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Why cicadas (Hemiptera: Cicadidae) develop so slowly

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Cicadas have amongst the longest development times and are also amongst the largest insects. Cicadas feed exclusively on xylem fluid, which is nutritionally dilute and difficult to obtain. One possible explanation for their slow development is that poor nutrition limits their growth rate. An analysis of 30 cicada species with known development times is consistent with this hypothesis as species with more equatorial distributions grew more rapidly than those at higher latitudes. A second possible explanation is that prolonged development maximizes net reproductive rate because there is little risk of mortality once early instar cicada nymphs establish feeding sites. Extended development probably allows nymphs to store resources and produce more offspring. Spittlebugs also feed obligately on xylem fluid and grow at similarly slow rates although they attain small adult sizes. Unlike cicadas, spittlebugs do not have steep survivorship curves and have shorter development times. The life histories of cicadas and spittlebugs are therefore consistent with both hypotheses. Cicada development times may be limited if (1) the risk of nymphal mortality equals increased fecundity associated with prolonging development, (2) fluctuating conditions sometimes favour rapid development times, or (3) host plant quality changes over time and penalizes nymphs that cannot relocate feeding sites.

ADDITIONAL KEYWORDS: body size – Cercopidae – generation time – growth rate – life history – longevity – spittlebugs – survival – xylem feeding.

INTRODUCTION

The generation time of most insects ranges from weeks to 1 year. A short development time to reproductive maturity is expected because it allows insects to reproduce rapidly, and their populations expand exponentially under favourable conditions (Lewontin, 1965). As a group, cicadas fail to fulfil this expectation. They develop slowly and reach reproductive maturity after 1–17 years. After a single episode of reproduction, cicadas die. Early entomologists were sceptical of the reality of a 17-year-long development time. C. L. Marlatt (1907) provided convincing evidence by introducing cicada eggs to uninfested trees in his garden and documenting their emergence 17 years later. Few insects are known to prolong development for this duration and these tend to be associated with extended diapause (Danks, 1992; Heliovaara *et al.*, 1994). The present essay will consider two hypotheses to explain this counterintuitive life history trait of cicadas and will evaluate the evidence supporting each of these explanations.

Two other features of cicada biology are relevant to these hypotheses. Not only are cicadas record holders for prolonged development, but they are also among the largest insects. For example, the giant Malaysian cicada, *Formotosena seebohmi*, is over 7 cm long and has a wingspan exceeding 21 cm, making it larger and heavier than some hummingbirds. Adult cicadas are larger than other Hemiptera, such that most cicada species are much larger than species of related taxa [Novotny & Wilson, 1997; although several relatively small cicadas have recently been described (Ewart, 2018; Bator *et al.*, 2021)]. If large adult body size is selectively favoured, growing large may require a long development time (Karban, 1986).

Cicadas are also unusual in feeding exclusively on xylem fluid (Cheung & Marshall, 1973; White & Strehl, 1978). It is possible that some adult cicadas may also feed on phloem sap although reports of this are unconfirmed. Cicadas share this habit of feeding on xylem fluid with all cercopids (froghoppers and spittlebugs) (Wiegert, 1964) and with some cicadellids (leafhoppers) (Houston *et al.*, 1947; Dietrich *et al.*, 2017). Feeding on xylem fluid is challenging for at least two reasons. First, it is nutritionally dilute,

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with the lowest concentrations of amino acids of the plant foods available to herbivores along with low concentrations of carbohydrates (Anderssen, 1929; Wiegert, 1964; Cheung & Marshall, 1973; Mattson, 1980; Raven, 1983; Dafoe & Constabel, 2009). Xylem-feeding insects compensate by processing large volumes of fluid through their digestive tracts. Second, xylem fluid is under tension or negative pressure as it moves up the plant (Raven, 1983). Extracting xylem fluid is energetically expensive and requires large cibarial muscles to pump against the negative pressure gradient (Novotny & Wilson, 1997).

NUTRITION LIMITS GROWTH RATE AND PROLONGS DEVELOPMENT

INTRASPECIFIC COMPARISONS

Growth rates of cicadas may be constrained because they are feeding on nutritionally poor xylem fluid (Lloyd & Dybas, 1966; Karban, 1986). Because root xylem fluid is under strong negative pressure under most circumstances, it is expensive and difficult to extract; this may limit the time when feeding is energetically profitable or even possible, particularly for early instar nymphs (Novotny & Wilson, 1997). For example, a xylem-feeding leafhopper was only able to extract xylem fluid during those times when pressures were less negative than 2.1 MPa (Andersen *et al.*, 1992). We know very little about when and at what rates cicada nymphs feed and grow. Cicada nymphs extract xylem fluid from small rootlets of their host plants, and plants may shed rootlets that lose too many nutrients or water to cicadas (Lloyd & Dybas, 1966; Addicott, 1982). A small cicada nymph associated with a rootlet that has been shed probably faces an energetically expensive and dangerous task of finding a new feeding site. However, I failed to find any evidence that feeding cicada nymphs caused abscission of rootlets (Karbon, 1985).

If cicada growth is limited by feeding on xylem fluid that contains few nutrients, then experimentally fertilizing their host plants should result in more rapid growth and shorter development times. Several fertilization experiments have been conducted involving intraspecific comparisons in fertilized and unfertilized conditions. When *Mogannia minuta* grew on its native *Miscanthus* grass host, most individuals required 3 years to complete development, but when they grew on fertilized sugarcane, most individuals matured in 2 years (Ito & Nagamine, 1981). Similarly, when *Diceroprocta apache* was grown on its unfertilized native hosts, most individuals required 3 years to complete development, but most individuals became adults on fertilized asparagus after two growing seasons (L. D. Anderson and E. L. Nigh, pers.

comm.). The Japanese cicada, *Cryptotympana facialis*, exhibited a median development time of 8 years when raised on native plants in outdoor cages, but only 5 years when raised on fertilized potted aloe plants (Numata and Shiyaki, 2007 reported by T. Sota).

Experimental fertilization increased the mean size of *Cicadetta calliope* adults of both sexes and of *Tibicen aurifera* females (Callaham *et al.*, 2002). Unfortunately, development time was not determined in that experiment. Researchers who have dug up cicada nymphs have observed that larger nymphs were associated with better feeding sites in orchards (White & Lloyd, 1975). Late instar *Magicicada septendecim* nymphs were larger beneath fertilized apple trees than from adjacent unfertilized forest trees (Maier, 1980; White & Lloyd, 1985). These fertilization experiments confirm the expectation that nutrition may limit cicada growth rates.

INTERSPECIFIC COMPARISONS

Often trends in life history traits are more visible in comparisons among species because the range of variation is greater than can be found within a species. If development of cicadas is limited by nutrition, we might expect that species living closer to the equator will grow more rapidly than species at higher latitudes. The rationale for this expectation is that the growing season is longer at lower latitudes, allowing cicadas to feed actively for a longer period each year. There are now 30 cicada species for which the development time is known (Supporting Information, Table S1), nearly double the number of species in a previous analysis (Karbon, 1986). There are three species of *Magicicada* that require 17 years to develop and four that require 13 years (Simon *et al.*, 2022). Development times for these species cannot be considered as independent observations so the seven species are included as only two data points.

For those species for which reliable information about development time was available, I acquired a range of body sizes from the literature or from museum specimens (Supporting Information, Table S1). I used body length, which varies more than estimates of hard morphological features such as wing length or mesonotum width. However, body length scales isometrically with both of these measures for cicadas (Novotny & Wilson, 1997). Growth rate was calculated as body length/development time.

Cicada species grow faster at lower latitudes [Fig. 1, Kendall's rank correlation, $N = 25$, Kendall's tau = -0.306 , $P = 0.035$ (R module rwasp-Kendall; Wessa, 2021)]. Higher temperatures and a longer growing season presumably allow individuals to feed over a longer period of time and to grow more rapidly. This trend is also exhibited by the seven species of

periodical cicadas in the genus *Magicicada*; the four species that develop in 13 years grow faster and are generally found at lower latitudes than the three species that develop over 17 years at higher latitudes (Koyama *et al.*, 2015; Simon *et al.*, 2022).

As mentioned above, cicadas are much larger than other related hemipterans and are among the largest insects (Lloyd & Dybas, 1966; Novotny & Wilson, 1997). Many insect species and other ectotherms exhibit a pattern termed the converse Bergman's Rule in which larger individuals are found at lower latitudes (Mousseau, 1997). For the species in my analysis, cicadas failed to show a significant relationship between latitude and body length (Fig. 2, Kendall rank correlation, $N = 25$, Kendall's tau = 0.030, $P = 0.85$). Among the *Magicicada* species, there was a significant trend for cicadas from lower latitudes to be larger, although this effect was slight (0–2%) (Koyama *et al.*, 2015; Beasley *et al.*, 2018).

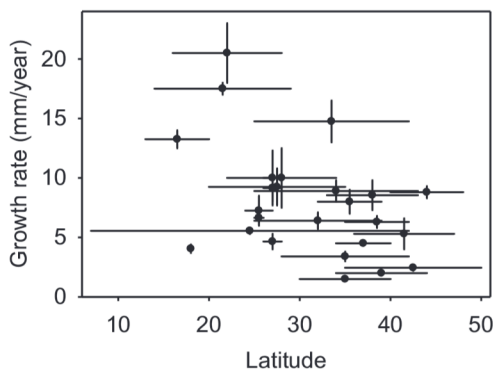


Figure 1. The relationship between cicada growth rate and latitude for each species for which development time is known. The bars show the range of values and points show the median of that range for each species.

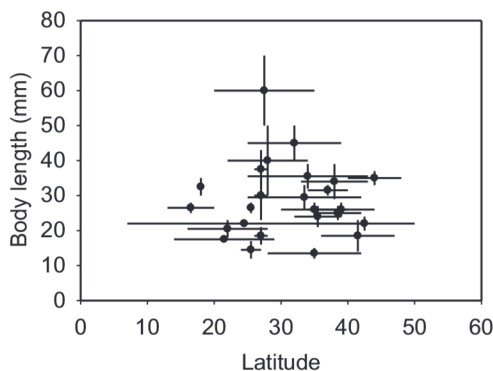


Figure 2. The relationship between cicada adult body size and latitude. The bars show the range of values and points show the median of that range for each species.

Presumably, selection for large body size applies to cicada species generally. Several factors may contribute to this hypothetical selection. Novotny & Wilson (1997) concluded that larger cicadas are more energetically efficient at extracting xylem fluid than smaller xylem feeders. Larger cicadas have lower cibarial pump loads and feeding does not require as much suction pressure per unit of body volume. In addition, large adult size in females has been correlated with greater fecundity in many insects (Honek, 1993). This linear relationship is likely to apply to female cicadas although I am not aware of any data to evaluate this hypothesis. Male cicadas attract mates by drumming or vibrating their tympana (singing) and cicadas are also the loudest insects (Pringle, 1957). Large body size allows male cicadas to be louder and presumably more attractive (Lloyd & Dybas, 1966). Larger males are able to produce lower frequency songs which carry farther than songs produced by smaller individuals (Bennet-Clark & Young, 1992). Larger *Magicicada cassini* males were more likely to copulate with conspecific females than smaller individuals (Karban, 1983), although this trend has not always been found (Cooley & Marshall, 2004).

If there is strong selection for body size, we would predict that large body size might be favoured independent of effects on development time. Body size was not significantly related to development time for the species with known development requirements (Fig. 3, Kendall's rank correlation, $N = 25$, Kendall's tau = 0.269, $P = 0.08$). This counterintuitive result suggests that growth rates are constrained by feeding on xylem fluid and/or that selection for large body size may be stronger than selection for shorter development time (see arguments above).

The hypothesis that growth rates are constrained by poor nutrition also predicts that species that

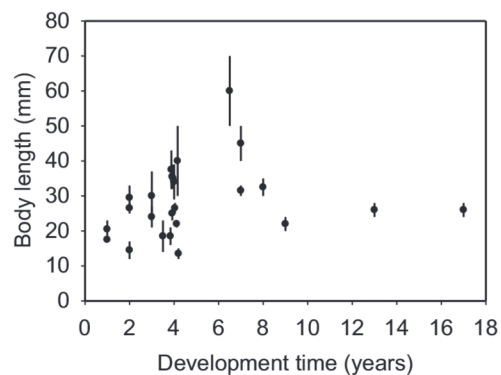


Figure 3. The relationship between adult body size and development time for each species for which development time is known. The bars show the range of values and points show the median of that range for each species.

grow more slowly will take longer to mature. This expectation was confirmed; species that took longer to develop grew more slowly than species that matured over a shorter period (Fig. 4, Kendall's rank correlation, $N = 25$, Kendall's tau = -0.626 , $P < 0.001$). This argument assumes that large adult size is generally favoured. This pattern was also observed for the seven *Magicicada* species as the 17-year species grew more slowly but attained approximately the same size at maturity as their 13-year counterparts in similar habitats (Koyama *et al.*, 2015).

DEMOGRAPHIC TRADEOFFS FAVOUR PROLONGED DEVELOPMENT

The fitness of individuals with different traits, in this case different development times, can be compared by calculating the net reproductive rates R_0 associated with those traits. Because cicadas have only one bout of reproduction at adulthood, net reproductive rate is the product of an individual's probability of surviving to reproductive age (l_a) and its fecundity at that age (m_a). So, $R_0 = l_a \times m_a$ for any development time or age a that is required to reach adulthood. Prolonging the time to reproduce (a) is expected to reduce survival (l_a) because staying alive longer always entails some risk. However, prolonging development is also expected to increase fecundity (m_a) because extra time to feed allows females to produce and provision more eggs. As long as the population is neither increasing nor decreasing on average, any age that maximizes R_0 should be favoured by natural selection (Mertz, 1971; Caswell, 1982; Karban, 1997).

For cicadas and many other insects, the early stages of development are extremely dangerous. Newly hatched cicada nymphs are small, soft, and relatively defenceless against desiccation and predation.

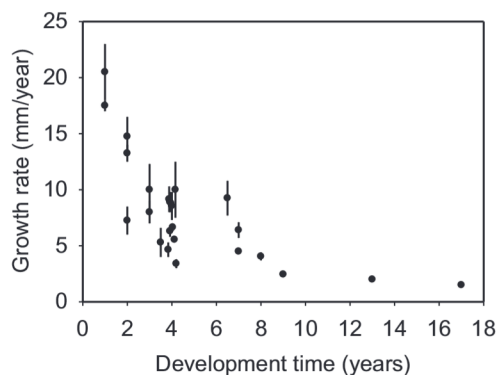


Figure 4. The relationship between growth rate and development time for each species for which development time is known. The bars show the range of values and points show the median of that range for each species.

Neonate nymphs burrow through the soil in search of a host rootlet into which they insert their stylets and pump xylem fluid against negative tension. Most individuals failed to successfully establish during this developmental phase for those cicada species that have been studied. For *Mogannia minuta* in sugarcane fields and native grasslands in Okinawa, Japan, survival of first instar nymphs was $<5\%$ (Fig. 5; Ito & Nagamine, 1981). Predation by ants and spiders was responsible for much of this early mortality. Once established, the risk of mortality was relatively low although a fungal disease, insect predators and heavy rains killed a small fraction of later instar nymphs. No information about age-specific fecundity was available for *Mogannia minuta*. A similarly steep survivorship curve has been reported for *Amphipsalta zealandica* reared on potted kiwi, ryegrass and dock (Logan *et al.*, 2014). When first instars were experimentally introduced to host plants, mortality ranged between 76 and 87% over the next 240–345 days, and this is probably an underestimate given that mortality that normally occurs during egg hatching and nymphal establishment was not included.

The survivorship curve for *Magicicada septendecim* is also steep with an estimated 95% of nymphs that hatched dying within their first 2 years (Fig. 6; Karban, 1997). Extending development from 13 to 17 years was associated with an increase in mortality risk of 29%. By comparing the weight of ovaries for individuals from a 13-year cohort and a 17-year cohort from similar habitats and latitudes, I estimated the increase in fecundity associated with extending development. For *Magicicada septendecim* and *M. cassini*, four extra years of feeding was associated with 16 and 80% greater fecundity, respectively (Karbon, 1997). As long as the increase in fecundity exceeds the increase in mortality associated with prolonging development, a

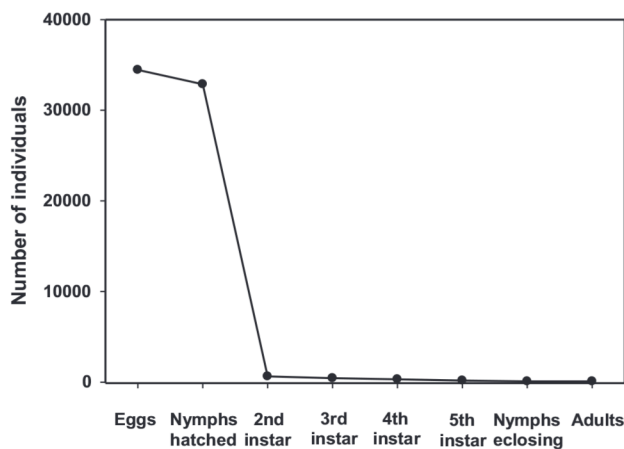


Figure 5. A survivorship curve for *Mogannia minuta*. Data are from Ito & Nagamine (1981).

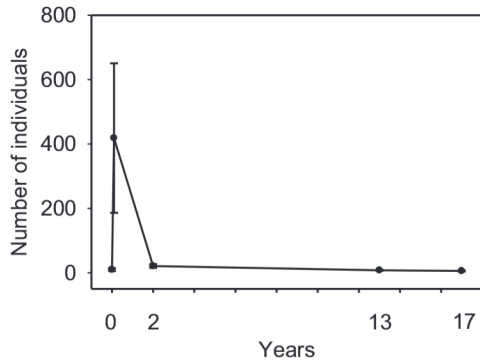


Figure 6. A survivorship curve for *Magicicada septendecim* (mean + 1 SE). Data are from Karban (1997).

demographic model predicts that natural selection can favour extending development times. It is unfortunate that age-specific estimates of fecundity are so difficult to obtain and therefore uncommon. The estimates for *Magicicada* species are consistent with the hypothesis that the tradeoff between survival and fecundity may have selected for prolonged development.

The situation for *Magicicada* spp. is unique because these species emerge synchronously in large numbers only once every 17 or 13 years at any site (Marlatt, 1907; Lloyd & Dybas, 1966). This life history allows them to satiate predators such that adult survival is greatest at sites with high densities (Karbon, 1982). Because nymphs develop at very different rates in a single locality (White & Lloyd, 1975), a long development time allows faster developing individuals to wait for slower individuals to catch up so that density at emergence and survival are maximized (Lloyd & Dybas, 1966; Martin & Simon, 1990). This situation provides an additional advantage that could have favoured long development time although this explanation would not apply as well to other cicada species that are not periodical.

COMPARISONS WITH OTHER XYLEM-FEEDING HEMIPTERA

Although xylem feeding is uncommon among insects, cercopids (spittlebugs) and a few leafhoppers (Cicadellini) also feed on this resource. Adult spittlebugs are smaller than cicadas but are still much larger than related phloem-feeding taxa (Novotny & Wilson, 1997; Dietrich *et al.*, 2017). Many spittlebugs complete their life cycles in a single year and some species complete several generations per year. This observation led Slansky (1980) to reject the hypothesis that xylem feeding led to prolonged development in cicadas because xylem is a poor source of nutrition that is difficult to extract. Two other facts are relevant

in considering Slansky's objection. First, cicada nymphs are much less mobile and therefore cannot easily choose among different sources of nutrition (hosts) compared to above-ground spittlebug nymphs (White & Lloyd, 1985). Second, the growth rates for the faster developing cicada species are now in line with those achieved by spittlebugs (compare Supporting Information, Table S1 for cicadas and Karban, 1986 for spittlebugs). As such, Slansky's argument that cicadas are slower developing no longer holds. In the future, it might be informative to compare leafhoppers that feed on xylem and phloem. A preliminary analysis of limited taxa failed to show differences in growth rates associated with these feeding habits (Novotny & Wilson, 1997).

For those few cicada species for which we have data, survival curves are very steep with very high rates of mortality early in life (Figs 5, 6). As a result, cicada nymphs suffer little risk of mortality as they feed underground and store resources that can be turned into eggs. This is not true for the few spittlebug species for which similar data are available. The probability of mortality was relatively constant (the survival curve was closer to linear) for *Neophilaenus lineatus* at two sites in England (Whittaker, 1971) and for *Philaenus spumarius* at two sites in North America (Wiegert, 1964). This implies that it is relatively riskier for spittlebug nymphs to prolong development compared to cicadas, and this observation is consistent with the hypothesis that demographic considerations favour prolonged development in cicadas, but not in spittlebugs.

WHAT LIMITS DEVELOPMENT TIME IN CICADAS?

The hypotheses that have been explored in this paper suggest that selection could favour prolonging development times either because growth rates are limited by poor nutrition and there is a premium on large body size or because prolonged development allows individuals to increase fecundity with little risk of mortality. If these hypothetical mechanisms are operating, this begs the question, why aren't development times even longer? I envisage three factors that limit the length of cicada life cycles.

First, although the survivorship curves were much steeper for early instar cicada nymphs than for established later instars, they were not completely flat later in development. In other words, there was some risk of dying before reproducing associated with extending development. For *Magicicada septendecim*, the estimated benefits of prolonging development in terms of increased fecundity (16% increase associated with four additional years) were roughly similar to the estimated costs in terms

of mortality risk (Fig. 6). When the mortality cost exceeds the fecundity benefit, selection will no longer favour longer development times. Estimates of age-specific survival and fecundity for additional cicada species are necessary to evaluate this argument.

Second, life history traits such as time to reproduction are influenced by a variety of complex factors. The simple demographic model that was presented above assumes that cicada populations are stable. There are relatively few multigenerational population studies, although cicada populations may be less variable in general than many other insect species (Ito, 1998). Over the long term, this assumption of stability ($R_0 = 1$) must be correct or cicadas would otherwise either dwindle to extinction or take over the world. However, populations experience fluctuating conditions allowing them to increase during certain times and to decrease during others. During periods when populations are increasing, a shorter generation time will probably be favoured while periods of declining populations will probably favour longer development times (Lewontin, 1965; Mertz, 1971; Caswell & Hastings, 1980; Oli & Dobson, 2003). However, the effects of fluctuating conditions on life history traits are complicated and simple predictions have rarely been supported (e.g. Oli & Dobson, 2003; Rees & Ellner, 2019).

A third factor that may limit cicada development is the combination of immobility and information degradation over time. Because cicada nymphs live underground in the soil, they have few opportunities to change host plants and moving through the soil without feeding is likely to be costly. When they oviposit, females select the host plants where their offspring will spend the vast majority of their lives. For example, *Magicicada* nymphs travelled only a few centimetres through the soil during their long underground development (White & Lloyd, 1975; Maier, 1980). Ovipositing females preferred sunlit branches at forest edges presumably because these sites will provide their offspring with actively growing roots over the next 13 or 17 years (Yang, 2006). The cues that females use to place their eggs are likely to contain reliable information although the quality of that information degrades over time. Trees that were actively growing during an adult emergence of 17-year cicadas had become senescent 17 years later (Karban, 2014). Cicada nymphs have no ability to track and respond to environmental changes during their development. The costs of habitat change may balance the benefits of associated with prolonged development.

CONCLUSION

Cicadas as a group are relatively larger and slower to develop than most other insects. Two hypotheses can

explain these life history patterns – their reliance on a poor source of nutrition and their very steep survivorship curve that flattens out after establishment. This study considered development times for approximately twice the number of cicada species compared with my earlier analysis (Karban, 1986) and found support for both of these non-exclusive hypotheses. Despite these additional recent data, we still know the development times for a very small fraction of species, and we have demographic information for even fewer. Because cicadas are at the tail of the distribution of insect life histories, understanding the selective forces that favoured their prolonged development and large body sizes can probably shed light on life history evolution more generally.

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DATA AVAILABILITY

The data used in this paper are presented in the Supporting Information (Table S1).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Growth rates and geographical ranges of cicada species.