THE ROYAL
SOCIETY

Sex, death and genetic variation: natural and sexual selection on cricket song

David A. Gray[*] **and William H. Cade**

Department of Biological Sciences, Brock University, St Catharines, Ontario, Canada L2S 3A1

Male field crickets, *Gryllus integer*, in Texas, USA, produce a trilled calling song that attracts female crickets, resulting in enhanced mating success. Gravid female parasitoid flies, *Ormia ochracea*, are also attracted to male cricket calling song, resulting in the death of the male within about seven days. Using playbacks of field-cricket calling song in the natural habitat, we show that both female crickets and female parasitoid flies prefer male calling song with average numbers of pulses per trill. Thus female crickets exert stabilizing sexual selection, whereas flies exert disruptive natural selection on male song. Disruptive natural selection will promote genetic variation and population divergence. Stabilizing sexual selection will reduce genetic variation and maintain population cohesiveness. These forces may balance and together maintain the observed high levels of genetic variation (*ca.* 40%) in male calling song.

Keywords: Fisher's fundamental theorem; genetic variation; female preference; parasitoid; phonotaxis

1. INTRODUCTION

According to Fisher's fundamental theorem, selection is expected to reduce genetic variation in fitness-related traits, a prediction largely borne out by empirical studies (Mousseau & Roff 1987). A number of mechanisms maintaining genetic variation in sexually selected traits have been proposed (Hamilton & Zuk 1982; Rowe & Houle 1996). Here we show that sexual selection and natural selection can act in opposition in such a way as to maintain genetic variation. Directional sexual and natural selection have long been viewed as acting in opposition in such a way as to stabilize the expression of sexual ornamentation (Lande 1981; Endler 1983; Andersson 1994). To our knowledge, neither the possibility nor the consequences of stabilizing sexual selection opposed by disruptive natural selection have been identified or discussed.

Using playbacks of male cricket song in the natural habitat, we investigated phonotaxis of female crickets, *Gryllus integer*, and of a phonotactic parasitoid fly, *Ormia ochracea*, to male song varying only in the number of pulses per trill (PPT). Male *G. integer* in Texas attract walking and flying females with a trilled calling song, ranging from 15 to 110 PPT (mean *ca.* 45 ± 20 (Souroukis *et al.* 1992; Gray & Cade 1999)). Calling song attracts female crickets for mating (Boake 1983; Walker & Masaki 1989), but it also attracts females of a parasitoid fly (Cade 1975). Attraction of female crickets enhances male mating success (Hedrick 1988; Cade & Cade 1992), whereas attraction of flies results in death within about seven days (Cade 1975). Recent laboratory work (Gray & Cade 1999) suggested that the female preference for PPT is stabilizing, with most females preferring 40–45 PPT.

2. METHODS

To test song preferences of female crickets and flies in the field, we used a repeated single pulse recorded from a male to construct three calling-song models, differing only in the number of PPT, namely 25, 45, and 65 PPT, or roughly the mean ± 1 s.d. Carrier frequency (5.0 kHz), inter-trill interval (175 ± 45 ms), and pulse rate (matched to temperature: 72 pulses per second at 22–23 °C; 78 pulses per second at 24–25 °C; and 84 pulses per second at 26 °C) were species-typical values and were identical for the three model songs. Three minutes of song were digitally transferred to CD-R disks.

We conducted phonotaxis trials from 13 to 22 September 1998 at the Brackenridge Field Laboratory in Austin, Texas. Speakers were placed 4 m apart at the corners of an equilateral triangle in a field with short grass and thatch. The speakers were within the natural range of nearest-neighbour distances and correspond to an aggregation of calling males (Cade 1981). Fly traps (Walker 1989) were placed over the speakers. Calling song was continuously broadcast from 20.00 (approximately sunset) to 00.00 Central Daylight Time each night. These are the peak times of fly (Cade *et al.* 1996) and cricket (Cade 1989) attraction. We played calling song at 95 dB (re: 20 μPa) peak pressure at 12.5 cm (Radio Shack 33-2055 meter). This sound level is at the upper limit of natural variation, *ca.* 2 s.d. above the mean (Cade 1979). Louder song attracts more crickets and flies (Cade 1979; Walker 1986, 1993). We played calling song from Sony D-181C Diskman CD players, via Radio Shack 32-2041 20 Watt amplifiers, broadcast through 2.54 cm dome tweeters (Radio Shack 40-1276B, 2–20 kHz). Speakers were placed facing skyward on bricks (19.5 cm × 19.5 cm × 4.5 cm) resting on 46.5 cm × 40 cm aluminium trays. On successive nights, we rotated the stimuli such that each song was broadcast from each position for three 4-h sessions. Due to rain, one stimulus–position replicate was conducted from 20.00 to 21.54 one night and from 22.37 to 00.43 a second night. Speaker positions were checked at least every 15 min; male and female crickets within 1 m of a speaker's centre were caught. Flies

---

[*] Author for correspondence (dgray@spartan.ac.brocku.ca).

Received 23 November 1998 *Accepted* 21 December 1998

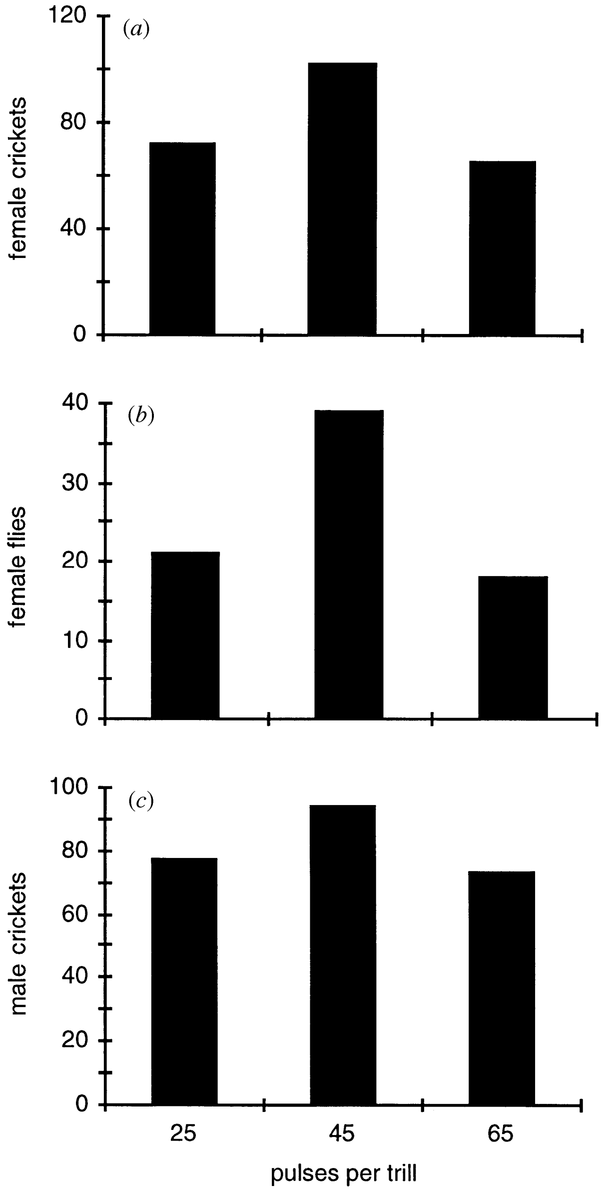

Figure 1. Attraction of female crickets (*a*), female parasitoid flies (*b*), and male crickets (*c*), to three calling-song models of 25, 45, and 65 pulses per trill. All song parameters were within the natural range of variation and were broadcast in the natural habitat. Both female crickets and female flies showed significant departures from random attraction.

in the traps were counted at the end of the playback session. Crickets and flies were not released except after the final night of the experiment; thus all data points are independent. We did not use silent control speakers and traps because traps without a sound source catch almost no crickets or flies (Cade 1975, 1989; Walker 1993).

3. RESULTS

We caught 239 female crickets and 78 female flies (figure 1*a*,*b*). Female crickets and flies both significantly differed from a null expectation of equal attraction (female crickets, $G_2 = 9.39$, $p = 0.0091$; flies, $G_2 = 9.42$, $p = 0.0090$). Both female crickets and flies preferred 45 PPT. This pattern was very robust, and was replicated across almost all nights of the study. Treating the nine nights as replicates, and assigning a rank of 1 to the most attractive, 0 to the second most attractive, and -1 to the least attractive (with 1/2 ranks for ties) such that for any one night the ranks summed to 0, we tested the average rank versus a null prediction of 0. For female crickets, 45 PPT had a mean ± s.e. rank of 0.78 ± 0.12; $T = 6.42$, $p = 0.0002$. For flies, the mean ± s.e. rank of 45 PPT was 0.72 ± 0.17; $T = 4.27$, $p = 0.0027$.

Male crickets also show phonotaxis to calling song. Some attracted males remain silent and attempt to intercept females attracted to another male's call. Silent males should maximize the number of females encountered by associating with calling males that females find most attractive (Waltz 1982). We caught 244 male crickets (figure 1*c*). Males did not differ from a distribution expected based on the empirical distribution of females ($G_2 = 1.83$, $p = 0.4012$), supporting this idea; however, they did not differ from random either ($G_2 = 2.30$, $p = 0.2234$). For males, 45 PPT had a mean ± s.e. rank of 0.39 ± 0.29; $T = 1.36$, $p = 0.2110$.

4. DISCUSSION

Studies of the same species of fly, but with different species of crickets, have shown that flies show song preferences (Walker 1993; Wagner 1996; Zuk *et al.* 1998). Female crickets and flies should exhibit song preferences if song is related to qualities of the male as a mate or host. We suggest that for *G. integer* male quality is unrelated to the number of PPT in male song. The number of PPT is not related to either male size or age, and has a substantial genetic component (Souroukis *et al.* 1992; Gray & Cade 1999). In the absence of song-associated benefits, we suggest that both female crickets and flies adaptively minimize search costs by preferring the most common male song. Although not well characterized, a variety of evidence suggests that female crickets suffer increased exposure to predation while searching for mates. This evidence includes a predominance of females in collections (Alexander 1957), direct observation of predation (Sakaluk & Belwood 1984) and changes in female selectivity with increased predation risk (Hedrick & Dill 1993). Search costs for female flies are currently unknown.

We conclude that males with average numbers of PPT are more attractive to female crickets and parasitoid flies. Female crickets exert stabilizing sexual selection, and female flies exert disruptive natural selection on male song. Disruptive natural selection promotes population divergence, but is counteracted by stabilizing sexual selection promoting population cohesion. Together, these forces diminish net selection on song and act to maintain genetic variation, currently estimated to be *ca.* 40% additive genetic variation (Gray & Cade 1999). Although not previously described, we suspect that opposing stabilizing sexual selection and disruptive natural selection may be more common than previously realized. Indeed, such a situation may be the rule in systems where both females and predators and/or parasitoids search for males in the same sensory modality, and the male signal is unrelated to male quality either as a mate or a prey item and/or host.

L. Gilbert and J. Crutchfield allowed access to the Brackenridge Field Laboratory of the University of Texas at Austin. D.A.G. is supported by a Brock University Postdoctoral Fellowship and W.H.C. by a Natural Science and Engineering Research Council of Canada operating grant.

REFERENCES

Alexander, R. D. 1957 The taxonomy of the field crickets of the eastern United States (Orthoptera: Gryllidae: *Acheta*). *Ann. Entomol. Soc. Am.* **50**, 584–602.

Andersson, M. 1994 *Sexual selection.* Princeton University Press.

Boake, C. R. B. 1983 Mating systems and signals in crickets. In *Orthopteran mating systems: sexual competition in a diverse group of insects* (ed. D. T. Gwynne & G. K. Morris), pp. 28–44. Boulder, CO: Westview Press.

Cade, W. H. 1975 Acoustically orienting parasitoids: fly phonotaxis to cricket song. *Science* **190**, 1312–1313.

Cade, W. H. 1979 The evolution of alternative male reproductive strategies in field crickets. In *Sexual selection and reproductive competition in insects* (ed. M. S. Blum & N. A. Blum), pp. 343–380. New York: Academic Press.

Cade, W. H. 1981 Field cricket spacing and the phonotaxis of crickets and parasitoid flies to clumped and isolated cricket songs. *Z. Tierpsychol.* **55**, 365–375.

Cade, W. H. 1989 Nightly and hourly rates of attraction of flying field crickets, *Gryllus integer*, to conspecific song. *Can. J. Zool.* **67**, 2540–2542.

Cade, W. H. & Cade, E. S. 1992 Male mating success, calling and searching behaviour at high and low densities in the field cricket, *Gryllus integer. Anim. Behav.* **43**, 49–56.

Cade, W. H., Ciceran, M. & Murray, A.-M. 1996 Temporal patterns of parasitoid fly (*Ormia ochracea*) attraction to field cricket song (*Gryllus integer*). *Can. J. Zool.* **74**, 393–395.

Endler, J. A. 1983 Natural and sexual selection on color patterns in poeciliid fishes. *Environ. Biol. Fish.* **9**, 173–190.

Gray, D. A. & Cade, W. H. 1999 Quantitative genetics of sexual selection in the field cricket, *Gryllus integer. Evolution.* (In the press.)

Hamilton, W. D. & Zuk, M. 1982 Heritable true fitness and bright birds: a role for parasites? *Science* **218**, 384–386.

Hedrick, A. V. 1988 Female choice and the heritability of attractive male traits: an empirical study. *Am. Nat.* **132**, 267–276.

Hedrick, A. V. & Dill, L. M. 1993 Mate choice by female crickets is influenced by predation risk. *Anim. Behav.* **46**, 193–196.

Lande, R. 1981 Models of speciation by sexual selection on polygenic traits. *Proc. Natl Acad. Sci. USA* **78**, 3721–3725.

Mousseau, T. A. & Roff, D. A. 1987 Natural selection and the heritability of fitness components. *Heredity* **59**, 181–197.

Rowe, L. & Houle, D. 1996 The lek paradox and the capture of genetic variance by condition dependent traits. *Proc. R. Soc. Lond.* B **263**, 1415–1421.

Sakaluk, S. K. & Belwood, J. J. 1984 Gecko phonotaxis to cricket calling song: a case of satellite predation. *Anim. Behav.* **32**, 659–662.

Souroukis, K., Cade, W. H. & Rowell, G. 1992 Factors that possibly influence variation in the calling song of field crickets: temperature, time, and male size, age, and wing morphology. *Can. J. Zool.* **70**, 950–955.

Wagner, W. E. Jr 1996 Convergent song preferences between female field crickets and acoustically orienting parasitoid flies. *Behav. Ecol.* **7**, 279–285.

Walker, T. J. 1986 Monitoring the flights of field crickets (*Gryllus* spp.) and a tachinid fly (*Euphasiopteryx ochracea*) in north Florida. *Fla. Entomol.* **69**, 678–685.

Walker, T. J. 1989 A live trap for monitoring *Euphasiopteryx* and tests with *E. ochracea* (Diptera: Tachinidae). *Florida Entomol.* **72**, 314–319.

Walker, T. J. 1993 Phonotaxis in female *Ormia ochracea* (Diptera: Tachinidae), a parasitoid of field crickets. *J. Insect Behav.* **6**, 389–410.

Walker, T. J. & Masaki, S. 1989 Natural history. In *Cricket behavior and neurobiology* (ed. F. Huber, T. E. Moore & W. Loher), pp. 1–42. Ithaca, NY: Cornell University Press.

Waltz, E. C. 1982 Alternative mating tactics and the law of diminishing returns: the satellite threshold model. *Behav. Ecol. Sociobiol.* **10**, 75–83.

Zuk, M., Rotenberry, J. T. & Simmons, L. W. 1998 Calling songs of field crickets (*Teleogryllus oceanicus*) with and without phonotactic parasitoid infection. *Evolution* **52**, 166–171.