

WINTER FRUIT REMOVAL IN FOUR PLANT SPECIES IN MAINE

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ABSTRACT - We monitored individual plants of winterberry (*Ilex verticillata*), highbush cranberry (*Viburnum opulus*), wild lily-of-the-valley (*Maianthemum canadense*), and partridgeberry (*Mitchella repens*) during two reproductive seasons to measure the disappearance of fruits (presumably removed by fruit-eating animals) in plant species whose fruits ripen in early fall but persist through the winter. Patterns of fruit removal were variable between species, individuals, and years, but in general removal rates for all species were slow and relatively constant. Only *Ilex* fruits showed visible deterioration during the winter. Exclosures placed around *Maianthemum* plants in the field and preliminary feeding trials suggested that mice (*Peromyscus* sp.) and other small mammals may remove most fruits and disperse many viable seeds of *Maianthemum*, as well as other low-growing plants with persistent fruits, such as *Mitchella*.

In the temperate zone the overwhelming majority of vertebrate-dispersed plant species ripen their fruits during the late summer and early autumn, a time which corresponds with the peak of fall migration of fruit-eating birds (Burger 1987; Sherburne 1972; Skeate 1987; Stiles 1980; Willson 1986). As a consequence, in many species most fruits are removed over a short period (Sargent 1990). However, a small number of plant species retain their fruits through much of the late fall and winter (Borowicz and Stephenson 1985; Burger 1987; Jones and Wheelwright 1987; Sallabanks 1992; Stiles 1980). Such fruits can persist in the face of microbial attack and damage from freezing because of their low lipid content and the presence of secondary compounds (Cipollini 1993; Herrera 1982; Stiles 1980), but those same compounds presumably reduce the attractiveness of the fruits to birds and slow their removal rates (Herrera 1982; Jones and Wheelwright 1987; Sorensen 1983). Moreover, the diversity and abundance of active seed dispersers are relatively low during the winter; plants must rely on resident birds and mammals for seed dispersal, or maintain fruits until spring migrants reappear. The disadvantages of presenting fruits during the winter months are presumably outweighed by the benefits of avoiding the season of heaviest damage to fruits and seeds by microbes, fungi and insects (Herrera 1982), and minimizing competition with other fruiting plants for a limited number of avian seed dispersers (McKey 1975; Wheelwright 1985).

In this study we examined disappearance rates of fruits of four wood-

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land plant species in southern Maine. The species — winterberry (*Ilex verticillata*), highbush cranberry (*Viburnum opulus*), wild lily-of-the-valley (*Maianthemum canadense*), and partridgeberry (*Mitchella repens*) — differ in habitat, secondary compounds, and fruit presentation patterns, but each produces persistent fruits eaten by vertebrates. Exclosures were used to determine the relative importance of birds, small rodents, and natural abscission in accounting for fruit disappearance in *Maianthemum canadense*. Preliminary feeding trials were conducted to clarify the role of mice (*Peromyscus* sp.) as potential seed dispersers or seed predators.

METHODS AND STUDY SPECIES

Our main study site was a mixed deciduous forest in North Yarmouth, Maine. *Viburnum opulus* was studied at a second site, in Brunswick, Maine, 20 km (12 mi) to the east. Censuses were conducted approximately weekly from late September, 1987 until low plants were covered by snow in December, and resumed at less frequent intervals from snow-melt until late April, 1988. Censuses resumed in early September, 1988 and continued at biweekly intervals until snowfall in mid-December. We refer to the September, 1987 to April, 1988 season as 1987, and the September, 1988 to December, 1988 season as 1988.

Viburnum opulus L. (Caprifoliaceae), a shrub found along forest edges and in the understory, produces 50-500 bitter, bright red drupes on terminal panicles which persist through the winter (Sherburne 1972; Jones and Wheelwright 1987). The fruit, whose diameter averages 11.0 mm (SD [\pm] = 0.5; N = 25), encases a single flattened seed (7.8 x 7.1 x 1.8 mm, N= 10). We found five shrubs of similar height (1.5-2.0 m) and fruit crop (300-400 fruits) growing along a dirt logging road in the forest. On each plant four infructescences, one from each side of the plant, were marked at the base of the panicle with a 1 x 5 cm piece of blue flagging. An average of 7.8 fruits were plucked from each infructescence to reduce it to 20 fruits and standardize infructescences (initial crops sizes of marked inflorescences in 1987: 27.8 ± 7.9). Fruit crop sizes were smaller in fall 1988 (initial crops sizes: 17.6 ± 5.5). Accordingly, in that period some infructescences were used with fewer than 20 fruits to repeat observations on the same shrubs (1987: N = 400 fruits; 1988: N = 313). Censuses began in both years before many fruits had been removed (empty pedicels per inflorescence: 1987: 1.3 ± 1.8 ; 1988: 0.6 ± 1.6).

Ilex verticillata (L.) Gray (Aquifoliaceae), a dioecious wetland shrub, grows to a height of 2.5 m and produces 10-1000 sessile orange-red drupes along its branches. The fruits, which are relatively dry, measure 7.7 mm in diameter (± 0.5 ; N = 25), with 4-7 seeds 3.3-4.1 mm in length. Ten shrubs were haphazardly selected along a 200 m stretch of a swampy power line roughly 75 m wide, edged by mixed coniferous and deciduous

trees. On each plant, two branches bearing at least 20 fruits each were chosen. The number of fruits on each branch was reduced to 20, and branches were inconspicuously marked with twined grass at the base. In fall 1988, the same shrubs were censused (1987: N = 400 fruits; 1988: N = 411).

Mitchella repens L. (Rubiaceae), a low-growing woody creeper of the forest floor, presents its red fruits singly in leaf axils. Its drupes, which have low water content, measure 7.8 x 6.4 mm (± 0.5 ; N= 6) and contain 4-7 seeds 2.9 mm in length (± 0.2 ; N = 20). Six plants growing beneath mixed hardwoods and conifers with little understory growth were haphazardly chosen and marked by blue flagging 1 m away. Plants were similar in size, covering about 0.5 m² of ground, and each bore 23-28 fruits (1987: N =157 fruits; 1988: N = 170). Once snow covered the plants in December, plants were not censused to avoid artificially exposing fruits to foraging animals.

Maianthemum canadense Desf. (Liliaceae) is a clonal herb 4-15 cm in height (Worthen and Stiles 1986). Fruits are presented on a single raceme per plant (technically, a ramet or physiologically independent portion of the clone) and number 6-15 per infructescence. The mean fruit diameter was 5.9 mm (± 0.8 ; N = 12) with 1-2 seeds per fruit averaging 3.5 mm in length (± 0.4 ; N = 16). In 1987, ten singly occurring fruiting ramets were located roughly 10 m apart along an old logging road in mixed forest. Each plant had 8-11 fruits (N= 89). In 1988, 25 ramets (6-15 fruits each, N = 239) were monitored at the same site. Plant locations were marked by tying 8 cm of cotton string to sticks placed 20 cm away.

Temporal patterns of disappearance of fruits as well as the firm attachment of fruits (periodically tested by shaking branches) and the general lack of fruits, seeds or pedicels beneath plants suggested that most fruits were removed by animals rather than simply abscised by plants. To determine the relative contributions of birds, small mammals, and natural abscission by the plant to fruit disappearance, in 1987 we constructed exclosures of 0.64 x 0.64 m wire netting cut and folded into cubes 10 cm on a side. Ten exclosures had no access holes, and 10 had 4.5 cm square holes cut into each side but not the top. A large dense patch of fruiting *Maianthemum* was located and 30 plants haphazardly selected. The plants were divided into three fruit crop size categories (6-10, 11-13, and >13 fruits) then randomly split into three groups. The first group's plants were covered by the complete exclosures (N = 86 fruits), the second group covered by the partial exclosures (N = 90 fruits), and the final group left as controls (N = 91 fruits).

A mouse (*Peromyscus* sp.), captured in December, 1987 and maintained on an *ad libitum* diet of millet and sunflower seeds, was used in two feeding trials to explore the role of small mammals as seed dispersers of *Maianthemum*. Trials consisted of leaving only *Maianthemum*

fruits and water in the cage overnight. In the morning, remaining seeds and fruits were removed, counted, and examined for visible damage. A second mouse of the same species was trapped in April, 1988 and three more trials were conducted with *Maianthemum* fruits gathered immediately after snowmelt.

Data are presented as $\bar{x} \pm 1$ SD throughout, except in Fig. 1-5, where standard errors are presented because of the large variance.

RESULTS

Removal rates of fruits were typically slow and relatively constant for all species in both years. However, there was considerable variation among individual plants, species, and years.

In 1987, *Viburnum* disappeared slowly until late November, when the proportion of fruits remaining dropped from 71.5% ($\pm 31.7\%$) to 20.7% ($\pm 30.8\%$) in less than a two-week period (Fig. 1). Three of the five shrubs lost all of their fruits during that time. Some panicles appeared to have been broken off, perhaps by seed-eating birds or squirrels (*Sciurus* and/or *Tamiasciurus*; Jones and Wheelwright 1987). In the case of this species in 1987 (but not 1988), however, most fruits seemed to have been abscised by the parent plant, judging from the fact that panicles had been dropped at the point of attachment and fruits lay for at least several days uneaten beneath the plant. Secondary removal of the fruits and seeds from beneath the shrubs was rapid and complete by early December. At that time, only 7% ($\pm 15.6\%$) of the original fruit crop remained on the shrubs. In 1988 fruit

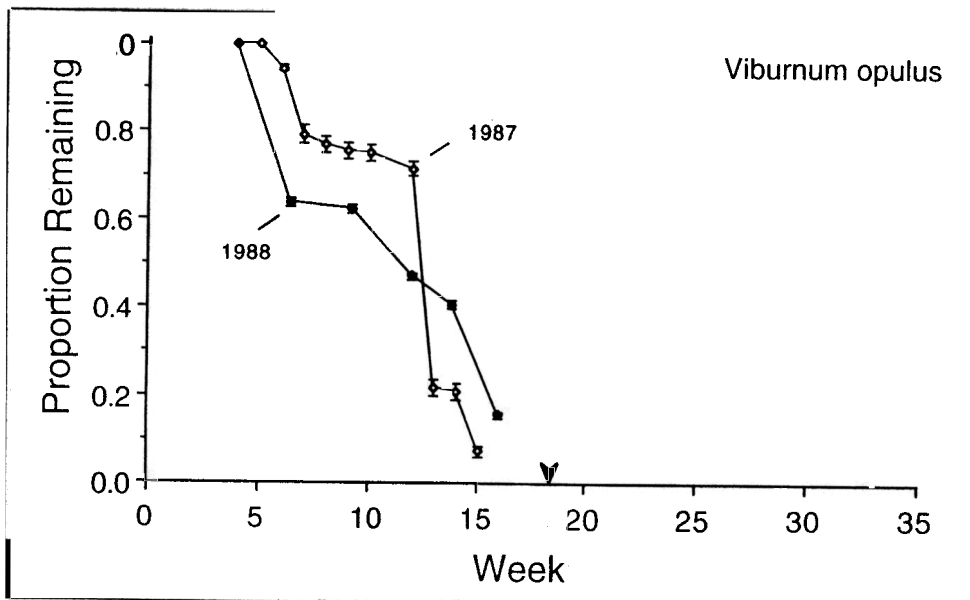


Fig. 1. Removal rates of *Viburnum opulus* fruits. Symbols designate the mean (averaged across plants) proportion of the original fruit crop remaining; bars represent ± 1 standard error. Week 1 = the week beginning September 1. The arrow marks January 1. 1987: N = 400 fruits. 1988: N = 313.

crop sizes in *Viburnum* were generally smaller. What fruits there were disappeared at a fairly constant rate, with only 16% ($\pm 14.0\%$) remaining in mid-December when sampling was discontinued. As in the previous year, some panicles were found on the ground in late autumn.

Ilex fruits were removed slowly but steadily in 1987, with little variation between individual plants (Fig. 2). At the end of April in the first year of the study, 11.5% ($\pm 12.3\%$) of the original fruits still remained firmly attached to the branches, although they had become brown and wrinkled after a prolonged cold spell in January; vigorous shaking failed to dislodge fruits. The following fall showed much faster rates of fruit removal. By the end of November, 1988, all fruits were gone from study plants as well as other *Ilex* in the population. Fruit crops of focal plants were reduced from 94.2% ($\pm 5.2\%$) on October 9 to 30.9% ($\pm 36.3\%$) by mid-November.

Removal rates of *Mitchella* were gradual and relatively constant prior to snowfall in both years, with 19.1% ($\pm 29.2\%$), and 29.8% ($\pm 25.0\%$) of the fruit crops remaining before snowfall covered the plants in December of 1987 and 1988, respectively (Fig. 3). Sampling was resumed in April, 1988, after snowmelt, revealing that 5.8% of the original fruits had disappeared in the interim. Fruits appeared unchanged by the winter conditions. Individual plants showed considerable variation in their fruit removal rates, with some plants retaining nearly all of their fruits and others becoming almost entirely depleted.

Maianthemum showed slow removal rates in 1987, with 50.9% ($\pm 43.6\%$) of the fruits remaining by the time plants were covered by snow (Fig. 4). After the snow melted, we observed that only 6.6% of the

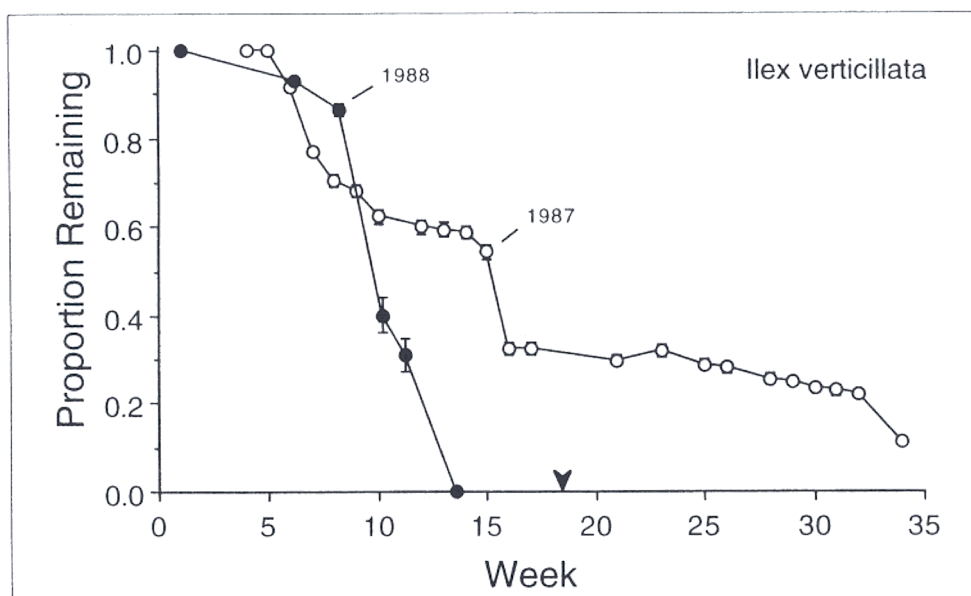


Fig. 2. Removal rates of *Ilex verticillata* fruits. Symbols as in Fig. 1. 1987: N = 400 fruits. 1988: N = 411.

original fruits had disappeared while under the snowpack, and fruits appeared unchanged by winter conditions. By the end of April, 1988, 37.8% ($\pm 48.9\%$) of the fruit crop still remained. In the autumn of 1988, fruit removal rates were much more rapid, with almost all fruits removed by early December. Fruit crops had declined to 12.6% ($\pm 28.0\%$) of the original size by late October. In both years, plants tended to lose either all of their fruits or none, as in *Mitchella*.

In the 1987 enclosure experiment involving *Maianthemum*, few fruits

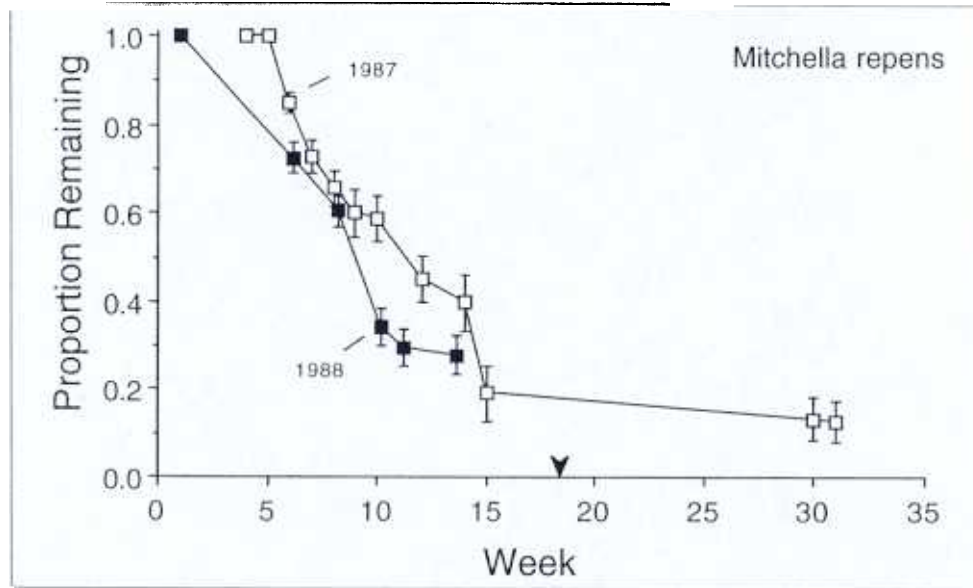


Fig. 3. Removal rates of *Mitchella repens* fruits. Symbols as in Fig. 1. 1987: N = 157 fruits. 1988: N = 170.

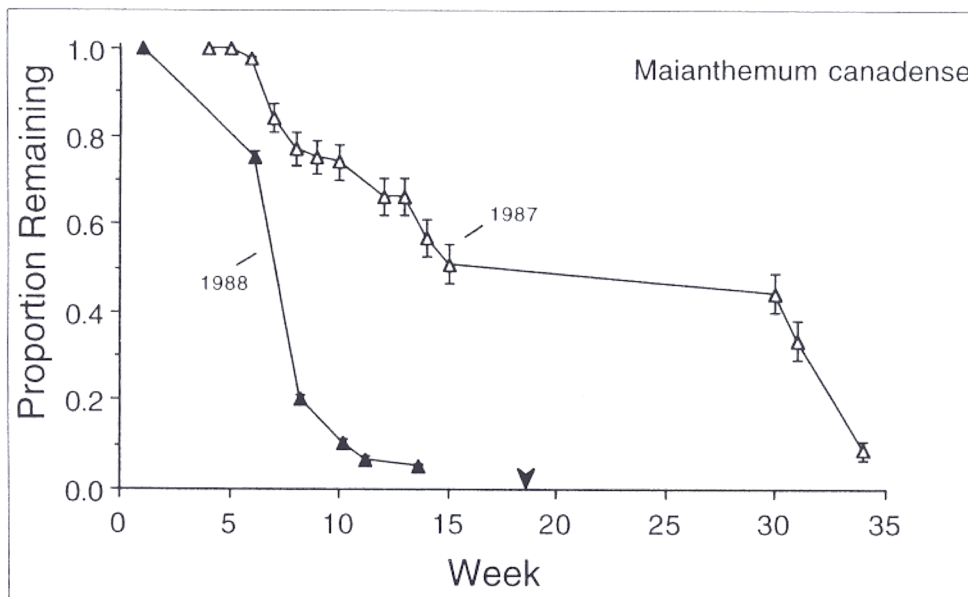


Fig. 4. Removal rates of *Maianthemum canadense* fruits. Symbols as in Fig. 1. 1987: N= 89 fruits. 1988: N= 239.

were removed from any of the plants during the first six weeks; during the next two weeks, fruits on the control plants and in the partial enclosures disappeared rapidly (Fig. 5). By mid-December, only 11.1% ($\pm 33.3\%$) of the control and 11.9% ($\pm 31.2\%$) of partial enclosure fruits remained. Most of these plants either had almost all their fruits taken, or fewer than three removed. In contrast, on average just two fruits per plant were missing by December from plants inside complete enclosures, and 78.5% ($\pm 17.8\%$) remained at the end of April, 1988.

In general, fruits disappeared more quickly in 1988 than in 1987, as indicated by the date at which half of the fruits had been removed (Figs. 1-4). This may have been due in part to the fact that observations were started earlier in 1988, which allowed more time for marked fruits to be removed that year. However, in 1987 we recorded little evidence of prior fruit removal. Moreover, in the case of *Maianthemum* at least, fruit removal in 1987 was minimal until late October. Temperatures were similar in both years, although November precipitation was greater in 1988 than in 1987.

In December, presented with 13 *Maianthemum* fruits, a captive mouse (*Peromyscus* sp.) ate the pulp of 11 fruits but consumed no seeds. In the second trial, it ate 10 of 12 fruits but no seeds. In April, presented with 12 fruits/trial, a different mouse of the same species ate 8 fruits and 6 seeds (trial 1), 9 fruits and 9 seeds (trial 2), and 12 fruits and 5 seeds (trial 3).

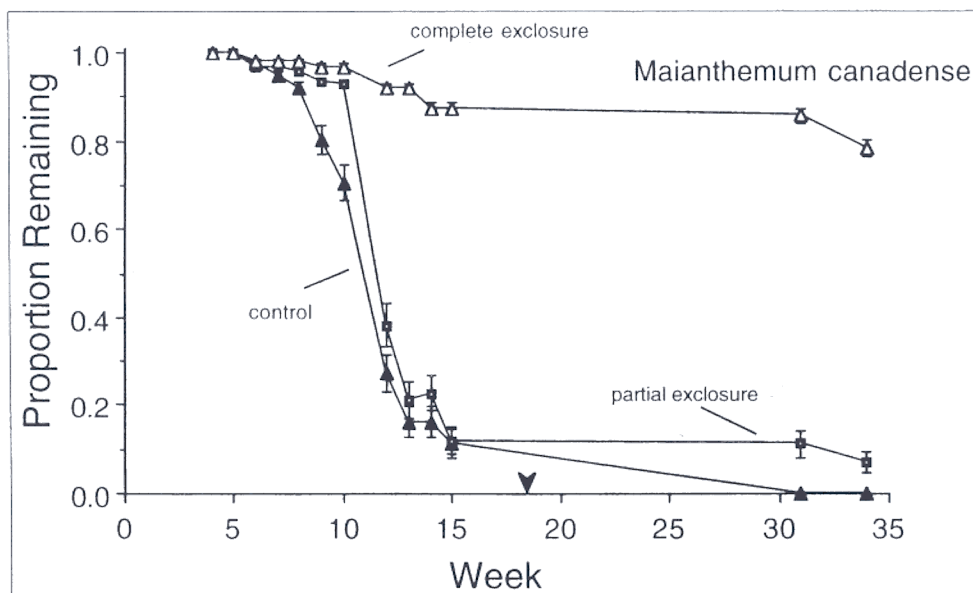


Fig. 5. Removal rates of *Maianthemum canadense* fruits. Plants completely enclosed by wire cages indicated by open triangles ($N = 86$ fruits); plants partially enclosed by wire cages with doorways cut in their sides by hollow squares ($N = 90$); and control plants without enclosures by closed triangles ($N = 91$). Triangles and squares designate the mean (averaged across plants) proportion of the original fruit crop remaining; bars represent ± 1 standard error.

DISCUSSION

Compared to other fleshy-fruited temperate zone species (e.g., Davidar and Morton 1986; Piper 1986a, b; Sargent 1990), plants whose fruits ripen relatively late in the season and are resistant to damage during the fall show low fruit removal rates, such as the four species in this study. Their persistent fruits do not appear to be a favorite food source for any local vertebrate. However, we found interesting differences in removal patterns between plant species and years.

For both years and all plants (with the exception of *Maianthemum* in 1988), less than 50% of the initial fruit crop was removed before the end of October. Given that most fruit-eating birds have left Maine by that time (pers. obs.), these plants must not rely heavily on fall migrant birds for seed dispersal. Yet all four species are capable of maintaining fruits throughout the winter, thus presenting them to both resident vertebrates and early spring migrant birds. Only *Ilex* fruits showed visible damage after cold weather.

Despite these broad similarities, plants with "persistent fruits" include a diversity of types of fruit presentation and are likely to have their seeds dispersed by different vertebrates. The two shrubs, *Viburnum* and *Ilex*, have large, showy fruit crops which may be effective in attracting late fall fruit-eating birds despite the birds' relative scarcity at that time and despite the fruits' distasteful secondary compounds. Fruit removal rates have been shown to increase with crop size within various species (Davidar and Morton 1986; Denslow 1987; Sargent 1990; Sallabanks 1992), and the same is probably true between species (after accounting for differences in fruit preferences).

Although secondary compounds in persistent fruits may reduce their appeal to potential seed dispersers (Herrera 1982; Jones and Wheelwright 1987; Sorensen 1983), naive animals such as immature individuals or newly arrived migrants may eat some in the process of becoming familiar with local fruits. The slow but constant removal rates of *Viburnum* and *Ilex* fruits suggest sampling by birds. The pattern of fruit disappearance is much more rapid and synchronous in species with more preferred fruits, such as *V. dentatum* (Sargent 1990; Wheelwright 1988).

The fruit removal patterns of *Mitchella* and *Maianthemum* differ from those of tall shrubs with persistent fruits probably because low-growing plants such as these present much smaller crops of fruits in far less conspicuous displays. The fruits of *Mitchella* are often hidden by the plant's leaves. Creeping shrubs and low herbs are also susceptible to burial by snow for much of the winter, which effectively precludes dispersal by birds during that period (small mammals may feed on fruits underneath the snow, but the few seeds that are not destroyed probably receive limited dispersal). Because of their small fruit crop sizes, plants

like *Mitchella* and *Maianthemum* are probably encountered by chance by potential seed dispersers, in contrast to shrubs with large numbers of fruits, which are remembered and revisited by birds (Sallabanks 1992). The fact that in both *Mitchella* and *Maianthemum* fruits tended to be either totally removed or neglected completely suggests random discovery of small fruit crops.

The pattern of fruit removal for the two low-growing species, and the results of the exclosure study in particular, also implicate small mammals as important consumers of fruits and potential dispersers of their seeds. *Peromyscus* mice are known to eat a variety of food types, including fruits and seeds, and display seasonal variation in diet (Sieg et al. 1986; Wolff et al. 1985). Our feeding trials indicate that, at least under certain circumstances, mice may play a role as seed dispersers of *Maianthemum*. Casual observations of *Maianthemum* clones revealed occasional piles of seeds on leaf litter near plants reminiscent of those left by captive mice. Although rodents are often considered seed predators, Stiles (1980) noted that *Vaccinium* seeds defecated by certain mice appeared unharmed. Even if they destroy most seeds, rodents may be effective seed dispersers by depositing at least some seeds in sites that are favorable for germination and establishment (Reid 1987).

Although fruit removal rates were generally slow and constant in plants with persistent fruits, they may show more year-to-year variation than species that ripen their fruits earlier in the season or whose fruits are preferred by birds. Perhaps in winters when alternative foods are unavailable, persistent fruits are more readily eaten and some of their seeds dispersed. The ability of such fruits to withstand exposure to microbes and harsh physical conditions may improve their prospects of successful seed dispersal at a time of year when seed predation and interspecific competition for dispersers are reduced.

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