Periodical Cicada (Homoptera: Cicadidae) Life-Cycle Variations, the Historical Emergence Record, and the Geographic Stability of Brood Distributions

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ABSTRACT The complex biogeography of the 13- and 17-yr periodical cicadas offers important opportunities for testing hypotheses of *Magicicada* evolution and ecology. However, misinterpretation of stragglers as on-schedule emergences, combined with systematic biases in search effort and the use of cross-generational brood maps, likely results in erroneous edge extension of adjacent broods and the appearance of sympatric shadow broods in published maps. Substantial recent changes in brood distributions have been inferred from the *Magicicada* historical record, the most significant being the decline and extinction of 17-yr brood X in the midwestern United States, the widespread expansion and contraction of 17-yr brood VI and 13-yr brood XXIII, and the displacement of brood XIII 17-yr cicadas in Illinois by 13-yr brood XIX in Illinois. Reanalysis of the historical data with an awareness of straggler-induced error suggests instead that brood distributions in these cases have remained stable.

KEY WORDS *Magicicada*, periodical cicada, life cycles, phenotypic plasticity, geographic distributions, brood extinction

THE PERIODICAL CICADAS (*Magicicada* spp.) of the eastern United States are characterized by long life cycles, dense populations, and synchronous development (Marlatt 1907; Alexander and Moore 1962; Lloyd and Dybas 1966a, 1966b; Williams and Simon 1995). All individuals emerge together as adults in the spring of one year and produce offspring that spend 13 or 17 yr underground as juveniles. Three morphologically and behaviorally distinct species of 17-yr cicadas (Table 1) inhabit the northern and plains states sympatrically and synchronically, and four 13-yr *Magicicada* species inhabit the southeastern and midwestern states (Marshall and Cooley 2000, Simon et al. 2000). The 17- and 13-yr life-cycle groups each have formed several largely allopatric broods that emerge in different years (Fig. 1). Each brood is given a Roman numeral indicating its temporal relationship to other same-cycle broods, from I to XVII for 17-yr cicadas and XVIII- to XXX for 13-yr cicadas. The term "brood" is used here in the strict sense of a population or set of populations of cicadas that reproduces on a particular 13- or 17-yr schedule. There are 12 extant 17-yr broods and three 13-yr broods, leaving many year-classes empty (Table 2).

These complex biogeographic patterns offer important opportunities for testing hypotheses of life-cycle evolution, brood formation, and the ecological and evolutionary interactions of 13- and 17-yr cicadas (e.g., Alexander and Moore 1962; Lloyd and Dybas 1966b; Lloyd and White 1976; Lloyd et al. 1983; Martin and Simon 1988, 1990a; Marshall and Cooley 2000, Simon et al. 2000). However, although brood distributions are well-known on a regional scale, there has been striking disagreement over the degree to which broods overlap, especially broods of different life-cycle types (e.g., Marlatt 1907; Bryce and Aspinwall 1975; Cox and Carlton 1988, 1991; Simon 1988). In addition, surveys in different emergence years have sometimes yielded radically different distributions for the same brood, suggesting substantial range changes. Analysis of these patterns suggests that much of the confusion has been caused by misinterpretation of off-schedule cicadas that emerge out of synch with the rest of the brood. This article first reviews and extends prior discussion (e.g., Lloyd and White 1976, Maier 1985, Moore 1993) of how such life-cycle variants contribute to erroneous patterns in *Magicicada* distribution maps. Then, historical hypotheses of recent *Magicicada* brood range changes are reanalyzed and argued to be based in part on misinterpretation of straggler emergences and other flaws in the historical record.

The Problem of Straggling and the *Magicicada* Historical Record

Although most cicadas in a *Magicicada* population emerge in synchrony, sometimes off-schedule *stragglers* appear, a term that applies to both premature and delayed cicadas. The cause of straggling is not yet

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Table 1. Periodical cicada complex

Subgroup	Species	Life Cycle
Decim	*Magicicada septendecim* (L.)	17
	Magicicada neotredecim Marshall & Cooley	13
	Magicicada tredecim (Walsh & Riley)	13
Cassini	*Magicicada cassini* (Fisher)	17
	Magicicada tredecassini Alexander & Moore	13
Decula	*Magicicada septendecula* Alexander & Moore	17
	Magicicada tredecula Alexander & Moore	13

known. Generally speaking, such life-cycle variations could be caused by novel mutations or gene combinations influencing life-cycle length or by novel environmental conditions that trigger developmental plasticity (Martin and Simon 1990b). Observations of cicadas emerging prematurely in recently cleared plots and beneath a greenhouse (Marlatt 1907) implicate climate effects as a likely trigger in some cases.

Straggler appearances most often occur 1 yr before or after the normal emergence (Kritsky 1987, Moore 1993), but multiple-year errors occur as well and should be expected in such long-lived organisms (see also Moore 1993). For example, apparent 4-yr premature (e.g., Dybas 1969, Simon 1988, Kritsky and Simon 1996; reviewed in Simon and Lloyd 1982) and 4-yr delayed (e.g., Young 1974, Maier 1985; see also *Appendix*) 17-yr cicadas have been observed on many occasions. In recent years, *M. cassini* adults in northern Illinois have emerged 2 and 3 yr early and 3, 4, 5, and 9 yr late (see *Appendix*). Off-schedule 17-yr cicadas were recorded on 10 separate year from 1944–1961 in southeast Ohio (Alexander and Moore 1962), where only three broods are known. Lloyd and Dybas (1966b) listed records of *Magicicada* stragglers from brood XIII emerging from 4 to 7 yr late in northeastern Illinois. These examples do not by any means represent an exhaustive list of known straggler records; they are given here to illustrate the range of forms that straggling can take.

Stragglers usually emerge in very small numbers of one to a few cicadas in a locality, but they can be more common, as might be expected given the extraordinary sizes of *Magicicada* populations. Population density estimates range from 8,355/ha (Maier 1982) to 3,700,000/ha (Dybas and Davis 1962), therefore even a minuscule rate of straggling could result in noticeable numbers of cicadas in off years. On rarer occasions, hundreds or thousands of periodical cicadas emerge off-schedule in dramatic surprise appearances. One emergence of this type involved 1-yr delayed cicadas (White and Lloyd 1979). Otherwise, there has been a tendency for the denser straggler emergences to occur 4 yr before an expected 17-yr emergence (e.g., Dybas 1969).

Past straggling probably formed the multiple temporally isolated broods of each life cycle (Alexander and Moore 1962, Lloyd and Dybas 1966b, Lloyd and White 1976, Simon and Lloyd 1982, Martin and Simon 1990b). However, successful reproduction by straggler cicadas, even in the larger off-schedule emergences, appears to be extremely rare because periodical cicadas are easily captured by predators (for an unusual case see White and Lloyd 1979). Flocks of birds have been observed annihilating introduced or straggler populations of up to a few thousand cicadas (e.g., Marlatt 1907, Beamer 1931, Alexander and Moore 1962, Dybas 1969, Chilcote and Stehr 1984); this has led to the characterization of *Magicicada* adults as "predator-foolhardy" (Lloyd and Dybas 1966a). Apparently, normal *Magicicada* emergences are dense enough to satiate local predator populations, which cannot respond numerically because of the long life cycle (Lloyd and Dybas 1966a, Karban 1982, Williams et al. 1993), and thousands or more cicadas per hectare must emerge across a substantial area for successful establishment of a new self-reproducing population by straggling, in part because the offspring of the straggler population must themselves be numerous enough to satiate predators.

Magicicada broods of the same life cycle are defined entirely by their temporal relationships. Conspecific cicadas of different broods have diverged slightly in wing morphology (Simon 1983, 1990) and allozymes (Simon 1979, Archie et al. 1985), but no fixed differ-

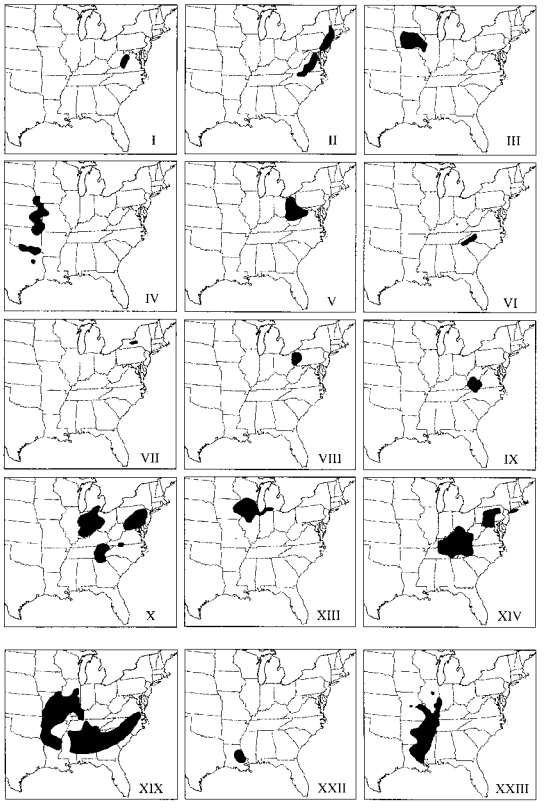

Fig. 1. General distributions of *Magicicada* broods, summarized from county-level maps in Simon (1988) and from 1997–1998 field observations in Illinois. I-XIV are 17-yr broods; XIX-XXIII are 13-yr broods. The remaining year-classes are not known to contain self-reproducing populations.

Table 2. Schedule of *Magicicada* broods

Year	17	13	Year	17	13	Year	17	13	Year	17	13	Year	17	13
1825	I		1863	V		1901	IX		1939	XIII		1977		
1826	II		1864	VI		1902	X		1940	XIV		1978	I	
1827	III		1865	VII		1903			1941			1979	II	
1828	IV		1866	VIII		1904			1942			1980	III	
1829	V	XIX	1867	IX		1905	XIII		1943			1981	IV	
1830	VI		1868	X	XIX	1906	XIV		1944	I		1982	V	
1831	VII		1869			1907		XIX	1945	II		1983	VI	
1832	VIII	XXII	1870			1908			1946	III	XIX	1984	VII	
1833	IV	XXIII	1871	XIII	XXII	1909			1947	IV		1985	VIII	XIX
1834	X		1872	XIV	XXIII	1910	I	XXII	1948	V		1986	IX	
1835			1873			1911	II	XXIII	1949	VI	XXII	1987	X	
1836			1874			1912	III		1950	VII	XXIII	1988		XXII
1837	XIII		1875			1913	IV		1951	VIII		1989		XXIII
1838	XIV		1876	I		1914	V		1952	IX		1990	XIII	
1839			1877	II		1915	VI		1953	X		1991	XIV	
1840			1878	III		1916	VII		1954			1992		
1841			1879	IV		1917	VIII		1955			1993		
1842	I	XIX	1880	V		1918	IX		1956	XIII		1994		
1843	II		1881	VI	XIX	1919	X		1957	XIV		1995	I	
1844	III		1882	VII		1920		XIX	1958			1996	II	
1845	IV	XXII	1883	VIII		1921			1959		XIX	1997	III	
1846	V	XXIII	1884	IX	XXII	1922	XIII		1960			1998	IV	XIX
1847	VI		1885	X	XXIII	1923	XIV	XXII	1961	I		1999	V	
1848	VII		1886			1924		XXIII	1962	II	XXII	2000	VI	
1849	VIII		1887			1925			1963	III	XXIII	2001	VII	XXII
1850	IX		1888	XIII		1926			1964	IV		2002	VIII	XXIII
1851	X		1889	XIV		1927	I		1965	V		2003	IX	
1852			1890			1928	II		1966	VI		2004	X	
1853			1891			1929	III		1967	VII		2005		
1854	XIII		1892			1930	IV		1968	VIII		2006		
1855	XIV	XIX	1893	I		1931	V		1969	IX		2007	XIII	
1856			1894	II	XIX	1932	VI		1970	X		2008	XIV	
1857			1895	III		1933	VII	XIX	1971			2009		
1858		XXII	1896	IV		1934	VIII		1972		XIX	2010		
1859	I	XXIII	1897	V	XXII	1935	IX		1973	XIII		2011		XIX
1860	II		1898	VI	XXIII	1936	X	XXII	1974	XIV		2012	I	
1961	III		1899	VII		1937		XXIII	1975		XXII	2013	II	
1862	IV		1900	VIII		1938			1976		XXIII	2014	III	XXII

ences are known. Therefore, the number and relative timing of broods in a location can be determined only by analysis of historical emergence patterns. Such analyses are greatly complicated by off-schedule emergences, because individual straggler cicadas do not look or sound any different from cicadas that emerge normally. However, the unique dependence of *Magicicada* populations on predator satiation means that small numbers of emerging periodical cicadas (i.e., up to hundreds per hectare) can be reliably interpreted either as stragglers or as the remnants of a soon-to-be-extinct brood. Unfortunately, most published records of *Magicicada* emergences do not include data on emergence density and therefore cannot be checked for the possibility of a straggler origin. In part because of this, and in part because of lack of awareness of the problem, past investigators have sometimes established brood locality records on the basis of one-time appearances of very small numbers of cicadas (e.g., 1–3 individuals at a location). Examples are given below in a discussion of three additional sources of error in *Magicicada* brood maps.

Use of Cross-Generation Brood Maps. Straggler-related error in the *Magicicada* historical record is increased by the use of distribution maps (Fig. 1) that lump records sharing a common 13- or 17-yr historical pattern (e.g., brood I maps lump records from 1995, 1978, 1961, and so on, whereas brood II maps include 1996, 1979, 1962, and so on). Such *cross-generation* maps do not include emergence dates; a dot indicates only that periodical cicadas appeared in one or more normal emergence years of a given brood. This practice makes it difficult to determine if a given record can be explained by straggling from a different brood. Examination of one unusual case in which the original data are available today illustrates this potential flaw. Marlatt (1898b) listed all localities reporting *Magicicada* to the USDA in 1898 and then assigned each record to either 13-yr brood XXIII or 17-yr brood VI, both of which appeared in that year (Table 2). Eight county records were assigned to 17-yr brood VI and 25 records were assigned to 13-yr brood XXIII (Fig. 2). Because only life cycle distinguishes 13- and 17-yr cicadas in central Illinois, these assignments must have been made using a priori range estimates. However, the range of brood XXIII in Illinois was not well-established in 1898 (Marlatt 1898a, 1898b), and brood VI had been recorded only sporadically. Brood assignments were therefore made more or less arbitrarily, with more northern emergences assumed to be from the expected 17-yr brood. Some populations from adjacent counties were attributed to different broods,

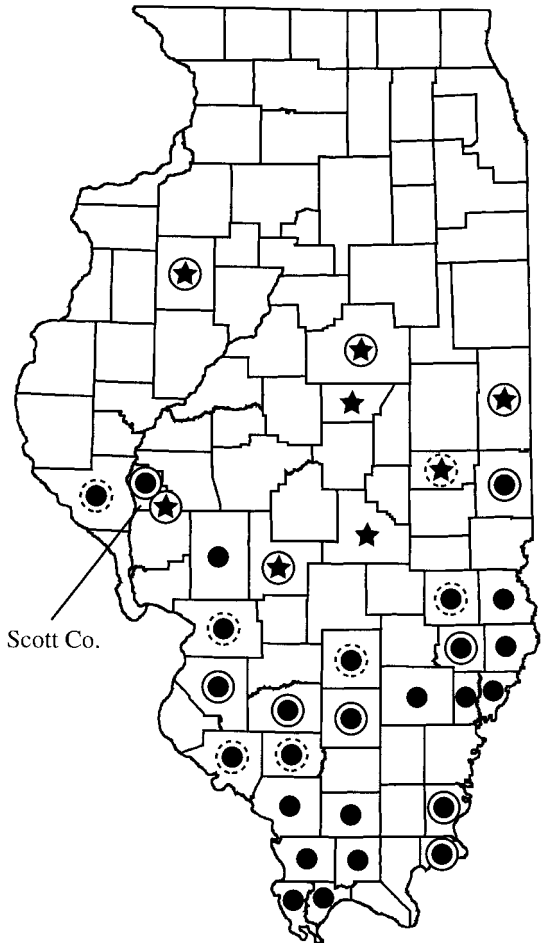

Fig. 2. Illinois periodical cicada emergence records from 1898 (Marlatt 1898b), listed by county with available emergence density data. Star, brood VI; dot, brood XXIII. No circle around symbol indicates dense population. Dashed circle around symbol indicates no data on emergence density. Circle around star indicates "few," "very few," or "sporadic." Circle around dot indicates "few," "one or two," "very limited numbers," "no great numbers," or "not so many as heretofore [1894]."

and records from two Scott County localities were assigned differently (Fig. 2). At least one of these assignments is known today to be incorrect (brood VI in DeWitt County; Lloyd et al. 1983). Furthermore, descriptive data accompanying the original records (Marlatt 1898b) show that many involved only a handful of cicadas (Fig. 2) and therefore suggest that the observed cicadas were merely stragglers. Because the 1898 cicadas appeared 4 yr after 13-yr brood XIX and 4 yr before 17-yr brood X (Table 2), which today inhabit many of the same localities, 4-yr straggling could explain many of these observations. As expected under this hypothesis, nearly all of the dense emergences were observed near the modern range of brood XXIII, whereas the sparse emergences mostly occurred outside this area but within the range of brood XIX. Marlatt's 1898 records survive in many cross-generation brood maps today, separated from the information required for recognition of their potential mis-assignment and straggler origin.

Edge Extension and Shadow Broods. Two important questions in *Magicicada* biology are the frequency of brood overlap and the relationship of overlap to temporal isolation. Some broods (e.g., 17-yr III and XIII) appear parapatric, while others (13-yr XIX and XXIII) appear broadly sympatric in some maps. Using Marlatt's (1907) cross-generation maps, Cox and Carlton (1991) discussed a "broad zone of overlap" between 13- and 17-yr cicadas, whereas recent fine-scale mapping in the Midwest indicates comparatively minor sympatry (Simon 1988). The apparent overlap of 13- and 17-yr broods in cross-generation maps could be explained by *edge extension* caused by chronic misinterpretation of stragglers. When stragglers from one brood (brood A) appear in the normal emergence year of an adjacent but nonoverlapping brood (B), brood A stragglers observed close to the anticipated range of brood B may be incorrectly identified as brood B cicadas, extending the recorded distribution of brood B. Brood A stragglers appearing far from the anticipated limits of Brood B may be disregarded, if they are noticed at all. The reciprocal process may extend the recorded distribution of brood A, until the two broods appear to overlap geographically. Because stragglers can appear many years early or late, adjacent 17- and 13-yr broods could leak stragglers into each other's emergence year in many different generations during a 221-yr cycle.

Broods of the same life cycle may also undergo edge extension. Such brood pairs share only one temporal path for straggler exchange, but the opportunity occurs in every generation. Edge extension between same-cycle broods may follow predictable patterns. First, some broods may be too far isolated in time to "exchange" many straggler records (e.g., 17-yr broods III and XIII). Second, if some forms of straggling are more common (e.g., 1- and 4-yr aberrations: Kritsky 1987, Moore 1993), then certain brood pairs will accumulate more distribution errors. Third, 4-yr straggling, being perhaps less often anticipated, may generate more erroneous records than 1-yr straggling. If true, the latter prediction could explain the observation that geographic overlap is generally limited to broods separated by 4 yr (e.g., 13-yr broods XIX and XXIII and 17-yr broods II, VI, X, and XIV) (Lloyd and White 1976, Simon and Lloyd 1982). Although 4-yr brood sympatry has been proven in several cases (e.g., Lloyd and White 1976, Simon et al. 1981, Simon and Lloyd 1982), other cases may involve a nonexistent *shadow brood* produced by recurring 4-yr stragglers (see also brood XXIII discussion below). Maier (1985) suggested that repeated 4-yr delayed stragglers from brood II have created the illusion of sympatric populations of brood VI on Staten Island; Lloyd and White (1976) proposed a similar explanation for brood XV.

Biased Search Effort and the Distribution of Brood VI. Uneven search effort may strongly influence patterns of straggler-induced error on *Magicicada* distri-

bution maps. Stragglers are probably more likely to be observed and recorded in heavily populated regions and near university towns. Stragglers are also more likely to be noticed when periodical cicadas are expected to emerge nearby or when large-scale mapping efforts are conducted. For example, the groups of 1–10 brood XIII stragglers observed in northern Illinois in 1994 (see *Appendix*) could have been recorded as populations of brood XVII by an inexperienced observer, but they were unlikely to be noticed at all because no broods were anticipated in 1994.

The apparently shifting distribution of 17-yr brood VI through history illustrates the interaction of nonrandom searching and straggler misidentification. In 1932 (USDA 1932), brood VI was described as "more widespread than any other 17-yr brood," with isolated populations described from many states. Later, Deay (1952) described brood VI as "a widespread, sparsely populated brood ranging from South Carolina north to northern New York and Wisconsin" and then noted that for Indiana "no dense swarms have been observed anywhere in the state; as a rule only a few specimens appear in each locality." Today, brood VI appears to be limited to Appalachian North Carolina, South Carolina, and Georgia (Fig. 1). The apparently changing distribution of brood VI and the scattered nature of many of its populations suggest that many records derive from misidentified stragglers (see also Lloyd and White 1976, Maier 1985, Kritsky 1987). Many of the questionable brood VI records fall within the ranges of 17-yr broods II, V, and X—all separated from brood VI by 1 or 4 yr. But if straggling underlies the many brood VI records from outside the southern Appalachians, then why have other year-classes with similar potential for straggler appearances remained empty (e.g., brood XV, which could accumulate 4-yr straggler records from broods II and XIV)? The answer may be that greater search efforts were conducted in the brood VI year-class, mainly as part of an unusually thorough 1898 USDA study (Marlatt 1898b) that yielded widespread records of stragglers and led to searches in future brood VI emergence years.

Brood VI maps before 1898 showed only six (Riley 1885, Walsh and Riley 1868) to 12 (Marlatt 1898a) records from no more than six states outside Wisconsin and Appalachian North Carolina, South Carolina, and Georgia. The 1898 USDA search increased this number to 90, from 21 states and the District of Columbia. This newly widespread distribution may have sparked interest in brood VI, because just two generations later the cumulative USDA list had grown to 310 localities (USDA 1932). At this point the inconsistency of the records was apparent, because only 84 of these localities actually reported cicadas in 1932, and these were concentrated in Appalachian North Carolina, South Carolina, and Georgia, and within the eastern part of brood X. Except for areas in Wisconsin and Michigan, nearly all of the locations that reported strong brood VI emergences 100 yr ago support the brood today (Simon 1988), whereas brood VI has not been recorded again from many locations where it was first noted in 1898. The strongest evidence that the apparent brood VI distribution was expanded by misinterpreted stragglers in 1898 is the data on emergence density for records of that year (Marlatt 1898b). Outside the modern brood VI range, low numbers were mentioned for 56% (61/106) of the counties, whereas abundant cicadas were reported in only 17% (18/106). No data on abundance were available for the remaining counties. Of the 18 counties that reported dense populations outside the modern range, 10 are localities in northern Michigan and Wisconsin where confusion with the morphologically similar *Okanagana* can occur (Maier 1985, Moore 1993) or in southern Wisconsin where anecdotal descriptions indicate unambiguously that brood VI populations existed in 1898 (Marlatt 1898b). Thus, the unusual historical record of brood VI is likely attributable to stragglers being recorded in a year of especially thorough search efforts.

Hypotheses of Recent Changes in *Magicicada* Brood Distributions

Historical evidence of recent shifts in brood distributions has been cited in discussions of many aspects of *Magicicada* ecology and evolution, including competition between broods (Lloyd et al. 1983), life-cycle genetics and hybridization (Lloyd et al. 1983, Cox and Carlton 1991), and life-cycle shifts (Martin and Simon 1988). The above discussion and earlier arguments suggest that one apparently declining brood (brood VI) has instead remained historically stable in its geographic distribution and that the appearance of historical change is in part due to straggler-related error. A reexamination of the supporting data in two additional cases leads to a similar conclusion.

Decline and Extinction of Midwestern 17-yr Brood X. Several papers (Lloyd et al. 1983; Martin and Simon 1988, 1990a; Cox and Carlton 1991) have cited historical evidence suggesting that 17-yr brood X declined to extinction across Missouri, Illinois, and northern Arkansas between 1868 and 1919, and that during this period it was replaced by new 13-yr cicada populations. Other than the apparent historical contraction of brood VI, no more substantial recent change in *Magicicada* brood distributions has been proposed, and the apparent disappearance of brood X has played a key role in important theories of *Magicicada* ecology and evolution. Kritsky (1989) and Cox and Carlton (1991) have challenged the second part of the hypothesis by noting historical records showing that 13-yr brood XIX was found in Illinois and Missouri before 1868. No one has yet challenged the central element of the hypothesis, that 17-yr brood X existed in the Midwest before 1868 and disappeared after 1902. This discussion adds to earlier arguments and shows that brood X was probably never present in the Midwest. The argument can be organized under three points.

(1) Thirteen-Year Broods XIX and XXIII Existed in Missouri and Illinois Before 1868. Kritsky (1989) noted that periodical cicadas emerged in parts of Illinois and Missouri in 1829, 1842, and 1855, suggesting populations with a 13-yr life cycle before 1868. Other sources

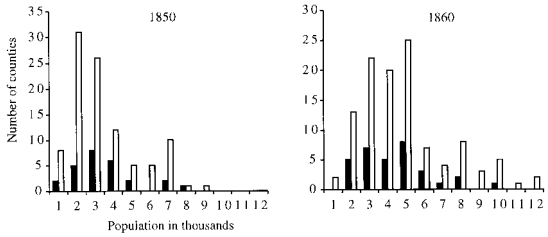

Fig. 3. Histograms of population sizes of Missouri counties. Black bars: counties that reported brood X in 1902. White bars: all Missouri counties. The brood X counties show a distribution of population densities that is typical for the state as a whole.

lend additional data to this conclusion. Cox and Carlton (1991) cited newspaper accounts suggesting a long history of 13-yr broods in eastern Missouri. Walsh and Riley (1868) described accounts of probable 13-yr cicadas near St. Louis (brood XXIII) in 1859. They also mention records from the same year for brood XXIII in Jackson County and Union County, IL, where the brood occurs today. While discussing stragglers, Walsh and Riley (1868) referred to 1-yr premature 13-yr cicadas in two Missouri counties (Luray County and Daviess County in 1854) and one county in western Illinois (Madison County in 1867). Marlatt (1907) included a chronology of records including some from "all southeast part" of Missouri in 1829, 1842, 1855, and 1868. Walsh and Riley (1868) wrote that brood XIX was found in "nearly the whole state" of Missouri, and cited 1868 records from many counties without qualification even though 1868 was also a brood X emergence year (Table 2). They apparently did not believe confusion with brood X to be a problem in Missouri and western Illinois, presumably because of the consistency of the records listed above.

(2) No Historical Evidence Indicates That 17-yr Brood X Cicadas Existed in Missouri or Western Illinois Before 1902. None of the primary sources of 19th century distribution information (Marlatt 1898a, Walsh and Riley 1868, Riley 1885) included a single record of 17-yr brood X in Missouri or western Illinois for years before 1868. Poor sampling is probably not the reason. The earliest summaries (Walsh and Riley 1868, Riley 1885) described records for all of the broods currently found in Missouri in approximately their modern distributions, including brood IV in the west, brood III in the north, brood XXIII in the southeast, and brood XIX throughout most of the state. In addition, mid-19th century census records indicate that the Missouri counties that reported apparent brood X cicadas in 1902 (discussed below) were not more sparsely populated than the rest of the state (Forstall 1996; Fig. 3). Cicadas did appear in Missouri in the brood X years 1868 and 1885. However, these emergences could not be assigned to a brood with certainty, because brood X emerged together with 13-yr brood XIX in 1868 and with 13-yr brood XXIII in 1885 (Unfortunately for early efforts to map the *Magicicada* broods, from 1855 to 1911 the important 17-yr broods XIV, X, VI, and II each emerged synchronously first with 13-yr brood XIX and then with 13-yr brood XXIII [Table 2].), and because 13- and 17-yr cicadas are morphologically and behaviorally indistinguishable in the Midwest. Nonetheless, later solo emergences of the 13-yr broods together demonstrated that the 1868 and 1885 populations were probably 13-yr cicadas, as concluded by Marlatt (1907, 1919) and suggested by the pre-1868 13-yr cicada records discussed above. The existence of 17-yr brood X in the region in the 19th century has been inferred entirely from historical records of 1902 and 1919, evidence disputed in number 3 below.

(3) Cicadas Emerging in the Brood X Years 1902 and 1919 likely were Stragglers from 13-yr Broods XIX or XXIII. The first year after 1851 in which 17-yr brood X emerged alone was 1902 (Table 2). Recognizing this opportunity, the USDA solicited records widely (Marlatt 1898b). Marlatt considered emergences of brood X in Illinois and Missouri a possibility, but only because he viewed the northern latitudes as more appropriate for 17-yr cicadas (Marlatt 1898b). The results apparently confirmed the pre-1868 historical record. In 1907, Marlatt (1907) wrote in reference to the 1902 data ". . . rather to our surprise, the substantial correctness of the old records is strikingly demonstrated. . . brood X stops, as hitherto believed, near the eastern line of Illinois, with a few scattering outposts. There is overlapping, but, in the main, south-central and western Illinois and eastern and central Missouri seem to belong to the 13-yr race, as hitherto believed." Marlatt (1919) later wrote "In 1902, for the first time since very careful study of the cicada began, it was not accompanied by a 13-yr brood, and its actual range was more nearly determined than before, although the old limits of distribution were pretty generally confirmed." Marlatt's subsequent distribution maps (1907, 1919) contain no Missouri records of brood X and just a few Illinois records where brood X exists today along the Indiana border. If these were the only sources available, there would likely be no controversy surrounding the historical distribution of this brood.

Uncertainty regarding brood X in Missouri exists because a different source (Haseman 1915; Fig. 4F) described 1902 emergences from 32 counties, citing J. M. Stedman, who "after careful culling of the reports received. . .found the brood to be quite generally tho' lightly distributed through the eastern half of the state." (Incidentally, Haseman also noted that brood X "has not heretofore been reported from this state," supporting the arguments made in number 2 above.) Marlatt (1898b) published brood XXIII records gathered by Stedman in 1898, so it is unclear why his later brood X maps did not include Stedman's 1902 data.

Most of the critical 1902 Missouri records were not replicated 17 yr later, when just four counties reported *Magicicada* (Cape Girardeau, Carter, Hickory, Perry; Haseman 1919). Only four subsequent records of putative brood X exist for Missouri (Simon 1988). Because these newer records are of "small populations" (Simon 1988) and do not correspond to the counties reporting cicadas in 1919, they remain of uncertain origin. The apparent decline from 1902 to 1919 in-

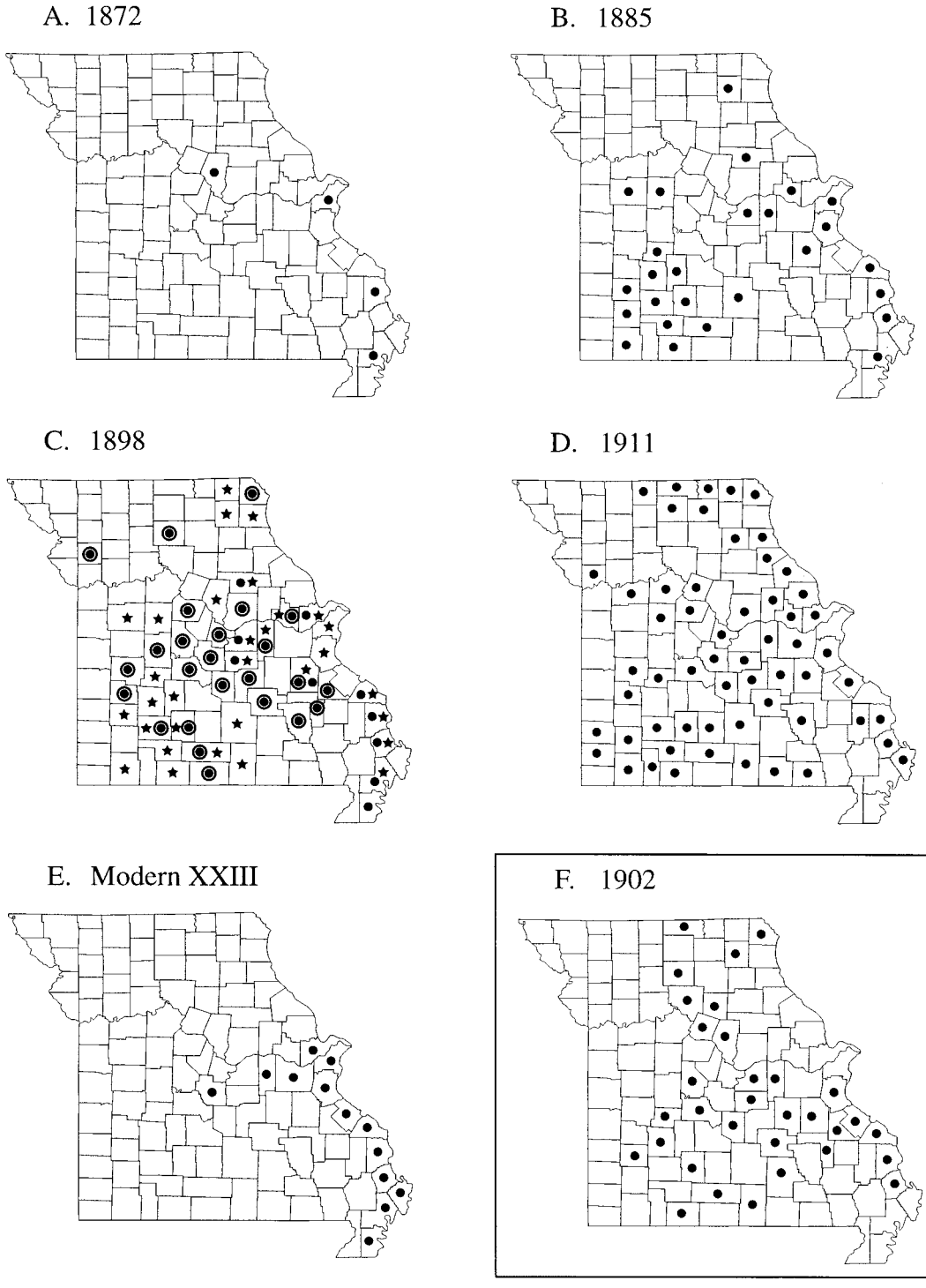

Fig. 4. Missouri *Magicicada* records plotted by county. (A–D) Brood XXIII emergence years 1872–1911. (E) Modern distribution of brood XXIII from Simon (1988). (F) Brood X emergence year 1902. Records from 1898 (C) include emergence density information when available (from Marlatt 1898b, 1907): Dot, dense populations reported; circled dot, sparse populations reported; star, emergences reported without abundance data. Records obtained from Froeschner (1952) –1911 St. Genevieve County only, Haseman (1915), Hyslop (1935) –1885 Barry County only, Marlatt (1898b 1907), Simon (1988), and USDA (1937) –1898 Scotland and Lewis counties only.

spired the theory that brood X became extinct after that period (Lloyd et al. 1983). However, the records from one of these two emergence years can be easily dismissed. Haseman (1919) pointed out that the 1919 cicadas emerged in small numbers and may have been 1-yr precursors of 13-yr brood XIX populations known from those counties. The evidence of brood X in Missouri and western Illinois therefore reduces to records from a single year, 1902. As argued below, the historical record suggests that the 1902 cicadas were delayed stragglers from one or both of the 13-yr broods XIX and XXIII. This discussion will focus on the more complete Missouri records, but the same hypothesis should apply to western Illinois (see Moore 1993).

The 1902 Missouri brood X cicadas appeared in the central, southern, and eastern parts of the state (Fig. 4F), areas inhabited today by 13-yr broods XIX and XXIII (Fig. 1). Therefore, if due to straggling, these records could be explained as 4-yr delayed brood XXIII cicadas, 8-yr delayed brood XIX cicadas, or a combination of both (Table 2) (assuming that brood XIX individuals due in 1907 could not have emerged in just their eighth year). There have been no clear published examples of multiple-year delayed 13-yr cicadas. However, because 1-yr life-cycle plasticity is documented for both life-cycle types, and multiple-year delayed emergences have been observed in 17-yr cicadas (see earlier discussion), such straggling seems plausible in 13-yr cicadas as well. Indeed, at least one recent straggler observation from Dewitt County, IL, appears consistent with a 4-yr delayed emergence from brood XXIII (see *Appendix*). All but one of Marlatt's (1907) mapped records of "Brood XXVI," a brood now regarded as extinct or doubtful from the start, fall within the geographically restricted distribution of brood XXII, suggesting a possible origin in a single bout of 4-yr delayed straggling. Furthermore, as discussed below, the arguments here offer a partial explanation for the apparently low frequency of multiple-year delayed straggling in 13-yr cicadas.

The simplest straggling hypothesis would explain the 1902 cicadas as 4-yr delayed brood XXIII. This hypothesis appears plausible at first because the historical brood XXIII data (Marlatt 1898b, Haseman 1915, USDA 1937; Fig. 4 A–D) do include most of the counties that reported cicadas in 1902. However, as argued below, the pattern of Missouri emergences from 1872 to the present day suggests that many brood XXIII records gathered around the turn of the century were based on mistaken observations of delayed brood XIX stragglers. If correct, this possibility would rule out brood XXIII as a source for many of the 1902 records, but it would also indirectly support the central hypothesis that the unexpected brood X records were caused by multiple-year delayed straggling in 13-yr cicadas. If 4-yr delayed brood XIX straggling occurred to an extent sufficient to cause widespread mistaken records of brood XXIII in 1898 and 1911, then it is possible that some of the same brood XIX stragglers emerged 8 yr late in 1902. Therefore, the discussion below will first analyze the Missouri distribution of 13-yr brood XXIII and then return to the argument that 1902 brood X cicadas were delayed 13-yr stragglers.

Simon's (1988) recent maps show 13-yr brood XXIII in 10 Missouri counties near the Mississippi and Missouri Rivers. However, earlier maps show brood XXIII in two to six times as many counties, including all but three of the counties reporting brood X in 1902 (Fig. 4). The list includes 26 counties in 1885 (USDA 1937), 50 in 1898 (Marlatt 1898b, USDA 1937), and 59 in 1911 (Haseman 1915, USDA 1937). In contrast to the apparently changing distribution of brood XXIII, 13-yr brood XIX has remained stable. The 1907 (Haseman 1915) and 1933 (USDA 1933) records show 13-yr brood XIX in all of Missouri except the northwestern counties, which are inhabited by 17-yr broods III and IV (Fig. 1). This description matches those of Walsh and Riley (1868), Riley (1885), and Simon (1988).

These data suggest at first that brood XXIII became more widespread after 1885, peaked in 1898 and 1911, and then declined sharply while brood XIX remained stable. However, given that midwestern populations of these two 13-yr broods contain the same species, there is little reason to believe that one brood could rapidly expand in distribution and then decline while another remains stable throughout the same general region. Brood XXIII populations in northern Indiana have been historically stable (Kritsky 1987) even though these populations are found at approximately the same latitude as the northernmost Missouri populations and share a similarly close geographic relationship to brood XIX (Fig. 1).

A simpler hypothesis would explain the apparently shifting distribution of Missouri brood XXIII as an artifact of repeated 4-yr delayed straggling from brood XIX from 1885 to 1911, a hypothesis supported by many details of the historical record: (1) The "core" brood XXIII distribution appears to have changed little since 1868. Except for a cluster of counties around Springfield in 1885, the pre-1898 records of brood XXIII are all from locations near the modern brood XXIII distribution (Walsh and Riley 1868, Riley 1885, USDA 1937; Fig. 4). (2) All counties listed by Marlatt (1898b, 1907) as containing dense brood XXIII populations are found within or near the modern-day range (Fig. 4), as are the localities for four brood XXIII specimen records from Froeschner (1952). (3) Many of the 1898 and 1911 populations were sparse. In 1898, 86% (31/36) of the within-county Missouri localities reporting data on abundance (36/71) noted small numbers (most reported "one," "one or two," "two or three," "few," or "very few"). Nearly all of these counties fall outside of the modern brood XXIII distribution (Fig. 4C; Marlatt 1898b). In addition, Haseman (1915) described the 1911 Missouri emergence as "much lighter than in former visitations" and "much less abundant than in 1907," attributing the pattern to an unusually dry spring. (4) Nearly all of the counties which have reported brood XXIII at least once contain brood XIX today (67 out of 75) or are located where brood XXIII certainly exists today (five out of 75), as expected if the brood XXIII distribution has not changed and brood XIX straggling caused most of the 1898 and

Table 3. Tabulation showing association between 1898 (apparent 13-yr brood XXIII) and 1902 (apparent 17-yr brood X) Missouri *Magicicada* emergence records, within the 90 Missouri counties known to contain populations of one or both 13-yr broods (Fisher exact two-tailed $P = 0.001$)

	Brood X	
	recorded (1902)	not recorded
Brood XXIII recorded (1898)	25	24
Brood XXIII not recorded	7	34

1911 records. The three exceptions are all counties that today harbor either brood III or IV 17-yr cicadas. Because the records from these counties all date to a brood III or IV year, or to 1 or 2 yr preceding a brood III or IV year, premature emergences of 17-yr cicadas are a plausible explanation. (5) There is inconsistency in the brood XXIII record across generations. Of the 77 counties listed by Marlatt (1898b) or Haseman (1915), 23 were reported only by Marlatt, and 24 were reported only by Haseman.

Four-year delayed stragglers from brood XIX may often be mistaken for brood XXIII cicadas, especially when emergence density is not considered, because such stragglers always appear synchronously with the later brood, and because only emergence timing distinguishes cicadas of the two broods. Because brood XIX accounts for more than two-thirds of the 13-yr range (Fig. 1), errors of this sort could account in part for the lack of published cases of multiple-year delayed straggling by 13-yr cicadas.

The discussion can now return to the question of 17-yr brood X in Missouri. If the above arguments are correct and brood XXIII has been restricted to east-central and southeastern Missouri for at least 150 yr, then many of the 1902 cicadas cannot be explained simply as 4-yr delayed stragglers from brood XXIII because they appeared outside the range of that brood, in locations containing only brood XIX. However, if many of the more widespread records of brood XXIII from 1885 to 1911 were caused by 4-yr straggling from brood XIX populations, then it is possible that other stragglers from the same populations delayed longer and emerged 8 yr late in 1902 as the unexpected brood X populations. The hypothesis that the 1902 straggler records were caused by a combination of 4- and 8-yr delayed straggling predicts that the 1902 counties should tend to be the same ones that observed apparent brood XXIII emergences in 1898. A test confirms this prediction: 25 of the 32 Missouri counties reporting brood X in 1902 also reported an apparent brood XXIII emergence in 1898 (Marlatt 1898b), a statistically significant association within the 13-yr Missouri range (Fisher exact two-tailed $P = 0.001$; Table 3). All of the 1902 counties today harbor either brood XIX or XXIII. The 13-yr straggler hypothesis also predicts the absence of 1902 brood X records from northwestern Missouri counties (Marlatt 1898b; Fig. 4), which are inhabited today only by 17-yr broods III or IV (Fig. 1). Cicadas from these broods are separated in time almost maximally from brood X (Table 2) and would have to emerge in their sixth, seventh, 23rd, or 24th yr of development (respectively) to produce false brood X records. These patterns strongly suggest that straggling from the 13-yr broods created false brood X records in 1902.

The hypothesis that midwestern 13-yr populations have in the past produced straggler cicadas as old as 21 yr is made more plausible by the phylogenetic and geographic relationships of the species in the Decim subgroup of *Magicicada* (see Table 1). One of the 13-yr species, *M. neotredecim,* appears to have been derived recently (perhaps <10,000 yr ago) from populations of its 17-yr relative *M. septendecim* (L.); the two species are distinguishable only by life-cycle length (Marshall and Cooley 2000, Simon et al. 2000). Observations of likely 4-yr delayed 17-yr cicadas have been made on several occasions (see earlier discussion and *Appendix*), and the recent derivation of 13-yr *M. neotredecim* from its 17-yr counterpart raises the possibility that *M. neotredecim* retains similar developmental plasticity. In contrast, the other 13-yr member of the Decim group, *M. tredecim* (Walsh & Riley), differs from *M. septendecim* in male calling song, in morphology, and in mitochondrial DNA by an estimated 2.6% sequence divergence, suggesting a more distant relationship to its 17-yr counterpart (Marshall and Cooley 2000, Simon et al. 2000). Perhaps *M. tredecim* cicadas are less likely to undergo multiple-year delayed emergences as a result. All *M. neotredecim* are found in brood XIX populations in the Midwest where, as argued above, multiple-year delayed straggling has created false records of brood XXIII and brood X. In the southern and southeastern parts of the 13-yr range, where only *M. tredecim* is present, similar confusion has not occurred. This hypothesis could be tested by comparing rates of delayed straggling in *M. neotredecim* and *M. tredecim* where the species are sympatric in northern brood XXIII populations of Illinois and Indiana (Simon et al. 2000).

Finally, it is important to acknowledge a related alternative hypothesis. The unexpected appearance of cicadas in 1902 could be explained in terms of two 4-yr delays rather than by one 8-yr delay. This would require that brood XIX stragglers emerge 4 yr late in 1885 in numbers sufficient to allow some reproduction, after which some of the offspring would also have to delay emergence by 4 yr. There is one case of documented substantial reproduction by stragglers (White and Lloyd 1979), but no evidence yet of straggling by the offspring of stragglers. It may never be practically possible to distinguish such a process from repeated independent straggling events across generations.

These arguments are relevant for another prominent hypothesis of *Magicicada* life-cycle evolution. Lloyd et al. (1983) proposed a single-locus model of *Magicicada* life-cycle genetics and suggested that hybridization between 17-yr brood X (AA or A-) and a 13-yr brood XIX (aa) gave rise to widespread new populations of 13-yr brood XXIII in Illinois, Missiouri, northern Arkansas, and Kentucky following F_1 interbreeding and Mendelian segregation of F_2 homozygotes. Historical records were cited showing the un-

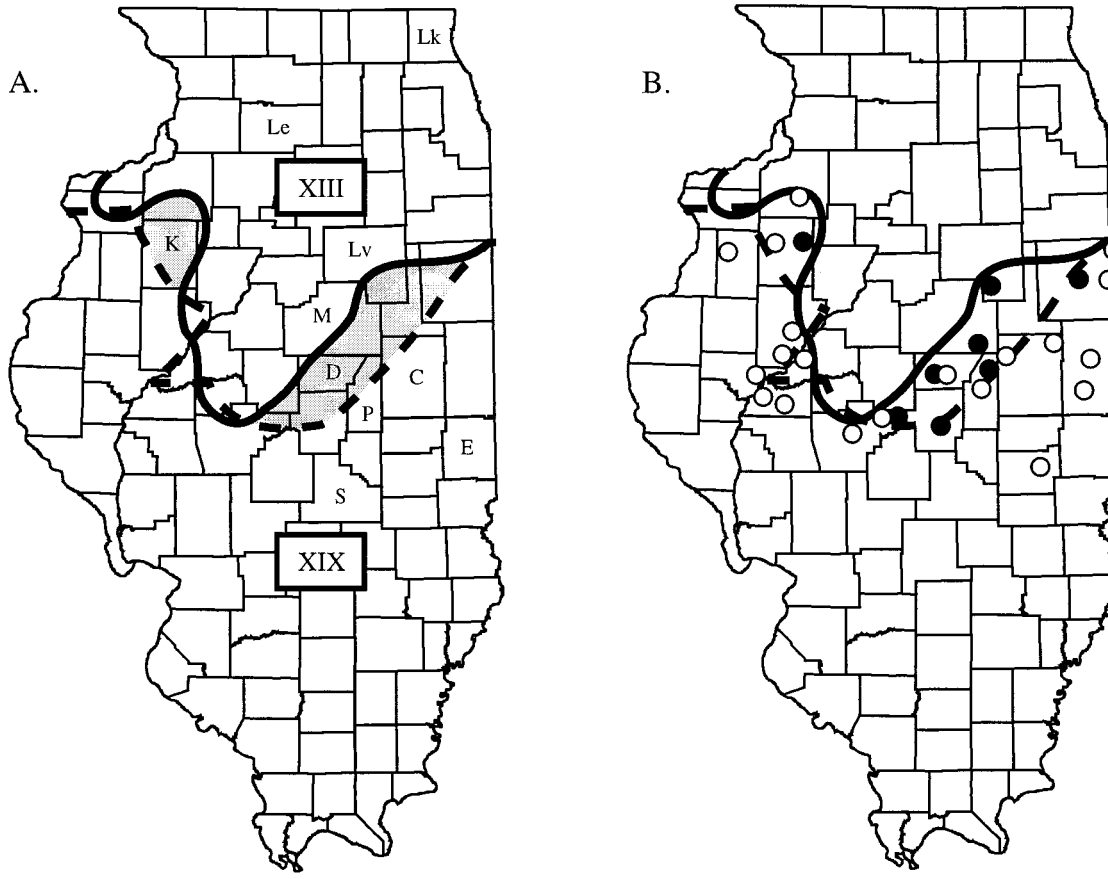

Fig. 5. (A) Apparent retreat (shaded region) of 17-yr brood XIII in central Illinois, adapted from Lloyd et al. (1983). Dashed line is estimated southern boundary of brood XIII in 1871 (LeBaron 1872). Solid line is estimated limit in 1973 (Stannard 1975). Counties mentioned in discussion are Champaign (C), Dewitt (D), Edgar (E), Knox (K), Lake (Lk), Lee (Le), Livingston (Lv), McLean (M), and Shelby (S). Other Illinois broods not shown. (B) Negative brood XIII records (open circles) used to infer retreat of brood XIII and positive brood XIX records (filled circles) used to infer presence (and implied advance) of brood XIX, from Stannard (1975).

expected appearance of brood XXIII populations throughout the region in 1898, 30 yr after the co-emergence of 13- and 17-yr broods XIX and X. The above discussions suggest that (1) unexpected emergences of brood XXIII can sometimes be accounted for by 4-yr straggling from 13-yr brood XIX (see also Cox and Carlton 1991), and (2) there is little evidence that brood X existed in much of the Midwest during the 19th century. In addition, Martin and Simon (1988) found no evidence of 13-/17-yr hybrid genomes in their genetic study of populations from the region. Other evidence cited in favor of the model was apparently not considered in light of the problem of straggling (see Moore 1993).

Thirteen-year Competitive Displacement of 17-yr Cicadas. Lloyd et al. (1983, p. 1170) proposed that the boundary between 13- and 17-yr broods in Illinois has shifted northward during the past century. The historical hypothesis was developed by comparing the southern distribution limit of 17-yr brood XIII in Illinois as mapped in 1871 by LeBaron (1872) to the same boundary as mapped in 1973 by Stannard (1975). The boundaries (Fig. 5A) suggest recent northward retreat of ≈50 km by brood XIII in eastern Illinois and in the Knox County/Henry County area in western Illinois. Lloyd et al. (1983) noted distribution records from Stannard (1975) indicating the presence of the 13-yr brood in the apparently vacated region and suggested that brood XIX cicadas had displaced the 17-yr brood. However, the data support neither the retreat of 17-yr brood XIII nor the advance of 13-yr brood XIX.

Stannard (1975) included both positive and negative search records in his maps. Fig. 5B shows the negative brood XIII records (from 1973) consistent with brood XIII retreat and the positive brood XIX records (1972) consistent with brood XIX invasion (those found on or north of the 1871 brood XIII boundary). The negative records show that almost no data support the position of the southern boundary drawn by Stannard (1975). Just two such records for brood XIII (in Henry and DeWitt counties) exist >10 km north of the 1871 limit estimated by LeBaron

(1872). Moreover, Stannard (1975) obtained two additional negative brood XIII records deep within the range of this brood in Lee and Lake counties (not plotted, but counties indicated in Fig. 5A), therefore it is not clear that the critical negative records indicate anything other than a patchy distribution.

The proposed recent advance of 13-yr brood XIX is also poorly supported for two reasons. First, very few positive records were listed for the disputed region. Stannard (1975) noted only four such records for 1972 within the entire 12,000-km^2 region apparently vacated by brood XIII (Fig. 5B). Second, three of these localities have probably contained 13-yr cicadas for at least a century. Walsh and Riley (1868) recorded brood XIX in eastern McLean County in 1868. Hyslop (1935) listed *Magicicada* in Wapella in Dewitt County for 1868 and 1885, consistent with either 17-yr brood X or 13-yr broods XIX and XXIII. Both 13-yr broods are probably found in this county today (Lloyd et al. 1983, Simon 1988). The Livingston County record matches records from the USDA (USDA 1933) and Marlatt (1907), although Walsh and Riley (1868) did not list the county for 1868. Stannard's (1975) Livingston County record is located farther north than any other from LeBaron's (1872) brood XIII line and is therefore most responsible for the appearance of northward brood XIX dispersal.

The remaining brood XIX 1972 record (Knox County) could be questioned because brood XIII is found in approximately this location and emerged 1 yr later in 1973. Stannard (1975) noted that the 1972 Knox County emergence could be interpreted as a 1-yr premature emergence of brood XIII, although there remains some question because apparently large numbers were involved. Unfortunately, the locality was not searched for brood XIII in 1973. Extensive searches in Knox County in 1998 did not locate brood XIX *Magicicada* (unpublished data).

Even if more supporting records were available, the conclusion that systematic brood distribution changes are occurring might not be warranted. Broods of periodical cicadas may not have simple margins on a local scale. LeBaron (1872, p. 132) described the 1871 brood XIII (northern Illinois brood) range limit with this comment:

> "... Neither must it be understood that no locusts were seen outside of this range. The locust line is not a simple and straight one, but more or less zig-zag, being necessarily much governed by the presence or absence of the timber which constitutes the natural depository of the insects' eggs. . .I may here remark that the Northern Illinois brood of locusts of 1871 meets and interlocks more or less with the Southern Illinois brood of 1868. . . ."

Finally, additional historical data cast some doubt on the thoroughness of Lebaron's brood XIII survey, which found that the Sangamon River approximates the southern limit of brood XIII. Riley (1885) published an apparently independent account of the 1871 brood XIII emergence, stating that "there seem to be detachments extending farther south, especially in the eastern portions of the State, and they occurred as far south as Shelby County." These "detachments" were reported from well south and east of the southern limit of LeBaron's (1872) distribution. As late as 1907, Marlatt's (1907) map showed brood XIII as far south as Champaign, Edgar, and Shelby counties, although later records for 1888, 1905, and 1922 (summarized in Lloyd and White 1976) did not include these counties. Neither of these counties was checked in 1973 by Stannard (1975), who mapped just nine negative emergence records for brood XIII in the entire eastern half of Illinois. To add to the confusion, Moore and Alexander (1958) mapped isolated brood XIII *M. septendecim* records for Champaign and Edgar counties in 1956, although they did not include specific information on abundance. The various Champaign, Edgar, and Shelby county records could be erroneous, or they could have been caused by straggling from broods XIX, XXIII, or X, or perhaps disjunct brood XIII populations have existed in these locations all along; there is little way to know without data on emergence density at least. The contrast between the LeBaron and Riley accounts is noted here only to illustrate the uncertainty inherent in the *Magicicada* record.

The Stability of Brood Distributions. Recent *Magicicada* brood distribution changes apparent in the historical record (the fluctuating ranges of broods VI, X, and XXIII and the northward displacement of the boundary between 13- and 17-yr broods in the Midwest) appear to be false patterns resulting in part from erroneous interpretation of straggling cicadas. Instead, the general range limits of the broods seem to have remained comparatively stable throughout recorded history. However, this conclusion is not intended to ignore other important forms of brood distribution changes, especially those happening on a more local scale. First, local straggling events of large magnitude may sometimes lead to the establishment of new self-reproducing brood populations (e.g., Simon and Lloyd 1982), although there is little evidence of this occurring during the period of the modern historical record. Reproduction in a straggler population was demonstrated by White and Lloyd (1979), but it is not known if the offspring population was large enough to satiate predators. Second, it has been suggested that repeated straggling events can gradually convert populations of one brood into another (e.g., brood XIV to brood X by 4-yr "acceleration;" Lloyd and White 1976). This could be correct, but the historical record is probably not long enough yet to show complete brood replacement by this process. Third, many authors (e.g., Marlatt 1907, Young 1958) have noted the widespread loss of local periodical cicada populations to forest fragmentation. This process has apparently not changed the general limits of the broods in part because *Magicicada* appear to thrive on woods edges and persist even in narrow strips of woods along prairie rivers. Finally, there is convincing evidence of the recent loss of a few geographically restricted broods (Williams and Simon 1995), such as

brood XI in Connecticut (Manter 1974) and brood XXI in peninsular Florida (Young 1958).

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Appendix: New Records of Periodical Cicada Stragglers Discussed in This Article

1993

Sangamon County, IL: Springfield, Riverside Park, south side of river, 16 June 1993. Heard one Cassini-type male singing in silver maple; 1330 hours R. D. Alexander and D. C. Marshall. Probably 3-yr-delayed *M. cassini:* This location lies at the border between broods XIII and XIX, but no cicadas emerged here in 1998 with brood XIX (R. D. Alexander and A. F. Richards, University of Michigan, personal communication).

DeWitt County, IL: Southwest of Clinton, on Rt. 400N at Salt Creek, 16 June 1993. Heard two calls from one Cassini-type male. R. D. Alexander and D. C. Marshall. Probably 4-yr-delayed *M. tredecassini* Alexander & Moore from brood XXIII: 13-yr broods XIX and XXIII have been recorded in the area, but no cicadas emerged here in 1998 with brood XIX (R. D. Alexander and A. F. Richards, University of Michigan, personal communication).

1994

Cook County, IL: Chicago, at Crooked Creek, 30 yards north of 107th Street, 14 June 1994. Three or more *M. cassini* males singing occasionally. Tape-recorded. D. C. Marshall. Four-year-delayed *M. cassini:* Only brood XIII has been recorded consistently from northern Illinois.

La Salle County, IL: Near Ottawa, southwest of town on Rt. 71 ≈0.2 miles northeast of Rt. 2650N, where road passes over creek, north side of road, 14 June 1994. One *M. cassini* male singing occasionally. Tape-recorded. D. C. Marshall. Four-year-delayed *M. cassini:* Only brood XIII has been recorded consistently from northern Illinois.

Warren County, IL: Near Surrey, southwest of Galesburg, just north of US34, 2000N and 1560E are the approximate coordinates. 14 June 1994. One *M. cassini* male singing. Tape-recorded. D. C. Marshall. Probably 3-yr-premature *M. cassini.* Brood III emerged here in 1997 (R. D. Alexander and A. F. Richards, University of Michigan, personal communication). However, brood XIII populations are not far away.

Sangamon County, IL: Springfield, Riverside Park, south side of river. 7 June 1994. Eight to 10 Cassini-type males singing occasionally. R. D. Alexander and D. C. Marshall. Probably 4-yr-delayed *M. cassini:* This location lies at the border between broods XIII and XIX, but no cicadas emerged here in 1998 with brood XIX (R. D. Alexander and A. F. Richards, University of Michigan, personal communication).

1995

Cook County, IL: Chicago, at Crooked Creek, 30 yards north of 107th Street, 13 June 1995. One or more *M. cassini* male(s) calling occasionally. Tape-recorded. J. R. Cooley and D. C. Marshall. Probably 5-yr-delayed *M. cassini.* Only brood XIII has been recorded consistently from northern Illinois.

Warren County, IL: Near Surrey, southwest of Galesburg, just north of US 34, 2000N and 1560E are the approximate coordinates. 14 June 1995. One *M. cassini* male singing occasionally. Tape-recorded. J. R.

Cooley and D. C. Marshall. Probably 2-yr-premature *M. cassini.* Brood III emerged here in 1997 (R. D. Alexander and A. F. Richards, University of Michigan, personal communication). However, brood XIII populations are not far away.

Piatt County, IL: Near Monticello, IL. Two locations north of town: (1) One *M. tredecassini* male singing occasionally at bridge over Goose Creek, at ≈800N/850E; (2) One or two *M. tredecassini* males singing near Interstate 72/Rt.105 interchange. 16 June 1995 (J. R. Cooley and D. C. Marshall). Tape-recorded at first location. Probably 3-yr-premature *M. tredecassini* from brood XIX, which emerged here in 1998 (R. D. Alexander and A. F. Richards, University of Michigan, personal communication).

1999

Cook County, IL: Flossmoor. Five to 10 nymphal skins and one or more teneral adults observed on 5 June 1999. Susan White.