

Reproductive Phenology of *Cryosophila warscewiczii* in Central Panamá

GREGORY H. ADLER, SCOTT A. MANGAN, AND THOMAS D. LAMBERT

Department of Biology and Microbiology, University of Wisconsin–Oshkosh, Oshkosh, Wisconsin 54901 USA

Palms have been the focus of numerous phenological studies, and many different reproductive patterns have been identified. In areas that experience seasonal changes in precipitation, most species appear to have distinct reproductive seasons (Kahn and Granville 1992). However, some species do not appear to be constrained to seasonal reproduction (Henderson 1995), and even in those species that reproduce seasonally, considerable variation exists within populations. For instance, DeSteven et al. (1987) studied reproductive phenologies of 13 species of palms in central Panamá and described species according to their degree of flowering synchrony. Of the 13 species, three showed highly synchronous flowering, six were moderately synchronous, and four showed little flowering synchrony. Despite the attention paid to palms, the reproductive phenologies of most Neotropical species remain poorly known.

Cryosophila warscewiczii (H. Wendl.) Bartlet is a solitary subcanopy palm that is found in lowland forests from southern Nicaragua to central Panamá (Evans 1995, Henderson et al. 1995). This species attains a height of 10–15 m (Croft 1978, Evans 1995, Henderson et al. 1995), with heights of reproductive individuals exceeding 5 m (DeSteven et al. 1987). Croft (1978) notes that flowering occurs from May to October and that fruits develop between August and December in Panamá. The mostly round fruits are 1–2 cm in diameter, are white when mature, and enclose a single globose seed (Croft 1978, Uhl and Dransfield 1987). Henderson (1984) identified two genera of beetles as probable pollinators of this palm (listed as *Cryosophila albida*) in Costa Rica. DeSteven et al. (1987), based on a study of only four individuals, found this species to display high intrapopulation flowering synchrony. Because little else is known of the reproductive phenology of *C. warscewiczii*, we present results

of a four-year study of the reproductive phenology of 137 marked individuals on a small island in the Panama Canal.

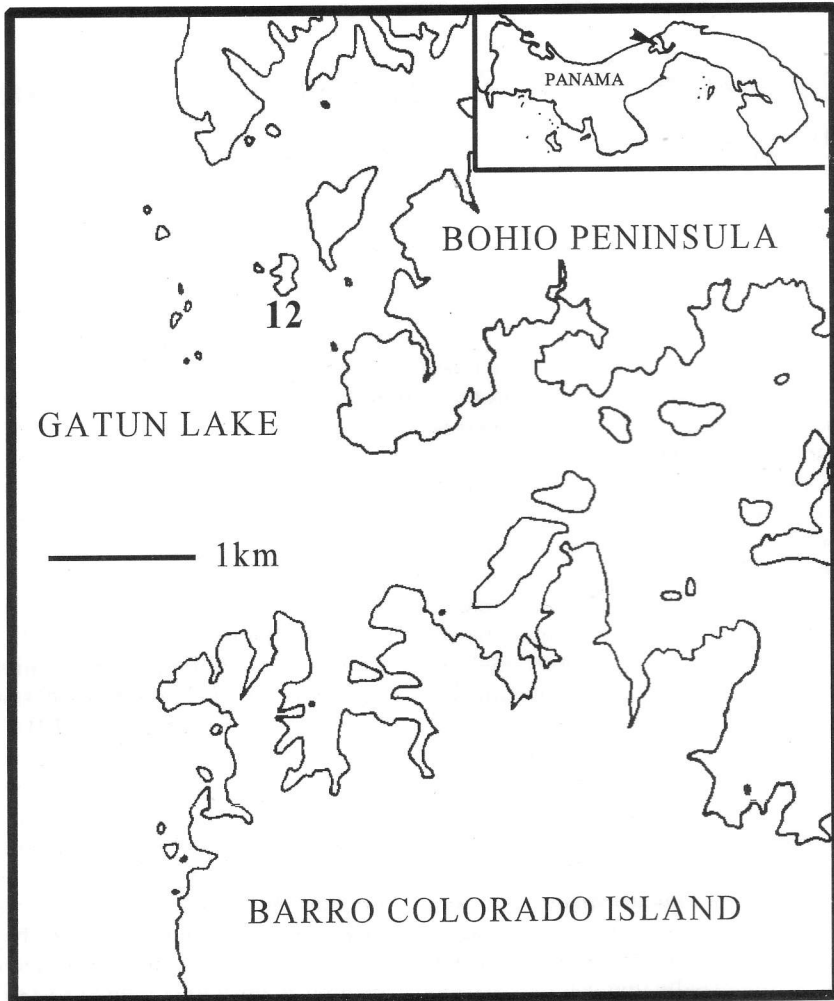
Study Area

The study area was a 1.8-ha island in the Panama Canal (Fig. 1) and was located 2 km north of Barro Colorado Island (BCI), where DeSteven et al. (1987) and Croft (1978) studied the reproductive phenology of *C. warscewiczii*. This island (locally known as Chicha and designated as Island 12 by Adler 1994) was formerly a hilltop that was isolated in 1914 by the rising water levels of Gatun Lake. The lake was created when the Chagres River was impounded during construction of the Panama Canal.

The study island is covered now with second-growth tropical moist forest. *C. warscewiczii* is the third most abundant arborescent plant of mature size on the island and is by far the most abundant palm, forming dense stands composed of both mature and immature individuals. The climate of the area is strongly seasonal, with an eight-month rainy season that is punctuated by a shorter but severe dry season. Less than 10% of annual precipitation falls during the dry season from mid-December until the end of April. Mean annual rainfall on BCI this century is 2612 mm (standard deviation = 446 mm) (Windsor 1990).

Methods

We marked 129 individuals of *C. warscewiczii* of reproductive size in 1991. A serially-numbered aluminum tag was affixed to each individual with grafting tape. We marked an additional four individuals in 1992, one in 1993, and three in 1994. Two marked individuals died between 1992–93 and 1993–94. We also established a permanent grid that covered the entire island, with 20-m intervals between adjacent points within the grid. Marked palms were then mapped



1. Location of the study island within the Panama Canal. The inset shows the location of the study area in central Panamá.

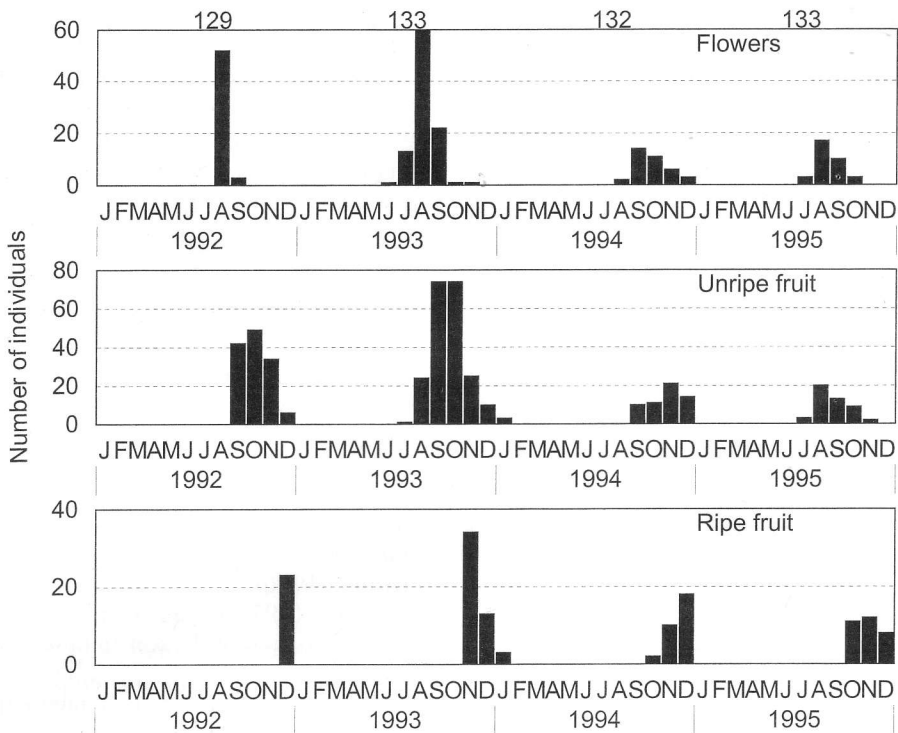
onto this grid. Marked individuals were censused every month from April 1992 through December 1995, and the numbers of inflorescences and either unripe or ripe infructescences produced by each individual were recorded.

We began the analysis by tallying the total numbers of individuals flowering and bearing unripe and ripe infructescences each month. We constructed contour maps of the total number of individuals marked over the four-year period and of the total numbers of individuals bearing ripe infructescences each year. We compared proportions of individuals that produced ripe infructescences (a measure of annual reproductive output) among years by constructing a linear model for repeated measures categorical (count)

data. We also constructed yearly histograms showing the numbers of individuals bearing a given number of ripe infructescences. We compared these numbers among years by again constructing a linear model, with categories represented by 1, 2, 3, or ≥ 4 ripe infructescences. In 1992, no individuals produced more than three infructescences. Because a count of zero prohibits complete parameter estimates, we replaced this zero with a one (Kleinbaum and Kupper 1978).

Results

C. warscewiczii showed only one reproductive period per year within this dense stand (Fig. 2). More individuals flowered in August than in any



2. Monthly numbers of individuals flowering and bearing unripe and ripe fruits. Numbers at the top of the figure indicate the total numbers of marked individuals each year.

other month each year, except in 1994 when more individuals flowered in September. The flowering season was longest in 1993, and lasted from June through November. Unripe fruits were present from July through January, although most unripe fruits were present from September through November. Ripe fruits were present from October through January, but within any given year ripe fruits were present for a maximum of only three months.

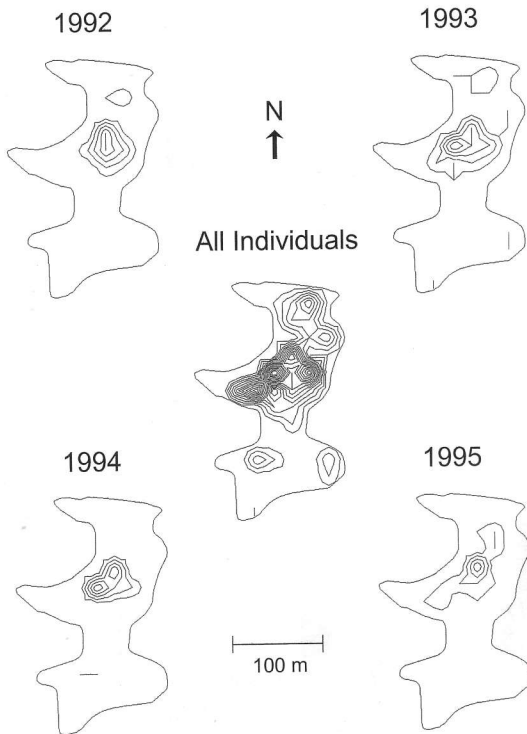
The distribution of mature individuals varied spatially, with the highest densities near the center of the island (Fig. 3). Lesser concentrations also occurred in the southern and northern portions of the island. The distribution of fruiting individuals varied both spatially and temporally (Fig. 3). Fruiting individuals were concentrated in the center of the island (where mature individuals were densest) during each of the four years, but other areas showed varying numbers of fruiting individuals across years, particularly in 1993.

Proportions of individuals with ripe fruit statistically varied among years (0.18 in 1992, 0.31 in 1993, 0.16 in 1994, and 0.17 in 1995 $\chi^2 =$

11.49, $df = 3$ $P = 0.0094$), which was due to the higher level of fruiting in 1993. The number of ripe infructescences borne by a single individual ranged from one to six (Fig. 4), and the counts of individuals within each infructescence category varied among years ($\chi^2 = 19.34$, $df = 9$, $P = 0.0225$). Individual production was least in 1992 and 1994, when one was the modal number of ripe infructescences. Production was greatest in 1993, when three was the modal number of ripe infructescences.

Discussion

Individuals within this dense stand of *C. warscewiczii* demonstrated highly seasonal reproductive activity, and our results corroborate those of DeSteven et al. (1987) with respect to the high level of flowering synchrony. Thus, most flowering occurred in a brief period of only two or three months centered around August. DeSteven et al. (1987) noted a mean period of two months in which individuals bore ripe fruit. In our much larger sample of individuals, we found a mean period of only 2.5 months in which individuals bore ripe fruit.



3. Contour maps of the spatial distribution of the total number of marked individuals over the four-year study period (central map) and yearly densities of individuals producing ripe infructescences. Each contour interval represents one palm.

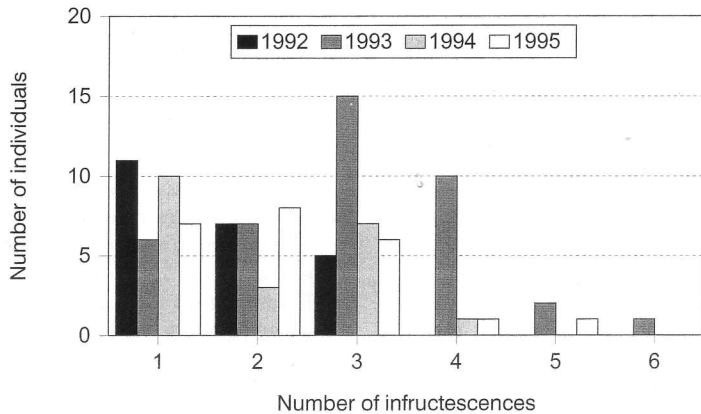
With respect to individual reproductive performance, DeSteven et al. (1987) found that the number of inflorescences produced per individual within a year ranged from only one to three. By contrast, we found a range of one to six ripe infructescences produced per individual within a year. However, a smaller percentage of plants out of the total pool of mature individuals produced ripe fruit in our study (21% vs. 43% in DeSteven et al. 1987). Fruit production over the four-year period varied and was greatest in 1993. While the causes of variation in individual reproductive output remain unknown, we suggest that pollinator diversity and abundance relative to the high density of mature individuals may be lower on this small island than on Barro Colorado Island. A lower pollinator diversity and abundance could account for the smaller percentage of individuals producing mature fruits. Temporal changes in pollinator abundance could also explain the higher fruit production in 1993.

The number of ripe infructescences serves only as a crude index of individual reproductive performance. Seed germination, seedling establishment, and recruitment into the mature age classes ultimately determine individual reproductive success. Seed and seedling predators may have a substantial impact on reproductive success. Rodents are often important predators of palm seeds (Vandermeer 1979, Hoch and Adler 1997, Adler and Kestell 1998). The only species of rodent present on the study island is *Proechimys semispinosus* (Central American spiny rat). *P. semispinosus* have been shown to eat not only the fruits but also the seeds of *C. warscewiczii* (Adler 1995). A year-long study of this rodent on Island 12 in 1991 revealed a mean density of 43.1 individuals/ha, with a maximum of 58.3/ha (Adler 1996). These densities are by far the highest yet recorded for this species (Adler 1996). Continuous monthly censuses through 1997 further demonstrate persistent high densities of *P. semispinosus* (unpublished data).

We observed enormous numbers of seeds destroyed by this rodent during each year of the present study. *P. semispinosus* are also abundant and widely distributed throughout the range of *C. warscewiczii*, and we therefore suggest that this rodent is an important determinant of seed survival of this palm. *C. warscewiczii* fruit at the time of lowest community-wide fruit production in central Panamá (Foster 1982). This phenology may render seeds particularly vulnerable to attack by granivorous rodents such as *P. semispinosus* because of low resource availability. However, such rodents may also serve as palm seed dispersers (Forget 1991, Adler and Kestell 1998), and *C. warscewiczii* may experience little competition with other plant species for rodents to disperse seeds. A complex interaction between fruit production and rodent density may therefore largely determine ultimate individual reproductive success of this palm. Further study of the interaction between *C. warscewiczii* and its pollinators and seed predators and dispersers such as *P. semispinosus* would further elucidate determinants of individual reproductive success.

Summary

We studied the reproductive phenology of *Cryosophila warscewiczii* by conducting monthly phenological censuses of 137 marked individu-



4. Yearly numbers of individuals bearing a given number of ripe infructescences.

als on a small island in the Panama Canal. Censuses were conducted from 1992 through 1995. Flowering occurred from June through November but was generally greatest in August. Ripe infructescences appeared from October through January, but within any given year ripe fruits were present for a maximum of only three months. The distribution of fruiting individuals varied spatially and temporally. Production of ripe fruits was greatest in 1993. The number of ripe infructescences borne by a single individual varied from one to six, and the modal number of infructescences varied yearly. We suggest that temporal changes in pollinator diversity and abundance may account for temporal differences in reproductive performance. We further suggest that ultimate reproductive success is strongly influenced by rodent seed predators.

Acknowledgments

We thank Nicole Casteel, Mark Endries, and Andrew Roper for help in the field. This study was supported by grants from the National Geographic Society (4893-92) and the National Science Foundation (DEB9628943) to GHA, and the Smithsonian Institution Scholarly Studies program to Egbert G. Leigh, Jr. and GHA.

LITERATURE CITED

- ADLER G.H. 1994. Tropical forest fragmentation and isolation promote asynchrony among populations of a frugivorous rodent. *J. Anim. Ecol.* 63:903-911.
- ADLER, G. H. 1995. Fruit and seed exploitation by Central American spiny rats, *Proechimys semispinosus*. *Stud. Neotrop. Fauna Environ.* 30:237-244.
- ADLER, G. H. 1996. The island syndrome in isolated populations of a tropical forest rodent. *Oecologia* 108: 694-700.
- ADLER, G. H., AND D. W. KESTELL. 1998. Fates of Neotropical tree seeds influenced by spiny rats (*Proechimys semispinosus*). *Biotropica*, in press.
- CROAT, T.B. 1978. *Flora of Barro Colorado Island*. Stanford University Press, Stanford, California, 94305 USA.
- DE STEVEN, D., D. M. WINDSOR, F. E. PUTZ, AND B. DE LEON. 1987. Vegetative and reproductive phenologies of a palm assemblage in Panama. *BIOTROPICA* 19:342-356.
- EVANS, R. J. 1995. Systematics of *Cryosophila* (Palmae). *Syst. Botany Monogr.* 46:1-70.
- FORGET, P.-M. 1991. Scatterhoarding of *Astrocaryum parmaca* by *Proechimys* in French Guiana: comparison with *Myoprocta exilis*. *Trop. Ecol.* 32:155-167.
- FOSTER, R.B. 1982. The seasonal rhythm of fruitfall on Barro Colorado Island. In: E.G. Leigh, Jr., A. S. Rand, and D. M. Windsor (eds.). *The ecology of a tropical rain forest: seasonal rhythms and long-term changes*. Smithsonian Institution Press, Washington, D.C., pp. 151-172.
- HENDERSON, A. 1984. Observations on pollination of *Cryosophila albida*. *Principes* 28:120-126.
- HENDERSON, A. 1995. *The palms of the Amazon*. Oxford University Press, Oxford, UK.
- HENDERSON, A., G. GALEANO, AND R. BERNAL. 1995. *Field guide to the palms of the Americas*. Princeton University Press, New Jersey, USA.
- HOCH, G. A., AND G. H. ADLER. 1997. Removal of black palm (*Astrocaryum standleyanum*) seeds by spiny rats (*Proechimys semispinosus*). *J. Trop. Ecol.* 13:51-58.
- KAHN, F., AND J.-J. GRANVILLE. 1992. *Palms in forest ecosystems of Amazonia*. Springer-Verlag, Berlin, Germany.
- UHL, N. W., AND J. DRANSFIELD. 1987. *Genera Palmarum: a classification of palms based on the work of Harold E. Moore, Jr.* Allen Press, Lawrence, Kansas, USA.
- VANDERMEER, J.H. 1979. Hoarding behaviour of captive *Heteromys desmarestianus* (Rodentia) on the fruits of *Welfia georgii*. *Trop. Ecol.* 20:17-26.
- WINDSOR, D. M. 1990. Climate and moisture variability in a tropical forest: long-term records from Barro Colorado Island, Panama. *Smithson. Contr. Earth Sci.* 29:1-145.