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Effects of a litter-disturbing bird species on tree seedling germination and survival in an Australian tropical rain forest

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ABSTRACT. The spatial and temporal variation in litter disturbance by a medium-sized bird, the chowchilla (*Orthonyx spaldingii* Ramsay, Orthonychidae) was documented, and its potential impacts on tree seed germination and early seedling survival in an Australian tropical rain forest experimentally investigated. Chowchilla disturbances occurred on ridges, slopes and drainages in all four seasons surveyed. In some areas litter was completely turned over as frequently as every 5 wk. Tethered seeds exposed to disturbance were moved farther and experienced significantly greater variation in litter cover than those protected from disturbance. When seeds of two canopy trees were placed in litter environments simulating those created by chowchillas, the seeds of one species showed significant effects of litter treatment on germination while those of the other showed no significant effects. Seedling cohorts of four tree species were followed for 6 wk soon after germination and all showed higher survival in vertebrate exclosures. The two most abundant species suffered 68% and 35% mortality in six wks, with the majority of that unambiguously due to chowchillas. It is argued that litter-disturbing birds increase litter heterogeneity and significantly impact early seedling mortality. These effects could be important in maintaining evenness and diversity of the seedling community.

KEY WORDS: chowchilla, disturbance, germination, leaf litter, rain forest, seedling

INTRODUCTION

Agents of mortality acting on seeds and seedlings have the potential to affect the abundance and distribution of adult trees and have been hypothesized to

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be one factor that could maintain diversity in tropical rain forests (Connell 1971, Grubb 1977, Janzen 1970). The effects of vertebrates on these early life stages have been studied primarily in terms of seedling herbivory, seed predation and seed dispersal. Less studied are the effects that litter-disturbing vertebrates may have by uprooting, burying and breaking seedlings, or altering the litter environment that seeds and seedlings encounter. Clark & Clark (1989) found that vertebrate activity accounted for 16–25% of the physical damage suffered by artificial tree seedling models over 1 y in the primary rain forest at La Selva, Costa Rica, suggesting that vertebrate disturbance could be an important agent of mortality in early seedling stages. However, few studies have quantified the effects of specific litter-disturbing vertebrates on living seedlings.

In tropical forest systems, variation in leaf litter can affect seed germination (Green, in press; Guzman-Grajales & Walker 1991, Metcalfe & Turner 1998, Molofsky & Augspurger 1992, Putz 1983) and seed survival (Cintra 1997). Diversity of microsites available for plant establishment has been argued to be an important factor maintaining tree species diversity in tropical forests (Denslow 1980, Grubb 1977, Ricklefs 1977), and litter heterogeneity could be one factor contributing to germination microsite diversity (Cintra 1997, Molofsky & Augspurger 1992). Most authors have stressed the variation in litter due to differences in accumulation of natural litter fall (Cintra 1997, Molofsky & Augspurger 1992) or that due to hurricanes (Guzman-Grajales & Walker 1991), but few have considered the role vertebrates play in creating, maintaining or increasing litter heterogeneity (Green, in press).

In temperate, subtropical and tropical rain forests of Australia, members of three avian groups can create significant litter disturbance in the course of foraging for litter invertebrates and vertebrates or in forming their nests (Adam 1992). One species of lyrebird (*Menura novae-hollandiae*) has been estimated to move 200 t of litter per hectare every year and may be vital in creating microsites necessary for regeneration of tree ferns (Ashton & Bassett 1997). Megapodes, or mound builders, include the Australian brush turkey (*Alectura lathami*) and orange-footed scrubfowl (*Megapodius reinwardti*). These birds create local disturbances by scratching litter into incubation mounds that can measure several metres in diameter (Jones 1988), and also create more widespread disturbance while foraging for insects and small vertebrates. Finally, logrunners (*Orthonyx temmincki*) and chowchillas (*Orthonyx spaldingii*) inhabit subtropical and tropical rain forests respectively. In the tropical rain forests of northern Queensland, chowchillas have been estimated to turn over all of the litter in their home range every month in the course of foraging (Jansen 1993). Fossil forms of congeners of the latter two species have been described from Miocene and Quaternary deposits (Baird 1993, Boles 1993), suggesting that these birds have been interacting with rain forest plants for considerable evolutionary time.

Our study focused on the impact one of these bird species, the chowchilla, has on seed germination and seedling survival of selected tropical rain forest tree species. We used field observations and experiments to determine (1) the extent of chowchilla disturbance in time and space, (2) the effect of chowchilla disturbance on litter heterogeneity, (3) the potential effects of litter heterogeneity on seed germination of two tree species, *Cryptocarya mackinonniana* and *Cryptocarya corrugata*, and (4) the direct effect of litter disturbance on the survival of newly germinated tree seedlings of four tree species, *Darlingia darlingiana, Franciscodendron laurifolium, Rockinghamia angustifolia* and *Apodytes brachystylis*.

METHODS

Study site and species studied

This study was conducted in a primary tropical rain forest in the Lamb Range of northern Queensland, Australia (see Connell *et al.* 1984 for a full description of the site). The site ranges from 800 to 900 m in elevation and receives *c.* 3000 ml of rain annually, with most of this falling December–April. Tree species used in this study included understorey and canopy trees (Table 1), but availability of seeds and seedlings precluded us from using all species in all experiments. Chowchillas are medium-sized birds (27 cm in length, weight 150 g) that spend most of their time searching the forest litter for invertebrates, moving through their home range in family groups of two to five individuals (Jansen 1993). They are well adapted for moving litter, with large feet and specialized tail feathers that act as additional support during the characteristic powerful sideways thrusts of one leg. Casual observations suggested that our study plot was used by three family groups of chowchillas, and they created the majority of the litter disturbance present on our plot. Other litter-disturbing vertebrates present included the Australian brush turkey and a small mammal, the long-nosed bandicoot, *Perameles nasuta*.

Table 1. Characteristics of seeds and seedlings of the tree species examined on the Davies Creek, Queensland, Australia study plot. Seedling height is that for seedlings of age < 6 mo.

Species	Family	Habit	Seed size (mg)	Germination	Seedling height (cm)
Apodytes brachystylis	Icacinaceae	UT	110	Epigeal	7
Cryptocarya corrugata	Lauraceae	CT	2800	Hypogeal	10
Cryptocarya mackinonniana	Lauraceae	CT	1100	Hypogeal	10
Darlingia darlingiana	Proteaceae	CT	200	Epigeal	8
Franciscodendron laurifolium	Sterculiaceae	CT	89	Epigeal	6
Rockinghamia angustifolia	Euphorbiaceae	UT	na	Hypogeal	7

Habit: UT = understorey tree, CT = canopy tree. na = not available.

Characteristics of chowchilla disturbances

To determine the prevalence of litter disturbance on our study site, five 20-m transect lines were haphazardly placed in each of three locations on our study plot: along the top of a ridge, across slopes and along creek drainages. These three sites were chosen to account for potential differences in both litter accumulation rates and habitat utilization by chowchillas. Both the total length of tape that passed over any type of disturbance and the length that could be unambiguously assigned to chowchillas were recorded in July, September and December of 1998. Disturbance by chowchillas was recognized by the characteristic cup-shaped hollows they created and could be distinguished from that of the two other major litter-disturbers on the study plot, brush turkeys, whose diggings were much larger in area and less distinct in shape, and bandicoots, whose diggings had a conical hole several cm deep dug in the centre of them. To monitor the temporal pattern of disturbance over a finer scale, ten 1-m × 1-m plots were monitored weekly during the months of January, June, September and December of 1998. Three of these plots were located in drainages near a creek, four were located on slopes, and three were located on the ridgetop.

To determine how chowchilla foraging affected litter depth, in November of 1997 we measured the size of 75 chowchilla disturbances, noting the depth of litter in the centre, on the edge and at 30 cm from the centre of each disturbance. Twenty-five of these sites were along the creek, 25 were on a slope and 25 were on a ridgetop.

Seed movement and germination

To assess whether seeds exposed to litter disturbance were more likely to experience variation in the litter microsite where they eventually came to rest, we compared movement of tethered seeds of *C. mackinonniana* and *C. corrugata* at three slope locations and two drainage locations on the study site. One end of a 1-m cotton thread was glued to the outside of each seed, and the other end tied to a metal wire stake, allowing the seed to move relatively freely within 1 m of the stake. Each stake had one seed of each species tied to it on opposite sides and stakes were spaced 0.5 m apart in a straight line for a total of 10 seeds of each species per location. At each location, one set of 20 seeds was placed in a vertebrate exclosure while the other set was placed on an unfenced control plot *c.* 10 m away. Vertebrate exclosures were 6-m × 7.5-m in area, fenced to a height of 1 m with poultry netting topped by a 0.3 m sheet of galvanized metal flashing. These fences significantly reduced litter disturbance by chowchillas, brush turkeys and bandicoots (T. C. Theimer & C. A. Gehring, unpubl. data). After 2 mo we assessed the distance each seed had moved and the depth of leaves that covered the seeds. The variance-ratio test (Zar 1984) was used to compare the variance of litter depths inside and outside of exclosures for each seed species.

To assess the potential effects of litter disturbance by chowchillas on seed germination, we created artificial chowchilla disturbances and placed eight seeds of two tree species, *C. mackinonniana* and *C. corrugata* in areas that simulated either

(1) the centre of a chowchilla disturbance (no litter, soil surface disturbed to a depth of 1 cm), (2) above or below litter piled to the depth found at the edge of a disturbance (5–6 cm), or (3) above and below undisturbed litter at 30 cm from a disturbance (2–3 cm). Seeds were collected below adult trees on our study plot in September 1998, and germination experiments were conducted from October–December, the period when these species naturally germinate. These experiments were conducted in seven vertebrate exclosures, for a total of 56 seeds above and 56 seeds below each litter treatment, and two sets of 56 seeds in no litter areas, each paired with either the above or below litter seed set. The experimental litter depths at each exclosure corresponded to the depths determined from natural chowchilla disturbances in that location. The number of successful germinants were determined by bi-monthly censuses conducted over the following 4 mo. Successful germination in this study was considered to be the point at which the seedling had roots anchored in the soil and the first leaves fully expanded. For each species, the effects of seed position and litter depth were tested using two-way ANOVA with germination data from the undisturbed and edge treatments only (there could be no seed position effects in the centre treatment as there was no litter). We then pooled the data for seeds above and below litter and analysed for differences among litter treatment using one-way ANOVA. In all analyses the percentage germination in each plot was arcsin square-root transformed. Tukey's multiple comparison tests were used to locate significant treatment effects.

Direct effect of chowchillas on seedlings

The direct effect of chowchilla disturbance on seedlings was assessed in two ways. First, 150 chowchilla disturbances were surveyed and the presence and condition of seedlings in and around these disturbances quantified. Second, cohorts of recently germinated seedlings (< 3 mo since germination) of four tree species were followed for 6 wk, checking each individual at weekly intervals to determine its fate. Seedling fates were categorized as (1) missing due to unknown causes, (2) uprooted by chowchillas, (3) buried by chowchillas, (4) broken by chowchillas (the leaves of the seedling were still present near the broken stem), or (5) stem only (only the stem remained but whether the seedling was broken by chowchillas or eaten by herbivores was impossible to determine). Six months after the initial 6-wk monitoring period, seedlings were resurveyed to determine subsequent mortality. This 6-mo mortality estimate of unfenced seedlings was then compared to the 6-mo mortality of seedlings of the same species that had germinated at the same time but were contained within three nearby vertebrate exclosures.

RESULTS

Characteristics of chowchilla disturbances

Chowchilla disturbances accounted for *c*. 15% of the length surveyed by line transects at each of the three census periods. The length disturbed on ridgetops (mean = 6.2%) was less than that of either slopes (15.4%) or drainages (20.8%) in each census period. These estimates were conservative, as only unambiguous and relatively recent disturbances were recorded at each census. Weekly monitoring of the ten 1-m plots during the months of January, June, September and November showed overall patterns similar to those indicated by the line transects. The mean percentage of the 1-m plot disturbed on the ridges was 11% wk^{-1}, while slope plots averaged 25% wk^{-1} and drainages 17.5% wk^{-1}. All plots were visited at least once per month by chowchillas at all time periods censused and the overall mean amount of each plot disturbed was 19% wk^{-1} (± 3.19 SE). This suggests that litter in these areas was completely turned over by chowchillas approximately once every 5 wk. A similar estimate was obtained indirectly by Jansen (1993) by calculating the amount of litter through which chowchillas would need to forage in order to meet their metabolic needs.

Based on our survey of 75 chowchilla disturbances, each chowchilla foraging bout typically resulted in an area of bare soil averaging 15 cm in diameter that was dug to a depth of 1–2 cm below the surface (ridge = –0.96 ± 0.19 cm SE, n = 25; slope = –0.91 ± 0.15 cm, n = 25; drainage = –2.4 ± 0.36 cm, n = 25). Drainage disturbances were deeper most likely because the thicker layer of humus and loose soil at these sites made digging easier. Around this central area bare of litter, litter was piled to a depth roughly two times that of undisturbed litter 30 cm away from the disturbed area (near disturbance: ridge = 5.16 ± 0.36 cm, slope = 5.74 ± 0.19 cm, drainage = 5.80 ± 0.32 cm; undisturbed litter: ridge = 2.2 ± 0.22 cm, slope = 3.4 ± 0.22 cm, drainage = 2.7 ± 0.19 cm).

Seed movement and germination

After 2 mo, tethered seeds placed in vertebrate exclosures had moved little (*C. mackinonniana* = 0.3 ± 0.22 cm SE, *C. corrugata* = 0.4 + 0.28 cm), while those exposed to vertebrates averaged 9.9 cm displacement (*C. mackinonniana* = 10.76 ± 1.96 cm, *C. corrugata* = 8.95 ± 1.74 cm). Variance in the depth of leaf litter covering seeds was significantly greater for seeds exposed to vertebrates than for those protected in exclosures (variance-ratio test, Zar, 1984) (F = 1.88, df = 49, 49; $P < 0.05$ for *C. mackinonniana* and F = 3.24, df = 49, 49; $P < 0.001$ for *C. corrugata*). These data indicated that seeds exposed to vertebrate disturbance were moved farther and experienced a greater range of litter microsites than did those protected from vertebrates.

Seeds of both *Cryptocarya* species placed in litter environments simulating undisturbed litter or the edge of a disturbance, where litter was kicked into mounds of greater depth, showed no significant effect of seed position (F = 0.554, df = 1, 24; P = 0.464 for *C. corrugata*, F = 0.639, df = 1, 24; P = 0.432 for *C. mackinonniana*), litter depth (F = 0.538, df = 1, 24; P = 0.471 for *C. corrugata*, F = 0.790, df = 1, 24, P = 0.383 for *C. mackinonniana*) or an interaction between the two (F = 0.141, df = 1, 24; P = 0.493 for *C. corrugata*, F = 0.008, df = 1, 24; P = 0.929 for *C. mackinonniana*). When germination successes of seeds above and

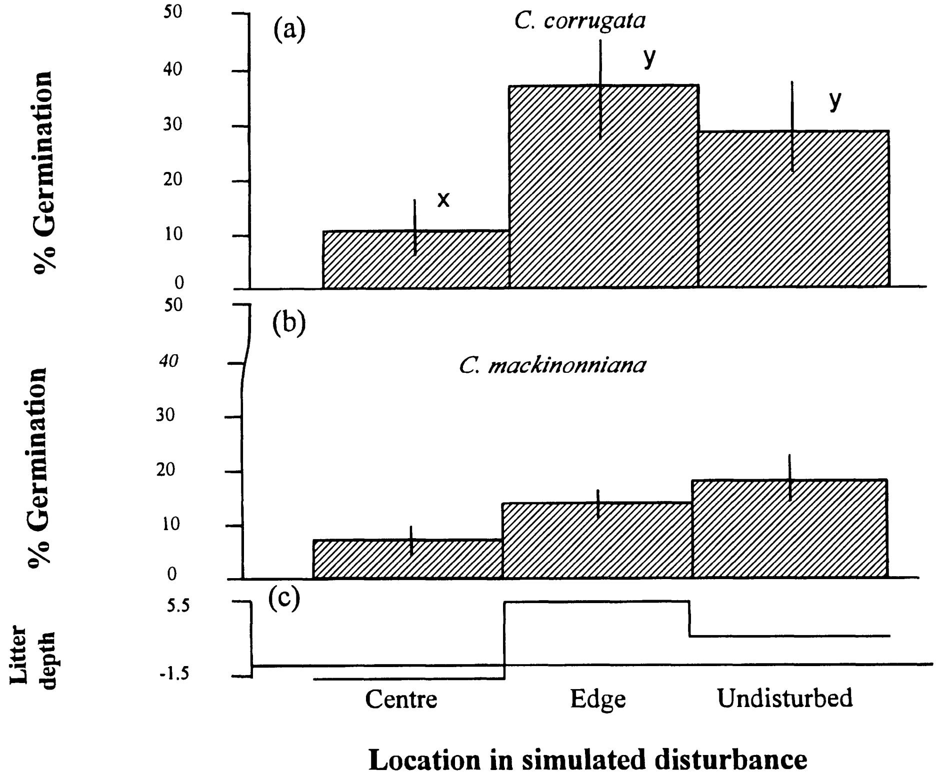

Figure 1. Percentage (±SE) of (a) *Cryptocarya corrugata* and (b) *Cryptocarya mackinonniana* seeds germinating in litter conditions simulating either the centre, the edge or an undisturbed area 30 cm away from a chowchilla disturbance. Because the position of seeds either above or below litter had no significant effect, categories were pooled for this figure. Letters above bars indicate where multiple comparisons tests showed significant differences. (c) Illustration of variation in litter depth at each location based on data from 75 natural chowchilla disturbances.

below litter were pooled, and undisturbed, mounded litter and no litter treatments compared, simulated chowchilla disturbances significantly affected germination of *C. corrugata*, (F = 4.69, df = 2, 18; P = 0.0229, Figure 1), but not *C. mackinonniana* (F = 1.595, df = 2, 18; P = 0.230, Figure 1). Tukey's multiple comparisons tests indicated that *Cryptocarya corrugata* germination was significantly lower in areas bare of litter, while germination was not significantly different between the two litter treatments.

Direct effect of chowchillas on seedlings

Sixty-eight of the 150 chowchilla disturbances we surveyed had one or more seedlings in or around them for a total of 90 seedlings of 13 different species. Of these 90 seedlings, 26% were either uprooted completely or were represented by a leafless stem. Another 42% were buried under leaf litter, while 36% were exposed in the bare soil patch left by the birds, many of these with their roots uncovered by the birds' vigorous scratching.

Table 2. Fates of seedling cohorts of four tree species followed over 6 wk soon after germination. Numbers in parentheses are the initial number of seedlings in each cohort. Numbers in columns are percentage of total cohort in each category. Percentage unambiguously due to chowchillas is the sum of those broken, uprooted and buried.

	Seedling fate (%)						
Tree species	Intact	Broken	Uprooted	Buried	Stem only	Missing	Chowchilla
Rockinghamia angustifolia (225)	32	15	17	11	18	7	43
Franciscodendron laurifolium (88)	65	13	6	8	3	5	27
Apodytes brachystylis (43)	81	2	0	0	0	17	2
Darlingia darlingiana (38)	92	3	0	5	0	0	8

The fates of the four seedling cohorts followed for 6 wk showed significant variation in their responses to chowchilla disturbance (Table 2). The greatest source of mortality for these seedlings was breakage/herbivory, where all that remained was a leafless stem. Although most of these stems were associated with chowchilla disturbances, herbivory could not be ruled out, as two small mammalian herbivores, the musky rat kangaroo (*Hypsiprymnodon moschatus*) and red-legged pademelon (*Thylogale stigmatica*) (a small kangaroo) were also present on our plot. The former has been documented to forage in association with chowchilla flocks in other areas (Jansen 1993) but was rarely encountered on our plot. More unambiguously associated with chowchilla effects were those seedlings that died due to burial or uprooting, or that had broken stems with the tops lying nearby. In the two species showing the greatest effects of chowchillas, *Rockinghamia* and *Franciscodendron*, this accounted for *c.* 63 and 77% of all mortality, respectively. By the end of the 6-wk monitoring period, surviving seedlings of *Rockinghamia* were often growing primarily in microsites that chowchillas could not effectively disturb, e.g. near the roots, trunks and buttresses of larger saplings and trees, amongst the branches of fallen limbs, or between rocks. The other tree species were more resistant to chowchilla effects, apparently because their stems were thicker and their cotyledons tougher so that they were less likely to be bent and subsequently broken and buried. *Darlingia* and *Apodytes* showed strikingly lower mortality over the 6-wk monitoring period. After 6 mo, the mortality of *Darlingia* and *Apodytes* outside vertebrate exclosures did not differ greatly from seedlings of the same species protected from vertebrates (Figure 2). In contrast, survival for *Rockinghamia* was greatly enhanced by protection over 6 mo, while *Franciscodendron* was intermediate (Figure 2). In all cases, most of the mortality occurred in the first 6 wk.

DISCUSSION

Leaf litter disturbance by chowchillas on our site was widespread, occurring in all major habitat types sampled, i.e. the slopes, the ridgetop and along the

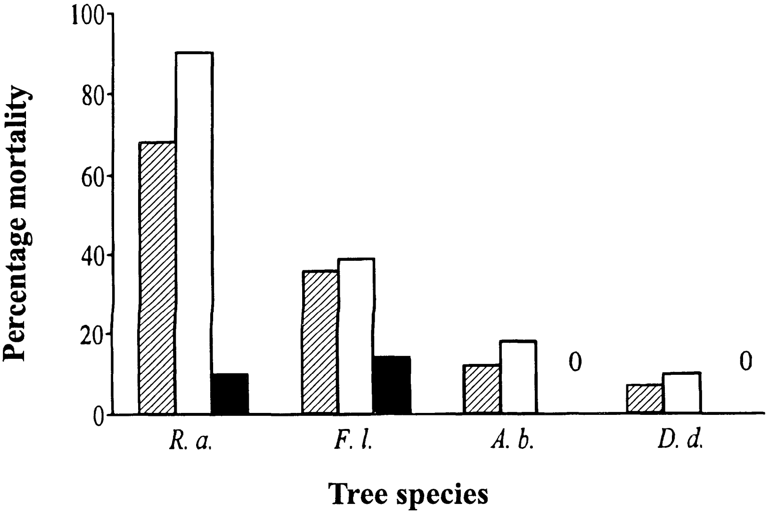

Figure 2. Percentage mortality of seedlings of four tree species during a 6 wk period soon after germination (striped bars), and at 6 mo after the initial survey (open bars) in areas unprotected from vertebrates compared to 6 mo mortality of seedlings of the same age growing in three nearby vertebrate exclosures (dark bars). Tree species: *R.a.* =*Rockinghamia angustifolia*, *F.l.* =*Franciscodendron laurifolium*, *A.b.* =*Apodytes brachystylis* and *D.d.* =*Darlingia darlingiana.*

drainage. Although level of disturbance varied across the four sampling periods, some level of disturbance occurred on our plot at each sampling period. This suggests that chowchillas, through their foraging activities, could affect seeds and seedlings at any time of the year, regardless of the timing of seedfall or seed germination.

Chowchilla litter disturbance had several important consequences for the tree seeds and seedlings studied. First, chowchillas altered the amount of litter that seeds could potentially rest above or below and this had differential effects on the ability of seeds to successfully germinate. Other studies of litter effects on tropical seedlings have emphasized natural litter fall (Cintra 1997; Green, in press; Guzman-Grajales & Walker 1991, Metcalfe & Turner 1998, Molofsky & Augspurger 1992), but this study documents that litter disturbing vertebrates are important agents creating litter variation in the field. In the presence of chowchillas and other vertebrates, tethered seeds were found in microsites ranging from areas bare of litter to those with overlying litter several times thicker than that naturally falling from the canopy. The depth of litter around chowchilla disturbances was roughly two-fold that at nearby undisturbed sites, and the action of these birds probably increases the incidence of ground bare of litter.

Areas without leaf litter may be especially important for tree species that produce small seeds. Small seeds may require higher light for germination or produce small seedlings that cannot penetrate litter (Kohyama & Grubb 1994, Metcalfe & Turner 1998, Molofsky & Augspurger 1992, Putz 1983). In contrast, large-seeded species like *C. corrugata* in our study and the neotropical tree *Gustavia superba* (Molofsky & Augspurger, 1992), may suffer from dehydration in the absence of a protective litter layer.

One caveat of our germination experiments was that they were carried out in vertebrate exclosures, so that once in place, subsequent vertebrate predation or litter disturbance was not possible. Under natural conditions, seeds could experience several different microsites before they eventually germinated, depending upon the length of time to germination. Seeds with long germination times could pass through successive periods of exposure and burial as chowchillas and other vertebrates repeatedly visited an area. Green (in press) hypothesized that the optimum litter microenvironment for another large-seeded tree species on our study plot (*Chrysophyllum* sp. nov) would be generated under such a scenario, in which seeds were either initially on bare soil, followed by subsequent burial by leaf litter, or initially atop the leaf litter and subsequently moved below the litter by some sort of disturbance.

Our results suggest that chowchillas could increase the chance that seeds falling to the forest floor would be subsequently buried by litter and might thereby gain whatever protection litter may afford. Some studies have indicated that litter cover can reduce seed predation (Cintra 1997) while others have found no or little advantage of an overlying litter layer (Schupp 1988, Willson 1988). In a study of four north Queensland tropical tree seeds, Willson (1988) found that only one species showed any reduction in removal rate due to litter cover, and that effect was evident in only one of several experimental trials with that species.

The second major effect of chowchillas was increasing seedling mortality through uprooting, breaking and burying seedlings. The four seedling cohorts we followed were all species that gave rise to relatively small seedlings, and would be hypothesized *a priori* to be potentially vulnerable to this type of disturbance. *Rockinghamia* showed the most striking effect, suffering 67% mortality in the 6 wk we followed it, with 43% mortality unambiguously due to chowchillas. Independent surveys of this species over a wider area of the study plot showed lower but still significant mortality rates during the same time period (40%) (P.T. Green, *pers. comm.*). After 6 mo, survival in vertebrate exclosures was higher for all four species, but this was most striking for *Rockinghamia* and *Franciscodendron*. In all species, most mortality over the 6 mo occurred in the earliest 6 wk of monitoring, suggesting that seedlings pass through an early period of vulnerability after which mortality rates decrease. This decline could have been due to seedlings growing into developmental stages that are more resistant to disturbance, though this seems unlikely given the slow growth of seedlings in the shaded understorey, or, more likely, because remaining seedlings occupied sites safe from disturbance. Germinating in areas protected from chowchilla disturbance could be one important aspect of microsites for species like *Rockinghamia angustifolia* and *Franciscodendron laurifolium*. High seedling mortality during the first few weeks after germination has been documented in other tropical forests (Garwood 1982), and our study may have under-estimated the earliest effects of chowchilla disturbance, as seedlings were several weeks old when we began monitoring them.

If seedling mortality by litter-disturbers is ubiquitous, litter disturbance could act as an additional force selecting either for large-seeded species that can produce larger, more robust seedlings, or for smaller seedlings to have more extensive root systems and stem and leaf architecture more resistant to disturbance. Grubb & Metcalfe (1996) argued that larger seed/seedling size may be selected for as a buffer against drought, herbivory and breakage by litterfall more than as a means of shade tolerance. We suggest that, in general, larger seeds and seedlings may be less susceptible to the effects of litter-disturbing vertebrates as well. However, seed and seedling size alone may not predict vulnerability to disturbance. Large-seeded species could experience a brief period of disturbance sensitivity during that time when the radicle is initially emerging and beginning to anchor the developing seedling. Also, seed and seedling size interacts with other seedling attributes to determine disturbance sensitivity. We have noted that some very small seedlings of *Randia fitzalanii* and *Doryphora aromatica* appear relatively resistant to chowchillas, presumably because of their short stature (2–3 cm), tough cotyledons, well-anchored root systems and resistance to the effects of burial under litter. Species like *Rockinghamia*, although germinating from a larger seed and producing an overall larger seedling, have relatively long stems susceptible to breakage, are easily uprooted, and die quickly when covered by litter.

We hypothesize that chowchilla disturbance may have two impacts on the seedling community. First, by increasing litter heterogeneity, chowchillas could allow a broader suite of species to successfully germinate given the variation in the response of tree species to litter environments documented in this and other papers (Cintra 1997, Molofsky & Augspurger 1992). This hypothesis assumes that litter heterogeneity in the absence of chowchillas would not be great enough to allow the same suite of species to germinate. This assumption could be tested by comparing areas with and without chowchillas or by long-term chowchilla exclosure experiments. Second, seedling mortality due to chowchillas may affect plant community evenness and diversity. For example, the seedling cohort sizes in our study reflected the relative initial seedling abundance in those areas surveyed, and abundances ranged from 225 *Rockinghamia* seedlings to 38 *Darlingia* seedlings. After 6 mo of disturbance, however, *Rockinghamia* abundance had fallen 10-fold, it was then the least common species, and abundances of the four species were far more even, ranging from 23 individuals to 54. On a larger spatial scale, the abundance of chowchilla-sensitive species could vary with the relative use of these areas by the birds. Areas used less, like those on ridges in our study, could serve as sites for successful recruitment of sensitive species, while recruitment would be much lower in areas of heavy use, and overall environmental heterogeneity in seedling abundance would be increased.

Our study suggests that in Australian tropical rain forests, litter disturbing birds can be important agents of mortality for tree seedlings and can significantly alter litter environments and thereby seed germination. In the *Eucalyptus regnans* forests of Australia, another bird species, the superb lyrebird, has also been shown to have important effects on seedling recruitment (Ashton & Bassett 1997). Litter-disturbing birds are an important component of the natural fauna of many tropical and subtropical forests worldwide and whether they have similar impacts in other forests deserves more attention. In the tropical rain forests of northern Queensland, chowchillas appear to be vulnerable to habitat fragmentation (Warburton 1997); while in other parts of the world potentially important litter disturbers such as turkey and jungle fowl are hunted by humans. If, as our study suggests, litter-disturbing birds play an important role in affecting tree recruitment, these anthropogenic effects may have much broader consequences for the forest ecosystem.

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