

Acoustic signals and speciation in cicadas (Insecta: Homoptera: Cicadidae)

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Abstract

Cicada species are separated by one or more of the following factors: geography, habitat, season, diurnal pattern of reproductive activity, and acoustic signals. A few species with unusually distinctive songs and broad habitat affinities have large geographic ranges, throughout which they show little acoustic or morphological variation. Most other species have far more restricted habitats and geographic ranges. *Tibicen lyricen* in eastern North America has evolved striking morphological varieties which all retain the same song.

The six species of periodical cicadas (*Magicicada*), with three distinctive but essentially invariant calling songs, have evolved extensive developmental and distributional complexity. Multispecies brood populations of both 13- and 17-year cicadas, isolated geographically and chronologically, have evidently persisted since the Pleistocene glaciation and have invaded glaciated regions. *Decim* cognate males' songs are heard by *Cassini* cognates even better than their own songs, which may

enhance assembly as chorusing, mixed-species, selfish herds. Sometimes adult stragglers emerge within a few years of the main brood emergence date; the most common straggling times are 1 year early or late, or 4 years late.

Tertiary fossils, representing all of the major subgroups of cicadas in North America, are known from the western United States.

INTRODUCTION

Tymballing cicadas are not host specific, but in North America are clearly associated (1) with general ecological habitats (such as deserts, eastern deciduous forests, grasslands, etc.), (2) with seasons (late spring and early summer, or mid-summer and fall), and (3) with time of day of reproductive activity.

The evolution of cicada acoustic signals seems to be linked to (1) the presence of other cicada species (commonly, 2–5 species representing 1 or 2 genera are active in a local area at the same time), (2) how long that association has persisted, and (3) how distinctive the species' song was at the time of first encounter with other species. Thus, geographic distribution, temporal occurrence and acoustic behaviour are closely linked.

A few examples in three genera are dealt with here. One focus is on the correlation of distribution and evolution of calling songs of males. Callings songs are the primary congregating mechanisms of sexually receptive adult cicadas, functioning as premating isolating mechanisms and initial mate-recognition signals. These songs are their most common sounds, usually produced by lone males, but in a few species they are produced by groups of chorusing males. The other focus is on evolution of very long developmental and reproductive cycles along with complex multispecies geographic ranges, given prior selection for very distinctive acoustic signals.

EXTENSIVE GEOGRAPHIC RANGE, LITTLE VARIATION

Only one cicada species, *Quesada gigas* (Olivier), is known whose range includes both North and South America. This species is common during local summers from south central Texas, through Mexico and Central America, and from east to west from northern South America to south of Buenos Aires, Argentina. *Q. gigas* is typically active in late afternoon and at dusk, and is one of the few species that continues singing at night under bright moonlight or streetlights. Its song is long and distinctive from all other cicada sounds in those regions, beginning with a buzz, followed by a staccato phrase lasting up to several seconds, and ending with a whine lasting up to several seconds. Without interruption, the staccato and whine sections may be repeated several times in a row during one singing bout by a male. Throughout its large geographic range of several thousand kilometres of temperate and tropical conditions, there is only modest morphological variation and essentially no variation in song.

It is not likely that *Q. gigas* has been transported passively by man, for it is not closely associated with any crop plants. Only one other species, also South American, is known in the genus, and no closely related fossils are known. There is no evidence on the timing or direction (s) that this great dispersal of *Q. gigas* followed. Similarly extensive geographic ranges, but in temperate climes from the Mediterranean eastward

across central Asia, also with little morphological or acoustical variation, are known for *Tibicen plebejus* (Scopoli) (= *Lyristes plebejus* (Scopoli)) and *Cicada orni* Linnaeus (Andrej Popov, personal communication; Claridge, Wilson & Singhrao, 1979).

SIMILAR SONGS, PLUS MORPHOLOGICAL VARIATION

Tibicen lyricen (De Geer) is a widespread summer species, active from July to the first frost in deciduous forests of eastern North America. It has three strikingly different morphs named as varieties (Fig. 1). Despite their distinctive appearances, these morphs show no clear geographic associations (Fig. 2), and there are no known barriers to introgression among the varieties. The generally larger variety with more heavily infuscated wings, *T. lyricen* var. *virescens*, has a more southerly and coastal distribution, but overlaps broadly with var. *lyricen*, in particular. Despite having evolved distinctive morphological varieties, as different as between many other species, the songs of males of all three varieties are virtually identical throughout eastern North America. They are composed of nondescript beginning and ending buzzes of lower intensity, and a middle distinctively buzzy vibrato that may last up to several seconds (Fig. 3, upper tracings). It is this middle 'vibrato' portion of songs in *Tibicen* that is distinguishing, and there are no other eastern species of *Tibicen* with closely similar songs.

The closest *Tibicen* with a similar song (Fig. 3, lower traces) occurs in the Bermuda Islands, associated with native trees there (*Juniperus bermudiana* L.). Adults are morphologically distinctive (Fig. 1, lower right), but the songs of *T. bermudianus* sound remarkably similar to those of *T. lyricen*. In both species the principle frequencies lie between 4 and 6 kHz. *Tibicen bermudianus* is the only cicada in the Bermuda Islands, so it may well have undergone little selection for differentiation of song through interaction with other species. The origin and age of the terrestrial flora and fauna of the oceanic subtropical Bermuda Islands, lying about 1000 km east of North America, is puzzling. Several endemic plant and animal species are known. Other native terrestrial organisms have their closest affinities with south-eastern U.S. coastal regions or the West Indies (Verrill, 1903; Britton, 1965:vii). The geological history of these islands is reasonably well-established, suggesting habitable land there for at least 200 000–125 000 years, and no prior land connections (Harmon *et al.*, 1983).

SIMILAR MORPHOLOGIES, STRIKINGLY DIFFERENT SONGS, COMPLEX RANGES

This final example involves some of the most distinctive and famous eastern North American animals: the six species of periodical cicadas (*Magicalcicada*). They are famous for: (1) their very similar morphology as adults and as juveniles; (2) the longest reproductive cycles of any animals (13–17 years); (3) their population density, sometimes exceeding 3 000 000 per acre; (4) their loud songs, produced by dense, commonly mixed-species choruses in early summer when few other insects are singing; (5) their apparent sudden appearance, short adult lives, and absence of defensive mechanisms, making them prime prey for nearly all general predators; (6)

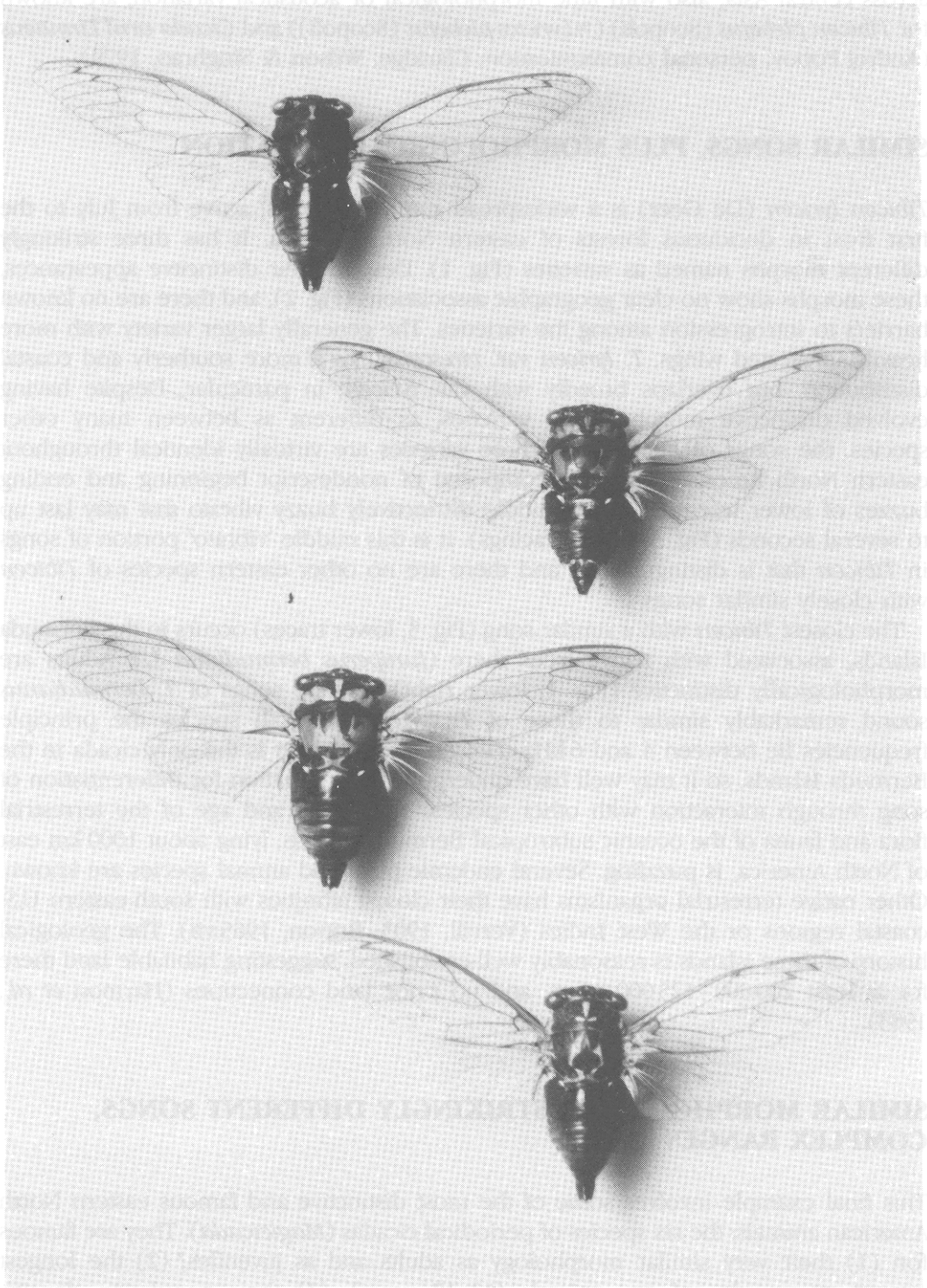


Figure 1 Dorsal views of adult males of two *Tibicen* species with very similar songs, one species with striking colour morphs. Upper left, *T. lyricen* var. *engelhardti* (Davis); upper right, *T. lyricen* var. *lyricen* (De Geer); lower left, *T. lyricen* var. *virescens* Davis; lower right, *T. bermudianus* (Verrill).

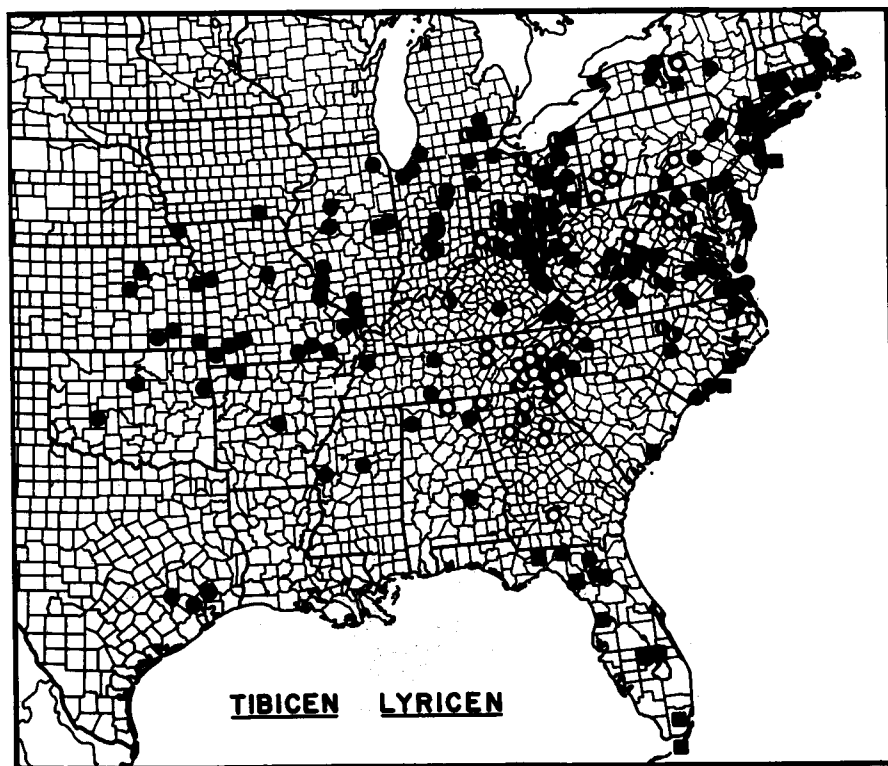


Figure 2 Geographic distribution of *Tibicen lyricen* (De Geer). Closed circles: var. *lyricen*; open circles: var. *engelhardti*; half-open circles, both var. *lyricen* and *engelhardti*; squares, var. *virescens*.

lack of distinctive habitat separations, daily redividing their habitats acoustically in unpredictable ways; (7) feeding regularly on xylem sap as juveniles and adults; and (8) their numerous and extensive mixed-species, chronologically and geographically disjunct populations called broods (Marlatt, 1923; Alexander & Moore, 1962; Williams & Smith, 1991).

The probable evolutionary relationships of the six species of periodical cicadas are shown in Fig. 4, based on morphological, developmental and behavioural characteristics. It is remarkable that each 17-year cicada has as its closest relative a 13-year cicada with essentially identical morphology and song. The songs and singing behaviour of the three 13-year species are shown in Fig. 5, and are essentially identical to the three 17-year species. The songs of the *Decim* cognates (*M. septendecim* and *M. tredecim*) centre between 1 and 3 kHz, those of both the *Cassini* (*M. cassini* and *M. tredecassini*) and the *Decula* (*M. septendecula* and *M. tredecula*) cognates centre between about 4 and 10 kHz. The songs of the *Decim* cognates are more musical, rising in pitch and in intensity before dropping in both characteristics at the end. The songs of the *Cassini* cognates sound like a series of rapid ticks, followed by a noisy buzz that rises in pitch and intensity before dropping in both at the end. The songs of the *Decula* cognates are about three times as long as a single song of the other two: a series of ticks separated by short buzzes, the buzzes becoming shorter and the ticks more closely spaced, ending with a series of ticks without buzzes between. These songs are about as different structurally as songs typically are

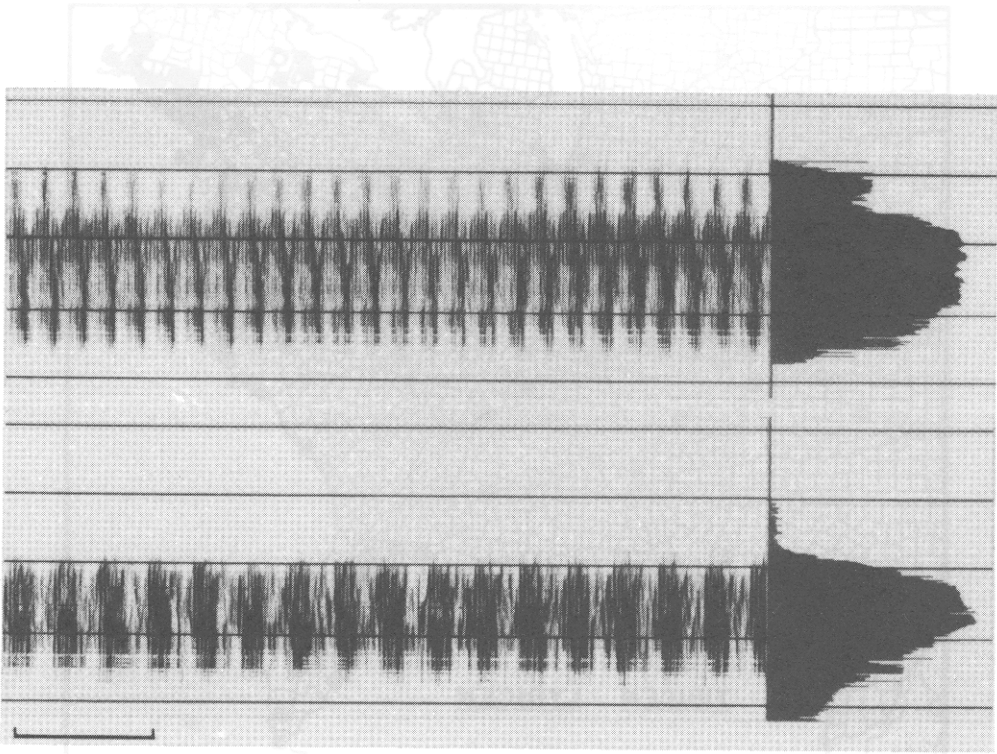


Figure 3 Audiospectrographs (left) and energy spectra (right) of vibrato middle portions of calling songs of *Tibicen lyricen* (upper) and *T. bermudianus* (lower). Time line for audiospectrographs, 0.1 s; amplitude scale relative; frequency scale marked at 2, 4, 6, 8 and 10 kHz.

between cicada genera, so they are well-distinguished by these signals, despite such similar adult appearance that the species were not distinguished until 1962 (Alexander & Moore, 1962). It is common for males of each species to sing one or a few songs, and then fly a short distance.

The three species of either 17-year or 13-year cicadas are thoroughly intermixed locally throughout most of their ranges, segregated together as mixed-species associates in chronologically and geographically isolated brood populations. It seems likely that some of these mixed-species populations have persisted since before Wisconsin glacialiation (Alexander & Moore, 1962; Cox & Carlton, 1988; Martin & Simon, 1990a; Cox, 1992). There are only 15 extant broods (Fig. 6), 12 of 17-year cicadas and 3 of 13-year cicadas, all designated by Roman numerals: I – XVII reserved for broods in any 17-year sequence, XVIII – XXX for those in any 13-year sequence. Brood VII, in upstate New York, includes only one species, *Magicicada septendecim*. All other broods include three species. One brood with the same single species, former brood XI in the Connecticut River valley, was still abundant, but reduced in range to one or at most a very few woodlots near Storrs, Connecticut, by 1954; by 1971 it had become extinct. Brood VII appears to be nearing a similar fate.

All three species of 17-year cicadas hear each other quite well, and hear a wide variety of other sounds, including birds, around them. In fact, *Magicicada cassini*

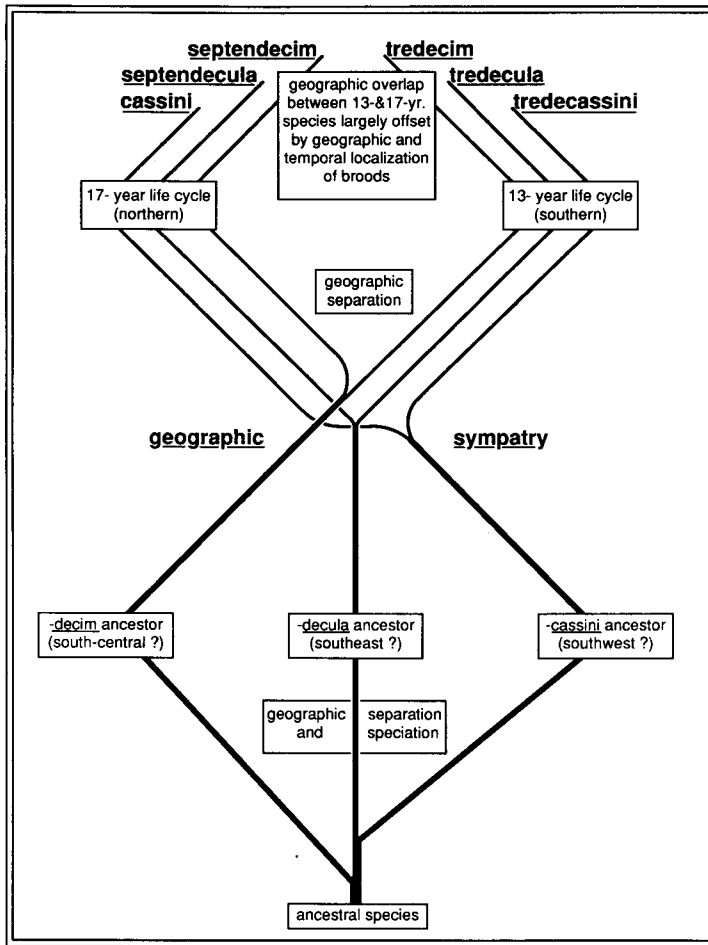


Figure 4 Diagram of probable phylogenetic relationships of 17-year and 13-year cicadas (*Magicicada*). (Modified from Alexander & Moore, 1962.)

hears *M. septendecim* (the species with which it most extensively occurs, whose peak of chorusing is reached earliest in the day, and whose song has the least intensity of the three) better than it hears its own songs (Huber *et al.*, 1990). This possibly enhances the formation of the typical complex mixed-species selfish herds (Hamilton, 1971) found in periodical cicadas, as the two later-chorusing species (*Cassini* and *Decula* cognates) daily move among the chorusing males and responding females once *Decim* males have begun to sing.

The only defences these species have against general predators are (1) surprise, emerging in huge numbers before their shorter-lived (and therefore inexperienced) potential predators have detected them, (2) accomplishing much of their reproductive activity quite early in an emergence, (3) emerging in such great numbers that they can satiate the predators once they are discovered, and (4) taking advantage of the buffering effect of the relative numbers of the other visually and behaviourally similar, sympatric, periodical cicada species by flocking together. Straggling individuals emerging in off years are at special risk, for their numbers are almost always so small

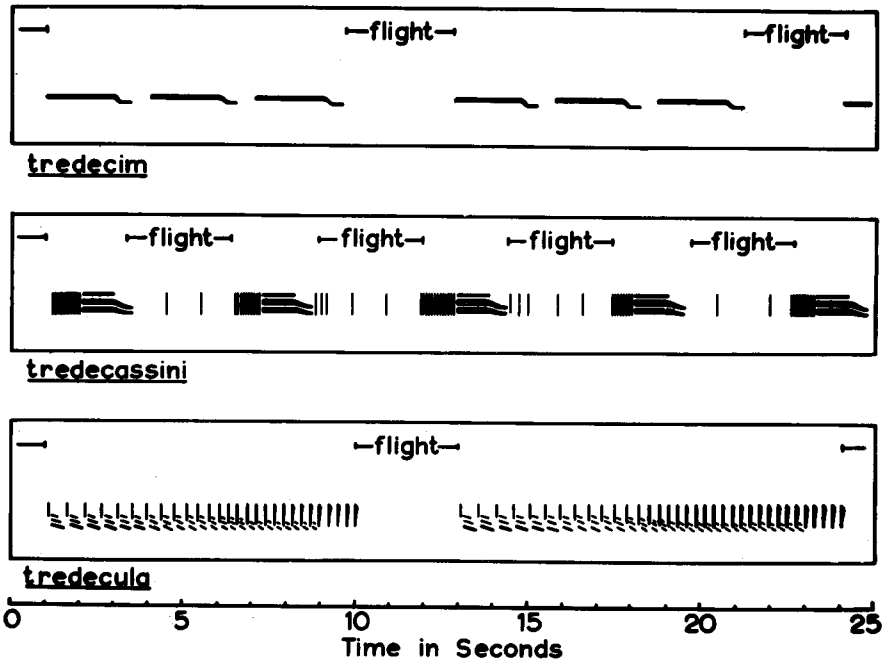


Figure 5 Diagrams of calling song audiospectrographs and typical chorusing behaviour in periodical cicadas (*Magicicada*). Song and behaviour patterns are essentially identical between cognate 13-year and 17-year cicadas: between *M. tredecim* (Walsh & Riley) and *M. septendecim* (L.), *M. tredecassini* (Alexander & Moore) and *M. cassini* (Fisher), and between *M. tredecula* (Alexander & Moore) and *M. septendecula* (Alexander & Moore). (From Alexander & Moore, 1962.)

that these populations are all eaten by predators within a few days, before they can lay sufficient eggs to sustain a subsequent emerging population of adults. This is particularly evident for the scattered stragglers in years after the main emergence.

The *Cassini* cognates usually emerge first in a brood (Williams & Smith, 1991; Moore, unpublished), and it is perhaps surprising that they are not more often the predominant species in an area, given the repeated opportunities to take advantage of predator surprise and the best singing and oviposition sites.

Whenever 17-year and 13-year broods occur in the same year, it is 13×17 , or 221, years before that happens again; and since Wisconsinan glacial times, a maximum of about 50 co-occurrences could have taken place between any such pairs of broods. Few such broods have the possibility of overlapping geographically as well as chronologically, however (cf. Fig. 6). Alexander & Moore (unpublished) brought large numbers of all three 13-year species (brood XXIII) from south-eastern Missouri into the range of all three 17-year species (brood III) in north central Illinois during the simultaneous emergence of adults of the two broods in 1963. By recording individual matings of marked animals, it was established that freely roaming cognates of 13- and 17-year cicadas would interbreed (*M. cassini* with *M. tredecassini*, *M. septendecim* with *M. tredecim*), that males and females of these species sometimes mate more than once, that subsequent matings by females may follow oviposition bouts, and that matings are not always preceded by courtship signals. The facts that intermatings will take place freely, that those few populations that could overlap in time and space

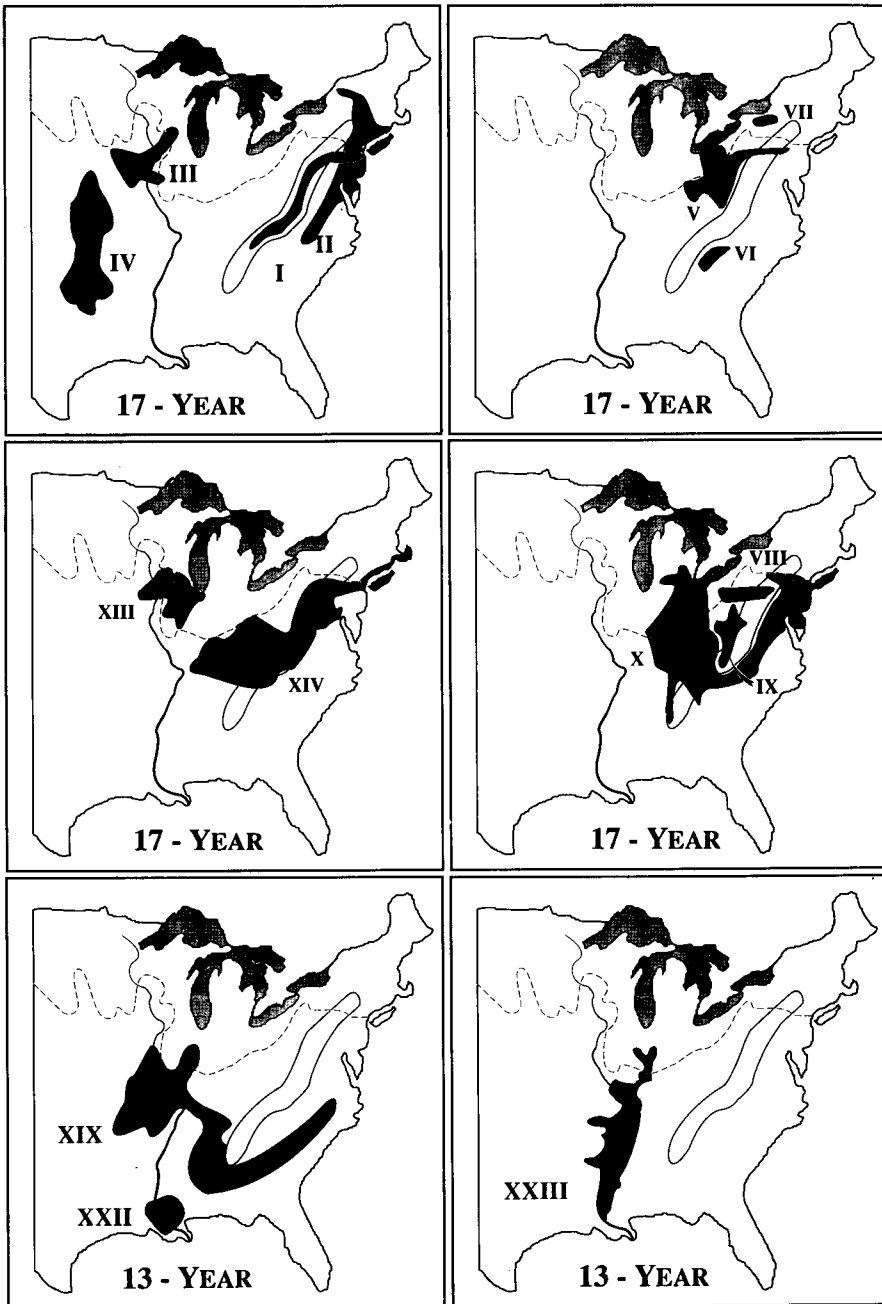


Figure 6 Generalized distributions of extant broods of periodical cicadas (*Magicicada*) in the eastern United States. All ranges include three species, except that of brood VII (*M. septendecim*, only). Upper four maps, 17-year cicadas (*M. septendecim*, *M. cassini*, *M. septendecula*); bottom two maps, 13-year cicadas (*M. tredecim*, *M. tredecassini*, *M. tredecula*). The Great Lakes, Mississippi River, Appalachian uplift area, and Wisconsinan (Pleistocene) glacial maximum boundary (dashed line) are also shown. (Modified from Alexander & Moore, 1962.)

have in fact moved further apart in nature with subsequent emergences, and that no sustained populations of intermediate emergence periods occur in regions of likely former overlap, all suggest that the natural experiments done on a grand scale whenever such 13- and 17-year broods have coincided as adults attest that viable adult offspring do not issue from such crossings. The handful of cross-matings reported within either 17-year or 13-year cicadas, in the hundreds of thousands of mating pairs observed, have always involved damaged individuals, have never been reported to have led to oviposition, and have not led to records of animals with intermediate songs or morphologies, suggesting insignificant introgression.

It might be expected that broods containing the species with the shorter life-cycle would out-reproduce 17-year cicadas wherever they overlapped, and spread more rapidly as forests expanded into new regions following Pleistocene glaciation, for in every 221-year period they would have four more generations. However, that has not been the clear case. One other expectation would be that if each of the 14 brood populations including three species remains isolated and persists long enough, sufficient differences will accumulate to make their members irreversibly separate from similar members of other broods, potentially producing 14×3 species of periodical cicadas. In order to understand where these species are today, and have been in the past (our best basis for predicting future associations), we need to show the locality and date records and the distribution maps for these broods by species (e.g. Fig. 7). This means using museum voucher specimens, tape-recordings, or records published by species and based upon competent identifications. Records and maps dealing with these six species as if they were one lead to a substantial loss of information and contribute to inadequate rigour in considering origins of broods. Comparisons of biochemical characteristics of less than all three species in each of the 14 extensive broods also are likely to contribute to incomplete or inadequate hypotheses (Simon, 1979, 1988; Simon & Lloyd, 1982; Cox & Carlton, 1988; Martin & Simon, 1988, 1990a, b; Cox, 1992).

There has always been concern about accepting presumed records, especially early records, for which no voucher specimens exist. Not only do these records usually lack precise locality and date, but also they are often reported from memory some time after the occurrence, usually by someone not familiar enough with cicadas to be certain even of generic identity. A prime example is the presumed earliest recorded emergence of 17-year cicadas (1633) in the first historical book published in America 36 years later (Morton, 1669:90–91). Morton (not Moreton) compiled his notes of the early 'New-Plimouth' colony largely from the journals of William Bradford and Thomas Winslow, noting that pages sometimes had fallen out, or were inserted in incorrect chronological order. Broods now known to have emerged in or near Massachusetts and expected to have emerged at about that period, none with vouchered records as far north-east as Plymouth (New-Plimouth), are XI (1631), XIV (1634), and II (1639). No other emergences are mentioned in Morton, specifically not for any of these years, nor for the next expected emergence in 1650 (or in 1651 – the date of the generally accepted first published emergence of 17-year cicadas (Anonymous, 1666; brood XIV) – if, as often assumed, the published date was incorrect by a year and the record represented brood XIV in 1634).

It is as likely that this 1663 record applies to *Okanagana rimosa* (Say), often confused for a 17-year cicada. It also is reddish and black, frequently occurs in very large populations at the same time of the year, sings loud songs in dense choruses

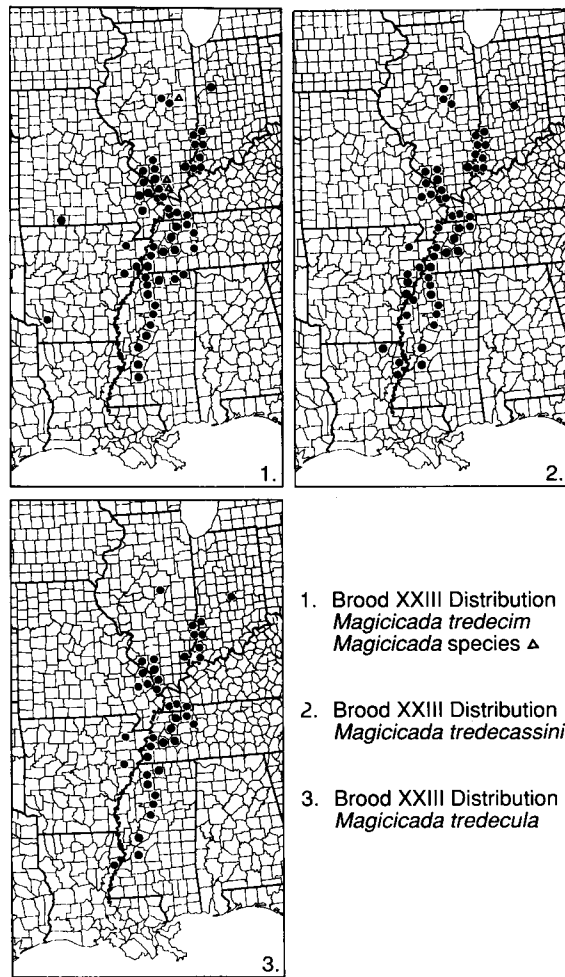


Figure 7 Distribution of the three species of 13-year cicadas in brood XXIII (*Magicicada*); consecutive emergence-years, 1976, 1989, 2002.

all day long, and has a fungus which rots off the tip of the abdomen, also characteristic of *Magicicada* species. *Okanagana rimosa* is known to occur from Long Island, New York, through Massachusetts, to the north-east, north, and westward through Canada and northern states to northern Iowa. We do not know a precise generation time for any *Okanagana* species; *O. rimosa* may average about 8–10 years in duration, and be variable.

Fidelity of *Magicicada* records, and their significance, has long been of concern (Marlatt, 1923; Alexander & Moore, 1962; Maier, 1985). Almost all records of adults emerging a few years before or a few years after an expected brood emergence-year (Fig. 7; cf. Alexander & Moore, 1962:50) are for either *M. septendecim* or *M. tredecim*, are within 4 years before or after a known major emergence and from known localities for existing broods, involve far fewer cicadas than a normal emergence, are eaten by birds or other predators within a week of emergence and before significant reproduction, and have rarely led to a corresponding emergence in more than one

subsequent generation. These early or late adults are called stragglers. The suggestion that periodical cicadas could switch between 13- and 17-year cycles (Martin & Simon, 1988, 1990b), proposed for straggling *Decim* siblings, is not supported by robust evidence, and is countered by the vast preponderance of repeated emergences occurring as expected in all species throughout the extensive ranges of each brood. Suggestions that such episodes are likely events accounting for the origin of broods ignore the powerful countering fact that these broods contain three independent species, each responding in its own way to genetic or environmental factors, making it extremely unlikely that the same cluster of species would so extensively coincide in 14 brood populations. For similar reasons, it is not rigorous to discuss the origin of broods by dealing with them as if the broods consisted of a single species; and doing so can mislead others who are not specialists on cicadas and diminish the value of insights they might be able to provide (Cox & Carlton, 1988; Cox, 1992). It is also important to realize that periodical cicadas feed freely on roots and branches, and lay eggs successfully in twigs, of white pine (*Pinus strobus* L.) and of red cedar (*Juniperus virginiana* L.) in addition to a wide range of deciduous forest woody plants (Moore, unpublished).

The preoccupation with the origin of 13-year cicadas, or of broods of either 13- or 17-year cicadas, just from stragglers appearing 4 years early not only ignores the evidence that a single species is usually straggling, and that the population numbers are too small and survive for too short a time to produce another generation, but also the records for stragglers 3, 2 and 1 year(s) early, as well as those 1, 2, 3, and 4 years late. Data based on vouchers indicate that stragglers are nearly always *Decim* cognates for all extant broods, departing from only 1–7 emergence-years per brood (mean, 3), as follows: 17-year cicadas – two broods 6 years early, one 5 years early, five 4 years early, four 3 years early, five 2 years early, eight 1 year early, nine 1 year late, five 2 years late, four 3 years late, five 4 years late; 13-year cicadas – one brood 3 years early, two 2 years early, one 1 year early, one 1 year late, one 2 years late, one 3 years late, two 4 years late. The most common straggling period is 1 year early, or late, next most common is 4 years late, 2 and 3 years early or late are as common as 4 years early (Moore, unpublished).

Careful comparison of the 865 periodical cicada brood records for Indiana given by Kritsky (1987), none by species, shows that 85% of them are for 17-year cicada brood X; of these, 71 are straggler records, 63% 4 years late, 27% 4 years early, and the few others representing 2, 3 and 5 years late as well as 2 years early. He missed the emergence of brood XIX (Posey Co., Indiana, *M. tredecassini*, 1972). Contrary to Kritsky's emphasis on 4-year accelerations of emergence, it would seem that the more common straggling times should be at least as likely to initiate broods as any one of the rarer ones. Far rarer decelerations or accelerations of whole brood populations, or of all three species in major portions of broods, seem as likely as sources of broods or of variability within broods, as ascribing origin to one of the less common periodicities of principally single-species stragglers.

Lloyd, Kritsky & Simon (1983) assume hybridization between 17-year and 13-year cicadas created at least some broods of periodical cicadas, and suggest that both broods XIX and XXIII of 13-year cicadas uniquely occur sympatrically at Weldon Springs State Park, DeWitt County, Illinois, following a 1976 emergence at the park. This county is at the northern boundary of the range of brood XIX, the northernmost brood of all 13-year cicadas, and not far from forests known to be occupied by 17-

year cicadas. They made several predictions based on their analyses of presumed historical correlations. Important among these predictions were that (a) brood XXIII would emerge there again in 1989, and (b) would emerge particularly in the same woods where brood XIX would have emerged in 1985. No cicadas emerged there in 1985, nor in any year since then (including 1989), although in 1985 brood XIX emerged within a few miles, in 1972 in nearby Clinton, and in 1969 (stragglers of the 1972 emergence of brood XIX ?) in the village of De Witt (Moore, unpublished). The 1963 emergence Lloyd *et al.* cite from De Witt County, as well as the 1976 emergence 13 years later that prompted their paper, are at least as likely to be accounted for by stragglers of prior brood XIX populations, perhaps delayed in emergence by a series of unusually cold years such as those cited by Hughes (1979) for 1812–17, as they are to be accounted for by their more complicated scenario. Brood XIX would have been expected to emerge in 1816, the coldest of the summers listed by Hughes, just four emergence periods prior to the 1868 emergence cited by Lloyd *et al.* Emergence of brood XIX is known from the two adjacent counties analysed by Lloyd *et al.* for the years 1868, 1881, 1894, 1907, 1920, 1933, 1946, 1959, 1972 and 1985; while likely straggling 4-years-late populations of brood XIX are known from De Witt County only in 1885, 1898, 1911, 1963 and 1976, and from those same two adjacent counties in 1963 and 1976. By comparison, Alexander & Moore (1962) reported stragglers from four southern Ohio counties in 10 different years across a span of 18 consecutive years in a region in which just three well-studied broods of 17-year cicadas are known. The hybridization hypothesized to have occurred between cognate pairs of 13- and 17-year cicadas by Simon & Lloyd (1982) and Lloyd *et al.* (1983), also seems less likely in view of the interpretation of their own data by Martin & Simon (1990a), in which they suggest finding no evidence of gene flow between 13-year and 17-year cicadas.

Whatever the interactions of periodical cicadas at Weldon Springs, the populations occurring at 13-year intervals from 1885 to 1911, and in 1963 and 1976, have become extinct; and there is no compelling evidence of 17-year cicadas such as brood X (possibly present in 1868) or of other 13-year cicadas (such as brood XXIII), as presumed by Lloyd *et al.* (1983), ever having occurred there (Moore, unpublished). One must emphasize the unlikelihood of periodical cicada broods, including three independent species of the six periodical cicadas, changing simultaneously into another brood through climatic influence, or changing chronology simultaneously by all six species successfully hybridizing in large numbers. The suggestion of single-year weather fluctuations or hybridizations involving one cognate pair, followed by a single 4-year life-cycle change persisting through several slightly varying emergence years, and overlooking the fact that the changes must be simultaneous in three different species (e.g. Martin & Simon, 1990b), runs counter to the abundant evidence of multiple years of climatic variation as well as multiple year-change events in several broods, often in the same general locality. Hopefully, comparative studies involving all three species in each of the 14 large broods of periodical cicadas will eventually provide more robust and consistent evolutionary hypotheses for broods.

Nymphal growth rates have seldom been measured by species; we can only identify genera for nymphs. However, in the Ann Arbor, Michigan, area there is only one species of one brood: *M. septendecim*, brood X. In mid-June, 2 years after the 1970 emergence, all nymphs sampled from a mature second-growth forest were still in the first instar. By mid-summer, 4 years after emergence, all were in the second

instar. In May, 8 years after emergence, 54% were in the third instar and 46% in the fourth, but by October of the same year only 21% remained in the third instar, while 79% were in the fourth. At 9 years, 9% were in fifth instar, and at 10 years from last emergence, 77% were in fourth and 23% were in fifth instar. By 13 years from last emergence, all were in fifth (final) instar, although none appeared mature enough to emerge. Other accounts of growth rates of nymphs of mixed, unknown species for both 17- and 13-year cicadas suggest, despite considerable variability in growth rates, that by the 8th or 9th year a significant percentage of nymphs have reached the fifth and final instar (Marlatt, 1923; White & Lloyd, 1975), which is not surprising, given the known pattern of straggling.

ORIGIN OF NORTH AMERICAN CICADAS

Quesada is a member of the subgroup of cicadas in which the tymbals are partially hidden from view by a dorsal abdominal flap, and in which the abdominal sternites are nearly transparent (see-through cicadas). *Tibicen* belongs to the subgroup of cicadas whose tymbals are completely concealed from view by a special dorsal abdominal flap (concealed-tymbal cicadas). *Magicicada* belongs to another subgroup in which the tymbals are completely exposed to view dorsally (exposed-tymbal cicadas). The exposed-tymbal condition is typical of the structure of most tymbals throughout the auchenorrhynchos Homoptera. One other subgroup, the wing-tapping cicadas, distinctive of western North America, has lost the tymbals while retaining an abdominal tracheal air chamber and ventral tympana typical of cicadas. Both males and females in this subgroup 'sing' by tapping their forewings to vibrate the wing surfaces.

All of these subgroups are known from the Tertiary of North America. *Lithocicada perita* Cockerell, a see-through cicada, is known from Miocene shales of Colorado; *Davisia bearcreekensis* Cooper, Palaeocene, Montana, and *Tibicen grandiosa* (Scudder), Miocene, Colorado, are both concealed-tymbal cicadas, similar to *Tibicen cultriformis* (Davis) or *Tibicen marginalis* (Walker); *Platypedia primigenia* Cockerell, Miocene, Colorado, is a wing-tapping cicada (Cooper, 1941). An undescribed rather complete fossil of *Okanagana* (Moore, unpublished), an exposed-tymbal cicada, is known from the Oligocene shales of the Ruby mountains of Montana (Becker, 1965). Thus, all of the major cicada subgroups now present in North America have been there for 25–60 million years. It seems likely that the six species of periodical cicadas (*Magicicada*) evolved and formed three-species broods sometime before the last Pleistocene glaciation. Seven 17-year broods, and two 13-year broods, have invaded, or re-invaded, these last glaciated areas (Fig. 6).

CONCLUSIONS

Cicadas are sometimes quite invariant morphologically and acoustically, despite great geographic ranges through many highly variable environments. Others vary morphologically, while showing almost no acoustic variation. The complex cluster of periodical cicadas (*Magicicada*) have evolved surprising developmental, biochemical

and distributional variability, despite little morphological or acoustic variation among the cognate 13-year/17-year species pairs.

REFERENCES

- ANONYMOUS, 1666. Some observations of swarms of strange insects and the mischiefs done by them. *Philosophical Transactions of London*, 1(8): 137.
- ALEXANDER, R.D. & MOORE, T.E., 1962. The evolutionary relationships of 17-year and 13-year cicadas, and three new species. *Miscellaneous Publications of the University of Michigan Museum of Zoology*, 121: 1–59.
- BECKER, H.F., 1965. Flowers, insects, and evolution. *Natural History*, 74(2): 38–45.
- BRITTON, N.L., 1965. *Flora of Bermuda (illustrated)*. New York: Hafner (reprinted from 1918).
- COX, R.T., 1992. A comment on Pleistocene population bottlenecks in periodical cicadas (Homoptera: Cicadidae: *Magicicada* spp.). *Evolution*, 46(3): 845–846.
- COX, R.T. & CARLTON, C.E., 1988. Paleoclimatic influences in the evolution of periodical cicadas (Insecta: Homoptera: Cicadidae: *Magicicada* spp.). *American Midland Naturalist*, 120(1): 183–193.
- CLARIDGE, M.F., WILSON, M.R. & SINGHRAO, J.S., 1979. The songs and calling sites of two European cicadas. *Ecological Entomology*, 4: 225–229.
- COOPER, K.W., 1941. *Davisia bearcreekensis* Cooper, a new cicada from the Paleocene, with a brief review of the fossil Cicadidae. *American Journal of Science*, 239: 286–304.
- HAMILTON, W.D., 1971. Geometry for the selfish herd. *Journal of Theoretical Biology*, 31: 295–311.
- HARMON, S.H., MITTERER, R.M., KRIAUSAKUL, N., LAND, L.S., SCHWARCZ, H.P., GARRETT, P., LARSON, G.J., VACHER, H.L. & ROWE, M., 1983. U-series and amino-acid racemization geochronology of Bermuda: implications for eustatic sea-level fluctuation over the past 250,000 years. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 44: 41–70.
- HUBER, F., KLEINDIENST, H.-U., SCHILDBERGER, K., WEBER, T. & MOORE, T.E., 1990. Acoustic communication in periodical cicadas: neuronal responses to songs of sympatric species. In F. G. Gribakin, K. Wiese & A. Popov (Eds), *Sensory Systems and Communication in Arthropods, Advances in Life Sciences*: 217–228. Basel: Birkhäuser.
- HUGHES, P., 1979. 1816. The year without a summer. *Weatherwise* 32(3): 108–111.
- KRITSKY, G., 1987. An historical analysis of periodical cicadas in Indiana (Homoptera:Cicadidae). *Proceedings of the Indiana Academy of Science*, 97(1987): 295–321.
- LLOYD, M., KRITSKY, G. & SIMON, C., 1983. A simple Mendelian model for 13- and 17-year life cycles of periodical cicadas, with historical evidence of hybridization between them. *Evolution*, 37(6): 1162–1180.
- MAIER, C.T., 1985. Brood VI of 17-year periodical cicadas, *Magicicada* spp. (Hemiptera: Cicadidae): new evidence from Connecticut, the hypothetical 4-year deceleration, and the status of the brood. *Journal of the New York Entomological Society*, 93(2): 1019–1026.
- MARLATT, C.L., 1923. The periodical cicada. *U. S. Department of Agriculture, Bureau of Entomology Bulletin*, 71: 1–183.
- MARTIN, A.P. & SIMON, C., 1988. Anomalous distribution of nuclear and mitochondrial DNA markers in periodical cicadas. *Nature (London)*, 336: 237–239.
- MARTIN, A. & SIMON, C., 1990a. Differing levels of among-population divergence in the mitochondrial DNA of periodical cicadas related to historical biogeography. *Evolution*, 44(4): 1066–1080.
- MARTIN, A. & SIMON, C., 1990b. Temporal variation in insect life cycles. Lessons from periodical cicadas. *BioScience*, 40(5): 359–367.
- MORTON, N., 1669. *New-Englands Memoriall: or, a Brief Relation of the Most Memorable and Remarkable Passages of the Providence of God, Manifested to the Planters of New-England in America; with Special Reference to the First Colony thereof, called New-Plimouth*. Cambridge, Massachusetts: Printed by S.G. and M.J. for John Usher of Boston.
- SIMON, C., 1979. Evolution of periodical cicadas: phylogenetic inferences based on allozymic data. *Systematic Zoology*, 28: 22–39.

- SIMON, C., 1988. Evolution of 13- and 17-year periodical cicadas (Homoptera: Cicadidae: *Magicicada*). *Bulletin of the Entomological Society of America*, 34(4): 163–176.
- SIMON, C. & LLOYD, M., 1982. Disjunct synchronic populations of 17-year periodical cicadas: relicts or evidence of polyphyly? *Journal of the New York Entomological Society*, 90(4): 275–301.
- VERRILL, A.E., 1903. The Bermuda Islands – their scenery, climate, productions, physiography, natural history and geology. *Transactions of the Connecticut Academy of Arts and Sciences*, 11(2): 413–957.
- WHITE, J. & LLOYD, M., 1975. Growth rates of 17- and 13-year periodical cicadas. *American Midland Naturalist*, 94: 127–143.
- WILLIAMS, K.S. & SMITH, K.G., 1991. Dynamics of periodical cicada chorus centers (Homoptera: Cicadidae: *Magicicada*). *Journal of Insect Behavior*, 4(3): 275–291.