

Fruit fate, frugivory, and fruit characteristics: a study of the hawthorn, *Crataegus monogyna* (Rosaceae)

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Summary. The fate of fruits from a population of European hawthorn (*Crataegus monogyna*) in western Oregon, USA, was examined over a two-year period. Only one frugivore, the American robin (*Turdus migratorius*) foraged on the *C. monogyna* fruits, making this an unusually straightforward fruit-frugivore system. Dispersal efficiency was low, with an average 21% of seeds being dispersed (carried away from parent plants) each year; the most common fate of fruits was to simply fall. Robins dropped 20% of the fruits that they picked, and defecated/regurgitated 40% of the fruits (seeds) that they swallowed, beneath parent plants. One trait, fruit abundance, strongly affected the probability of bush visitation by robins, bushes with larger fruit displays being preferred. Both absolute dispersal success (number of seeds) and dispersal efficiency (proportion of seeds; success per propagule) were also found to be correlated most strongly with initial fruit abundance. Individual plant fecundity and fruit quality were found to vary little between years; as a result, dispersal efficiencies for individual plants were also annually consistent. Larger (older) plants produced more fruits and therefore had higher fitness. These results suggest that the optimal fruiting strategy for *C. monogyna* is therefore to get as big as possible as quickly as possible by delaying fruiting until later in life.

Key words: Seed dispersal – Seed waste – Fruit abundance – American robins

Fruiting plants produce fleshy fruits as a reward for seed dissemination by frugivores (Howe 1986). Plants that evolve traits that both attract dispersers and provide higher rewards will therefore be visited more by frugivores, will experience greater dispersal efficiency, reproductive success, and hence fitness. Early predictions concerning fruiting plant strategies and dispersal success

have been tested, but with mixed results (e.g. see Howe and Smallwood 1982; Estrada and Fleming 1986; Willson 1986, and Wheelwright 1988 for reviews).

The number of fruits produced by individual plants is one trait thought to particularly affect dispersal success and hence the evolution of fruiting-plant strategies (Snow 1971; Howe and Estabrook 1977). Plants with larger fruit displays should achieve higher fitness for two reasons: they will be serviced by more frugivores because such plants are more conspicuous, and frugivores will prefer them because less time is spent in search and travel. Studies that have addressed the importance of fruit abundance (e.g. Howe and De Steven 1979; Howe and Vande Kerckhove 1979, 1981; Howe 1980, 1983; Moore and Willson 1982; Manasse and Howe 1983; Davidar and Morton 1986; Murray 1987) together provide equivocal evidence that it influences dispersal success (Howe and Smallwood 1982). Such variability in results both reflects the complexity commonly found in fruit-frugivore systems, and the likelihood that general predictions should be reconsidered.

In this paper I report on a two-year study of an unusually straightforward fruit-frugivore system in which one fruiting plant, the hawthorn (*Crataegus monogyna* Jacq.) (Rosaceae) was served by one frugivore, the American robin (*Turdus migratorius* L.). Complicating factors (e.g. predation pressure, interspecific competition, and insect infestations) were negligible. I used this system to examine fruit fate, dispersal success (defined as the absolute number of seeds dispersed), dispersal efficiency (defined as the proportion of initial fruit crop dispersed; dispersal success per propagule), and the relationship between plant traits and plant fitness. Specifically, I report on results from a test of the hypothesis that individual plants with larger fruit crops experience greater dispersal success and efficiency and then discuss optimal fruiting strategies.

Study site and study species

Field-work was conducted on the Nature Conservancy's Cogswell-Foster Reserve in Linn County, western Ore-

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gon, USA. *C. monogyna* (the one-seeded European hawthorn) was introduced to the study site approximately 100 years ago (Love and Feigen 1978) and has since spread vigorously throughout the area. The native five-seeded black-fruited hawthorn (*C. douglasii* Lindl. var *sucksdorfii* Sarg.), and hybrids between the native and non-native hawthorn, also occur on the reserve. *C. monogyna* is now the dominant hawthorn at the study site, however, comprising over 70% of the total hawthorn population (Love 1980). Although European hawthorn and American robin are species with no recent coevolutionary history, *Turdus* and *Crataegus* co-occur extensively throughout the Holarctic. Hence, although we cannot make strong adaptive arguments based on the interactions between *C. monogyna* and *T. migratorius*, it is probable that these represent evolutionary lineages with a long history of contact.

C. monogyna fruits ripen during Sept–Oct and, if uneaten, persist throughout the winter (a season). *C. monogyna* is dispersed by (primarily avian) frugivores (e.g. De Boer 1979, Manzur and Courtney 1984; Courtney and Manzur 1985; Herrera 1987; but see Bass 1990). There are no data on dispersal of *Crataegus* by frugivores in the United States and field studies addressing frugivory in robins are also rare (but see Wheelwright 1986a). At the study site, the only dispersers of *C. monogyna* were robins during the two-year study reported here. Cedar waxwings (*Bombycilla cedrorum* Vieillot) were occasionally observed flying overhead but rarely foraged on fruits during this study. However, because waxwings are a relatively nomadic species, in years when they do forage on hawthorn fruits they could potentially cause important episodic dispersal events; robins, therefore, are not necessarily the primary dispersal agents of *C. monogyna*.

Methods

Calculation of fruit consumption

Fruit consumption by robins was calculated using a simple model modified from equations derived by Courtney and Manzur (1985). Fruit abundance per bush (T) changes as a function of the number of fruits actually eaten by birds (E), the number of fruits picked by birds, but subsequently dropped (a) (identified by characteristic beak-marks; see also Manzur and Courtney 1984), and the number of fruits fallen naturally (b).

$$\text{Hence, } T_o - T_i = E + a + b \quad (1)$$

T was measured directly (to the nearest 100 fruits) for all bushes by systematically counting the number of fruits on all branches. Because a and b could not be measured directly, I instead calculated $a/(a+b)=p$, the proportion of beak-marked fruits under a bush. p was estimated for all bushes by scoring all fruits, collected from eight randomly placed quadrats (25×50 cm) beneath bushes, as either having beak-marks, or not.

Using the identities E/E and a/a , Eq. (1) can be rewritten:

$$\begin{aligned} T_o - T_i &= E + (a+b) \cdot (E/E) \cdot (a/a) \\ &= E \cdot (1 + (1/p) \cdot (1/(E/a))) \end{aligned} \quad (2)$$

Rearranging Eq. (2) gives:

$$E = (T_o - T_i) / (1 + (1/p) \cdot (1/(E/a))) \quad (3)$$

The only unknown quantity in Eq. (3) is E/a , the ratio between eaten and beak-marked fruits.

E/a was measured in the following way. In Sept 1989, plastic sheeting was stretched beneath five arbitrarily chosen fruiting *C. monogyna* bushes at the study site so as to catch all fruits falling from the canopy. For these bushes, fruit abundance was estimated to the nearest 100 fruits by systematically counting the number of fruits on all branches. Fruit abundance was redetermined on 21 Dec 1989 and 3 Mar 1990 for all five bushes. In Sept 1990, similar fruit-traps were built beneath 20 arbitrarily chosen bushes. Fruit abundance was redetermined on 27 Oct 1990, 1 Dec 1990, 12 Jan 1991 and 24 Mar 1991 for all 20 bushes. In both years, fruit-traps were emptied at weekly intervals and the numbers of beak-marked and unbeak-marked fruits counted. Unbeak-marked fruits were assumed to have fallen naturally. Knowing fruit abundance (T_o and T_i), the total number of fruits naturally fallen (b), and the total number of bird-dropped fruits (a), the number of fruits actually consumed by robins (E) was estimated by subtraction for all fruit-trap bushes (see Eq. (1)). Knowing E and a therefore, E/a was calculated for all fruit-trap bushes at each recount date.

In the 1989 season, variation in E/a was tested with a two-way ANOVA without replication for paired comparisons (Sokal and Rohlf 1981). Prior to the ANOVA, an F-test found the two samples to be homoscedastic ($F=2.6$, $df=4,4$, $P=0.42$). E/a did not vary between recounts ($F=0.46$, $df=1,4$, $P=0.70$) or among bushes ($F=1.69$, $df=4,4$, $P=0.41$). The mean value for E/a (mean ± 1.96 SE = 3.80 ± 0.57) was therefore used as a constant in Eq. (3) to calculate E for all bushes in the 1989 season.

In the 1990 season, variation in E/a was again tested with a two-way ANOVA without replication. Prior to the ANOVA, Bartlett's test (Sokal and Rohlf 1981) found the samples to be homoscedastic ($X^2=1.14$, $df=3$, $P=0.78$). E/a did not vary among recounts ($F=0.50$, $df=3,57$, $P=0.69$) or among bushes ($F=1.53$, $df=19,57$, $P=0.10$). The mean value for E/a (mean ± 1.96 SE = 4.21 ± 0.73) was therefore used as a constant in Eq. (3) to calculate E for all bushes in the 1990 season.

Traits measured

In Sept 1989, I located and tagged 210 fruiting *C. monogyna* bushes at the study site. At this time, I estimated (initial) fruit abundance (T_o) to the nearest 100 fruits for all bushes by systematically counting the number of fruits on all branches. In Oct 1989 (when robins began foraging on fruits), I arbitrarily sampled approximately 20–50 fruits from all tagged bushes (because fruit abundance ranged from approximately 500–40000 fruits per bush, the effects of sampling 20–50 fruits were assumed to be negligible). Within 48 h, 20 fruits were drawn from each sample, measured in diameter, and weighed whole to the nearest milligram. Seeds were then dissected from each fruit, cleaned of pulp, and weighed. I then calculated pulp weight and pulp-to-seed ratio. For each bush I calculated a mean value of fruit diameter, fruit weight, pulp weight, seed weight, and pulp-to-seed ratio. Each bush therefore had six measured traits (five fruit traits plus initial fruit abundance). On 21 Dec 1989 and 3 Mar 1990, I redetermined fruit abundance for all tagged bushes.

In Sept 1990, I located 53 fruiting *C. monogyna* bushes as in the previous year. Thirty of these bushes were tagged in 1989, the remaining 23 bushes being new additions to the study. As before, initial fruit abundance was estimated at the time of location. In Oct 1990, fruits were sampled and analyzed for the five traits measured in 1989 and averaged for each bush. In addition, for each bush, I measured bush height, bush width, and distance to the nearest cover (defined as dense oak/hawthorn thicket). From measures of bush height and bush width I estimated canopy surface area and canopy volume by assuming bush canopies to be rectangular boxes. Fruit densities were also calculated by dividing initial fruit abundance by canopy surface area. Each bush therefore had

twelve measured traits (five fruit and seven bush). On 27 Oct 1990, 1 Dec 1990, 12 Jan 1991 and 24 Mar 1991, I redetermined fruit abundance for all tagged bushes.

Classification of fruit fate

For all bushes in both years, I classified fruits into the following categories: (I) remaining on the bush; (II) bird-dropped; (III) defecated/regurgitated; (IV) dispersed; and (V) naturally fallen beneath parent plants. The number of fruits in each of these categories was calculated as outlined below and then converted to a proportion of initial fruit abundance. Although insect seed predators are known to attack *Crataegus* fruits (Roitberg et al. 1982; Manzur and Courtney 1984; Courtney and Manzur 1985), insect infestation was rare in the population studied here and any effects were therefore considered negligible. Robins rarely foraged for fruits on the ground, and fallen fruits were invariably eaten by deer mice (*Peromyscus maniculatus* Wagner) (R. Sallabanks, personal observation); fallen fruits were therefore unlikely to be dispersed.

I. Remaining fruits. The number of fruits remaining on bushes was determined at each recount date (see section on traits measured).

II. Bird-dropped fruits. For all recount dates, I estimated the number of fruits eaten by robins for all bushes. Knowing the number of fruits eaten (E), and the ratio of eaten to bird-dropped fruits (E/a), the number of bird-dropped fruits was simply calculated as $E/(E/a)$.

III. Defecated/regurgitated fruits. To calculate the ratio of eaten fruits (E) to defecated/regurgitated fruits (d), on 20 Jan 1989, I directly observed 37 foraging bouts by 20 individual robins and recorded their behavior on audio tape. I then arbitrarily collected 246 robin defecations from beneath bushes where robins had been foraging and determined the number of seeds per defecation ($\text{mean} \pm 1.96 \text{ SE} = 2.00 \pm 0.20$). Tapes were then analyzed for the number of fruits eaten, and the number of defecations or regurgitations made. By assuming that each regurgitation was of only one seed, I then calculated E/d , the ratio of eaten to defecated/regurgitated fruits to be 2.52 (because *C. monogyna* fruits contain only one seed, the number of seeds defecated equals the number of fruits eaten that weren't regurgitated). Hence, the number of fruits defecated/regurgitated by robins was simply $E/2.52$.

IV. Dispersed fruits. I calculated the number of fruits dispersed as $E - (E/2.52)$, the difference between the number of fruits eaten and the number defecated/regurgitated. Throughout this paper, "dispersal" is defined as the number of seeds carried away from parent plants. Estimates of seed and seedling survivorship were not made and it should therefore be remembered that "dispersal" is a correlate of plant fitness, and not a measure of it.

V. Fallen fruits. I simply calculated the number of fallen fruits as the difference between initial fruit abundance and the sum of the above four categories.

Data analysis

The quantity of fruits eaten by birds is only one component of the dispersal process; whether or not frugivores even visit a plant is another (Murray 1987). To distinguish between these two components is important, and for this reason, I first compared bushes visited by birds (defined as having at least one fruit eaten) with bushes not visited by birds; this enabled me to identify which characters were important in the bush-selection process.

Subsequent analyses were then restricted to bird-visited bushes only. Correlation coefficient matrices were constructed to deter-

mine the relationships among the traits measured; values for seed dispersal and seed waste (a seed was considered wasted if it was not dispersed) were also included in these matrices to examine their relationship with bush and fruit characters.

Results

The fate of fruits

Fruit crops were persistent and the majority of fruits fell beneath parent plants in both years (1989: Fig. 1a; 1990: Fig. 1b). By December, few fruits had been removed by birds (1989: mean = 9%; 1990: mean = 26%) and even fewer had actually been dispersed (1989: mean = 4% (Fig. 1a); 1990: mean = 12% (Fig. 1b)).

By March, the most common way for fruits to have left bushes was to fall (1989: mean = 44% (Fig. 1a); 1990: mean = 17% (Fig. 1b)). In total, approximately 60% of fruits landed (i.e. fell, were dropped by birds, or defecated/regurgitated) beneath parent plants (1989: mean = 60%; 1990: mean = 62%). Twice as many fruits were consumed by birds in 1990 compared with 1989 (1989: mean = 24%; 1990: mean = 48%). Similar differences were found in the proportion of fruits actually dispersed (1989: mean = 14%; 1990: mean = 29%). In

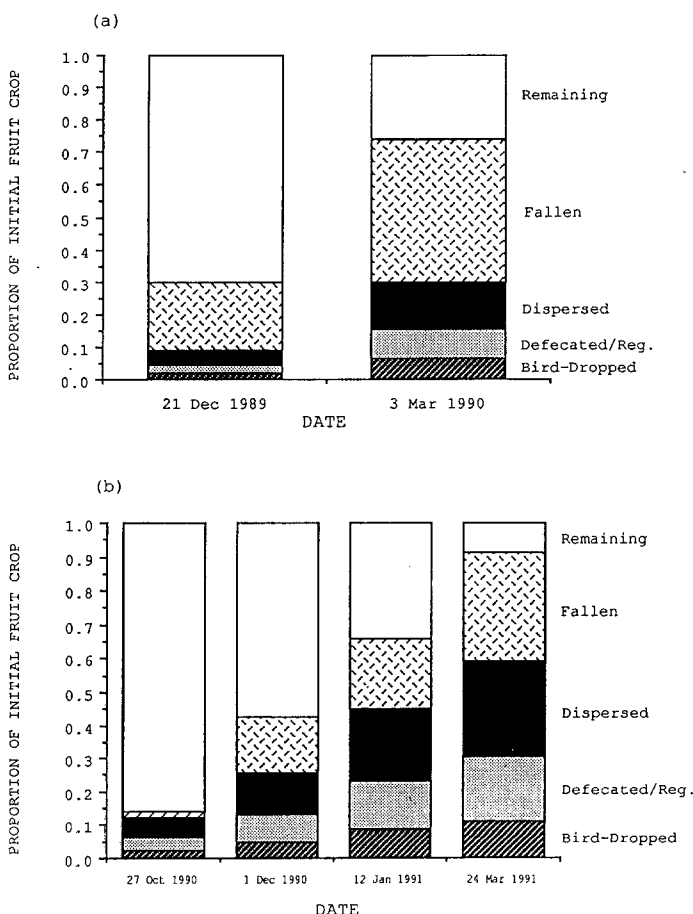


Fig. 1. (a) Fate of fruits from the *C. monogyna* population in the 1989 season ($n=210$ bushes). (b) Fate of fruits from the *C. monogyna* population in the 1990 season ($n=53$ bushes)

Table 1. Comparison between bushes visited and not visited by birds during the period 18 Sept–21 Dec 1989. Traits were measured in Sept/Oct 1989 (prior to bird visitation) and values are means \pm 1.96 SE

	Visited (<i>n</i> = 43)		Not visited (<i>n</i> = 167)		Mann-Whitney U-test	
					U	<i>P</i>
Frt abundance (frt/bush)	5620	\pm 2102	1975	\pm 446	2180.0	<0.001
Fruit diameter (mm)	9.38	\pm 0.31	8.97	\pm 0.12	2730.5	<0.025
Fruit weight (mg)	520.95	\pm 40.20	476.22	\pm 14.15	2871.0	<0.05
Pulp weight (mg)	408.28	\pm 36.51	363.52	\pm 12.60	2733.0	<0.025
Seed weight (mg)	112.84	\pm 6.61	112.74	\pm 3.72	3590.5	ns
Pulp-to-seed ratio	3.69	\pm 0.25	3.38	\pm 0.14	2777.5	<0.025

Table 2. Comparison between bushes visited and not visited by birds during the period 3 Sept–27 Oct 1990. Traits were measured in Sept/Oct 1990 (prior to bird visitation) and values are means \pm 1.96 SE

	Visited (<i>n</i> = 42)		Not visited (<i>n</i> = 11)		Mann-Whitney U-test	
					U	<i>P</i>
Frt abundance (frt/bush)	7930	\pm 872	4911	\pm 403	1007.5	<0.01
Fruit diameter (mm)	8.35	\pm 0.09	8.10	\pm 0.11	1124.5	ns
Fruit weight (mg)	431.96	\pm 12.23	406.40	\pm 13.81	1158.0	ns
Pulp weight (mg)	334.31	\pm 9.99	308.24	\pm 10.89	1170.0	ns
Seed weight (mg)	102.22	\pm 2.11	98.29	\pm 3.87	1211.0	ns
Pulp-to-seed ratio	3.34	\pm 0.09	3.23	\pm 0.10	1329.0	ns
Bush width (m)	2.12	\pm 0.04	2.11	\pm 0.03	1374.0	ns
Bush height (m)	3.75	\pm 0.11	3.54	\pm 0.14	1332.0	ns
Canopy surf area (m ²)	41.63	\pm 1.72	38.94	\pm 1.36	1330.0	ns
Canopy volume (m ³)	17.99	\pm 1.16	15.94	\pm 0.74	1277.0	ns
Fruit density (frt/m ²)	467.37	\pm 36.90	357.52	\pm 50.51	1019.5	<0.025
Distance to cover (m)	18.45	\pm 3.54	12.45	\pm 2.23	1392.5	ns

Table 3. Correlation matrix of (log-transformed) traits measured in Sept/Oct 1989 (*n* = 157 bushes visited by birds during the period 18 Sept 1989–3 Mar 1990). Values of seed dispersal and seed waste are also for this period. Correlation coefficients (above diagonal) and all significant relationships (below diagonal) are shown. Fr ab = initial fruit abundance (frt/bush); Fr dm = fruit diameter (mm); Fr wt = whole fruit weight (mg); Pp wt = pulp weight (mg); Sd wt = seed weight (mg); Pp:Sd = pulp-to-seed ratio; # Disp = no. seeds dispersed; # Wast = no. seeds wasted

	Fr ab	Fr dm	Fr wt	Pp wt	Sd wt	Pp:Sd	# Disp	# Wast
Fr ab		−0.181	−0.137	−0.118	−0.114	−0.029	0.883	0.993
Fr dm	0.05		0.818	0.811	0.397	0.384	−0.078	0.202
Fr wt	ns	0.001		0.966	0.563	0.395	−0.032	−0.160
Pp wt	ns	0.001	0.001		0.335	0.611	−0.014	−0.141
Sd wt	ns	0.001	0.001	0.001		−0.519	−0.067	−0.125
Pp:Sd	ns	0.001	0.001	0.001	0.001		0.022	−0.039
# Disp	0.001	ns	ns	ns	ns	ns		0.829
# Wast	0.001	0.01	0.05	0.05	ns	ns	0.001	

both years, of the fruits removed by birds (1989: mean = 30%; 1990: mean = 59%), less than 50% were actually carried away from parent plants (1989: mean = 48%; 1990: mean = 49%).

Correlates of seed dispersal: annual trends

There were significant differences between bushes visited by birds and bushes not visited by birds in both years (1989: Table 1; 1990: Table 2). However, fruit abundance was the only trait found to differ significantly in both years (greater for bird-visited bushes). In 1989,

fruit abundance and fruit diameter still differed significantly between bushes visited and bushes not visited by the end of the season (3 Mar 1990). In 1990, however, no significant differences were found between bushes visited and bushes not visited at any recount date other than 27 Oct 1990.

When only bird-visited bushes were considered, many of the traits measured were correlated with one another in both years (1989: Table 3; 1990: Table 4). Similar correlations occurred when all bushes, irrespective of visitation, were considered. Seed dispersal and seed waste were consistently and most highly correlated with initial fruit abundance. Regression analysis demonstrated that

Table 4. Correlation matrix of (log-transformed) traits measured in Sept/Oct 1990 ($n=52$ bushes visited by birds during the period 3 Sept 1990–24 Mar 1991). Values of seed dispersal and seed waste are also for this period. Correlation coefficients (above diagonal) and all significant relationships (below diagonal) are shown. Bh ht=bush height (m); Bh wd=bush width (m); Cy sa=canopy surface area (m²); Cy vl=canopy volume (m³); Fr dy=fruit density (fruits/m²); D cov=distance to nearest cover (m). For all other abbreviations see Table 3

	Fr ab	Fr dm	Fr wt	Pp wt	Sd wt	Pp:Sd	Bh wd	Bh ht	Cy sa	Cy vl	Fr dy	D cov	# Disp	# Wast
Fr ab														
Fr dm	ns	0.000	-0.089	-0.041	0.058	-0.097	0.669	0.326	0.574	0.598	0.441	0.035	0.840	0.963
Fr wt	ns	0.001	0.521	0.938	0.639	0.558	-0.004	-0.359	-0.256	-0.219	0.246	0.562	0.054	-0.031
Pp wt	ns	0.001	0.001	0.551	0.325	0.369	-0.068	-0.212	-0.184	-0.169	0.090	0.342	-0.070	-0.088
Sd wt	ns	0.001	0.001	0.001	0.536	0.716	-0.046	-0.359	-0.278	-0.245	0.229	0.575	0.055	-0.088
Pp:Sd	ns	0.001	0.05	0.001	ns	-0.205	0.091	-0.155	-0.073	-0.039	0.108	0.096	0.092	0.045
Bh wd	0.001	ns	0.01	ns	ns	ns	-0.134	-0.288	-0.264	-0.254	0.177	0.594	-0.017	-0.139
Bh ht	0.05	0.01	ns	ns	ns	0.05	0.01	0.378	0.789	0.829	-0.185	-0.130	0.551	0.638
Ca sy	0.001	ns	ns	0.05	ns	ns	0.001	0.001	0.865	0.831	-0.569	-0.525	0.368	0.259
Cy vl	0.001	ns	ns	ns	ns	ns	0.001	0.001	0.001	0.997	-0.479	-0.422	0.538	0.513
Fr dy	0.01	ns	ns	ns	ns	ns	ns	0.001	0.001	0.001	-0.455	-0.395	0.553	0.540
D cov	ns	0.001	0.05	0.001	ns	0.001	ns	0.001	0.01	0.01	0.001	0.481	0.314	0.466
# Disp	0.001	ns	ns	ns	ns	ns	0.001	0.01	0.001	0.001	0.05	ns	-0.044	0.066
# Wast	0.001	ns	ns	ns	ns	ns	0.001	ns	0.001	0.001	0.001	ns	0.001	0.670

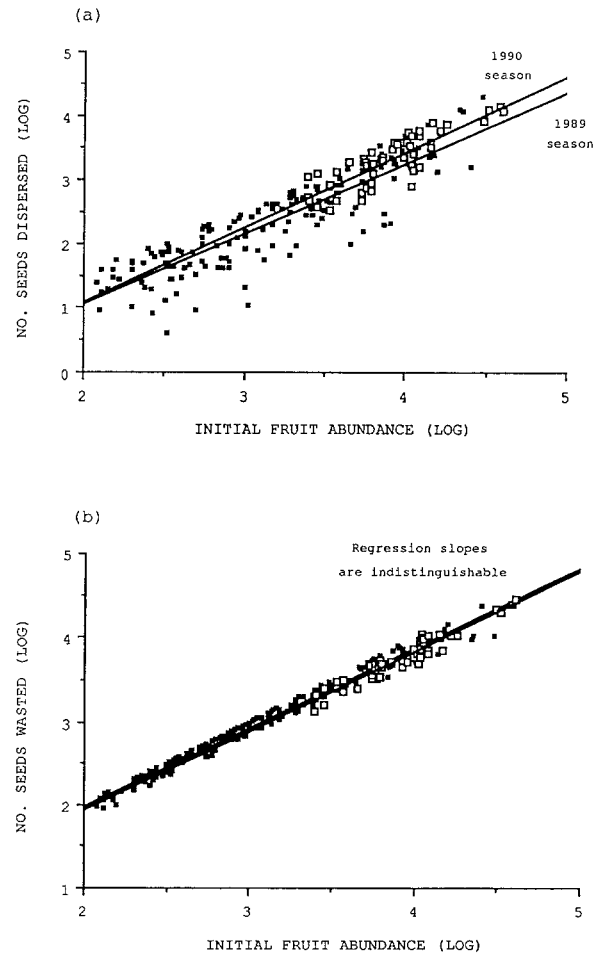


Fig. 2. (a) The number of seeds dispersed from bird-visited bushes as a function of initial fruit abundance (18 Sept 1989–3 Mar 1990, open squares: $y = 1.09x - 1.12$, $r^2 = 0.77$, $df = 1,155$, $P < 0.001$; 3 Sept 1990–24 Mar 1991, closed squares: $y = 1.17x - 1.24$, $r^2 = 0.71$, $df = 1,50$, $P < 0.001$). (b) The number of seeds wasted by all bushes as a function of initial fruit abundance (18 Sept 1989–3 Mar 1990, open squares: $y = 0.95x + 0.07$, $r^2 = 0.98$, $df = 1,208$, $P < 0.001$; 3 Sept 1990–24 Mar 1991, closed squares: $y = 0.95x + 0.03$, $r^2 = 0.92$, $df = 1,51$, $P < 0.001$)

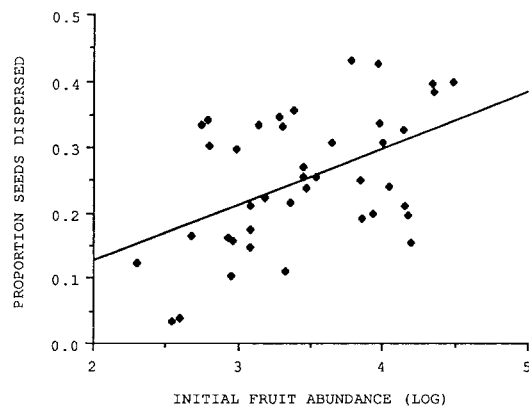


Fig. 3. The (angular-transformed) proportion of seeds dispersed from bird-visited bushes during the period 18 Sept–21 Dec 1989 as a function of initial fruit abundance ($y = 0.09x - 0.04$, $r^2 = 0.23$, $df = 1,41$, $P < 0.001$)

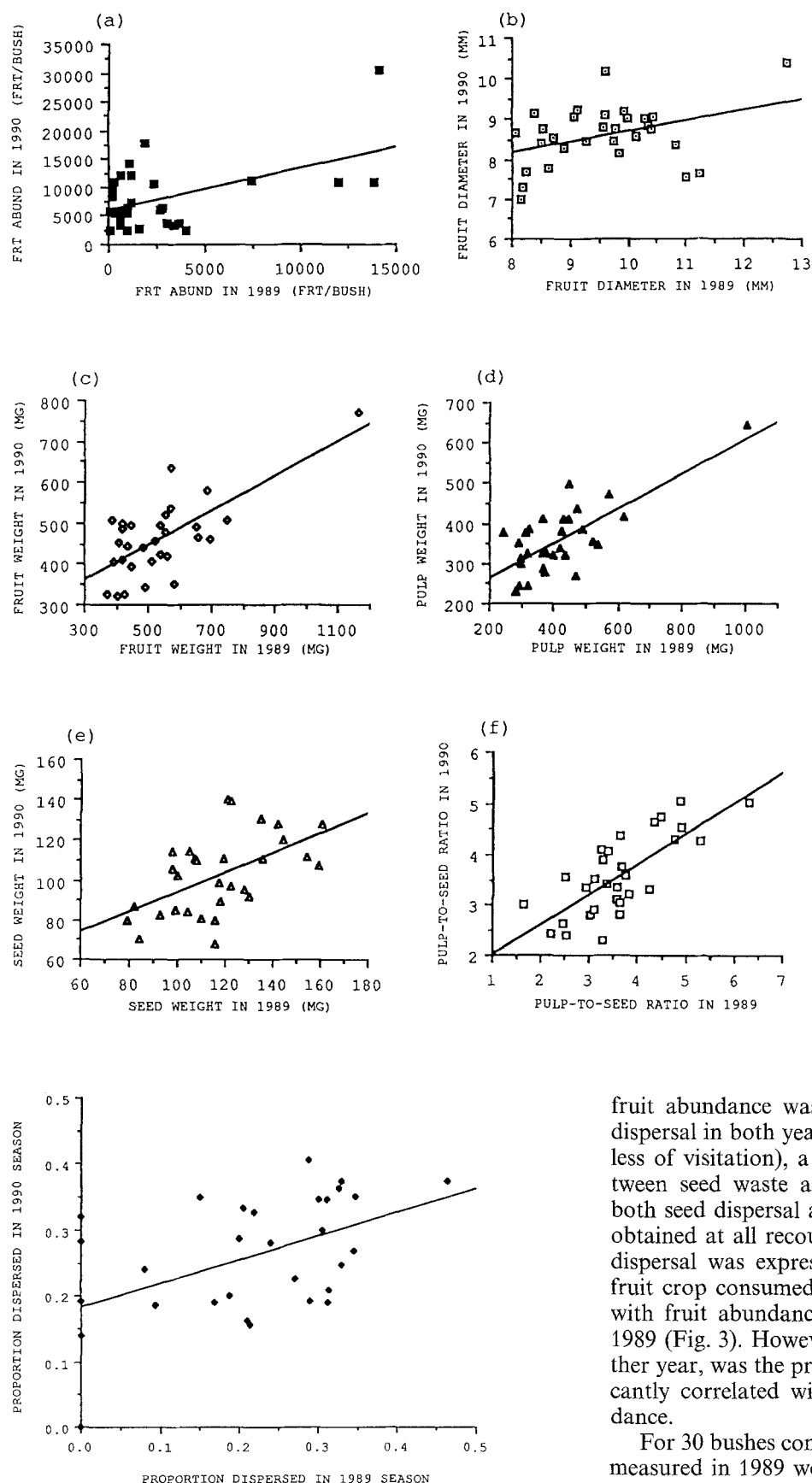


Fig. 4a-f. The relationship between traits in the 1989 season and the 1990 season for 30 bushes common to both years. (a) Fruit abundance ($y = 0.75x + 6182$, $r^2 = 0.26$, $df = 1, 28$, $P < 0.01$); (b) Fruit diameter ($y = 0.26x + 6.15$, $r^2 = 0.14$, $df = 1, 28$, $P < 0.05$); (c) Fruit weight ($y = 0.42x + 235.36$, $r^2 = 0.49$, $df = 1, 28$, $P < 0.001$); (d) Pulp weight ($y = 0.43x + 179.50$, $r^2 = 0.55$, $df = 1, 28$, $P < 0.001$); (e) Seed weight ($y = 0.49x + 45.24$, $r^2 = 0.29$, $df = 1, 28$, $P < 0.01$); (f) Pulp-to-seed ratio ($y = 0.60x + 1.43$, $r^2 = 0.56$, $df = 1, 28$, $P < 0.001$).

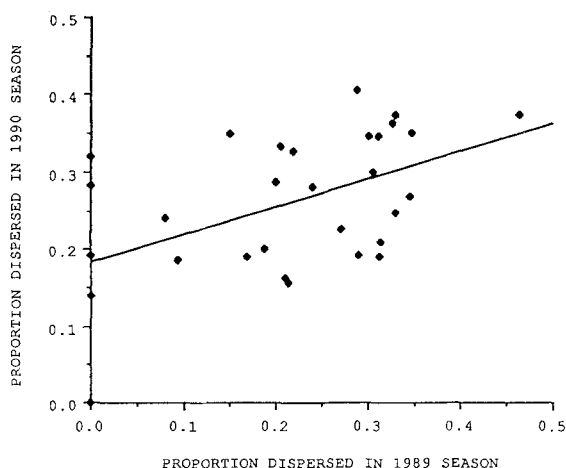


Fig. 5. The relationship between the (angular-transformed) proportion of seeds dispersed in the 1989 season and the 1990 season for 30 bushes common to both years ($y = 0.35x + 0.18$, $r^2 = 0.24$, $df = 1, 28$, $P < 0.01$).

fruit abundance was indeed a good predictor of seed dispersal in both years (Fig. 2a). For all bushes (regardless of visitation), a similar relationship was found between seed waste and fruit abundance (Fig. 2b). For both seed dispersal and seed waste, similar results were obtained at all recount dates in both years. When seed dispersal was expressed as a proportion of the initial fruit crop consumed, a significant positive relationship with fruit abundance was found in the mid-season of 1989 (Fig. 3). However, at no other recount date, in either year, was the proportion of fruits consumed significantly correlated with any trait, including fruit abundance.

For 30 bushes common to both years, all six variables measured in 1989 were significantly correlated between years (Fig. 4). Similarly, the proportion of seeds dispersed by individual bushes in the 1989 season was significantly correlated with the proportion dispersed the following year (Fig. 5).

Discussion

Fruit fate and dispersal efficiency

Most fruiting plants have relatively high dispersal efficiencies with fruit removal rates ranging from 50–100% (e.g. Howe and Vande Kerckhove 1979, 1981; Herrera and Jordano 1981; Sorensen 1981; Jordano 1982, 1987, 1989; Borowicz and Stephenson 1985; Burger 1987). In their study of *C. monogyna* in England, Courtney and Manzur (1985) report that approximately 65% of fruits were eaten by birds. In contrast, I found that, on average, robins consumed between 24% (1989 season) and 48% (1990 season) of initial fruit crops. The proportion of fruits actually carried away from bushes (i.e. dispersed) was even less (1989: mean = 14%; 1990: mean = 29%). These figures translate into an average 79% of seeds wasted each year. Such high seed waste has only rarely been reported (Howe 1980).

Low dispersal efficiency in this system appears to be a function of both disperser availability and behavior. The avifauna of western Oregon is relatively devoid of frugivores; other than robins, cedar waxwings (*Bombicilla cedrorum*) are the only species that regularly eat fruits. Fewer than 50% of fruits removed from bushes by robins are actually dispersed; robins drop 20% of the fruits they pick, and defecate/regurgitate 40% of the fruits (seeds) they swallow before leaving bushes. Such dropped and defecated/regurgitated fruits are subject to intense competition beneath parent plants or are eaten by deer mice (*Peromyscus maniculatus*). Furthermore, calculations of seed dispersal refer only to maximum potential dispersal rates. Seeds carried away from parent plants can suffer high post-dispersal predation (Howe et al. 1985; Thompson 1985; Willson and Whelan 1990) and low germination rates. Indeed, during freezing winter spells, robins are known to defecate *C. monogyna* seeds in huge clumps (> 1000 seeds) at communal drinking sites (Sallabanks and Courtney 1992). Such clump-dispersed seeds suffer intense intra-specific competition and rarely survive (Howe 1989).

Weather effects may also be important. Dispersal success is clearly related to fruit production (Figs. 2a and 3), which may explain why twice as many fruits were dispersed in the 1990 season as in the previous year: on average, almost four times as many fruits were produced in the 1990 season (mean = 10131 fruits/bush) as in the 1989 season (mean = 2721 fruits/bush). In addition to increased quantity in the 1990 season, the fruits produced were also of higher quality, being larger and having higher pulp-to-seed ratios. Fruit production can itself be dependent upon pollination success (e.g. Phipps and Muniyamma 1980). Annual variation in dispersal efficiency will therefore be dependent upon disperser availability, pollination, and hence fruit production, all of which are probably controlled by weather (e.g. Stephenson 1981; Foster 1982; Herrera 1982; Howe 1983).

If *C. monogyna* has a low dispersal efficiency, why is it such a successfully invasive species? It is possible that dispersal is episodic (e.g. by large nomadic flocks of waxwings) and therefore unlikely to be documented

in a two-year study such as this. Alternatively, dispersal success is perhaps only meaningful when compared with other native fruiting species. Indeed, *C. monogyna* was found to be far more attractive to robins than the native *C. douglasii suksdorfii* (Sallabanks 1992).

Correlates of seed dispersal and plant fitness

Fruiting plant fitness is correlated with absolute dispersal success (the number of seeds dispersed) or relative dispersal success per propagule (the proportion of seeds dispersed) (Howe 1980); which is the best estimator of reproductive success is unclear, however. Murray (1987) argues that reproductive success for iteroparous plants (i.e. *C. monogyna*) is best estimated by dispersal success per propagule; such plants should maximize the ratio of surviving offspring to reproductive effort expended. The proportion of fruits dispersed would therefore be the best estimator of plant fitness for *C. monogyna*. In either case, those *C. monogyna* bushes with larger fruit displays had more fruits dispersed (Figs. 2a and 3) and therefore potentially higher fitness. Furthermore, highly fecund plants were more likely to be visited by robins in both years (Tables 1 and 2). Plants producing more fruits may also disperse a larger absolute number of seeds to distant sites through statistical effects (Howe 1980). Other studies have found fruit abundance to affect frugivore choice (Howe and De Steven 1979; Howe and Vande Kerckhove 1979, 1981; Howe 1980, 1981; Jordano 1982; Davidar and Morton 1986; Murray 1987), but none have found positive linear relationships between the proportion of fruits dispersed and fruit abundance.

Despite population differences in fruit production between years, *C. monogyna* plants with high fitness one year (i.e. high fruit removal rates) also enjoyed high fitness the following year (Fig. 5). This is probably because some bushes were consistently more fecund and consistently produced higher quality fruits (e.g. pulp-to-seed ratio; Fig. 4). While fecund individuals may simply be older (see below), or growing in better locations, low individual year-to-year variation in fruit abundance and quality may indicate that such traits are heritable. Invasion of new habitat by *C. monogyna* begins from scattered plants that have established at random distances from the source, probably by avian dispersal, followed by population expansion (Williams and Buxton 1986). Therefore, if fitness-related traits such as fruit abundance are heritable, one fecund individual could potentially inundate uncolonized habitats by dispersing genetically similar offspring.

Consequences for fruiting strategies

Because dispersal efficiency increases linearly with fruit abundance, dispersal success will increase disproportionately with fruit abundance. That more fecund plants are more dispersal efficient therefore suggests the optimal

fruiting strategy for *C. monogyna* is to produce large quantities of fruits as quickly as possible. Plant fecundity was closely correlated with bush size (Table 4), and therefore plant age (e.g. Williams and Buxton 1986). To produce large fruit crops as quickly as possible, therefore, *C. monogyna* should maximize its growth rate early in life. Fruiting should therefore be delayed because resources allocated to reproduction would cause slower growth rates (Harper 1977; Foster 1982; Wheelwright 1986b). Such an optimal strategy may explain why Williams and Buxton (1986) found few flowering and fruiting *C. monogyna* plants to be less than 20 years old. The only plants with abundant fruit or flowers were those 30–40 years old.

The results presented in this paper have demonstrated the importance of plant fecundity – a likely correlate of plant fitness. Such results from a fruit-frugivore system provide rare support for predictions of both optimal foraging theory (Pyke et al. 1977) and models of the evolution of fruiting strategies (Snow 1971; McKey 1975). Typically, fruit-frugivore systems are more complex (multiple fruiting plant and frugivore species) than the one studied here; this complexity may explain why most studies that address patterns of seed dispersal provide mixed results. I suggest that predictions of seed dispersal patterns receive mixed support because complexity is real and predictable patterns simply do not exist in most cases.

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