Patchiness, Density, and Aggregative Behavior in Sympatric Allochronic Populations of 17-Year Cicadas

Chris Simon, Richard Karban, Monte Lloyd

Ecology, Volume 62, Issue 6 (Dec., 1981), 1525-1535.

PATCHINESS, DENSITY, AND AGGREGATIVE BEHAVIOR
IN SYMPATRIC ALLOCHRONIC POPULATIONS
OF 17-YEAR CICADAS[1]

Chris Simon[2]
*Department of Ecology and Evolution, State University of New York at Stony Brook,
Stony Brook, New York 11790 USA, and Department of Biology,
University of Chicago, Chicago, Illinois 60637 USA*

Richard Karban
*Department of Biology, University of Pennsylvania,
Philadelphia, Pennsylvania 19104 USA*

AND

Monte Lloyd
*Department of Biology, University of Chicago,
Chicago, Illinois 60637 USA*

Abstract. Densities of two allochronic, geographically overlapping populations of periodical cicadas were censused in the eggnest stage in order to test the hypothesis that larger populations can be supported when the root-feeding nymphs are of different ages. In a frequently burned chest-high stand of scrub oak (*Quercus ilicifolia*) on Long Island, *Magicicada septendecim* emerged in 1974 (Brood XIV), then again in 1978 (Brood I) from under the same individual plants over an area of about 1.2 × 3.5 km. Adjacent to this, in the same vegetation, periodical cicadas emerged in 1974 but not in 1978. A nested scheme of sampling revealed significantly higher total eggnest densities when Broods I and XIV occupied the same ground than when Brood XIV existed by itself. The major component of variation in density was among quadrats within plots. That is, cicadas exhibited patchiness on a small scale (metres) which was not reflected in patchiness on a larger scale (tens of metres).

Microspatial distributions were thus patchy in both Brood I and Brood XIV, yet dense patches of one brood were usually not correlated with dense patches of the other. Apparently the vegetation appears about as uniform to the cicadas as it does to the human observer, the primary cause of the patchy oviposition pattern being either mutual attraction among ovipositing females or lack of dispersal from the chorusing and mating centers. The degree of patchiness is inversely density-dependent, in that the most patchy distributions were invariably those with lowest density. However, several plots with low density were not very patchy. This pattern makes biological sense, remembering that mutual attraction cannot operate unless the animals perceive one another, and at low densities they may sometimes do so and sometimes not. Further analysis, plotting mean crowding against mean density (following Iwao 1968) suggests that mutual attraction among females is weakened at high densities. As modes of data analysis, both kinds of plots—mean crowding vs. mean density and patchiness vs. mean density—bring out patterns that would not otherwise be apparent. In this connection, we offer an empirical definition for the concept, "density-independent aggregation."

Key words: aggregation; density; Magicicada; *mean crowding; patchiness; 4-yr acceleration theory.*

Populations of periodical cicadas (Homoptera: Cicadidae: *Magicicada* spp.) exhibit the highest biomass recorded for any terrestrial animal under natural conditions (Dybas and Davis 1962). Their high densities are inseparably linked to other unusual life history characteristics: periodicity and the long life cycle. Fifth-instar nymphs emerge within a period of a few days once every 17 yr at a given locality (13 yr in the southern and Mississippi Valley states). There are three perfectly synchronized species of periodical cicadas emerging together in most areas, although one

or two of these drop out at the extremes of the range (Alexander and Moore 1962, Dybas and Lloyd 1974, Simon 1979). Cicadas in different parts of the range are out of phase, producing year classes (called broods) such that there will be substantial populations of periodical cicadas emerging somewhere in the eastern United States during 176 out of every 221 yr (counting 12 17-yr broods and 4 13-yr broods: 12 × 13 + 4 × 17 − 12 × 4 = 176), or about 4 yr out of every 5. Despite the fact that different areas readily get out of phase with each other, the species never do. Predator satiation is an important part of periodical cicada ecology and is theoretically the link that so firmly binds the three species together (Lloyd and Dybas 1966)—an hypothesis that is currently being tested by field work (R. Karban, *personal observation*).

It is rare to find more than one brood existing sympatrically in the same woods, but cases do occur (Craig 1941, Bryce and Aspinwall 1975, Lloyd and White 1976). The present report concerns a particularly unusual case of sympatric coexistence occurring at Ridge (Long Island), New York, USA. The study area is located approximately 0.5 km northeast of the intersection of the William Floyd Parkway and New York Route 25. This section of eastern Long Island appears to be a microcosm of cicada evolution in that periodical cicadas emerge in five of every 17 yr (corresponding with Broods I, V, IX, X, and XIV) in a relatively small area. Brood XIV occupies much of the eastern United States, including most of Suffolk County west of Riverhead, and was very abundant in 1974. The other four year-classes (I, V, IX, and X) are located nowhere near the main ranges of their respective broods and are probably related to them in name only. For example, Brood I is primarily located in the Shenandoah Valley of Virginia some 480 km south of the Long Island populations. Relationships of the Long Island populations to their southerly namesakes can be tested because Simon (1979a and b) has demonstrated that periodical cicada broods in general are distinct evolutionary units identifiable on the basis of allozyme frequencies and wing morphology. Such a test is presented for the Ridge population of Brood I by C. M. Simon et al. (*personal observation*).

The present study examines the ecological relationship between two overlapping populations of Brood XIV and Brood I. Brood XIV has been recorded in this area of Long Island since the mid-1800's (Marlatt 1907, Davis 1924). Brood I was recorded from our study area in 1910, 1927, and 1944 (W. T. Davis, *unpublished observations*). In 1978, we traveled to the area pinpointed in Davis' correspondence and found that Brood I had emerged at this site over an area of approximately 1.2 × 3.5 km. In this same pigmy forest, 4 yr earlier, Brood XIV had emerged and covered a much larger area such that it was sympatric with and completely surrounded the smaller Brood I emergence area. This was apparent from field inspection in 1978 because 4-yr-old eggnest scars are easily distinguished from those of the current year. Because this is the northern edge of the range of periodical cicadas, only one species, *Magicicada septendecim*, was present.

We use this overlap situation as a natural experiment to test the hypothesis that a given area has a higher carrying capacity for two sympatric but allochronic populations than it has for a single population—provided that the nymphs of the two populations are not too similar in age. This hypothesis is related to the theory of brood formation as discussed by Lloyd and Dybas (1966), Lloyd and White (1976), and C. M. Simon et al., (*personal observation*).

Also of interest are the patterns of distributions.

Periodical cicada populations, like many others, are notable for their patchy distributions. Although among-population patchiness today is accentuated by habitat destruction, patchiness in undisturbed habitats remains a mystery. A given population can occur in huge numbers in one section of a forest and be absent from adjacent, seemingly identical areas. We test the hypothesis that periodical cicadas are also patchy within populations. We demonstrate that in addition to large-scale patchiness (measured in kilometres) these cicadas are patchy on a microscale (metres) which is, surprisingly, not reflected in patchiness at a higher level (i.e., tens of metres). We attempt to explain the microscale patchiness in terms of periodical cicada behavior.

In most ecological situations, one has no way of knowing whether patchiness stems from inhomogeneities in the habitat or from mutual attraction among the animals, or both. The circumstances of our study should allow separation of the two possibilities, in that two different broods oviposit in the same uniform habitat independently, 4 yr apart. Because *Quercus ilicifolia*, the dominant woody plant, grows so slowly, the habitat would scarcely change in appearance in 4 yr. If inhomogeneities in the habitat were important, then the cicadas should react to these similarly on both occasions. For the most part, this was not the case.

METHODS

The situation in our study area was simplified by having only one cicada species, by having virtually only one plant species, and above all by the "canopy" being accessible at chest height so that it could be sampled randomly on foot (Fig. 1). Each female *Magicicada septendecim* lays up to 500 eggs, inserted into woody twigs 3–11 mm in diameter (White 1973). Eggnests, each 1 cm long and containing about 20 eggs, are typically laid in a "run" of several in tandem along a twig. This leaves a permanent scar, identifiable to cicada species when fresh (White 1980) and still recognizable as eggnest damage after 4 yr of growth (Lloyd and White 1976). Since twigs grow only at their tips, the number of eggnests represented by a scar can be determined from its length even after 4 yr, by which time the individual eggnests are not always distinguishable.

Sixteen 25 × 25 m plots were chosen based on cicada broods present (see Fig. 2). Eight plots supported Brood XIV only (designated the XIV-only zone); the remaining eight plots, having both broods, were chosen to include four plots near the edge of the distribution of Brood I (interface zone) and four plots farther inside the emergence area of Brood I (overlap zone). Each plot was sampled using a coordinate system in which square metre quadrats were selected randomly and located by pacing in from measured bound-

FIG. 1.   The study area is an oak scrub on sandy soil. The almost pure stand of *Quercus ilicifolia* burns at erratic intervals and is seldom more than 1.5 m tall. Interspersed are occasional pitch pines (*Pinus rigida*) and white oaks (*Quercus alba*), 3–4 m high. Blueberries (*Vaccinium* sp.) and huckleberries (*Gaylussacia* sp.) are also found, as well as sweet fern (*Comptonia peregrina*), bracken fern (*Pteridium aquilinum*) and winged sumac (*Rhus copallina*).

aries. Most plots were sampled with 13–15 quadrats; a few had 16–20. From each quadrat, all eggnest-bearing twigs were clipped, placed in a separate paper bag, counted and measured in the laboratory, and classified as belonging to Brood I (fresh wounds) or to Brood XIV (showing growth of scar tissue).

RESULTS AND DISCUSSION

J. White (*personal communication*) has abundant evidence indicating that the mean number of *M. septendecim* eggnests occurring per "run" in other host species is far greater than we found in *Quercus ilicifolia* (Fig. 3). Undoubtedly, the explanation lies in the slow growth rate of scrub oak and the short internodes that result. *Magicicada* usually avoids ovipositing in nodes; presumably the wood is much harder there.

Counts of total eggnests in each quadrat for each plot are summarized in Table 1. Brood I was sparsely represented in the interface zone, but more abundantly in the overlap zone. A glance at these data shows that the microdistribution is extremely patchy: variance-to-mean ratios are significantly greater than unity in every case. Part of this patchiness stems from the clustering of eggnests in runs, but even if we count runs instead of eggnests, variance-to-mean ratios are still

significantly higher than random expectation ($P < .001$) in 20 out of 24 cases. Since patchiness results in a correlation between variance and mean, it is inappropriate to use analysis of variance to compare eggnest densities in the three zones unless the data are first subjected to a variance-stabilizing transformation. We have used the one suggested by Iwao and Kuno (1968, see also Beall 1942), namely the inverse hyperbolic sine function $f(x) = \log_e(\sqrt{wx} + \sqrt{wx + 1})$ where $w = 0.0198 = (\beta - 1)/(\alpha + 1)$, $\alpha = 9.139$ and $\beta = 1.201$. Values for α and β were calculated by fitting a least-squares line to a plot of mean crowding vs. mean density, as explained in a later section.

Table 2 gives the results of the analysis of variance. First we look only at the data for Brood XIV, ignoring Brood I entirely. We use a two-level nested analysis of variance, sampling randomly within plots (Sokal and Rohlf 1969:256). The abundance of Brood XIV, taken by itself, is not significantly different in the three zones. Apparently no zone is intrinsically more favorable for cicadas than any other. When the data for Brood I are added to the analysis, the zones do differ significantly in cicada abundance ($P < .01$). In other words, the sandy oak scrub habitat can support more periodical cicadas if the cicadas occur in two different broods 4 yr apart.
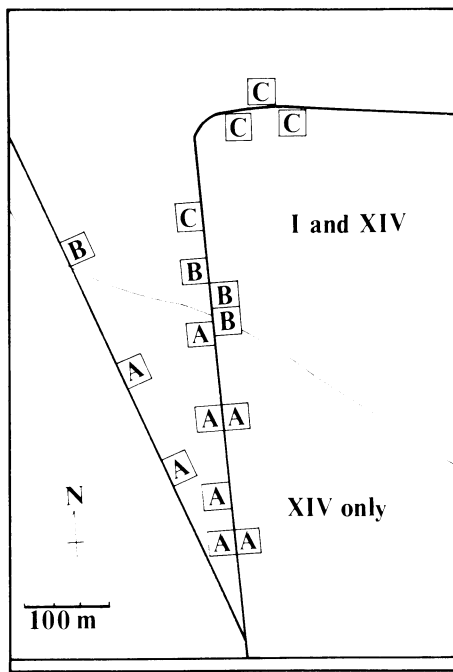
FIG. 2. Map of the study area, located approximately 0.5 km northeast of the junction of New York Route 25 and the William Floyd Parkway. Route 25 forms the lower boundary of the figure. The Brood-XIV-only zone (containing eight 25 × 25 m plots marked A) is demarcated from the other two zones (interface zone—four plots marked B, and overlap zone—four plots marked C) by a thin line. The heavy lines are fire lanes (sandy one-lane roads). A constant nonrandom feature of plot locations is that each appears to have a fire lane as one of its edges. However, the actual boundary was placed at least 1 m from the edge of the vegetation so that no quadrat fell on an edge. This vegetation is owned by Brookhaven Township and forms the southern boundary of the town public rifle range.

FIG. 3. Top: numbers of eggnests per "run" found in the present study, all plots combined. Cross-hatched = Brood XIV; solid shading = Brood I. Most of these eggnests occurred in scrub oak (*Quercus ilicifolia*). Bottom: data for comparison kindly supplied by Dr. JoAnn White, taken from eggnests produced by *Magicicada septendecim* in redbud (*Cercis canadensis*) in Kentucky in 1974. Our point is to show that the present collection is atypical for *M. septendecim* in that many eggnests occurred singly, with seldom more than 2, 3, or 4 in tandem, whereas in most collections it is routine to find up to 20 or more eggnests in tandem in a "run." Dr. White found it expedient to cut through many of the runs in her material in order to fit the twig segments conveniently into a collecting bag. Therefore, her average of 4.3 eggnests in tandem is a gross underestimate of the numbers of eggnests actually occurring in a run, yet this is still greater than the average of 2.4 eggnests per run that we found in scrub oak.

Nymphal carrying capacity

The hypothesis that the variation in total number of cicadas supported is due to differences in habitat quality among the zones is not supported by the data. There was no significant difference in the Brood XIV density among zones (Table 2), the plant species composition was remarkably uniform (Fig. 1), and there was little variation in soil composition (Table 3). To what, then, can we attribute the increased carrying capacity of the overlap zone?

Data from other sources suggest that resource partitioning may explain how the overlap zone could support many more nymphs than the Brood-XIV-only zone. White and Lloyd (1979) found that larger cicada nymphs tend to occur at greater depths where Broods X and XIV overlap in Kentucky. Second instars were found entirely above 15 cm, whereas about three-quarters of the third instars were below 15 cm. By feeding, presumably, on different-sized roots, the instars may
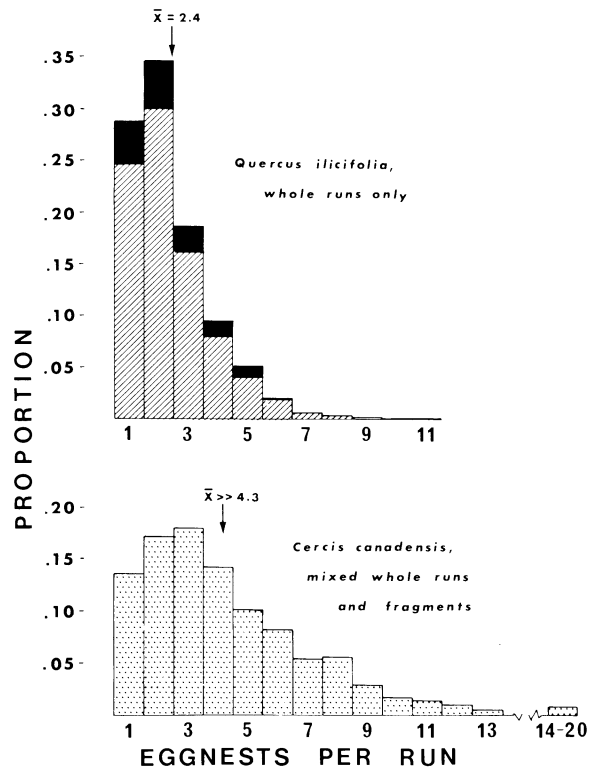
avoid interference competition for at least the initial years of their lives.

To some extent, 17-yr cicada nymphs of a single brood mimic the presumed advantage gained by two allochronic overlapping broods because, within a population of a single brood, nymphs grow at different rates. Marlatt (1907) did not report this. He believed that the first instar lasted approximately 1 yr, the second lasted 2 yr, the third 3 or 4 yr, the fourth 3 or 4 yr, and the 5th lasted the remaining 6–8 yr. More recent digging studies (White and Lloyd 1975) demonstrated that 17-yr cicada nymphs grow at widely different rates. In a population of 9-yr-old nymphs in Oklahoma, they found 18% in the fifth instar, 79% in

TABLE 1. The numbers of eggnests in each quadrat. There were 13 to 20 quadrats per plot; counts are listed from left to right in order of abundance of Brood XIV. Fig. 2 is a map of the area. Detailed statistics are given in Table 4. Weighting each plot equally, means ± standard errors for Brood XIV are: Brood-XIV-only zone—21.2 ± 4.4, interface zone—22.0 ± 6.2, overlap zone—27.2 ± 8.7. These are statistically homogeneous (see Table 2).

Plot	No. quadrats	Eggnest counts in individual quadrats*																		
Brood-XIV-only zone																				
1	15	0	0	0	3	5	5	7	8	9	10	15	16	19	20	58				
2	15	0	3	3	6	10	14	15	15	16	23	24	46	49	54	76/2				
3	15	5	11	11	13	15	22	25	25	30	31	31	35	43	47	47				
4	14	2	4	7	7	8	10	11	20	21	23	49	51	57	89					
5	17	0	0	0	4	5	7	8	10	11	18	20	24	25	33	40	43	54		
6	19	0	0	2	2	7	7	15	16	17	18	21	25	25	26	31	32	36	58	86
7	15	7	8	9	10	11	14	14	16	24	25	25	26	31	31	49				
8	20	0	1	1	11	12	14	15	15	17	20	21	24	24	27	30/1	31	36	38	55 55
Interface zone																				
9	15	3/0	3/3	9/0	12/0	14/2	18/5	20/7	22/2	24/3	26/4	31/0	32/0	33/8	51/0	56/0				
10	13	1/0	6/0	13/2	17/2	23/13	26/0	27/0	30/0	38/0	39/1	51/2	54/13	62/4						
11	13	2/0	3/8	3/0	3/0	11/9	11/12	12/0	15/0	17/6	17/9	18/15	19/0	32/8						
12	15	3/0	7/6	8/0	13/21	14/4	17/0	17/1	17/2	20/12	27/2	29/9	30/0	31/17	46/0	53/14				
Overlap zone																				
13	16	0/0	2/13	3/0	3/10	4/6	4/15	5/32	6/0	7/6	12/3	14/0	17/5	17/16	22/4	40/43	54/40			
14	15	0/11	6/28	7/3	9/10	11/4	17/7	22/13	23/3	24/10	34/21	35/14	39/17	44/30	65/20	68/62				
15	14	8/0	9/15	12/12	13/7	19/2	24/2	26/1	32/15	39/5	41/5	44/12	47/2	77/19	98/13					
16	14	9/1	19/0	23/5	27/11	31/7	36/5	36/15	37/9	37/9	41/11	42/8	44/4	44/11	50/6					

* Where two numbers appear, Brood IV count precedes and Brood I count follows the slant line.

the fourth, and 3% in the third. A 9-yr-old population of nymphs from Iowa was composed of 77% fourth-instar nymphs, 18% third instars, and 5% second instars. Earlier, Lloyd and Dybas (1966) had also noted this size variation among periodical cicada nymphs of the same age. Presumably, interference competition will be reduced if nymphs of different instars feed on roots of different sizes and/or at different depths.

Lloyd and White (1976) hypothesized that crowding underground might be a stimulus capable of producing an acceleration in the life cycle. If a fraction of a crowded cicada population were to shorten the life cycle and emerge 4 yr early (in sufficient numbers to satiate predators) then the progeny of these individuals might have a better chance of surviving underground. They would have escaped the crowding stimulus and would presumably return to the 17-yr life cycle. Since they would not be synchronized with the original population, they would not be competing with as many nymphs of their own size. They would, if self-perpetuating, belong to a new brood. This phenomenon may have occurred at Ridge. We have data supporting the hypothesis that rather than being a relict of a formerly large Brood I, the Ridge population of "Brood I" is independently derived, probably from Brood XIV in several steps (C. M. Simon et al., *personal observation*).

Patchiness

Perhaps the most significant result of the analysis of variance (Table 2) is that in all zones the majority of the variation is among the quadrats within each of the 16 plots. There is very little variation among plots within each of the three zones (Table 2). In other words, within this local distribution the cicadas exhibit patchiness on a small scale (metres) which is not reflected in patchiness at a larger scale (tens of metres).

In view of the monotonous appearance of the habitat (Fig. 1), the extreme patchiness of the cicadas is surprising and demands an explanation. Are the ovipositing cicadas aware of subtle differences in habitat from place to place to which human eyes are not attuned, or are they simply attracted to each other? Or

TABLE 2. Analysis of variance of transformed counts of eggnests in random quadrats among different plots.

	df	SS	MS	F	% var†
Brood XIV considered alone					
Among zones	2	.159	.0793	.75 (NS)‡	0
Among plots	13	1.374	.1057	2.76**	10
Within plots	229	8.750	.0382		90
Broods I and XIV combined					
Among zones	2	1.070	.5352	6.92**	13
Among plots	13	1.004	.0773	1.95*	8
Within plots	229	9.083	.0397		79

* $P < .05$.
** $P < .01$.
† % var = percent of the total variation which is accounted for by variation at each of the levels.
‡ NS = not statistically significant.

TABLE 3. Soil analyses in duplicate samples from the three zones: topsoil and subsoil. Data are percent organic matter (% O), alkalinity (pH), and eight mineral nutrients, expressed as kilograms per hectare.*

	% O	pH	P	K	Mg	Ca	Mn	Al	NO$_3$	NH$_3$
Topsoil:										
Brood-XIV-only zone	9.6	3.9	2	157	50	190	7	470	18	7
	7.4	3.7	2	78	34	146	10	157	11	7
Interface zone	5.4	3.8	1	62	39	157	4	190	6	4
	9.8	3.6	2	73	45	157	8	118	<6	7
Overlap zone	8.2	3.8	1	134	67	224	9	291	6	6
	23.6	3.7	2	134	50	157	7	369	11	8
Subsoil (20 cm):										
Brood-XIV-only zone	3.4	4.1	<1	56	17	39	1	644	6	4
	1.8	4.2	<1	34	11	39	6	280	6	3
Interface zone	2.0	4.4	<1	28	11	39	4	364	<6	4
	1.2	4.4	<1	22	11	34	1	325	<6	3
Overlap zone	3.6	4.3	<1	50	39	45	1	560	6	3
	3.1	4.3	<1	67	17	39	3	504	<6	4

* Analyzed by the Soil Test Laboratory, Department of Agronomy, Cornell University, originally expressed as pounds per acre (ton of soil); converted to kilograms per hectare by multiplying by 1.12 and rounding.

are both processes involved, and if so, to what extent is each responsible for the patchiness?

With the two allochronic cicada populations interspersed, we have an opportunity to resolve this question. There were no fires on the study site between 1974 and 1978, and the oak scrub grows slowly, so when they emerged, the two broods were confronted with practically identical habitats. If the cicadas are patchy because they are responding to subtle differences in habitat, then there should be a strong correlation between the eggnests deposited in a given quadrat on the two emergences. If there is no such correlation, then we conclude that the females are either attracted to chorusing males, or to each other; the particular spots where they happen to aggregate would then depend upon accidents of history rather than habitat quality.

Fig. 4 shows the numbers of eggnests of Brood I vs. those of Brood XIV in each quadrat, all eight plots superimposed. Ranking the data, seven of the eight plots showed no significant correlations, Kendall's (1955) tau ranging from $\tau = +.01$ to $+.34$ ($P = .50$ to .07). Even when all seven of these one-tailed probability values are combined using Fisher's (1954:99) method, there is still no significant correlation: $\chi^2 = 21.1$, df = 14, $P = .10$. In Fig. 4, notice the many points lying directly on the vertical axis, some of them quite high. These represent quadrats where Brood XIV females laid a considerable proportion of the eggnests received by all samples in the whole plot (the three highest points are around 15%), yet these quadrats were completely ignored by Brood I females. The fact that there is no *negative* correlation between the numbers of Brood I vs. Brood XIV eggnests in a given quadrat rules out the possibility that females avoid areas of previous heavy oviposition (with many

scarred branches); the fact that there is no *positive* correlation indicates that the cicadas can perceive no consistent environmental differences among the quadrats.

In one of the plots, however (plot 14, shown as stars in Fig. 4), there was a significant correlation: $\tau = +.61$, $P = .0015$. In retrospect, it seems that the agreement between Broods I and XIV eggnest locations in this plot may have been due to the occurrence of several taller (3–4.5 m) white oak trees. These trees stand out above the scrub oaks and may therefore differentially attract cicadas. When we include this plot (as we should, since we had no a priori reason to single it out) then the total evidence for a positive correlation is $\chi^2 = 30.1$, df = 16, $P = .017$, statistically significant. Nevertheless, the overall correlation is weak (Fig. 4), indicating that, by and large, the vegetation appears as monotonous to the cicadas as it appears to us (Fig. 1). Consequently, habitat heterogeneity can be ruled out as a *major* cause of the patchiness seen in these periodical cicada populations.

Interestingly, plot 14 had the highest combined eggnest density of the eight plots containing both Broods I and XIV. This suggests that when crowded the females may be stimulated to become more discriminating of habitat quality, or perhaps conversely, the taller white oak trees in plot 14 attracted cicadas from elsewhere, causing the higher local density (it is reasonable to assume that these individual trees would be equally attractive to cicadas of both Broods I and XIV). In either case, we would expect that the τ-values from each plot, though not individually significant, might be positively correlated with overall plot densities. These are plotted in Fig. 5. The trend is suggestive but fails to reach statistical significance ($\tau = +.21$, $P = .27$). The lack of a relationship may simply mean

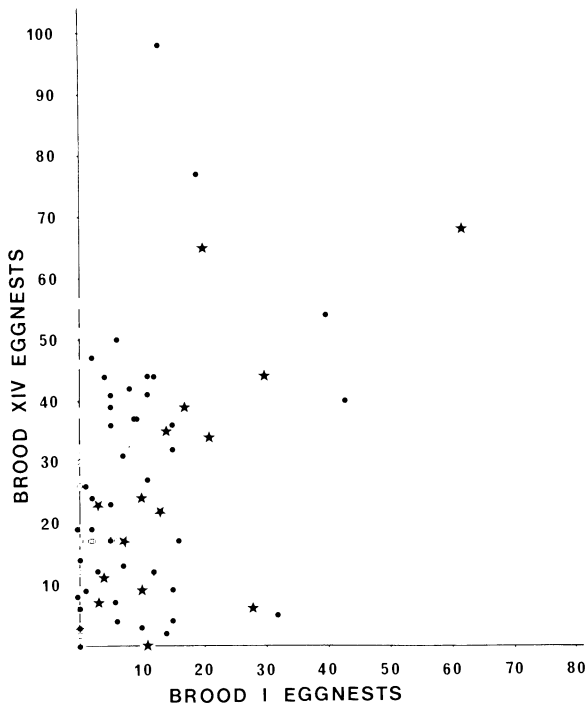FIG. 4. The poor correlation between number of eggnests laid in an individual quadrat by Brood I in 1978 vs. those laid in the same quadrat by Brood XIV 4 yr earlier. Data from eight plots in which both Broods I and XIV occur are superimposed. Open circles: quadrats from plots near the edge of the Brood I range (interface zone). Solid symbols: quadrats from plots within the strong chorusing zone of Brood I (overlap zone). Stars: quadrats from plot 14 in the overlap zone, the only plot to show a significant correlation. The inference is that, except for plot 14, the patchiness is not caused by habitat heterogeneity; otherwise cicadas of the two broods should prefer the same quadrats.
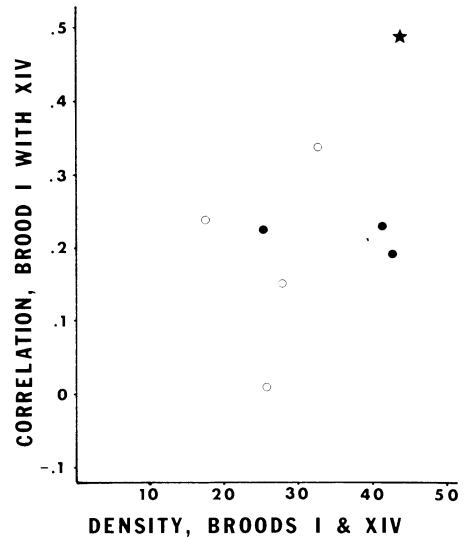

FIG. 5. Possible relationship between population density (eggnests per square metre) and the correlation (τ) between eggs laid in a given square metre by successive broods. Symbols are the same as in Fig. 4. Although none of the τ-values (correlation coefficients) are negative, only one (the star, plot 14) is statistically significant. There is not a convincingly consistent relationship with density.

that in vegetation as uniform as our study area, the cicadas have very little habitat diversity with which to discriminate.

Mean crowding vs. mean density

Lloyd (1967) defined "mean crowding" (x) as the mean number per individual of other individuals in the same quadrat, and suggested the ratio of mean crowding to mean density $(x/\bar{x})$ as a measure of patchiness Maximum-likelihood estimates (Bliss and Fisher 1952, Lloyd 1967) for these quantities in each of our 16 plots are given in Table 4. Anscombe's (1950) third moment test was applied to see whether any of the plots differed significantly from the negative binomial. In no case did the sample third moment differ from its expected value by as much as 1.5 standard errors. However, there is a consistent trend, in that the third moments tend to be a little less than their expectations, so if the total evidence is accumulated (Fisher 1954:99) we have $\chi^2 = 24.4$, df $= 48$, 2-tailed $P < .01$.

Iwao (1968) proposed plotting x vs. $\bar{x}$, which we have done in Fig. 6. If the habitat is uniform and the individuals establish themselves independently, then the distribution is random, x and $\bar{x}$ are equivalent, and one expects a straight line through the origin with slope unity. Mutual repulsion would produce points below that line, but above a parallel line having intercept minus unity, i.e., $x = \bar{x} - 1$. (No points can fall below the line $x = \bar{x} - 1$, because that would imply negative variances.)

A slope greater than unity, as in our case where $\beta = 1.2$, shows a patchy distribution stemming either from habitat heterogeneity or from mutual aggregation, or both. In the absence of aggregation, the amount by which the slope exceeds unity measures habitat heterogeneity, as it is perceived by the organisms, and we expect the line to be perfectly straight (Iwao 1968). Now, if the habitat is uniform but the individuals aggregate, this will produce a slope greater than unity near the origin, but in the absence of a precise specification of how the machinery of aggregation works, it is not possible to say whether the Iwao line should be straight or not. As a temporary expedient we think it would be useful to define "density-independent aggregation" as any pattern of aggregation that results in a plot of x vs. $\bar{x}$ that is straight, and hence is operationally indistinguishable from habitat hererogeneity. By contrast, density-dependent aggregation bends the Iwao line downwards at its upper end: patchiness becomes less as density increases, as found, for example, by Morisita (1971).

TABLE 4. Maximum-likelihood estimates of mean density, mean crowding, patchiness, and the k-value in the negative binomial distribution, with standard errors.

	Plot	Variance	Mean density	SE	Mean crowding	SE	Patchiness	SE	k-value	SE
Nonoverlap area, Brood XIV only (plots 1–8)	1	208.4	11.67	3.67	27.97	11.04	2.40	0.57	0.72	0.29
	2	501.1	23.60	6.15	46.66	14.85	1.98	0.36	1.02	0.38
	3	179.8	26.07	3.64	32.68	5.34	1.25	0.11	3.94	1.65
	4	672.2	25.64	6.48	47.54	14.38	1.85	0.31	1.17	0.42
	5	274.3	17.77	5.10	41.61	14.89	2.34	0.50	0.75	0.28
	6	452.6	22.32	5.50	47.10	14.33	2.11	0.38	0.90	0.31
	7	134.9	20.00	2.82	24.94	4.10	1.25	0.11	4.05	1.73
	8	241.3	22.35	4.32	38.05	9.17	1.70	0.25	1.42	0.50
Overlap area, Brood XIV only (plots 9–16)	9	239.7	23.60	4.22	33.93	7.30	1.44	0.17	2.29	0.90
	10	344.5	29.77	6.13	45.16	11.31	1.52	0.22	1.93	0.81
	11	73.8	12.54	2.51	18.08	4.44	1.44	0.20	2.26	1.05
	12	197.3	22.13	3.61	29.96	5.82	1.35	0.14	2.83	1.15
	13	221.7	13.13	3.39	26.13	8.24	1.99	0.36	1.01	0.37
	14	426.5	26.93	6.05	46.31	12.81	1.72	0.28	1.39	0.54
	15	684.2	34.93	6.47	50.72	11.15	1.45	0.17	2.21	0.84
	16	124.9	34.00	3.26	37.36	3.98	1.10	0.05	10.11	5.22
Overlap area, Brood I only (plots 9–16)	9	7.4	2.27	0.87	6.27	3.42	2.77	1.07	0.57	0.34
	10	21.8	2.85	1.40	10.76	6.79	3.78	1.50	0.36	0.20
	11	29.1	5.15	2.45	19.29	11.91	3.74	1.48	0.37	0.20
	12	49.7	5.87	2.30	18.45	9.17	3.14	0.96	0.47	0.21
	13	201.1	12.06	4.20	34.48	14.90	2.86	0.73	0.54	0.21
	14	225.7	16.87	3.36	25.90	6.22	1.54	0.21	1.87	0.72
	15	39.7	7.86	1.90	13.29	4.09	1.69	0.32	1.45	0.67
	16	17.1	7.29	1.22	9.14	1.98	1.25	0.17	3.94	2.68
Overlap area, Broods XIV and I combined (plots 9–16)	9	239.7	25.87	4.32	35.69	7.13	1.38	0.15	2.63	1.05
	10	424.4	32.62	6.83	50.19	12.77	1.54	0.22	1.86	0.77
	11	135.6	17.69	3.64	26.41	6.62	1.49	0.21	2.03	0.88
	12	289.6	28.00	4.56	38.13	7.39	1.36	0.14	2.76	1.09
	13	712.2	25.19	6.13	48.09	14.29	1.91	0.33	1.10	0.39
	14	1070.2	43.80	7.72	63.19	13.16	1.44	0.16	2.26	0.82
	15	859.1	42.79	7.12	58.38	11.42	1.37	0.14	2.74	1.06
	16	188.7	41.29	4.20	46.25	5.26	1.12	0.06	8.31	3.94

Note—Sample estimates for k in the negative binomial were calculated by the iterative maximum likelihood procedure described by Bliss and Fisher (1953), who also give standard errors for k and for mean density, $\bar{x}$. Mean crowding is then estimated as $x = \bar{x}(1 + k^{-1})$ and patchiness as $x/\bar{x} = 1 + k^{-1}$. Formulas for standard errors are given by Lloyd (1967).

A third, unrelated cause of patchy distributions is that the females lay their eggs in clutches (or in our case, their eggnests in runs). The beauty of the Iwao line is that it provides an objective way to distinguish this cause of patchiness from the other two: eggs laid in clutches produce a nonzero intercept in the plot of x vs. $\bar{x}$. The intercept should be approximately equal to mean clutch size (Iwao 1968). In our case, there is a marked discrepancy; we know from independent evidence (Fig. 3) that the average number of eggnests per run is 2.4, yet the empirical intercept in Fig. 6 is much higher: $\alpha = 9.1$. A reasonable interpretation is that the true Iwao line is a curve that bends downward as it approaches the vertical axis. It has an intercept at about 2.4, an initial slope much greater than 1.2, and approximately unit slope at high density. In other words, we have evidence for a density-dependent weakening of aggregative behavior as crowding increases, which makes ecological sense and would be expected. Admittedly, the scatter of points in Fig. 6 (and their associated standard errors—see Table 4) is

too great to demonstrate curvature in the line statistically, yet the discrepancy between theoretical and observed intercepts strongly suggests it.

It can be argued that the inscribed stars in Fig. 6 (and later Fig. 7), which represent Broods I and XIV combined, should be deleted, since they are not independent of the other points and concern events happening at different times, but even if they are deleted, the patterns discussed still apply. They were, in fact, deleted in calculating the least-squares line.

Even though there are ecological reasons to doubt the linearity of Fig. 6, the points are still close enough to linear so that the two fitted parameters α and β can serve in a useful variance-stabilizing transformation (Iwao and Kuno 1968), as described earlier.

Aggregative behavior

To summarize: (1) we have reason to believe that habitat heterogeneity is a minor cause of patchiness in this case (i.e., the poor correlation between oviposition sites independently selected by the two
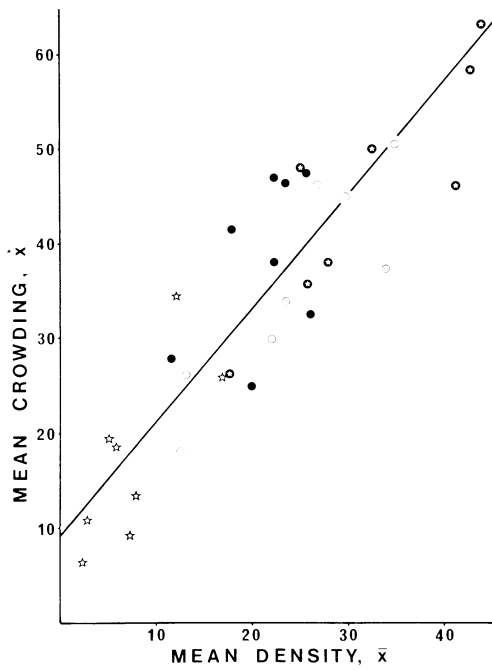
FIG. 6. The Iwao line, mean crowding (x) plotted against mean density (x̄, eggnests per square metre), where x is the mean number per eggnest of other eggnests falling in the same square metre. The data are shown both grouped and ungrouped in the same figure, as follows. Area of no overlap: open circles = Brood XIV only. Area of overlap: solid circles = Brood XIV only; open stars = Brood I only; stars inscribed in circles = XIV and I combined. See text for explanation.
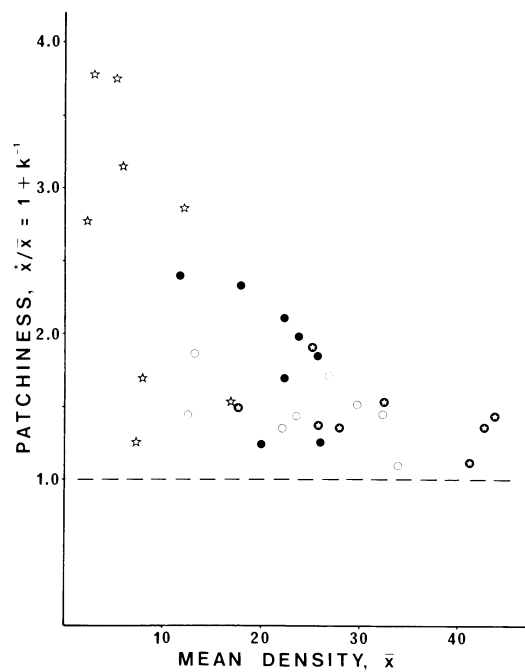
FIG. 7. The inverse relationship between patchiness and density (eggnests per square metre), a relationship that disappears at low densities, probably because at low densities individuals are sometimes not aware of each other's presence, hence cannot be mutually attracted. A patchiness of unity indicates an approximately random distribution; mutual repulsion would be shown by a value slightly below unity. All these distributions are significantly patchy. Symbols are the same as in Fig. 6. Patchiness, x/x̄, is an estimate of the ratio of mean crowding to mean density. This ratio was estimated by $1 + k^{-1}$, where k is the parameter of the negative binomial distribution, fitted by maximum likelihood (Lloyd 1967).

broods); (2) patchiness is inversely density-dependent, but the relationship stems from two quite different causes: oviposition of eggnests in runs, and a weakening of mutual attraction at high densities. If we now directly plot patchiness against mean density, as in Fig. 7, another pattern becomes evident: the inverse density-dependence of patchiness disappears at low densities! All the very patchy plots have low densities, but not conversely; some of the low-density plots are not much more patchy than random. In other words, *variability* in patchiness is far greater at low density. Assuming that the patchiness stems at least partly from aggregative behavior, this pattern makes good ecological sense; at low density, the ovipositing females will sometimes be *aware* of each other and sometimes not, hence mutual attraction will sometimes operate and sometimes not.

Fig. 7 shows that none of the plots have both high patchiness and high density. This is not simply a mathematical artifact of having the same variable on both axes, since there would be nothing to prevent one from constructing an artificial distribution with both density and patchiness high enough to fall in the upper right-hand part of Fig. 7. Obviously, there are limits to the cicadas' aggregative tendencies.

The ecological result of patchiness is that young nymphs must be more crowded underground than they would have been had the females oviposited in the vegetation at random and laid their eggnests singly rather than in runs. In Table 4, patchiness is the ratio of mean crowding to mean density, with the standard error of that ratio (Lloyd 1967). Mean crowding of eggnests ranges from 1.1 ± .05 to 3.8 ± 1.5 times its random expectation, when each brood is considered separately. To translate that into the equivalent number of other nymphs falling into the same square metre, as viewed by an average nymph, multiply mean crowding by 15 hatching nymphs per eggnest (20 eggs per eggnest × 75% fertility, White 1980). Thus, in different plots, the average Brood XIV nymph had between 271 ± 67 and 761 ± 167 others competing with it to get established in the same square metre of ground! It is not surprising, then, that the aggregative tendencies of ovipositing females seem to be weakened when their density is high; such weakening reduces the crowding suffered by their offspring.

One still has to inquire why there should be any tendency to aggregate at all, since it would appear to be maladaptive. One should remember that periodical cicadas usually find themselves in much more diverse vegetation than our study area. In a roadside area of diverse vegetation, White (1980) demonstrated strong preferences for certain host species. She also showed that fertility of the eggs differed according to host species (although the correlation between host preferences and fertility was somewhat obscured by infertility owing to overcrowding in the most preferred hosts). Herein may lie the selective advantage for aggregative behavior; the sight of another female busily ovipositing probably means that the other female has found a favorable host, and it may be quicker and easier to share that particular host plant than to find another favorable host for oneself. Kiester (1979) refers to such behavior as "conspecific cueing," and points out that it can account for a patchy distribution even in a uniform habitat. Such aggregative behavior can be maladaptive in a perfectly uniform habitat if crowding causes competition, but then, most periodical cicada habitats are not uniform.

In diverse vegetation, mutual attraction and host preference (habitat heterogeneity) are probably both important factors in determining the patchy distribution. Lloyd and White (1976) showed significant local differences in the way the same diverse vegetation was used by Broods X and XIV where they overlap in Kentucky—differences that showed no consistent pattern between different study areas. This finding is understandable if historical accidents of mutual attraction, i.e., conspecific cueing, routinely play a part in determining the patchy distribution of eggnests, hence nymphs.

A second behavioral explanation for the observed aggregation of eggnests may lie in the periodical cicadas' movement patterns prior to mating. Patchiness could result from aggregative mating at chorusing centers followed by poor dispersal of fertile females. Both sexes are attracted to the congregational chorus of the males (Alexander and Moore 1958). If females do not move far away from the chorusing centers to oviposit, a patchy pattern of eggnests would result. R. Karban (*personal observation*) has examined this possibility.

LITERATURE CITED

Alexander, R. D., and T. E. Moore. 1958. Studies on the acoustical behavior of seventeen-year cicadas (Homoptera: Cicadidae: *Magicicada*). Ohio Journal of Science **58**:107–127.

Alexander, R. D., and T. E. Moore. 1962. The evolutionary relationships of 17-year and 13-year cicadas, and three new species (Homoptera, Cicadidae, *Magicicada*). Miscellaneous Publication 121, Museum of Zoology, University of Michigan, Ann Arbor, Michigan, USA.

Anscombe, F. J. 1950. Sampling theory of the negative binomial and logarithmic series distribution. Biometrika **37**:358–382.

Beall, G. 1942. The transformation of data from entomological field experiments so that the analysis of variance becomes applicable. Biometrika **32**:243–262.

Bliss, C. I., and R. A. Fisher. 1953. Fitting the negative binomial distribution to biological data and note on the efficient fitting of the negative binomial. Biometrics **9**:176–200.

Bryce, D., and N. Aspinwall. 1975. Sympatry of two broods of the periodical cicada (*Magicicada*) in Missouri. American Midland Naturalist **93**:450–454.

Craig, F. W. 1941. Observations on the periodical cicada. Journal of Economic Entomology **34**:122–123.

Davis, W. T. 1924. The seventeen-year cicada on Long Island with particular reference to its appearance in 1923. Brooklyn Entomological Society, Bulletin **19**:182–184.

Dybas, H. S., and D. D. Davis. 1962. A population census of seventeen-year periodical cicadas (Homoptera: Cicadidae: *Magicicada*). Ecology **43**:432–444.

Dybas, H. S., and M. Lloyd. 1974. The habitats of 17-year periodical cicadas (Homoptera: Cicadidae: *Magicicada* spp.). Ecological Monographs **44**:279–324.

Fisher, R. A. 1954. Statistical methods for research workers. 12th edition. Oliver and Boyd, London, England.

Iwao, S. 1968. A new regression method for analyzing the aggregation pattern of animal populations. Researches on Population Ecology **10**:1–20.

Iwao, S., and E. Kuno. 1968. Use of the regression of mean crowding on mean density for estimating sample size and the transformation of data for the analysis of variance. Researches on Population Ecology **10**:210–214.

Kendall, M. G. 1955. Rank correlation methods. Charles Griffin, London, England.

Kiester, A. R. 1979. Conspecifics as cues: a mechanism for habitat selection in the Panamanian grass anole (*Anolis auratus*). Behavioral Ecology and Sociobiology **5**:323–330.

Lloyd, M. 1967. 'Mean crowding.' Journal of Animal Ecology **36**:1–30.

Lloyd, M., and H. Dybas. 1966. The periodical cicada problem. Evolution **20**:133–149 and 466–505.

Lloyd, M., and J. White. 1976. Sympatry of periodical cicada broods and the hypothetical four-year acceleration. Evolution **30**:786–801.

Marlatt, C. L. 1907. The periodical cicada. Bulletin 71 (new series), Bureau of Entomology, United States Department of Agriculture, Washington, D.C., USA.

Morisita, M. 1971. Measuring of habitat value by the 'environmental density' method. Pages 379–401 *in* G. P. Patil. E. C. Pielou, and W. E. Waters, editors. Statistical ecology, Volume 1. Spatial patterns and statistical distributions. Pennsylvania State University Press, University Park, Pennsylvania, USA.

Simon, C. M. 1979*a*. Evolution of periodical cicadas: phylogenetic inferences based on allozymic data. Systematic Zoology **28**:22–39.

Simon, C. M. 1979*b*. Evolutionary relationships among the 13- and 17-year periodical cicadas. Dissertation. State University of New York, Stony Brook, New York, USA.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry. Freeman, San Francisco, California, USA.

White, J. 1973. Viable hybrid young from crossmated periodical cicadas. Ecology 54:573–580.

———. 1980. Resource partitioning by ovipositing cicadas. American Naturalist 115:1–28.

White J., and M. Lloyd. 1975. Growth rates of 17- and 13-year periodical cicadas. American Midland Naturalist 94:127–143.

White, J., and M. Lloyd. 1979. 17-year cicadas emerging after 18 years: a new brood? Evolution 33:1193–1199.