

Prior reproduction and weather affect berry crops in central Ontario, Canada

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Abstract Populations of many perennial plants intermittently produce large seed crops—a phenomenon referred to as mast seeding or masting. Masting may be a response to spatially correlated environmental conditions (the Moran effect), an adaptive reproductive strategy reflecting economies of scale, or a consequence of the internal resource budgets of individual plants. Fruit production by endozoochorous plants representing eight genera varied synchronously over much of central Ontario, Canada, 1998–2009. We tested for effects of weather and prior reproduction on fruit production by comparing AIC_c values among regression models fit to time series of fruit production scores and partitioning contributions by different predictors to multiple R^2 into independent and joint contributions. Fruit production by mountain ash (*Sorbus* spp.), juneberry (*Amelanchier* spp.), dogwoods (*Cornus* spp.), nannyberry (*Viburnum lentago*), and possibly cherries (*Prunus* spp.) was inversely related to production in the previous year. These effects were independent of weather conditions, suggesting that intrinsic factors such as internal resource budgets or an adaptive strategy of variable reproductive output influenced fruit production. To our knowledge, this is the first evidence of masting in members of the genera *Cornus*, *Viburnum*, and *Amelanchier*, and in members of *Prunus* and *Sorbus* in North America. All species produced fewer fruits when weather conditions were dry, so the Moran effect could have synchronized fruit production both within and among species. Patterns and causes of variation in berry crops have implications for ecosystem

dynamics, particularly in boreal and subArctic environments where berry crops are important wildlife foods.

Keywords Berry crops · Endozoochory · Masting · Moran effect · Pulsed resources · Seedfall

Introduction

Populations of many polycarpic plants intermittently produce large seed crops (Herrera et al. 1998; Kelly and Sork 2002). This phenomenon is referred to as mast seeding or masting, and several explanations for it have been proposed (Kelly 1994; Isagi et al. 1997; Kelly and Sork 2002). Seed crops could simply vary in response to spatially correlated environmental conditions (referred to as resource matching, climatic forcing, or the Moran effect; Royama 1992). However, resource matching alone is inadequate to explain the magnitude and regularity of variation in seed crops by many species (Kelly 1994; Koenig et al. 1994; Koenig and Knops 2000). Masting may be an adaptive reproductive strategy reflecting economies of scale if large, intermittent reproductive efforts are more efficient than constant efforts (Janzen 1978; Norton and Kelly 1988). For example, masting can enhance wind and insect pollination (Nilsson and Wästljung 1987; Crone and Lesica 2006), and seed survival by satiating predators during mast years (Janzen 1971; Silvertown 1980; Kelly et al. 2008a). Masting may be of no benefit or detrimental to dispersal in endozoochorous species (those with fleshy fruits dispersed by mutualist frugivores) because dispersers would be saturated in mast years (Janzen 1971; Silvertown 1980; Herrera et al. 1998), unless dispersers were attracted to, or can show a rapid numerical response to, large seed crops (Kelly 1994; Vander Wall 2002). Indeed, reviews and meta-analyses

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have shown that masting is less common in endozoochorous species and shrubs than other plants (Silvertown 1980; Herrera et al. 1998; Kelly and Sork 2002), though shrubs and North American endozoochorous species were under-represented in the masting literature (Kelly and Sork 2002). Studies demonstrating negative impacts of masting on dispersal of endozoochorous seeds have focused on avian frugivores (Davidar and Morton 1986; Herrera et al. 1994; Herrera 1998). However, recent work from Spain suggests that mammals, particularly carnivores, opportunistically exploit large fruit crops and can be important dispersers of endozoochorous seeds (Martínez et al. 2008; Fedriani and Delibes 2009; Guitiàñ and Munilla 2010; Matías et al. 2010). Among North American carnivores, American black bears (*Ursus americanus*), brown bears (*U. arctos*), raccoons (*Procyon lotor*), coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), gray foxes (*Urocyon cinereoargenteus*), and American martens (*Martes americana*) are highly frugivorous and can be effective dispersers because they harvest fruits effectively, carry many seeds, may move several kilometers before depositing seeds, and deposit viable seeds (Willson 1993; Borchert and Tyler 2010; also see Koike et al. 2010).

For any fitness benefits of masting to be realized, temporal variation in seedfall must first become synchronized among individuals. The Moran effect was suggested as a likely synchronizing agent (Silvertown 1980). Masting could then evolve via selection favouring individuals with common responses to environmental cues and high inter-annual variation in seedfall (Silvertown 1980; Kelly and Sork 2002). Theoretical work with resource budget models has shown that density-dependent pollen limitation could also synchronize intermittently reproducing individuals in a population. This would result in population-level masting even in the absence of either environmental fluctuations or fitness benefits, provided that most plants produced few seeds in some years (Isagi et al. 1997; Satake and Iwasa 2000). Empirical studies have shown that both the Moran effect and density-dependent pollen limitation can synchronize interannual variation in seedfall by some species (Selås 2000; Rees et al. 2002; Schaubert et al. 2002; Crone et al. 2005, 2009; Kon et al. 2005; Lamontagne and Boutin 2007), and updated resource budget models demonstrate that both mechanisms acting in concert would produce the strongest correlations in seedfall among individuals (Satake and Iwasa 2002).

Considerable annual variation in fruit production by endozoochorous shrubs and small trees was apparent in seedfall data from central Ontario, Canada, 1998–2009. All the plant species we monitored are insect-pollinated, primarily by bees, or in the case of *Sambucus* spp., primarily by flies, and are also visited by other insects including wasps, beetles, butterflies, and moths. Seeds of these species are

dispersed by passerine and gallinaceous birds (Stiles 1980; Willson 1986), and mammals including ungulates, rodents, and lagomorphs, but particularly carnivores such as raccoons, coyotes, red foxes, American martens, and American black bears (Willson 1993). All of these potential dispersers were common on our study area. We questioned whether the observed variation in seedfall was adequately explained by spatially correlated weather conditions, or if prior reproductive output had an effect independent of weather conditions. Independent effects of prior reproduction would suggest that intrinsic factors such as the internal resource budgets of individual plants or an adaptive strategy of variable reproductive output contributed to the observed pattern. We assessed synchrony of weather conditions and seedfall data, and tested for effects of fruit production in year $t - 1$, and soil moisture during fruiting in year t , on fruit production by endozoochorous species representing eight genera. The study area covered more than 65000 km² within Canada's boreal shield ecozone (Ecological Stratification Working Group 1996; Fig. 1), and was largely covered by forests and wetlands with tree and shrub species typical of both boreal and eastern North American deciduous forests (Rowe 1972), interspersed with open water and agricultural, rural, and urban development.

Methods

Five Ontario Ministry of Natural Resources (OMNR) administrative districts monitored fruit and seed availability for wildlife in central and eastern Ontario from 1998–2009. Fruit or seed production by eight species, or groups of species, of endozoochorous trees and shrubs (Table 1) was ranked on a five point scale in each district, where 0 represented crop failure and 4 represented a bumper crop. Sample sizes of observations varied among districts and years. Not all districts completed surveys in all years, and no district recorded fruit production by all eight species in all 12 years. Furthermore, some district-specific rankings were consistently based on multiple observations from different locations (e.g., townships) within the district, but in other cases single values reflecting fruit production across entire districts were assigned by an individual or by consensus among observers. Observers in some but not all districts visited the same sites each year, but fixed monitoring plots were not established. Despite these differences in collection methods, the data showed consistent temporal patterns in fruit production across the region (Ontario Ministry of Natural Resources, unpublished data; Obbard et al. 2003). Noyce and Coy (1990) showed that a similar index of fruit production was consistent with quantitative data and sufficient to demonstrate differences among years and forest stands.

Fig. 1 Location of the study area (*shaded grey*) in central Ontario, Canada. Boundaries between Ontario Ministry of Natural Resources administrative districts are shown as *black lines* within the greater study area. *Black circles* are weather stations

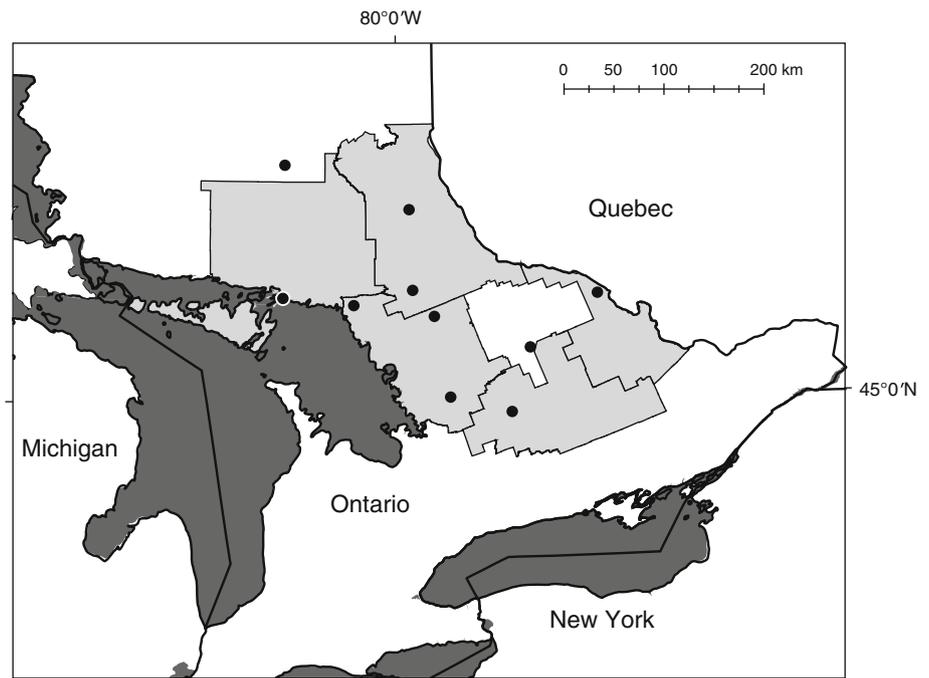


Table 1 Plant species or groups of species monitored in central Ontario, Canada, 1998–2009

Common name	Family	Genus	Species included
Mountain ash	Rosaceae	<i>Sorbus</i>	<i>S. americana</i> , <i>S. decora</i>
Cherry	Rosaceae	<i>Prunus</i>	<i>P. serotina</i> , <i>P. pensylvanica</i> , <i>P. virginiana</i>
Juneberry (serviceberry/ saskatoonberry/shadbush)	Rosaceae	<i>Amelanchier</i>	<i>A. alnifolia</i> , <i>A. Canadensis</i> , <i>A. arborea</i> , <i>A. laevis</i> , <i>A. bartramiana</i>
Red raspberry	Rosaceae	<i>Rubus</i>	<i>R. ideaus</i>
Nannyberry	Adoxaceae	<i>Viburnum</i>	<i>V. lentago</i>
Elderberry	Adoxaceae	<i>Sambucus</i>	<i>S. canadensis</i> , <i>S. pubens</i>
Dogwoods	Cornaceae	<i>Cornus</i>	<i>C. stolonifera</i> , <i>C. alternifolia</i> , <i>C. rugosa</i> , <i>C. racemosa</i>
Blueberry	Ericaceae	<i>Vaccinium</i>	<i>V. angustifolium</i> , <i>V. myrtilloides</i>

To assess synchrony in seed production among districts, we calculated Buonaccorsi et al.'s (2001) measure indicating whether pairs of time series from different districts changed in agreement (A) and average A across pairs of series (\bar{A}). Because district-specific time series had missing values and one missing value in a time series reduced the number of possible comparisons between any two districts across consecutive years by two, sample sizes for some measures of agreement were small. We did not calculate A where there were fewer than 4 possible comparisons within the 11 year time series, or \bar{A} where there were less than 3 pairwise comparisons between Districts with adequate data to calculate A .

A drought code (DC) was calculated as part of Ontario's Forest Fire Weather Index. It described the dryness of the organic soil layer below the fine fuel and duff layers and was calculated from daily rainfall and

evapotranspiration data over the previous 52 days (Turner 1972; Van Wagner 1987). The DC therefore combined weather variables to provide a measure of the amount of soil moisture available to plants. We selected DC values on 15 August each year from the ten weather stations in our study area for which continuous data were available (Fig. 1). We tested for synchrony in DC data using the modified correlogram procedure (Koenig and Knops 1998) with 1000 trials. We were more interested in whether DC varied synchronously within the entire study area than the decline in synchrony with distance within the study area, so we applied the test to the complete data set, and to two subcategories based on distance between weather stations. Means and variances of station-specific DC data were not correlated with each other ($R^2 < 0.10$), and no trends were apparent, so the tests were applied to untransformed data.

We averaged seed production scores across districts and DC values across weather stations before fitting regression models to test for effects of weather and prior reproduction on fruit production by each species or group of species. We first averaged fruit production scores across multiple reports from within each district and year (where available) to give equal weight to data from each district. We then averaged scores across districts in each year to obtain regional time series for each species. By averaging fruit production scores, we avoided missing values in the time series; however, we also removed any spatial variation in seed production among districts and were required to assume that seed production scores from a subset of districts was representative of production across the entire study area in some years. We calculated A (Buonaccorsi et al. 2001) between regional average fruit production scores for each pair of species to assess whether fruit production varied synchronously among species across the region.

We duplicated fruit production data for each species or group of species at a 1-year lag. Prior to fitting regression models, we examined Pearson correlation coefficients (r_p ; 1) among fruit production scores of the different species or groups of species, (2) between production by each species or group of species in year t ($prod_t$) and in year $t - 1$ ($prod_{t-1}$), (3) between $prod_t$ and DC, and (4) to assess collinearity between predictors, between $prod_{t-1}$ and DC. The same set of four linear regression models was then fitted to regional data (1999–2009) for each species or group of species to test for effects of fruit production in year $t - 1$ and summer weather conditions in year t on fruit production in year t . Regression models were a null (intercept only) model, models with effects of each of $prod_{t-1}$ and DC, and a model with additive effects of both predictors. We compared models using AIC_c (Hurvitch and Tsai 1989). We hierarchically partitioned coefficients of multiple determination (R^2) from the additive model into independent and joint contributions by each predictor (Chevan and Sutherland 1991). Statistical analyses were performed using R software (R Development Core Team 2009).

Results

DC values varied synchronously across the study area (mean r_p across all pairs of weather stations 0.66, SD 0.17, $P = 0.002$ by the modified correlogram procedure applied to the entire data set). Synchrony declined slightly with distance (mean r_p across weather stations an average of 111 and 263 km apart = 0.70 and 0.61, respectively), but was significant ($P < 0.05$) at both distance categories.

The mean (SD) number of OMNR Districts estimating fruit production annually was 4.2 (0.80), and the mean annual number of observations was 31 (6.5). The number of Districts reporting species-specific fruit production annually averaged 4.1 (0.79) for mountain ash, 3.3 (0.75) for dogwood, 3.7 (0.78) for juneberry, 2.4 (1.17) for nannyberry, 4.2 (0.84) for cherry, 3.9 (1.00) for elderberry and blueberry, and 4.1 (0.80) for raspberry. Fruit production by all species for which we calculated \bar{A} tended to increase or decrease relative to the previous year synchronously across the study area (Table 2). Mountain ash and dogwood always fluctuated in the same direction across all pairs of districts for which data were available. Relative fruit production in consecutive years by other species agreed in 62–78% of cases (Table 2). Mean fruit production by mountain ash, nannyberry, juneberry, dogwood, cherry, and elderberry fluctuated synchronously across the region (Table 3). Fluctuations in fruit production by blueberry were in the same direction as fluctuations by other species 55% of the time, and fluctuations in fruit production by raspberry were in the same direction as fluctuations by other species 55–73% of the time.

Fruit production by some species, such as raspberry, appeared to vary inversely with DC, whereas for other species, such as mountain ash, a pattern of good and poor fruit production in alternating years was apparent (Fig. 2). Poor fruit production by species that exhibited a biennial pattern still coincided with dry conditions, which were most severe in 2001, 2005, and 2007 (Fig. 2).

Correlation coefficients between $prod_t$ for different species were all positive; those between $prod_t$ and DC were all negative, as were those between $prod_t$ and $prod_{t-1}$ except in the case of raspberry (Table 4). Collinearity between DC and $prod_{t-1}$ as predictors of $prod_t$ was not a major concern $r_p < 0.3$; Table 4). Distributions of regional fruit production scores and DC values did not differ from normal (Shapiro–Wilk's $W > 0.88$; $P > 0.10$ in all cases). Nonlinearity of relationships was not apparent in plots of $prod_t$ versus DC and $prod_{t-1}$. Relative AIC_c values among the four models fit to data for each species indicated that fruit production by mountain ash, dogwood, juneberry, nannyberry, and possibly cherry was affected by fruit production in the previous year, and that fruit production by juneberry, nannyberry, cherry, elderberry, blueberry, and raspberry was affected by dry summer weather conditions (Table 5). Hierarchical partitioning further revealed that prior reproduction accounted for more of the explained variation in fruit production by mountain ash, dogwood, and juneberry, whereas weather conditions accounted for more of the explained variation in fruit production by cherry, elderberry, blueberry, and raspberry; contributions to nannyberry production were similar (Table 5). Joint

Table 2 Agreement in the direction of change in fruit production scores among administrative districts in central Ontario, Canada, 1998–2009

Species	\bar{A}	Mean # comparisons contributing to pairwise A (maximum = 10 time intervals)	Number of pairwise A values contributing to \bar{A} (maximum = 10 pairs of Districts)
Mountain ash	1.00	6.3	7
Dogwood	1.00	5.0	3
Juneberry	0.72	6.0	3
Nannyberry	n/a	5.0	1
Cherry	0.78	6.3	8
Elderberry	0.62	6.2	5
Blueberry	0.67	5.4	5
Raspberry	0.68	6.1	7

\bar{A} measures the mean proportion of time intervals during which pairs of series agreed in their change of direction (Buonaccorsi et al. 2001)

Table 3 Proportions of years with the same direction of change in the amount of fruit produced by pairs of plant species in central Ontario, Canada, 1998–2009

	NN	JN	DW	CH	EL	BB	RA
MA	1.00	1.00	1.00	1.00	1.00	0.55	0.73
NN		1.00	1.00	1.00	1.00	0.55	0.64
JN			1.00	1.00	1.00	0.55	0.64
DW				1.00	1.00	0.55	0.73
CH					1.00	0.55	0.64
EL						0.55	0.64
BB							0.55

MA mountain ash, NN nannyberry, JN juneberry, DW dogwood, CH cherry, EL elderberry, BB blueberry, RA raspberry

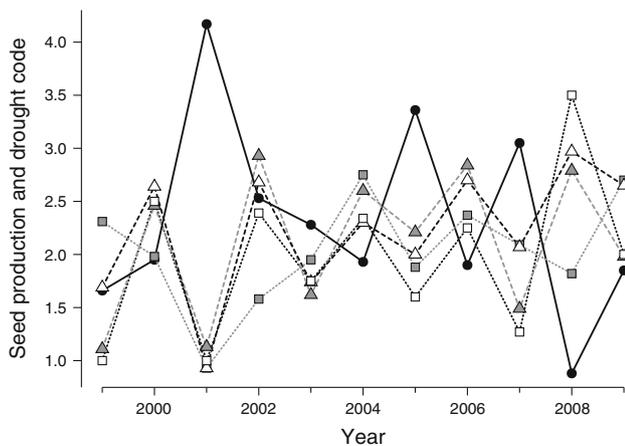


Fig. 2 Drought code values (circles, solid line) on 15 August, and fruit production scores for mountain ash (grey triangles and grey dashed line), raspberry (grey squares and grey dotted line), cherry (white triangles and black dashed line), and nannyberry (white squares and black dotted line) in central Ontario, Canada, 1999–2009. Drought code values were scaled by dividing by 100

contributions were consistently smaller than independent contributions (Table 5), so high R^2 values were not attributable to collinearity between predictors (Chevan and Sutherland 1991). Plots of residuals versus fitted values from the most general model fit to data for each species did not suggest violations of the assumptions of homoscedasticity of errors or linearity of relationships. Relationships

between standardized residuals and theoretical quantiles were approximately linear suggesting errors were normally distributed.

Discussion

Our data describe a system where weather conditions varied synchronously, and fruit production by several species of endozoochorous shrubs and small trees appeared to fluctuate synchronously, over more than 65000 km² of boreal-deciduous transitional forests in eastern North America. To our knowledge, this is the first evidence of masting in the genera *Cornus*, *Viburnum*, and *Amelanchier*, and in members of *Prunus* and *Sorbus* in North America. Fruit production was low when weather conditions during fruiting were dry, but variation in fruit production by mountain ash, dogwood, juneberry, nannyberry, and possibly cherry was better explained by inverse relationships between fruit production in the current and previous year, or a combination of such relationships and weather conditions, than by weather conditions alone. We conclude that the observed interannual variation in fruit production was not solely a result of a Moran effect, and that other factors such as an evolved strategy of variable reproductive output (Kelly 1994), or the energetic costs of reproduction in combination with density-dependent pollen limitation

Table 4 Pearson correlation coefficients between fruit production scores for different species or groups of species, between productivity scores in year t and in year $t - 1$, and between drought code values on 15 August (DC) and fruit production scores in the same and in previous years in central Ontario, Canada, 1999–2009

	DCA	MA	NN	JN	DW	CH	EL	BB	RA	MA ₋₁	NN ₋₁	JN ₋₁	DW ₋₁	CH ₋₁	EL ₋₁	BB ₋₁	RA ₋₁
DCA	1	-0.46	-0.68	-0.44	-0.52	-0.72	-0.7	-0.65	-0.61	0.26	0.15	0.08	0.27	0.14	0.06	0.02	0
MA		1	0.86	0.83	0.96	0.85	0.83	0.38	0.22	-0.79	-0.76	-0.83	-0.77	-0.81	-0.55	-0.18	-0.46
NN			1	0.8	0.9	0.85	0.93	0.37	0.17	-0.76	-0.69	-0.65	-0.66	-0.6	-0.47	-0.18	-0.39
JN				1	0.86	0.8	0.73	0.25	0.12	-0.74	-0.79	-0.79	-0.62	-0.72	-0.61	-0.01	-0.68
DW					1	0.92	0.85	0.38	0.18	-0.76	-0.75	-0.83	-0.69	-0.71	-0.5	-0.11	-0.38
CH						1	0.84	0.42	0.47	-0.59	-0.52	-0.62	-0.52	-0.52	-0.26	0.07	-0.29
EL							1	0.5	0.34	-0.59	-0.6	-0.49	-0.53	-0.51	-0.33	-0.1	-0.29
BB								1	0.37	0.07	-0.07	0	-0.07	-0.05	0	-0.31	0.06
RA									1	0.15	0.25	0.11	0.1	0.13	0.41	0.55	0.17
MA ₋₁										1	0.89	0.86	0.94	0.9	0.83	0.24	0.45
NN ₋₁											1	0.86	0.87	0.88	0.9	0.21	0.43
JN ₋₁												1	0.79	0.83	0.7	0.05	0.46
DW ₋₁													1	0.94	0.86	0.32	0.29
CH ₋₁														1	0.88	0.36	0.53
EL ₋₁															1	0.42	0.45
BB ₋₁																1	0.27
RA ₋₁																	1

MA mountain ash, NN nannyberry, JN juneberry, DW dogwood, CH cherry, EL elderberry, BB blueberry, RA raspberry

Table 5 Model comparisons and hierarchical partitioning of R^2 values from linear regression models fit to fruit production data for different species or groups of species in central and eastern Ontario, Canada 1999–2008

	Model selection							Partitioning R^2			
	Null	prod _{t-1}		DC		prod _{t-1} + DC		Contribution to R^2			Ratio of independent contributions to R^2 %(prod _{t-1}): %(DC)
	ΔAIC_c	ΔAIC_c	R^2	ΔAIC_c	R^2	ΔAIC_c	R^2	prod _{t-1}	DC	Joint	
Mountain ash	6.95	0.00	0.63	8.23	0.21	2.98	0.68	0.56	0.14	0.07	80:20
Dogwood	3.23	0.00	0.48	3.69	0.27	2.36	0.60	0.40	0.20	0.08	67:33
Juneberry	7.21	0.25	0.63	8.74	0.20	0.00	0.77	0.60	0.17	0.02	78:22
Nannyberry	9.66	6.39	0.48	6.71	0.47	0.00	0.82	0.42	0.40	0.06	51:49
Cherry	4.04	4.44	0.27	0.00	0.52	0.03	0.70	0.23	0.47	0.05	33:67
Elderberry	3.60	6.28	0.11	0.00	0.50	3.26	0.58	0.09	0.48	0.01	16:84
Blueberry	2.16	4.96	0.10	0.00	0.43	3.33	0.52	0.09	0.42	0.00	18:82
Raspberry	1.11	4.71	0.03	0.00	0.37	4.69	0.40	0.03	0.37	0.00	8:92

Shown are ΔAIC_c values among models fit to the same data ($\Delta AIC_c \leq 1$ appear in bold), coefficients of determination (R^2) for each model, independent contributions to multiple R^2 by each of productivity in the previous year (prod_{t-1}) and the drought code on 15 August (DC), the joint contribution to R^2 , and the ratio of independent contributions to R^2 as a percent of the total explained variation

(Isagi et al. 1997) contributed to the observed variation. Our results support previous research that showed the Moran effect to be insufficient to explain masting (Kelly 1994; Koenig et al. 1994; Koenig and Knops 2000), but they do not allow us to infer whether pollen limitation affected fruit production, or whether masting was adaptive. Pollen limitation is widespread in angiosperms but there have been few studies of it in the species we monitored (Burd 1994; Ashman et al. 2004; Knight et al. 2005). Enhanced seed survival through predator satiation is a common benefit of masting in animal-pollinated plants (Sork 1993; Kelly and Sork 2002), and was apparent in studies of *Sorbus* and *Prunus* elsewhere (Kobro et al. 2003; Li and Zhang 2007), but we are not aware of studies of pre-dispersal seed predation of the species we monitored. Mammalian carnivores common on our study area could satisfy the conditions necessary for masting to enhance dispersal, in that they are attracted to large fruit crops, may not be satiated in mast years, and effectively disperse endozoochorous seeds (Willson 1993; Borchert and Tyler 2010; Guiti an and Munilla 2010).

Fruit production by mountain ash, dogwood, nannyberry, juneberry, cherry, and elderberry always fluctuated in the same direction between years, and blueberry and raspberry production fluctuated in the same direction as other species more than 50% of the time. Annual variation in fruit production by different endozoochorous species including several of the ones we monitored was also synchronous over 20 years in a similar ecosystem in Minnesota (Garshelis and Noyce 2008); berry crops in southwest Yukon tended to covary among species as well (Krebs et al. 2010). Flower, berry, and seed production by several plants including *Vaccinium myrtillus* and *Empetrum nigrum* varied synchronously in Fennoscandia, with summer precipitation

apparently causing the synchrony among species (Laine and Henttonen 1983; Sel as 1997). Here, the DC was supported as a predictor of fruit production in six of the eight species monitored, and production by the other two species was also poor in dry years. Spatially correlated weather conditions may therefore have synchronized interannual variation in fruit production both within and among species on our study area. Other studies identified positive relationships between fruit production and precipitation in the same year (Sel as 2000; Sel as et al. 2001; Krebs et al. 2009).

Density-dependent pollen limitation might also have contributed to the intraspecific synchrony we observed (Isagi et al. 1997; Rees et al. 2002; Crone et al. 2005, 2009). Furthermore, since the species we monitored share pollinators, release from pollen limitation could promote synchrony among species if pollinator populations were attracted to, or responded numerically to, large flowering efforts (Satake and Iwasa 2002; Tachiki et al. 2010). If density-dependent pollen limitation is necessary to synchronize individuals (Satake and Iwasa 2002), spatially correlated weather conditions such as droughts or spring frosts that kill flower buds (e.g., Usui et al. 2005) could provide the years of low population-level fruiting success which are required for synchrony to occur under these models (Isagi et al. 1997; Satake and Iwasa 2000).

Pulses of food resources produced in mast years cascade through ecosystems (Ostfeld and Keesing 2000; Liebhold et al. 2004) and effects on higher trophic levels are well-documented (King 1983; Satake et al. 2004; Kelly et al. 2008b; Schmidt and Ostfeld 2008). Most studies demonstrating effects of variable seedfall on North American seed consumers focused on responses to seedfall from trees (Eiler et al. 1989; Koenig and Knops 2001; Bowman et al.

2005, 2008; Falls et al. 2007), but Kelly et al. (2008b) showed that the effects of masting on other trophic levels vary among ecosystems. Effects of masting by endozoochorous plants may be more apparent in boreal forests where the relative importance of berries to wildlife is greater. For example, in Fennoscandia, abundance of grouse, voles, and raptors, and mass of moose calves correlated with annual variation in fruit production by bilberry (*Vaccinium myrtillus*) and cowberry (*V. vitis-idaea*; Laine and Henttonen 1983; Selås 1997; Selås et al. 2001). In the southwestern Yukon, Canada, autumn abundance of the four dominant rodent species was explained well by variation in berry crops (Krebs et al. 2010), and in the boreal forest of Ontario, Canada, population-level reproductive failures by black bears occurred when berry crops failed (Obbard and Howe 2008).

Data limitations reduce the strength of our inferences. We analyzed rank data collected by different observers with little standardization of data collection methods, and fruit production data were specific to a group of species rather than a single species in six of eight cases which could have obscured species-specific patterns. We tested for negative autocorrelations between current and prior reproduction at a 1-year lag only but plant populations could have masted at longer or variable intervals (e.g., Selås 1997; Satake and Bjørnstad 2008), and we did not test for effects of all weather variables that might have affected fruit production. Synchrony in fruit production among districts, though apparent, could not be demonstrated statistically. Asynchrony among districts would dampen interannual variation in regional average rankings, potentially increasing the risk of type II error in tests for effects of prior reproduction. Despite these limitations we think that our novel findings raise interesting questions that will encourage future studies of this subject.

Our results suggest testable hypotheses about the contribution of adaptive reproductive strategies and pollen limitation to masting in endozoochorous plants. Studies could avoid the limitations of our dataset by collecting quantitative seedfall data at fixed locations over a longer time period while monitoring seed survival and responses of pollinators and consumers. In particular, knowledge of rates of pre-dispersal seed predation and the role of mammals as dispersers might suggest adaptive benefits, and manipulative experiments such as those conducted by Crone et al. (2005, 2009) could be used to test for effects of resource accumulation and pollen limitation.

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