Periodical cicadas (Magicicada spp.): Predator satiation, or too much of a good thing?

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Periodical Cicadas (*Magicicada* spp.): Predator Satiation, or Too Much of a Good Thing?

John R. Cooley¹,* and Greg Holmes²

¹Department of Ecology and Evolutionary Biology, The University of Connecticut Hartford, 10 Prospect Street, Hartford CT 06103.
²TheLope.com, Hutchinson KS 67501
*Corresponding author: (e-mail: john.cooley@uconn.edu)

Abstract

We report a novel mode of ecdysis failure in periodical cicadas (Hemiptera: Cicadidae: *Magicicada* spp. Davis) tied to the cicadas’ reliance on high densities for survival in the face of predation. Under extremely high densities, cicadas can disrupt others undergoing ecdysis by knocking them loose from their perches, trapping them, or causing physical damage. Our observations raise the possibility that while periodical cicadas thrive at high densities, it is possible that some densities are so high that they inhibit success.

**Keywords:** Periodical cicadas, nymph, crowding, molting, ecdysis failure

The mass emergences of periodical cicadas (Hemiptera: Cicadidae: *Magicicada* spp. Davis 1955) attract widespread attention because of the noise, activity, and sheer numbers of insects present (sometimes between 0.5–1.5 million per acre; Dybas and Davis 1962). Indeed, periodical cicadas generally seem to require high densities, or at least densities sufficient to satiate predators (a “quorum”) as a means to reduce their per capita predation risk (Karban 1982, Simon et al. 2022). Surprisingly, emergences sometimes include large numbers of cicadas that fail to properly complete their final molt. For example, Cory and Knight (1937) found an approximately 31% failure rate during heavy emergences in Brood X cicadas from 1936. White et al. (1979) found that up to 31% of the cicadas emerging in extreme numbers under isolated sugar maples in a suburban lawn during the 1976 emergence of Brood XXIII died from failed ecdysis. These observations suggest that in some circumstances, high densities may be a liability.

At some point prior to molting, likely associated with the appearance of dorsal black thoracic patches, 5th instar periodical cicada nymphs undergo irreversible physiological changes that commit them to ecdysis and impose a time limit on the process (White et al. 1979, Williams and Simon 1995). When a nymph is ready, it exits the ground and starts to climb. The nymph may crawl for quite a while before eventually settling on a perch; once it has done so, it probes with its forelegs (presumably to lock its claws in to the surface) and then walks no more. Molting, or ecdysis, begins when the dorsal surface splits along the midline from the clypeus to the metanotum. The emerging cicada arches its back, pulling its head free from the nymphal skin; then it leans backwards to pull the legs free, after which it bends forward to pull the abdomen free. Once free, the cicada remains on or near its shed skin while it inflates its wings; once the wings are fully inflated, the cicada closes them in typical tent-like fashion over the abdomen (Marlatt 1907, Myers 1929). Throughout this process, the cicada remains callow and pale, dependent on hemolymph pressure to move, expand tissues, and maintain its shape (Saldedo et al. 2023). Once the cicada has taken its adult form, its exoskeleton darkens and hardens; no further changes to body form (other than wear or damage) are possible. During this process, cicadas are vulnerable to predation (Harvey et al. 2006, Nagamine et al. 1975) and if a cicada is knocked off its perch while still callow, the result is fatal.

During the 2021 emergence of *Magicicada* Brood X, we observed a novel kind of interference among nymphs that leaves few obvious traces. We noted that an isolated silver maple in a lawn seemed to be a deathtrap, such that dead or dying cicadas that failed to emerge properly accumulated rapidly on the trunk and around the base. Curious, we watched the tree at dusk. Large numbers of nymphs emerged from the lawn and moved toward the tree. Some crawled far into the canopy, but others did not travel far up the trunk before settling and initiating ecdysis. For those nymphs undergoing ecdysis on the tree trunk, other nymphs encountering them bumped into them or even walked over them,
sometimes knocking them to the ground or sometimes stopping to initiate ecdisys on top of them, trapping them in the process (Fig. 1). More interestingly, we observed that if a crawling nymph walked over another nymph undergoing ecdisys, the crawling nymph’s tarsi often ripped the delicate skin of the molting nymph. Seemingly slight damage could prove fatal, as elevated hemolymph pressure during molting enlarged even small nicks or cuts, leading to significant fluid loss (Fig. 2) and ecdisys failure. Even though the actual immediate damage caused by nymphs crawling over each other may be inconspicuous, the results can be just as fatal as when an interfering cicada traps another or knocks it off its perch.

Nymphs can interfere fatally with each other several ways: They can trap each other (relatively rare), they can knock other off their perches, or they can cause inconspicuous but severe damage that results in fluid loss and molting failure. Each type of interference is expected to leave slightly different evidence: Nymphs that are trapped by others are immediately apparent, because a successfully shed exoskeleton remains atop the trapped nymph; those that are dislodged by others during ecdisys are expected to appear in the litter at the bases of trees, while failures due to puncture damage should remain on their perches. Since Cory and Knight (1937) conducted a survey of nymphs on tree trunks, while White et al. (1979) conducted an overall survey of a suburban yard and did not conduct separate censuses of ground litter and perches, these earlier datasets do not shed light on these different causes of molting failure. Our study, based on our observations above, aims to revisit these earlier observations of molting failure.

**Methods and Results**

We conducted surveys of failed ecdisys at six different locations during the 2021 emergence of periodical cicada Brood X (Table 1). Trees at all sites had strong choruses of periodical cicadas, dominated by *M. septendecim* (L) and *M. cassini* (Fisher; See Marshall 2022 concerning the spelling of *M. cassini*), and all sites were in the later stages of the emergence, so considerable quantities of shed nymphal skins had accumulated over several weeks. Each site was
visited only once, no earlier than midday, so that nymphs that had emerged the night before had completed their molt (or not) and moved on. At each site, we chose a focal tree that was isolated in a mowed lawn and not less than 1.5 m dbh and no shorter than 20 m canopy height.

Litter around the bases of our focal trees contained the shed skins of cicadas that had successfully undergone ecdysis as well as the bodies of dead or dying cicadas that were dislodged during ecdysis (Fig. 3). To census this litter, we constructed a 0.5 m × 0.5 m sampling frame out of stout, flexible cord. To sample, we haphazardly tossed the frame on the accumulated litter already on the ground, squared it up, pinned the corners into the ground, and collected all the material within the frame. We then sorted the material into two categories: “successful” (including successfully shed skins, normal living adults), and “failed” (including failed emergences, dead nymphs, and malformed adults). The number of days and locations suitable for ground sampling was severely limited by the fact that the litter decayed rapidly into a brown mash and it quickly became impossible to sort the material with any confidence.

Table 1. Sampling locations during 2021 Brood X emergence.

<table>
<thead>
<tr>
<th>State</th>
<th>City</th>
<th>Location</th>
<th>Lat</th>
<th>Lon</th>
<th>Date</th>
</tr>
</thead>
<tbody>
<tr>
<td>MD</td>
<td>Flintstone</td>
<td>Post Office</td>
<td>39.70392</td>
<td>-78.5711</td>
<td>31 May 2021</td>
</tr>
<tr>
<td>MD</td>
<td>Flintstone</td>
<td>United Methodist Church</td>
<td>39.70464</td>
<td>-78.5699</td>
<td>12 June 2021</td>
</tr>
<tr>
<td>MD</td>
<td>Cumberland</td>
<td>St. Mary’s Cemetery</td>
<td>39.60342</td>
<td>-78.7357</td>
<td>30 May 2021</td>
</tr>
<tr>
<td>IL</td>
<td>Oakwood</td>
<td>Kickapoo State Park</td>
<td>40.13806</td>
<td>-87.7481</td>
<td>5 June 2021</td>
</tr>
<tr>
<td>IL</td>
<td>Marshall</td>
<td>Lincoln Trail State Park</td>
<td>30.34667</td>
<td>-87.7036</td>
<td>6 June 2021</td>
</tr>
<tr>
<td>PA</td>
<td>Schellsburg</td>
<td>Shawnee State Park</td>
<td>40.03937</td>
<td>-78.6328</td>
<td>28 May 2021</td>
</tr>
</tbody>
</table>

We also sought to quantify instances in which cicadas failed but remained attached to their perches. We quantified these failures by pinning the sampling frame to the trunk of a survey tree at heights of between 2 and 3 meters and counting all the material within the frame, sorting it into the same categories as above. Trees at some of the locations were large enough to permit repeated samples of different locations around a single tree, to reduce the chances that outlier samples would bias our results. At two sites, we also attempted to sample trees along nearby forest edge that were similar to the isolated trees. We had difficulty completing trunk samples on these edge trees because of the lack of cicadas on the tree trunks, and we had difficulty completing ground samples, because of the density of understory vegetation. The results of our surveys are summarized in Table 2. The sample sizes were too small to permit meaningful statistical analysis.

Discussion

Our ground surveys are consistent with those of White et al. (1979) and suggest that crowding and direct interference are substantial problems on isolated trees. White et al. (1979) noted that some instances of faulty ecdysis in periodical cicadas seem clearly attributable to direct interference, such as when crowded nymphs knock each other off their perches, while other instances occur without obvious interference. Because failed nymphs had a lower moisture content than successful nymphs, (White et al. 1979) speculated that deficient nutrition may be the cause of molting failure. However, our observations reveal that failure can also be caused by inconspicuous damage that ruptures the soft skin of molting cicadas, leading to loss of hemolymph, molt failure, and low moisture content.

Ecdysis is a complex and delicate process, and the extremely high stakes involved would seem to provide a context in which selection would minimize fatal errors. Some factors that affect ecdysis, such as temperature or humidity (Cory and Knight 1937, Harvey et al. 2006) are beyond an insect’s control, though they can minimize...
Table 2. Results of our surveys of ground litter and cicadas on tree trunks at several different locations, divided by sample type and sorted in order of decreasing failure rate. Isolated trees were the bulk of our samples; we also attempted to sample similar trees along forest edges, with limited success. For sites in which replicate measurements were made, replicates were combined. “Failure Rate” is number of failed emergences divided by total sample size.

<table>
<thead>
<tr>
<th>Sample Type</th>
<th>Tree Location</th>
<th>Location</th>
<th>Number of samples</th>
<th>Failure Rate</th>
<th>Sample Size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trunk</td>
<td>Isolated</td>
<td>Flintstone Post Office</td>
<td>3</td>
<td>29.3%</td>
<td>82</td>
</tr>
<tr>
<td>Trunk</td>
<td>Isolated</td>
<td>Shawnee State Park</td>
<td>2</td>
<td>28.6%</td>
<td>14</td>
</tr>
<tr>
<td>Trunk</td>
<td>Isolated</td>
<td>Lincoln Trail State Park</td>
<td>1</td>
<td>10.7%</td>
<td>28</td>
</tr>
<tr>
<td>Trunk</td>
<td>Isolated</td>
<td>St. Mary's Cemetery</td>
<td>1</td>
<td>6.0%</td>
<td>50</td>
</tr>
<tr>
<td>Ground</td>
<td>Isolated</td>
<td>Kickapoo State Park</td>
<td>1</td>
<td>65.7%</td>
<td>102</td>
</tr>
<tr>
<td>Ground</td>
<td>Isolated</td>
<td>Flintstone Post Office</td>
<td>3</td>
<td>33.3%</td>
<td>2177</td>
</tr>
<tr>
<td>Ground</td>
<td>Isolated</td>
<td>Lincoln Trail State Park</td>
<td>3</td>
<td>32.2%</td>
<td>841</td>
</tr>
<tr>
<td>Ground</td>
<td>Isolated</td>
<td>St. Mary’s Cemetery</td>
<td>1</td>
<td>20.5%</td>
<td>117</td>
</tr>
<tr>
<td>Ground</td>
<td>Isolated</td>
<td>Flintstone Methodist Church</td>
<td>1</td>
<td>18.8%</td>
<td>442</td>
</tr>
<tr>
<td>Ground</td>
<td>Forest Edge</td>
<td>Kickapoo State Park</td>
<td>1</td>
<td>23.5%</td>
<td>17</td>
</tr>
<tr>
<td>Ground</td>
<td>Forest Edge</td>
<td>Flintstone Post Office</td>
<td>1</td>
<td>0</td>
<td>3</td>
</tr>
</tbody>
</table>

Figure 4. Nymphs and adults in unmown vegetation along the forest edge in Flintstone MD.

The danger by commencing the process only under suitable conditions. Periodical cicadas, however, apparently face an additional hazard related to their reliance on extremely high densities; high densities overwhelm potential predators, but extreme densities create circumstances that lead to high rates of ecdisis failure. The inability of periodical cicadas to avoid such a self-defeating density trap seems odd; many aspects of periodical cicada life history, such as long life cycles, periodicity, “predator foolhardiness” (Lloyd and Dybas 1966), unusually complex mating behaviors (Cooley and Marshall 2001), and optimal reproductive success only at high densities (Karban 1982) seem shaped by a selective context of high densities. Why should ecdisis failure seem so common in these insects, when so many other aspects of their life histories seem attuned to high densities?

White et al. (1979) suggested that high failure rates were an indication that the population they observed was “out of control,” and they may have observed extraordinarily high densities because of their focus on isolated suburban trees with relatively open canopies, which are known to attract cicadas (Yang 2006). This possibility hints at a novel factor promoting ecdisis failure—human development, or more specifically, forest clearing and urbanization. While much discussion of urbanization is centered on studies of climate change (e.g. Chapman et al. 2017), and how it affects species distribution and phenology (e.g. Parmesan 2006, Hill et al. 2011), spatial modifications of the environment may also cause novel problems for some species. The three-dimensional structure of natural landscapes is complex enough that emerging cicada nymphs can spread out, an observation supported by our extreme difficulty conducting meaningful surveys of trees along forest edges (Fig. 4). But structurally simplified habitats consisting of lawns bordered by a few trees can have particularly immediate and fatal effects by concentrating nymphs into small areas (Fig. 3) thereby elevating the risks associated with sensitive parts of their development. We wonder whether such subtle anthropogenic pathologies are more common than is generally appreciated.
Dedication

This note is dedicated to Dr. David Wagner, who has done so much to advance our understanding of how anthropogenic factors affect insects.

Acknowledgments

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Literature Cited


