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Colour and pattern in relation to sexual and aggressive behaviour in the Bluehead wrasse *Thalassoma bifasciatum*

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Abstract

Terminal phase adult male bluehead wrasse show rapid and frequent changes of body colour from bright green to opalescent. Green body colour is associated with aggressive chases of other fish, opalescent with courting females and spawning and so the body colour gives an indication of the fish's 'intention' over the next few seconds. Pectoral fin spots appear during courtship and a hypothesis is suggested for their function.

Key words: Aggression; Bluehead wrasse; Colour change; Courtship; Intention; Signalling

Introduction

The colour patterns of fish have been shown to correlate with sexual and aggressive behaviour with varying degrees of reliability (e.g. Barlow, 1963; Fernald, 1977; De Boer, 1980; Martin and Hengstebeck, 1981; Baerends et al, 1955; 1986; Hulscher-Emeis, 1991). We here describe rapid changes (that is, completed within a few seconds) in the body coloration and fin patterns of adult male bluehead wrasse that are strongly correlated with behaviour over periods of a few seconds and minutes and therefore potentially indicate 'intention' (Maynard Smith, 1979; Caryl 1979; Waas, 1991; Hauser and Nelson, 1991).

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The bluehead wrasse is a small (up to 15 cms) coral reef fish which is common throughout the western Caribbean Sea, Florida and the Bahamas (Warner and Robertson, 1978). Adults occur in two colour phases: Initial Phase (IP) individuals which are either male or female and are variable in colour but usually striped yellow and black or barred grey-green, and Terminal Phase (TP) individuals which are larger and always male and which have intense blue heads, a green body and a prominent white vertical stripe separated by two black bars over the pectoral region (Fig. 1). TP males can arise either from IP males or from IP females through sex change (Warner et al., 1975). Males in the two colour phases adopt different mating strategies (Feddern, 1965). IP males show aggregate spawning, with groups of several males clustering around a single female that spawns following a quick rush towards the surface accompanied by the males. They have large testes, apparently an adaptation to the sperm competition experienced during this aggregate spawning. The TP males, by contrast, defend individual spawning territories – typically outcrops of coral on the edge of a patch reef (Warner, 1987) – against all other males and spawn singly with females. The eggs are pelagic and females choose TP males with spawning territories where water currents are best for placing eggs in the plankton (Warner, 1987; 1990). The testes of the TP males are typically about half the size of the IP males (Warner and Robertson, 1978).

Courtship and spawning takes place throughout the year but are restricted to a period of about 2 h each day (Warner and Robertson, 1978). During this time, a given male may spawn several times per hour and will intersperse periods of courting females with aggression towards other males. Aggression mainly takes the form of high speed chases in which TP males swim after intruder males using the rapid rowing movements of the pectoral fins that are characteristic of the labrid fishes.

Methods

Observations on adult TP male bluehead wrasse were carried out on patch reefs in Tague Bay, St. Croix, US Virgin Islands. Eleven individual territorial males were observed continuously for about 30 min at a time from the water surface with face masks and using underwater slates to record data (approximately 6 h of observation were made leading to a total of 4 h and 59 min of recorded data). Observations were made between 13:00 and 15:30h (the time of day when the fish were spawning) during August 1991. The fish were between 1.5 and 3 m below the surface.

The following activities of TP males were recorded:



Fig. 1. Terminal phase (TP) male bluehead wrasse showing distinctive white pectoral stripe. The head is a bright blue and the rest of the body is either green or opalescent grey (see text). Diagram shows the dark pectoral fin spot.

Sexual behaviour

Circling: the male swims in tight circles around and above the female. **Fin fluttering:** a series of repeated movements by the male in which his pectoral fins are moved rapidly backwards and forwards across his body in the region of the black/white/black stripe markings (Fig. 1). **Spawning:** the female turns her head upwards (Warner and Swearer, 1991) and then dashes rapidly to the surface accompanied by the male. At the top of the spawning dash, the female turns upside down and releases her eggs which the male immediately attempts to fertilise.

Aggressive behaviour

Chasing: Males chase all conspecifics away from the territory except females. The close resemblance between females and IP males means that a TP male will, occasionally, spend some time investigating a fish before either courting or chasing it. In addition to chasing target fish, the males often swim considerable distances (5–10 m) away from the centre of their territories.

The males were also recorded as being 'on-territory' or 'off-territory'. At the centre of a territory there was usually a prominent object such as a piece of coral and each male defended an area 1–3 m diameter around this. The precise outer boundaries of territories were not measured.

The following colour changes of TP males were recorded:

1. **Body colour.** The back two-thirds of a male's body (behind the black-white-black stripe) was scored as either green (a bright bottle green colour with a metallic sheen) or opalescent (a pink-grey pearl). The colour changes were generally easy to score, although occasionally intermediate colours were seen. In such cases no change was recorded until the colour had become obvious.

2. **Pectoral fin spots.** The pectoral fins were recorded as either no spot (fins clear and completely transparent) or with spot (with a distinct black circle of about 4 mm diameter at the distal end, as shown in Fig. 1)

The time when a male changed from one body colour to another was recorded. The presence or absence of the pectoral fin spots was noted at this moment of change. The occurrence of the various behaviour patterns was then recorded during the phase that followed one colour change and ended at the next colour change. The position of a male (on- or off-territory) was noted whenever fin-fluttering or spawning occurred and whenever a chase was initiated.

Results

The fish changed frequently between green and opalescent body colour during the periods of observation (a mean of 43.18 times $sd = 16.56$). Figure 2 shows that different behaviour patterns were clearly associated with the fish showing green or opalescent body colour. In particular, green body colour was significantly associated with chasing and the opalescent body colour with courting, fin-fluttering and spawning. Since each fish spent different proportions of the period for which it was observed in the two body colour phases, the expected number of occurrences of each behaviour in each colour phase was calculated for each fish as the total number of occurrences of that behaviour \times proportion total time spent with that body colour. The observed and expected values shown in Fig. 2 are the means for all 11 fish. Binomial tests on the observed and expected values for each

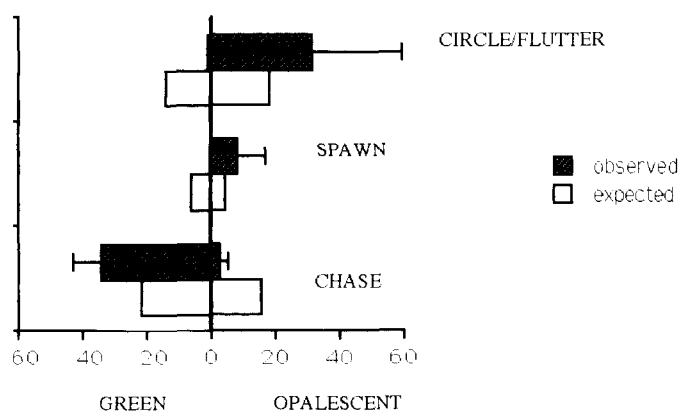


Fig. 2. Observed and expected numbers of instances of circling/fin-fluttering, spawning and chasing that occurred in fish with different body colours. The figures shown represent the means for 11 fish and the bars on the observed values are standard deviations. For the calculation of expected values, see text. Circling/fin-fluttering was significantly more likely than expected to occur when fish were opalescent ($P < 0.001$, Binomial test, $n = 11$) as was spawning ($P < 0.001$). Chasing was more likely to be initiated when fish were green ($P < 0.001$).

of the 11 fish were used to determine whether observed and expected values differed significantly. Fin-fluttering was significantly more likely than expected to occur when a fish was opalescent in body colour ($P < 0.001$; $n = 11$), as were circling ($P < 0.001$) and spawning ($P < 0.001$). Chasing, on the other hand, was significantly more likely to occur when the fish was green ($P < 0.001$).

The relationship between the presence of pectoral fin spots and changes in body colour is shown in Table 1. Fin spots were more likely to be present when the fish had just changed from green to opalescent body colour than when they changed from opalescent to green. Chi-square tests on each fish showed that this relationship was significant for each of the 11 fish (1 case $P < 0.05$; 1 case $P < 0.01$; 9 cases $P < 0.001$). Of the 238 changes to opalescent observed over the 11 fish, 94.9% were associated with the appearance of the pectoral spot. Whereas of the 237 changes to green observed, 90.7% were associated with the absence of the pectoral spot. Table 1 shows the mean values over the 11 fish. This indicates that the spots were most likely to be present when the fish were courting, fin-fluttering and spawning and disappeared when they were chasing other fish.

Courting, fin-fluttering and spawning were also associated with the males being at or near the centres of their territories (Fig. 3). Since precise durations of their being on or off

TABLE 1

Numbers of body colour changes associated with presence or absence of pectoral fin spots

	Change to green	Change to opalescent
Fin spots present	1.1	20.5
Fin spots absent	19.5	2.0

The figures shown are means of 11 fish.

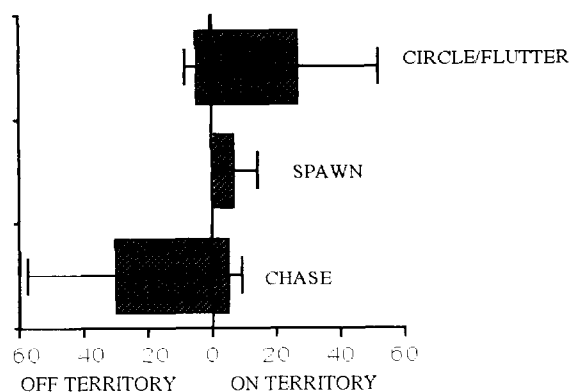


Fig. 3. Observed numbers of instances of circling, fin-fluttering, spawning and chasing that occurred in fish when they were on- or off-territory. Figures shown represent the means of 11 fish and the bars are standard deviations.

territory were not be recorded, it was not possible to calculate expected values, so no statistical analysis of these results is attempted. However, it is clear that whilst most circling/fin-fluttering and all spawning occurred on-territory, most chasing was initiated off-territory.

Discussion

Many fish use colour patterns to signal dominance (e.g. Rasa 1969; Wyman and Ward, 1973; Fernald, 1977; Fernald and Hirata, 1977; Stacey and Chiszar, 1978) or sexual receptivity (e.g. Farr and Travis, 1986; Rowland et al, 1991). In addition they may also use such patterns to signal their motivational state and the behaviour that they are likely to show in the immediate future (e.g. Barlow, 1963; Martin and Hengstebeck, 1981; Baerends et al., 1955; 1986). Rasa (1969) demonstrated that *Pomacentrus jenkinsi*, a damselfish found on Hawaiian reefs, signals aggressive motivation by a darkening of the normally yellow eye and showed that it was possible to predict the outcomes of fights from the respective colouring of the two combatants. De Boer (1980), studying another damselfish, *Chromis cyanea*, on reefs off Curacao, showed that iridescent or light blue colouring in the males was associated with chasing other males or fleeing whereas when the males were soliciting females, their backs became very dark. Colour patterns may therefore serve an analogous function to the badges of status shown, for example, by many birds (Whitfield, 1987; Maynard Smith and Harper, 1988) with the added advantage that they are far more flexible and changeable over the short term than most plumage badges, and comparable to those that can be temporarily covered (Hanson and Rowher, 1986).

The very close correlation between colour pattern and behaviour shown by the bluehead wrasse in the present study can be related to the mating strategies of the two sexes. Females initiate the spawning dash to the surface (Warner and Swearer, 1991) where they lay their eggs. Successful fertilisation therefore depends on the male following the female closely and fertilising the eggs before they have been swept away by the currents that are a feature of preferred mating sites (Warner, 1987). For males, on the other hand, successful reproduction depends both on being able to court females and on

chasing intruding males off the territory, activities that are mutually incompatible. It is therefore important for the female to spawn only when the male is ready to follow her and not when he is about to chase other males. At the same time, it is important for the male that the female should not release eggs when other males are around, or when the male is not ready or prepared to fertilise them. It is therefore in the interest of the female to know the intentions of the male and in the interest of the male to display them – conditions that should encourage reliable intention signalling. A male that signals his intention to spawn clearly with a distinctive colour pattern would be giving the visual equivalent of a male stickleback ‘quivering’ on the tail of a female about to lay eggs (Tinbergen, 1951) or the ‘tail touch’ a female newt gives to a male as a stimulus for him to deposit a spermatophore (Halliday, 1975).

The dark spots on the pectoral fins are a striking feature of sexual behaviour in the bluehead wrasse, particularly because the fin fluttering movements cause the spots to appear and disappear rapidly as they move across the black/white/black stripes on the body. The body stripes appear to accentuate the movements of the fins when the female is close and could potentially signal finning or muscle strength through fin-fluttering rate. Many species of fish use spots to attract attention (Guthrie, 1986) and the bluehead fin spots may be particularly attractive to females because of their resemblance to moving prey such as copepods (McFarland, 1991). In addition, the stripes also seem to function as a longer-distance signal that is conspicuous in the blue waters of the Caribbean (Lythgoe, 1979). Warner and Schulz (1992) have shown that variation in the width of the white stripe is related to variation in mating success and may itself be an indicator of male quality. This means that the body stripes may have evolved both as an indicator of quality and also, in conjunction with the fin spots, as accentuators of the fin movements. They thus contribute to the efficacy (Guilford and Dawkins, 1991) of the entire suite of courtship signals (stripes, spots and fin movements).

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