

Effects of fly parasitoids on nightly calling duration in field crickets

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The song of male field crickets, *Gryllus integer* (Orthoptera: Gryllidae), attracts flies, *Euphasiopteryx ochracea* (Diptera: Tachinidae). Flies deposit larvae on male crickets and the larvae burrow in and consume the host. Effects of fly parasitism on duration of calling in *G. integer* were studied. Male crickets were collected at street lights and placed in jars and were electrically monitored for calling song. Calling duration was measured for 7 nights. Fly larvae were then placed on males and calling duration was measured for an additional 7 nights. In two replicates, males called significantly less following parasitism, and average calling duration declined gradually before death. Other males which remained free of fly larvae showed no reduction in calling. Field-collected males which subsequently died from fly parasitism called significantly less than non-parasitized males. Acoustically orienting flies reduce the ability of parasitized males to attract females acoustically.

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Le chant des grillons mâles *Gryllus integer* (Orthoptera: Gryllidae) attire la mouche *Euphasiopteryx ochracea* (Diptera: Tachinidae). Les mouches déposent leurs larves sur les mâles et celles-ci s'enfouissent dans l'hôte et en consomment la chair. Les effets du parasitisme sur la durée des chants de *G. integer* ont fait l'objet d'une étude. Des grillons mâles ont été recueillis près de lampadaires et placés dans des pots où leurs cris étaient enregistrés électriquement. La durée des cris a été mesurée durant 7 nuits. Ensuite, des larves de mouches ont été placées sur les grillons et la durée de leurs chants a de nouveau été mesurée durant 7 nuits. Dans deux des expériences, les mâles parasités émettaient significativement moins de cris et la durée moyenne des cris a diminué graduellement jusqu'à la mort. D'autres mâles qui sont restés sains n'ont pas subi cette diminution d'émission de cris. Des mâles récoltés en nature qui sont finalement morts du parasitisme émettaient significativement moins de cris que des mâles sains. Les mouches qui s'orientent au son pour effet de diminuer, chez les mâles qu'elles parasitent, la capacité d'attirer des femelles par des cris.

[Traduit par le journal]

Introduction

Male field cricket song attracts conspecific females and matings result (Alexander 1975; Otte 1977). In central Texas the song of the field cricket, *Gryllus integer*,¹ also attracts female flies, *Euphasiopteryx ochracea*, which deposit larvae onto males; these burrow inside and feed on their host for several days before emerging and pupating. Parasitized males always die shortly before or after fly emergence. Acoustically orienting flies have probably resulted in the evolution of silent or irregular calling behaviour by some male *G. integer* in field populations. Silent or irregularly calling males are usually not parasitized by flies and some (the so-called satellites) may intercept females attracted by calling males (Cade 1975, 1979a, 1980; Cade and Wyatt 1984). Parasitoids often debilitate their hosts before death (Vinson and Iwantsch 1980), and the present research was intended to determine if the amount of cricket calling is affected by fly parasitism before crickets die. Any reduction in male calling time following parasitism may affect male ability to attract female crickets.

Methods of study

Artificial infestation

In July 1978, in San Antonio, Texas, male *G. integer* were collected under electric street lights where flying crickets had landed (see Cade 1979b). Males were placed in individual 4.2-L glass jars, each of which contained a crystalline microphone attached to a sound-activated relay. The relay caused 24-h clock to operate when a male called and stopped operation within 4 s when a male stopped calling. Relays were sensitive to sounds between 4 and 6 kHz and a sound pressure level of 50 dB, a frequency and sound intensity characteristic of *G. integer* (Cade 1979a, unpublished). Jars were placed

close to the open windows of a private residence in San Antonio, and were therefore exposed to the normal photoperiod and temperatures for that time of year (approximately 24–37°C, 15 h light : 9 h dark). Jars were placed from 0.5 to 1.2 m apart, a distance corresponding to the minimum distance between calling males in the field (Cade 1981a). Purina Cat Chow®, lettuce, and a water vial with a cotton plug were placed inside each jar. The amount of time that a male called the previous night was determined each day. Individual male calling times were measured for 7 nights following capture, a time long enough to allow flies to emerge if a male was already parasitized. Males were removed from jars and discarded if they did not call or called less than 1 h per night on average.

Female flies were collected by broadcasting tape recorded *G. integer* song in the field using loudspeakers fitted with traps (see Cade (1979a) for a description of song-broadcasting equipment and techniques). Several larvae were dissected from captured flies, and a dissecting needle was used to place three to seven larvae on the membranous area around the front and middle legs of each cricket. This number of larvae is within the range found in parasitized males collected in the field (W. H. Cade, unpublished). There was no control sample of unparasitized males used in this first replicate.

Essentially the same procedure was followed with *G. integer* in September and October 1982, with some exceptions. Males were collected under lights in Austin, Texas, and placed inside sound-monitored jars. Jars were placed close to windows at the Brackenridge Field Laboratory, University of Texas, Austin. Males were exposed to the outside photoperiod (approximately 14 h light : 10 h dark), and the temperature was relatively constant at 17–19°C. After individual male calling durations were measured for 7 nights, fly larvae were placed on some of the males. Other males were not infested with fly larvae and served as a control to this replicate of the infestation experiment.

Natural infestation

In September, October, and November 1982, male *G. integer* which were calling in field populations in and near Austin were collected and placed in sound-monitored jars in the laboratory. Individual male calling times were recorded until a male died from fly parasitism

¹This species has been routinely referred to as *G. integer*, but the name is no longer valid and the species is under taxonomic revision (R. D. Alexander and W. H. Cade, in preparation).

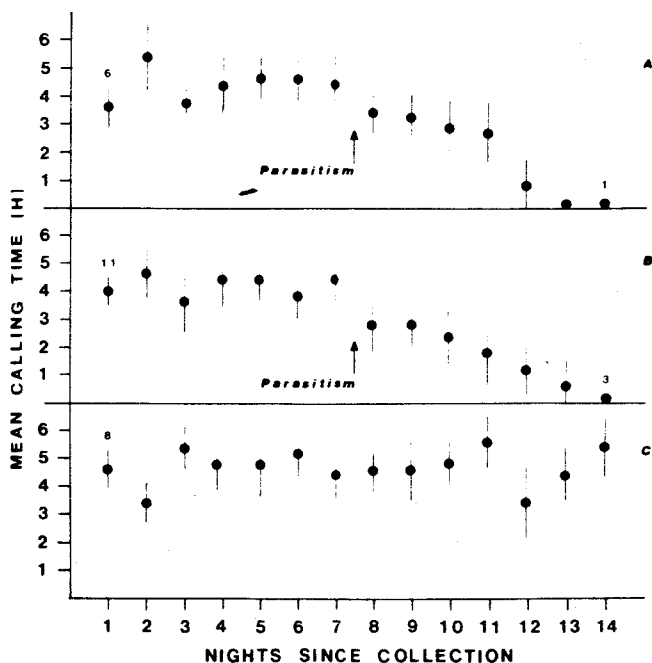


FIG. 1. The average calling time per 24-h period in laboratory jars for *G. integer* males collected under electric street lights before and after being parasitized by *E. ochracea* larvae in (A) 1978 and (B) 1982 or (C) which remained unparasitized in 1982. SE bars and sample sizes for the first and following nights are shown.

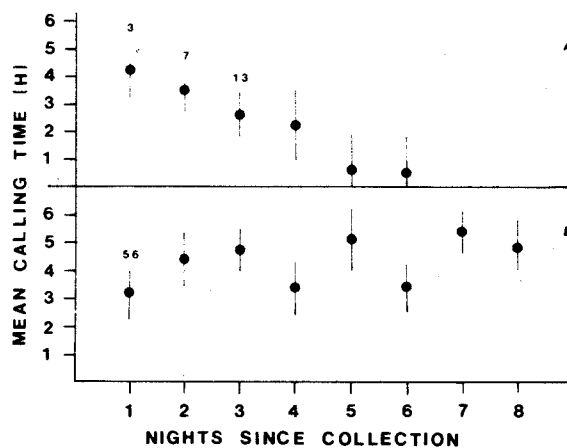


FIG. 2. The average calling time in laboratory jars for *G. integer* males collected while they were calling in the field in 1982. (A) Calling times for crickets from which *E. ochracea* larvae subsequently emerged. (B) Calling times for crickets from which larvae did not emerge and which were therefore classified as nonparasitized. SE bars and sample sizes for the first and following nights are shown. The sample size increases in A since only males who lived for at least 4 nights following collection are included, and of the 13 males, 3 lived 6 nights, and 4 lived 5 nights.

or for at least 8 nights following capture. These data were used to compare the duration of nightly calling between naturally parasitized and nonparasitized *G. integer*. Males were placed in the nonparasitized category if fly larvae did not emerge from them or if the males did not die during the experiment.

Results

The average calling times per 24 h for 6 *G. integer* males collected under lights in 1978 and for 11 males in 1982 are shown in Figs. 1A and 1B, respectively. Before parasitism in 1978, males called an average of 4.4 h (SD = 2.1; range, 1.2–6.1) and 1982 males called 4.2 h (SD = 2.2; range, 1.2–7.5). In 1978, five of the six males died on night 7 following parasitism and three males died on night 8. The average calling time per night following parasitism on nights 8–13 when all males were alive was 2.1 h (SD = 2.4; range, 0–5.1) in 1978, and 2.3 h (SD = 2.7; range, 0–6.7) in 1982. Mean calling time before parasitism was significantly greater than the mean for nights 8–13 in 1978 (paired *t*-test; $t = 6.0$, $df = 5$, $p < 0.002$) and 1982 ($t = 5.7$, $df = 10$, $p < 0.0002$). No males called on night 13 in 1978, the sixth night after parasitism and the night before they died. But in 1982, three males called from 0.7 to 1.5 h on night 13, the night before they died. All other males in 1982 stopped calling completely by night 13, or six nights after infestation by fly larvae. None of the males collected under lights and kept in sound-monitored jars for the duration of the experiment in 1978 or 1982 had been parasitized previously by *E. ochracea*.

The mean calling time for eight males collected under street lights in 1982 but who did not have fly larvae placed on them is shown in Fig. 1C. Males called an average of 4.4 h (SD = 2.3; range, 1.2–5.7) the first 7 nights after collection, and 4.3 h (SD = 2.2; range, 1.3–6.7) on nights 8–14. There was no significant difference in the mean calling time between nights 1–7 and 8–14 ($t = 0.8$, $df = 7$, $p < 0.05$).

Seventy-three calling males were collected in field populations in Austin in 1982 and placed in sound-monitored jars. From one to five fly larvae ($\bar{X} = 2.3$, $SD = 1.2$) subsequently emerged from 17 of these males. The average duration of calling in the laboratory for parasitized and nonparasitized males is shown in Fig. 2A and 2B, respectively. Only those parasitized males who lived for at least 4 nights following collection are included in Fig. 2A. Thirteen males lived at least 4 nights, and of these seven lived for 5 nights, and three lived for 6 nights following collection. Mean calling duration was 1.9 h in the parasitized group (SD = 2.5; range, 0–6.2), and 4.6 h in the nonparasitized males (SD = 2.6; range, 1.2–5.8). These two groups differed significantly in the mean duration of calling (unpaired *t*-test; $t = 3.9$, $df = 67$, $p < 0.001$).

Discussion

The attraction of acoustically orienting female flies to male cricket song represents a cost of sexual behaviour. Although calling males attract female crickets, parasitism decreases male survival. Noncalling or irregularly calling *G. integer* males often occur close to calling conspecific males. One benefit of noncalling or satellite behaviour is probably the interception of females attracted by the calling of other males (Cade 1979a). Cricket songs are energetically expensive to produce (Prestwich and Walker 1981), and satellite males also benefit by avoiding this cost of signaling. In addition, satellite males are infrequently parasitized by *E. ochracea* fly larvae, and avoidance of parasitoids is another advantage of noncalling males (Cade 1975). Burk (1982) reviewed evolutionary aspects of the attraction of predators and parasitoids to the sexual signals of male insects and other animals.

The data reported here indicate that parasitism by *E. ochracea* also reduces the duration of male *G. integer* calling, and thus the ability to attract females before death. Once parasitized by fly larvae, the duration of calling declined gradually. Most males called very little the last few nights of life, and did not call the night before they died. Control males collected under lights and nonparasitized males from field populations

did not, however, show any reduction in calling behaviour with time. The calling behaviour of these nonparasitized males was very similar to that of male *G. integer* raised in the laboratory which also showed no variation in calling with increasing time (Cade and Wyatt 1984). In the present study, all artificially and naturally parasitized crickets died within 8 nights of fly infestation, whereas none of the control males or the apparently nonparasitized males from field collections died during the course of the experiments. None of the *G. integer* collected under lights and kept in sound-monitored jars for the duration of the experiments had been parasitized previously. The absence of fly larvae from these light-collected males is probably because flying males have not yet established calling territories and many are satellite males (Cade 1979a, 1979b). Some light-collected males were discarded which did not call or called infrequently during the first few nights of the experiment, however, and some of these males may have been parasitized by *E. ochracea*.

Acoustically orienting flies are likely to influence calling behaviour in other species of singing insects. *Euphasiopteryx* and related flies parasitized various crickets and other acoustical Orthoptera (Sabrosky 1953), and flies probably orient to the species-specific male calling song in most cases (Mangold 1978). For example, *Neoconocephalus robustus* (Orthoptera; Tettigoniidae) is parasitized by *E. brevicornis*, a close relative of the fly studied here. Parasitized katydids also called up to a few days before death, although actual calling times were not measured (Nutting 1953). In similar situations, the katydid, *Neoconocephalus triops* (Orthoptera; Tettigoniidae), is parasitized by the acoustically orienting fly, *Ormia lineifrons* (Burk 1982), and calling males cicadas, *Okanaga rimosa* (Homoptera; Cicadidae), are parasitized by the acoustically orienting fly, *Colcondamyia auditrix* (Diptera; Sarcophagidae). In contrast with the situation in crickets and katydids, male cicadas become incapable of calling once they are parasitized (Soper *et al.* 1976). Parasitoids induce numerous morphological and physiological changes within their hosts (Vinson and Iwantsch 1980), but no information exists regarding the physiological effects of fly larvae on acoustical insects which might account for the observations reported here.

Population density, time of night, availability of females, and other factors influence male calling behaviour (Alexander 1961; Cade 1979a; Cade and Wyatt 1984; Walker 1983). Laboratory experiments have also demonstrated additive genetic variation underlying the duration of calling by male *G. integer* (Cade 1981b). The data reported here are further evidence that fly parasitoids, *E. ochracea*, have been a selective force on calling behaviour in *G. integer*. Other evidence that flies select against calling in *G. integer* include the greater frequency of parasitism of calling males compared with non-singing males (Cade 1975, 1979a), and the overall reduction in calling behaviour for *G. integer* compared with other apparently nonparasitized species of field crickets (Cade and Wyatt 1984).

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- ALEXANDER, R. D. 1961. Aggressiveness, territoriality, and sexual behavior in field crickets. *Behaviour*, **17**: 130–223.
- 1975. Natural selection and specialized chorusing behavior in acoustical insects. *In* *Insects, science, and society*. Edited by D. Pimental. Academic Press, New York. pp. 35–77.
- BURK, T. 1982. Evolutionary significance of predation on sexually signaling males. *Fla. Entomol.* **65**: 90–104.
- CADE, W. 1975. Acoustically orienting parasitoids: fly phonotaxis to cricket song. *Science* (Washington, D.C.), **190**: 1312–1313.
- 1979a. The evolution of alternative male reproduction strategies in field crickets. *In* *Sexual selection and reproductive competition in insects*. Edited by M. S. Blum and N. A. Blum. Academic Press, New York. pp. 343–379.
- 1979b. Field cricket dispersal flights measured by crickets landing at lights. *Tex. J. Sci.* **31**: 1–6.
- 1980. Alternative male reproductive behaviors. *Fla. Entomol.* **63**: 30–45.
- 1981a. Field cricket spacing, and the phonotaxis of crickets and parasitoid flies to clumped and isolated cricket songs. *Z. Tierpsychol.* **55**: 365–375.
- 1981b. Alternative male strategies: genetic differences in crickets. *Science* (Washington, D.C.), **212**: 563–564.
- CADE, W., and D. WYATT. 1984. Factors affecting calling behaviour in field crickets, *Telegryllus* and *Gryllus* (age, weight, density, and parasites). *Behaviour*. In press.
- MANGOLD, J. R. 1978. Attraction of *Euphasiopteryx ochracea*, *Corethrella* sp. and gryllids to broadcast songs of the southern mole cricket. *Fla. Entomol.* **61**: 57–61.
- NUTTING, W. L. 1953. The biology of *Euphasiopteryx brevicornis* (Townsend) (Diptera, Tachinidae), a parasite in the cone-headed grasshoppers (Orthoptera, Copiphorinae). *Psyche*, **60**: 69–81.
- OTTE, D. 1977. Communication in Orthoptera. *In* *How animals communicate*. Edited by T. A. Sebeok. Indiana University Press, Bloomington, IN. pp. 334–361.
- PRESTWICH, K. N., and T. J. WALKER. 1981. Energetics of singing in crickets: effect of temperature in three trilling species (Orthoptera: Gryllidae). *J. Comp. Physiol.* **143**: 199–212.
- SABROSKY, C. W. 1953. Taxonomy and host relations of the tribe Ormiini in the western hemisphere (Diptera, Larvaevoridae). *Proc. Entomol. Soc. Wash.* **55**: 167–183.
- SOPER, R. S., G. E. SHEWELL, and D. TYRRELL. 1976. *Colcondamyia auditrix* nov. sp. (Diptera: Sarcophagidae), a parasite which is attracted by the mating song of its host, *Okanagana rimosa* (Homoptera: Cicadidae). *Can. Entomol.* **108**: 61–68.
- VINSON, S. B., and G. F. IWANTSCH. 1980. Host regulation by insect parasitoids. *Q. Rev. Biol.* **55**: 143–165.
- WALKER, T. J. 1983. Diel patterns of calling in nocturnal Orthoptera. *In* *Orthopteran mating systems*. Edited by D. T. Gwynne and G. K. Morris. Westview Press, Boulder, CO. pp. 45–72.