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QUANTITATIVE GENETICS OF SEXUAL SELECTION IN THE FIELD CRICKET, *GRYLLUS INTEGER*

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Abstract.—Major theories of sexual selection predict heritable variation in female preferences and male traits and a positive genetic correlation between preference and trait. Here we show that female Texas field crickets, *Gryllus integer*, have heritable genetic variation for the male calling song stimulus level that produces the greatest phonotactic response. Approximately 34% of the variation in female preferences was due to additive genetic effects. Female choosiness, that is, the strength of the female response to her most preferred stimulus relative to her average response to all stimuli, did not show significant genetic effects. The male calling song character was not related to male size or age but did show significant genetic effects. Approximately 39% of the variation in the number of pulses per trill was due to additive genetic variation. The genetic correlation estimated for the field population was 0.51 ± 0.17. The number of pulses per trill produced by males is under stabilizing sexual selection.

Key words.—Crickets, genetic correlation, *Gryllus*, heritability, sexual selection.

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Although once controversial, today it is an empirical certainty that females of many species exhibit mating preferences for particular types of male traits (Andersson 1994). Accordingly, research attention has focused more closely on mechanisms of mate choice (Real 1990; Dombrovsky and Perrin 1994) and the benefits, if any, of female preferences (Andersson 1994). Theoretical models of mate choice, and its consequences, abound (reviewed in Andersson 1994; see also Kirkpatrick 1996; Johnstone 1997; Holland and Rice 1998). Almost all models of the evolution of mate choice and associated male traits require heritable variation in both the female preference and the male trait. Preexisting female-bias models (Basolo 1990; Ryan and Keddy-Hector 1992; Ryan and Rand 1993)neither require nor preclude variation, genetic or otherwise, in female preferences. Both good-genes and Fisherian models of mate choice predict a positive genetic correlation between the female preference and the male trait (Pomiankowski 1988). The genetic correlation may arise through assortative mating or pleiotropy (Boake 1991). Bakker and Pomiankowski (1995) recently reviewed both evidence suggesting a genetic basis to female mate choice and evidence for a genetic correlation between female preferences and male traits. Despite several examples of species- and/or population-level genetic differences and of both discrete and additive genetic effects within populations, there are to date only four quantitative genetic estimates of preference heritability—and two of these are of male preferences for females (Bakker and Pomiankowski 1995). Similarly, several studies have examined the genetic correlation between female preferences and male traits, yet only one significant quantitative estimate of the genetic correlation exists (in the three-spined stickleback, *Gasterosteus aculeatus*, $r_A = 0.75 \pm 0.31$; Bakker 1993).

No studies have examined the heritability of female choosiness, that is, the degree of discrimination shown by females in the expression of their preference. Choosiness and preference are conceptually distinct aspects of female choice, that is, female choice is the expressed outcome of female preference (for discussion see Wagner 1998). For example, two females may have the same preference (male trait value that elicits the greatest response), but differ in their degree of discrimination against less preferred males (choosiness). Adaptive mate search models predict that the expression of preferences in females is dependent on nongenetic factors such as predation risk, female age, quality, or other factors associated with motivation to mate (Real 1990; Dombrovsky and Perrin 1994; Johnstone 1997). Some empirical evidence supports facultative rather than fixed female choosiness (Forsgren 1992; Hedrick and Dill 1993).

In the species studied here, *Gryllus integer*, males call with a trilled song (Fig. 1). Each trill is composed of a number of pulses; each pulse is produced by a single wing closure. Previous work has documented phenotypic variation in the number of pulses per trill (PPT; Souroukis et al. 1992) and in female preferences for PPT (Wagner et al. 1995). Here we demonstrate that female *G. integer* show heritable variation in female preference for male calling song. Specifically, females show genetic variation in the number of PPT that elicit the greatest directed phonotactic response. We also show that the magnitude of the female response to her most preferred stimulus, relative to her average response to all stimuli (her choosiness) is not heritable. We additionally show that male song, specifically the number of PPT, has a genetic basis. Finally we examine the genetic correlation between the female preference for PPT and male PPT.

METHODS

Female crickets were collected in late September and early October 1997 from three sites within Austin, Texas, USA (a golfcourse, the University of Texas at Austin main campus, and the University of Texas–Austin Brackenridge Field Laboratory). Because this species has very strong flight capability, we consider this to be one population. Crickets were collected where they had flown to lights (approximately 70% of females) or a broadcast tape-playback of male calling song

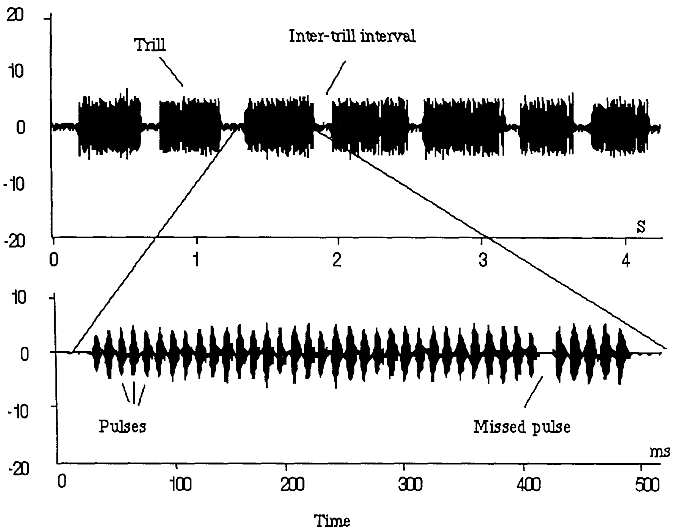

FIG. 1. Calling song of male Texas *Gryllus integer*. The top panel shows a series of trills as amplitude versus time in seconds. The bottom panel shows an expanded trill (millisecond scale), revealing the individual pulses that comprise a trill. The amplitude scale units are arbitrary.

(approximately 30%). Most female crickets collected in this manner are inseminated (Cade 1979a). Crickets were brought to Brock University (Ontario, Canada), where all experiments were conducted.

The offspring of the wild-caught females were reared under standardized conditions (controlled temperature and photoperiod: 28 ± 1°C, 13:11 L:D reversed photoperiod; uncontrolled relative humidity). Offspring were reared at low densities: family groups of five or fewer were reared in 500-mL containers, family groups of six to 15 were reared in approximately 2.5-L plastic containers (21.5 × 14 × 10 cm). All containers were provided with cat food, water in cotton-plugged vials, and cardboard for shelter. Rearing containers were checked weekly for food, water, and last-instar juveniles. Containers with last-instar crickets were checked daily. Newly molted adults were removed, weighed to the nearest 1 mg (Ohaus TS120 electronic balance), and placed in 500-mL individually marked containers with food, water, and cardboard shelter.

We adopted a multigeneration approach that allows repeated estimation of genetic parameters. We first tested the offspring of the wild-caught females. Because female field crickets commonly remate (Sakaluk and Cade 1983; Solymar and Cade 1990a) and last male sperm precedence is incomplete ($P_2 \simeq 72\%$ in this species; Backus and Cade 1986), family groups of these crickets were siblings, but they may not have been full siblings. Genetic parameters were, nonetheless, estimated using a full-sibling model. A subset of these individuals were then mated and their offspring were tested. Individuals were paired for mating using a random number generator; if the randomly selected pairing would have resulted in a sibling-pair or the duplication of a cross-family pairing, then we rerandomized and selected a new pairing. Not all pairs were randomly assigned at the same time. As additional crickets of the parental generation were tested, they were added to the pool of potential mates. Thus, the pairings were random with respect to the female preference and the male song characters, but not all possible pairings were considered. The offspring of these pairs formed full-sibling groups, but also allowed for genetic estimation via parent-offspring regression. We obtained three estimates of the heritability of female preference and choosiness, three estimates of the heritability of male song, and two estimates of the genetic correlation.

In the F_1 generation (offspring of wild-caught females), we divided families with at least four offspring into two rearing environments. One group was reared at a lower temperature (20 ± 2°C) for 30 days. This accomplished two things: (1) it effectively slowed down development, making it logistically possible to test more individuals; and (2) allowed for estimation of common environmental effects through Nested ANOVA (environment nested within families). Not all families were of sufficient size, thus not all families were split into two environments. Because these crickets were later paired to obtain the F_2 and parent-offspring estimates, with some pairings made across rearing environments, this method had the potential to introduce some environmental effects in subsequent estimates. However, environmental effects were nonsignificant (see Results).

Female Preference/Choosiness Trials

Female phonotaxis to synthetic male calling song was tested with virgin females age five to 17 days (virgin females more than 20 days old of this and other cricket species show reduced phonotactic selectivity; Prosser et al. 1997; D. A. Gray, unpubl.). Female phonotaxis was tested using a Kugel, as described in detail previously (see especially fig. 1 of Wagner et al. 1995), based on the design of Doherty and Pires (1987). Briefly, the Kugel consists of a lightweight (34.4-g) plastic sphere (51-cm circumference) that floats on a column of air. Melted beeswax was used to attach a female cricket dorsally to a small piece of balsa wood (approximately 4 × 8 × 1.75 mm) that had a 38-mm long, 0.44-mm diameter, insect mounting pin protruding from the upper surface. The mass of the pin and balsa mounting was 0.145 g when the wood was saturated with beeswax. The pin was pushed through a vertical sleeve of a metal arm that then held the cricket in place on top of the sphere. Crickets could walk normally on the sphere and rotate 360°; movement by the cricket caused the sphere to move. Sphere movement was monitored by two rollers connected to a personal computer that measured the speed and direction of cricket movement relative to an active speaker once per second. The sphere was housed within a large circular semi-anechoic test chamber (47-cm height, 102-cm diameter) lined on all interior surfaces with 2.5–5.5-cm thick corrugated foam padding. Four speakers (linear, B-4-5 JO) were placed 35.4 cm from the cricket tether point. Movement scores were converted to net vector phonotaxis scores as the cosine of the angle of movement (relative to the active speaker, designated as 0°) multiplied by the speed of movement, summed for each second of the trial. The net vector scores thus measure directed female phonotaxis toward male calling song. Because phonotaxis in crickets is physiologically, developmentally, and functionally related to mating (Stout et al. 1976; Cade 1979b; Loher 1981;

Sakaluk 1982; French and Cade 1987; Hedrick 1988; Solymar and Cade 1990b), preferences expressed during phonotaxis are considered mating preferences, although they are not necessarily the only mechanism of female choice.

Females were tested with artificially created song-stimulus sets. We tested females during the crickets' nighttime hours with stimulus sets ranging from 15 to 75 PPT, in intervals of 10 PPT. Pulse repetition rates were matched to the temperature within the Kugel. Appropriate pulse rates were determined from previous work (Smith and Cade 1987; Souroukis et al. 1992). The temperature and corresponding pulse rates were (°C: pulses/sec): 25:81, 24:78, 23:75, 22:72. From 17°C to 23°C, there is no dependence of the number of PPT on temperature (Souroukis et al. 1992), suggesting temperature effects from 22°C to 25°C are minimal if present. Within a stimulus set, intertrill intervals varied from 85 msec to 265 msec (mean ± SD 172.4 ± 52.4 msec). This variation was introduced to reduce habituation. The pattern and duration of intertrill intervals were identical for all stimuli sets and for all females. Intertrill intervals are highly variable within individual male calling song (D. A. Gray and W. H. Cade, unpubl. data; see also Webb and Roff 1992), and in this species in the laboratory show no dependence on temperature from 18°C to 23°C (Souroukis et al. 1992). Each calling song was broadcast for 120 sec with 15-sec silences between sequential songs. These times allow for sufficient female response to a stimulus and a diminishing of response to the previously played stimulus (Wagner et al. 1995; W. E. Wagner Jr., pers. comm., D. A. Gray, pers. obs.). Songs were broadcast at 84 dB SPL (re: 20 μPa) at the female tether point. All song parameters used were within the natural range of variation (Souroukis et al. 1992). We randomized the order songs were played and which speaker played which song; these were rerandomized for each female. Most unresponsive females were retested a minimum of 2 hours later, usually the next day. Most retested females later showed phonotaxis and so were included. Females that were repeatedly unresponsive (minimum of four attempts, $n = 36$ females total) were excluded. For each female, each song was played twice, 35 PPT was played three times. The average score for each stimulus was used in analyses. Figure 2 shows the relationship between female response and male song for a single female and illustrates the definitions of female preference and female choosiness used here.

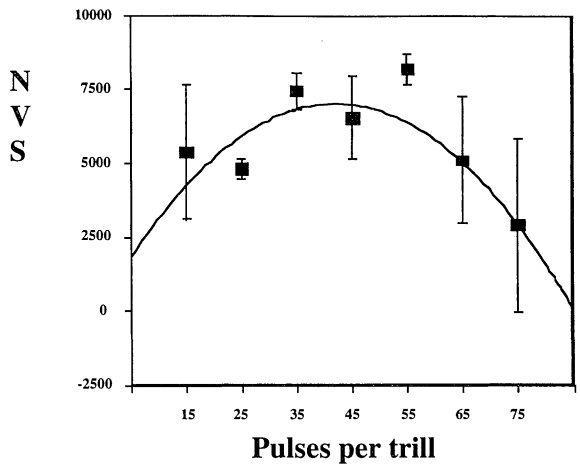

FIG. 2. Exemplar female response graph. Shown are the mean ± SD responses of a single female as a function of the number of pulses per trill. Female response was measured as a net vector score (NVS) of directed phonotaxis toward male calling song. Female preference was defined as the male trait value (number of pulses per trill) that elicited the highest average female response (for this female, preference = 55). Female choosiness was defined as the number of NVS standard deviations the female's response to her most preferred stimulus was from her average response to all stimuli.

Male Song Recording and Analysis

Males were recorded on TDK SA90 IEC Type II tapes in a portable recorder (Sony WM-D3 Professional Walkman) via a foam covered parabolic reflector (14-cm diameter) fitted with an Archer electret microphone (No. 270090 PC). The parabolic reflector was placed directly over a calling male's container. The males were recorded at 28 ± 1°C.

Due to logistical constraints, males were not acoustically isolated. The lack of isolation caused some males to produce abnormal calling song with extreme numbers of PPT (e.g., one male produced a single trill with > 3000 pulses). Males with greater than 110 PPT were excluded from the analysis ($n = 27$ in the F_1 sibling generation; in the F_2 generation, abnormal songs were not recorded and/or not computer analyzed; 20 of the 27 F_1 males served as fathers for the F_2 parent-offspring comparison, thus the sample size for the parent-offspring regression was reduced from 80 full-sib families to 60 parent-offspring comparisons). The cut-off point of 110 PPT corresponds to the highest number of PPT previously reported for this species (Souroukis et al. 1992). Exclusion of these males was a priori given their abnormal song (in ca. 20 years of field research with this species, such males have never been heard in the field; W. H. Cade, pers. obs.), but we note that inclusion of these males would cause heritability estimates of male song to be nonsignificant.

Recorded calling song was analyzed using Canary 1.2 (Cornell Laboratory of Ornithology, Ithaca, NY, licensed to W. H. Cade) on a Macintosh Performa 5260/120 PowerPC with 22-kHz sample rate and 8-bit resolution (calling song has a carrier frequency of approximately 5 kHz, thus, with 22-kHz sampling, aliasing is not a concern). Background noise was filtered out if necessary using the filtering capabilities of the software. Twenty-five trills were analyzed for each male. For each male we determined an average pulse rate based on five 10-pulse sections of song. In some males the pulse rate slows down near the end of a trill, thus we sampled pulse rates from the beginning, middle, and end of different trills. We then measured the length of each trill to the nearest 0.1 msec. From the pulse rate information and the duration of each trill, we then estimated the number of PPT. Males occasionally miss pulses within a trill (see Fig. 1); our estimated number of PPT includes missed pulses. To assess the accuracy of this method, we counted the number of pulses for 10 trills for each of 10 males and then regressed the actual number of PPT on the estimated number of PPT. For this method to be accurate, the regression should have an intercept of zero, a slope of one, and a high r^2 value. For each male, the regression was highly significant ($P < 0.0001$

TABLE 1. Heritability estimates (%; ± SE) and genetic correlations by generation.

Trait	F_1 siblings	F_2 full-siblings	Parent-offspring
Female preference	32 ± 15	47 ± 21	34 ± 17
Female choosiness	0	0	−2 ± 14
Male song	37 ± 13	40 ± 14	39 ± 19
Genetic correlation	0.51 ± 0.17[1]	−0.20 ± 0.42[2]	

[1] Estimate applies to field population.

[2] After one generation of random mating.

for all males). The mean ± SD intercept (n = 10 males) was 0.057 ± 0.812, not significantly different from zero (t = 0.223, P = 0.8287); the mean ± SD slope was 0.996 ± 0.029, not significantly different from one (t = 0.400, P = 0.6984); the mean ± SD r^2 was 0.992 ± 0.014. Thus we are confident that this method accurately estimated the true number of PPT.

Data Analysis

Analyses were conducted using SAS software (SAS Institute 1989). For sibling analyses, we used ANOVA to test for significant family effects. For the offspring of wild-caught females, rearing environment was nested within family. Type III sums of squares were used (PROC GLM). Variance components were estimated using restricted maximum-likelihood estimation (PROC VARCOMP). We calculated standard errors of the sibling heritability estimates according to Becker (1992). We considered estimates significant if they were two or more SE from zero. Simons and Roff (1994) demonstrate that the SE estimated from ANOVA produces a lower 95% confidence interval that is too low, thus this is a conservative approach. Parent-offspring hertitabilities were assessed using weighted regression following Falconer (1989). Standard errors of parent-offspring heritabilities were calculated from the SE of the slope. Genetic correlations were estimated using ANOVA (Fry 1992). As recommended by Fry (1992), we estimated the among-family variances for the separate traits from separate one-way ANOVAs, thus avoiding the assumption of equal among-family variances for males and females. Standard errors were calculated following the approximation given by Falconer (1989) using the heritabilities and their associated SEs obtained from the parent-offspring regression.

Means are reported with SDs, whereas genetic estimates are reported with SEs. Two-tailed statistical tests are reported throughout, with the exception made in the case of the genetic correlation. All theoretical models of sexual selection predict a positive correlation, therefore a one-tailed test is more appropriate.

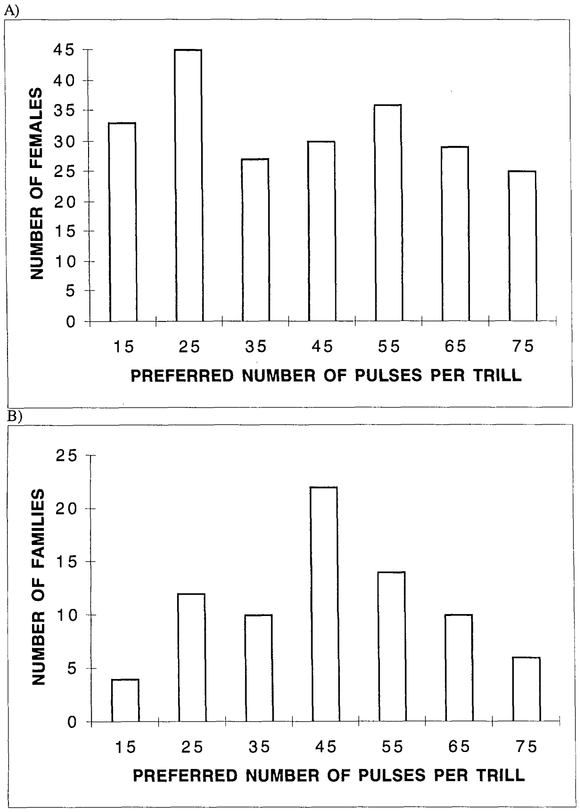

FIG. 3. Distribution of female preference. (A) The preferences of individual females. (B) Female preferences have been collapsed into family means. These family means provide the best estimate of the distribution of female preferences in the field.

RESULTS

A summary of the major results is presented in Table 1. Detailed results are presented by generation below.

F_1 Siblings

Female Preference.—A total of 225 females from 78 families were tested (corrected mean family size, k′ = 2.87; Becker 1992). Female preference averaged 43 ± 20 PPT. Figure 3 shows the distribution of female preferences for individual females as well as family averages. The distribution of family averages represents the best estimate of the distribution of preferences in the field. Preference was unrelated to female mass, female age, Kugel temperature, average net vector score (NVS), or female choosiness. Nested ANOVA showed a significant family effect, but no effect of common environment on preference (family: $F_{77,105}$ = 1.85, P = 0.0017; environment [family]: $F_{42,105}$ = 1.22, P = 0.2094). Heritability was estimated to be 32 ± 15%, which is 2.13 SE from zero.

Female Choosiness.—Choosiness averaged 1.47 ± 0.30 standard deviations and was unrelated to female mass and age, but was positively related to temperature (r = 0.197, P = 0.0030) and negatively related to average NVS (r = −0.174, P = 0.0089). Neither female choosiness nor residual choosiness after correcting for temperature and average NVS showed significant family or common environmental effects; (choosiness, family: $F_{77,105}$ = 0.81, P = 0.8389; environment

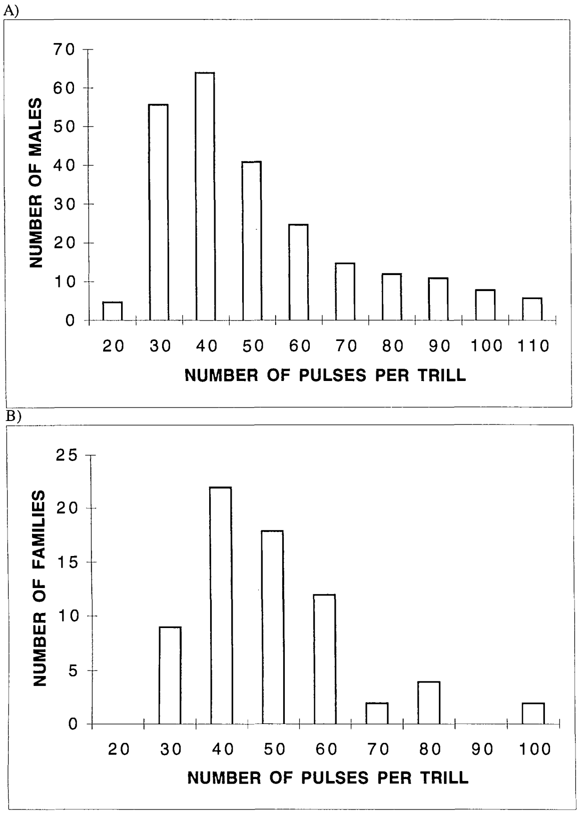

FIG. 4. Distribution of the number of pulses per trill (PPT) in male calling song. (A) PPT for individual males. (B) The distribution of calling song collapsed into family means.

[family]: $F_{42,105}$ = 1.03, P = 0.4431; residual choosiness, family: $F_{77,105}$ = 0.78, P = 0.8777; environment [family]: $F_{42,105}$ = 1.02, P = 0.4553). Given the absence of family effects, heritability estimates are not reported (variance component estimated to be zero).

Male Song.—Figure 4 shows the distribution of the number of PPT in male calling song. The analysis consisted of 243 males from 69 families (k′ = 3.5). Males averaged 46 ± 21 PPT. Neither male mass nor age was related to the number of PPT (r = 0.082 and 0.033 for mass and age, respectively). There was a significant family effect on the number of PPT, but no effect of common environment (family: $F_{68,129}$ = 1.73, P = 0.0039; environment [family]: $F_{45,129}$ = 0.88, P = 0.6794). Heritability was estimated to be 37 ± 13%, which is 2.85 SE from zero.

Genetic Correlation.—The genetic correlation between female preference for PPT and male PPT was significant ($F_{79,66}$ = 1.49, P = 0.0489) and positive (0.51 ± 0.17).

F_2 Full-Siblings

Female Preference.—A total of 162 females from 74 families were tested (k′ = 2.07). Females preference averaged 42 ± 19 PPT and was unrelated to female mass, age, Kugel temperature and average NVS, but was significantly related to female choosiness (r = −0.184, P = 0.0193). ANOVA showed a significant family effect on female preference (preference; $F_{73,88}$ = 1.73, P = 0.0070; residual preference correcting for choosiness; $F_{73,88}$ = 1.88, P = 0.0024). Preference heritability was estimated to be 47 ± 21%, which is 2.24 SE from zero; residual preference heritability was estimated to be 54 ± 20%, which is 2.64 SE from zero. Parent-offspring heritability of female preference was 34 ± 17% ($F_{1,72}$ = 3.859, P = 0.0533). Residual preference heritability by parent-offspring regression was 39 ± 17% ($F_{1,72}$ = 5.120, P = 0.0267).

Female Choosiness.—Choosiness averaged 1.41 ± 0.28 standard deviations and was unrelated to female mass and temperature, but negatively related to average NVS (r = −0.181, P = 0.0215) and female preference (r = −0.184, P = 0.0193) and marginally positively related to age (r = 0.153, P = 0.0519). Given the marginal significance of female age, we corrected for average NVS, female preference, and age in calculating residual choosiness. Neither female choosiness nor residual choosiness showed significant family effects (choosiness; $F_{73,88}$ = 1.02, P = 0.4543; residual choosiness; $F_{73,88}$ = 1.05, P = 0.4097). Given the absence of family effects, heritability estimates are not reported (estimated variance component equals zero). Parent-offspring heritability of female choosiness was −2 ± 14% ($F_{1,72}$ = 0.021, P = 0.8844). Residual choosiness heritability was 7 ± 14% ($F_{1,72}$ = 0.251, P = 0.6182).

Male Song.—The full-sibling analysis consisted of 226 males from 80 families (k′ = 3.28). Males averaged 39 ± 12 PPT. Neither male mass nor age was related to the number of PPT (r = −0.027 for both mass and age). There was a significant family effect on the number of PPT ($F_{79,146}$ = 1.71, P = 0.0026). Heritability was estimated to be 40 ± 14%, which is 2.86 SE from zero. Heritability of PPT by parent-offspring regression was 39 ± 19% ($F_{1,58}$ = 4.132, P = 0.0467).

Genetic Correlation.—The estimated genetic correlation between female preference for PPT and male PPT was negative (−0.20 ± 0.42) and not significant ($F_{84,68}$ = 0.88, P = 0.7106).

DISCUSSION

Studies of hybrid cricket behavior (Fulton 1933; Hoy 1971; Bentley and Hoy 1972; Hoy and Paul 1973; Hoy et al. 1977; Mousseau and Howard 1998) have shown that there is some genetic control of male song and female preferences in crickets. Intra-specific quantitative genetic studies have examined variation in cricket calling behavior and song structure (Cade 1981; Hedrick 1988; Webb and Roff 1992). The heritability of correlates of song structure, for example, forewing morphology (Webb and Roff 1992) and body size (Simmons 1987), have also been examined. However, this is the first study of crickets to document heritable variation in both male song structure and in female preference for variants of male song.

The genetic estimates obtained in this study address fundamental predictions of major theories of sexual selection. In accordance with prediction, both the female preference and the male trait show heritable genetic variation. No effects of common environment were detected for either the female preference or the male trait. Female choosiness was not influenced by genetic effects, but rather showed influences from other factors such as temperature, and age. Whether female choosiness varies in accordance with predictions from theoretical work on optimal mate searching (e.g., Real 1990; Dombrovsky and Perrin 1994; Johnstone 1997) is not addressed here, rather we simply note that choosiness varies in response to nongenetic factors and is not fixed. This supports the operation of facultative mate-search tactics and suggests that past selection on female mating behavior may have favored females with the ability to vary their level of discrimination against less preferred male phenotypes.

A positive genetic correlation between female preferences and male traits is predicted when both preference and trait are under genetic control and females effectively mate with their preferred males. This prediction is independent of whether female preferences are directional or stabilizing and whether they are initiated or maintained by good genes or arbitrary mate choice. The strength of the genetic correlation required to sustain runaway evolution depends on stabilizing natural selection acting on the female preference and the male trait (Kirkpatrick and Barton 1995). Our estimate of the genetic correlation between the female preference and the male trait in the field is 0.51 ± 0.17. The genetic correlation disappeared after only one generation of random mating. Genetic correlations among unlinked genes maintained by assortative mating are expected to be reduced by 50% per generation with random mating (Bakker and Pomiankowski 1995), thus it is not surprising that the estimated correlation was reduced.

We conclude that (1) female preference for the number of PPT in male song is stabilizing (see also Gray and Cade 1999); (2) female preference is heritable, but female choosiness is not; (3) the number of PPT in male song is heritable; and (4) a moderate genetic correlation exists between preference and trait alleles in the population studied here. These results strongly support assumptions of major theories of sexual selection. It appears, however, that neither Fisherian-runaway nor good-genes selection are currently operative in this system: The female preference is stabilizing and the male trait is unrelated to a priori measures of male quality, that is, male size and age.

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