

Title: Extended flowering intervals of bamboos factorize into small primes

Authors: Carl Veller^{1,2,3,*}, Martin A. Nowak^{1,2,4}, Charles C. Davis²

Affiliations:

¹ Program for Evolutionary Dynamics, Harvard University, Cambridge, Massachusetts 02138, USA

² Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138, USA

³ Department of Economics, Harvard University, Cambridge, Massachusetts 02138, USA

⁴ Department of Mathematics, Harvard University, Cambridge, Massachusetts 02138, USA

*Correspondence to: carlveller@fas.harvard.edu

Abstract:

Many bamboo species collectively flower and seed at dramatically extended, regular intervals, some as long as 120 years. These collective seed releases (termed ‘masts’) are thought to be a strategy to overwhelm seed predators. But why are the intervals so long, and how did they evolve? We propose a simple mathematical model that supports their evolution as a two-step process: First, an initial synchronization phase in which a mostly annually-flowering population synchronizes onto a small multi-year interval. Second, a phase of successive small multiplications of the initial synchronization interval, resulting in the extraordinary intervals seen today. A prediction of the hypothesis is that mast intervals observed today should factorize into small prime numbers. Using a historical data set of bamboo flowering observations, we find strong evidence in favor of this prediction. Although little is known about the genetic and developmental basis of the biological clock in masting bamboos, our hypothesis provides a first theoretical explanation for the mechanism underlying this remarkable phenomenon.

One sentence summary: The extraordinary flowering intervals of bamboos have evolved through an irreversible process of successive, small multiplications, rendering these intervals factorizable into small prime numbers.

Main text:

Understanding the basis of species' phenology—the timing of life history events such as plant flowering and bird migration—is a key area of biological research (1). Easily one of the most captivating phenomena in this regard is the extended synchronous flowering and fruiting intervals exhibited by tropical woody bamboos (2, 3). Although numerous bamboo species flower and fruit at more modest time intervals, there are many extraordinary examples of bamboos with greatly extended intervals (Fig. 1). For example, the Asian bamboos *Bambusa bambos*, *Phyllostachys nigra* f. *henonis*, and *P. bambusoides* flower every 32, 60, and 120 years respectively (2, 4-9), with historical records for the latter two species dating back as far as 813 C.E. and 999 C.E. respectively (4). In each of these cases, individuals of a species collectively flower and fruit in enormous quantities (referred to as 'masting') only to die back, leaving behind seeds which subsequently germinate. The cycle then repeats. In some documented cases, this synchrony is maintained even after plants are transplanted far from their native ranges (5, 7, 10, 11).

Though some other plant species mast (most notably the Dipterocarpaceae clade in Southeast Asia (12, 13)), none is known to exhibit either the regularity or the extraordinary interval length of the mast cycles observed in bamboos. Despite its broad interest to biologists, however, the evolution of these prolonged regular flowering intervals has received surprisingly little quantitative investigation. The leading explanation for masting in bamboos is attributed to Janzen (2, 13), who proposed that the enormous number of propagules (fruits or seeds) released during these episodes satiate local predator populations, ensuring that more seeds survive than with sporadic, and thus less abundant, propagule release (14, 15). In the case of bamboos, these predators typically include rats, birds, and pigs (2). The stabilizing selection underlying the predator-satiation hypothesis requires that a plant releasing its propagules out of synch with its cohort will likely have them all eaten by predators. Support for this comes from measurements of seed predation rates during and outside of masting episodes, for bamboos (16) and other masting species (17-20). But while the predator satiation hypothesis provides an explanation for the success of synchronous seeding in bamboos, a more intriguing puzzle remains: what explains the remarkable regularity and length of bamboo mast cycles? Here, we propose and test a novel mathematical model of the evolution of bamboo masting to solve this puzzle.

The puzzle is twofold. First, how was synchrony achieved on the shorter, regular multi-year intervals that have been hypothesized to be ancestral in bamboos (2)? Second, given the strong stabilizing selection for maintaining a regular interval, how did the shorter ancestral intervals lengthen to the extraordinary intervals seen today?

We first hypothesized that initial synchronization on a multi-year cycle can evolve naturally from a population of annual flowerers when two conditions are met. First, plants that wait longer to flower release more seeds, and/or seeds that are better protected (e.g., with thicker coats). This delay allows plants to accumulate greater energy resources to be invested in producing more or better-protected seeds (21). Second, total potential seed predation varies from year to year, but is typically high, amounting to a significant proportion of maximum possible seed release. Evidence for this assertion comes from observations of enormous predation rates in minor mast years among well studied woody tree species (17-20).

These conditions can be incorporated into a simple mathematical model (Fig. 2). Here, we assume a fixed environmental carrying capacity, and begin with a population comprising mostly plants that seed annually, but with some variation in seeding time, so that a small number of plants seed every two years. These two-year plants may be distributed across odd and even years in this two year cycle, forming two distinct ‘cohorts’. Under a broad class of parameterizations, a common outcome of our model is synchronization onto a single cohort of two-year plants, following a year where all annual plants and one cohort of two-year plants are eliminated by predation (Fig. 2). Importantly, our model is not restricted to synchronization onto a two-year cycle: longer intervals of synchronization are possible in a similar model if we extend the variation in the initial population to include plants with longer flowering intervals, including three, four, and five years (Supplementary Fig. S2).

Once synchronization has been established in a population, say, on a three year mast interval, stabilizing selection should maintain the synchrony. A plant flowering out of sync—e.g., after two or four years—would release its seeds alone, and they would be completely consumed by predators. Given such strong selection for synchrony, how could flowering intervals have increased to the extraordinary lengths observed today? Janzen noted (2) that a plant flowering at an interval twice that of its clump—at six years, in the case of a three year mast cycle—would always flower during a masting year (i.e., every second mast), and thus be buffered against predation. Indeed, this holds for a mutant flowering at any multiple of the initial mast

interval, not just double. And since plants waiting longer to mast release more propagules (or better protected ones), during times of low population growth (when delaying seeding would not represent a significant ‘missed opportunity’), such mutants would likely be favored. For example, if a mutant with a flowering interval twice that of its clump releases $s\%$ more seeds than the average single-interval plant (or, equivalently, seeds that are better protected and thus suffer $s\%$ less predation), and if average clump growth is $g\%$ per period, a simple population growth model (see SI) predicts that selection will favor the mutant if $s > g$. This is likely to hold especially when population growth, g , is low. Analogous conditions for mutants of higher-multiple intervals can be derived (see SI)—these are also likely to hold for reasonably low g . So when clump growth is low, multiple-interval mutants can emerge, be selected for, and fix. Under this scenario, the population’s flowering period increases to a multiple of its initial synchronized interval.

The converse, however, is not true: if a population’s growth rate increases, mutants with intervals a fraction—say half—of the cohort’s would not survive because they would seed out of synch with the population every second period of their reduced interval. So, earlier initial flowering intervals are not recoverable, and thus the population’s flowering interval can only increase. The evolution of extended flowering intervals in bamboos may therefore represent an instance of Dollo’s law, or irreversibility in evolution (22).

Finally, the logic underlying this mechanism of interval growth yields a simple, testable numerical prediction. If the extraordinary flowering intervals observed today are the result of successive multiplications of the initial synchronization interval, then they should be decomposable back into those multiples. Though the theory is consistent with multiples of any size if population growth is sufficiently low, and though the mechanics of the genetic clock in bamboos are poorly understood (23), small multiples seem more likely than larger ones. The physiological and underlying genetic adjustments necessary for much larger single interval multiplications would likely render such multiplications implausible. Thus, we hypothesize that the extended mast intervals of bamboos should be factorizable into small prime numbers.

So, do the data support our small primes hypothesis? An initial survey of the most well-studied examples is promising (Fig. 1): *Phyllostachys bambusoides* (120 yrs = 5 yrs \times 3 \times 2 \times 2 \times 2), *P. nigra* f. *henonis* (60 yrs = 5 yrs \times 3 \times 2 \times 2), and *Bambusa bambos* (32 yrs = 2 yrs \times 2 \times 2 \times 2 \times 2) (2, 4-9). These examples support our hypothesis on several fronts. First, all of these

intervals are factorizable into small primes (5 or smaller). Second, the smallest primes appear most often in each factorization, consistent with smaller prime multiples being more likely. Third, the 120 year mast interval of *P. bambusoides* is a small multiple of the 60 year interval of the closely related *P. nigra* f. *henonis*, suggesting a common ancestral interval from which the two have evolved.

Other bamboo species with extended intervals are less well studied. For these species, a number of factors are likely to increase measurement error in estimates of mast intervals (2). These include geographic variation in observations of masting, observations gathered at different stages of consecutive masting episodes (many of which can last more than one year), and misidentification of species, as well as natural variation around mean flowering intervals within species (24).

Nonetheless, a broader inspection of the estimated mast intervals of these less well-studied species, together with their phylogenetic placement (Fig. 1) corroborates our hypothesis. In the two monophyletic genera in our data that exhibit variation in mast intervals across more than two species, *Phyllostachys* and *Chusquea*, these mast intervals show clear signs of having arisen through a multiplicative process (Fig. 3). The three *Phyllostachys* species in our data appear to share a common base interval of 15 years (15 yrs, 60, 120), which under our hypothesis would itself have arisen from a shorter (3 or 5 yr) initial synchronization interval. Allowing for measurement error, the three *Chusquea* species appear to share a base interval of 8 years (16 yrs, 23, 32). Similar patterns of multiples in bamboo flowering intervals have previously been noted as anomalous (25)—this anomaly is resolved as a natural consequence of our multiplication model.

To test our hypothesis more formally, we developed a simple, robust nonparametric test to determine if estimated mast intervals (Table 1) are more tightly clustered around numbers factorizable into small primes ('NFSP', here defined as primes 5 or smaller) than would be expected by chance under an appropriate null hypothesis. Here, our null hypothesis is that extended mast intervals evolved gradually (instead of via the discrete multiplications we have hypothesized), resulting in a smooth, continuous distribution of interval lengths (see SI for details of the estimation of this null distribution). Compared to samples generated from such a null distribution, the measured flowering intervals were significantly closer to NFSP ($p = 0.0041$) and contained significantly more NFSP ($p = 0.0024$). These results strongly support

the small primes hypothesis. Moreover, they are robust to changes in the construction of the null distribution, and alternative definitions of NFSP (see SI).

To our knowledge, our study is the first to develop a mathematical theory of the mechanism underlying extended mast intervals in bamboos. Here, an initial phase of synchronization onto a small interval is followed by successive multiplication of the interval by small numbers. Three key assumptions underlie our multiplication model: i.) strong stabilizing selection that maintains interval synchrony, ii.) that later seed release allows for greater seed release (and/or for better protected seeds), and iii.) approximately regular, endogenously timed mast intervals. These assumptions may explain why other masting plant species, such as members of the Dipterocarpaceae clade, do not exhibit such greatly extended intervals as the bamboos do. In particular, while assumptions i.) and ii.) above are likely to apply to many masting plants, assumption iii.) appears to be unique to bamboos. This assumption, which is crucial to the survival of multiple-interval mutants in our model, may thus be the key distinction that has allowed bamboos to achieve such dramatically extended flowering intervals.

The only other organisms that are well known to exhibit long-intervaled synchrony are the periodical cicadas (genus *Magicicada*), whose synchronized emergence from an underground larval state on 13- and 17-year intervals has similarly been attributed to predator satiation (26-28). Evolutionary explanations have been proposed for their large prime lifecycles (29-31), which clearly cannot be factorized into small primes, and thus stand in contrast to our hypothesis for the evolution of long-intervaled masting in bamboos. This suggests distinct evolutionary and genetic mechanisms underlying the periodical lifecycle of cicadas in comparison to long-intervaled masting in bamboos. Along these lines, the small primes hypothesis offers a framework upon which comparative analyses may be devised to explore the genetic and developmental basis of this striking behavior in bamboos.

References:

1. M. E. Visser, Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings of the Royal Society B: Biological Sciences* **275**, 649-659 (2008).
2. D. H. Janzen, Why bamboos wait so long to flower. *Annual Review of Ecology and Systematics* **7**, 347-391 (1976).
3. S. J. Gould, *Ever since Darwin: Reflections in natural history*. (W.W. Norton & Company, London, 1992).
4. S. Kawamura, On the periodical flowering of the bamboo. *Japanese Journal of Botany* **3**, 335-342 (1927).
5. M.-Y. Chen, Giant timber bamboo in Alabama. *Journal of Forestry* **71**, 777 (1973).
6. M. Numata, Conservation implications of bamboo flowering and death in Japan. *Biological Conservation* **2**, 227-229 (1970).
7. W. Seifriz, Observations on the causes of gregarious flowering in plants. *American Journal of Botany* **10**, 93-112 (1923).
8. W. Seifriz, Gregarious flowering of *Chusquea*. *Nature, London* **165**, 635-636 (1950).
9. A. F. W. Schimper, *Plant-geography upon a physiological basis*. (Clarendon Press, 1902), vol. 2.
10. D. Morris, *Chusquea abietifolia*. *Gardeners' Chronicle* **Oct 23**, 524 (1886).
11. D. Brandis, Biological Notes on Indian Bamboos. *Indian Forester* **25**, 1-25 (1899).
12. P. Ashton, T. Givnish, S. Appanah, Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *American Naturalist* **132**, 44-66 (1988).
13. D. H. Janzen, Tropical blackwater rivers, animals, and mast flowering by the Dipterocarpaceae. *Biotropica* **6**, 69-103 (1974).
14. D. Kelly, The evolutionary ecology of mast seeding. *Trends in Ecology & Evolution* **9**, 465-470 (1994).
15. D. Kelly, V. L. Sork, Mast seeding in perennial plants: why, how, where? *Annual Review of Ecology and Systematics*, 427-447 (2002).
16. T. Kitzberger, E. J. Chaneton, F. Caccia, Indirect effects of prey swamping: differential seed predation during a bamboo masting event. *Ecology* **88**, 2541-2554 (2007).
17. L. M. Curran, M. Leighton, Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecological Monographs* **70**, 101-128 (2000).
18. M. Crawley, C. Long, Alternate bearing, predator satiation and seedling recruitment in *Quercus robur* L. *Journal of Ecology* **83**, 683-696 (1995).
19. J. O. Wolff, Population fluctuations of mast-eating rodents are correlated with production of acorns. *Journal of Mammalogy* **77**, 850-856 (1996).
20. S. G. Nilsson, U. Wastljung, Seed predation and cross-pollination in mast-seeding beech (*Fagus sylvatica*) patches. *Ecology* **68**, 260-265 (1987).
21. M. Fenner, *Seed ecology*. (Chapman and Hall, 1985).
22. L. Dollo, Les lois de l'evolution. *Bull. Soc. Belge. Géol. Pal. Hydr* **7**, 164-167 (1893).
23. R. Nadgouda, V. Parasharami, A. Mascarenhas, Precocious flowering and seeding behaviour in tissue-cultured bamboos. *Nature* **344**, 335-336 (1990).
24. D. C. Franklin, Synchrony and asynchrony: observations and hypotheses for the flowering wave in a long-lived semelparous bamboo. *Journal of Biogeography* **31**, 773-786 (2004).

25. C. Guerreiro, Flowering cycles of woody bamboos native to southern South America. *Journal of Plant Research* **127**, 307-313 (2014).
26. M. Lloyd, H. S. Dybas, The periodical cicada problem. I. Population ecology. *Evolution* **20**, 133-149 (1966).
27. M. Lloyd, H. S. Dybas, The periodical cicada problem. II. Evolution. *Evolution* **20**, 466-505 (1966).
28. M. Bulmer, Periodical insects. *American Naturalist*, 1099-1117 (1977).
29. J. Yoshimura, The evolutionary origins of periodical cicadas during ice ages. *American Naturalist*, 112-124 (1997).
30. E. Goles, O. Schulz, M. Markus, Prime number selection of cycles in a predator-prey model. *Complexity* **6**, 33-38 (2001).
31. R. M. May, Periodical cicadas. *Nature* **277**, 347-349 (1979).
32. S. A. Kelchner, Higher level phylogenetic relationships within the bamboos (Poaceae: Bambusoideae) based on five plastid markers. *Molecular phylogenetics and evolution* **67**, 404-413 (2013).
33. A. E. Fisher, J. K. Triplett, C.-S. Ho, A. D. Schiller, K. A. Oltrogge, E. S. Schroder, S. A. Kelchner, L. G. Clark, Paraphyly in the bamboo subtribe Chusqueinae (Poaceae: Bambusoideae) and a revised infrageneric classification for *Chusquea*. *Systematic Botany* **34**, 673-683 (2009).
34. J. K. Triplett, L. G. Clark, Phylogeny of the temperate bamboos (Poaceae: Bambusoideae: Bambuseae) with an emphasis on Arundinaria and allies. *Systematic Botany* **35**, 102-120 (2010).

Acknowledgments:

We thank A. Berry, K. Borusyak, B. Franzone, L. Hayward, M. Hoffman, A. Knoll, E. Kramer, J. Libgober, J. Losos, A. Peysakhovich, H. Sarsons, J. Wakeley, and Z. Xi for helpful comments.

Figure 1. Long-interval flowering in bamboos. A recent phylogeny of the bamboos as inferred by Kelchner *et al.* (32). Twenty-one species with long-interval flowering are displayed across their associated bamboo subtribes. These are species whose flowering intervals can be estimated from the data summarized by Janzen (2) (see SI for details of interval estimation). Species names have been updated to reflect current taxonomy.

Figure 2. An evolutionary model of initial synchronization in bamboos. (A, B) Blue phase: Initially, the population comprises mostly annual-flowering bamboos, with a small number flowering every two years (symmetric across odd and even years). At first, owing to their higher individual seed release (or seeds better protected from predation), the two-year plants increase in numbers over time (A). As they do, the total annual seed release declines, as the population's seeding becomes increasingly diluted over the odd and even years of the two-year cohorts (B). Red phase: When total annual seed release declines below maximum potential predation (B), the population is at risk of having an annual seed release completely consumed by predators. When complete predation of a seed release eventually occurs, all of the annual plants, as well as the two-year cohort seeding in that year, are eliminated (A). Green phase: If predation is not unusually high in the following, the seed release of the remaining two-year cohort will fill the environmental carrying capacity, establishing synchrony onto that cohort's two year cycle.

Figure 3. Mast intervals within bamboo subclades appear to have arisen from a multiplication process. Two hypothesized patterns of small interval multiplications along phylogenies (33, 34) of *Phyllostachys* (A) and *Chusquea* (B), here including species from our data set for which more than two species possess reliable flowering intervals. The mast intervals of these species are consistent with the multiplication model we propose, allowing for small measurement error in the case of *C. ramosissima* (estimated interval 23 yrs vs. predicted interval 24 yrs). Hypothesized intervals, ancestral and extant, are displayed in boxes; measured intervals from our data set are displayed on the bottom lines.





