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Choosy males in Jamaican field crickets

Susan M. Bertram [a, *], Michelle J. Loranger [a], Ian R. Thomson [a], Sarah J. Harrison [a], Genevieve L. Ferguson [a], Mykell L. Reifer [a], Deborah H. Corlett [a], Patricia Adair Gowaty [b, c]

[a] Department of Biology, Carleton University, Ottawa, ON, Canada
[b] Department of Ecology and Evolutionary Biology and Institute of Environment and Sustainability, University of California Los Angeles, USA
[c] Smithsonian Tropical Research Institute, Panama

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Male mate choice is an often neglected aspect of sexual selection studies. While theory predicts that females should exhibit mate choice due to their comparatively greater investment in gametes, males may also exhibit mate choice for a variety of reasons, including seeking mates with greater fecundity. Furthermore, males may exhibit discriminant or indiscriminate mate choice as a function of their own intrinsic characteristics, such as body size or condition. Here we experimentally evaluated male Jamaican field cricket, *Gryllus assimilis*, mating preferences using randomly selected females and determined how both male and female morphology (body size and residual mass) and male signalling behaviour influence male mate preference. Results show that male crickets exhibit mating preferences, with larger males tending to exhibit more consistent mate preferences than smaller males. Contrary to predictions, males did not prefer larger or relatively heavier females, suggesting that males may not be basing their choosiness on these proxy measures of female fecundity. Our findings highlight the need for continued research on male mate choice and identifying the intrinsic characteristics of both sexes that drive them.

Sexual selection theory since Darwin's time has been pervaded by distinct sex roles in which females are often depicted as the choosy sex over competitive males (Darwin, 1874). Here we define mate choice as the process that results in the tendency of one sex to mate nonrandomly with members of the opposite sex, based on mating preferences for one or multiple traits expressed by the opposite sex (Heisler et al., 1987; Kokko, Brooks, Jennions, & Morley, 2003; Wagner, 1998). It is now well known that female mate choice can be influenced by internal properties of the chooser as well as environmental factors (Ah-King & Gowaty, 2016; Gowaty & Hubbell, 2009; Wagner, 1998) and often exerts strong selection forces resulting in the elaboration of male traits (reviewed by Andersson, 1994). However, male mate choice is often neglected in studies of sexual selection (Gillingham et al., 2009; Pizzari & Bonduriansky, 2010; Wright et al., 2008). This neglect is somewhat surprising given that males regularly exhibit mating preferences (Amundsen & Forsgren, 2001; Anderson, Kim, & Gowaty, 2007; Bel-Venner, Dray, Allaine, Menu, & Venner, 2008; Bonduriansky, 2001; Cornwallis & Birkhead, 2006; Drickamer, Gowaty, & Holmes, 2000; Edward & Chapman, 2011; Gowaty, Drickamer, & Schmid-Holmes, 2003; Gowaty, Steinichen et al., 2003; Pizzari, Cornwallis, Lovlie, Jakobsson, & Birkhead, 2003; Reading & Backwell, 2007; Reinhold, Kurtz, & Engqvist, 2002; Rubolini et al., 2006; Wedell, Gage, & Parker, 2002). Consider the extreme example presented by *Drosophila pseudoobscura*, which has one of the greatest known degrees of anisogamy in the genus, with males ejaculating two sizes of tiny sperm relative to the vastly larger eggs produced by females (Snook, Markow, & Karr, 1994). Anisogamy theory predicts therefore that female *D. pseudoobscura* should exhibit stronger mate choice behaviour than males. However, even in this extreme case, males still display similar mate choice frequencies that affect their fitness in much the same way as female mate choice of *D. pseudoobscura* (Anderson et al., 2007; Gowaty, Steinichen, & Anderson, 2002; Gowaty, Steinichen et al., 2003). In fact, studies of mutual mate choice in a wide array of species have unambiguously demonstrated that males and females can both simultaneously exhibit mate choice (Drickamer, Gowaty, & Wagner, 2003; Gowaty, Drickamer et al., 2003; Gowaty, Steinichen et al., 2003).

Theoretical research suggests that male mate choice can evolve under a broad range of circumstances (Barry & Kokko, 2010; Gowaty & Hubbell, 2009; Hubbell & Johnson, 1987; Kokko & Johnstone, 2002; Kokko & Monaghan, 2001; Servedio & Lande,

* Correspondence: S. M. Bertram, Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, ON K1S 5B6, Canada.
E-mail address: Sue_Bertram@carleton.ca (S. M. Bertram).

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2006). For example, male mate choice is theoretically likely to evolve (1) in populations with female-biased sex ratios where males have higher encounter rates with potential mates (Gowaty & Hubbell, 2009; Hubbell & Johnson, 1987), (2) in mating systems where males encounter multiple females simultaneously (Barry & Kokko, 2010), (3) when males have high survival probabilities (Gowaty & Hubbell, 2009; Hubbell & Johnson, 1987), (4) in species where females exhibit highly variable levels of fertility, (5) when males court intensively and females exhibit strong preferences for intense courters (South, Arnqvist, & Servedio, 2012) and (6) in species where males transfer costly ejaculates/gifts during mating (Gwynne & Simmons, 1990).

Here we report tests of male field crickets' precopulatory mate preference. Male field crickets produce long-range acoustic signals to attract females from a distance. Once females come into contact, the males switch from producing mate attraction signals to producing short-range acoustic courtship signals (Alexander, 1961, 1962). While female field crickets regularly exhibit strong mate preferences (Gray, 1997; Hedrick, 1986, 1988; Hedrick & Weber, 1998; Hedwig & Poulet, 2005; Hennig & Weber, 1997; Pacheco & Bertram, 2014; Scheuber, Jacot, & Brinkhof, 2004; Simmons, 1986; Simmons & Ritchie, 1996; Wagner, 1996; Wagner, Murray, & Cade, 1995), far less is known about male field cricket mate preference.

Male field crickets could exhibit mate preferences for a variety of reasons including eschewing inbreeding, seeking compatible genes and/or seeking mates with greater fecundity (Bradford & Roff, 1993; Bretman, Wedell, & Tregenza, 2004; Carriére, Simons, & Roff, 1996; Shoemaker, Parsons, & Adamo, 2006; Simmons, Beveridge, Wedell, & Tregenza, 2006; Simmons & Garcia-Gonzalez, 2007; Stahlschmidt & Adamo, 2015; Stahlschmidt, Rollinson, Acker, & Adamo, 2013; Tregenza & Wedell, 2002). For example, male field crickets could preferentially court larger females (Bateman & Fleming, 2006b) because larger females often oviposit more eggs (Bateman, 2001; Bertram et al., 2016; Bonduriansky, 2001; Loranger & Bertram, 2016b). Conversely male field crickets might not discriminate among attracted females because males tend to attract females sequentially rather than simultaneously (Alexander, 1961), and theoretical work shows that male mate choice is less likely to evolve when encounters are sequential (Barry & Kokko, 2010). Male field crickets may also not discriminate among attracted females because of the costs of missing a mating opportunity (Bonduriansky, 2001) or because of the energetic costs associated with acoustic mate attraction signalling (Prestwich, 1994; Prestwich & O'Sullivan, 2005; Prestwich & Walker, 1981).

Hubbell and Johnson (1987) provided a mathematical proof demonstrating that, under a very wide array of demographic circumstances, fixation for extreme mate choice behaviours (exhibiting universally discriminate or indiscriminate behaviour) should be selected against in favour of plasticity (Gowaty & Hubbell, 2005; Hubbell & Johnson, 1987). Furthermore, in an exhaustive review of 200 experimental studies of phenotypic plasticity in mate preferences, Ah-King and Gowaty (2016) found that individuals switch between discriminate and indiscriminate mating behaviours depending on variation in the chooser's predation risk, presence of rivals, health status, parasite load and encounter probabilities with potential mates. Ah-King and Gowaty's (2016) review indicates that the intrinsic variation in the characteristics of the choosers' may be as important and sometimes much more important to an individual's reproductive decision making than the intrinsic variation in the traits of potential mates.

Male crickets clearly exhibit some form of mate discrimination behaviour. For example, *Acheta domesticus* transfer more sperm to larger females (Gage & Barnard, 1996), *Teleogryllus oceanicus* provide less viable sperm to multiply mated females (Thomas & Simmons, 2007) and male *Gryllus bimaculatus* court larger females with significantly higher effort than smaller females (Bateman & Fleming, 2006b). While these studies suggest that male field crickets may regularly exhibit mate discrimination behaviour, it is surprising that male cricket mate choice is a relatively understudied topic. This lack of published data may result from an underappreciation of the importance of male mate choice (Gillingham et al., 2009; Pizzari & Bonduriansky, 2010; Wright et al., 2008), or from males not exhibiting mate choice and the well-renowned publication bias against negative results (Begg & Mazumdar, 1994; Fanelli, 2012; Macaskill, Walter, & Irwig, 2001; Pham, Platt, McAuley, Klassen, & Moher, 2001; Sterne, Gavaghan, & Egger, 2000).

To test whether male field crickets exhibit mate preference, we allowed male Jamaican field crickets, *Gryllus assimilis*, to repeatedly choose between two randomly selected females. This approach resulted in some male mate preference tests with females that were quite different in size, while other male mate preference tests had females that were similar in size, a situation akin to the trait distribution males would naturally encounter (Anderson et al., 2007; Bluhm & Gowaty, 2004; Gowaty, Drickamer et al., 2003; sensu Moore, Gowaty, Wallin, & Moore, 2001). We assessed male mate preference based on the males' spatial proximity to females in dichotomous preference tests, allowing us to separate mate preference from mate choice (the act of mating), as male mate choice is confounded by the female's behaviour (whether or not she wants to mate, since she controls mounting) (Heisler et al., 1987; Wagner, 1998). We repeated this dichotomous preference test with each male after we swapped the females' sides, enabling us to quantify whether males exhibited consistent mate preference. We then tested whether male mate preference was associated statistically with the males' traits and/or with variation in female morphological traits.

METHODS

We conducted our study during May–August 2013 and our experiments complied with the guidelines set out by the Canadian Council on Animal Care. Detailed methods are provided in our companion paper on female mate preference (Bertram et al., 2016). We used laboratory-reared *G. assimilis* field crickets descended from wild crickets captured in Smithville, Texas, U.S.A., during 15–24 September 2007. We collected hundreds of individuals from the field, allowed them to mate freely and then imported the resultant several thousands of eggs to initiate our laboratory population (Canadian Food Inspection Agency permit number 2007–03130). We reared our laboratory population from egg to final juvenile instar using several large communal plastic containers (49 × 35 and 40 cm tall). Our rearing conditions ensured all crickets were continuously exposed to a variety of social cues including physical interactions with members of both sexes and nearly continuous mate attraction signalling of conspecific adult males housed in nearby containers. We ensured all crickets had shelter (stacked egg cartons) and provided them with ad libitum water and food (Harlan's Teklad Rodent diet 8604M; 24.3% protein, 40.2% carbohydrate, 4.7% lipid, 16.4% fibre, 7.4% ash). We maintained the crickets under a 14:10 h light:dark illumination regime at a temperature of 28 ± 2 °C.

Starting in mid-May 2013, we sorted crickets and placed ~50 wing bud stage juvenile (nymph) males and females from each of the nine communal containers into two new communal experimental containers. These juveniles were free to interact with each other and were exposed to conspecific mate attraction signals of males housed nearby. We removed all adult crickets (individuals