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Retention Time of Seeds in Bird Guts: Costs and Benefits for Fruiting Plants and Frugivorous Birds

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Abstract **Fruiting plants and frugivorous birds are known to interact. In endozoochory, frugivorous birds consume fruits and subsequently disperse seeds. It follows that fruit characteristics would have evolved to allow birds to consume fruits easily. However, one's benefit does not always mean the other's. There are several conflicts between fruiting plants and frugivorous birds in terms of nutrient content, retention time and number of seeds in a fecal pellet. Retention time of seeds in guts is particularly interesting. Longer retention time benefits plants directly by increasing seed dispersal distance but may involve indirect costs through birds' preference by reducing their consumption. To understand the exact role of seed dispersers in the reproductive success of fruiting plants, we should pay more attention to the possible conflicts between fruiting plants and frugivorous birds.**

Key words: **retention time, frugivorous birds, seed dispersal, plant-animal interaction.**

Fruiting plants and frugivorous animals interact through endozoochory, and provide an example of "diffuse coevolution" (Jordano, 1987). The key aspect of endozoochory is that seeds must enter animals' guts. Ingestion of indigestible seeds is a cost for frugivores because they can only digest the fleshy parts of fruits. On the other hand, production of the fleshy parts of fruits is a cost for plants. Thus, animals' benefits do not always coincide with plants' benefits. Little research attention has been paid to such conflicts between fruiting plants and frugivores in comparison with their mutualistic aspects (Howe and Smallwood, 1982). In this paper, from the perspective of costs and benefits for plants and animals, I discuss the way retention time of seeds in guts influences seed dispersal.

1. *Advantages and Disadvantages of Fruits as a Food*

Fruit is an important food for animals. Many species of birds, monkeys, and even carnivorous mammals consume fruits and disperse their seeds (Howe and Smallwood, 1982). Among them, frugivorous birds have been well studied as efficient seed dispersal agents (Snow and Snow, 1988). Approximately one-third of bird species in temperate and tropical communities consume fruits (Herrera, 1982; Willson, 1986; Wheelwright and Janson, 1985). Plants have evolved special features of fruits for attracting dispersal animals (Gautier-Hiron et al., 1985; Willson and Whelean, 1990; Willson, 1991; Jordano, 1995). For instance, fruits with seeds dispersed by mammals (olfactory animals) have a strong odor but dull color, whereas those consumed by birds (visual animals) have vivid color but little odor. Among bird-dispersed fruits, nutritional characteristics differ between summer and winter fruits coinciding with seasonal differences in nutrient requirements of birds (Herrera, 1982).

Such characteristics of fruits are advantageous for frugivores. At the same time, however, most wild fruits contain a large proportion of indigestible seeds (Herrera, 1987). This indigestible material puts a load on frugivore digestive systems (Sorensen, 1984; Levey and Grajal, 1991). Thus, fruits have both advantageous and disadvantageous features as a food.

2. *How Do Birds Manage the Disadvantages of Fruits as a Food?*

Food retention in guts prevents animals from consuming additional food until the guts have been emptied (Westby, 1974; Sorensen, 1984; Karasov et al., 1986). This is called "gut limitation," and it frequently occurs in animals with a high-bulk diet. Gut limitation is also known in frugivorous birds (Sorensen, 1984; Karasov et al., 1986; Levey, 1987; Levey and Grajal, 1991). In experiments using captive brown-eared bulbuls, the number of fruits eaten in a foraging bout was negatively correlated with the size of fruit and seed: the birds ate more than 20 fruits of *Callicarpa dichotoma* (fruit 3.5 mm and seed 1.9 mm in length), about 10 intermediate-sized fruits (fruit, 5.0–11.0 mm; seed, 1.8–6.5 mm), five of *Dahnipyllum macropodum* (fruit, 12.0 mm; seed, 9.3 mm), and only one of *Aucuba japonica* (fruit, 16.5 mm; seed, 16.1 mm) (Fukui, unpubl.). This observation strongly suggests that gut limitation may control the foraging behavior of bulbuls.

There are two ways to overcome gut limitation. One is enlargement of the gut volume, as is seen in large herbivorous mammals (Westby, 1974). This solution cannot be used by most frugivorous birds because body weight is sharply restricted in flying birds.

The other way is rapid food processing. In this context, there are two types of frugivorous birds. One type are mashers, like tanagers and finches. They crush fruits, separate pulp from seeds with their bills, and ingest only the pulp. Thus, they solve the problem of gut limitation without ingesting seeds but have a higher cost in handling time while foraging. The other type are gulpers like manakins, bulbuls, waxwings, or thrushes. They swallow whole fruits, and separate pulp from seeds in their guts. Therefore, they must offset the gut limitation by rapid voiding of seeds (Levey and Grajal, 1991; Levey and Duke, 1992; Countney and Sallabank, 1992; Murray et al., 1994). Since mashers usually drop seeds under the parent tree, they are considered to be poor seed dispersers. Hereinafter I will discuss only gulpers.

3. *Retention Time of Seeds in Guts*

Retention time is defined as the time from the eating of a fruit to the depositing of its seed(s). Table 1 summarizes the literature to date on the retention times of seeds in birds. The retention times are shorter than 60 minutes in most cases. Four factors are known to determine the retention time: seed size, bird body size, degree of specialization in frugivory, and chemical compounds in pulp.

There is a negative correlation between seed size and retention time (Johnson et al., 1985, Sorensen, 1984; Levey, 1987; Levey and Grajal, 1991). Large seeds are more frequently regurgitated than small ones (Sorensen, 1984; Johnson et al., 1985; Levey, 1987; Murray et al., 1994). Such seeds do not pass through the whole length of the gut and are voided rapidly (Johnson et al., 1985). However, the negative correlation between seed size and retention time was also observed in brown-eared bulbuls that regurgitated hardly any seeds (Fukui unpubl.). It is suggested that large seeds are separated from pulp more quickly in the gizzard and pass more quickly through the digestive tract than small seeds (Levey and Duke, 1992).

Retention time tends to be shorter in small birds than in large ones (Johnson et al., 1985), because small birds regurgitate seeds more frequently (Sorensen, 1984; Johnson et al., 1985; Levey, 1987; Jevey and Grajal 1991).

Birds highly specialized in frugivory—e.g., mistletoebirds and waxwings—can void seeds more quickly than unspecialized frugivores like honeyeaters, American robins, and European starlings (Murphy et al., 1993; Levey and Karasov, 1994). It has been suggested that frugivorous birds have evolved the ability to process seeds rapidly (Levey and Karasov, 1990). Rapid voiding of seeds is an important adaptation to escape gut limitation because it allows an increased consumption rate (Murray et al., 1994). This is supported by the evidence for physical changes in a frugivore's gut; the guts of American robins, for example, change physiologically with a switch of diet between insects and fruits (Wheelwright, 1988).

Murray et al. (1994) reported that soluble chemicals involved in the pulp of *Witheringoa solanacea* (Solanaceae) played an important role in determining the retention time of its seeds in the gut of *Myadestes melarops* (Muscicapidae: Turdinae). They made artificial fruits by coating seeds with agar and measured the retention times while changing the ingredients mixed into the agar. The retention time was shorter when the agar coat included the pulp extract than when it was pure. This result clearly shows that the presence of some soluble chemicals in the pulp of *Witheringoa solanacea* speeds the passage of its seeds through the gut of *Myadestes melarops*. To my knowledge, this is a pioneering study demonstrating the effect of fruit chemicals on retention time. Increasing attention to such fruit chemicals in the future may uncover other cases, identify the relevant chemicals, and reveal their roles and mechanisms.

Although our knowledge is still limited, fruit characteristics undoubtedly play an important role in determining retention time. In the following sections, I will discuss how retention time affects seed dispersal in relation to fruit removal rate, germination success, seed dispersal distance, and density-dependent mortality.

4. *Fruit Removal Rate*

In most studies on endozoochory, the amount of dispersed seeds has been equaled to the amount of removed fruits. Optimal foraging theory predicts that birds select food items to maximize the energy gain relative to handling cost. Frugivores' preferences are influenced by not only factors that increase the energy gain but also factors that decrease these costs (Howe and Estabrook, 1977; Herrera, 1982; Moermond and Denslow, 1983; Sorensen, 1984). Foraging costs include searching time, handling time, and digestion time (Sorensen, 1981, 1984; Levey, 1987; Hedge et al., 1991; Levey and Grajal, 1991; Courtney and Sallabanks, 1992; Levey and Duke, 1992). In particular, Courtney and Sallabanks (1992) emphasized that retention time should be incorporated into digestion cost. As for the searching and handling costs, some characteristics of fruits—e.g., color or size—help birds in decreasing these costs. A decrease in searching and handling costs, in turn, enhances the consumption rate of fruits. In this context, the animal's benefit is congruent with the plant's.

Sorensen (1984) indicated that fruit preferences were affected by retention times. Levey and Grajal

Table 1. Retention times of seeds in birds' guts.

Frugivorous birds (body weight)	Fruit (fruit diameter, seed diameter, No. seeds/fruit)	Retention time (in minutes)	Reference
Turdus merula blackbirds	*Sambus nigra* (0.14mm, 0.07mm, 2.7)	25.5(f/D), 33.8(l/D)	Sorensen (1984)
	Rubus fructicosa (1.1mm, 0.70mm, 19)	39.1(f/D), 50.4(l/D)	
	Cratagus monoggna (0.3mm, 0.13mm, 1)	8.6(f/R)	
	Prunus spinosa (1.4mm, 0.65mm, 1)	7.8(f/R)	
	Rosa canina (0.9mm, 0.43mm, 8.6)	29.2(f/D), 37.0(l/D)	
	Hedaera helix (0.3mm, 0.13mm, 3.3)	6.5(f/R), 8.9(l/R)	
Catharus gullata Hemit thrushes	16 species of fruits (0.028–0.76g,-,0.025–0.218g, 1–35.9)	30–31(D)	Johnson et al. (1985)
	16 species of fruits (0.028–0.76g,-,0.025–0.218g, 1–35.9)	10–11(R)	
Turdus migratoris American robin (77g)	16 species of fruits (0.028–0.76g,-,0.025–0.218g, 1–35.9)	30 (D)	Johnson et al. (1985)
	16 species of fruits (0.028–0.76g,-,0.025–0.218g, 1–35.9)	19 (R)	
Bombycilla cedrorum Cedar waxwing	*Amerancher arborea*	30,31(f), 129,122(l)	Robinson (1986)
Pipra mentalis Manakin (15g)	seven species of fruits (4.06–11.64mm,-, 1–300)	17.0(mo), 12.5(f) mean of 9 bird species	Levey (1986)
Manacus candei Manakin (34g)	seven species of fruits (4.06–11.64mm,-, 1–300)		Levey (1986)
Arremon aurantirostris Emberized finches (34g)	seven species of fruits (4.06–11.64mm,-, 1–300)		Levey (1986)
Caryothraustes poliogaster Emberized finches (35g)	seven species of fruits (4.06–11.64mm,-, 1–300)		Levey (1986)
Euphonia gouldi Tanager (12g)	seven species of fruits (4.06–11.64mm,-, 1–300)		Levey (1986)
Tachphous delatrii Tanager (20g)	seven species of fruits (4.06–11.64mm,-, 1–300)		Levey (1986)
Ramphocelus passerinii Tanager (30g)	seven species of fruits (4.06–11.64mm,-, 1–300)		Levey (1986)
Thraupis palmarum Tanager (39g)	seven species of fruits (4.06–11.64mm,-, 1–300)		Levey (1986)
Mitrospingus cassinii Tanager (42g)	seven species of fruits (4.06–11.64mm,-, 1–300)		Levey (1986)
Bulbul *Pycnonotus xanthopygos*	*Asparagus aphyllus*	20.0(D)	Barena et al. (1991)
	Ephedra campylopod	12.0(D)	
	Mornus nigra	16.4(D)	
	Myrtus communis	27.3(D)	
	Rhamnus alaterus	17.1(D)	
	Rhamnus palaestinus	32.8(D)	
	Rubia tenuifolia	16.5(D)	
	Rubia sanctus	13.5(D)	
	Smilax aspera	21.0(D)	
Bulbul *Pycnonotus xanthopygos*	*Tamus communis*	8.7(D)	
	Viscum cruciatum	20.8(D)	
blackbirds *Turdus merula*	*Arum hygrophium*	30.7(f/R)	Barena et al. (1991)
	Asparagus aphyllus	13.0(f/D,R)	
	Ephedra campylopod	16.5(f/D,R)	
	Mornus nigra	44.4(f/D)	
	Myrtus communis	30.9(f/D,R)	
	Rhamnus alaterus	20.5(f/D,R)	

Table 1. Retention times of seeds in birds' guts (continued).

Frugivorous birds (body weight)	Fruit (fruit diameter, seed diameter, No. seeds/fruit)	Retention time (in minutes)	Reference
	Rhamnus palaestinus	40.7(f/D,R)	
	Rubia tenuifolia	15.0(f/R)	
	Rubia sanctus	20.8(f/D)	
	Smilax aspera	16.2(f/R)	
	Tamus communis	17.9(f/R)	
	Viscum cruciatum	73.7(f/D)	
Pipra mentalis manakins (15.3g)	*Ardisia nigropuncta* (7.16mm, 4.54mm, 1)	13.0(f/D)	Levey (1987)
	Dieffenbachia sp. (11.64mm, 9.68mm, 1)	7.8(f/D)	
Manacus candei Manakin (18.2g)	*Ardisia nigropuncta* (7.16mm, 4.54mm, 1)	25.8(f/D)	Levey (1987)
	Dieffenbachia sp. (11.64mm, 9.68mm, 1)	6.7(f/D)	
Bombycilla cedrorum cedar waxwing	small seeded artificial fruit (-, 2.5mm, 4)	23.3	Levey and Grajal (1991)
	large seedes artificial fruit (-, 4.0mm, 1)	19.2	
Dicaeum nirundinaceum mistletoebirds (specialist)	*Amyera qyandang*	820 sec.	Murphy et al. (1993)
Acanthagenys refularis honeyeater (un-specialist)	*Amyera qyandang*	2434 sec.	Murphy et al. (1993)
cedar waxwing (34 g)	several species of fruits (unkown)	13	Levey and Karasov (1986)
American robin (78 g)	several species of fruits (unkown)	16	
Europian strling (75 g)	several species of fruits (unkown)	18	
Myadestes melanops black faced solitaire	*Witheringia solanacea*	about 15	Murray et al. (1994)
	artificial fruit with pulp extract	about 15	
	artificial fruit without pulp extract	about 27	
Hypsypetes amaurotis brown-eared bulbuls (78g)	*Aucuba japonica* (16.5mm, 16.1mm,1)	11.6, 6.0, 17.6 (m,f,l/D)	Fukui unpublished
	Cornus florida (11.0mm, 5.3mm, 1)	13.1, 6.8, 29.8 (m,f,l/D)	
	Ilex serrata (5.0mm, 2.5mm, 5)	16.8, 9.5, 43.0 (m,f,l/D)	
	Viburnum dilatarum (5.1mm, 5.0mm, 1)	28.0, 11.6, 59.1 (m,f,l/D)	

mo; mode voided, f; first voided, m; mean voided, l; last voided, D; defecated, R; regurgitated

(1991) fed cedar waxwings on two types of artificial fruits with equal fruit size and seed loads but different seed sizes. The waxwings consumed significantly more fruits with few large seeds than fruits with many small seeds. Fruit consumption rate was negatively correlated with retention time, since large seeds were defecated more rapid than small seeds. Frugivorous birds may prefer fruits with short retention times, and hence some fruits with long retention times may remain uneaten on trees in the field.

However, in my field studies, all fruits but insect-infested ones of mountain ash were eventually consumed by the end of winter in Sapporo, northern Japan, and most fruits of 53 plant species were also consumed in Tsukuba, central Japan (Fukui, unpubl.). In temperate regions, birds face shortages of insect food due to the seasonal decline from autumn to winter. But most fruits ripen during these seasons of low insect abundance. Under such conditions, most fruits are eventually consumed.

Fruits are likely to be consumed in a preferential order. Consumption rate of fruits differed among fruit species. If there is pressure from seed predators such as squirrels, rapid consumption of fruits by efficient seed dispersers becomes important for reproductive success. Thus, by enhancing the fruit consumption rate, shortening of the retention time may increase reproductive success.

Sorensen (1984) argued that seed volume also determines fruit preferences of birds. A large seed occupies a larger space in the gut; in other words, the larger a seed, the stronger the gut limitation. However, retention time becomes shorter with an increase in seed size. It can, therefore, be presumed that the cost of seed processing in the gut is relatively constant regardless of the seed size.

5. *Seed Dispersal Distance*

The retention time of seeds in the gut corresponds to the traveling time of seeds. Several studies have documented that the seeds' dispersal distance is a function of the retention time, and those small seeds with long retention times tend to be carried farther than large seeds with short retention times (Hoppes, 1988; Murray et al., 1994). Because seeds deposited near their source may suffer from competition with the parent plant or density-dependent predation, longer dispersal distances would be more advantageous for seeds (Augspurger, 1984; Clark and Clark, 1983). Thus, the retention time affects the reproductive success of dispersed seeds.

6. *Germination*

The pulp of most fruit species inhibits germination physiologically and chemically (Krefting and Roe, 1949; Karasawa, 1978; Barnea et al., 1991; Fukui, 1996). I conducted germination experiments using three kinds of seeds: seeds within intact fruits, seeds with the pulp removed artificially, and seeds ingested and defecated by brown-eared bulbuls. In 16 out of 20 plant species examined, seeds within intact fruits did not germinate, whereas pulp-removed seeds did germinate in all 20 species studied. Thirteen species did not differ significantly in germination success between defecated seeds and pulp-removed ones. A little pulp often remains around the seeds in fecal pellets but is easily washed away by rain in the field. Thus, pulp removal is necessary for seed germination. Passing through a bird's guts is quite effective for pulp removal but is not a prerequisite for germination.

It is also known that long retention of seeds in guts can either enhance or inhibit germination. Barnea et al. (1991) investigated the germination of seeds that had been ingested by bulbuls and blackbirds. Seeds ingested by blackbirds usually had a higher germination rate than those ingested by bulbuls. This was explained by longer retention times in blackbirds than in bulbuls. Long retention in the gut may increase abrasion of the seed coat and improve germination rate. Scanning electron micrographs of the surfaces of these seed coats supported this hypothesis (Barnea et al., 1990). The cedar waxwing separated pulp from seed in the gizzard (Levey and Duke, 1992), and during this process the gizzard may abrade the seed coat.

Murray et al. (1994) showed, however, that if seeds were retained in the gut for longer than a certain period, the germination rate decreased markedly with increasing retention time. Over long retention in the gut may decrease the seed viability.

7. *Seed Clump Size and Density-dependent Mortality*

If the mortality of seeds and seedlings is dependent on their densities, the number of seeds dispersed together has a negative effect on seed and/or seedling survival. The number of seeds included in a fecal pellet is one of the factors that determine the seed density at a site. Moreover, large clump size may cause sibling competition among seeds dispersed together.

In the case of brown-eared bulbuls, the number of seeds in a fecal pellet (y) was almost determined by the number of seeds in a fruit (x): $y = x + 0.9$ (Fukui unpubl.). This result implies that sib-competition is more pronounced when a number of seeds are packed in a fruit. Although the clump size of dispersed seeds has been little considered in previous studies (but see Loiselle, 1990), this is an important factor affecting the reproductive success of fruiting plants.

There is a trade-off between the seed size and the seed number in a fruit. Many small seeds in a fruit may subject them to sib-competition, but long retention time may benefit them because they escape the effects of the parent plant. On the other hand, a single or a few

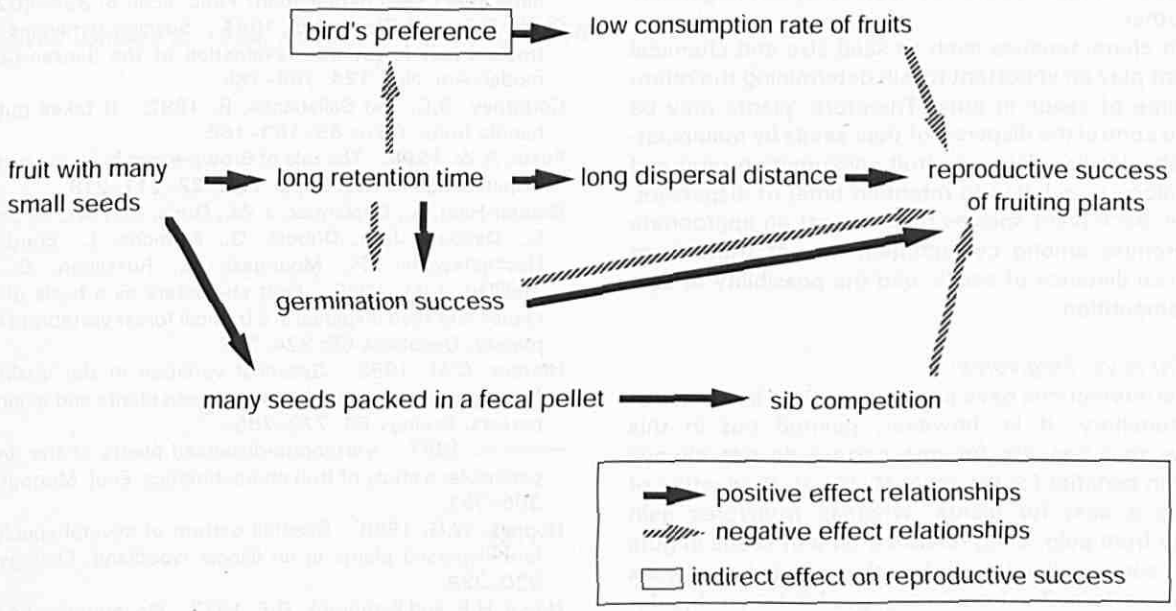

Fig. 1. Relationships among various factors affecting the reproductive success of plants producing fruits with many small seeds.

Table 2. Relationships between fruits and frugivores.

Factors governing seed dispersal	Functional significance		Correlation
	Fruits (benefit)	Frugivore (benefit)	
Retention time	seed dispersal distance (long)	food processing time (short)	conflict
Nutrient content in pulp	productive cost (little)	energy gain (much)	conflict
Seed number in a fecal pellet	size of seed clump (few)	rate of food processing (many)	conflict
Amount of consumed fruits	amount of dispersed seeds (many)	amount of food (many)	mutualism

large seed(s) in a fruit could escape sib-competition but may not be free from negative effects imposed by the parent plant.

8. *Reproductive Success of Fruiting Plants*

Figure 1 summarizes the multiple effects of various factors relevant to reproductive success in the case of plants producing fruits with many small seeds. The effects can be either positive or negative. The relationship between positive and negative effects is just reversed in the case of fruits with a few large seeds. The key point is that retention time can have both positive and negative effects on reproductive success through different processes. The longer seeds are retained in the gut, the greater is the dispersal distance. This benefits reproductive success by reducing negative impact from the parent plant on its offspring. On the other hand, long retention time loads birds with high gut limitations. Birds prefer fruits with less gut limitation and consume them at a higher rate. In consequence, long retention time has a negative effect on the reproductive success of the plant, by reducing the consumption rate through birds' preferences. Thus, retention time functions positively in one way but negatively in another.

Fruit characteristics such as seed size and chemical content play an important role in determining the retention time of seeds in guts. Therefore, plants may be able to control the dispersal of their seeds by manipulating behavior (in relation to fruit consumption rate) and physiology (in relation to retention time) of dispersers. Hence, each plant species might select an appropriate compromise among consumption rate of fruits, long dispersal distance of seeds, and the possibility of sibling competition.

9. *Fruits vs. Frugivores*

Mutual interactions have been emphasized in studies of endozoochory. It is, however, pointed out in this review that benefits for one partner do not always result in benefits for the other (Table 2). Production of pulp is a cost for plants, whereas frugivores gain energy from pulp. Long retention time of seeds in guts gives some advantages for the plant but forces frugivores to suffer from heavy gut limitation. Insofar as they can, frugivores pack as many seeds as possible into a fecal pellet to empty their guts rapidly. On the other hand, a large clump size of seeds in a fecal pellet may cause sib-competition among those seeds. Thus, a large clump size of seeds in a fecal pellet gives an advantage to frugivores but a disadvantage to plants. Growing knowledge reveals that there are conflicts between fruits and frugivores in some aspects of endozoochory.

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