

## Photoperiodically determined dimorphic calling songs in a katydid

MALES of most species of katydids (Orthoptera, Tettigoniidae) make calling songs that attract conspecific females<sup>1–4</sup>. These songs, like those of crickets, cicadas, and some grasshoppers, are species specific and can be produced in perfect form by males that have never heard a similar song<sup>5</sup>. The fact that insect calling songs are the same even though conditions during their development varied from generation to generation and between field and laboratory has led to the inference that the ontogeny of such songs is free of environmental modification<sup>6</sup>. We show here, however, that the calling songs of a katydid are dimorphic and photoperiodically determined.

The narrowness of intraspecific variation in insect calling songs is coupled with a narrow range of acoustic parameters that are optimally attractive to conspecific females. Consequently species that call together do not confuse one another. If two species were to use confusingly similar calling songs at the same time and place, rapid evolution towards unambiguously different songs would be expected<sup>7</sup>. Katydids that produce different calling songs generally belong to different species, and calling songs have provided a means of initially recognising species that are morphologically indistinct<sup>8–10</sup>. A major complication in identifying species by their calling songs is that the rate of the male's sound-producing wingstrokes is a function of ambient temperature<sup>11</sup>. Differences in rates of sound-producing wingstrokes are often the only important differences among calling songs of similar species<sup>12,13</sup>. Comparisons must therefore be made between calling songs made by males at the same ambient temperature, or wingstroke rates must be corrected to compensate for temperature differences. The rates to which females are attracted are also a function of ambient temperature<sup>12</sup>.

*Neoconocephalus triops* is a coneheaded katydid (Copiphorinae) found in southern United States, the Caribbean, and northern South America. In northern peninsular Florida, Walker<sup>14</sup> noted two seasonally distinct populations of adults that differed in the wingstroke rate and continuity of the calling song. Winter males (calling January–April) produced approximately 90 wingstrokes s<sup>-1</sup> at 25°C and called for minutes without interruption after initially hesitating about once per second. Summer males (calling July–August) produced approximately 110 wingstrokes per second at 25°C and continually interrupted their calls at ~1 s intervals (Fig. 1). Although he found no non-overlapping morphological differences, Walker interpreted northern Florida *N. triops* as two species, each with a distinctive univoltine life cycle and calling song. Whitesell<sup>15</sup> refuted this interpretation by periodically sampling field populations and by rearing in outdoor cages. He established that all summer adults are progeny of adults of the previous winter while some winter adults are progeny of adults of the previous summer and some are progeny of adults of the previous winter. Both univoltine and bivoltine life cycles occur in the same deme with summer adults containing only part of the deme's gene pool while winter adults contain all of it. Whitesell also demonstrated that photoperiod was one determinant of whether particular progeny of winter adults became summer or winter adults. Those progeny that made the final molt during photoperiods similar to those of July became reproductively active without delay; shorter photoperiods resulted in adults that were in reproductive

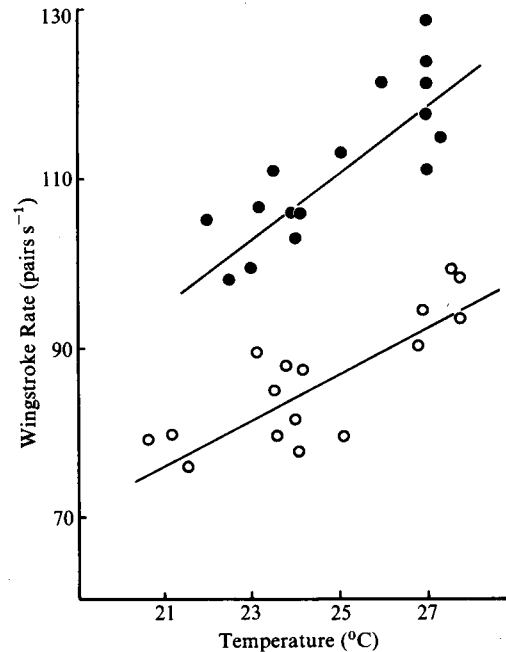


Fig. 1 Wingstroke rates of north Florida (Alachua Co.), field-collected adults. Regression lines: ●, (summer, July–August)  $\hat{y} = 3.99x + 12.13$ ; ○, (winter, January–April)  $\hat{y} = 2.61x + 22.19$ , ( $x = ^\circ\text{C}$ ). (Coefficients of determination,  $r^2$ , are 0.71 and 0.65.)

diapause—as shown by the silence of the males and the unenlarged ovaries of the females. In outdoor conditions adult diapause ends in January or February but Whitesell discovered that diapausing individuals could be brought to reproductive readiness at any time by exposing them to 15-h photoperiods for a few weeks.

Since northern Florida *N. triops* had proved to be one species rather than two, we sought causes of the unprecedented circumstances of a single species making different calling songs at different seasons.

Specimens for experiments were captured near Gainesville, Florida, and caged individually in screen-topped jars with food and water. Two photoperiod chambers, each illuminated by two 15-W fluorescent bulbs and maintained at ambient temperature  $\pm 1^\circ\text{C}$  by exhaust fans, provided day lengths of 11 and 15 h—approximately equivalent to the shortest and longest local days. The chambers and control jars were housed in a screened insectary that provided outdoor photoperiods and near-outdoor temperatures. Calling songs were recorded at 38 cm s<sup>-1</sup> within the first week that an individual began to sing. High-speed cinematography demonstrated that the calling song is produced by alternate long and short closures of the wings<sup>16</sup>. Rates for complete cycles of wing movement, consisting of two openings and two closings, were calculated from audiospectrograms.

When reared in 15-h photoperiods (Table 1) progeny of summer adults made songs characteristic of summer adults. When reared in 11-h photoperiods (and kept in diapause for 3 months), they made songs similar to those of winter adults.

The males in Table 1 that produced near-winter songs had been adults for more than 3.5 months when they began to sing.

The males producing summer songs had been adults less than one month. Therefore, the differences in calling songs might be attributed to age<sup>15,17</sup>, to the events of diapause, or to both. To compare the effects of age and diapause, we collected 30 diapausing males from 19–28 September 1972 and kept them in the screened insectary at outdoor temperatures and photoperiods. Successive groups of 10 were moved to a 25±1 °C, 15L:9D room on 1 October, 15 November, and 1 January, and their songs were recorded as soon as diapause ended and singing began (Table 2). Even though the earliest group sang when 2 months younger than the latest group, their songs were not significantly different. The proximal causes of seasonally distinct calling songs in *N. triops* are apparently associated with diapause or its initiation or termination.

The ultimate or adaptive causes of the different calling songs are unknown. At one extreme they may simply be by-products of the physiology of diapause. At the other extreme they may be specific, evolved responses—that is, one or both songs may have changed from the ancestral song because of increased reproductive success of individuals that had the changed song(s). If the latter is the case, the critical events of natural selection probably occurred in conditions different from those in northern Florida at present. However, a clue to what may have happened is the simultaneous singing of *Neoconocephalus retusus* and summer *N. triops* in August in north Florida. The calling song of *N. retusus* has wingstroke rates and continuity like that of winter *N. triops*. If summer *N. triops* used the winter song, females of each species would be falsely attracted during their several weeks of overlap.<sup>15</sup>

**Table 1** Calling songs of males reared from a single collection of nymphs that were progeny of summer adults

	Rearing Photoperiod	
	15-h	11-h
Date of collection	11 Aug 1972	11 Aug 1972
Month of moult to adults	Sept. 1972	Sept. 1972
Date of transfer to recording room*	21 Sept. 1972	1 Jan. 1973
Age of males when recorded	1 month	3.5 months
No. of males recorded	6	4
Song characteristics:		
Phrasing†	summer	winter
Wingstroke rate		
Range	106–116	95–104
Mean	109‡	98‡
S.e.m.	2	2

Specimens at outdoor temperatures and 15- or 11-h photoperiods until transferred to 25±1 °C, 15L:9D room prior to tape recording.

\* Males from 15-h treatment were singing before transfer; males from 11-h treatment began singing 2 weeks after transfer.

† Summer phrased songs are continuously interrupted at ~1 s intervals. Winter-phrased songs become continuous after initial interruptions.

‡ Means significantly different at  $P \leq 0.005$  (Student's *t*-test).

**Table 2** Effect of early termination of diapause on wingstroke rates

	Group		
	a	b	c
Date of transfer	1 Oct. 1972	15 Nov. 1972	1 Jan. 1973
Date of first singing	25 Oct.	2 Dec.	4 Jan.
No. of males recorded	4	4	4
Song characteristics:			
Phrasing*	winter	winter	winter
Wingstroke rate			
Range	96–104	92–104	101–103
Mean	100†	99†	102†
S.e.m.	2	2	1

All males collected 19–28 September 1972 and kept at outdoor temperatures and photoperiods until transfer to 25 °C, 15L:9D room.

\* Winter-phrased songs become continuous after initial interruptions.

† No two means were significantly different at  $P = 0.05$  (Student's *t*-test).

Variation in the morphology of the male genitalia of the leafhopper *Euscelis plebejus* seems to us analogous to that of *N. triops* calling songs<sup>18</sup>. What were originally described as two species on the basis of aedeagal differences were shown by E. J. Muller to be seasonal dimorphs controlled by photoperiod. As in *N. triops* no clear cut adaptive significance is evident for a photoperiodically-triggered dimorphism in a reproductively important aspect of the phenotype.

We thank Drs J. E. Lloyd, G. K. Morris and R. C. Paul for criticising the manuscript and the NSF for financial support.

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Received 15 February; accepted 30 June 1978.

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