

Original Article

# Experimental evidence that immediate neighbors affect male attractiveness

Sophia Callander, Catherine L. Hayes, Michael D. Jennions, and Patricia R.Y. Backwell

Evolution, Ecology and Genetics, Research School of Biology, The Australian National University, Canberra 0200 ACT, Australia

If female mate choice is based on comparison of locally available mates rather than absolute, fixed criteria, a male's attractiveness might depend on the attractiveness of his immediate competitors. We use robotic models to test whether the number of females that a male fiddler crab, *Uca mjoebergi*, attracts depends on his immediate neighbors' size. Larger males are, on average, more attractive to females and are also more likely to win male–male fights. Larger males can partially influence who their territorial neighbors are because they assist smaller neighbors to repel intruders that attempt to acquire the neighbor's burrow (defence coalitions). This assistance might allow a male to avoid the costs of renegotiating territorial boundaries with new neighbors, who will also tend to be larger than the previous neighbor. In this study, we show that males are more likely to attract females if they court immediately alongside smaller males. This represents an additional potential benefit of defence coalitions, by ensuring that large males compete against smaller neighbors when courting. *Key words*: courtship, defence coalition, fiddler crab, mate choice, sexual selection. [*Behav Ecol*]

## INTRODUCTION

Theoretical models of mate choice have considered various mate sampling tactics (Janetos 1980). These include whether mating preferences are fixed (i.e., a single peak male trait value), asymptotic (i.e., lower marginal gain in attractiveness as male trait value increases), or open-ended (i.e., linear or increasing marginal gains as male trait value increases; Andersson 1994). In addition, it has been necessary to consider female “choosiness” (Jennions and Petrie 1997), and how females sample males (e.g., mate with the first male that exceeds a threshold value or use best-of-N sampling; Janetos 1980) and to determine whether female choice is influenced by information acquired while viewing potential mates so that it is “comparative” (e.g., thresholds change due to a “previous mate” effect; Wong et al. 2004).

The available empirical data suggest that a male's attractiveness is often influenced by which other males a female encounters, and is not an absolute function of his sexual signaling (Bateson and Healy 2005). Comparative female choice can arise due to temporal shifts in mating preferences (i.e., information on the distribution in male phenotypes acquired from previously encountered males) and/or spatially restricted mate choice (e.g., choice among a current, limited set of males). This yields an obvious question. Should a male display alongside less attractive competitors to increase his relative attractiveness? To date, however, there have been few rigorous, experimental tests of whether males benefit by associating with inferior competitors (Bateson and Healy 2005; for an observational study see Oh and Badyaev 2010). Studies

quantifying the social structure of animal populations show that choice of social partners can affect an individual's fitness. For example, individual female's shoaling preference predicts subsequent cooperative interactions in guppies (*Poecilia reticulata*) (Croft et al. 2006). The potential for nonrandom associations of individuals to emerge is therefore high, given that local social structure can influence an individual's access to key resources such as food and mates (Krause et al. 2007; Wey et al. 2008; Sih et al. 2009).

If a male's attractiveness is increased when displaying alongside inferior rivals, could some males benefit by controlling the identity of their neighbors? The stability of such a strategy is unclear. For example, in lekking species, males might strategically adjust their position relative to their rivals to limit a female's outside options (Patricelli et al. 2011). Alternatively, males could select which lek to join to improve their relative rank, but low-ranked males might then benefit by leaving the lek to seek out another comprised of even weaker rivals. Unless there are costs to movement between leks and/or effects of lek size/composition on the rate at which it attracts females, the situation is unstable (Kokko et al. 1998). In territorial species, the situation might be more stable. There are obvious high costs to vacating a territory, especially when it contains essential resources (e.g., refuge from predators, water source). Interestingly, there are a few territorial species where some (but not all) males influence who acquires abutting territories: rock pipits (*Arthus petrosus*; Elfström 1997) and 3 fiddler crabs (*Uca mjoebergi*, *U. annulipes*, and *U. elegans*; Backwell and Jennions 2004; Bookmythe et al. 2010; Detto et al. 2010).

In fiddler crabs, females prefer larger males (e.g., Reaney 2009) and larger males tend to win male–male fights (Morrell et al. 2005). Resident males sometimes intervene in fights when intruders attempt to usurp a smaller neighbor's territory. This mainly occurs when the neighbor is smaller than the intruder and therefore likely to lose his territory; and the helper is larger than the intruder (Backwell and Jennions

Author correspondence to S. Callander. E-mail: [sophia.callander@anu.edu.au](mailto:sophia.callander@anu.edu.au).

Received 15 June 2012; revised 5 October 2012; accepted 30 October 2012.

2004; Detto et al. 2010). Theoretical models show that such “defense coalitions” can be adaptive because a successful intruder is likely to be stronger than the former neighbor. A larger neighbor will reduce the potential helper’s territory size and impose costs associated with renegotiating territory boundaries (Backwell and Jennions 2004; Mesterton-Gibbons and Sherratt 2009). In fiddler crabs, retaining a smaller, familiar neighbor is one benefit of helping (Detto et al. 2010; Booksmythe et al. 2012). There is, however, another reason to help neighbors: large males might gain a mating advantage by having smaller neighbors if female choice is comparative. In this study, we test if smaller neighbors increase male mating success in *U. mjoebergi*.

## MATERIALS AND METHODS

### Study system

Fiddler crabs inhabit highly dense, mix-sexed, intertidal communities. Both sexes own a burrow that is surrounded by a territory (approximately 10–20 cm in diameter). During the 5–6 day mating period of each semilunar tidal cycle, gravid females leave their territories to mate underground in a chosen male’s burrow. Males court mate-searching females by waving their greatly enlarged major claw and compete with males holding immediately abutting territories to attract a female (Callander et al. 2011). Females preferentially approach the burrows of males with larger claws, faster wave rates, and those that are the first within their group to wave (i.e., produce “leading” waves; Reaney et al. 2008; Reaney 2009). These characteristics increase the likelihood that a male has his burrow “sampled” by a female. Females “sample” a burrow by briefly dangling their legs into the entrance and their final mate choice decision appears to be based on burrow properties. After mating, a female remains in the burrow to incubate her eggs. Several features of the burrow (e.g., stability, temperature, and size) influence her reproductive success (Christy 1983; Christy 1987; deRivera 2005; Reaney and Backwell 2007). A male’s burrow is therefore an essential resource for breeding, which is strongly defended against other males.

### Experimental design

Fieldwork was conducted in Darwin, Australia (September to October 2011) during the mating period. We used robotic male crabs to quantify female mating preferences. Each robotic unit comprises an exact claw replica affixed to a metal arm. To obtain claw replicas, we make a plaster cast from the latex mould of an autotomized claw. The cast is then painted (Dulux Tintytin) to within the natural color variation of a *U. mjoebergi* male claw (details in Detto et al. 2006). The metal arm is powered by a motor that is embedded in the sediment to generate movements mimicking courtship waving. These robots have been successfully used in several studies of female choice (e.g., Reaney et al. 2008; Reaney 2009; Callander et al. 2011).

Mate choice experiments were conducted on an area of mudflat that did not contain any resident crabs. If new crab burrows appeared in the arena during the experiment, small shells were placed over the burrow entrance. We used naturally occurring mate-searching females ( $N = 40$  females/treatment). To be defined as mate searching, we followed burrowless females and ensured that they visited at least 1 waving male prior to being caught. We caught females by waiting for them to reappear after they had hidden inside a burrow and then blocking the burrow entrance with a stick. Each female was then placed individually in a plastic cup

containing seawater and kept in the shade. Females were randomly allocated to trials and used as soon as possible after capture. At the start of each trial, a single female was placed in a transparent container and allowed to observe 2 complete waves by the robots (hereafter “males”). The container was then remotely lifted. We scored a positive mate choice decision if the female directly approached within 2 cm of a male.

We compared female responses between 2 treatments to test whether female preferences depend on the claw size of a male’s immediate neighbors. In each treatment, females chose among 5 males, spaced 5 cm apart on an arc that was 20 cm from the female release point. The central “focal” male always had an 18.1-mm long claw. All 5 males waved synchronously (8.4 waves/min) to control for a known female preference for leading waves (Reaney 2009).

### Treatments

In the “large neighbors” treatment, the 2 males on either side of the focal male (hereafter “immediate neighbors”) had larger claws (24.1 mm) than the focal male. The 2 males on either side of the immediate neighbors (hereafter “outer males”) had smaller claws (12.2 mm). In the “small neighbors” treatment the immediate male neighbors had smaller claws (12.2 mm) than the focal male, and the outer males had larger claws (24.1 mm) (Figure 1). We included the 2 outer males, rather than testing a focal male with 2 neighbors to ensure that we could determine whether the focal male’s size relative to that of his immediate neighbors influenced female choice. For example, the use of only 3 males might simply show that females tend to choose the largest male from those available in each mating trial. Our design explicitly kept the total size distribution of males identical in both treatments (i.e., the size of the focal male relative to alternate mates). Consequently, we can causally attribute any change in the proportion of females choosing the focal male to the position of males rather than the group’s composition.

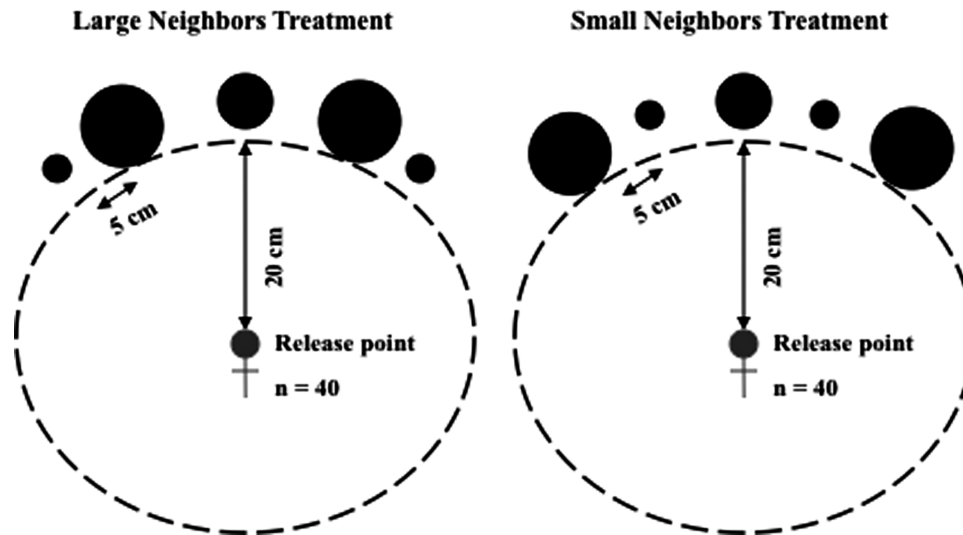
## RESULTS

The size of a focal male’s immediate neighbors significantly affected his mating success. A male with 2 smaller neighbors was significantly more likely to be approached by a female than one with 2 larger neighbors (Fisher’s Exact test:  $n = 40, 40$ ,  $P = 0.048$ ). In the small neighbors treatment, 22.5% of females chose the focal male (9 of 40). In the large neighbors treatment only 5% of females chose the focal male (2 of 40).

A small male was chosen in 5 of 40 (12.5%) small neighbor trials [the 2 immediate neighbors were a large and a focal (medium-sized) male] and in 10 of 40 (25%) large neighbor trials (the single immediate neighbor was a large male). Females chose a large male in 26 of 40 (65%) small neighbor trials and in 28 of 40 (70%) large neighbor trials. There was no significant difference in the relative success of small and large males between treatments ( $\chi^2 = 0.53$ ,  $df = 1$ ,  $P = 0.47$  with Yates correction). Unlike the case for focal males, however, this result cannot be used to directly test for an effect of immediate neighbor size: both the position of the males and the number of immediate neighbors changed between treatments (i.e., males were in the inner or outer position).

## DISCUSSION

We have experimentally shown that a male’s immediate neighbors could significantly influence his likelihood of mating in *U. mjoebergi*. Males immediately alongside 2 smaller neighbors were chosen significantly more often by females than males with 2 larger neighbors. This result is not simply attributable to females generally preferring larger males: in



**Figure 1**

Diagrammatic representation of “large” and “small neighbors” treatment. (Small black circles = males with a 12.2-mm long claw; medium black circles = focal males with a 18.1-mm long claw and large black circles = males with a 24.1-mm long claw. All robotic claws are waving in synchrony at 8.4 waves/min.)

both treatments the size distribution of the set of males was identical (i.e., there were always 2 males larger and 2 smaller than the focal male).

Why was the same (focal) male with a medium-sized claw more attractive when his immediate neighbors were smaller rather than larger? In general, when options are evaluated, perceptual biases can influence choice decisions (Bateson and Healy 2005). First, a female’s ability to discriminate between male ornaments diminishes with the absolute size of the stimuli (Weber’s Law, see Jennions and Petrie 1997). It might, therefore, be easier for females to distinguish between medium and small claws than medium and large claws. Second, perceptual biases might arise due to a visual illusion. In humans, the perceived size of the identical objects depends on the size of the surrounding stimuli (Ebbinghaus circles illusion; e.g., Parron and Fagot 2007). This phenomenon has yet to be shown in animals (Parron and Fagot 2007; Nakamura et al. 2008), but recent work shows that male great bowerbirds (*Chlamydera nuchalis*) influence their mating success by maintaining size–distance gradients of objects in their display courts (Kelley and Endler 2012). Third, in many species male harassment influences female behavior (Krupa et al. 1990; Stone 1995; Darden and Croft 2008; Darden et al. 2009), including mate choice (e.g., Mesnick and Leboeuf 1991). There is scope for male harassment to influence female mating behavior in *U. mjoebergi*. Larger males are stronger competitors (Morrell et al. 2005), so females might prefer males with smaller neighbors to lower any harassment costs imposed by the chosen male’s neighbors. To test this will, however, require a detailed future study that quantifies levels of harassment.

It is noteworthy that “comparative” choice by female *U. mjoebergi* was due to a highly localized effect. The focal male always had both a large and small male on either side, only their relative positions differed. There should be no difference in focal male mating success between treatments if females simultaneously assess all 5 males and their spatial position did not affect evaluation of size. Future studies will be required to understand the proximate basis of this result. At the function level, however, it is clear that the identity of a male’s courting companions during communal displays to females will affect his likelihood of attracting a female, hence

his mating success. This makes it beneficial for males to have smaller neighbors.

In fiddler crabs, defence coalitions increase the likelihood of retaining smaller neighbors. Previous studies show that coalitions are beneficial because they remove the costs of renegotiating territorial boundaries with stronger individuals (Backwell and Jennions 2004; Detto et al. 2010). Our current study suggests that there is an addition potential mating benefit of defence coalitions. Male *U. mjoebergi* mainly compete with their immediate neighbors when courting (Callander et al. 2011). Defence coalitions affect the identity of neighbors, hence the identity of a male’s immediate competitors. Our findings differ from those for “hotshot” models of lek formation, where subordinate males might choose to display near superior competitors who attract more females and thereby increase their likelihood of mating success simply by attracting more females into their vicinity (Beehler and Foster 1988). Interestingly, a recent observational study of house finches, *Carpodacus mexicanus*, found that less attractive males improve their pairing success by shifting into new social groupings (Oh and Badyaev 2010). Future studies might well reveal that this is a widespread pattern, but a key challenge will be to explain stability in social structure when all males benefit from having less attractive competitors. In fiddler crabs, stability might be maintained by the inability of small males to evict large neighbors and by the high movement costs to small males of relinquishing a burrow in search of a better territory (burrowless males that lack a refuge are far more susceptible to predators).

## FUNDING

This work was supported by the Joyce W. Vickery Research Fund from the Linnean Society of New South Wales (to S.C.); Sigma Xi Grants in Aid of Research (to S.C.); American Museum of Natural History Lerner-Gray Fellowship (to S.C.); and the Australian Research Council (to P.R.Y.B. and M.D.J.).

We thank Tim Maricic, Tegan Dolstra, and Andrew Kahn for their assistance in the field. We would also like to thank Mark Briffa and 2 anonymous reviewers for their helpful comments.

**Handling editor:** Alison Bell

## REFERENCES

- Andersson MB. 1994. Sexual selection. Princeton: Princeton University Press.
- Backwell PRY, Jennions MD. 2004. Coalition among male fiddler crabs. *Nature*. 430:417.
- Bateson M, Healy SD. 2005. Comparative evaluation and its implications for mate choice. *Trends Ecol Evol*. 20:659–664.
- Beehler BM, Foster MS. 1988. Hotshots, hotspots, and female preference in the organization of lek mating systems. *Am Nat*. 131:203–219.
- Booksmythe I, Hayes C, Jennions MD, Backwell PRY. 2012. The effects of neighbor familiarity and size on cooperative defense of fiddler crab territories. *Behav Ecol*. 23:285–289.
- Booksmythe I, Jennions MD, Backwell PRY. 2010. Interspecific assistance: fiddler crabs help heterospecific neighbors in territory defence. *Biol Lett*. 6:748–750.
- Callander S, Jennions MD, Backwell PRY. 2011. Female choice over short and long distances: neighbor effects. *Behav Ecol Sociobiol*. 65:2071–2078.
- Christy JH. 1983. Female choice in the resource-defense mating system of the sand fiddler crab, *Uca pugilator*. *Behav Ecol Sociobiol*. 12:169–180.
- Christy JH. 1987. Female choice and the breeding behavior of the fiddler crab *Uca beebei*. *J Crust Biol*. 7:624–635.
- Croft DP, James R, Thomas POR, Hathaway C, Mawdsley D, Laland KN, Krause J. 2006. Social structure and co-operative interactions in a wild population of guppies (*Poecilia reticulata*). *Behav Ecol Sociobiol*. 59: 644–650.
- Darden SK, Croft DP. 2008. Male harassment drives females to alter habitat use and leads to segregation of the sexes. *Biol. Lett.* 4:449–451.
- Darden SK, James R, Ramnarine IW, Croft DP. 2009. Social implications of the battle of the sexes: sexual harassment disrupts female sociality and social recognition. *Proc R Soc B*. 276:2651–2656.
- Detto T, Backwell PRY, Hemmi JM, Zeil J. 2006. Visually mediated species and neighbour recognition in fiddler crabs (*Uca mjoebergi* and *Uca capricornis*). *Proc R Soc B*. 273:1661–1666.
- Detto T, Jennions MD, Backwell PRY. 2010. When and why do territorial coalitions occur? Experimental evidence in a fiddler crab. *Am Nat*. 175:E119–E125.
- Elfström ST. 1997. Fighting behavior and strategy of rock pipit, *Anthus petrosus*, neighbors: cooperative defense. *Anim Behav*. 54:535–542.
- Janetos AC. 1980. Strategies of female mate choice: a theoretical analysis. *Behav Ecol Sociobiol*. 7:107–112.
- Jennions MD, Petrie M. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biol Rev*. 73:283–327.
- Kelley LA, Endler JA. 2012. Illusions promoting mating success in Great Bowerbirds. *Science*. 335:335–338.
- Kokko H, Sutherland WJ, Lindström J, Reynolds JD, Mackenzie A. 1998. Individual mating success, lek stability, and the neglected limitations of statistical power. *Anim Behav*. 56:755–762.
- Krause J, Croft DP, James R. 2007. Social network theory in the behavioural sciences: potential applications. *Behav Ecol Sociobiol*. 62:15–27.
- Krupa JJ, Leopold WR, Sih A. 1990. Avoidance of male giant water striders by females. *Behaviour*. 115:247–253.
- Mesnick SL, Leboeuf BJ. 1991. Sexual-behavior of male northern elephant seals: II. Female response to potentially injurious encounters. *Behaviour*. 117:262–280.
- Mesterton-Gibbons M, Sherratt TN. 2009. Neighbor intervention: a game theoretical model. *J Theor Biol*. 256:263–275.
- Morrell LJ, Backwell PRY, Metcalfe NB. 2005. Fighting in fiddler crabs *Uca mjoebergi*: what determines duration? *Anim Behav*. 70:653–662.
- Nakamura N, Watanabe S, Fujita K. 2008. Pigeons perceive the Ebbinghaus-Titchener circles as an assimilation illusion. *J Exper Psychol Anim Behav Proc*. 34:375–387.
- Oh KP, Badyaev A. 2010. Structure of social networks in a passerine bird: consequences for sexual selection and the evolution of mating strategies. *Am Nat*. 176:E80–E89.
- Parron C, Fagot J. 2007. Comparison of grouping abilities in humans (*Homo sapiens*) and baboons (*Papio papio*) with the Ebbinghaus illusion. *J Comp Psychol*. 121:405–411.
- Patricelli GL, Krakauer AH, Mcelreath R. 2011. Assets and tactics in a mating market: Economic models of negotiation offer insights into animal courtship dynamics on the lek. *Curr Zool*. 57: 225–236.
- deRivera CE. 2005. Long searches for male-defended breeding burrows allow female fiddler crabs, *Uca crenulata*, to release larvae on time. *Anim Behav*. 70:289–297.
- Reaney LT. 2009. Female preference for male phenotypic traits in a fiddler crab: do females use absolute or comparative evaluation? *Anim Behav*. 77:139–43.
- 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, Sims RA, Sims SWM, Jennions MD, Backwell PRY. 2008. Experiments with robots explain synchronized courtship in fiddler crabs. *Curr Biol*. 18:R62–R63.
- Sih A, Hanser SF, McHugh KA. 2009. Social network theory: new insights and issues for behavioral ecologists. *Behav Ecol Sociobiol*. 63:975–988.
- Stone GN. 1995. Female foraging responses to sexual harassment in the solitary bee *Anthophora plumipes*. *Anim Behav*. 50:405–412.
- Wey T, Blumstein DT, Shen W, Jordan F. 2008. Social network analysis of animal behaviour: a promising tool for the study of sociality. *Anim Behav*. 75:333–344.
- Wong BMB, Jennions MD, Keogh JS. 2004. Sequential male mate choice in a fish, the Pacific blue-eye *Pseudomugil signifer*. *Behav Ecol Sociobiol*. 56:253–256.