Ann Rev. Ecol. Syst. 1974 7:347–91

WHY BAMBOOS WAIT SO LONG TO FLOWER

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INTRODUCTION

In the years 919 and 1114, the mainland Chinese bamboo ***Phyllostachys bambusoides*** seeded en masse. Sometime between 1716 and 1735, and again in 1844-1 847, it seeded in Japan, long after being introduced there from China (135). In the late **1960s,** transplanted stocks of this bamboo in England, Alabama, and Russia, as well as their parental Japanese stock, flowered again ***(60,* 181, 182, 192). *P. bambusoides*** thus has a seeding cycle of about 120 years. Many other species of bamboo have shorter yet still very long times between successive synchronized reproductions by seed (Table 1). I hypothesize that this behavior is an extraordinary example of satiation of seed predators at the level of the prey population, and here explore the literature on the natural history of bamboo to determine if this hypothesis is reasonable. It is probably untestable in most contemporary habitats, owing to the destruction of the relevant organisms or their interactions.

Nearly all species of bamboo seem to have one of two life histories. Some species outside of the Indian-Asian tropics, and a very few in, have populations composed of individuals (clones) that grow to maturity and then flower/seed annually for many years. Such behavior has been recorded for ***Bambusa forbesii* (114), *Arundinaria wightiana, Arundinaria elegans, Arundinaria glomerulata, Ochlandra rheedei* [= *0. scriptoria,* (162)], *Ochlandra stridula* (39), *Shibataea kumasaca* (254),** and ***Bambusa lineata*** (254) in Asia, and implied for some neotropical species (163). These populations of apparently iteroparous bamboos are not recorded as displaying conspicuous seeding synchrony at greater than yearly intervals, and are not discussed further.

Many of the more common Indian-Asian species [at least 137 **(40)]** have populations made up of individuals that seed synchronously at regular and long **supra-**annual intervals. In his 1966 review of bamboo biology, McClure (162) reached the opposite conclusion, but he worked almost entirely with cultivated or feral

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Table 1 Fairly reliable records for the intermast period of mast-seeding bamboos

Species	Locality	Flowering dates	Intermast period	References
Arundinaria alpina	Kenya	?	about 40-plus	P. J. Greenway, J. B. Gillett (personal communication)
Arundinaria falcata	Lansdowne,	1911		
	U.P.	1946	35	(145)
Arundinaria falconeri	Darjeeling	1900	20-25?	(91)
	England	1847		J. S. Keesing
	(introduced from	1875-1877	28-30	(personal communication)
	Himalaya)	1902-1908	25-32	(32, 246)
		1929-1932	21-30	
		1964-1967	32-38	
Arundinaria intermedia	Eastern Himalaya	1848		
	(mixed localities)	1868	10 (= 20/2)	
		1879	11	(49)
Arundinaria maling	Eastern Himalaya	not in living memory		
		1951	50-plus	(208)
Arundinaria racemosa	Sikkim	1857		
		1888	31	(105)
Arundinaria simonii	England	1877		
	(introduced)	1907	30	(32, 162)
Arundinaria spathiflora	Western Himalaya	1821		
	(mixed localities)	1881-1882	10 (= 60/6)	
		1892-1893	10-11	(49)
Bambusa arundinacea	Malabar, South Kanara	1804		
	(Wynaad & Corg)	1836	32	
		1866	30	(46, 49, 142)
	Narbudda River	1839		
		1870	31	(49)
	Kanara	1878		
		1912	34	(250)

Bambusa arundinacea (continued)	Dehra Dun	1836		
	(planted)	1881	45	
		1926	45	**(39, 42)**
	Brazil	1804		
	(introduced)	1836	32	
		1868	32	
		1899	31	**(78)**
	Upper Weinganga Valley,	1818		
	Balaghat District	1865-1870	47-52	(177)
	Dehra Doon	1832		
		1882	50	(177)
	Chandka Range,			
	Puri Forest Division	1929?		
	Orissa	1969	40	(72, 167)
	South Travancore	1816-1817		
		1869-1870	52-54	**(25)**
	Martaban	?	32	(50)
Bambusa indusager	Paraguay	1972	long interval	(230)
Bambusa polymorpha	Burma	?	at least 68	(224)
	Burma	1853	at least 50	**(263)**
	Prome Division Burma	1859-1860,1914	54-55	(48)
Bambusa vulgaris	Pantropical	?	150 years plus	**(162)**
Chimonobambusa quadrangularis	Japan and Europe, in cultivation	?	greater than 100	**(162)**
Chusquea abietifolia	Jamaica	1884-1886, 1918,	32-34	
		1948-1949	30-31	(115, 172, 223,225)
Chusquea culeou	Chile	?	15-20	**(98)**
Chusquea quila	Chile	?	15-20	**(98)**
Chusquea ramosissima	Brazil	1893, 1916	23	**(78)**

Table I (Continued)

Species	Locality	Flowering dates	Intermast period	References
Chusquea tenella	Brazil	1901		
		1916	15	
		1932	16	(78)
Dendrocalamus giganteus	Burma-Ceylon	1831?		
	(introduced)	1908-plus	about 76	(150)
Dendrocalamus hamiltonii	Lakhimpur Forest, Assam	1905	30?	(57)
	Cachar, Assam	1912		
		1956	44	(100)
Dendrocalamus hookerii	Assam	1850		
		1967	117	(99)
Dendrocalamus strictus	Garhwal, outer	1872-1876		
	Himalayan tract	1909-1913	36-40	(250)
	Madhya Pradesh	?	20-30	(139)
	Paniali	1909		
		1948	39	(102)
	Cachar Hills, Assam	1879		
		1922	43	
		1966	44	(100)
	India	1921-1922		
		1968	46	(226, 231)
	Saharanpur Siwaliks	1883-1886		
		1926-1927	40-44	(102)
	Bhadravathi, Mysore State	1905-1908		
		1932-1933	24-28	(132)
	Uttar Pradesh	1870		
		1909-1910	39-40	
		1949-1953	39-44	(102)

Table 1 (Continued)

Dendrocalamus strictus (continued)	Taiwan	1922		
	(introduced	1969	47	(260)
	Burma:			
	Tharawaddy	Based on Deogun's	23	—
	Zigon	summary of his own	15, 27	
	Ruby mines	records (73)	9[a]	
	Thayetmyo		21	
	Henzada		32	
	Prome		12-15	
	Tauguin		8[a]	
	Central Provinces:			
	Chanda		21	—
	Seoni		22	
	Balaghat		20	
	Madras:			
	Vizagapatam		28	
	United Provinces:			
	Garhwal Outer Himalayas		36	
	Saharanpur Siwaliks		40	(73)
Guadua trinii	Argentina	1923		
		1953	30	(185)
	Brazil	1902		
		1934	32	(78)
Melocanna bambusoides	Mizo Hills, Assam	1863-1866		
		1892-1893	26-30	
		1900-1902	7-10	
		1933	33-31	
		1960	27	(58)

Table 1 *(Continued)*

Species	Locality	Flowering dates	Intermast period	References
Melocanna bambusoides (continued)	Lushai Hills, Assam	1864		
		1911-1912	47-48	(186)
	Chittagong,	1863-1866		
	East Pakistan	1908-1912	42-49	
		1958-1959	46-51	(116)
Merostachys anomala	Brazil	1876		
		1906	30	(78)
Merostachys burchellii	Brazil	1877		
		1907	30	(78)
Merostachys fistulosa	Brazil	?	30-34	(187)
Merostachys sp.	Brazil	?	11	(187)
Neehouzeaua dullooa	Cachar, Assam	1951-1953		
		1967-1968	14-17	(100)
Ochlandra travancorica	Travancore	1875		
		1882		(24, 25)
Oxytenanthera abyssinica	East, South, and			
	Central Africa	?	7-21	(84)
	Malawi	1925-1930		
		1943	13-18	(63)
	Malawi	?	about 15	(2)
Phyllostachys bambusoides	China	999		
	China	1114	115	
	Japan (introduced)	1716-1735	120 (= 602/5)	
	Japan	1844-1847	120	
	Japan, United States	1966-1969	120	(60, 135, 181)
Phyllostachys edulis	Japan	?	greater than 48	(254)

Table 1 *(Continued)*

Phyllostachys henonis	Japan (introduced from China)	813		
		931	59 (= 118/2)	
		1247	63 (= 316/5)	
		1666	60 (= 419/7)	
		1786	60 (= 120/2)	
		1848	62	
		1908	60	(135)
Phyllostachys reticulata	Japan	?	greater than 60	
			probably greater than 100	(254)
Phyllostachys aurea	Introduced to Europe and England	1876	28-29 (2 X 14-15)	J. S. Keesing (personal communication)
		1904-1905		
		1919-1921	14-17	
		1934-1938	13-19	
Sasa tessellata	Japan in cultivation	?	greater than 115	(162)
Schizostachyum elegantissimum (=Nastus elegantissimum)	Bandong, Java	?	3	(142)
Sinocalamus copelandi	Northern Shan States, Upper Burma	1896		
		1943	47	(202)
Thamnocalamus spathiflorus	Jaunsar-Bawar, Northwestern Provinces	1865-1866		
		1882	16-17?	(214)
Thyrsotachys oliverii	In cultivation from Burma	1891		
		1939	48	(162)

[a] For unknown reasons, Deogun (73) suggested discarding these records.

plants-plants that for the reasons discussed throughout this paper may be expected to lose their synchrony with sympatric conspecifics. A brief and idealized life history for one of these mast-seeding semelparous species is the following. After growing by rhizome and branch production for a species-specific period of 3– 120 years (Table 1), nearly all the members of one species in one area produce wind-pollinated flowers, set large quantities of seed, and die. This seed germinates immediately or when the first rains come, but is preyed upon very heavily by local animals, highly nomadic animals, and, apparently, the offspring of both. This seed predation is heaviest on the tails of the seeding distribution, thus maintaining the synchrony. The new cohort of seedlings then grows vegetatively for the same length of time as did its parents and repeats the process. The timing of seeding in these semelparous species is set by an internal physiological calendar rather than an external weather cue, and thus differs from iteroparous mast-seeding trees (126, 127).

The questions that such a life cycle bring to mind are dealt with in turn below; this phenomenon has been of interest to academic biologists since the middle of the 19th century (see 20, 38–40, 49, 73, 111, 135, 162, 180, 208, 224, 242, 254), to Chinese and Japanese temple recorders since at least 919 AD (135), and to agriculturalists as long as man has lived around bamboo plants. In the hundreds of pages of description and puzzlement this interest has generated, not a single sentence attempts to define the adaptive significance of synchronized seeding by bamboos, although I suspect that many an Indian or Asian farmer or hunter-gatherer could give the correct answer.

TERMINOLOGY

Must seeding is the synchronized production of seed at long intervals by a population of plants. The term derives from oak mast, beech mast, etc, as traditionally used to describe the large amount of acorns, beech seeds, etc on the ground beneath midlatitude forests in a mast year (cf 126, 127). I prefer mast seeding to the traditional term ***gregarious flowering,*** which is often applied to bamboos; the latter implies a collective and deliberate behavioral action by the plants at a time when the plant in seed probably has no way of directly perceiving that other individuals are seeding. The proximal cause of synchronization of mast seeding is 1. selective mortality, which removes those seeds or seedlings out of phase with the rest of the cohort (e.g. bamboo), or 2. caused by the synchronization of adult members of an iteroparous population by a weather cue (as in oaks, beeches, conifers, and Dipterocarpaceae). Mast-seeding bamboos, as well as the ***Strobilanthes*** discussed at the end of this review, are usually "monocarpic" or semelparous plants in that they seed once and die. Bremekamp (52) coined ***plantae plietesiae*** or ***plietesials*** for synchronized perennial monocarpic plants, but I find this to be an unnecessary addition to our vocabulary.

THE SEED PREDATORS OF MAST-SEEDING BAMBOOS

Who eats bamboo seed? Everybody does. Bamboo seed has a nutrient quality slightly greater than rice and wheat (1,23, 58,98, 122, 167, 181,205,206,244,265, 274, 277). There is no evidence that bamboo seed contains the toxic secondary compounds normally found in tropical tree seeds, but bamboo seeds can cause diarrhea if eaten in excess, and they are not eaten when other grains are available (264). In addition to being chemically unprotected, bamboo seeds are easily located since they fall onto ground relatively bare of understory shrubbery, owing to the dense shade cast by the parents. The seeds range from the size of a rice kernel up to 100-350 grams (116) (and see 191, 192, 194, 213, 239, 254), and may cover the ground to as much as 5-6 inches in depth below the parent plant (74). A surveyor reported in 1867 that in a 6000 square mile patch of Indian *Melocanna bambusoides,* the pear-sized seeds were falling so thickly that he had to give up work because they were breaking his plane tables and theodolites (239). A 40 square yard clump of Indian *Dendrocalamus strictus* can produce 320 pounds of seed (68) [there are 800-1000 *D. strictus* seeds to the ounce (73)]. A mast seeding by two species of wild Madagascar bamboos produced an estimated 50 kg of seed per ha over 100,000 ha (203).

Humans have been major predators on bamboo seed throughout recorded history (23, 34, 61, 73, 74, 92, 142, 146, 167, 175, 213, 235) and probably long before. *D. strictus* seed kept over 35,000 people alive during the 1899-1900 drought in the Central Provinces of India (146). By hand gathering and threshing, an adult can collect 4-6 pounds of seed per day (213).

> . . . in 1864 there was a general flowering of the Bamboo in the Soopa jungles, and . . . a very large number of persons, estimated at 50,000, came from Dharwar and Belgaum districts to collect the seed. Each party remained about ten or fourteen days, taking away enough for their own consumption during the monsoon months, as well as some for sale. . . . Tens of thousands of pounds have been sold in the English bazaar at Malda; and large quantities have been sent to Sultangunge and other places twenty-five to thirty miles distant . . . (175).

Indigenous people harvested *Chusquea* seeds during mast crops in Chile (98) and *Sasa* seeds in times of famine in Japan (18 1). It is becoming popular to view early man as heavily granivorous (140), and thus the predation on bamboo seeds by man may go back a very long way.

Predation by humans on bamboo seeds differs in a very important way from seed predation by the other animals listed below. Humans probably ignored the leading and following tails of the seeding distribution within a mast crop, especially for the small-seeded species such as *Dendrocalamus strictus.* I expect that they concentrated on the center of the distribution, where seeds would be the densest and the most easily gathered. Their predation could thus promote a breakdown of the mast-cropping synchrony by favoring late- and early-seeding individuals. It is probably significant that almost all the examples cited above of humans gathering bamboo seed are for *D. strictus,* the species of bamboo for which poorly synchronized mast crops and sporadic flowering were most frequently recorded (see discussion).

. Local animals should be major predators on bamboo seeds from the day the mast crop begins until the day it ends. In addition to the local individuals of the more nomadic species of animals (described below), all regions (with the exception of

Jamaica) with mast-cropping bamboos have a number of indigenous species of terrestrial rodents of various sizes. In India and neighboring areas, *Nesokia, Mus, Rattus, Golunda, Rhizomys, Hystrix,* and others would be present (129). With the exception of porcupines *(Hystrix),* these rodents produced the "rat" population explosions that were caused by bamboo mast crops (58, 138, 152,176, 186,220,245, 255, 274). As the seed is exhausted through predation and germination, the rats emigrate. "Rats are so fond of bamboo seeds that the widespread seeding of [Burmese] bamboos may induce a regular plague of them in the neighborhood. This sometimes results in famine and is followed by epidemics and disease since the number of rats increases to such enormous proportions that the sowing of field crops becomes impossible" (255). There are *Clethrionomys* outbreaks in the year following Japanese *Sasa* mast crops (181, 244, 253), which are undoubtedly due to the very large amounts of bamboo seed and seedlings. In Madagascar, bamboo mast crops contributed an estimated 40-60 million *Rattus* to nearby 10,000 ha of crops, which were destroyed before the rats starved to death (203). That this could happen with a mast crop of only 5 months' duration is not surprising since rats have 6-12 young per litter and attain reproductive maturity in 2-3 months. In the Brazilian "rat plagues" following mast crops of *Guadua* bamboo, wild rodents *(Holochilus, Oryzomys, Hesperomys, Akodon)* caused comments such as "Mr. Mercer, who plants annually about fifty acres of corn, replanted six times last year, and finally gave up in despair" (74) [see (78) and (96) for additional examples]. Mast crops of *Merostachys fistulosa* in Brazil caused rat outbreaks *(Heligmodontia, Oxymycterus, Akodon),* and even *Rattus rattus* populations increased in the wild (187). Chilean rat outbreaks on *Chusquea* seeds were conspicuously rich in *R. rattus* and even *R. norvegicus* (98). Arboreal rodents should also do well by bamboo mast crops. "Fox Island was full of game from my earliest recollections up to the year 1850, when the cane *[Arundinaria tecta]*, with which it was covered, went to seed and then all died. The seed grew in clusters and resembled oats, and all the animals and fowls got rolling fat from eating this seed. The squirrels were so fat that their kidneys were covered. . . but this was the end of the cane on Fox Island as it all died the following winter and was either carried off by the high water or rotted on the ground" (119) (near New Harmony, Indiana, United States).

The animals may not have been satiated in the previous case. After a Burmese mast crop of *Cephalostachyum pergracile,* the absence of seedlings "is attributed to the destruction of the seed by a plague of rats" (9). Such total destruction of a mast crop was probably a rare thing, but the mast crops large enough to attract attention were those least likely to fail to satiate wild seed predators. Local extinction of very small bamboo cohorts by seed predation, or fragments of them, was probably a common event in habitats with a full complement of animals.

Small local bamboo seed predators are of special importance in bamboo seed predation because they are likely to have a powerful reproductive response to the abundant food. This trait is well known for small rodents and especially *Rattus, a* genus with native species sympatric with Indian and Asian mast-seeding bamboos.

Larger animals should have a powerful nomadic response to a bamboo seed crop (and a reproductive one as well, if the seeding period is long enough), as exemplified by the wild chicken (jungle fowl, *Gallus* spp.) and other pheasants in India and Burma. However, only hints remain of the importance that these once abundant birds must have had as bamboo seed predators. In 1907 Ellis tried to find seed after a minimum of 295 square miles of *Cephalostachym pergracile* had a mast crop in lower Burma:

> Some seed has been collected, but the Karens say that owing to the collection having been left too late, viz., May, it is hard to find, as pheasants, jungle fowl, parrots and doves to say nothing of four-footed animals, have eaten it all up. Some 4½ baskets have been obtained and it seems fairly good seed. Little of this was found on the ground, however, most being rubbed by hand out of the infrutescences still hanging on the bamboo. It is curious how jungle fowl and pheasants swarm this year where last year they were scarcely to be heard or seen, but then there is any quantity of *C. pergracile* seed this year. (82)

Baker (29, 138) said of *Gallus bankiva* in Burma:

> Jungle-fowl are extra-ordinarily numerous in the Garo, North Cachar and other hills south of the Brahmapootra, and it is often possible to see hundreds in a morning's or afternoon's wandering. Like the domestic fowl the jungle-fowl is practically omnivorous but is by preference rather a vegetarian than an insect eater. All kinds of seeds, grain, etc. are greedily devoured, and also many kinds of roots, buds and young shoots. Bamboo seeds are a very favorite food, and where there are stretches of bamboo which have seeded and the seeds are beginning to fall, these birds-and others-collect in almost incredible numbers into a very small area.

> . . . a morning's beating was done at Taungbon [Burma) . . . a well known spot for jungle fowl where usually hundreds of birds are seen in a morning's beating. On the morning in question not a single bird was put out. It was discovered that [the bamboo] **thanatwa** *(Thyrosostachys oliveri)* had flowered gregariously a few miles away and all the birds had deserted their usual dwelling places around Taungbon village and migrated to the flowered area.

A Thai jungle fowl cock had 519 bamboo seeds in its crop (67). Other observers of polyplectrons, pheasants, and related birds have made similar comments (5, 28, 29, 31, 33, 66, 67, 112, 156, 232, 250, 274). Just as domestic chickens lay on very heavy fat deposits when there is excess feed, so do wild phasianids (28). Being largely terrestrial, chickens may be the pigs of the bird world.

The opportunity for a jungle fowl population explosion is great when the bamboo mast crop lasts for a couple of years. On a bamboo mast year, jungle fowl have "larger and earlier broods" (5,232). Maximum food for domestic chicks can lower the age of sexual maturity from 186 to 135 days (199). Since the chicks of gallinoid birds seem to depend heavily on insects for early growth, an excess of bamboo seed might appear to not be sufficient for a chicken population explosion. However, domestic chicks can subsist on a diet of crushed grain alone, and Collias & Saichuae (67) recorded a downy jungle fowl chick with 20 rice grains and 68 termites in its stomach. A jungle fowl hen on optimal food can produce 62 eggs within 500 days of birth and domestic chickens have their first egg at about 160 days of age (120). A jungle fowl nest may contain as many as 11 eggs (106) while the usual clutch size is 5-8 (33) or 6–10 (71). Since the egg-laying rate can be greatly increased by selection in commercial chickens (76), I expect that local jungle fowl reproductive rates are genetically adjusted to match the relative frequency of local bamboo mast crops. Chickens lay eggs year-round in the tropics (267) and jungle fowl should do the same in the presence of ample food. The jungle fowl in the San Diego Zoo may have two broods per year (N. E. Collias, personal communication).

Pheasants can be induced to lay eggs continually by providing day-length regimes roughly like those in the tropics; they may lay as many as 44 eggs in a season (55). As an example of the possibilities for population growth, ***Phasianus colchicus,*** introduced onto predator-free and grain-rich Pelee Island in Lake Erie, went from 36 birds to an estimated 20,000 in five years (6). Almost all 33 species of Asian Phasianidae occur in habitats containing bamboo and many feed on bamboo seeds and sprouts (33). Hens of some species of pheasants can produce very large broods (33, 266), and I expect that, in the presence of a mast crop, they may well have produced a reproductive response as well as a nomadic one. Since jungle fowl feed on the flowers (245) as well as the seeds, they are guaranteed nearly a year of abundant food even with the most tightly synchronized species of bamboos. Jungle fowl have been found in very fat and healthy condition migrating by the thousands (95, 173); this is probably emigration from exhausted bamboo (or ***Strobilanthes, see*** later) mast crops. Small wonder that local Indian tribes invented tales of monstrous animals “half rat and half jungle fowl” (186) that appear during famines-famines that may well have been brought on by bamboo seeding. Beebe (33) concluded that “while the name junglefowl is quite correct, bamboofowl would be even more appropriate, as they are especially fond of this type of vegetation . . . rarely, I have found them in heavy tropical forest devoid of bamboo” (and see 67).

I expect smaller birds to congregate at bamboo mast crops as well, but only from Africa is there any published information. The African weaver finches (***Quelea spp.***) must migrate by the millions to keep up with the ripening of wild and domestic grains (262). They may have been attracted to mast crops (or even sporadic seeding) of the most common lowland bamboo in eastern and central Africa, ***Oxytenanthera abyssinica.*** However, the pied mannikin (***Lonchura fringilloides,*** Estrildidae, a weaver-finch) is apparently a specialist on the mast crops of ***0. abyssinica*** and moves long distances among cohorts out of phase with each other (123). In February–March of 1975, an introduced clump of ***Phyllostachys*** bore seed on the edge of the rainforest on Barro Colorado Island, Canal Zone. The clump attracted a large number of small birds, including ***Pheucticus ludovicianus*** (rose-breasted grossbeak), ***Cyanocomposa cyanoides*** (blue-black grossbeak), ***Geotrygon montana*** (ruddy quail dove), ***Clavaris prefiosa*** (blue ground dove), ***Leptotila cassinii*** (gray-chested dove), ***Oryzoborus funereus*** (thick-billed seedeater), ***Sporophila nigrocallis*** (yellow-bellied seedeater), and ***S. aurita*** (varied seedeater) (C. Augsperger, personal communication). I expect that passenger pigeons (***Ectopistes migratorius***) and Carolina parakeets (***Conuropsis carolinensis***) made good use of mast crops of ***Arundinaria tecta,*** the common canebreak bamboo of the southeastern United States. ***E. migratorius*** fed on cane seeds (221), and ***C. carolinensis*** was also a highly mobile generalist predator on tree seeds (97, 117). It is even possible that the very rapid demise of the large canebreaks in the last half of the 1800’s by fire, grazing, and draining (119) may have contributed to the rapid extinction of these birds. Bobwhite quail and turkeys congregate on mast crops of beech, oak, and pine (22 1, 222, **241)**, and probably moved into cane mast crops.

There are no detailed records of wild pigs feeding on bamboo seeds. However, they are fond of other species' mast crops **(51a**, 108, 128, 240, 248) and domestic grain crops (7, 87, 128, 248). I am certain that they would have traveled to bamboo mast crops. Indeed, in 192 1, Troup (250) said that in India "the fleshy fruits of ***Melocanna bambusoides*** attract bison, deer, pig, and other animals," and others have made similar comments (35, 138, 274). Pigs are also very fond of bamboo seedlings (17,249). In 1874 Jerdon commented that "the wild hog is found throughout India" and that "***Sus Cristatus*** travel great distances for their food in some parts of India." In 1894 the Indian Mathesan Hill jungle people told Mason that "a large number of wild pigs came up on to the hills every year during the rains in order to feed on the snails which are very plentiful there at that time of the year" (153). It was said as late as 1940 of ***Sus scrofa*** in south China that "in some sections so great is the damage they do to growing crops, that farming has been entirely abandoned over large areas which in former times produced quantities of rice, while numerous hamlets have been deserted on account of the raids of the animals, which utterly destroyed the crops" (7). A bamboo mast crop should have proved equally attractive. Feral pigs in tropical Australia have 10-15 miles as their daily foraging distance, and they "tend to concentrate in areas where food is plentiful, following the ripening of natural crops of tubers and fruits . . ." (200). I have postulated that the spectacular pig migrations in Borneo (15, 85, 113, 195) may be either in search of, or emigrating from, mast crops of Dipterocarpaceae (127). Interestingly, these migrating or nomadic animals are not in a reproductive state (113). The spectacular pig outbreaks in Europe (e.g. 118) may well have been the outcome of beech or oak mast crops. That pigs were the only large mammals to widely colonize the Malay Archipelago beyond the Molluccas (166, 259) also attests to their nomadic abilities.

The wild pig is a specialist at moving long distances to a large but temporary food source and then making very good use of it. As mentioned earlier, a 40 square yard clump of ***Dendrocalamus strictus*** can produce 320 pounds of seed (68). A wild boar X Berkshire cross requires only 530 pounds of starch or equivalent to grow from 66 to 220 pounds in 158 days (107). When presented with superabundant food, a wild Bomean hog may put on a layer of fat 3-6 cm deep in a week (195). Pigs store 3 times as many calories of what they eat as do other livestock (248). In contrast to other herbivores of equal body weight, a pig such as the Indian ***Sus cristatus*** may have as many as two litters of 4-6 piglets per year (36). Wild European hogs may produce a litter of 4-12 twice a year (71) and be sexually mature in 1½ years (240, 258) or as little as 8-10 months (85). They differ widely from other ungulates in having a gestation period of only 114-175 days and having large litters (85). "The rate of growth and development of the suckling pig surpasses that of all other farm animals . . . the young pig is almost unique among our farm animals in its ability to utilize feeding stuffs other than milk at a remarkably early age . . ." Suckling pigs begin to feed for themselves before they are three weeks old and they are capable of an independent existence at an age of six weeks (45). Even as far north as North

Carolina, wild pigs breed year-round (240). No information of like nature is available from other areas with bamboo mast crops. However, a herd of 1000 white-lipped peccaries has been reported from Paraguay (128) as have thousands of acres of mast-seeding bamboo (230). In Paraguayan Indian mythology, the bamboo was brought from the east by tajasu, the big wild pig (56). It appears that for a bamboo mast crop of 1-2 years duration, pigs could easily have both a nomadic and reproductive response.

Amazingly, there are only two specific records of Indian elephants (*Elephas maximus*) feeding on bamboo seeds (138, 165). However, there is no reason to suppose that they did not, since where they still run wild they are severe predators on grain crops. As late as 1874, wild elephants were still common in most of the large forests of India (129) and as late as the 1500s a herd in the Indo-Gangetic plains might have contained as many as a thousand (151). The yearly ivory input to England in 1831 and 1832 required the death of 4000-5000 elephants (128); thus there is little doubt that elephants were abundant. An adult Indian elephant can eat 600-700 pounds of green fodder per day (36). While it would be unlikely to consume this much of a concentrated food such as bamboo seeds [they require only about 60 kg per day of digestible vegetable matter (164)], the amount that a herd of elephants could eat is nonetheless very great. Their highly nomadic behavior could easily have resulted in heavy concentrations at a bamboo mast crop. Malcolm Coe told me that in the year of a mast crop of *Arundinaria alpina* on Mt. Kenya (1957), the hillsides in the bamboo stands were thoroughly covered with elephant trails; elephants are not normally encountered in this habitat in ordinary years. Elephants are also very fond of bamboo foliage (17, 164).

Other large mammals with a generation time too long to have a reproductive response to a bamboo mast crop probably removed substantial amounts of seed. *Rhinoceros* were common and widespread in India (36). Burmese *Rhinoceros sumatrensis* (= *Didermocerus sumatrensis*) "like most herbivorous animals, is very fond of the flower and fruit of *Melocanna bambusoides*, " and *R. sumatrensis* "wanders" for many miles (245). Such wanderings could result in a very large number of rhinos congregating at a mast crop, especially when the flowering and seeding takes several years. There were three wild species of Bos in India and Burma, and *B. gaurus* was once "found in all the larger forest-tracts of the Indian Peninsula from the Ganges to Cape Comorin" (37). From its very generalized diet, which included bamboo shoots (129), it likely fed on bamboo seeds when available (138). Thorn reported in 1935 (245) that "many animals gathered in these flowering patches of bamboo to gorge themselves on the pear-shaped fruit. I have known of village cattle gorging themselves on the fruit to such an extent as to die subsequently from the effects of overeating." The other numerous species of Indian bovids and cervids were also avid bamboo seed predators, if I may judge from the eagerness with which they decimate grain crops when the chance avails. It is mind-boggling to think what a herd of 8000 Indian *Antilopa bezoartica* (129) would have done to a bamboo mast crop. Numerous artiodactyls and perissodactyls were available as potential seed predators of the two African mast-cropping bamboos, *Oxytenanthera abyssinica* and *Arundinaria alpina.* Henkel (111) believed that the spiny fruits of *O. abyssinica* must have protected them from animals but this seems very unlikely in view of the spiny things eaten by many African herbivores. I would expect nonhuman primates to feed on bamboo mast, but there is only one record. Blue monkeys (*Cercopithecus midas*) in Zaire feed on *A. alpina* flowers and seeds (H. Schlichte, personal communication).

I expect carnivores to likewise congregate at bamboo mast crops to feed on superabundant prey. Local Burmese legend has it that tigers become more common in the year of a bamboo mast crop (274). Small predators congregated at the rat population explosions associated with Chilean *Chusquea* mast crops (98) and Japanese *Sasa* mast crops (244).

There are almost no reports of insect predation on bamboo mast crops. However, considering the imprecision with which vertebrate seed predators have been recorded for bamboo mast crops, insects may simply have been overlooked. An unidentified moth larva killed a large percentage of the developing seeds of an *Arundinaria tecfa* mast crop in North Carolina (119). The pentatomid bug *Ochrophora montana* purportedly destroyed all the *seed* of a *Dendrocalamus strictus* mast crop over 1200 square miles of Chanda District, Central Province, India (73), and the wild-collected seed of *Dendrocalamus longispathus* was found to be heavily attacked by insects (12). An unidentified insect drilled emergence holes out of the *Phyllostachys* seeds from Barro Colorado Island.

There is only one habitat that contains a mast-seeding bamboo yet appears to lack a substantial mammal population. *Chusquea abietifolia* in Jamaica exists in a very animal-poor habitat. Jamaica had, however, a complex mammal fauna in the past (157, 158, 227). Today it has only the very rare hutia *(Geocapromys brownii)*, which belongs to a genus with. a life history (64) that does not impress with potential for massive seed predation. However, it was once very abundant in Jamaica (258) and close attention should be given to the next Jamaican mast crop, due in 1979-1980 (Table 1).

There is no doubt that some mast crops are large enough to attract large numbers of animals. In India, there are records of 1200 square miles and of 96,000–104,600 acres of *Dendrocalamus strictus*, 6000 square miles of *Melocanna bambusoides*, 60 square miles of *Thyrsostachys oliveri*, more than 295 square miles of *Cephalostachyum pergracile*, 11 square miles of *Dendrocalamus hamiltonii*, and hundreds to thousands of square miles of *Bambusa polymorpha* in synchronized flower or seed (11, 82, 209, 235, 239, 263). It is unclear whether these old records are for somewhat natural stands, although I suspect they are. In Kenya there are stands of *Arundinaria alpina* of 63,000 hectares (18), 200 square miles, and 250 square miles (273). Seifriz (223-225) said that an area of *Chusquea abietifolia* ten miles long and extending from 4000 to 7000 feet elevation had a mast crop in Jamaica. 100,000 hectares of two species of Madagascar bamboos produced a mast crop in 1917, 1942, and 1965 (203). A Paraguayan tract of wild bamboo large enough to yield 200,000 tons of stems annually had a mast crop *(230)*. The *Arundinaria tecta* canebrakes of the southeastern United States still occupied many thousands of square miles in the late 1700s (109). Pure stands of mast-cropping *Sasa* cover thousands of hectares of Japanese national forests (183). In addition to these records, many old references refer to synchronized bamboo seeding over "large areas."

The variety of seed predators mentioned in the previous paragraphs makes it clear that the pattern and intensity of seed predation on a bamboo seed crop will vary strongly, depending on who arrives when. Likewise, there are traits of the seed crop itself that should influence the response of the seed predators once at the crop. When the seed biomass is divided into trillions of rice-sized grains such as those of *Dendrocalamus strictus,* the animals that can do very well on them may be quite different from those that do well when there are many fewer seeds each the size of a pear, such *as Melocanna, Ochlandra,* and *Melocalamus.* Cohorts that seed over only one year should produce different kinds of population explosions of seed predators than those that require 2-5 years to complete flowering and fruiting. For example, the very concentrated mast crops of *Melocanna bambusoides* in Assam produced massive emigrations of rats while the slightly less synchronized mast crops of sympatric *Dendrocalamus hookeri* and *Bambusa tulda* produced much less severe rat outbreaks; in the same habitat, *Cephalostachyum capitatum* mast crops did not produce any rat outbreaks at all (186).

A conspicuous trait of the animals postulated to be important bamboo seed predators is that they are extreme generalists and thus may be expected to have a maximum chance of surviving between mast crops (in space or time). In addition to living off of their fat deposits, "swine are a race that can subsist on almost anything placed within their reach" (128) (and see 51a, 85, 108,240). That rats and humans are omnivores requires no documentation. Chickens eat any small thing that moves or grows, as do jungle fowl and pheasants (6, 29, 30, 33, 112, 275). Pheasants can even exist on herbage alone (6).

A second important trait of these animals is that none have a social structure inimical to rapid population increase when food is abundant. Jungle fowl males just form bigger harems as females become more abundant (33), and tightly packed flocks may contain as many as 48 birds (65). Pigs and many species of rats obviously do not have strong behavioral barriers to great local abundance. Collared peccaries may have 50 or more individuals in a herd with amazingly little conflict among themselves (238); old world suids are generally not territorial (85). It is somewhat of a mystery how these animals know where to go to find a bamboo mast crop, but since the crop lasts many months, nomadic wandering would be moderately effective at locating bamboo seeds. Since jungle fowl males call loudly each morning to establish each other's presence, a domino theory of movement toward a bamboo seed crop seems in order.

In summary, there are numerous potentially important predators that can be selecting heavily against the tails of the bamboo seeding distribution, against small cohorts, and against sporadically flowering/fruiting individuals. They should maintain the synchrony of the mast crop within a cohort. However, I cannot find a single detailed documentation of this interaction. The best is offered by an unidentified Indian forest officer (68) who said in 1883 "the result of a general seeding of *Dendrocalamus strictus,* notwithstanding that vast quantities of the seed must be destroyed chiefly by rats and birds, and in unprotected forests by fire, is a dense mass of young plants which spring up after the first few showers of rain." I should emphasize that not only should the tails of the seeding distribution be preyed upon heavily, but the seeds of isolated clumps far out of phase should also be preyed upon heavily. However, there is only one direct observation: "in the Cochin State Forests one solitary clump of ***Bambusa arundinacea*** flowered and seeded. No other clump has seeded anywhere close by though the whole forest is about two miles as the crow flies from the forests where the bamboos have flowered, and this clump was bodily pulled down by wild elephants and the panicles eaten up" (165).

THE HABITATS OF MAST-SEEDING BAMBOOS

Wild mast-seeding bamboos do not appear to be distributed evenly through the global bamboo distribution, though virtually all tropical and subtropical areas now have one or more introduced species under cultivation or feral. All originate in subtropical or tropical habitats with conspicuous dry and/or cold seasons. The vast majority occur from India east through Burma, Thailand, and China (20, 38–40, 49, 62, 162, 224, 254). Burma has 42 species of bamboo (90), most of which probably have mast crops. Troup concluded in 192 1 that "so far as is known the vast majority of Indian bamboos flower gregariously" (250). On the other hand, Holttum (114) made the generalization that "the bamboos of the wet tropics usually do not die after flowering. Many of them flower at the end of leafy branches, some almost continually." Except for Jamaica, the several hundred species of bamboos of the American wet tropics are not noted for mast seeding (163). However, there are no detailed records of their seed production, and I suspect that many are also mast-seeding species. For example, the very common ***Chusquea subtessellata*** at 2800-3300 meters elevation in central Costa Rica has not had a mast crop between 1963 and 1975, but sporadic flowering was recorded in 1975. Local inhabitants say it flowers at about 15-year intervals. There are approximately a dozen mast-seeding species in South America, all located in midlatitude, subtropical, or tropical seasonal habitats (74, 78, 96, 98, 187, 230, 255). The mast-seeding species in Madagascar live in a seasonal habitat (203), as do the canebrake bamboos of the southeastern United States and the native bamboos of Japan.

In attempting to understand the habitats in which bamboo mast seeding evolved, I am unfortunate in that most of the old flowering or seeding records come from India, and "the destruction of natural habitats by man has been far more extensive and complete in India than perhaps anywhere else in the world" (15 1). In 1972 Khan (139) said of the most common mast-seeding bamboo in Madhya Pradesh: "The extensively occurring ***Dendrocalamus strictus*** forests are under a severe strain of local and industrial use. Local people residing around such forests are allowed a fixed number of bamboos annually either free or at a very nominal rate of royalty. Due to laxity in enforcing rigid administrative control over such extractions, bamboo forests have already been wiped out from many sizeable areas, and are in danger of annihilation from many more." "Bamboo, the major long fibered raw material resource for the pulp industry in India, is fast becoming scarce" (228). In 1903, several authors (143, 263) lamented that a mast seeding was due in wild Indian populations of ***Bambusa polymorpha*** and wasn't anybody going to take advantage of this marvelous opportunity to eliminate the bamboo and replace it with valuable lumber trees?!

The seed predators are very relevant parts of the mast-seeding bamboos' habitats; the ranges of most large wild animals in the Indian subcontinent have been reduced 90–99% during the past 200 years, with most of the change occurring within the past 100 years (36, 151). The jungle fowl is now classified as nonmigratory (54), although it still migrates in Thailand (13 1) and Ceylon (112), and was apparently highly nomadic in the old days. Habitat destruction has probably taken the major toll of these bamboo seed predators, but hunting may have contributed as well. Between 1895 and 1900, 1,149,354 pounds of bird feathers and skins (mostly pheasants and partridges) were exported from India. When export of skins was prohibited in 1902, two firms in Calcutta had on hand 6000 skins of argus and impeyan pheasants, and a single railway station to the north of Sind had exported 30,000 skins of black partridges in a few months. In 1909 someone attempted to smuggle a shipment of 823 jungle fowl skins out of Bombay (75). Beebe (33) refers to a harvest of 45,000 impeyan pheasants in the early 1900s. These birds are all potential bamboo seed predators. Perhaps in the wilder parts of the Himalayas, Burma, Thailand, and southern South America, enough bamboo seed predators still exist to allow us to observe their interaction with bamboo, but probably not on the scale that apparently led to the evolution of mast seeding.

Not only have the habitats been destroyed and the animals for the most part removed from them, but the bamboos themselves have been moved around so much that today it is difficult to determine in what microhabitats they lived and the structure of their interspecific synchronization. For example, in 1895 Nicholls what was proudly reported that he took seeds from an *1882* flowering of ***Bambusa arundinaria*** in Jubbulpore and raised young plants "which were distributed in great part along the Great Indian Peninsula line of Railway" (177). In 1908-1909, seeds of ***Dendrocalamus strictus*** and ***Bambusa arundinacea*** were obtained from different localities in and near the Central Provinces and used to establish a wide variety of plantations (204). As late as 1966, feral ***Phyllostachys bambusoides*** (a Chinese species) was found in the Indian foothills of the Himalayas (136). It was suggested in 1969 that the African ***Oxytenanthera abyssinica*** be introduced to India to replace forest understory vegetation with a valuable plant (229). Two species of introduced ***Phyllostachys*** cover 143,000 hectares of Japan (254), and there are 20,000 hectares of introduced ***Sinocalamus latiflorus*** in Taiwan (133, 260, 261).

The literature does allow the general and expected conclusion that different species of wild bamboos specialized on habitats such as riverside floodplains, peculiar soil types, dry hills, heavily forested sites, disturbed sites, etc (73, 79, 132, 148, 201, 207, 276). As might be expected of a plant that seeds only after a long interval and then dies, mast-seeding bamboos are extremely plastic and vigorous in vegetative growth and have very broad geographic distributions. ***Oxytenanthera abyssinica,*** for example, is native from Ethiopia to Rhodesia and across central Africa, from sea level to 2000 m elevation, and in almost all soils and areas with 3-7 month dry seasons; it tolerates 700-2000 mm of total annual rainfall (16, 18, 84, 111, 123, *170). Dendrocalamus srrictus* seems to have had a distribution from southern India all the way to the foothills of the Himalayas *(73). Arundinaria tecta* ranged from Maryland to Florida and across to the Mississippi River Valley (109, 163).

HOW LONG IS THE MAST CROP CYCLE?

It is evident from Table 1 that different species (and perhaps different cohorts of the same species) have different intermast periods. These range from 3 to 120 years; most are between 15 and 60 years. There are precious little data that simultaneously document the presence and the length of the mast crop cycle for a particular bamboo cohort, but the skimpy data are bolstered by a large body of circumstantial evidence. Ideally, I would like specific information on a particular cohort in its intact native habitat over a number of generations. Such information has never been gathered for bamboo (but *see Strobilanthes kunthianus* below). Additionally, I would like the same information for a cohort growing in a foreign habitat free from seed predators. The best record is Parodi's (185) from Argentina. He gathered seedlings from a 1923 flowering of *Guadua trinii,* kept track of them under a wide variety of garden conditions, and then recorded that they all flowered 30 years later at the same time as their parental population.

Records of wild plants are skimpy because 1. they take so long to accumulate, and thus one person is not likely to do it; 2. virtually all previous recorders of mast crops or fragments thereof have failed to note precisely which plants were seeding; 3. little or no distinction is made between native and introduced plants; and 4. there has been no motivation by virtue of the existence of a hypothesis to be tested with the data. However, Seifriz (223-225) did add 1948-1949 and 19 18 to an old record in 1884-l 886 (172) to document three successive mast crops of wild *Chusquea abietifolia* in Jamaica and obtain an intermast period of 30-34 years. Dutra's (78) records of 1901, 1916, and 1932 for *Chusquea tenella* in Brazil are probably for wild plants of one cohort (15 and 16 year intermast periods), as are his records of 1870, 1902, and 1934 for Brazilian *Bambusa riograndensis* (= *Guadua trinii) (*32 year intermast periods). For all the records of bamboo mast seeding in India, southeast Asia, and China, I have been able to find only three sets of data for at least three successive mast crops for a native bamboo cohort in situ. *Dendrocalamus srrictus* apparently had a mast crop in the Cachar Hills of Assam in 1879, 1922, and 1966 (43-44 year intermast period) (100), and in Uttar Pradesh in 1870,1909-1910, and 1949-1953 (39-40 and 39-44 year intermast periods) (102). *Melocanna bambusoides* had mast crops in Chittagong, East Pakistan in 1863-l 866, 1908-19 12, and 1958-1959 (42-49 and 46-5 1 year intermast periods) (116). However, enough records of two successive crops exist to give a good impression of how long the cycles will be when long-term records become available (Table I), if they ever do.

There are in addition, records from transplants of the Indian-Asian species of mast-seeding bamboos. *Phyllostachys henonis,* introduced from China in "ancient times," flowered in Japan in 8 13, 93 1, 1247, 1666, 1786, 1848, and 1908, which yields an intermast *period* of *59-63* years (135). *Bambusa arundinacea,* planted at Dehra Dun in northern India, had a mast crop in 1836, 188 1, and 1926, yielding an inter-mast period of 45 years (39, 42). Introduced to Brazil, a cohort of this species flowered in 1804, 1836, 1868, and 1899, yielding an intermast period of 3 l-32 years (78). This seed was most likely derived from a cohort of *B. arundinacea* different from that planted at Dehra Dun. Blatter (38) reported a mast crop of *B. arundinacea* on the coast of India in 1804; these plants could well have the same parental cohort as the plants introduced to Brazil. Finally, there is *Phyllostachys bambusoides* with its 120-year inter-mast period, described in the first paragraph of this paper. As described in the following section, there have been numerous introduced bamboos in midlatitude greenhouses and botanical gardens that flowered in synchrony with their parental cohort in its native (?) habitat, but very few of these have yielded published records of successive generations (largely because they rarely set seed).

One of the most serious problems in determining the length of the intermast period is that flowering records are very commonly made for the species rather than for cohorts of bamboos within a species. For example, Chattejee (58) reported mast fruiting by *Melocanna bambusoides* in 1863-1866, 1892-1893, 1900-1902, 1933, and 1960 in the Mizo Hills of Assam. If I treat the first two records as from one cohort and the last three as from another, the inter-mast period is about 30 years. If I treat them as all belonging to one cohort, I get two intermast periods of 30 years and one intermast period of 7-10 years, a period that barely allows attainment of adult size, to say nothing of having enough reserves to flower and fruit. Furthermore, the other records of *M. bambusoides* all show intermast periods of more than 40 years, so perhaps the Chattejee (58) records are for three different cohorts. Blatter (39) was particularly frustrated by this problem. He pointed out that there were mast crops of *Dendrocalamus strictus* in "Tharrawaddy," India in 1865, 1888, 1895, and 1912-1913. This yields a cycle of 23, 7, and 17-18 years, but he noted that "Tharrawaddy is a comparatively large area." It is likely that the 1895 flowering represents a different cohort than the 1865, 1888, and 1912-1913 mast crops. If this is so, the Tharrawaddy data give intermast periods of 23 and 24 years.

Finally, some of the records are undoubtedly based on synonyms and misidentifications. In 1900-l 901, Rogers (211, 2 12) cited a case where three locally named Indian "species" all turned out to be *Arundinaria falconeri*. In one case, even *Dendrocalamus longispathus* was apparently mistaken for *Melocanna bambusoides* (100).

WHAT IS THE INTERNAL CALENDAR?

As has been much debated and worried over in the reviews mentioned in the introduction, there is no convincing evidence that the intermast period is set by an external cue and no logical reason to believe that such an external cue has been overlooked, or even that there is one. It was frequently suggested in the older literature that the Indian bamboos seeded in the years of famine brought on by drought [e.g. (146)]. This idea has, however, been thoroughly discarded (49, 142, 224, 250). As Nicholls pointed out in 1895, "whereas coincidence [of famine and bamboo mast crops] attracts attention, the opposite condition passes unnoticed" (177). There are numerous cases where large bamboo seed crops were produced in normal crop years (186, 223, 224). There also have been severe drought years in which Indian bamboo did not fruit (49, 234). Since a bamboo clump that is going to flower does not produce new vegetative culms (stems) the year before (73, 142, 250), the decision to flower must have been entered into well before a drought at the time of seeding could occur. Furthermore, as discussed below, transplant experiments show clearly that weather cues are not involved in synchrony of most species of mast-seeding bamboos.

I assume here that bamboo mast seeding is timed by an internal calendar possessed by each member of the cohort. The only external feedback is the reestablishment of the cohort by an even-aged cohort each time a mast crop occurs, The intensity of synchronization (extent of even-agedness) produced by such a feedback system is directly related to the effectiveness of the seed predator community at pruning off the tails of the seeding distribution, and the rate of production of genetic and physiological variance by each bamboo species. No one has ever reported conducting a physiological search for the internal calendar in a mast-fruiting bamboo, although it might be done by growing bamboo in a bioclimatic chamber with foreshortened years. The various physiological changes reported in a bamboo at the time of flowering and seeding, such as reduction in starch and nitrogen content (133, 254), are those expected of any plant when it reproduces. The following account of the traits of the internal calendar should be of aid in a search for it, but the thing most needed, a wild cohort in situ with a known mast crop pedigree, is probably not available to any physiologist in the world.

1. The internal calendar is very well buffered from environmental impact both with respect to weather and photosynthate production. In 1867 Kurz (142) "observed in Burma pygmaean plants of tinwa (*Cephalostachyum pergracile*) of only about ½ to 1 foot height, which had been continuously burnt down by jungle fires, and which flowered together with their unhurt companions of 30 to 40 feet high!" In a mast seeding of *Dendrocalamus strictus* in Orissa in 1967 even plants only 2-3 feet tall flowered, and Singh (228) concluded "after close visual inspection of the dug up root stocks . . , that the so-called bamboo seedlings have been dying back repeatedly over a number of years, maybe 15-20 years in some cases, mainly due to the severe annual fires." Many species of mast-fruiting bamboos do not have their flowering timing perturbed by severe cutting or shipment of seeds or rhizomes to very different latitudes and climates (4,21,23, 24, 32,40, 41, 51, 73, 111, 133, 135, 172, 185, 198, 223, 224, 233, 243a, 250, 254). Indian "natives tell one that . . . however widely distributed may be the progeny of offsets deriving from any one general seeding, all the progeny and all the offsets must flower, seed, and die simultaneously" (177). In Japan, Ueda (254) concluded that for mast-seeding species, "all bamboos . . . of a rhizome system flower in the same stage even though rhizomes of the same group are separated and transplanted in different places." The *Phyllostachys bambusoides* in Chiba Prefectural Forest in Japan were planted from genetically different clones from various parts of Japan in 1923, yet they all flowered in the 1960s (182), roughly in schedule with the rest of the world. Offsets of *Arundinaria japonica*, introduced from Japan in 1850, flowered simultaneously at Bois de Boulogne, Sceaux, Marseilles, and Algiers in 1867-1868. *Arundinaria fal-*

cata flowered about 35 years after introduction from India in Brittany, Normandy, Luxembourg, Angers, Nantes, Algiers, Ireland, and Paris. *Phyllostachys flexuosa* brought from China in 1864 flowered at Hamma, Toulon, and Paris in 1876 (49, 250). *Chusquea abietifolia,* taken from Jamaica to England in the 1880s, flowered in synchrony with its parent cohort 4-5 years later (172, 223, 224). Argentinian *Guadua trinii* seedlings planted in optimal conditions of an arboretum and in the dismal conditions of a city park flowered in perfect synchrony with each other and their siblings back home 30 years later (185). On the other hand, "bamboos belonging to the group that have a different flowering stage do not flower in the same time even though in the same grove" (254).

Numerous authors have given examples where damage to mast-fruiting bamboos (burning, grazing, cutting, ditching, transplanting) apparently caused an advance in the length of the intermast period (3, 23, 32, 40, 49, 53, 73, 84, 89, 90, 94, 102, 142, 163, 168, 212, 261). Unfortunately, these reports are even more anecdotal than most of the data on which I am forced to rely. A Forest Officer in central India wrote in 1833 that "it is the opinion of natives, and one which is believed in by many Forest Officers and others, that seeding of *Dendrocalamus strictus* is prevented or retarded by heavy working" and that "steady working retards seeding may be fairly assumed from the fact that in the forests most worked, the seeding of the species is least common" (68). To prevent having all their bamboos die and flower at one time, Indian villagers were reported "to dig up a small portion of the stock with a shoot of the year, and plant it in the beginning of the rains. This method of cultivation is, of course, known wherever bamboo exists, but it is a fact which I have seen nowhere recorded . . . that though the rhizomes of both bamboos are of the same stock, the mother tree will flower and die long before the young plants" (83). On the other hand, Osmaston said that the small and lightly harvested forests of *D. strictus* have had no mast crops for 80 years (Punjab) but the adjoining private forests have been heavily worked and have had two mast crops at an interval of three years (73, and see 102). Such forests could well be planted forests with different seed origins, and such comments must be viewed in the light of Kawamura's and Ueda's conclusion that no degree of perturbation could alter the timing of the seeding and death of a number of native and introduced species of mast-seeding bamboos in Japan (135,254). Gupta (101) said that systematic cutting of bamboo causes flowering to occur early! Finally, I must stress that *D. strictus* is probably the most variable of all the Indian mast-fruiting bamboos. A few clumps are in flower almost every year [e.g. (102)]. While it may be that *D. strictus* has an internal calendar with an exceptionally thin shield, it is also possible that its complex use and cultivation by man may have genetically and geographically mixed the cohorts and severely relaxed the selection against poorly timed individuals.

2. Whatever the internal calendar counts, it must be contained in all the plant's parts, since the timing is maintained by the parts of a plant that has been fragmented. It cannot be measuring stored reserves, since the health and size of the plant within very large bounds does not affect the timing of the mast crop. The calendar must be the annual or daily accumulation or degradation of a temperature-insensitive photosensitive chemical. On the one hand, days or nights would seem easier to count

than years, but only 1/365 as many physiological events need occur if years are counted. In all parts of the world where bamboo grow, there is enough annual variation in daylength to count the passage of a year, especially if the timing of the count within that year is unimportant. It is particularly interesting in this context that accurate mast-seeding bamboos are unknown from closer than about 5 degrees from the equator. The closer to the equator, the more equal (and minimal) are the two annual cycles of day lengthening and shortening. The African *Oxytenanthera abyssinica,* which has cohorts with intermast periods ranging from 7 to 21 years, much sporadic flowering, and relatively unsynchronized cohorts (2, 16,81, 84, 11l), has a distribution bracketing equatorial Africa.

3. I expect the sensitivity of the internal calendar to perturbations to be proportional to the degree and predictability of the fluctuations normally experienced by the bamboo in its native habitat (124). Both transplanting and agroeconomic perturbations of bamboo cohorts have without doubt created environmental conditions more extreme than those that the physiological shields for the internal calendar were evolved to block. For example, if 95% of the individuals in a bamboo cohort are usually not at the edge of a dense monoculture of bamboo, the genome is not likely to have a good physiological shield against the extremes of productivity and desiccation that occur at the edges. Man's harvesting and clearing of bamboo stems may place 95% of the surviving plants at an edge.

There is only one recorded case where it appears that a species or cohort of bamboo may not be simultaneously buffered against two quite different environments. In the Mahandi basin (Orissa, inland from the Bay of Bengal) it was observed in 1922 (178) that

> on coarse-grained *dry* soils *Dendrocalamus strictus* generally flowers only sporadically in isolated clumps and not in groups or gregariously. On the other hand on moister soils, which are not however too moist for this species to thrive moderately well, simultaneous flowering over areas several hundred acres in extent is not uncommon. In or immediately after abnormally dry years gregarious flowering may be induced on all soils . . .

However, since I know nothing of either the patterns of pollen flow in the area or of the fate of seeds in the two adjacent and interdigitated habitats, it is impossible to know if this apparently bimodal behavior is adaptive, an unavoidable response by the plants, or due to seed and pollen flow between the two habitats (or even due to past introductions of *D. strictus*).

4. The internal calendar is without doubt a genetic trait. By transplanting rhizomes and seeds, humans have maximized the changes of intercohort and interspecific hybrids. Not only should this produce plants with altered intermast periods, but it should produce plants with altered physiological shields to environmental perturbations. The stock on which the physiologist does experiments must be very carefully chosen.

Just as with other genetic traits, it is reasonable to expect the calendar length and shielding to vary among some cohorts or populations. As Deogun concluded in 1936, when speaking only of *Dendrocalamus strictus,* "The cycle does appear to vary in different localities for the same species."

VARIATION OF INTERMAST PERIOD WITHIN A COHORT

There has never been a quantitative description of the seeding distribution of a bamboo cohort's mast crop. However, there is some information on the types of variation present.

1. As Kawamura (135) stressed, there is a distribution of flowering and seeding intensity within a mast crop-a concept largely ignored by all before and after in their documentation of bamboo flowering or seeding. He described the mast crop of ***Phyllostachys** henonis* (probably derived from a single introduction of seeds or rhizomes in ancient times, and now distributed widely in Japan) as beginning in 1903 and continuing until 1912. ***Phyllostachys** bambusoides* flowered over 31% of its range in Japan (introduced) in 1966, and the species as a whole began flowering in Japan about 1960 (1 81, 182). Here, it appears that the variation was due to different clumps (clones) within the cohort that were slightly out of phase with each other, but no attention is given to separating within- and between-habitat variation, or genetic versus phenotypic variation. These descriptions bring to mind one of the more debilitating of the flaws in how bamboo mast crops are recorded. No one has been careful to distinguish between the flowering time and the seeding time. Since a single clump of a mast-fruiting bamboo may require as long as a year from the initiation of flowering until the fall of the last seed, this imprecision makes it impossible to ask detailed questions about the variance in the intermast period for any species.

The causes of interclone intracohort variation in seeding time are potentially very diverse. *(a)* In the previous mast crop there may have been atypical selection against one portion of the seeding distribution. *(b)* There may be mutants for internal calendars of different length. Out of many thousands of seeds of ***Dendrocalamus strictus*** planted in March of 1895, 5 flowered and died in April-July 1896 (49). A seedling of ***D. strictus*** did the same (3). (c) There may be mutants for different physiological shields against the environment. *(d)* There may never have been sufficient selection to produce an internal calendar of more than a certain degree of accuracy, or it may be that to do so would be biochemically or physiologically impossible. (e) In introduced species, such *as **P.** henonis* and ***P.** bambusoides* in Japan, there may be no selection against the tails of the seeding distribution except when they get so far out of phase that failure of cross-pollination lowers the seed crop size. *(f)* In strictly agricultural circumstances, adults may be prevented from dying after seeding by fertilizing weakened rhizomes and protecting them from competition (e.g. 171, 182). I have no idea what sort of intermast periods such phenotypic monsters would have. (g) Finally, a cohort may be contaminated by seed and pollen flow from an adjacent conspecific cohort that is slightly out of phase.

2. A bamboo mast crop is generally "heralded" by scattered clumps (clones) of bamboo coming into flower in the previous year. This leading tail of the seeding distribution may be caused by the variation-inducing processes mentioned previously. For example, in **Prome** Division, Burma, a few quarter-acre clumps of ***Bambusa polymorpha*** flowered in 1913, and then in 1914, 3 square miles flowered (48). When *Arundinaria **maling*** had its first mast crop in living memory in the Eastern

Himalayas in 195 1, it was heralded by sporadic flowering in 1950 (208). Writers only rarely mention clones that are in flower an equal distance after the peak time of seed production. It is possible that they have not bothered with those flowering late in the mast crop because they are less spectacular than those that appear early after many years of vegetative growth. However, it is also possible that the trailing tail is foreshortened in comparison with the leading tail of the seeding distribution. If so, I expect this to be due to more intense seed predation on the trailing than on the leading tail. The trailing tail should be preyed upon by a full complement of starving local and nomadic seed predators and their offspring.

3. There are a few observations in India (14, 39, 49, 274) such as where the flowering of *Bambusa arundinacea* "has been observed to spread like a wave in a definite direction, taking a few years to extend over the whole flowering area" (250). Here, a peak in the seeding distribution can be defined only with respect to a specific piece of habitat and a cohort gets stretched in time. I find variance of this type most surprising and doubt that it is natural. However, it has been described for apparently natural *Bambusa polymorpha* forests in Burma (274). In continuous bamboo forest, animals that have built up on early-seeding plants should produce very intense predation on the seeds of the later-seeding plants. It is possible that the forests in which this was described were either planted or cultivated by man. Such a pattern could be generated by planting in temporal succession or by planting from seed derived from conspecific cohorts that are slightly out of phase with each other. On the other hand, wavelike flowering has also been described for *Oxytenanthera abyssinica* in Malawi (2, 63), where it is unlikely to have been planted. It makes one wonder about plant pheromones.

4. The best understanding of genetic variation in the length of the intermast period might be derived from introduced plants, but no records have ever been kept to this end. There are hints, however. *Arundinaria falconeri* was introduced as seed to Kew Gardens, England, from the Himalayas in 1847 (246) and all the plants seeded between 1875 and 1877. The adults from these seeds then produced a seeding distribution lasting from 1902 to at least 1907 (32). In the two following seedings, a 9- and 6-year spread were recorded (Table 1). A similar increase in range, perhaps owing to relaxed selection against the tails of the seeding distribution, might be responsible for the 5-12-year seeding distribution recorded for introduced *Phyllostachys* in Japan.

5. It has never been recorded, but there should be geographic variation in the location of the seeding distribution with respect to the seasons. While warm weather may allow the more tropical bamboo species to flower and seed at any time of the year [in tropical areas with severe dry seasons every month of the year has some tree species in full flower or fruit (86, 125)], there seems to be a seasonal pattern to bamboo mast seeding. In Japan the "tropical types" tend to flower in November to February and bear seeds in April and May (254). This would place the seeds on the ground within a month of the beginning of the monsoon (rainy season) in most parts of southern Asia. If the seeding distribution is to move backwards from this time, there must be compensations for any increased mortality that should occur through the seeds being on the ground during a greater part of the dry season and

therefore exposed to seed predators longer before germination. If it is to move forward from this time, the seedlings will have a shorter portion of the rainy season in which to become established before the next dry season arrives. Ueda also noted that *Phyllostachys* (primarily a subtropical genus) flowers in April through June and bears seeds through autumn in Japan. Again, a shift off of this timing could generate increased juvenile mortality through increased seed predation and inclement weather.

6. There is one source of variance that is very unlikely, and that is the variance that would be generated by seed dormancy of more than a few months. Bamboo seeds can be dormant for several months if kept dry (116, 268) but apparently no longer (there was a hasty rush to distribute bamboo seed whenever available in colonial India--see advertisements in the pages of the *Indian Forester*). In view of the potentially very strong selection against plants that bear seed in the tails of the seeding distribution, I would expect strong selection against seed dormancy of more than a few months duration if the internal calendar does not start running until germination. There is no evidence for dormancy in wetted bamboo seeds.

WHY IS THE INTERMAST PERIOD SO LONG?

To explain the length of the intermast period, I need first to hypothesize how the intermast period of a bamboo can lengthen and shorten. It is very unlikely to lengthen by gradual increments. A mutant that waits 1-2 years longer than the usual intermast period to bear seed may have difficulty outcrossing, and its seeds should fall into the mouths of many starving animals. If it flowers 5-10 years later than the mast crop, it is likely to have an insurmountable pollination problem. Even if it can self-pollinate, its seeds should be a major attraction for all local animals. A lengthened cycle appears possible only if the intermast period is doubled in the mutant genotype. This gives the new genotype the usual protection of seeding when its relatives are seeding. A genotype with a double intermast period would be favored because it should have twice as much reserve for seed production and thus lose a smaller percent of its seeds to the seed predators at each mast crop. This, however, requires that not all the major seed predators focus their attention on bamboo clones (clumps) that are bearing particularly heavily, or that the rhizomes of heavy bearers be well intertwined with those of light bearers. As the mutant comes to constitute a progressively larger proportion of the genome in the cohort, the plants with the parental (short) intermast period should make up a progressively smaller fraction of the cohort. Collectively, the parental type would be progressively less likely to produce a mast crop large enough to satiate the seed predators when they seed halfway between the seed crops of the new genome. Incidentally, this process could occur, although perhaps less successfully, with a bamboo mutant whose intermast period is 1.5 times that of the parent-every other mast crop would gain protection from its relatives.

An intermast period may be shortened by the following pattern of seed predation. When a mast crop begins, I expect heavy predation on the early tail of the seeding distribution. In many cases, nomadic animals should arrive shortly and locals should begin to multiply; thus the primary source of seed consists of those seeds that survive through straightforward predator satiation in the middle of the peak of the seeding. However, there may be some cases where the seed production builds up very rapidly, satiating the local animals before the nomads arrive and local reproduction can occur. This could result in the greatest proportion of surviving seeds coming not from the exact center of the peak of the seeding distribution but from the earlier (leading) side of the peak. The outcome of such an event would be a gradual shortening of the intermast period by a few months each time the seed predators were a bit tardy in accumulating. The same process would operate if the usual number of nomadic seed predators did not arrive because, for example, the cohort was too small to attract attention or it was accidentally synchronized with a much larger mast crop nearby.

It is important to understand the source of the variation on which the selection described in the previous paragraph is operating. If those clones that seeded just before the peak did so because of environmental plasticity rather than because they were mutants with slightly shorter internal calendars, the outcome of this pattern of seed predation would be a gradual shifting backward in time of the cycle, but no reduction in the length of the inter-mast period for the cohort. If the earlier seeding plants are mutants, then the intermast period should both shift backwards and become shorter.

If only the processes discussed above were responsible for the lengths of the intermast periods, I would expect the values in Table 1 to be rather uniformly distributed from very small to rather large numbers. However, there is a conspicuous shortage of intermast periods of less than about 15-20 years. A number of ecological processes come to mind that should result in the elimination of bamboo cohorts with short intermast periods. Such elimination is a kind of group selection, where the cohort can be viewed as the unit of selection.

1. A bamboo cohort with a short intermast period has a distinct chance of not having enough reserves accumulated to produce a large enough seed crop to satiate the local and nomadic seed predators. The definition of a "short" intermast period depends on: (a) the seed productivity of the species, (b) the seed productivity of the site occupied by the cohort, (c) the area1 extent of the cohort, and (d) the proximity in time and space of other cohorts. What is a "large enough" seed crop depends on: (a) the ability of the local guild of bamboo seed predators to eat seeds and reproduce on them, (6) the tightness of the seeding synchrony within the cohort, and (c) the conspicuousness or attractiveness of the cohort to nomadic seed predators. The combination of these factors should result in different inter-mast periods being optimal in different parts of the range of a widely distributed bamboo species, and should even result in interspecific geographic trends in the duration of inter-mast periods. "The clump forming species in tropical regions generally flower at shorter intervals than that of [midlatitude Chinese] ***Phyllostachys*** species" (254). Whatever the overall patterns with wild plants, the data in Table 1 generally suggest that intermast periods of less than about 15 years are generally not adequate to accumulate enough reserves for predator satiation. This conclusion is made more robust by the observation that there is always selection favoring cohorts with short intermast

periods just because they have a shorter generation time than those with long ones.

2. For a cohort with a short inter-mast period, the same seed predators that accumulated on the first crop may still be present for the second crop. However, the length of time for seed predator levels to fall to that before the mast crop depends upon the animal species. Small rodents should be down to precrop levels within a year or two, and it is doubtful if insects are going to be able to wait out a period of more than about 2-4 years between crops. However, large animals have longer life spans and it may take much longer for their density to fall to precrop levels. The reason for this delay is that the pulse of superabundant food provided by a bamboo mast crop may allow a large number of pigs, jungle fowl, porcupines, and other animals of similar size to make it through the difficult juvenile years. It is of interest here that, for maximum growth and muscle development, domestic pigs require feed supplements in addition to their mother's milk after 3 weeks of age (107). In nature, a bamboo mast crop could provide this supplement. Newborn pigs are a far smaller portion of the mother's body weight than is the case with other ungulates (85); the sow makes a very small initial investment, requiring a large pulse of outside resources to bring off a litter. Once pigs or jungle fowl have grown to adult size, they may be able to exist in a semistarved and rarely reproducing state for many years on food levels that would never have allowed their initial survival to adulthood. There are no records on the longevity of any of these animals in the wild, but domestic roosters can live as long as 24-30 years, hens 6–10 years (33, 120), and pigs live for 15-20 years (258).

Extension of a cohort's intermast period beyond 10–20 years is not likely to reduce the number of nomadic animals that arrive at the seed crop. If a cohort is so large that it occupies the entire range through which a nomad might move, then the nomad should probably be termed a local seed predator.

3. The presence of other mast-fruiting cohorts in the area should select against cohorts with short intermast periods for the following reasons.

(a) If a cohort should happen to produce a mast crop within l-2 years after that of a neighboring cohort, it will only survive if it has produced a much larger seed crop than the other species. The longer its inter-mast period, the larger its seed crop is likely to be.

(6) If a region contains two equal sized cohorts, one with a short intermast period and one with a long one, the long one is likely to eliminate the short one in the following manner. If the short one, with its smaller seed crop, should happen to seed just before the long one, it is less likely to eliminate the long one than in the reverse case. Each time it bears seed, the cohort with the long inter-mast period is guaranteed to have had the other cohort's mast crop a few years before. However, within every few generations by the cohort with the short inter-mast period, one of its small mast crops is guaranteed to have been shortly preceded by a very large seed crop.

(c) If a pair of cohorts with a short and a long inter-mast period start out perfectly timed so that they never seed near each other, a process described earlier should result in the demise of the cohort with the short intermast period. At each generation, the cycle should drift slightly backward in time, and/or gets slightly shorter in time. The cohort with the short inter-mast period will back up at a faster absolute rate than the cohort with a long intermast period. It is doomed to eventually find itself seeding for several cycles in the following tail of the seeding distribution of the cohort with the long intermast period.

In order to evaluate the possible mutual impact that cohorts may have on each other, I need some information on the degree of sympatry of cohorts of the same and different species. In most contemporary Asian habitats this is impossible because of man's movement of bamboos. There is not a single description of all the populations of various species of bamboos in any Indian or Asian habitat or area. There may be as many as 7 potentially mast-seeding species at one site: the Chittagong Hill Tracts in Bengal have commercially important (native?) stands of *Bambusa tulda, Oxytenanthera auriculata, Dendrocalamus iongispathus, Melocalamus compactiflorus, Teinostachyum bambusoides,* and *T. griffithii (59).*

There are a few incomplete records of sympatric mast crops. In 1904 there were three mast crops of *Melocanna bambusoides* in a "limited area" during a 12-year period in the Garo Hills of Assam *(239).* Since *M. bambusoides* has an intermast period of somewhere between 30 and 50 years (Table 1), these three records almost without doubt represent three conspecific and roughly sympatric cohorts. *Bambusa polymorpha* flowered in Burma in 1854, 1862, and 1871 (93); since each was at a slightly different site and since *B. polymorpha* has an intermast period of at least 50 years (Table 1), I suspect that this also represents three cohorts. In 1931 Parry (186) described an area in Assam where the most common species, *M. bambusoides,* had a highly synchronized mast crop about every 50 years and then about 12 years after this *Dendrocalamus hookeri* and *Bambusa tulda* both had a mast crop over about a four-year period. At another site in Assam, Parry said that *Cephalostachyum capitatum* mast crops were sympatric with those of *M. bambusoides,* but out of phase *Bambusa tulda* flowered in 1934 in the Sitapahar range of the Chittagong Hill tracts and in 1931 in Patiya range of the same tracts (13). Three species of bamboos produced mast crops in the Dehra Dun valley in 1836 and 1881 (42). However, this area has been an important source of commercial bamboo for hundreds of years and thus their synchronization could simply be the result of planting from seed of simultaneously flowering allopatric cohorts brought from elsewhere. Kurz (142) stated that "all three sorts of bamboo flowered at Simla in 1858." In Burma in 1916 there was at least one mast crop of *Melocanna, Oxytenanthera albociliata, Cephalostachyum pergracile, Dendrocalamus hamiltonii, D. strictus, D. longispathus, Bambusa tulda, B. pallida, B. arundinacea,* and *Thyrsostachys oliveri* (9). In eastern Brazil, there appear to be two common and locally allopatric species of *Merostachys* that are out of phase with each other by five years (96). In Japan, four apparently adjacent species of *Sasa* had a synchronized mast crop in 1954–1955 on Mt. Turugi (244). In Jamaica and the southeastern United States, there is only one species of mast-seeding bamboo each, and the Jamaican species seems to be made up of only one cohort as well. Incidentally, it is appropriate to add here that the presence of slightly allopatric mast-seeding bamboos with unsynchronized cohorts is the ideal circumstance for the evolution of eruptive nomadic behavior by seed predators.

Sympatry by mast-seeding bamboos is very much a matter of scale. At the level of the Indian subcontinent a mast crop was recorded for *Dendrocalamus strictus* every year but 12 between 1870 and 1934 (73). It is quite likely that many mast crops went unrecorded, especially since all 12 "sterile" years were before 1906. Between 1804 and 1896, there were 17 years in which ***Bambusa arundinacea*** mast crops were recorded in India (49). Six cohorts could produce this amount of flowering, since ***B. arundinacea*** appears to have an inter-mast period of about 30 years (Table 1). Except for 1855 and 1867, every year in India between 1850 and 1918 at least one bamboo species (and often many more) was recorded to have a mast crop (38). The same may be said of every year between 1958 and 1971(230).

On a smaller scale, Blatter (38) pulled together miscellaneous mast crop records for "Sikkim" for the following bamboos; ***Arundinaria aristata* (1895), *A. falconeri* (1876), *A. hookeriana* (*1848, 1868,* 1879), *A. maling* (1904), *A. polystachya* (1868), *A. racemosa*** (1857, ***1887,*** 1890, **1892), *Cephalostachyum capitatum*** (1848, 1866, 1874, **1878),** and ***Pseudostachyum poiymorphum*** (1857, ***189*1**). ***Ochlandra travancorica*** apparently has the exceptionally short intermast period of seven years, and where it lives in the foothills of the Himalayas, "different valleys flower at different times" (25).

There are cases where Indian conspecific cohorts are out of phase yet very close to each other. There is, however, no way of knowing if this is the result of humans moving them around. In 1895 Nicholls reported that south of the Acchankovil River, ***Bambusa arundinacea*** flowered in 1870 and north of the river in 1879-1880 (177). He also said that he saw different large patches of ***Dendrocalamus strictus*** seeding on the "same hills" 9 years apart. In 1918 most of the ***B. arundinacea*** in the Thekkadi leased forest of Tunacadaun Range flowered and seeded, but in the Cohin State Forests which touch the leased forest on the western side, they did not (165). In 1895 the ***Bambusa polymorpha*** forests in the watershed of the Pegu River in Thaukyeghat District did not flower but the cohort on the adjacent Yoma Range (watershed for the Irrawaddi and Hlaing Rivers) did (49).

WHY DOES THE PARENT DIE?

It is perplexing that the adult mast-seeding bamboos usually die after bearing seed in a mast year. The literature marvels over the phenomenon, but makes little effort to explain it. Nicholson (178) made the only real attempt by postulating that the adults die to remove the intense shade that they often cast, so that the seedlings of the bamboo can become established. It is certainly true that, following the death of a cohort, the light regime at ground level dramatically increases. There are, however, two problems-although perhaps not insurmountable ones-with this interpretation. First, its evolution probably requires that the seeds of an individual parent (clone, clump) usually end up directly below the parent. Otherwise, the individual parent would be dying to open a site for the offspring of other individuals, which is not too likely unless the members of a cohort are closely related (which they of course may be after many generations of inbreeding within a cohort). Second, the bamboo parent need not die to create an open area beneath itself. All it need do is drop its leaves for a year (as it does at the time of flowering) and live off reserves stored in the rhizomes or photosynthate from a few leafy stems.

I would favor a different interpretion of the death of the adult. There is obviously very heavy selection for producing a large seed crop in any mast-seeding species, and especially the bamboo. Only a small amount of resources could be saved to reestablish the adult after seeding. However, in a natural habitat it seems that a small amount of resource would not be enough to maintain an adult plant in the face of (a) competition with large numbers of its own seedlings and other species of plants, (*b*) the usual challenges by herbivores and diseases faced by adults, and (c) the unusual challenge of many herbivores attracted by the seed and seedling crop. For the adult plant to hold back enough resource to survive in this circumstance could seriously jeopardize the size of its seed crop. In this context, it is of great interest that some of the longer lived and larger species of bamboos will survive flowering if they are free of normal forest competition and fertilized heavily (171, 182, 251, 273).

There may also be a major physiological problem with a semelparous mast-seeding bamboo becoming iteroparous. It will not only have to have an internal calendar to tell it how long it has been since it germinated, but also it will need another calendar to tell it when it last flowered.

POLLINATION

There have been numerous places in the above paragraphs where it would have been appropriate to add in the pollination component of the interaction. However, this is impossible since there is no direct information as to whether bamboos are outcrossed, obligatorily or otherwise. The only detailed study of flower anthesis and phenology did not attempt cross-pollination but noted that self-pollinated plants did not set seed (191). They are apparently wind-pollinated since they have inflorescences like those of other grasses. There is even a report in 1895 of a “hay-fever”-like fever in areas of mass flowering (179). As might be predicted of a wind-pollinated plant (269), most of the mast-seeding species drop their leaves at the time of flowering rather than when they die some months later (2, 23, 92, 137, 142, 202, 223,239,250). One inflorescence may require as long as two weeks to flower as only 1 or 2 flowers per inflorescence open each day (193).

On the other hand there is a hint that bamboos may be at least in part insect-pollinated. Bodekar (43) recorded “bees” hovering around the flowers of ***Bambusa polymorpha*** in Burma, and Gunckel (98) suggested that a Chilean ***Chusquea*** was pollinated by wind “and by some small insects.” ***Bambusa polymorpha*** (Burma) and ***Chusquea abietifolia*** (Jamaica) have purple glumes with bright yellow anthers (48, 172) and a number of other bamboos have rather showy inflorescences. A number of the putative ancestors of bamboos have insect-pollinated flowers (236, 237). If some pollen flow can occur through insect pollination, it would tend to operate against synchronization of mast crops, since individuals slightly out of phase could be more readily pollinated.

It is possible to conclude from indirect evidence that mast-seeding bamboos are obligatory outcrossers. McClure (164), after a lifetime of experience with bamboos, concluded that it is common for bamboo to flower without setting seed but then went on to note that those that do set a lot of seed are usually wild plants. An isolated wild clump that is flowering well out of phase with the main mast crop may set little or no seed (68, 92, 93, 162). Such a clump is likely to be a clone based on a single seed. Most of the plants that McClure worked with were introduced or cultivated. In Taiwan, the approximately 40 species of introduced bamboos set very little seed when they flower (133, 260, 261). I interpret this to mean that they have been derived originally from very small samples from within a cohort. It seems likely that introductions will commonly be in the form of pieces cut from one large rhizome system or as seeds gathered from one point in a mast crop. The propagules will therefore have a high chance of not containing whatever type of heterozygosity is required for compatibility among offspring.

Pollination by wind may place a spatial constraint on obligatorily outcrossed bamboos. Most wind-pollinated woody plants grow in stands where it is commonplace for conspecifics to stand crown to crown. In like manner, it may be that clumps of bamboo that are spatially far from their cohort may suffer reduced pollination even if they flower in synchrony. The outcome of such a phenomenon may be to maintain the spatial as well as temporal integrity of the cohort.

When a small bamboo plant flowers but does not set seed, it is generally regarded as having failed to reproduce. However, if bamboo regularly outcross, such plants may be simply acting as males by reproducing in direct proportion to the amount of pollen they produce.

EVOLUTION OF MAST SEEDING BY BAMBOO

How might a mast-seeding bamboo have evolved in the first place? The most uncomplicated starting point would be annually iteroparous species that grew for a number of years before attaining reproductive maturity. The only population-level synchrony would be the timing of flowering within the year. There is one way that an individual of such a species can substantially increase its seed crop size. If, upon first reproduction, it puts all of its reserves into seeds, it is likely to produce a much larger seed crop than will its associates that are retaining a major part of their reserves for continued growth. The ecological circumstance that favors such a semalparous mutant would be a habitat where satiation of the small set of animals in the immediate vicinity of the mutant bamboo clump was an effective method of escape from seed predators. The most prominent cost levied against a semelparous bamboo would be that if seedling establishment were to fail that year, the mutant would be eliminated irrespective of how many seeds escaped the predators. I would thus expect such a mutant to survive first in tropical areas where the occurrence of the rainy season was fairly predictable, and where seed predators were highly territorial and did not allow territory decomposition in the presence of large amounts of food.

Once some such semelparous mutants exist, they may further increase their seed crop size by waiting a longer period before having their one and only seed crop. However, the population that contains them will have many fewer individuals in seed in any given year than will a purely iteroparous population, and thus the seed predators are likely to concentrate their activity on the few clumps (clones) in seed. This should make it much more difficult for a territory holder to keep the seed predator density down to a level whereby the animals in range of the clump are satiated. As the mutant comes to constitute more of the population, a disproportionate amount of the bamboo vegetative material in the habitat will belong to the mutant cohort. This means that, during years when it does not seed, there will be fewer total bamboo seeds and the parent genotype should be headed for local extinction. If there were any variance in the time to reproductive maturity by the individuals in the mutant cohort, it would be strongly selected against at this time. At this time, the intermast period of the dominant cohort will become the basic period, which, as I postulated earlier, will be doubled by mutation.

OTHER MAST-SEEDING PLANT GROUPS

The system that I have described for bamboo differs in a very important way from that of most mast-seeding trees. Oaks, beeches, conifers, and Dipterocarpaceae all display mast seeding in populations of adults of unequal ages and use environmental cues to synchronize their mast crops, which are produced by reserve materials stored since the last mast crop (110, 126, 141). These iteroparous perennials produce numerous seed crops during their life spans and require an external cue to become synchronized with the population as they attain reproductive size or age. The same kind of cue, such as an exceptionally dry spring, is then used repeatedly in later life.

However, there is one dicotyledonous group of widespread woody plants that behaves exactly as do mast-seeding bamboos. This is the acanthaceous genus ***Strobilanthes*** and related genera of the India subcontinent and southeast Asia. Owing to the taxonomic muddle over the generic delimitations of these plants (52,156), I refer to them here by one of their vulgar names, niloo [other names are the Sanskrit nelu (44), karvia, nillus nillu]. At least 50 out of several hundred species of strobilanthoids were known or suspected to have mast crops at the time of Bremekamp's 1944 revision (52) (cf 49, 188). Mast-seeding species of niloo are woody shrubs to small trees that grow as a cohort for a species- and perhaps cohort-specific intermast period of 3-16 years, flower and seed synchronously, and die (19,22,26,27,44,47, 52, 77, 88,92, 103, 104, 121, 156, 159, 160, 161, 169, 174, 184, 188, 197,215-219, 243,270,271). Other species in the same or related genera are iteroparous perennials (52). Within a cohort, plants of all sizes and health flower at the time of the mast crop (44, 188, 215, 217), but there are a very few individuals that flower in the year before (184), and even a few that flower completely out of phase (103, 104, 188, 197). The seeds display no dormancy (250). Transplants flower on time with the cohort from which they were removed (134, 188). The best set of records are for ***Strobilanthes kunthianus [= Phlebophyllum kunthianum, (52)]***. What is apparently one cohort of ***S. kunthianus*** flowered in the Nilgiris and Palnis Hills of southern India in 1838, 1850, 1862, 1874, 1886, 1898, 1910, 1922, 1934, 1946, 1958, and 1970, which establishes a precise 12 year inter-mast period for this cohort of this species (155, 156, 210). Two different cohorts of ***Strobilanthes sexennis*** in Ceylon have flowering pedigrees for 1857,1869,1881,1893, 1905, and 1917, and for 1850,1862, 1874, 1886, 1898, 1910, and 1922 (188).

A single cohort of niloo may cover an area of many square miles and be so dense as to appear to carpet the hills or forest understory with its blue flowers (88,92, 121, 188, 217). Several mast-seeding species of niloo may occur in the same habitat in India or Ceylon, and yet not be synchronized with each other (44, 188). Different but immediately adjacent cohorts of the same species can be out of phase (44, 188, 217). A number of the species have intermast periods that are even multiples of those of other species, suggesting that the period may lengthen by doubling.

There are two root parasites of niloo (*Campbellia*), one of which flowers and dies in synchrony with its host (189) and is thus a semelparous perennial parasite, and one of which is iteroparous (190) and probably survives by connecting up with roots of new seedlings as the parent niloo dies.

The seeds are oil rich and have been gathered as human food (134) and for poultry feed (70) in India. There are numerous records of jungle fowl congregating in very large numbers to feed on niloo crops (5, 29, 44, 70, 147, 149, 173, 188, 257), and Henry (112) stated:

> When nillu flowers and seeds in up-country [Ceylon] jungles, jungle fowl [*Gallus lafayettii*] migrate to these areas in large numbers to fatten on the abundant seed. They are also very fond of the seeds of the small hill-bamboo which, like the nillu, seeds only at long intervals. Like the jungle fowl [the Ceylon spurfowl, *Galloperdix bicalcarata*], numbers increase greatly in up-country in nillu-flowering years. The highest elevations are visited [by the very common Ceylon bronze-winged pigeon, *Chalcophaps indica*] only when nillu is seeding up-country (about once in eleven years), when it migrates to exceptional heights to feed on the seeds.

In 1917, Baker (29) cited Davison's comments that

> ordinarily, as already remarked, jungle fowl are found scattered; but when a tract of bamboo comes into seed, or any other particular food is locally abundant, they collect there in vast numbers, dispersing again as soon as the food is consumed. I remember on one occasion when the undergrowth of the Sholas about Pykarra [India] (which consists almost entirely of *Strobilanthes* sp.) seeded, the jungle fowl congregated there in the *greatest* numbers. I mean by hundreds, and were excessively numerous for more than a fortnight, when they dispersed, owing, I believe, not so much to the seeds having all been eaten, as to what remained of them having been sprouted and so become uneatable

In 1971, Matthew (156) said "The season of dispersal of [niloo] seeds was reported to have caused mass migration of jungle fowls from the foothills on the Nilgiris. These, however, are a memory of the past, with the area under the plant fast diminishing owing to denudation of virgin land for cultivation. The flowering of 1958, and more so that of 1970, was conspicuous for the absence of such visitors." There is one record of livestock feeding on the mature infrutescences (250) and no reason to believe that smaller mammals would not have gathered the seed. There is a hint that over-indulgence in the seed made Ceylonese jungle fowl and rats dizzy (44,112). There is a Javanese finch, *Serinus estherae,* which appears to be an obligate specialist on mast-seeding niloo seed and migrates from one mast-seeding cohort to another (26). Not only did niloo and bamboo share some important seed predators, but there is even one record in Burma where "the general flowering of bamboos ... has been followed by a dense growth of *Strobilanthes auriculatus* which threatens to exterminate the bamboo" (10).

The odoriferous (8) and showy blue to white or yellow flowers are insect-pollinated (8, 52, 196, 210, 265) and attract very large numbers of honeybees (apparently *Apis dorsata* in most cases) (149, 156, 210, 272). As Watt said in 1908, *Apis dorsata* the rock bee is in India "most prevalent in localities where species of *Strobilanthes* abound, and is reputed to move from one locality to another with the somewhat spasmodic flowering of the plants" (265). During the 1922 flowering of *S. kunthianus* there were as many as 28 *Apis dorsata* hives hanging from one eucalyptus tree near Kodaikanal (India) and 32 on an overhanging rock (210). The 1942 flowering of about 400 square miles of niloo on the Nilgiri Plateau "produced a huge invasion of the big rock bee which builds exposed combs. There were several hundreds of these combs hanging on the *Grevillea* shade trees of 100 acres of coffee near here. These bees undoubtedly follow the *Strobilanthes* flowering, as there have been no nests here at all this year (1944), though the country is full of the usual annual flowers and flowering trees" (272). After such an immigration in 1892, "most of these bees at high elevations perished during the frosts of January and February 1893, and the ground, in places, was covered with their dead bodies" (149). There was even a migration of honey-eating hill bears (*Melursus ursinus*) into the population explosion of bee nests recorded in 1934 (210).

To make the analogy with the Asian mast-seeding bamboos complete, some of the African perennial *Acanthaceae* are semelparous mast-seeding species. *Mimulopsis solmsii* has a mast crop every 9-10 years (69, 252) or 7 years (J. B. Gillett, personal communication) in Kenya. Gillett cited one case where the *M. solmsii* plants flowered seven years after the seed was planted. *Brillentarsia nitens* and perhaps *Mimulopsis solmsii* appear to seed in synchrony at greater than annual intervals in the rainforest around Fort Portal, Uganda, and their seeds are heavily preyed on by primates (W. Freeland, personal communication).

A few other tropical trees are semelparous and some even synchronized [e.g. *Spathelia excelsa* in Brazil (210a), *Cerberiopsis candelabrum* in New Caledonia (256)]. Phenological studies underway with *Tachigalia* (Leguminosae) in Panama suggest that there may be several sympatric cohorts of these rainforest trees with intra- but not intercohort synchronization. They produce a mast seed crop and then die after growing for many years into a large tree (R. Foster, personal communication). The semelparous talipot palm (*Corypha umbraculifera*) may have had an intermast period of 37–44 years in southern India, if the behavior of garden trees (130, 188, 247) represents that of wild plants in the natural dense stands in which they used to occur.

DISCUSSION

Throughout this paper I have been stressing the synchrony of the mast seeding bamboos. However, the most important bamboo in India, *Dendrocalamus strictus*, is particularly difficult to characterize. As has been mentioned, it has mast crops clearly originating from synchronized cohorts. However, it also is famous for populations (?) with a wide variety of intermast periods and for sporadic flowering. Mathauda (154) kept close track of the latter phenomenon, and between 1934 and

1947, the percentage of the clumps (clones) that flowered in five different parts of India was 31.6, 6.6, 3.8, 3.6, and 3.6, respectively (total clumps in each sample ranged from 500 to 900). Furthermore, of those clumps that flowered, 8%-27% survived flowering. To review the possible causes of this variability will highlight some of the more important points to emerge from the literature review in the previous pages. *D. strictus* rhizomes and seeds have been moved about India for at least 500 years and probably much longer; the chance of genetic and physiological mixing of cohorts is immense. *D. strictus* is the-most preyed on by humans, humans that should select against the center rather than against the tails of the seeding distribution of mast crops. Further, humans generally do not eat bamboo seedlings. This bamboo is the most widespread in India, with respect to both geography and habitat type. This versatility may be the product in part of human activity and therefore be subjecting the bamboo to physiological stress it is not set up to handle. On the other hand, it may not be possible to make a physiological system that functions well in intracohort synchrony in all habitat types, or, it may be that there are (were) many cohorts of *D. strictus,* each adapted to its own peculiar combination of habitat and seed predators. That some *D. strictus* survive after flowering may be simply due to human care of plantation clones, or it may be that a widespread bamboo species finds itself occasionally in habitats that especially favor the survival of badly weakened adults. In short the difficulties that attend interpreting *D. strictus* are the same ones that attend interpreting the behavior of any mast-seeding bamboo or other tropical plant. The old literature does not contain the definitive data, and contemporary habitats do not allow us to gather that data.

My interpretations of the interactions between mast-seeding semelparous perennial plants and seed predators are of economic importance in determining how and which seeds and rhizomes should be drawn from a native bamboo population if a new self-perpetuating plantation is to be established. All the Asian bamboo species of major economic importance are mast-seeding species. As foresters pointed out long ago (e.g. 35,250) the vulnerable time in a bamboo's (and niloo's) life is the year of the mast crop. It is at this time that seedlings of other plants get their chance, and at this time man has the chance to create or destroy a monoculture of a mast-seeding species. In addition, the interaction itself is of great historical importance, since we may well have the bamboo (and other mast-seeding species) to thank for the ease of domestication of the chicken, rat, and pig. Man has simply replaced the mast crop with farms and their annually **masting** fields of grain.

In 1927, Kawamura concluded somewhat dejectedly that "I am compelled to believe that the periodical cicadas and some bamboos are remarkable representatives of living things which have special characteristics of periodical as well as simultaneous reproduction, and that this emergence has no relation to climate, soil or any other external conditions" (135). Recent papers on periodical cicada evolutionary biology (80, 144) reveal no conspicuous qualitative difference between these insects and bamboo (and niloo) except perhaps in the way they physiologically count years. After all, it was for the interaction between cicadas and their predators that the term "predator satiation" was invented.

I caution the reader at this point to note that it has not been demonstrated that predator satiation is the natural selection process that has produced extreme supra-annual synchronized semelparity in bamboos. I offer predator satiation as a hypothesis, a hypothesis that could be tested by field biologists fortunate enough to witness bamboo mast-seeding in habitats with approximately natural complements of seed predators. Such biologists need to record the fraction of the seeds that are eaten throughout the seeding distribution. To demonstrate that predator satiation is operating, they have to show that the seed predators take the smallest percentage of the seeds somewhere in the central portion of the seeding distribution and the largest percentages of the seeds in the tails of the distribution. Of special importance are seeds that fall very far out in the tails; these indicate that there were enough plants in flower for cross-pollination to occur (provided that cross-pollination is necessary). If they are heavily preyed on, this supports the idea that selection for synchronization merely to ensure pollination is unlikely to have been the only driving force for the synchronization. Of equal importance is the establishment in many long-lived botanical gardens of a number of bamboo cohorts from large seed samples from one and from many parents, followed by careful records over the years of the timing of their flowering, that of their children, grandchildren, etc. Special attention should be given to documenting any changes in the variance of the intermast periods for these cohorts not under selection by herbivores. If bamboos are too daunting a prospect for such a program, niloo would make an adequate substitute.

I conclude by noting the inadequacy of the data presented in my review of bamboo and niloo evolutionary biology. Again, I defend a review at this poor state of the art with the simple fact that it is now nearly impossible to gather most of the critical information needed to answer most of the questions I have posed. The species may not yet be extinct, but the interaction is.

ACKNOWLEDGMENTS

This study was financially supported by NSF GB 35032X and BMS 14268, but could not have been completed without the services of the Oxford Forestry Library and the library of the Edward Grey Institute, Oxford. The following persons were most helpful in commenting on the manuscript, the ideas, and in finding obscure references: D. Adams, J. Adams, C. Augsperger, H. G. Baker, I. Baker, W. Benson, E. Bünning, B. L. Burtt, R. Carroll, M. Coe, N. E. Collias, H. S. Dybas, J. F. Eisenberg, R. Foster, J. Fox, W. Freeland, J. B. Gillett, P. J. Greenway, G. Hughes, D. Janos, J. S. Keesing, E. Leigh, M. Lloyd, D. McKey, S. Miller, E. Moore, R. A. Morse, M. Numata, G. Orians, M. J. Parrot, C. M. Perrins, C. M. Pond, G. R. Proctor, D. Rabinowitz, P. W. Richards, R. Rickson, W. Schaffer, T. Soderstrom, 0. Solbrig, J. Straugh, B. Tomlinson, J. Vandermeer, J. L. Vial, and A. Winfree.

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