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ABSTRACT: This paper comments on a recent study of the phonotactic response of female katydids (Conocephalus nigropleurum) to various models of the male sexual signal. Females approached a number of song models, including conspecific calls and those of an allopatric Conocephalus species, but did not show this response to the song of a species that coexists in the habitat. These results suggest that female C. nigropleurum have evolved to avoid mispairings or mismatings with a closely related species not through the usual postulated mechanism of recognition and response only to conspecific song but instead by recognition and lack of response to the "problem" species.

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Crickets and katydids (Orthoptera, Ensifera: Gryllidae and Tettigoniidae, respectively) are well-known for their species-specific acoustic signals produced by males prior to sexual pair-formation. These "calling songs" (sensu Alexander, 1967), produced by movements of the forewings, are known to attract sexually-receptive females (Regen, 1912; Beier, 1930).

A number of studies have concluded that female crickets or katydids respond phonotactically to conspecific calling song but not to the songs of other species (references cited below). However, a recent study by Morris and Fullard (1983) demonstrated that, although female katydids (Conocephalus nigropleurum) showed no response to the song of another Conocephalus species from the same habitat, they were otherwise indiscriminate in their response to various song patterns, including that of a third Conocephalus, a species not found in the same locations as C. nigropleurum.

We discuss this case of "selective heterospecific recognition" in katydids in relation to theories on the origins of behavioural isolation.

HETEROSPECIFIC RECOGNITION AND ORTHOPTERAN CALLING SONGS

Morris and Fullard (1983) investigated the response of female meadow katydids, Conocephalus nigropleurum, (Tettigoniidae, Conocephalinae) to tape-recorded playback of various sound models. The calling songs of most species in this genus, for which information is available, share the same broad ultrasonic carrier frequency band (28-50 kHz) (Sales and Pye, 1974). However, the songs of different species differ dramatically in their patterns of amplitude-modulation (Morris and Fullard, 1983). Females of C. nigropleurum proved remarkably indiscriminate: even in the presence of the song of a conspecific male they were attracted to sounds departing substantially from the species-specific pattern. They approached the song of a congener, C. attenuatus, a species that produces pulse-trains of sound at a rate double that of their own males. They treated conspecific song, from which time-amplitude elements (putative wing-opening sounds) had been removed, as equivalent to intact conspecific calling song (Morris et al. 1978). They even approached random noise, sound with energy in the appropriate ultrasonic frequency band (Beranek, 1954), when it was placed in

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competition with the song of their own male (Morris and Fullard, 1983).

However, there was one acoustic stimulus which these females did not respond to, even though it contained the same carrier frequencies as their conspecific song, and even when it was presented to these sexually-deprived females as the only stimulus available - the calling song of Conocephalus brevipennis. This species is usually found together with C. nigropleurum and the life cycles of both species are synchronic: they share oviposition sites (certain plant galls) in locations where they have been collected (near Alpine, New York [Pipher and Morris, 1974] and in the Credit River Valley, Ontario [the site where insects for the Morris and Fullard study were obtained, Morris, unpubl.]); in the lab, nymphs of both species hatched at similar times from eggs brought in from the field (Morris, unpubl.). There is no report of C. attenuatus, the species to which females did respond, being found in the same sites as C. nigropleurum (Morris and Fullard, 1983).

Thus, C. nigropleurum females recognized C. brevipennis song (Morris and Fullard, 1983). The critical feature appeared to be the distinctive amplitude modulation pattern. In confirmation of this, when the songs of a sufficient number of C. brevipennis males were overlapped in a tape-recording, the pattern was obscured to the point that C. nigropleurum females began to respond to, in effect, the carrier frequency band characteristic of the genus.

Both response to conspecific song alone and a more indiscriminate response combined with no response to a habitat-sharing species may exist in other species of ensiferan Orthoptera. Female katydids, Ephippiger spp., respond phonotactically to the song of an allopatric congener (Walker, 1957) even in trials where conspecific song is present (Dumortier, 1963). Females will even approach a number of sounds very different from male calling, including those produced by certain whistles (Busnel and Dumortier, 1954). Experiments with the cricket Gryllus bimaculatus (Gryllidae) showed that females responded to 'very rough models' near the frequency range of calling; these models included a continuous tone (Popov and Shuvalov, 1977). However, females rejected a model calling song with the amplitude modulation pattern of the sympatric G. campestris. As Morris and Fullard (1983) suggest, this may parallel the "heterospecific recognition" shown by the katydids in their study.

Many studies of phonotaxis by female katydids and crickets purport to show preference for conspecific song alone (Walker, 1957; Bailey and Robinson, 1971; Hill et al., 1972; Zaretsky, 1972; Nevo and Blondheim, 1972; Hoy and Paul, 1973; Ulagaraj and Walker, 1973; Paul 1976; Moiseff et al., 1978; and Forrest, 1983). Because many of these studies were done with sympatric (and possibly syntopic) assemblages of species, however, demonstrations of females responding only to conspecific song have rarely excluded the possibility that experimental females were avoiding the songs of habitat-sharing species and that females may respond to the sounds of species that they do not encounter in nature.

However, there are experimental demonstrations of females responding only to conspecific song. Of the studies mentioned above, Bailey and Robinson (1971), Nevo and Blondheim (1973) and Forrest (1983) show female preference for conspecific signals over signals of allopatric congeners. Also research with Teleogryllus crickets supports this hypothesis by showing preference of female interspecies hybrids for hybrid song (Hoy and Paul, 1973; Hoy et al., 1977). Interestingly, other behavioral experiments with these crickets indicate that "auditory matching" by females to an internal template of the song does not occur (Pollack and Hoy, 1979).

KATYDID SONGS AND THE ORIGINS OF SPECIES-SPECIFIC SIGNALS

Two theories address the origins of species-specific signalling systems as exemplified by orthopteran calling songs (see Heth and Nevo, 1981). One argues

that the species-isolation properties of these systems do not actually evolve as isolating mechanisms; rather they arise during allopatry as incidental effects of selection in some context other than species-recognition (Darwin, 1859; Muller, 1940; Mayr, 1942, 1970). West-Eberhard (1983, 1984) and Thornhill and Alcock (1983) pointed out that differences in sexual selection pressures are expected to result in rapid divergence in allopatry of premating signals. Paterson (1985) also regards the isolating properties of signalling systems as results of incidental effects. However, he attributes these properties not to an evolutionary history of biological interactions, such as through sexual selection, but as a result of adaptations to physical features of "preferred" habitats²

The second theory, reinforcement theory, contends that differences in species-isolating properties of signalling systems have not resulted from selection pressures in allopatry but that certain of these systems actually evolved to prevent mispairing or mismating which, historically, resulted in a selective disadvantage (due to time and energy costs in responding to heterospecific males or in the production of hybrid offspring with decreased fitness). Thus differences in premating displays, and/or the response to these displays, have been reinforced as the incipient species became sympatric, and thus display differences resulted only in conspecific pairings (Dobzhansky, 1940; Fisher, 1958; Littlejohn, 1969; and see Walker [1974] for acoustic insects).

The studies of signal response in Conocephalus katydids appear to support aspects of both theories dealing with the origins of species-specific signals:

(1) The lack of response of C. nigropleurum females to the song of their syntopic congener, C. brevipennis, supports the premise of reinforcement theory, namely that ancestral C. nigropleurum suffered a cost through pairing or mating mistakes due to the presence of C. brevipennis. However, in this case avoidance of mispairings has not been achieved by the mechanism outlined in the theory, i.e. by reinforcement of female response to conspecific song or in reinforcement of conspecific song parameters. The features of C. brevipennis song, against which ancestral C. nigropleurum females first discriminated were likely to have been present at the very onset of the process; i.e. such features are unlikely to have been selected for in an interspecific context due to unproductive interactions between male C. brevipennis and female C. nigropleurum. (Selection is expected to have operated on the signal-receiving female nigropleurum rather than the signalling male brevipennis as it is the female conocephaline katydid that is the discriminating sex as well as the sex that has more to lose in a mispairing due to the effort expended [both risks-taken and energy-expended] in moving between signalling mates [Feaver, 1977]).

(2) However, in support of the assumption of the incidental origins theory, the existence of recognition and lack of response to a habitat-sharing species as an alternative mechanism to "response only to conspecific" suggests that the fitness cost due to mispairings with other species has not been a strong selection pressure influencing the signalling system of this group. If a species has had a history of potential mismatches with a number of other species an innate releasing mechanism reacting only to unique components of conspecific signal would have been likely to evolve. Direct recognition of heterospecific songs would not be expected to evolve due to the cost and complexity of maintaining mechanisms each aimed at a different species. However, if the potential for mispairings with other species is a rare phenomenon in nature, heterospecific recognition by response to signal parameters of a "problem species" on the rare occasion that it

²Paterson (1975) views a species as a population of organisms sharing a common "specific mate-recognition system", an example being a coadapted signal-response chain. The signal and response of C. nigropleurum does not qualify as such a system since females do not distinguish conspecific calls over those of the allopatric C. attenuatus (Morris and Fullard, 1983).

is encountered should have been as likely to evolve as a mechanism of preference only for the conspecific signal.

Although the most plausible interpretation of recognition of and lack of response to the song of a syntopic species by females is that it is a mechanism that evolved to avoid mispairings or mismatings³ evidence that females recognize and prefer conspecific signal is not exclusive support for this hypothesis; sexual selection is expected to produce species-specificity by reducing variation in important male signal parameters (Zahavi, 1980; West-Eberhard, 1984). In calling Orthoptera females may respond to conspecific song features that indicate a male of high quality (for example, see Crankshaw, 1979), with preference for conspecific song over songs of heterospecifics being simply an effect of this process. Song parameters discerned by females that choose mates from among conspecifics appear to be those that traditionally have been regarded as functioning in species isolation: in an undescribed katydid species, spectral frequencies of song are good predictors of the amount of important resources that males supply to females (Gwynne, unpubl.; see also Gwynne, 1982); in crickets song modulation patterns are important in female choice among males (Hedrick, unpubl.). In addition, complex signals such as orthopteran calling songs (see review by Doherty and Hoy, 1985) need not have evolved to provide information of functional benefits that males might provide; characters preferred by females may be "aesthetic", i.e. arbitrary characters produced by the process of runaway sexual selection envisioned by Fisher (1930).

However, data on song preferences by Conocephalus nigropleurum females indicate that preference for conspecific song as an effect of female choice among conspecific males is not always the case as females of this species do respond to other sound models, including the song of an allopatric congener. This is not to say that C. nigropleurum females are indiscriminate in their response to conspecific male songs. They respond preferentially to the sounds of a chorus of males over that of a single male, (Morris et al., 1978) and prefer to mate with the larger of two calling males, apparently using cues from the calling song (Gwynne, 1982).

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REFERENCES

- Alexander, R.D. 1967. Acoustical communication in arthropods. *Ann. Rev. Entomol.* 12: 495-526.
 Baier, L.J. 1930. Contribution to the physiology of stridulation and hearing in insects. *Zool. Jb.* 47: 151-243.
 Bailey, W.J. and D. Robinson. 1971. Song as a possible isolating mechanism in the genus Homorocoryphus (Tettigonioidae, Orthoptera). *Anim. Behav.* 19: 390-397.
 Beranek, L.C. 1954. *Acoustics*. McGraw-Hill, New York.

³Thornhill (pers. comm.) has suggested that the case of "heterospecific recognition" of C. brevipennis song may be a mechanism whereby C. nigropleurum females detect and avoid an area where ecological competition with the congener may be likely to occur. However, this hypothesis predicts that females should actively avoid C. brevipennis song. The results of Morris and Fullard (1983) show that females do not avoid the song, they simply do not respond to it.

- Busnel, R-G. and B. Dumortier. 1954. Observation sur le comportement acoustico-sexuel de la Q'd'Ephippiger bitterensis. Compt. Rend. Soc. Biol. 148: 1589-1592.
- Crankshaw, O.S. 1979. Female choice in relation to calling and courtship songs in Acheta domesticus. Anim. Behav. 27: 1274-1275.
- Darwin, C. 1859. On the Origin of Species. A facimile of the first edition. Harvard University Press, Cambridge.
- Dobzhansky, T. 1940. Speciation as a stage in evolutionary divergence. Amer. Nat. 74: 312-371.
- Doherty, J. and R. Hoy. 1985. The auditory behavior of crickets: some views of genetic coupling, song recognition, and predator detection. Q. Rev Biol. 60: 457-472.
- Dumortier, B. 1963. Ethological and physiological study of sound emissions in Arthropoda. In: Acoustic Behaviour of Animals, (Busnel, R-G., ed.) Elsevier press, Amsterdam, pp. 583-584.
- Feaver, M. 1977. Aspects of the behavioral ecology of three species of Orchelimum. Ph.D. Thesis, University of Michigan.
- Fisher, R.A. 1958. The Genetical Theory of Natural Selection. Dover Publications, New York.
- Forrest, T.E. 1983. Phonotaxis and calling in Puerto Rican mole crickets (Orthoptera: Gryllotalpidae). Ann. Entomol. Soc. Amer. 76: 797-799.
- Gwynne, D.T. 1982. Mate selection by female katydids (Orthoptera: Tettigoniidae, Conocephalus nigropleurum). Anim. Behav. 30: 734-738.
- Heth, G. and E. Nevo. 1981. Origin and evolution of ethological isolation in subterranean mole rats. Evolution 35: 259-274.
- Hill, K.G., J.J. Loftus-Hills and D.F. Gartside. 1972. Pre-mating isolation between the Australian field crickets Teleogryllus commodus and Teleogryllus oceanicus (Orthoptera: Gryllidae). Aust. J. Zool. 20: 153-163.
- Hoy, R.R., J. Hahn and R.C. Paul. 1977. Hybrid cricket auditory behavior: evidence for genetic coupling in animal communication. Science 195: 82-84.
- Littlejohn, M.J. 1969. The systematic significance of isolating mechanisms. In: Systematic Biology: Proceedings of an International Conference. National Academy of Sciences, Washington, DC., pp. 459-482.
- Mayr, E. 1942. Systematics and the Origin of Species. Columbia University Press, New York.
- Mayr, E. 1970. Populations, Species and Evolution. Belknap Press, Harvard University, Mass.
- Moiseff, A., G.S. Pollack and R.R. Hoy. 1978. Steering responses of flying crickets to sound and ultrasound: mate attraction and predator avoidance. Proc. Nat. Acad. Sci. 75: 4052-4056.
- Morris, G.K. and J.H. Fullard. 1983. Random noise and congeneric discrimination in Conocephalus (Orthoptera: Tettigoniidae). In: Orthopteran Mating Systems: Sexual Competition in a Diverse Group of Insects, (Gwynne, D.T. and G.K. Morris, eds.) Westview Press, Boulder, pp. 73-96.
- Morris, G.K., G.E. Kerr and J.H. Fullard. 1978. Phonotactic preferences of female meadow katydids (Orthoptera: Tettigoniidae, Conocephalus nigropleurum). Can. J. Zool. 56: 1479-1487.
- Muller, H.T. 1940. Bearings of the 'Drosophila' work on systematics. In: The New Systematics, (Huxley, J., ed.) Oxford Univ. Press, London, pp. 185-268.
- Nevo, E. and S. Blondheim. 1972. Acoustic isolation in the speciation of mole crickets. Ann. Entomol. Soc. Amer. 65: 980-981.

- Paterson, H. 1985. The recognition concept of species. In: Species and Speciation (Vrba, E.S., ed.) Transvaal Museum Monograph No. 4, Transvaal Museum, Pretoria, pp. 21-29.
- Paul, R.C. 1976. Species specificity in the phonotaxis of female ground crickets (Orthoptera: Gryllidae: Nemobiinae). *Ann. Entomol. Soc. Amer.* 69: 1007-1010.
- Pipher, R.E. and G.K. Morris. 1974. Frequency modulation in Conocephalus nigropleurum, the black-sided meadow katydid (Orthoptera: Tettigoniidae). *Can. Entomol.* 106: 997-1001.
- Pollack, G.S. and R.R. Hoy. 1979. Temporal pattern as a cue for species-specific calling song recognition in crickets. *Science* 204: 429-432.
- Popov, A.V. and V.F. Shuvalov. 1977. Phonotactic behavior of crickets. *J. Comp. Physiol.* 119: 111-126.
- Regen, G.S. 1912. Experimentelle Untersuchungen über das Gehör von Liogryllus campestris L. *Zool. Anz.* 40: 305-316.
- Sales, G. and D. Pye. 1974. *Ultrasonic Communication by Animals*. Chapman and Hall, London.
- Thornhill, R. and J. Alcock. 1983. *The Evolution of Insect Mating Systems*. Harvard University Press, Cambridge, Mass.
- Ulagaraj, S.M. and T.J. Walker. 1973. Phonotaxis of crickets in flight: attraction of male and female crickets to male calling songs. *Science* 182: 1278-1279.
- Walker, T.J. 1957. Specificity in the response of female tree crickets to the calling songs of the males. *Ann. Entomol. Soc. Amer.* 50: 626-636.
- Walker, T.J. 1974. Character displacement and acoustical insects. *Amer. Zool.* 14: 1137-1150.
- West-Eberhard, M.J. 1983. Sexual selection, social competition, and speciation. *Q. Rev. Biol.* 58: 155-183.
- West-Eberhard, M.J. 1984. Sexual selection, competitive communication and species-specific signals in insects. In *Insect Communication* (Lewis, T., ed.) Academic Press, London, pp. 283-324.
- Zahavi, A. 1980. Ritualization and the evolution of movement signals. *Behaviour* 72: 77-81.
- Zaretsky, M.D. 1972. Specificity of the calling song and short term changes in the phonotactic response by female crickets Scapsipedus marginatus (Gryllidae). *J. Comp. Physiol.* 79: 153-172.