



Behavioral Ecology (2014), 00(00), 1–5. doi:10.1093/behco/art125

## Original Article

## Fiddlers on the roof: elevation muddles mate choice in fiddler crabs

Luke Holman, Andrew T. Kahn, and Patricia R.Y. Backwell

Division of Ecology, Evolution &amp; Genetics, Research School of Biology, Australian National University, Canberra, Australian Capital Territory 0200, Australia

Received 24 May 2013; revised 7 November 2013; accepted 1 December 2013.

Biological signaling usually occurs in complex environments, yet signals are most often studied in controlled experiments that strip away this complexity. Male fiddler crabs possess one enlarged claw that is waved during courtship displays, and females preferentially respond to larger claws and faster waves. Fiddler crab vision is evolutionarily specialized to their predominantly level mudflat habitats, although some populations inhabit topographically complex environments. Here, we investigated how the elevation of signaling males relative to receiving females affects attractiveness. Experiments with robotic crabs revealed a strong female aversion to males signaling from atop small (>2 cm) mud mounds. This aversion entirely masked previously documented strong preferences for large claws and faster waving. Our results suggest that variation in signaling environment might substantially weaken selection on males, thereby helping to maintain genetic variation in courtship traits.

**Key words:** error-prone signaling, sexual selection, *Uca mjoebergi*, visual communication.

## INTRODUCTION

Temporal and spatial variations in mate choice preferences have important implications for sexual selection. Just as fluctuating natural selection can preserve genetic polymorphism, variable female preferences could help to maintain genetic variation in male sexual signals (Chaîne and Lyon 2008). The lek paradox (Kirkpatrick and Ryan 1991) questions why male sexual ornaments and weapons remain variable despite persistent sexual selection, yet the paradox lessens or disappears if female preferences are sufficiently variable (Chaîne and Lyon 2008). Such variation in female preferences might result from adaptive plasticity: females might choose a mate that best complements their current needs based on variable biotic and abiotic factors (Qvarnström et al. 2000). For example, female fiddler crabs display a stronger preference for males with large claws in summer, potentially because claw size correlates with the size and temperature of the burrow provided by the male (Milner, Detto, et al. 2010).

Variation in signaling traits might also be maintained if environmental factors introduce errors to receivers' perception or assessment of signals (Endler and Basolo 1998). Examples include the masking of auditory signals by background noise (e.g., Samarra et al. 2009) or visual signals by turbid water (e.g., Candolin et al. 2007). When the environment adversely affects the receiver's response (from the signaler's perspective), selection should favor

those signalers that evolve means to overcome this effect. For example, some *Anolis* species and *Amphibolurus muricatus* lizards adjust the structure (Peters et al. 2007) and speed (Ord et al. 2007) of their visual displays to improve signal transmission against backgrounds of moving vegetation. Furthermore, signalers could use the environment to manipulate receivers if it biases receiver response in a favorable way. For example, male great bowerbirds (*Ptilinorhynchus nuchalis*) maintain decorations around their bower to create "forced perspective" (Endler et al. 2010), which makes the bowers appear larger to females and improves males' mating success (Kelley and Endler 2012).

Fiddler crabs (*Uca* spp.) are excellent models for studies of sexual selection, signaling, and mate choice. Males possess one greatly enlarged claw, which is used as a weapon during territorial fights (Pratt et al. 2003) and waved in a stereotyped, species-specific pattern during courtship and threat displays (How et al. 2008). Previous experiments have found that females prefer males with large claws, as well as males that wave rapidly (Reaney 2009). Though the strength of this preference varies across seasons and tidal cycles, selection on claw size and waving behavior might nevertheless be under directional selection because females consistently prefer high values of these traits (Milner, Detto, et al. 2010; Kahn et al. 2013). However, both traits show considerable intraspecific variation (e.g., Jennions and Backwell 1998; How et al. 2008; Lailvaux et al. 2009). In a study explicitly testing for environmental effects on male courtship signaling in *Uca mjoebergi*, Milner et al. (2008) found no effect of light level or foreground and background

Address correspondence to L. Holman. E-mail: luke.holman@anu.edu.au.

complexity on female mate choice behavior. However, other contextual or environmental factors may introduce variability into the outcome of female mate choice.

Here, we investigated whether the elevation of a courting male affects female mate preferences in the fiddler crab *U. mjoebergi*. Fiddler crab vision is well suited to their largely flat environment: their eyes sit atop long vertical stalks and provide a panoramic view of the mudflat (Zeil and Hemmi 2006). Experiments suggest that fiddler crabs approximate the distance and size of external objects by comparison with their horizon line (Zeil et al. 1986; Layne 1998). Furthermore, crab vision is hypothesized to be separated into 2 main areas: movements above the crab's visual horizon elicit antipredator responses (e.g., freezing or entering a nearby burrow), whereas those below do not (Layne et al. 1997). The claw-waving of courting males crosses this visual boundary when signaler and receiver are both on a flat surface (How et al. 2009), and male waving is speculated to exploit female responses to elevated stimuli, for example, by startling wandering females into freezing near the male's burrow or bolting into it (Layne et al. 1997). A link between intersexual signaling and antipredator responses may also explain why some fiddler crab species build mud structures next to their burrows: the structures attract females by mimicking natural refugia (Christy 1995; Christy et al. 2003).

In light of this previous work, it is unclear whether male fiddler crabs waving at different elevations should appear more or less attractive to females. Elevated males might appear larger because their claws reach higher areas of the female's field of vision (Zeil et al. 1986) and could thereby have inflated attractiveness. In line with this prediction, the waving behavior of many fiddler crab species appears to have evolved to maximize the wave's height (How et al. 2008); in *U. mjoebergi*, the legs are straightened at the apex of the wave, further elevating the claw. Accordingly, females appear to prefer tall waves rather than large males or claws per se (Murai and Backwell 2006). Conversely, females might fail to recognize elevated males as potential mates if they occupy the visual space above females' horizon lines and hence are perceived as potential threats (Layne 1998; Zeil and Hemmi 2006). Males living atop small hills on the mudflat may therefore be unattractive. Adding to the uncertainty, antipredator behavior could influence mate choice (Christy 1995; Christy et al. 2003): rugged areas of the mudflat might be more dangerous and hence avoided by females (e.g., if crabs were less able to locate burrows or perform evasive sprints on uneven surfaces), or conversely, they could provide more refugia and thereby be attractive to females.

## METHODS

Fieldwork was conducted in mangrove mudflat habitats in East Point Reserve, Darwin (12.41°N, 130.83°E).

### Spatial distribution of courting males

To assess whether male density and traits affecting fighting ability are related to elevation, we randomly sampled natural *U. mjoebergi* populations. Some areas of the mudflat are level ("flat sites"), whereas others contain aggregations of long-lasting (across years) mud mounds up to 25 cm high ("elevated sites") created by larger burrowing crustaceans such as the mangrove lobster, *Thalassina squamifera*. To compare male density between site types, we identified all male *U. mjoebergi* burrows inside randomly thrown 35 cm<sup>2</sup> quadrats ( $n = 20$  per site type). This was accomplished by marking all burrows with numbered flags and waiting for all crabs to reemerge.

For each burrow, we used calipers to measure burrow diameter  $\pm 0.1$  mm (highly correlated with the size of the occupant; Reaney and Backwell 2007). We recorded the distance to the nearest male burrow ( $\pm 0.1$  cm) and the number of male burrows within 15 cm. We also noted whether the male had an original or regenerated claw, as the latter impedes fighting (Reaney, Milner, et al. 2008). For elevated sites, we also recorded the elevation of the burrow entrance above the lowest point in the quadrat ( $\pm 0.1$  cm).

All statistical analyses were performed in R 3.0.2. Mixed models and generalized linear mixed models (GLMMs) were performed using the function *glmer* in the lme4 package (GLMMs were used when residual plots revealed nonnormal error structures).

### Mate choice experiments with robotic crabs

We collected mate-searching female crabs that had responded to courtship by visiting the burrow of at least 1 waving male. Captured females were stored individually in cups of seawater in the shade and used in mate choice trials within 2 h. For practical reasons, females were collected from a largely flat area of the mangrove mudflat.

Mate choice trials utilized "Robocrab," a crab-sized robotic arm fitted with a model of a *U. mjoebergi* major claw that mimics the courtship waves of male *U. mjoebergi* (Reaney, Sims, et al. 2008). We mounted 2 Robocrab units (hereafter "males") in a 60 × 60-cm plastic arena covered in moist sand from the mudflat, with their claws orientated toward a release mechanism made from a transparent plastic cup (diameter: 6 cm) housing a female. The 2 robotic males were 5 cm apart and equidistant (20 cm) from the female. One male was elevated either 2.1 or 4.2 cm above the arena using plastic spacers, which were then covered in mud that was smoothed into a gentle slope. Note that these elevation treatments were very subtle relative to the natural range: males were observed living and signaling atop much larger mud hills in the field (Figure 1).

In each choice trial, we released the female after 3 wave cycles. A choice was recorded when the female contacted a male. We recorded a trial as unsuccessful if the female 1) displayed a startle response on release, 2) left the arena, or 3) did not choose within 180 s. If a trial was unsuccessful, the female was retested. If 3 consecutive trials were unsuccessful, we excluded that datum from the statistical analysis (51/300 data points from 28 females were excluded in this manner).

We first performed a pilot study using no-choice trials to confirm that females can detect an elevated male, recognize it as a potential mate, and climb the hill to reach it. We elevated a single male by either 2.1 or 4.2 cm, fitted an 18 mm claw, and programmed it to wave every 4 s. For both height treatments, 5/10 females contacted the male and performed stereotyped courtship behavior (tapping the robot with their legs); the remaining trials ended with "no-choice" results. These results suggest that females do recognize elevated males as potential mates and are easily capable of reaching them.

### Experiment 1: elevation and claw size

We assessed the joint effect of elevation and claw size on male attractiveness ( $n = 30$  females). Females were given a choice between an elevated male and a nonelevated male. There were 2 elevation treatments (elevated male raised by 2.1 or 4.2 cm relative to the substrate and the other male), whereas the claw size treatment had 3 levels: 1) both males had medium-sized claws (18 mm), 2) the elevated male had a large claw (22 mm) and the other had

a small claw (14mm), and 3) the nonelevated male had a large claw and the other had a small claw. The medium claw is close to the mean, and the small and large claws are close to the mean  $\pm 1$  SD, respectively, at our field site (Kahn et al. 2013). Every female received all 6 treatment combinations, in a random order. Robotic males waved synchronously (interwave interval: 4 s). The experiment was conducted in the first 2 days of the breeding cycle because the female preference for large claws is strongest at this time (Kahn et al. 2013).

**Experiment 2: elevation and wave rate**

We next investigated the combined effect of elevation and wave rate on male attractiveness ( $n = 30$  females). The 2 elevation treatment levels were as in Experiment 1 (+2.1 or +4.2 cm), and both males had 18mm (“medium-sized”) claws. There were 2 wave rate treatments: 1) the elevated male waved at twice the rate of the nonelevated male and 2) the nonelevated male waved twice as fast as the elevated one (interwave intervals: 4 and 8 s). The slower male always waved in synchrony with the faster one, and every female received all 4 treatments in a random order.

In both Experiments 1 and 2, the position (left vs. right) of the elevated male and the positions of the individual Robocrab units were rotated every few trials to prevent bias. The elevated male was in the left position in 50% of trials, and each Robocrab unit spent an equal number of trials in the left and right, and elevated and nonelevated, positions. Experiments 1 and 2 were conducted one after the other, and are hence not directly comparable, and used 2 different sets of  $n = 30$  females each.

**Statistical analysis**

All statistical analyses were performed in R 3.0.2. Mixed models and GLMMs were performed using the function *glmer* in the lme4 package (GLMMs were used when residual plots revealed nonnormal error structures).



**Figure 1**  
A crab’s eye view of 3 male *Uca mjoebergi* standing by their burrows on a mud mound.

**RESULTS**

**Spatial distribution of courting males**

Burrows were smaller at flat sites than elevated sites, implying that elevated sites might be occupied by larger males (flat:  $6.6 \pm 0.10$  mm, elevated:  $7.1 \pm 0.12$  mm; mixed model with plot as a random factor:  $t_{38} = 2.54$ ,  $P = 0.015$ ). There was no difference in the total number of males present in flat and elevated sites (flat:  $5.6 \pm 0.49$ , elevated:  $6.75 \pm 0.60$ ; Poisson generalized linear model [GLM]:  $z_{38} = 1.46$ ,  $P = 0.14$ ) and no difference between site types in the percentage of males with a regenerated claw (flat:  $30.4 \pm 3.6\%$ , elevated:  $34.4 \pm 4.6\%$ ; binomial GLM:  $z_{38} = 0.65$ ,  $P = 0.52$ ). There was also no difference between flat and elevated sites in nearest-neighbor distances (flat:  $8.0 \pm 0.3$  cm, elevated:  $7.1 \pm 0.3$  cm; mixed model with plot as a random factor:  $t_{38} = 1.60$ ,  $P = 0.12$ ) or the number of male burrows within 15 cm of the focal burrow (flat:  $3.8 \pm 0.2$ , elevated:  $4.0 \pm 0.2$ ; GLMM with plot as a random factor and Poisson errors:  $z = 0.71$ ,  $n = 247$ ,  $P = 0.48$ ).

We also analyzed the data for just the elevated sites, for which we had measurements of the elevation of each burrow. There was no relationship between elevation and burrow diameter ( $t_{112} = 0.33$ ,  $P = 0.74$ ), claw type ( $t_{112} = 0.03$ ,  $P = 0.98$ ), or their interaction ( $t_{112} = 0.35$ ,  $P = 0.72$ ).

**Experiment 1: elevation and claw size**

There was an extremely strong female preference for nonelevated males. The elevated male was only chosen 3 times out of 138 successful trials. Each of these 3 events occurred in a different claw size treatment (Table 1). Because so few females chose the elevated male, we cannot meaningfully test for a treatment effect or a treatment  $\times$  elevation interaction. Similarly, the female preference for the elevated male would be statistically supported whatever test one chose to use. For example, even if we discard all trials for each female except the first one (making the data fully independent), we find that 0/30 females chose the elevated male (binomial test:  $P < 10^{-8}$ ).

**Experiment 2: elevation and wave rate**

The elevated male was only chosen in 4/110 successful trials. In all 4 cases, the elevated male had the higher wave rate, which provides

**Table 1**  
**Data from the mate choice trials**

Height of elevated Robocrab	Claw size/wave rate treatment	Elevated Robocrab chosen	Nonelevated Robocrab chosen
2.1 cm	Equal	1	26
	Elevated Robocrab has smaller claw	0	27
	Elevated Robocrab has larger claw	0	28
4.2 cm	Equal	0	16
	Elevated Robocrab has smaller claw	1	20
	Elevated Robocrab has larger claw	1	19
2.1 cm	Elevated Robocrab waves faster	3	25
	Elevated Robocrab waves slower	0	29
4.2 cm	Elevated Robocrab waves faster	1	26
	Elevated Robocrab waves slower	0	26
Total		7	242

Females almost always chose the nonelevated Robocrab, masking the previously documented effects of claw size and wave rate. The numbers show the preferences of each of the females used in Experiments 1 and 2 ( $n = 30$  for each); the choices do not sum to 30 because females did not always make a choice (see text).



some evidence that fast waving overcame females' aversion to elevation in rare cases (Table 1). However, with only 4 events, we cannot confidently reject the null hypothesis that the probability of the female picking the elevated male is independent of wave rate treatment. As before, discarding all the data except for the 30 females' first trials (a highly conservative approach) yielded strong support for a preference for the nonelevated male: 0/30 females chose the elevated male ( $P < 10^{-8}$ ).

## DISCUSSION

We found that elevation has profound effects on the outcome of courtship in *U. mjoebergi* fiddler crabs. Robotic crabs waving from a modestly elevated position were far less attractive, even when they had a larger claw or waved twice as fast as their nonelevated rival. Claw size and wave rate typically have a large effect on attractiveness in *U. mjoebergi*; for example, females preferred larger claws in 63/80 Robocrab trials and faster wavers in 65/80 Robocrab trials in Reaney (2009). However, these effects were completely masked by elevation in our experiments. Therefore, females mate-searching in areas of variable elevation may impose relatively weak selection on male signaling traits compared with those in flat areas.

It is unclear why females have such a strong aversion to males waving from above, but there are several possibilities. The female preference might have no direct adaptive function; for example, it might arise as a by-product of a tendency to equate sufficiently elevated movements with predators (Zeil and Hemmi 2006). However, we do not think this can completely explain the results observed here: females exhibited stereotyped mate-searching behavior during the trials and visited elevated males in our pilot no-choice trials. This suggests that females did not consistently classify the waves of elevated Robocrabs as potential threats. Alternatively, the female preference might be the product of selection. For example, elevated burrows might tend to have less stable temperature or be dry. There may also be a cost to movement on elevated parts of the mudflat, for example, crabs might be less able to sprint to escape predators on a rugged surface. Females preferentially moving toward nonelevated males might therefore choose males with better burrows or be less at risk of predation.

Males did not appear to avoid elevated sites and might even compete over them, as implied by the presence of larger burrows at elevated sites (although this pattern could conceivably be caused by differences in substrate structure between flat and elevated areas). This seems odd given that elevation so strongly decreases male attractiveness. There are several potential explanations for this result. First, an elevated burrow may be less costly to male attractiveness than suggested by our experiment. When males are courting, they leave the burrow and move closer to the female while displaying (How and Hemmi 2008), which should decrease the difference in elevation. Even so, elevation likely still inflicts some cost on males. Males frequently stand at their burrow and wave when no females are nearby, presumably to attract distant females (females can perceive waving males at distances of more than a meter; Peso et al. 2014), and also wave in response to other males' waves (effectively eavesdropping on males that have detected a female; Milner, Jennions, et al. 2010). Second, it might also be very costly for a male to desert a high burrow in search of a lower one. Males without a burrow cannot mate or take shelter and must fight until they can evict a resident. Third, burrows on high ground might be superior in some respect; for example, they might be deeper. If so, the cost of attracting fewer females to an elevated burrow might

be offset if more of these females find the burrow acceptable and remain to mate.

Our results have implications for studies of animal communication. Although manipulative experiments in which "all else is equal" are effective at precisely identifying selective pressures, they may misrepresent the strength of selection by stripping away environmental and spatial complexity. Previous experimental studies of fiddler crabs holding everything constant except claw size and wave rate found evidence of strong female preferences (e.g., Reaney 2009), yet in our study, these preferences vanished when a third (environmental) variable was added. Similarly, another mate choice study of fiddler crabs found that females are more likely to visit the burrows of closer males, even when the closest male is of lower quality (Booksmythe et al. 2008). Studies in other taxa also suggest that the stochastic positions of males relative to mate-searching females are an important predictor of male mating success, which may largely override differences in attractiveness. In strawberry poison frogs *Oophaga pumilio*, females chose the closest calling male and apparently did not discriminate among males based on their call, body size, and territory quality (Meuche et al. 2013). Female *Hyperolius marmoratus* frogs lost their usual preference for low-frequency calls in a 2-choice playback experiment when the inferior call had better perches nearby (Backwell and Passmore 1990), and female crickets chose unattractive calls that were close to refugia (Hedrick and Dill 1993). In another frog species, females selected males with low-frequency calls when a background chorus of male calls was absent, but adding a chorus completely masked this preference (Wollerman and Wiley 2002).

Our study also provides a reminder that estimates of the strength of selection are context specific. A strong selective pressure in one environment (level mudflat) may be weak or absent in another (hilly mudflat). Similarly, in sticklebacks, male color signals are strongly correlated with attractiveness and dominance in clear water but are relatively unimportant in murky water (Wong et al. 2007). In great tits *Parus major*, females lose their usual preferential response to low-frequency songs in the presence of urban noise, which interferes more with low-frequency male songs than high (Halfwerk et al. 2011). In light of such results, we recommend that experimental estimates of selection be measured in as natural a context as possible (and preferably in multiple contexts) and that caution be applied when making evolutionary inferences based on estimates of selection from experiments.

## FUNDING

This work was funded by an A.R.C. Discovery Project grant to P.R.Y.B.

We are grateful to the staff of the North Australia Research Unit for providing research facilities and to M. Jennions for comments on the manuscript.

**Handling editor:** Glauco Machado

## REFERENCES

- Backwell P, Passmore NI. 1990. Suitable approach perches affect female phonotaxis in an arboreal frog. *Herpetologica*. 46:11–14.
- Booksmythe I, Detto T, Backwell PRY. 2008. Female fiddler crabs settle for less: the travel costs of mate choice. *Anim Behav*. 76:1775–1781.
- Candolin U, Salesto T, Evers M. 2007. Changed environmental conditions weaken sexual selection in sticklebacks. *J Evol Biol*. 20:233–239.
- Chaine AS, Lyon BE. 2008. Adaptive plasticity in female mate choice dampens sexual selection on male ornaments in the lark bunting. *Science*. 319:459–462.
- Christy JH. 1995. Mimicry, mate choice, and the sensory trap hypothesis. *Am Nat*. 146:171–181.

- Christy JH, Baum JK, Backwell PRY. 2003. Attractiveness of sand hoods built by courting male fiddler crabs, *Uca musica*: test of a sensory trap hypothesis. *Anim Behav*. 66:89–94.
- Endler JA, Basolo AL. 1998. Sensory ecology, receiver biases and sexual selection. *Trends Ecol Evol*. 13:415–420.
- Endler JA, Endler LC, Doerr NR. 2010. Great bowerbirds create theaters with forced perspective when seen by their audience. *Curr Biol*. 20:1679–1684.
- Halfwerk W, Bot S, Buikx J, van der Velde M, Komdeur J, Cate ten C, Slabbekoorn H. 2011. Low-frequency songs lose their potency in noisy urban conditions. *Proc Natl Acad Sci USA*. 108:14549–14554.
- Hedrick AV, Dill LM. 1993. Mate choice by female crickets is influenced by predation risk. *Anim Behav*. 46:193–196.
- How MJ, Hemmi JM. 2008. Courtship herding in the fiddler crab *Uca elegans*. *J Comp Physiol A*. 194:1053–1061.
- How MJ, Hemmi JM, Zeil J, Peters R. 2008. Claw waving display changes with receiver distance in fiddler crabs, *Uca perplexa*. *Anim Behav*. 75:1015–1022.
- How MJ, Zeil J, Hemmi JM. 2009. Variability of a dynamic visual signal: the fiddler crab claw-waving display. *J Comp Physiol A*. 195:55–67.
- Jennions MD, Backwell PRY. 1998. Variation in courtship rate in the fiddler crab *Uca annulipes*: is it related to male attractiveness? *Behav Ecol*. 9:605–611.
- Kahn AT, Dolstra T, Jennions MD, Backwell P. 2013. Strategic male courtship effort varies in concert with adaptive shifts in female mating preferences. *Behav Ecol*. 24:906–913.
- Kelley LA, Endler JA. 2012. Illusions promote mating success in great bowerbirds. *Science*. 335:335–338.
- Kirkpatrick M, Ryan MJ. 1991. The evolution of mating preferences and the paradox of the lek. *Nature*. 350:33–38.
- Lailvaux SP, Reaney LT, Backwell PRY. 2009. Dishonest signalling of fighting ability and multiple performance traits in the fiddler crab *Uca mjoebergi*. *Funct Ecol*. 23:359–366.
- Layne JE. 1998. Retinal location is the key to identifying predators in fiddler crabs (*Uca pugilator*). *J Exp Biol*. 201:2253–2261.
- Layne JE, Land M, Zeil J. 1997. Fiddler crabs use the visual horizon to distinguish predators from conspecifics: a review of the evidence. *J Mar Biol Assoc UK*. 77:43–54.
- Meuche I, Brusa O, Linsenmair KE, Keller A, Pröhl H. 2013. Only distance matters—non-choosy females in a poison frog population. *Front Zool*. 10:29.
- Milner RNC, Detto T, Jennions MD, Backwell PRY. 2010. Experimental evidence for a seasonal shift in the strength of a female mating preference. *Behav Ecol*. 21:311–316.
- Milner RNC, Jennions MD, Backwell PRY. 2008. Does the environmental context of a signalling male influence his attractiveness? *Anim Behav*. 76:1565–1570.
- Milner RNC, Jennions MD, Backwell PRY. 2010. Eavesdropping in crabs: an agency for lady detection. *Biol Lett*. 6:755–757.
- Murai M, Backwell PRY. 2006. A conspicuous courtship signal in the fiddler crab *Uca perplexa*: female choice based on display structure. *Behav Ecol Sociobiol*. 60:736–741.
- Ord TJ, Peters RA, Clucas B, Stamps JA. 2007. Lizards speed up visual displays in noisy motion habitats. *Proc R Soc Lond B*. 274:1057–1062.
- Peso M, Telford L, Backwell PRY. 2014. Comparison shopping: detectability and mate preferences in a fiddler crab. *Anim Behav*. 88:107–111.
- Peters RA, Hemmi JM, Zeil J. 2007. Signaling against the wind: modifying motion-signal structure in response to increased noise. *Curr Biol*. 17:1231–1234.
- Pratt AE, McLain DK, Lathrop GR. 2003. The assessment game in sand fiddler crab contests for breeding burrows. *Anim Behav*. 65:945–955.
- Qvarnström A, Pärt T, Sheldon BC. 2000. Adaptive plasticity in mate preference linked to differences in reproductive effort. *Nature*. 405:344–347.
- Reaney LT. 2009. Female preference for male phenotypic traits in a fiddler crab: do females use absolute or comparative evaluation? *Anim Behav*. 77:139–143.
- Reaney LT, Backwell PRY. 2007. Temporal constraints and female preference for burrow width in the fiddler crab, *Uca mjoebergi*. *Behav Ecol Sociobiol*. 61:1515–1521.
- Reaney LT, Milner RNC, Detto T, Backwell PRY. 2008. The effects of claw regeneration on territory ownership and mating success in the fiddler crab *Uca mjoebergi*. *Anim Behav*. 75:1473–1478.
- Reaney LT, Sims RA, Sims SWM, Jennions MD, Backwell PRY. 2008. Experiments with robots explain synchronized courtship in fiddler crabs. *Curr Biol*. 18:R62–R63.
- Samarra F, Klappert K, Brumm H, Miller P. 2009. Background noise constrains communication: acoustic masking of courtship song in the fruit fly *Drosophila montana*. *Behaviour*. 146:1635–1648.
- Wollerman L, Wiley RH. 2002. Background noise from a natural chorus alters female discrimination of male calls in a Neotropical frog. *Anim Behav*. 63:15–22.
- Wong BBM, Candolin U, Lindström K. 2007. Environmental deterioration compromises socially enforced signals of male quality in three-spined sticklebacks. *Am Nat*. 170:184–189.
- Zeil J, Hemmi JM. 2006. The visual ecology of fiddler crabs. *J Comp Physiol A*. 192:1–25.
- Zeil J, Nalbach G, Nalbach HO. 1986. Eyes, eye stalks and the visual world of semi-terrestrial crabs. *J Comp Physiol A*. 159:801–811.