

FRUIT LAXATIVES AND SEED PASSAGE RATES IN FRUGIVORES: CONSEQUENCES FOR PLANT REPRODUCTIVE SUCCESS¹

K. GREG MURRAY, SUSAN RUSSELL, CHRISTOPHER M. PICONE,²
KATHY WINNETT-MURRAY, WENDY SHERWOOD, AND
MARK L. KUHLMANN³
Department of Biology, Hope College, Holland, Michigan 49423 USA

Abstract. To explore how plants may influence dispersal of their own seeds by manipulating the behavior and physiology of their dispersers, we studied the effect of a soluble chemical (or chemicals) in the fruits of *Witheringia solanacea* (Solanaceae), a Costa Rican cloud forest shrub, on passage of its seeds through the guts of one of its major dispersers, the Black-faced Solitaire, *Myadestes melanops* (Muscicapidae: Turdinae). Using artificial fruits containing natural seeds, we found that the presence of a crude pulp extract reduced the median seed retention time by nearly 50%. Estimation of seed dispersal distance as a function of retention time suggested that more rapid seed passage results in shorter average dispersal distances, especially for seeds retained <20 min. At the same time, germination trials revealed that seeds voided rapidly were far more likely to germinate than those remaining longer in *Myadestes* guts. We propose that “laxative” chemical(s) in *Witheringia* fruits balance these positive and negative consequences of ingestion by *Myadestes*.

Key words: Costa Rica; frugivory; “laxative” chemicals; *Myadestes melanops*; seed dispersal; seed germination; *Witheringia solanacea*.

INTRODUCTION

Ever since McKey's (1975) influential paper on plant–frugivore coevolution, a recurrent theme in the study of seed dispersal mutualisms has concerned the degree to which plants can influence disperser behavior in order to maximize their own reproductive success. Most studies have concentrated on plant characteristics that serve to increase the likelihood of frugivore visitation or the rate at which they remove fruits (e.g., Howe and Estabrook 1977, Thompson and Willson 1979, Howe and Vande Kerckhove 1980, Stiles 1980, Herrera 1981, Sorensen 1981, 1983, 1984, Levey et al. 1984, Johnson et al. 1985, Murray 1987, Skeate 1987, Murray et al. 1993). Plant characteristics that influence reproductive success by manipulating disperser physiology have received much less attention. In many bird species large seeds are voided by regurgitation while smaller ones are defecated (Sorensen 1984, Johnson et al. 1985, Levey 1986, 1987, Murray et al. 1993). As a result, small seeds are retained longer in the gut and might travel farther from the parent plant, even though longer retention might reduce seed viability. A recent study by Levey and Grajal (1991) demonstrated the negative relationship between seed size and retention time in

Cedar Waxwings, even among seeds that are invariably defecated.

We report here the results of experiments that demonstrate the influence of a soluble fruit chemical (or chemicals) on seed passage rates of a Costa Rican cloud forest plant. We show that the “laxative” chemical(s), which reduce(s) seed retention times and thus lead(s) to more restricted seed shadows, may actually increase plant fitness by reducing mortality of seeds retained in the gut for long periods of time.

STUDY SITE AND METHODS

Data were collected from 12 June to 12 August 1990 and 11 June to 26 July 1991 in the Monteverde Cloud Forest Reserve, Provincia de Puntarenas, Costa Rica (10°18' N, 84°48' W). Most of the reserve, which straddles the continental divide and includes some 10 000 ha, consists of pristine Lower Montane Rain Forest (LMRF; Holdridge life zone classification system, Holdridge 1967) and Lower Montane Wet Forest (LMWF). Fruits and birds used in experiments reported here were collected in the transition zone between LMRF and LMWF, at ≈1450–1550 m. Thorough descriptions of the geography, climate, and forest types of the reserve are provided by Lawton and Dryer (1980).

The plant species used in this study, *Witheringia solanacea* (Solanaceae), is a common pioneer (i.e., gap dependent) shrub in forests from sea level to 2000 m (Standley 1937), and ranges from Mexico to Brazil (D'Arcy 1973). Previous studies at Monteverde by one of us (K. G. Murray) showed that the major disperser

¹ Manuscript received 1 February 1993; revised and accepted 31 August 1993; final version received 27 September 1993.

² Present address: Department of Biology, University of Michigan, Ann Arbor, Michigan 48109-1048 USA.

³ Present address: Department of Biological Sciences, Florida State University, Tallahassee, Florida 32306 USA.

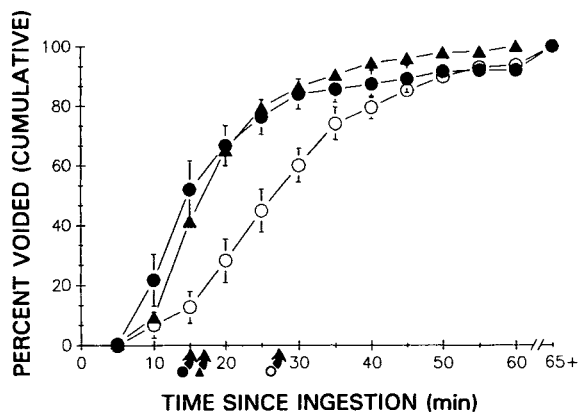


FIG. 1. Cumulative passage time distributions for *Witheringia solanacea* seeds in three fruit types: natural fruits (▲), artificial fruits with pulp extract (●), and artificial fruits without extract (○). Error bars indicate ± 1 SE. Arrows below the x axis represent median retention times. Total numbers of seeds were 1366, 232, and 336 for natural fruits, artificial fruits with pulp extract, and artificial fruits without extract, respectively. Data on natural fruits are from Murray (1988) and lack error bars because data were collected differently in that study.

of *W. solanacea* at Monteverde is the Black-faced Solitaire, *Myadestes melanops* (Muscicapidae: Turdinae); of all *W. solanacea* seeds recovered from frugivore feces in an intensive 2-yr study, nearly all came from *M. melanops* (Murray 1988).

Captive *M. melanops* were maintained in separate $0.5 \times 0.5 \times 0.5$ m cages during and between experiments, and were provided with food and water ad libitum at all times. Maintenance food consisted of natural fruits commonly eaten by *M. melanops* (primarily *Conostegia bernouliana* and *Gonzalagunia rosea*) and an "artificial" maintenance diet similar to that described by Denslow et al. (1987). All birds ate the diet readily and maintained approximately constant mass for the captive period. Most birds were held for 3–5 d, and all were released unharmed.

Seed passage rates.—Seed passage rates were determined as described by Murray (1988). After removing maintenance food from the cage, we presented each bird with 10 experimental fruits, either on a wire "inflorescence" or in a petri dish attached to the perch. Five minutes after the first fruit was consumed, all remaining fruits were removed, and the maintenance food was replaced in the dish. The midpoint of the 5-min consumption interval was then considered as the time of ingestion for all experimental fruits. At 5-min intervals thereafter a single sheet of newspaper was removed from the cage floor, and all defecated seeds were recovered and counted.

Chemical control of seed passage rate.—To determine whether fruit chemicals affect seed passage rates, we constructed artificial "fruits" from a solution of 2.0 g agar, 7.5 g glucose, 7.5 g fructose, 100 mL boiling water, and 45 drops of red food coloring. The hot mix-

ture was injected into a spherical mold (7.75 mm diameter) containing 10 *Witheringia solanacea* seeds. Half of the artificial fruits so produced were soaked in a small amount of crude extract from *W. solanacea* fruits (prepared by simply crushing natural fruits and discarding the seeds, pulp, and fruit skins) overnight before retention time experiments. Thus we obtained two types of artificial fruit identical in all respects save one: the presence/absence of soluble chemicals from *W. solanacea* pulp. With each of six *M. melanops*, we performed two trials with each fruit type.

Germination success and rate vs. passage rate.—To determine how the length of gut treatment affects germination success (defined as the proportion of seeds germinating), we conducted retention time experiments similar to those described above with natural fruits in five *M. melanops*. Seeds emerging in each 5-min interval were then planted in shallow trays of soil in a large clearing. Germination success of control seeds (20–40 seeds carefully removed by hand from fruits of each of the 14 plants used as fruit/seed sources above) was measured in the same way. To prevent additional seed input and disturbance by direct rainfall, trays were protected by a plastic canopy. Seeds were checked approximately every other day and watered when necessary for at least 60 d after planting. We scored seeds as germinated when the root had penetrated the soil and the cotyledons had fully emerged from the seed coat. Although this is more properly called "establishment" than germination, we use the latter term throughout this paper.

RESULTS

Seed passage rates

Birds consumed 1–8 (median 2.8; $n = 48$) fruits during the 5-min ingestion period, invariably swallowing them whole. In all cases, the first seeds emerged within 10 min of ingestion, and $\approx 90\%$ had emerged by 45 min. The resulting retention time distributions (Fig. 1) show that seed passage rates from artificial fruits with pulp extract were very similar to those from natural fruits. In contrast, seeds from artificial fruits without pulp extract were passed significantly more slowly (median passage time ≈ 27 min) than those with extract (≈ 15 min) (Kolmogorov–Smirnov $D = 0.2429$, $P < .001$). The presence of some (as yet undetermined) soluble chemical(s) in *W. solanacea* apparently increases seed passage rates in *M. melanops*, perhaps by increasing gut motility.

To verify that the difference in seed passage rate between artificial fruits with and without pulp extract was consistent among individual birds, we compared mean seed retention times between treatments with a two-way ANOVA. Data used in the analysis were the two median retention time determinations per bird per treatment. The effect of the extract was highly significant (Table 1, effect TREATMENT), and although

TABLE 1. Results of two-way ANOVA on mean retention times of *Witheringia solanacea* seeds from agar fruits with and without pulp extract. Since TREATMENT is a fixed effect, its MS is tested over the interaction (BIRD \times TREATMENT) MS rather than over the ERROR MS (See Sokal and Rohlf 1981: 339–340).

Source	SS	df	MS	F	P
TREATMENT	467.65	1	467.65	15.80	<.02
BIRD	613.09	5	122.617	3.80	<.05
BIRD \times TREATMENT	147.95	5	29.59	0.92	>.5
Error	387.17	12	32.27
Total	1615.86	23

some individuals passed seeds more rapidly than others overall (effect BIRD), the extract produced similar effects in all individuals (no significant BIRD \times TREATMENT interaction).

Consequences of seed passage rate for germination success and dispersal distance

Germination success of *W. solanacea* seeds was strongly affected by gut passage. On the one hand, proportional germination was higher among seeds passed through Black-faced Solitaire guts (62.8%; all retention times combined) than among those removed from fruits by hand (51.7%; $\chi^2 = 12.8$, $P < .001$). On the other hand, among gut-treated seeds germination success decreased monotonically with increased time spent in the gut (Fig. 2), even though all seeds, regardless of retention time, appeared intact. Thus, short periods of treatment in Black-faced Solitaire guts are advantageous, but this advantage diminishes rapidly with longer retention times. This effect was similar, but not identical, among birds: regression lines fit separately for each of the five birds were parallel, but had different y intercepts (Table 2).

To determine the relationship between retention time and seed dispersal distance, we used a method devised by Murray (1988:297–298) that combines retention time distributions like those in Fig. 1 with data on bird movement patterns. Here, we estimated the median dispersal distance for seeds retained for 5, 10, 15, . . . , 60 min, using 96.2 h of movement data obtained previously for four *M. melanops* individuals (Murray 1988). Fig. 3 shows that predicted median dispersal distance increases dramatically with increasing retention time up to ≈ 30 min, but only slightly thereafter. The asymptotic increase results from the fact that Black-faced Solitaires restrict their foraging to reasonably well-defined home ranges.

DISCUSSION

Effects of gut treatment on germination success

Numerous studies document enhanced germination success of seeds that pass through the guts of birds (e.g., Noble 1975, Temple 1977, Noble and Whalley 1978, Glyphis et al. 1981, Holthuijzen and Sharik 1985, Barnea et al. 1990, 1991, Izhaki and Safriel 1990) as well as mammals (e.g., Lamprey et al. 1974, Applegate et

al. 1979, Lieberman et al. 1979, Fleming and Heithaus 1981, Estrada and Coates-Estrada 1986, Utzurrum and Heideman 1991) compared with those removed from fruits by hand. Such enhancement is far from universal however; many of the studies cited above, as well as others (e.g., Howe and Vande Kerckhove 1981, Lieberman and Lieberman 1986), failed to show any positive effects of gut treatment in some of the fruit–frugivore pairs tested.

Results of the present study suggest that simple comparisons of germination success in seeds ingested by frugivores with those not ingested obscure an important aspect of the plant–frugivore interaction. Although germination success of seeds passed rapidly through *Myadestes* guts was higher than that of those removed from fruits by hand, viability of those retained longer decreased markedly with increasing passage time (Fig.

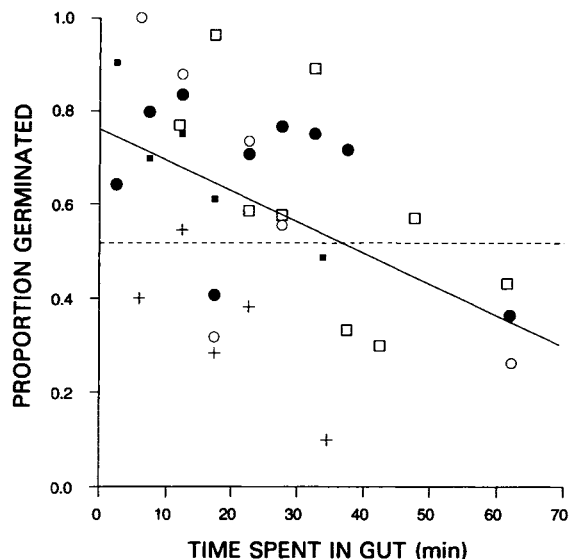


FIG. 2. Germination success of *W. solanacea* seeds vs. retention time in five *Myadestes melanops* guts. Each point represents the proportion of seeds (retained by one individual for a particular time) that eventually germinated. \square represents bird 1, \blacksquare bird 2, \circ bird 3, \bullet bird 4, and $+$ bird 5. Total number of seeds processed was 1355 and ranged from 149 to 508 per bird. The regression equation for all birds combined is $y = 0.007x + 0.76$. F and P values are 10.1 with $df = 1, 32$ and $P < .005$, respectively. The dashed horizontal line represents germination success of seeds removed from fruits by hand, hence not treated in Black-faced Solitaire guts.

TABLE 2. Two ANCOVA tests for the effects of treatment in different birds' guts on germination success (data in Fig. 2). (A) Test for homogeneity of slopes (Sokal and Rohlf 1981) among the regressions fitted separately for each of five birds. (B) Test for equivalence of γ intercepts among individual regressions. Germination success was arcsine transformed for all analyses.

Source	SS	df	MS	F	P
A) AMONG REGRESSIONS	428.20	4	107.05	0.80	>.5
Error	3212.70	24	133.86
B) AMONG INTERCEPTS	2307.08	4	576.77	4.44	<.007
Error	3640.90	28	130.03

2). Both effects may result from chemical and/or mechanical abrasion of the seed coat in the gut (cf. Barnea et al. 1990). Mild abrasion may facilitate water imbibition or perception of germination cues (probably light, cf. Vazquez-Yanes 1977, 1980, Vazquez-Yanes and Smith 1982, Vazquez-Yanes and Orozco-Segovia 1984). As retention time increases, however, abrasion may be sufficient to damage seeds, perhaps by causing premature germination. All else being equal, we might expect selection for fruit characteristics that result in more rapid seed passage.

Effects of gut treatment on dispersal distance

Despite the advantage of rapid seed passage acting through seed viability, rapid passage also appears to have negative consequences for plant reproductive success. Seeds voided quickly are deposited nearer the parent plant (Fig. 3), and such reduced dispersal distance is likely to lower reproductive success in at least three ways. First, seeds deposited near their source may suffer from direct competition with the parent plant. Second, since the density of dispersed seeds is a function of dispersal distance, and since many seed and seedling predators forage in a density-dependent manner, seeds voided near the parent may suffer increased predation risk (Howe and Primack 1975, Janzen et al. 1976, Platt 1976, Salmonson 1978, Clark and Clark 1981, Augspurger 1983a, b, 1984a, b, Howe et al. 1985). Third, for pioneer species like *W. solanacea*, repro-

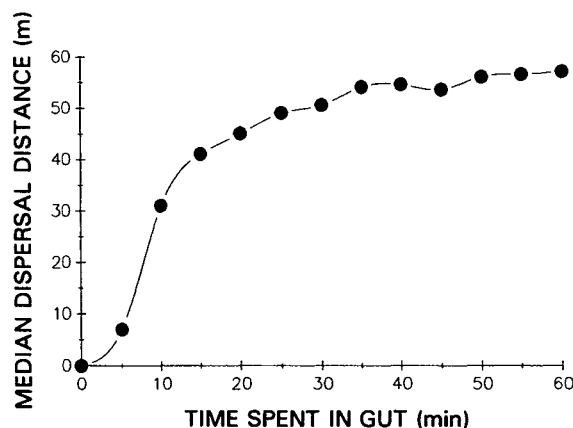


FIG. 3. Median seed dispersal distance as a function of time spent in *Myadestes melanops* guts.

ductive success depends strongly on dispersal distance, since seeds deposited nearer their parents are less likely to encounter recently opened gaps (Murray 1988). Especially in pioneers then, we might expect selection to favor not faster, but slower seed passage. Despite the advantages of greater dispersal distance, however, very long seed retention times are unlikely to result in ever-increasing dispersal distances. As Fig. 3 shows, median dispersal distance increases little for seeds retained longer than 30 min, because Black-faced Solitaires forage on well-defined home ranges.

Effects of fruit "laxatives"

To our knowledge, this is the first study to demonstrate the existence of a soluble fruit chemical (or chemicals) that mediates seed passage rate: seeds from artificial fruits that also included a crude extract from *W. solanacea* pulp were voided much more rapidly than seeds from fruits without the extract (Fig. 1). The implication of a laxative chemical is strengthened by the fact that the retention curve for artificial fruits treated with pulp extract is almost indistinguishable from that for natural fruits.

It is tempting to propose that fruit chemicals that increase seed passage rates have evolved in response to conflicting selection pressures imposed by the seed viability vs. dispersal distance trade-off suggested above. However, since we lack detailed knowledge of the precise nature of the trade-offs between fitness components associated with germination success and dispersal distance, such an adaptive explanation for the existence of a laxative chemical must remain speculative.

Laxative chemicals may have other effects as well. If fruit laxatives increase the frequency of defecation, for example, seeds from a given fruit might be deposited in a greater number of fecal clumps (cf. Putz 1993). Presumably, both predation and competition would be reduced for seeds in smaller clumps. Although we did not collect data on seed number per individual defecation in this study, our results suggest that the laxative in *Witheringia* pulp may actually decrease the number of sites at which seeds from a given fruit are deposited: the variance in percentage of seeds emerging in each 5-min time interval was actually higher for seeds from fruits with pulp extract (86.9) than for those from fruits without it (32.7). At least in *Witheringia* then, laxative

chemicals are more likely to decrease, rather than increase, reproductive success via effects on seed clump size.

Laxative chemicals might indirectly affect fruit preferences as well. Recent studies with artificial fruits show that rapid seed passage makes possible higher fruit consumption rates in Cedar Waxwings (*Bombycilla cedrorum*; Levey and Grajal 1991) and American Robins (*Turdus migratorius*; Murray et al. 1993) and that many birds form strong preferences for fruits whose seeds are passed most rapidly. Working with natural fruits, Sorensen (1984) also found that feeding preferences of European Blackbirds (*Turdus merula*) were correlated with seed passage rates. Presumably, the effects of a laxative chemical would even extend to other fruits present in the gut at the same time. Birds might thus derive benefits from fruits like *W. solanacea* that are entirely unrelated to the nutrient content of the fruits themselves. By consuming small numbers of *W. solanacea* fruits, birds may be able to increase the rate at which they can consume and process all fruits. On the other hand, more rapid passage of gut contents may be at the expense of complete extraction of nutrients from the fruit pulp. Indeed, frugivores in general are notorious for intrinsically rapid processing rates, and Karasov and Levey (1990) explain these as a strategy to increase the net rate of energy gain from nutrient-poor foods by process-limited animals. Future work with *W. solanacea* and other species should focus on identifying the chemicals responsible for rapid seed passage as well as exploring their consequences for feeding efficiency in birds on mixed-fruit diets.

Consequences of intraspecific variation in gut treatment effects

Individual *Myadestes* used in this study varied significantly in both seed passage rates (Table 1) and treatment effects on seed viability (Fig. 2, Table 2). Such variation has important general implications for studies of plant-frugivore interactions. Obviously, if we hope to detect and interpret differences in the fitness consequences to plants of ingestion by different species of dispersers, we must first understand the extent and nature of variation in treatment effects within species. Some studies have based comparisons of treatment effects on fewer than four individuals of some bird species (e.g., Levey 1986, Murray 1988, Izhaki and Safriel 1990). Izhaki and Safriel (1990), for example, suggest that the differential effects of ingestion by different bird species on germination rate serve to spread the risk associated with synchronous germination. If significant variation exists within bird species, however, we might overestimate the fitness advantages of a broad disperser coterie relative to those of a single disperser species. Future studies should include adequate replication in order to accurately represent the variation within disperser species as well as allow meaningful comparisons among different ones.

ACKNOWLEDGMENTS

Personnel of the Tropical Science Center (especially W. Aspinall, G. Bello, and J. Tosi) kindly facilitated our use of the Monteverde Cloud Forest Reserve. D. Levey and C. Martinez del Rio provided invaluable criticism of an earlier version of the manuscript, and R. Boyce, B. Keas, S. Kulp, T. Long, E. Lundquist, and R. Ostertag assisted with field work. The authors were supported by NSF grants BSR-9006734 and BSR-9146650 and an American Philosophical Society grant-in-aid to K. G. Murray and NSF REU grants (BBS-8712566, BBS-8804082, DIR-9000984, and BBS-9100398) to Hope College.

LITERATURE CITED

- Applegate, R. D., L. L. Rogers, D. A. Castell, and J. M. Novak. 1979. Germination of cow parsnip from grizzly bear feces. *Journal of Mammalogy* 60:655.
- Augspurger, C. K. 1983a. Offspring recruitment around tropical trees: changes in cohort distance with time. *Oikos* 40:189-196.
- . 1983b. Seed dispersal by the tropical tree, *Platypodium elegans*, and escape of its seedlings from fungal pathogens. *Journal of Ecology* 71:759-771.
- . 1984a. Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. *Oecologia* 61:211-217.
- . 1984b. Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. *Ecology* 65:1705-1712.
- Barnea, A., Y. Yom-Tov, and J. Friedman. 1990. Differential germination of two closely related species of *Solanum* in response to bird ingestion. *Oikos* 57:222-228.
- Barnea, A., Y. Yom-Tov, and J. Friedman. 1991. Does ingestion by birds affect seed germination? *Functional Ecology* 5:394-402.
- Clark, D. A., and D. B. Clark. 1981. Effects of seed dispersal by animals on the regeneration of *Bursera graveolens* (Burseraceae) on Santa Fe Island, Galapagos. *Oecologia* 49:73-75.
- D'Arcy, W. G. 1973. Solanaceae. In R. E. Woodson, Jr. and R. W. Schery, editors. *Flora of Panama*. *Annals of the Missouri Botanical Garden* 60:573-780.
- Denslow, J. S., D. J. Levey, T. C. Moermond, and B. C. Wentworth. 1987. A synthetic diet for fruit-eating birds. *Wilson Bulletin* 99:131-134.
- Estrada, A., and R. Coates-Estrada. 1986. Frugivory by howling monkeys (*Alouatta palliata*) at Los Tuxtlas, Mexico: dispersal and fate of seeds. Pages 93-104 in A. Estrada and T. H. Fleming, editors. *Frugivores and seed dispersal*. W. Junk, Dordrecht, The Netherlands.
- Fleming, T. H., and E. R. Heithaus. 1981. Frugivorous bats, seed shadows, and the structure of tropical forests. *Biotropica* 13 (supplement):45-53.
- Glyphis, J. P., S. J. Milton, and W. R. Siegfried. 1981. Dispersal of *Acacia cyclops* by birds. *Oecologia* 48:138-141.
- Herrera, C. M. 1981. Fruit variation and competition for dispersers in natural populations of *Smilax aspera*. *Oikos* 36:51-58.
- Holdridge, L. 1967. Life zone ecology. Tropical Science Center, San Jose, Costa Rica.
- Holthuijzen, A. M. A., and T. L. Sharik. 1985. The avian seed dispersal system of eastern red cedar (*Juniperus virginiana*). *Canadian Journal of Botany* 63:1508-1515.
- Howe, H. F., and G. F. Estabrook. 1977. On intraspecific competition for avian dispersers in tropical trees. *American Naturalist* 111:817-832.
- Howe, H. F., and R. B. Primack. 1975. Differential seed dispersal by birds of the tree *Casearia nitida* (Flacourtiaceae). *Biotropica* 7:278-283.

- Howe, H. F., E. W. Schupp, and L. C. Westley. 1985. Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). *Ecology* **66**:781-791.
- Howe, H. F., and G. A. Vande Kerckhove. 1980. Nutmeg dispersal by tropical birds. *Science* **210**:925-927.
- Howe, H. F., and G. A. Vande Kerckhove. 1981. Removal of wild nutmeg (*Virola surinamensis*) crops by birds. *Ecology* **62**:1093-1106.
- Izhaki, I., and U. N. Safriel. 1990. The effect of some mediterranean scrubland frugivores upon germination patterns. *Journal of Ecology* **78**:56-65.
- Janzen, D. H., G. A. Miller, J. Hackforth-Jones, C. M. Pond, D. Hooper, and D. P. Janos. 1976. Two Costa Rican bat generated seed shadows of *Andira inermis* (Leguminosae). *Ecology* **56**:1068-1075.
- Johnson, R. A., M. F. Willson, J. N. Thompson, and R. I. Bertin. 1985. Nutritional values of wild fruits and consumption by migrant frugivorous birds. *Ecology* **66**:819-827.
- Karasov, W. H., and D. J. Levey. 1990. Digestive system trade-offs and adaptations of frugivorous passerine birds. *Physiological Zoology* **63**:1248-1270.
- Krebs, C. J. 1989. *Ecological methodology*. Harper & Row, New York, New York, USA.
- Lamprey, H. F., G. Halevy, and S. Makacha. 1974. Interactions between *Acacia*, bruchid seed beetles and large herbivores. *East African Wildlife Journal* **12**:81-85.
- Lawton, R., and V. Dryer. 1980. The vegetation of the Monteverde cloud forest reserve. *Brenesia* **18**:101-116.
- Levey, D. J. 1986. Methods of seed processing by birds and seed deposition patterns. Pages 147-158 in A. Estrada and T. H. Fleming, editors. *Frugivory and seed dispersal*. W. Junk, Dordrecht, The Netherlands.
- . 1987. Seed size and fruit-handling techniques of avian frugivores. *American Naturalist* **129**:471-485.
- Levey, D. J., and A. Grajal. 1991. Evolutionary implications of fruit processing limitations in Cedar Waxwings. *American Naturalist* **138**:171-189.
- Levey, D. J., T. C. Moermond, and J. S. Denslow. 1984. Fruit choice in neotropical birds: the effect of distance between fruits on preference patterns. *Ecology* **65**:844-850.
- Lieberman, D., J. B. Hall, M. D. Swaine, and M. Lieberman. 1979. Seed dispersal by baboons in the Shai Hills, Ghana. *Ecology* **60**:65-75.
- Lieberman, M., and D. Lieberman. 1986. An experimental study of seed ingestion and germination in a plant-animal assemblage in Ghana. *Journal of Tropical Ecology* **2**:113-126.
- McKey, D. 1975. The ecology of coevolved seed dispersal systems. Pages 159-191 in L. E. Gilbert and P. H. Raven, editors. *Coevolution of animals and plants*. University of Texas Press, Austin, Texas, USA.
- Murray, K. G. 1986. Consequences of seed dispersal for gap-dependent plants: relationships between seed shadows, germination requirements, and forest dynamic processes. Pages 187-198 in A. Estrada and T. H. Fleming, editors. *Frugivores and seed dispersal*. W. Junk, Dordrecht, The Netherlands.
- . 1987. Selection for optimal fruit crop size in bird-dispersed plants. *American Naturalist* **129**:18-31.
- . 1988. Avian seed dispersal of three neotropical gap-dependent plants. *Ecological Monographs* **58**:271-298.
- Murray, K. G., K. Winnett-Murray, E. A. Cromie, M. Minor, and E. Meyers. *In press*. The influence of seed packaging and fruit color on feeding preferences of American Robins. *Vegetatio*.
- Noble, J. C. 1975. The effects of emus (*Dromaius novaehollandiae* Latham) on the distribution of the nitre bush (*Nitraria billardieri* DC.). *Journal of Ecology* **63**:979-984.
- Noble, J. C., and R. D. B. Whalley. 1978. The biology and autecology of *Nitraria* L. in Australia. II. Seed germination, seedling establishment and response to salinity. *Australian Journal of Ecology* **3**:165-177.
- Platt, W. J. 1976. The natural history of a fugitive prairie plant (*Mirabilis hirsuta* (Pursh) MacM.). *Oecologia* **22**:399-409.
- Putz, F. E. 1993. On diarrhea. *Bulletin of the Ecological Society of America* **74**:177.
- Salmonson, M. G. 1978. Adaptations for animal dispersal of one-seeded juniper seeds. *Oecologia* **32**:333-339.
- Skeate, S. T. 1987. Interactions between birds and fruits in a northern Florida hammock community. *Ecology* **68**:297-309.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. Second edition. W. H. Freeman, New York, New York, USA.
- Sorensen, A. E. 1981. Interactions between birds and fruit in a temperate woodland. *Oecologia* **50**:242-249.
- . 1983. Taste aversion and frugivore preference. *Oecologia* **56**:117-120.
- . 1984. Nutrition, energy and passage time: experiments with fruit preference in European blackbirds (*Turdus merula*). *Journal of Animal Ecology* **53**:545-557.
- Standley, P. C. 1937. *Flora of Costa Rica*. Publications of the Field Museum of Natural History, Botanical series **18**.
- Stiles, E. W. 1980. Patterns of fruit presentation and seed dispersal in bird-disseminated woody plants in the eastern deciduous forest. *American Naturalist* **116**:670-688.
- Temple, S. A. 1977. Plant-animal mutualism: coevolution with dodo leads to near extinction of plant. *Science* **197**:885-886.
- Thompson, J. N., and M. F. Willson. 1979. Evolution of temperate fruit/bird interactions: phenological strategies. *Evolution* **33**:973-982.
- Utzurum, R. C. B., and P. D. Heideman. 1991. Differential ingestion of viable vs. nonviable *Ficus* seeds by fruit bats. *Biotropica* **23**:311-312.
- Vazquez-Yanes, C. 1977. Germination of a pioneer tree (*Trema guineensis* Fieahlo), from equatorial Africa. *Turrialba* **23**:301-302.
- . 1980. Light quality and seed germination in *Cecropia obtusifolia* and *Piper auritum* from tropical rain forest in Mexico. *Phyton* **38**:33-35.
- Vazquez-Yanes, C., and A. Orozco-Segovia. 1984. Ecophysiology of seed germination in the tropical humid forests of the world: a review. Pages 37-50 in E. Medina, H. A. Mooney, and C. Vazquez-Yanes, editors. *Physiological ecology of plants in the wet tropics*. W. Junk, Dordrecht, The Netherlands.
- Vazquez-Yanes, C., and H. Smith. 1982. Phytochrome control of seed germination in the tropical rain forest pioneer trees *Cecropia obtusifolia* and *Piper auritum* and its ecological significance. *New Phytologist* **92**:477-485.