ANIMAL BEHAVIOUR, 2008, **76**, 1565–1570
doi:10.1016/j.anbehav.2008.07.014

Does the environmental context of a signalling male influence his attractiveness?

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(Received 5 May 2008; initial acceptance 19 June 2008;
final acceptance 17 July 2008; published online 5 September 2008; MS. number: D-08-00294)

How sexually selected male signals and female sensory systems have evolved so that females can continue to detect and discriminate between potential mates in the face of environmental noise and changes in signaller density has been well studied for acoustic signals. Far less is known about visual signals. We examined the influence of the local signalling environment on male signal attractiveness in the fiddler crab *Uca mjoebergi*. We used custom-built robotic crabs in two-stimulus mate choice experiments. Females were presented with two identical signals produced in two different signalling environments (simple and complex). The conspicuousness/attractiveness of male claw waving was unaffected by the local environment (physical or social). Male *U. mjoebergi* appear to produce a signal that is highly conspicuous across a wide range of naturally occurring signalling environments and females seem to have a sensory system that is capable of coping with high levels of environmental noise.

Keywords: female choice; fiddler crab; signal conspicuousness; *Uca mjoebergi*; visual noise

Communication systems involve the exchange of a signal between a sender and a receiver to the benefit of both parties (Bradbury & Vehrencamp 1998). An effective signal is one that the intended receiver can detect against background noise and that allows discrimination of salient characteristics from those of other signals. Numerous environmental factors can affect these processes, including competing signals from other conspecifics, extraneous environmental noise and predation risk, all of which can influence the type of signal emitted (Guilford & Dawkins 1993).

Mate attraction signals are subject to strong sexual selection imposed by environmental factors that determine the most effective mode of communication as well as finer-scale characteristics of the behaviour and physiology of senders and receivers (e.g. Witte et al. 2005; Doucet et al. 2007). Males with signals that are easier to detect and locate are more likely to mate. To maximize signal efficacy, both sender and receiver evolve traits that increase signal detectability and fidelity. Signals tend to match well the environment in which they are produced, while receivers evolve sensory systems that compensate for environmentally induced signal degradation during transmission (Endler 1992). For example, while most frogs use acoustic signals to attract mates, noise from cascading water has led to the partial loss of such signals in the Panamanian golden frog, *Atelopus zeteki*. Instead, visual signals comprising limb movements are used as they are more efficacious in an acoustically noisy environment (Lindquist & Hetherington 1996).

For a visual signal, detectability or conspicuousness is largely determined by the extent to which it is a nonrandom sample of the surrounding environment (Uy & Endler 2004). This is achieved by (1) colour, (2) brightness, (3) pattern geometry and (4) movement contrast (Bradbury & Vehrencamp 1998). Signals evolve to increase the signal to noise ratio (Ryan 2007), with receivers often responding preferentially to those that are bigger, brighter, faster and offer more visual contrast (Andersson 1994). Fine-scale aspects of signalling behaviour, such as microhabitat choice by signallers, can further boost the signal to noise ratio and reduce potential signal degradation (Endler 1992; Chunco et al. 2007). For example, in golden-collared manakins, *Manacus vitellinus*, males behaviourally enhance their conspicuousness by altering

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0003–3472/08/$34.00/0

their signalling environment: they clear a circular court and then display to females who assess males from elevated perches (Endler & Thery 1996). A cleared court provides a simple visual background that improves display conspicuousness (Uy & Endler 2004). Similarly, there is evidence from guppies, *Poecilia reticulata* (Endler 1991), wire-tailed manakins, *Pipra filicauda* (Heindl & Winkler 2003a) and the moth *Hepialus humuli* (Andersson et al. 1998) that males exploit specific light environments that increase within-body contrast of colour patches used in sexual displays and elevate contrast with the background (Heindl & Winkler 2003b).

There is relatively good information on how the physical environment (e.g. understorey density, canopy cover) and environmental noise affect the detectability of acoustic signals. The masking effect of background noise on call detectability has been shown for many species (Morton 1975; Wollerman 1999; Wollerman & Wiley 2002; Slabbekoorn & Peet 2003; Witte et al. 2005; Patricelli & Blickley 2006; Warren et al. 2006; Swaddle & Page 2007). It selects for shifts in signal properties. For example, urban great tits, *Parus major*, that live in noisy industrial locations differ from those in quiet residential areas by using higher minimum frequencies in their song, presumably to reduce the masking effect of low-frequency noise from cars and planes (Slabbekoorn & Peet 2003). In contrast, we know far less about environmental effects on visual signals in the field (Stuart-Fox et al. 2007). It is only because of recent advances in robotics, video playback and spectrometry that field studies of visual communication systems have become possible (Ryan 2007). For example, Ord et al. (2007) provided one of the first studies illustrating the influence of movement-based visual noise on visual displays, showing that signal speed in two Puerto Rican lizards (*Anolis cristatellus* and *A. gundlachi*) had to be increased to improve communication in environments of rapidly moving vegetation.

The presence of other signallers can also have a pronounced effect on a receiver's ability to detect and discriminate relevant signals (Wollerman & Wiley 2002). Psychophysical studies of humans show that an excess of signals can generate an erroneous response or lack of response because of 'cognitive overload' (Hutchinson 2005). Similarly, for acoustic signals used by animals, changes in the density and distribution of calling males can impair a female's ability to discriminate between potential mates (Wollerman 1999; Wiley 2006). Again, however, there is less evidence for this type of 'confusion effect' for visual signals, largely because of the practical difficulties of generating artificial signals in the field.

We used robots to test how the conspicuousness, and thus attractiveness, of visual courtship signals produced by male fiddler crabs (*Uca mjoebergi*) is influenced by the signalling environment. Male fiddler crabs wave their greatly enlarged claw to attract females as mates. In most species, including *U. mjoebergi*, there is great variation in the environment in which males wave and females select mates (Crane 1975). For example, some males display in full sunlight on exposed mudflat, while others are shaded by mangrove trees; some wave among mangrove roots and a moving background of waving leaves, while others are in the flat, treeless habitat of the open mudflat (Nobbs 2003). There is also substantial variation in the social environment because of changes in the local density of waving males (Christy 1980). Our aims in this study were to investigate the influence of (1) light level, (2) background complexity, (3) foreground complexity, (4) a combination of these factors, and (5) social complexity on male signal conspicuousness/attractiveness.

METHODS

Uca mjoebergi is a small fiddler crab (carapace width 5–20 mm) that inhabits intertidal mudflats in northern Australia (Crane 1975). They occur in dense, mixed-sex colonies (Reaney & Backwell 2007a). Both sexes defend territories that are centred on a burrow. Males have one greatly enlarged claw (an order of magnitude longer than the feeding claw), which they wave at females during courtship (Reading & Backwell 2007). During the mating period, receptive females leave their territories and visit the burrows of a series of courting males before eventually selecting a mate (Reaney & Backwell 2007b). Females are usually simultaneously faced with several potential mates. Observations in the wild show that females more often approach males with higher wave rates and bigger claws (L. T. Reaney, unpublished data). Playback experiments using robotic crabs confirm that females have preferences for specific male traits (e.g. claw size, wave rate and wave leadership, i.e. waves beginning before those of its neighbours; Reaney et al. 2008; E. Curran, M. D. Jennions & P. R. Y. Backwell, unpublished data). Our study was undertaken at East Point Reserve, Darwin, Australia. Mate choice trials were run for 5–6 days during peak mating periods each neap tide from September to December 2007.

We surveyed the habitat of *U. mjoebergi* along seven 20 m transect lines, placed 8 m apart and set perpendicular to the shoreline. At 50 cm intervals along each transect, the closest male crab (<30 cm) was selected and his immediate habitat (<10 cm) was scored for shade (absent, mottled or heavy), the presence of mangrove roots (≥3 roots = present), and presence of shells or leaves (for both, ≥1 = present).

The field site used for the mate choice trials was an environmentally homogeneous clearing within the natural distribution of *U. mjoebergi*. All conspecific and heterospecific crabs within 2 m of the choice arena were removed and released elsewhere on the mudflat. For the experiments we used custom-built robotic crabs (see Reaney et al. 2008 for construction details). In brief, each robotic crab has a claw movement engineered to resemble closely that of a courting male *U. mjoebergi*. For all experiments we set the wave rate at 8.4 waves/min and the artificial claw size was 17.5 mm (population mean ± SE = 17.79 ± 0.124 mm, $N = 704$, Morrell et al. 2005), and both claws waved in synchrony to avoid a leadership effect (Reaney et al. 2008). The two robotic crabs were placed 5 cm apart and 20 cm from the female release point. These distances fall within the natural ranges of intermale distances during a bout of waving (5 cm) and the distances between a female and a set of displaying males when she makes her mate choice (20 cm). The motors moving the claws were buried underground so that only the claw was visible to the female. The area surrounding the choice