

## Temporal and Geographic Variation in Predispersal Seed Predation on *Hibiscus moscheutos* L. (Malvaceae) in Ohio and Maryland, USA

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**ABSTRACT.**—Seed predation has the potential to strongly reduce seed production and thereby act as a selective force on the evolution of flowering traits and other defenses against herbivory. We characterized levels of predispersal seed predation on *Hibiscus moscheutos* (Malvaceae) during 2001 and 2002 at four sites in Ohio and Maryland, USA. The seed predators were a weevil, *Conotrachelus fissinguis* (Coleoptera, Curculionidae) and a bruchid beetle, *Althaeus hibisci* (Coleoptera, Bruchidae). The weevil occurred at three of the four sites and damaged 24% to 94% of fruits in these populations. The bruchid occurred at all four sites, where it destroyed 4% to 27% of the seeds. Seed predation varied between years and among sites for both predators and year-by-site interactions were common. Variation in predation levels indicates that seed predators did not influence this species uniformly, but they were often abundant and sometimes destroyed nearly all of the seeds produced. At one of the Ohio sites, we assessed levels of seed predation at 5-d intervals during the 2001 flowering season. At this population, bruchid damage was greatest for seeds produced by flowers that opened in late July, when flowers were scarce, whereas weevil damage was greatest in mid-August and coincided with peak flowering. The timing and greater extent of weevil damage suggest that they may have a greater effect on plant fitness than bruchids.

### INTRODUCTION

Seed predation can influence plant populations by limiting seed output and reducing seedling recruitment (De Steven, 1983; Greig, 1993; Ehrlén, 1996; Brody and Mitchell, 1997; Sperens, 1997; Hemborg and Després, 1999). By acting directly on fecundity, seed predation has the potential to be an agent of natural selection and plants may ultimately evolve strategies to circumvent seed predators. In addition, if a population is seed-limited, seed predation might influence population size and the spatial distribution of plants. Characterizing the extent of seed predation within and among populations can aid in understanding the evolutionary forces that shape these populations and the demographic parameters that affect population dynamics (*e.g.*, Louda, 1983; Louda and Potvin, 1995; Froberg and Eriksson, 2003).

The potential impact of seed predation on plant populations and their evolution can be substantial. For example, Kaye (1999) demonstrated that predispersal seed predation limited seedling recruitment of the rare mountain perennial, *Astragalus australis*, and was a previously undetected impediment to conservation efforts. Seed predation can also influence the evolution of floral displays and flowering phenology. Brody and Mitchell (1997) found that artificially increasing the number of flowers per plant caused greater seed predation in *Ipomopsis aggregata*. In addition, the direction of phenotypic selection on calyx

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length differed between pollinators and seed predators in this species (Cariveau *et al.*, 2004). Thus, opposing selective pressures from pollinators vs. seed predators may act on floral characteristics. Mahoro (2002) reported that later flowering plants experienced higher levels of seed predation than earlier ones in *Vaccinium hirtum* populations, while Pilsen (2000) found that wild *Helianthus annuus* plants that flowered late in the season, when key seed predators were scarce, had higher fecundity than neighboring plants that flowered earlier. These studies suggest that seed predation could influence selection on flowering time, which is a heritable trait in *H. annuus* (Pilsen, 2000). Different predators may predominate in different regions, setting up distinctive regional selection pressures and corresponding evolutionary responses.

*Hibiscus moscheutos* L. (Malvaceae) often experiences high levels of damage from predispersal seed predators (Cahoon and Stevenson, 1986; Spira, 1989; Kudoh and Whigham, 1998) and, thus, is a convenient species for studying temporal and spatial variation in seed predation. Kudoh and Whigham (1998) manipulated petal size in *H. moscheutos* and found that although seed predators were attracted to larger flowers, flower size did not affect levels of seed predation. By knowing the intensity, among-population variability and timing of the impacts of the major predators, it may be possible to infer whether it is likely that the observed predation could exert selection pressure on related aspects of floral biology. This could include, but not be limited to, a shift in flowering period towards times when the predators are scarce or absent. Accordingly, the goal of our study was to examine geographic and temporal variation in predispersal seed predation levels in *H. moscheutos*. We investigated the following questions: (1) To what extent does predation by each species of seed predator vary among sites and years? (2) Within a season, how does predation by each species of seed predator vary temporally, relative to the changing abundance of flowers in the population?

#### STUDY SYSTEM

Commonly known as rose mallow, *Hibiscus moscheutos* occurs in fresh and brackish marshes in the eastern United States, often forming dense, nearly monospecific populations. A typical plant grows 1 to 2 m tall and consists of an estimated 10–30 shoots arising from a perennial non-rhizomatous rootstock (Spira, 1989). Flowering occurs from late July to early September, and the plants produce large pink or white blossoms that remain open for 1 to 2 d. The flowers are self-compatible, but selfing is apparently minimized by spatial separation of the stigma and the anthers, and by the fact that relatively few flowers per plant are open simultaneously (Snow *et al.*, 1995). The flowers are pollinated by certain large bees of the Family Apidae, Subfamily Apinae: *Ptilothrix bombiformis* Cresson and bumblebees including, in Maryland, *Bombus pennsylvanicus* Deeger (Spira, 1989). *Ptilothrix* is obligately associated with this and a few closely related *Hibiscus* species, while bumblebees are generalist pollinators (Spira *et al.*, 1992; Kearns and Thompson, 2001). In Maryland, previous studies showed that seed set is not pollen-limited and fruit set is typically high (Snow and Spira, 1991; Spira *et al.*, 1992; Kudoh and Whigham, 1998). High fruit set (>85%) is also common in Ohio (A. Snow, unpubl. data). This indicates that beetle predation has the potential to substantially diminish fecundity (Spira, 1989; Kudoh and Whigham, 1998). Fruit capsules ripen approximately 1 mo after flowering and generally dehisce in October and November, releasing ~100 hard-coated 3 mm diameter seeds (Blanchard, 1976; Spira, 1989).

The major seed predators on *Hibiscus* are beetles that feed on pollen as adults and on developing seeds as larvae (Kudoh and Whigham, 1998). One is a curculionid weevil, *Conotrachelus fissinguis* LeConte, and two others are closely related bruchid beetles, *Althaeus*

*hibisci* Oliver and *A. folkersti* Kingsolver. Although both *Althaeus* species occur regionally in the vicinity of our study sites, *A. hibisci* was the only bruchid seed predator that we observed. Both the weevil and bruchid seed predators specialize on *H. moscheutos*. *Conotrachelus fissinguis* has only been reported from rose mallows (Arnett *et al.*, 2002), and the bruchid beetles are obligate parasites of rose mallows (*Hibiscus* section *Muenchhusia*) and the introduced European weed *Abutilon theophrasti* (Kingsolver *et al.*, 1989).

Adult weevils lay their eggs inside the young seed capsule. The larvae consume several to many seeds as they develop, while the fruit continues to mature. Eventually each larva bores a hole of ~2 mm in diameter in the fruit wall to exit from the capsule. The larvae then drop to the ground and begin pupation in early September (Weiss and Dickerson, 1919). Bruchid beetles lay eggs on the immature capsule soon after the petals abscise. Shortly after hatching, their larvae burrow through the ovary wall and each enters an ovule, within which larval development and pupation take place. Infested seeds reach their full size and appear normal, but they are hollow and dead. Adult beetles emerge from the seeds during late autumn (after the fruit capsule has dehisced) through a 1 mm diameter hole in the hard seed coat (Weiss and Dickerson, 1919). Competitive interactions between these two species of seed predators have not been studied. It is possible that weevils, which eat developing seeds, affect the survivorship of bruchids that develop inside the seeds.

## METHODS

### VARIATION IN SEED PREDATION AMONG SITES AND YEARS

We quantified levels of seed predation in four populations of *Hibiscus moscheutos*, hereafter referred to as *Hibiscus*, in Ohio and Maryland during two consecutive years. The two Ohio populations are Stage's Pond (Pickaway County, central Ohio), consisting of a few thousand individuals bordering an isolated pond, and the Winous Point Marsh Conservancy (Portage County, northern Ohio), consisting of tens of thousands of individuals situated along the shoreline of Lake Erie. The two Maryland populations, which are located at the Smithsonian Environmental Research Center (Anne Arundel County), are Mill Swamp, a riverine freshwater wetland where several hundred plants occur, and Hog Island, consisting of roughly a thousand individuals in a brackish marsh adjacent to Chesapeake Bay. These two populations are 2 km apart. *Hibiscus* plants at the brackish Hog Island marsh appeared to be smaller and more widely spaced than plants at the other three sites.

In 2000 and 2001 weevil damage was assayed on ten fruits gathered from each of 30–50 plants (total fruits per site = ~450) at each site in mid-October, when fruits were mature but had not yet released their seeds. On each plant, fruits were gathered from a variety of early, mid-season and late-blooming flowers, as indicated by their relative positions on the plants' shoots, to obtain a representative, season-long sample. No attempt was made to re-sample plants in successive years, so the samples are independent from one another. We calculated the average numbers of exit holes per fruit and the proportions of fruits with weevil damage for each plant. To assess bruchid damage, the fruits were incubated in paper envelopes in a laboratory at room temperature for >90 d during which bruchid maturation and emergence took place. Dissection of a subsample of seeds indicated that the seeds fell into two distinct categories: intact seeds without bruchid damage and hollow seeds with an exit hole. Bruchid damage was quantified for 100–600 seeds sampled equally from the ten fruits per plant. We recorded the number of seeds with exit holes and calculated the average proportion of bruchid-damaged seeds per plant.

For all measures of predation, differences among sites and years were compared using two-way ANOVAs (data were arcsin square root transformed). Dependent variables were the

TABLE 1.—Analysis of variance for percent of fruits damaged by the weevil *Conotrachelus fissinguis* and percent seeds killed by bruchid beetle larvae (*Althaeus hibisci*) at Hog Island, MD, Mill Swamp, MD, Stage's Pond, OH, and Winous Point, OH in 2000 and 2001. Replication for each location each year ranged from 30 to 50 individual plants

Source of variation	df	Mean square	F	P
Percent fruits damaged by weevils				
Year	1	1.62	0.48	0.559
Location	2	16.54	4.93	0.168
Year*Location	2	3.35	38.62	<0.001
Rep (Year*Location)	268	0.087		
Number of weevil holes per fruit				
Year	1	22.47	0.63	0.511
Location	2	136.57	3.83	0.207
Year*Location	2	35.69	28.92	<0.0001
Rep (Year*Location)	267	1.23		
Percent seeds consumed by bruchids				
Year	1	3.187	2.97	0.184
Location	3	0.103	0.10	0.957
Year*Location	3	1.075	47.10	<0.0001
Rep (Year*Location)	337	0.023		

proportion of fruits attacked by weevils, the average number of weevil emergence holes per fruit, and the proportion of seeds parasitized by bruchids per plant (Table 1).

#### PHENOLOGY OF SEED PREDATION WITHIN A SEASON

We studied the phenology of seed predation at Stage's Pond, Ohio. In early July 2001, ~2 wk before the initiation of flowering, 60 multi-stemmed plants were randomly selected and marked along a meandering transect through a portion of the marsh that was densely occupied by *Hibiscus* plants. Five bud-bearing stems per plant were tagged with plastic flagging. Beginning on 26 July 2001 (an estimated 1–3 d after the initiation of flowering at the site) and continuing at 5-d intervals until flowering ceased in mid-September, we revisited these plants, recorded the number of open flowers per stem and tagged each open flower with plastic flagging that was color-coded to indicate the date. The resulting fruits were collected during September and October, when they had begun to dehisce but had not yet released any seeds. Twenty-six to 30 fruits from each of the first seven sampling dates were retained for analysis. (Fruits from flowers that were initiated after the seventh sampling date did not contain mature seeds.) As above, the fruits were incubated in paper envelopes in a laboratory at room temperature for >90 d, during which bruchid maturation and emergence took place. Weevil damage was assessed by recording the number of larval emergence holes in the fruit wall, using 26–30 fruits per flowering date and bruchid damage was assayed by examining a pooled sample of 300 seeds sampled equally from these fruits.

## RESULTS

#### WEEVIL DAMAGE AMONG SITES AND YEARS

The proportion of fruits that were damaged by weevils varied tremendously among sites, from zero at Winous Point, Ohio, to more than 90% per plant at Stage's Pond,

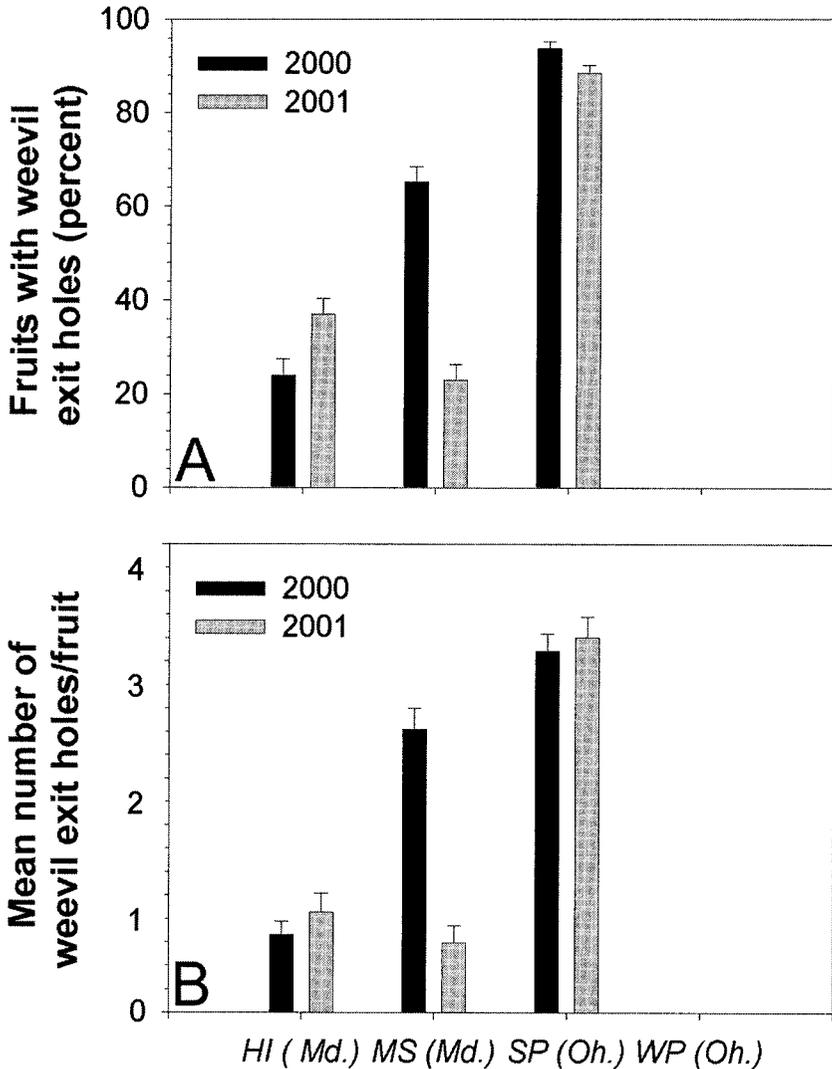


FIG. 1.—A. Average percent of fruits damaged by the weevil *Conotrachelus fissinguis* in 2000 and 2001. B. Average number of exit holes per fruit from the weevil *C. fissinguis* in 2000 and 2001. Sites are Hog Island, MD (HI), Mill Swamp, MD (MS), Stage's Pond, OH (SP), and Winous Point, OH (WP). Mean  $\pm$  1 SE, N = 50 plants. No weevil damage occurred at WP

Ohio (Fig. 1A). At these two sites, similar levels of weevil predation were seen in both years of the study. The two sites in Maryland had intermediate levels of damage and were less consistent between years. At Mill Swamp, an average of 65% of the fruits were damaged by weevils in 2001, while only 23% were damaged in 2002. In contrast, the average percent of fruits damaged at Hog Island increased from 24% in 2000 to 37% in 2001. Excluding the Winous Point population, where no weevil damage was seen in either year, a

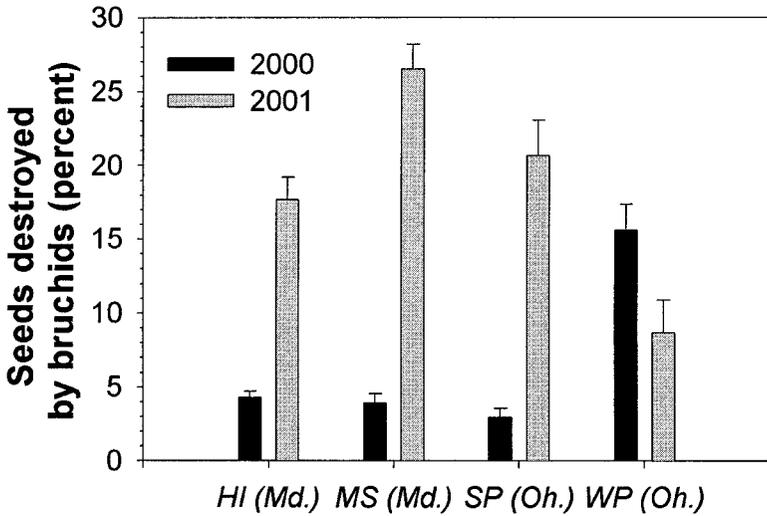


FIG. 2.—Average percent of seeds killed by bruchid beetle larvae (*Althaeus hibisci*) at Hog Island, MD (HI), Mill Swamp, MD (MS), Stage's Pond, OH (SP), and Winous Point, OH (WP) in 2000 and 2001. Mean  $\pm$  1 se; N = 50 plants (100–600 seeds were sampled per plant)

two-way ANOVA revealed a significant site-by-year interaction ( $P < 0.001$ ) and no significant main effects of site or year.

Variation in the intensity of fruit damage, as reflected by the average number of exit holes per fruit, paralleled the pattern described above (Fig. 1B). Fruits with three or more emergence holes produce very few viable seeds (A. Snow, pers. obs.), so we used this value as a convenient reference point for evaluating seed mortality due to weevils. In both years, plants at Stage's Pond, Ohio, had an average of about three holes per fruit at Stage's Pond, Ohio, while plants at Hog Island, Maryland, averaged  $\sim 0.6$ – $0.8$  holes per fruit, which is considerably less severe. Fruit damage was intermediate at Mill Swamp, Maryland, averaging 2.5 holes per fruit in 2000 and only 0.6 holes per fruit in 2001. In summary, seed mortality due to weevils was very high at Stage's Pond in both years and was quite high at Mill Swamp in 2000. In contrast, no weevil damage was seen at the population in Winous Point, Ohio, in 2000 or 2001 and damage at Hog Island was relatively low.

#### BRUCHID DAMAGE AMONG SITES AND YEARS

Bruchid damage was observed at all locations during both years of the study and exhibited considerable spatial and temporal variation (Fig. 2). At three of the sites, only  $\sim 4\%$  of the seeds were killed by bruchids in 2000 vs.  $\sim 20$ – $25\%$  in 2001, representing a large difference between years. Bruchid damage at Winous Point did not show this pattern, however. There, an average of 16% of the seeds were destroyed by bruchids in 2000 and 10% in 2001. This resulted in a significant site-by-year interaction in the two-way ANOVA ( $P < 0.001$ ), which did not reveal main effects site for year affecting the proportion of seeds killed by bruchids.

#### PHENOLOGY OF DAMAGE WITHIN A SEASON

In 2001 flowering at the Stage's Pond population began during the last week of July, peaking sharply in mid-August, and continuing until early September (Fig. 3). Flowers that

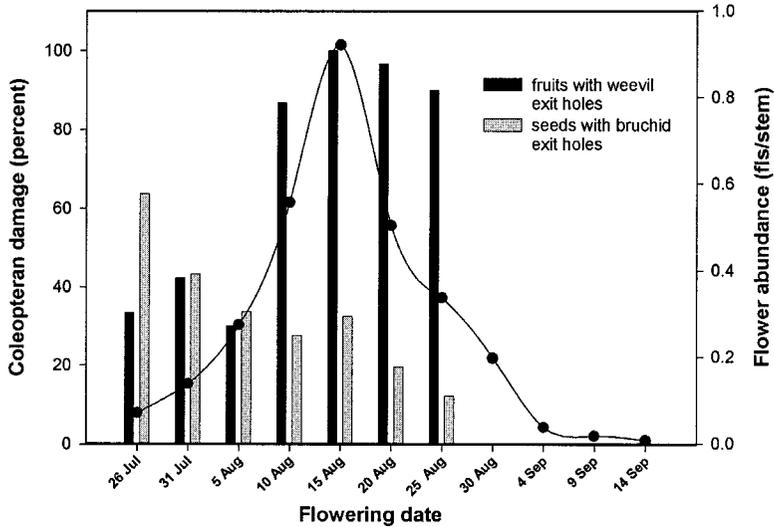


FIG. 3.—Phenology of seed predation and flowering at Stage's Pond, OH, in 2001. Flowering data are the average numbers of flowers per stem ( $N = 60$  plants; averaged for five stems per plant) on each flowering date. Damage data show the percent of fruits damaged by weevils and the percent of seeds killed by bruchids in fruits from each flowering date (from 26–30 fruits for each date)

opened after the last week of August did not produce viable seeds, probably due to the onset of cooler weather. A few plants in the population flowered earlier or later than the 60 study plants, but we did not attempt to quantify seed predation on these plants.

The intensity of predation by the two beetle species varied markedly over the course of the flowering season (Fig. 3). Fruits that were initiated during the first flowering interval, on 26 July, experienced the greatest seed losses from the bruchids (64% mortality). Bruchid damage declined fairly steadily to its lowest level (12% mortality) in fruits from flowers that bloomed on 25 August. Weevils, by contrast, peaked on 15 and 20 August, when  $\sim 100\%$  of the fruits bore emergence holes. The average number of holes per fruit was 1.2 during the first week of flowering and 9.0 during the week of peak flowering (15 August). The combined damage from both seed predators was relatively high throughout the flowering period at this site, as described above.

#### DISCUSSION

We found that levels of seed predation in *Hibiscus* populations can vary a great deal from year-to-year and site-to-site, making it difficult to generalize about the magnitude of potential effects of seed predation on demographic or evolutionary processes after two years of monitoring. However, damage caused by the weevil was very high at one of the four sites during both years. By comparing the timing of seed predation and flowering within a season, we documented greater potential of the seed predator acting mainly during peak flowering, *i.e.*, the weevil *Conotrachelus fissinguis*, to exert selective pressure on flowering time as compared to the bruchid, *Althaeus hibisci*. Below, we discuss key differences between the two predators, describe possible causes of the variation that we observed, and offer suggestions for further research.

Weevil damage was fairly constant between years at one of the Maryland sites (Hog Island), a noteworthy finding in view of the fact that insect populations often show great year-to-year variability. Damage by weevils was also consistent between years on Ohio, but dramatically differences were seen between the two sites. Weevil damage did not occur at Winous Point, located along Lake Erie in northern Ohio, but at Stage's Pond in central Ohio we observed damage by an average of ~3 larvae per fruit in 2000 and 2001 (enough to destroy most of the developing seeds in the population). To find out whether the lack of weevils at the northern site was an isolated event, we surveyed several nearby populations during September 2001 and found no fruits with weevil exit holes. Likewise, no weevils were seen there in 2004. It is unclear whether weevils are absent along Lake Erie because: (1) their natural range does not extend this far north, (2) other factors have prevented them from persisting there or (3) they could persist but have yet to be introduced to this region. Weiss and Dickerson (1919) reported that along the Atlantic coast, *Conotrachelus fissinguis* occurred as far north as New Jersey, which is similar to northern Ohio in latitude but has warmer monthly temperatures in January (averaging 4.7 C warmer; National Climatic Data Center, 2004). It will be interesting to monitor northern *Hibiscus* populations over the next few years to see if weevils become established.

Weevils have been common at the Maryland sites since at least 1988 (Spira, 1989; and Whigham, 1998), Kudoh and probably much longer (Weiss and Dickerson, 1919; Cahoon and Stevenson, 1986). Interestingly, descriptive records from Stage's Pond show that weevils were completely absent at this site in 1993 and were rare in 1994, while they have been common from 1994 to the present (A. Snow, pers. obs.; exception: in 1999 a severe drought prevented most flowers from setting fruit). We have no information about weevil abundance at Stage's Pond prior to 1993. Before this date, weevil populations may have been decimated temporarily, or they may have been absent from the region. Based on our observations at Stage's Pond and Winous Point, it is possible that *Hibiscus* populations in Ohio have a shorter history of exposure to weevil predation than those in Maryland.

Bruchid beetle predation was more variable within sites than weevil damage. Some of the year-to-year variation we observed in bruchid impact may be related to exceptionally dry summers. Bruchids specialize on *Hibiscus* seeds during their larval development, and a sharp decline in their food source may cause population declines. In 1999, a severe widespread drought occurred during the growing season in both Ohio and Maryland. Very few seeds were produced by the stunted, drought-stressed *Hibiscus* plants at Stage's Pond (A. Snow, pers. obs.) and Mill Swamp (Dennis Whigham, pers. comm.). It is possible that the drought reduced the numbers of bruchids that overwintered and oviposited on *Hibiscus* fruits in 2000 at three of our study sites: Hog Island, Mill Swamp, and Stage's Pond. This is suggested by low levels of bruchid damage at these sites in 2000 (~5% seed mortality), followed by greater levels in 2001 (~18–26% seed mortality, Fig. 2). The more stable abundance of bruchids at Winous Point may reflect the capacity of Lake Erie and the local hydrology to buffer the very dry conditions that affected the other populations. At the same time, however, this pattern of lower abundance in 2000 versus 2001 was not seen in weevil damage at these sites, despite the fact that weevils also specialize on *H. moscheutos*.

Despite the spatial and temporal variation that we documented, we suggest that seed predation in *Hibiscus* has the potential to be strong enough to act as a selective force on traits such as flowering phenology. This inference is based on the substantial amount of seed and fruit damage that was observed, coupled with the fact that the damage occurred late in the reproductive process, after substantial maternal investment in seeds and past the point when their loss could be compensated by additional reproductive effort. Given the relatively short growing season that is available for flowering in these wetland perennials, a sharply

peaked flowering period as documented at Stage's Pond may be the best way for individuals to minimize their exposure to seed predators. At sites where weevils are less abundant, these predators could be satiated by the large numbers of flowers that are available during peak flowering. We cannot be certain that the flowering phenology data from Stage's Pond population are typical, but a sharp peak in flowering was also documented in 1999 (E. Bauman, pers. obs.), occurring 3 d later than the peak in 2000. Further studies are needed to examine how seed predation in *Hibiscus* varies within seasons relative to flowering phenology and factors that affect the population dynamics of seed predators, including extreme weather and competition between weevils and beetles for developing seeds. At northern sites like Winous Point, where weevils are absent, it would be interesting to investigate whether plants that bloom later in the season are less likely to be affected by bruchids, while benefiting from the current absence of weevils. so, selection might favor delayed flowering relative to the onset of autumn conditions that inhibit fruit maturation.

Our study illustrates that patterns of seed predation that are documented in one growing season or part of a season may be reversed in another year due to annual variation or differences in sampling dates. Likewise, predator damage at one or a few sites may not be representative of an entire region. Clearly, variation in predation that occurs among and within sites and years must be taken into account when designing studies of seed predation, and conclusions should be limited to appropriate time frames and localities. Other studies also provide ample evidence for spatial and temporal variation in seed predation. In Europe, for example, predispersal seed predation in *Juniperus communis* varied significantly among populations, and was lowest at the northern limit of the range in subarctic tundra (Garcia *et al.*, 2000). Geographic and year-to-year variation in predispersal seed predation also have been reported in *Lathyrus vernus* (Ehrlén, 1996) and *Primula veris* (Leimu *et al.*, 2002). A goal for future studies is to examine how spatial and temporal variation in seed predation affect seedling recruitment and, ultimately, plant fitness and population growth rates (*e.g.*, Louda and Potvin, 1995; Ehrlén, 1996; Brody, 1997; Froberg and Eriksson, 2003).

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