Phonotaxis in Female *Ormia ochracea* (Diptera: Tachinidae), a Parasitoid of Field Crickets

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Gravid females of Ormia ochracea *locate their hosts by homing on their hosts' calling songs. At Gainesville, Florida, O.* ochracea *females were attracted in greatest numbers to broadcast sounds that simulated the calling song of* Gryllus rubens. *Other candidate hosts and the attractiveness of their songs relative to the simultaneous song of G.* rubens *were G.* fultoni *(9%), G.* integer *(4%), G.* firmus *(3%), Orocharis luteolira (1%), Scapteriscus borellii (1%), and S.* vicinus *(0%). The response of female O.* ochracea *to simulated G.* rubens *songs that have different pulse rates changes with temperature in parallel with temperature-induced changes in the pulse rate of natural songs. Speaker stations ≤ 16 m apart in an apparently uniform environment produced strikingly different fly counts (e.g., 852 and 2163). The song of G.* rubens *at 21°C approximates a continuous sequence of 4.6-kHz pulses at a rate of $45 \ s^{-1}$ and with a duty cycle of 50%. When two of these parameters were held constant and the third systematically varied in steps of 0.4 kHz, $10 \ s^{-1}$, and 10–20%, maximum attraction occurred at 4.4 kHz, $45 \ s^{-1}$, and 20–80%. Omitting as many as half the pulses in a* rubens *simulation (e.g., 1, 2, 4, or 16 pulses followed by an equivalent silence, and repeat) did not significantly reduce the counts of O.* ochracea, *proving that chirping (producing pulses in brief groups) is no safeguard from call-seeking O.* ochracea. *Phase shifting of pulses in successive chirps sometimes decreased fly counts. When songs were first broadcast, flies came within seconds. Flies that landed at sound often stayed for minutes, even when the sound was turned off.*

KEY WORDS: phonotaxis; cricket; *Ormia; Gryllus;* parasitoid; bioacoustics.

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INTRODUCTION

Larvipositing females of at least three species of ormiines (Ormiini, Tachinidae, Diptera) locate katydid or cricket hosts by homing on their hosts' calling songs. Cade (1975), at Austin, Texas, attracted gravid females of *Ormia ochracea* to the taped calling song of *Gryllus integer* and showed that they larviposited on crickets at the sound source. Burk (1982), in Gainesville, Florida, attracted *Ormia lineifrons* to the taped calling song of the copiphorine katydid *Neoconocephalus triops*, a species it heavily parasitizes. Fowler and Kochalka (1985) attracted *Ormia depleta*, a South American species that parasitizes mole crickets of the genus *Scapteriscus*, to synthesized calling songs of *S. borellii* (= *S. acletus*). Lakes-Harlan and Heller (1992) gave strong circumstantial evidence that females of a fourth ormiine species, *Therobia leonidei*, locate males of the katydid *Poecilimon veluchianus*, in Greece, by their calls. Phonotaxis is not known in males or nongravid females for any ormiine.

Whether phonotactic ormiine females locate hosts other than by acoustic cues is unknown. The only evidence that they do is that hosts that never call are sometimes parasitized. For example, Walker and Wineriter (1991) found that *O. ochracea* parasitized males and females of two *Gryllus* spp., at Gainesville, Florida, at similar levels. Since female *Gryllus* do not call, this suggests other means of host finding. However, the other means may be that larvae, not their mother, find silent hosts. Larvae deposited at a call may be placed near rather than on the caller and may attack silent hosts that encounter them.

Little is known of the acoustical specificity of phonotactic ormiines. *O. lineifrons* is attracted to the song of *Neoconocephalus triops* (Burk, 1982) and, presumably, to the similar songs of other *Neoconocephalus* spp. that it parasitizes. It has not been reared from females. I have attracted small numbers to synthetic song of *Scapteriscus vicinus* (3.3 kHz, 130 pulses s^{-1}) but not to cricket songs of lower pulse rates. Thus all calls known or suspected to attract *lineifrons* are continuous or nearly continuous pulse sequences with pulse rates of more than 100 pulses s^{-1}.

Fowler (1987) studied phonotaxis in *O. depleta* by simultaneously broadcasting synthesized calls of five species of mole crickets: *S. vicinus*, *S. borellii*, *S. imitatus*, *S. didactylus*, and *Neocurtilla hexadactyla*. He captured 24 or more *O. depleta* at calls of each of the first three species and none at calls of the last two. *N. hexadactyla* has a notably lower carrier frequency (1.7 kHz) than the other species and produces short chirps instead of a long-continued trill. The failure of *S. didactylus* calls to attract *O. depleta* is not easily explained. Relative to the trills of other species that attracted *O. depleta*, the trill of *S. didactylus* is intermediate in carrier frequency and pulse rate (Forrest, 1983). This suggests that *O. depleta* females have acoustical templates for particular host species, rather than responding to all mole-cricket-like calls issuing from the soil. Because

Fowler did not report the physical characteristics of the synthesized sounds he used, his transposing the songs of *S. imitatus* and *S. didactylus* cannot be excluded. Forrest (1983), in describing mole cricket calling songs, listed these two species only as "*Isabella changa*" and "*Dorado changa*," respectively. *S. imitatus* has a carrier frequency of 4.5 kHz, well above the 2.7- to 3.5-Hz range of the other three *Scapteriscus* species. Complicating this picture further, Fowler and Mesa (1987) reared *O. depleta* from field-collected *Anurogryllus* sp. and felt "confident that the songs of *Anurogryllus* are attractive to . . . *depleta*, based upon preliminary tests with taped *Anurogryllus* songs in the field." Calling songs of *Anurogryllus* spp. have carrier frequencies of 4.7 to 7.4 kHz (Walker, 1973).

Three workers have studied phonotaxis in *O. ochracea*. Cade (1975, 1979, 1981) attracted it to tape-recorded songs of *G. integer* and of "a tree cricket." He failed to attract it with a high frequency whistle and with a tape recording of bullfrog croaking. Mangold (1978) attracted it to a tape-recorded song of *Scapteriscus borellii*. Walker (1986, 1989) attracted it to synthetic *G. rubens* song but failed to attract it to synthetic *G. firmus* song.

The present study of phonotaxis in *O. ochracea* began in 1986 and sought to answer these questions: (1) Which calls, among those of potential hosts, attract gravid females? (2) Do the acoustical templates of host-seeking females change with temperature, in keeping with changes in hosts' songs? (3) What features of a call make it attractive? Tests of question 3 were completed first, but 1–3 is the logical sequence for presenting the results.

WHICH CALLS ATTRACT?

Methods

Attraction of *O. ochracea* to calls of hosts and selected candidate hosts was studied in two series of tests. Because *Gryllus rubens* is the most abundant natural host in north Florida and because preliminary tests showed that its song was by far the most attractive of those tested, attraction to its call was made the standard by which other calls were measured.

In the most extensive series of tests, 27 July to 11 Dec. 1991, the standard and one other call were played simultaneously each night, and attracted flies were killed prior to counting, assuring that a fly could score but once. Tests were performed in a 5-ha Bermuda and Bahia grass pasture surrounded by woods of slash pine and mesic hardwoods (NW corner of sect. 31, tp. R19E, T9S, Alachua Co., FL) (Site 1) and on a Bahia grass lawn east of the University of Florida Entomology and Nematology Building (UF Bldg. 970) (Site 2). At each site three stations defined an equilateral triangle 50 m (Site 1) or 16 m (Site 2) on a side. Each station was equipped with a slit trap for *Ormia* (Walker, 1989)

and a programmable, microprocessor-based "artificial cricket." Each artificial cricket consisted of an electronic sound synthesizer, an amplifier, and a speaker, mounted in a 15 × 12.5 × 10 (l × w × h)-cm metal box (e.g., Walker, 1988, 1990). One station broadcast *G. rubens'* call, one broadcast the call of a test species, and the third was a silent control. Test species were *Gryllus fultoni*, *G. firmus*, *G. integer*, *Orocharis luteolira*, *Scapteriscus borellii*, and *S. vicinus*. Parameters of test calls approximated those of natural calls at 25° (Table I). Songs were synthesized by turning a carrier frequency on and off at a constant rate to produce a pulse train (trill) with pulses and pulse intervals of equal duration (Fig. 1A). To produce chirping calls the trill was turned on and off. Prior to placing the slit trap over the artificial cricket, a Bruel & Kjaer Model 2219 sound level meter was used to adjust sound levels of trills to 106 dB at 15 cm. For chirping calls, a microphone (at 15 cm) and an oscilloscope were used to adjust pulse amplitudes to match those of the 106-dB *G. rubens* trill. In tests to investigate the effect of relative sound levels on numbers attracted, the *rubens* call was set at 94 dB while test calls remained at 106 dB.

Broadcasts were started before 1–3 h before sunset and stopped 1–3 h after sunrise. Captured *O. ochracea* were killed and counted daily. When cumulative captures at the three stations exceeded nine (often after 1 night), the synthesizers

Table I. Number of *O. ochracea* Trapped at Synthetic Calls of Known and Potential Hosts, Compared to Numbers Trapped at a Synthetic Call of *G. rubens* (4.8 kHz, 50 p/s)[a]

Test call	Parameters of test call (kHz, p/s; p/ch, ch/s)[b]	Replicates Site 1	Replicates Site 2	Trapped at Test call	Trapped at *rubens* call	Test call as % of *rubens* call
106-dB test call vs 106-dB *rubens* call						
G. fultoni	4.5, 35; 3, 2	2	1	36	420*	8.6
G. integer	5.3, 85	2	2	8	206*	3.9
G. firmus	4.4, 17; 4, 2	2	2	13	383*	3.4
O. luteolira	5.7, 70; 6, 0.5	2	2	5	416*	1.2
S. borellii	2.7, 50	0	2	3	470*	0.6
S. vicinus	3.3, 130	0	2	0	245*	0.0
106-dB test call vs 94-dB *rubens* call						
G. integer	5.3, 85	0	1	4	73**	5.5
G. firmus	4.4, 17; 4, 2	0	1	0	96**	0.0
S. borellii	2.7, 50	0	1	3	211**	1.4
G. rubens	4.8, 50	3	0	159	68	233.8

[a]Calls played for >14 h, simultaneously.
[b]p/s, pulses per second; p/ch, pulses per chirp; ch/s, chirps per second.
*Number at test call significantly less than number at *rubens* call (chi-square, $P < 0.001$).
**Number at test call, relative to number at *rubens* call, not significantly different from results with 106-dB *rubens* call (chi-square, $P > 0.10$).
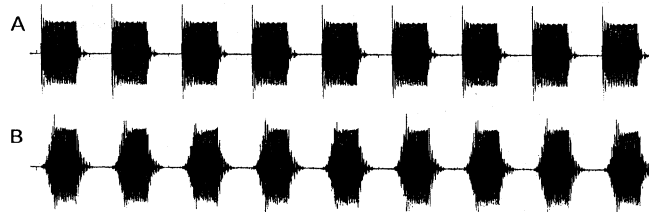
Fig. 1. Oscillograms of broadcast pulse trains, at 45 p/s, produced by sound synthesizers. (A) "Artificial cricket" (synthesizer, amplifier, and speaker in a small box). (B) "Virtuoso Cricket" (computer-based synthesizer used to make tapes for subsequent use).

were rotated among the stations and the test was continued. A replicate of a given comparison was completed when the required rotation would return the synthesizers to their original positions (i.e., each sound had played at each position).

In the other test series, run 14–20 Nov. 1988 at Site 1, calls of the five species listed in Table II were played sequentially and flies that landed at a call were counted but not captured and, hence, could be counted again. *G. rubens* calls in this series were made with the "Virtuoso Cricket" described more fully below (What features attract?). Carrier frequency was 4.6 kHz and pulse rate was 45 s^{-1}. Other calls were made with artificial crickets, as described above. Prior to starting an evening's series of tests, the sound level was set at 106 dB, as described above. Beginning at dusk, a call was started every 60 s and played for 30 s. As the call played, *O. ochracea* landing on a 0.5 × 0.5-m cloth platform just above the speaker were observed and the greatest number seen at once was recorded. During the 30 s between calls, flies were fanned from the platform and the next call-producing unit was installed beneath. Tests were continuous during an evening until replicates were completed. Calls were randomized within replicates.

Prior to pooling, the replicates of each test were tested for heterogeneity with chi-square. For unreplicated tests and pooled replicates of tests with homogeneous results, the null hypothesis of identical attractiveness was tested (chi-square, $P\alpha \leq 0.05$).

Results and Discussion

Tables I and II list results of tests that compared attraction of *O. ochracea* to *G. rubens* calls with attraction to calls of other known or potential hosts. Replicates of the same test were never significantly heterogeneous. In tests that included silent control traps, the control traps caught no flies. In all tests, in both series, the null hypothesis of equal attraction to calls of *rubens* and the test species was rejected ($P < 0.001$).

Table II. Numbers of *O. ochracea* Landing at Synthetic Calls of Known and Potential Hosts, Compared to Numbers Landing at a Synthetic Call of *G. rubens*[a]

Call played	Parameters of call (kHz, p/s; p/ch, ch/s)[b]	No. landing	No. landing at call as % of *rubens* call
G. rubens	4.6, 45	217	100.0
G. fultoni	4.5, 35; 3, 2	3*	1.4
G. firmus	4.4, 17; 4, 2	0*	0.0
S. borellii	2.7, 50	10*	2.3
S. vicinus	3.3, 130	0	0.0

[a]Calls played for 30 s, sequentially. Site 1, 17 replicates.
[b]p/s, pulses per second; p/ch, pulses per chirp; ch/s, chirps per second.
*Number at call, relative to number at *rubens* call, significantly different from top of Table I (chi-square, $P < 0.025$).

Rankings in the two series were similar for the four test species in common, but attraction to songs of *G. firmus*, *G. fultoni*, and *S. borellii*, relative to attraction to *rubens* song, was significantly different between the two series (chi-square, $P < 0.025$). Because the two series differed in many features, including what was scored as attraction and details of the *rubens* calls (e.g., pulse shape; Figs. 1A and B), the differences in relative attraction cannot be attributed to any one feature. The importance of the sequential tests is that they establish that few flies are attracted to non-*rubens* calls even in the absence of a competing *rubens* call and with many flies in the vicinity (demonstrated by high counts at *rubens* calls played as part of the same test sequences).

In addition to *rubens*, three species of *Gryllus* occur in north peninsular Florida. Calls of *G. firmus* and *G. fultoni* attract only a few *O. ochracea* compared to *G. rubens*. *G. firmus*, but not *G. fultoni*, is known to be a natural host, yet in both test series *fultoni*'s call proved more attractive. It may be pertinent that the calling season of *G. fultoni* is restricted largely to spring, a season with few to no phonotactic *O. ochracea*. The remaining species, *G. ovisopis*, mates solely in autumn, when *O. ochracea* is abundant. However, it produces no calling song (Walker, 1974) and apparently completely escapes parasitism by *O. ochracea*—though it is a suitable host in laboratory tests (Walker and Wineriter, 1991). Both *fultoni* and *ovisopis* occur in woods rather than in the open areas favored by *rubens* and *firmus*. However, *rubens* calls played in a woods attracted as many *O. ochracea* as calls played in a nearby pasture (Walker, 1989, Fig. 2).

The call of *G. integer*, a field cricket whose range extends into western Florida, attracted fewer than 4% as many *O. ochracea* as *G. rubens*'s call (Table I). Yet in Texas, *G. integer* is heavily attacked by *O. ochracea*, and Cade (1981) attracted large numbers to broadcasts of its taped calling song. Thus, geographical variation in the acoustical template of *O. ochracea* seems likely,

and a comparison of *integer* and *rubens* songs in central Texas, where *rubens* does not occur, would be expected to contrast with the present results.

The call of *Orocharis luteolira*, a common, arboreal, eneopterine cricket, attracted few *O. ochracea* compared to the call of *rubens* (5 vs 416) (Table I). However, in these tests *Ormia dominicana*, not known previously to find its host by phonotaxis, was attracted in substantial numbers to *luteolira* song but not to *rubens* song (35 vs 0). The elevated calling sites of *luteolira* would probably not deter attraction of *O. ochracea*. Although the known hosts of *O. ochracea* call from the ground, I have attracted it to *rubens* calls played 4.7 m above ground level.

Calls of *S. borellii* and *S. vicinus*, two species of mole crickets introduced from South America, attracted few and no *O. ochracea* (Tables I and II). *S. borellii* supports development of *O. ochracea* in the laboratory, though it is not known to be a natural host; *S. vicinus* is apparently unsuited to parasite development (Walker and Wineriter, 1991).

Setting the call of *G. rubens* at 94 dB while leaving the test calls at 106 dB did not significantly change the attractiveness of the test calls relative to the *rubens* call (Table I) (chi-square, $P > 0.10$). These tests were at Site 2, where the sound traps were 16 m apart. Over that distance a sound level measured at 15 cm should, through spreading loss, drop about 40 dB. Thus even at the lower level, the *rubens* call likely reached the station broadcasting the test call well above the hearing threshold of *O. ochracea*, measured at about 20 dB by Robert *et al.* (1992). A fly at a test call in this second series of tests was still hearing two calls and choosing between them.

When 106- and 94-dB *rubens* were played simultaneously, the stronger song attracted 2.3 times as many *O. ochracea* as the weaker (Table I). In similar tests with the attraction of *Scapteriscus borellii* to synthetic *S. borellii* calls, Walker and Forrest (1989) caught 8.2 times as many at 106 as at 94 dB. The relative attraction of female crickets to male calls that differ in sound level was modeled by Forrest and Green (1991). Their model predicts that a call 12 dB stronger than another will attract four times as many flies if the range of the weaker call is entirely outside the range of the stronger. If the range of the weaker call is entirely within the range of the stronger, the model predicts the stronger will attract 11.5 times as many. Almost certainly, for *O. ochracea*, the range of the 94-dB call was entirely within the range of the 106-dB call. The two were only 50 m apart, and provided that the fly's response threshold was <40 dB [cf. the 20-dB hearing threshold measured by Robert *et al.* (1992)], the range of the 106-dB call exceeded that of the 94-dB call by more than 200 m. Because the stronger *rubens* call trapped substantially fewer than four times as many flies, one or more of Forrest and Green's assumptions were apparently not met. The relevant assumptions are that (1) the traps radiate sound evenly in all directions and that the females (2) fly in straight lines, (3) have some thresh-

old of hearing and respond with straight-line flight toward a source if it is above threshold, (4) fly toward the louder source when two are heard simultaneously, and (5) come from outside the spheres of attraction. Which assumption(s) is(are) not met is not obvious. If most flies that were trapped resided in the vicinity of the traps, violating assumption 5, the ratio of loud-to-soft attractions would be reduced. However, the removal of hundreds of flies at trapping stations, apparently without affecting future catches, speaks against this being the case. Forrest and Green (1991) showed that their model's predictions approximated experimental results in tests of female choice of male calling songs in mole crickets, meadow katydids, and frogs. Thus the failure of the *O. ochracea* trapping data to conform is not trivial and merits further study.

DOES THE TEMPLATE CHANGE WITH TEMPERATURE?

Methods

To determine whether the acoustical template of *O. ochracea* changes with temperature, as do the songs of its hosts (Walker 1962), *G. rubens* songs appropriate to ambient temperature were tested against songs appropriate to 4°C above or below ambient at Site 1. Ambient temperatures were measured to the nearest 1°C with a thermocouple inserted in the body of a recently killed *G. rubens* placed at ground level between two artificial crickets 4 m apart. Immediately above the speaker of each unit was a framed 12 × 14-cm sheet of 0.05-mm polyethylene covered with Tack Trap stickum. Pulse rates of synthesized calls were varied in accord with the regression of *G. rubens* pulse rate on temperature: $-13.12 + (2.756 * T)$, where T = degrees centigrade (Walker, 1962). Carrier frequency, which in *G. rubens* calling songs varies little with temperature (Walker, 1962), was held constant at 4.8 kHz. All calls were played at 92 dB, measured 15 cm above the sticky surface. Tests began at sunset, with one unit playing the pulse rate that matched the ambient temperature and the other playing a pulse rate 11 pulses s^{-1} higher or lower, i.e., appropriate to a 4°C higher or lower temperature. Every 10 min, ensnared *O. ochracea* were counted and removed and the synthesizers switched in position. When ambient temperature dropped 1°C, a new test, with appropriate songs, was started. When ambient temperature was 25 to 28°C, the test call was 4°C below; when ambient was 17 to 20°C, the test call was 4°C above; when ambient was 21–24°C, the test call was 4°C above and 4°C below in alternate tests.

Replicates were subjected to heterogeneity chi-square analysis before pooling. Pooled data were used to test the null hypothesis of equal attractiveness of songs appropriate to ambient temperature and to temperatures deviating 4°C from ambient.

Results and Discussion

The acoustic template of host-seeking *O. ochracea* does change with temperature. In seven tests of calls appropriate to ambient and 4°C above ambient, totals of 66 and 39 *O. ochracea* were ensnared. In six tests of calls appropriate to ambient and 4°C below ambient, 64 and 36 were caught. The data for each of the two sets of tests proved suited to pooling; and the null hypotheses, of equal attractiveness of songs appropriate to ambient temperature and to temperatures 4°C above and below, were rejected (chi-square, $P < 0.01$).

"Temperature coupling," reviewed by Doherty and Hoy (1985), occurs when the receiver of a poikilotherm-produced signal changes its signal recognition behavior in parallel with temperature-induced changes in the signal. For example, female crickets are attracted to faster pulse rates when they are warm than when they are cool, and the rate at which their preference changes approximates the rate at which the wing-stroke rates of conspecific males change. Previous examples of temperature coupling have been between males and females of the same species of cricket, grasshopper, firefly, or frog. This is the first example of interspecific temperature coupling. Conspecific temperature coupling may result from the same neural network, under the same genetic control, generating both the signal pattern in males and the sensory template in females (Doherty and Hoy, 1985). In interspecific coupling, sender and receiver do not come from a common gene pool, and the match in their temperature responses can be attributed only to their common poikilotherm physiology or to the evolution of one or both to match the other. In this case, the receiver but not the sender benefits from the match.

WHAT FEATURES ATTRACT?

Methods

To determine what features make cricket calls attractive to *O. ochracea*, systematically modified synthetic *G. rubens* calls were broadcast outdoors during autumn, the season of greatest fly abundance. Within a mowed area at Site 1, six speaker stations were spaced evenly on the circumference of a 16-m-diameter circle (Fig. 2). Each station had a Realistic 7.6-cm piezoelectric speaker mounted in a 15 × 12.5 × 10 (l × w × h)-cm metal box along with a potentiometer for adjusting sound level and an input transformer (6.3 to 120 V). The metal box, with speaker directed upward, was centered in a 50 × 50 × 13-cm box of 1.6-cm plywood. The plywood box was closed above with a 50 × 50-cm square of perforated, 3-mm, tempered fiberboard (Peg-Board) that had a 30-cm-diameter hole at its center, over the speaker, and was covered with black cloth. The six stations were numbered clockwise from north, with alternate speaker stations assigned to trios *A* (Nos. 1, 3, 5) and *B* (Nos. 2, 4, 6).
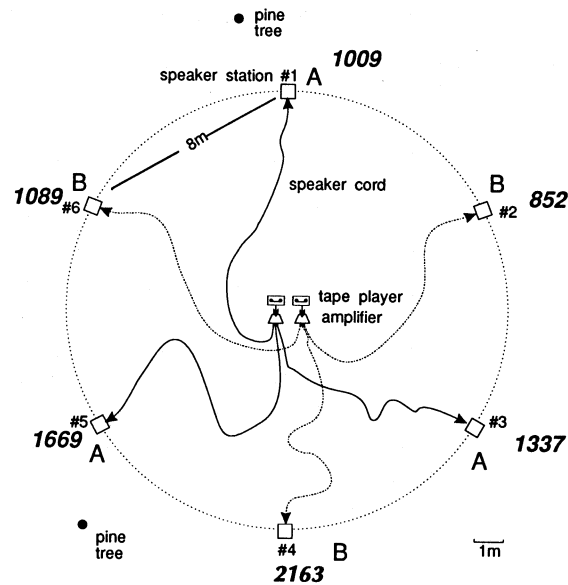
Fig. 2. Experimental layout for testing variations of *Gryllus rubens* calls. Speaker stations, numbered 1 to 6, are 60° apart on the circumference of a 16-m-diameter circle in a pasture. Numbers in italics are total counts of *O. ochracea* at each station, during fall of 1986 and 1987. (North is 10° west of Station 1.)

Test signals were generated with the Virtuoso Cricket, a computer-based sound synthesizer custom built by Oldacre Electronics, Gainesville, Florida. Parameters that could be varied were (1) carrier frequency, (2) pulse rate, (3) pulse ramp duration (all pulses began with a linear increase in intensity to the set value and ended with a linear decrease in intensity to zero; for these tests, each ramp was set at 10% of the total pulse duration), (4) duty cycle (pulse duration as a percentage of pulse period), (5) pulse train duration (here expressed as the number of pulse periods in the train), and (6) pulse train interval (here expressed as the number of silent pulse periods between trains). Prior to use, test signals were tape-recorded at 19 cm s^{-1} on a Kudelski Nagra E recorder. Test tapes were made at standard amplifier settings on both the synthesizer and the recorder, thereby equalizing the amplitude of the recorded carrier frequency, and of the pulses made from it, for all tapes in a set of songs.

Duplicate Nagra E tape players and portable amplifiers were placed at the center of the circle of speaker stations, with one player and amplifier serving the three A stations and the other serving the three B stations (Fig. 2). Coin flips determined which player in combination with which amplifier would drive a given trio of speakers during an entire evening of testing. Sound level was set

using a Model 2219 Bruel & Kjaer sound-level meter and a standard continuous trill, recorded at the same time as the set of tapes being tested. With the meter 15 cm above the cloth covering of each speaker, the potentiometer was adjusted (by means of an extension passing through the front of the outer box) to the desired value (usually 106 dB). In tests of intermittent pulse trains or of varied duty cycles, this procedure produced equal pulse amplitudes in the test broadcasts. Peak sound level, rather than total sound power, was held constant.

Tests began shortly after sunset, when phonotaxis becomes common. A unit test consisted of two 5-min broadcasts of two signals, with the initial station assignment determined by coin flip and with the signals switched between the A and the B stations between broadcasts. Before each broadcast, flies that remained on the cloth-covered platforms were fanned away. During the first 2 min of each broadcast, if the nature of the test signals permitted, I checked sound levels and adjusted any that deviated from the desired value. During the third minute, all platforms were inspected and the number of *O. ochracea* was recorded. Additional counts were made during the fourth and fifth minutes. Each count started at Station 1 and proceeded clockwise around the circle. When natural light faded, a dimmed light was used briefly to illuminate each platform. At the end of a 5-min broadcast a score for each station was calculated by summing its three counts. For example, if four flies were counted at a speaker during each of the final 3 min of a broadcast, the score for that station would be 12. Tests were ended each night when few or no flies came to normally attractive sounds—usually about 90 min after sunset or when the temperature dropped to about 18°C.

Scores were adjusted to compensate for differences in average numbers of flies at the six stations (see Results). The Mann–Whitney test (Zar, 1984) was then used to test the two-tailed null hypothesis that a pair of sounds was of equal attraction to *O. ochracea* ($P\alpha = 0.05$). When more than one test had been made comparing the same pair of sounds, the 12 scores per test were pooled prior to running the Mann–Whitney. No adjustment was made for differences in mean scores among the tests.

Tests were run 26 Oct.–16 Nov. 1986 and 16 Oct.–15 Nov. 1987. Pilot tests were run to determine what sound level should be used and whether flies were attracted to silent stations or to stations broadcasting unmodulated continuous tones. Then series of tests were run to compare songs differing from a standard synthetic *G. rubens* song in each of these features: (1) carrier frequency, (2) pulse rate, (3) duty cycle, and (4) continuity of pulse train. Finally, the effect of phase shifts in pulse trains was tested, but only in regularly interrupted songs.

Because of a seeming discrepancy in the results of tests with pulse rate and pulse train continuity, a test of the combined effect of duty cycle and pulse rate was run 15–21 Nov. 1991 using the three equidistant trapping stations at Site 1

(see above). These songs were played simultaneously: 45 p/s, 50% duty cycle; 22.5 p/s, 50%; and 22.5 p/s, 25%. Carrier frequency was 4.6 kHz. Traps and other aspects of test protocol were the same as for the principal test series under "Which Calls Attract?"

Results and Discussion

Pilot Tests. O. ochracea seldom landed on silent stations. In nine tests of three silent stations paired with three broadcasting stations, the total counts were 1 and 188. *O. ochracea* showed no tendency to land on stations emitting unmodulated tones. In three tests, no flies came to unmodulated tones of 4.6 or 4.8 kHz, whereas counts for pulsed tones of the same frequencies were 6, 14, and 8. Because of these results, silent control stations were not used, and only pulsed sounds were tested further.

In studies of phonotaxis of crickets to cricket calls, higher sound levels have always attracted larger numbers (e.g., Ulagaraj and Walker, 1975; Walker and Forrest, 1989). This can be attributed to more powerful calls exceeding some lower threshold level over a larger area, and not exceeding some upper threshold above which the cricket is repelled or its audition fails. In my tests I wanted to attract large numbers of *O. ochracea* in order to reveal small differences in attraction among the test signals. A test of synthetic *G. rubens* call at 106 and 94 dB produced counts of 75 and 6, respectively—confirming that *O. ochracea* would come to sounds far louder than the 75 to 85 dB of natural *G. rubens* calls and suggesting that songs as loud as 106 dB would attract more flies than softer ones. All further tests were at 106 dB.

Station Effect. The circle of six stations was in a homogeneous area of a pasture with scattered large pines. To ensure uniformity further, the circle and a 1-m buffer were closely mowed. Because every station broadcast both test signals for 5 min during each test, approximately the same numbers of flies should have come to each station in the course of the study. Such was not the case. Station 4 attracted more than 2.5 times as many *O. ochracea* as Station 2 (only 14 m away) (Fig. 2). Speakers and the cloth-covered landing platforms were rotated from night to night and thus could not account for the bias. Once the "station effect" was apparent, plywood boxes were swapped among stations, but that did not change the bias.

The effect was first noted and evaluated in 1986 (2622 fly counts). In 1987 (5497 counts) a similar effect occurred, with the same stations having the highest and lowest counts (Fig. 3). In 1986, station counts, expressed as percentage of the expected count (2622/6), were 73, 51, 100, 182, 126, and 68 (starting with Station 1). In 1987, the corresponding counts were 75, 69, 98, 149, 122, and 87. Although the gross pattern lasted at least 2 years, the details changed significantly during the course of the study. For example, the patterns for the 2
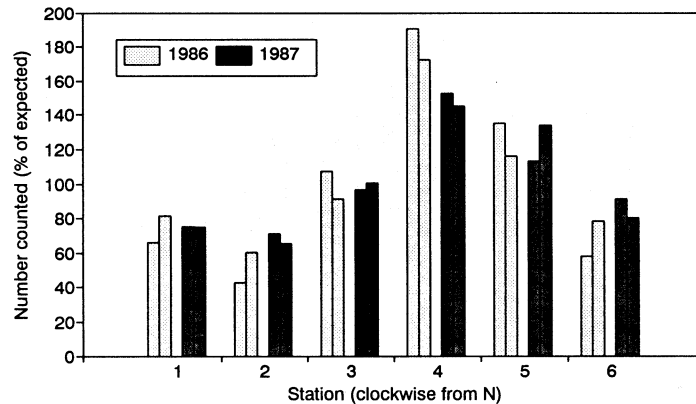
Fig. 3. Effect of station position on counts of *Ormia ochracea*. Bars show counts at each station (Fig. 2) relative to the number expected if *O. ochracea* are equally likely to land at any station. Shaded bars are for 1986 (total counts = 2622); black bars are for 1987 (total counts = 5497). For each year the bar on the left is for the first half of tests, and the bar on the right is for the second half of tests.

years and for the first and last halves of tests each year were different (Fig. 3; chi-square, $P < 0.001$).

The only obvious nonuniformities near the study area were two large slash pine trees (about 34-cm DBH). The circle had been positioned to minimize any tree effect, and each tree was 2.5 m outside (Fig. 2). One tree was nearest Stations 1, 2, and 6, the stations with the lowest counts; the other was nearest Stations 3, 4, and 5, the ones with the highest counts. Neither tree had limbs below 8 m.

The uneven counts remain unexplained, but the fact that stations separated by 8 or 14 m can yield drastically different counts of flies should be taken into account in field studies of ormiine phonotaxis.

Carrier Frequency. In 1986, 4.8 kHz and 50 p/s were used for the standard *G. rubens* call in most tests. Such a call had attracted many *G. rubens* in previous studies (e.g., Walker, 1986), but the 1986 *Ormia* tests indicated that *O. ochracea* was more attracted to 4.6 kHz than to 4.8, and 4.6 was made the standard for 1987. Furthermore, the pulse rate of the standard (and of the calls that varied in carrier frequency) was dropped to 45 p/s, a rate more appropriate to fall temperatures. Because of these changes, the 1986 tests of carrier frequencies cannot be combined with those of 1987 and are not reported here (but are recorded by Walker, 1987).

In 1987, 12 carrier frequencies, from 2.4 to 6.8 kHz, in 0.4-kHz increments, were tested against the standard 4.6 (Fig. 4A). Three replications were
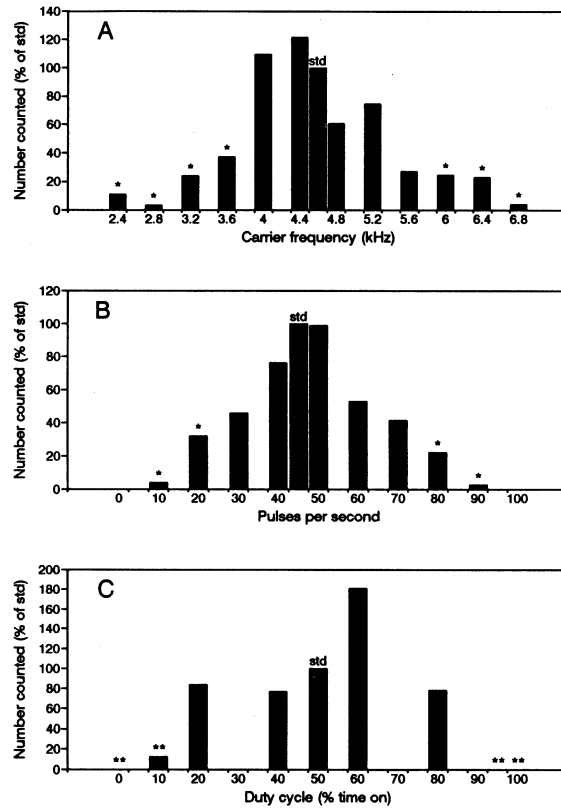
Fig. 4. Counts of *O. ochracea* at stations broadcasting simulated *G. rubens* calls that systematically differ from a standard of 4.6 kHz, 45 p/s, and 50% duty cycle. (*, **) Counts that differ significantly from those of the standard at $P_\alpha \leq 0.05$ and $P_\alpha \leq 0.01$, respectively. (A) Carrier frequency; (B) pulse rate; (C) duty cycle.

planned, with the 12 frequencies randomized within each. Because the first two replications showed 2.4, 2.8, and 6.8 kHz to be significantly less attractive than 4.6, those tests were dropped in favor of tests of other features. A fourth test of 4.8 kHz was run, making a total of 34 carrier frequency tests in 1987.

Carrier frequencies of 4.0, 4.4, 4.8, 5.2, and 5.6 kHz did not differ significantly from the standard in their fly counts (Mann–Whitney, $P > 0.05$). The overall response to carrier frequency seems to be a bell-shaped curve with a peak at 4.4 kHz (Fig. 4A). The carrier frequency of *G. rubens* calling song changes very little with temperature (Walker, 1962), making it unlikely that the irregularities in the data are a result of temperature differences among tests.

Temperatures measured at 1 m above ground level during carrier frequency tests were 18 to 25°C, with a mean of 21°C.

Natural songs of *G. rubens* are generally between 4 and 5 kHz. Walker (1962, Fig. 8) showed an average of about 4.8 kHz for Gainesville males, and Doherty and Callos (1991) reported an average of about 4.2 kHz for males from Grafton, Virginia.

Pulse Rate. In 1986, 12 tests of pulse rate, mostly against a standard of 50 p/s, were run. Like the 1986 tests of carrier frequency, these are omitted here but are reported elsewhere (Walker, 1987). In 1987, nine pulse rates, from 10 to 90 p/s in increments of 10, were tested against a standard of 45 p/s (Fig. 4B). Three replications, with the treatments randomized in each, were run. Two additional tests of 50 p/s and one of 40 p/s were run, bringing the total to 30.

Pulse rates of 10, 20, 80, and 90 produced significantly lower counts of *O. ochracea* than did 45 p/s (Mann–Whitney, $P < 0.05$). The pattern of response to pulse rate is apparently a bell-shaped curve centered at 45 to 50 p/s (Fig. 4B). Temperatures during the 1987 pulse rate tests varied from 17 to 24°C, with a mean of 21°C. The expected pulse rates for *G. rubens* at these temperatures are 34, 53, and 45 (Walker, 1962). Since the acoustic template of *O. ochracea* changes with temperature (see above), pulse rate preference should have been sharper if all tests had been at 21°C.

Duty Cycle. In 1987, six duty cycles (*viz.*, 10, 20, 40, 60, 80, and 95%) were tested against a standard of 50% in randomized sequence. Tests of 10 and 95% were repeated, for a total of eight tests. Pilot test data of silence (0% duty cycle) and unmodulated tones (100% duty cycle) were used to complete Fig. 4C.

Duty cycles from 20 to 80% were not significantly different from the standard in these tests, but without replication this means little. Recent tests using a different protocol suggest that optimal duty cycle may be substantially less than 50% (work in progress). However, these recent tests used a synthesizer that could not "ramp" pulses (cf. Figs. 1A and B), thereby introducing another, untested variable.

Continuity of Pulse Train. In 1986 and 1987, tests were run to determine the attraction of *O. ochracea* to regularly broken pulse trains, compared to unbroken pulse trains of the same carrier frequency (4.6 or 4.8 kHz), pulse rate (45 or 50), and duty cycle (50%). The discontinuous pulse trains were made by inserting intervals equivalent to one or more pulse periods (i.e., a pulse and its following interval). For example a 4:1 train consisted of an endlessly repeating cycle of four pulses and a one-pulse gap (Fig. 5C). (Note: The gap between groups of four pulses is actually longer than a pulse period, since it includes the pulse interval of the preceding pulse). The interrupted trills tested were 4:1 (3 replicates), 1:1 (5 replicates), 2:2 (6), 4:4 (5), and 16:16 (3).

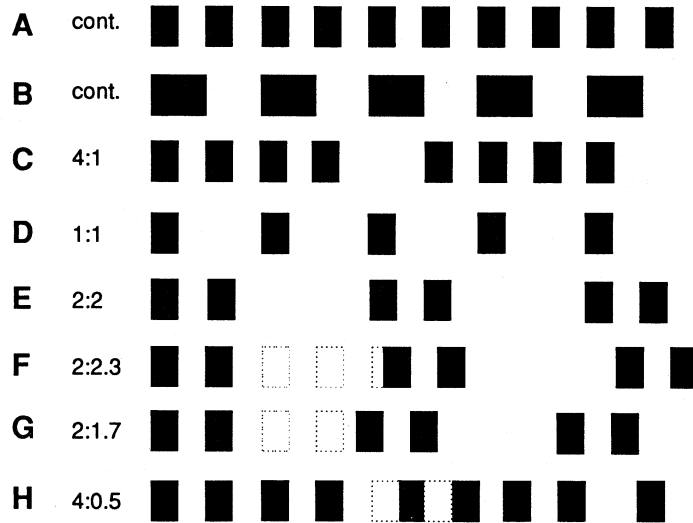*O. ochracea* females do not need long-continued pulse trains to home on

Fig. 5. Pulse patterns of selected test calls. Dotted boxes in F–H reveal degree and direction of phase shifting. (A) Continuous trill, 50% duty cycle. (B) Continuous trill, 50% duty cycle, half the pulse rate of A. (C) Four pulses on:one pulse off (4:1). (D) One pulse on:one pulse off (1:1). Equivalent to B (continuous trill) with a 25% duty cycle. (E) 2:2. (F) 2:2.3. (G) 2:1.7. (H) 4:0.5.
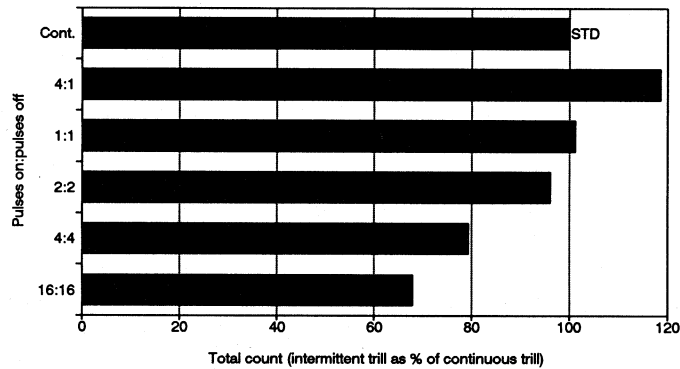

Fig. 6. Effect of pulse train continuity on counts of *O. ochracea* at stations broadcasting simulated *G. rubens* calls. Calls were 4.6 kHz and 45 p/s except the 4:1 test (4.8 and 50) and three of six replicates of 2:2 (4.6 and 50). Counts at interrupted trills did not differ significantly from those for continuous trills (Mann–Whitney, $P \leq 0.05$).

their hosts' calling songs (Fig. 6). Furthermore, attraction to a call does not directly diminish with reduction in percentage "on time." Omitting 50% of the pulses in a continuous trill caused no significant reduction in attraction in tests with 1:1, 2:2, 4:4, and 16:16. The fact that relative counts were less with longer intervals (e.g., 68% for 16:16) could be a matter of cruising flies passing by during the silent period (0.4 s for 16 pulses). It seems evident that as the 50%-time-off intervals get longer, relative counts should approach 50% (cf. 1 h on:1 h off). A question not addressed was the effect of leaving the On time the same (e.g., 4 pulses) and making the Off time greater (e.g., 4, 16, 64 pulses). The song of *G. fultoni* that attracted 8.6% as many *O. ochracea* as did *G. rubens* song (Table I) was equivalent to 3 pulses on:14.5 pulses off; i.e., the 35 p/s sec trill was off 83% of the time.

The results with the 1 pulse on:1 pulse off call seemed to contradict the results of the pulse rate study. The 1:1 call, derived from a 45-p/s trill, was equivalent to a 22.5-p/s trill (Fig. 5D). That pulse rate should have yielded a relative count of about 40% (Fig. 4B) rather than 101% (Fig. 6). However, the attractive 22.5-p/s call had a duty cycle of 25%, whereas the trills tested in Fig. 4B had 50% duty cycles. Figure 7 shows results of 1991 tests that addressed this matter. At 22.5 p/s, the 25% duty cycle attracted 3.5 times as many *O. ochracea* as the 50% duty cycle. However, this version of 1:1 attracted only 35% as many flies as its continuous trill counterpart (rather than 101%). This difference might result from different test protocols (trapping and removing flies vs counting those that had landed at the call) or it might result from unwanted differences in the synthesized signals. Pulses synthesized for the 1986–1987 tests were ramped 10% fore and aft (Fig. 1B), whereas the artificial crickets used in 1991 produced only square pulses (Fig. 1A). The frequency spectrum
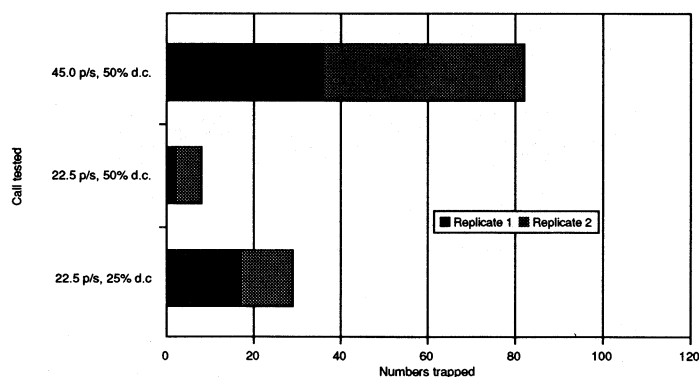

Fig. 7. Numbers of *O. ochracea* trapped at three calls. The 22.5-p/s, 25% duty cycle call is equivalent to the 45-p/s, 50% duty cycle, 1 pulse on:1 pulse off (Figs. 5 and 6).

produced by 100% amplitude modulation of a sine wave is broader with square pulses than with ramped pulses.

Phase Shifts. Phase shifts in the pulse train were investigated because calling males of *G. rubens*, unlike those of other cricket species, often pause momentarily during the silent, opening portion of tegminal movement [unpublished results of high-speed photography (see Walker *et al.*, 1970)]. The effect is to change the phase of the stridulatory cycle and, therefore, of the pulses in the trill. Since substantial numbers of *G. rubens* males die from attacks of *O. ochracea*, their unusual habit of periodically changing the phase of their pulses might have evolved as a means of thwarting phonotactic parasitoids. This would be accomplished if the parasitoids depended on matching a train of pulses to a template that could accommodate pulses being dropped but not phase shifted. Such benefit to calling male *rubens* would of course have to exceed any cost in fewer female *rubens* attracted.

In 1986, to determine if phase shifting influenced counts of flies attracted to synthetic *rubens* calls, calls of 4:1 and 4:0.5 were compared (4.5 kHz, 50 p/s, and 50% dc; three replicates) (Figs. 5C and H). Even though the phase-shifted song had more power (because sound occurred 44% of the time rather than 40%), its fly counts were substantially, but not significantly, lower (Fig. 8). In 1987, 2:2 songs were compared with 2:2.3 and with 2:1.7 songs (4.6 kHz, 45 p/s, 50% dc; three replicates) (Figs. 5 and 8). The 2:2.3 song produced slightly higher fly counts than the non-phase-shifted, 2:2 song, whereas the 2:1.7 song produced significantly lower counts.

These limited tests indicate that the flies' phonotaxis is sometimes affected by phase shifting but do not define the circumstances. It may be relevant that the two test series with reduced counts were with songs achieved by shortening
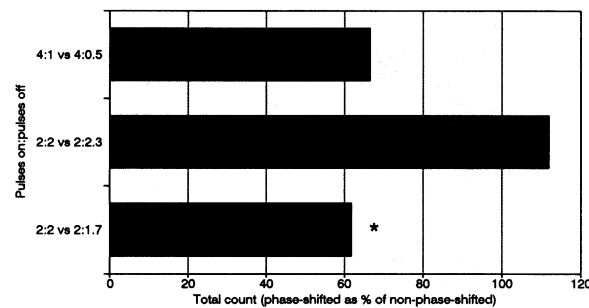

Fig. 8. Effect of phase shifting of pulses on counts of *O. ochracea* at stations broadcasting simulated *G. rubens* calls. The 4:1 vs 4:0.5 test used 4.5 kHz and 50 p/s; the other two used 4.6 and 45. (*) Non-phase-shifted trill significantly more attractive than phase-shifted trill (Mann–Whitney, $P \leq 0.05$). Counts for the three tests totaled 102, 142, and 190, respectively.

a pulse period (by 50 or 30%), whereas the series with no reduction in counts was with a song modified by lengthening a pulse period (by 30%) (Figs. 5F–H). Males of *rubens* probably cannot shorten pulse periods as they call (because of the nature of the neural oscillator that determines stridulatory rhythm) but can and do lengthen them. Minor pauses (<0.5 of the pulse period), which are frequent in *rubens* trills, apparently do not deter phonotaxis in *O. ochracea*. However, pauses of 1.5 or 1.7 pulse periods, which are infrequent, would accomplish phase shifts identical to the shifts in 4:0.5 and 2:1.7 songs and might reduce parasitism. Of more certain relevance is that my tests of phase shifting used brief pulse trains (two or four pulses). Tests of frequent phase shifts within otherwise long-sustained trills would have been more germane, but the sound synthesizers used in these tests could not produce such calls.

Behavior of Flies. When the first *rubens* call was played to set the sound levels for an evening's tests, one or more *O. ochracea* usually landed within a few seconds. As the call continued, more flies would arrive, but the total number at the sound would often diminish. Examples of numbers after 10, 20, and 30 s are 15, 12, 12 (25 Oct.), 1, 3, 4 (30 Oct.), and 7, 5, 3 (10 Nov.). Whether flies arriving quickly were flying by or were perched in the grass or on a nearby tree trunk ready to fly to a calling *rubens* is not known. Whatever the case, a calling *rubens* should have little chance of remaining unparasitized for long. Walker and Wineriter (1991) exposed laboratory-reared males of *G. rubens* at site 1 for 5 days and reported 54% parasitism of nonmuted males and 0% parasitism of muted males. The frequency of calling by nonmuted males was not determined.

After the first 2 min of each broadcast, counts of flies at each station remained fairly stable, but flies continued to come and go. Some flies flew toward the station but veered away instead of landing. Of the flies on the cloth-covered platform of a station, some ran in tight circles above the broadcasting speaker, a few walked about, and most sat quietly. When I scored the behavior of 300 landed flies during 5 nights, 7% were running a circle, 1% were walking, and 92% were motionless. One fly was doing a headstand over the speaker. When a station was illuminated briefly to count flies after dark, very few seemed to leave in response to the light. Many had to be fanned from the platforms between tests and some were difficult to dislodge. If flies were not fanned from the platforms, many would remain for long periods. In a pilot study of flies left undisturbed after the sound was turned off, 20 of 35 (57%) remained after 5 min. When observations were continued beyond 5 min, two of seven flies remained after 20 min.

The generally sedentary behavior of *O. ochracea* at sound is quite different from that reported for the mole-cricket-seeking *O. depleta* in Brazil. Fowler (1987) reported that, of 20 female *O. depleta* he watched arrive at a synthetic *Scapteriscus vicinus* call, none stayed longer than 3 s. While at the sound they

"quickly circled" on the substrate and deposited larvae. Field observations of (recently introduced) *O. depleta* in Florida showed that females landed at *S. borellii* call and moved about the substrate for 1–11 s (mean, 2.7 s) while depositing 1–10 larvae. Females that did not land or that only touched down deposited no larvae (J. Amoroso and Walker, unpublished).

GENERAL DISCUSSION

When a *G. rubens* male calls, a sexually responsive *G. rubens* female may hear and approach, leading to courtship and mating. On the other hand, a male that calls even a few minutes in the fall, at Gainesville, is likely to attract an *O. ochracea* female, which will deposit larvae that are lethal in 7–10 days. The ecological life expectancy of a male *G. rubens* in the absence of *O. ochracea* is unknown, but field-collected females, caged outdoors, often live 6 weeks or more. The cost/benefit ratio of calling by *G. rubens* males probably changes greatly with the abundance of gravid *O. ochracea* females. In fact the numbers of calling *G. rubens* are low in late summer and fall at the same time that populations of both *O. ochracea* and *G. rubens* are high. In spring, when both populations are low, the numbers of calling *G. rubens* males are high (Walker, 1986, unpublished).

The various tests in this study prove that gravid females of *O. ochracea* are attracted to some subset of cricket-like calls, i.e., trains of pulses of relatively pure carrier frequency. Cricket calling songs can be envisioned as occupying an acoustical hyperspace in which major dimensions are carrier frequency, pulse rate, duty cycle, pulse train continuity, chirp duration, and chirp rate. My tests explored a tiny fraction of this hyperspace and used as base camp the hypervolume occupied by calls of *G. rubens*, the putative principal host of *O. ochracea* in north Florida. The main multidimensional foray from base camp was the broadcast of songs of six other crickets that were known or suspected hosts (Table I). Nearly all of the remaining tests were sallies along single dimensions (e.g., Fig. 4) and neglected other nearby parts of hyperspace. This neglect led to an incomplete picture of *O. ochracea*'s phonotactic world, as illustrated by results of the test in which both pulse rate and duty cycle were changed from the values typical of *rubens* (Fig. 7) and the tests of shifts in pulse phase in regularly interrupted trills (Fig. 8).

My tests did not refute the hypothesis that gravid females of *O. ochracea* in north Florida have a single mode of acoustical attraction, i.e., that songs decreasingly like the song of *G. rubens* are always and correspondingly decreasingly attractive. For example, the song of the other known natural host of *O. ochracea* in north Florida, *G. firmus*, attracted no more flies than might be expected on the basis of resemblance to the song of *G. rubens*. Another chirping

Gryllus, *G. fultoni*, attracted more flies than *G. firmus* and is substantially closer to *G. rubens* in pulse rate.

Future studies of ormiine phonotaxis should further explore the effects of pulse phase, duty cycle, and pulse train continuity in *O. ochracea* and look for multiple modes of acoustical attraction in species with multiple hosts in single localities, such as *Ormia depleta* and *O. lineifrons*. These studies should benefit and be benefited by neurophysiological studies of ormiine audition, as recently initiated in the United States and Germany (Robert *et al.*, 1992; Lakes-Harlan and Heller, 1992).

ACKNOWLEDGMENTS

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