



## Artificial enhancement of an extended phenotype signal increases investment in courtship by three-spined sticklebacks

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Interactions between the components of a multiple-signal sexual display can be complex, and previous work has shown that alteration of one component can lead to changed investment in either the altered or other display components. Extended phenotype signals (nonbody structures that carry a signalling function) provide an ideal means to manipulate signal quality in a noninvasive manner, to investigate investment patterns in display components. We made three predictions as to how males might alter investment in display components in response to artificial enhancement of an extended phenotype signal, and tested those predictions using three-spined sticklebacks, *Gasterosteus aculeatus*. The addition of brightly coloured ornaments (threads) to the nests of male sticklebacks led to increased investment in both courtship of females and nest construction. In a field experiment, males offered coloured threads spent increased time engaged in interactions with females, and in the laboratory, they built nests that were neater and more compact (better quality), relative to males offered dull threads. Our findings support a hypothesis based on resource budgeting, and suggest that resources saved by having an artificially enhanced nest are reallocated to other courtship behaviours. The study provides a framework for investigating the interaction between signal components, and demonstrates that manipulation of extended phenotype signals can provide insight into the ways in which animals balance investment in interacting signal components in sexual displays.

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Sexual displays can be complex, involving multiple signal components, often across different sensory modalities (Candolin 2003; Hebets & Papaj 2005). For instance brightly coloured ornamentation may be combined with vocalizations or courtship displays. Multiple traits may convey similar ('redundant' or 'backup signals') or different ('multiple messages') information about underlying male quality, or interact to enhance the information content of the signals ('emergent messages', 'signal enhancers' and 'amplifiers'). Alternatively, different signals may contain

information for different receivers ('multiple receivers'), or may represent adaptation to fluctuating environments or dynamic variation in selection pressures (reviewed in Candolin 2003; Hebets & Papaj 2005; Bro-Jørgensen 2010). Although it has been argued that multiple ornaments may be only weakly condition dependent (Møller & Pomiankowski 1993), other studies support the idea that multiple signals are honest indicators of underlying male quality (Candolin 2003; van Doorn & Weissing 2004) and that males invest optimally in signalling (Andersson 1982; Delcourt & Rundle 2011).

The interaction between signal components is likely to be complex (Candolin 2003), making it difficult to predict how animals might respond to changes in their signal quality. For example, activation of the immune system in birds can reduce the behavioural display component of a signal, but the reduction is lower in individuals expressing plumage-based signals indicative of high quality (Garamszegi 2004; Loyau et al. 2005). Experimental manipulation of individual signal components is perhaps challenging, particularly where signals are correlated (Candolin 2003), but can provide insight into how traits interact to convey information to a receiver. Wolf spiders (*Schizocosa* spp.) use a combination of visual and vibratory (seismic) signals in courtship. When

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placed on a substrate that does not allow for the transmission of vibratory signals (granite), males increase investment in the visual component of courtship display (Gordon & Uetz 2011) allowing them to maintain courtship success (Hebets & Papaj 2005).

'Extended phenotype signals' are nonbody structures (such as nests, burrows and bowers) built by males that can act to inform mate choice (Schaedelin & Taborsky 2009). Females prefer to mate with males with particular signal characteristics that indicate either male quality or enhance the survival of eggs (birds: Hansell 2005; fiddler crabs, *Uca annulipes*: Backwell & Passmore 1996; bowerbirds: Borgia 1995; Humphries & Ruxton 1999; Madden 2003). Evidence suggests that many extended phenotype signals are condition dependent, and honestly signal builder quality (e.g. Barber et al. 2001; Soler et al. 2001; Olsson et al. 2009). Thus, extended phenotype signals provide an ideal means to manipulate signal quality experimentally without potentially confounding direct physical or physiological impacts on signaller behaviour (Schaedelin & Taborsky 2009, 2010; Sergio et al. 2011). This allows for investigation into how male investment in display components is influenced by manipulation of the extended phenotype signal.

When an extended phenotype signal is experimentally manipulated, males may alter their investment in either the manipulated trait or alternative components of their display. In the black wheatear, *Oenanthe leucura* (Soler et al. 1996) and the Lake Tanganyika cichlid *Cyathopharynx furcifer* (Schaedelin & Taborsky 2006), males compensated for alteration to their nests and mating craters, respectively, through increased investment in building behaviour and rapid reconstruction of the signals to their original dimensions. In contrast, satin bowerbirds, *Ptilonorhynchus violaceus*, increased investment in bower construction when bower decorations were experimentally removed (Bravery & Goldizen 2007), and barn swallows, *Hirundo rustica*, with experimentally lengthened tails reduced nest-building effort (Soler et al. 1998). Here, we investigated how male three-spined sticklebacks, *Gasterosteus aculeatus*, alter investment in behaviour and nest construction, in response to artificial enhancement of the quality of their nest, which acts as an extended phenotype signal in this species.

In sticklebacks, the males build nests from sediment and plant material, and are solely responsible for parental care (Van Iersel 1953). The nests are held together with a kidney-secreted protein called spiggin (Jakobsson et al. 1999), and are known to have a courtship-signalling function (von Frisch 1974; Barber et al. 2001; Östlund-Nilsson 2001; Östlund-Nilsson & Holmlund 2003). Females are first alerted to the presence of males via olfactory cues (McLennan 2003), after which the male uses his courtship display to lead females to the nest (Candolin 1997); thus, nest inspection by females occurs late in the courtship sequence. Nest quality, measured as neatness and compactness, increases with both male quality and immunological function (Barber et al. 2001; Östlund-Nilsson 2001); so nests act as an honest signal of male quality. Males may also 'decorate' their nest with algae of contrasting colours or artificial materials provided experimentally (such as threads, foil sticks and sequins), and females prefer males with nests decorated with brightly coloured objects over undecorated nests (Östlund-Nilsson & Holmlund 2003). The provision of brightly coloured objects therefore provides a simple experimental means of manipulating perceived nest quality.

We manipulated nest quality by providing male sticklebacks with brightly coloured cotton threads. In a field experiment, we investigated behavioural investment in nest building, courtship of females, male–male aggression and other fitness-related behaviours in response to nest enhancement (relative to a control). In a complementary laboratory study, we investigated investment in nest construction by analysing nest quality. We tested three hypotheses linking nest quality to behaviour.

(1) Decreased investment hypothesis: when one trait (here, the nest) is enhanced, investment in other aspects of courtship could be reduced so that the overall level of signalling remains the same, and honestly indicates male quality. This may explain the reduction in nest-building effort by male barn swallows with lengthened tails (Soler et al. 1998), and may be particularly relevant when female preferences are based on the simultaneous, combined effect of multiple cues (Lehtonen et al. 2007; Lancaster et al. 2009). This hypothesis predicts that stickleback males with enhanced nests will decrease the time invested in courtship behaviour and decrease nest quality relative to males with control nests.

(2) Resource-budgeting hypothesis: if males have a limited resource (e.g. energy, time) budget to allocate to mate attraction, increasing the quality of one trait could allow for increased investment in other aspects of mate attraction, as lower resource allocation to the enhanced trait is needed. This hypothesis predicts that stickleback males with enhanced nests will increase the time spent courting females, and increase nest quality, relative to males with control nests.

(3) Alternative allocation hypothesis: as an alternative to hypothesis 2, male resources could be allocated to other behaviours outside the mate attraction sphere, such as foraging or resting. This hypothesis is perhaps particularly relevant to species in which males provide parental care, and resources must be allocated to, or retained for, continued investment in offspring provisioning or survival (Kokko et al. 2002). This hypothesis predicts that stickleback males with enhanced nests will increase the time spent resting and/or foraging relative to males with control nests, while time spent courting and nest quality will not differ between enhanced and control nests.

## METHODS

### Study System

The three-spined stickleback is a small shoaling fish, native to freshwater, brackish and marine habitats in the northern temperate region. In the breeding season (May–July in the U.K.) males leave their groups and develop bright nuptial coloration (see below). Males establish small territories in shallow water (<1 m), in which they construct a nest from plant material and spiggin. This nest, the male's breeding coloration and a courtship dance attract females to lay their eggs in his nest, which he will then fertilize and care for alone (Van Iersel 1953; Wootton 1984).

### Field Experiment

Our field experiment was carried out in an artificial brackish fishing pond in Saltfleet, Lincolnshire, U.K. (53° 25.2'N, 0° 11.4'E; OS Explorer 283 map grid reference 459939), measuring approximately 115 × 40 m, between April and July 2009. The pond was created in 1980 and has had a resident stickleback population since 1981 (local fishermen, personal communications). The pond is characterized by wide, shallow silt banks providing both suitable stickleback nesting habitat and areas from which to observe nesting sticklebacks.

In total, 50 nests were identified as being suitable for study. These were nests made by males whose entire territory could be identified from the bank, positioned less than 1 m from the shore, and at a depth of 30 cm or less, allowing reliable observations to be made from the bank. Nests were required to be almost complete (defined by the presence of a visible nest entrance; Barber et al. 2001; Rushbrook et al. 2008), yet still under construction (defined by males carrying and adding material to the nest, and so the nest would be unlikely to contain eggs; Van Iersel 1953).

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