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Pair-Forming Phonotaxic Strategies of Phaneropterine Katydids (Tettigoniidae: Phaneropterinae)

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ABSTRACT. Species of Phaneropterinae form sexual pairs as a result of males and/or females moving toward the sounds produced by the opposite sex. A heretofore undetermined pair-forming phonotaxic strategy is described in which conspecific males and females simultaneously move toward constant intensity sounds produced by the opposite sex. This contrasts to three previously described phonotaxic strategies, in which only the male or the female moves at a given time, and in which differences in sound intensity may elicit different responses. [KEY WORDS: Tettigoniidae, Phaneropterinae, pair-formation, sound production, phonotaxis, *Amblycorypha, Montezumina*]

Species of Phaneropterinae form sexual pairs largely as a result of males and females moving toward the sounds produced by the opposite sex. Once aggregated, other parameters (size, loudness) may be important in final mate selection (Galliart and Shaw 1991, Gwynne 1986). From experiments involving tape recorded sounds broadcast to individual specimens in an experimental cage Spooner (1968a) reported three different strategies (Figure 1, Strategies 1,2,3) of pair-forming movements in phaneropterines. Differences in the strategies involve either a male or a female moving all the way or part-way to stationary conspecific individuals, depending on the intensity of the sound received. In each strategy the male initiates the interaction. Two sounds by males are a calling song (CS), which attracts females, and a call that elicits ticks from females (FTE = female tick elicitor). The female's simple answering tick (AT) is made at species-specific timings after FTE (Spooner 1968ab, Heller and von Helversen 1986). In Strategy 1 males emit only FTE, females answer with AT, and males move the whole distance to females. In Strategies 2 and 3 males produce CS interspersed with or regularly combined with FTE. In Strategy 2 males move partway toward females answering at a distance (males receive AT at low intensity), and females move the final distance to males (females respond to CS only at high intensity). Strategy 3 is similar to Strategy 2 except that the movement patterns are reversed. Females move toward CS from a distance (*i.e.*, receive CS at low intensity) but stop before reaching a singing male. Females answer FTE with AT, which at close range attracts males (receive AT at high intensity) to move the remaining distance to the stationary females. Spooner (1968a) proposed that an undetermined fourth strategy would be expected among phaneropterines. In Strategy 4 males would produce combined CS and FTE, females would answer, and both males and females would move toward each other simultaneously (Figure 1).

Recently I became cognizant of the probable significance of the lack of separate CS and FTE components of the male acoustic repertoire as well as the importance of differences in broadcast intensity of male singing among different phaneropterine species that was missed in earlier studies. Males of Strategy 3 species produce CS and FTE as separate events and regularly lower the intensity of their calls once a female has answered (Spooner 1968a). This has the double effect of reducing the chance of other males homing toward an answering female (Spooner 1968b) as well as attracting females closer to a male CS. Males of non-Strategy 3 species typically do not vary the intensity of their calls even in the presence of answering females (males of some species have been noted at times to slightly lower their intensity of calling when first answered by a female). Males of *Montezumina modesta* (Brunner), *Inscudderia strigata* (Scudder), *Amblycorypha oblongifolia*

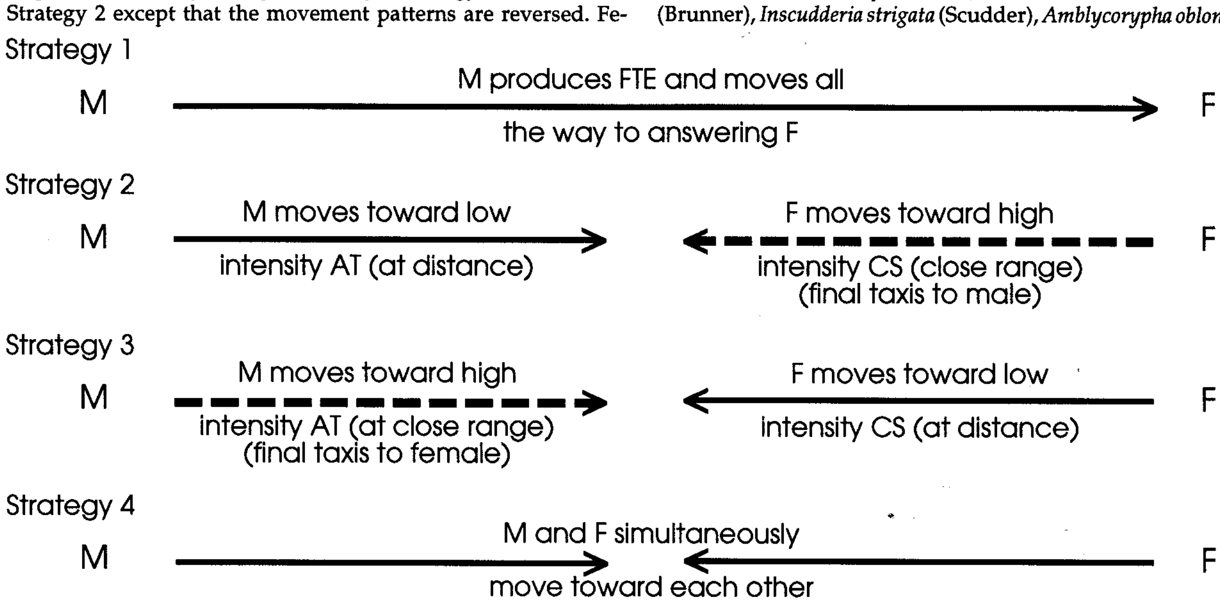

Fig. 1. Graphic representations of phonotactic pair-forming strategeis of phaneropterine katydid species in which both males and females produce sounds. Solid line—initial phonotaxis. Broken line—secondary phonotaxis. M—male. F—female. AT—answering tick of females. CS—calling song of males. FTE—female tick elicitor (sound that elicits tick from females).

Table 1. Results of experiments with virgin males and females of the "slow clicker" form of *Amblycorypha rotundifolia* to determine phonotaxes to sounds produced by conspecific individuals in uncovered cages (high intensity sounds received by the free individual) and covered cages (low intensity sounds received). See text for test set-up. M = male, F = female, + = moved all the way to caged indiv. P = moved only partway.

Uncaged Test Indiv. (free)[1]	Degree of Movement of free indiv. toward caged conspecific individ.			
	Uncovered cage		Covered cage	
	Test 1	Test 2	Test 1	Test 2
M1	+	+	+	+
M2	+	+	+	P
M3	+	+	+	+
M4	+	+	+	P[1]
M5	+	+	+	+
F1	+	+	+	+
F2	+	+	+	+
F3	P	+	P	P
F4	+	+	+	+
F5	+	+	+	+

[1]This individual moved past caged individual to one side. See text.

Table 2. Results of experiments with virgin males and females of the "slow clicker" form of *Amblycorypha rotundifolia* that were both free to move in response to sounds of the conspecific individual. See text for test set up. M1, F1, etc. are test individuals.

Uncaged male (free to move)	Phonotaxic response to conspecific individual: Met nr. midway between cages	Phonotaxic response to conspecific individual: Did not meet between cages	Uncaged female (free to move)
M1	+		F1
M2		+[1]	F3
M4	+		F5
M5	+		F4
M3	+		F2

[1]Moved partway toward each other, ended about 1 m apart at end of test.

(DeGeer), *Microcentrum retinerve* (Burmeister), and three cryptic species currently recognized as *Amblycorypha rotundifolia* Scudder typically produce songs consisting of trains of pulses or trains of phrases that apparently serve as both CS and FTE. Except for increasing intensity during the first few sound emissions in a train, these species usually do not vary the intensity of their calls after establishing a train, even in the presence of an answering female. Differences in intensity of sound received are affected only by differences in distance between sender and receiver. This study tested the hypothesis that the production of constant intensity sound in species that combine CS and FTE is correlated with Strategy 4.

This study included three pairs of *Montezumina modesta* and five pairs of *Amblycorypha rotundifolia* "fast-clicker"[1]. *Montezumina modesta* males produce a series of short lisps (average 19 msec ea) followed by long lisps (average 30 msec ea), both of which are answered by females (Spooner 1968a). "Fast clicker" males produce, in a single acoustical performance, click-like sounds—multi-pulsed phonatomes suggestive of the sound of male *Amblycorypha parvipennis* Stål (Shaw *et al.* 1990)—in successive trains, *e.g.*, 2,3,3,4,4,20+ clicks per train (Spooner 1964).[1] Females often do not answer the first couple of short trains, but usually vigorously answer the remaining short trains with one, two, or three ticks. Females also begin vigorously answering the long train before the end of the train and continue answering with several ticks after the end of the long train (unreported).

Table 3. Results of experiments with males and females of *Montezumina modesta* to determine phonotaxes to sounds produced by conspecific individuals in covered cages (low intensity sounds received by the free indiv) and uncovered cages (high intensity sounds). See text for test set-up. M1, F1, etc = test males and females, +v = vigorous response all the way to caged indiv., +s = slow movement all the way, P = moved only partway.

Uncaged Test Indiv. (free)	Degree of movement of free indiv. toward caged conspecific indiv.			
	Uncovered cage		Covered cage	
	Test 1	Test 2	Test1	Test 2
M1	+s	+s	+v	+v
M2	+s	P	+v	+v
M3	P	+s	+v	+v
F1	+v	+v	P	+s
F2	+v	+v	P	P
F3	+v	+v	P	+s

Test specimens were virgins obtained by rearing from last instar nymphs. Test specimens of "fast clicker" had been acoustically active for two and three days, of *M. modesta* for seven and nine days. Males and females of both species were kept in separate rooms in 6.2 cm x 10 cm glass jars with metal screen tops and fed vitamin-enriched whole grain cereal and water for 24-48 hours before any test observations were made. One pair at a time was studied. Caged individuals were placed 4 m apart on a carpeted floor and allowed to acclimate after having been moved. An overhead dim white light illuminated the room at a brightness which just allowed the taking of notes and observing the movements of the katydids. No movements were ever observed which could be correlated to my presence or to the light. Variation of sound intensity was accomplished by placing cloth towels across a cage to muffle the sound. A test began when the male started to sing. One or both cage lids were gently removed, and observations were made for either 1) 15 min, 2) until single individuals reached the cage of the conspecific individual, or 3) until a pair made contact. Each individual was tested twice for response to a covered conspecific individual (low intensity sounds) and twice for response to an uncovered conspecific individual (high intensity sounds). The sequences of testing response to covered or uncovered calling individuals were randomized. On the day following the tests with single individuals five tests were conducted with "fast clicker" and three tests with *M. modesta* in which both the male and female were released simultaneously.

Test results with "fast clicker" are shown in Tables 1 and 2. Both males and females of the "fast-clicker" moved toward sound produced by the opposite sex. In 18 of 20 tests uncaged males went

[1] Alexander (1960) informally described two song forms of *Amblycorypha rotundifolia* as "rattler" and "clicker." Spooner (1964) further referred to two song forms of clicker as "fast clicker" and "slow clicker."

vigorously toward the answering female and climbed on her cage whether the female was covered or uncovered. In one test male M4 walked past the female about 30 cm to one side and moved away. In the remaining test male M2 simply did not move and sang vigorously to the uncovered answering female. Tests with females were similar. In 17 of 20 tests uncaged females went straight to the male cage while answering the male. In the other three tests the female moved somewhat in the direction of the male but did not reach the male cage. In four tests in which both the male and the female were released (Table 2), each moved toward the other simultaneously and met somewhere between their two cages. The fifth pair moved toward each other sporadically but mostly sang loudly. At the end of the test they were about one meter apart. The fifth pair were the same ones that did not go all the way to the opposite cage when released in a one-free-at-a-time test.

Montezumina modesta results are shown in Table 3. Females went all the way to the uncovered male cage in six of six tests, all the way to the covered male in two of six tests, and part way to the covered male in the remaining four tests. Males went rapidly to the covered female cage in six of six tests, hesitantly but all the way to the uncovered female in four of six tests, and only part way to the uncovered female in two tests. In all three tests with both the male and female free to move, both sexes moved toward each other with the female moving more vigorously than the male. They always met closer to the male cage.

The "fast clicker" results strongly support the hypothesis that a fourth pair-forming phonotaxic strategy, as defined earlier, does operate. The *M. modesta* results may weakly support the hypothesis. Spooner (1968a) reported Strategy 3 for *M. modesta*. In that study females answered tape recorded short and long lisps at all intensities "but moved very little towards the short lisps... Long lisps attracted females when broadcast at high intensity." Note that the females did move toward the short lisps. The single male in that study moved toward low intensity AT. In the present study *M. modesta* makes Strategy 4 movements, although males show stronger response to low intensity AT and females to high intensity long lisps (CS).

These tests demonstrate that, in species that combine CS and FTE at non-varying intensity in each acoustic broadcast, either sex may move toward the other under high or low intensity circumstances. In individual cases a given male or given female may move all the way to the opposite sex, or both may move simultaneously toward the other. The whole context of combined CS and FTE, non-varying intensity of calling, and movement of either sex at any intensity of sound received constitutes the Strategy 4 system. Determining the scope of Strategy 4 clarifies the operative context of Strategy 3, which requires that CS and FTE be produced as isolated, unrelated events with no predictable frequency. Strategy 3 species enhance the effectiveness of Strategy 3 calling and corelated phonotaxes by male reduction of loudness in the presence of an answering female.

Spooner (1968a) concluded that there would probably be few cases of Strategy 4 due to the difficulty of homing toward a moving source of sound in coarse vegetation. The conclusion is unfounded. I have had numerous occasions since then to observe different phaneropterines moving across vegetation toward conspecific sounds with remarkable directionality. In Strategy 4 the task should be no more difficult, because both individuals call to each other more or less continuously while moving toward each other.

A Strategy 4 pair-forming system is an understandable evolutionary accomplishment in phaneropterine phonotaxic systems. In the presence of answering females the simultaneous movement of both sexes may have the desirable effect of reducing the time required for the pair to make contact and return to silence. Reduction of calling time conserves energy spent on mating effort (Bailey 1995, Bailey *et al.* 1993) as well as reducing the chances of predators (Walker 1964) and parasitoids (Cade 1975) locating a calling individual. Conservation of energy spent on mating effort may allow for greater partitioning of energy spent on parental investment through the spermatophylax (Simmons *et al.* 1992). It would be informative to compare the size of the spermatophylax relative to total body weight of Strategy 3 and Strategy 4 males.

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