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# Male and female crickets modulate their courtship behaviour depending on female experience with mate availability

## Robin M. Tinghitella\*

Department of Biological Sciences, University of Denver, Denver, CO, U.S.A.

### ARTICLE INFO

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Keywords: Acheta domesticus age cricket mate choice plasticity population density Ecological factors like demography can shape competition for mates, altering the strength and direction of sexual selection via changes in courtship behaviour, choosiness and postcopulatory mechanisms. Demography is also quite dynamic, frequently changing within the life span of individual organisms. In this paper, I ask whether and how female experience with mate availability and female age interact to influence both male and female mating decisions. I housed female Acheta domesticus crickets individually at low or high density throughout their adult lives in screen cages that allowed low- and high-density crickets acoustic, visual and tactile contact with conspecifics. I assessed mating behaviour in courtship trials with naïve (untreated) males at two time points, early and late in life. Females that experienced high and low density initiated courtship by approaching and contacting males more frequently than did females that were housed in isolation. Older females also initiated courtship more often than young females. Female mating decisions (whether the female mounted the male and her latency to mount), however, did not depend on experience with population density, age, or their interaction, perhaps because females remained virgin throughout the experiment. Naïve males were able to assess females' prior experience, perhaps through variation in how frequently females approached them, and preferentially courted females that experienced high density. They did not differentially court females depending on their age or the interaction of age and population density. My results suggest that males assess mate competition using sociosexual cues derived from potential mates and adjust their behaviour accordingly.

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Ecological factors can alter sexual selection by facilitating or constraining the expression of courtship behaviour, preferences and investment in offspring, making it critical to understand sexual selection in the context of realistic ecology (Kokko & Rankin, 2006). Demographic factors like sex ratio and population density can shape competition for mates and may be particularly important in this regard (Emlen & Oring, 1977). Mating behaviour also commonly depends on intrinsic factors like age, condition, reproductive state and mating history (e.g. Burley & Foster, 2006; Gray, 1999; Hunt, Brooks, & Jennions, 2005; Lynch, Rand, Ryan, & Wilczynski, 2005; Moore & Moore, 2001; Prosser, Murray, & Cade, 1997). Because demography can be quite dynamic, changing within individuals' lifetimes, we might expect plastic responses to change with age, for instance, as the costs and benefits of various mating decisions change (Real, 1990; Tuomainen & Candolin, 2011). Yet extrinsic (e.g. demography) and intrinsic factors (e.g. age)

E-mail address: robin.tinghitella@du.edu.

affecting mate choice are rarely investigated together. In this study, I investigate the manner in which male courtship and female mating behaviour and decisions vary in response to population density, female age and their interaction.

From the male perspective, when females are the choosier sex, high population density means more competition for mates, including sperm competition when females mate multiply (reviewed in Wedell, Gage, & Parker, 2002). Males are sensitive to sociosexual cues indicating sperm competition and vary their reproductive behaviour accordingly. In many cases, we expect males to put more effort into courtship, mating, mate guarding and competition with rivals when the risk of sperm competition is high (Wedell et al., 2002). For instance, Mougeot, Arroyo, and Bretagnolle (2001) manipulated the risk of extrapair copulations by presenting decoys to paired Montagu harriers, Circus pygargus, and found that males spent more time with females and copulated more frequently and for longer periods of time when male decoys were presented compared to controls. This is consistent with predictions coming from risk models of sperm competition (Parker, Ball, Stockley, & Gage, 1997). The effects of density on male reproductive investment, however, can be system specific, and



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<sup>\*</sup> Correspondence: R. M. Tinghitella, Department of Biological Sciences, University of Denver, Denver, CO 80208, U.S.A.

predictions can be more complex depending on female remating rates and patterns of sperm utilization (Engqvist & Reinhold, 2006). For instance, as sperm competition intensity (the number of competing ejaculates) increases above two, males should invest less because the advantage of investing heavily decreases as the number of competing sperm increases (Engqvist & Reinhold, 2006; Parker, Ball, Stockley, & Gage, 1996). Sperm competition risk models, then, predict increased reproductive investment when the probability of sperm competition is high, and sperm competition intensity models predict reduced reproductive investment when the number of competitors increases above two (Wedell & Cook, 1999). As paternity is biased more towards the first male to mate, theory predicts that the relative difference between allocation to matings with virgin and already mated females should be higher (Parker et al., 1997).

From the female perspective, when females are the choosy sex, high population density (assuming an equal sex ratio) means a higher relative mate encounter rate, relatively low search costs and the opportunity to choose mates on the basis of quality (Kokko & Mappes, 2005). Models incorporating mate encounter rates typically predict that females should become less selective at lower population densities (Crowley et al., 1991; Hubbell & Johnson, 1987; Kokko & Mappes, 2005) because the cost of searching for a new mate is high. However, empirical results are mixed. In some systems female choice even breaks down at particularly high densities because of the difficulty in assessing so many males and the potential for harassment by males (Kokko & Rankin, 2006).

Importantly, mate availability is not static. Instead, metrics like population density change over space and time, both predictably and in response to stochastic fluctuations in weather and food availability (e.g. Taff, Freeman-Gallant, Dunn, & Whittingham, 2013). Some of these changes take place within seasons and individual lifetimes (e.g. Forsgren et al., 2004; Kasumovic, Bruce, Andrade, & Herberstein, 2008; Tinghitella, Weigel, Head, & Boughman, 2013). This means that we may observe changes in behavioural responses to extrinsic cues like population density throughout individuals' lives as they age. Classic life-history theory predicts that residual reproductive value should decline with age (Roff, 1992; Stearns, 1992), so females are predicted to be choosiest and males most competitive early in life (Jennions & Petrie, 1997; Real, 1990), although this may be overly simplistic. Numerous studies (e.g. Kodric-Brown & Nicoletto, 2001; Moore & Moore, 2001; Prosser et al., 1997) have confirmed that females are less choosy late in life, including one study in house crickets, Acheta domesticus, the study system I use here (Gray, 1999).

In this study, I asked whether there are age-dependent changes in responses to population density. I housed female house crickets under conditions that mimicked isolation, low density and high density throughout their adult lives, and assessed mating behaviour and decisions both early and late in life when encountering novel males. Because experimental males were pulled from laboratory stock populations and were naïve to females' experience, I was also able to determine whether males detect and respond to cues about females' previous experience with mate availability. This is biologically important because in species with internal fertilization in which individuals do not regularly interact with one another (for instance, males do not congregate around females, guard females or mate in the presence of competitors), males may rely on cues other than their own physical experience with rivals to assess sperm competition risk (Gray & Simmons, 2013; Thomas & Simmons, 2009). Female experience with population density may be communicated through variation in female receptivity or interest behaviours (Rodriguez, Haen, Cocroft, & Fowler-Finn, 2012) or via chemical cues like contact pheromones (the females' or those deposited by males during previous interactions; Thomas & Simmons, 2009).

I made several predictions about female and male responses to female experience with population density and age. If population density affects female mating behaviour, I expected females from the isolated treatment to be most willing to mate, those from the high density treatment to be least willing to mate and those from the low density treatment to be intermediate, because the cost of searching for a new mate should be greatest for isolated females and lowest for females experiencing high population density (Kokko & Mappes, 2005). If female age influences mating decisions, consistent with earlier work in house crickets (Gray, 1999) and lifehistory theory (Roff, 1992; Stearns, 1992), I expected old females to be more motivated to mate and to be less choosy than young females. If mate availability and age interact, a number of outcomes are possible. One prediction is that differences in female mate choice across densities (described above) may only be detectable early in life. Female crickets remate at relatively high rates (French & Cade, 1989; Simmons & Beveridge, 2010; Tregenza & Wedell, 1998, 2002). If males can assess females' previous experience with population density, and that previous experience reliably predicts the risk of sperm competition, I expected them to put more effort into courting high-density females, consistent with sperm competition risk models (Parker et al., 1997). If males can reliably assess females' previous experience with population density, and that previous experience indicates the number of previous mates (sperm competition intensity), I expected them to discriminate against high-density females (Engqvist & Reinhold, 2006; Parker et al., 1996; Thomas & Simmons, 2009). If males can detect female age. I expected them to put more effort into courting young females because they have higher relative reproductive value (Real. 1990). Again, if the two interact, a number of outcomes are possible. One possible prediction was that males would prefer young females from the isolated treatment, because they were most likely to be virgin, reducing sperm competition risk.

#### METHODS

#### Animal Maintenance

I obtained crickets, *A. domesticus*, from Armstrong's Crickets (West Monroe, LA, U.S.A.) in January of 2012. Unlike many commercial cricket breeders, Armstrong's has continuously raised *A. domesticus* without infection by the widespread *A. domesticus* densovirus (AdDNV; Weissman, Gray, Pham, & Tijssen, 2012). I maintained the cultures in 16-litre boxes with egg carton for shelter, ad libitum access to Fluker's cricket chow (for juveniles) or cat food (for adults) and water from cotton-filled oviposition dishes, and housed the boxes in a temperature controlled room set to 25 °C on a 12:12 h light:dark cycle.

#### Female Experience with Population Density

When sex differences became apparent (females had visible, stubby ovipositors, about the seventh instar), females were assigned randomly to one of three treatments: isolated, low density or high density, and transferred to treatment boxes (16-litre) to control for sociosexual experience. The 16-litre boxes were 37 cm long, 26 cm wide and 16.5 cm tall. Isolated females were transferred to treatment boxes containing no other individuals. Low-density females were transferred to treatment boxes that contained a total of five females and five males. High-density females were transferred to treatment boxes, nine replicate low-density treatment boxes (five marked, caged females in each) and nine replicate high-density treatment boxes (five marked, caged females in each).

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