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**Orthopteran
Mating Systems**
Sexual Competition in a
Diverse Group of Insects

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Chapter 4

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4. Random Noise and Congeneric Discrimination in *Conocephalus* (Orthoptera: Tettigoniidae)

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Phonotactic bioassay of Ensifera began with Regen (1913): female crickets, *Gryllus campestris*, performed an oriented locomotion to a disembodied male call, relayed by a speaker. Many workers since have experimented with the information content of cricket and katydid calling songs by observing behavior in response to speaker broadcasts: Busnel et al. (1956), Walker (1957), Hill et al. (1972), Zaretsky (1972), Morris (1972), Ulagaraj and Walker (1973), Morris et al. (1975), Paul (1976), Morris et al. (1978), Popov and Shuvalov (1977), Moiseff et al. (1978), Pollack and Hoy (1979), Forrest (1980). This area of study was reviewed recently by Elsner and Popov (1978) who drew attention to the tendency of females in choice situations to approach those "signals which have the higher probability of being the conspecific song" by a process these authors termed "recognition preference". The insect is hypothesized to compare the physical structure of the perceived sound against species-characteristic features encoded in its central nervous system (see also Popov and Shuvalov 1977). Sounds can sometimes evoke approach, even if they deviate greatly from this ideal, but only if presented in the absence of a 'better' stimulus.

As part of a phonotactic bioassay investigating effective parameters of tettigoniid calling song, we broadcast random noise to *Conocephalus nigropleurum* females. Noise is random when the instantaneous sound amplitude changes over time according to a normal distribution curve (Beranek 1954). Since species-unique patterns of amplitude modulation (AM) are such an important feature of ensiferan calling songs, we did not expect this signal, lacking any patterned AM, to evoke response. Our intention was to use noise as a neutral sound emission, a raw material onto which we could impose AM patterns and test their role in evoking taxis. To our surprise some females were attracted to this signal. This occurred even when the noise was presented in

competition with the song of a conspecific male, an apparent contradiction of 'recognition preference'. These females were also attracted to the song of another species, *Conocephalus attenuatus*, again, even in the presence of conspecific song and in spite of the distinctive AM pattern of *attenuatus*.

But not all of the stimuli we tested were effective. The broadcast song of another congener, *Conocephalus brevipennis*, produced no phonotaxis, in spite of the fact that this species employs essentially the same ultrasonic carrier band in its song as *nigropleurum*. Even if *brevipennis* song was the only stimulus, females of *nigropleurum* failed to exhibit phonotaxis.

It is common practice in phonotactic bioassay to isolate female subjects from males, thereby maintaining sexual receptivity and responsiveness to the calling song. This procedure has been criticized (Forrest 1980), quite properly, as possibly leading to abnormally low response thresholds and a lack of discrimination. Were it not for the discrimination of *brevipennis* song by *nigropleurum* females, such an explanation might be advanced here.

C. nigropleurum females do not appear to require the presence of their species-specific AM pattern to execute phonotaxis: they will respond to unstructured, broad-band ultrasonic noise. Yet they will not approach a virtually identical broad-band ultrasonic carrier when there is superimposed upon it the AM pattern of a sympatric congener. The rationalization of these observations, with reference to the applicability here of recognition preference, is the subject of this paper.

CONOCEPHALUS CALLING SONGS

Conocephalus is a very large genus of relatively small (<2 cm body length) katyids. More than 100 valid species have been described worldwide (Pitkin 1980). They live at much higher densities than most other tettigoniids. At the peak of their singing season, a population of *nigropleurum* singers exhibited a density of $0.42/m^2$ in a preferred sedge habitat (Morris 1967). Compare this for example with *Mygalopsis marki* at $0.01/m^2$ (Bailey and Thiele 1982) or with *Amblycorypha parvipennis* at $0.004/m^2$ (Shaw et al. 1981).

Conocephalus katyids are typically diurnal in a characteristically nocturnal family. Visual stimuli may be more important to them than to other tettigoniids; they respond readily to human movement during stalking. They prefer moist, weedy, herbaceous sedge and grass habitats. The males produce faint calling songs in which broad-band ultrasonics predominate. Beyond the human

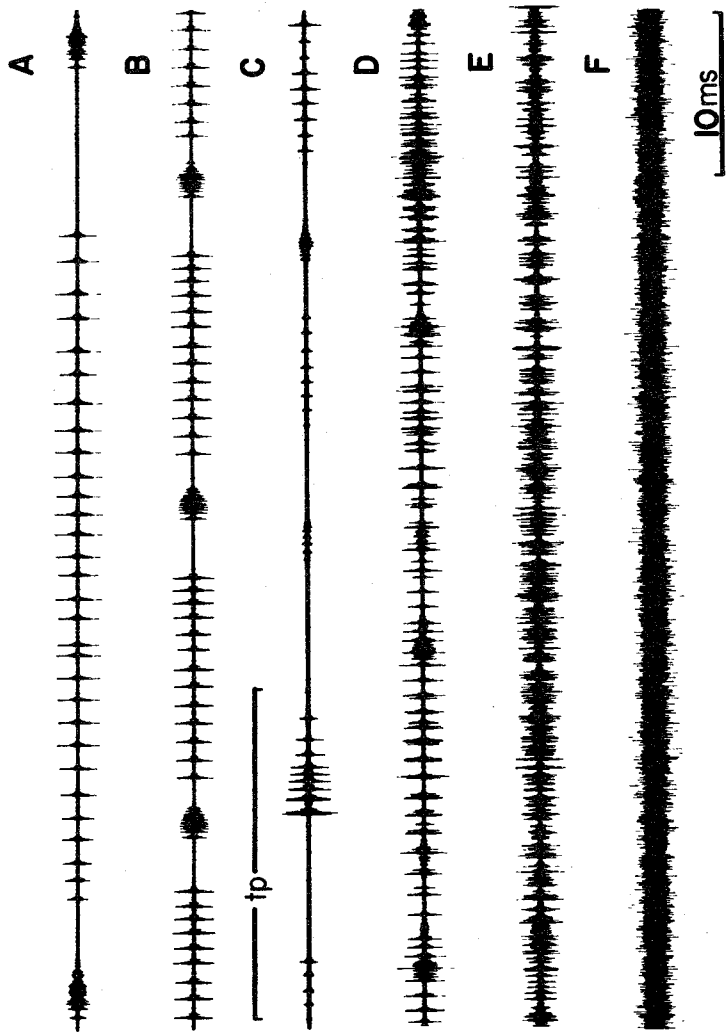


Fig. 1. Oscillograms of *Conocephalus* spp. and of random noise, prepared at the same time base and with the same recording temperature. A. One male of *nigropleurum*. B. One male of *brevipennis* during the buzz. C. A single tick phonatome of *brevipennis* immediately prior to buzz onset. D. Ten superimposed songs of 10 individuals of *nigropleurum*. E. Ten superimposed songs of 10 individuals of *brevipennis*. F. Random noise.

frequency range their songs are actually quite intense: readings of more than 90 dB at 10 cm (linear, fast) are typical (Morris, unpub.). However the density of the vegetation in their habitats can be expected to substantially reduce the perceived intensity of these ultrasonic calls (Griffin 1971).

Each cycle of wing movement generates a 'phonatome' (Walker and Dew 1972, 'syllable' of Samways 1976) comprised of one minor and one major pulse train (Fig. 1A). Each passage of the anal edge of one forewing across a tooth series on the underside of the other forewing, produces a succession of rapidly damping pulses. The rapid-decay nature of these pulses results in their clear temporal separation, at least in major pulse trains, a feature contrasting markedly with the sustained sinusoidal pulse produced by crickets on each file run (Morris and Walker 1976).

The waveform of each pulse is complex and this complexity is manifest in a noisy spectrum of carrier frequencies, continuous from the low audio to beyond 100 kHz (Morris and Pipher 1967, Pipher and Morris 1974). *C. nigropleurum*, *C. attenuatus*, and *C. brevipennis*, the three temperate-zone North American species considered here, all share this same noisy, but remarkably consistent, frequency spectrum (Fig. 2A,B,C). A more intense energy band occurs between 28 and 50 kHz, with a broad principal peak near 40 kHz (Morris and Pipher 1967). In *nigropleurum* during the major pulse train, frequencies in the 30-45 kHz range shift downward about 5000 cycles (Pipher and Morris 1974); the signal function, if any, of this frequency modulation remains unknown.

Phonatomes recur at high speed, e.g. about 15/sec in a male of *nigropleurum* measured at 25°C. To our ear this appears as a steady buzz, though as emphasized above, there is much silence between the component pulses (Morris et al. 1978). *C. nigropleurum* continues its buzz uninterrupted for minutes at a time. The calling song of *attenuatus* is also a buzz but at about double the phonatome rate of *nigropleurum* for any given temperature. *C. brevipennis* (Fig. 3) differs by possessing a chirp structure ('echeme' of Samways 1976): short buzzes of about a second in duration are interspersed with two to several single phonatomes (Fig. 1C) of an AM pattern distinct from that of the buzz phonatome (Morris and Walker 1976). These single phonatomes are heard by human observers as discrete ticks; the phonatome rate of *brevipennis* during the buzz is about triple that of *nigropleurum* for any given temperature.

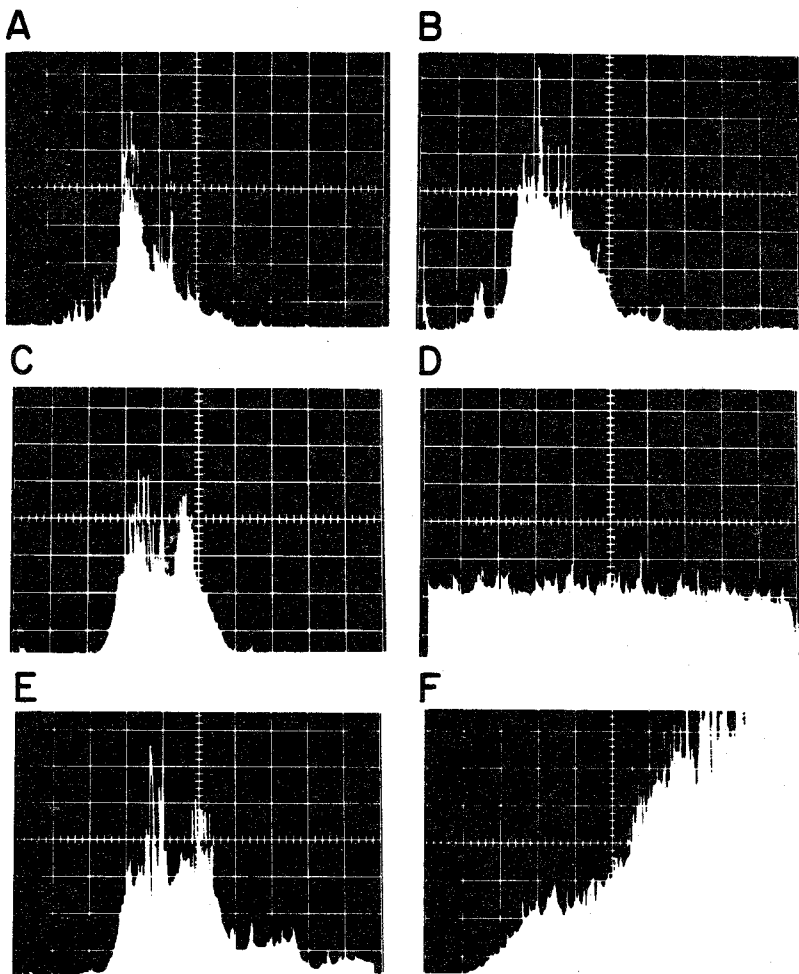


Fig. 2. Frequency spectrograms of *Conceptualus* songs, and of random noise, made with Tektronix 3L5 analyser at 20 ms/div. continuous sweep. Each division on the x axis 10 kHz, range 0-100 kHz. A, B and C of *brevipennis*, *attenuatus* and *nigropleurum* respectively; each is based upon a 10-s song sample of a single male taken directly from the Analog-7 output. D is a spectrogram of the random noise signal as it appeared at the Philips output. E and F show the effect on carrier frequency of signal transmission via the power amplifier and speaker. E is of the *nigropleurum* male, F of the random noise. E and F were obtained by analysing the output of a B and K 2204 sound level meter and 1/4" microphone, the latter placed 10 cm in front of an arena speaker.

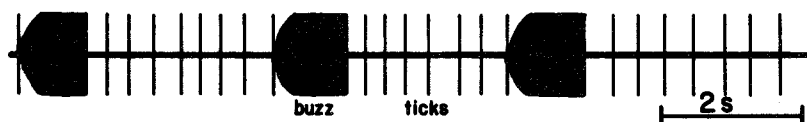


Fig. 3. Diagram of the buzz-tick sequence of a *brevipennis* male at 30°C.

PHONOTACTIC BIOASSAY EXPERIMENTS: PROTOCOLS

C. nigropleurum specimens were reared from field-collected eggs (Pipher and Morris 1974) and sound stimuli presented to animals released singly at the center of a circular arena. The arena surface was fiberglass screen (6 strands/cm), stitched with thread to the rim of an aluminum hoop 140 cm in diameter. This hoop was suspended horizontally about 1 m below the ceiling in a room modified to reduce reverberation and the penetration of external sounds. Insects were introduced from beneath via an opening in the screen 6 cm in diameter at the arena center. The animals were held between trials in a glass cylinder cage (10 cm high, 8 cm in diameter) with a screen top but no bottom. In preparation for a trial this cage was inverted beneath the opening with a card held against the open end to prevent premature exit; to begin a trial the card was slipped to one side, and as the insect walked voluntarily out of its cage and up through the opening, playback was started.

Four speakers built to specifications given by McCue (1961) were suspended above the arena on an aluminum frame. They were located at the hoop periphery with their centers 10 cm above the arena plane. Each speaker faced into an equal quadrant of the arena. Two concentric centered circles were drawn on the screen surface with 30 and 60-cm radii and each quadrant was marked off into three sectors, the middle sector symmetrical about a speaker. The sector (or quadrant) in which a first crossing of the 60-cm circle occurred established direction of exit as the criterion of response. Two power amplifiers (McCue 1961) were symmetrically placed on the floor beneath the arena. Four symmetrically positioned incandescent lights illuminated from above.

Experiment temperatures were always within 1°C of those at which song stimuli had been recorded and are specified on figures summarizing exit results. In single-stimulus presentations the broadcast was randomized to occur from any one of the four quadrant speakers. With simultaneous presentation of two

sound models, broadcast quadrants were always adjacent, the second stimulus randomized to the right or left of the first. Randomization included which of the two power amplifiers received the output of a Philips Analog-7 instrumentation tape recorder, located in an adjoining room; the sound stimuli to be presented were stored on a tape loop on different tracks of this recorder. The Philips recorder was less responsive to sound frequencies above 40 kHz, while the amplifier-speaker system increasingly emphasized ultrasonics. The two systems combined fortuitously to produce a *Concephalus* sound spectrum very close to that of the real insect.

The noise signal used originated with a General Radio 1390B random noise generator; it was transferred to a track of the Philips recorder. The 'randomness' of random noise is a reference to its amplitude characteristics (see above) and not to its spectral content. In this case the virtually flat spectrum of the Philips output (Fig. 2D) was shaped by the speaker and power amplifier to an increasing emphasis of ultrasonics (Fig. 2F).

Broadcast sound levels were the same for all stimuli. Using one of the two power amplifiers set at an arbitrary gain, the particular Analog-7 amplifier, for each track on which a sound stimulus had been recorded, was adjusted to produce 90-92 dB (linear, fast) 10 cm directly in front of the speaker. This sound level was measured with a clamped Bruel and Kjaer condenser microphone (4135) and sound level meter (2204). (Levels for the song of a single *brevipennis* male were set by reading the peak displacement achieved and held by the meter needle during the short buzz of this species.) Subsequently the gain of the second power amplifier was set by broadcasting a model for which the Analog-7 had already been adjusted and obtaining the same 90-92 dB output sound level. To correct for differences in the broadcast fields of the four speakers, the microphone was clamped vertically at the arena center with its sensitive element in the arena plane; using a pure tone test sound, the four speakers were manipulated in their orientation until a uniform sound level was achieved at the arena center.

In creating multiple singer recordings, songs of individual males were each recorded on a different channel of the Philips recorder. To produce, for example, a single track incorporating the songs of five different *nigropleurum* males, the outputs of all five amplifiers were directed into one channel of a Lockheed 417 instrumentation tape recorder. The resulting five-male recording was transferred in turn onto one channel of a new Philips tape loop for broadcast in arena trials.

TAXIS TO RANDOM NOISE

Unmated adult *nigropleurum* females were tested for their phonotactic response to random noise in single-stimulus presentation. They exited from the random noise speaker quadrant in numbers inconsistent with an hypothesis of no stimulus effect (Fig. 4A). We conclude that attraction occurred to a sound entirely lacking in patterned amplitude modulation.

As mentioned above, it is at first puzzling that sound, devoid of an AM pattern, should be attractive. But based upon studies with crickets, when only one stimulus is offered even a very rough model may evoke positive taxis (Elsner and Popov 1978). If the *nigropleurum* female is given a choice between the random noise and song of her own species, she should demonstrate 'recognition preference' and discriminate strongly in favor of her male's call.

Virgin females were presented with simultaneous broadcasts of random noise and the song of a lone conspecific male. Attraction to the acoustic half of the arena was highly significant (Fig. 4B), indicating the phonotactic responsiveness of the tested insects; but there was no discrimination between the two stimuli. Thus, recognition preference notwithstanding, female *nigropleurum* will respond to an imperfect stimulus even in the presence of an ideal.

C. *nigropleurum* females will in general tolerate wide departures from the AM patterning of their calling song without discriminating against an acoustic model. For example, the calling song of a male of *nigropleurum* was broadcast simultaneously with the same recorded song from which minor pulse trains had been deleted (Morris et al. 1978). Females responded readily to both sound sources but did not show a significant preference for the intact song. The same result is seen in a dual presentation of conspecific calling song and the song of *attenuatus* (see below).

It can be argued that the response to random noise is an artefact of experimental design. Critical AM patterns having evoked recognition, localization might proceed indiscriminantly to any perceptible (ultrasonic?) source. Thus in dual-stimulus presentations such as those described above, presentations involving conspecific calling song and some less than ideal acoustic model, e.g. random noise, the species-specific pattern would always be present to evoke taxis. Orientation by some females to random noise would not then represent a choice of random noise, but an error brought about by activation of a species recognition center (template) in the nervous system.

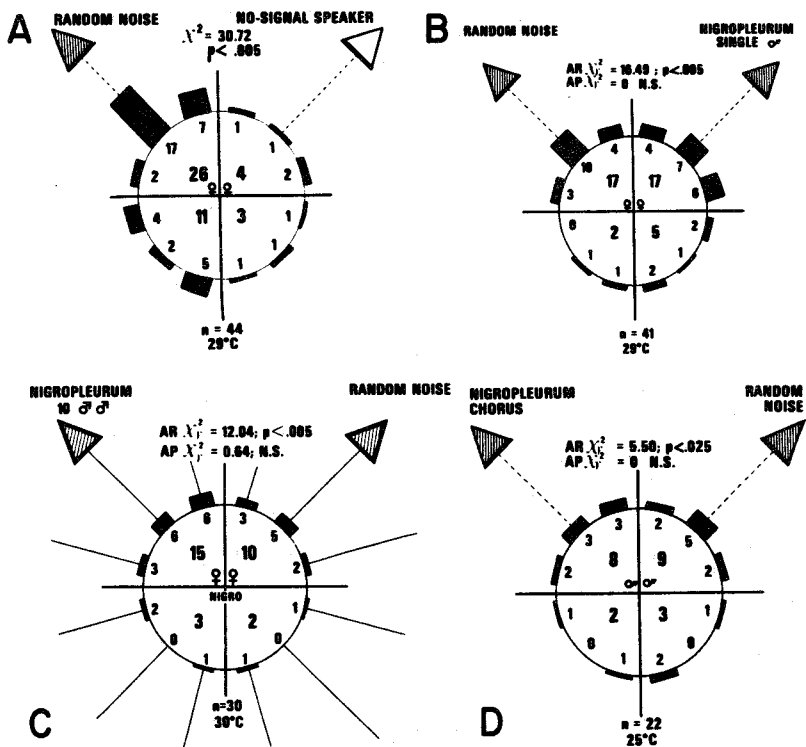


Fig. 4. A. Response of **nigropleurum** females to random noise in a single-stimulus presentation. B. Dual-stimulus presentation of the song of a **nigropleurum** male and random noise to **nigropleurum** females. C. Response of **nigropleurum** females to the overlapped songs of 10 conspecific males broadcast with random noise. D. Response of **nigropleurum** males to a multi-singer recording of conspecific males broadcast with random noise.

This interpretation is unlikely for several reasons. 1) It does not account for the approach of the insects to random noise in single-stimulus presentation. 2) It does not explain why **nigropleurum** females fail to approach **brevipennis** song in the presence of their own male's calling song (see below). 3) It does not explain the success of models where the species-specific AM pattern is masked by the overlap of many songs (see 10-male model below). 4) The inefficient pairings such a

mechanism would invite in nature are unlikely to be tolerated by natural selection: if this mechanism obtained, insects within earshot of both their own species and the songs of congeners, would often misdirect their pairing activities.

If response to random noise is not the result of indiscriminant localization in the presence of the species-specific calling song, could it represent a distinct tactic response occurring normally in the life of this species?

TAXIS TO AGGREGATE SONG: AN HYPOTHESIS

In addition to recognition preference Elsner and Popov (1978) draw certain conclusions about information coding in cricket calling songs. They identify two kinds of parameter, 1) stereotyped, species-distinctive parameters that function in species recognition, 2) variable, graded, contextually influenced parameters that function in motivation. Motivational parameters (e.g. echeme repetition rate) change with the internal state of the emitter: they are rates of display, 'power parameters', involving altered amounts of sound energy over time. Recognition parameters are primarily patterns of amplitude modulation, the output of classic ethological fixed action patterns.

The songs of *Conocephalus* spp. are already very like random noise in terms of their frequency spectra. Energy occurs at every frequency between 1 and 100 kHz; the principal (ultrasonic) energy band is more than 20 kHz wide. Whatever the sensitivity curve of a *Conocephalus* ear (Suga 1966), a female would perceive about the same band of sound energy in a random noise broadcast that she does in the conspecific song. Her differing sensitivity across the carrier spectrum would 'carve out' an appropriate ultrasonic carrier band from the random noise spectrum. Only the AM patterning would be absent from a random noise stimulus.

Successful transmission of an AM pattern, i.e. of recognition parameters, requires a favorable signal-to-noise ratio. The signal in this case will be the AM pattern of any singer which an approaching female elects as an individual goal; noise will be any background sounds tending to obscure this pattern. In their habitat these *Conocephalus* spp. are the only diurnal organisms producing sustained intense sound in the 28-50 kHz ultrasonic carrier band; therefore they will themselves constitute the major source of noise. Perception of a clear signal will obviously improve as the receiver nears the signal source, because the approach distance will have become shorter than distances to any competing noise

sources. In most katydid species singing males may maintain fairly large interindividual distances relative to the average distance of phonotactic approach. But the extremely high singer densities of *Conocephalus* mean that distances to noise sources are very short and females must be very close to their goal for a given male's signal to predominate.

Consider a female of *nigropleurum* in two contrasting field situations, 1) in the midst of an aggregation of conspecific singers and 2) relatively isolated at a distance of 10 m or more from such an aggregate, perhaps a female that is dispersing. The density of singer aggregates has already been stressed. The distribution of calling males within such a grouping is highly regular. In a large population of *nigropleurum* (Morris 1967), R of Clark and Evans (1954) was 1.67, indicating a significant ($p < .01$) departure in the direction of regularity from the frequency distribution of nearest neighbor distances to be expected under an hypothesis of random spacing between singers. The mean nearest neighbor distance of the singers was 90 cm (Morris 1967).

Case I. A female in an aggregation cannot on average be more than half the mean nearest neighbor distance (45 cm) from a singing male. In a perfectly regular aggregate the AM patterns of at least the nearest ring of six singers will certainly be perceptible and could be brought further above the background noise by changes in the female's orientation or in the alignment of her hearing organs. Use of AM patterns for species recognition in this situation is perfectly feasible. But the close proximity of so many potential mates and the ready availability of alternative stimuli by which mates could be localized and assessed (vibratory, olfactory and especially visual) raises doubts about necessary reliance on sound.

Case II. The female, assuming her ears are sufficiently sensitive, should perceive the distant aggregate as confined to a limited arc of the horizon. The pulses of tens of males, delivered at rates of several hundreds each second, each male singing independently of the others (i.e. asynchronously), should fill in the inter-pulse intervals of silence and produce a collective calling song that resembles the time course of random noise very closely (compare D and F of Fig. 1). Only the carrier band should be preserved at this long range, a band that cannot contribute to species recognition since it is apparently shared by most species in the genus.

If this reasoning is valid a female in situation two is not close enough to any aggregate male to recognize his song. There is no significantly nearer male and hence all signals are received at about the same peak

amplitude. Amplitude modulation patterns would seem to be unavailable for long-range species recognition in *Conocephalus*. The random noise signal of our experiments could be providing a female with exactly the same limited information provided by a distant aggregate of singers in the field.

We hypothesize an evolved phonotactic aggregation response in *nigropleurum*, distinct from phonotaxis to individuals. We suggest that under the conditions usually experienced by isolated dispersing individuals phonotaxis can occur to any sound sufficiently sustained and with appreciable energy in the 28-50 kHz band. AM patterns, even if perceptible, are not effective in this instance and species recognition is not involved.

The existence of such a response accords with previous experimental results involving *nigropleurum*. Females offered a choice between the combined, hence louder, sound output of a 'group' of two males and the simultaneous and equidistant broadcast of one male's song, significantly preferred the group (Morris et al. 1978). Females of *nigropleurum* have also been shown to mate preferentially with the heavier of two males (Gwynne 1982a). Males of many tettigoniid species including *nigropleurum*, transfer nutrients to the female during mating and thereby undergo a substantial weight loss (Gwynne 1982b); the capacity of a male to make this contribution varies with his size and recent mating history (Gwynne 1982b) and females should benefit reproductively by discriminating heavier males as mates.

These experimental results combine to support a sexual selection model proposed by Alexander (1975, see also Greenfield and Shaw 1982). Alexander argues that females in many acoustic insects may have been selected to place themselves in a group situation where they can have the "greatest opportunity to compare males". By their attraction to aggregations of singers, females of *nigropleurum* may be maximizing the nutritional investment they obtain from their mate.

A sound model was constructed to test the equivalence of random noise and unison singing¹; it involved the simultaneous stridulation of 10 different *nigropleurum* males. Individual singers were recorded at

¹ Greenfield and Shaw (1982) define chorusing and include 'unison singing' as an example of its simplest form. *C. nigropleurum* are probably capable of unison singing, i.e. they sing in response to each other's song over "the same extended time period without consistent temporal relationships between any song units".

30°C on five tracks of the Philips recorder. These were then transferred together to one track of the Lockheed. The process was repeated with another five males and then the two five-male tracks were rerecorded simultaneously to produce a single 10-male recording. Chance inherent in their assembly governed the phase of these superimposed signals; the resulting model was examined on an oscilloscope for any fortuitous exact synchronization of pulse trains and none was found.

Broadcast in competition with random noise, this 10-male acoustic model was not significantly better in attracting *nigropleurum* females (Fig. 4C). Both stimuli evoked taxis in the females ($p < .005$) and random noise was treated as equivalent to the artificial song aggregation. It should also be noted that the species-characteristic AM pattern is most unlikely to have survived the 10-male overlap; this experiment is therefore further confirmation that the species-specific AM pattern need not be present to evoke phonotaxis.

A phonotactic aggregation response should not be limited to females: males must also approach conspecific song as a necessary part of aggregation formation. (For a discussion of the reasons why males should closely approach male competitors see Greenfield and Shaw 1982.) *C. nigropleurum* males were tested in a dual-stimulus presentation. One speaker broadcast random noise, the other a 'chorus' of conspecific males (Fig. 4D). This multisong recording was produced in one operation from a cluster of caged, calling males. Twenty were confined individually in small, cylindrical, screen cages (10 cm high, 4.5 cm in diameter), the cages placed contiguously on a flat, fiberglass screen surface. The combined output of an undetermined number of singers was recorded 1 m from the center of the cage cluster. Males released, one at a time in the arena, exited significantly more often in the acoustically active half ($p < .025$) but failed to discriminate between the two stimuli.

Males as well as females are attracted by random noise and do not distinguish it from unison singing of conspecifics. In the field the effect of such behavior by both sexes should be aggregation. Failure of males to discriminate in favor of a real chorus, strengthens the contention that at long range, individual AM patterns are submerged in the calls of neighbors and unavailable to the insect's perceptive system as species-recognition cues.

TAXIS TO CONGENERS

If *nigropleurum* females are attracted to any reasonably persistent sound that occupies the ultrasonic

band typical of the genus, they must sometimes approach singer aggregations of other *Conocephalus* species and expose themselves to the risk of interspecific matings. Some form of species recognition has to occur at close range. Of course over short distances and with a visually competent diurnal insect, sound as a beacon may not be so important. But it is unlikely that use of calling song in recognition has been supplanted completely by visual or olfactory stimuli, otherwise the species-unique and diverse AM patterning of the genus becomes difficult to explain.

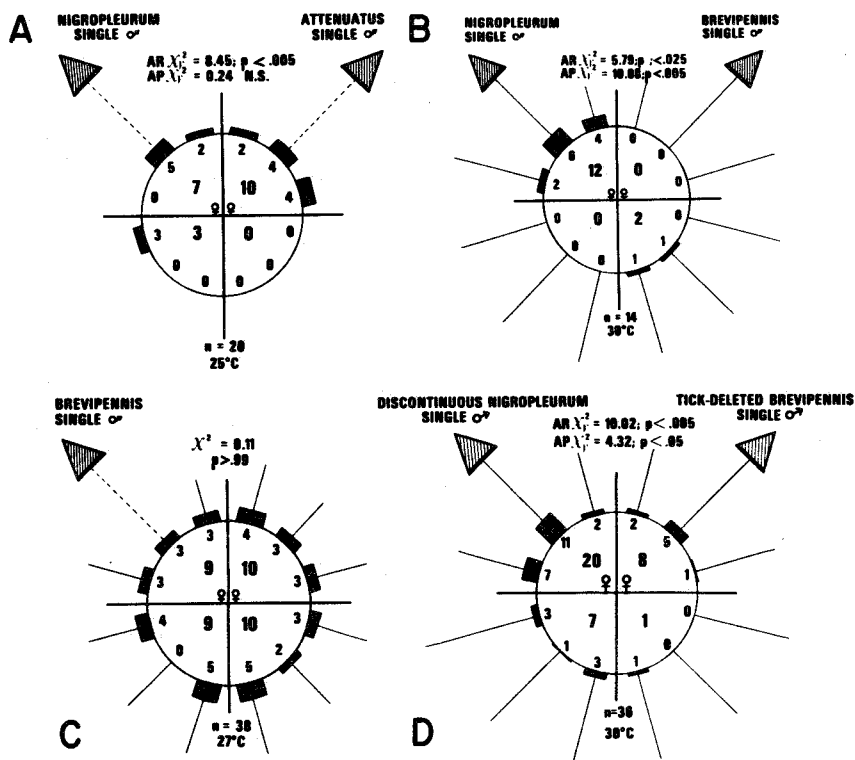


Fig. 5. Broadcasts to *nigropleurum* females. A. The song of a single *nigropleurum* male vs that of a male of *attenuatus*. B. Dual-stimulus presentation of the song of one *nigropleurum* male and that of a male of *brevipennis*. C. Response to *brevipennis* song in a single-stimulus presentation. D. Dual-stimulus presentation of *nigropleurum* song, interrupted to resemble *brevipennis* buzz durations, and *brevipennis* song from which ticks have been deleted.

An experiment was undertaken with the song of a congeneric: *C. attenuatus*. At a given temperature this species moves its wings to and fro twice as fast as does *nigropleurum*. Its AM pattern should be easily distinguished by *nigropleurum* females. A recording of a single *attenuatus* singer was broadcast simultaneously with the song of a *nigropleurum* male. Females of *nigropleurum* exhibited positive phonotaxis, but showed no significant preference for their own song (Fig.5A). In the presence of the acoustic display of their own conspecific male, they approached the highly AM-distinctive song of a congeneric. This is counter to the result predicted by 'recognition preference' but consistent with our hypothesis of general responsiveness to an ultrasonic carrier.

Though the ranges of *attenuatus* and *nigropleurum* in temperate North America overlap broadly (Alexander 1957), there is no report of these insects occurring syntopically. Populations of the two species have been observed only a few kilometers apart but never within earshot of each other (Morris, unpub.). The attraction of *nigropleurum* females to *attenuatus* song may not present problems in nature if these insects are separated geographically for ecological reasons.

C. nigropleurum is commonly found within earshot of *brevipennis* in swale habitats in southern Ontario. Populations appear to be contiguous rather than intermingled (Morris, unpub.). When song of a single male of *brevipennis* was tested against that of a single *nigropleurum* male (Fig. 5B), *nigropleurum* females exited only toward their own species ($p < .005$). More impressively, when *brevipennis* song was presented alone (Fig. 5C), phonotactically responsive *nigropleurum* females (determined previously) exited the arena in randomly selected directions ($p > 0.99$). Even though *brevipennis* song provided abundant sound energy in the genus-characteristic ultrasonic band, these insects, so indiscriminant in their signal preferences in other contexts, remained unattracted in a 'no choice' situation.

Rejection in single presentation, even though a model is highly similar to the natural calling song, was also observed in *Gryllus bimaculatus* (Popov and Shuvalov 1977). *G. bimaculatus* occurs in Azerbaydzhan district, in the Caucasus near the border with Turkey, where it is sympatric (and syntopic?) with *G. campestris*. The carrier frequencies of the two species are virtually identical at 5 kHz. *G. bimaculatus* males produce 4 or 5-pulse chirps while *campestris* males produce only 3-pulse chirps. Whereas female *bimaculatus* from these populations readily approached chirps of 4, 5 and higher numbers of pulses, 80% of receptive females ($n=20$) failed to execute a phonotaxis to 3-pulse chirps. This result

might be a parallel to that observed in the case of *brevipennis* and *nigropleurum*. Physical parameters, predictive of congenericity with which pairing mistakes may have been common in the past, could carry a special potency in the avoidance of positive phonotaxis.

C. brevipennis also form dense aggregations of singing males. As argued above on theoretical grounds, the species-characteristic AM pattern of *brevipennis* should be obscured for a receiver monitoring the chorus at long range. If enough *brevipennis* are singing simultaneously, with unrelated phasing of their echemes (and there is no evidence of synchronized chorusing in *brevipennis*), all that can survive to the ear of a distant *nigropleurum* female is the genus-specific ultrasonic carrier band. To this band, according to our hypothesis, she should respond with positive phonotaxis.

Three dual-stimulus experiments tested this prediction. Receptive *nigropleurum* females were offered a

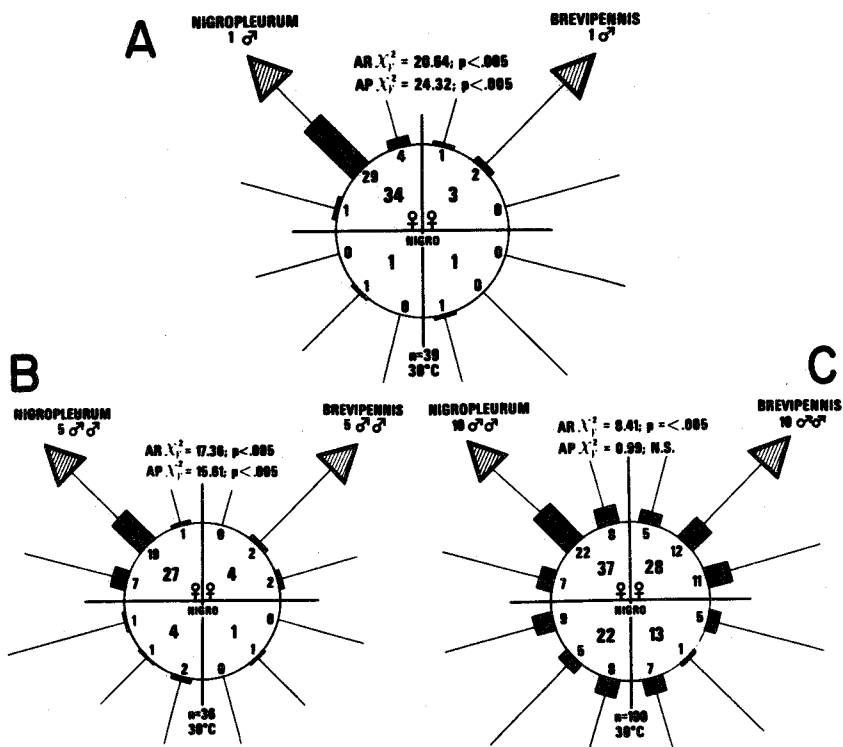


Fig. 6. Response of *nigropleurum* females to their own species' song and that of *brevipennis* in dual-speaker broadcasts when the stimuli involve A) single male songs, B) 5 overlapped songs, and C) 10 overlapped songs.

choice between songs of a lone **nigropleurum** and a lone **brevipennis** male (Fig. 1A, B); the females approached their conspecific stimulus but not the heterospecific (Fig. 6A). When the choice was between the output of five simultaneously singing males of **nigropleurum** and five of **brevipennis** (five different individuals were used in each case to construct the playback tape), females were still able to discriminate in favor of their own species (Fig. 6B). When the number of singers was increased to 10 for each species (Fig. 1C,D; Fig. 6C), the **nigropleurum** females exited significantly more often in the acoustic half of the arena ($p < .005$) but no longer discriminated their own species over **brevipennis**.

These results support the contention that many simultaneous songs, perceived at a suitable distance, can obscure AM patterning. They affirm the attractiveness of conspecific song even when its AM pattern is hidden, for it is difficult to imagine the AM pulse pattern of **nigropleurum** (Fig. 1C) surviving the overlap of 10 songs. Most significantly, these experiments suggest that only perception of the AM pattern of **brevipennis** prevents phonotaxis to this stimulus; the carrier band of **brevipennis** is quite acceptable.

It seems inevitable that in the field **nigropleurum** females and males must sometimes approach **brevipennis** singer aggregations. This may ultimately bring **nigropleurum** into contact with their own kind since the two species so commonly occur together. But what mechanisms of close range recognition might actually be used?

HETEROSPECIFIC RECOGNITION?

Two mechanisms seem plausible, both following after the initial long-range **unspecific** phonotaxis toward the ultrasonic band. As a **nigropleurum** female perceives the AM pattern rising out of the background ultrasonics created by neighboring songs, she will presumably enter a recognition phase directed at the output of a single individual. Mechanism I supposes she would somehow match this individual's acoustic output against a neuronal template encoded to respond only in the presence of certain diagnostic AM features found in the song of **nigropleurum**. This is the procedure considered by Elsner and Popov (1978) to underlie recognition preference. **C. brevipennis** song, since it lacks the critical AM patterning, would fail to engage such a template; failure to respond would be due to the **absence** of species-specific features.

Suppose as an alternative mechanism (II) that **nigropleurum** does not rely on its AM pattern for recognition but responds positively to the ultrasonic

band until contact is made in other modalities. The conspecific nature of the sound source might then be confirmed by visual or olfactory cues. For females motivated to mate, approach to a conspecific could be completed with the song complementing other stimuli. If the AM pattern of a *brevipennis* male was perceived above the background chorus, further close-range approach to that particular source might be inhibited by a neuronal template, the template activated by AM features in the song of *brevipennis*. By employing such a mechanism females would in effect be recognizing heterospecific song. Failure to respond to *brevipennis* would be due not to the absence of a characteristic conspecific patterning but to the presence of a particular heterospecific one.

We have already discussed the reasons why taxis of *nigropleurum* females to *attenuatus* song (Fig. 5A) should not be explained as activation of a species-recognition template by a conspecific song that is present but not approached. If *nigropleurum* females utilize a species-recognition template it seems more reasonable to argue that it was activated in this case by the same stimulus to which the insects oriented. In other words, *attenuatus* song was able to satisfy the (hypothetical) template and provide the necessary diagnostic AM features. But a template is not very precisely diagnostic if it finds acceptable, pulse train rates double those of its own species. Recognition preference is envisaged as using a much more restrictive template match than this. In two-stimulus presentations, departures from the ideal template should suffer in comparison to the calling song, not perform just as well. Conspecific song from which minor pulse trains were removed should not be as effective as calling song; yet it is as effective in the case of *nigropleurum* (Morris et al. 1978). With an AM pattern as straightforward and relatively simple as is that of *nigropleurum*, loss of a minor pulse train or doubling of phonotome rates above those characteristic for the temperature, represent rather drastic changes. Such considerations have led us to doubt the likelihood of a species-recognition template in this species.

It might however be the case that such a template operates in *nigropleurum* on the basis of AM pattern continuity. As long as sound pulses recur within a critical time interval, neural elements would remain active, the species-specific template would be satisfied and phonotaxis proceed. The buzz-tick structure of *brevipennis* song involves silent breaks of several hundred milliseconds and might not therefore provide the necessary continuity. Conspecific song, *attenuatus* song, random noise and even conspecific song from which minor pulse trains were deleted (about 16 ms of silence between major pulse trains results from such a deletion)

would involve renewed pulse activity within the critical interval and so phonotaxis would occur to all of these stimuli. Under such a scheme phonotaxis would fail to take place to the song of a *brevipennis* male due to the absence rather than the presence of a feature, the feature being continuity.

We discount this hypothesis on the basis of a dual-speaker experiment in which the song of an individual *brevipennis* was presented to *nigropleurum* females simultaneously with that of *nigropleurum* (Fig. 5D). Ticks had been deleted from the *brevipennis* recording and sections of the *nigropleurum* song had been deleted so that what remained approximated *brevipennis* buzz durations. In other words, the *nigropleurum* song was even more discontinuous, since no ticks were present, than would be the case with normal *brevipennis* song. A significant phonotactic response was established. Twenty females exited in the quadrant of the altered *nigropleurum* song, but only eight in the *brevipennis* quadrant. Discontinuity in excess of that seen in *brevipennis* did not preclude significant discrimination of their own song by *nigropleurum* females ($p < .025$).

There is no indication that *nigropleurum* females set narrow limits on the AM patterns they will approach. This species does not seem to fit a model in which recognition comes about by responding exclusively to a set of narrowly defined species-unique song parameters. The suggested alternative, heterospecific recognition, explains the avoidance of a normally attractive carrier band when it is offered in the presence of a particular AM pattern, but our results do not prove its existence. It is possible however to suggest a plausible basis for the evolution of heterospecific recognition.

C. nigropleurum has a simple and probably primitive song. For each temperature there is a single unvarying wingstroke rate, suggesting the output of a co-opted flight oscillator. There is no echeme patterning, only a buzz of indefinite duration. There is an ultrasonic carrier band, held in common with virtually all members of the genus. Ancestral *Conocephalus* song was probably much like this. And for an ancestral stem form, attraction to the ultrasonic band probably sufficed for reproductive isolation.

Species-distinctive song patterns of sympatric acoustic insects are considered important premating mechanisms of reproductive isolation (Alexander 1960, Mayr 1963). General models for the origin of such mechanisms are discussed by Dobzhansky (1951), Mayr (1963) and Kaneshiro (1980). Suppose two previously isolated populations establish contact and gene flow occurs. Given that pairing between the members of the two groups is reproductively disadvantageous, selection

should operate to favor individuals that successfully discriminate their own kind as mates. Females in a species where the males sing might exercise a genetically based preference for certain physical features of the song that predict a true conspecific. This preferential mating would produce sexual selection on male song structure. A set of features uniquely diagnostic of each of the species would emerge in each of the two populations. Females would discriminate mates by means of a species-specific recognition template.

But suppose of the two incipient species that make contact, one already possesses a highly distinctive song feature that permits the other a sure diagnosis of a singer as an undesirable sound source. Suppose ancestral *nigropleurum*, pairing as now, by attraction to the ultrasonic band, came into contact with ancestral *brevipennis*. *C. nigropleurum* females would inevitably be attracted to heterospecifics. If *brevipennis* already possessed some very distinctive song feature (perhaps ticks evolved in the context of male spacing -- Alexander 1960) a means would be immediately available for the sure prediction of this pairing error. If any *nigropleurum* female should appear with a genetically based tendency to inhibit her phonotaxis in response to such a feature, she would enjoy a reproductive advantage. Such a female would rapidly leave progeny possessing nervous systems capable of heterospecific recognition.

It would of course be quite inefficient to maintain a large repertoire of heterospecific recognition mechanisms, one for each species with which interbreeding was a risk. If such a system began to develop it would in many cases be supplanted by the appearance of the far less costly process in which a single set of parameters codes exclusively for one's own kind. But where the potential for breeding errors was limited to only one other species, and a case can be made for this situation in *nigropleurum*, which has a very limited range in North America, heterospecific recognition should be at no disadvantage relative to species recognition and could maintain itself indefinitely.

The final result might be much as we presently observe in *nigropleurum*: reliance in conspecific pairing on a very simple acoustic response, combined with detection and avoidance of the only possible reproductive mistake: attraction to the song of its sympatric congener.

SUMMARY

1. Three *Conocephalus* species share essentially the same broad-band ultrasonic carrier frequency. 2. At long

range the collective output of the dense singer aggregates characteristic of the genus should prevent perception of the species-specific amplitude modulation (AM) patterns considered to function in species recognition. 3. In the laboratory, females of *C. nigropleurum* were attracted to broadcast random noise; they treated as equivalent this random noise stimulus and the superimposed songs of 10 conspecific males. The same behavior is seen in males of this species and may have evolved to promote aggregation. 4. *C. nigropleurum* females often exhibit an indiscriminant phonotactic response to perceived AM patterns: they do not distinguish the song of the sympatric but nonsyntopic *C. attenuatus* from that of their own species, though the AM patterns of the two are very different. 5. Pairing mistakes should be a hazard for *nigropleurum* females responding to the genus-characteristic ultrasonic band generated by an aggregation of congeneric singers. These errors could be minimized by geographic and temporal separation (*attenuatus*) or by recognition of a heterospecific AM pattern. 6. The song of *C. brevipennis*, a sympatric syntopic congener with which mating errors are possible, is not approached by *nigropleurum* females even if it is the only stimulus present. 7. Attraction to *brevipennis* song is possible if sufficient recorded songs are overlapped to obscure the species-characteristic AM pattern. 8. *C. nigropleurum* seems to combine an indiscriminant, perhaps primitive, positive phonotactic aggregation response with recognition of the AM pattern of the one congeneric with which interspecific breeding is most likely.

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