

Seasonal changes in the fruits of *Viburnum opulus*, a fleshy-fruited temperate-zone shrub

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Certain temperate-zone plant species retain their fleshy fruits through the fall and winter. The production of "persistent fruits" has been interpreted as an adaptive reproductive strategy because plants can offer "low-investment" fruits when competition with other plants for seed dispersers is low. In theory fruits are defended chemically against fall pathogens, and palatability improves seasonally with cold-induced chemical changes. We studied the ecology of persistent fruits in *Viburnum opulus* (Caprifoliaceae), a fleshy-fruited temperate-zone shrub. *Viburnum opulus* fruits remained uneaten through the fall until most were removed, apparently by avian seed predators. Some shrubs retained fruits through May. Birds in the field and laboratory preferred all other fruit species tested over *V. opulus*. Palatability of *V. opulus* fruits to captive American Robins declined rather than improved throughout the winter, contrary to expectation. Tannins and pH remained constant, while sucrose concentration doubled over a 6-month period. Seeds regurgitated by robins in the spring germinated at similar rates as seeds processed the previous fall. Although *V. opulus* showed some of the theoretically expected adaptations for delayed seed dispersal (chemical defense, germination following spring dispersal), it did not show others (seasonal improvement in palatability). Plants with persistent fruits may depend on years of severe weather and food scarcity for seed dispersal.

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Certaines espèces végétales de la zone tempérée retiennent leurs fruits charnus durant l'automne et l'hiver. L'on a interprété la production de «fruits persistants» en tant que stratégie d'adaptation à la reproduction puisque les plantes peuvent fournir des fruits à «faible investissement» lorsque la compétition avec d'autres plantes pour les agents de dispersion des semences est faible. Théoriquement, les fruits possèdent une défense chimique contre les pathogènes automnaux et leur palatabilité s'améliore avec les changements chimiques saisonniers induits par le froid. L'écologie des fruits persistants de *Viburnum opulus* (Caprifoliaceae) a fait l'objet de la présente recherche. Ces fruits demeurent dans les arbustes au cours de l'automne, jusqu'à ce que la plupart soit mangé apparemment par les oiseaux. Certains arbustes retiennent leurs fruits jusqu'en mai. Les oiseaux, tant au champ qu'au laboratoire, préfèrent les fruits de toutes les autres espèces à l'étude à ceux de *V. opulus*. La palatabilité des fruits de *V. opulus* pour les merles d'Amérique décline au cours de l'hiver. Les tannins et le pH restent constants; la concentration en saccharose double au cours d'une période de 6 mois. Les graines régurgitées par les merles germent au printemps à des taux similaires à celles récoltées à l'automne précédent. Bien que *V. opulus* montre certaines adaptations à un délai de dispersion des semences (défense chimique, germination suite à la dispersion au printemps), il n'en révèle pas d'autres (amélioration saisonnière de la palatabilité). Les plantes aux fruits persistants peuvent dépendre des années où la température est rigoureuse et les aliments rares pour la dispersion de leurs graines.

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Introduction

In the temperate zone, most fleshy-fruited plant species ripen their fruits in the fall and rely mainly on migratory birds for dispersal of their seeds (Snow 1971; Sherburne 1972; Thompson and Willson 1979; Stiles 1980). Plants benefit by having their fruits eaten and their seeds dispersed as soon as possible after ripening. The fruits that remain on the plant risk damage to the pulp or seeds by microbes, invertebrates, or vertebrates, which decreases the likelihood that seeds will be dispersed (Janzen 1971; Thompson and Willson 1978, 1979; Jordano 1983, 1987; Herrera 1982; Manzur and Courtney 1984).

Nonetheless, a number of temperate-zone plant species retain ripe fruits through the fall and winter: e.g., *Rhus* spp. (Graber and Powers 1981; E. Jones and N. T. Wheelwright, personal observations); *Symphoricarpos albus* (Best 1981), *Rhamnus purgatoria* (Sherburne 1972); *Smilax* spp. (Thompson and Willson 1979); *Mitchella repens*, *Viburnum acerifolium*, and others (Stiles 1980). These "persistent fruits" gradually disappear during winter and spring (Sherburne 1972;

Stiles 1980) and presumably individuals benefit by retaining their fruits on the plant until the fruit crops of their competitors for seed dispersers have been depleted. However, to reduce the risk of fruit damage while "waiting" on the plant, fruits must be nutritionally inadequate to predators and pathogens (Stiles 1980) or chemically repellent (Herrera 1982). If their fruits escape damage, such plants can achieve dispersal of their seeds with relatively little investment in pulp nutritional value, while avoiding competition with fall-fruited plant species (Stiles 1980). Another possible benefit of fruit persistence applies when seeds are more susceptible to predators on the ground (following fall dispersal but preceding spring germination) than on the plant. Even though seeds are conspicuous and clumped on the plant, they may be at a greater risk after being dispersed if terrestrial predators such as *Peromyscus* spp. are common. Using pulp unpalatability to postpone dispersal could be one more mechanism (along with delayed fertilization or variable fruit development times (Wheelwright 1985; Gorchov 1985)) by which plants could stagger the timing of effective fruiting to reduce competition or the risk of predation.

The trade-off from the perspective of the plant is that fruits defended chemically against predators and pathogens may be rejected by seed dispersers because of their unpalatability (Stiles 1980; Best 1981; Herrera 1982). Yet many species with

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distasteful, persistent fruits are widely disseminated nonetheless, which raises the question, under what conditions do animals choose such fruits? Protective secondary compounds and digestibility-reducing substances (e.g., Feeny 1975; Levin 1976) have been hypothesized to degrade or become inactivated with freezing and thawing, making persistent fruits attractive to spring migrants (Sherburne 1972). Best (1981), for example, found that *Symphoricarpos albus* fruits offered to Cedar Waxwings (*Bombicilla cedrorum*) in October before the fruits had been exposed to freezing temperatures were less palatable than fruits experimentally frozen or fruits picked in December after having been frozen.

This view of the evolution of persistent fruits as an adaptive reproductive strategy leads to several predictions: (i) avian seed dispersers should favor nonpersistent fruits over chemically defended persistent fruits in the fall; (ii) the biochemistry of persistent fruits should change seasonally with freezing; (iii) the palatability of persistent fruits to avian seed dispersers should improve with time and exposure to winter conditions; and (iv) seeds from fruits that overwinter on the plant should still be capable of germinating in the spring after digestion by birds. An alternative view of persistent fruits is that such fruits remain on plants because they stay firmly attached and are produced in superabundance (Willis 1966; Wheelwright 1985) or are ignored by birds until preferred food sources have been depleted (Sherburne 1972; Baird 1980; Stiles 1980). Such a view does not necessarily predict seasonal changes in pulp chemistry, seasonal improvements in palatability, or the capacity for germination in the spring.

We tested these predictions in a study of *Viburnum opulus* (Caprifoliaceae). The red, fleshy fruits of *V. opulus* persist on the plant for much of the winter. The fruits are apparently chemically defended and mildly toxic and have a bitter, sour taste (Sherburne 1972). They are also discriminated against by birds, the presumed major dispersers of *V. opulus* seeds. *Viburnum opulus* fruits were removed very slowly under natural conditions in one study in England; none of the 14 common fruit-eating bird species were seen to eat *V. opulus* fruits in the field (Sorensen 1981; see also Docters van Leeuwen 1954). Artificial fruits soaked in extracts of ripe *V. opulus* fruits ranked 7th of 11 fruit species presented to fruit-eating birds in choice tests (Sorensen 1983). Sherburne (1972) speculated that *V. opulus* fruits are eaten in the spring after cold-induced reduction in toxicity; in fact, the bitterness of *V. opulus* fruits decreases somewhat over the winter (Williams 1984). Thus, *V. opulus* seemed an appropriate species for investigating the phenomenon of persistence of temperate-zone animal-dispersed fruits.

Methods

Study species

Viburnum opulus, commonly known as guelder rose or highbush cranberry, grows in moist, well-drained soils. Originally found in Europe and Asia, it was introduced into North America, where it has escaped cultivation and currently ranges across Canada and the northern United States (Gill and Pogge 1974). It is closely related to the native *Viburnum trilobum* (*V. opulus* var. *americanum*), with which it is considered conspecific by some authorities (e.g., Muenscher 1950; Fernald and Kinsey 1958). The plants observed in this study were identified as *V. opulus* on the basis of their sessile petiole glands (E. Cope, personal communication; Anonymous 1976). Voucher specimens are housed in Cornell's Bailey Hortorium.

The plants produce bright red, fleshy drupes on slender terminal panicles (Gill and Pogge 1974). Fruits ripen in August and September

and are eaten by birds and mammals (Sherburne 1972). Most fruits, however, remain uneaten on the plant all winter (Sherburne 1972; E. Jones and N. T. Wheelwright, personal observations). Fruits in our study area averaged 9.1 ± 0.6 mm ($n = 81$) in diameter. The mean wet weight of 20 fruits collected in November 1984 was 0.68 g, with an average water content of 94%. Lipids make up approximately 1.6% of the dry pericarp weight (T. Stiles, personal communication).

Removal of fruits in the field

A preliminary study demonstrated that *V. opulus* fruits were removed much more slowly than *Viburnum lentago*, *Viburnum dentatum*, or *Cornus racemosa* fruits from shrubs, artificial infructescences, and bird feeders in the field and from displays offered to captive birds from the beginning of October to the beginning of December in 1984 (E. Jones and J. Bower, unpublished data). In 1985 we measured the rate of fruit removal from eight individual *V. opulus* shrubs from October until all fruits disappeared in January. The study population was located among second-growth vegetation at the edge of a wooded area of ca. 50 ha, near the southeast corner of the Moakley Golf Course in Ithaca, NY (42°27' N, 76°27' W).

In late October 1985, four or five panicles on each focal shrub were marked with a 0.6×4.4 cm piece of orange fluorescent tape wrapped around the base of its branch (total: 36 panicles, 720 fruits). Focal panicles were randomly selected from among those borne at least 1.8 m above the ground (to protect them from browsing by deer) and bearing at least 20 fruits. The number of fruits on each focal panicle was reduced to 20 by picking excess fruits; the remainder were monitored on October 26, December 1, and January 15, at which point all fruits on focal shrubs had disappeared. We assumed that fruits had been removed by animals rather than by abscission because fruits that remained on other shrubs did not fall until March with vigorous shaking of the branches. Fewer than 5% of all fruits had been removed from focal plants between ripening (late August – early September) and the beginning of our censuses, as indicated by the scarcity of empty peduncles (which remain on the plant for weeks or months). After all marked fruits had disappeared, we made casual observations of fruit removal from other local *V. opulus* plants.

The fate of fallen fruits was examined by recording the removal of fruits placed in 0.3×0.3 m plots beneath five *V. opulus* shrubs in April 1985. Twenty single fruits and a panicle of 10 fruits were placed in each plot, and their disappearance was monitored.

Fruit measurements

The refractive index of the crushed pulp of *V. opulus* fruits was measured monthly from December through April with an Atago pocket refractometer to estimate sugar content. Fruits were collected from the eight focal trees in the study site, as well as from nearby shrubs. Refractive index values were also obtained for 10 samples of 10 frozen *V. dentatum* fruits. (The limitations of using refractometry to estimate sugar content are discussed by White and Stiles (1985), who note that refractive values give a reasonably good measure of fruit juiciness but are not specific for sugars; see, however, Coombe (1960) and Wheelwright and Janson (1985)). We measured the pH of *V. opulus* fruits monthly from January through April, by probing five individual fruits from each of four shrubs with a radiometer combination spearpoint probe with a radiometer portable pH meter. The pH of six *V. dentatum* fruits was also measured. Two-hundred *V. opulus* fruits and 400 frozen *V. dentatum* fruits preserved in 95% ethyl alcohol were analyzed at Colorado State University for chlorogenic acid concentration because of the suspected role of chlorogenic acid in antiherbivore defense (Greig-Smith and Wilson 1985).

Preference trials

We measured consumption rates and relative preferences for *V. opulus* fruits by six captive American Robins under controlled conditions for each month from October through April. The robins were maintained together in a $3 \times 4 \times 5$ m free-flight room with a natural photoperiod and reduced seasonal temperature cycles (15–20°C). Except during feeding trials, the birds were fed a standard laboratory diet (dog food, cottage cheese, grated carrots, turkey starter, calcium glucomate, vitamins, mealworms) and water *ad libitum*.

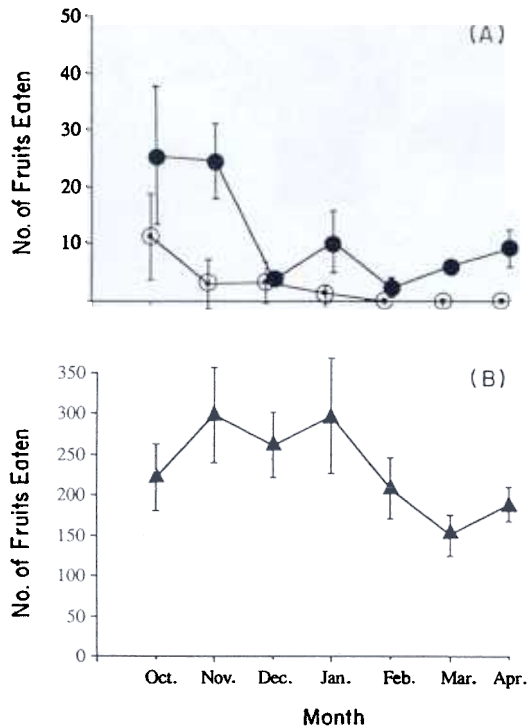


FIG. 1. (A) Mean number of *V. opulus* fruits eaten by six American Robins over a 3-h period when presented alone (●) and with *V. dentatum* (○). (B) Mean number of *V. dentatum* fruits eaten by six American Robins over a 3-h period. Fruits of both species were presented *ad libitum* in all trials. Note differences in scale on y-axes. Each point represents three feeding trials per month. Bars designate 1 SD of the mean.

Two types of feeding trials were performed: (i) *V. opulus* fruits alone (VO trials) and (ii) *V. opulus* offered with *V. dentatum* (VO versus VD trials), a highly preferred fruit species (Stiles 1980). In both types of trials, fruits were presented *ad libitum* in evenly spaced Petri dishes placed on the floor in two 2 m diameter circles, with equal numbers of dishes in each circle. Biases due to location of fruits were eliminated by alternating the position of dishes containing *V. opulus* and *V. dentatum* fruits. In October and November, we presented 15 *V. opulus* fruits in each of six Petri dishes in both trial types. Owing to the unanticipated depletion of the supply fruits in the census site (see below) and low feeding rates during the trials (cf. Fig. 1), sample sizes were reduced thereafter to 10 dishes with 8 *V. opulus* fruits in the VO trials, and 6 dishes of 5 *V. opulus* fruits in the VO versus VD trials. Six dishes of 75 *V. dentatum* fruits were used in the latter trials. Because *V. opulus* fruits are much larger than *V. dentatum* fruits and all fruits were concentrated in Petri dishes, the size of the visual display of the two fruit species differed only slightly.

Trials began at about 09:00 and lasted 3 h, during which all other food was removed from the room. Birds were not starved before experiments but because of the length of the experiments and the fact that they were performed early in the morning, birds that did not feed during trials manifested clear signs of hunger (e.g., active searching around the room). Each trial type was replicated three times monthly. Thus, each monthly data point represents 54 "bird-hours" of feeding trials. In most months VO trials alternated with VO versus VD trials on consecutive days beginning on the 3rd or 4th day of each month.

Viburnum opulus fruits were collected each month from a shrub at the census site until fruits were depleted by predators in mid-January. In subsequent trials an equal number of fruits were gathered from each of five shrubs located 300 m away. Fruits from the two areas did not differ in appearance, sugar concentration, or pH and there were no differences in the results of preference trials. After collection, fruits were stored for several days in a refrigerator until used. *Viburnum*

dentatum fruits were collected in September, immediately placed in liquid nitrogen, and preserved in a deep freeze at -60°C . These fruits served as a standard for measuring robins' relative preference for *V. opulus* fruits.

Germination experiments

Each month we collected *V. opulus* seeds regurgitated by the captive robins and planted them at a density of ca. 1 seed/10 cm² at a depth of 1 cm in a 1 × 1 m outdoor garden plot, in a Latin square design to control for microenvironmental variation. Seeds were not watered other than by naturally occurring rainfall. By mid-July none had germinated. The seeds were then excavated and transported in paper envelopes with soil at ambient temperature to Brunswick, ME (because of a change of address by N.T.W.), where they were replanted within a week in sterile soil in separate peat pots placed outside and monitored monthly.

Results

Removal of fruits in the field

Although *V. opulus* fruits ripen in late August or early September, few fruits had been removed by October 26, by which time most fall migratory fruit-eating birds had left the area (Thompson and Willson 1979; Stiles 1980). However, by December 1, 73% of all fruits ($n = 720$) on marked panicles had been removed. By January 15, 100% of the fruits had been removed, although we never observed birds or mammals feeding on marked *V. opulus* fruits. The disappearance of fruits coincided with a local irruption of Pine Grosbeaks (*Pinicola enucleator*), and observations of grosbeaks damaging fruits of various species (G. Butcher, personal communication; E. Jones and N. T. Wheelwright, personal observations) implicated these avian seed predators. Each focal shrub had numerous fruits and broken panicles scattered beneath; empty fruit skins were left hanging on panicles and cracked seed coats lay on the ground and branches. Although the fruit crops of all of our focal shrubs were entirely depleted of fruits, some nearby smaller shrubs, as well as large shrubs in other areas, were bypassed. Casual observations of other *V. opulus* shrubs in the area showed very low removal rates of fruits and plants retained fruits throughout the winter. By late March, most fruits had withered on the plants and fell easily with shaking of the branches. A few plants held fruits through May.

Of the fruits experimentally placed on the ground ($n = 150$), 5% disappeared after 1 day, 8% after 4 days, and 66% after 16 days. In three of the five plots, remains of seed coats were found. Small incisor marks on the seed coats suggested that predation was caused by rodents such as *Peromyscus* spp. or *Tamias striatus*.

Preference trials

The rate of consumption of *V. opulus* fruits by captive robins in the VO trials declined abruptly after November and remained low for the last 4 months (Spearman rank correlation between month and number of fruits eaten: $P < 0.01$; Fig. 1). In the VO versus VD trials, the number of *V. opulus* fruits eaten also showed a sharp seasonal decrease. No *V. opulus* fruits were eaten during the last 3 months of feeding trials (Fig. 1). *Viburnum dentatum* consumption remained relatively constant through January, declined sharply through March, and then showed a slight increase in April (Fig. 1). Robins consistently preferred *V. dentatum* to *V. opulus* fruits (Wilcoxon signed rank test: $P < 0.01$) even when corrected for the larger size of *V. opulus* fruits (ca. 6.7 times the volume and 1.6 times the dry pericarp mass of *V. dentatum* fruits). The birds ate fewer *V. opulus* fruits when simultaneously offered

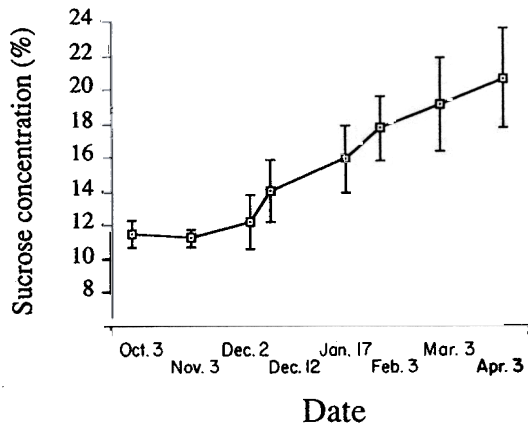


FIG. 2. Mean refractive index of *V. opulus* fruits collected at monthly intervals. $n = 10$ fruits in October and November, and >20 fruits per month from at least four shrubs thereafter. Bars designate 1 SD of the mean.

V. dentatum than when *V. opulus* fruits were offered alone ($P < 0.02$). Earlier experiments with artificial fruit displays in the field and laboratory showed that robins and other fruit-eating birds preferred most species of fruits (e.g., *Cornus racemosa*, *Lindera benzoin*, *Vitis* sp., *Lonicera tatarica*) to *V. opulus* (J. Bower and E. Jones, S. Sargent, N. T. Wheelwright, unpublished data).

Fruit measurements

The mean monthly refractive index for *V. opulus* fruits increased from 11.5 ± 0.8 to 20.6 ± 2.9 between October and April (Spearman rank correlation: $P < 0.01$; Fig. 2). Mean pH of *V. opulus* fruits varied little ($\text{pH } 2.8 \pm 0.1$ to 3.0 ± 0.1) and nonsignificantly ($P > 0.01$) over a 4-month period. *Viburnum opulus* fruits were significantly more acidic than *V. dentatum* fruits ($\text{pH } 5.1 \pm 0.0$; Mann-Whitney U test: $P < 0.05$). Individual *V. opulus* fruits contained approximately 2.5 mg chlorogenic acid (6% of dry pericarp weight); no chlorogenic acid was discovered in *V. dentatum* fruits (F. Stermitz, personal communication). In an independent study (M. Witmer and S. Sargent, unpublished data) in the same area, fall and spring samples of *V. opulus* pericarp were similar in water, ash, and tannin content. Thus, only sugar concentration showed a seasonal change in *V. opulus* fruits.

Seed germination

Between mid-July and mid-August 1986, 50% of the *V. opulus* seeds had germinated ($n = 124$). Another 11.3% germinated by mid-September. There was no difference in germination success or timing as a function of month of processing by birds (Kruskal-Wallis test: $P = 0.60$ for August; $P = 0.49$ for September) or whether they had been regurgitated and planted before ($n = 58$) or after ($n = 66$) February (chi-square test: $P > 0.50$). Although we cannot rule out the possibility that seeds germinated in response to a sudden change in treatment, this appears unlikely because the conditions of transport and replanting were not highly unusual compared with the normal variation in rainfall and temperature characteristic of Ithaca summers.

Discussion

The fruits of *V. opulus* share many traits traditionally associated with persistent fruits of bird-dispersed plants. They remain uneaten on the plant until long after fall migratory fruit-

eating birds have flown south for the winter. They are rejected in the field and laboratory by fruit-eating birds given a choice of alternative fruits. They are chemically protected. Our first prediction (presaged by numerous earlier reports: Sherburne 1972; Williams 1984), that the fruits of *V. opulus* would persist uneaten on plants, was supported. Very few fruits were removed between August and late November. The reason that *V. opulus* fruits persisted was not that they were produced in superabundance: *V. opulus* shrubs bear relatively few fruits. Observations and experiments in the field and laboratory demonstrated clearly that birds prefer all other local fruits tested over those of *V. opulus*. Birds' distaste for *V. opulus* fruits was apparently due to more than simple nutritional inadequacy, judging from the fact that birds often rejected the fruits despite clear signs of hunger (cf. Sorensen 1983). The chemical basis for the relative unpalatability of *V. opulus* fruits may be their low pH (considerably more acidic than those of their congener, *V. dentatum*), unusually high levels of chlorogenic acid (Greig-Smith and Wilson 1985), reduced lipid content (T. Stiles, personal communication), or perhaps the presence of secondary compounds not measured in this study but known to occur in *V. opulus* leaves (e.g., flavonoids, saponins, arbutins (Frohne and Pfander 1983)). Low pH and high levels of chlorogenic acid may interact to play a role in protecting *V. opulus* fruits against pathogens. Hulme and Edney (1960) found that, at a pH of 2.8 (which is similar to the pH of *V. opulus* fruits), chlorogenic acid inhibited the germination of fungal spores; under less acidic conditions (pH 4.0), spore germination was merely delayed.

Our second prediction, that pulp composition would change seasonally, was only partially upheld. *Viburnum opulus* fruits underwent few apparent seasonal chemical changes. Only sucrose concentration changed noticeably, nearly doubling over a 6-month period with an accompanying subjective improvement in flavor (to humans). Other pulp components (tannins, water concentration, ash content) did not change over time or with freezing (M. Witmer and S. Sargent, unpublished data). Fruit pH remained constant and low throughout the winter and spring. Although Best (1981) noticed seasonal changes in palatability of *Symphoricarpos albus* fruits, she detected no change in the concentration of nitrogen, fats, or carbohydrates after freezing. Grieg-Smith and Wilson (1985) discovered no consistent changes in *Fraxinus excelsior* fruit chemistry after ripening.

Contrary to our third prediction, absolute consumption of *V. opulus* fruits by robins, as well as preference of *V. opulus* fruits relative to *V. dentatum* fruits, decreased rather than increased over the winter. The results of the monthly preference trials indicated that, if any chemical changes occurred in the field in *V. opulus* fruits between October and April, they had a negligible or even a negative effect on palatability to American Robins, which are one of the most important avian seed dispersers of North America (Wheelwright 1986). The fact that the robins' consumption of *V. dentatum* fruits (whose composition probably changed little, if at all, because they were preserved at -60°C ; see Lee (1970)) also fell as spring approached indicates that this decline in *V. opulus* consumption may in part reflect innate seasonal changes in diet preferences in fruit-eating birds (N. T. Wheelwright, unpublished data). Regardless of the possible complications introduced by seasonal patterns of fruit eating, our third prediction (an increase in the preference of persistent fruits with time and freezing) was not upheld, at least for robins. Thus, *V. opulus* plants probably do not benefit from higher dispersal rates in the

spring because of cold-induced flavor improvements. Despite its membership in a genus known to be dispersed by birds and its small, red, fleshy fruits which fit the syndrome of avian seed dispersal (van der Pijl 1969; Janson 1983), *V. opulus* could of course be dispersed by mammals in addition to or instead of birds, in which case this and other studies (Sherburne 1972; Sorensen 1981, 1983) of avian consumption of *V. opulus* fruits are incomplete.

The final prediction, that the seeds of *V. opulus* fruits eaten in the spring would still be capable of germination, was confirmed. In fact, there was no difference in the timing or success of germination of seeds processed by birds in the fall versus the spring. Consequently, seeds processed in the spring germinated in less time than seeds processed in the fall (median elapsed time between processing and germination for seeds of fruits eaten in November was 9 versus 4 months for those eaten in April). These results contradict earlier reports (e.g., Gill and Pogge 1974) that germination of *V. opulus* seeds was difficult and did not occur during the 1st year following dispersal.

In conclusion, even though *V. opulus* showed certain adaptations for winter and spring seed dispersal (defense of fruits against pathogens, capacity for germination following spring dispersal), it did not show other characteristics theoretically associated with persistent fruits (seasonal change in pH and tannin levels, seasonal improvement in palatability to birds). While our results do not strongly support current hypotheses about the strategy of bearing persistent fruits, they do not favor at least one alternative view, namely, that fruits simply remain over winter because they are produced in superabundance. The captive-bird experiments offer some support for the notion that persistent fruits remain because foraging animals prefer alternative foods. Even when no other fruits were available, however, robins did not readily eat *V. opulus* fruits.

Assuming that *V. opulus* is representative of other species with persistent fruits, it appears that plants selected for whatever reason to have chemically defended (or otherwise distasteful) fall fruits may be "stuck" with relatively unpalatable fruits and poor seed dispersal in the winter and spring. Nonetheless, under certain conditions a strategy of fruit persistence could be successful. The low frequency of removal of *V. opulus* fruits by legitimate seed dispersers during our study may reflect unusually mild climatic conditions during the spring of 1986. Temperatures in March and April in Ithaca normally average 0.2 and 6.9°C, respectively; in 1986 temperatures were higher (2.0 and 8.1°C). In addition, there was less snowfall than usual when migratory fruit-eating birds returned in March 1986 (10.7 cm versus a March average of 31.5 cm) (Cornell University Department of Meteorology, unpublished data). Because avian metabolic requirements are greater and the availability of more preferred foods (especially invertebrates) is probably lower under severe spring conditions, the seeds of *V. opulus* and other species with persistent fruits may be adequately dispersed in unusually cold winters and springs. During unseasonal snow storms, many birds switch to a fruit diet (N. T. Wheelwright, personal observations). If this line of reasoning is correct, chemically defended, persistent fruits should be rare in short-lived plants and most common in moderately long lived shrubs, which can produce fruits over a number of years (cf. Herrera 1982).

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