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Author(s): Alan E. Burger
Source: *Oikos*, Vol. 49, No. 1 (May, 1987), pp. 3-10
Published by: Wiley on behalf of Nordic Society Oikos
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OIKOS 49: 3–10. Copenhagen 1987

Fruiting and frugivory of Cornus canadensis in boreal forest in Newfoundland

Alan E. Burger

Burger, A. E. 1987. Fruiting and frugivory of *Cornus canadensis* in boreal forest in Newfoundland. – Oikos 49: 3–10.

The fate of fruits of bunchberry *Cornus canadensis* was monitored for three autumn seasons in boreal forest in Newfoundland. On average, 53% of the berries were removed while intact, 23% damaged by slugs and other invertebrates, 18% infected by microbes, 3% shrivelled, 1% fell to the ground and 2% remained intact until covered by snow. Observations and exclosure experiments showed that birds were major dispersers, rodents and shrews had negligible effects and hares or squirrels ate <6% of the fruits. Most removals occurred in five-week periods, coinciding with the passage of migrant birds. Dispersers tended to avoid damaged or infected fruits: 92% of the dispersed fruits were intact when removed, 6% were damaged and 2% infected. The frequency of removals varied significantly between seasons and between plots, and was not correlated with the size of the berry crop in each plot. Frugivory within a boreal ecosystem is discussed.

A. E. Burger. Dept of Biology, Grenfell College, Memorial Univ., Corner Brook, Newfoundland, Canada A2H 6P9 (present address: Bamfield Marine Station, Bamfield, B.C., Canada VOR 1B0).

Introduction

Plant-frugivore interactions in boreal ecosystems have received little attention, unlike tropical and mid-latitude temperate systems (Thompson and Willson 1979, Stiles 1980, Herrera 1982a, 1985, Howe and Smallwood 1982). Few boreal trees have seeds disseminated as fruit (Stiles 1980) but many shrubs bear fleshy fruits (Ryan 1978). The more restricted fruiting seasons and the paucity of frugivorous birds (Godfrey 1979) in these latitudes may lead to patterns of fruiting and dispersal which differ from those further south.

This paper reports on fruit-frugivore interactions involving bunchberry *Cornus canadensis,* a common plant of forest floors across boreal and cool-temperate North America. During three autumn seasons I documented the fates of ripe fruits, and recorded the numbers of dispersal agents and predators of the fruits. Exclosure experiments tested the importance of birds as dispersers and the durability of fruits. One aim of the study was to determine whether concepts emerging from studies of fruit, frugivores and fruit pests in mid-latitude temperate regions applied to a boreal species. First, I examined the hypothesis (Snow 1971, Thompson and Willson 1979, Stiles 1980) that autumn-fruiting plants maximize seed dispersal by presenting ripe fruit at the time of bird migration in the region. Fruit presentation should thus be inversely correlated with latitude; my data come from more northerly latitudes than similar studies in North America.

Second, I investigated the proposal that fruits in eastern North America show divergent characteristics for either bird or mammal dispersal (Stiles 1980). *C. canadensis* is of particular interest because it exibits characteristics of both bird and mammal dispersed fruit (Stiles 1980). The genus *Cornus* has large interspecific variations in fruit quality (Stiles 1980, Borowicz and Stephenson 1985, Johnson et al. 1985) and detailed study of this genus might reveal whether ecological adaptations for seed dispersal are constrained by taxonomic relationships. Third, I examined Stiles' (1980) suggestion that low quality fruits should be adapted for prolonged

Accepted 13 October 1986

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exposure to dispersers, to compensate for their relative unattractiveness to frugivores. Finally, the effects of damage to fruit by invertebrates and microbial infection were determined. The interactions between fruiting plants, invertebrate fruit pests and frugivorous, vertebrate seed-dispersers are largely unexplored in temperate regions (Herrera 1982a, 1984, Manzur and Courtney 1984, Courtney and Manzur 1985).

Study area and study species

The study area was in second-growth forest bordering the campus of Grenfell College on the outskirts of Corner Brook, Newfoundland (49°N, 58°W). The vegetation was typical of boreal forest in western Newfoundland (Damman 1967, Bouchard et al. 1978), dominated by balsam fir *Abies balsamea* with white spruce *Picea glauca,* black spruce *P. mariana* and white birch *Betula papyrifera* also common trees. The canopy was discontinuous and there were frequent patches where trees had fallen or small clearings had been cut.

Cornus canadensis is a low (10–20 cm) plant with erect herbaceous stems each bearing a whorl of annual leaves rising from a woody underground rhizome (Gleason and Cronquist 1963). It is common on forest floors in western Newfoundland, particularly where understorey foliage is absent or sparse. Flowering occurs from June through July, and fruits ripen in late August. The fruits are single-stoned drupes, about 8 mm in diameter, each borne on a short (3–5 mm) pedicel. The infructescence consists of a tight cluster of berries (average 7 berries per bunch, range 1–18) at the tip of a slender stalk rising vertically about 5 cm above the horizontal whorl of leaves. The bunch of bright red berries contrasts conspicuously with the green foliage.

Fruits of *C. canadensis* from Maine analysed by D. W. White and E. W. Stiles (unpubl.) averaged 148.6 mg, with seeds 7.9 mg, resulting in a seed load of 5.32%. The fleshy pulp was of low quality, relative to other fruit from eastern North America, having a high water content (91.3%) with the dried pulp having a high soluble carbohydrate content (49.1%) but little lipid (1.2%), protein (3.3%) and energy (17 kJ g^{-1}).

Methods

Bunchberry fruits were monitored in 1982, 1984 and 1985 in 1 m^2 plots, located in dense aggregations of berries 20–200 m apart. Each infructesence was labelled with small letters inked on the leaves below. Plots were visited regularly, usually every 3–7 d, from the time berries ripened until snow covered the plants.

At each visit the berries were allocated to one of the following categories.

1) *Removed.* These were berries which had disappeared since the previous visit. Intact fruit was recorded separately from fruit blemished by invertebrates, microbes or shrivelling.

2) *Damaged.* These were fruits which had been wholly or partially eaten by invertebrates leaving the seed and some flesh still attached to the infructescence.

3) *Infected.* These were fruits visibly affected by infections of fungi or other microbes. The fruits were discoloured, and the flesh was no longer firm.

4) *Shrivelled.* These were fruits which had shrunk without visible evidence of infections.

5) *Fallen.* The ground below bunches where fruits had disappeared was carefully searched for fallen fruit.

I recorded invertebrates found on fruits, and mammals and birds seen in the forest during the 2 h visits to the plots. Birds were also censused, between 0830–0930 hours, along a 2.1 km transect situated 0.5–2.0 km from the fruit plots, covering residential areas with gardens (56%), parks (30%) and boreal forest (14%). Such repeated counts by a single observer produce crude estimates of bird density suitable for monitoring migration, and changes in relative densities of post-breeding birds (Erskine 1981).

In 1985, exclosure experiments were used at five sites: two 20 m apart and all others > 100 m apart. At each site, two square frames (1 m^2) of light wooden lath were positioned 15–20 cm over adjacent patches of *C. canadensis* berries. One frame, the exclosure plot, was covered with wire netting (mesh diameter 25 cm), which excluded birds, squirrels and hares but allowed invertebrates, shrews and small rodents to enter. The adjacent control plot was left uncovered (open plot), and the berries in all plots were checked regularly.

Results

The fate of ripe fruit

In open plots, averaged over three years, 53% of the ripe berries were removed before being attacked by invertebrates or microbes and were presumably dispersed by vertebrates (Tab. 1). Invertebrates damaged 23% of the berries leaving the seeds in place, and most of these berries were later infected by microbes, although this was not quantified. A further 18% of intact berries were infected by microbes, 3% shrivelled, 1% fell to the ground and were not removed and 2% were still intact when covered with snow in November (Tab. 1).

Significant differences occurred between years in the proportions of berries removed, infected and intact when snow-covered, but no differences in the proportions of berries damaged, shrivelled or fallen (Tab. 1). The inter-year differences were due to higher frequencies of removals in 1984, leaving fewer berries to rot or be snow-covered in that year. Comparisons of the same sites in two seasons, 1982 and 1984 (Tab. 2) showed that the rates of removal were randomly distributed among plots (rank correlation test, $r_s = -0.02$, $P > 0.10$); no site had consistently high or low removal rates. The plots used in 1985 were in slightly different sites and therefore not directly comparable. There was no signifi-

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Tab. 1. The fate of ripe berries of *Cornus canadensis* in open plots. The numbers and percentages (in parentheses) of the original ripe crop allocated to each category are shown.

Fate of berries	Year				Differences between years[1]
	1982	1984	1985	All years	
Removed intact	396 (48)	406 (63)	282 (50)	1084 (53)	***
Damaged	195 (23)	159 (25)	110 (19)	464 (23)	NS
Infected	180 (22)	40 (6)	137 (24)	357 (18)	***
Shrivelled	23 (3)	22 (3)	24 (4)	69 (3)	NS
Fallen	13 (2)	11 (2)	6 (1)	30 (1)	NS
Intact when snow-covered	23 (3)	3 (1)	10 (2)	36 (2)	*
Berries in original crop	830	641	569	2040	

[1] χ^2-test: *** $P<0.001$; * $P<0.05$; NS = no significant difference ($P>0.05$).

Tab. 2. Percentage of the original berry crop (sample size in parentheses) removed from each open plot in different years. The same plots were used in 1982 and 1984, but different ones were set up in 1985 for the exclosure experiments.

Plot (1982 & 1984)	1982	1984	Plot (1985 only)	1985
A	26 (244)	62 (138)	A2	95 (116)
B	19 (64)	67 (39)	B2	74 (105)
C	44 (133)	52 (179)	C2	43 (87)
D	52 (122)	66 (86)	–	–
E[1]	51 (140)	82 (105)	E2	41 (138)
G	99 (127)	62 (94)	G2	37 (123)

[1] The 1984 plot was 10 m distant from the 1982 plot, in the same type of vegetation.

cant correlation between the density of berries per plot and the percentage removal per plot (data from Tab. 2, percentages arcsine transformed and tested for linear correlation, $P>0.05$ for each year and for all years combined).

Berries which had been damaged by invertebrates, infected by microbes or had shrivelled comprised only 6%, 7% and 13% of the fruits removed from open plots in 1982, 1984 and 1985, respectively, and 8% in all years combined (Tab. 3). Damaged, infected and shrivelled fruits were removed significantly less frequently, and intact fruits more frequently, than expected (Tab. 3). Damaged fruits seemed to be taken more frequently than infected fruits but nearly all damaged fruits suffered subsequent infections, making rigorous comparisons impossible.

Dispersal agents

Potential fruit dispersers seen in the study area are listed in Tab. 4. In addition, snowshoe hares *Lepus americanus* and meadow voles *Microtus pennsylvanicus* were common, as indicated by the frequency of their tracks in the early winter snow. The shrews were also more common than indicated by sightings. No mammals were seen to eat *C. canadensis* berries.

The American robin *Turdus migratorius,* hermit thrush *Catharus guttatus* and white-throated sparrow *Zonotrichia albicollis* are major consumers of fruit of the size and structure of *C. canadensis,* in other parts of eastern North America (Thompson and Willson 1979, Stiles 1980, Baird 1980, Johnson et al. 1985). American robins and white-throated sparrows were seen to eat

Tab. 3. Condition of the *C. canadensis* berries when removed. The numbers of berries actually removed (percentages in parentheses) are compared with numbers expected if removal was random and in proportion to the number of berry-days exposed to dispersers (see Figs 1–3).

Berry condition when removed	1982		1984		1985		All years combined
	Observed	Exp.	Observed	Exp.	Observed	Exp.	
Intact	396 (94)	318	406 (93)	205	282 (87)	204	1084 (92)
Damaged	21 (5)	75	22 (5)	176	25 (8)	65	68 (6)
Infected	3 (1)	21	8 (2)	39	12 (4)	45	23 (2)
Shrivelled	1 (0)	7	1 (0)	17	4 (1)	9	6 (0.5)
Total	421	421	437	437	323	323	1181
χ^2-value[1]	78.6***		371.5***		82.1***		

[1] *** $P<0.001$.

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Tab. 4. Numbers of sightings of birds and mammals which might eat *C. canadensis* fruits, recorded during visits to the fruit plots.

Species	1984	1985
Mammals		
Red squirrel *Tamiasciurus hudsonicus*	26	18
Masked shrew *Sorex cinereus*	1	0
Birds		
Ruffed grouse *Bonasa umbellus*	4	5
Northern flicker *Colaptes auratus*	0	1
Blue jay *Cyanocitta cristata*	32	12
Gray jay *Perisoreus canadensis*	1	0
Common raven *Corvus corax*	3	3
American crow *Corvus brachyrhynchos*	33	11
Black-capped chickadee *Parus atricapillus*	35	5
Boreal chickadee *P. hudsonicus*	48	16
American robin *Turdus migratorius*	38	31
Hermit thrush *Catharus guttatus*	0	2
Yellow-rumped warbler *Dendroica coronata*	11	3
White-throated sparrow *Zonotrichia albicollis*	22	12
Pine grosbeak *Pinicola enucleator*	9	10
No. of visit-days	21	12

these fruits in my study area and intact seeds were found in the droppings of ruffed grouse *Bonassa umbellus*. The white-throated sparrows might act as seed predators by crushing seeds (Thompson and Willson 1979).

Berries were removed in two ways: by being plucked off the infructesence leaving part of the pedical behind; or when the whole infructesence was bitten off leaving only the vertical stalk. Biting, interpreted as being caused by squirrels or hares, accounted for 9.5% (N = 421), 0% (N = 437) and 9.3% (N = 323) of all berries removed from open plots in 1982, 1984 and 1985, respectively, and 5.9% (N = 1181) overall. Plucking, interpreted as resulting from frugivory by birds, accounted for 94% of berry removals.

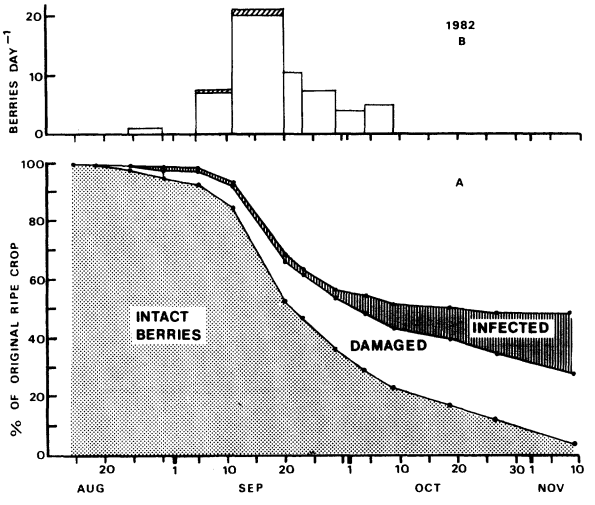

Fig. 1. The phenology of fruiting and frugivory of *C. canadensis* berries in 1982 showing: A) the availability and condition of fruit; B) the rate of removals, between visits, of intact berries (open columns) and damaged or infected berries (hatched). Observations were made from the time the fruit were ripe until snow covered the plants.

Invertebrate frugivores

Small slugs of an unidentified species, usually < 10 mm long, were major invertebrate consumers of *C. canadensis* fruits. Twelve were found on fruits in 1982, nine in 1984 and 12 in 1985. Typically, the slugs made small holes in the fruit integument and then ate out much of the inner flesh leaving the seed and skin attached to the plant.

Springtails (Collembola), one small snail, an isopod and two small lepidopteran caterpillars also ate the fruits. Many invertebrate predators, including slugs, might have been primarily nocturnal and thus seldom seen. Damage to seeds by invertebrates was not seen, but seeds were not systematically examined.

Phenology of frugivory

Intact ripe fruits were available from late August to early November (Figs 1–3). Removals began soon after ripening and most occurred in a five week period in each year: 97% (N = 421) of all removals occurred between 5 September and 9 October in 1982; 92% (N = 437) between 26 August and 1 October in 1984; and 82% (N = 323) between 10 September and 16 October in 1985. The removals of berries were thus highly synchronised, with some variation in timing between years.

Following these periods of peak removals, the remaining intact berries comprised 24, 11 and 18% of the original crops in 1982, 1984 and 1985, respectively, and were outnumbered by damaged and infected berries (Figs 1–3). Damage to fruit by invertebrates occurred throughout the observation period, declining after September. Most of the berries remaining in October and early November were infected by microbes.

Periods of intense removals of berries in 1984 and 1985 co-incided with the presence of American robins and other migratory birds in the study area (Figs 2 and 3), and in nearby mixed-habitat areas where birds were censused (Fig. 4). The numbers of birds seen during each visit to fruit plots (Figs 2C and 3C) were compared with the average of the removal rates of fruits preceding and following each visit (Figs 2B and 3B). In 1984 there were no significant correlations between rates of berry removals and numbers of American robins ($r = 0.11$, $df = 18$, $P > 0.05$) or all migratory birds ($r = 0.08$, $df = 18$, $P > 0.05$).

In 1985, by contrast, removal rates were correlated significantly with numbers of American robins ($r = 0.85$, $df = 8$, $P < 0.01$) and all migratory birds ($r = 0.93$, $df = 8$, $P < 0.01$). The reasons for this difference between years are not clear but might be due to rapid removals of berries which occurred very early in 1984

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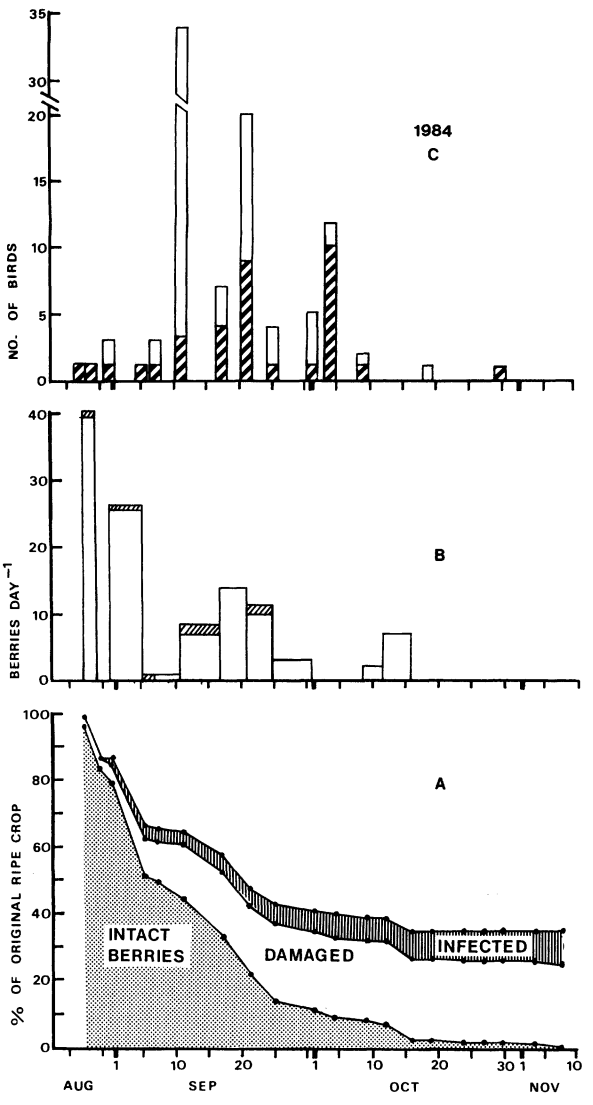

Fig. 2. The phenology of fruiting and frugivory of *C. canadensis* berries in 1984: A) and B) as in Fig. 1; C) numbers of American robins *Turdus migratorius* (hatched columns) and other migratory birds (unshaded) recorded during visits to fruit plots.

leaving fewer berries for subsequent removal despite continued pulses of migratory birds.

Exclosure experiment

When birds, squirrels and hares were excluded with wire mesh, only 2% of the intact berries were removed, compared with 50% in adjacent open plots (Tab. 5). The 12 berries which disappeared were all near the periphery of the exclosures and might have been removed by birds which poked their heads through the mesh. Clearly, voles, shrews and invertebrates, which could have entered exclosures, were not dispersers of *C. canadensis* fruits in this area.

With dispersers excluded, significantly more berries in exclosures remained to be infected by microbes or snow-covered than in the open control plots (Tab. 5, Fig. 5). There were no significant differences in the frequencies of damaged, shrivelled or fallen fruit in exclosures and open plots. Prolonged availability of the berries did not appear to benefit invertebrate frugivores, which tended to be restricted by cold temperatures in late autumn.

Discussion

The major dispersers of C. canadensis

Rigidly co-evolved plant-animal relationships are not a feature of most fruit-frugivore interactions (Howe and Smallwood 1982), particularly in temperate regions (Herrera 1985, Borowicz and Stephenson 1985). The dispersers tend to be omnivores with broad trophic

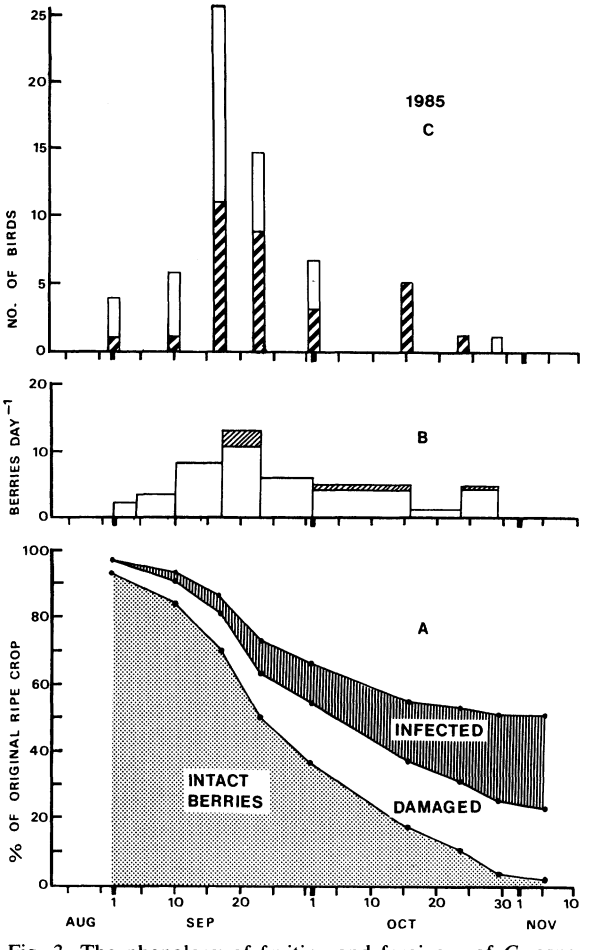

Fig. 3. The phenology of fruiting and frugivory of *C. canadensis* berries in 1985: A) and B) as in Fig. 1; C) as in Fig. 2.

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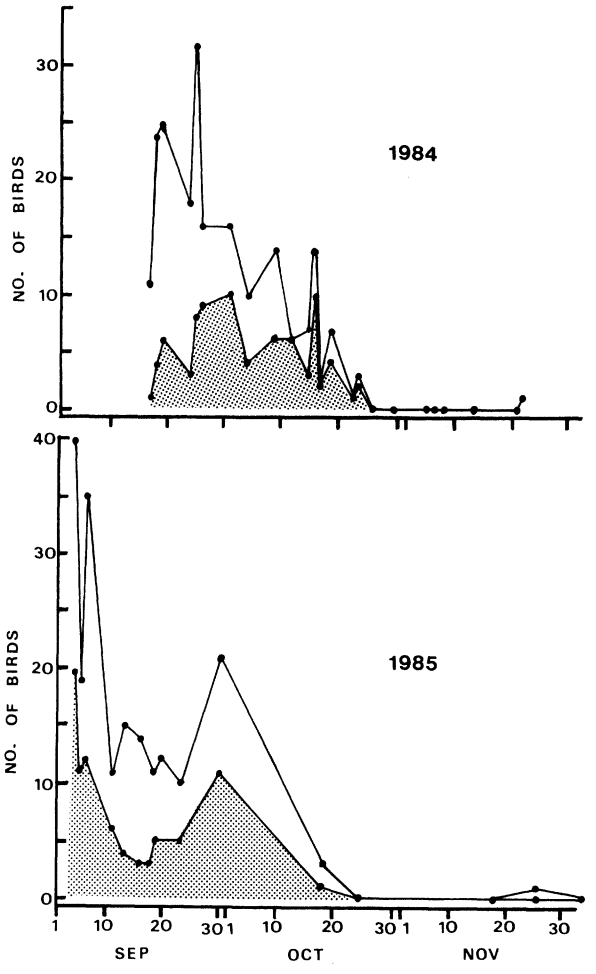

Fig. 4. American robins (shaded) and other migratory birds (unshaded) counted along a transect through residential areas, parks and boreal forest in Corner Brook, Newfoundland in 1984 and 1985.

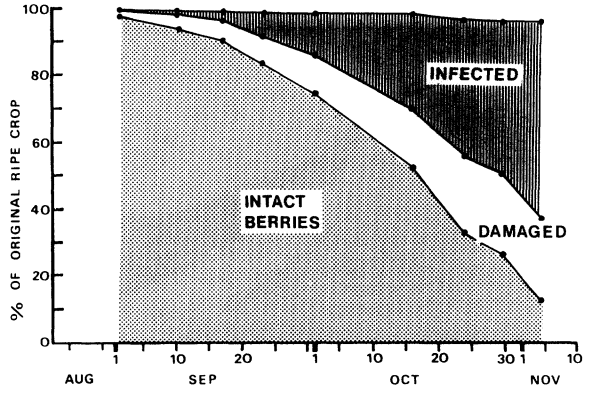

Fig. 5. The availability and condition of *C. canadensis* fruits in five exclosure plots in 1985, from the time of ripening until snow covered the plants. Compare these results with those from adjacent open plots in Fig. 3A.

Tab. 5. Fate of berries in five open and five exclosure plots in 1985. The numbers of berries and (in parentheses) percentages of the original crop are given.

Fate of berries	Open plots	Exclosures	χ^2-test[1]
Removed intact.....	282 (50)	12 (2)	***
Damaged	110 (19)	133 (24)	NS
Infected.....	137 (24)	290 (53)	***
Shrivelled.....	24 (4)	37 (7)	NS
Fallen	6 (1)	8 (1)	NS
Intact when snow-covered.....	10 (2)	64 (12)	***
Berries in original crop.....	569	544	

[1] *** $P<0.001$; NS = no significant difference ($P>0.05$).

niches and the fruits appear to have evolved to exploit guilds of frugivores rather than isolated species (Stiles 1980, Herrera 1985, Johnson et al. 1985). It has been suggested that fruits of eastern North America can be broadly categorized on the basis of fruiting time (summer vs autumn), major dispersers (birds vs mammals), fruit quality (high vs low energy and lipid content) and other features such as fruit chemistry, seed size and plant structure (Stiles 1980, Stiles and White 1982). This classification has been criticized (Herrera 1982b, Borowicz and Stephenson 1985) but it is useful as a set of hypotheses to be tested in the field and laboratory.

Cornus canadensis is difficult to categorize. It has characteristics of both the the autumn deciduous category, comprising autumn-fruiting species, mostly shrubs, having low-quality fruit which tend to be bird dispersed, and the similar autumn herbaceous category (Stiles 1980, D. W. White and E. W. Stiles, unpubl.). Its herbaceous above-ground structure separates it from the other common members of its genus in North America, which are small trees or shrubs (Gleason and Cronquist 1963). Stiles (1980) speculated that this species, because of its low growth and relatively small seeds, might have adaptations to avoid seed predation by rodents or alternatively use rodents as seed dispersers.

The exclosure experiments indicated that voles and shrews did not disperse or prey on *C. canadensis* fruits in Newfoundland. Red squirrels or snowshoe hares ate small numbers of berries (< 6%), but mammals appear to be unimportant in the dispersal of seeds. The island of Newfoundland does, however, have a depauperate small mammal fauna. Eleven species of rodents and five Insectivora found on the adjacent mainland in Labrador or Nova Scotia are absent from Newfoundland (Banfield 1977). A study of seed dispersal of *C. canadensis* in areas with richer small mammal faunas would make an interesting comparison.

Migrant birds were the major dispersers of *C. canadensis* fruit in Newfoundland. Birds were seen to eat the fruits and when they were excluded, removals were neg-

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ligible. Removals coincided with the presence of migrant birds and in 1985 removal rates were significantly correlated with migrant numbers. The virtual cessation of removals following migration suggests that overwintering birds were not important dispersers. American robins, which are major dispersers of fruiting plants over a wide geographic range (Thompson and Willson 1979, Stiles 1980, Baird 1980), probably disperse many seeds of *C. canadensis*. Their mode of foraging (Paszkowski 1982) and their preference for more open forest patches, make them ideal dispersers for this plant which tends to be overgrown by dense vegetation and have brief tenure in successional forest patches.

Phenology and frequency of fruit removals

It has been hypothesised that the fruiting phenology of many temperate plants has evolved to match the autumn migratory movements of frugivorous birds (Snow 1971, Thompson and Willson 1979, Stiles 1980). The coincidence of fruiting and bird migrations is itself insufficient evidence to indicate a causal relationship. In the case of bunchberry in Newfoundland, however, migrant birds are clearly the major dispersers of seeds and significant rates of berry removals occurred only while these birds were present. The coincident timing of bunchberry fruit removals and bird migration therefore points to an evolutionary link. *Cornus canadensis* did not have adaptations allowing fruit to persist until dispersed by wintering birds or spring migrants, unlike some other low quality fruits (Stiles 1980, Courtney and Manzur 1985). Fruit remaining on the plants in October rotted, even when removals were prevented by the exclosures. As might be expected by the more northerly location, maximum removals of berries and maximum numbers of birds, occurred somewhat earlier in Newfoundland (late August to early October) than in New Jersey (late September to early November; Baird 1980), and Illinois (September through mid-October; Thompson and Willson 1979).

The dispersal rates of *C. canadensis* fruits differed between some years and between plots. About half of the original crop of ripe berries was removed, on average, in contrast to removals approaching 100% in high quality fruit elsewhere in eastern North America (Thompson and Willson 1979, Baird 1980, Borowicz and Stephenson 1985). The inconsistent and modest dispersal rates of *C. canadensis* might be attributed to a number of factors. The fruits are of relatively low lipid content and other species with better quality fruits might have attracted the available frugivores. Damage by invertebrates and microbes reduced the availability of intact fruits favoured by dispersers (see below). The absence from Newfoundland (Godfrey 1979) of many of the major frugivores common further south (Thompson and Willson 1979, Stiles 1980) and the departure of migrant birds before the fruit had been depleted were probably contributing factors. At this stage it is impossible to judge whether these results are typical of boreal ecosystems.

I found no correlation between the size of the berry crop in each plot and the proportion of the crop removed. The numbers of berries which disappeared between visits to plots was highly variable, but large numbers of berries were seldom removed from a plot simultaneously. This suggests that the frugivores involved were very mobile, were probably eating other foods in addition to bunchberry fruits and perhaps had rather unpredictable foraging movements and food patch selection. Several other studies have failed to find a simple correlation between fruit abundance and the activities of frugivores (see Courtney and Manzur 1985).

The effects of invertebrate and microbial frugivores

Invertebrate and microbial frugivores disrupt seed dispersal (Janzen 1977, Stiles 1980, Herrera 1982a), but this has seldom been quantified in temperate regions (Herrera 1984). Thompson and Willson (1978) found that damage to fruit by ants and harvestmen (Phalangids) affected up to 62% of the fruit of certain plants in Illinois. Insects damaged an average of 37% (range 10–60%) of fruits on hawthorn *Crataegus monogyna* bushes in England (Courtney and Manzur 1985). These damaged hawthorn fruits were seldom taken by avian dispersers, and the presence of damaged fruits also reduced the dispersal rates of nearby undamaged fruits (Manzur and Courtney 1984). Parasitic flies damaged 13–20% of the fruits of *Cornus amomum* in Pennsylvania and probably reduced the plants' dispersal success (Borowicz and Juliano 1986).

Invertebrate and microbial frugivores clearly retarded dispersal of bunchberry seeds in Newfoundland. During three seasons, 23% of the bunchberry fruits were damaged by invertebrates, 18% infected by microbes and 3% of fruit shrivelled and might also have been infected. Damaged, infected and shrivelled fruit comprised only 8% of the fruits removed by dispersers, but comprised 76–89% of fruits remaining on the plants after the periods of peak removals. The activities of invertebrates appeared to be curtailed by cold toward the end of the autumn season, as was found in Illinois (Thompson and Willson 1978). Three-way interactions between fruiting plants, vertebrate seed dispersers and organisms which infect or damage fruit are evidently important in cool boreal forests, as they are in warmer temperate or tropical regions (Janzen 1977, Herrera 1982a, 1984). A more detailed synthesis of these interactions in northern latitudes requires further quantitative studies.

Acknowledgements – I thank E. Stiles and D. White for advice and access to their unpublished manuscript, D. Duncan for helpful comments on the manuscript and M. Simpson for technical assistance. During this study I was supported, in part, by a grant (A0306) from the Natural Sciences and Engineering Research Council of Canada.

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References

Baird, J. W. 1980. The selection and use of fruit by birds in an eastern forest. – Wilson Bull. 92: 63–73.

Banfield, A. W. F. 1977. The mammals of Canada. – Univ. of Toronto Press for Nat. Mus. Canada, Toronto.

Borowicz, V. A. and Stephenson, A. G. 1985. Fruit composition and patterns of fruit dispersal of two *Cornus* spp. – Oecologia (Berl.) 67: 345–441.

– and Juliano, S. A. 1986. Inverse density-dependent parasitism of *Cornus amomum* fruit by *Rhagoletis cornivora*. – Ecology 67: 639–643.

Bouchard, A., Hay, S. and Rouleau, E. 1978. The vascular flora of St. Barbe South District, Newfoundland: an interpretation based on biophysiographic areas. – Rhodora 80: 228–308.

Courtney, S. P. and Manzur, M. I. 1985. Fruiting and fitness in *Crataegus monogyna:* the effects of frugivores and fruit predators. – Oikos 44: 398–406.

Damman, A. W. H. 1967. The forest vegetation of western Newfoundland and site degradation associated with vegetation change. – Unpubl. Ph.D. thesis, Univ. Michigan.

Erskine, A. J. 1981. Adapting generalized instructions to specific situations in planning count work. – Stud. Avian Biol. 6: 570–574.

Gleason, H. A. and Cronquist, A. 1963. Manual of vascular plants of northeastern United States and adjacent Canada. – Van Nostrand, Princeton, NJ.

Godfrey, W. E. 1979. The birds of Canada. – Nat. Mus. Canada, Ottawa.

Herrera, C. M. 1982a. Breeding systems and dispersal-related maternal reproductive effort of southern Spanish bird-dispersed plants. – Evolution 36: 1299–1314.

– 1982b. Some comments on Stiles' paper on temperate bird-disseminated fruits. – Am. Nat. 120: 819–822.

– 1984. Avian interference of insect frugivory: an exploration into the plant-bird-fruit pest evolutionary triad. – Oikos 42: 203–210.

– 1985. Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. – Oikos 44: 132–141.

Howe, H. F. and Smallwood, J. 1982. Ecology of seed dispersal. – Ann. Rev. Ecol. Syst. 13: 201–228.

Janzen, D. H. 1977. Why fruits rot, seeds mold, and meat spoils. – Am. Nat. 111: 691–713.

Johnson, R. A., Willson, M. F., Thomson, J. N. and Bertin, R. I. 1985. Nutritional values of wild fruits and consumption by migrant frugivorous birds. – Ecology 66: 819–827.

Manzur, M. I. and Courtney, S. P. 1984. Influence of insect damage in fruits of hawthorn on bird foraging and seed dispersal. – Oikos 43: 265–270.

Paszkowski, C. A. 1982. Vegetation, ground, and frugivorous foraging of the American robin. – Auk 99: 701–709.

Ryan, A. G. 1978. Native trees and shrubs of Newfoundland and Labrador. – Parks Div., Govt. of Newfoundland and Labrador, St. John's, Nfld.

Snow, D. W. 1971. Evolutionary aspects of fruit-eating by birds. – Ibis 113: 194–202.

Stiles, E. W. 1980. Patterns of fruit presentation and seed dispersal in bird-disseminated woody plants in the eastern deciduous forest. – Am. Nat. 116: 670–688.

– and White, D. W. 1982. Additional information on temperate bird-disseminated fruits: response to Herrera's comments. – Am. Nat. 120: 823–827.

Thompson, J. N. and Willson, M. F. 1978. Disturbance and the dispersal of fleshy fruits. – Science 200: 1161–1163.

– and Willson, M. F. 1979. Evolution of temperate fruit/bird interactions: phenological strategies. – Evolution 33: 973–982.

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