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Pre- and post-dispersal seed predation in *Tachigali versicolor* (Caesalpiniaceae): effects of timing of fruiting and variation among trees

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ABSTRACT. Fruiting phenology, habitat types and proximity to conspecific fruiting adults may influence the degree of escape from pre- and post-dispersal seed predators. Successful predator escape by means of satiation is considered to be especially important for selection of masting and monocarpic reproduction in trees, such as exhibited by *Tachigali versicolor*, a tropical canopy tree. How pre- and post-dispersal predation rates varied with dispersal timing and among trees in *T. versicolor* was examined in young and old forests on Barro Colorado Island in Panama during a 4-mo period. Seeds were collected from above-ground traps to assess predispersal predation by bruchid beetles, and from quadrats on the ground to record predation and removal by terrestrial mammals. Proportion of seeds aborted varied greatly among trees (range 6–30 %, mean 16 %), and was especially high for trees on the edge of the island with fruiting conspecifics nearby during the early part of fruiting season. The proportion of seeds killed by bruchid beetles varied less among trees (14–25 %, mean 20 %), and remained constant throughout the fruiting season. Seeds on the ground were attacked mostly by rodents, and possibly by deer (26 % of all seeds and 43 % of intact dispersed seeds). The post-dispersal predation level was higher in the young forest than in the old forest (61 and 26 % of intact dispersed seeds, respectively), and was unaffected by the proximity of fruiting conspecifics. Temporal satiation of seed predators was evident only for post-dispersal mammalian predators in the old forest.

KEY WORDS: *Amblycerus tachigaliae*, Barro Colorado Island, Bruchidae, edge effect, masting, rodents, satiation, seed abortion, seed predation, *Tachigali versicolor*.

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INTRODUCTION

Escape of seeds from pre- and post-dispersal seed predators may have strong fitness implications for a plant population (Louda 1982, Louda & Potvin 1995). Hence, seed predation is considered to be a selective force for the evolution of masting behaviour in trees (Janzen 1974, 1976; Kelly *et al.* 1992, Silvertown 1980). Predators may be satiated by an abundance of seeds during mast years while they experience starvation during non-mast years with little or no availability of seeds. Consequently, successful escape from seed predators is often limited to mast years (Forget 1997a, Jensen 1985, Kelly *et al.* 1992, Ligon 1978; but see Ballardie & Whelan 1986, Donaldson 1993). The most extreme case of masting is monocarpic reproduction with population-level synchronization (Kelly 1994). Predator satiation may be more pronounced in monocarpic masting species than in polycarpic masting species, because monocarps allocate all of their resources to reproduction and create dense seed shadows around individual parents. This type of reproduction is rare for dicotyledonous trees, but is found in the tropical canopy tree, *Tachigali versicolor* (Caesalpiniaceae): every 4 or 5 y several individuals come into fruit, disperse seeds and die (Foster 1977). Previous studies have identified predispersal seed predation by bruchid beetles and post dispersal predation by terrestrial vertebrates to be both important causes of seed mortality in this species (Foster 1977, Kitajima & Augspurger 1989).

Although there is a positive evidence for local satiation of terrestrial predators in the dense shadows around parent trees relative to areas without any fruiting trees (Augspurger & Kitajima 1992), for a complete demonstration of predator satiation, the temporal dynamics of seed predation rates during development and dispersal of seeds need to be examined. Other factors being equal, seed predation rate is likely to be lowest when seeds are most abundant within a given seed shadow. This may not be the case, however, if fruiting phenology of other conspecific and heterospecific trees in the community affect predator behaviour. In *T. versicolor*, timing of flower initiation, fruit maturation and dispersal differ by several months among individual trees (Foster 1977). If temporal satiation of predispersal seed predators takes place, trees fruiting closer to the population peak may suffer less mortality than those fruiting at other times (Augspurger 1981, Donaldson 1993). For post-dispersal predators, predator satiation may occur for late fruiting trees, as seeds tend to accumulate on the ground with time (Forget 1993, 1996; Wright 1990). These predictions imply that pests cannot consume all the seeds where and when seeds are most abundant, a limitation which would reflect the natural history of the pest species, such as their mobility, their generation time, and the duration of seed vulnerability (Ims 1990, Janzen 1971a).

Seed predator escape may also depend on ecological factors other than seed abundance, including microclimatic conditions (Kelly *et al.* 1992; Louda 1982, 1983), distances to other reproductive individuals (Janzen 1978, Silander 1978,

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Vandermeer 1974, but see De Steven 1983, Traveset 1991) and fruiting phenology of other species in the community (Forget 1992, 1993; Forget *et al.* 1994; Foster 1982). Fragmentation of a forested habitat and accompanying microclimate changes at the edges are known to affect pollination success, the level of seed abortion and seed output (Aizen & Feinsinger 1994, Murcia 1995, Renner 1998, Powel & Powel 1987), with consequences for the number of seeds available to predators. Environmental conditions and habitat types often influence pre-dispersal predation levels (Auld 1983, Auld & Myerscough 1986, Donaldson 1993, Willson 1988). Many studies have demonstrated that the probability of post-dispersal seed predation differs among habitat types; between the inside and the edge of a forest stand (Burkey 1993, Sork 1983), between open fields and woods (Webb & Willson 1985, Whelan *et al.* 1991; Willson & Whelan 1990), between forest stands of contrasting successional ages (De Steven & Putz 1984, Forget 1992, Hammond 1995) and between gap and forest microhabitats (Forget 1997b, Schupp 1995). In *T. versicolor*, the degree of predator satiation near parent trees was greater in the old forest than in the young forest (Augspurger & Kitajima 1992). Thus, it is important to address the influences of ecological factors associated with parent trees in a study of temporal dynamics of seed predation.

Our main question in this study was how pre- and post-dispersal seed predation rates would vary with time of dispersal and among trees. To meet this goal, we observed the phenology and among-tree variation in seed damage in the canopy tree *T. versicolor* on BCI. We examined two hypotheses with regard to predator satiation in time. The first hypothesis was that predation level should be highest for early-maturing seeds within a given tree. The second hypothesis was that both pre- and post-dispersal seed predation level should be highest for trees with long fruiting tail (asynchronous seed production) and/or overall early seed production (early mean fruit dispersal time). However, we also expected that the outcome would depend on habitat types where individual trees were standing. We chose three factors likely to affect pre- and post-dispersal predation levels on BCI: degree of relative isolation from conspecific fruiting trees, difference in forest type due to stand ages, and proximity to forest edges. We expected that predation level should be lower in trees standing in clumps than in isolated trees, because local seed density is higher for the former than the latter. We compared the predation levels between trees standing in old and young forest communities on BCI, because fruiting phenology of other species is likely to influence predator behaviour. Lastly, we examined the effects of proximity to forest edge, taking into consideration that BCI is a fragmented forest stand surrounded by an artificial lake.

STUDY SITE AND SPECIES

The study was conducted in 1990 in the tropical moist forest on Barro Colorado Island (BCI), Panama (Leigh *et al.* 1982). The forest on BCI consists of two

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types of contrasting ages: young (< 150 y) and old (> 500 y) (Foster & Brokaw 1982, Piperno 1990). The community has two fruiting peaks, the first peak in April-May (both wind- and animal-dispersed species) and the second one in September-October (animal-dispersed species) (Foster 1982).

Tachigali versicolor exhibits monocarpic reproduction. In the population of *T. versicolor* on BCI, 18 to 90 canopy trees initiated flowering in 1970, 1974, 1978, 1984, 1989 and 1993, and following seed dispersal in the following year, died rapidly (Foster 1977; R. Foster, *pers. obs.*). Asynchronous individuals flowering in other years were extremely rare; there may be one or two trees flowering on BCI during the year immediately preceding or mast years.

Seeds of *T. versicolor* are dispersed by the seasonal north-northeast trade wind during the dry season (January–April), i.e. when the number of fruiting species is increasing (Foster 1982). Each fruit is a flat symmetrical indehiscent samara (4 cm × 15 cm) and contains one large flat seed (dry mass = 500–600 mg, length 20–25 mm, Kitajima & Augspurger 1989). Seeds do not germinate until the second month of the rainy season (June). Seeds of *T. versicolor* suffer high pre-dispersal mortality from three bruchid beetles which, as yet, have been found on seeds of no other species. Bruchid beetles lay eggs only on green fruits, still on trees, whose exo- and endocarps are not yet tough and dry. These bruchid species do not have multiple generations within a given fruiting season (P.-M. Forget and K. Kitajima, *pers. obs.*). If the bruchid species on *T. versicolor* are host specific without alternate food sources for larvae, these bruchids have to survive as adults during intervening years when there are no *T. versicolor* fruits available in the region. After dispersal, seeds are eaten by terrestrial rodents. Preliminary surveys of over 50 trees fruiting in 1978 and 1985 found that both pre- and post-dispersal predation levels varied greatly among trees including some trees with 100 % seed mortality, but reasons for this variance was not examined (R. Foster, unpubl. data).

METHODS

Of 26 flowering trees of *T. versicolor* in 1989, we selected nine trees for this study (Figure 1, Table 1). We avoided trees that had suffered heavy crown damage from a storm in June 1989, trees that had severe loss of green fruits to parrots, and trees whose fruits matured very early. Since samaras are predominantly dispersed south of the parent trees (Kitajima & Augspurger 1989), we avoided trees on the Island's southern shore. Further, we chose trees more than 100 m from the nearest fruiting tree, to the north, in order to avoid overlap of seed shadows. With a map of all *T. versicolor* flowering on BCI in 1989 (Lyn Loveless, *pers. comm.*; Figure 1), we classified the relative degree of isolation from other conspecific flowering trees as 'scattered' and 'clumped', i.e. trees with no neighbour and trees with one or several neighbours within 100 m, respectively (Table 1 and Figure 1). Forest types (old vs. young forest) of trees were determined according to the vegetation map of Foster & Brokaw

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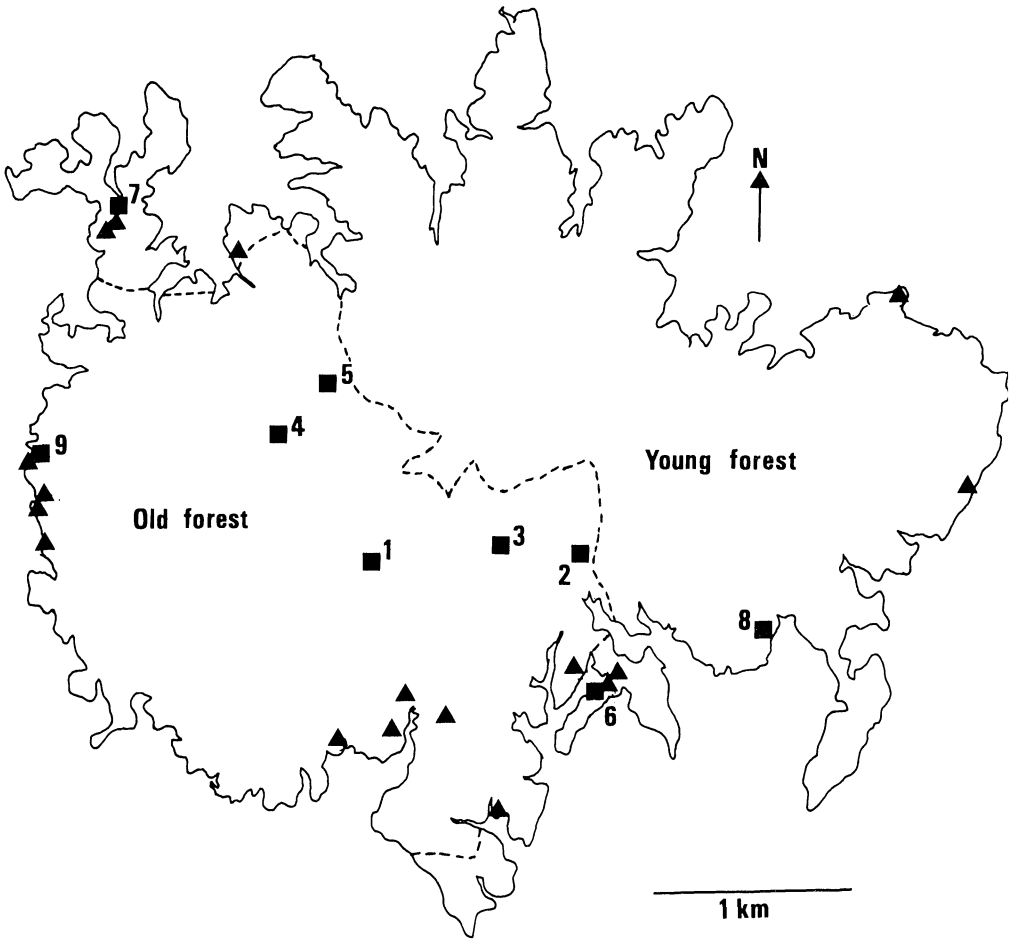


Figure 1. Map of Barro Colorado Island, Canal of Panama, with locations of reproductive *T. versicolor* trees in 1989 (L. Loveless, *pers. comm.*). Squares and triangles indicate location for fruiting trees included and not included in the study, respectively. Numbers refer to trees in Table 1.

(1982) and our direct observations (Table 1 and Figure 1). We also classified tree locations as 'inland' vs. 'edge', as the shore of the island is subject to more frequent and severe wind disturbance due to this edge effect (Murcia 1995) than inland locations. Incidentally, two of the three trees in clumps were in the young forest, and most sample trees in the young forest and one of the trees in the old forest were close to the edge of the island (Table 1 and Figure 1).

We quantified the level of pre- and post-dispersal seed predation by collecting dispersed samaras in above-ground traps (n = 3 per tree) and from ground quadrats (n = 3 per tree) placed within a 45–50° segment south of each of the nine study trees at 15–20 m from the base. Each trap and quadrat had the same area of 1.69 m^2 (1.3 m × 1.3 m). Traps were made of nylon shade cloth and hung at 1.8 m above the ground by tying them to nearby trees with

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Table 1. Summary of the data of phenology, pre-dispersal and post-dispersal seed predation and damage among nine *Tachigali versicolor* trees on Barro Colorado Island, Panama. Time was measured as number of weeks from 12 February 1990. Each tree was classified according to its phenology (E: early vs. L: late), location (I: inland vs. E: edge of the island), forest type (Y: young vs. O: old), and relative adult isolation (S: scattered vs. C: clumped).

Tree	1	2	3	4	5	6	7	8	9
Phenology	E	E	E	L	L	L	L	L	L
Location	I	I	I	I	I	E	E	E	E
Forest	O	O	O	O	O	Y	Y	Y	O
Distribution	S	S	S	S	S	C	C	S	C
Timing of dispersal of all seeds (wk)									
Median	0–2	2–4	2–4	4–6	2–4	4–6	4–6	4–6	4–6
Mean	1.5	2.5	4.0	4.7	5.0	5.1	5.2	5.4	5.7
SD	2.3	3.21	2.69	2.7	3.86	2.35	2.87	3.57	2.49
Timing of dispersal for mature seeds only (wk)									
Mean	2.01	3.28	4.13	8.0	5.13	6.42	7.03	5.27	8.73
SD	2.23	3.05	2.67	2.87	3.87	2.59	2.65	3.31	2.17
Skewness[1]	1.51	1.01	1.01	−0.30	0.68	0.89	0.14	0.74	−0.55
Kurtosis[1]	4.01	1.20	0.76	−0.41	−0.64	0.48	−0.73	−0.56	−0.95
CV	106	93.1	64.7	36.3	75.8	40.5	37.8	62.9	25.0
Number of seeds collected in traps	142	287	435	199	129	248	374	135	173
% all damaged[2]	35.2	34.1	31.7	33.2	31.8	73.8	37.2	40.0	63.1
% abortion[2]	7.7	7.7	8.0	10.1	6.2	41.1	20.3	17.0	28.4
% parasitism-all[2]	23.9	15.0	19.1	19.6	19.4	25	13.9	18.5	21.6
% parasitism-non-aborted[3]	26.0	16.2	20.8	21.8	20.7	42.5	17.4	22.3	30.2
Number of intact fallen seeds collected on ground	183	317	364	218	133	155	426	141	85
% all damaged[4]	58.5	36.3	31.3	17.9	22.6	76.8	65.7	64.5	10.6
% large rodents[5]	52.3	62.2	5.6	51.3	36.4	94.1	3.2	6.0	77.8
Number of seeds on ground	260	533	551	299	189	335	611	206	209
% all damaged[6]	70.4	62.1	54.8	42.8	45.5	89.3	76.1	75.7	71.8

[1] See Sokal and Rohlf (1980), pp. 114–119
[2] of the number of all seeds fallen in traps
[3] of the number of non-aborted seeds fallen in traps
[4] of the number of intact seeds fallen on ground
[5] of the number of intact seeds eaten by vertebrates
[6] of the number of intact and aborted seeds fallen on ground

strings. The ground quadrats were delimited with a string tied to plastic stakes at each corner. Traps and quadrats were positioned alternately at 2–3 m intervals. In order to capture a sufficient number of seeds to follow temporal patterns, we avoided setting traps and quadrats under dense palm foliage. The traps were set at six trees by 16 January, and at three others by 29 January. Thus, we did not collect data for the first 2-wk period for these three trees. All samaras and remains of torn samaras in traps and ground quadrats were collected biweekly between 12 February (time zero) and 20 May 1990, and brought to the laboratory to determine the type of damage.

Trap contents served to quantify pre-dispersal seed mortality, while ground quadrats were used for estimation of post-dispersal seed predation. A few samaras in the traps had beak marks and were torn open by parrots. We dissected

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all remaining samaras to examine the condition of the seeds inside. Seeds were classified as intact green (intact and green with soft integument), intact dry (intact and mature with hard integument), damaged (killed by abortion, bruchid beetle predation, other predispersal damage, or post-dispersal mammalian predation). Intact green seeds were yet to complete dehydration and hardening, but they had developed to the full size and would germinate normally in nurseries (K. Kitajima, *pers. obs.*). If seeds were extremely small (<10 mm long) or not visible, they were classified as aborted.

We described phenology both in terms of all fruits collected in the traps, as well as in terms of fruits containing intact dry seeds. For intact dry seeds, we also calculated skewness and kurtosis (Sokal & Rohlf 1980) of dispersal time for each tree. Skewness was used as a supplementary measure to mean and median to describe whether fruit dispersal timing was biased early or late within each tree. Skewness was positive if the peak of dispersal time occurred earlier, and negative if it occurred later, than the peak of a statistically normal distribution. In contrast, kurtosis was used to measure the degree of synchrony of fruit dispersal: positive if the distribution was more synchronous (peaked) and negative if is was less synchronous (flatter) than a normal distribution. Coefficient of variation (CV) was also a standard measure of the degree of synchrony (smaller for more synchronous seed production), but without a reference to a normal distribution .

Presence of an insect larva, pupa, adult, or exit hole on a samara was used as evidence of bruchid beetle infestation. We measured the diameter of exit holes with vernier callipers to ± 0.1 mm. As no larvae were of early instars, all bruchid oviposition must have taken place while fruits and seeds were still green, but not after fruits were dispersed. Percentage seed predation by bruchid beetles was calculated in two ways, (1) relative to the total number of seeds and (2) relative to the total number of non-aborted seeds. Post-dispersal seed predation by ground-dwelling mammals was quantified by counting torn-open samaras. For samaras shredded into pieces, we counted the number of peduncles in the collection. Beak marks of parrots were easy to distinguish from damage by ground-dwelling mammals. In both cases, vertebrate predators appeared to attack fruits containing intact seeds, but not aborted or beetle-infested seeds.

Due to small sample sizes for individual traps, we pooled contents of all traps and of all ground quadrats, respectively, at each tree for analysis. We used multivariate analysis of repeated measures with SYSTAT 7.0 (SYSTAT 1997) to examine the effects of census time, ecological factor associated with parent trees ('between subject effect') and interactions between them. In order to have sufficient sample size for each time period, data from several censuses at the beginning and at the end of censuses (week 0–2, 2–4, 4–6 and 6–14), resulting in four census times in the analysis. A separate analysis was run for each ecological factor, namely phenology type (early vs. late), habitat type (old

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vs. young), location (edge vs. inland), and relative isolation of adult tree (scattered vs. clumped). To be conservative, significance level should be set at $P = 0.0125$ according to Bonferonni correction to account for multiple testing with the same data set. Arcsine square-root transformations were applied when data were not normally distributed.

RESULTS

Fruit dispersal phenology

In total, 2125 and 3193 seeds were collected in traps and ground quadrats, respectively, between 29 January and 20 May 1990. Samples ranged from 129–435 seeds per tree from the traps, and 189–611 seeds per tree from the ground quadrats (Table 1). Median and mean of dispersal timing, determined as time from 12 February (time = 0), varied among the nine study trees (Table 1, Figure 2). The mean of mean dispersal timing for nine trees was 4.3 wk. Accordingly, we grouped trees into two phenology types, those with mean dispersal timing earlier than 4.3 wk ('early') and the rest ('late'), respectively (Table 1). Most dispersal timing of dry mature seeds was typically 1–2 wk later than that of all dropped fruits at each tree, but the phenology ranking of trees did not change. Skewness and kurtosis of the dispersal time of intact dry seeds varied greatly among trees (Table 1 and Figure 2). Mean dispersal time was negatively correlated with both skewness and kurtosis ($n = 9$ trees; Pearson's correlation coefficient, $r = -0.93$ and -0.81, respectively). In other words, trees with later mean dispersal time had less synchronous dispersal occurring later than expected from the statistically normal distribution.

Pre-dispersal damage and predation

Overall pre-dispersal mortality ranged between 32 and 75 % of seeds collected in the traps (mean = 42 % of nine trees). Most mortality was caused by infestation by bruchid beetles and abortion (mean = 20 and 16 %, respectively), while attack by parrots and apparent fungal damage accounted for the rest (6 %). Mean, skewness, and kurtosis of seed dispersal time for individual trees were not correlated with the level of pre-dispersal mortality by any cause ($r^2 < 0.42$, $P > 0.06$).

The level of seed abortion varied widely among trees, ranging between 6 and 41 % with an average of 16 % (Table 1). Abortion rate was higher near the shore ($F = 28.8$, $df = 1,7$; $P = 0.001$), among clumped trees ($F = 27.4$, $df = 1,7$; $P = 0.0012$), in the young forest ($F = 6.7$, $df = 1,7$; $P = 0.037$). Late fruiting trees suffered from somewhat higher abortion ($F = 5.3$, $df = 1,7$; $P = 0.055$). There was no effect of census time or interaction of time with any factor (all $P > 0.10$). The greatest contrast was observed in location comparisons; inland trees had much lower abortion rates (7.9 %) than edge trees (26.7 %). While abortion level remained low inland throughout (6–10 %), it decreased with time in edge trees (as high as 70 % in February, and <10 % in May) (Figure 3).

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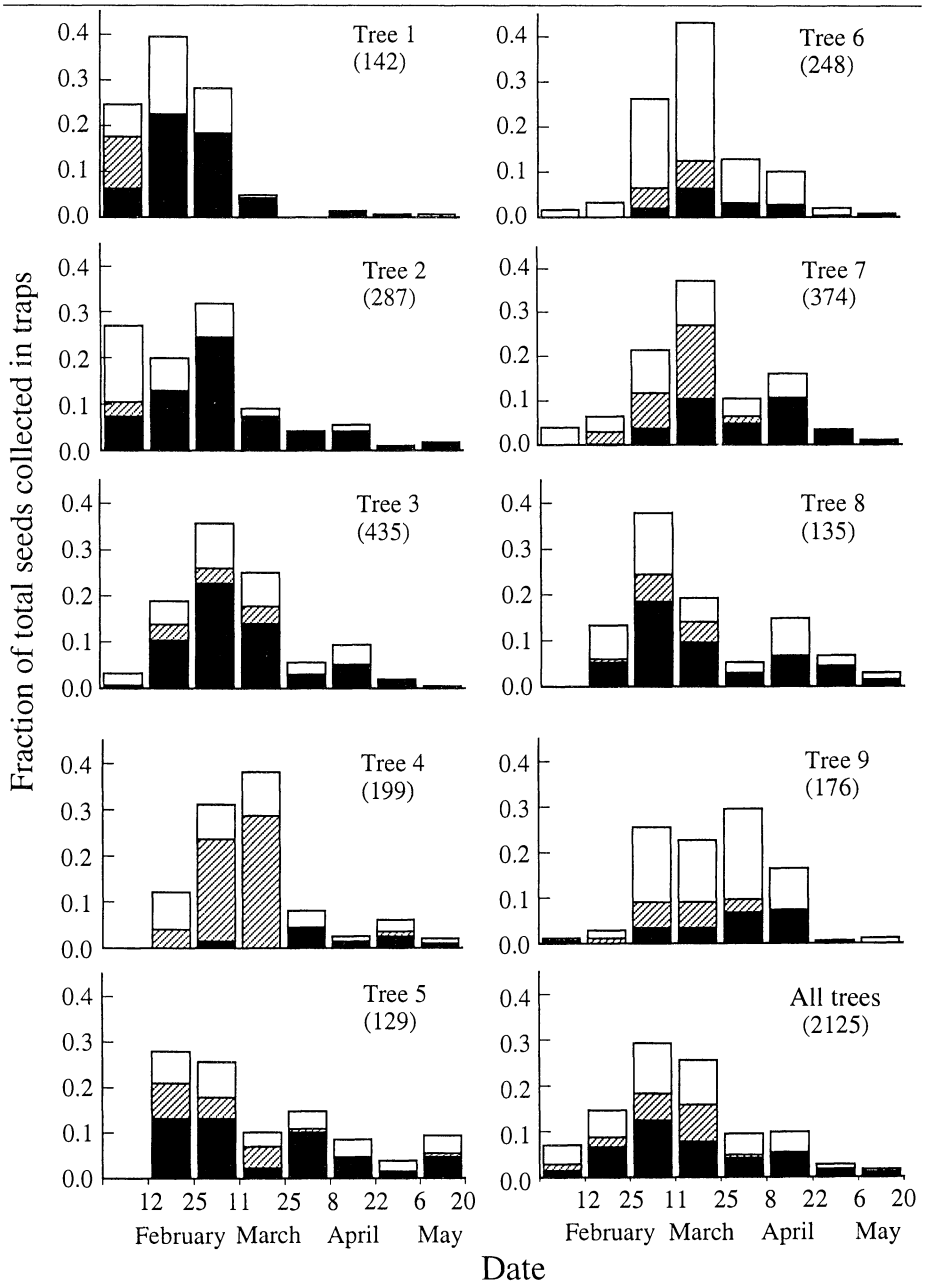


Figure 2. Temporal pattern of fruit fall and seed damage types for fruits collected in traps (n = 3 per tree) located outside the limit of the crowns of nine *Tachigalia versicolor* trees in Barro Colorado Island, Panama. The vertical axis is the percentage of the total number of fruits falling in traps between 16–29 January and 20 May 1990 (shown in parenthesis). Data for the first period are missing for three trees (no. 4, 5 & 8). Filled, intact dry seeds; hatched, intact green seeds; open bars, dead seeds (aborted, infested by bruchid beetles, consumed by parrots, or killed by other causes).

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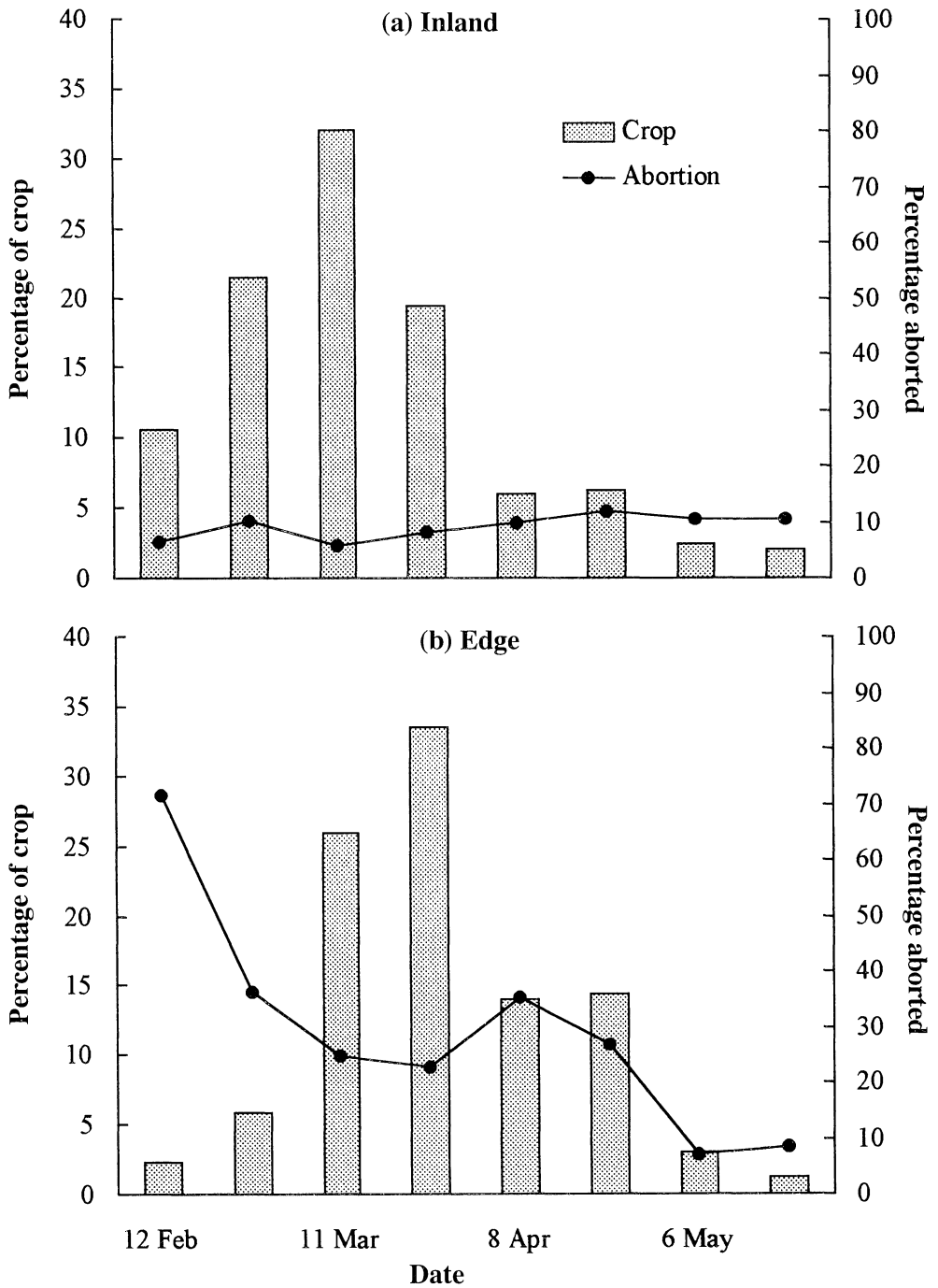


Figure 3. Temporal pattern of fruit dispersal and seed abortion levels in *T. versicolor* trees located (a) in the interior (n = 5), or (b) at the edge (n = 4) of Barro Colorado Island, Panama, in 1990. Abortion level is expressed as percentage of all fruits falling in traps in each 2-wk period. The first census period covered 2–4 wk depending on the exact dates when the traps were set up. See text for details of the census schedule.

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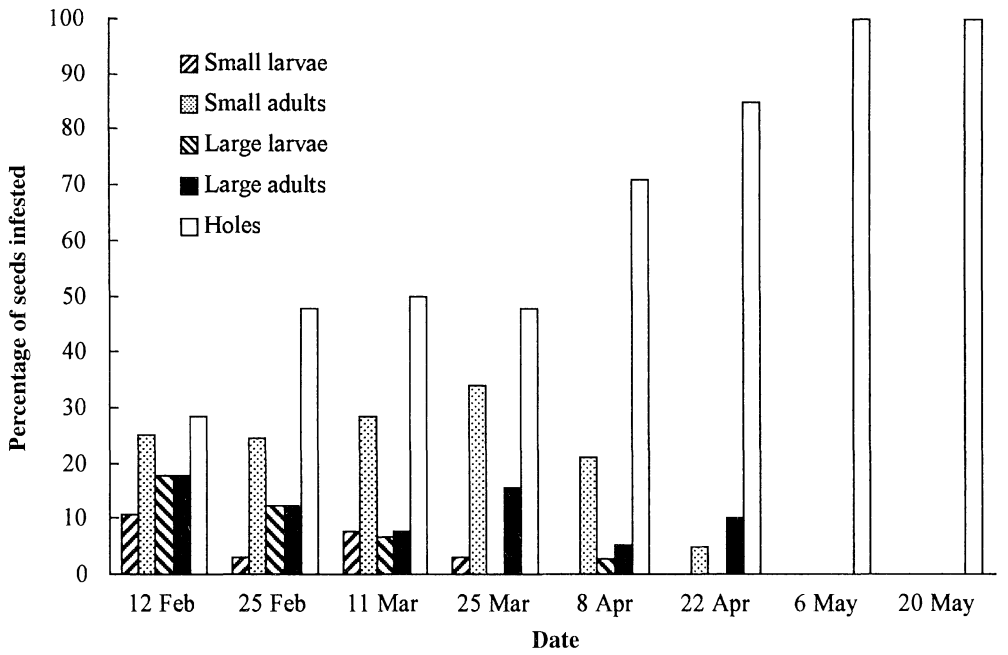


Figure 4. Temporal change of the relative representation of larvae and adults of small and large beetle species and emergence holes in *T. versicolor* fruits collected in traps, expressed as percentage of total bruchid-infested seeds collected during each census period ending on the specified date in 1990.

In addition to *Amblycerus tachigaliae*, a beetle which had been previously reported to infest *T. versicolor* seeds (Kingsolver 1976, Kitajima & Augspurger 1989), we found smaller bruchid species infesting our seed collections. They were less than 2/3 the body length of *A. tachigaliae*. Four samples of these beetles were identified as two undescribed species in an undescribed genus close to *Sennius* in Bruchidae (J. Kingsolver, *pers. comm.*). We did not distinguish the two small species; they were similar in body size and morphology and their adults emerged much earlier than *A. tachigaliae* (Figure 4). Smaller holes were probably made by the two smaller bruchid species, but the overlap between the sizes of their holes and those of *A. tachigaliae* holes was great enough so that holes made by *A. tachigaliae* could not be distinguished unambiguously from the others (Shapiro-Wilk W-test, $P < 0.0001$; the primary peak at 3.5 mm and a second and smaller peak at 5.5 mm, range 1.7 mm to 7.5 mm, $n = 547$). Of all seeds ($n = 178$) containing larvae or adults, *A. tachigaliae* accounted for 79 %. The actual proportion of fruits infested by the smaller beetle species was perhaps higher, because the smaller beetle species had overall earlier time of emergence (Figure 4) and many probably had emerged before seed collection. The level of bruchid predation remained relatively constant through time at about 20 % of the total fruits or 24 % of the non-aborted seeds (Figure 5). Bruchid predation was not significantly affected by time or any of the four ecological factors examined in the analysis of repeated measures (all $P > 0.10$).

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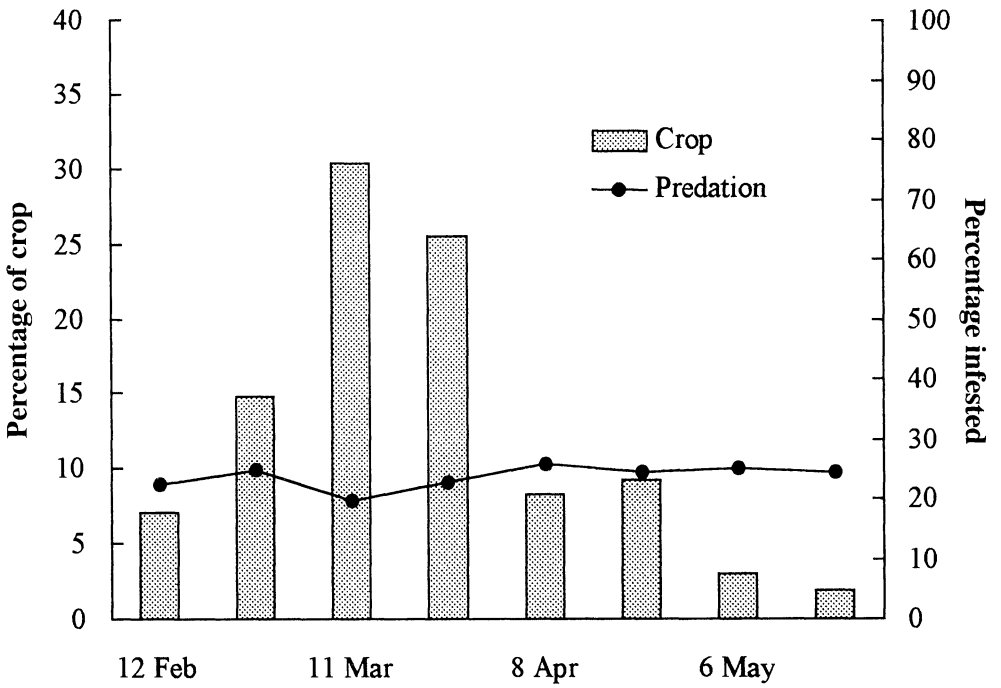


Figure 5. Temporal pattern of fruit fall (bars) and average percentage of seed parasitism by bruchid beetles (solid circles) in all nine *T. versicolor* trees sampled on Barro Colorado Island, Panama, in 1990. Percentages are expressed of all full-size fruits excluding those with aborted seeds. See text for sampling periods.

The level of bruchid predation, when expressed as a proportion of non-aborted seeds, was correlated with the level of abortion ($r^2 = 0.77$, $P = 0.015$ with arcsine-square root transformation of both variables). The level of pre-dispersal mortality by all causes was higher for trees near island edges ($F = 8.04$, $df = 1,7$; $P = 0.025$) and for trees with conspecifics nearby ($F = 12.1$, $df = 1,7$; $P = 0.010$), while fruiting phenology and forest type were not significant factors ($F < 3.5$).

Post-dispersal predation

Post-dispersal predation was only by mammalian vertebrates. Two types of damage could be recognized on the fruit remains. In the first type, pods were open on both sides with tooth marks of 5–6 mm in width, perhaps made by large rodents, most likely by *Dasyprocta punctata*. In the second type, pods were torn apart into small pieces, presumably by small rodents such as *Proechimys semispinosus* and *Oryzomys* spp. or by deer *Mazama americana*. The occurrence of these two types of damage varied from tree to tree without any particular trends. The level of post-dispersal predation by terrestrial vertebrates depended on forest type ($F = 10.71$, $df = 1,7$; $P = 0.014$) but not on fruiting phenology, proximity to edge, or isolation from other conspecific fruiting trees

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(all $P > 0.26$). There was no effect of time or its interaction with these ecological factors (all $P > 0.11$). On average, seed predation by terrestrial vertebrates was 30 % in the old forest versus 69 % in the young forest. Contrasting temporal patterns of post-dispersal predation levels were observed between old and young forest. In the old forest, the level of post-dispersal predation was high at the both tails of the fruiting period and low during the peak fruiting time, whereas in the young forest, it rapidly increased with the seasonal increase of seed fall and remained high (Figure 6).

Overall seed predation

There were significant effects of both location ($F = 14.95$, $df = 1,7$; $P = 0.006$) and forest type ($F = 7.96$, $df = 1,7$; $P = 0.026$) on overall seed mortality as a cumulative consequence of pre- and post-dispersal seed predation. The average seed predation was 55 % in the inland locations and 78 % at the edge of the island. When forest types were compared, overall seed predation level was 58 % in the old forest versus 80 % in the young one. Because these ecological factors associated with the trees were correlated with each other in this study, we can not analyze interactions among them.

DISCUSSION

Was there predator satiation?

Our results suggest temporal satiation of seed predators in *T. versicolor* trees only after dispersal, and only in trees in certain areas. Post-dispersal seed predation rate by ground-dwelling vertebrates in the old forest site was lower during the peak fruiting time than at the beginning and the end of the fruiting period. But, this pattern was not found in the young forest. If predation level was lower in trees with conspecifics fruiting nearby than in isolated trees, it would suggest an occurrence of local predator satiation. However, neither pre- or post-dispersal predation level was affected by the degree of adult tree isolation.

We predicted that if seed predators are satiated in time, seed mortality should be highest for early maturing trees (i.e. early mean dispersal time and positive skewness) and lowest for trees maturing seeds later and/or in trees that mature seeds more synchronously (i.e. with high skewness of dispersal time within a tree). Timing and degree of synchrony in fruit maturation and dispersal were not important sources of variation in predation levels among trees. However, our results should be interpreted with caution, because fruiting phenology was confounded with proximity to edges and forest type, which affected the seed abortion levels and post-dispersal predation levels, respectively.

Factors responsible for seed abortions

Seed abortion was more important than seed predation in determining phenological patterns of predispersal seed mortality in *T. versicolor* as in other

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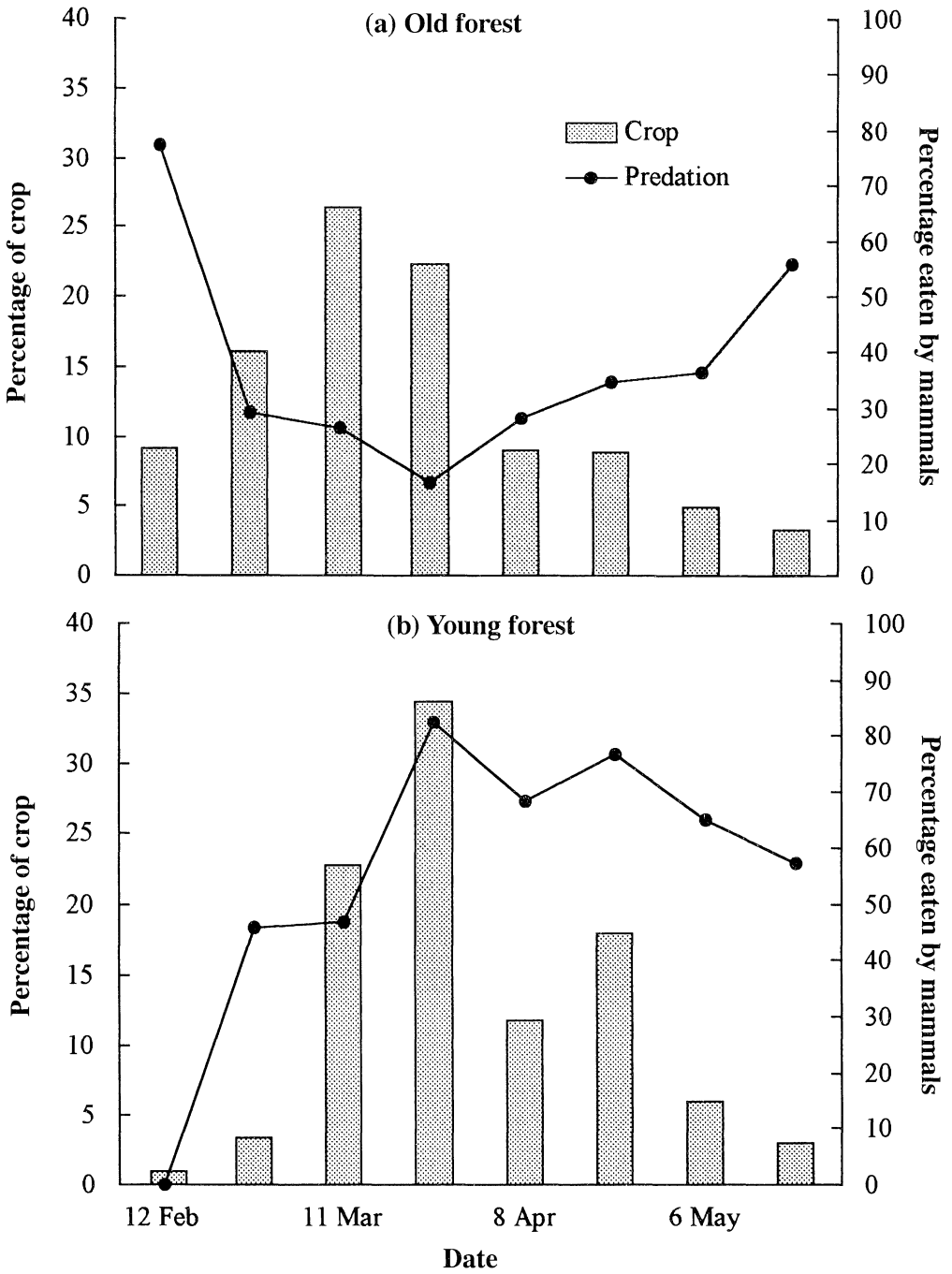


Figure 6. Temporal patterns of fruit fall (bars) and average percentage of vertebrate seed predation (dots) in *T. versicolor* trees in (a) the old (n = 6), and (b) the young forest (n = 3) of Barro Colorado Island, Panama, in 1990. Percentages are expressed of all full-size intact fruits (i.e., excluding those with pre-dispersal damage) falling on the ground quadrats (n = 3 per tree). See the text for sampling periods.

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tropical species (e.g. Augspurger 1981, Traveset 1995). Both seed abortion level in full-size fruits and overall seed mortality declined with time for trees fruiting near shore but not inland, the former tending to be more clumped than the latter (Fig. 3). However, as these three factors were highly correlated with each other for the nine study trees, it is impossible to conclude unambiguously which of these factors was actually responsible for the observed pattern.

Ovule and ovary abortions may be due to failure of pollination, especially in fragmented habitats (reviewed by Renner 1998), resource limitation, attack by seed predators, or inbreeding depression (reviewed by Wiens 1984). Adults flowering synchronously in clumps may attract more pollinators from farther away (Augspurger 1981). However, if pollination is restricted within a clump and trees within a clump are genetically related to each other, clumped trees may suffer from inbreeding depression and consequent seed abortion. Clumped adult trees may also attract more ovipositing bruchid beetles. As typical for many legumes, seeds of *T. versicolor* fill after pods reach their full size. If beetles oviposit on pods whose seeds are yet to develop, such pods containing minute seeds may be dropped soon, as found for two tropical shrub species (Augspurger 1981, De Steven 1981). Elevated levels of seed abortion in clumped trees may thus be a response to bruchid beetle oviposition. High abortion level in the edge habitat may also be due to unfavourable microenvironmental conditions at the island edges. Strong winds and drier conditions at the island's edges may cause a physiological stress and resource limitation on trees at the edges of fragmented forests (Solbreck & Sillén-Tullberg 1986, Kapos 1989, Kapos *et al.* 1993).

Lack of satiation in pre-dispersal seed predation

Apparently, selection was not strong enough to synchronize fruiting phenology of *T. versicolor* within a given year. Mean dispersal time of mature dry seeds varied by more than 2 mo among nine study trees. Individual seeds are developmentally appropriate for successful colonization by bruchid larvae only for a short time (Center & Johnson 1974, Toy & Toy 1992, Traveset 1991). Population sizes of adult beetles are finite and decline with time, because the three bruchid species attacking *T. versicolor* do not have multiple generations within a given fruiting year. Given these, escape from these bruchids should be promoted by synchronous fruiting within a crown or within the tree population. However, predation level was not correlated with kurtosis (peakedness relative to a normal distribution) and CV of dispersal timing of mature fruits. Nor was there a significant tendency of a lower predation level for individual fruits maturing at the peak fruiting time of a given tree or of the population. Whether fruiting and dispersal occurred early or late did not influence the level of predispersal predation either. Adults of the two smaller beetle species appear to emerge earlier than the larger beetle species, *A. tachigaliae*. Interactions among multiple bruchid species (Johnson 1981, Southgate 1979) may influence the overall level and temporal dynamics of seed predation. What

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remains unknown, but potentially important for temporal dynamics of predispersal predation, is the timing of attack by each beetle species relative to development of individual seeds and fruits.

Masting and longer inter-mast intervals are considered to help satiate predators (Janzen 1971a, b, 1975a, 1976; Silvertown 1980, Kelly 1994). The current masting behaviour in *T. versicolor* may be ensuring escape of some seeds from bruchid beetles. However, we cannot reject other potential advantages of reproductive synchrony, such as attracting pollinators (Augspurger 1981), and storing sufficient reserves until favourable weather conditions for flowering occur (Fenner 1991), as key selective forces for the supra-annual reproductive synchronization of *T. versicolor*. The level of bruchid infestation for a tree on the mainland that fruited in 1989 out of synchrony was high (25 % of 433 fruits collected from the ground were infested by beetles; K. Kitajima, unpubl. data), although within the range for the nine trees reported here (14–25 %). In contrast, other studies have found that trees fruiting in non-masting years suffer vastly higher seed predation than trees fruiting in mast years (Auld 1986, De Steven 1983, Donaldson 1993).

Although the level of bruchid beetle attack may differ between habitat types (Janzen 1975b), we found no clear difference in overall bruchid predation levels between the forest types or between the edges and the inland. Neither did we find a significant effect of local adult density on pre-dispersal seed predation levels. In other studies, a greater number of seeds escape predation when local fruit density is high but it is not necessarily related to tree clumping (Augspurger 1981, Augspurger & Kitajima 1992, De Steven 1981, Franson & Willson 1983).

Timing of bruchid infestation in *T. versicolor* had almost no overlap with the timing of post-dispersal seed predation by rodents. Most beetles had either emerged (223 of 401 infested seeds) or were adults that were ready to emerge (72 % of the remaining infested fruits) at the time of seed collection (Figure 4). This may be advantageous for the bruchid species in avoiding accidental consumption by rodents. The percentage of trapped fruits infested by bruchid beetles (mean = 19.6 % for the nine trees) was not significantly higher than the percentage of bruchid-infested seeds collected from the ground (15.8 %). Thus, rodent seed predators probably avoided fruits contained bruchids or aborted seeds.

Most studies of pre-dispersal predation, including this study, focused on invertebrate seed predators (Crawley 1992). Parrots, monkeys, and arboreal rodents, however, may cause major seed losses. Unfortunately, removal of fruits by these arboreal vertebrates is hard to quantify and appears to vary more from tree to tree. During the late part of fruit maturation, parrots (Psittacidae spp) attacked some trees, causing almost complete destruction of green fruits when seeds were still green inside. Parrot attack is apparently limited to a narrow window of time. In two of our nine census trees, 12 and 6 % of trapped

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fruits were killed by parrots. Much higher levels of parrot damage would be found had we included trees with severe parrot damage. Diet selection by parrots (Galletti 1993, Higgins 1979) and how spatial and temporal patterns of parrot predation modify the potential advantage of reproductive synchrony deserve future attention.

Janzen (1976) remarked that seeds of masting species, such as bamboos, are generally not toxic. *T. versicolor*'s seeds, however, apparently contain a high level of alkaloids (R. Foster, unpubl. data). Based on the analysis of 38 bruchid species and 44 host plant species, Center & Johnson (1974) concluded that bruchid beetle species have evolved to circumvent defensive responses of host plants, including toxins and synchronized seed set. Our results are in agreement with this conclusion, given the lack of advantage of synchronization against bruchid beetles. Yet, synchronization of *T. versicolor* seeds may be important for local satiation of post-dispersal mammalian seed predators.

Satiation of post-dispersal predation: the importance of habitat

The extent of predation of *T. versicolor* seeds by terrestrial vertebrates was highly dependent on habitat type. We found a greater level of predator satiation in old than in young forest, as found during the 1985 fruiting episode (Augspurger & Kitajima 1992, Kitajima & Augspurger 1989). Predation of *T. versicolor* was lowest during the peak time of fruit dispersal (March 1990) in the old forest, but it increased and remained high during the fruiting period in the young forest. The level of post-dispersal seed predation by rodent seed predators is strongly influenced by the availability of alternative and more desirable food sources in the community (Forget 1992, 1993, Forget *et al.* 1994). In both young and old forests, we occasionally saw fruiting trees of other species near *T. versicolor*, that may have been more attractive to seed predators. For instance, *Dipteryx panamensis* (Papilionaceae) was fruiting near the tree 7 (in young forest), which had the lowest proportion of seed damage from large rodents (with large teeth marks) of any of the nine sample trees. In *Dipteryx* as well, rodent damage level was lowest in March 1990 (Forget 1993), suggesting a community-wide temporal satiation of rodent seed predators in the old forest (see also De Steven & Putz 1984). In contrast, there were no plants producing fruits suitable for agoutis near our tree 6 (also in young forest) when it was fruiting and this tree suffered the highest level of attack by large rodents. Besides differences in plant species composition and food availability, rodent populations may also be highly different between locations within BCI (Glanz 1990, Wright *et al.* 1994). The level of seed removal and of seed predation may be higher in forest habitat where the diversity and density of rodents are greater (Forget *et al.* 1998, Osunkoya 1994). Future studies of post-dispersal seed removal and predation by terrestrial seed predators should be coupled with better description of habitat attributes including alternative food resources available in the community.

Local satiation of seed predators is a case of positive density dependency of

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seed survival, which has received much less attention than negative density dependency in the history of tropical tree recruitment ecology (e.g., Clark & Clark 1984). Nevertheless, satiation of rodent-seed predators may be a common and important mechanism for successful recruitment of tropical trees as found by Burkey (1994) for *Brosimum alicastrum* and Schupp (1992) for *Faramea occidentalis*. The outcome of local predator satiation during the seed and early seedling stage in *T. versicolor* continues to be a determining factor of local distribution of recruits even 4 y after germination (Augspurger & Kitajima 1992). Positive density dependency deserves more attention, given masting and irregular seed production is widespread among tree species in tropical forests.

Following the creation of BCI about 1914, the structure and dynamics of the forest at the edges of this island have been greatly changed. Wind perturbation is common at the island edges where trees are directly exposed to the wind sweeping across the lake surface (see Leigh *et al.* 1993). Recruitment and growth of *T. versicolor* may have been promoted in the edge habitat, as this species exhibits a very high phenotypic plasticity and positive growth response to increase in light availability (Kitajima & Augspurger 1989). However, currently, recruitment probability of seedlings appears to be low in these trees occurring in clumps at the forest edge, due to the high levels of seed abortion and post-dispersal seed predation. At a regional scale, even the 'inland' locations on BCI should be classified as a part of a fragmented habitat. Results from similar studies in more continuous forests, when compared to our results, will contribute to a better understanding of ecological or environmental effects of habitat fragmentation on seed abortion, seed predation and seedling recruitment. These observations point to the importance of seed ecology and long-term studies in examining tree population dynamics.

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