Periodical cicadas

(Magicicada spp.): A GIS-based map of Broods XIV in 2008 and "XV" in 2009

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The 17-year periodical cicadas (*Magicicada* spp.) of eastern North America are divided into 12 extant "broods" or regional, synchronized emergences defined by year of adult emergence. Most existing brood maps are not GIS-based and consist largely of county-level records derived from 19th-century USDA maps (Fig. 1; Marlatt 1923) whose low resolution limits their utility for testing hypotheses about brood formation and ecology (Marshall 2001). In addition, existing maps often fail to distinguish between typical emergences, which rely on predator satiation and involve densities of tens of thousands to millions of cicadas per acre (Beamer 1931; Dybas and Davis 1962; Lloyd and Dybas 1966; Dybas 1969; Karban 1982a, b; Williams and Simon 1995) and emergences of small numbers of cicadas or scattered individuals, which may be explained as expressions of latent variation in life-cycle length ("stragglers"; Alexander and Moore 1962; Dybas 1969; Marshall 2001). Even though revisions have corrected some mapping problems (Simon 1988; Kritsky 1992; Irwin and Coelho 2000; Cooley et al. 2009), most broods are in need of detailed, GIS-based study.

Of particular interest is Brood XIV, which has a remarkable geographic extent, reaching from New England to Georgia and west through central Tennessee and Kentucky (Marlatt 1923; Simon 1988). It has been suggested that Brood XIV is the source of at least some or all of the other 17-year *Magicicada* broods (Lloyd and Dybas 1966) through a process of brood formation that involves climate-mediated life cycle mistakes occurring on regional scales (Alexander and Moore 1962). However, these hypotheses are difficult to evaluate using outdated maps of Brood XIV. Here we present a newly generated map of the 2008 emergence of periodical cicada Brood XIV. We compare this map to a previously published map of the 2004 emergence of Brood X (Cooley et al. 2009) and other unpublished records of adjoining periodical cicada broods. Using these records, we discuss the nature of apparent brood overlaps and the possible interdependence and intermixing of some populations along brood boundaries, and the pattern of "shadow broods" or populations that are not self-sustaining (Marshall 2001). We conclude with a map of periodical cicada reports during 2009; these records are unequivocally off-cycle stragglers from other broods, since no emergence was expected in 2009

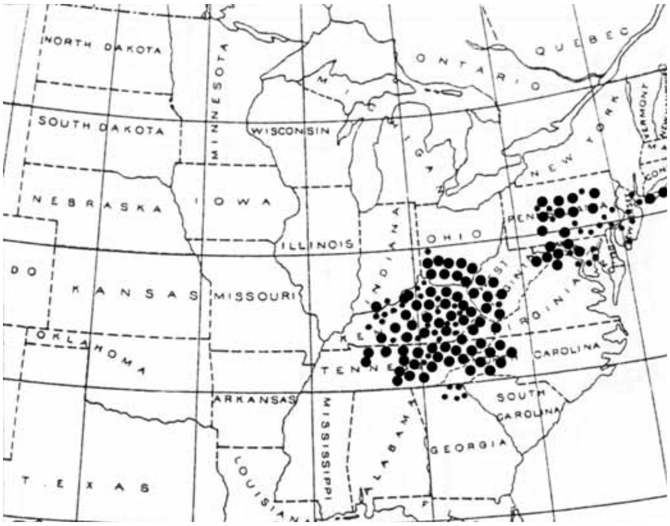

Fig. 1. Existing map of Brood XIV, redrawn from Marlatt (1923) Fig. 17 and Simon (1988) Fig. 1. Larger symbols indicate greater estimated population density.

Methods

Record Criteria. We obtained "field-verified" records by searching for physical evidence of cicadas (emerging nymphs, cast skins, adults, etc.). We also listened for singing cicadas by driving slowly (< 60 km/h) along roads with vehicle windows open, noting chorus densities and species present. Where possible, we estimated chorus densities by categorizing records as single individuals, low-density populations (e.g., only a handful of individuals, or single calls audible), or full emergences (chorusing with individual calls indistinguishable from general chorus sound; if no chorusing, large numbers of individuals visible). We obtained negative records by searching or listening for a minimum of two minutes at appropriate times and under appropriate weather conditions for periodical cicada activity. Even such a short period of listening is sufficient to establish the absence of a typical periodical cicada population because of the densities and high activity levels that occur during a typical emergence (Marshall et al. 1996).

Geographic Sampling. Our search was not exhaustive. Rather than attempting to search the entire historically reported distribution of Brood XIV (Marlatt 1923; Simon 1988), we concentrated our efforts on mapping edges of the brood, locating areas of contact with other broods, and following up on unverified records or reports of periodical cicadas. Because our ability to collect records was strongly affected by weather patterns and emergence phenology, we had no regular sampling scheme; instead, our sampling could best be described as opportunistic, educated by past experience, and guided by reports from the general public.

We collected locality information with handheld GPS units (Garmin, various models). We also collected records using four custom dataloggers consisting of a laptop computer with a GPS antenna attached to the vehicle. At each keystroke, software recorded latitude, longitude, time (GMT), elevation, species present, and chorus density. All GPS units used the WGS84 map datum. When taking records, we noted the time, temperature, and weather conditions. At some locations, we also made voucher collections and recorded choruses using a digital recorder sampling at 48 kHz. The maximum resolution of our data set is 10 m (i.e., no two records are closer than 10 m), but sampling resolution and record density varied across the brood range. These variations should not be taken to imply qualitative differences in the nature of the emergence in different regions. It should also be noted that for any given location, only negative records provide certain evidence that periodical cicadas were absent; the lack of a positive record indicates only that the location was not visited. Records from other broods were collected using similar criteria and methods.

Records from the General Public. In addition to our verified records, we collected "unverified records" submitted by the general public through a Web site (http://magicicada.org) in response to media solicitations. We collected these records during the 2008 emergence of Brood XIV and also during 2009, when no *Magicicada* emergence was expected. Records submitted by the public included locality information, sighting information, and comments. Locality information consisted of a street address, intersection, public park, latitude/longitude, or map location and was automatically geocoded using Google Maps API. Visitors to the Web site were allowed to adjust the geocoded location using a graphical interface prior to final submission. Sighting information consisted of a series of illustrated radio buttons that visitors could choose to indicate quantities or developmental stages of cicadas that they were reporting. Visitors could also include text comments to accompany their reports.

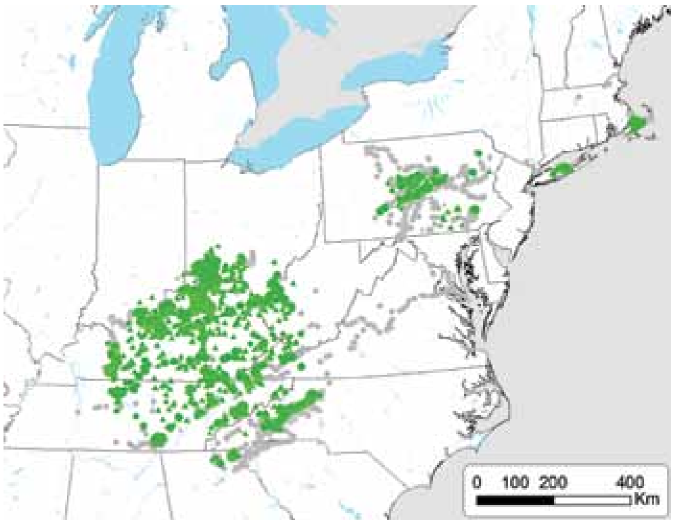

Fig. 2. 2008 Brood XIV records. Circles are verified records; triangles are unverified records submitted by the general public. Green indicates positive (presence) record; gray indicates negative (absence) record. Size of symbol indicates rough estimate of population density.

Duplicate unverified records and records that could not be geocoded based on address information were discarded, as were records that fell outside the known distribution of periodical cicadas (2009 records) or more than 50 km outside the estimated range of Brood XIV (2008 records). To estimate the known range of Brood XIV, we used our 2008 verified records and an additional 57 verified Brood XIV records collected during previous emergences (1974 and 1991). We divided this combined dataset into New England, Long Island, Appalachian, and Ohio Valley regions and constructed four convex hulls encircling all records within each region. We chose convex hulls rather than more stringent detailed hulls, since we could not be certain that we had completely sampled all the edges of the brood. We then added a 50 km external buffer to each convex hull, and we combined the four buffered hulls into a single shapefile used to clip (discard) all unverified records falling outside. All verified records

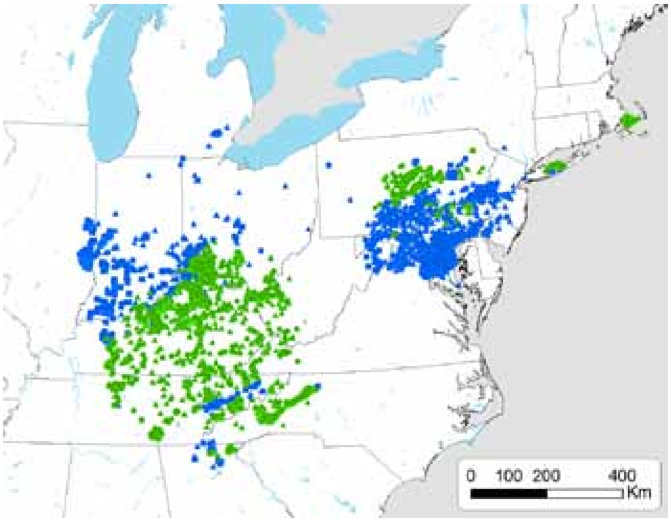

Fig. 3. 2008 Brood XIV records and 2004 Brood X records. Green circles are verified 2008 records; green triangles are unverified 2008 records submitted by the general public. Blue squares are verified 2004 Brood X records; blue triangles are unverified 2004 records submitted by the general public.

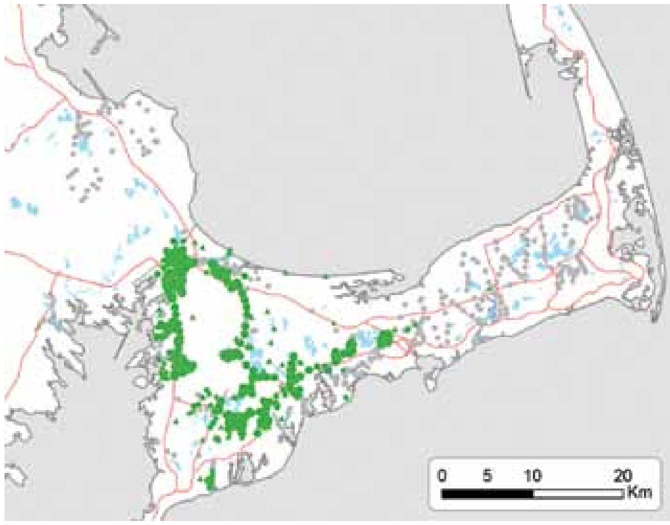

Fig. 5. Plymouth and Barnstable Counties, Massachusetts records of the 2008 Brood XIV emergence. Circles are verified records; triangles are unverified 2008 records. Green indicates positive (presence) record, gray indicates negative (absence) record. Red lines are major roads.

and all unverified records meeting the criteria above were archived in a publicly available database (http://hydrodictyon.eeb.uconn.edu/projects/cicada/).

Results

In 2008, we collected 6,438 positive, verified ("presence") records and 3,075 negative, verified ("absence") records of Brood XIV. The general public submitted 3,139 unique geocodable records. Of these unverified records, 2,081 positive records and 69 negative records fell within the 50 km boundary encircling all 1974-2008 verified Brood XIV records (Fig. 2).

The new Brood XIV records fell into New England, Appalachia, and the Ohio Valley/Cumberland regions, and in some areas, Brood XIV appeared where observations attributed to Brood X had been made in 2004 (Fig. 3). Emergences of Brood XIV in New England were scattered on Long Island and on or near Cape Cod and consisted only of M. septendecim. On Long Island (Fig. 4), some populations, such as those in Brookhaven NY, contained extremely loud choruses and later experienced significant "flagging" or twig death due to female oviposition. In Massachusetts (Fig. 5), most records were in Barnstable County, with few emergences noted east of Hyannis. Appalachian emergences (Fig. 6) were mostly in Pennsylvania's Centre, Clinton, Huntingdon, Mifflin, and Juniata Counties. However, isolated emergences were found in Lackawanna, Berks and Luzerne Counties, PA, and in Washington County, MD.

The largest section of Brood XIV was found in a contiguous region roughly occupying portions of the Ohio Valley, part of the Cumberland Plateau, and the mountains to its south and east. In some parts of LaRue, Nelson, and Bullitt Counties, KY, *Magicicada* choruses were found in locations where single individuals or small numbers of individuals emerged during 2004 (Fig. 7). **[Fig. 7 near here]** In North Carolina and Georgia, Brood XIV emerged within eyesight or earshot

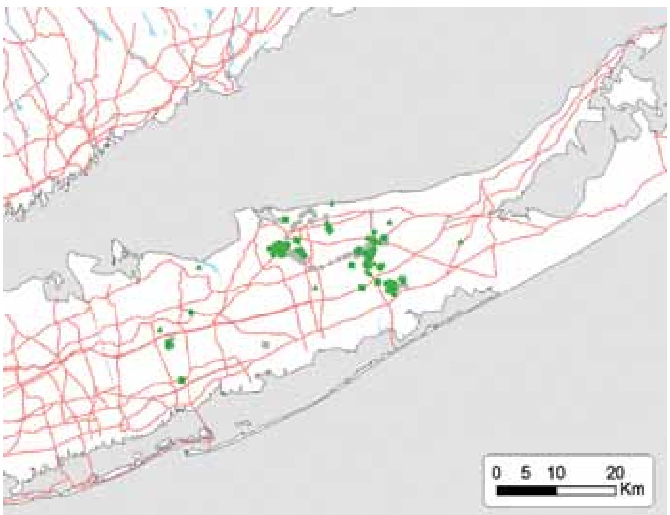

Fig. 4. Suffolk County, Long Island records of the 2008 emergence of Brood XIV. Circles are verified records collected in 2008; triangles are unverified 2008 records. Squares are verified Brood XIV localities from 1974 and 1991. Green indicates positive (presence) record; gray indicates negative (absence) record. Red lines are major roads.

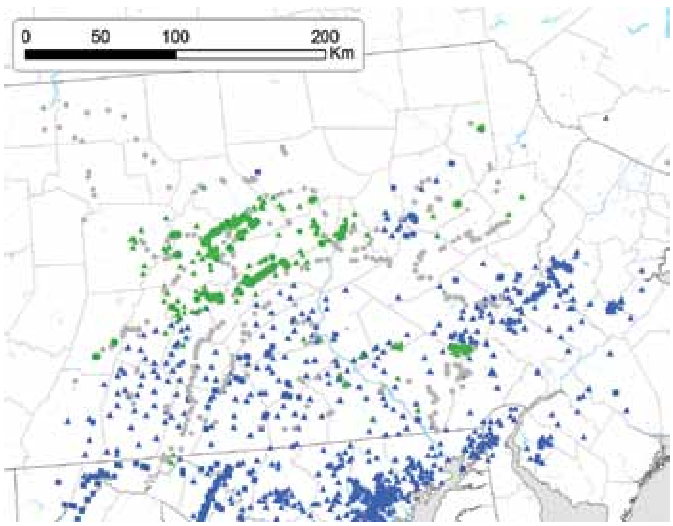

Fig. 6. Appalachian region records of the 2008 Brood XIV emergence. Green circles are verified 2008 records; green triangles are unverified 2008 records submitted by the general public; gray symbols are negative records (absence). Blue squares are verified 2004 Brood X records; blue triangles are unverified 2004 records submitted by the general public.

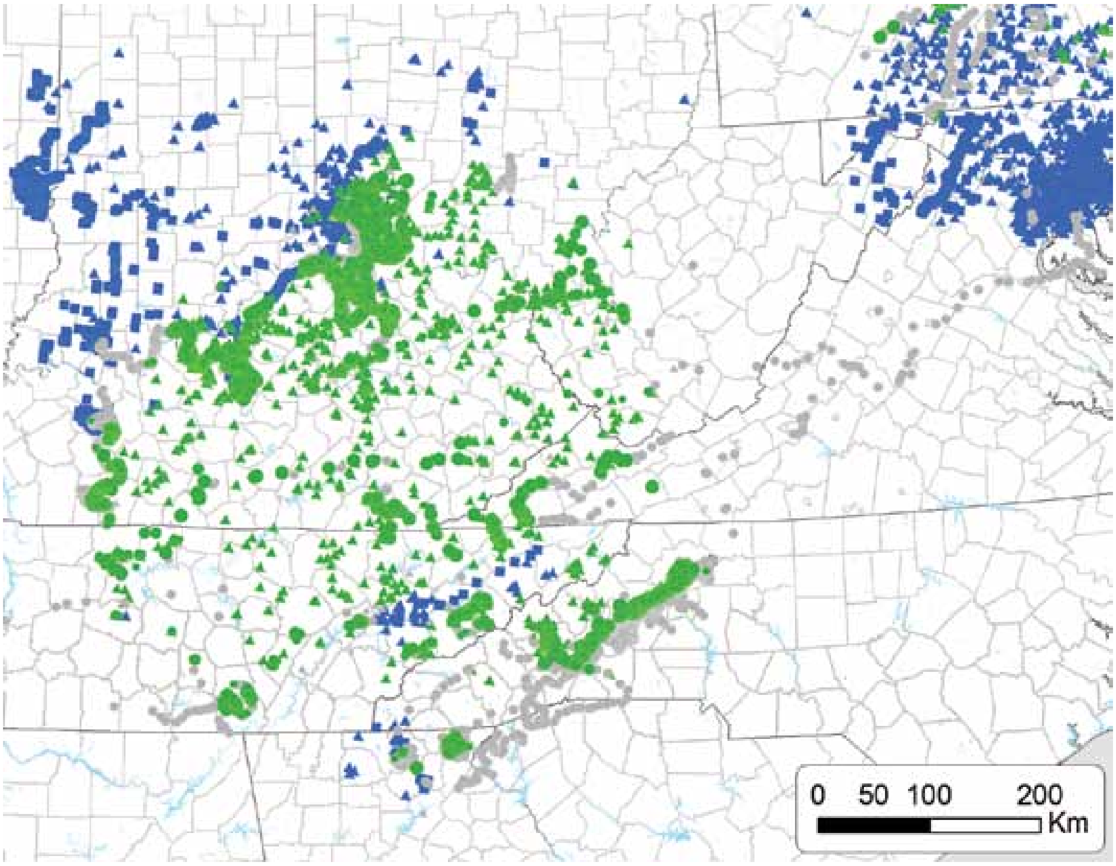

Fig. 7. Ohio Valley region records of the 2008 Brood XIV emergence. Green circles are verified 2008 records; green triangles are unverified 2008 records submitted by the general public; gray symbols are negative records (absence). Blue squares are verified 2004 Brood X records; blue triangles are unverified 2004 records submitted by the general public. The large gap with no records in eastern Ohio, western Pennsylvania, northern West Virginia, Virginia, and North Carolina hosts populations of 17-year Broods I, II, V, VIII, and IX, which will be appearing in 2012, 2013, 2016, 2019, and 2020, respectively.

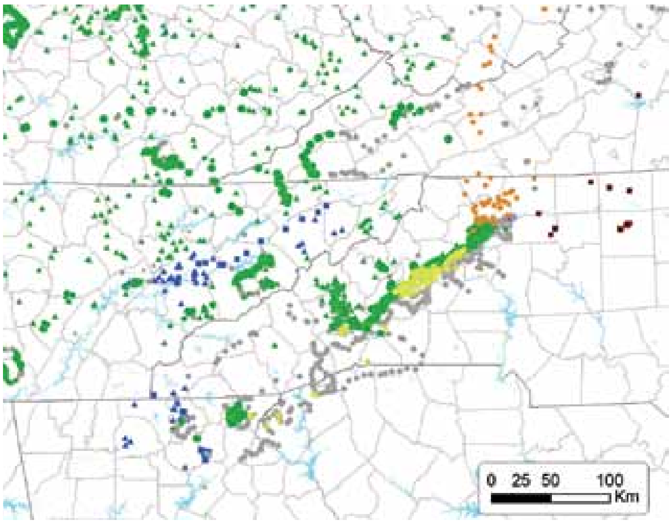

Fig. 8. Detail of Brood XIV map in Kentucky and North Carolina. Green circles are verified 2008 records; green triangles are unverified 2008 records submitted by the general public; gray symbols are negative records (absence). Blue squares are verified 2004 Brood X records; blue triangles are unverified 2004 records submitted by the general public. Also included are verified records from 1995 Brood II (maroon squares), 2000 Brood VI (yellow diamonds), and 2003 Brood IX (orange squares). Major hydrological features shown in light blue.

of locations where Broods VI, IX, and X emerged in prior years (Fig. 8).

During 2009, we received 109 unverified records of periodical cicadas from within the known range of all periodical cicada broods (Fig 9). No brood was scheduled to emerge this year, and most, though not all, of these records were from within the published range of Brood II, scheduled to emerge four years later in 2013 (Marlatt 1923; Simon 1988). Reports from southern states fall within the range of 13-year Brood XIX.

Discussion

The general outlines of our map match earlier maps, with Brood XIV divided into four regions. We found no unequivocal evidence that the range of Brood XIV has changed since it was first mapped, since differences between our map and others can mostly be attributed to differing map criteria and resolution. Intriguingly, Brood XIV appears to be largely absent from Campbell County, KY, where White and Lloyd (1979) reported an unexpected Magicicada emergence in 1975 following the particularly heavy 1974 emergence of Brood XIV in the same area. Cicadas again emerged unexpectedly in this general area 13 years later in 1988, followed by another emergence 13 years after that in 2001 under the same trees marked during the

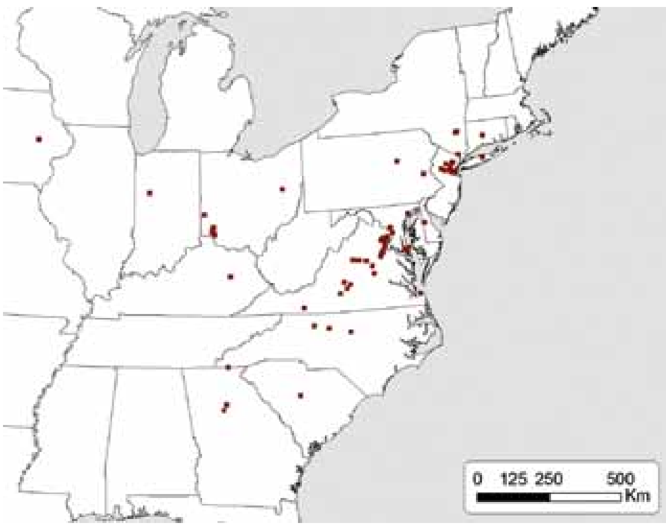

Fig. 9. Records submitted by the public during 2009, a year when no periodical cicada brood emerged.

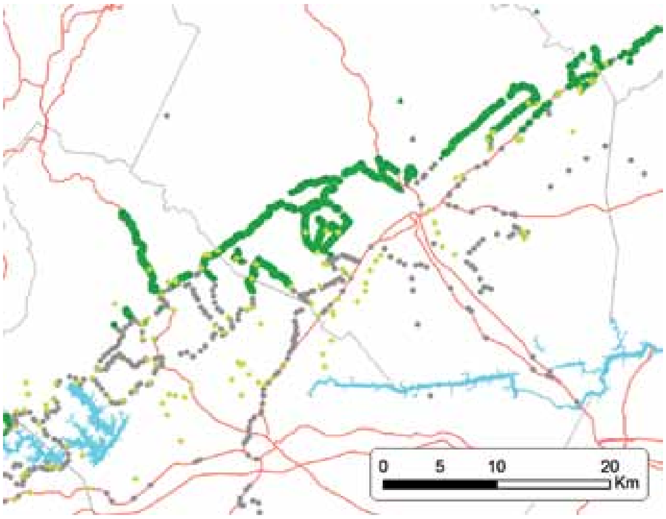

Fig. 10. Detail of boundary between Broods VI and XIV in Burke and Caldwell Counties, NC. Green circles are verified 2008 records; green triangles are unverified 2008 records submitted by the general public; gray symbols are negative records (absence). Yellow diamonds are 2000 Brood VI records. Major hydrological features shown in light blue. Red lines are major roads.

1988 emergence (Kritsky 2004). Historical records suggest past emergences in this area consistent with a 13-year cycle, though these earlier records tend to lack precise locality or date information (Kritsky 2004)[1]. If, in 2014, a population of 13-year cicadas is found to exist in this area, then unlike any other known populations of 13-year cicadas, it would be completely embedded within the general range of 17-year cicadas.

The most southern populations of Brood XIV occur in higher-elevation areas surrounding Lake Burton and near the town of Tiger, in extreme northeast Georgia. A roughly 100 km gap separates these populations from populations that continue northward in the Brushy Mountains towards Elkin, NC (Fig. 7). Between Morganton and Elkin, NC, populations of Brood XIV are within eyesight or earshot of populations belonging to Broods VI, IX, and X, though the broods are mostly parapatric and interleaved, with only slight overlaps (Fig. 10). These extreme southern populations of 17-year cicadas appear to be largely disjunct isolates from the main bodies of their respective broods. Elsewhere, such as on Long Island and Martha's Vineyard, separate populations of *Magicicada* Broods I, V, VIII, IX, X, and XIV have been explained as independently-derived populations synchronous with broods occurring elsewhere (Simon and Lloyd 1982).

Earlier maps show that Broods X and XIV are closely associated, even appearing to overlap over a large portion of Kentucky in some publications (Lloyd and White 1976). Our map shows that Broods X and XIV exhibit sharp, parapatric boundaries in places, while in other places, 2008 Brood XIV records were taken from locations near or coincident with locations where cicadas occurred during the 2004 emergence of Brood X (Kritsky et al. 2009). In a few cases, emergences in both 2004 and 2008 seemed scattered or sparse, such as in Berks and Luzerne Counties, PA (Edwards et al. 2005). Because of the small numbers and scattered nature of the 2004 emergences, Edwards et al. (2005) suggested that the 2004 emergences were likely early stragglers from Brood XIV. But during 2008, emergences in this area were also scattered and not always coincident with 2004 emergence sites. Thus, the precise relationships of the broods in this area are difficult to resolve. More than evidence of brood overlap, they seem to be declining relicts of once-larger populations, similar in some respects to populations of Brood VII further north (Cooley et al. 2004).

In other cases, 2004 emergences attributed to Brood X seemed to be of insufficient density to satiate predators, while sympatric emergences of Brood XIV were regional and characterized by densities of several million per acre (Dybas and Davis 1962). For example, during 2004 in parts of LaRue, Nelson, and Bullitt Counties, KY, scattered cicadas were common enough that it was possible to drive many miles along roads (e.g., KY 61 near Fort Knox) and reliably hear one or a few cicadas at any given location, though never a typical chorus.

[1] The Cincinnati Enquirer reported that cicadas emerged in 1871, but did not include any locality information. Records for cicadas in specific areas in Ohio and Kentucky were reported to the Bureau of Entomology in 1923 and 1936. The 1923 cicadas coincided with Brood XIV, and the 1936 cicadas coincided with Brood X; thus, they were not recognized as remarkable. Periodical cicadas also emerged in 1962, when they were noticed during the construction of the Meldahl Lock and Dam

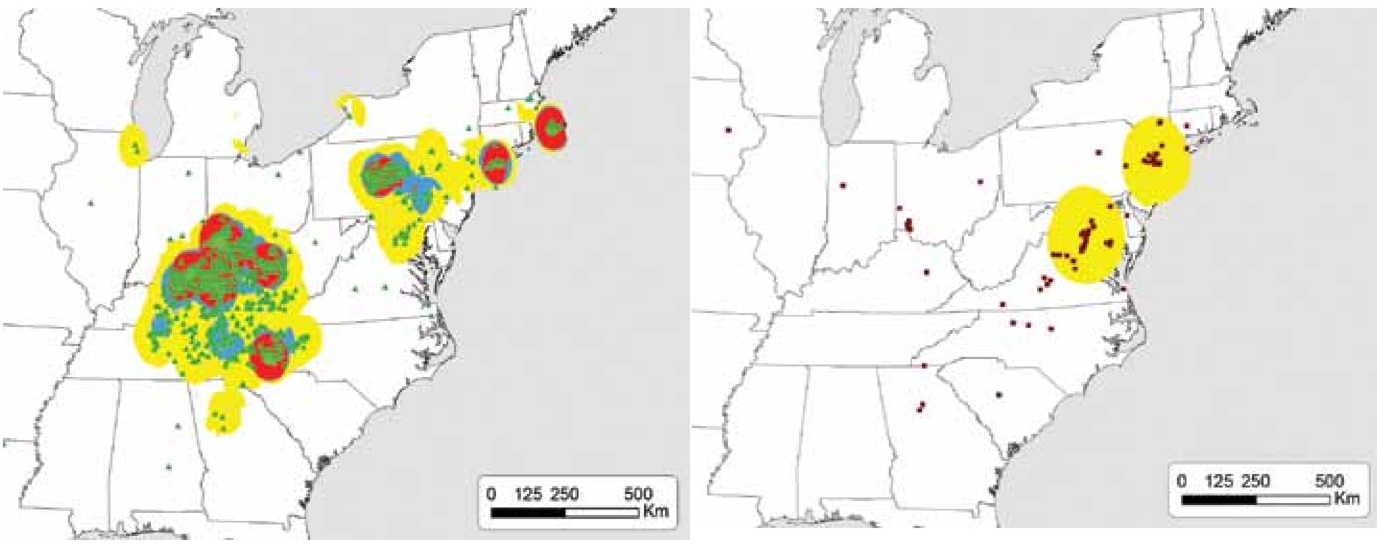

Fig. 11. Point density contours of 2008 (panel A; green triangles) and 2009 (panel B; maroon squares) unedited, unverified reports of periodical cicadas. A circular neighborhood around each record was used to estimate record density. Scale roughly corresponds to quantiles in the 2008 data, although the lower quantile has been adjusted downward. White: Under 3 records/km²; yellow: 3-30 records/km²; blue: 30-50 records/km²; red: more than 50 records/km².

These cicadas were attributed to Brood X, but their unusually low densities were noted (Cooley et al. 2009). During 2008, we found dense Magicicada choruses in these same areas; these clearly belong to Brood XIV.

Are these situations truly evidence of brood overlap? Interpreting sparse, scattered cicadas as self-sustaining populations is problematic, because such emergences should be especially vulnerable to predation (Beamer 1931; Dybas 1969; Karban 1982a, b; Williams and Simon 1995). An alternative interpretation that sparse cicadas are simply coincidentally synchronic stragglers from dense populations of a neighboring brood is also dissatisfying, because such sparse populations were not reported throughout the range of Brood XIV, although it is also true that the entire range was not searched in 2004. One salient feature of the 2004 sparse populations is that they are from areas where Broods X and XIV adjoin.

Historically, the brood concept was a bookkeeping tool for organizing emergence schedules (Fitch 1854), so that any emergence, whether high or low density, was assigned to the brood (or year-class) with which it was synchronized. But this method of brood assignment may not reflect real population structure in Magicicada. Because there is no known method for determining the age of an adult periodical cicada, it is possible that populations in areas of apparent overlap contain adults of different ages and origins. In the case of our reported 2004 Kentucky emergences, some of the cicadas could have been spatial emigrants moving away from the main body of Brood X, while others could have been four-year advance stragglers (or "temporal immigrants") from Brood XIV. If so, then the cicadas emerging at low densities in Kentucky during 2004 would have been a mixed population with members hailing from both Brood X (individuals who emigrated away from the main body of the brood) and Brood XIV (individuals who straggled and were coincident with Brood X).

A hypothesis that these populations are of mixed brood origin requires that four-year advance straggling must be reasonably common among 17-year cicadas. Some indication of the prevalence of four-year advance straggling comes from studies of stragglers (e.g., Dybas 1969; Marshall et al. 2011), as well as from records of cicadas emerging in 2009. Cicadas emerging in this year were members of "Brood XV," a brood that Marlatt noted was apocryphal. Like earlier records of this spurious brood (Simon and Lloyd 1982), most of our 2009 records were from within the territory of Brood II, scheduled to emerge four years later in 2013 (Fig. 9). Thus, the periodical cicadas emerging in 2009 are best explained as four-year early stragglers from Brood II (or, in a few cases, miscellaneous stragglers from other broods), and they are unlikely to be an autonomous, self-sustaining brood for several reasons. First, many of the 2009 records were reports of single individuals or small numbers of cicadas, not enough to effect predator satiation. While some unverified records were of "thousands of individuals," spot checks of these records did not confirm such densities. Second, the individual records from 2009 are widely scattered. To put these records into context, the point densities of records submitted via the Web site in 2008 and 2009 can be calculated and visualized as a contour map. The 2008 contour map shows expected patterns, with greater numbers of records from near major population centers, and with few areas of sparse records within the estimated boundary of the brood (Fig. 11a). This map demonstrates that people affected by a periodical cicada emergence cannot avoid noticing and recognizing them, and that our publicity was effective enough to cause many of those people to report the emergence on our Web site. By contrast, a point density contour map of the 2009 reports shows few areas of dense records, with most records falling into the lowest density categories (Fig. 11b); in fact, point densities of 2009 records throughout most of the range of "Brood XV" were comparable to point densities of 2009 records from the Chicago metropolitan area—cicadas that were clearly two-year-late stragglers from the 2007 emergence of Brood XIII. [Fig. 11 near here] For these reasons, 2009 records are almost undeniably records of stragglers (e.g., "Brood XV" does not exist), and since most are from within the range of Brood II, they are four-year early stragglers. Thus, their existence demonstrates that four-year early straggling is reasonably common in 17-year cicadas.

Cicadas in such mixed "shadow brood" populations can potentially interbreed in spite of their different temporal origins. Unlike sparse populations that have difficulty maintaining themselves over multiple generations in the face of predator pressure, these "shadow broods" would be continually replenished by individuals from two separate source broods. Therefore, these low-density populations may have a capacity for persistence in spite of their vulnerability to predators. In addition, shadow brooding could serve to permit gene flow between broods of the same life cycle, and thus may be a factor in maintaining the relative genetic homogeneity of the 17-year broods (Heliövaara et al. 1994). If "shadow brooding" is a real phenomenon, then other instances, involving other brood pairs, should be discoverable.

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