

Developmental Plasticity of Life-Cycle Length in Thirteen-Year Periodical Cicadas (Hemiptera: Cicadidae)

DAVID C. MARSHALL,^{1,2} JOHN R. COOLEY,^{1,3} AND KATHY B. R. HILL¹

Ann. Entomol. Soc. Am. 104(3): 443–450 (2011); DOI: 10.1603/AN10087

ABSTRACT Speciation in periodical cicadas (*Magicicada* Davis) is closely tied to changes in life-cycle length, which presents a paradox because these organisms depend on emergence synchrony for survival. Recently proposed speciation models invoke developmental plasticity as a possible solution: Environmentally triggered “4-yr accelerations” occur in 17-yr cicadas, suggesting that canalization of induced plasticity could change 17-yr populations into temporally isolated 13-yr populations. However, the reverse shift, 13-yr cicadas emerging in 17 yr, has never been documented. We searched 4 yr after the normal emergence of a 13-yr brood (and in a year with no expected periodical cicada emergences anywhere) and found periodical cicadas active at 26 of 92 sites, with examples of all four 13-yr species. At one location, we found evidence of at least 1,724 cicadas per ha emerging. Few males were heard singing at most sites, so these off-schedule cicadas apparently did not survive long in the face of predation. We also found one 13-yr species singing 8 yr late within the range of a different 13-yr brood, suggesting an 8-yr delayed emergence or consecutive generations of 4-yr-delayed cicadas. Developmental plasticity in life-cycle length seems to be similar in 13- and 17-yr cicadas—both types possess the ability to switch to the opposite life cycle and to emerge 1 yr early and/or late. The confirmation of a reverse life-cycle switch in 13-yr cicadas suggests improvements to theories of life-cycle evolution in *Magicicada* and strengthens the case for developmental plasticity in speciation.

KEY WORDS phenotypic plasticity, speciation, allochronic isolation, predator-satiation, *Magicicada*

The periodical cicadas (genus *Magicicada* Davis, Fig. 1A) of eastern North America are renowned for precisely timed and prime-numbered life cycles of 13 or 17 yr, nearly all spent underground as nymphs, as well as for synchronous emergences of up to millions of adults per hectare (Marlatt 1907, Williams and Simon 1995). Three morphologically, ecologically, and behaviorally distinct 17-yr species each have a phenotypically similar 13-yr counterpart and a fourth 13-yr species completes the genus (Alexander and Moore 1962, Marshall and Cooley 2000) (Fig. 1B). Species of the same life-cycle length always emerge together, and these 17- and 13-yr communities are broken into multiple allochronically isolated “broods” inhabiting largely nonoverlapping geographic regions (Simon 1988, Cooley et al. 2009).

Because sister-species always possess different life cycles (Fig. 1B), speciation in periodical cicadas seems to involve changes in life-cycle length. However, such shifts are difficult to explain because periodical cicadas are “predator foolhardy”—emergences of fewer than thousands of cicadas per hectare seem unable to satiate and survive predators (Lloyd and

Dybas 1966b, Karban 1982, Williams et al. 1993). This dependence on emergence synchrony makes modes of speciation involving small populations or individual life-cycle mutants seem extremely unlikely.

A solution to this problem is suggested by the phenomenon of “straggling” or off-schedule *Magicicada* emergences. Historical records show that 17-yr cicadas sometimes emerge from 6 yr early to 5 yr late, with all three species appearing in some records (reviewed in Marlatt 1907, Maier 1985, Moore 1993, Marshall 2001). Some of these unexpected emergences, particularly those occurring 4 yr prematurely, have involved thousands of stragglers at once (e.g., Dybas 1969). The scale of these larger straggling events is consistent with developmental plasticity in life-cycle length, rather than mutations in life-cycle genes. The causes of mass straggling are uncertain—most studies suggest climate-related triggers (Alexander and Moore 1962, Marshall et al. 2003), but other mechanisms such as widespread fires (Young 1958) and nymphal crowding (Lloyd and White 1976) have been discussed as well.

Developmental plasticity is an important component of some theories of evolutionary innovation and speciation, in part because plasticity can facilitate phenotypic transitions across adaptive valleys (West-Eberhard 2003, Pigliucci et al. 2006). For *Magicicada*, plasticity in life-cycle length may allow population densities to remain high enough for predator satiation,

¹ Department of Ecology and Evolutionary Biology, University of Connecticut, 75 N. Eagleville Rd., Storrs, CT 06268-3043.

² Corresponding author, e-mail: david.marshall@uconn.edu.

³ Department of Evolution, Ecology, and Organismal Biology, The Ohio State University, 318 West 12th Ave., Columbus, OH 43210-1293.

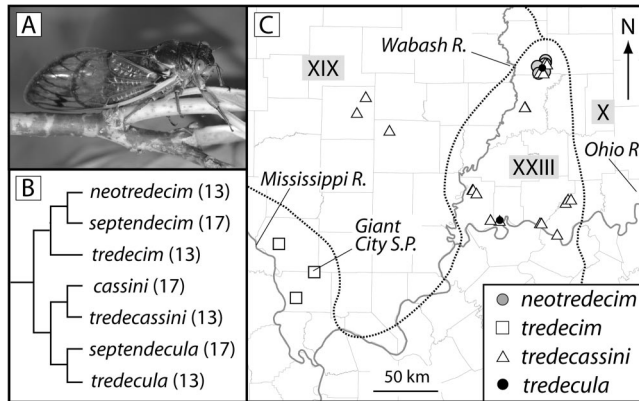


Fig. 1. (A) *Magicicada septendecim* (L.) individual (morphologically similar 17-yr sibling of *M. tredecim* and *M. neotredecim*). (B) Phylogenetic relationships and life cycles of the seven *Magicicada* species based on behavioral, morphological, and genetic data (Alexander and Moore 1962, Williams and Simon 1995, Marshall and Cooley 2000, Simon et al. 2000, Cooley et al. 2001a). (C) Locations of adult 13-yr *Magicicada* observed in southern Illinois and Indiana in 2006. Dotted line approximates the border between 13-yr brood XXIII (last emerged in 2002), 13-yr brood XIX, (last emerged in 1998) and 17-yr brood X (last emerged in 2004). Cicadas observed within the territory of brood XXIII were probably 4-yr late cicadas; those in the range of brood XIX could have been 8-yr late cicadas or 4-yr-late offspring of 4-yr-late parents from 1989.

as long as the cue affects many cicadas at once. Short-term cueing of life-cycle variation (over one or a few generations) should allochronically isolate populations and lead to minimal genetic change—this is presumably how the various 17- and 13-yr broods were formed (Marlatt 1907, Young 1958, Alexander and Moore 1962, Lloyd and Dybas 1966a, Lloyd and White 1976). Sustained cueing of an alternative life cycle over many generations, however, may allow natural selection to canalize the expression of the new cycle, especially if the cue gradually ameliorates (Lloyd and Dybas 1966b, Lloyd and White 1976, Marshall and Cooley 2000, Cooley et al. 2001, Marshall et al. 2003, but see Cox and Carlton 2003).

Climate-triggered developmental plasticity is appealing as a general mechanism for *Magicicada* speciation but for one complication: Although examples of 4-yr-premature 17-yr cicadas have been observed many times, there have been no records of the reverse switch—4-yr-delayed 13-yr cicadas. Even 1-yr premature or delayed emergences are poorly documented for the 13-yr species. This has caused theorists to assume that life-cycle plasticity does not exist in 13-yr cicadas (e.g., Hoppensteadt and Keller 1976) and led to an emphasis on plasticity as a mechanism relevant only for deriving 13-yr species from 17-yr ancestors (e.g., Simon and Lloyd 1982).

A few recent articles (Martin and Simon 1990b, Marshall 2001) have suggested that 13-yr cicadas may be able to prolong development and emerge 4 yr late, mirroring developmental plasticity found in 17-yr cicadas. We tested this prediction in 2006 by searching for adult periodical cicadas at locations where we had observed normal 13-yr emergences in 2002. We selected both the brood (XXIII) and the year (2006, a year with no “scheduled” emergences) to minimize the possibility of coemergence of cicadas from other broods (Table 1). We also searched within the range

of brood XIX, which last emerged in 1998, to check for cicadas appearing 8 yr late.

Materials and Methods

Location of Study. In 2006, we visited 92 sites located within the range of 13-yr brood XXIII, 56 in Indiana and 36 in Illinois (Fig. 1C). The sites were selected to avoid brood overlap zones, by using our detailed emergence maps of the region (Cooley et al. 2009; unpublished data) together with historical records (Marlatt 1907, Stannard 1975, Kritsky 1987, Simon 1988). Three broods occupy nearly exclusive sections of this region. Thirteen-year brood XIX (last

Table 1. Schedule of recent *Magicicada* brood emergences

Yr	17	13
1995	I	
1996	II	
1997	III	
1998	IV	XIX
1999	V	
2000	VI	
2001	VII	XXII
2002	VIII	XXIII
2003	IX	
2004	X	
2005		
2006		
2007	XIII	
2008	XIV	
2009		
2010		
2011		XIX
2012	I	

The 12 extant 17-yr and three 13-yr broods are given Roman numerals according to their relative year of emergence, with the 17-yr numbers beginning with I (through XVII) and the 13-yr numbers beginning with XVIII (through XXX). Broods XI (17-yr) and XXI (13-yr) went extinct in the early 20th century.

emergence in 1998) covers most of southern Illinois but is found in only the southwestern-most Indiana county (Posey Co., Moore 1993). Brood XXIII (last emergence in 2002) is found in Illinois primarily near the Wabash and Mississippi rivers, and in southwestern Indiana. Seventeen-year brood X (last emergence in 2004) borders brood XXIII to the north in Indiana and Illinois. We also opportunistically searched 14 locations in Wayne and Marion counties, IL, for stragglers of 13-yr brood XIX. All sites were sampled only once, by one or more of us.

Sample Methodology. An efficient way to locate cicadas and other singing insects is to drive to selected sites and listen for the songs of males under good conditions for adult cicada behavior (Marshall et al. 1996, Riede 1998, Hill and Marshall 2009). At each site, we listened from the location of our vehicle for 4 min with the car engine off and pinpointed singing individuals to estimate the minimum number of active males. We digitally recorded (when possible) and identified each male to species, by using their species-specific song characteristics (Alexander and Moore 1958, Alexander and Moore 1962, Marshall and Cooley 2000). We also noted any additional males that sang after the 4-min interval while we prepared to depart. We took records only when conditions were appropriate for singing, e.g., temperature $>21^{\circ}\text{C}$ ($>70^{\circ}\text{F}$) or temperatures $>18^{\circ}\text{C}$ ($>65^{\circ}\text{F}$) with full sun and minimal wind (Heath 1964, 1967; Heath et al. 1971). All observations were made from 3 to 5 June 2006, within or just after the period of maximum adult activity observed in the southern Indiana-Illinois region in 2002 and 2004 (unpublished data).

In one location (Giant City State Park, Jackson County, IL) where singing was noted and many *Magicicada* nymphal exuviae were observed, we collected all of the exuviae we could find in a 15.24- by 15.24-m plot that contained 25 trees. Both the tree trunks and the ground around the trees were searched, to a 1-m radius around each tree trunk. The location, a campground, had been recently mowed and the soil was partly bare. We used the exuviae count to estimate a minimum number of straggling cicadas at that site. We also scored the exuviae from that sample, plus a small number of additional exuviae found opportunistically outside the plot, for sex and species, by using calipers—*M. -decim* siblings can be reliably distinguished from *-cassini* and *-decula* siblings using the morphological criteria of Dybas and Lloyd (1974). Exuviae also were collected opportunistically from a second site in Randolph County Conservation Area, IL. Nymphal exuviae and pinned specimens have been deposited at the University of Connecticut Biological Collections Facility.

Equipment. Locations were geocoded with Garmin GPS V or Garmin GPS III handheld GPS units, with the map datum set to WGS84. Records were plotted using ArcGIS 9.3. Digital sound recordings, sampled at 44.1 or 48 kHz, were made using Marantz PMD-670 flash-memory digital recorders and Sennheiser ME-62 omnidirectional microphones installed in Sony PBR-330 parabolic re-

flectors. Dominant frequencies of single-phrase song samples were estimated using Raven Pro version 1.2 (Cornell Lab of Ornithology, Ithaca, NY). Audio files are available from us on request.

Results

Seventeen-Year Stragglers of 13-Yr Brood XXIII.

One or more periodical cicadas were heard singing at 26 of the 92 sites checked within the range of brood XXIII, and each of the four 13-yr *Magicicada* species was heard in at least two locations (Fig. 1C; Table 2). In all, we heard a minimum of 71 periodical cicadas across these locations (all male, because female cicadas do not sing). At 25 of the 26 sites where we heard cicadas singing, we noted one or more males during the 4-min sampling period.

The most commonly heard species was *Magicicada tredecassini* Alexander & Moore (minimum 40 singing males over 20 sites), followed by *Magicicada neotredecim* Marshall & Cooley (Table 2). Three of the four *Magicicada tredecim* (Walsh & Riley) males heard were recorded and their dominant song frequencies were 1.1, 1.18, and 1.20 kHz. In total, 13 *M. neotredecim* males were recorded, nine from within the *M. neotredecim*/*M. tredecim* overlap zone and four from north of the overlap zone. Males within the overlap zone had song frequencies >1.5 kHz, which positively identify the cicadas as *M. neotredecim* (Cooley et al. 2006). The other four had dominant frequencies ranging from 1.38 to 1.45 kHz, as expected from their locations outside the overlap zone.

At four sites, we found evidence indicating mass emergences. At Moody Cemetery in Sullivan Co., IN, scattered *M. neotredecim* males were heard singing in a nearly continuous chorus with few silent moments, and we estimated a minimum of five males singing at any given time. Near the United Methodist Church in Yankeetown (Warrick Co., IN), we heard a continuous low chorus of *M. tredecassini*, with a minimum of 10 males singing at once. More significantly, large numbers of nymphal exuviae were found at two sites. At the campground in Giant City State Park, Jackson Co., IL (where we observed a massive emergence on schedule in 2002), *Magicicada* exuviae were common on and beneath the trunks of trees throughout the woods and on our study plot: 40 exuviae and three isolated wings were found in the 232-m² plot, corresponding to an emergence density of 0.1724 cicadas per m² or 1,724 cicadas per ha. Sex and species counts for these 40 exuviae plus 18 additional exuviae found close to the study plot were as follows: *M. tredecim* or *M. neotredecim*: nine males, 15 females; *M. tredecassini* or *Magicicada tredecula* Alexander & Moore: 16 males, 18 females. The combined sex ratio was not significantly different from 50:50 (binomial one-tailed $P = 0.179$ for observed ≤ 25 when $n = 58$). Only two males (both *M. tredecim*) were heard singing at Giant City State Park during this collection work. Finally, at Randolph County Conserva-

Table 2. Locations and counts of late-emerging 13-yr periodical cicadas in 2006

County	State	Brood	NEO	TRE	CAS	DEC	OTH	Latitude	Longitude
Vanderburgh	Indiana	XXIII			1	1		37.945	-87.647
Posey	Indiana	XXIII			1			37.950	-87.723
Warrick	Indiana	XXIII			2			37.928	-87.311
Warrick	Indiana	XXIII			10			37.926	-87.298
Spencer	Indiana	XXIII			1			37.851	-87.170
Spencer	Indiana	XXIII			1			38.061	-87.096
Spencer	Indiana	XXIII			2			38.082	-87.077
Spencer	Indiana	XXIII			2			38.082	-87.051
Sullivan	Indiana	XXIII	3		2			38.982	-87.256
Sullivan	Indiana	XXIII	5		1			38.982	-87.256
Sullivan	Indiana	XXIII			2			38.967	-87.250
Sullivan	Indiana	XXIII	4					38.967	-87.260
Sullivan	Indiana	XXIII	3			1		38.947	-87.283
Sullivan	Indiana	XXIII			1			38.931	-87.279
Sullivan	Indiana	XXIII			1			38.921	-87.279
Sullivan	Indiana	XXIII	2					38.950	-87.317
Sullivan	Indiana	XXIII	1		2			38.917	-87.307
Sullivan	Indiana	XXIII	1		2			38.921	-87.279
Knox	Indiana	XXIII			2			38.692	-87.429
Knox	Indiana	XXIII			2			38.692	-87.431
Posey	Indiana	XXIII			3			38.150	-87.874
Posey	Indiana	XXIII			1			38.148	-87.868
Posey	Indiana	XXIII			1			38.126	-87.841
Jackson	Illinois	XXIII		2			Exuviae ^a	37.597	-89.186
Jackson	Illinois	XXIII		1				37.779	-89.483
Randolph	Illinois	XXIII					Exuviae ^b	37.972	-89.808
Jackson	Illinois	XXIII		2				37.425	-89.335
Wayne	Illinois	XIX			1			38.538	-88.571
Marion	Illinois	XIX			2			38.758	-88.771
Marion	Illinois	XIX			2			38.654	-88.846

Values are the minimum numbers of males heard singing during a 4-min sampling window. NEO, *M. neotredecim*; TRE, *M. tredecim*, CAS, *M. tredecassini*, DEC, *M. tredecula*, OTH, other records. Brood XXIII cicadas were 4 yr late. Brood XIX cicadas were 8 yr late, or perhaps 4-yr-late cicadas of 4-yr-late parents. These numbers probably represent severe underestimates of the numbers of emerged cicadas as illustrated at two sites where the ground was exposed, allowing the collection of exuviae (see text).

^a Forty exuviae in a 232-m² survey plot.

^b Forty-nine exuviae informally collected.

tion area, IL, 49 exuviae and five isolated wings were observed during an informal search over 25 min. Emergence holes also were noted at both of these latter sites. No singing was heard at the Randolph County site.

Cicada exuviae generally break down within a few months of deposition, and those that remain over the winter seem visually weathered and pick up detritus and spiderwebs (White and Sedcole 1993). All of the exuviae we found were clean and shiny; thus, all of these exuviae were from recent emergences and could not have been left over from the main emergence 4 yr earlier.

Stragglers of 13-Yr Brood XIX. We found evidence of adult periodical cicadas at three of the 14 sites checked within the range of brood XIX, 8 yr after the most recent main emergence. One *M. tredecassini* was heard singing and was audio recorded at Sassafras Point, Sam Dale Lake Conservation Area, Wayne Co., IL. Two *M. tredecassini* were heard singing and were recorded at each of two sites in Marion Co., IL—at Lost Creek on Wilson Rd. and 0.2 miles north of Quail Run Rd. on Kinmundy Rd. (Table 2; Fig. 1C). One of the males at the latter site was captured and pinned. Finally, one *Magicicada* exuvia was found clinging to a tree at Stephen A. Forbes State Park (Marion Co., IL).

Discussion

Evidence for Environmentally Induced 4-Yr-Late Straggling in 13-Yr Cicadas. Seemingly novel life-cycle phenotypes can be explained by mutation of life-cycle genes or by environmental induction of developmental plasticity. Observations of large numbers of cicadas delaying emergence at once are important because they seem to exclude mutation as a possibility. We estimated that a minimum of 0.1724 cicadas per m² emerged at Giant City State Park in 2006. The population density at that site is unknown, but published adult density estimates for *Magicicada* range from ≈ 1 to 372 per m², suggesting that $\approx 0.172-0.00046$ of the adult population emerged 4 yr late. Photographs we took from this campground during the 2002 emergence, which was impressive, show individual trees with hundreds of exuviae on or around them, so the true straggling fraction was probably not on the high end of that scale. Nonlethal mutations have been estimated to occur at a rate of 10^{-6} per replication per locus (Drake et al. 1998) or roughly one mutation per genome per replication (also see Mukai et al. 1972, Baer et al. 2007). The frequency of lethal recessives has been estimated at 1.9 and 1.4 per individual in two fish species (e.g., McCune et al. 2002). For rates such as these to account for the frequency of straggling in

Magicalcada, a large fraction of the genome would have to be directly involved in the genetic architecture of life-cycle length. In addition, mutation does not explain high variation in the incidence of straggling across generations, as implied by “unprecedented” events like the Chicago premature emergence reported by Dybas (1969) (see below). We conclude that such “mass” off-schedule emergences by both 13- and 17-yr cicadas are evidence of induced developmental plasticity in life-cycle length.

Although most direct evidence for life-cycle plasticity derives from observations of mass off-schedule emergences, Karban et al. (2000) experimentally induced a 1-yr acceleration of emergence, in an unspecified species of 17-yr cicada, by accelerating the annual cycle of trees on which nymphs were feeding. Karban's findings strengthen the long-held supposition that life-cycle plasticity in periodical cicadas can be induced by changes in climate, especially temperature (Alexander and Moore 1962, Lloyd and Dybas 1966a, Marshall et al. 2003). For 17-yr cicadas, temperature also is known to influence the specific date of emergence in the 17th yr (Marlatt 1907).

Four-year acceleration in 17-yr cicadas has been observed repeatedly in recent decades (see below), yet our study is the first to document the reverse shift—or any off-schedule emergence involving large numbers of cicadas—in the 13-yr species. Although 13-yr cicadas are not found in the nation's largest eastern metropolitan areas (New York, Chicago, Washington, DC), their geographic range nearly equals that of the 17-yr broods and includes many smaller cities, so detection bias is probably not the reason for lack of reports from the 13-yr species (brood maps can be found in Alexander and Moore 1962 and Simon 1988). It may simply be that the 13-yr species have been less likely to emerge off-schedule during the period of the historical record or that they have tended to do so in smaller numbers. There are almost no published estimates of straggler emergence densities, but anecdotal statements suggest that the off-schedule emergences we observed in 2006 probably involved fewer cicadas than the largest reported “4-yr accelerations” of the 17-yr species. Specifically, Dybas (1969) reported that two young Chicago citizens presented him with a container of 2,350 *Magicalcada* exuviae from the 4-yr-premature emergence of the 17-yr species in 1969, all collected from “a small area”. Zyla (2004) described a collection of 2,908 exuviae taken over a period of 25 d in the yard of a Maryland entomologist 4 yr before an anticipated emergence of 17-yr brood (Marshall et al. 2003) also reports that enough 17-yr cicadas emerged 4 yr prematurely in Cincinnati in 2004 to create “sustained choruses” with mating pairs. As for other forms of evidence, the existence of only four historically well-documented 13-yr broods compared with thirteen 17-yr broods is also consistent with a lower incidence of straggling by 13-yr cicadas. This could be due to reduced developmental plasticity in the 13-yr species or to reduced frequency or magnitude of develop-

ment-influencing cues in areas inhabited by 13-yr cicadas.

Confirmation of the potential for 4-yr delayed emergence in 13-yr cicadas is relevant to recent debate over historical evidence of brood distribution shifts, patterns that have been cited in support of influential theories of periodical cicada ecology and evolution. In one widely cited example (Lloyd et al. 1983), 19th century emergence records from midwestern states were interpreted as evidence for the regional decline and extinction of a 17-yr brood following hypothesized coemergence and hybridization with a competitively superior 13-yr brood (also see Martin and Simon 1988, 1990a; Simon et al. 2000). The existence of the hypothetical 17-yr population was later disputed (Marshall 2001) and the historical records attributed in part to 4-yr delayed emergences by the two 13-yr broods long known from the region (also see Kritsky 1989). At that time, however, no documented examples of multiple-year delayed 13-yr cicadas could be cited.

These results also confirm the high population densities required for predator satiation and successful reproduction in *Magicalcada* (Williams et al. 1993). At the Giant City State Park site, at least 0.1724 cicadas per m² emerged on our study plot, but this value is only approximately one sixth of the lowest published emergence densities, which range ≈ 1.0 per m² (Karbon 1982, Maier 1982, Rodenhouse et al. 1997). If the straggling rate on the Giant City study plot was representative of the local rate, it is remarkable that only two males were heard singing. These observations suggest that natural *Magicalcada* populations with adult densities of 1.0 per m² are perilously close to failing to satiate predators. Furthermore, the observations suggest that many more cicadas had emerged at other sites where we recorded just one or two individuals singing.

Comparing Life-Cycle Spectra in 13- and 17-Yr Cicadas. Considering evidence from emergences of large numbers of off-schedule cicadas, developmental plasticity in life-cycle length seems to be similar in 13- and 17-yr cicadas (Fig. 2). Both types possess the ability to switch to the other life cycle, and both types sometimes emerge 1 yr early and/or late (see references in Fig. 2 legend). For the 17-yr cicadas, recent evidence suggests that induced emergence 4 yr late also occurs. Marshall (2001) (p. 398) reported multiple *Magicalcada cassini* (Fisher) singing at two brood XIII (17-yr) sites in 1994 (near Chicago and Springfield, IL), 4 yr after an emergence of that brood. An emergence large enough to generate chorusing behavior (“some chorusing . . . but not anywhere near the volume or extent that a typical emergence would generate”) was observed at Fontanelle Forest near Omaha, NE, in 2002, 4 yr after the normal emergence of 17-yr brood IV (C. Hensley, personal communication). Brood IV is the only population known from the Omaha area. Emergences after 21 yr have not yet been directly observed in 13-yr cicadas, although Marshall (2001) suggested the possibility from historical emergence patterns. The discovery during this study of *M. cassini* individuals singing (and nymphal exuviae) within the range

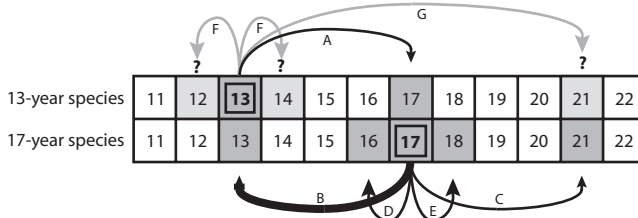


Fig. 2. Evidence for life-cycle length plasticity in 13- and 17-yr cicadas from experiments or from observation of cicadas emerging off-schedule in numbers too large to be plausibly accounted for by mutation. Evidence is limited because most historical records do not include data on emergence density. Overall, the evidence is strongest for 1-yr premature and/or delayed emergences and for jumps of 4 yr. Supporting data for each capital-letter-labeled life-cycle variant are as follows: (A) Data from this study, including specific information for multiple 13-yr species. (B) Many published examples (Dybas 1969, Kritsky 1988, Kritsky and Simon 1996—*M. cassini*, Marshall et al. 2003 citing G. Kritsky—all three species, Zyla 2004), including specific evidence for large numbers of both *M. septendecim* and *M. cassini* in the 1969 example according to Simon and Lloyd (1982). (C) Maier (1985) and multiple unpublished observations (see text). (D) Published observations (Marlatt 1907, p. 24; Boyd 1952) and experimental data (Karban et al. 2000). (E) Published observations including White and Lloyd (1975, 1979), but see Kritsky (2004). Indirect evidence suggesting 1- and/or 4-yr shifts in emergence timing (including F) is found in the biogeography of the various broods of both life cycles, which are generally assumed to have originated via mass shifts in life-cycle timing (Marlatt 1907, Alexander and Moore 1962, Lloyd and Dybas 1966a, Lloyd and White 1976). Eight-year-delayed emergence of 13-yr species (G) has been suggested by Marshall (2001) based on historical data, and it is weakly suggested by our observations of adult cicadas in 2006 within the range of brood XIX.

of brood XIX in 2006, 8 yr after an emergence of that brood, suggests that additional search efforts aimed at uncovering such developmental plasticity would be worthwhile. Multiple-year premature emergence of 13-yr cicadas also has not yet been documented.

Straggling events involving large numbers of cicadas are not well established for differences other than plus or minus 4 yr, for either life-cycle type. White and Lloyd (1979) reported an example of millions of cicadas from brood XIV emerging 1 yr late, but Kritsky (2004) (p. 105) has since argued that the cicadas belonged to a previously unrecognized, disjunct population of 13-yr brood XXII. A review of historical records in Indiana (Kritsky 1987) showed 1- and 4-yr accelerations to be most common in 17-yr cicadas, but most of the records do not include data on emergence density.

Although we did not measure the number of 13-yr cicadas that emerged at our study sites 1, 2, and 3 yr late, a numerical exercise suggests that our 2006 observations probably did not represent the tail end of normally distributed life-cycle variation. Given a mean life-cycle length of 13 yr, an assumption of normally distributed life-cycle variation, and an assumed population density of 200,000 per ha (toward the high end of the published range), an SD of 1.505 is necessary to account for $1,724/200,000 = 0.86\%$ of the population emerging 4 yr late. But under these assumptions tens of thousands of cicadas (21% of the population) would emerge 1 yr late, and 11% would emerge 2 yr late, etc. White and Lloyd (1975) found just 0.7% of 17-yr cicadas emerging in the 18th year in a study plot beneath an apple tree, in an abandoned orchard where they believed delayed development was especially likely. Significantly, when they dug up their study plot in the 19th year they found evidence suggesting a bimodal distribution of emergence times—fifth-instar nymphs, amounting to 1.7% of the population, still in the ground.

Different *Magicicada* species with the same life cycle seem to respond similarly to environmental triggers affecting emergence timing. All three 17-yr species have been observed emerging together after 13 yr, and we observed all four 13-yr species during our search for delayed cicadas in 2006 (see references in Fig. 2 legend). *M. tredecula* was observed only as singletons in 2006, but this may be attributed to the fact that the *-decula* siblings are usually rare compared with the other *Magicicada* species (Alexander and Moore 1962, Lloyd and White 1983). The fact that we heard more *M. tredecassini* stragglers may be due to the louder, higher pitched, and more obvious song of this species. Approximately equal numbers of *M. 13-yr -decim* and *M. tredecassini* or *M. tredecula* were observed in the exuviae counts from Giant City State Park.

Parallel 13- and 17-Yr Developmental Plasticity and *Magicicada* Life-Cycle Evolution. Many evolutionary mechanisms and historical scenarios have been offered to explain the origin of the seven periodical cicada species and their long, prime-numbered life cycles. All begin with a nonperiodical ancestor with a shorter cycle length more like those observed today in other temperate zone cicadas (i.e., up to 11 yr, Karban 1997). Some scenarios derive the first fully periodical 13- and 17-yr forms independently (Cox and Carlton 1988, Yoshimura 1997), whereas others propose the evolution of periodicity first in one form (e.g., a 13-yr ancestor), followed by a life-cycle shift to derive the other form (Marlatt 1907, Lloyd and Dybas 1966a). Developmental plasticity plays an important role in hypotheses of both types, but its generality has been limited by the absence, until now, of evidence that the extant 13-yr species possess latent potential to emerge in 17 yr. For example, Yoshimura (1997) proposed a theory deriving long, periodical life cycles independently during Pleistocene cold shocks that would have nonadaptively extended life length, increased juvenile

mortality, and then selected for strict emergence synchrony as a consequence of lower population density. To account for the two life-cycle types, he proposed a second evolutionary phase in which multiple new life-cycle forms are weeded down to prime-number alternatives by synchrony-disrupting brood hybridization events that preferentially eliminate populations with nonprime cycle lengths (Yoshimura 1997). Although mathematically possible (Yoshimura et al. 2009), the second stage is not well supported by the present-day geography of the various 13- and 17-yr broods, in which populations with different life cycles show only minimal overlap (Williams and Simon 1995, Marshall 2001, Cooley et al. 2009). Instead, Yoshimura's hypothesis can be modified to derive the 13-yr ancestor as originally proposed, but then derive the 17-yr ancestor in one jump through induced and canalized developmental plasticity (Waddington 1953). The same modification can be used to simplify a related scenario offered by Cox and Carlton (1988), which also depends on brood hybridization to weed out nonprime cycles. Furthermore, the observation of developmental delays in 13-yr species means that one need not begin with a 17-yr ancestor and then jump back to 13 (as in Lloyd and Dybas 1966a, Lloyd and White 1976, Simon and Lloyd 1982); thus, whether the most recent common ancestor of *Magicicada* had a 13-yr or a 17-yr cycle remains an open question.

A complete theory of developmental plasticity and speciation must account for the origins of developmental flexibility as well as the details of the speciation process. Few studies have considered the possibility that a general tendency for 4-yr developmental shifts exists in *Magicicada*, as suggested by Fig. 2, probably because evidence for four-year delays of both the 13- and 17-yr species is only now beginning to appear. We need to continue refining our understanding of patterns of life-cycle variation across the seven *Magicicada* species—to determine which phenotypes are possible and what their relative frequencies are, as well as what environmental cues induce them. Information of this sort will help to separate life-cycle switches that are adaptive in origin (Lloyd and White 1983, Martin and Simon 1990b, Simon et al. 2000, Yoshimura et al. 2009), from those that are atavistic (Yoshimura et al. 2009) or predictable side effects of cicada life-history attributes (Karban 1997, West-Eberhard 2003).

Acknowledgments

An anonymous reviewer provided important criticisms and suggestions for statistical characterization of straggling rates. Normal distribution calculations were made with the help of the Finite Mathematics & Applied Calculus Resource Page, copyright Stephen Waner, at <http://www.zweigmedia.com/RealWorld/index.html>. Chris Simon critiqued an early version of the manuscript. Partial support was contributed by the National Science Foundation under grants DEB 04-22386, DEB 05-29679, and DEB-0722101 to Chris Simon (University of Connecticut), and by the National Geographic Society.

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Received 27 May 2010; accepted 19 January 2011.