Ornithol. Sci. 2: 41–48 (2003)

SPECIAL FEATURE Ecology of seed dispersal

Relationship between seed retention time in bird's gut and fruit characteristics

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ORNITHOLOGICAL SCIENCE

Abstract Seed retention time (SRT) of 16 fruit species in the guts of the Brown-eared Bulbul (*Hypsipetes amaurotis*), a major fruit consumer in central Japan, was studied to examine the relationship between SRT and fruit characteristics, i.e. fruit size, seed size, seed weight, and water content. Caged bulbuls were videotaped after feeding on fruits, and the time of defecation of each seed was recorded. Most seeds were always defecated in fecal pellets, with the exception of *Aucuba japonica* (the largest of the seeds studied), a seed of which was regurgitated on one occasion. Bulbuls defecate large seeds more rapidly than small seeds. The SRT of the last defecated seed, mean SRT, and standard deviation of SRT were significantly negatively correlated with seed size, fruit size, and seed weight, while SRT of the first defecated seed and water content were not correlated with any of the fruit characteristics examined. This suggests that Brown-eared Bulbuls are somehow able selectively to eliminate bulky seeds from the gut rapidly in order to overcome digestive limitations. If birds would prefer fruit species with large seeds that they can regurgitate and with short seed retention times in the gut, the results suggest that large seeds have the advantage of quantity of seed dispersed. Small seeds retained in the gut for longer have the advantage of being carried further and thus can achieve greater dispersal distances and more diverse destinations. The evolutionary interaction between fruiting plants and avian seed dispersers, may affect the diversity of fruit characteristics mediated by the length of retention time in a bird's gut.

Key words Frugivorous birds, Gut limitation, *Hypsipetes amaurotis*, Seed retention time, Seed size

Mutual interactions between birds and plants species have been emphasized in a range of studies of endozoochory, during which frugivorous birds consume fruit and subsequently disperse plant seeds (Snow 1971; Herrera 1985, 1995; Jordano 1995). There are, however, various conflicts between fruiting plants and frugivorous birds, for example, fruit pulp production is costly for plants, but provides frugivores with energy (Sorensen 1984; Fukui 1996). Fruiting plants and frugivorous birds are also in conflict over seed retention time (SRT), which is defined here as: the time from ingesting a fruit to the time when its seed(s) are eliminated, corresponding to the time spent passing through the bird's digestive system.

(Received 28 August 2002; Accepted 12 December 2002)

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Several studies have suggested that seed dispersal distance is a function of SRT, however, small seeds tend to be dispersed further (Hoppes 1988; Murray et al. 1994), indicating a relationship between seed size and SRT. Small seeds tend to remain in the gut longer than large seeds. Furthermore, long SRT in the avian gut apparently enhances seed germination (Barnea et al. 1991). Seeds ingested by blackbirds *Turdus merula* usually had a higher germination rate than those ingested by bulbuls *Pycnonotus xanthopygos*. This differential rate in germination has been explained by longer SRT in blackbirds than in bulbuls. Longer SRT may increase abrasion of the seed coat by the avian digestive system and thus improve germination rate. SRT represents part of the handling cost of food for birds. Ingested seeds also represent a cost to frugivorous birds because the seeds displace gut volume that could otherwise be filled with digestible fruit pulp. Furthermore, the seed mass increases the energy demands for locomotion. Thus whereas long SRT is advantageous for fruiting plants, it is disadvantageous for frugivorous birds.

There are several ways to overcome gut limitations. One is enlargement of gut volume, as seen in large herbivorous mammals (Westby 1974). Gut volume enlargement is a less helpful solution for frugivorous birds as they must be highly mobile to visit ephemeral fruiting sources; increased gut volume brings the disadvantage of increased body weight and thus a severe restriction for actively flying birds. An alternative solution is more rapid food processing.

To reduce the ingestion cost of bulky seeds, frugivorous birds have several mechanisms for processing fruit quickly (Countney & Sallabanks 1992; Levey & Duke 1992). Levey (1987) identified two types of frugivorous birds in terms of their fruit processing mechanisms: mashers, and gulpers. Mashers include the tanagers Thraupidae and the finches Fringillidae, which crush fruits, separating the pulp from the seeds with their mandibles before ingesting only the pulp. Mashers solve the gut limitation problem by not ingesting seeds, but, as a result, their handling time costs are higher. Gulpers, including the manakins Pipridae, waxwings Bombycillidae, and thrushes Turdidae, ingest whole fruit, and separate the pulp from the seeds in their digestive system. Gulpers must offset their gut limitation by rapid elimination of seeds.

Gulpers ingest all seeds, regardless of seed size, then eliminate the seeds by either regurgitation or defecation (Levey 1987, 1992). Levey (1987) showed that seed size influenced processing methods and time. Frugivorous birds more frequently regurgitate large seeds (>4 mm) than small seeds (<2 mm). Median regurgitation times for two manakin species *Pipra mentalis* and *Manacus candei* were significantly less than that of defecation (Levey 1992). Regurgitated seeds only pass through part of a bird's digestive system, whereas defecated seeds pass through the whole process, and this may explain why regurgitation time is usually shorter than defecation time. Size is important in determining how quickly a seed can be voided with fecal matter (Levey 1992). Large seeds had a significantly shorter SRT in the Cedar Waxwing *Bombycilla cedrorum* than did small seeds. Rapid elimination of large bulky seeds may be one way for gulpers to overcome their gut limitations.

Understanding the relationship between seed size and seed retention time is essential when studying interactions between frugivorous birds and fruiting plants. Seed size is an important factor determining the foraging efficiency of frugivorous birds. Seed size affects SRT, which is important for fruiting plants as it affects survival into the next generation. A number of studies have examined SRT in relation to seed size for various plant species (Sorensen 1984; Johnson et al. 1985; Levey 1987; Levey & Grajal 1991).

In this study, I examined fruit size and water content as well as seed size, since these characteristics appear to influence the foraging behaviour, digestion, and SRT of the Brown-eared Bulbul *Hypsipetes amaurotis*. The Brown-eared Bulbul is one of the major fruit consumers in central Japan, and an efficient seed disperser (Fukui 1995). When feeding, bulbuls usually gulp whole fruit, except when larger fruits are close in size to the gape width.

Sixteen fruit species with a wide range of fruit properties were used in feeding experiments with Brown-eared Bulbuls, and the relationship between fruit characteristics and SRT were analyzed statistically. The questions raised during this research, and discussed here are as follows: 1) Does the Brown-eared Bulbul regurgitate large seeds more frequently than small seeds?, 2) Does the bulbul eliminate large bulky seeds more rapidly than small seeds?, and 3) What properties of fruits affect seed retention time in the gut?

MATERIALS AND METHODS

1) Study area

This study was conducted on the University of Tsukuba campus, in southern Ibaraki Prefecture (36°06′N, 140°06′E), from 1989 to 1991. Six species of frugivorous birds were observed in the study area. These were the Brown-eared Bulbul, Gray Starling *Sturnus cineraceus*, Azure-winged Magpie *Cyanopica cyana*, Dusky Thrush *Turdus naumanni*, Pale Thrush *T. pallidus*, and Daurian Redstart *Phoenicurus auroreus*. The Brown-eared Bulbul was the most abundant of the six, and the only one resident in the study area throughout the year.

2) Fruit characteristics

The Brown-eared Bulbul is a gulper known to feed on the fruits of 53 plant species from 24 families occurring in this study area (Fukui 1995). These fruits vary in diameter from 3.5 mm *Callicarpa mollis*, Verbenaceae to 12.0 mm *Aucuba japonica*, Cornaceae, and all were smaller than the maximum width of the bulbul's gape (17.0±1.7 mm [mean±SE]). Sixteen common fruiting plants preferred by wild Brown-

Table 1. Characteristics of fruits examined.

Plant species	Seed size (mm)	Fruit size (mm)	Seed weight (mg)	Water content (%)
Aucuba japonica	16.1	16.5	0.69	74.36
Daphniphyllum macropodum	9.3	12.0	0.23	68.23
Elaeagnus umbellata	6.5	10.0	0.10	68.08
Cinnamomum camphora	6.3	8.5	0.12	56.29
Paederia scandens	6.2	6.2	0.029	65.68
Ligustrum japonicum	5.4	6.5	0.046	66.43
Cornus florida	5.3	11.0	0.091	64.9
Nandina domestica	5.1	6.5	0.10	66.98
Viburnum dilatum	5.0	5.1	0.025	74.15
Ilex crenata	4.8	6.0	0.058	56.54
Celastrus orbiculatus	3.8	7.5	0.023	71.12
Phytolacca americana	3.0	8.0	0.0076	73.29
Ilex serrata	2.9	5.0	0.008	78.57
Pyracantha angustifolia	2.8	5.5	0.025	73.00
Callicarpa mollis	1.9	3.5	0.0031	79.35
Eurya japonica	1.8	6.0	0.0023	70.87

eared Bulbuls were chosen for this study (see Table 1). All 16 species produce fruit in autumn and winter. To minimize intraspecific variation in fruit features, I collected fruits for the experiments from a single mother tree within a five-day period.

For each of the 16 fruit species, four characteristics (Table 1) were recorded: fruit size, seed size, seed weight, and water content. Twenty or more fruits of each species were measured. Fruit and seed sizes, were the diameters of the longest axis measured using a pair of vernier callipers. Forty fresh fruits of each species were weighed individually with a Mettler balance. Seeds were removed from half of the 40 fruits and weighed. Another 20 fruits were dried in an oven at 60°C until their weights became constant. Water content was defined as the difference between dry weight and fresh fruit weight.

3) Seed retention times

Seven wild Brown-eared Bulbuls were captured with mist nets between September 1988 and March 1990. When captured they weighed 78.7 ± 9.6 g (mean±SE). These seven birds were housed indoors in separate cages ($1.0 \times 1.0\,m^2 \times 0.5$ m high) and maintained on diets of wild fruits, pieces of apple, commercially-available food for fruit-eating birds, and water. All birds were fed commercially-available food overnight between the days of experiments and they were deprived of food for an hour prior to the onset of the experiments. Each bird was kept for a week then released. All birds remained in good health throughout the duration of the experiments.

The SRT for the bulbuls was determined as follows. During experiments, each bulbul was fed on a single species of fruit and provided with plenty of water. From 1 to 20 fruits were supplied depending on fruit size (Table 1). Ten fruits of each of 16 plant species with intermediate sized fruits were given during experiments. There were three exceptions. Twenty fruits of *Callicarpa mollis* were supplied as this species bears very small fruit. Five fruits of the large fruit bearing *Daphniphyllum macropodum* were given, and just one fruit of the very large fruited *Aucuba japonica* was given. The number of experimental replications for each fruit ranged from 3 to 32, because the number of bulbuls available for testing varied from time to time.

Several experiments were carried out sequentially in a single day. One experiment consisted of supplying fruit followed by about two-hours of observation. Different fruit species were fed to a bird in successive experiments so as to be able to distinguish the seeds from each experiment. In each experiment the bulbuls consumed all the fruits within 20 seconds of them being provided. Each experiment was videotaped, and a sheet of graph paper on the floor of the cage made it possible to identify exactly the positions of feces, the condition of each fecal pellet, and the number of seeds in each fecal pellet. The time at which seeds were either defecated or regurgitated was available in seconds from the video record. The SRT of each type of seed was calculated as the period between feeding and elimination.

Four indices were used to define the relationship between SRT and fruit characteristics: mean SRT, first SRT, last SRT, and standard deviation of SRT. Mean SRT was defined as the overall mean of the mean retention time for all defecated seeds in an experiment using a single fruit species. First SRT was defined as the overall mean SRT for the first defecated seed of each experiment. Last SRT was defined as the overall mean SRT for the last defecated seed of each experiment. The standard deviation of SRT was defined as the overall mean of the standard deviations of SRT for all defecated seeds in an experiment. The first three indices represent the SRTs of first, mean, and last defecated seeds of a given species, and thus they provide some indication of the expected dispersal distance and dispersal range of seeds by wild bulbuls. The standard deviation of SRT indicates the degree of variation in seed destination dispersal by birds, which, in addition to seed dispersal distance, is an important parameter of seed dispersal success for plants.

4) Analysis of seed retention time and fruit characteristics

Relationships between each index of seed retention time and fruit characteristics were analyzed using Pearson's correlation coefficient. All the data, except water content, were log-transformed before analysis. Water content data was transformed to arcsine square root in order to satisfy the requirement of normality.

RESULTS

1) Treatments of seeds

All but one of the seeds of all of the plant species used in the experiments were defecated by captive bulbuls. The exception was a single seed of *A. japonica*, which was regurgitated. The retention time of the regurgitated *A. japonica* seed was 14.2 minutes (N=1), but it was excluded from the calculation of retention time. All of the observed feces contained only seeds of a single species.

2) Individual difference between bulbuls

It was not practical to examine every fruit species with every bird, because the fruiting periods of the plants examined varied and each bulbul was retained for experimentation for just one week. One-way ANOVA was applied to the five fruit species for which SRTs were measured for two or three individual bulbuls. No significant differences were found among individual bulbuls in any of the experiments (Table 2).

3) Seed retention times

In most cases, seeds were defecated within one hour (Table 3). The mean SRT for all seed species was 20.8 minutes. The shortest SRT recorded was 2.4 for *Pyracantha angustifolia*, and the longest SRT recorded was 123.0 minutes for *C. mollis*.

4) Relationships between fruit characteristics and seed retention times

Last SRT and mean SRT were significantly negatively correlated with seed size, fruit size and seed weight (last SRT vs. seed size: $r=-0.68$, $N=16$, $p=0.0028$; mean SRT vs. seed size: $r=-0.56$,

Table 2. Comparison of retention time between individual birds.

Plant species	Individuals birds (# of seeds examined)	df	MS	*F*-ratio	P
Ligustrum japonicum	A vs B vs C (10, 10, 10)	2	317.63	.71	.50
Pyracantha angustifolia	A vs B vs C (80, 83, 91)	2	20.83	1.34	.26
Ilex crenata	C vs D vs E (20, 57, 51)	2	267.83	2.65	.07
Aucuba japonica	E vs F vs G (4, 13, 12)	2	6.15	.20	.82
Cornus florida	A vs B (46, 4)	1	4.91	.11	.74

Table 3. Seed Retention Times by Brown-eared Bulbul.

Plant name	N*	Mean of mean	Mean of first	Mean of last
Aucuba japonica	32	11.6±4.9	6.0	17.6
Daphniphyllum macropodum	17	15.7±5.5	9.5	30.0
Elaeagnus umbellata	4	19.8±7.2	7.0	31.8
Cinnamomum camphora	9	13.1±4.8	6.2	22.5
Paederia scandens	3	24.2±3.6	16.0	37.0
Ligustrum japonicum	4	12.1±7.4	3.0	26.5
Cornus florida	6	13.1±6.0	6.8	29.8
Nandina domestica	6	20.8±5.4	15.3	26.0
Viburnum dilatum	4	28.0±15.5	11.6	59.1
Ilex crenata	4	21.5±12.0	2.5	53.6
Celastrus orbiculatus	4	26.9±10.6	14.5	42.5
Phytolacca americana	11	21.1±16.7	5.2	45.3
Ilex serrata	4	16.8±11.5	9.5	43.0
Pyracantha angustifolia	8	16.7±17.2	2.8	45.0
Callicarpa mollis	4	41.5±14.4	26.3	76.3
Eurya japonica	6	21.1±7.9	6.8	40.6

N* shows replications of trials of each fruit species.

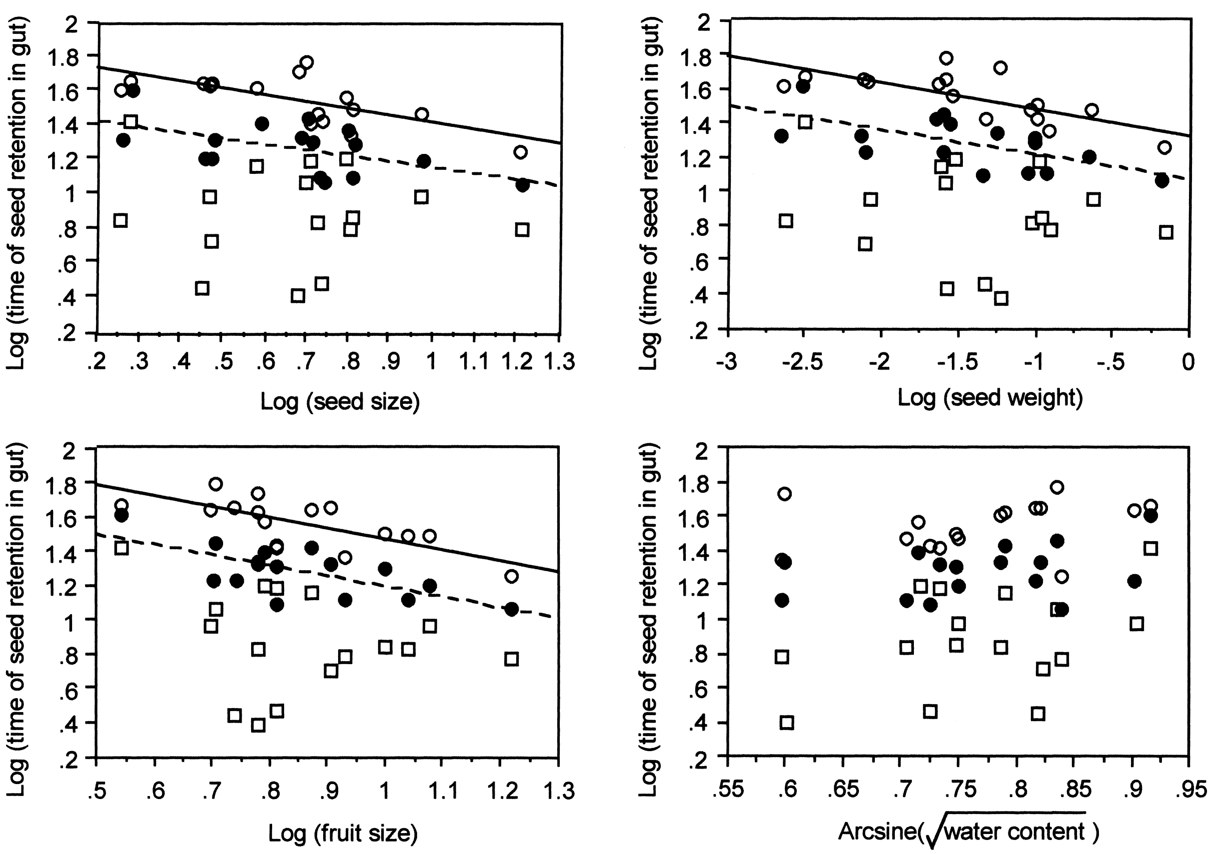

Fig. 1. Correlations between three indices of seed retention time (first SRT, mean SRT, and last SRT) and four fruit features (seed size, fruit size, seed weight and water content). Open squares=first SRT; solid circles=mean SRT, and open circles=last SRT. Unbroken lines indicate interactions between last SRT and each fruit feature. Broken lines indicate interactions between mean SRT and each fruit feature.

N=16, p=0.022; last SRT vs. fruit size: r=−0.71, N=16, p=0.0014; mean SRT vs. fruit size: r=−0.68, N=16, p=0.0031; last SRT vs. seed weight: r=−0.71, N=16, p=0.0014; mean SRT vs. seed weight: r=−0.63, N=16, p=0.0077) (see Table 1, Fig. 1). The first SRT did not have significant correlation with any fruit characters (seed size: $r=-0.12$, $N=16$, $p=0.66$; fruit size: r=−0.24, N=16, p=0.38; seed weight: r=−0.23, N=16, p=0.41). Water content was not significantly correlated with SRT (first SRT: r=0.41, N=16, p=0.12; mean SRT: r=0.37, N=16, p=0.17; last SRT: r=0.28, N=16, p=0.30).

The standard deviation of SRT was significantly negatively correlated with seed size (r=−0.65, N=16, p=0.0053), fruit size (r=−0.57, N=16, p=0.021), and seed weight (r=−0.60, N=16, p=0.013), but was not correlated with water content (r=0.49, N=16, p=0.054) (see Fig. 2).

DISCUSSION

As the key aspect of endozoochory is that plant seeds must pass through a bird's gut, seed retention time is a significant factor for both plants and birds. Brown-eared Bulbuls are gulpers, and so might be expected to overcome any gut limitation by rapid voiding of seeds, such as by regurgitation. During my experiments, a bulbul only once regurgitated a seed, and that was of *A. japonica*, which produces the largest seed of the fruits examined. Studies of manakins indicate that seed regurgitation is one way of voiding seeds rapidly in order to offset gut limitation because regurgitated seeds do not pass through the gut (Levey 1992). Levey (1992) found that manakins regurgitated large seeds more frequently than small seeds, whereas small seeds were always defecated. Like manakins, Brown-eared Bulbuls defecated small seeds and regurgitated a very large seed, although in the bulbul the average length of time to regurgitation

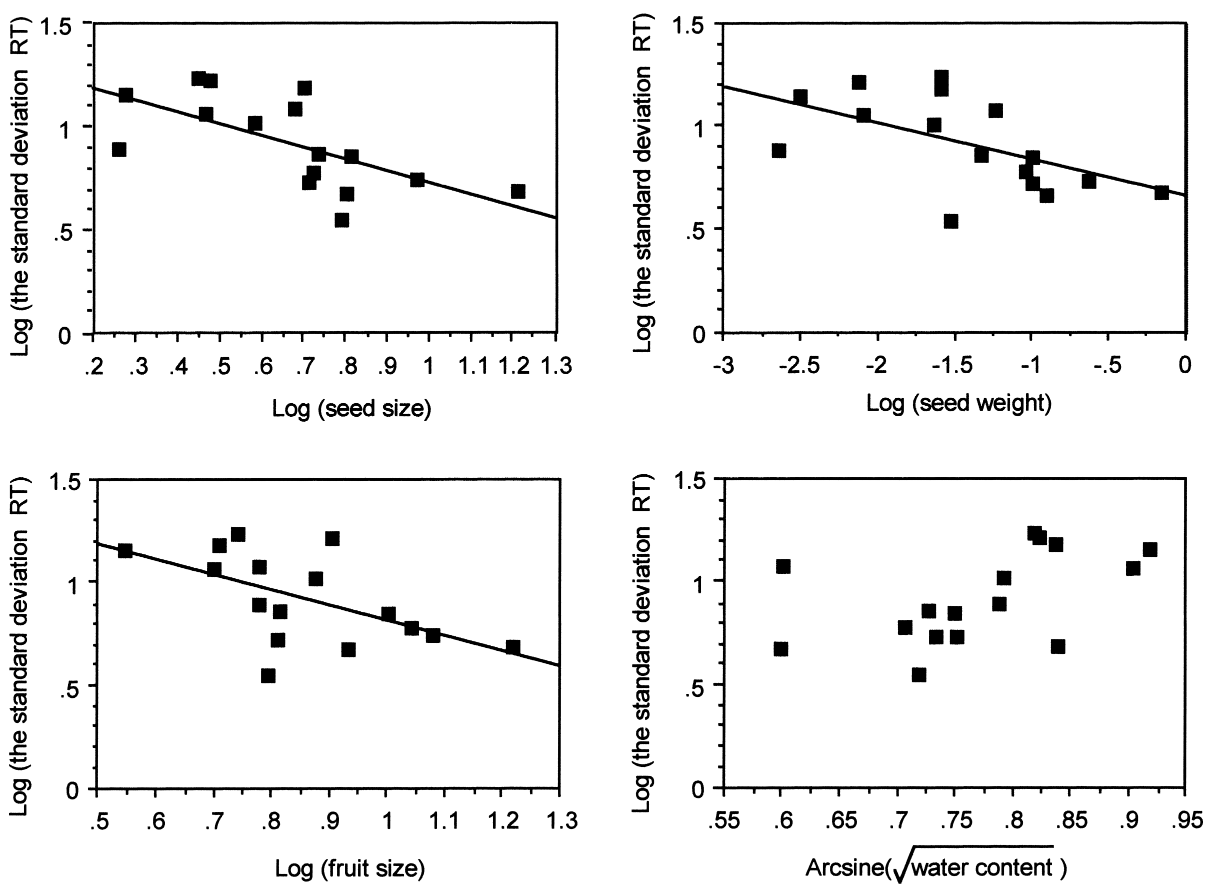

Fig. 2. The correlation between the standard deviation of SRT and four fruit features (seed size, fruit size, seed weight and water content). Unbroken lines indicate interactions between the standard deviation of SRT and each fruit feature (seed size, fruit size and seed weight).

is not known because regurgitation was observed only once.

The Brown-eared Bulbul defecated large bulky seeds more rapidly than small seeds (last SRT and mean SRT were both significantly negatively correlated with seed size, fruit size, and seed weight; see Fig. 1). These three fruit characteristics, representing bulk to frugivorous birds, being negatively correlated with SRT demonstrate that fruits and seeds with bulky characteristics are processed more quickly. In contrast, water content was not correlated with any indices of retention time, perhaps representing nutrient reward to frugivorous birds rather than bulk. It is concluded that it is important for bulbuls to process bulky seeds quickly. The first (shortest) SRT was not correlated with any of the four fruit characteristics examined (Fig. 1), indicating that gut limitations do not apply to first SRT.

For fruiting plants, rapid seed processing by birds is disadvantageous for their seed dispersal success. Since last SRT and mean SRT are considered to represent seed dispersal distances, the results imply that small seeds, which are retained in the gut longer, have longer dispersal distances than large seeds.

A large standard deviation of SRT is likely to correspond to high diversity of seed destination. If so, small seeds have a higher diversity of seed destination than large seeds because there was a negative correlation between seed size and the standard deviation of SRT (Fig. 2). The standard deviation of SRT was also negatively correlated with fruit size and seed weight. Thus, it is concluded that seeds within a small fruit or light seeds are dispersed at various destinations as well as at greater distances than larger, bulkier seeds.

Endozoochorous plants have evolved special features of their fruit to allow their dispersal agents to consume fruit easily (Gautier-Hion et al. 1985; Willson & Whelan 1990; Jordano 1995). Fruiting plants depending on frugivorous birds for their seed dispersal, are characterized by vivid colors (Willson & Whelan 1990). Among bird-dispersed fruits, nutritional characteristics differ between summer and winter fruit, coinciding with seasonal differences in the nutrient requirements of birds (Herrera 1982). Although such fruit characteristics are advantageous for frugivores, other characteristics, e.g. seed size, are disadvantageous (Sorensen 1984). Thus there exists a conflict between fruiting plants and frugivorous birds, although seed dispersal interactions have been discussed from the viewpoint of mutualism.

How quickly and how thoroughly seeds are processed has important evolutionary consequences for both fruiting plants and frugivores (Herrera 1995; Murray et al. 1994). Fruits are generally considered to be a food resource high in bulk (Herrera 1987), and bulk overloads the gut thereby reducing ingestion rate. Rapid seed processing may clear the gut and thus allow an increased ingestion rate (Levey & Grajal 1991; Levey 1992). Waxwings fed two types of artificial fruit (agar-based sugar solution as pulp and plastic beads as seeds) with equal seed loads but with different seed sizes consumed significantly more of the larger-seeded fruits. Because large seeds were defecated more quickly than small seeds, the increase in fruit consumption indicated that waxwings were process rate limited (Levey & Grajal 1991). Levey (1992) reported that freely feeding manakins took natural and artificial fruits very quickly after regurgitation. Evidence from various birds suggests that the seeds already in a bird's gut limit the rate of ingestion of more fruit. If rapid seed processing results in increased nutritional gain, then development of such an advantageous mechanism would spread through a population of frugivorous birds.

From the viewpoint of fruiting plants, seed dispersal success is determined by two factors: the quantity of seeds dispersed, and the distance over which seeds are dispersed. There is evidence that fruit species with seeds that are regurgitated, or with seeds that have short seed retention times (e.g. hawthorn *Crataegus monogyna*, sloe *Prunus spinosa*, and ivy *Hedera helix*) were the fruits most preferred by birds (Sorensen 1984). By implication, such fruit species have better chances of achieving higher removal rates of seeds, than other less-favored species. Considering that large seeds tend to have short retention times (Fig. 1), plant species producing large seeds benefit from the food preferences of birds and are able to disperse large numbers of their seeds, though their seed destinations may be limited because of the short throughput time. In contrast, plants producing small seeds (tending to have longer retention times) are more likely to achieve longer dispersal distances (corresponding to longer SRTs), which results in a greater diversity of seed destinations. Therefore, plants producing large seeds have the advantage of greater quantity of their seeds dispersed, whereas plants producing small seeds have the advantage of greater dispersal distances of their seeds.

The results from this study of the Brown-eared Bulbul imply that there are two types of fruit characteristic associated with frugivorous birds in term of seed dispersal success. This evolutionary interaction between fruit plants and seed dispersers may affect the diversity of fruit features, e.g. seed size, fruit size and seed weight, mediated by the length of time the seeds are retained in a bird's gut.

ACKNOWLEDGMENTS

I am very grateful to: T. Saitou and H. Banno, who gave valuable suggestions during the experiments; Y. Kominami, S. Matsuoka and N. Noma, who provided helpful discussions; M. Yasuda, who gave numerous valuable comments on early versions of the manuscript, and finally, members of the Laboratory of Animal Ecology, University of Tsukuba, who gave valuable advice and encouragement during this study.

REFERENCES

Barnea A, Yom-Tov Y & Friedman J (1991) Does ingestion by birds affect seed germination? Func Ecol 5: 394–402.

Countney SC & Sallabanks R (1992) It takes guts to handle fruits. Oikos 65: 163–166.

Fukui A (1995) The Role of Brown-eared Bulbuls as a Seed Dispersal Agent. Res Popul Ecol 37: 211–218.

Fukui A (1996) Retention Time of Seeds in Bird Guts: Costs and Benefits for Fruiting Plants and Frugivorous Birds. Plant Sp Biol 11: 141–147.

Gautier-Hion A, Duplantier J-M, Quris R, Feer F, Sourd C, Decoux J-P, Dubost G, Emmons L, Erard C, Heckestsweiler P, Moungazi A, Russilhon C & Thiollay J-M (1985) Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. Oecologia 65: 324–337.

Herrera CM (1982) Seasonal variation in the quality of fruits and defuse coevolution between plants and avian dispersers. Ecology 63: 773–785.

Herrera CM (1985) Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. Oikos 44: 132–141.

Herrera CM (1987) Vertebrate-dispersed plants of the Iberian peninsula: A study of fruit characteristics. Ecol Monogr 57: 305–331.

Herrera CM (1995) Plant-vertebrate seed dispersal systems in the Mediterranean: Ecological, evolutionary, and historical determinants. Ann Rev Ecol Syst 26: 705–727.

Hoppes WG (1988) Seedfall pattern of several species of bird-dispersed plants in an Illinois woodland. Ecology 69: 320–392.

Johnson RA, Willson MF & Thompson JN (1985) Nutritional values of wild fruits and consumption by migrant frugivorous birds. Ecology 66: 819–927.

Jordano P (1995) Angiosperm flesh fruits and seed dispersers: a comparative analysis of adaptation and constraints in plant-animal interactions. Am Nat 145: 163–191.

Levey DJ (1987) Seed size and fruit-handling techniques of avian frugivorous. Am Nat 129: 471–485.

Levey DJ (1992) Digestive processing of fruits and its consequences for fruit-frugivore coevolution. Acta XX Congresses Internationalis Ornithologici 1624–1629.

Levey DJ & Duke GE (1992) How do frugivores process fruit?: Radiographic studies of gastrointestinal transit in cedar waxwings (*Bombycilla cedrorum*). Auk 109: 722–730.

Levey DJ & Grajal A (1991) Evolutionary implication of fruit-processing limitations in Cedar waxwings. Am Nat 138: 171–189.

Murray KG, Russell S, Picone CM, Winnett-Murray K, Sherwood W & Kuhlmann ML (1994) Fruit laxatives and seed passage rates in frugivores: consequences for plant reproductive success. Ecology 75: 989–994.

Snow DW (1971) Evolutionary aspect of fruit-eating by birds. Ibis 113: 194–202.

Sorensen AE (1984) Nutrition, energy and passage time: Experiments with fruit preference in European blackbirds. J Anim Ecol 53: 545–557.

Westby M (1974) An analysis of diet selection by large generalist herbivores. Am Nat 108: 290–304.

Willson MF & Whelan CJ (1990) The evolution of fruit color in flesh-fruited plants. Am Nat 136: 790–809.