



Context-dependent preferences vary by multicomponent signals in a swordtail



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Female mating preferences can be both context dependent and based on the assessment of multicomponent male signals. Here, we assess the social context dependence of female mating preferences for two components of a male's multicomponent signal. We dissected the visual signal of male *Xiphophorus nigrensis* swordtails, a species in which males vary by both size and degree of courtship, to test (1) how the identity of males in a given choice influences female mating preferences and (2) how females perceptually integrate a male's multicomponent signal. We used validated male animations that generate repeatable female responses to test mating preferences for size and courtship vigour, separately and together, using dichotomous choice tests. When keeping courtship vigour constant, females discriminated between males only when there was a large size difference between them. When keeping size constant, the identity of males in a choice reversed a preference for a vigorously courting male. We found no evidence that females perceptually bind the separate components of a male's signal additively. However, females were faster to approach males when the males varied in both size and courtship than when the males only varied in size, perhaps favouring the evolution of multicomponent signals in males. © 2017 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Although Darwin and Wallace agreed on many things, the relative importance of male ornamentation to a female's mate choice decision was not one of them. While Darwin contended that ornamentation was more important to females (Darwin, 1859), Wallace maintained that courtship vigour was the main interest (Wallace, 1889) and that ornamentation simply amplified the intensity of the male's courtship. Although the surge of interest in the past three decades on female mating preferences has mostly focused on the importance of ornamentation, there is evidence to suggest Wallace might have been right as well (Byers, Hebets, & Podos, 2010; Cornuau, Rat, Schmeller, & Loyau, 2012).

Male mating signals of the sort that Darwin and Wallace disagreed about are 'multicomponent signals' if females perceive the parts of the signal—e.g. ornamentation and courtship vigour—in a single sensory modality (Rowe, 1999). Multimodal signals span modalities, like vision and audition (Hebets & Papaj, 2005). Both types of signals, which we call 'complex signals' (following Hebets & Papaj, 2005), are ubiquitous in mating interactions (Candolin, 2003) in part because they are thought to be more detectable, eliciting faster reactions from females (Rowe, 1999). The study of

complex signalling is indebted to the descriptive categorizations of Johnstone (1996) and Møller and Pomiankowski (1993) that were later expanded by Partan and Marler (1999, 2005). These categorizations are useful in understanding how different components of a complex signal interact to affect some response in a receiver. A common assumption is that females can independently assess the different components of a signal and integrate them by additively combining them (Hebets, 2005; Hebets & Papaj, 2005; Stange, Page, Ryan, & Taylor, in press), although this need not be the case.

One of the challenges still facing the study of complex signal processing and design is understanding how females process multiple signal components that vary continuously. As noted by Wagner (1998), presentation of two extremes of a signal component (i.e. presence and absence) is best suited for testing for directional preferences. In many species, the components of a signal vary continuously, and work in treehoppers (Fowler-Finn & Rodríguez, 2012; Rodríguez, Hallett, Kilmer, & Fowler-Finn, 2013), guppies (Blows, Brooks, Kraft, & Phillips, 2003; Cole & Endler, 2015) and crickets (Bentsen, Hunt, Jennions, & Brooks, 2006; Gray, Gabel, Blankers, & Hennig, 2016; Reichert, Finck, & Ronacher, 2017) shows that female preferences for components of male traits are often not directional. Smith and Evans (2013) recognized this limitation and encouraged researchers to consider continuous variation in signal components when studying multimodal communication. Ronald,

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Zeng, White, Fernández-Juricic, and Lucas (in press) further expanded on this work and created a theoretical framework for understanding how continuously varying signal components influence the overall response to a complex signal.

At the same time, evolutionary biologists interested in the patterns of multivariate selection that females impose on males have studied complex signalling for decades. Female guppies, for example, impose complex linear and nonlinear selection on male coloration (Blows et al., 2003; Brooks & Endler, 2001; Cole & Endler, 2015). These studies used statistics to understand patterns of female preference for the separate components of a male's coloration. But by relying on naturally occurring variation in male traits, it becomes difficult to fully understand the individual contributions of signal components on the receiver's response. Use of live males also makes it difficult to partition a female's response to the male's coloration from other components of his visual signal, such as his behaviour. Correlations between signal components make teasing apart these contributions even more difficult. A more powerful approach would be to synthetically engineer signals (Bentsen et al., 2006; Gray et al., 2016; McClintock & Uetz, 1996; Reichert et al., 2017; Rosenthal & Evans, 1998), giving the researcher precise control over the signal and the ability to decouple signal components that might typically be tightly correlated, although this has rarely been done for visual signals.

While most of the ideas about how complex signals are perceived by receivers assume that signals will be perceived the same way regardless of context, female mating preferences can also be influenced by the environment (Jennions & Petrie, 1997). For example, female mating preferences for colourful males can be abolished in the presence of a predator (Forsgren, 1992; Godin & Briggs, 1996). Although context-dependent or plastic preferences are often studied by examining how mating preferences change in different physical (e.g. lighting) environments (Fuller & Noa, 2010; Maan, Seehausen, & Van Alphen, 2010), the social environment is increasingly recognized as playing a large role in shaping a female's choice of mate (Rodríguez, Rebar, & Fowler-Finn, 2013). Mate choice copying is one example where the presence of a conspecific interacting with a potential partner can increase that individual's perceived attractiveness by an observer (Auld & Godin, 2015; Schlupp, Marler, & Ryan, 1994; Witte & Ryan, 2002). Furthermore, multiple experiments have demonstrated that exposure to specific male types at developmental (Fowler-Finn & Rodríguez, 2012; Hebets, 2003; Verzijden & Rosenthal, 2011) or adult (Tudor & Morris, 2011) life stages can alter female responses towards males during subsequent encounters.

Here we explore how the immediate social environment, specifically the available set of males that a female is deciding among (the 'choice set' of males), influences her choice behaviour. This relatively unexplored mechanism of how the social environment could affect mating preference is particularly important with multicomponent signals that show continuous variation. How will a female respond when confronted with two males, each more attractive for a different component of his multicomponent signal? In humans (Huber, Payne, & Puto, 1982) and other animals (Lea & Ryan, 2015; Locatello, Poli, & Rasotto, 2015; Royle, Lindström, & Metcalfe, 2008), the options immediately available to a female chooser can alter her choice behaviour (Bateson & Healy, 2005). In túngara frogs, *Engystomops pustulosus*, for example, an initial preference for one of two male calls in a dichotomous choice test can be reversed by adding a third call to the 'choice set' of available calls (Lea & Ryan, 2015). This mechanism is distinct from the social exposure experiments outlined above because all females have the same exposure to male signals: the difference is in the males that are immediately available for comparison (Patricelli & Hebets, 2016). Many studies

that measure female mating preferences for different male signals use no-choice tests (Fowler-Finn & Rodríguez, 2012; Girard, Elias, & Kasumovic, 2015; Hebets, Vink, Sullivan-Beckers, & Rosenthal, 2013; Wagner, Smeds, & Wiegmann, 2001). These are tests in which a female is presented with a single type of male or male signal and her response to that signal alone is recorded. Thus the role that the choice set of males has on female preferences for different males has often been neglected in studies of mate choice behaviour, and even more so in studies of complex signalling.

Here, we study context dependence of female mating preference for two continuously varying components of a male multicomponent signal in the El Abra pygmy swordtail *Xiphophorus nigrensis*. Males of this species have genetically based alternative mating phenotypes: large males court females, small males attempt coercive matings with females, and intermediate males can do both (Ryan & Causey, 1989; Zimmerer & Kallman, 1989). Females prefer large males over small males in dichotomous tests with live males (Cummings & Mollaghan, 2006; Wong, So, & Cummings, 2011) and respond to synthetic animations of males (Rosenthal, Wagner, & Ryan, 2002), allowing the decomposition of a male's visual signal. *Xiphophorus nigrensis* is therefore an attractive species in which to test both perceptual integration of signals and context dependence.

Our goals in this study were three-fold. First, we wanted to test whether females perceptually bind two components of a male's multicomponent signal in an additive or nonadditive way. To do this, we presented female swordtails with a series of animated males that differed (1) only in size, (2) only in courtship vigour or (3) in both size and courtship vigour. This dissection of a male's visual signal allowed us to measure female mating preferences for each component separately and together. To test for additive preferences, we compared female preference responses in each of the single component trials to the combined multicomponent trials. If females bind separate components of a male's visual signal in a strictly additive way, then their preference scores for the multicomponent trials should be predicted by the summed quantity of their responses for each of the individual component trials.

Second, we tested whether female preferences for specific male components (his size or courtship rate) were absolute or varied depending on the expression of these components between the available males present (the 'choice set' of males). To test the influence of a female's choice set, for each signal component we created three types of males that varied in component properties (small, intermediate and large males that displayed either no, low or high levels of courtship). We tested female mating preferences in dichotomous choice tests for each pairwise combination of males. This allowed us to assess female mating preferences for a given type of male when paired against two other types of males. If female preferences for specific components are absolute, then preferences for that male component should be constant across different choice sets. If, however, a female's preference for male signal components is dependent on how those signals are perceived in the presence of other males with different component states, then we predicted that female preferences would vary across choice sets.

Third, to test a possible adaptive function of multicomponent signalling, we tested whether multicomponent signals evoke faster reaction times than individual stimuli (as predicted by Rowe, 1999). To test this hypothesis, we examined whether latency to approach males in our experiments was shorter when males varied in both courtship intensity and size relative to the single component experiments. We predicted that females would approach males more quickly when males varied in size and courtship compared to when males varied in only one dimension (size or courtship).

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