Context-dependent female mate preferences in leaf-footed cactus bugs

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Abstract

Female mate preferences can shape sexual selection and evolution. Thus, it is important to understand the factors that affect mating decisions. Here, we examine context-dependent mate preferences in the leaf-footed cactus bug, *Narnia femorata* Stål (Hemiptera: Coreidae), a species that experiences distinct seasonal changes and spatial variation in the quality of their food, cactus. Previous work has shown that cactus with fruit is a superior resource for these insects, however they must sometimes develop, mate, and reproduce without cactus fruit. We reared males on *Opuntia humifusa* (Raf.) (Cactaceae) cactus pads with and without cactus fruit. We found that females preferred the odour of males that had developed on cactus fruit over males that developed only on cactus pads. However, the current cactus context also affected female preference. Females were more likely to choose males that developed with cactus fruit when cactus fruit was currently available. Our results suggest that natural fluctuations in resource availability during development and adulthood may result in fluctuations in the strength of sexual selection via female mate choice.

1. Introduction

Sexual selection in nature occurs within temporally and spatially dynamic environments (Cornwallis & Uller, 2010; Miller & Svensson, 2014), but how environmental variation affects sexual selection is rarely considered. A major agent of sexual selection is female mate choice, with females often selecting for those males with the most elaborate ornaments (Andersson, 1994). Much discussion has focused on 'good genes' for ornament expression, but developing in high quality environments can also facilitate elaborate ornament expression in males (Griffith et al., 1999; Qvarnström, 1999; Griffith & Sheldon, 2001; Jensen et al., 2006). The context where males are encountered may also influence mating decisions, and more studies are needed to examine the effects of different, ecologically-relevant contexts on mate choice (Jennions & Petrie, 1997; Cotton et al., 2006; Miller & Svensson, 2014). Environmental effects on mate choice may be important because they can lead to fluctuations in sexual selection on male traits, potentially reducing the loss of genetic variation or even changing evolutionary trajectories (Ellner, 1996; Siepielski et al., 2009, 2011; Bell, 2010).

Here, we examined the effect of resource quality on female mate preferences in the leaf-footed cactus bug, *Narnia femorata* Stål (Hemiptera: Coreidae). *Narnia femorata* feeds, mates and oviposits on prickly-pear and cholla cactus (*Opuntia* and *Cylindropuntia* spp.) in the southern United States and Mexico (Baranowski & Slater, 1986; Palomares-Pérez et al., 2012). Males often defend cactus territories, with larger males more likely to be dominant over smaller males (Procter et al., 2012). Cacti with red, ripe fruit are a superior resource for these insects. Females lay 56% more eggs on cactus with fruit than on cactus without fruit (Miller et al., 2013). Offspring developing on host plants with cactus fruit develop faster (Nageon de Lestang & Miller, 2009) and mature as larger adults (Gillespie et al., in review). Males that develop with cactus fruit become superior competitors over males reared without cactus fruit (Nageon de Lestang & Miller, 2009; Nageon de Lestang, 2010). Although cactus is widespread and plentiful, these plants only produce fruit once per year, and abundance wanes throughout the summer and fall (Gillespie et al. in review). Furthermore, ripe cactus fruit are a popular food of rodents, birds, deer, and other vertebrates, and some areas are rapidly denuded of cactus fruit (C.W. Miller, unpublished data). Thus, cactus fruit availability is limited in time and variable across space, and some *N.*

femorata must sometimes develop, compete, mate, and produce eggs in the absence of cactus fruit.

In this study, we provided insects with cactus pads with or without cactus fruit during development. We later tested female preferences using odour cues from their host plant (cactus) and males. We first examined female preferences for a host plant versus a host plant with a male, using males that developed either with or without cactus fruit. Existing work has demonstrated measureable effects of cactus fruit during development on male size and quality; therefore, we predicted more females would choose the cactus with a male when the male offered had developed with cactus fruit.

We next examined the effect of context on female preferences. We simultaneously offered females the choice between the odours of a male that developed with cactus fruit and the odours of one that developed without cactus fruit. These males were both either held on cactus with fruit or cactus without fruit. We expected that the difference in context would affect female preferences. Based on previous results (Gillespie et al., data not shown), we predicted that females would be more likely to move towards odours from the male that developed with cactus fruit when cactus fruit was currently available.

2. Material and methods

The insects used in these experiments were descended from individuals collected locally at the University of Florida Ordway-Swisher Biological Station (29°41′N, 82°W) in the autumn of 2009 and reared subsequently as part of a laboratory colony. We reared *Narnia femorata* nymphs from egg to fourth instar on *Opuntia humifusa* cactus with red-ripe cactus fruit in the spring of 2011. Young nymphs commonly aggregate, thus we raised them in sibling groups of up to 12 individuals in a greenhouse setting. When nymphs reached the fourth instar, we transferred them into new containers in groups limited to five individuals to minimise competition for resources. At that time, they were randomly assigned either a potted *O. humifusa* pad with red fruit or one without fruit. Removal of red fruit during juvenile development occurs commonly in fall, winter, and early spring as frugivores move through an area consuming cactus fruit, thus, our treatments with and without cactus fruit for late development replicate natural circumstances.

Juveniles remained in the treatments of a cactus pad with fruit or without fruit through their fourth and fifth instars, until they moulted into adults.

Nymphs greatly increase in size during these final two instars, thus nutrition experienced during this time period was expected to affect adult condition and related traits. Newly-emerged adults were isolated within 24 h of emergence and placed on a cactus pad with a red fruit until they were between 14 and 21 days post-eclosion to ensure reproductive maturity (C.W. Miller, unpublished data). Females used in this experiment were kept with potted cactus pads and fruit throughout development until testing. All of the insects from fourth instar onwards were maintained in the laboratory at 26°C with 0% humidity and 12 h of light each for 24 h. Cacti within the containers were watered twice a week, and if cactus quality declined, insects were given fresh potted cactus.

These insects were reared in the winter and early spring when red cactus fruit was becoming increasingly scarce under natural circumstances. By the time the wild counterparts of these insects mature and look for mates, red fruit is largely unavailable. However, cactus bloom in April and May, and produce fresh green cactus fruit. To replicate these natural conditions and increase the relevance of our study, we reared insects with and without red fruit, but only offered green cactus fruit during the mate preference experiments described below.

Males in *N. femorata* and related species are territorial (Mitchell, 1980; Miyatake, 1997; Eberhard, 1998; Miller & Emlen, 2010; Procter et al., 2012), and females typically fly to visit males on their territories for mating. Female mate choice probably includes a multi-step process of long-distance detection and movement followed by physical contact and a final mating decision. Here, we evaluated preferences likely relevant to the long-distance portion of this process by presenting individual females with male odours in a glass Y-tube olfactometer and documenting female movement towards one odour source or the other. We found that approximately 80% of other randomly paired, unmated males and females from this cohort mated soon after contact, demonstrating that female movement towards a male is likely important to eventual mating.

To set up the experiment, we connected the two arms of the Y-tube olfactometer (common arm, 15 cm; right and left arms, 12 cm) to sealed 4-l domed glass chambers containing the odour sources. The cacti used in the domes were paired according to weight (20–25 g) and according to fruit number. All cacti provided during the experiment had recently produced fresh green fruit. Male *N. femorata*, if provided (see below), were introduced into the

glass chambers and allowed to move freely. Hydrated, filtered air was forced at a constant pressure of 70 bar (using commercial flowmeters) into the glass domes and then into the arms of the Y-tube olfactometer. Potential visual distractions were reduced by placing a cardboard screen between the Y-tube and the observer and the Y-tube and the glass domes.

We placed females into small plastic tubes with only moistened paper towel and without food the night before each experimental trial period. At testing time, a single female was slowly introduced into base of the common arm of the Y-tube olfactometer over the course of 5–10 min with efforts to minimise stress. A female was deemed to have made a choice and the trial was terminated if the female walked at least 5 cm into an arm of the Y-tube and stayed in the arm for at least five minutes. Female preference was therefore estimated using a binary response. Females that did not respond or did not remain in a single arm after thirty minutes had passed were removed from the Y-tube and tested again on a subsequent day. Those that did not respond on more than one occasion were removed from the experiment and were not included in the analyses. Responsive females were only used once for each experiment, and each male pair was tested with 5–11 different females. We reversed the odour sources after five females had made a choice to reduce the potential for a bias due to a directional preference by the females. After every 5 females tested, the Y-tube was rinsed using 95% ethanol to remove any odour residues. After every 10 females were tested the Y-tube was cleaned using an odour-free glass cleaner, rinsed in 95% ethanol and then baked overnight in an oven at 200°C.

We conducted two experiments in April and May 2011 (Figures 1A, C and 2A, C). First, we estimated female preferences for a host plant versus a host plant with a male (Figure 1A, C). To do so, we offered females the odours of cacti with fruit in the glass domes on each end of the Y-tube, with a male placed randomly on one of the two cacti the day before testing to allow acclimatisation. Males provided were either reared with fruit or without fruit during their final two instars to assess whether females would be more likely to move towards the cactus pad with a male if the male developed with cactus fruit. Testing of preferences for a cactus alone and a cactus with a fruit-reared male occurred on three separate days. Testing of preferences for a cactus pad alone versus one with a male that developed without fruit occurred over a different, but interspersed, three days.
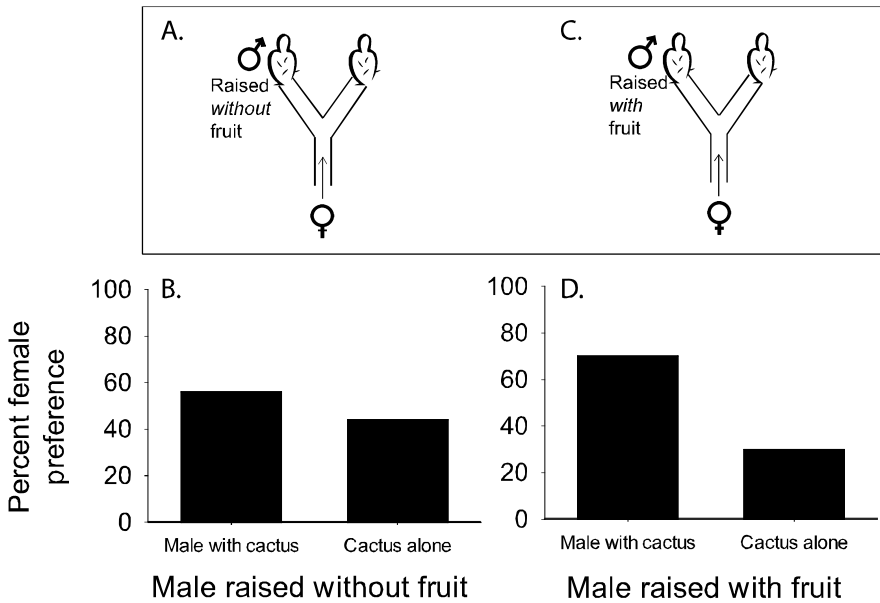
Figure 1. In the first experiment, females were presented with odours from two cacti with fruit. One of the provided cacti held a male, while the other did not. When the male provided had developed without cactus fruit (A and B), females preferred the cactus with the male only 56% of the time (27 versus 22 females, $\chi^2_1 = 0.75$, $p = 0.39$). When the male provided had developed on cactus with fruit (C and D), 70% of females preferred the cactus with the male over a cactus alone (35 versus 15 females, $\chi^2_1 = 8.0$, $p < 0.01$).

In the second experiment, we simultaneously offered females the choice between a male reared with red cactus fruit and a male reared without cactus fruit (Figure 2A, C). As before, males were randomly paired and placed in the chambers the day before testing for acclimatisation. In this experiment, both males were simultaneously held either on cacti with fruit or simultaneously held on cacti without fruit.

2.1. Statistical analyses

For the data from the first experiment, we initially explored the potential for non-independence due to the repeated use of males across multiple females. We used a repeated measures logistic regression model (generalised estimating equations) that suggested observations were independent (within-male correlation -0.027). Thus, we continued with a chi square analysis for simplicity. We analysed female preference for a cactus pad with a male versus a cactus pad without a male separately by male developmental environment
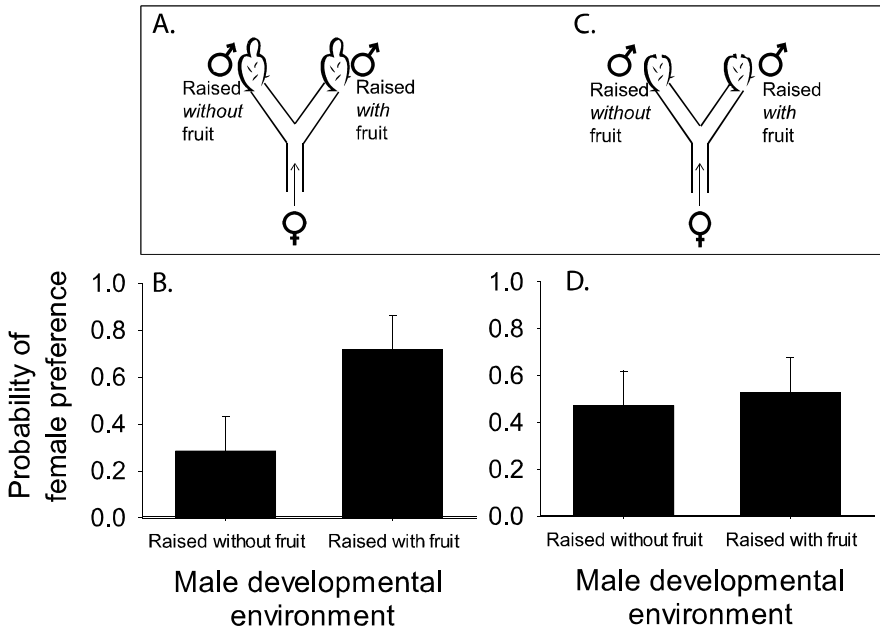
Figure 2. In Experiment 2, a subset of females placed into a Y-tube olfactometer were presented with odours from two cacti with fruit (A), while other females were presented with odours from two cacti without fruit (C). In both cases, one cactus held a male that developed with cactus fruit (the high-quality developmental environment) while one held a male that developed without cactus fruit (the low-quality developmental environment). The context of males influenced female preferences (B and D; parameter estimates ±SE). When the two cacti presented had cactus fruit (B), females were more likely to prefer the male that had also developed on cactus fruit. When the two cacti presented did not have cactus fruit (D), there was no detectable difference in preference.

($N = 50$ for females offered males that developed with fruit, and $N = 49$ for females offered males that developed without fruit).

We used proc logistic in SAS 4.3 for the data from our second experiment. Our statistical model included male developmental environment (with fruit or without fruit) and the interaction of male developmental environment with the current context (with fruit or without fruit). We did not include the current context as a main effect in this model because there was only one current context provided each time females were offered a choice of males (i.e., conditional logistic regression; Allison, 1999). Our model allowed us to treat the male pair used to test female preferences as a random effect. For this experiment we had a total of eleven blocks (six male pairs in the current

treatment of cactus with fruit, and five pairs in the current treatment of cactus without fruit) with a total of 95 females tested.

3. Results

3.1. Experiment 1

Female preferences for odours of their host plant alone versus their host plant with a male differed depending upon the developmental environment of the male. When presented with odours from a cactus and a cactus with a male reared without cactus fruit, 56% of females chose the cactus with the fruit-reared male (27 versus 22 females, $\chi_1^2 = 0.75$, $p = 0.39$; Figure 1B). In contrast, 70% of females preferred males reared with fruit over a lone cactus time (35 versus 15 females, $\chi_1^2 = 8.0$, $p < 0.01$; Figure 1D).

3.2. Experiment 2

Consistent with our hypotheses and the results seen in Experiment 1, we found that females overall preferred the odours of males that developed with fruit over the odours of males that developed without fruit (WALD $\chi_1^2 = 10.267$, $p < 0.01$; Figure 2). However, this pattern was context dependent (significant interaction between the current environmental context and the male developmental environment, WALD $\chi_1^2 = 3.7142$, $p = 0.05$). Females more often preferred males that developed with cactus fruit when the males were held on cactus with fruit as the current context (Figure 2B).

4. Discussion

We found that female responses to males in *Narnia femorata* depended upon male developmental environment and the current context of the male (Figures 1 and 2). These patterns were detected using simple resource differences that these insects encounter routinely during development and later when assessing mates. Our results thus provide evidence of context-dependent female preferences in *N. femorata*.

When cactus with fruit was present, female *N. femorata* moved towards the odours of males that developed with cactus fruit over those that developed without cactus fruit (Figures 1 and 2B). Importantly, all males were provided potted cactus with cactus fruit upon reaching adulthood, and were held in this environment for at least two weeks prior to the assay. Thus,

despite having the opportunity to feed on fruit as adults, males whose development occurred in a low-quality environment were not as attractive to females. These results demonstrate that, for *N. femorata*, adult male feeding in a high-quality environment during sexual maturation does not immediately compensate for juvenile development in a low-quality environment. It is well known that poor early nutrition in many species can lead to large, negative effects on adult life history traits (Lindstrom, 1999; Metcalfe & Monaghan, 2003). However, in some species, individuals can compensate for poor conditions early in life if better conditions are experienced later (Nicieza & Metcalfe, 1997; Birkhead et al., 1999). However, an inability to fully compensate for poor early nutrition has been demonstrated in a wide variety of taxa including cockroaches (Barrett et al., 2009) and songbirds (Nowicki et al., 2002).

Why might females prefer males that developed with cactus fruit? Males that develop with cactus fruit are on average larger (Gillespie et al., data not shown), and larger male *N. femorata* may be more likely to defend high quality cactus territories (Procter et al., 2012), that would provide nutrition for females and their offspring. Male size is fixed upon adult emergence, so later nutritional improvements would not affect this important characteristic. Also, males that develop with red cactus fruit have greater testes mass (Sasson et al., unpublished data) and can fertilise more of a female's eggs (Hamel et al., unpublished data). Female *N. femorata* used in this experiment were unmated, and many Hemipterans, including *N. femorata*, are constrained to continually produce a small number of eggs, even if they are not fertilised (Gordon & Loher, 1968; Sakurai, 1996). Thus, it is likely to the benefit of females to quickly find a mate and fertilise as many eggs as possible with a single mating, otherwise females may need to remate sooner or produce wasted eggs. Other benefits of choosing a male reared with cactus fruit are certainly possible, and further research is needed.

Although females are more responsive to the odours of males that developed with cactus fruit than those of males that developed without cactus fruit (Figure 1B, D), we found evidence that female preferences in *N. femorata* are context-dependent (Figure 2B, D). Context-dependence in female mate preferences has recently attracted substantial attention (Jennions & Petrie, 1997; Cotton et al., 2006; Chaine & Lyon, 2008). Females alter their preferences due to, for instance, risk of predation (Godin & Briggs, 1996), the behaviours of other females (Wade & Pruett-Jones, 1990; Valone & Templeton, 2002),

and their own physical condition (Cotton et al., 2006). Shifts in preferences may be adaptive, resulting from spatial and/or temporal fluctuations in selection on preferences (Cotton et al., 2006; Chaine & Lyon, 2008). Here, we found that females more often preferred males that developed with cactus fruit when the males were held on cactus with fruit as the current context (Figure 2B). These results, based on chemical cues alone, mirror those found in another behavioural study of this species where males and females were allowed to directly interact (Gillespie et al., data not shown).

Why are female *N. femorata* responses context dependent? One possibility is that females modify their preferences according to the anticipated developmental environment of offspring (Candolin, 2003). Females often lay eggs soon after mating, so the mate-encounter environment can be the same as the offspring developmental environment. Further studies are needed to examine whether offspring reared on cactus with fruit benefit from having a father that also developed on cactus with fruit.

Another, perhaps more parsimonious possibility is that males that developed with fruit alter their odour cues based on the quality of cactus where they are located. Males in the family Coreidae and the closely related family Alydidae are known to produce aggregation pheromones (Aldrich et al., 1976; Numata et al., 1990; Blatt & Borden, 1996; Wada et al., 1997; Schaefer & Panizzi, 2000) and may produce a different blend or greater quantity of compounds when they are located on a high-quality resource (Yasuda et al., 2007). In the absence of cactus fruit in the current context, *N. femorata* females were as likely to choose males that developed without cactus fruit as those that developed with cactus fruit (Figure 2D). Thus, males that developed with cactus fruit may restrict their pheromone production to when they are in the presence of cactus fruit. Males reared without cactus fruit may be unable to emit sufficient quantities of attractive compounds regardless of context. Thus, although female preferences for males in *N. femorata* change according to whether cactus fruit is present, the underlying cause may be context-dependence in male pheromone production. Why high-condition *N. femorata* males would not continually produce attractive odours is unclear, but in closely-related insects, males that produce aggregation pheromones attract both males and females. Thus, it may benefit males to only produce aggregation pheromones when they are located on a resource worth defending. Alternatively, males may only be physiologically able to produce the

highly-attractive odour if they experienced a high-quality developmental environment and are also currently feeding on a high-quality host plant. If so, odours may be an honest indicator of both male condition and the quality of the territory where the male is found. Similar context-dependent pheromone production is seen in the bean bug, *Riptortus clavatus* (Thunberg) (Heteroptera: Alydidae), where males actively feeding on soybeans produce an important attractant chemical that is found in lesser quantities in individuals that have not fed on soybeans recently (Yasuda et al., 2007).

Further research is needed to explore whether context-dependent female preferences are due to short-term changes in honest indicators provided by males. This possibility stresses the importance of establishing whether modification of female preferences is due to context-dependent changes in male phenotypes or whether females continuously and simultaneously assess their contexts and the males within them (Cotton et al., 2006). Both situations can lead to fluctuations in sexual selection, though the targets of selection may be different.

4.1. Conclusions

In conclusion, female *N. femorata* were more likely to move towards the odours of males that developed on a high-quality environment (Figures 1 and 2), but preference was influenced by male context (Figure 2B, D). More females selected males that developed on cactus with red fruit when those males were held on cactus with fruit. The mechanisms responsible for the context-dependent female preference are unknown, but the results here provide many exciting hypotheses for further experimentation. One underexplored possibility is that context-dependent male signalling is a mechanism behind changes in female mate preferences.

A hotly-debated topic in the field of sexual selection has been how genetic variation in male traits is maintained in spite of directional selection by females (Kirkpatrick & Ryan, 1991; Miller & Moore, 2007; Radwan, 2008). Here, we show that female preferences may vary due to simple changes in environmental factors. This variation can result in weakened or fluctuating selection pressures that slow down the erosion of genetic variation (Jennions & Petrie, 1997; Radwan, 2008). Recent theoretical work has shown that flexible mate choice may lead to an enhancement of the runaway process and elaboration through sexual selection (Bailey & Moore, 2012). Sexual selection takes place in nature where heterogeneity in environmental factors is

ubiquitous (Cornwallis & Uller, 2010). Incorporating this heterogeneity into studies of sexual selection has great promise to yield an improved understanding of how sexual selection operates in the real world and help explain the diversity of animal form and behaviour.

Acknowledgements

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