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Avoidance by birds of insect-infested fruits of Vaccinium ovalifolium

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This study investigates the interaction between the insects (a sawfly and a moth) that infest the fruits of *Vaccinium ovalifolium* (Ericaceae) and the birds that act as seed dispersers of this plant in a temperate rainforest of Southeastern Alaska. Experiments and observations were performed in the field and with captive birds in an aviary. Intact fruits are round whereas those that are attacked by an insect usually acquire a deformed shape; thus, birds have a cue to discriminate among the blueberries. Infested berries are not necessarily larger or smaller than intact berries, so fruit size cannot be used as a cue to discriminate between them. Results from the aviary experiments showed that the two avian species examined, varied thrushes and American robins, consumed significantly less insect-infested fruits than uninfested ones. In the field, birds also showed a preference for round fruits over deformed ones. Here, the probability of removal of an insect-infested berry depends on the type of habitat where the plant is located. Avian fruit removal was higher in an open site than inside the forest while the incidence of insects was greater in the latter. The presence of deformed fruits did not decrease the removal of uninfested fruits in either site.
Not all seeds in an infested fruit are killed by the larvae, so animals may still be dispersers of the viable seeds if the infested fruit is consumed. The larger the fruit the higher the number of seeds within it. The two species of birds preferred large over small fruits in the aviary. Therefore, a seed in a large berry – infested or not by insects – might have a greater probability of being dispersed than one in a smaller fruit (although to assess this we need to know which other factors affect fruit selection).
There is no apparent competition between birds and insects that results in a non-overlapping use of the resources (fruits). The two insect species risk mortality by vertebrate frugivores, as larvae develop within ripe fruits. The evolutionary implications of the bird-insect interaction for plant fitness are apparently negligible, mainly because insects do not seem to kill many seeds and also because the bird-insect encounters are rather few.

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Fruit choices by vertebrate frugivores usually respond to differences in traits such as ripeness, chemical composition, fruit size and shape, and accessibility (see Jordano 1992 for a recent review). The presence of insect larvae in the fruits (either in the pulp or inside the seeds) can alter some of those attributes, with the potential implication of increasing or decreasing fruit attractiveness to vertebrate dispersers. For instance, fruit ripening can be precluded in *Ilex opaca* (Krischik et al. 1989) and in *Pistacia terebinthus* (Traveset 1993) by the presence of larvae of cecidomyiid flies and chalcidoid wasps, respectively. Insect larvae in fruits also change the chemical composition of the pulp with their excreta and, usually, also by introducing microbes that give the fruit a bitter

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taste. The change in palatability deters vertebrates from eating those infested fruits of several species (e.g., Stiles 1980, Manzur and Courtney 1984, Burger 1987, Jordano 1987, Borowicz 1988, Buchholz and Levey 1990, Christensen and Whitman 1991). Likewise, insect larvae increase the nutritional value of the fruit, mainly by increasing the protein level (Piper 1986, Drew 1988), which may cause some vertebrates such as primates (Freeland 1979, Redford et al. 1984) and birds (Valburg 1992a, b) to prefer the infested over the uninfested fruits. Insect-infested seeds have also shown to be preferred by rodents (Davis 1907, Linduska 1942; but see Semel and Anderson 1988 and Weckerly et al. 1989), peccaries (Kiltie 1980) or avian seed predators such as cockatoos (Scott and Black 1981).

Frugivorous insects can alter the color of fruits (e.g., Carter 1939, Krischik et al. 1989 and references therein, Traveset 1993), their size and shape (Highland 1964) and even their texture (Carter 1939), making it possible for vertebrates to visually discriminate between infested and intact fruits. An alteration mostly visible in fruit shape has been found in several species of *Vaccinium* (Ericaceae) that are infested by a sawfly and a moth larva which feed upon the seeds (Gaither unpubl.). The objectives of the present study were to learn whether avian seed dispersers distinguish intact fruits (completely round) from infested ones (deformed) in one such species, *Vaccinium ovalifolium* Sm. (early blueberry), and whether they prefer one over the other. This species is infested by the moth *Lotisma trigonana* (Walsingham) (Lepidoptera: Copromorphidae) and by the sawfly *Melastola resinicolor* (Marlatt) (Hymenoptera: Tenthredinidae). The deformation usually consists of one protuberance in the horizontal axis but sometimes a fruit can be greatly deformed and have two or three. Early- and mid-season infestation by *L. trigonana* nearly always results in grossly deformed and stunted fruit. *M. resinicolor*, in contrast, infests fruit approximately one month later in the season, when most berries have already achieved full development, having much less of an impact on fruit size and shape than *L. trigonana*.

Experiments and observations were made in the field and with captive birds in an aviary. If birds consume infested fruits, they might still act as seed dispersers if some viable seeds are left intact by the larvae. Also, if large berries contain more seeds than small ones and the former are preferred by birds, a seed in a large fruit might have a greater chance of being dispersed, assuming that larvae eat similar amounts of seeds per fruit and that other effects (crop size, plant location, etc.) are not as important as fruit size for removal. Thus, we were also interested in determining 1) how many seeds remain viable after larvae have left the fruit, 2) whether there is a correlation between number of seeds and fruit size, and 3) whether birds prefer large over small fruits.

V. ovalifolium is found in moist coniferous forests and openings and also in bogs, from low to subalpine elevations. At low altitudes, where this research took place, the first ripe fruits (blue-colored) appear in mid to late June. Generally, by mid-July the entire fruit crop has turned blue. The berries remain on the plants through September. Cool temperatures in the autumn result in fruit and leaf drop. Average fruit diameter was found to be 11.04 ± 1.02 (s.d.) mm (n = 208), and the total number of seeds per fruit was 85.70 ± 29.21 (s.d.) (n = 84), ranging from 20 to 141.

There is often mold inside a fruit which has been infested by insects. Larvae feed on seeds and deposit frass within the interior of the fruits. The mold, not visible from the exterior, usually grows on such frass, but also on head casings, partially eaten seeds, and rotting pulp.

The berries are dispersed by several species of birds and also by brown and black bears (*Ursus arctos* and *U. americanus*, respectively). At present, it is unknown which of the two groups (birds or bears) is the most efficient as seed dispersers of this species in the areas where they both coexist.

Methods

The experiments required that we accurately judged whether a fruit was deformed and hence infested, or round and thus not infested. To determine the probability of judging correctly we dissected 115 berries considered not infested and 139 berries considered infested. Although infested fruits tend to be smaller than intact fruits (see Results section), they cannot be distinguished simply by size due to the high variation in diameter of both types of fruits. In order to describe the deformations, the ratio of the two perpendicular axes of 30 deformed fruits was calculated and compared with that of 30 round fruits.

Infested and intact berries are similar in texture and color, so birds cannot discriminate between them on these bases. To determine differences in fruit weight which could affect fruit choice and handling by birds, we weighed 50 deformed fruits and 50 round fruits.

A total of 35 fruits that bore an insect exit hole were collected in the field and dissected under the microscope to record the number of viable seeds remaining.

Aviary experiments

Three individual juveniles of *Ixoreus naevius* (varied thrushes) and three juveniles of *Turdus migratorius* (American robins) were used for these experiments, all performed during the fruiting season. The two species are highly frugivorous (Willson 1994, and pers. obs.) and we have often seen them in the field feeding upon blueberries. They were chosen mainly because they do well in captivity. All six individuals were placed in separate cages and were maintained on a diet consisting of artificial fruit (Denslow et al. 1987), Science Diet TM Kitten kibble, and earthworms.

Table 1. Number of round (uninfested) and deformed fruits (with a high probability of being infested) eaten by three individuals (each row represents an individual) of each bird species during experiments 1 and 2. Number of large (> 10 mm diameter) and small (< 10 mm diameter) fruits eaten by three individuals of each bird species during experiment 3. * P<0.05.

Species	Exp. 1		Exp. 2		Exp. 3	
	Round	Deformed	Round	Deformed	Large	Small
Varied thrush	26	15	10	3	8	2
	22	16	41	31	7	3
	24	11	21	10	6	4
Total	72	42*	72	44*	21	9*
American robin	26	21	25	18	10	0
	18	16	34	18	7	3
	4	1	14	12	6	4
Total	48	38	73	48*	23	7*

In experiment 1, lasting from 9 August to 14 August 1993, we sought to determine whether the birds preferred either round or deformed fruits. Two Petri dishes, one with five deformed fruits and the other with five round fruits, all of similar size, were placed close to each other in each bird cage. Dishes were checked every 30–90 min (depending upon the birds' appetite). Ten trials were performed for each individual bird.

In experiment 2, carried out between 15 August and 22 August, our goal was the same as in experiment 1, but we altered the experiment by changing the method of fruit presentation. Five round and five deformed fruits were placed alternately on a single tray. Trays were checked periodically, recording the number of fruits remaining of each type. Ten trials were again performed for each individual bird.

Experiment 3 consisted of determining whether there was any preference by birds for a given fruit size. Sixty large and sixty small fruits, all mature and round, were collected from different shrubs. Their diameter and weight were measured. One large fruit (> 10 mm) and one small fruit (< 10 mm) were placed on a Petri dish. Birds were observed from a blind within the aviary, recording their first fruit choice. A total of 10 trials were carried out for each individual. The experiment took place on 23–24 August.

Avian fruit removal in the field

We marked a total of 20 stems of *V. ovalifolium* in an area off Fish Creek (58°20'N, 134°34'W), on Douglas Island, about 10 km from Juneau, Alaska, USA. Ten of the stems were haphazardly selected from an open site. The other ten stems were haphazardly chosen from a nearby site under partial tree cover inside the forest, which is dominated by hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*). For each marked stem, the total number of deformed and round fruits per branch were recorded on 1 August and were counted weekly until 30 August. In the open site, the deformed fruits were much scarcer than in the forested site, and they were individually marked for easy detection in the following counts. Fruit removal in all experimental plants was done by birds since no bear visitation was evidenced in the area. Bears usually eat most berries from a branch along with the foliage and their footprints are quite obvious.

Data analysis

Chi-square tests were used to determine fruit preference by birds both in the aviary and in the field. Fruit removal in the field was summed over all days to obtain total fruit removal per stem. Two Chi-square tests, one for each site, were used to test for significant differences in fruit removal between round and deformed fruits. Both Pearson and Spearman's tests were used to search for significant correlations between variables measured in the field.

Results

Of the 115 berries examined and judged to be free of insect larvae, 113 (98.3%) actually were free of larvae upon dissection. The probability of being correct when predicting that a deformed fruit bore an insect larva was lower: of the 139 fruits judged to be infested, 77% contained an insect larva, but 23% did not. Those fruits that were greatly deformed always bore a larva but those that were only slightly deformed sometimes did not (this might be due to an early death of the larva within the fruit, although we do not have any evidence).

The maximum diameter of deformed fruits tends to be slightly smaller than that of round fruits (9.4 ± 0.2 mm vs 10.1 ± 0.2 mm; $F_{1,58} = 6.07$, $P = 0.02$). The range of the latter (7.2–1.17) encompasses that of the former (7.2–1.12) and that is why infested and intact berries cannot be told apart just by looking at fruit size. The ratio of the two perpendicular axes appears to be greater in deformed fruits (1.33 ± 0.02) than in round fruits (1.25 ± 0.02) ($F_{1,58} = 10.52$, $P = 0.02$).

Table 2. Number of round and deformed fruits that were consumed from the 10 stems marked in the field at each of the two sites examined.

	Open		Intermediate	
	Round	Deformed	Round	Deformed
Fruits eaten	274	37	109	13
Fruits uneaten	414	48	139	140

Experiment 1 indicated that varied thrushes discriminated between round and deformed fruits, preferring the former (Table 1) whereas American robins showed no discrimination or preference. When the two types of fruits were offered on the same tray (experiment 2), thrushes still preferred round fruits and robins now consumed more round than deformed fruits also, possibly because they had learned the distinguishing cues (Table 1).

Both species displayed a preference for large fruits over small ones (Table 1, experiment 3). The number of seeds per fruit is significantly correlated with fruit size ($r=0.65$, $P=0.0001$, $n=42$); thus by eating more large fruits birds are dispersing more seeds than by eating small ones. The correlation, however, varies from site to site and from year to year (Gaither unpubl.). Total seed load per fruit is also positively correlated with fruit size ($r=0.75$, $P=0.0001$, $n=42$). Fruit weight was not significantly different between infested and intact berries (0.34 ± 0.16 g (s.d.) vs 0.38 ± 0.15 g, respectively, $n=50$).

The average number of viable seeds left intact after insect infestation was 14.5 ± 14.7 (s.d.) ($n=35$), which represents about 10% of the initial number of seeds. Thus, even fruits that are or were infested can still have some of their seeds dispersed if they are consumed by a vertebrate.

Fruit removal by birds in the field was not significantly different between round and deformed berries in the open site ($X^2=0.43$, $P=0.51$) but round fruits were preferred over deformed ones in the forested area ($X^2=56.2$, $P<0.001$) (Table 2). Removal of round and deformed fruits through time is shown in Fig. 1 for the two areas.

Total fruit production was larger in the open than in the forested site, although the proportion of deformed berries was greater in the latter. The total number of fruits per stem was, on average, 77.3 ± 10.9 (s.e.) ($n=10$ stems) in the open area but only 40.1 ± 6.7 ($n=10$) in the forested site. The number of deformed fruits per stem, in contrast, was significantly higher in the forested than in the open site (15.3 ± 1.5 (s.e.) vs 8.5 ± 1.7; $F_{1,18}=9.4$, $P=0.007$).

Total avian fruit removal was higher in the open (40%) than in the forested area (30%) (Table 2). Considering both sites together, there was a significant positive correlation between total number of fruits removed (infested or not) and number of fruits produced per stem ($r_s=0.60$, $P=0.005$). When the sites were considered separately, such correlation was significant only for the stems in the forested site ($r_s=0.84$, $P=0.002$).

A regression analysis showed that the proportion of deformed fruits in each stem does not influence significantly the removal of round fruits or the total fruit removal per stem in either the forested or the open site ($P>0.05$).

Discussion

The experiments performed both in the aviary and in the field showed that birds are able to discriminate between insect-infested fruits and intact fruits by recognizing the shape of the blueberries. In the aviary, the preference for non-infested fruits was detected for both varied thrushes and robins; the latter might take longer to discriminate between fruits as significant differences in removal were observed in the second but not in the first experiment. Bird preference for non-infested fruits has also been found in other studies (Manzur and Courtney 1984, Burger 1987, Jordano 1987, Christensen and Whitman 1991). It remains unknown, however, whether infested fruits deter birds because of toxins produced by pathogens or because of other reasons. In *Vaccinium*, it might be the mold that grows on frass left by insects inside the fruits what is toxic or unpalatable to birds. Only in two studies, as far as we know, have birds shown a preference for insect-infested fruits: Scott and Black (1981) found cock-

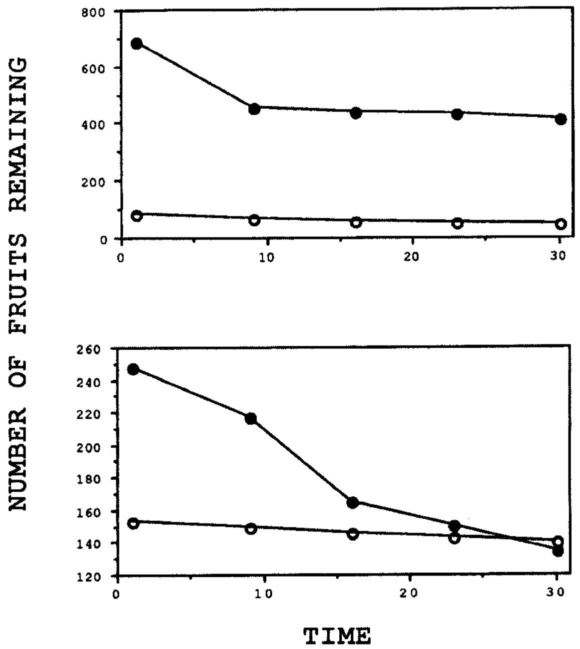

Fig. 1. Removal by birds of deformed (○) and round fruits (●) in the open (above) and the forested site (below) during the month of August. 10 stems examined from each site.

atoos to prefer seeds that contained insect larvae over those that did not, and Valburg (1992a, b) found tanagers to prefer berries, the pulp of which was mined by a dipteran larva. Valburg (1992b) also found that the same species of bird may prefer the infested fruits of a plant species but the uninfested fruits of another species. The effect of larval infestation on fruit removal by vertebrates has received little attention so far, and we still need more studies, with other species and in different areas, in order to make any generalization.

In the field, we found that the probability of removal for an insect-infested berry depended upon the area where the stem is located. In the open site, where deformed fruits were scarcer and avian fruit removal was higher (probably due to a greater bird abundance), the probability that such fruits were taken by birds was greater than in a nearby site inside the forest where insect infestation was more common and avian fruit removal was lower. The same patterns have been found in other open and forested sites in nearby areas by one of us (Gaither unpubl.).

Birds usually use a set of criteria more complex than form alone in their fruit selection. In the aviary, for instance, we observed that large fruits were preferred over small fruits by the two species studied; thus, size is also an important trait determining fruit choice. A recent study of fruit selection by American robins (Sallabanks 1993) also shows that this species prefer large over small fruits of *Crataegus monogyna*. This author found that robins hierarchically used fruit abundance, fruit size and fruit pulpiness as decision cues to select a shrub where to feed; once a shrub was selected, robins then made visual choices among fruits correlated with fruit size. In the present system, we know from the aviary experiments that both fruit size and shape are important as decision cues. The question remains, however, which trait is used first in the visual choice. Given that infested fruits tend to be smaller than intact fruits, (although the size cue is not sufficient to tell them apart due to the variation within and among plants), what is certain is that by choosing large and round fruits the probability that a bird eats an infested berry is minimized.

From an evolutionary viewpoint, the bird-insect interaction may have important consequences for seed dispersal (Manzur and Courtney 1984, Jordano 1987). In the present case, however, as found also in other systems (e.g. Traveset 1993), the implications for plant fitness of such interaction might be negligible, especially if the insects do not represent an important seed mortality factor (at least in the year of study, the incidence of insects in the fruits was rather low). Moreover, the bird-insect encounters appear to be very few; in the area with higher insect infestation avian fruit removal is lower and vice versa. The relative role of bears vs birds in the dispersal system of *V. ovalifolium* is unknown. Both brown and black bears consume large quantities of fruits of this species (probably not discriminating between infested and uninfested ones), evidenced by the great amount of seeds found in their faeces in some areas, but they might not be as efficient as birds because of the high seed density in those faeces, for instance.

The fact that some viable seeds always remain in infested fruits and that they may still be successfully dispersed if such fruit is consumed by a vertebrate (bird or mammal) leads one to think that selection to avoid insect infestation is probably very low. The two bird species used in the aviary experiments showed a preference for large fruits over small ones. If the other avian dispersers have the same preferences, there might be selection favoring individuals that produce large fruits. Insects, which infest fruits that are still developing, might exert a selection on fruit size only in the case they leave more intact seeds in large than in small fruits. We do not have any data so far to show this.

It is often assumed that, in general, insect and vertebrate frugivores compete for resources (Sallabanks and Courtney 1992, but see Traveset 1993) and that such competition results in a selection against those insects whose development overlaps with vertebrate fruit consumption. A few studies (Bigler and Delucchi 1981, Drew 1987) suggest that vertebrates are the major natural enemies of insects that feed on fruit pulp, and that larvae leave the fruits to pupate in the soil as an adaptation to escape vertebrate ingestion. In the present system, however, we do not find a common pattern of insect behavior which may lower the probability of being eaten by vertebrate frugivores. The moth larvae cause more conspicuous fruit deformation than the sawfly larvae. Moth larvae pupate outside the fruit, whereas sawfly larvae pupate inside the fruit, and both species risk mortality by vertebrate frugivory during their larval development. In the case of insects that develop inside seeds, no evidence of vertebrate-insect competition exists so far, and it has been shown (Chung and Waller 1986, among others) that vertebrates may even act as mutualists of insects rather than as competitors by transporting larvae within their guts to different places.

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