Pre-dispersal Seed Predation by a Granivorous Bird, the Masked Grosbeak (*Eophona personata*), in Two Bird-dispersed Ulmaceae Species

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ABSTRACT: Pre-dispersal seed predation by a granivorous bird, the masked grosbeak (*Eophona personata*, Fringillidae), was investigated in two bird-dispersed trees, *Celtis sinensis* and *Aphananthe aspera* (Ulmaceae). The objectives of this study were to 1) measure direct damage of predation by grosbeaks on plant crops, 2) reveal the temporal pattern of predation within each tree species and its causal factors, and 3) test whether foraging grosbeaks hinder foraging of frugivorous birds, thereby indirectly impacting the reproduction of both tree species. A substantial amount of fruit and seed crop was consumed by grosbeaks (24.3% in *Celtis*; 55.5% in *Aphananthe*), and only 17.7% (*Celtis*) and 16.7% (*Aphananthe*) were removed by frugivorous birds. At the study site, the grosbeak population size fluctuated greatly during the fruiting seasons of both plant species. As for *Celtis*, predated seed density also fluctuated temporally, and the local population size of grosbeaks was responsible for predated seed density. In *Aphananthe*, predation was not fully explained by grosbeak populations or plant phenology, but its peak coincided with that of grosbeak population. These results suggest that pre-dispersal seed predation by granivorous birds can have large negative impacts on the bird-dispersed plants. Changes in local population size of granivorous birds can influence predatation and can affect reproductive success of the bird-dispersed plants available to the birds.

Key words: Fleshy fruit, Granivory, Plant-animal interaction, Plant phenology, Seed dispersal

INTRODUCTION

Pre-dispersal seed predation is one of the major factors limiting plant reproductive success and has a large impact on plant population dynamics (Crawley 1992, Ehrlén 1996, Hulme and Benkman 2002). Bird-dispersed plants with fleshy fruits whose seeds are removed and dispersed by frugivorous birds (van der Pijl 1982) also suffer pre-dispersal seed predation by various organisms (Herrera 1982, Traveset 1994, Whitney and Stanton 2004). Among various organisms that consume seeds, granivorous birds are thought to be the main agents of pre-dispersal seed predation (Crawley 1992, Hulme and Benkman 2002). Granivorous birds have several characteristics that make them important seed predators; they have special organs (thick bills or muscular gizzards) to destroy hard pericarps, and they can effectively feed on both the embryo and endosperm inside seeds (Traveset 1994). In addition, some granivorous birds form flocks, and often migrate and feed on seeds in flocks (Cody 1971, Benkman 1988, 1997). These flocks of granivorous birds have the potential to consume large amounts of seeds on trees.

However, in bird-dispersed plants, pre-dispersal seed predation by granivorous birds has received little attention, and its impacts on

plant reproduction are poorly understood (Snow and Snow 1986). Granivorous birds can damage fruiting plants in two ways. At first, they damage fruiting plants directly by destroying seeds that might otherwise be dispersed by frugivorous birds (Jordano 1982, Englund 1993, Traveset 1994). Secondly, they may indirectly damage fruiting bird-dispersed plants through interactions between birds (Snow and Snow 1986); granivorous birds feeding on plants, especially when the birds are in flocks, may interfere with foraging of frugivorous birds and thereby hinder seed dispersal.

The temporal pattern of seed predation reflects the behaviors of seed predators and may have serious implications with regard to plant damage (Forget et al. 1999, Hammond et al. 1999). In the case of flock-forming granivorous birds, their local population can fluctuate greatly around a fruiting tree, depending on the flock migration. At the same time, the amount of ripe seeds on the plant, i.e., the food available to seed predators, changes temporally according to the fruiting phenology of the plant and the consumption of fruit and seeds by birds (Okamoto and Kitajima 1988). Although these factors are expected to define a pattern of predation, the temporal pattern of predation in a tree and the associated causal factors have not been clearly determined. Moreover, temporal patterns of seed predation and seed removal can reflect foraging interactions among

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granivorous and frugivorous birds. If foraging by granivorous birds hindered foraging by frugivorous birds, seed removal by frugivorous birds would have been expected to decrease, while consumption of seeds by granivorous birds would been expected to increase. Thus, by comparing temporal patterns of seed predation and plant seed removal, we can test whether granivorous birds are hindering seed dispersal by frugivorous birds.

In this study, we focused on the relationships between a granivorous bird, the masked grosbeak (*Eophona personata*, Fringillidae) and two bird-dispersed Ulmaceae trees, *Celtis sinensis* and *Aphananthe aspera*. These two trees are common bird-dispersed trees in lowland forests in temperate regions of Japan and are sometimes dominant in these forests. As indicated by several reports in the literature (Kiyosu 1951, Chiba et al. 1972, Kanagawa Branch of Wild Bird Society of Japan 2007), masked grosbeaks often consume *Celtis* and *Aphananthe* seeds in flocks. Consequently, masked grosbeaks would be expected to have a large negative impact on these trees. We investigated predispersal seed predation by grosbeaks continuously throughout the fruiting period in one tree of each species. The objectives of this study were as follows: (1) to measure direct damage caused by granivorous birds to seed predation of fruiting plants, in particular *C. sinensis* and *A. aspera*; (2) to investigate the temporal pattern and determinants of seed predation within these plants; and (3) to test whether granivorous birds indirectly damage fruiting plants by hindering foraging of frugivorous birds. Thus, we addressed the following questions: (1) What proportion of the whole crop is predated by grosbeaks? (2) How does the size of the granivorous bird population change temporally? (3) What is the temporal pattern and determinants of predation within plants? (4) Do granivorous birds hinder foraging by frugivorous birds?

MATERIALS AND METHODS

Study Site

The study was conducted in a forested botanical garden of the Graduate School of Science, Kyoto University (N35° 2′, W135° 47′; 70 m elevation) in central Japan, from July to December 2004. This region falls in a temperate climate zone, with an annual mean temperature of 16.1℃; the annual precipitation in 2004 was 1994 mm (Field Science Education and Research Center of Kyoto University 2007). The study site (about 2 ha), which comprises a botanical garden (founded in 1923) neighboring the Kyoto University campus, is located in an urban area of Kyoto City at about 900 m from the mountain forests. The abundant surrounding green areas have encouraged a diverse population of birds (Nimura 1993). The forest includes cultivated trees, but is now dominated by naturally grown trees, such as *C. sinensis* and *A. aspera* (Hatakeyama et al. 1973).

Established at the site are 14 *C. sinensis* trees and 17 *A. aspera* trees with diameters at breast height (DBH) > 5 cm. For this study, we selected one adult fruiting individual from each species (*Celtis*: DBH = 53 cm, height = 25 m; *Aphananthe*: DBH = 45.2 cm, height = 20 m). We selected these trees because of the following reasons: (1) they are middle-sized trees among the other conspecific trees at the site; (2) their canopies did not spatially overlap with those of neighboring conspecific trees; and (3) they produced an abundant crop in the study year. The trees of the two species show considerable among-year variation in crop size, producing only small crops in some years; however, these variations are not synchronous within their populations (T. Yoshikawa, unpublished data). Therefore, our focal trees were selected as representative of the trees with fertile crops in their populations.

The site also constitutes other fleshy-fruited plants, such as *Ficus erecta*, *Ilex chinensis*, *Ramnella fraguloides*, *Swida macrophylla*, and *Celtis biondii*, whose fruiting periods overlap those of our focal trees. Frugivorous birds such as the brown-eared bulbul and Japanese white-eye presumably consume the fruits of these plants; however, the biomass of these plants at our site is smaller than our focal trees. Grosbeaks rarely consume the seeds of these plants, except those of *Celtis biondii* (Ulmaceae; five trees at the site), which bear ripe fruits from October to December (T. Yoshikawa, unpublished data). Grosbeaks also consume seeds of some wind-dispersed trees (e.g., *Acer palmatum*, *Zelkova serrata,* or *Ailanthus altissima*) at the site.

Plant Species

Celtis sinensis (Ulmaceae, hereafter *Celtis*) is a bird-dispersed, deciduous tall tree that is distributed in Japan, Korea, and China and grows in open habitats with moderate humidity. Bisexual and male flowers bloom from March to April (Satake et al. 1999) and fruits grow rapidly in May (Okamoto and Kitajima 1988). In August, unripe (green) fruits begin ripening (orange). The ripe drupe of *Celtis* (6 mm in radius) comprises a single, nearly round seed (3 mm radius) surrounded by a fleshy pulp. No insect seed predators were found at the study site, although a species of weevil fed on sap on the surface of unripe fruits in early summer (T. Yoshikawa, personal observation).

Aphananthe aspera (Ulmaceae, hereafter *Aphananthe*) is also a bird-dispersed, deciduous tall tree. It is distributed in Far East Asia around Japan and grows in open habitats. Female and male flowers bloom in April~May (Satake et al. 1999). The fruits grow rapidly in May, but unripe (green) fruit begins ripening (black) in September, shortly after *Celtis* (Okamoto and Kitajima 1988). A ripe drupe (10 mm in radius), which is larger than that of *Celtis,* consists of a single, nearly round seed (6 mm in radius) surrounded by a fleshy pulp.

At the study site, fruits of *Celtis* and *Aphananthe* are eaten by similar assemblages of frugivorous birds. Frugivorous birds, including the brown-eared bulbul (*Microscelis amaurotis*, Pycnonotidae), jungle crow (*Corvus levaillantii*, Corvidae), carrion crow (*C. corone*, Corvidae), and dusky thrush (*Turdus naumanii*, Turdidae), swallow fruits and disperse seeds of both plant species, whereas the Japanese white-eye (*Zosterops japonica*, Zosteropidae) disperses only seeds of *Celtis*, because of its small gape size (T. Yoshikawa, personal observation). In addition, *Celtis* and *Aphananthe* have a characteristic pattern of asynchronous fruit ripening (Gorchov 1985, Okamoto and Kitajima 1988). In *Celtis* and *Aphananthe* individuals, fruits do not ripen all at once. The fruits ripen gradually so that only a small portion of the total crop is ripe at any given time.

Avian Species

The masked grosbeak is a granivorous passerine (body size: 23 cm) distributed in Far East Asia around Japan. In Japan, grosbeaks breed in deciduous and coniferous forests of mountain areas in spring and summer. In autumn, grosbeaks migrate to lowland deciduous forests and live there in flocks (Kiyosu 1951). Grosbeaks feed on plant seeds and insects, although in the non-breeding season, they feed mainly on seeds of various plants (Chiba et al. 1972). In Kyoto, around the study site, the grosbeak population is small in summer and increases in autumn and winter (T. Yoshikawa, personal observation).

Grosbeaks often forage seeds of *Celtis* and *Aphananthe* (Kiyosu 1951, Chiba et al. 1972, Nimura 1993) in autumn and winter seasons. They have thick bills to destroy hard pericarps and are able to consume the embryos and endosperm inside the seeds. A grosbeak feeds on seeds of *Celtis* and *Aphananthe* as follows; a grosbeak picks a fruit from a branch, and after peeling the pulp and cracking the pericarp with its bill, it consumes the embryo and endosperm. In most cases, grosbeaks discard the peeled pulps and broken pericarps to a site directly beneath the location from which they pick the fruit from the tree. However, they were infrequently observed to pick fruit with the fly-catching behavior. Hence, broken pieces of pulp and pericarp are typically scattered on the ground beneath these trees. Because grosbeaks crush and destroy the seeds completely, they never act as seed dispersers of these tree species. The only other granivorous bird populating the site the hawfinch *Coccothraustes coccothraustes* crushes seeds of *Celtis* and *Aphananthe* (Kanagawa Branch of Wild Bird Society of Japan 2007). However, the hawfinch is much rarer at this site than grosbeaks and was not observed during the monitoring periods.

Measuring Direct Damage from Grosbeak Predation

To estimate the total number of seeds destroyed by grosbeaks per tree, the cross-trapping method (Kawaguchi et al. 1995, Naito et al. 2008) was used. Seed traps (with <1-mm mesh, 0.25 m^2 per trap) were set in four directions from the canopy center of each tree at 2-m intervals (19 traps for *Celtis* and 11 for *Aphananthe*). The canopy center of each tree was determined by analyzing the projected crown area (*Celtis*: 133 m^2; *Aphananthe*: 95 m^2). Throughout the fruiting seasons of both trees in 2004, trap contents (pieces of pericarp broken by grosbeaks, fallen seeds, and conspecific naked seeds excreted by avian frugivores) were sampled regularly. In *Celtis*, sampling was conducted 14 times at $7 \sim 14$-day intervals from 4 August to 20 December. In *Aphananthe*, sampling was conducted nine times at $8 \sim 19$-day intervals from 18 August to 26 November. These periods covered most of the period during which ripe fruits were found in both species. For each trap, total numbers of predated and fallen seeds were counted for each sampling period, and cumulative seed density throughout all the periods was calculated at each trap. The number of predated seeds per trap was calculated [(dry mass of broken pericarp in the trap) / (average dry mass of pericarp in sound seeds; *Celtis*: 0.026 ± 0.006 g, n = 20; *Aphananthe*: 0.073 ± 0.005 g, n = 11)].

The total number of predated and fallen seeds per tree was estimated as follows. We analyzed trap data using a normal distribution model (Kawaguchi et al. 1995). According to Kawaguchi et al. (1995), we assumed that seed density at χ meters from the center of the canopy [$d(x)$] follows a normal distribution expressed by the equation $d(x) = (n/\pi\alpha^2) * \exp(-\chi^2/\alpha^2)$, where α is the standard deviation and n is a constant. The total number of seeds under the plant was then calculated as $G = \int_0^\infty 2\pi xy\,dx = n$. The values of parameters were determined by a non-linear regression with the Gauss-Newton algorithm using R version 2.4.1.

In both trees, total seeds (fruits) within trees were estimated as the average number of seeds per branch (about 1 cm in diameter, $n = 30$) multiplied by the number of branches per tree. In late July, before fruit ripening and removal, the number of seeds per branch and the number of branches per tree were counted by direct observation with binoculars ($\times 8$) and a telescope ($\times 15$). The total number of fruits removed by frugivorous birds was then calculated [(total seeds) $-$ (total predated seeds) $-$ (total fallen seeds)].

Seasonal Changes in Bird Populations at the Study Site

To investigate seasonal changes in populations of grosbeaks and frugivorous birds, line censuses were conducted 14 times between 16 July and 21 December, at $8 \sim 18$-day intervals. The census line passed through the botanical garden and neighboring campus and wooded areas. Every census was carried out in early morning, $30 \sim 60$ minutes after sunrise. An investigator walked along the route

slowly (about 2 km/h) and recorded birds that appeared within 30 m on both sides of the route, using binoculars (×8). We conducted censuses twice, including the initial walk and the return, along the route (total 36 minutes) and recorded the maximum number of individuals of each species in the two censuses.

Fruiting Phenology of the Plants

We continued to monitor fruits in the canopies of the *Celtis* and *Aphananthe* study trees during their fruiting seasons to investigate patterns of fruit ripening and disappearance within the trees. In the canopy of each tree, we randomly selected 13 branches (<5 mm in diameter) of *Celtis* and 15 branches (<10 mm in diameter) of *Aphananthe*, which bore 269 (*Celtis*) and 291 (*Aphananthe*) fruits in total at the start of observation period. Monitoring was conducted from 4 August to 21 December (14 times, at 8∼18-day intervals) for *Celtis*, and from 7 September to 7 December (9 times at 8∼18-day intervals) for *Aphananthe*. In *Aphananthe*, fruit monitoring began about 20 days later than the start of seed trapping. At each observation, total numbers of ripe and unripe fruits on all branches were recorded using binoculars (×8) and a telescope (×15). Fruit ripeness was judged from its color. Whole fruit abundance (WFA) was defined as the total number of remaining fruit in a day divided by the initial number of fruits (*Celtis*: 269; *Aphananthe*: 291). Similarly, ripe fruit abundance (RFA) was defined as the total number of ripe remaining fruit in a day divided by the initial number of fruits.

Temporal Pattern of Predation within a Plant

Using traps beneath both trees, we regularly sampled pieces of pericarp broken by grosbeaks. In the case of *Celtis*, some of the fleshy pulp was stuck to the surface of the pericarp material broken by grosbeaks. When the pulp on the pericarp was green, we judged that the pericarp was from an unripe fruit. Because no pulp was found on the surface of pericarp pieces in *Aphananthe*, we were not able to judge by whether grosbeaks consumed seeds from unripe fruits.

To detect factors affecting temporal patterns of predation in *Celtis* and *Aphananthe*, we conducted multiple regression analysis. We considered the daily mean density of predated seeds (no. $\times$ m^{-2} $\times$ day^{-1}) in all seed traps (*Celtis*: 19; *Aphananthe*: 11) in each period as the dependent variable, and observed grosbeak populations, RFA, and WFA in each period as the independent variables. Because some periods lacked data on grosbeak populations or fruit abundance, we used a data set including ten periods (*Celtis*) and six periods (*Aphananthe*) for the analysis.

Testing for Indirect Damage by Grosbeaks

To test whether grosbeaks hinder foraging of frugivorous birds

in *Celtis* and *Aphananthe*, we compared the temporal pattern of seed removal by frugivorous birds to that of seed predation by grosbeaks. As an index of seed removal by frugivorous birds, we used naked conspecific seeds excreted under the tree, which were similarly sampled by the traps. These seeds can include the seeds transported from other fruiting trees, but can be used as the index of fruit removal in the trees (Herrera 1984, García et al. 2001). If foraging grosbeaks interfere with that of frugivorous birds within the fruiting tree, seed removal by frugivorous birds is expected to decrease during the periods when grosbeaks are vigorously feeding on seeds. Hence, we conducted a Pearson correlation test between seed removal by frugivorous birds and seed predation by grosbeaks for each period.

RESULTS

Measuring Direct Damage of Predation by Grosbeaks

In the *Celtis* tree, the total numbers of predated and fallen seeds per tree were estimated as 35,045 and 83,601, respectively. The total number of seeds in the entire canopy was estimated at 144,083. The number of seeds per branch was 111.4 ± 57.4 (mean ± SD), and the total number of branches was 1,293. The proportions of seeds predated by grosbeaks, fallen seeds, and seeds removed by frugivorous birds were 24.3%, 58.0%, and 17.7%, respectively. More than half of the whole seeds (58.0%) had fallen beneath the tree, and the total number of seeds removed by avian frugivores was less than the total number of seeds destroyed by grosbeaks.

In the *Aphananthe* tree, total numbers of predated and fallen seeds per tree were estimated at 4,694 and 2,348, respectively. The total number of seeds in the entire canopy was estimated at 8,447. The number of seeds per branch was 24.1 ± 10.2 (mean ± SD), and the total number of branches was 350. The proportions of seeds predated by grosbeaks, fallen seeds, and seeds removed by frugivorous birds were 55.5%, 27.8%, and 16.7%, respectively. Seeds predated by grosbeaks represented more than half of the entire crop. This predation was much more prevalent than seed removal by frugivores.

Seasonal Changes in Bird Populations at the Study Site

Throughout the observation periods, the average number of grosbeaks was greatest among other avian species feeding on fruits of *Celtis* and *Aphananthe*, but the grosbeak population showed large temporal fluctuations and peaked in October (Fig. 1a). Among frugivorous birds, the brown-eared bulbul was most abundant and its population reached the maximum level on October (Fig. 1b). Japanese white-eyes and crows (jungle crows and carrion crows) were few in number. The dusky thrush, a winter migratory species, first
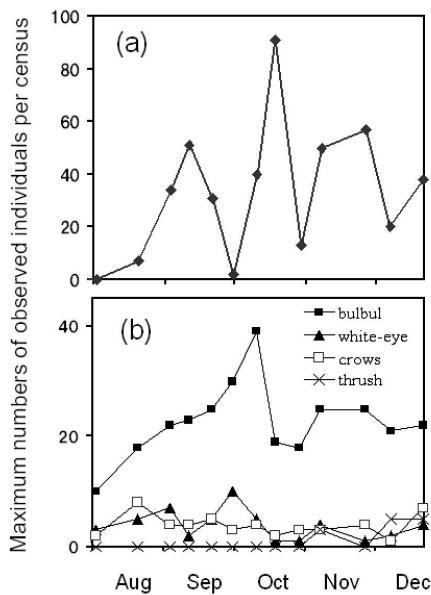
Fig. 1. Seasonal population changes in (a) grosbeaks and (b) four fru-
givorous birds, as determined by line census twice a day
conducted 14 times between July 16, 2004, and December 21,
2004, at 8~18-day intervals. The y-axis indicates the maxi-
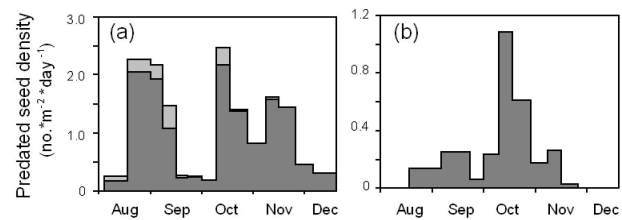mum observed number of each bird species per census.

Fig. 2. Temporal patterns of predation by grosbeaks on (a) *Celtis* and
(b) *Aphananthe*. The y-values indicate the daily mean number
of predated seeds per m^2 (no. $\times$ m^{-2} $\times$ day^{-1}) for all seed traps
within each period. In Fig. 2(a), the light-gray area indicates
predated seeds from unripe (green) fruits, and dark gray indi-
cates predated seeds from ripe (orange or red) ones.

appeared in late autumn, but did not persist.

Temporal Pattern of Predation within Plants

In the *Celtis* tree, predation by grosbeaks continued throughout
the fruiting period, although predated seed density fluctuated greatly
(Fig. 2a). In early August, when fruits began ripening in the ca-
nopy, predated seed density was low; however, it increased rapidly
from late August to mid-September. From mid-September to early
October, predated seed density diminished markedly, but in mid-
October, suddenly increased and reached its peak. Thereafter, the
level fluctuated but eventually decreased in December. Grosbeaks
consumed the seeds of both ripe and unripe fruits, but consumed
many more ripe fruit seeds (Fig. 2a) even in the early fruiting
season when ripe fruits are scarcer than unripe fruits in the canopy.
In the *Aphananthe* tree, predation by grosbeaks continued from
mid-August to November (Fig. 2b). Predated seed density remained
relatively low from August to early October, but increased rapidly
in mid-October; the density then decreased gradually and ceased in
late November.

As mentioned previously, predated seed density peaked sharply
in September and mid-October in the *Celtis* tree, coinciding with
rapid increases in the grosbeak population. In multiple regression
analysis (Table 1a), grosbeak population size, RFA, and WFA were
selected as independent variables, but only grosbeak population size
had a significant effect on predated seed density, although regre-

ssion itself was not significant ($P = 0.09$). In the *Aphananthe* tree,
multiple regression analysis showed that neither the grosbeak
population RFA nor WFA affected this temporal pattern (Table 1b).
However, the peak in predation coincided with the peak in grosbeak
population size in mid-October.

Testing for Indirect Damage by Grosbeaks

In both tree species, there was no negative correlation between
seed predation by grosbeaks and fruit removal by frugivorous birds
in each period (*Celtis*: $r = 0.400$, $P = 0.156$; *Aphananthe*: $r = 0.493$,
$P = 0.178$). In *Celtis*, fruit removal by frugivorous birds continued
throughout the fruiting season (Fig. 3a). Although predated seed
density increased in mid-October, seed removal by frugivorous
birds did not decrease markedly. In the *Aphananthe* tree (Fig. 3b),
the peak in seed removal by frugivorous birds coincided with the
peak in seed predation by grosbeaks in mid-October.

DISCUSSION

We quantified pre-dispersal seed predation by granivorous birds
in tall bird-dispersed tree species. Pre-dispersal seed predation by
grosbeaks reached 24.3% (*Celtis*) and 55.5% (*Aphananthe*) of the
tree crops. The data available on predispersal seed predation by gra-
nivorous birds in bird-dispersed plants (Englund 1993, Traveset
1994), especially in tall trees (but see Jordano 1982) is limited. Our
study revealed that predispersal seed predation by granivorous birds
can directly affect crops in fertile tall trees. On the other hand, only
17.7% of *Celtis* and 16.7% of *Aphananthe* crops were removed by
avian frugivores. In this study, the number of seeds (fruits) that fell
directly under the mother plant, particularly in *Celtis*, was con-
siderably high, a finding which was also reported by Okamoto and
Kitajima (1988). This fact suggests overabundance of crops relative
to the fruit consumption of the birds (Howe and de Steven 1979,
Hampe 2008). This overabundance of crops might act as a buffer

Table 1. Results of multiple regression analysis in the (a) *Celtis* tree and in the (b) *Aphananthe* tree, with daily mean predated seeds in each period as the dependent variable, and ripe fruit abundance (RFA), whole fruit abundance (WFA), and observed grosbeak population size in each period as independent variables. RFA and WFA were adjusted by arcsine-transformation prior to the analysis. Stepwise procedures were conducted for variable selection.

(a) *Celtis*

	Coefficient	Standard error	T value	P
Intercept	−0.0020	0.0154	−0.127	0.903
RFA	−0.1363	0.0727	−1.875	0.110
WFA	0.0353	0.0149	2.366	0.056
Grosbeak	0.0007	0.0003	2.725	0.034[*]

Adjusted R^2: 0.443, F-statistic: 3.39 on 3 and 6 DF,
p-value: 0.0948; [*] $P < 0.05$

(b) *Aphananthe*

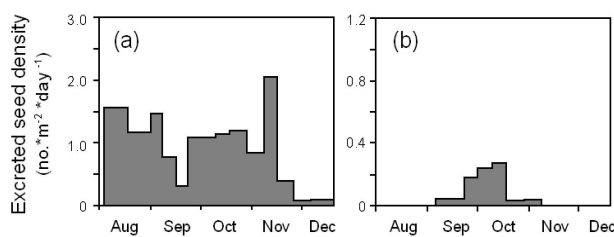|	Coefficient	Standard error	T value	P
Intercept	0.3795	0.1650	2.300	0.070

Fig. 3. Temporal patterns of seeds excreted by frugivorous birds within (a) *Celtis* and (b) *Aphananthe*. The y-values indicate the daily mean number of excreted seeds per m^2 (no. $\times m^{-2} \times day^{-1}$) for all seed traps within each period.

against seed loss by granivorous birds, thus guaranteeing successful fruit removal by frugivorous birds. In addition, these fallen seeds can be dispersed by mammals, or by water in habitats along rivers and may contribute to plant reproductive success. In this site, however, some of the fallen seeds may be consumed by grosbeaks, which feed on seeds on the ground as well as on fruiting trees.

Snow and Snow (1986) reported interference behaviors between birds feeding on fruits in the same tree and suggested that such interactions between birds could alter the reproductive output of plants. In our study, however, results suggest that grosbeaks did not hinder foraging of frugivorous birds markedly in the fruiting plants and *vice versa*. Thus, indirect damage by granivorous birds was not found in these *Celtis* and *Aphananthe* trees. We believe that this

could be attributable to the smaller body size of the grosbeak than that of primary frugivorous birds, such as the crow, bulbul, or thrush; hence, it is likely that the grossbeak is unable to interfere with frugivorous birds in a significant manner. In addition, *Celtis* and *Aphananthe* are tall tree species with broadly spreading canopies. Such large canopies and abundant crops might enable both seed predators and dispersers to eat seeds and fruits together within the same plant.

During the fruiting seasons of *Celtis* and *Aphananthe*, the grosbeak population fluctuated greatly at the study site. Conversely, populations of frugivorous species were temporally more stable than grosbeaks, suggesting different patterns of population change between granivorous and frugivorous birds. Since grosbeaks live in flocks in autumn-winter (Kiyosu 1951), observed fluctuations in their population size at the study site were assumed to reflect their seasonal and/or local migration. In multiple regression analysis (Table 1), grosbeak population size had some influence on predated seed density in *Celtis*, but we found no association between the two factors in *Aphananthe*. This indicates that other factors, e.g., availability of other food sources (such as *Celtis sinensis* and *C. biondii*) at the site or selection of feeding trees by the birds, might influence the process of predation, especially in *Aphananthe*. Nevertheless, peaks of predation in both trees were coincident with that of the grosbeak population (mid-October); hence, grosbeak population may have an impact on plant crops even in *Aphananthe*. The population dynamics of frugivorous birds in relation to seed dispersal of bird-dispersed plants (Thompson and Willson 1979, Noma and Yumoto 1997, Kimura 2003) have been investigated extensively; however, comparable studies on granivorous birds have been limited. Migrating populations of some seed-eating birds are known to show large annual fluctuations (Koenig and Knops 2001, Newton 2006). In addition, there is considerable between-year variation in crop sizes and fruiting phenology in bird-dispersed plants. Therefore, further studies are needed to understand between-year variations in seed loss by granivorous birds in the focal plants.

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