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William E. Wagner Jr.

University of Nebraska-Lincoln, wwagner1@unl.edu

Alexandra L. Basolo

University of Nebraska-Lincoln, basolo@unl.edu

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The Relative Importance of Different Direct Benefits in the Mate Choices of a Field Cricket

William E. Wagner, Jr., and Alexandra L. Basolo

School of Biological Sciences, University of Nebraska–Lincoln, Lincoln, Nebraska, USA

wagner@unl.edu & basolo@unl.edu

Abstract

Discussions about the evolution of female mating preferences have often suggested that females should express multiple strong preferences when different male traits are correlated with different mating benefits, yet few studies have directly tested this hypothesis by comparing the strength of female preferences for male traits known to be correlated with different benefits. In the variable field cricket, *Gryllus lineaticeps*, females receive fecundity and fertility benefits from mating with males with higher chirp rates and life-span benefits from mating with males with longer chirp durations. Although females prefer higher chirp rates and longer chirp durations when the other trait is held constant, it is possible that they give priority to one of these song traits when both vary. In this study, we examined the relative importance of chirp rate and chirp duration in female mate choice using single-stimulus presentations of songs that varied in both chirp rate and chirp duration. Females expressed both directional and stabilizing preferences based on chirp rate, responding most strongly to a chirp rate approximately one standard deviation above the population mean. Females did not express preferences based on chirp duration, and did not express correlational preferences. These results suggest that females may give priority to the reproductive benefits provided by males that produce higher chirp rates.

Keywords: Calling song, direct benefits, female mate choice, field cricket, *Gryllus lineaticeps*, mating preference.

Male animals often express multiple sex-limited traits, such as color patterns, morphological structures, acoustic signals, and courtship displays, and each of these sexually dimorphic traits can be complex, varying along multiple axes (Hebets and Papaj 2005). Whether females should express strong preferences for multiple male traits has been controversial. A number of hypotheses have been proposed for why females should express multiple preferences (Candolin 2003; Hebets and Papaj 2005), including: (1) different male traits might be predictive of the same mating benefit, and females might improve the accuracy with which they assess benefit quality by using multiple male traits (Møller and Pomiankowski 1993; Johnstone 1996); (2) different male traits might be predictive of different mating benefits, and females might obtain multiple benefits by assessing multiple male traits (Møller and Pomiankowski 1993; Johnstone 1996); and (3) females might have sen-

sory or cognitive biases that evolved in another context, and these biases might be stimulated by multiple male traits (Basolo 1990; Ryan and Rand 1993; Endler and Basolo 1998; Rowe 1999). In contrast, some models have predicted that females should often express a single strong preference; when the cost of assessing multiple traits is high, females should tend to select mates based on the one trait correlated with the most important mating benefit (Schluter and Price 1993; Iwasa and Pomiankowski 1994; but see Johnstone 1996).

The hypothesis that females should express multiple preferences when different male traits are correlated with different mating benefits has received substantial empirical attention, but support for this hypothesis is mostly weak. A strong test of the hypothesis requires evidence that females receive multiple types of mating benefits from males, and that different male traits are correlated with different mating benefits. Numer-

ous studies have shown that different male traits provide information about different male qualities (Candolin 2003), such as age and parasite resistance (Lindström and Lundström 2000) or juvenile and adult condition (Scheuber et al. 2003). These male qualities, however, may or may not be indicative of different female mating benefits, or indeed, of any mating benefits. Because few studies have shown that different male traits are correlated with different mating benefits, there are currently a limited number of systems available for testing the hypothesis that females express multiple preferences to obtain multiple benefits from males.

Even in systems where females can receive multiple benefits from expressing multiple preferences, it is necessary not just to test whether females have preferences for each male trait, but also to examine the relative importance of each trait in female mate choice (Jennions and Petrie 1997). In many animals, for example, females have been shown to express preferences for multiple male traits, or trait components, when all other traits are experimentally held constant (e.g., Gerhardt 1991; Borgia 1995; Parri et al. 1997; Basolo and Trainor 2002). Although such experiments can reveal whether females have preferences based on a particular trait, females may select mates primarily based on a single trait when multiple traits vary. A relatively small number of studies have examined female preferences when multiple male traits are varied (e.g., Basolo 1998; Jang and Greenfield 1998; Ryan and Rand 2003; Olvido and Wagner 2004; Brooks et al. 2005).

We examined the relative importance of two male traits in female mate choice in the variable field cricket, *Gryllus lineaticeps*. Males of this species sing from the ground near the entrances of holes or cracks in the soil, and they produce a calling song consisting of a series of short, repeated chirps to attract females. Male calling songs vary in chirp rate and chirp duration, and in two-speaker choice tests, where females are presented with songs that vary only in chirp rate or chirp duration, females prefer higher chirp rates to lower chirp rates and longer chirp durations to shorter chirp durations (Wagner 1996; Wagner and Resier 2000). Females have the potential to directly benefit from both of these mating preferences; they receive fecundity and fertility benefits from males that produce higher chirp rates, and they receive life-span benefits from males that produce longer chirp durations (Wagner and Harper 2003). These benefits appear to result from products transferred in male seminal fluid (Wagner et al. 2001a; Wagner and Harper 2003). The primary objective of this study was to test whether females more strongly prefer the song character indicative of the reproductive benefits (chirp rate), the song character indicative of the life-span benefit (chirp duration), or express strong preferences based on both traits. To do so, we presented females with 25 songs with different combinations of chirp rate and chirp duration and used multiple regression methods to estimate the linear, quadratic (stabilizing or disruptive), and cor-

Table 1. Chirp rate and chirp duration values used to construct the 25 test stimuli. These values ranged from approximately 2 SD above to 2 SD below the population mean.

Value	Chirp rate (chirps/s)	Chirp duration (ms)
+2 SD	4.2	150
+1 SD	3.6	135
mean	3.0	120
-1 SD	2.4	105
-2 SD	1.8	90

relational components of female preferences for these two song characters (Lande and Arnold 1983; Blows and Brooks 2003; Brooks et al. 2005).

Materials and Methods

The females used were from a laboratory population of *G. lineaticeps* maintained at the University of Nebraska-Lincoln. To establish this laboratory population, we collected adult females from Tucker's Grove Park, Santa Barbara, California. Most adult females that are captured in the field have mated at least once prior to capture, and thus lay fertile eggs when brought into the laboratory. The females used in the preference tests were either from the first laboratory generation (hatched from eggs laid in the laboratory by a wild-caught mother) or from the second laboratory generation (hatched from eggs laid in the laboratory by a first laboratory generation female mated to a first laboratory generation male). When we arranged matings to produce the second laboratory generation, we only paired males and females from different families (offspring of different field-caught mothers). Nymphs were raised in family containers until the penultimate instar, at which time they were transferred to individual containers and placed in a room acoustically isolated from singing males. Females were thus known to be virgins at the time of testing, and they had no exposure to male song as adults. The individual containers were checked daily, and the day on which each female reached sexual maturation was recorded. Females were tested seven to 12 days following sexual maturation. All females were provided with ad libitum water and cat chow as both nymphs and adults, and all family and individual containers had a paper towel substrate and cardboard shelters.

We examined female chirp rate and chirp duration preferences in a manner similar to that described by Olvido and Wagner (2004) for the ground cricket, *Alloxemobius socius*. Five chirp rates and five chirp durations were chosen that ranged from approximately 2 SD below the population mean to 2 SD above the population mean (Wagner and Reiser 2000; Wagner, unpublished; Table 1). Twenty-five calling song stimuli were then constructed using all possible combinations of these five chirp rates and five chirp durations. To con-

struct each song type, a single pulse was selected from a natural chirp (pulse duration = 11 ms, dominant frequency = 5.17 kHz). This pulse was then copied to produce five chirps that contained between six and 10 pulses, and thus chirps that varied in duration (inter-pulse interval was held constant at 4 ms). Five song loops that varied in chirp rate were then constructed for each of the five chirp durations by varying the duration of the interchirp interval.

Female responses to the test songs were measured in a $2.2 \times 2.2 \times 2.7$ m chamber that had foam-lined walls to reduce echoes. A KLH 970 speaker was placed at the center of a cardboard circle with an arbitrary radius of 0.26 m (the area of the circle was 4.4% of the area of the arena). The circle was placed in one corner of the arena and positioned such that edges were 5 cm from the wall. As a result, a female wandering along the wall of the arena would never enter a circle. At the beginning of a test, a female was placed under a cup at the center of the arena for a 10-min acclimation period. In the final minute of the acclimation period, a song was broadcast through the speaker from a Macintosh Quadra 840AV computer and Optimus SA-155 amplifiers. The songs were broadcast at amplitudes of 70 dB SPL (re: 20 μ Pa) at a distance of 30.5 cm from the speakers, and the broadcast amplitudes were calibrated using a Brüel and Kjær 2236 sound level meter (fast RMS) prior to the start of each trial. After the acclimation period, the cup was lifted and the female was observed for 10 min using a Panasonic WV-BP100 video camera mounted in the ceiling of the chamber and a Panasonic CT-1384Y monitor outside of the chamber. The time that the female spent in the circle around the speaker was recorded using a stopwatch.

Each trial consisted of two consecutive tests. A female was first tested with an average song type (average chirp rate and average chirp duration). The female was then immediately placed back under the cup at the center of the arena. Following another 10 min acclimation period, the female was then tested with one of the 25 test songs for 10 min (test songs were randomly assigned to females). The initial test with the average song type was conducted for two reasons. First, in single stimulus presentations, females may respond strongly to even unattractive song types if they have never been exposed to male song as adults, whereas they may show strong preferences if exposed to a standard song type prior to testing (Wagner, unpubl. data). Presenting all females with the same average song in the first test ensured we would have the opportunity to detect differential responses to the test songs and that all females had exactly the same adult experience with song (experience with different song types is known to affect female responses in this species; Wagner et al. 2001b). Second, the initial test provided a measure of female responsiveness to song that could be used to control for differences in female responsiveness in the preference test. This was important because two females that have identical pref-

erences (i.e., that show the same degree of discrimination between two song types) might differ in their response to a given song type because they differ in their responsiveness to broadcast song (see Reinhold et al. 2002; Syriatowicz and Brooks 2004).

Each female was only used in one trial, and four females were tested with each of the 25 stimuli (total females and trials = 100). Because each female was tested only once, this study examined population-level mating preferences, not individual mating preferences (Wagner 1998). Immediately following a trial the temperature in the test arena was recorded (range = 20.5 to 25.0 °C) and the female was weighed to the nearest 0.0001 g (range = 0.28 to 1.03 g).

Data were analyzed using multiple regressions to derive estimates for the magnitude of linear, quadratic, and correlational preference gradients (Blows and Brooks 2003; Brooks et al. 2005; Bentsen et al. 2006). In these analyses, female response in the preference test was the dependent variable and chirp rate and chirp duration were the independent variables. Because female response in a preference test was correlated with female response in the initial test (see Results), we statistically controlled for variation in female responsiveness prior to subsequent analysis based on the regression of response in the preference test on response in the initial test using the following formula: adjusted response = observed response + slope (mean responsiveness – observed responsiveness), where slope = 0.382 and mean responsiveness = 186.19 sec. To produce estimates for the linear (β), quadratic (γ), and correlational components of female preferences that are compatible with evolutionary models of selection, we divided female responses in the preference tests by the mean response of all females (resulting in a mean of one for these relative female responses), and standardized the independent variables (Lande and Arnold 1983). Linear preference gradients were estimated by regressing female response on chirp rate and chirp duration. Quadratic and correlational preference gradients were estimated by regressing female response on chirp rate, the square of chirp rate, chirp duration, the square of chirp duration, and the cross product of chirp rate and chirp duration.

Because female responses were not normally distributed, bootstrap analyses were used to test the statistical significance of the estimated preference gradients. For each preference gradient, 100 samples were drawn from the dataset with replacement, and a preference gradient was calculated using the appropriate multiple regression model. This procedure was then repeated for a total of 10,000 replications. We then calculated 95% and 99% confidence intervals using the percentile method. If a confidence interval for a given preference gradient estimate did not overlap zero, the estimate was judged significant at $P < 0.05$ or $P < 0.01$. Other methods of calculating the bootstrap confidence intervals (normal, bias corrected, bias corrected, and accelerated) resulted in identical statistical inferences.

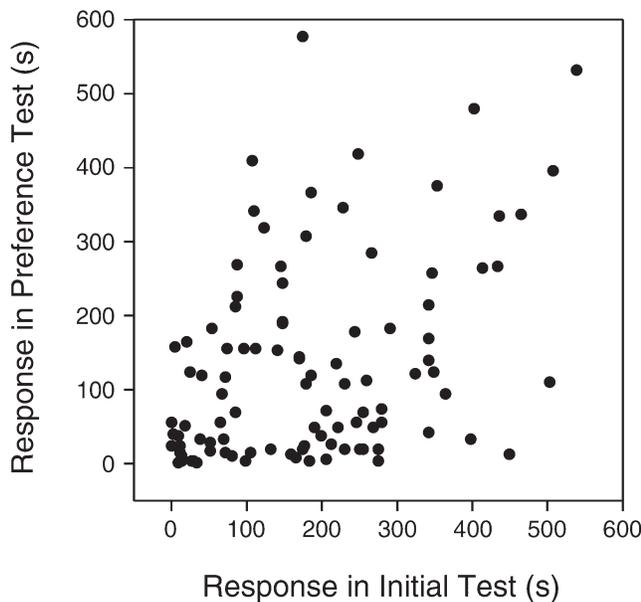


Figure 1. Correlation of female response in the preferences test and response in the initial test with the average song type.

Results

Female response to the initial average song type was positively correlated with response in the preference test ($r_{98} = 0.39$, $P < 0.001$; Figure 1). As a result, some of the variation in female response to a given test song resulted from some females being more responsive, regardless of the nature of the song. Because variation among females in responsiveness can confound preference measures using single stimulus presentations, the relationship between female response in the initial test and response in the preference test was used to statistically control for variation in female responsiveness prior to subsequent statistical analysis (see Methods). There was no association of female mass ($r_{98} = 0.00$, $P = 0.992$), age ($r_{98} = 0.11$, $P = 0.274$) or testing temperature ($r_{98} = -0.07$, $P = 0.498$) with response in the preference test.

Standardized linear, quadratic, and correlational preference gradients are presented in Table 2. Females expressed significant directional preferences for higher chirp rates. In addition, females expressed significant nonlinear preferences based on chirp rate. This nonlinear

Table 2. Standardized linear selection gradients (β) and the matrix of standardized quadratic and correlational selection gradients (γ).

Song character	β	γ	
		Chirp rate	Chirp duration
Chirp rate	0.225**	-1.745*	0.169
Chirp duration	-0.026		-0.515

Bootstrap confidence intervals: * $P < 0.05$; ** $P < 0.01$.

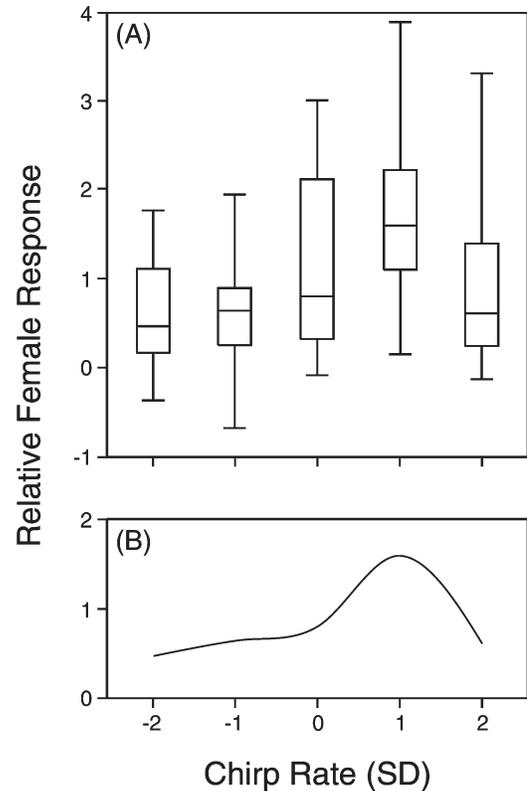


Figure 2. (A) Box plot showing variation in relative female response with variation in chirp rate, controlling for variation in female responsiveness. Lines within boxes indicate median female responses. The upper and lower edges of the boxes indicate 75th and 25th percentiles, respectively. The upper and lower whiskers indicate the maximum and minimum responses, respectively. Negative values represent females that were highly responsive in the initial test but showed little response in the preference test. Chirp rates are presented in standard deviation (SD) units. (B) The shape of the female chirp rate preference. The curve represents a cubic spline fit to the median response for each chirp rate.

chirp rate preference was stabilizing, centered approximately one standard deviation above the mean population chirp rate (Figure 2). Females did not express significant directional or nonlinear preferences based on chirp duration, and there was no evidence of correlational preferences.

Discussion

There has been substantial discussion about whether females should express strong preferences based on multiple male traits when these traits are correlated with different mating benefits (Møller and Pomiankowski 1993; Schluter and Price 1993; Iwasa and Pomiankowski 1994; Johnstone 1996). Addressing this question has been difficult because relatively few studies have shown that females receive multiple types of benefits from males, and that different male signals are correlated with different benefits. The results presented here sug-

gest that although male chirp rate and chirp duration in *G. lineaticeps* are correlated with different mating benefits (Wagner and Harper 2003)—chirp rate with fecundity and fertility benefits, and chirp duration with a life-span benefit—chirp rate has a substantially larger effect on a female's mating response than does chirp duration. Females of this population thus appear to give priority to the song trait correlated with the reproductive benefits. It should be noted here that females in the previous study benefited from mating with males with higher chirp rates primarily when they were nutritionally stressed, whereas the females tested in this study were not nutritionally stressed. It is not yet known whether nutritional condition affects female preferences in this species. Nutritional condition affects female preferences in some animals (e.g., Bakker et al. 1999; Hingle et al. 2001; Hunt et al. 2005), but does not affect female preferences in others (e.g., Syriatowicz and Brooks 2004).

Assessment costs are expected to favor female choice based on the one trait correlated with the greatest fitness benefit (Schluter and Price 1993; Iwasa and Pomiankowski 1994). For female field crickets, it seems likely that current reproductive benefits will have a greater effect on female fitness than life-span benefits. Field crickets rarely live more than three weeks as adults under natural conditions (Simmons and Zuk 1994; Murray and Cade 1995), but can have adult life spans in the laboratory of many months (Wagner et al. 2001a; Wagner and Harper 2003). Because they rarely realize their maximum life spans under natural conditions, selection may favor females that give priority to reproductive benefits, which can be realized quickly, over life-span benefits, which may only occasionally be realized. Whether assessment costs have favored selective attention to male chirp rate is not known. Even in the absence of assessment costs, selection may favor females that attend primarily to a single male trait if the male traits that are correlated with different mating benefits are negatively correlated with each other. In *G. lineaticeps*, for example, there is a negative phenotypic correlation between male chirp rate and chirp duration (Wagner and Harper 2003). Because females may often have to trade one benefit off against the other, selection may favor females that select mates primarily based on the trait correlated with the most important mating benefit.

Given that the reproductive benefits females receive from males increase with male chirp rate (Wagner and Harper 2003), it seems puzzling that females would have a stabilizing component to their preferences. There may, however, be costs of being in association with males that produce the highest chirp rates. In the population studied, males were attacked in the recent past by the phonotactic parasitoid fly, *Ormia ochracea* (Wagner 1996), although the flies have not been observed at this site for over five years (Wagner, unpubl. data). These flies use male calling song to locate their field crickets hosts (Cade 1975; Walker 1986), and when attacking *G. lineaticeps*, they preferentially orient to the calling songs with

the highest chirp rates (Wagner 1996). It is possible that female chirp rate preferences reflect a historical balance between the benefits of mating with males with higher chirp rates and the predation costs of being in association with these males. Another reason females might discriminate against very high chirp rates is to avoid heterospecific matings; if sympatric congeners produce high chirp rates, females might minimize heterospecific matings by avoiding males with high chirp rates. The only sympatric congener for the population we studied is *G. assimilis* (Wagner, unpubl. data). Because *G. assimilis* tends to produce much lower chirp rates than *G. lineaticeps* (Weissman et al. 1980), an avoidance of heterospecific matings might at least partially explain why female *G. lineaticeps* discriminate against very low chirp rates, but cannot explain why they also discriminate against very high chirp rates. It is possible, however, that *G. lineaticeps* interacted in the past with a high chirp rate species, and that this past interaction has influenced the current form of female preferences. Finally, the males used to examine the direct benefits of female mating preferences by Wagner and Harper (2003) had maximum chirp rates that were lower than the highest chirp rate used in this study (3.8 vs. 4.2 chirps/sec). It is possible that males with chirp rates that are greater than 3.8 chirps/s provide lower quality benefits to females than do males with chirp rates that are near 3.8 chirp/sec, and that this is why females discriminate against very high chirp rates. There was no evidence for diminishing benefits at very high chirp rates in the previous study, but we cannot entirely reject this possibility.

A relatively small number of studies have examined multivariate female preferences (e.g., Basolo 1998; Jang and Greenfield 1998; Ryan and Rand 2003; Olvido and Wagner 2004). In one of these studies, using the Australian field cricket *Teleogryllus commodus*, Brooks et al. (2005) manipulated five song characters and found evidence for directional and stabilizing components to female preferences based on intercall duration (a trait that is roughly proportional to the inverse of call rate), evidence for correlational preferences between intercall duration and trill number, and evidence for multivariate stabilizing preferences. As in *T. commodus*, we found both directional and stabilizing components to female preferences based on call rate in *G. lineaticeps*, but no evidence of correlational preferences based on call rate and duration. It should be noted, however, that we only manipulated two properties of male song; manipulations of more song characters might reveal the presence of correlational preferences. Little is known about correlational mating preferences, but testing for such preferences is essential for understanding both the nature of female preferences and how they affect the evolution of male traits.

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