

## HOLOCENE CLIMATE SHIFTS, LIFE-CYCLE PLASTICITY, AND SPECIATION IN PERIODICAL CICADAS: A REPLY TO COX AND CARLTON

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Periodical cicadas (*Magicicada*), with their unusual life-history mix of long prime-numbered life cycles, synchronized multispecies emergences every 13 or 17 years, and dependence on predator satiation via high adult population densities, present an especially intriguing speciation problem (Williams and Simon 1995). Each of the seven species is most closely related to a geographically adjacent counterpart with the alternative life cycle, suggesting that life-cycle changes may contribute to speciation in the genus. Allochrony, or isolation in time, has been of interest in speciation theory as a means by which populations may become genetically isolated without geographic isolation. However, to be plausible, allochronic speciation scenarios for *Magicicada* must account for the apparently ancient dependence on predator satiation—emergences of periodical cicadas appear unlikely to survive avian predators unless they number many thousands per hectare (Lloyd and Dybas 1966a; Karban 1982; Williams et al. 1993).

The unusual biogeography of the periodical cicada complex both complicates the problem and offers clues (Fig. 1). Three 17-year species coexist in near-perfect sympatry and synchrony across the northeastern United States to the Great Plains. Two of these 17-year species (*M. cassini* and *M. septendecula*) each have one closely related 13-year counterpart (*M. tredecassini* and *M. tredecula*, respectively) (Fig. 1); these 13-year relatives are found in sympatry and synchrony across the southern and midwestern states. The remaining 17-year species (*M. septendecim*) has two close relatives (*M. tredecim* and *M. neotredecim*) which coexist in synchrony with the other 13-year forms, but in only partial sympatry with one another, overlapping along a 50–150-km zone reaching from southern Indiana to northern Arkansas. The 13- and 17-year species groups meet with almost no overlap along a wandering line reaching from coastal Maryland to eastern Oklahoma. Along this line, adjacent populations emerge in synchrony every 221 years. To further complicate the picture, the 13- and 17-year populations have become separated into regionally distinct broods that emerge on different 13- or 17-year schedules; there are twelve 17-year broods (I–X, XIII, XIV) and three 13-year broods (XIX, XXII, XXIII) numbered in order of appearance (brood maps can be found in Simon 1988). Because only minimal differences have been found between cicadas of different broods of the same life cycle, most broods are presumed to have postglacial origins (Wil-

liams and Simon 1995). Recent discussions of life-cycle change in periodical cicadas have involved mainly the two large 13-year broods XIX and XXIII, both of which extend into the Mississippi valley and Midwest.

Debate surrounds the evolution of the recently described 13-year species *M. neotredecim*. In the 1985 emergence of Brood XIX, Martin and Simon (1988, 1990a) discovered that midwestern and southern 13-year cicadas (both then described as *M. tredecim*) differ in both morphology and mtDNA. Cicadas from southern areas of Brood XIX have mostly orange ventral abdominal coloration and a mitochondrial DNA (mtDNA) haplotype that differs in sequence from that of 17-year *M. septendecim* by an estimated 2.6%. In contrast, -decim cicadas from the midwestern part of the 13-year range are indistinguishable in mtDNA haplotype and abdominal coloration (mostly black) from *M. septendecim*. Simon et al. (2000) found the same pattern in northern versus southern -decim populations of Brood XXIII, as well as population phenotypes that suggested overlap, rather than mixing and hybridization, of the two forms in northern Arkansas and southern Missouri, Illinois, and Indiana. Finally, Marshall and Cooley (2000) described this midwestern 13-year -decim form as a new species, *M. neotredecim*, upon discovering that the two kinds overlap in the same region in Brood XIX and possess distinctive calling songs and female song preferences that reproductively isolate them. The southern form retained the name *M. tredecim*. They further showed that the song and preference difference is exaggerated in the area of overlap, in a pattern of reproductive character displacement.

Two historical scenarios for the evolution of 13-year *M. neotredecim* have been offered: a “selective introgression” model proposed by Cox and Carlton (1991, 2003), and a set of “life-cycle shift” models presented by Martin and Simon (1988, 1990a), Simon et al. (2000), and Marshall and Cooley (2000). Both scenarios (1) incorporate well-known evolutionary processes as well as special factors unique to *Magicicada*, (2) invoke climate and habitat change as causal events in life-cycle evolution, and (3) assume that the new 13-year species is recently derived from populations of 17-year *M. septendecim*, based on the lack of divergence in mtDNA and morphology. We argue below that the life-cycle shift models are more plausible and better incorporate related aspects of *Magicicada* biology, such as straggling (off-schedule emergences) and brood-formation.

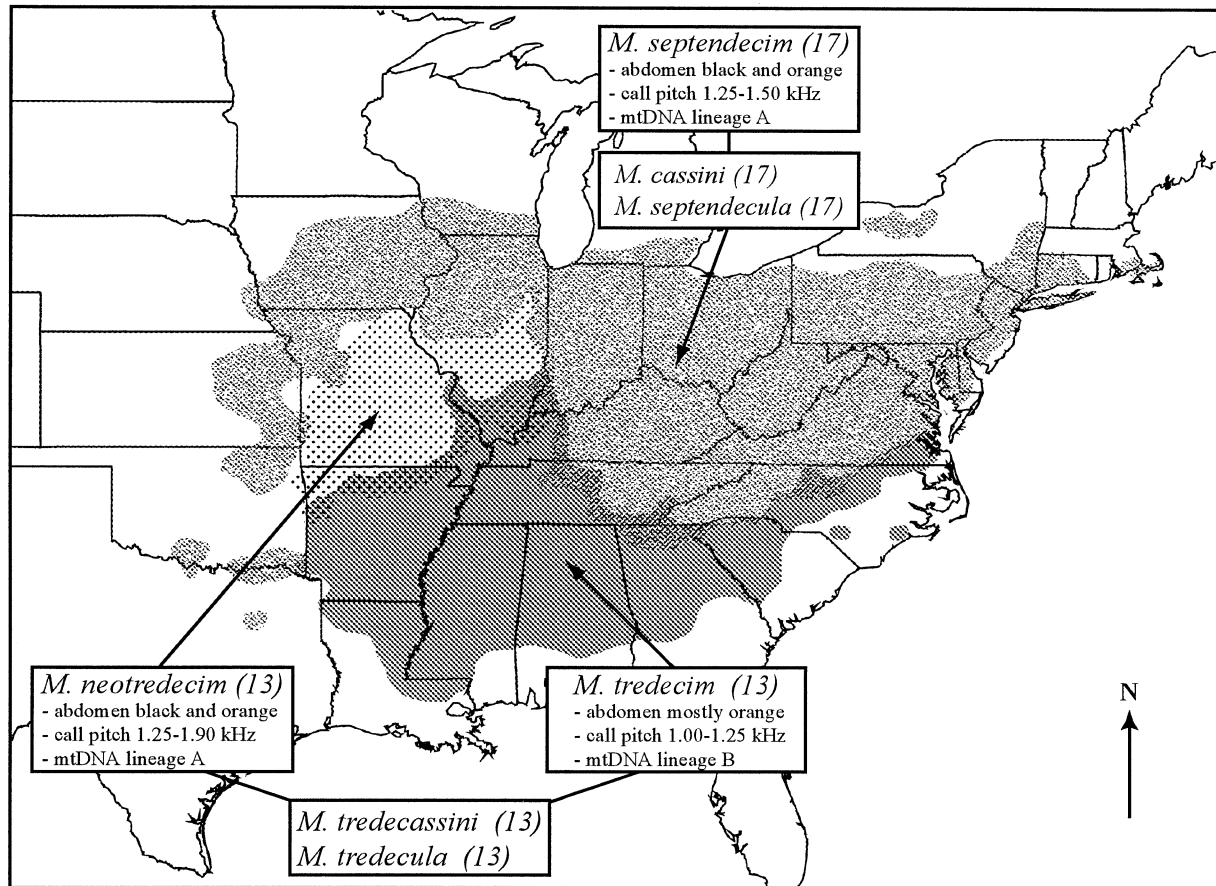


FIG. 1. *Magicicada* species distributions summarized from county-level maps in Simon (1988) and from 1993–1998 field surveys in Illinois. The 17-year species are sympatric except in peripheral populations; *M. cassini* alone inhabits Oklahoma and Texas, while only *M. septendecim* is found in some northern populations (Dybas and Lloyd 1974). Two 13-year species (*M. tredecassini* and *M. tredecula*) are sympatric across the entire 13-year range, while the remaining 13-year species, *M. tredecim* and *M. neotredecim*, overlap only in the central United States. County-level maps overestimate distribution limits, hence the overlap between the 13- and 17-year populations is probably exaggerated. Characters distinguishing -decim species are noted; the -cassini and -decula siblings are distinguishable only by life cycle. Call pitch is the dominant pitch of male call phrase; mtDNA lineage refers to types described in Martin and Simon (1990a).

Marshall and Cooley (2000) and Simon et al. (2000) propose that *M. neotredecim* formed from midwestern populations of *M. septendecim* by a life-cycle shift, and that reproductive character displacement occurred after secondary contact between the new species and its 13-year counterpart. Such a shift could have taken place by cueing of latent phenotypic plasticity in life-cycle length by new environmental conditions, such as a sudden warming (Lloyd and Dybas 1966b; Marshall and Cooley 2000; Cooley et al. 2001), and it could have occurred once over a large area (Marshall and Cooley 2000) or in progressively more northern locations over several co-emergences (Simon et al. 2000). Both 13- and 17-year cicadas exhibit such life-cycle variations today (Martin and Simon 1990b; Marshall 2001), and modern 17-year cicadas seem especially prone to four-year accelerations (Lloyd and White 1976; Maier 1985; Williams and Simon 1995), although such “stragglers” do not usually appear in numbers sufficient to sate predators. For example, in 2000, 17-year cicadas of all three species emerged four years early throughout the range of Brood X and in numbers large enough to form sustained choruses in the Cincinnati area (G. Kritsky pers. comm.); a similar four-year acceleration occurred in the

Chicago area in 1969 (Dybas 1969). If a plasticity-cueing climate shift were to occur rapidly and remain in place for generations, natural selection would favor genes that stabilized or canalized the new 13-year phenotype, particularly if the climate gradually reverted in the direction of the initial conditions (see Fig. 11 in Marshall and Cooley 2000). Such a pattern of change appears to have occurred in midwestern North America during the mid-Holocene (Hypsithermal) (Wright 1976; Webb et al. 1993). Temperatures rose and precipitation fell rapidly about 8000 years ago as the last remnants of the continental glacier vanished and Arctic air masses retreated, and these conditions have been largely maintained to the present, with some gradual amelioration (King 1981; Bartlein et al. 1984). An extreme climatic stimulus might cue large numbers of cicadas to shift, perhaps even enough to satiate predators, but smaller numbers might still survive to found the new species if they repeatedly emerged in synchrony with an overlapping 13-year brood to the south (Marshall and Cooley 2000; Simon et al. 2000; Cooley et al. 2001). Predator protection afforded by a “nurse” brood would thus explain the initial synchrony of

the new 13-year species with one or more of the other 13-year broods to the south.

Simon et al. (2000; see also Martin and Simon 1990b) proposed a different mechanism for the proposed life-cycle shifts—each 17-year female commits a certain fraction of her offspring to a 13-year cycle as a “bet-hedging” strategy, and that co-emergence with an overlapping 13-year brood could shield the new 13-year cicadas from predators. As long as the tendency to produce some 13-year offspring was also passed on, natural selection would tend to canalize the 13-year cycle in these lineages.

While offering little discussion of the above models, Cox and Carlton (2003) re-introduce a hypothesis first offered in 1991 to explain the unexpected patterns in “*M. tredecim*” mtDNA and morphology described by Martin and Simon in 1988, patterns that contributed to the eventual recognition of *M. neotredecim*. They argue that no modification of their 1991 hypothesis is required to account for the findings of overlap between *M. tredecim* and *M. neotredecim* in Brood XXIII as well as in Brood XIX, or the discovery of reproductive character displacement in *M. neotredecim* male song pitch and female pitch preferences.

In the Cox and Carlton (1991) model for the evolution of *M. neotredecim*, hybridization along the western portion of the 13-year/17-year contact zone (occurring progressively farther north every 221 years during local co-emergences) led to selective introgression of a dominant 13-year life-cycle allele from *M. tredecim* into midwestern *M. septendecim* populations, beginning about 8000 years ago with the onset of mid-Holocene warming (see below). This introgression gradually converted those populations into 13-year cicadas, isolating them genetically from other *M. septendecim* populations and synchronizing them with the 13-year broods to the south. In its general form, this model is similar to one proposed by Lloyd et al. (1983), which suggested a recessive rather than dominant 13-year allele. To explain why the 13-year allele migrated northward more than 500 km in the Midwest, but apparently not at all along the remainder of the *M. tredecim*/*M. septendecim* contact zone to the east, Cox and Carlton (1991) propose that a contrast in infection rates by the entomopathogenic fungus *Massospora cicadina* (Soper et al. 1976) may have existed between humid deciduous forests of the south (high infestations) and prairie-savanna habitat of the Midwest (low infestations), but not between southern and northeastern forests. This contrast then set the stage for biased dispersal from the south to the Midwest by 13-year periodical cicadas seeking to avoid infection. They note that the *M. neotredecim*/*M. tredecim* overlap zone matches the mid-Holocene transition between southern deciduous forests and midwestern prairie-savannah—the southern margin of the Prairie Peninsula (Transeau 1935). To account for the lack of northward introgression by 13-year mtDNA, which is inherited through females only, they suggest that the dispersal may have occurred largely in males, citing data showing a greater tendency of males to disperse (Karban 1981; Maier 1982), greater flight abilities of healthy males compared to infected males, and the absence of such superior flight ability in healthy females compared to infected females (White et al. 1983). Finally, Cox and Carlton (2003) suggest a northward spread of humid deciduous forest habitat in the

late Holocene led to northward migration of *M. tredecim* cicadas, and subsequent reproductive character displacement with the new 13-year *M. neotredecim* species.

Cox and Carlton were the first to note the relationships between the range of 13-year *M. neotredecim* and the Holocene paleoecology of the Midwest, and this focus has been a strength of their arguments. However, the *Massospora*/selective introgression model for the evolution of *M. neotredecim* is unnecessarily complicated and depends on too many unlikely circumstances and untested speculations, especially given that the simpler life-cycle shift models can predict similar correlations between Holocene paleoenvironments and the range of the new 13-year species.

The selective introgression model depends on the idea that periodical cicadas can detect high local abundance of *Massospora* and disperse to areas of low infestation before becoming infected. Although Lloyd et al. (1982) speculated on this possibility, they did not explain what proximate cues of local infestation would be available to uninfected cicadas, and they noted that no evidence exists to support or refute the hypothesis. If the evolution of such adaptive dispersal were possible, one would expect both sexes to benefit from such behavior, but the selective introgression model requires that males alone disperse away from areas of *Massospora* infestation. Furthermore, while experimental data do suggest that healthy males disperse marginally farther than healthy females, the hypothesis requires essentially zero dispersal by females because there is no evidence of any northward movement of *M. tredecim* mtDNA; this unrealistic expectation is contradicted by observational data from many sources (Williams and Simon 1995). Furthermore, Cox and Carlton’s additional observation that female periodical cicadas disperse only after mating does not explain why some northward mtDNA migration would not occur via the offspring of dispersing mated females.

Cox and Carlton (1991) admit that the proposed historical pattern of high *Massospora* infestation in the south and low infestation in the Midwest remains entirely speculative as well. But even if this historical pattern is assumed, it does not explain the complete absence of 13-year introgression along the eastern half of the 13-/17-year contact zone. *Massospora* is found today throughout eastern 13- and 17-year populations, and there is no reason to suspect its absence in the past. Because dispersing cicadas cannot “know” whether distant habitat is more or less infested with *Massospora*, one would expect dispersal and 13-year introgression in the east, as well as the Midwest.

Plausible theories of *Magicicada* speciation must be compatible with the unique dependence of periodical cicadas on predator satiation via high adult population density, but this raises a serious hurdle for the selective introgression model. Under this hypothesis, introgression occurs by way of males that move north out of the 13-year/17-year overlap zone during a co-emergence and reproduce within pure 17-year populations. For this to work, dispersing males must find still-unmated *M. septendecim* females (a scarce commodity, since *Magicicada* females mate once; White 1973; Cooley and Marshall unpubl. data) and produce offspring at a rate sufficient for those offspring to satiate predators when they emerge on their own 13 years later—despite presumably costly nymphal

competition from the sympatric 17-year brood (both same- and different-cycle brood overlap is rare; see Williams and Simon 1995). The problem is reduced if one argues that the dispersing males do not move far from the parent 13-year populations, but the approximately 400-km north-south extent of the *M. neotreddecim* range in Missouri requires that at least 650 m of northward dispersal occur in each 13-year generation to create the overlap over 8000 years. In contrast, the life-cycle shift models need only to account for the development of the 150-km *M. neotreddecim*/*M. treddecim* overlap zone. This could have developed over 8000 years with only 200 m of combined *M. treddecim*/*M. neotreddecim* dispersal (consistent with published dispersal estimates; e.g., Lloyd et al. 1982). Furthermore, predator satiation presents no difficulty for the life-cycle shift models since the dispersing cicadas are always sympatric with Brood XIX or Brood XXIII.

One other key requirement of the selective introgression model appears inconsistent with the need for predator satiation in *Magicicada*. To account for the complete absence of *M. treddecim*-like traits other than life cycle in cicadas just north of the *M. neotreddecim*/*M. treddecim* overlap zone, Cox and Carlton suggest that only the 13-year life-cycle allele is favored by selection within a 17-year genetic background. This component of the model implies strong selection against most *M. treddecim* × *M. septendecim* hybrids, but if hybrids are strongly selected against, they are even less likely to emerge in numbers sufficient to cause predator satiation.

We believe that the important paleoecological patterns identified by Cox and Carlton, as well as related patterns of *Magicicada* biogeography and the important phenomenon of frequent accelerations, are better accommodated by our general life-cycle shift model for the evolution of *M. neotreddecim*. Seventeen-year periodical cicadas today exhibit the facultative variation in life-cycle length required by our model, and paleoclimatic data suggest that shifts in Holocene climate occurred in a manner that could have triggered large-scale expression of the latent 13-year phenotype followed by canalizing natural selection. A climate-related trigger occurring over a large region would be expected to incidentally lead to correlations between habitat type and cicada populations that did or did not respond to the cue with a life-cycle shift, in part because the strength of the climate stimulus will be influenced by physical features of the underlying habitat (e.g., elevation, latitude, vegetation type). For example, the mid-Holocene changes in temperature and precipitation caused rapid conversion of forests to prairie in the Midwest (King 1981; Baker et al. 1990). Loss of buffering forests could have amplified the warming stimulus and increased its rate of change for the cicadas occupying the remaining narrow strips of woods along rivers, leading to a correlation between the ancient Prairie Peninsula and the range of the new 13-year species. The greatest problem of our theory is that there is little data available to pinpoint exactly what environmental changes cue straggling events of the sort observed in Brood X in 2000. Anecdotal evidence, such as premature emergences beneath greenhouses and in recently cleared areas (Marlatt 1907), does suggest a role for temperature (see also Heath 1968), but no systematic study has been conducted to relate patterns in straggling emergences to historical weather patterns. It remains possible that other proximate mecha-

nisms, such as bet-hedging (Martin and Simon 1990b; Simon et al. 2000) and underground nymphal crowding (Lloyd and White 1976), may be involved, especially if these mechanisms can be triggered in part by climate changes. Further analysis is also needed to determine if similar phylogeographic patterns are found in the -cassini and -decula siblings, which may have experienced the same historical influences. This theory fits a general class of speciation mechanism (such as some host shifts) in which phenotypic plasticity facilitates initial reproductive isolation of subpopulations that later diverge genetically through divergent natural selection (West-Eberhard 1989, 2002).

## LITERATURE CITED

- Baker, R. G., C. A. Chumbley, P. M. Witinok, and H. K. Kim. 1990. Holocene vegetational changes in eastern Iowa. *J. Iowa Acad. Sci.* 97:167–177.
- Bartlein, P. J., T. Webb III, and E. Fleri. 1984. Holocene climate change in the northern Midwest: pollen-derived estimates. *Quat. Res.* 22:361–374.
- Cooley, J. R., C. Simon, D. C. Marshall, K. Slon, and C. Ehrhardt. 2001. Allochronic speciation, secondary contact, and reproductive character displacement in periodical cicadas (Hemiptera: *Magicicada* spp.): Genetic, morphological, and behavioral evidence. *Mol. Ecol.* 10:661–671.
- Cox, R. T., and C. E. Carlton. 1991. Evidence of genetic dominance of the 13-year life cycle in periodical cicadas (Homoptera: Cicadidae: *Magicicada* spp.). *Am. Midl. Nat.* 125:63–74.
- . 2003. A comment on gene introgression versus en masse cycle switching in the evolution of 13-year and 17-year life cycles in periodical cicadas. *Evolution* 57:428–432.
- Dybas, H. S. 1969. The 17-year cicada: A four-year “mistake”? *Bull. Field Mus. Nat. Hist.* 40:10–12.
- Dybas, H. S., and M. Lloyd. 1974. The habitats of 17-year periodical cicadas (Homoptera: Cicadidae: *Magicicada* spp.). *Ecol. Monogr.* 44:279–324.
- Heath, J. E. 1968. Thermal synchronization of emergence in periodical “17-year” cicadas (Homoptera: Cicadidae: *Magicicada*). *Am. Midl. Nat.* 80:440–447.
- Karban, R. 1981. Flight and dispersal of periodical cicadas. *Oecologia* 49:385–390.
- . 1982. Increased reproductive success at high densities and predator satiation for periodical cicadas. *Ecology* 63:321–328.
- King, J. E. 1981. Late-Quaternary vegetational history of Illinois. *Ecol. Monogr.* 51:43–62.
- Lloyd, M., and H. S. Dybas. 1966a. The periodical cicada problem. I. Population ecology. *Evolution* 20:133–149.
- . 1966b. The periodical cicada problem. II. Evolution. *Evolution* 20:466–505.
- Lloyd, M., G. Kritsky, and C. Simon. 1983. A simple Mendelian model for the 13- and 17-year life cycle of periodical cicadas, with historical evidence for hybridization between them. *Evolution* 37:1162–1180.
- Lloyd, M., and J. White. 1976. Sympatry of periodical cicada broods and the hypothetical four-year acceleration. *Evolution* 30:786–801.
- Lloyd, M., J. White, and N. Stanton. 1982. Dispersal of fungus-infected periodical cicadas to new habitat. *Environ. Entomol.* 11:852–858.
- Maier, C. T. 1982. Observations on the seventeen-year periodical cicada, *Magicicada septendecim* (Hemiptera: Homoptera: Cicadidae). *Ann. Entomol. Soc. Am.* 75:14–23.
- . 1985. Brood VI of 17-year periodical cicadas, *Magicicada* spp. (Hemiptera: Homoptera: Cicadidae): New evidence from Connecticut (USA), the hypothetical 4-year deceleration, and the status of the brood. *J. NY Entomol. Soc.* 93:1019–1026.
- Marlatt, C. L. 1907. The periodical cicada. *U.S.D.A. Bur. Entomol. Bull.* 71:1–181.
- Marshall, D. C. 2001. Periodical cicada (Homoptera: Cicadidae)

- life cycle variations, the historical emergence record, and the geographic stability of brood distributions. *Ann. Entomol. Soc. Am.* 94:386–399.
- Marshall, D. C., and J. R. Cooley. 2000. Reproductive character displacement and speciation in periodical cicadas, with description of a new species, 13-year *Magicicada neotredecim*. *Evolution* 54:1313–1325.
- Martin, A., and C. Simon. 1988. Anomalous distribution of mitochondrial and nuclear gene markers in periodical cicadas. *Nature (Lond.)* 336:237–239.
- . 1990a. Differing levels of among-population divergence in the mitochondrial DNA of periodical cicadas relating to historical biogeography. *Evolution* 44:1066–1080.
- . 1990b. Temporal variation in insect life cycles: lessons from periodical cicadas. *BioScience* 40:359–367.
- Simon, C. 1988. Evolution of 13- and 17-year periodical cicadas (Homoptera: Cicadidae). *Bull. Entomol. Soc. Am.* 34:163–176.
- Simon, C., J. Tang, S. Dalwadi, G. Staley, J. Deniega, and T. R. Unnasch. 2000. Genetic evidence for assortative mating between 13-year cicadas and sympatric “17-year cicadas with 13-year life cycles” provides support for allochronic speciation. *Evolution* 54:1326–1336.
- Soper, R., A. J. Delyzer, and L. F. R. Smith. 1976. The genus *Massospora* entomopathogenic for cicadas. Part II. Biology of *Massospora levispora* and its host *Okanagana rimosa*, with notes on *Massospora cicadina* on the periodical cicadas. *Ann. Entomol. Soc. Am.* 69:89–95.
- Transeau, E. N. 1935. The Prairie peninsula. *Ecology* 16:423–437.
- Webb, T., III, P. J. Bartlein, S. P. Harrison, and K. H. Anderson. 1993. Vegetation, lake levels, and climate in eastern North America for the past 18,000 years. Pp. 415–467 *in*: H. E. Wright, Jr., J. E. Kutzbach, T. Webb III, W. F. Ruddiman, F. A. Street-Perrott and P. J. Bartlein, eds. *Global climates since the last glacial maximum*. Univ. of Minnesota Press, Minneapolis, MN.
- West-Eberhard, M. J. 1989. Phenotypic plasticity and the origins of diversity. *Annu. Rev. Ecol. Syst.* 20:249–278.
- . 2002. *Developmental plasticity and evolution*. Oxford Univ. Press, Oxford, UK.
- White, J. 1973. Viable hybrid young from crossmated periodical cicadas. *Ecology* 54:573–580.
- White, J., P. Ganter, R. McFarland, N. Stanton, and M. Lloyd. 1983. Spontaneous, field tested, and tethered flight in healthy and infected *Magicicada septendecim* L. *Oecologia* 57:281–286.
- Williams, K. S., K. G. Smith, and F. M. Stephen. 1993. Emergence of 13-year periodical cicadas (Cicadidae: *Magicicada*): phenology, mortality, and predator satiation. *Ecology* 74:1143–1152.
- Williams, K. S., and C. Simon. 1995. The ecology, behavior, and evolution of periodical cicadas. *Annu. Rev. Entomol.* 40: 269–295.
- Wright, H. E., Jr. 1976. The dynamic nature of Holocene vegetation: a problem in paleoclimatology, biogeography, and stratigraphic nomenclature. *Quat. Res.* 6:581–596.

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