Character Displacement and Acoustic Insects

THOMAS J. WALKER

*Department of Entomology and Nematology, University of Florida, Gainesville,
Florida 32611*

SYNOPSIS. Crickets, katydids, grasshoppers, and cicadas should be ideal for illustrating character displacement. Their species-specific calling songs are of direct importance to reproductive success, and species with similar songs and overlapping ranges should develop greater differences in their songs in areas of sympatry. Although many pairs of species have suitably similar songs and overlapping ranges and the data concerning songs are extensive for crickets and katydids, no convincing example of character displacement has been found in acoustic insects. Lack of such examples can be attributed to false premises, to divergence completed in allopatry, to elimination of geographical variation in song by gene flow between the zone of sympatry and the zones of allopatry, and to the scanty sample that has been intensively studied.

INTRODUCTION

The term *character displacement* was proposed by Brown and Wilson (1956, p. 63) to denote "the situation in which, when two species of animals overlap geographically, the differences between them are accentuated in the zone of sympatry and weakened or lost entirely in the parts of their ranges outside this zone." They concluded that natural selection in the zone of overlap should act to cause each of a pair of similar species to diverge from the other because of ecological competition and/or reproductive interference. Subsequently, researchers often interpreted their data as illustrating character displacement, and textbook writers (e.g., Keeton, 1972) began treating character displacement as a well-established corollary of natural selection that is generally applicable to similar spe-

cies with overlapping ranges. As Grant (1972) and others have pointed out, many of the presumptive examples of character displacement depend on data that are insufficient to refute other plausible hypotheses concerning the pattern of geographical variation. Furthermore, even if the pattern is that of character displacement, the causes may be unrelated to the occurrence in the same area of two similar species. The difficulty of interpreting geographical variation is further illustrated by the occurrence of *character convergence*— the situation opposite to that discussed by Brown and Wilson. Cody (1973) summarized cases of species having greater similarity in sympatry than in allopatry. Mayr (1970, p. 53) was right when he concluded that it is time for "an unbiased analysis of unselected cases of overlapping species to permit the establishment of valid generalizations."

Insects that make sounds loudly and frequently enough to attract the attention of the casual observer—i.e., *acoustic insects*—provide an optimal opportunity for studying large numbers of unselected cases. Only four families are involved: Cicadidae (cicadas; Homoptera), Acrididae (grasshoppers; Orthoptera), Tettigoniidae (katydids; Orthoptera), and Gryllidae (crickets; Orthoptera), but these include at least 20,000 species worldwide and 500 in the United States. Many pairs of similar species have overlapping ranges. The cicadas and grass-

hoppers evolved their noisiness independent of one another and of the katydids and crickets (which had a common acoustical ancestor), but the four groups are alike in that males are the principal noise makers and most of the noises they make are species-characteristic calling songs functioning in sexual-pair formation. Usually the female simply walks or flies to the calling male, but in some taxonomic groups she makes an answering sound and the male moves toward the female (Alexander, 1968b).

Species that are acoustically active at the same time and in the same locality nearly always have different calling songs. Such interspecific differences make it possible for sexually ready females to respond to conspecific males and to avoid responding to males of other species. On the other hand, species that are acoustically active only at different times or in different localities sometimes have indistinguishable calling songs. Here the sameness of the songs leads to no interspecific interference in pair formation. Therefore, when formerly conspecific populations become species in allopatry, they may maintain identical or similar songs. If such populations subsequently overlap geographically, reproductive character displacement [1] would be expected in regard to characteristics of the calling songs of males. Understanding the evolution of such differences depends on knowing that the ontogeny of calling songs is under rigid genetic control—the environment, including the acoustical environment, has practically no lasting effect on the nature of the sound produced (for reviews see Walker, 1962b, and Alexander, 1968b). Within a deme, individual males show minor but consistent differences in calling song parameters, and females presumably show similar differences as to the acoustic stimuli required to release their optimal response. If reproductive interference occurs because of similar calling songs of overlapping species, those females that have

optimal responses to calling song variations that are more frequent in their own species will have greater reproductive success and the genes responsible will become more frequent in the population. As the females change in their mean optimal response, those males that produce the cues that more and more conspecific females rely upon and those that produce them in a more prominent or extreme manner will have greater reproductive success. In other words, shifts in the population means for features of the male calling songs would be expected to result from shifts in the population means of features important to female response to calling song. Shifts in the responses of females may have a more direct effect on male song than proposed above—the genes that determine the neural template used by females in responding to song may directly control corresponding features of the male's song (suggested but not proved by Hoy and Paul, 1973).

When looking for reproductive character displacement in acoustic insects, one should concentrate on the parameters of the calling songs that are important to the species-specific responses of females. Experiments with natural and synthetic signals have helped identify these parameters in some instances (Walker, 1957, Loftus-Hills et al., 1971, Ulagaraj and Walker, 1973). The parameters of demonstrated importance have these two characteristics: (i) low variability within species and (ii) consistent differences between species that sing together. Consequently, one can identify the parameters that are likely to prove important for species not studied experimentally.

Not only do calling songs provide specific features that are expected to exhibit reproductive character displacement, they make acoustic insects exceptionally easy to locate and identify in the field. A person with a knowledge of insect songs can drive along a road at the proper time of day or night and find demes at localities along a geographical transect. Modern tape recording equipment and the readiness with which males of most acoustic insects sing make it easy to sample the calling songs of

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1 *Reproductive character displacement* results from reproductive interference between individuals of two similar species. Character displacement resulting from competition should be termed *ecological* (Grant, 1972).

individuals from the selected demes either in the field or later in cages in the laboratory. Once the songs are stored on tape, they can be analyzed with an audiospectrograph, an oscilloscope, or a digital computer.

In spite of these attributes of acoustic insects, few studies have dealt with geographical variation in their songs and in only one instance (Hill et al., 1972) was character displacement of primary concern. This paper will summarize what is known of reproductive character displacement in crickets and katydids. Cicadas and grasshoppers are omitted from further discussion because no relevant data are available. Dr. Daniel Otte, University of Texas, has studied acoustic behavior of U.S. grasshoppers extensively (e.g., 1970) but has so far detected no instance that he interprets as character displacement (personal communication, 1973).

Ambient temperature influences rates within the calling songs of crickets and katydids making corrections necessary before comparing a song recorded at one temperature with songs recorded at other temperatures. Fortunately such temperature effects are generally stereotyped, species-specific, and predictable (Walker, 1969b, and unpublished). In the cases discussed below, except *Anurogryllus*, all rates were corrected to some medial temperature (usually 25 C) by assuming that rate was a linear function of temperature with the rate declining to 0 at 4 C (Walker, 1962b). In *Anurogryllus*, the available data (Walker, 1973) did not fit the usual rate-vs.-temperature pattern; therefore, a regression line was calculated for all points for each species and the two resulting slopes were used in adjusting the rates to 25 C.

POTENTIAL CASES OF CHARACTER DISPLACEMENT IN CRICKETS AND KATYDIDS

A valid criticism of most of the supposed cases of character displacement is that they have been selected for description because they agree with the hypothesis. No indication is given of how many examples were ignored in which character displacement

was expected but not found or in which character convergence was found instead. I have attempted to analyze the entire cricket

TABLE 1. *Analysis of potential cases of reproductive character displacement in crickets and katydids of the United States and Canada.*

	Gryllidae	Tettigoniidae
Total number of species	135	119 [a]
Number of pairs of closely related [b] species having distributions appropriate for character displacement [c]	57	107
And with similar songs [d]	25	18
And with song data sufficient for revealing character displacement [e]	18	4
Pairs perhaps showing reproductive character displacement	3 ½ [f]	0
Pairs perhaps showing character convergence	1 [g]	0

[a] This figure omits 137 species of western Dectici-nae and Phaneropterinae in which congeneric species are generally allopatric. Little is known of their calling songs.

[b] Species are treated as closely related if they belonged to the same species group (species in *Anaxipha, Amblycorypha, Conocephalus, Oecanthus, Orchelimum*) or to the same genus (species in other genera).

[c] Distributions are classed as appropriate for character displacement if at least one species of the pair has a zone of allopatry extending at least 160 km beyond a zone of sympatry of at least 160 km. In cases where only one species has such a distribution, it can show character displacement by its allopatric populations resembling the other species more than its sympatric populations. In such cases the other species had no substantial area of allopatry, and cannot show character displacement.

[d] Songs are classed as similar if they differ in the zone of sympatry by less than X2 in the feature that is most likely to permit conspecific responses by females.

[e] Song data are classed as sufficient if they include at least five tape recordings of one species from each of two localities, one allopatric and one sympatric, at least 160 km apart.

[f] *Oecanthus quadripunctatus* and *argentinus-nigricornis-pini* are counted as one pair since only one *quadripunctatus* changes. The other two are *Oecanthus exclamationis* and *niveus* and *Oecanthus fultoni* and *rileyi*. None of these makes a particularly convincing example (see text).

[g] *Orocharis luteolira* and *saltator*, number of pulses per chirp (see text).

and katydid fauna of the United States and Canada for potential cases of reproductive character displacement and of character convergence (Table 1).

As can be seen from Table 1 and the remainder of this paper, few potential cases are known well enough to substantiate small but significant degrees of geographical variation in calling songs. The cases discussed in detail below are those that have been mentioned in the literature as potential examples, those for which the data are most adequate, and those listed in Table 1 as suggestive of reproductive character displacement.

Oecanthus fultoni and O. rileyi (Fig. 1-3)

The earliest report of geographical variation in insect song suggestive of character displacement concerned two sibling species of tree crickets. One of these, O. fultoni (formerly O. niveus), is the best known insect musician in North America. Its low-pitched regular chirps issue from doorway shrubs during summer months (and from TV sets whenever the hero steps outside on a warm night). The other species, O. rileyi, is restricted to the western United States (Fig. 1) and is most easily distinguished from fultoni by its slower chirp rate.

B. B. Fulton (1925) described ecological and behavioral differences between fultoni and rileyi in Oregon and presented extensive data on their chirp rates. He reported chirp rates of 190 per minute at 25 C for Oregon fultoni and 112 at 25 C for rileyi. He noted that chirp rates of fultoni in eastern United States were significantly lower than in Oregon. An Iowa specimen, for instance, chirped 165 times per minute at 25 C. In 1962, I reported chirp rates for fultoni in five Western and three Eastern states and for rileyi at five localities in California and Oregon (Walker, 1962a). These chirp rates were similar to those noted by Fulton and I concluded, "it seems likely that the occurrence of a slow chirping species (O. rileyi) on the West Coast is responsible for the evolution of a faster chirp rate in the western populations of O. fultoni" (Walker, 1962b, p. 427). In

other words, the pattern of variation suggested reproductive character displacement. I later recorded fultoni chirp rates at 9 more localities, mostly in the Southwest, and rileyi chirp rates from the Chiricahua Mountains in southeastern Arizona. These data plus those previously published are plotted in Figures 2 and 3.
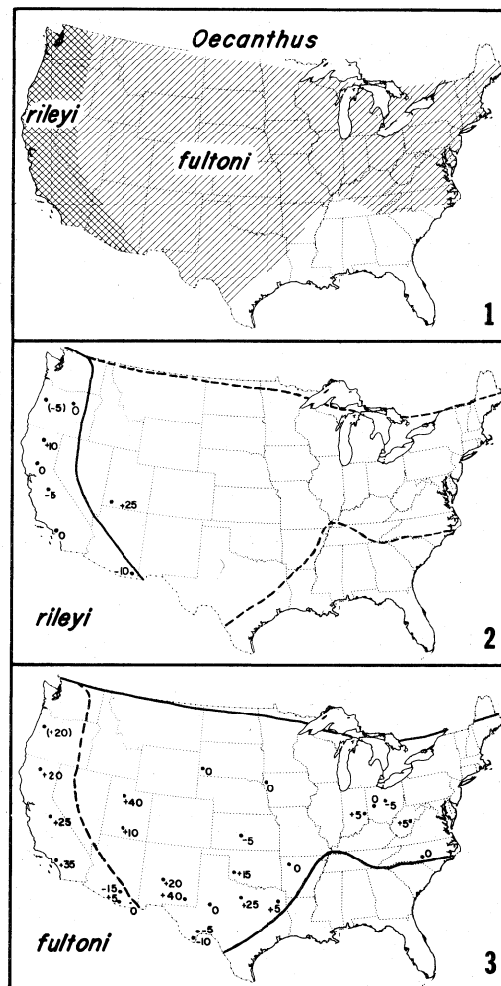

FIG. 1-3. Oecanthus rileyi and O. fultoni. FIG. 1. Diagonal lines show generalized distributions of the two species. FIG. 2. Chirp rates of O. rileyi. Each number on map shows the difference between the mean chirp rate (corrected to 25 C) at the locality and 115 chirps per minute. The Utah record may not be rileyi (see text). FIG. 3. Chirp rates of O. fultoni. Each number shows the difference between the mean chirp rate (corrected to 25C) at that locality and 170 chirps per minute. (Records in parentheses are from B. B. Fulton, 1925.)

The pattern of variation is too complex to be explained by a simple hypothesis of character displacement. The chirp rate of *rileyi* is nearly the same throughout its range as I know it (Figs. 1,2). However, Alexander and Loftus-Hills report that they have found *rileyi* as far east as Colorado (personal communication). On this basis I included in Figure 2 a record from Zion National Park, Utah, based on two individuals singing anomalous songs resembling *rileyi* more than *fultoni* (134 and 143 chirps per minute at 25 C, Walker, 1962*a*). The chirp rates of *fultoni* (Fig. 3) are apparently uniformly high in the West Coast states and uniformly low in the East. In between, the variation is erratic. Especially noteworthy are the high rates in northcentral Texas (Palo Pinto Co., 196 chirps per minute) and southwestern Oklahoma (Kiowa Co., 186), where no *rileyi* occurs, and the low rates in the Chiricahua Mountains (170), where *rileyi* was taped, and in other localities in southeastern Arizona (Madera Canyon, Santa Cruz Co., 173; Molino Basin, Pima Co., 156).

The rates for Figures 2 and 3 are from field observations. I estimate that differences in rates of more than 15 per minute are unlikely to be attributable to errors in measuring temperature or to sampling individuals that were singing at rates nonrepresentative of their deme. This estimate is based on the repeatability of field observations in the East and on the low intrademe variation of laboratory recorded individuals (see Fig. 12 in Walker, 1962*a*).

Laboratory experiments with taped natural and synthetic signals proved that the chirp rhythm is essential to the positive phonotaxis of female *fultoni* to the calling song (Walker, 1957). The pulse rate within the chirp and the carrier frequency can hardly be of importance to female specificity in *rileyi* and *fultoni* because the two species are nearly identical in these parameters (Walker, 1962*a*). How great the difference in chirp rate must be and whether difference in pulse number (i.e., chirp length) are important are unknown. The chirp rates of *fultoni* in the East (170) and of *rileyi* on the West Coast (115) are propor-

tionally more different (170/115 = 1.5) than the pulse rates to which certain other female tree crickets exhibit species-specific responses: For instance, Walker (1957, Tables I and II) showed that females of *quadripunctatus* had strikingly different responses to pulse rates that differed by factors of 1.2 and 1.3. In other words, the chirp rates to which allopatric *fultoni* respond may be fast enough to avoid interference from the West Coast *rileyi*. On the other hand the Zion Park, Utah, "*rileyi*" and Eastern *fultoni* differ in chirp rates by a factor of approximately 1.2. More data from southwestern United States are needed to clarify the patterns of variation in chirp rates. Thus far, reproductive character displacement does not explain the observed patterns.

Gryllus fultoni *and* G. veletis

Two field crickets with similar songs and overlapping distributions are *Gryllus fultoni*, occurring throughout the southeastern United States, and *G. veletis*, occurring throughout the northeastern United States (Alexander, 1968*a*). The area of overlap extends from southern Ohio and Missouri to Tennessee and northern Arkansas. Alexander (1957, p. 595-596) observed that "*fultoni* chirps with considerably more regularity in southern Ohio than it does across the Appalachians in Virginia and North Carolina. . . . If uniform or rhythmical intervals in these songs are behaviorally significant, this introduction of an additional and different rhythmical element into the song of *fultoni* may be associated with its occurrence together with *pennsylvanicus* [=*veletis*], an irregular chirper." This is potentially a case of reproductive character displacement; however, it cannot be confirmed or refuted until the geographical variation in chirp regularity is known in greater detail and the importance of this parameter to the species-specific responses of the female is established (Alexander, 1967).

Teleogryllus commodus *and* T. oceanicus

Two Australian field crickets of the genus *Teleogryllus* are so similar that they were

believed to represent a single species until work with laboratory colonies showed post-mating reproductive isolation (Bigelow and Cochaux, 1962) and distinctive calling songs (Leroy, 1965). Hill et al. (1972) reported that the more northern species, *T. oceanicus,* overlaps in range with the more southern species, *T. commodus,* by at least 420 km. They tape recorded calling songs of *commodus* at three localities in the allopatric zone at distances of approximately 1400, 800, and 100 km from the zone of sympatry and at three localities within the zone of sympatry. They recorded the calling songs of *oceanicus* at the same three sympatric localities and depended on recordings of a laboratory colony from Ayr, Queensland, for information on *oceanicus* in allopatry. The northern limit of *commodus* is unknown but evidently lies between Ayr and the northernmost sympatric locality sampled (Emu Park, 530 km southeastward of Ayr).

The calling songs of *commodus* and *oceanicus* are exceptionally complex in amplitude modulation pattern, and the number of parameters that might be used by females making species-specific responses is great. However, the seven parameters of *commodus* songs and the six of *oceanicus* songs that Hill et al. (1972) analyzed showed no significant intraspecific variation between localities. Included among these parameters were three that occurred in both *commodus* and *oceanicus* and had low intrademe variability: repetition rate of longer pulses, repetition rate of shorter pulses, and carrier frequency (all corrected to 18 C). Of these three only carrier frequencies were nonoverlapping between species.

Hill et al. (1972) not only tested for accentuation of calling-song differences between sympatric *commodus* and *oceanicus* but also assayed for improved discrimination by females. They played *commodus* and *oceanicus* songs to laboratory-reared, mature, virgin females of both species from both allopatric and sympatric localities. In one series they played two songs simultaneously and in another series they played only one song at a time. In neither series did the

females from the sympatric locality, compared to those from allopatric localities, show a significant difference in conspecific phonotactic responses.

Thus, in the most carefully and extensively studied presumptive case of reproductive character displacement in acoustic insects, no geographical variation was demonstrated.

Oecanthus quadripunctatus *and* O. argentinus-nigricornis-pini

The *nigricornis* group of the genus *Oecanthus* consists of seven species of North American tree crickets (five of which are most frequently found on forbs). The calling songs of the seven species are similar except for pulse rates (Walker, 1963). Laboratory experiments have demonstrated that for species calling together, differences in pulse rate alone are generally sufficient to enable females to go chiefly to conspecific songs (Walker, 1957).

The distributions of none of the seven species are coextensive but all are included within the range of *quadripunctatus*. Eleven pairs from these seven species have potential for character displacement but the only geographical variation in calling song detected, in spite of extensive tape recording and analysis, is for *quadripunctatus* (Walker, 1963, p. 779). A sample of 42 tapes of 12 individuals from Alachua County, Florida, averaged 3.6 pulses/sec faster at 27 C than the 45 pulse/sec predicted from the regression line based on tape recordings of *quadripunctatus* from Franklin County, Ohio, and no recording was at a pulse rate as low as 45.

Those tapes were made under laboratory conditions that permitted exceptionally accurate determination of temperature. Only in the southeastern United States does *quadripunctatus* occur without either *argentinus* or *nigricornis* (see Fig. 12), and in peninsular Florida *pini* is absent as well. These three species have average pulse rates at 27 C of 57, 59, and 49 per second respectively (see Table I in Walker, 1962b). They each occur with *quadripunctatus* in old fields and the song of *quadripunctatus*

may have been influenced by their presence. However, the present data on geographical variation in allopatric *quadripunctatus* are too scant to interpret as character displacement. That there is significant variation is based on a single group of individuals from one site, and their deviation from *quadripunctatus* populations sympatric with *argentinus* and *nigricornis* was so small that it would not have been detected under less rigidly controlled circumstances.

Oecanthus exclamationis *and* O. niveus

The tree cricket *Oecanthus exclamationis* occurs in three widely separated areas: eastern United States, the mountains of southeastern Arizona, and southern Mexico (Walker, 1962a, 1967). Its song is known only from the first two areas. In central Ohio 18 tapes of the songs of 7 individuals showed a pulse rate of 79.5 $\pm$ 1.8 per second ($\overline{X}$ $\pm$ SD) at 25 C, while in southeastern Arizona 9 tapes of 7 individuals showed a pulse rate of 74.5 $\pm$ 1.6.

In southeastern Arizona no tree crickets with similar songs occur with *exclamationis*. Throughout the range of *exclamationis* in eastern United States two such tree crickets sing with it: *Oecanthus niveus*, with an average pulse rate of 71.5 at 25 C, and *Neoxabea bipunctata*, with an average pulse rate of 112. If the ancestral population of *exclamationis* sang like Arizona populations sing today, the Ohio populations may have undergone character displacement. The present distributions of *exclamationis* and *niveus* make it impossible to get convincing evidence of character displacement in *exclamationis*.

Orocharis saltator *and* O. luteolira (*Figs. 4-5*)

Two United States bush crickets, *O. saltator* and *O. luteolira*, have similar songs and partially overlapping ranges (Fig. 4) (Walker, 1969). The calling song of each species is a series of irregularly timed chirps, but *luteolira* has a higher pulse rate within its chirps than *saltator* and a lesser number of pulses per chirp. The two species broadly overlap in the carrier frequencies of their calling songs (Walker, 1969).

The pulse rate shows less intrademe variation than the other parameters of the calling song and is most likely the principal cue that females of the two species use in going to conspecific songs. Sympatric populations of *saltator* and *luteolira* show no greater differences in pulse rate than do allopatric populations (Fig. 5). For allopatric and sympatric *saltator* the pulse rates ($\overline{X}$ $\pm$ SD) are 53.6 $\pm$ 2.4 and 54.3 $\pm$ 1.7. For *luteolira* the comparable figures are 70.4 $\pm$ 4.9 and 68.0 $\pm$ 2.6.

The only geographical variation detected for the song of either species was in the number of pulses per chirp of *luteolira* (Walker, 1969). In south Florida *luteolira* has 4 to 6 pulses/chirp whereas farther north it has 6 to 9. Since *saltator* has more pulses per chirp (10 to 18) than does *luteolira*, the variation is in the direction of character convergence.

Anurogryllus celerinictus *and* A. muticus (*Figs. 6-7*)

Two similar species of Caribbean short-tailed crickets overlap in distribution (Fig. 6). Males of both species produce very intense trills, but the trills of *A. celerinictus* have a faster pulse rate than those of *A. muticus*. The carrier frequencies of their calling songs broadly overlap (Walker, 1973). Pulse rate is the only likely basis for conspecific responses by females to the two songs. Nevertheless, *muticus* has a higher pulse rate in Jamaica where it is sympatric with *celerinictus* than it has in Puerto Rico where it is allopatric (Fig. 7). The pulse rate of allopatric *celerinictus* is known from only two tape recordings, and little can be concluded about geographical variation in the song of that species. Tapes of songs of *celerinictus* from Cuba, of songs of *celerinictus* and *muticus* from Hispaniola, and of songs of *muticus* from the Lesser Antilles would clarify the patterns of geographical variation. However, the data thus far run counter to the hypothesis of reproductive character displacement.
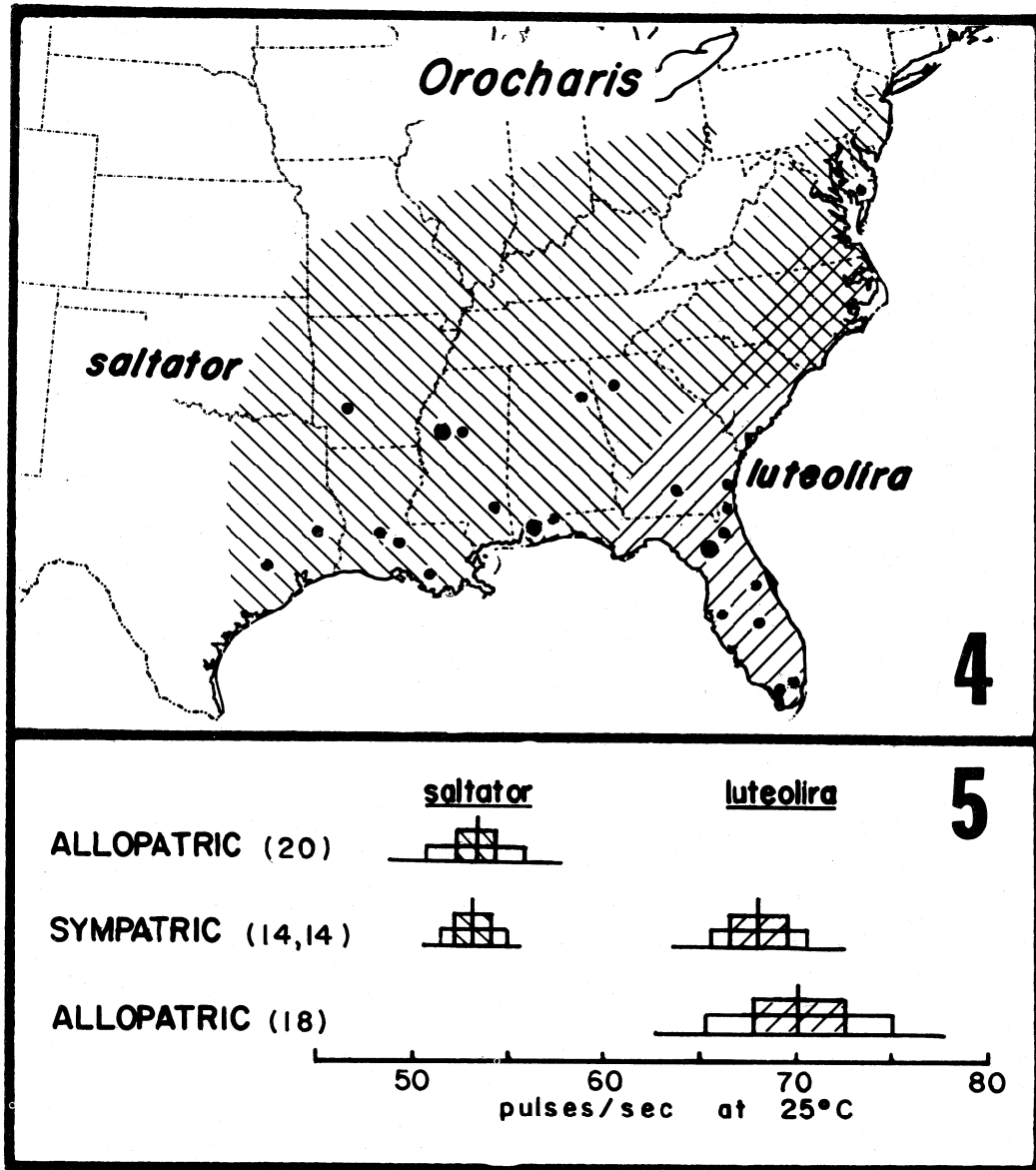
FIG. 4-5. *Orocharis saltator* and *O. luteolira*. FIG. 4. Diagonal lines show distributions of the two species. Dots show localities for the 38 allopatric songs summarized in Fig. 5. Small dots indicate 1 or 2 individuals were taped; large dots indicate 3 or 4 individuals were taped. Sympatric songs came from the following counties: S. CAR., Dillon (5 *saltator*, 6 *luteolira*), Chesterfield (*3 s*, 1 *1*), Marion (2 *1*), Clarendon (1 *s*, 1 *1*), Orangeburg (2 *s*); N. CAR., Hoke (*3 s*); VIR., Northampton (*3 1*). FIG. 5. Geographical variation in pulse rate. The horizontal lines show the ranges of values, the vertical lines are the means, the open bars indicate one standard deviation on either side of the mean, and the shaded boxes include the 95% confidence limits on either side of the mean. (Numbers of taped individuals in parentheses.) Only field tape recordings made between 20 and 30 were used, and all were corrected to 25C.
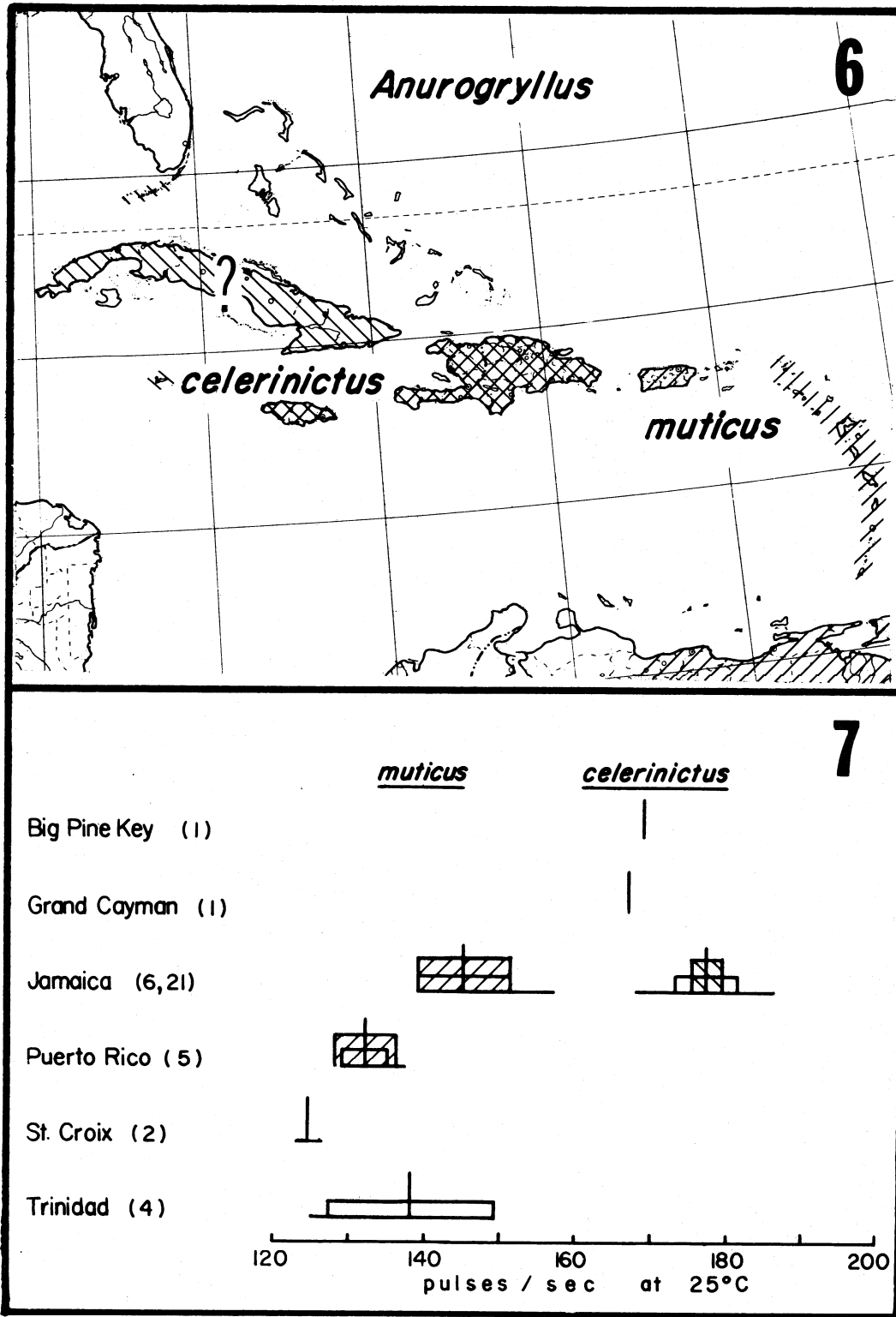
FIG. 6-7. *Anurogryllus celerinictus* and *muticus*. FIG. 6. Diagonal lines show distributions of the two species. FIG. 7. Geographical variation in pulse rate (corrected to 25C). (Numbers of taped individuals in parentheses.) The horizontal lines show the ranges; the vertical lines, the means; the open bars, one standard deviation on either side of the mean; the shaded boxes, the 95% confidence limits on either side of the mean.

Gryllus integer *and* G. rubens *(Fig. 8-10)*

The two most abundant field crickets in southern United States have overlapping distributions (Fig. 8). The calling songs of the two species are irregularly interrupted trills with the pulse rate for *G. integer* being higher than that of *G. rubens*. The carrier frequencies of the two species are broadly overlapping, so again the pulse rate is apparently the only parameter that would allow a female of either species to go consistently to the conspecific song.

I have assayed the pulse rates of *integer* and *rubens* at numerous localities. All data for *integer* are similar (Fig. 9), while the pulse rates for *rubens* are variable but average slightly higher westward (Fig. 10). What geographical variation there is cannot be explained by reproductive character displacement.

The variation in pulse rate determinations between individuals of a deme and from time to time for the same individual are greater for *integer* and *rubens* than for other crickets and for most tettigoniids with which I've worked. Introgression may contribute to the former and thoracic heating during calling to the other, but both of these hypotheses are presently as unsubstantiated in crickets as is character displacement.

Summary of examples

For the other pairs of species for which data are sufficient to reveal character displacement (Table 1), the data are less extensive and are not compatible with displacement. These cases plus the cases described in detail above do not support the contention that reproductive character displacement generally occurs in acoustic insects with overlapping ranges and similar calling songs. Indeed for the cases with the most extensive data the score reads: displacement, 0; convergence, 1 (*Anurogryllus*); no significant geographic variation, 2 (*Orocharis, Teleogryllus*); complex geographic variation, 2 (*Oecanthus fultoni, Gryllus rubens*).
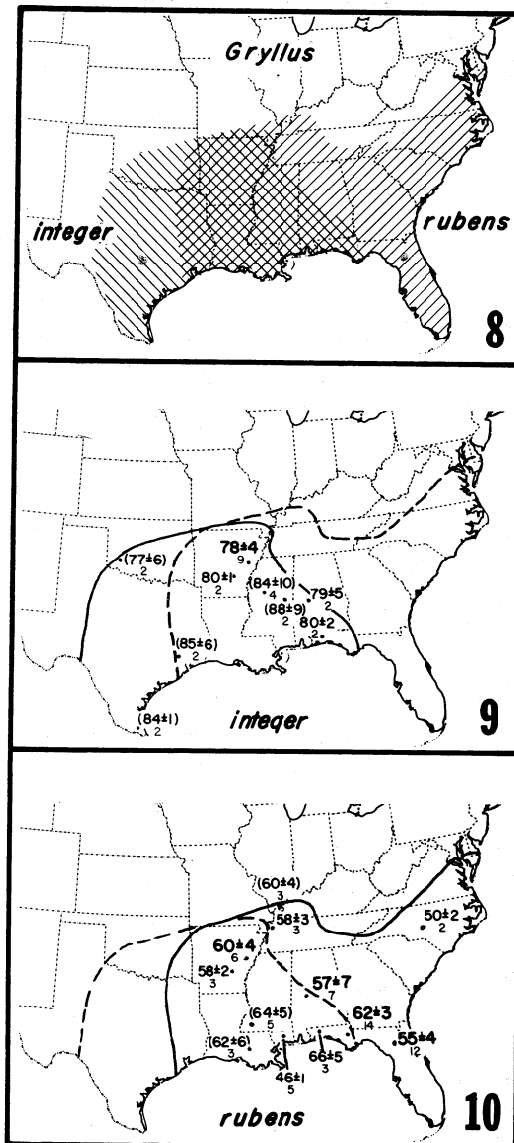

FIG. 8-10. *Gryllus integer* and *rubens*. FIG. 8. Diagonal lines show distributions of the two species. FIG. 9. Geographical variation in pulse rate (corrected to 25C) of calling songs in *integer*. For each locality the numbers are $\overline{X} \pm$ SD and *n*. Large numbers are for sample sizes of 6 or more individuals. Small numbers indicate *n* = 2 to 5 individuals. Numbers in parentheses are from field tape recordings. Other numbers refer to recordings made in the laboratory. FIG. 10. Geographical variation in pulse rate (corrected to 25C) of calling songs of *rubens*. Numbers have same meanings as in Fig. 9.

DISCUSSION

Why should examples of reproductive character displacement be scarce in crickets and katydids? Some possible answers are outlined below.

1) Perhaps sympatric enhancement of calling song differences does not occur. (a) Calling songs may not be as critical to conspecific sexual pair formation as supposed. For instance, a number of cricket species lack calling songs but form pairs anyway (Alexander and Otte, 1967; Walker, 1974), and Hill et al. (1972) found that sympatric *Teleogryllus* spp. females went to non-conspecific songs in single-choice trials. Nevertheless, laboratory experiments and evidence from the field point to calling songs being of great importance in the efficient forming of pairs in most species of crickets and katydids (Spooner, 1968a,b; Ulagaraj and Walker, 1973; and others already cited). (b) Calling songs may diverge sufficiently in allopatry such that when newly speciated populations became sympatric the songs are different enough so that no additional divergence occurs. Divergence in allopatry is sometimes strongly indicated by present distributions. For instance, *Borinquenula martorelli* and *B. caritensis* are allopatric cognate species with strikingly different songs (Walker and Gurney, 1972), yet they have apparently evolved their differences on isolated mountain ranges and have never been in contact. However, other allopatric cognate species have not diverged in song—for instance, *Gryllus veletis* (U.S.) and *G. campestris* (Europe) (Alexander, 1967) and *Orchelimum nigripes* and *O. pulchellum* (Fig. 11). The lack of detectable geographic variation in the songs of widespread species with low vagility is another indication of the slowness with which allopatric populations diverge in song. For instance, demes of *Belocephalus sabalis* and of the closely related species (or subspecies) *B. sleighti* and *B. davisi* occur allopatrically or parapatrically throughout Florida. These copiphorine katydids are flightless and their geographical variation in morphology suggests minimal gene flow. However, the songs of these demes are indistinguishable

(Walker, unpublished). The comparative evidence suggests that allopatric speciation often occurs without significant changes in the calling songs of the cognate species.

2) Sympatric enhancement of calling song differences occurs, but is difficult to detect. (a) The sympatric enhancement may occur without ever producing the pattern of geographic variation termed character displacement by Brown and Wilson (1956). Hill et al. (1972) point out that if one species arises from a small peripheral population of the other, sympatric selection for song differences could precede the expansion of the new species into an extensive allopatric range. Another possibility is that if the songs of cognate species are nearly identical at the time they come into contact geographically each species may interfere with the pair formation of the other to such an extent that only one can occupy any area, the winner for each area being determined by other aspects of the physical and biotic environments. Such interaction would result in parapatric distributions of cognate species with near-identical songs. Examples having this pattern are *Orchelimum nigripes* and *O. pulchellum* (Fig. 11) (Morris and Walker, unpublished) and *Oecanthus celerinictus* and *O. forbesi* (="fast-trilling nigricornis") (Walker, 1963). Calling song interference at the line of contact and extensive intraspecific gene flow might eventually result in divergence in important parameters of the calling songs without there ever being a substantial zone of sympatry. Such parapatric divergence in calling songs might occur even though the parapatry was caused by something other than reproductive interference.

(b) Perhaps the sympatric enhancement of calling song differences occurs and produces the pattern of geographic variation termed character displacement by Brown and Wilson. (i) Too small a sample has been studied intensively to prove that this pattern of variation is scarce in United States crickets and katydids. In only 22 of 43 presumptive cases have I the minimal data for showing displacement (Table 1), and in only a few of these have I sufficient data to show minor geographic variation.
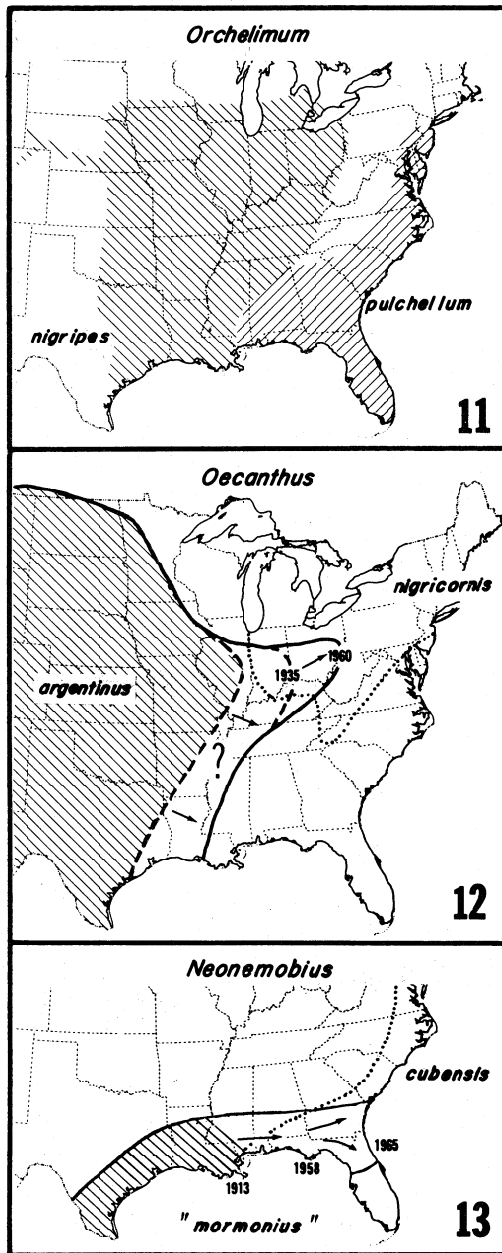
FIG. 11. Distributions of *Orchelimum nigripes* and *O. pulchellum*, two species with indistinguishable calling songs. FIG. 12. Distribution of *Oecanthus argentinus*, a prairie species that has spread eastward during this century. Solid line indicates eastern limits. Dashed lines are guesses as to former range. Dotted line indicates approximate southern and western limits of *O. nigricornis*, a species with a calling song similar in pulse rate to that of *argentinus*, and which was termed "slow-trilling *nigri-*

(ii) The features of the songs that have been analyzed may not be the ones that the females are using to make their conspecific responses. The results with temperature-altered natural songs (Walker, 1957) and with synthetic songs discredit this idea at least for the groups so studied. (iii) The diagnostic pattern of geographic variation may be rapidly lost because differences arising in the zone of sympatry spread into the zones of allopatry. The spread need not depend on differential reproduction favoring the change in song in the zone of allopatry, but simply on a biased exchange of alleles between the zones of allopatry and of sympatry. Ehrlich and Raven (1969) cautioned against unsupported assumptions about gene flow. Other than circular argument (i.e., I don't find much geographical variation in song; therefore, gene flow must be extensive) the evidence for extensive gene flow is as follows: large numbers of many species of acoustic insects are captured at light and the simplest interpretation is that these nocturnal flights are dispersive (e.g., Callahan et al., 1972; Ulagaraj and Walker, 1973). Allozyme studies of one such species, *Gryllus integer*, "demonstrated a surprising degree of geographic uniformity in both allele frequencies and level of genic heterozygosity" (Wagner and Selander, 1974, p. 128). Two prairie species of crickets have apparently spread hundreds of miles eastward in the past 60 years. One of these, the prairie tree cricket, *Oecanthus argentinus* (Fig. 12), is discussed by Walker (1963, p. 774). The other is a ground cricket of the genus *Neonemobius*. It is similar to *N. mormonius* (type locality, Utah) but is probably undescribed. When I first started studying Florida crickets (1958) it was one of the most abundant crickets in West Florida (Fig. 13). Yet in Hebard's (1913) revision of ground crickets, the easternmost record of "*mormonius*" was Biloxi, Mississippi. During extensive field work in the

cornis" in Walker (1962a). FIG. 13, Distribution of *Neonemobius* "*mormonius*", a species that has spread eastward to the Atlantic during this century. Dotted line indicates northern and western limits of *N. cubensis*, a species with a calling song similar in pulse rate to that of "*mormonius*."

1930's, T. H. Hubbell failed to find *"mormonius"* in the Gainesville area (1938 mimeographed list of Orthoptera of Alachua County, Florida). In 1961 I first found it in Gainesville, and in a few years it had become the most abundant ground cricket inhabiting well-drained, grassy roadsides and pastures. It has remained abundant in Gainesville and is perhaps still spreading southward and northward. The extreme records are Lake County, Florida (1970), and Chatham County, Georgia (1964). Both *N. mormonius* and *O. argentinus* demonstrate a rapid (eastward) gene flow that would have gone undetected except that range extensions resulted. Similar but undetected gene flow probably occurs in these species in other directions and in many species in all directions.

Obviously acoustic insects still have the potential for convincingly illustrating reproductive character displacement, but surprisingly little positive evidence has turned up thus far. Further studies are desirable, especially if they are directed toward the strongest presumptive cases. If rapid erosion of geographic variation in song by gene flow is a major contributor to the scarcity of examples, two types of cases deserve special study: pairs of species with low vagility and pairs of species that have achieved their geographical overlap recently. An example of the former are *Gryllus fultoni* and *G. veletis* (see above). *G. fultoni* is 100% micropterous while *G. veletis* is 96% micropterous (Alexander, 1968a). Two examples of the latter are provided by *O. argentinus* and *N. "mormonius"* (Figs. 12, 13). Each has recently spread into the range of a species with a similar song. For *argentinus*, the species overlapped is *nigricornis*. The fact that *argentinus* is bivoltine while *nigricornis* is univoltine reduces the contact betwen singing adults of the two species, but in September in Ohio both species call in the same weedy fields (Walker, 1962a). The occurrence of faster-*(Oecanthus forbesi* = fast-trilling *nigricornis* of Walker, 1963) and slower-*(Oecanthus quadripunctatus)* pulsed calling songs in the same habitats restricts the possibilities for displacement of pulse rates in *argen-*

tinus and *nigricornis;* consequently, displacement in some other calling song parameter or accentuation of seasonal or habitat differences seems probable. For *N. "mormonius"* the newly acquired overlap is with *N. cubensis.* The pulse rate of the songs are broadly overlapping but carrier frequencies and the manner in which each trill is begun provide possible cues for conspecific responses. Whether these are used or whether sympatric divergence in calling song parameters has occurred is not known.

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