Evolutionary Ecology Research, 2005, **7**: 1067–1076

Does mimicry occur between fleshy-fruits?

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ABSTRACT

Goal: Test for mimicry in two bird-dispersed fruit species.

Site: British Columbia, Canada

Species: *Rubus parviflorus* Pursh and *R. spectabilis* Nutt.

Background: *Rubus parviflorus* produces red fruits, while *R. spectabilis* produces both red and orange fruits. The two colour forms of *R. spectabilis* are otherwise similar, but birds prefer the red form. Both *Rubus* species are dispersed by the same frugivores, co-occur in close proximity, and have overlapping fruit phenologies, but birds prefer *R. parviflorus* fruits over *R. spectabilis* fruits.

Experiment: I conducted a field experiment to test whether avian preferences for red *R. spectabilis* fruits are associated with their closer similarity to *R. parviflorus* fruits. Red and orange fruits of *R. spectabilis* were displayed in close proximity to *R. parviflorus* fruits, or close to *R. spectabilis* fruits. The latter served as a control.

Results: The red form of *R. spectabilis* was removed more rapidly than the orange form when displayed close to *R. parviflorus* fruits. The difference disappeared in the control treatment.

Conclusions: Birds appear to mistake the red form of *R. spectabilis* for *R. parviflorus* fruits when they are displayed close together.

Keywords: birds, fleshy-fruits, frugivore, fruit colour, mutualism, seed dispersal.

INTRODUCTION

Some plant species produce brightly coloured seeds that superficially resemble fleshy-fruits yet offer no nutrient reward (see McKey, 1975; Van der Pijl, 1982; Schaefer *et al.*, 2004). Previous experiments have shown that seed-dispersing birds sometimes mistake coloured seeds for similarly coloured fleshy-fruits (Foster and Delay, 1998; Galetti, 2002). Therefore, experimental evidence for fruit mimicry has been found in investigations of 'mimetic' seeds (but see Peres and van Roosmalen, 1996). Similar relationships could also occur between high- and low-quality fleshy-fruits (Willson and Whelan, 1990). However, evidence for mimicry between fleshy-fruits has not been previously documented (Cipollini and Levey, 1997).

This study presents the results of the first experimental test for fruit mimicry between fleshy-fruits. The experiment was conducted on two raspberry species, *Rubus parviflorus*

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Nutt. and *Rubus spectabilis* Pursh, in a temperate rainforest in British Columbia, Canada. Both species are similar in most respects. However, *R. parviflorus* produces red fruits, while *R. spectabilis* is colour polymorphic, producing both red and orange fruits. Although both colour forms of *R. spectabilis* are phenotypically similar (Traveset and Willson, 1998), birds consistently prefer the red form (Gervais *et al.*, 1999). While collecting fruits for a previous experiment (Burns and Dalen, 2002), I repeatedly mistook the red form of *R. spectabilis* for the red fruits of *R. parviflorus*. This led me to question whether seed-dispersing birds are similarly fooled.

Roy and Widmer (1999) outline several criteria necessary to demonstrate evidence for flower mimicry. Species involved in the proposed interaction must share the same pollinator species, have overlapping flower phenologies and spatial distributions, and require pollinators for seed set. Morphological similarity between flower species must also influence plant fitness. Using these criteria as a general guide, I made several observations and conducted an experiment to test for evidence of fruit mimicry. I conducted field observations to quantify: (1) the types of frugivore species consuming each fruit species to determine whether both fruit species share the same seed dispersers; (2) the spatial distributions and fruit phenologies of each species to determine whether they co-occur in space and time; (3) fruit size and shape to determine their morphological similarity; and (4) fruit removal rates from isolated fruiting plants to determine whether frugivores prefer *R. parviflorus* fruits over *R. spectabilis* fruits. I then conducted a fruit removal experiment to evaluate whether the red form of *R. spectabilis* is removed more rapidly than the orange form when they are displayed in close proximity to *R. parviflorus* fruits.

METHODS

Study site and species

All data were collected on the west coast of Vancouver Island, British Columbia, Canada. The prevailing vegetation type is conifer forest; however, angiosperm shrubs are common in the forest understory. Most shrub species at this site produce fleshy-fruits that are commonly consumed by birds, which subsequently act as dispersal vectors (see Burns, 2004). All data were collected from a 1 ha plot of old-growth temperate rainforest on the grounds of the Bamfield Marine Sciences Centre (48°50′N, 125°22′W). Klinka *et al.* (1989) provide a detailed description of the area's climate, vegetation and natural history.

Rubus spectabilis Pursh (Rosaceae) is a common shrub species in Western North America (Hitchcock and Cronquist, 1994). Its fruits are compound drupelets produced on solitary peduncles. Plants either produce red or orange fruits. The two colour forms are nearly identical in morphology, phenology, seediness and nutrient composition (see Traveset and Willson, 1998). However, orange fruits are longer (2.32 ± 0.03 cm) than red fruits (2.21 ± 0.04 cm). Although both colour forms are present throughout its geographic range, the relative abundance of red fruits increases with latitude (Gervais, 1996). *Rubus spectabilis* commonly occurs in large clonal patches that result from rhizomatous growth (Tappeiner *et al.*, 1991).

Rubus parviflorus Nutt. is a similarly common shrub species in Western North America. It produces red compound drupelets that are generally similar to those of *R. spectabilis*. However, *R. parviflorus* fruits are born on racemes, not solitary peduncles, and are more cup-shaped in appearance. Both species are similar in stature (1–3 m), branching architecture, growth form and leaf morphology (Klinka *et al.*, 1989; Hitchcock and Cronquist, 1994).

However, *R. parviflorus* has slightly larger, pubescent leaves and lacks thorns, which are common in *R. spectabilis*.

Five frugivorous birds are common at the site. The American robin (*Turdus migratorius*), cedar waxwing (*Bombycilla cedrorum*) and Swainson's thrush (*Catharus ustulatus*) migrate to the study site in the summer to breed. The northwestern crow (*Corvus caurinus*) and Steller's jay (*Cyanocitta stelleri*) are year-round residents. Hatler *et al.* (1978) and Campbell *et al.* (1997) give detailed descriptions of the avifauna.

Observations

Frugivores

The identities of frugivore species consuming each fruit species were quantified in foraging observations of free-ranging birds. Observations were made three times a week throughout the 2001 fruiting season along a series of small trails. To avoid multiple observations of the same bird during each census, observations were halted after each sighting and resumed 10 m down the trail. Observations were halted if interrupted by strong winds or heavy rainfall. A contingency table test was conducted to evaluate differences in the number of fruits removed by each frugivore species.

Fruit phenologies and spatial distributions

Fruit phenologies were quantified in observations of marked plants in 1998 and 1999. A single branch on each of 10–12 plants was permanently marked and visited 20 times throughout each fruiting season at approximately 10 day intervals (see Burns and Dalen, 2002). During each census, the total number of ripe fruits occurring on marked branches was noted. Interspecific differences in the number of plants with ripe fruits were compared between censuses with a separate contingency table test for each year. Spatial distributions of each species were assessed by placing a 1 m^3 quadrat in 100 random locations along the same forest trails used in frugivore observations. The presence of each species was noted in each sample, and the resulting data were used to determine how often each species co-occurred in the same cubic metre.

Fruit morphology

The size and shape of both fruit species were measured to assess their morphological similarity. A total of 10 fruits were haphazardly collected from five plants in 2000. From these 10 fruits, six were randomly selected, and their length (maximum diameter) and width (minimum diameter) were measured to the nearest millimetre with vernier calipers. Differences in fruit length and width were assessed with analysis of variance (ANOVA), using species as a fixed factor and parent plant as a random factor. Analyses were conducted in SPSS (2002) using the GLM procedure. Data were log-transformed to meet normality and homoscedasticity assumptions.

Avian fruit preferences

Bird preferences for each fruit species were assessed by comparing fruit removal rates between fruit species. The fruiting stalks of six fruits on 12 plants of each species were marked with small pieces of green tape (1 cm^2) in 1999, and their fates followed though time. Six *R. spectabilis* plants produced red fruits and the other six produced orange fruits. Plants chosen for analysis were located at least 10 m from congeners. Characteristic markings are left on fruiting stalks after removal by birds (Traveset and Wilson, 1998; Gervais *et al.*, 1999; Burns and Dalen, 2002). Therefore, fruit removal rates were quantified through periodic observations of marked peduncles. The ground below marked fruits was checked during each census to ensure that fruits falling from parent plants were not miscategorized as being dispersed. Seventy-two fruits of both species were originally marked; however, samples sizes varied due to pre- and post-ripening fruit mortality. The number of days marked fruits spent on parent plants before removal by birds was compared between species with a Mann-Whitney *U*-test, as data could not be transformed to meet assumptions of ANOVA.

Experiment

A fruit removal experiment was conducted to test whether red *R. spectabilis* fruits are removed more rapidly when displayed in close spatial proximity to *R. parviflorus* fruits, relative to when they are displayed in close proximity to *R. spectabilis* fruits. Using small pieces of green tape, one red and one orange *R. spectabilis* fruit were attached to 30 fruiting plants of *R. parviflorus*. One red and one orange fruit were also attached to 30 fruiting plants of *R. spectabilis*, which served as a control. Fruits were placed on non-fruiting branches 25–100 cm from naturally occurring fruits. Both colour morphs were separated by at least 30 cm. Displays were monitored every 4 (daylight) hours for 3 days. Fruits that were not removed at the end of the observation period were scored as being removed 4 hours after the last census. Two consecutive trials, beginning on 27 July and 2 August 2001, were conducted. Differences in fruit removal rates, or the number of hours until fruit removal, were analysed with three-way ANOVA, using the GLM procedure in SPSS (2002). Fruit type (red or orange) and display species (*R. spectabilis* and *R. parviflorus*) were considered fixed, while trial was treated as a random factor. The interaction term between fruit type and display species was used to test the hypothesis that the red colour morph of *R. spectabilis* is removed more rapidly than the orange colour morph when displayed in close proximity to *R. parviflorus* fruits. The data were log transformed to meet normality and homoscedasticity assumptions.

RESULTS

Both *R. spectabilis* and *R. parviflorus* were dispersed by the same bird species. *Rubus spectabilis* was dispersed by American robins ($n = 22$ observations, 41%), northwestern crows ($n = 18$ observations, 33%) and Swainson's thrushes ($n = 14$ observations, 26%). *Rubus parviflorus* was also dispersed by American robins ($n = 60$ observations, 55%), northwestern crows ($n = 25$ observations, 23%) and Swainson's thrushes ($n = 24$ observations, 22%). The total number of fruits consumed by each frugivore species did not differ between fruit species ($\chi^2 = 2.1$, $P > 0.10$). No other vertebrate species was observed eating the fruits of either species during the observation period.

Both species produced fruit at approximately the same time and in similar locales. Phenological observations showed that *R. spectabilis* were more abundant earlier in the season than *R. parviflorus* ($\chi^2 > 23.4$, $P < 0.001$ for both years). However, their phenologies overlapped for approximately one month in both years (41 and 29 days, respectively). Previous work has shown that the phenology of red and orange *R. spectabilis* fruits does not differ (Traveset and Willson, 1998). Quadrat sampling showed that both species co-occurred in nearly half of vegetation samples ($n = 41$). *Rubus spectabilis* was found alone in 13 quadrats, *R. parviflorus* was found alone in 44 quadrats and neither was found in 2 quadrats.

Differences in fruit morphology were observed between species. *Rubus spectabilis* fruits averaged 17.0 ± 2.5 mm (mean ± standard error; range = 13.6–23.1 mm) in length and 14.9 ± 2.7 mm (range = 11.3–22.2 mm) in width. *Rubus parviflorus* fruits averaged 14.2 ± 2.0 mm (range = 10.8–18.8 mm) in length and 8.6 ± 1.8 mm (range = 5.6–12.7 mm) in width. Statistical analyses showed that fruit length and width varied more strongly among plants than between species. Fruit length differed strongly among plants ($F_{8,50} = 12.8$, $P < 0.001$), and a weak, statistically insignificant, difference was observed between species ($F_{1,8} = 4.3$, $P = 0.071$). Fruit width differed both among plants ($F_{8,50} = 24.8$, $P < 0.001$) and between species ($F_{1,8} = 20.1$, $P = 0.002$). Traveset and Willson (1998) previously showed that the red form of *R. spectabilis* was smaller than the orange form, suggesting that the red form was more similar to *R. parviflorus* fruits, both in colour and size.

Avian frugivores removed each fruit species at different rates ($U = 353$, $P < 0.001$). *Rubus spectabilis* fruits spent longer periods (mean ± standard error: 7.6 ± 0.9 days, $n = 50$) on parent plants prior to removal than *R. parviflorus* fruits (1.9 ± 0.8 days, $n = 27$). Differences in removal rates between species suggest that birds prefer *R. parviflorus* fruits over *R. spectabilis* fruits.

Few differences in fruit removal rates were observed in the experiment. The only statistically significant result was a first-order interaction between fruit type and display species (Table 1), indicating removal rates of red and orange *R. spectabilis* fruits differed among display species.

Specifically, the red form of *R. spectabilis* was removed more rapidly than the orange form when attached to *R. parviflorus* plants. However, both colours were removed at similar rates when attached to *R. spectabilis* plants (Fig. 1). A weak, statistically insignificant, interaction was also observed between display species and trial, indicating that regardless of colour, fruit removal rates were slightly higher on *R. spectabilis* plants in the second trial relative to the first.

Table 1. Results of three-way ANOVA of fruit removal rates (number of hours until fruit removal by frugivores) of red and orange *R. spectabilis* fruits (fruit type) after attachment to either *R. parviflorus* or *R. spectabilis* plants (display species)

Source of variation	d.f.	MS	*F*	*P*
Fruit type	1	1541	12.84	0.173
Display species	1	30	0.08	0.823
Trial	1	441	0.91	0.463
Fruit type × display species	1	701	210.25	0.044
Fruit type × trial	1	120	36.00	0.105
Display species × trial	1	368	110.25	0.060
Fruit type × display species × trial	1	3	0.02	0.887
Error	112	165	–	–

Note: Two consecutive trials were conducted (trial). The only statistically significant result was a first-order interaction between fruit type and display species, indicating that red *R. spectabilis* fruits were removed more rapidly than orange *R. spectabilis* fruits when they were displayed on *R. parviflorus* plants.

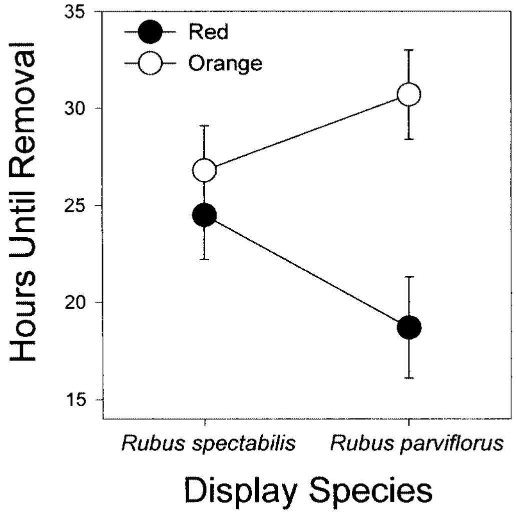

Fig. 1. Results of a field experiment comparing removal rates of red and orange *Rubus spectabilis* fruits after attachment to either *Rubus parviflorus* (treatment) or *Rubus spectabilis* (control). Symbols are the mean number of hours fruits spent on plants before removal by birds (± standard error).

DISCUSSION

Overall, the results fit within the general framework of biological mimicry. A common pool of frugivores dispersed the fruits of both species, which collectively generate patterns in fruit removal. Although *R. spectabilis* produced fruit earlier than *R. parviflorus*, both fruit species were present together for at least one month in both years. Both fruit species commonly occurred in close spatial proximity, indicating that frugivores are likely to simultaneously encounter their fruits on small spatial scales. Both species were similar morphologically, although *R. parviflorus* fruits were narrower than those of *R. spectabilis*. Interestingly, the red fruits of *R. spectabilis* are smaller than the orange ones (Traveset and Willson, 1998). Therefore, the red form of *R. spectabilis* appears to be morphologically more similar to *R. parviflorus* fruits than the orange form of *R. spectabilis*. Observations of isolated fruiting plants showed that *R. parviflorus* fruits were removed more rapidly than *R. spectabilis* fruits. Therefore, birds appear to prefer *R. parviflorus* fruits over *R. spectabilis* fruits.

Experimental results showed that birds treat red and orange *R. spectabilis* fruits differently when they are displayed on different parent plants. The red form of *R. spectabilis* was removed more rapidly than the orange form when displayed in close proximity to *R. parviflorus* fruits. In contrast, both colour forms were removed at similar rates when they were displayed close to *R. spectabilis* fruits. Therefore, birds appear to confuse the red form of *R. spectabilis* for *R. parviflorus* fruits when they co-occur in close proximity. If this interpretation is correct, results constitute the first experimental support for mimicry between fleshy-fruits.

Foster and Delay (1998) and Galetti (2002) obtained similar results in experiments on 'mimetic' seeds. Some species (primarily legumes, Fabaceae) produce brightly coloured seeds, which persist on parent plants for long periods and superficially resemble fleshy-fruits (see McKey, 1975; Van der Pijil, 1982; Schaefer *et al.*, 2004). Although they offer no reward to dispersers, these seeds are sometimes consumed by birds, which apparently mistake them for fleshy-fruits (but see Peres and van Roosmalen, 1996). A similar situation may occur in New Zealand, where I have observed waxeyes (*Zosterops lateralis*) consuming the large, black seeds of *Melicope ternata* Forster et Forster f. (Rutaceae), which resemble fleshy-fruits yet offer no nutrient reward.

Several other types of mimicry have been reported in seed dispersal mutualisms. Webb (1985) describes another New Zealand plant (*Corokia cotoneaster* Raoul, Escalloniaceae) whose leaves senesce when its fruits mature. As the leaves abscise, they obtain a yellow hue, which matches the colour of ripe fruits. Webb (1985) suggests this pattern might enhance seed dispersal fitness by creating the illusion of greater fruit abundances. Groom *et al.* (1994) documented the opposite phenomenon in *Hakea trifurcate* Smith (Proteaceae), which is susceptible to seed predation by parrots before ripening. The plant produces dimorphic leaves, with one leaf-type superficially resembling unripe, green fruits. In a series of experiments and observations, they showed that the similarity of unripe fruits and leaves is a form of 'self-crypsis', which deters parrot seed predation.

My results also provide some insight into the cues used by birds to identify particular fruit species. The effect of fruit type on experimental removal rates indicates that birds use fruit colour, size or both to distinguish between fruit species. The effect of display species indicates that birds also use some aspect of vegetative morphology, such as leaf morphology, branching patterns or thorniness, to differentiate among fruit species. However, fruit type interacted with display species, suggesting that birds use a combination of fruit and vegetative characteristics to distinguish between fruit types. This result is in line with those of Willson and Comet (1993), who found that birds do not use simple foliar cues to distinguish between fruit species.

Mimicry in plants is usually documented in flowers. Although small relative to the literature on animal mimicry (see Joron and Mallet, 1998), a growing number of studies have documented a variety of mimetic interactions between flower species (see Gigord *et al.*, 2001; Johnson *et al.*, 2003 and references therein). In a critique of the evidence for mimicry in flowers, Roy and Widmer (1999) classified two general types of floral mimicry. Flower species that converge on the same phenotype to jointly attract pollinators were referred to as Müllerian floral mimics. Rewardless species that attract pollinators because they resemble species producing nectar rewards were classified as Batesian floral mimics. Roy and Widmer's (1999) classification system can be usefully applied to fruits. Previous tests for fruit mimicry with mimetic seeds clearly fall under the heading of Batesian fruit mimicry. Brightly coloured yet rewardless seeds (mimics) appear to have evolved bright colours to resemble fleshy-fruits (models), which offer nutrient rewards for the dispersal services of birds. However, results from this study share similarities with both Müllerian and Batesian mimicry, and do not fit precisely into either classification. Results are similar to Müllerian fruit mimicry because all three fruit types present rewards to dispersers. However, results are also similar to Batesian fruit mimicry, because a clear model and mimic could be identified.

Another distinct feature of this study is that the evolutionary implications of the observed interactions are not clear. The results simply show that birds have difficulties discerning between morphologically similar fruits that co-occur in space and time. How these difficulties might shape the evolution of fruit morphology represents a major challenge to future studies (Schaefer *et al.*, 2004). Similarly, results do not appear to explain the maintenance of the fruit colour polymorphism in *R. spectabilis*. Gervais *et al.* (1999) found that birds prefer the red form in both Oregon and Alaska. However, *R. parviflorus* was not listed as present at either site. Therefore, the specific processes observed in British Columbia apparently do not apply to previously investigated geographic locales, and the mechanisms maintaining the polymorphism across its geographic range remain unknown.

Although results are consistent with the general phenomenon of mimicry, other interpretations are possible. First, birds may have confused orange *R. spectabilis* fruits with unripe *R. parviflorus* fruits. Fleshy-fruits often pass through a series of colours as they mature, and unripe *R. parviflorus* fruits are an orange-red hue before ripening. However, the orange form of *R. spectabilis* is more yellow in appearance and is easily distinguished from unripe *R. parviflorus* fruits. While I repeatedly mistook red *R. spectabilis* fruits for ripe *R. parviflorus* fruits, I never had difficulties discerning orange *R. spectabilis* fruits and unripe *R. parviflorus* fruits. Nevertheless, this explanation cannot be ruled out entirely because fruit colours were not compared quantitatively (cf. Schmidt *et al.*, 2004). Second, *R. spectabilis* and *R. parviflorus* may be antagonistic resources, which reduce a consumer's fitness when ingested simultaneously (see Whelan *et al.*, 1998). If the two fruit species are antagonistic, birds may have avoided orange *R. spectabilis* fruits when they were displayed on *R. parviflorus* plants because they had previously consumed nearby *R. parviflorus* fruits. This explanation still assumes that birds have difficulties distinguishing red *R. spectabilis* fruits from *R. parviflorus* fruits; however, the mechanism generating fruit removal patterns differs. Lastly, a fully reciprocal experimental design (i.e. *R. parviflorus* fruits transplanted to both *R. parviflorus* and *R. spectabilis* plants) could have provided additional insight into bird–fruit interactions. However, this design proved to be infeasible. *Rubus parviflorus* fruits cannot be transported because they are weakly attached to peduncles and usually fall off during transplantation. Future tests of fruit mimicry would certainly benefit from such a design.

Bird-dispersed fruits are a remarkable example of functional convergence. Fleshy-fruits that rely on animal consumption for seed dispersal have evolved repeatedly in unrelated plant lineages (Herrera, 2002a). Numerous explanations have been offered to explain the evolutionary dynamics of fleshy-fruits (for recent discussions, see Lord, 2004; Voigt *et al.*, 2004). However, the most widely accepted explanation is that evolutionary constraints, such as geographically inconsistent selection pressures or pleiotropic effects, limit the co-evolution of specific fruit characters to match the preferences of particular frugivore species (Thompson, 1994; Herrera, 2002b). Results from this study suggest an alternative explanation. It is conceivable that Müllerian fruit mimicry between groups of fruits and frugivores has resulted in the morphological convergence of fleshy-fruits (see also Cipollini and Levey, 1997). However, evidence for this hypothesis awaits future tests for fruit mimicry among groups of fruits and frugivores, and further conceptual refinement of the phenomenon.

ACKNOWLEDGEMENTS

Thanks to the staff, researchers and students at the Bamfield Marine Science Centre for their hospitality. Several research assistants at BMSC provided invaluable help in the field. I am also indebted to J. Dalen, M. Rosenzweig and C. Whelan who carefully reviewed the manuscript.

REFERENCES

Burns, K.C. 2004. Scale and macroecological patterns in seed dispersal mutualisms. *Global Ecol. Biogeogr.*, **13**: 289–293.

Burns, K.C. and Dalen, J. 2002. Foliage color contrasts and adaptive fruit color variation in a bird-dispersed plant community. *Oikos*, **96**: 463–469.

Campbell, W.R., Dawe, N.K., McTaggert-Cowan, I., Cooper, J.M., Kaiser, G.W., McNall, M.C.E. *et al.* 1997. *The Birds of British Columbia*, Vol. 3. Vancouver, BC: University of British Columbia Press.

Cipollini, M.L. and Levey, D.J. 1997. Secondary metabolites of fleshy vertebrate-dispersed fruits: adaptive hypotheses and implications for seed dispersal. *Am. Nat.*, **150**: 346–372.

Foster, M. and Delay, L.S. 1998. Dispersal of mimetic seeds of three species of *Ormosia* (leguminosea). *J. Trop. Ecol.*, **14**: 389–411.

Galetti, M. 2002. Seed dispersal of mimetic fruits: parasitism, mutualism, aposematism, exaptation. In *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation* (D.J. Levey, W.R. Silva and M. Galetti, eds.), pp. 177–191. New York: CAB International.

Gervais, J.A. 1996. Geographic variation in fruit-color polymorphism of *Rubus spectabilis*. Masters thesis, Humboldt State University, Arcata.

Gervais, J.A., Noon, B.R. and Willson, M.F. 1999. Avian selection of the color-dimorphic fruits of salmonberry, *Rubus spectabilis*: a field experiment. *Oikos*, **84**: 77–86.

Gigord, L.D.B., MacNair, M.R. and Smithson, A. 2001. Negative frequency-dependent selection maintains a dramatic flower color polymorphism in the rewardless orchid *Dactylorhiza ambucina* (L.) Soo. *Proc. Nat. Acad. Sci. USA*, **98**: 6253–6255.

Groom, P.K., Lamont, B.B. and Duff, H.C. 1994. Self-crypsis in *Hakea trifurcate* as an avian granivore deterrent. *Funct. Ecol.*, **8**: 110–117.

Hatler, D.F., Campbell, R.W. and Dorest, A. 1978. *Birds of the Pacific Rim National Park*. Victoria, BC: British Columbia Provincial Museum.

Herrera, C.M. 2002a. Seed dispersal by vertebrates. In *Plant–Animal Interactions: An Evolutionary Approach* (C.M. Herrera and O. Pellmry, eds.), pp. 185–208. Oxford: Blackwell.

Herrera, C.M. 2002b. Correlated evolution of fruit and leaf size in bird dispersed plants: species-level variance in fruit traits explained a little further? *Oikos*, **97**: 426–432.

Hitchcock, C.L. and Cronquist, A. 1994. *Flora of the Pacific Northwest*. Seattle, WA: University of Washington Press.

Johnson, S.D., Peter, C.I., Nilsson, A. and Ågren, J. 2003. Pollination success in a deceptive orchid is enhanced by co-occurring rewarding magnet plants. *Ecology*, **84**: 2919–2927.

Joron, M. and Mallet, J.L.B. 1998. Diversity in mimicry: paradox or paradigm? *Trend. Ecol. Evol.*, **13**: 461–466.

Klinka, K., Krajina, V.J., Ceska, A. and Scagel, A.M. 1989. *Indicator Plants of Coastal British Columbia*. Vancouver, BC: University of British Columbia Press.

Lord, J. 2004. Frugivore gape size and the evolution of fruit size and shape in Southern Hemisphere floras. *Austral. Ecol.*, **29**: 430–436.

McKey, D. 1975. The ecology of coevolved seed dispersal mutualisms. In *Coevolution of Animals and Plants* (L.E.Gilbert and P.H. Raven, eds.), pp. 159–191. Austin, TX: University of Texas Press.

Peres, C.A. and van Roosmalen, M.G.M. 1996. Avian dispersal of ‘mimetic seeds’ of *Ormosia lignivalvis* by terrestrial granivores: deception or mutualism? *Oikos*, **75**: 249–258.

Roy, B.A. and Widmer, A. 1999. Floral mimicry: a fascinating yet poorly understood phenomenon. *Trend. Plant Sci.*, **4**: 325–330.

Schaefer, H.M., Schaefer, V. and Levey, D.J. 2004. How plant–animal interactions signal new insights in communication. *Trends Ecol. Evol.*, **19**: 577–584.

Schmidt, V., Schaefer, H.M. and Winkler, H. 2004. Conspicuousness, not colour, as a foraging cue in plant–animal signaling. *Oikos*, **106**: 551–557.

SPSS Inc. 2002. *Statistical Analysis Software*, version 11.05. Chicago, IL: Lead Technologies.

Tappeiner, J., Zasada, J., Ryan, P. and Newton, M. 1991. Salmonberry clonal and population structure: the basis for persistent cover. *Ecology*, **72**: 609–618.

Thompson, J.N. 1994. *The Coevolutionary Process*. Chicago, IL: University of Chicago Press.

Traveset, A. and Willson, M.F. 1998. Ecology of the fruit-color polymorphism in *Rubus spectabilis. Evol. Ecol.*, **12**: 331–345.

Van der Pijl, L. 1982. *Principles of Dispersal in Higher Plants*. New York: Springer.

Voigt, F.A., Bleher, B., Fietz, J., Ganzhorn, J.U., Schwab, D. and Böhning-Gaese, K. 2004. A comparison of morphological and chemical fruit traits between two sites with different frugivore assemblages. *Oecologia*, **141**: 94–104.

Webb, C.J. 1985. Fruit flags in a temperate evergreen shrub Corokia cotoneaster (Escalloniaceae). *NZ J. Bot.*, **23**: 343–344.

Whelan, C.J., Schmidt, K.A., Steele, B.B., Quinn, W.J. and Dilger, S. 1998. Are bird-consumed fruits complementary resources? *Oikos*, **83**: 195–205.

Willson, M.F. and Comet, T.A. 1993. Food choices by northwestern crows: experiments with captive, free-ranging and hand-raised birds. *Condor*, **95**: 596–615.

Willson, M.F. and Whelan, C.J. 1990. The evolution of fruit color in fleshy-fruited plants. *Am. Nat.*, **136**: 790–809.