. 1998). In the lagoon goby, a short-living species with low variability in fecundity (coefficient of variation=30.65%, calculated from Massironi et al. 2005), the observed strong preference for more fecund females may be particularly rewarding because males usually take care of only one egg clutch at a time (Massironi et al. 2005).

In the third experiment, where the two investigated traits were tested together, males exhibited a greater preference for the size of the yellow belly than for that of body. Dummy fecundity estimates project that the female dummy preferred by nine out of ten males would have fewer eggs (0.7 times than the other dummy) or, considering the confidence limits, at best an equal number of eggs than the larger one. These results might suggest that the yellow belly patch acts as an amplifier of body size, as it has been demonstrated for other sexually dimorphic fish traits (Berglund 2000; MacLaren et al. 2004). In this scenario, females with larger belly patch would exploit male

preference for partners with larger body size, appearing larger to the prospective mates. Although this possible sensory bias offers one explanation of the male preference for females with larger belly patch, other explanations, related to the information on female quality conveyed by this ornament, may account for it. Indeed, in addition to signal female fecundity (Massironi et al. 2005) the yellow belly patch has been found to contain carotenoids (Pizzolon and Mazzoldi, unpublished data). These pigments, respon-sible for the yellow and red colouration of several sexual ornaments (Gray 1996; Kodric-Brown 1989; Wedekind et al. 1998; Blount et al. 2000; Svensson et al. 2006; Griggio et al. 2007), are considered to honestly signal individual condition (Hill 1991; von Schantz et al. 1999) because of their role as anti-oxidants and in the immune defence (Chew 1996; Edge et al. 1997; Olson and Owens 1998). A tradeoff between the use of these pigments to maintain health and to signal to potential mates implies that individuals in good condition are able to display more brightly coloured or larger ornaments (Lozano 1994; Olson and Owens 1998; Blount 2004). In the lagoon goby, it has been shown that females displaying larger yellow patches are more fecund than expected for their size (Massironi et al. 2005). In this scenario, a male choosing a female with a large patch could gain an immediate direct benefit because of his mate condition and/or indirect benefits in terms of her genetic quality and, consequently, that of her offspring. Female ornaments could also signal the quality of the eggs, in terms of overall size, yolk size or carotenoid content (Svensson et al. 2006; Cornwallis and Birkhead 2007). In the lagoon goby, the size of the yellow patch is not related to egg or yolk size or to the size of hatching larvae (Massironi et al. 2005). The carotenoid content of lagoon goby eggs has not been investigated, but the concentration of these substances does not always reflect egg or larval quality, as recently demonstrated in *G. flavescens*, a species where the female ornament expression is positively corre-lated with egg carotenoids (Svensson et al. 2006). However, that the size of the yellow patch could reflect female capacity to provide eggs with components that are directly related to egg quality, such as lipids, carbohydrates, vitamins and hormones, cannot be ruled out (Brooks et al. 1997; Rennie et al. 2005).

In conclusion, we found that the nuptial colouration of female *K. panizzae* is selected by male choice and may convey multiple signals. While exactly which qualities of the female and/or the eggs are signalled by the yellow patch calls for investigation, this female ornament is expected to convey to males, in addition to fecundity, crucial informa-tion because they are ready to pay a price in terms of fecundity by choosing a smaller female with a larger yellow patch.

References

Amundsen T (2000) Why are female birds ornamented? Trends Ecol Evol 15:149–155

Amundsen T, Forsgren E (2001) Male mate choice selects for female coloration in a fish. Proc Natl Acad Sci USA 98:13155–13160

Amundsen T, Forsgren E, Hansen LTT (1997) On the function of female ornaments: male bluethroats prefer colourful females. Proc R Soc Lond B Biol Sci 264:1579–1586

Andersson M (1994) Sexual selection. Princeton University Press, Princeton, NJ

Bagenal TB (1966) A short review on fish fecundity. In: Gerking SD (ed) The biological basis of freshwater fish production. Blackwell, Oxford, UK, pp 89–11

Barlow GW (2005) How do we decide that a species is sex role reversed? Q Rev Biol 80:28–35

Beeching SC, Gross SH, Bretz HS, Hariatis E (1998) Sexual dichromatism in convict cichlids: the ethological significance of female ventral coloration. Anim Behav 56:1021–1026

Berglund A (2000) Sex role reversal in a pipefish: female ornaments as amplifying handicaps. Ann Zool Fenn 36:1–13

Berglund A, Rosenqvist G, Svensson I (1986) Mate choice, fecundity and sexual dimorphism in two pipefish species (Syngnathidae). Behav Ecol Sociobiol 19:301–307

Blount JD (2004) Carotenoids and life-history evolution in animals. Arch Biochem Biophys 430:10–15

Blount JD, Houston DC, Møller AP (2000) Why egg yolk is yellow. Trends Ecol Evol 15:47–49

Bonduriansky R (2001) The evolution of male mate choice in insects: a synthesis of ideas and evidence. Biol Rev 76:305–339

Brooks S, Tyler CR, Sumpter JP (1997) Egg quality in fish: what makes a good egg? Rev Fish Biol Fisher 7:387–416

Chew BP (1996) Importance of antioxidant vitamins in immunity and health in animals. Anim Feed Sci Technol 59:103–114

Clutton-Brock TH, Parker GA (1992) Potential reproductive rates and the operation of sexual selection. Q Rev Biol 67:437–456

Clutton-Brock TH, Vincent ACJ (1991) Sexual selection and the potential reproductive rates of males and females. Nature 351:58–60

Cordoba-Aguilar A, Salamanca-Ocana JC, Lopezaraiza M (2003) Female reproductive decisions and parasite burden in a calopterygid damselfly (Insecta: Odonata). Anim Behav 66:81–87

Cornwallis CK, Birkhead TR (2007) Experimental evidence that female ornamentation increases the acquisition of sperm and signals fecundity. Proc R Soc Lond B Biol Sci 274:583–590

Côte IM, Hunte W (1989) Male and female mate choice in the redlip blenny: why bigger is better. Anim Behav 38:78–88

Darwin C (1871) The descent of man, and selection in relation to sex. Murray, London, UK

Domb LG, Pagel M (2001) Sexual swellings advertise female quality in wild baboons. Nature 410:204–206

Dosen L, Montgomery R (2004) Female size influences mate preferences of male guppies. Ethology 110:245–255

Edge R, McGarvey DJ, Truscott TG (1997) The carotenoids as anti-oxidants—a review. J Photochem Photobiol B 41:189–200

Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. Science 197:215–223

Fitzpatrick S (1994) Colourful migratory birds: evidence for a mechanism other than parasite resistance for the maintenance of 'good genes' sexual selection. Proc R Soc Lond B Biol Sci 257:155–160

Gabor CR (1999) Association patterns of sailfin mollies (*Poecilia latipinna*): alternative hypotheses. Behav Ecol Sociobiol 46:333–340

Gandolfi G, Zerunian S, Torricelli P, Marconato A (1991) I Pesci delle acque interne italiane. Istituto Poligrafico e Zecca dello Stato, Roma, Italy

Gray DA (1996) Carotenoids and sexual dichromatism in North American passerine birds. Am Nat 148:453–480

Griggio M, Valera F, Casas A, Pilastro A (2005) Males prefer ornamented females: a field experiment of male choice in the rock sparrow. Anim Behav 69:1243–1250

Griggio M, Serra L, Licheri D, Monti A, Pilastro A (2007) Armaments and ornaments in the rock sparrow: a possible dual utility of a carotenoid-based feather signal. Behav Ecol Sociobiol 61:423–433

Hamilton WD, Zuk M (1982) Heritable true fitness and bright birds: a role for parasites? Science 218:384–387

Hanssen SA, Folstad I, Erikstad KE (2006) White plumage reflects individual quality in female eiders. Anim Behav 71:337–343

Heinsohn R, Legge S, Endler J (2005) Extreme reversed sexual dichromatism in a bird without sex role reversal. Science 309:617–619

Hill GE (1991) Plumage coloration is a sexually selected indicator of male quality. Nature 350:337–339

Itzkowitz M, Draud MJ, Barnes JL, Haley M (1998) Does it matter that male beaugregory damselfish have a mate preference? Behav Ecol Sociobiol 42:149–155

Jawor JM, Gray N, Beall SM, Breitwisch R (2004) Multiple ornaments correlate with aspects of condition and behaviour in female northern cardinals, *Cardinalis cardinalis*. Anim Behav 67:875–882

Johnsen TS, Hengeveld JD, Blank JL, Yasukawa K, Nolan V Jr (1996) Epaulet brightness and condition in female red-winged blackbirds. Auk 113:356–362

Johnstone RA, Reynolds JD, Deutsch J (1996) Mutual mate choice and sex differences in choosiness. Evolution 50:1382–1391

Kodric-Brown A (1989) Dietary carotenoids and male mating success in the guppy: an environmental component to female choice. Behav Ecol Sociobiol 25:393–401

Kokko H, Monaghan P (2001) Predicting the direction of sexual selection. Ecol Lett 4:159–165

Kraak SM, Bakker TCM (1998) Mutual mate choice in sticklebacks: attractive males choose big females, which lay big eggs. Anim Behav 56:859–866

Kvarnemo C, Forsgren E (2000) The influence of potential reproductive rate and variation in mate quality on male and female choosiness in the sand goby, *Pomatoschistus minutus*. Behav Ecol Sociobiol 48:378–384

Kvarnemo C, Simmons LW (1999) Variance in female quality, operational sex ratio and male mate choice in a bushcricket. Behav Ecol Sociobiol 45:245–252

Lande R (1980) Sexual dimorphism, sexual selection, and adaptation in polygenic characters. Evolution 34:292–305

LeBas NR, Marshall NJ (2000) The role of colour in signalling and male choice in the agamid lizard *Ctenophorus ornatus*. Proc R Soc Lond B Biol Sci 267:445–452

LeBas NR, Hockham LR, Rotchie MG (2003) Nonlinear and correlational sexual selection on 'honest' female ornamentation. Proc R Soc Lond B Biol Sci 270:2159–2165

Lozano GA (1994) Carotenoids, parasites, and sexual selection. Oikos 70:309–311

MacLaren RD, Rowland W, Morgan N (2004) Female preferences for sailfin and body size in the sailfin molly, *Poecilia latipinna*. Ethology 110:363–379

Massironi M, Rasotto MB, Mazzoldi C (2005) A reliable indicator of female fecundity: the case of the yellow belly in *Knipowitschia panizzae* (Teleostei: Gobiidae). Mar Biol 147:71–76

McGraw KJ, Adkin-Regan E, Parker RS (2005) Maternally derived carotenoid pigments affect offspring survival, sex ratio, and sexual attractiveness in a colourful songbird. Naturwissenschaften 92:375–380

Nordeide JT (2002) Do male sticklebacks prefer females with red ornamentation? Can J Zool 80:1344–1349

Nordeide JT, Rudolfsen G, Egeland ES (2006) Ornaments or offspring? Female sticklebacks (*Gasterosteus aculeatus* L.) trade off carotenoids between spines and eggs. J Evol Biol 19:431–439

Olson VA, Owens IPF (1998) Costly sexual signals: are carotenoids rare, risky or required? Trends Ecol Evol 13:510–514

Pélabon C, Borg ÅA, Bjelvenmark J, Forsgren E, Barber I, Amundsen T (2003) Do male two-spotted gobies prefer large fecund females? Behav Ecol 14:787–792

Pizzari T, Cornwallis CK, Lovlie H, Jakobsson S, Birkhead TR (2003) Sophisticated sperm allocation in male fowl. Nature 426:70–74

Potti J, Merino S (1996) Decreased levels of blood trypanosome infection correlate with female expression of a male secondary sexual trait: implications for sexual selection. Proc R Soc Lond B Biol Sci 263:1199–1204

Ptacek MB, Travis J (1997) Mate choice in the sailfin molly, *Poecilia latipinna*. Evolution 51:1217–1231

Rennie S, Huntingford FA, Loeland A-L, Rimbach M (2005) Long term partial replacement of dietary fish oil with rapeseed oil; effects on egg quality of Atlantic salmon *Salmo salar*. Aquaculture 248:135–14

Roulin A, Riols C, Dijkstra C, Ducrest A-L (2001) Female plumage spottiness signals parasite resistance in the barn owl (*Tyto alba*). Behav Ecol 12:103–110

Sargent RC, Gross MR, Van den Berghe EP (1986) Male mate choice in fishes. Anim Behav 34:545–550

Simmons LW, Kvarnemo C (2006) Costs of breeding and their effects on the direction of sexual selection. Proc R Soc Lond B Biol Sci 273:465–470

Svensson PA, Pélabon C, Blount JD, Surai PF, Amundsen T (2006) Does female nuptial coloration reflect egg carotenoids and clutch quality in the two-spotted goby (*Gobiusculus favescens*, Gobiidae)? Funct Ecol 20:689–698

Torres R, Velando A (2005) Male preference for female foot colour in the socially monogamous blue-footed booby, *Sula nebouxii*. Anim Behav 69:59–65

Vincent A, Ahnesjö I, Berglund A, Rosenqvist G (1992) Pipefishes and seahorses: are they all sex role reversed? Trends Ecol Evol 7:237–241

von Schantz T, Bensch S, Grahan M, Hasselquist D, Wittsell H (1999) Good genes, oxidative stress and condition-dependent sexual signals. Proc R Soc Lond B Biol Sci 266:1–12

Wedekind C, Meyer P, Frischknecht M, Niggli UA, Pfander H (1998) Different carotenoids and potential information content of red coloration of male three-spined stickleback. J Chem Ecol 24:787–801

Whitehead PJP, Bauchot M-L, Hureau J-C, Nielsen J, Tortonese R (1986) Fishes of the north-eastern Atlantic and the Mediterranean. UNESCO, Paris, France

Wolf WL, Casto JM, Nolan V, Ketterson ED (2004) Female ornamentation and male mate choice in dark-eyed juncos. Anim Behav 67:93–102