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MORPHOLOGICAL DIFFERENTIATION IN WING VENATION AMONG BROODS OF 13- AND 17-YEAR PERIODICAL CICADAS

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It has traditionally been assumed that no morphological differences exist between the 13- and 17-year life cycle forms of the periodical cicadas. Thus, differences among year-classes (broods) within a single species and life cycle would not be expected. In the first published description of the two life cycle forms, Walsh and Riley (1868) wrote, "there are absolutely no perceptible specific differences between the 17-year and the 13-year broods, other than in the time of maturing." The possibility of differentiation among broods, within a life cycle was never mentioned. Walsh (1870) asserted that, "it has been impossible for me, on the closest examination of very numerous specimens to detect any specific differences between the two forms." Riley (1869) commented that, "Mr. Walsh informs me that Charles Darwin, Asa Gray and Dr. Hooker all agree in the belief that the 17-year and 13-year forms ought not to be ranked as distinct species, unless other differences besides the period of development could be discovered."

Although later authors (Alexander and Moore, 1962) did not completely reject the possibility of differentiation among the broods, Lloyd and Dybas (1966) noted that, "no one has yet succeeded in demonstrating statistically significant differences between either broods or life cycles in any of the three species but modern methods of numerical taxonomy (Sokal and Sneath, 1963) have never been applied to this problem." In this paper I demonstrate that 13- and 17-year periodical cicada broods

can be differentiated based on multivariate analysis of wing morphology.

Background

Periodical cicadas (Homoptera: *Magicalicada*) are found only in the U.S. east of the Great Plains. The 13-year life cycle is confined to the central Mississippi Valley and southeastern states while the 17-year cycle is found in the northern, eastern, and western sections of the range (Marlatt, 1907). A given population of cicadas appears only once every 13 or 17 years, but the year of adult emergence differs depending upon the geographic location of a particular population. Populations which emerge in the same year are, by definition, members of the same *brood*. Some broods are large and extend over much of the eastern U.S., while others are small and extend over only a few hundred square miles. Broods are numbered sequentially according to the year of their emergence. Seventeen-year broods are numbered I–XVII while 13-year broods are numbered XVIII–XXX. Some of the numbered broods have never existed or are known to have gone extinct. At present, there are 14 broods of 17-year cicadas and three broods of 13-year cicadas.

Almost every brood of periodical cicadas contains three morphologically distinct species which differ in song, coloration, size, behavior, microhabitat preferences and body proportions (Alexander and Moore, 1962; Dybas and Lloyd, 1974; Lloyd and White, 1976*b*; Dunning et al., 1979; White, 1980), however, the range of states of many of these characters overlap considerably and these differences have not been quantified.

The 13- and 17-year counterparts of each

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TABLE 1. *Sample sizes for morphometric analysis of wing veins.*

Species group	Life cycle	Brood	Total sample size	Number of populations	Sample size per population
Cassini	13	XXIII	100	5	20
Decim	13	XXIII	80	8	10
Decim	17	XIV	80	8	10
Decim	17	XIII	100	2	80, 20

of the three morphologically distinct species have not been found to differ consistently in any characteristics. Nevertheless, Alexander and Moore (1962) recognized six species: three 17-year forms (*Magicicada septendecim*, *M. cassini*, and *M. septendecula*) and their 13-year counterparts (*M. tredecim*, *M. tredecassini*, and *M. tredecula*). The three morphologically distinct forms have conventionally been abbreviated Decim, Cassini, and Decula unless it was desirable to specify the life cycle duration. Decula will not be discussed in this paper.

Wing Morphology

The wings of insects are more extensively used in classification than any other portion of the body. Since wing characters are peculiarly conspicuous and tangible, it might be supposed that taxonomists have chosen them for the identification of groups to a larger extent than their relative importance warrants simply because they present easily recognized characters. One has but to make comparison however, of wing characters with those based on other parts of the body to be led irresistibly to the conclusion that they are of exceptionally high value. It is not too much to say that of all structures the wings have preserved the most nearly complete record of the course of the phyletic history of insects. The confidence with which wing characters are selected for the differentiation of groups results, in large part, from the recognition of this high phylogenetic significance, and the conviction that groups so defined are natural.

Woodworth, 1906

The phylogenetic significance of wing characters, described in the above quote, lies chiefly in the determination of relationships among higher taxa (families, orders), but wing characters can be useful in studies of more closely related taxa such as species and species complexes. Previously difficult taxa may now be separable using modern techniques of semi-auto-

matic data recording and computerized data handling which allow the processing of large amounts of information. Such detailed information may also be valuable in discerning phylogenetic relationships.

Magicicada wings are appealing as a source of systematic information because they are large and durable with many easily measured veins (Fig. 1). But, before any systematic analysis can be performed using these characters, it must first be determined whether and in what manner they differ among the groups to be examined. The purpose of the analyses presented in this paper is to demonstrate how wing veins vary within and among the broods and species of periodical cicadas. Do broods differ in wing morphology? Can broods be identified on the basis of wing morphology? Past entomologists have assumed broods to be morphologically indistinguishable. The fact that broods are, more or less, isolated from each other in time, calls this assumption into question. Allochronic broods should act as independent evolutionary units. Thus, they may have accumulated consistent morphological differences. Factors operating against morphological differentiation of these cicada broods are large population size (Lloyd and Dybas, 1966), similar selection pressures (populations from two broods are often sympatric or parapatric), and short amount of time since divergence of broods (Simon, 1979a).

UNIVARIATE ANALYSES

The present study examines variation in wing vein dimensions within and among three broods of periodical cicadas. Two of these broods are 17-year (Broods XIII and XIV) and one is a 13-year (Brood XXIII).

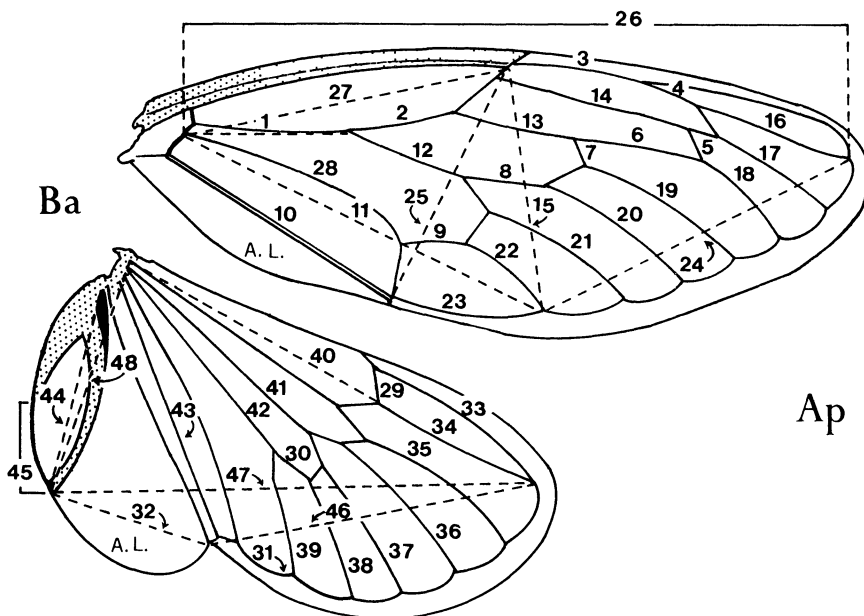


FIG. 1. The 49 wing characters measured. The fore wing is drawn above the hind wing. The costal (anterior) margin of the fore wing is stippled. The basal portion of both wings (labelled Ba) is closest to the insect's body. The apical portion of the wing is labelled Ap. Character numbers are written just above or to the right of the vein they identify unless otherwise indicated. Dashed lines describe length and width characters. A.L. is the abbreviation for anal lobe in both wings. Characters 11 and 43 measure the diagonal width of the anal lobes of the fore and hind wings, respectively.

The analysis concentrates on the *Decim* species, the only species found to be allozymically variable among broods (Simon, 1979a). Five populations of the morphologically distinct *Cassini* (*M. tredecassini*, Brood XXIII) are added later in the analysis to provide a comparison between the variation due to differences among life cycles and the variation due to differences among the morphologically distinct species. Table 1 gives sample sizes used in the various analyses.

All four wings of each specimen were mounted between clear acetate sheets and the veins of one fore wing and one hind wing (chosen randomly) were measured to the nearest .01 inches using a Hewlett-Packard 9864A digitizer. Coordinates of vein intersections were stored directly on magnetic tape and later transmitted to a larger computer for analyses. From these coordinates, the lengths of 48 different

wing vein dimensions were calculated (Fig. 1).

A two-level nested analysis of variance (ANOVA; Sokal and Rohlf, 1969 p. 204) was performed for each of the 48 wing-vein characters to discover the percent and significance of variation among broods (level 2), versus variation among populations within broods (level 1), versus variation within populations (level 0). An a posteriori grouping test, the sum-of-squares simultaneous test procedure (SS-STP), was used to describe the source of the among-brood variation. This test was necessary to determine whether significant variation in a character was due to differences among all broods or merely between one or two brood(s) and the others.

Character Variation in Decim

The results of the analyses of variance (Table 2A) showed that for the *Decim*

TABLE 2. Average percent of variance (\pm standard error) from 48 two level nested analyses of variance of wing vein characters.

Broods	Among broods	Among populations	Within populations
A. Decim Broods XIII, XIV, and XXIII: ¹	18.2 \pm 2.0	9.3 \pm 0.8	72.2 \pm 2.6
B. Decim Broods XIII, XIV, and XXIII and Cassini Brood XXIII: ²	53.2 \pm 3.0	4.5 \pm 0.4	42.3 \pm 3.0

¹ Ten characters were not significantly different ($P < .05$) among broods: 2, 4, 8, 18, 33, 34, 40, 41, 46, 47. Twelve characters were not significantly different ($P < .05$) among populations: 1, 4, 5, 7, 8, 9, 12, 13, 18, 29, 30, 31.

² All characters were significantly different among broods. Twelve characters were not significantly different ($P < .05$) among populations: 1, 4, 5, 7, 8, 9, 12, 13, 18, 29, 30, 31.

species, broods differed significantly for 79% of the 48 wing characters measured; only ten characters did not vary among broods. Sixty percent of the characters were significantly different among populations.

The majority of the variation (average 72.5% for the 48 characters) was within populations. Cicadas emerging at any one locality varied a great deal in size and shape of the wing. Of the remaining variation, 18.2% was among broods and 9.3% was among populations (Table 2A). Allochronically isolated broods which are probably no older than Pleistocene in origin (Simon, 1979a), have developed morphological differences.

Measurement error was calculated by measuring *all* Decim from Broods XXIII and XIV twice; an entire sample was measured and then re-measured. Analysis of variance using these replicated measurements showed that an average of only $6.99 \pm 0.8\%$ of the within population variation was the result of measurement error (see Simon 1979b for separate error estimates for each character).

Character Variation in Cassini Versus Decim

In order to compare variation between the morphologically distinct Decim and Cassini, five populations of Cassini (*M. tredecassini*) from Brood XXIII were measured (Table 1), and added to the Decim data set for the analyses of variance. Cassini was added to the nested ANOVAs at the "brood level" (i.e., level 2) rather

than adding a third "species" level, because this procedure would facilitate later partitioning of the variance. That is, an SS-STP analysis could then be used to compare variation among all four groups (three Decim plus one Cassini). The alternative, a comparison of Decim lumped versus Cassini, would not be as informative.

The results of the ANOVAs are shown in Table 2B. Again a large percentage of the variation was within populations (42.3%) but as expected with the addition of the much smaller Cassini, a greater percentage of the variation (53.2%) was at the highest level (among Decim of Broods XIII, XIV, XXIII, and Cassini of Brood XXIII). An average of only 4.5% of the total variation was among populations.

The SS-STP bar diagrams of Figure 2 depict the variation among broods of Decim and Cassini. Broods which were not significantly different constitute *homogeneous groups*. These are shown in the figure connected by a solid bar. Half of the 48 characters show one pattern of variability (Fig. 2, pattern A). This pattern shows no difference between the two 17-year broods while 17's as a group differ from the 13-year Decim and the 13-year Cassini. Five of the characters show a similarity between Decim of Broods XIII and XIV as well as a similarity between XIV and XXIII (pattern B). Four of the characters do not differ between *septendecim* of Brood XIV and *tredecim* of Brood XXIII (pattern C). Two of the characters are similar for all Decim (pat-

CHARACTERS	N ₁	N ₂	DECIM	DECIM	DECIM	CASSINI
			17	17	13	13
			XIII	XIV	XXIII	XXIII
A. 1 5 9 10 17-22 27 30-32 34-39 24 42 44 45 48		1	_____	_____	_____	_____
B. 2 13 33 40 47	5	2	_____	_____	_____	_____
C. 12 16 24 46	4	1	_____	_____	_____	_____
D. 8 41	2	1	_____	_____	_____	_____
E. 4	1	2	_____	_____	_____	_____
F. 6	1	2	_____	_____	_____	_____
G. 7	1	3	_____	_____	_____	_____
H. 14	1	1	_____	_____	_____	_____
I. 29	1	2	_____	_____	_____	_____
J. 3 11 15 23 25 26 28 43	8	0	_____	_____	_____	_____

FIG. 2. Sum-of-squares simultaneous test procedure (Sokal and Rohlf, 1969 p. 237) among all four groups studied. Solid horizontal lines identify homogeneous subgroups. For example characters 12, 16, 24, and 46 do not differ significantly between the Decim of Broods XIV and XXIII. Characters 3, 11, 15, 23, 25, 26, 28, and 43 are the only characters which differ significantly among all four groups (zero homogeneous subsets). N₁ = the number of characters which show the given pattern. N₂ = the number of homogeneous subgroups making up the pattern. The life cycle durations are indicated just below the species name abbreviations.

tern D). Eight of the characters are different among all four groups (pattern J). The remaining ten characters show various patterns of differentiation (patterns E–I). In three of these, Cassini is not significantly different at the brood level from more than one of the Decim groups.

The results of the SS-STP analyses demonstrate that some characters do not follow the classical expectation that 17-year broods of Decim should be more similar to each other than any one is to a 13-year brood of Decim. It is also surprising to find three characters for which Cassini and Decim do not differ significantly despite the smaller body size of Cassini.

MULTIVARIATE ANALYSES

Discriminant Function Analysis

Although groups of populations may overlap with respect to many characters viewed singly, the same groups may be entirely distinct when characters are viewed jointly (Jolicoeur, 1959). Discriminant function analysis (Lachenbruch, 1975) separates groups by giving less

weight to groups with high within-group relative to among-group variances. For k groups to be discriminated using p characters, there are $k - 1$ discriminant functions (or p discriminant functions if p is less than k); however, not all discriminant functions are guaranteed to be significant. Each discriminant function is made up of a linear combination of all characters but the relative importance of each character—its standardized discriminant weight—varies across discriminant functions. Discriminant function analysis can be used as an identification procedure to assign individuals to preexisting groups or, as used here, as an ordination procedure to help visualize group differences by plotting the groups in a space which is distorted such that among group distances are maximized.

Because of the large amount of among brood variation and the small amount of among population variation observed in this study, it seemed likely that broods of periodical cicadas could be differentiated but that populations within broods could

not. In total, 23 populations of 10–20 individuals each (Table 1) were subjected to discriminant function analysis.

The results of the discriminant function analysis upheld expectations; that is, populations within broods overlapped considerably whereas broods formed separate clusters (see below). The first three discriminant functions accounted for 79% of the total discrimination and seven of the 22 possible discriminant functions were significant at or above the .05 level.

Two dimensional plots of the population centroids and 95% confidence ellipses about these bivariate means (see below) in the estimated discriminant space for axes 2 versus 3 are shown in Figures 3A and 3B. Each population is represented by an ellipse calculated from its individual variance-covariance matrix. Although no information on brood membership was used in this analysis, the populations were grouped with other populations of their respective broods with little or no overlap. The small amount of among population variability present within broods did not allow separation of populations by even this most powerful technique.

In Figure 3 (and 4) the area encompassed by each confidence ellipse has a 95% probability of including the true population mean. The size of the ellipse depends on population sample size. The tilt of the ellipse depends on the covariances along each discriminant axis. The shape of the ellipse—the relative lengths of major and minor axes—depends on the amount of within-population variation along each discriminant function axis.

In the calculation of discriminant functions, within population variation is standardized such that variation along the major and minor axes is equal. In this new (Mahalanobis) space, confidence ellipses would appear circular and among population differences would be maximized. Standardization, however, does not insure that all the population's confidence contours will be circular. Only the *average* population's confidence contours will be circular. This is because standardization is performed on the *pooled* (averaged over

all populations) within-groups variance-covariance matrix. Discriminant function analysis *assumes* that within population variation (measured by the within-groups variance-covariance matrix) is equivalent for each population. Therefore in this ideal case, all confidence contours, once standardized, would be circular.

Violation of the assumption of equal variances does not preclude the use of discriminant function analysis. Indeed, in Figures 3 and 4, variances appear unequal in that ellipses are of different shapes. Tests of equality of variances confirmed this fact: 1) For discriminant function 1, Bartlett's adjusted Chi-square = 36.3 with 22 degrees of freedom (*d.f.*) and $P < .05$; also $F_{MAX} = 17.4$ with 9/9 *d.f.* and $P < .001$; 2) For discriminant function 2, Bartlett's Chi-square = 40.4 with 22 *d.f.* and $P < .01$; also $F_{MAX} = 8.3$ with 9/9 *d.f.* and $P < .01$; 3) For discriminant function 3, Bartlett's Chi-square = 16.9 with 22 *d.f.* and it is not significant but $F_{MAX} = 5.9$ with 9/9 *d.f.* and $P < .01$. Despite these unequal variances, populations were lumped into their respective broods with little or no overlap.

The primary value of confidence ellipses is heuristic rather than inferential. Degree of overlap of confidence ellipses should not be used as a test of significant differences. Their purpose, according to Pimentel (1979), is to facilitate "rough appraisal of differences and similarities among groups." In order to demonstrate significance, a multivariate analysis of variance was performed using all 48 characters. This test showed that the *septendecim* from Broods XIII and XIV (the groups with the closest confidence ellipses) were significantly different in wing morphology (Rao's F approximation = 4.67, *d.f.* = 48/130; $P < .001$).

If discriminant function analysis includes tests of significance of centroids or tests of equality of variances, an assumption of multivariate normality of the data is implied; however, no good test for multivariate normality exists. There are tests for univariate normality but even if all characters are univariately normal, this

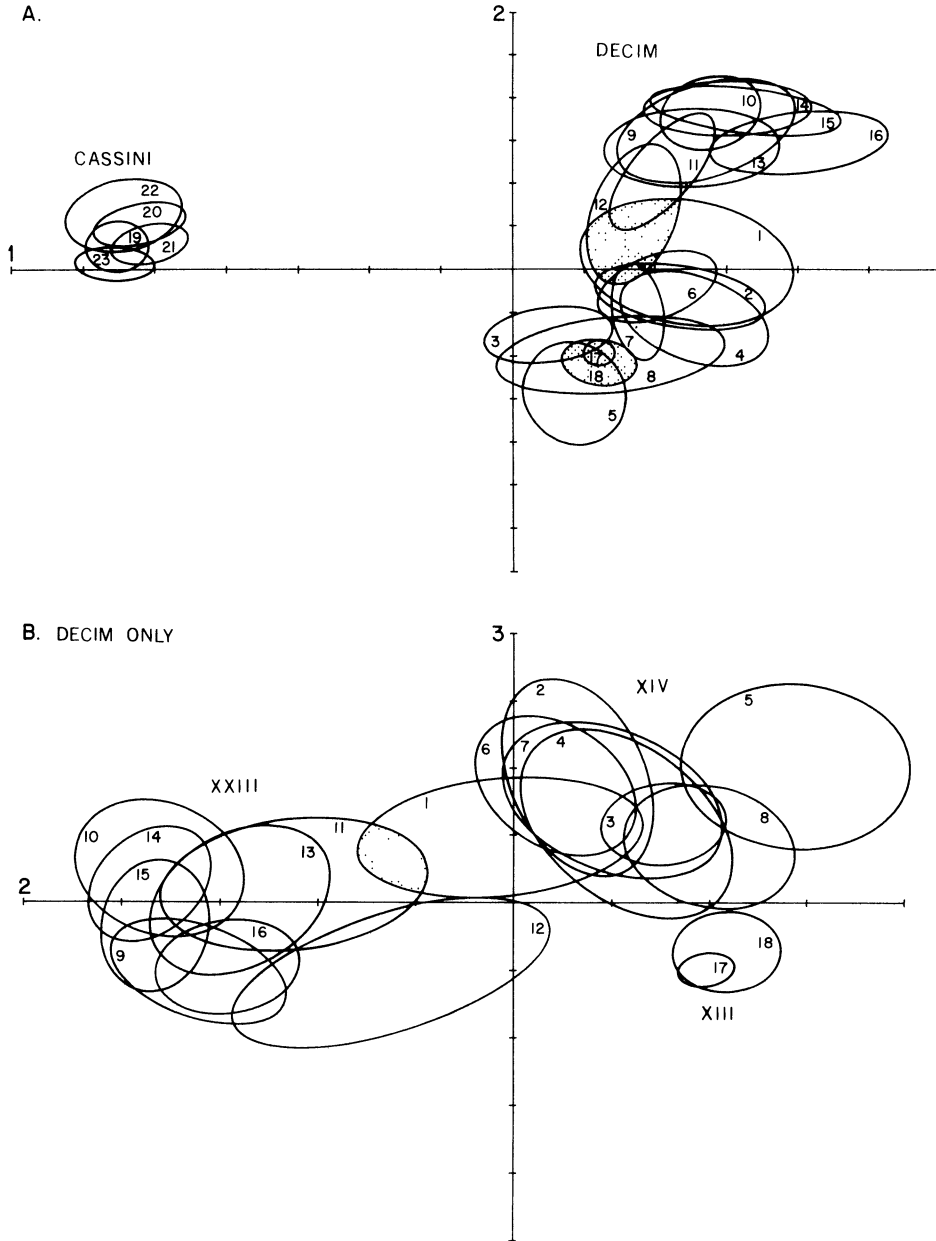


FIG. 3. Ninety-five percent confidence ellipses about population centroids plotted: (A) on discriminant axes 1 and 2; (B) on discriminant axes 2 and 3. Populations 1–8 are of Brood XIV (*septendecim*), 9–16 are of Brood XXIII (*tredecim*), 17 and 18 of Brood XIII (*septendecim*), 19–23 of Brood XXIII (*tredecassini*). The Cassini populations are left out of the drawing of Figure 3B (but not left out of the analysis) because they lie directly behind the main cluster (but well behind the plane of the picture were the third dimension drawn) and would only add confusion to the drawing. Note especially that the *septendecim* of Broods XIII and XIV do not overlap when viewed from this perspective. Stippled areas indicate brood overlap, but note that were the figure drawn in three dimensions, overlap of confidence ellipses would be negligible. The axes are labelled in Mahalanobis distance units. One tic mark = one distance unit. The scale on the ordinate is compressed relative to that of the abscissa making the ellipses appear less circular than they actually are. Also note that the scale in 3A is smaller than 3B because of the greater length of axis 1.

is no guarantee that they will be multivariate normal (Cooley and Lohnes, 1971).

Identifying Useful Characters

In order to determine which characters were most important in separating broods, discriminant functions were calculated using broods instead of populations as the a priori groups. All three of the discriminant functions were highly significant. Plots of the brood mean scores and character coefficients are shown in Figure 4A for discriminant axes 1 and 2 and in Figure 4B for axes 1 and 3. The inset shows characters represented as vectors which join the bivariate plot of their coefficient on each axis with the origin (a similar illustrative technique was used by Jolicoeur, 1959). Only those characters which are most important in discriminating groups are shown. Refer to the wing diagram, Figure 1, to match wing-veins with their character numbers in Figure 4.

The character vectors which are longest and most parallel to an imaginary line connecting any two brood centroids (the ellipse centers) represent the characters which are most important in separating those two broods in those two dimensions. In the Figure 4A and B insets, the labelled dashed lines are parallel to these imaginary lines and can be used as a reference to choose more easily the characters most important in each separation.

Figure 4A shows the broods plotted on discriminant axes 1 and 2. The characters most important in the separation of Decim (Broods XIII and XIV) from Cassini (Brood XXIII) are 9 and 22 (the lengths of the lower mid-sections of the fore wing) and 41 and 42 (the length of the basal half of the hind wing). The characters most important in separating Decim of Brood XXIII from Cassini of Brood XXIII are 11 and 28 (the length of the anal lobe of the fore wing) and to a lesser degree 9 and 22 (as above). To view the characters most useful in separating the Decim broods from each other, it is best to look at Figure 4B.

A graph of discriminant axes 1 and 3 (Fig. 4B) shows the characters most important in separating the two *septendecim*

broods (XIII and XIV): 10 (the half-length of the anal lobe of the fore wing) and 27 (the length of the basal half of the fore wing). The *tredecim* of Brood XXIII differ from *septendecim* of Brood XIV primarily in the following characters: 26 (total length of the fore wing) and not surprisingly, 3, 4, and 16 (costal length of the apical half of the fore wing). Character 46 (width of the apical portion of the hind wing) is also of use here. The following characters separate the *tredecim* of Brood XXIII from the *septendecim* of Brood XIII: 39 (a vein bordering the posterior-most apical cell of the hind wing), 44 (depth of the anal lobe of the hind wing) and to a lesser degree 27 and 10 (as described above).

For each pair of broods a different combination of characters is important for discrimination. Additional broods might best be separated using a different fraction of the characters. It is for this reason that it would be unwise to discard any characters which have not been examined in all groups under consideration.

DISCUSSION

Membership in a particular brood of periodical cicadas is determined solely by year of adult emergence. Lloyd and Dybas (1966) and Lloyd and White (1976) discuss a theory of brood formation in which broods are derived from parent broods through one- or four-year accelerations in the life cycle. In other words, either a proper subset or a mosaic subsection of a brood emerges from the ground one or four years early and once established never comes in reproductive contact with the parent brood again.

The 4-year acceleration hypothesis was suggested to Lloyd and Dybas (1966) by the fact that the four largest broods of 17-year cicadas were essentially overlapping and separated in time by four years. This hypothesis was strengthened by: 1) a massive emergence of periodical cicadas in the Chicago area which occurred in 1969 four years ahead of the scheduled 1973 emergence. (An even larger emergence occurred in 1973 in the exact same suburban yards.) 2) Many instances in which broods

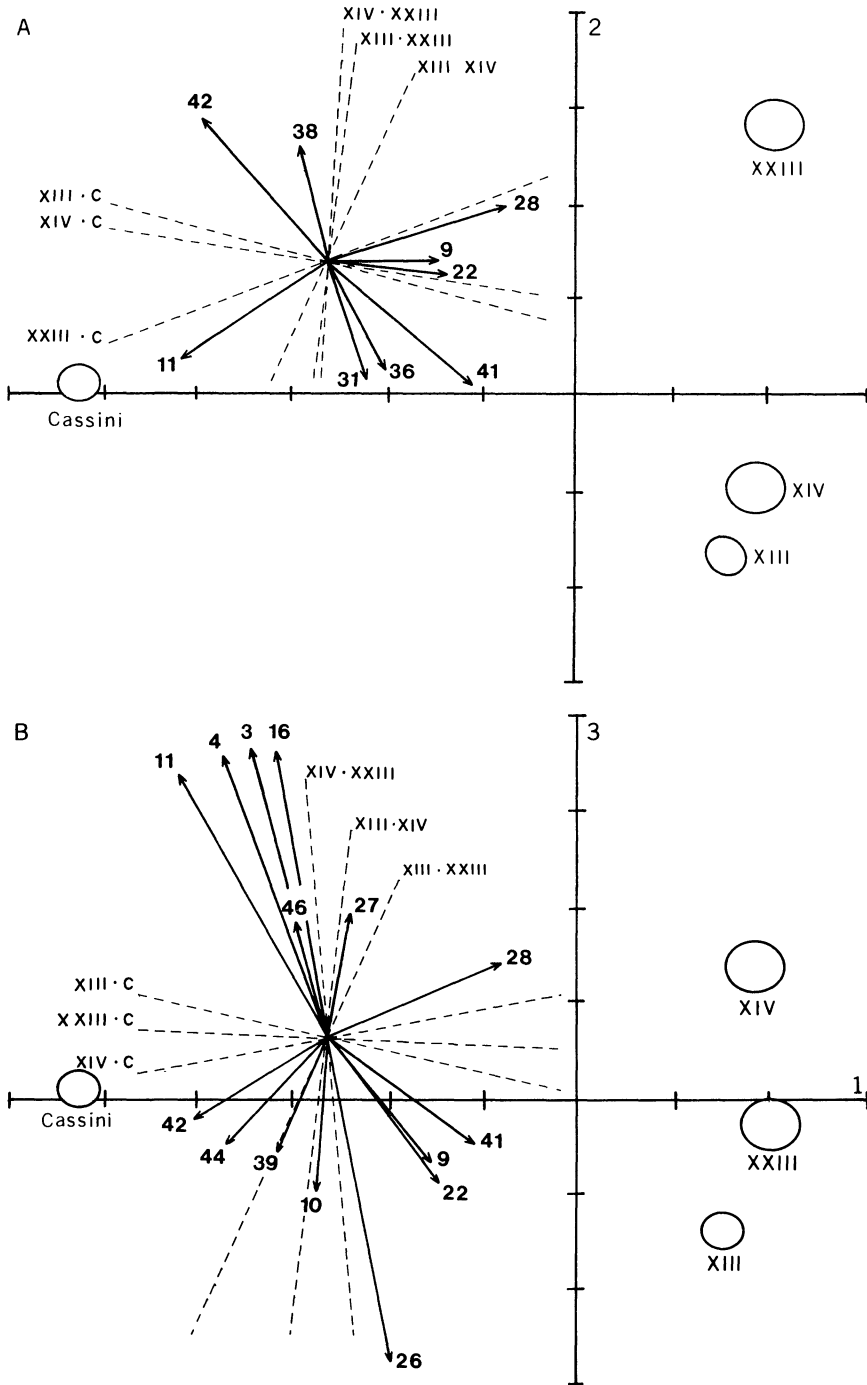


FIG. 4. Ninety-five percent confidence ellipses about brood centroids (A) on discriminant axes 1 and 2; (B) on discriminant axes 1 and 3. Labelled vectors represent characters most important in separating groups. Dashed lines labelled with brood numbers are parallel to imaginary lines connecting the centers of each pair of ellipses and represent the direction of variation of each group from each of the other groups. Only those

differing by four years in adult emergence time were found sympatrically (evidenced by egg scars laid four years apart on the same trees), but never cases in which two or more sympatric broods were more similar in emergence time (Simon et al., 1981). 3) The often noted examples of local emergences of periodical cicadas four years early in sites of extreme abundance. 4) White and Lloyd's (1975) discovery that nymphs of 17-year cicadas grow more slowly than 13-year nymphs in the first four years of life. The evidence for the four-year acceleration theory is discussed in detail in two forthcoming papers (Simon and Lloyd, 1982; Lloyd et al., unpubl.).

Broods of periodical cicadas which are separated in time by one year are often geographically adjacent but never overlap (Lloyd and White, 1976; Simon and Lloyd, 1982). It has been suggested that 1-year accelerations are caused by climatic shifts and that 4-year accelerations are caused by crowding of the nymphs underground. One case is known where, in an extremely crowded population in Kentucky, a large percentage of the population emerged one year late (White and Lloyd, 1979).

Although no cases are known in which accelerated or retarded populations of periodical cicadas have reproduced successfully and established permanent populations, it is possible that such events have occurred resulting in broods of polyphyletic origin. Assuming uniformity of process, there is no reason to doubt that accelerations are happening in recent times. In accord with the theory of predator satiation, given that an individual cicada shortens its life cycle by four years, it will have a better chance of survival if it accelerates *into a sympatric preexisting brood*. Such an acceleration event could lead to one way gene flow from preceding broods to later emerging broods. The efficacy of predator satiation for periodical cicadas has

been demonstrated; Karban (1982) found that an individual cicada's risk of capture decreases as cicada density increases.

The hypothesis of one-way migration through time may be testable in 1987 when Brood X of the 17-year cicadas emerges. In one section of Kentucky, Brood X and XIV live in the same woods as evidenced by egg scars on the tree branches (Lloyd and White, 1976). Brood XIV has been shown to be uniform in gene frequency at four polymorphic loci over its entire range. If Brood X is similarly homogeneous over its entire range *and* if it is different in gene frequencies from Brood XIV, then the gene frequencies in the overlap zone in Kentucky should be intermediate if there is appreciable gene flow. To be sure, many "ifs" are involved.

In this paper, and earlier (1979a, 1979b), I present evidence which suggests that broods are not mosaic in origin. Allozyme frequencies at four polymorphic loci for both 13- and 17-year cicada broods sampled over a wide range (10–12 populations per brood, 96 individuals per population) do not vary significantly in gene frequency. Populations located in coastal xerophytic pine-oak forests are no more similar to each other than they are to populations located hundreds of miles away in diverse Appalachian mesic forests. There are, however, significant differences in allozyme frequency *among* broods. A phenogram constructed from these data agrees well with the geographic distribution of the broods and can be explained in terms of Lloyd and Dybas' 1- and 4-year acceleration theory.

As with the allozyme data, the morphological variation in wing vein dimensions is much lower among populations within broods than it is among broods. This is reflected by the fact that broods, but not populations within broods, are clearly separable on the discriminant axes. Wing

←

characters with discriminant weights greater than 40 (an arbitrary cutoff) are shown; other characters would be less important discriminators. See the text for a complete description of the information present in this figure. Refer to Figure 1 for character number identification. Scales are the same as in Figure 3.

vein information, therefore, is useful in identifying broods. Whether this information will provide useful phylogenetic information awaits morphometric analyses of additional broods (in progress).

SUMMARY

Broods of periodical cicadas are allochronically isolated, presumed incipient, species which have traditionally been considered to be morphologically identical. Forty-eight wing dimensions, largely corresponding to lengths of various veins, were measured for three broods (two 17-year and one 13-year). The analyses primarily concerned *Magicicada septendecim* and *M. tredecim* but several *M. cassini* populations were added later in the analysis for comparison.

Most characters measured showed significant among brood variation, high levels of variation within populations and low levels of variation among populations within broods. Discriminant function analysis identified combinations of characters by which these broods could be separated in three dimensions. The results of these morphological analyses agree with recent allozymic studies which indicate that, for a given species of periodical cicada, broods are definable evolutionary units.

The low level of among population variation (9%) in wing vein morphology contrasted with the higher level of among brood variation (18%) suggests that in morphology, as well as allozymes, populations respond very little to local environmental conditions. They retain a similarity with other populations of their respective broods which is very likely the result of a common evolutionary history.

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