



Sexual selection is influenced by both developmental and adult environments

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Sexual selection is often assumed to be strong and consistent, yet increasing research shows it can fluctuate over space and time. Few experimental studies have examined changes in sexual selection in response to natural environmental variation. Here, we use a difference in resource quality to test for the influence of past environmental conditions and current environmental conditions on male and female mate choice and resulting selection gradients for leaf-footed cactus bugs, *Narnia femorata*. We raised juveniles on natural high- and low-quality diets, cactus pads with and without ripe cactus fruits. New adults were again assigned a cactus pad with or without fruit, paired with a potential mate, and observed for mating behaviors. We found developmental and adult encounter environments affected mating decisions and the resulting patterns of sexual selection for both males and females. Males were not choosy in the low-quality encounter environment, cactus without fruit, but they avoided mating with small females in the high-quality encounter environment. Females were choosy in both encounter environments, avoiding mating with small males. However, they were the choisiest when they were in the low-quality encounter environment. Female mate choice was also context dependent by male developmental environment. Females were more likely to mate with males that had developed on cactus with fruit when they were currently in the cactus with fruit environment. This pattern disappeared when females were in the cactus without fruit environment. Altogether, these results experimentally demonstrate context-dependent mate choice by both males and females. Furthermore, we demonstrate that simple, seasonal changes in resources can lead to fluctuations in sexual selection.

KEY WORDS: Condition dependence, context dependence, Coreidae, Hemiptera, selection analysis, selection gradient.

Fluctuations in sexual selection over time appear to be common (Siepielski et al. 2011) in part because of the environmental context dependence of mate choice (Jennions and Petrie 1997; Cotton et al. 2006; Chaine and Lyon 2008; Cornwallis and Uller 2010; Milner et al. 2010; Prudic et al. 2011). Females are known to alter their mating decisions due to, for instance, predator pressure (Godin and Briggs 1996), the decisions made by other females (Wade and Pruett-Jones 1990; Valone and Templeton 2002), their own condition (Cotton et al. 2006), and developmental history (Clark et al. 1997).

Variation in female mate choice may result in variation in the form, direction, and intensity of sexual selection on males. Siepielski et al. (2011) reviewed 89 studies of temporally replicated estimates of selection and concluded that the strength of sexual selection on males is stronger and more variable over time than survival selection. Such fluctuations in selection may have important evolutionary implications, such as maintaining genetic variation in sexually selected traits (Ellner and Hairston 1994; Radwan 2008; Bell 2010). Much of the existing work on variation in sexual selection has been tied to differences in social

environments, such as population density and composition (McLain 1992; Oh and Badyaev 2006; Gosden and Svensson 2008; Siepielski et al. 2011). It is less well known how seasonal changes in food and territory quality may directly affect sexual selection.

Males, like females, can be choosy (Cunningham and Birkhead 1998; Bonduriansky 2001; Clutton-Brock 2007) and their decisions can be context dependent (Simcox et al. 2005; Bel-Venner et al. 2008; Heubel and Schlupp 2008; Venner et al. 2010; Edward and Chapman 2011). Thus, sexual selection on females due to male mate choice should vary. However, only a handful of studies have estimated selection on females resulting from male choice (LeBas et al. 2003; Chenoweth and Blows 2005; Chenoweth et al. 2007; Bussière et al. 2008; Robson and Gwynne 2010; Wheeler et al. 2012), and even fewer have measured temporal or spatial changes in sexual selection on females. Selection studies are rarely able to identify the causal agents responsible for changes in selection because the majority of selection studies are observational (Kingsolver et al. 2001). Replicated experimental studies are needed to allow detection of changes in selection and to explore the causative factors (Wade and Kalisz 1990; Losos et al. 2006; Kelly 2008a; Siepielski et al. 2011; Miller and Svensson 2014). Here, we use experimental manipulations of a common natural resource to examine effects of past environmental conditions and current environmental conditions on mate choice and resulting sexual selection gradients for both male and female leaf-footed cactus bugs, *Narnia femorata* (Hemiptera: Coreidae).

We provided insects with cactus pads with or without ripe cactus fruit during development and later during encounters with potential mates. We then examined the influence of environmental context on male and female mating decisions and resulting sexual selection. *Narnia femorata* live, feed, mate, and produce offspring on prickly pear and cholla cacti, *Opuntia* and *Cylindropuntia* spp. (Baranowski and Slater 1986). Males are territorial, and the larger individuals are more likely to be dominant and successfully defend a cactus territory (Procter et al. 2012). Adults and juveniles feed on cactus fruit when it is available. When insects are not feeding, they often descend from the fruit and reside on cactus pads. Cactus fruits are valuable to these insects; those *N. femorata* raised on cactus with red, ripe fruits develop faster (Nageon de Lestang and Miller 2009), grow larger, and achieve greater reproductive success as adults than those raised without fruit (C. W. Miller, unpubl. data). Females lay on average 56% more eggs when provided with ripe fruit during the first two weeks of egg laying relative to females not provided cactus fruits (Miller et al. 2013). Thus, cactus with fruit is a superior resource; yet, *N. femorata* develop and breed throughout the year, even when cactus fruit is unavailable. Cactus fruits are only produced in the spring each year and ripen in the summer and fall (Fig. 1). Ripe cactus fruits are rapidly removed and consumed by tortoises, birds, deer, raccoons,

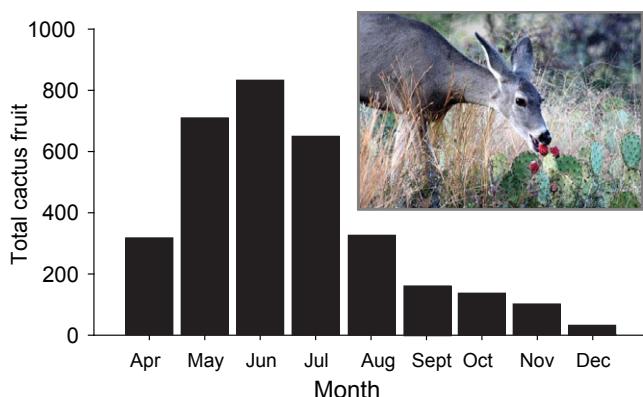


Figure 1. *Opuntia humifusa* fruits are rapidly depleted in the field, primarily due to herbivory. Bars indicate the total cactus fruit present in 2010 in a 160 × 1 m area at the Ordway-Swisher Biological Station in North-Central Florida. The seasonal pattern of cactus fruit abundance is similar across years. Insects have been found developing and breeding throughout the year. Photo: Erin Willett.

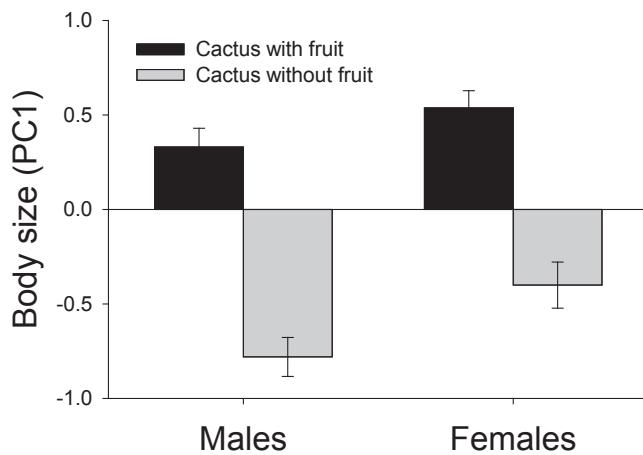


Figure 2. Body size (PC1) of *N. femorata* that developed on cactus with or without cactus fruits, mean ± 1 standard error. Both males and females that developed without cactus fruit are smaller as adults.

and rodents (Gonzalez-Espinosa and Quintana-Ascencio 1986; Hellgren 1994). Herbivore pressure is also greater in some areas than in others (C. W. Miller, pers. obs.). Thus, a temporal and spatial mosaic of cactus fruit abundance is the result, with a proportion of *N. femorata* mating, reproducing, and developing without this important resource.

We measured how sexual selection on size changed as a result of resource differences during juvenile development and later adult mate choice. Large female *N. femorata*, like larger females of many other invertebrate species, produce more eggs than small females (Honěk 1993). Thus, size can serve as a cue of fecundity. We predicted that male *N. femorata* would be overall more likely

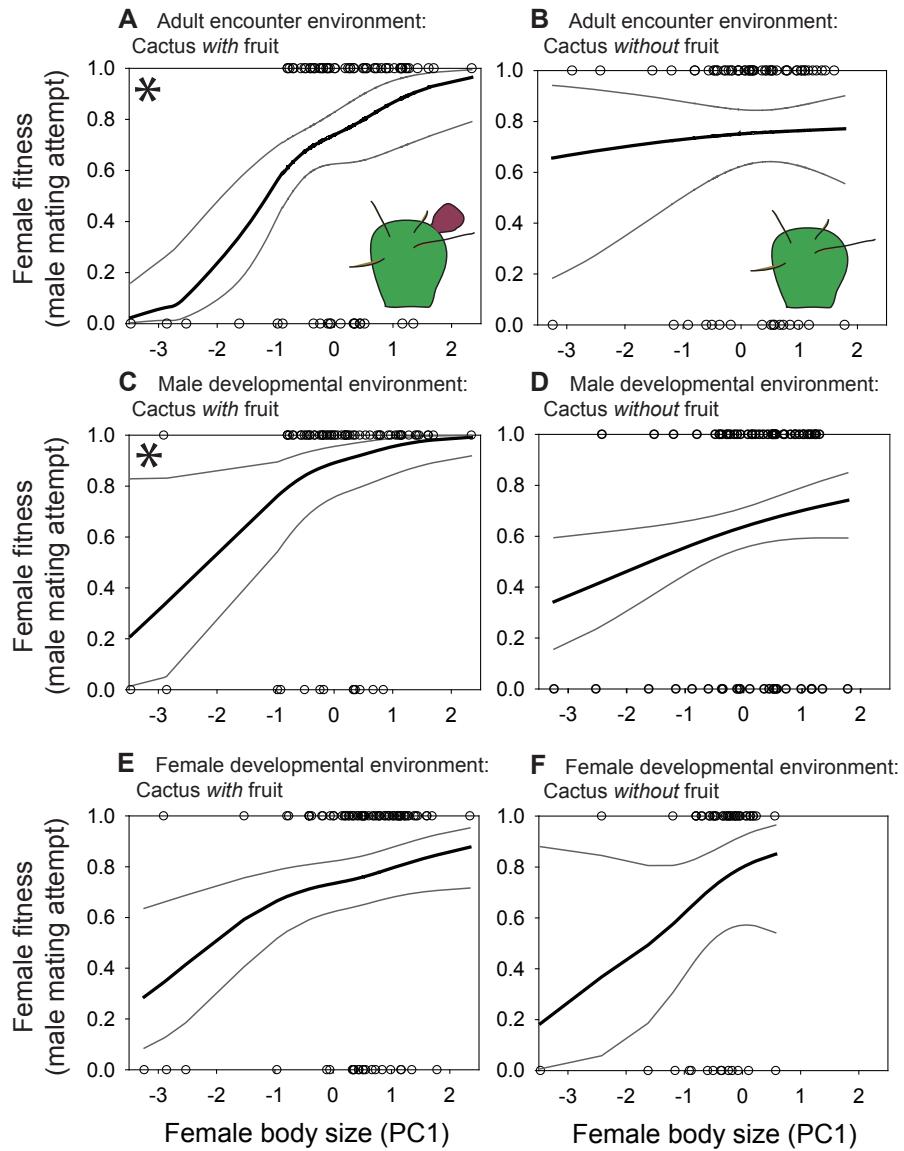


Figure 3. Nonparametric cubic splines representing the univariate fitness surfaces for female body size using fitness scores based on male mounting. (A and B) illustrate selection in adult encounter environments, (C and D) male developmental environments, and (E and F) female developmental environments. Gray lines are the standard errors of the fitness surface generated from 50 bootstraps. λ is the smoothing parameter. Significant selection gradients are denoted by “*.”

to choose larger females than smaller females, a pattern commonly seen in invertebrates (Bonduriansky 2001; Edward and Chapman 2011). We predicted that the adult encounter environment should modify male mating decisions. Ripe cactus fruits are a valuable resource, so we predicted that males on territories with cactus fruits would be choosy in their mating effort because mating would mean reduced time feeding. Males may also be choosy in this environment because numerous females may visit such high-quality territories in natural settings. We predicted that males on the low-quality territories (without cactus fruits) would be relatively indiscriminate in their mating attempts based on patterns seen in other taxa (Itzkowitz and Haley 1999). We

predicted that males that developed without cactus fruit would be less choosy or even prefer smaller females, because small males often incur costs and risks from pursuing high-quality females (Venner et al. 2010). To explore factors leading to the discovered patterns, we examined the influence of male developmental environment on whether males fed during the observational period and the influence of male size on whether males attempted intromission with females.

We predicted that females would overall choose larger rather than smaller males, as is common in many species (Andersson 1994). However, unlike with males, we predicted females should be less choosy in the presence of cactus fruit. Cactus fruit is

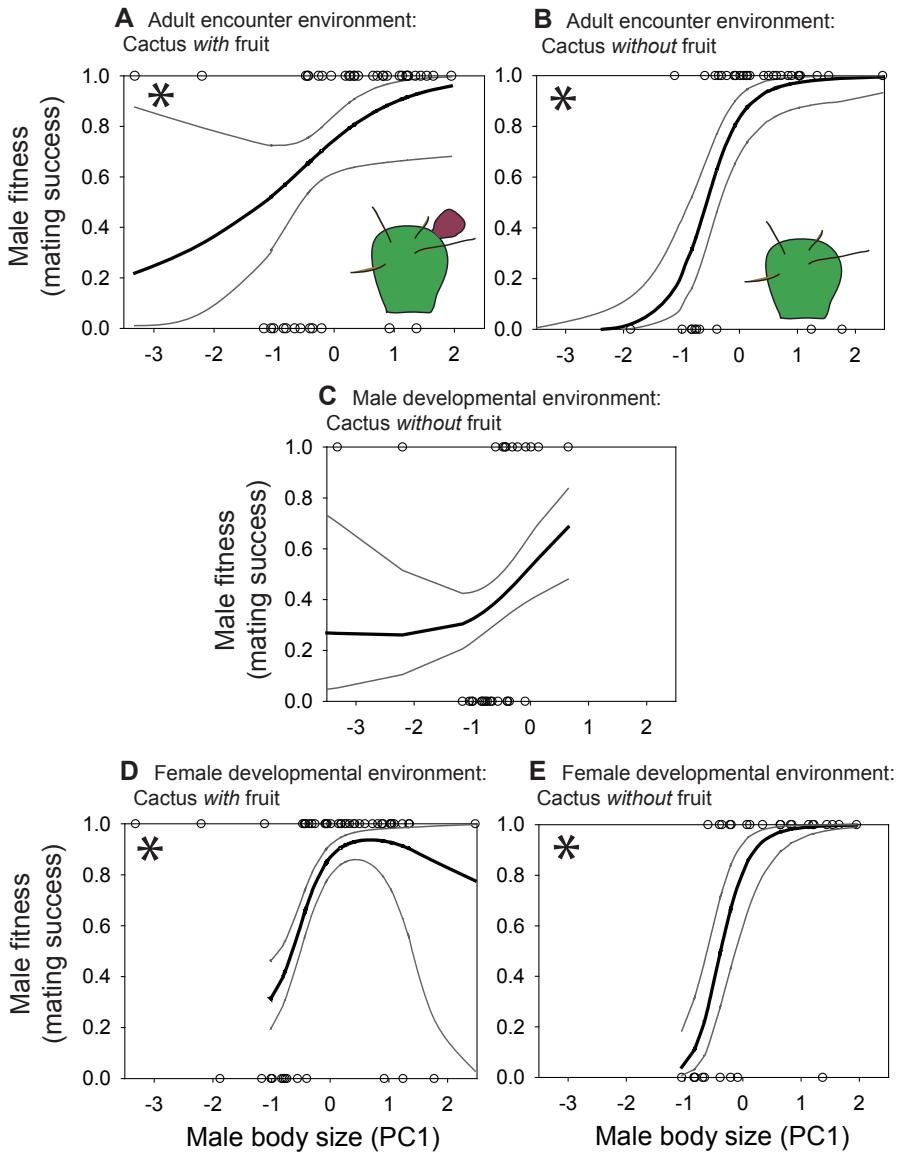


Figure 4. Nonparametric cubic splines representing the univariate fitness surfaces for male body size using fitness scores based on male mating success. (A and B) illustrate selection in adult encounter environments, (C) male developmental environment of cactus without fruit, and (D and E) female developmental environments. We did not calculate a spline for male developmental environment of “cactus with fruit” because the vast majority of males in this category mated, and there were too few males that did not mate to calculate reliable splines. Gray lines are the standard errors of the fitness surface generated from 50 bootstraps. λ is the smoothing parameter. Significant selection gradients are denoted by “*.”

a high-quality food for both females and their offspring, thus we predicted the presence of the direct benefit would result in greater willingness to mate with any male defending the fruit. In addition, we predicted females that developed without cactus fruit would be less choosy because females in poor condition often have decreased choosiness (Hunt et al. 2005; Cotton et al. 2006; Hebets et al. 2008). After examining the environmental dependence of mate choice, we examined the resulting patterns of sexual selection on males and females through univariate selection analyses (Lande and Arnold 1983).

Materials and Methods

EXPERIMENTAL DESIGN

We reared *N. femorata* (Hemiptera: Coreidae) between February and May 2009 in a greenhouse with a summertime photoperiod of 14 h of light per day. Developmental time in *N. femorata* from egg to adult is six to eight weeks in favorable environments. The experimental individuals were the offspring of adults and juveniles collected from the University of Florida Ordway-Swisher Biological Station ($29^{\circ}41'N$, $82^{\circ}W$) in the fall of 2008. Nymphs commonly aggregate, thus we raised laboratory insects in family

groups of four to 12 individuals through the first three instars. Thirty-two families provided the 286 offspring used in this experiment, with a maximal number of 18 offspring per family. We initially provided all juveniles with *Opuntia humifusa* cactus pads and red, ripe fruits from our local area.

We employed a factorial experimental design, with male and female insects placed in all possible combinations of two developmental environments and two adult environments. In natural situations, removal of fruit by other herbivores can occur at any point during development. When *N. femorata* individuals reached their fourth instar (of five), we randomly placed sibling pairs into one of the two developmental environments: (1) one cactus pad with a large, ripe fruit (the high-quality environment) or (2) one cactus pad without a fruit (the low-quality environment). By separating them into pairs at this stage, we reduced food competition and minimized common environment effects. The insects in this study on average quintupled their weight during these final two instars. The fruit used from the penultimate instar onwards was ripe fruit from *Opuntia engelmannii* var. *linguiformis*. This cactus species is a host of *N. femorata* in its native range. Insects were isolated individually within 24 h of adult emergence. Two weeks before behavioral testing, females were randomly assigned one of the two encounter environments (cactus with or without cactus fruit). Males remained isolated in their developmental environment (cactus with or without cactus fruit) until just before behavioral testing when they were put into female containers, their adult encounter environments.

BEHAVIOR TESTING

We replicated mate encounters as they commonly occur under natural circumstances, where a single male and female meet on a host plant. Each male was randomly placed in a high- or low-quality adult encounter environment and observations were begun. We watched 10–15 pairs at a time concurrently for 4 h. This species is excellent for simultaneous observations because they have low activity levels (mean time active, 8%) and behaviors are typically slow and easy to observe (Video S1). Behavioral scoring was conducted using the event recorder Jwatcher (Blumstein and Daniel 2007).

In *N. femorata*, a male mounts a female by climbing onto her back. Attempted intromissions are easy to observe because a male must first mount a female, line up his body parallel to hers, lean to one side, and match up their terminal abdominal segments. Females commonly keep their genital plates closed and prevent insertion of the male genitalia (Video S1). If intromission is achieved, males twist 180 degrees, resulting in an end-to-end connection. Copulation duration ranges between several minutes to several hours.

We used male mounting of a female as our metric of male mate choice. We used a successful intromission as our metric

of female mate choice. For females to allow mating, contact of terminal abdominal segments (an attempted intromission) must have occurred first, giving females an option to allow intromission or not. Thus, we analyzed mate choice for only those females where contact of the terminal abdominal segments occurred. We took this conservative approach because occasionally mountings did not result in contact of the terminal abdominal segments. Usually the reason appeared to be that the female rejected the male, but in some cases it may have been due to rejection of the female by the male. At the end of the observation period, bugs were individually frozen for morphometrics.

MORPHOMETRICS

Each insect used in the behavior trials was photographed and measured. Digital photographs of insects were captured with a Canon EOS 50D camera and Leica M 165C microscope. We took linear measurements of the following: pronotal width (from dorsal view), mouthpart length (from ventral view), head length (from dorsal view), front femoral length, and front tibiae length using ImageJ 1.42q software (Rasband 2009). We estimated the area of the hind femora and hind tibiae using the ImageJ threshold function. This tool interactively sets the lower and upper threshold values, segmenting grayscale images into features of interest and background.

GENERAL STATISTICAL ANALYSES

All measured morphological traits were highly correlated (Table S3). We chose to use a composite measure of overall size, rather than using the original traits, because high phenotypic correlations between morphological traits can cause problems of multicollinearity in regression analyzes of selection and make interpretations of selection coefficients difficult (Mitchell-Olds and Shaw 1987). We used principal component analysis (PCA) to reduce our measures to a single composite measure of size (Table S4). The first principal component of the PCA explained 85% of the variation in the data and was used in subsequent analysis as the metric of body size. Body size followed a normal distribution, thus we used generalized linear models (GLM) assuming a normal error distribution to examine the influence of developmental environment on body size (PC1). We first tested (1) the effect of male body size on whether males attempted intromission with females, and (2) the effect of developmental environment on whether individuals fed during the behavioral observations. For these two analyses, we used GLM with a logit-link functions and assumed binomial error distributions.

Context-dependent mate choice can result in fluctuating selection pressures (Qvarnström 2001; Chaine and Lyon 2008). Therefore, we took a combined statistical approach, using GLM to examine influences on mate choice, and selection analyses (Lande and Arnold 1983; Brodie et al. 1995) to examine resulting

changes in selection. We analyzed environmental effects on male mate choice and female mate choice separately. We used GLM with logit-link function and assumed a binomial error distribution. The mounting of a female by a male was used as our metric of male mate choice. Our initial full model tested the effect of female size, male and female developmental environments, the adult encounter environment, and all two way interactions on this binary response variable (mounting or no mounting). Mating following an attempt at intromission by the male was used as our binary metric of female mate choice (intromission or no intromission). Our initial full model for female mate choice was the same as above; however, male size was substituted for female size in the model. We used the “stepwise elimination modelling procedure” (described in Hardy and Field 1998), specifically, all nonsignificant interactions (set conservatively a priori at $P > 0.15$) were removed sequentially from our models. All models were nonnested models.

SELECTION ANALYSES

Our goals with selection analyses were to measure sexual selection on body size as a result of mate choice and to visualize differences in the strength of selection as a result of alternate adult encounter and developmental environments. We separately calculated selection coefficients on body size (PC1) for each adult encounter environment, male developmental environment, and female developmental environment. We used the convention for sexual selection analyses of assigning fitness scores based on mating behaviors (Lande and Arnold 1983; Brodie and Janzen 1996; Kingsolver et al. 2001; Siepielski et al. 2011).

For females in this study, a “fitness” score of 0 reflects that the female was not mounted by a male. A score of 1 reflects that the female was mounted by a male. For males, a fitness score of 0 reflects that the male mounted and contacted the female’s terminal abdominal segments (an attempted intromission), but that the female did not allow him to mate. A score of 1 means that there was an attempt at intromission, and the male was successful in mating. Although we use the convention for selection analyses of assigning fitness scores, it is important to note that we have only measured one potential aspect of fitness. Fitness is likely influenced by a great many other factors in natural situations. Also, we measured selection gradients in a laboratory setting. Selection gradients may differ for wild populations, although a recent meta-analysis found that selection measured in experimental studies is generally comparable to selection measured in unmanipulated natural populations (C. M. Caruso, R. A. Martin, N. Sletvold, J. G. Kingsolver, M. J. Wade, K. Augustine, S. M. Carlson, A. D. C. MacColl, and A. M. Siepielski, unpubl. results).

Selection analyses were performed and cubic splines were constructed for each environment separately (Figs. 3, 4). Before each selection analysis, we transformed body size (PC1) to

Table 1. Generalized linear model results for mate choice by males. Male mounting was used to estimate male mate choice.

Source	χ^2	<i>P</i>
Female developmental environment (FD)	0.315	0.574
Male developmental environment (MD)	7.205	0.007
Encounter environment (EE)	0.185	0.667
Female body size	5.501	0.019
EE × female body size	3.829	0.050

Degrees of freedom of each factor = 1; $n = 141$.

All nonsignificant interactions ($P > 0.15$) were removed sequentially from our models.

mean = 0, standard deviation = 1 for the individuals in each environment (the subgroup). We also estimated relative fitness by dividing each individual fitness score by the average score of the subgroup (Janzen and Stern 1998). Selection coefficients (Lande and Arnold 1983; Arnold and Wade 1984) were obtained from linear regression analyses with relative fitness as the dependent variable and standardized body size as the independent variable. We used logistic regression analyses to determine the significance of the selection coefficients (Fairbairn and Preziosi 1996). Analyses were conducted in PASW Statistics version 18.0. We constructed cubic splines with GLMS version 4.0/glmsWIN 1 (Schluter 1988) using the fitness scores of 0 and 1 to visualize the form of selection. Standard errors were generated through bootstrapping.

Results

Narnia femorata that developed on ripe cactus fruit for the final two instars were larger (GLM: $F_{1,268} = 109.741$, $P < 0.001$, Figs. 2, S1). Males that developed without cactus fruit were more likely to feed in the encounter environment than males that developed with cactus fruit (GLM: Wald $\chi^2 = 4.790$; $P = 0.029$). All females were moved to the encounter environment for the two weeks prior to testing, and we found no effect of developmental environment on the probability of female feeding in the encounter environment during our observation period (GLM: Wald $\chi^2 = 0.019$; $P = 0.889$).

Of the 141 male–female pairings, 104 of the males mounted females. Larger males were more likely to mount females than were small males (GLM: Wald $\chi^2 = 8.752$; $P = 0.003$). Intromission was attempted by males in 84 of the 105 mountings. In 24 of these 85 pairs, females did not open their genital plates, and thus no mating occurred. Mountings and successful intromissions were influenced by both developmental environments and encounter environments (Tables 1, 3), and our selection analyses revealed variation in the strength and form of sexual selection across these environmental contexts (Tables 2, 4; Figs. 3–5).

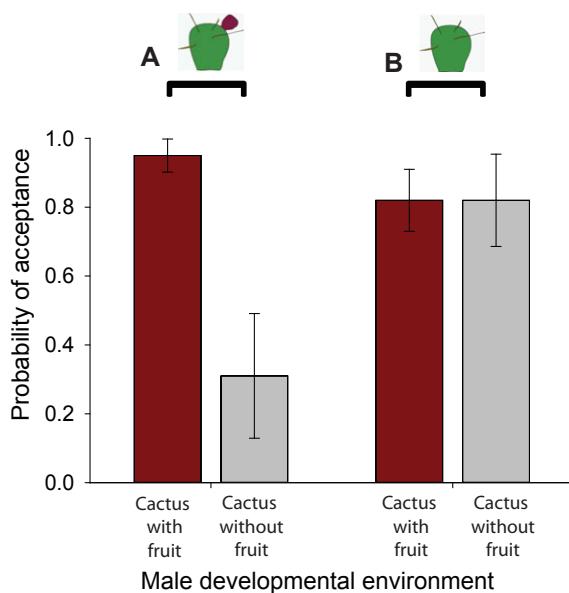


Figure 5. Female receptivity after an attempted intromission (± 1 standard error; Table 3). (A) When red cactus fruit was present, females were less likely to mate with males that developed without cactus fruit. (B) In contrast, females in a cactus-only encounter environment showed an equal and high probability of mating with males that developed with and without red cactus fruit.

MALE MATE CHOICE AND CONSEQUENCES FOR SELECTION ON FEMALES

The pattern of male mate choice differed across adult encounter environments (significant interaction between encounter environment and female size, Table 1). In the adult encounter environment of cactus with fruit, males were more likely to mount large females rather than small females (Table 1; Fig. 3A). No evidence of male mate choice was seen in the lower quality encounter environment, cactus without fruit (Fig. 3B). The six smallest females had a large influence on these results. When we removed these individuals from the analysis, the statistical significance of the female size and the interaction term in the ANOVA was lost (three females removed from each encounter environment; female size, $P = 0.331$,

encounter environment \times female size, $P = 0.270$). These results suggest that the differences in male mountings across adult encounter environments were largely due to a rejection of the very smallest females in the cactus with fruit environment (Fig. 3A).

Although males might be expected to prefer females that developed on cactus with fruit (the high-quality environment), male mate choice was not influenced by female developmental environment (Table 1). Males that developed with cactus fruit were more likely to mount females than males that developed without cactus fruit (Table 1). Effect sizes of factors in the GLM are available in Table S1.

Selection analyses revealed that male mate choice resulted in positive linear selection on female body size in the cactus with fruit encounter environment (Table 2; Fig. 3A). In contrast, no evidence of selection on female body size was found in the cactus without fruit encounter environment (Table 2; Fig. 3B). We detected significant linear selection on female size from males that developed on cactus with fruit (Table 2; Fig. 3C). All other selection gradients were nonsignificant; however, the nonparametric cubic splines illustrate that larger females have an overall selective advantage (Fig. 3).

FEMALE MATE CHOICE AND CONSEQUENCES FOR SELECTION ON MALES

Across environments, females were more likely to mate with the larger males (Table 3; Fig. 4). However, when cactus fruit was present in the adult encounter environment, smaller males had a better chance of mating than when cactus fruit was not present in the adult encounter environment (significant interaction between encounter environment and male size; Table 3; Fig. 4A, B). The four smallest males were integral to this pattern of context dependence; when data were re-analyzed with the four smallest individuals removed, statistical significance of the interaction term in the ANOVA was lost (two males removed from each encounter environment; encounter environment \times male size, $P > 0.10$). These results suggest that the differences in female mate choice across adult encounter environments were largely

Table 2. Results of univariate selection analyses for female body size using mounting by a male as the metric of female fitness.

Environmental factor	β (SE)	n	χ^2	P
Adult encounter environment				
Cactus with fruit	0.212 (0.069)	73	6.686	0.010
Cactus without fruit	0.026 (0.071)	68	0.140	0.708
Male developmental environment				
Cactus with fruit	0.132 (0.053)	73	4.813	0.028
Cactus without fruit	0.114 (0.091)	68	1.512	0.219
Female developmental environment				
Cactus with fruit	0.119 (0.061)	91	3.391	0.066
Cactus without fruit	0.155 (0.088)	50	2.444	0.118

Table 3. Generalized linear model results for female mate choice. Female acceptance of intromission was used to estimate choice.

Source	χ^2	P
Female developmental environment (FD)	0.503	0.478
Male developmental environment (MD)	6.802	0.009
Encounter environment (EE)	0.078	0.779
Male size	4.380	0.036
EE × MD	3.924	0.048
FD × male body size	4.920	0.027
EE × male body size	5.442	0.020
MD × male body size	2.553	0.110

Degrees of freedom of each factor = 1; n = 84.

All nonsignificant interactions ($P > 0.15$) were removed sequentially from our models.

due to a rejection of the very smallest males in the cactus without fruit environment (Fig. 4B).

Male developmental environment affected female mate choice (Table 3), but the pattern was context dependent (significant interaction between encounter environment and male developmental environment; Table 3; Fig. 5). In the adult encounter environment of cactus with fruit, females were more likely to mate with males that developed in the high-quality environment, cactus without fruit (Fig. 5A). However, when cactus fruit was not present in the adult encounter environment, females showed no preference for male developmental background (Fig. 5B).

Female developmental environment did not affect female receptivity during the observation period (Table 3); however, it did subtly influence the use of male size in mating decisions (significant interaction between female developmental environment and male size; Table 3; Fig. 4D, E). Effect sizes of factors in the GLM are available in Table S2.

Selection analyses revealed that female mate choice resulted in positive linear selection on male size in both encounter environments. In addition, larger males were favored whether females developed on cactus with fruit (Table 4). Nonparametric cubic splines illustrate that larger males have an overall selective advantage, although there is variation in selection across environments (Table 4; Fig. 4).

Discussion

We found that male and female mating decisions in *N. femorata* were affected by their developmental environments and the environments where they encountered potential mates (Figs. 3–6, S1; Tables 1, 3). These effects led to changes in the strength of sexual selection on both sexes (Figs. 3, 4). We detected these patterns using a simple resource difference in the life history of this organism—the presence or absence of cactus fruit. Because this

Table 4. Results of univariate selection analyses for male body size using female acceptance of intromission as the metric of male fitness.

Environmental factor	β (SE)	n	χ^2	P
Adult encounter				
Cactus with fruit	0.201 (0.090)	44	3.859	0.049
Cactus without fruit	0.323 (0.100)	40	5.970	0.015
Male development				
Cactus with fruit	0.998 (0.054)	53	0.831	0.362
Cactus without fruit	0.197 (0.219)	31	0.788	0.375
Female environment				
Cactus with fruit	0.209 (0.082)	54	4.926	0.026
Cactus without fruit	0.410 (0.111)	30	6.497	0.011

resource varies both seasonally and spatially, our results provide insight into dynamic patterns of sexual selection that likely occur over space and time in nature.

MALE MATE CHOICE AND CONSEQUENCES FOR SELECTION ON FEMALES

The environment where males encountered females affected patterns of male mate choice (Table 1; Fig. 3A, B). In the high-quality environment, cactus with fruit, males avoided the smallest females (Fig. 3A). Males were not choosy in the lower quality encounter environment, cactus without fruit (Fig. 3B). Why are males choosy in one context but not the other?

The evolution of male mate choice is expected when females differ in quality and males have more opportunities to mate than their capacity to fertilize females (Edward and Chapman 2011). Female *N. femorata* differ markedly in size (Fig. S1) and fecundity (Miller et al. 2013). Male *N. femorata* show a decline in fertility (via offspring production) across sequential pairings, consistent with sperm limitation (C. W. Miller, unpubl. data). When cactus with fruit is present, it may benefit males to prioritize feeding on this valuable resource over mating with low-quality females. In addition, males on cactus with fruit may predictably have more opportunities to mate than males on cactus without fruit. Thus, it may benefit males to reject low-quality females to conserve sperm for more fecund females. More research is needed to investigate these patterns and the frequency of context-dependent male mate choice across taxa. Work on sperm competition has demonstrated that males in many species allocate sperm differently according to the social environment and cues of female quality (Kelly and Jennions 2011), thus it should not be surprising that male mating decisions should also be context dependent (Itzkowitz and Haley 1999; Simcox et al. 2005; Bateman and Fleming 2006; Bel-Venner et al. 2008; Heubel and Schlupp 2008; Venner et al. 2010; Takahashi and Watanabe 2011; Jordan and Brooks 2012).

The developmental environment of males affected their mating behaviors (Table 1). We found male *N. femorata* that developed without cactus fruit were less likely to mount females than males that developed with cactus fruit (Table 1). Why would males that developed in the poor-quality environment be less likely to mount females? Two lines of evidence show that it is not because they are simply more selective based on female size. First, the statistical interaction between male developmental environment and female size was not significant and was removed from the final model (Table 1). Second, male mate choice resulted in a significant linear selection gradient on female body size only for the subset of males that developed with cactus fruit (Fig. 3C), not the subset that developed without cactus fruit (Fig. 3D). Males that developed on cactus without fruit spent more time feeding in the encounter environment. These males may lack important nutrients, and may consequently prioritize feeding on ripe cactus fruit before attempting mating. Another reason that poor-quality males may generally avoid females early in life may be to reduce the risk of confrontation with other males (Shine et al. 2001; Fawcett and Johnstone 2003; Shine et al. 2003; Härdling and Kokko 2005; Bel-Venner et al. 2008; Venner et al. 2010). However, evidence in *N. femorata* suggests that small males become more aggressive with other males, not less, when females are present (Procter et al. 2012).

Variation in male mate choice across environments had consequences for selection on female body size (Table 2; Fig. 3). Overall, changes in selection gradients were modest. The most striking difference was related to the adult encounter environments (Fig. 3A, B). We found positive directional selection on female size when cactus fruit was present in the adult encounter environment but not when it was absent. Although studies of male mate choice are becoming increasingly common (reviewed in Bonduriansky 2001; Edward and Chapman 2011), the consequences for sexual selection on females have only rarely been measured (LeBas et al. 2003; Chenoweth and Blows 2005; Chenoweth et al. 2007; Bussière et al. 2008; Robson and Gwynne 2010; Wheeler et al. 2012; Fritzsche and Booksmythe 2013). Existing work in katydids has found that the potential exists for sexual selection on females to be as strong as sexual selection on males (Lorch et al. 2008). Directional and stabilizing selection have been detected for female ornamentation in dance flies, *Rhamphomyia tarsata* (LeBas et al. 2003), and *R. longicauda* (Wheeler et al. 2012). Mormon crickets experience sex-role reversal and male mate choice of females (Gwynne 1981), yet positive linear selection for female ornamentation or weapons has not yet been found (Robson and Gwynne 2010). Our study is the first to our knowledge to measure sexual selection gradients on females across levels of natural resource availability. Additional comparisons of sexual selection across natural environments will reveal if fluctuations in sexual selection on females are common.

FEMALE MATE CHOICE AND CONSEQUENCES FOR SELECTION ON MALES

As with males, the environment where females encountered potential mates affected mate choice (Table 3; Fig. 4A, B). However, the patterns were reversed. In the *low-quality* environment, cactus without fruits, females avoided the smallest males (significant encounter environment \times male size interaction, Table 3; Fig. 4B). In contrast, males were choosiest in the *high-quality* environment (significant encounter environment \times female size interaction, Table 1; Fig. 3A). These opposing patterns of context dependence highlight likely differences in the value of size for the two sexes. For males, larger females may provide a direct fitness benefit because larger females are more fecund (Miller et al. 2013). For females, the value of mating with larger males is likely indirect and possibly weak. Body size in *N. femorata* has low heritability (C. W. Miller and A. J. Moore, unpubl. ms.) and is highly sensitive to developmental environment (Fig. 2). Thus, the genetic benefit to offspring of having a large father may be very small. In contrast, cactus with fruit provides a clear direct benefit to females and their offspring. Jennions and Petrie (1997) have argued that females in the presence of direct benefits should relax their preferences for size or other cues of male quality, which is consistent with the pattern we see here (Fig. 4A, B).

We found an intriguing interaction between the environment where females encountered potential mates and the developmental background of males (Table 3; Fig. 5A). Females in the high-quality encounter environment (cactus with fruit) were more likely to mate with males that developed with cactus fruit (Fig. 5A), whereas females in the low-quality environment (cactus without fruit) showed no difference in response to males from the two different developmental backgrounds (significant encounter environment \times male developmental environment interaction, Table 3; Fig. 5B). In fact, in the low-quality context, males that developed in either developmental background had a high probability of mating (Fig. 5B). This unexpected experimental result is robust; similar results have been found using only odor cues and offering females a choice of two males simultaneously (Addesso et al. 2014). Recent work suggests that female mate choice on cactus with fruit leads to greater offspring production, but the benefit is absent when fruit is absent (J. Hamel, unpubl. data).

Female developmental environment did not affect their probability of mating (Table 3). However, it did have subtle effects on female selectivity for male size (Table 3; Fig. 4D, E). These effects of female developmental environment on mating patterns were not as pronounced as those seen in other taxa (Hunt et al. 2005; Cotton et al. 2006; Moskalik and Uetz 2011).

Female mate choice led to overall directional selection on male body size (Table 4; Fig. 4). Selection gradients varied across environments (Table 4; Fig. 4). As predicted by patterns of female mate choice, directional selection for male body size was stronger

in the environment without cactus fruit than the environment with cactus fruit (Table 4; Fig. 4A, B).

PHENOTYPIC VARIATION, MATE CHOICE, AND TOTAL SEXUAL SELECTION

The context dependence of both female and male mate choice was strongly influenced by the acceptance or rejection of the very smallest individuals (Figs. 3A, B and 4A, B). As seen here, selection may commonly act on the tails of the phenotypic distribution (Anholt 1991). Some of the major benefits of using natural resource variation are that a realistic range of phenotypes can be generated and realistic patterns of selection can be estimated. Artificial laboratory diets may generate extreme sizes and unrealistic phenotypic variation that can be problematic for studies of selection.

Our study examined selection originating from mate choice at close range. Female mate choice decisions likely begin before this point, with females using odors to assess resource quality and male quality simultaneously from a distance. Reproductive female *N. femorata* should seek the best available resource for themselves and their offspring, and such high-quality resources may be defended by the highest quality males (Procter et al. 2012, see also Kelly 2008b). Thus, females visiting cactus with fruit may still end up mating with large males, even though they are relatively less choosy for size in this environment (Fig. 4A). It would be particularly informative to combine field studies of sexual selection with additional laboratory experiments to partition the relative contributions of resource choice, mate choice, male–male competition, and their interactions on sexual selection (Hunt et al. 2009; Miller and Svensson 2014).

Conclusions

Our results suggest dynamic sexual selection for *N. femorata* in nature. We found that mate choice and resulting selection gradients in *N. femorata* are influenced by both present and past environmental contexts. As the seasons change from summer through fall and winter, herbivores rapidly remove ripe cactus fruits, leaving many insects without this high-quality resource (Fig. 1). Many organisms such as *N. femorata* breed over long time periods each year during which time environments can vary substantially. Few studies have examined changes in selection across time within breeding seasons (Oh and Badyaev 2006; Kasumovic et al. 2008; Kasumovic and Andrade 2009; Punzalan et al. 2010; Steele et al. 2011). This study is one of the first experimental demonstrations that seasonal variation in resource quality can affect sexual selection on both males and females. Seasonal variation in resources is common across species and habitats, and such changes may result in predictable fluctuations in sexual selection over time.

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DATA ARCHIVING

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1. Parameter estimates from a GLM model testing the factors influencing male mounting of females.

Table S2. Parameter estimates from a GLM model testing the factors influencing female acceptance of intromission.

Figure S1. Body size histograms for adult (A) males and (B) females by developmental environment.

Video S1. A male *Narnia femorata* attempts mating with a female on a cactus fruit.