Effects of forest edges, fruit display size, and fruit colour on bird seed dispersal in a New Zealand mistletoe, *Alepis flavida*

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Abstract: This study examined how forest edges, fruit display size, and fruit colour influenced rates of seed dispersal in an endemic, bird-dispersed, New Zealand mistletoe species, *Alepis flavida*. To examine rates of seed dispersal, fruit removal rates were compared between plants growing on forest edges and in forest interior, and also between two morphs of plants with different coloured fruits. Two aspects of fruit display size were examined: plant size and the neighbourhood of conspecific plants. There was no overall difference in fruit removal rates on forest edges and in forest interior, but birds removed fruits from red-fruited plants at a faster rate than from orange-fruited plants. Proximity of plant neighbours interacted with edges to influence fruit removal rates. The smaller the distance to nearest neighbours, the greater the fruit removal rates for orange-fruited plants in both habitats, but this relationship was significant for red-fruited plants only in the interior. Plant size affected fruit removal rates for orange-fruited plants, but not for red-fruited plants, and these differences were consistent in both habitats. Thus, fruit colour had the strongest effects on rates of fruit removal in this system, but forest edges also affected fruit removal rates, via altering the effects of neighbouring plants. Although birds prefer red fruits, there appears to be little selection pressure against orange-fruited plants because fruit removal rates are very high for both morphs.

Keywords: *Alepis flavida*; edge effect; forest fragmentation; frugivory; fruit colour; fruit display size; fruit removal rates; mistletoe; seed dispersal.

Introduction

Habitat fragmentation is a major contributor to the increased rates of species extinctions worldwide in the past decade (Cracraft and Grifo, 1999). There are many components of habitat fragmentation, including patch size, connectivity, and surrounding matrix, but one of the most important components is edge effects. Recent studies have shown edge effects for a variety of both plant and animal species (Laurance *et al.,* 1998; Kremsater and Bunnell, 1999; Davies *et al.,* 2000; Gehlhausen *et al.,* 2000). However, we know very little about the mechanisms responsible for differences in population densities in edge *v.* interior environments. Forest edges have been shown to affect plants by altering the physical environment, either the availability of resources or the microclimate (Laurance *et al.,* 1998; Sizer and Tanner, 1999). More interestingly, forest edges can alter important interactions that plants have with animals, including herbivory, pollination, and seed dispersal. Cunningham (2000) found that insect fruit predation was higher in linear strips of woodland habitat than in large reserves. Aizen and

Feinsinger (1994) studied 16 plant species in tropical dry forest, and consistently found decreased pollination rates in more fragmented habitats than in continuous forest, whereas other studies have found increased pollination rates on edges (Jules and Rathcke, 1999; Kelly *et al.,* 2000; Kremen and Ricketts, 2000). Dispersal of seeds has also been shown to be more effective on edges (Restrepo and Gomez, 1998; Restrepo *et al.,* 1999; Dale *et al.,* 2000).

Edge effects on rates of seed dispersal by animals can result from a number of different mechanisms. Animal densities or foraging patterns could vary in edge *v.* interior habitats. Alternatively, the importance of other factors influencing dispersal rates could differ on forest edges and in forest interior. One important factor influencing seed dispersal rates is fruit display size. In the case of birds, rates of fruit removal are influenced by plant size and vigour (Jordano and Schupp, 2000) and the presence or absence of neighbouring plants that are fruiting at the same time (Nogales *et al.,* 1999). It seems likely that bird seed dispersers might respond differently to plant size or the presence of fruiting neighbours in edge habitats (with

their associated greater visibility) than in forest interior.

The purpose of this study was to investigate effects of forest edges on rates of seed dispersal in the native New Zealand mistletoe, *Alepis flavida* (Loranthaceae). Declines in the populations of all seven native species of New Zealand mistletoes are of concern because five of the species are endemic to New Zealand; six of the species are officially categorized as "threatened" (Norton and Reid, 1997). No studies have examined edge effects *per se* on mistletoes, but effects of forest fragment size have been investigated for one mistletoe species. Kelly *et al.* (2000) found that smaller forest fragments had improved reproduction in the New Zealand mistletoe, *Peraxilla tetrapetala*, because flower predation decreased and pollination success increased in fragmented habitats. In that study, there was no apparent trend in seed dispersal rates with forest fragment size.

Seed dispersal is particularly critical for New Zealand mistletoes for two reasons. First, past research on mistletoes has shown that seed dispersal is not adequate in some years (Ladley and Kelly, 1996). Recent evidence suggests that bird scarcity may be responsible for inadequate mistletoe dispersal, as well as pollination (Robertson *et al.,* 1999; Murphy and Kelly, 2001). Second, and most important, seedling recruitment is absolutely dependent on bird dispersal, because birds must defecate seeds onto branches of host trees for seed germination to occur (Ladley and Kelly, 1996). Thus, in the case of mistletoes, fruit removal rates by birds are identical to seed dispersal rates, at least in terms of dispersal quantity (*sensu* Schupp, 1993). For this reason, fruit removal rates were used as the measure of seed dispersal rates in this study. It must be noted that dispersal quality (e.g. whether seeds are voided by birds in germinable condition and what fraction of seeds are voided onto suitable host branches) was not addressed in this study.

The question of bird seed dispersal is of particular interest for *Alepis flavida* because of the existence of a polymorphism in fruit colour. Plants either have fruits that ripen from green through yellow to orange, or from green through yellow and orange to red. Fruit colour influences rates of frugivory in other systems (Willson *et al.,* 1990) and birds prefer red over orange fruits in another plant that is polymorphic for fruit colour, *Rubus spectabilis* (Traveset and Willson, 1998; Gervais *et al.,* 1999). It seems likely that colour preferences might vary on forest edges and in forest interior, because of their associated differences in visibility.

This study addressed four specific questions: (1) Do rates of fruit removal vary on forest edges and in forest interior? (2) How do conspecific fruiting neighbours and plant size influence rates of fruit removal? (3) How do fruit removal rates vary for red-fruited *v.* orange-fruited plants? and most importantly, (4) Do effects of neighbours, plant size, and/or fruit colour vary on forest edges compared with forest interior (i.e. are there interactive effects)? We predict greater fruit removal rates for plants growing on forest edges, for larger displays of fruits (larger plants and/or plants with more neighbours), and plants with red fruits. We also predict that these preferences will vary for plants growing on forest edges and forest interior.

Methods

The system under study

The loranthaceous mistletoe, *Alepis flavida*, has been reported on nine indigenous host species in New Zealand, but *A. flavida* is the most host-specific of all the New Zealand mistletoes, with over 80% of host records from *Nothofagus solandri* (Norton, 1997). Flowering occurs from January to February, and a lepidopteran feeds on flower buds (C. E. Bach and D. Kelly, *unpubl.*). In a related mistletoe species, *Peraxilla tetrapetala*, flower predation by a specialist caterpillar destroyed up to 48% of the flowers on a plant (Kelly *et al.,* 2000). Although birds are essential pollinators of flowers of related mistletoes in New Zealand (Robertson *et al.,* 1999), *Alepis flavida* can self-pollinate, and thus does not require birds for pollination (Ladley *et al.,* 1997).

Fruiting in *Alepis flavida* occurs from March to May. Fruits are dispersed by several native New Zealand bird species: bellbirds (*Anthornis melanura*, Meliphagidae), silvereyes (*Zosterops lateralis,* Zosteropidae), and tuis (*Prosthemadera novaeseelandiae,* Meliphagidae). Ripening fruits first become yellow and then orange. In some plants, orange fruits ripen further to red (henceforth called red plants), whereas in other plants even over-ripe fruits remain orange (henceforth orange plants). This existence of two colour morphs of plants has not been previously reported for *A. flavida*, but has been found in other plants with fleshy, animal-dispersed fruits (Willson, 1983; Willson and O'Dowd, 1989; Traveset and Willson, 1998; Traveset *et al.,* 2001), including a lizard-dispersed New Zealand species, *Coprosma cheesemanii* (Lord *et al.,* 2002).

Rates of fruit removal

To examine the patterns by which forest edges influenced fruit removal rates, a field experiment was conducted at Jacks Pass (43° 09'S, 171° 43'E, elevation 940m a.s.l.) in Craigieburn Forest Park, South Island, New Zealand. The site has been used for previous studies on mistletoe reproduction (Ladley and Kelly,

1996; Ladley *et al.,* 1997; Robertson *et al.,* 1999; Kelly *et al.,* 2004). At this site, the host for *Alepis flavida* is mountain beech, *Nothofagus solandri* var. *cliffortioides*. For the principal study, nine to ten individuals of *A. flavida* were chosen at each of six sites: three sites with plants occurring next to roads (henceforth designated as "forest edge"), and three sites with plants occurring in forest interior, which was defined as occurring at least 10m (but in practice usually > 50m) from a road or opening (henceforth designated as "forest interior"). The three edge sites were along roads traveling north, east, and southeast from Jacks Pass, and each interior site was nearby one of the edge sites. Thus, edge and interior sites were interspersed throughout the study site, which is completely forested except the roads that receive very little use. At each site, we chose study plants varying in neighbouring-plant densities, from fairly isolated individuals to plants with a number of close neighbours of *A. flavida*, thus providing a good range of plant densities. All study plants were chosen so that they could be reached without a ladder. The study included a total of 29 edge plants and 28 interior plants, because only nine plants were located at one edge and two interior sites.

All plants were tagged on 10 January 1998 and fruit production and fruit removal rates were then measured from March through June. On each of ten dates (1, 13, 19, 25, and 31 March, 8, 15, and 30 April, 12 May, and 9 June), fruits were counted and categorized as: unripe, yellow, orange, red, or overripe (= over-mature).

Because we calculated rates of fruit removal indirectly from fruit counts (i.e. using disappearance of fruits as a measure of fruit removal by birds), rather than directly from observations of bird foraging behavior, it was necessary to conduct several additional experiments to: (1) confirm the rate of natural fruit abscission in the absence of birds (the mesh bag exclosure experiment; see below), (2) confirm that birds were removing different colours of ripe fruits as well as overripe fruits (the marked fruit experiment; see below), and (3) confirm the rate of fruits being knocked off plants during bird foraging (the fruit trap experiment; see below).

Mesh bag exclosure experiment

To determine how long fruits stay on plants when birds do not have access to fruits, we conducted an exclosure experiment using ten branches on ten different plants. These plants were located in one of the edge sites ($n = 5$) and one of the interior sites ($n = 5$). The fruits on each of the experimental branches were counted on 14 March 1998, and then a mesh bag was placed over each branch. On each of six dates in the next 6-week period (19, 26, and 31 March, 8, 15, and 30 April), the mesh bags were carefully removed, and the number of fruits on each branch was counted, divided into the same ripeness categories as above. The fruits that had fallen off into each bag were also counted and removed. Because cages had to be removed in order to count fruits (which provided some disturbance), these data probably slightly over-estimate natural fruit abscission rates in the absence of birds.

Marked fruit experiment

To calculate disappearance rates for different colours of ripe and overripe fruits, a marking experiment was conducted. On each of nine of the 57 study plants (1–3 plants at each of four sites), eight inflorescences were marked with coloured wire on 14 March 1998. Six of these were orange plants, and three were red. The fate of each fruit was followed as we had recorded its position on the inflorescence. The marked inflorescences were sampled every 2–8 days for a period of 1 month (16, 18, 23, 26, and 31 March, 8 and 15 April).

Fruit trap experiment

To directly measure the number of fruits knocked off (rather than consumed) during bird foraging, fruit traps made of white cloth sheets (approximately 1m × 1m) were placed on the ground and anchored with stakes under six of the plants used in the marked fruit experiment on 13 March. Counts of all fruits present in the sheets were made on 19, 25 and 31 March, and 8 and 15 April. Obviously the rates of fruit fall into these traps include not only fruits being knocked off during bird foraging, but also fruits naturally abscising from plants. Analyses found no significant difference between mean fruit removal rates on the six plants with sheets on the ground ($\bar{x} = 8.9 \pm 0.9\%$ fruits removed/day) compared with plants without sheets ($\bar{x}$ $9.8 \pm 0.3\%$ fruits removed/day), thus data for the six plants with sheets were included in all analyses.

Plant size and neighbour sampling

As an index of plant size, the total number of leaves on each plant was counted on 23–25 March. The methodology for sampling neighbouring plants involved locating the four closest fruiting plants of *Alepis flavida* to each study plant, constrained by a maximum search distance of 5m (including vertically). Only fruiting neighbours were sampled, because we were interested in how bird seed dispersers would respond to the size of fruiting displays. For each neighbouring plant, the following information was recorded: (1) distance from study plant, (2) length, width, and height of each plant (to allow a calculation of volume, assuming that the shape of each plant was approximated by an ellipsoid, as in Norton *et al.,* 1997).

To determine whether bird seed dispersers might

also be responding to size and/or proximity of neighbours, neighbour size (volume) and neighbour proximity (distance) were analyzed separately. Because the scale of neighbour effects can never be known beforehand, neighbour variables were analyzed at two different scales: the nearest neighbour (volume; distance), and the neighbouring community, which included the four closest neighbours within the 5m sampling area (total volume; mean distance). Because these latter variables would only be valid if all plants had four neighbours, the missing neighbours for each plant with less than four neighbours within 5m were coded as having a volume of 0 and a distance of 510cm. Obviously, this mean distance represents a lower bound, because the next closest neighbours may in fact have been much farther away. Only analyses of the neighbouring community (four closest neighbours) are presented, because analyses at the scale of the single nearest neighbour showed very similar patterns.

Sugar concentrations as a function of fruit colour

Fruits were analyzed for sugar concentration in 2001. Fifteen plants of the 57 tagged in 1998 (9 red; 6 orange) were located on 22 March, all ripe fruits were removed, and mesh bags were placed over the remaining unripe fruits on each plant (so that all fruits collected on the next visit would be of approximately the same age). On 12 April, 8–10 ripe fruits were then collected from each plant, and the percentage of sugar was then measured on each fruit individually, using a refractometer. We compared the sugar concentrations of orange *v*. red plants by using *t*-tests with means of the individual fruits for each plant.

Analyses

To assign a colour morph status to each plant, we used several criteria. Clearly, all plants that had at least one red fruit present on any sampling date were designated as red plants ($n = 26$). If a plant had over 20 orange fruits and no red fruits over the season, then it was designated as an orange plant ($n = 24$). If a plant had less than 20 orange fruits and no red fruits over the season, then it was designated as an orange plant only if there were significantly more orange fruits than expected by chance, based on the proportion of red fruits on known red plants, and tested by a χ^2 test ($n = 2$). Five plants could not be definitively assigned to a colour morph category because they had no ripe fruits, only yellow fruits, or 3 or fewer orange fruits. These five plants were revisited in 2001, and one more identification was verified (orange); the other four plants were either not fruiting in 2001 or could not be located. The above criteria are conservative in that results from the marked fruit experiment, in which a total of 62 orange fruits were marked on red plants,

showed that there was not a single case of an orange fruit on a red plant remaining orange for more than two days.

Fruit removal rates were calculated for each time period as the number of ripe and overripe fruits disappearing during the time period divided by the number of ripe and overripe fruits available for dispersal. Available fruits for dispersal consisted of all ripe and overripe fruits on the first sampling date, plus any unripe fruits that changed to ripe during the time period (= number of unripe fruits on first sampling date minus number of unripe fruits on next sampling date). Thus, proportion fruit removal = (total fruits on the first sampling date – total fruits on the next sampling date)/ (total fruits on the first sampling date – number of unripe fruits on next sampling date). Experimental evidence from the mesh bag, marked fruit, and fruit trap experiments supports two important assumptions underlying the validity of this equation: (1) birds remove both ripe (yellow, orange, and red) and overripe fruits (see Results), and (2) unripe fruits do not abscise from plants or get knocked off plants at a measurable rate during bird foraging (see Results). Fruit removal rates were then converted to a daily rate by dividing by the number of days between sampling dates. The mean rate of fruit removal over the five time periods with the highest removal rates (from 13 March to 15 April) and the removal rate over the period of highest fruit abundance (25–31 March) were analyzed. All proportions were arcsine transformed prior to analysis.

To examine the effect of forest edge, plant size and neighbour variables, and the potential interactive effect of forest edge with these other variables, mean fruit removal rates were analyzed by ANCOVA. For each of the plant size and/or neighbour variables, a separate model tested for effects of forest edge (edge *v*. interior), the plant size or neighbour variable, and the interaction between these two variables. For all models in which the main effect of forest edge and the interaction term were not significant, a follow-up analysis examined just the effects of the plant size or neighbour variable using a linear regression. These models were carried out separately for orange-fruited plants and red-fruited plants, because fruit removal rates were significantly different for the two colour morphs in initial 2-way ANOVAs testing for effects of colour morph, forest edge, and an interaction between colour morph and forest edge (see Results).

To enable comparisons of fruit disappearance rates in the mesh bag experiments and those on the study plants, fruit disappearance rates were calculated for the mesh bag experiments using the same formula as for the study plants (see above). Throughout the Results, means are presented with the standard error of the mean.
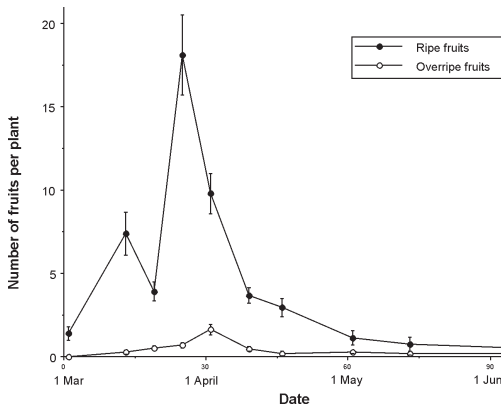
Figure 1. Number of ripe and overripe fruits per *Alepis flavida* plant from 1 March to 9 June. Means and standard errors are presented for the 57 plants.

Table 1. Results from 2-way ANOVAs (*F*-values, degrees of freedom, and *P*-values) on fruit removal rates in *Alepis flavida*, testing for effects of fruit colour morph, forest edge, and an interaction between colour morph and forest edge.

Effect	F	df	P
(a) Mean removal rates (13 Mar–15 Apr)			
Colour morph	6.8	1, 49	0.012
Forest edge	0.23	1, 49	0.63
Colour * forest edge	0.084	1, 49	0.77
(b) Peak removal rates (25–31 Mar)			
Colour morph	7.7	1, 48	0.008
Forest edge	0.63	1, 48	0.43
Colour * forest edge	1.36	1, 48	0.25

Results

Rates of fruit removal

Plants had ripe fruits present from 1 March until 9 June, but numbers showed a clear peak on 25 March, at which time plants had an average of over 17 ripe fruits (Fig. 1). Numbers of overripe fruits remained low over the entire season, but were greatest on 31 March, the sampling date directly following the date of peak numbers of ripe fruits (Fig. 1).

Fruit removal rates were significantly affected by colour morph, both for mean rates over the five dates of highest fruit removal (13 March–15 April) and for peak removal rates during the period of highest fruit abundance from 25–31 March (Table 1). Removal rates were significantly higher for plants with red fruits
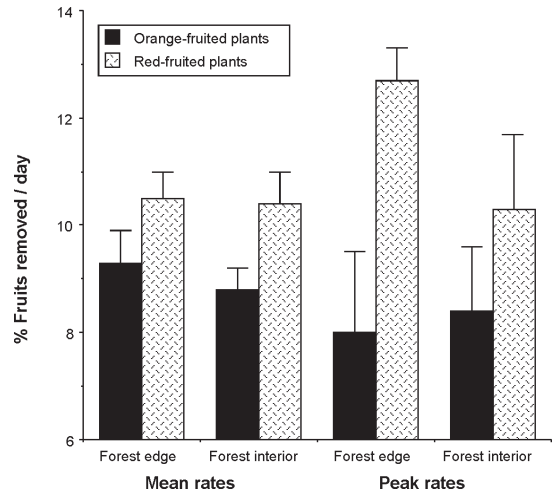

Figure 2. Fruit removal rates (% fruits removed/day) in *Alepis flavida* for two time periods: Mean removal rates from 13 March–15 April; and Peak removal rates from 25–31 Mar, the time of highest fruit abundance. Means and standard errors are presented for orange-fruited plants growing on forest edge (*n* = 13) and in forest interior (*n* = 14), and red-fruited plants growing on forest edge (*n* = 14) and in forest interior (*n* = 12).

than for plants with orange fruits (Fig. 2), whereas there was no significant difference between removal rates for edge and interior plants (Table 1). The preference for plants with red fruits over plants with orange fruits was consistent in both habitats, as shown by the insignificant interaction effects between colour morph and forest edge (Table 1). However, for peak removal rates over the season (Fig. 2), the difference between removal rates for red-fruited and orange-fruited plants appears to be greater on the forest edge. Because of the strong effect of colour morph on fruit removal rates, all subsequent analyses were carried out separately for orange-fruited and red-fruited plants.

Fruit removal rates were strongly affected by the proximity to neighbours, but this effect of neighbours varied depending on whether plants had orange fruits or red fruits, and whether the plants were growing on edges or in the interior (Fig. 3). For orange-fruited plants, the closer the four nearest neighbours were, the greater the fruit removal rates, regardless of location (edge *v.* interior: Table 2, Fig. 3). Red-fruited plants also showed higher removal rates when neighbours were closer, but only for interior plants (there was a significant interaction term: Table 2, Fig. 3). Models testing for effects of neighbour size did not reveal any significant effects of forest edge, neighbour size, or the interaction between edge and size on mean removal
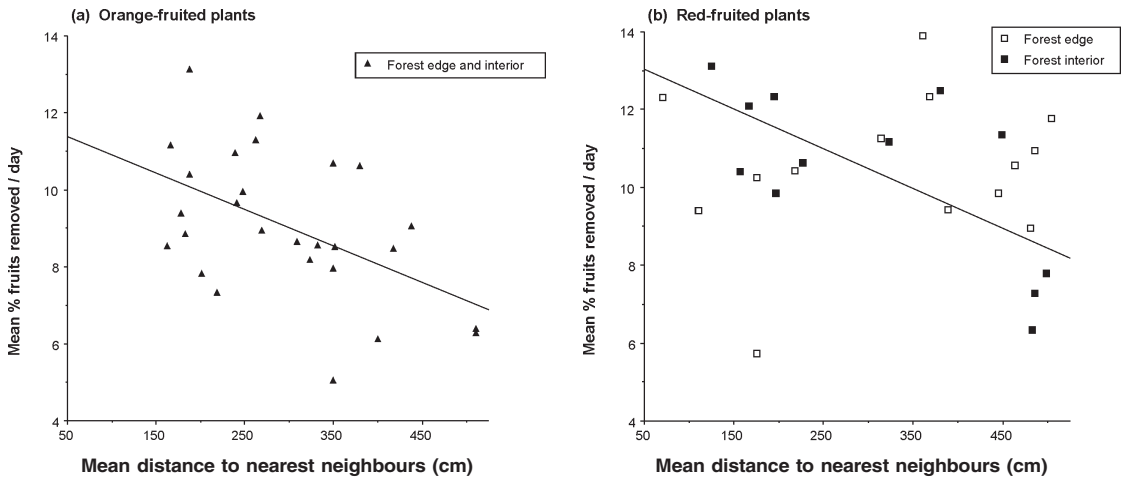
Figure 3. Fruit removal rates in *Alepis flavida* as a function of mean distance to the four nearest fruiting neighbours (cm) for: (a) orange-fruited plants, and (b) red-fruited plants. For (a), the equation for the regression line is: $y = -0.10x + 11.9$ ($R^2 = 0.26$, $n = 27$, $P = 0.006$); data for plants growing on forest edge and in forest interior are plotted together, because there was no significant interaction effect between neighbour distance and forest edge. For (b), forest edge and forest interior plants are plotted separately, because there was a significant interaction between neighbour distance and forest edge. The relationship between fruit removal rate and neighbour distance was not significant for forest edge ($R^2 = 0.029$, $n = 14$, $P = 0.56$), but was highly significant for forest interior ($R^2 = 0.46$, $n = 12$, $P = 0.016$; $y = -0.10x + 13.6$).

Table 2. Results from ANCOVAs (*F*-values, degrees of freedom, and *P*-values) on mean fruit removal rates in *Alepis flavida*, testing for effects of forest edge (edge. *v.* interior), neighbour distance (mean distance to the four nearest neighbours), and an interaction between forest edge and neighbour distance.

Effect	Orange-fruited plants			Red-fruited plants		
	F	df	*P*	*F*	df	*P*
Forest edge	0.98	1, 23	0.33	4.4	1, 22	0.047
Neighbour distance	9.1	1, 23	0.006	2.4	1, 22	0.14
Forest edge * distance	0.96	1, 23	0.34	5.8	1, 22	0.025

Table 3. Results from linear regressions (R^2 values, sample sizes, and *P*-values) between mean fruit removal rates in *Alepis flavida* and (a) neighbour size (total volume of neighbours) and (b) plant size (number of leaves). Regressions were conducted separately for orange plants and red plants.

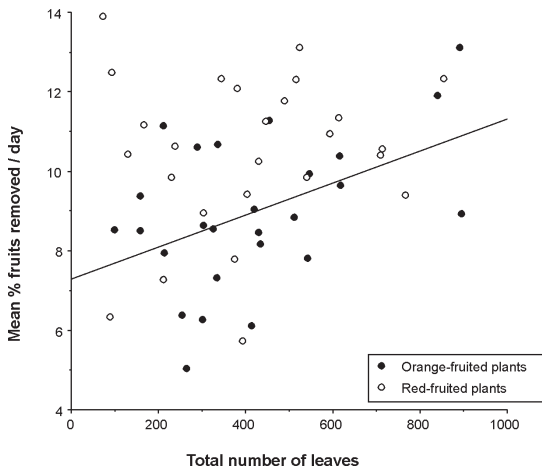| Effect	Orange-fruited plants			Red-fruited plants		
	R^2	*n*	*P*	R^2	*n*	*P*
(a) Neighbour size	0.083	27	0.15	0.004	26	0.76
(b) Plant size	0.21	26	0.018	0.019	26	0.50

Figure 4. Relationship between fruit removal rate (mean percent of fruits removed/day) in *Alepis flavida* and plant size, measured as the number of leaves. Data are plotted separately for orange-fruited plants and red-fruited plants. The equation for the regression line for orange-fruited plants is: $y = 0.004x + 7.3$ ($R^2 = 0.21$, $n = 26$, $P = 0.018$). The relationship was not significant for red-fruited plants ($R^2 = 0.019$, $n = 26$, $P = 0.50$).

rates, either for orange-fruited or red-fruited plants ($P > 0.05$ for all effects). Separate linear regressions between mean removal rates and neighbour size also were not significant (Table 3).

Plant size (number of leaves) did not significantly affect mean removal rates in the models examining effects of forest edge, plant size, and the interaction between the two factors, either for plants with orange or red fruits ($P > 0.05$ for all effects). However, separate linear regressions between plant size and removal rates showed a strong effect of total number of leaves on removal rates, but only for orange-fruited plants (Fig. 4). There was a significant positive relationship between mean fruit removal rates and number of leaves for orange-fruited plants, but not for red-fruited plants (Table 3).

Mesh bag exclosure experiment

Fruits remained on plants for much longer periods of time in the absence of birds than in the presence of birds (Fig. 5). For example, by 8 April, approximately one month after bags were placed on plants, 80% of the original fruits remained on bagged plants, compared with less than 20% on unbagged plants (Fig. 5). It is clear that overripe fruits remained on bagged plants, whereas overripe fruits were always very rare on study plants (Fig. 5b), an indication of high removal rates by
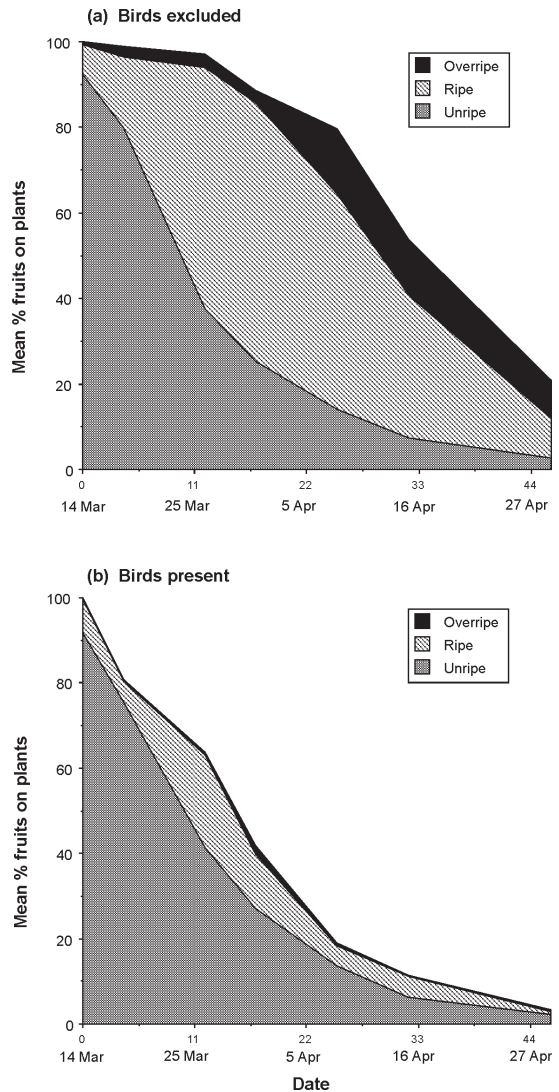

Figure 5. Mean percentage of *Alepis flavida* fruits on plants that were unripe, ripe, and overripe from 14 March until 30 April for: (a) plants with birds excluded (in mesh bags; $n = 10$), and (b) plants with birds present (in field study; $n = 57$).

birds. It is also clear that birds do remove overripe fruits since the difference between numbers of fruits on plants with birds excluded (Fig. 5a) v. birds present (Fig. 5b) is just as great for overripe fruits as for ripe fruits.

The rates of fruits falling off into the mesh bags were very low for the first month of the experiment (from 0.5 to 2% per day). These fruit disappearance rates were 18.5 times lower than those on the principal
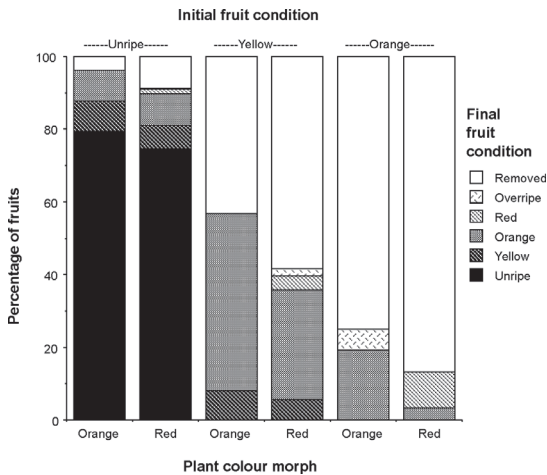
Figure 6. Percentage of *Alepis flavida* fruits in the marked fruit experiment that were removed (disappeared), underwent transitions to overripe, red, orange, or yellow, or remained unripe. Data are presented separately for orange-fruited and red-fruited plants, and for transitions starting with unripe, yellow, and orange fruits. Transitions represent time periods from 2–8 d.

study plants for the first two weeks, and five times lower for the next two weeks. Not until one month after the bags were placed on plants did substantial numbers of fruits begin to fall off plants (5.2%/day compared with 9.4%/day for the principal study plants). Mesh bags contained orange, red, and overripe fruits, but no yellow fruits were ever found in bags, indicating that yellow fruits do not readily abscise from plants. These rates of natural fruit abscission in mesh bags, especially from 26 March onwards, are gross overestimates of the rates occurring on plants exposed to bird foraging, because birds removed fruits so quickly that very few fruits remained on plants long enough to become overripe (Fig. 5). Thus, the mesh bag experiment clearly documents that some fruits naturally fall off plants, but this fruit abscission represents only a small portion of the total fruit disappearance.

Marked fruit experiment

Data from this experiment yielded a total of 1613 fruit transitions from one sampling date to the next. Overall, there were significant differences between the proportions of fruits remaining v. removed as a function of fruit colour ($\chi^2 = 33.1$, df = 3, $P < 0.001$). Yellow fruits were removed at a lower rate (50%) than were orange (79%), red (88%), or overripe fruits (76%). However, birds clearly did remove yellow fruits, because there is no evidence that yellow fruits ever fell

off plants, either from the mesh exclosure or the fruit trap experiments (see below).

Plant colour morph had very strong effects on rates of fruit disappearance for all categories of fruits. First, in terms of transitions from unripe fruits, the two colour morphs differed significantly in the proportion of fruits that remained unripe, ripened, or were removed ($\chi^2 = 13.8$, df = 2, $P = 0.001$). Fruit disappearance rates were much greater for red plants than for orange plants (Fig. 6). Furthermore, unripe fruits remained on red plants for significantly shorter lengths of time before removal ($\bar{x} = 5.0 \pm 0.26$ d) than on orange plants ($\bar{x} 7.2 \pm 0.23$ d; $t = -6.0$, df = 71, $P < 0.001$). Second, data on transitions from yellow fruits also showed a greater proportion of fruits removed from red plants (Fig. 6), but this difference was not quite significant ($\chi^2 = 2.88$, df = 1, $P = 0.089$). Third, in terms of transitions from orange fruits, the two colour morphs showed a significant difference between the proportions of fruits remaining ripe, turning overripe, and being removed ($\chi^2 = 7.4$, df = 2, $P = 0.025$). Again for orange fruits, there were greater disappearance rates on red plants than on orange plants (Fig. 6). In fact, orange fruits on red plants were removed at the same rate (86.9%) as red fruits on red plants (87.5%; $\chi^2 = 0.004$, df = 1, $P = 0.95$). Thus, even though some proportion of orange fruits on red plants probably turned red before removal, the marked fruit experiment documents that the greater fruit removal rates on red plants than orange plants in the field study clearly result from greater removal rates of all categories of fruits on red plants.

Fruit trap experiment

Results from the fruit traps placed under plants to obtain an estimate of the number of fruits knocked off during bird foraging showed that low numbers of fruits fell into traps. A total of 44 fruits were found in all six traps from 13 Mar to 15 April. No unripe fruits ever fell into fruit traps; a total of 26 ripe (orange or red) and 18 overripe fruits were found, but no yellow fruits were found in traps.

Rates of fruit fall into each trap were calculated by dividing the number of fruits found in the trap over the one-month period by the number of fruits that disappeared from the plants during the same time (= number of fruits on 13 March – number of fruits on 15 April). An average of 8.45% of fruits fell into the fruit traps, which means that over 90% of the fruits that disappeared from plants were removed by birds. These rates of fruit fall obviously could include fruits naturally falling off plants, fruits dropped by birds that were trying to eat them, and fruits knocked off plants by birds. However, the process of birds causing some fruits to fall off plants during foraging represents a small portion of the total fruit disappearance.

Sugar concentrations as a function of fruit colour

Sugar concentrations for orange fruits ($\bar{x} = 14.4 \pm 0.4\%$, $n = 9$) and red fruits ($\bar{x} = 14.2 \pm 0.5\%$, $n = 6$) were nearly identical ($t = 0.30$, df = 13, $P = 0.77$).

Discussion

The overall conclusion of this study, which considers the effects of forest edges, fruit colour, and display size, is that birds showed a strong preference for red fruits, but this preference was most strongly expressed at peak fruiting times (when competition for disperser attention is most acute) and on edges (where the visual signals of fruit colour can be seen from the greatest distance). Of the three factors addressed in this study, only fruit colour showed significant main effects on fruit removal rates. Both edge effects and effects of fruit display size occurred only via interactions with colour morph, again emphasizing the importance of fruit colour in this system. This study is in contrast to others that report significant effects of the edge component of habitat fragmentation (Restrepo and Gomez, 1998; Restrepo *et al.,* 1999; Dale *et al.,* 2000) and fruit display size (Nogales *et al.,* 1999).

The strong preference for red-fruited plants in this study involved more than just a preference for red fruits, because all fruit types (unripe, yellow, and orange) were removed at a faster rate from red-fruited plants than from orange-fruited plants. Because red-fruited plants and orange-fruited plants did not differ in numbers of fruits, the preference for red fruits clearly did not result from differences in fruit display size. Puckey *et al.* (1996) demonstrated a preference for red fruits in one of the frugivores present at Craigieburn, silvereyes, although silvereyes have been shown to prefer white over red fruits in the polymorphic *Rhagodia parabolica* (Giles and Lill, 1999). For *Rubus spectabilis*, which also has orange and red-fruited morphs, birds showed similar preferences to those reported in this study: Red fruits were preferred over orange fruits (Traveset and Willson, 1998), resulting in greater removal rates of red fruits in experimental field displays (Gervais *et al.,* 1999). For a different plant, polymorphic for fruit colour, *Myrtus communis,* fruit removal rates did not differ for blue and white morphs (Traveset *et al.,* 2001).

Effects of fruit display size also varied as a function of colour morph, both for plant size and the presence of fruiting neighbours. Larger plants had greater fruit removal rates, but only for orange plants. This result agrees with those of Giles and Lill (1999), who found that preference by silvereyes for the less-preferred fruit colour was enhanced when fruit abundance was increased. Orange plants with closer neighbours had greater fruit removal rates in both edge and interior habitats. In contrast, proximity of neighbours only affected fruit removal rates on interior red plants, not edge red plants. Apparently red plants are so highly preferred that birds are attracted to red plants of any size. To receive equivalent attention, orange plants have to be large, and/or have close fruiting neighbours. Red plants are only affected by display size in the forest interior, where proximity of neighbours was perhaps compensating for lower visibility or accessibility of plants.

The fruit colour morphs in *A. flavida* are most likely genetic. There was not a single case of a plant changing in fruit colour over the three years between 1998 and 2001. In addition, red and orange plants grow in exactly the same habitat, and the mean percentage of orange plants at the six sites was $50.8 \pm 3.8\%$. The presumed genetic basis of this colour polymorphism leads to the important question of why orange plants persist in the population, when red plants are more highly preferred by bird seed dispersers. One possible answer is that there is little cost (in dispersal terms) of being orange. Although there were significantly greater removal rates for red plants, by the end of the season, nearly all fruits had been removed even on orange plants. Thus, dispersal did not appear to be limiting in this species at our study site in 1998. A four-year study (1995–1998) at this site of dispersal of both *Alepis flavida* and *Peraxilla tetrapetala* also concluded that nearly all fruits were successfully dispersed by the end of each season (Kelly *et al.,* 2004). Therefore, bird numbers at this site are sufficient for good dispersal of both fruit-colour morphs, and there would be little selection pressure in favour of the red morph. This picture for dispersal contrasts strongly with results for pollination of *P. tetrapetala* at this site, where there is strong pollen limitation due to inadequate flower visitation by the same bird species involved in fruit visitation (Robertson *et al.,* 1999). It appears that pollination is more sensitive than seed dispersal in mistletoes, and perhaps generally (Kelly *et al.,* 2004).

We note one caveat on the use of fruit removal as a measure of seed dispersal. Fruit removal only measures dispersal quantity (*sensu* Schupp, 1993); the plants will also be affected by dispersal quality, such as whether seeds are voided by the birds in germinable condition, and what fraction of them are voided onto a suitable host branch. The two major losses during reproduction by seed are presumably seeds voided in unsuitable locations (rocks, soil, etc.), and seeds that landed and germinated on host branches but failed to establish a haustorial connection (Ladley and Kelly, 1996). There is no reason to believe that any of these measures of dispersal quality are affected by fruit colour morph, therefore our measures of fruit removal

do probably give a good indication of the relative amount of effective dispersal. There may be relationships between edge habitats and later stages in regeneration (e.g. if birds spend more time on edges, seeds are more likely to be voided there; seedlings deposited in higher light situations may have higher survival or growth rates), but such questions are beyond the scope of the present study. There are some indications that establishment and growth of *Alepis flavida* seedlings are not related to light intensity, but are related to growth of the host tree which may itself be affected by edge position (Norton and Ladley, 1998; Norton *et al.,* 2002).

In conclusion, birds showed strong preferences for red fruits, most especially during the peak fruiting season, but nearly all fruits were removed for both morphs in both habitat types by the end of the fruiting season. Plant size affected fruit removal rates, but only for the less-preferred orange-fruited morphs. Fruit removal rates for the red-fruited morphs were greater for plants with closer neighbours only in the interior. It appears that the major effect of forest edges is their role in changing the visibility and accessibility of plants to birds.

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