SEED DISPERAL, SEED PREDATION, AND SEEDLING RECRUITMENT OF A NEOTROPICAL MONTANE TREE

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Abstract. Postdispersal fate of seeds from Ocotea endrissiana (Lauraceae), a bird-dispersed Neotropical montane tree, was studied in Costa Rica to determine the influence of seed dispersers, seed predators, and microhabitat characteristics on seedling recruitment. Particular emphasis was placed on finding naturally dispersed seeds in order to study the link between dispersal and postdispersal fate of seeds. Four species of birds (Emerald Toucanet, Aulacorhynchus prasinus; Resplendent Quetzal, Pharomachrus mocinno; Three-wattled Bellbird, Procnias tricolor; and Mountain Robin, Turdus plebejus) dispersed the seeds by regurgitation, and one species (Black Guan, Chamaepetes unicolor), by defecation. Most seeds (80%) were dispersed within 25 m of parent trees and under high (>92%) canopy cover. Bellbirds deposited 52% of the seeds they dispersed under habitual song perches in standing dead trees on the edges of treefall gaps >25 m from parent trees. In contrast, the other four species dispersed only 6% of the seeds they dispersed >25 m from parent trees, and <3% of the seeds were dispersed to gaps. Thus, male bellbirds provided predictable, nonrandom dispersal to a different microhabitat than the other four species.

Seed predation, germination, and one-year seedling survival were assessed for naturally dispersed seeds and for seeds placed at randomly located sites. Seed predation during the first 12 mo after dispersal was extremely high (99.7%). At least 50% of seed removal was attributable to small rodents, such as Peromyscus mexicanus, with no evidence of scatterhoarding or secondary dispersal. Seeds dispersed >20 m from parent trees were removed more slowly than seeds directly under the crown, but over the course of the fruiting season seed predation approached 100%, throughout the study site. Seed predation did not differ between gaps and forest understory.

Germination of seeds protected from mammals was high (70–90%), regardless of microhabitat or seed size. Seeds regurgitated by birds and seeds removed from fruits by hand germinated equally well (98%), but seeds in intact fruits did not germinate. Seeds defecated by guans and regurgitated by other species in the field had similar germination success. Thus, dispersal by birds is important for removal of pulp but does not otherwise affect germination. Seedlings were taller in gaps (<90% canopy cover) than in closed-canopy forest (>90% cover). Fungal pathogens killed fewer seedlings in gaps than in understory, while other causes of seedling mortality were similar among microhabitats. Consequently, bellbirds, the most likely species to disperse seeds to gaps, had a disproportionate influence on seedling recruitment. Nevertheless, the absolute number of seedlings was higher in closed-canopy forest, because the great majority of seeds (85%) landed there. The overall pattern of recruitment, averaged among trees, had a large peak corresponding with bellbird song perches in gaps, as well as a smaller peak near the parent tree corresponding with the seeds dispersed by other species. The relative height of these peaks is opposite that of the original pattern of dispersal. Frugivorous birds that use habitual perches may have disproportionate effects on plant recruitment. To test this idea further, it is necessary to study each stage of the recruitment process, including seed dispersal, postdispersal seed survival, and seedling survival.

Key words: Aulacorhynchus prasinus; birds, seed dispersal; Chamaepetes unicolor; Neotropical cloud forest in Costa Rica; Ocotea endrissiana (Lauraceae); Pharomachrus mocinno; Procnias tricolor; recruitment; rodents, seed predation; seed dispersal and predation; seedling survival; Turdus plebejus.

INTRODUCTION

Seed dispersal determines the spatial arrangement and physical environment of seeds from which the next cohort of seedlings is selected. The links between seed dispersal and seedling recruitment, however, are poorly understood. Dispersal is the first of a series of events that may be important in limiting recruitment. For vertebrate-dispersed plants, these stages include fruit removal, seed dissemination, postdispersal seed predation, potentially secondary dispersal, germination, and
seedling establishment. Previous studies have generally focused on only one or a few of these stages (Herrera et al. 1994, Schupp and Fuentes 1995).

Despite many studies on fruit consumption and seed handling by birds and mammals, seed shadows (spatial patterns of dispersed seeds) generated by animals are poorly known (Willson 1993). While concentrations of seeds under or near fruiting trees have been noted and, indeed, are expected (Janzen 1970, Howe 1989, Willson 1993), the pattern of seed distribution farther from fruiting trees is likely to be the most important part of the seed shadow for plant fitness and population ecology (Portnoy and Willson 1993, Schupp and Fuentes 1995). In particular, the tail of the distribution is often heterogeneous because of disperser behavior (McDonnell and Stiles 1983, Hoppes 1988, Chavez-Ramirez and Slack 1994, Julliot 1996). Fruit-eating vertebrates differ in foraging behavior (Cruz 1981, Santana and Milligan 1984, Trainer and Will 1984, Moermond and Denslow 1985), fruit removal rates (Howe and Vande Kerckhove 1980, Bronstein and Hoffman 1987, Englund 1993), seed-handling techniques (Janzen 1983, Levey 1987, Corlett and Lucas 1990, Stiles and Rosselli 1993), and effects on seed germination (Krefting and Roe 1949, Compton et al. 1996, Traveset and Willson 1997). Few studies, however, have compared seed shadows generated by different dispersers (but see Thomas et al. [1988] and Chavez-Ramirez and Slack [1994]), or the consequences of dispersal pattern on recruitment (but see Howe [1989, 1990a], Herrera et al. [1994], Schupp [1995], and Schupp and Fuentes [1995]).

After dispersal, seed predation and seedling mortality are often extensive for tropical trees (DeSteven and Putz 1984, Howe et al. 1985, Chapman 1989, Hammond 1995, Cimbra and Horna 1997, Porcs et al. 1997) and may be important in influencing the spatial pattern of recruitment (Connell 1970, Janzen 1970, Harper 1977, Hubbell 1980, Clark and Clark 1984, Becker et al. 1985, McCann 1985, Howe 1989). In addition, studies on forest dynamics have suggested that canopy gaps are often crucial recruitment sites for tree seedlings (Hartshorn 1978, Denslow 1987, Swaine and Whitmore 1988, Swaine 1996). Few studies, however, have examined seed predation as a link between seed dispersal and seedling recruitment. In fact, aside from research on Virola in Panama (Howe and Vande Kerckhove 1980, Howe et al. 1985, Howe 1990b, 1993), Philibertia in Spain (Herrera et al. 1994, Jordano and Herrera 1995), and Ficus in Borneo (Lama 1995, 1996a, b), I know of no studies that consider the various stages leading to recruitment for any species of fleshy-fruited, vertebrate-dispersed plant. Furthermore, some plant species, typically considered to be bird or mammal-dispersed, may have a second (or even third) stage of dispersal by an entirely different dispersal vector (Robertson and Heithaus 1986, Clifford and Monteith 1989, Forget and Milleron 1991, Estrada et al. 1993, Levey and Byrne 1993, Nogales et al. 1996, Wenny 1999). To understand the relative importance of seed dispersers and seed predators in forest dynamics, it is necessary to study each stage leading to recruitment (and, ideally, to reproductive age).

The main factor that limits our understanding of the link between seed dispersers and seedling recruitment is the difficulty of finding dispersed seeds (Harper 1977, Janzen 1983, Schupp and Fuentes 1995). Thus, most studies on vertebrate-dispersed plants have assessed the importance for plant fitness of different dispersers by the amount of fruit in the diet and gut treatment of seeds, and have not considered postdispersal fate of seeds (reviewed by Howe [1986], Stiles [1989], Jordano [1992], Willson [1992], and Levey et al. [1994]). Similarly, studies on seed predation and seedling recruitment have relied on experimentally dispersed seeds, usually without data on the actual patterns of seed rain (Price and Jenkins 1986, Crawley 1992, Hulme 1993, Schupp 1995).

The objective of this study was to link patterns of seed dispersal and seed predation with those of seedling recruitment, by determining the locations of naturally dispersed seeds, and then following the fate of those seeds after dispersal. I studied a common tree, Ocotea endressiana Mez (Laureaceae), in an old-growth montane forest in Costa Rica, to answer the following questions: (1) Do the main fruit consumers of O. endressiana generate different patterns of seed rain and, thus, subsequently influence germination and the pattern of seedling recruitment? (2) What proportion of the dispersed seeds are subsequently killed by seed predators, and what animals are the most important seed predators? (3) Do scat-hoarding rodents provide a second stage of dispersal? (4) What proportion of the dispersed seeds germinate and establish as seedlings under different microhabitat conditions? To answer these questions, I used a combination of natural and manipulative experiments to assess the types of sites to which seeds are dispersed and how the habitat characteristics and spatial arrangement of these sites relative to the parent trees influence postdispersal survival. In a previous paper (Wenny and Levey 1998), based a subset of the data from this study, I described some elements of the first question and found that one of the five disperser species deposited seed disproportionately in sites suitable for seedling survival. In the current paper, I examine this idea in more detail, by incorporating data on seed predation and seedling establishment, as well as additional data on dispersal not included in the previous paper.

Methods

Study site

This study was conducted during May 1993-July 1996 in the Monteverde Cloud Forest Preserve (10°12' N, 84°42' W) in the Cordillera de Tilaran, northern...
Costa Rica. This 10,000-ha preserve is adjacent to other protected lands encompassing one of the largest areas of relatively unbroken forest in Costa Rica. The study area contains the full complement of birds and mammals, including top predators that have historically occurred in the area (Young and McDonald 1999), although certainly the abundance of some species has changed (Fogden 1993). Other characteristics of the fauna are described by Nadkarni and Wheelwright (1999).

The study area was in relatively undisturbed lower montane rain forest (Hartshorn 1983) along the continental divide at 1600-m elevation. A 5-ha area, 500 m from the beginning of the Valley Trail (Sendero El Valle), was mapped (using sighting compasses and measuring tapes) and marked into 10 × 10 m quadrats with PVC tubing at every grid point. The study area was relatively level with a change in elevation of only 10 m from north to south (excluding stream banks). The forest canopy is 25–30 m tall and dominated by several species of Lauraceae, *Sapindus insigne* (Euphorbiaceae), *Ficus crassa* (Moraceae), *Inga* sp. (Leguminosae), and *Pouteria viridis* (Sapotaceae). The vegetation of the area is described in more detail by Lawton and Dryer (1980) and Nadkarni et al. (1995).

Canopy gaps caused by falling trees and branches are common and may be an important habitat for recruitment of some plants in the study area (Lawton and Putz 1988, Lawton 1990). Although gaps may be formed at any time of year, most are formed during the dry season, when strong winds are more frequent (K. G. Murray, personal communication). Gaps are also formed under standing dead trees, especially *Sapindus*, which shed large limbs for several years before the remainder of the trunk falls (personal observation; C. Guindon, personal communication). Approximate boundaries of gaps were sketched on to the map of the study site, the area of each gap was estimated from the map, and the proportion of the study site in gaps was calculated from the sum of those estimates. Approximately 5.3% of the mapped study area was in gaps ≥10 m², with vegetation ≤2 m tall (sensu Brokaw 1982), including two *Sapindus* gaps. Mean canopy cover (measured with a spherical densiometer 1.2 m above the ground) in gaps and gap edges was 90.7% (±9.6, range 60–92%, N = 78), while closed-canopy forest had mean cover of 96.2% (±4.3, range 91–100%, N = 234). These values are similar to those at other Neotropical forest sites (Howe et al. 1985, Levey 1988, Clark 1994).

Most woody plants at Monteverde are animal dispersed, as is typical of Neotropical forests in general and tropical montane forests in particular (Gentry 1982, Howe and Smallwood 1982, Tanner 1982, Stiles 1985, Levey and Stiles 1994). Bird dispersal predominates: 77% of the understory trees and shrubs and 63% of the canopy trees have fruit morphology suggesting dispersal by birds (Stiles 1985). At least 70 resident and migrant bird species feed on the fruits of >150 species of trees and shrubs (Wheelwright et al. 1984). Most of these birds regurgitate or defecate seeds intact (Wheelwright et al. 1984, Murray 1988).

The mean annual rainfall at 1520 m on the Pacific slope 3 km from the study site is ~2500 mm, with most of the precipitation occurring during May–November. Actual rainfall in the study site was probably >2500 mm, but the seasonal pattern was similar (Nadkarni and Wheelwright 1999). Rain gauges underestimate the amount of precipitation from mist and cloud interception, which contribute ≥50% of the precipitation in some Neotropical montane forests (Cavelier 1996). Temperatures recorded in the forest understory at the study site during this project ranged 15–22°C.

**Study species**

The Lauraceae is an important family in Neotropical forests in terms of species richness, a food resource for birds, and economic value (Wheelwright 1983, 1985a, 1991, Burger and van der Werff 1990, Gentry 1990, Martínez-Ramos and Soto-Castro 1993, Guindon 1996). Members of the Lauraceae are also important dietary components for frugivorous birds in Africa, Southeast Asia, and Australia (Crome 1975, Snow 1981, Sun et al. 1997). *Ocotea endresiana* Mez (listed as *O. austini* in Wheelwright et al. [1984], Wheelwright [1985a, 1986]) is a common canopy tree in montane forests in central and northwestern Costa Rica at 1100–2300 m elevation (Burger and van der Werff 1990). In the Monteverde area it occurs between 1550 and 1700 m along the continental divide. In the same area, 20–30 other species of Lauraceae occur (Wheelwright 1985a, 1986, Haber 1991). *Ocotea endresiana* is monocious and begins flowering in August, the mid-rainy season, and is pollinated by small flies and other insects. Fruits ripen the following May and June in the early rainy season. Ripe fruits (18 × 9 mm, 1.2 g) have blue-black skin, lipid-rich pulp, and are held in a shallow reddish receptacle, typical of the Lauraceae genera *Ocotea* and *Nectandra* (Wheelwright et al. 1984, Burger and van der Werff 1990). Most of the volume of the fruit is a single seed (15 × 8 mm, 0.75 g, fresh mass) composed of a small embryo and two large cotyledons surrounded by a thin (0.3-mm) seed coat. Seeds begin germination ~6 wk after dispersal. Although small compared to some other Lauraceae species, *O. endresiana* fruits and seeds are among the largest at Monteverde (Wheelwright et al. 1984). Twenty-one *O. endresiana* trees >20 cm dbh were in the 5-ha study site, and all but one produced fruit in both years. Fruits and seeds for some experiments were collected from 17 additional trees outside the main study area. Large fruit crops (2110 ± 1495 fruits/tree) were produced in 1993 and 1995, but not in 1994. Each *O. endresiana* tree was a mean distance of 36.5 m (±12.1) from the three closest conspecific adults.

The most common avian visitors to fruiting Laurae-
ceae include the largest and most frugivorous species at Monteverde (Wheelwright et al. 1984). *Ocotea endresiana* fruits are eaten primarily by five species of birds: Emerald Toucanet (Ramphastidae: *Aulacorhynchus prasinus*), Resplendent Quetzal (Trogonidae: *Pharomachrus mocinno*), Three-wattled Bellbird (Coerebidae: *Procnias tricolorula*), Mountain Robin (Turdidae: *Turdus plebejus*), and Black Guan (Cracidae: *Chamaepetes unicolor*), all of which breed in the study site during the fruiting season. The first four species swallow fruits intact and regurgitate seeds in viable condition. Seeds in this size range are generally regurgitated 15–30 min after ingestion (Wheelwright 1991). Guans defecate seeds in viable condition (Wheelwright 1991). These bird species (especially quetzals) typically remain in a fruiting tree after eating several fruits, and often regurgitate seeds under the same tree or nearby (Wheelwright 1983, 1991). Seed processing times for guans are unknown, but they generally leave a fruiting tree before defecating the seeds from that foraging bout (personal observation). Several other bird species (Wheelwright et al. 1984), as well as spider monkeys (*Ateles Geoffroyi*), occasionally eat *O. endresiana* fruits and probably disperse viable seeds (e.g., Chapman 1989).

**Experimental design**

A combination of observational and experimental data was collected to determine the probability of seedling establishment and one year survival for seeds dispersed by birds. In particular, the focus of this project was to find the locations of seeds dispersed naturally, and to compare the postdispersal fate of those seeds with experimentally placed seeds, with the goal of determining the influence of dispersers on seedling recruitment. The locations of seeds naturally dispersed by birds were classified in two categories, according to their position relative to the parental tree crown. Seeds were classified as nondispersed if dispersed under the crown of a fruiting *O. endresiana* tree, or as dispersed if not under such a tree. Even though all dispersed and nondispersed seeds in this study had been regurgitated or defecated by birds (and therefore “dispersed” sensu Janzen [1983]), it is generally believed that seeds deposited under the parent trees have very little chance of survival (e.g., Janzen 1970, Howe et al. 1985, Hulme 1997). For convenience, I will refer to sites of dispersed seeds as dispersed sites and of nondispersed seeds as nondispersed sites.

**Seed dispersal**

Seeds were located by following birds until they dropped, regurgitated, or defecated seeds, and by systematic ground searches. These ground searches were started at the base of a fruiting tree and proceeded along 10 m wide transects to 50–60 m from the trunk. It was impossible to search the entire site with equal intensity, but an effort was made to cover the entire site at least once every two weeks, so that, over the course of the two-month season of fruit ripening, each 10 × 10 m plot was checked at least four times. Bird observations began whenever one of the five major consumers of *O. endresiana* fruits was located, and continued as long as the bird was visible or until the bird regurgitated or defecated seeds. During 193 hr spent following birds, 184 seeds were found. I assumed that the distribution of seed locations found by the combination of methods would be representative of the entire population of seeds.

In addition to these dispersed and nondispersed seeds, other seeds were experimentally placed at randomly selected sites to determine if birds deposited seeds in sites with specific or random characteristics. Random numbers generated on a hand calculator were used as site coordinates within the 5-ha grid. The postdispersal fate of seeds at these random locations was compared to the fate of seeds at the dispersed and nondispersed locations.

**Microhabitat characteristics**

For all seed locations, including random sites, I measured seed characteristics and microhabitat variables that I thought might influence seed predation, germination, or seedling survival. Seed length and width were measured with dial calipers, and seed mass was measured ±0.05 g with a spring balance. Canopy cover was estimated with a spherical densiometer (Lemmon 1957). Leaf litter was the number of leaves pierced by a metal stake thrust into the soil once at the site of each seed. Vegetation density was the number of stems within a 50-cm radius of the site. The distances to the nearest woody stem >1 m in height, tree >10 cm dbh, trunk of fruiting *Ocotea* tree, and fallen log were measured with a fiberglass measuring tape. These variables were selected based on their demonstrated importance in previous studies. Seed size may influence the probability of seed predation (Price and Jenkins 1986, Hulme 1993) or seedling size (Howe and Richter 1982). Canopy cover (light availability) is known to be an important factor for germination and tropical seedling growth (Howe et al. 1985, Mulkey et al. 1996, Swaine 1996). Vegetation density and distance to objects may influence rodent activity and seed predation (Smythe 1978, Kittle 1981, Ritchings and Levey 1981). Finally, leaf litter may influence seed predation or germination (Schupp 1988, Molofsky and Augspurger 1992, Myster and Pickett 1993).

**Postdispersal seed predation**

At each dispersed, nondispersed, and random site, a marked seed was used to assess rate of seed predation, to identify seed predators, and to determine if secondary dispersal occurred. For this treatment, I used seeds that were regurgitated by birds and collected under fruiting trees adjacent to the study site. Seeds were marked by gluing 50–75 cm of unwaxed dental floss
to the seed, and tying ~50 cm of flagging tape to the distal end of the floss. Because the glue held best on seeds with a dry seed coat, seeds were taken inside a lab room and allowed to dry for 1–3 h before gluing. Each marked seed was placed at a site the next morning. To determine if presence of dental floss and flagging tape influenced seed removal, I conducted a pilot study in May 1993. Fifty marked seeds and 50 unmarked seeds were placed singly at random locations and censused one week later. Removal of marked and unmarked seeds was not significantly different (49 and 47 seeds removed, respectively; $\chi^2 = 0.047, df = 1, P > 0.10$). Thus, the marking of seeds was assumed to have no effect on seed removal.

Note that these marked seeds were placed next to the cages protecting the original seeds deposited by birds (see cage description in Methods: Germination and seedling survival). The cages may have served as cues for visually searching seed predators, but I believe that is unlikely for two reasons. First, at the beginning of the study in 1993, cages were novel items and would not have been associated with seeds by the seed predators. Second, because most marked seeds were removed, but the cages were left at the sites for several months, most cages were not good indicators of seed availability. Olfactory cues left by marking and handling the seeds are another possible confounding factor, but the frequent rains probably diminished these (Whelan et al. 1994).

In 1993, all marked seeds were censused once each week for three weeks, and then at weeks 5 and 10. Because most seeds were removed during the first week after dispersal in 1993, marked seeds in 1995 were checked more often: on days 1, 3, and 7, and once each week afterwards until week 10. If a marked seed was removed, the surrounding area was searched to find the flagging tape-dental floss assembly. The end of the floss where the seed had been attached was examined to determine the fate of the seed. If a seed was entirely removed, or if a piece of the seed coat remained attached to the floss, the seed was classified as killed by seed predators, because captive Peromyscus treated O. endrestana seeds with dental floss in that manner when they consumed them (Wenny, unpublished data). The distance from the dispersal site to the predation site was measured, and each site of a removed seed was classified in the following categories: in burrow; in, under, or near a fallen log ($>10$ cm diameter); at the base of a large tree; in dense vegetation (defined as $\geq50\%$ cover of plants $<50$ cm tall within a $50$-cm radius of site, assessed visually); under or beside a clump of fallen branches, or on the leaf litter. If a marked seed was removed but not eaten, it was left in the new location and included in subsequent censuses.

**Distance effect.**—Two other experiments (one in 1995 and one in 1996) were conducted with marked seeds to determine the effect of distance on seed removal, as well as whether most seed removal occurs during the day or at night. In 1995, one seed was placed at the base of each of 12 fruiting trees and at 20, 40, 60, and 80 m from the base of the tree. The orientation of each transect was carefully selected to avoid approaching within 80 m of other fruiting O. endrestana trees. Seeds at these sites were censused on the same schedule as the other marked sites in 1995. In 1996, a similar experiment was conducted, except the seeds were 5 and 40 m from each of 22 trees. Shorter and fewer distances were used so that more trees could be included, and because data from the previous year, as well as other studies (e.g., Howe et al. 1985), indicated that the distance effect can be detected beyond 20 m from a conspecific adult. In this case, the compass directions were randomly selected, although some directions were discarded if the 40-m treatment was not $\geq40$ m from all fruiting conspecifics. This experiment was run twice, once in the early fruiting season (late May) and once two weeks later, during the peak fruiting season (mid-June). During the second of these trials, all sites were checked at dusk and dawn for two consecutive days to determine whether most seed removal occurred during the day or night. Removal during the day likely could be attributed to the diurnal agouti, while removal at night likely would be from nocturnal species, such as Peromyscus or other small rodents.

**Exclusions.**—To determine the amount of seed predation attributable to large or small mammals, 38 sets of exclusions were established in early 1995. Each set had three treatments, each 1 m$^2$ in area: (1) “no rodents” exclusions made of 1-cm$^2$ galvanized wire mesh, 0.9 m tall; (2) “small rodents only” exclusions made of chicken wire mesh with 6-cm holes, 0.9 or 1.35 m tall; and (3) “all rodents” control plots with only wooden stakes marking the corners. The bottom edges of the wire exclusions were buried 5 cm below ground and held with two or three 25-cm metal stakes on each side. The corners were supported by 1.25-m lengths of 10 mm thick metal stakes. The tops were open to allow normal accumulation of fallen leaves. Although small rodents can probably climb such cages, the results show that the “no-rodent” treatment was successful. Each set was located where convenient (avoiding trees and fallen logs), within randomly located 10 $\times$ 10 m quadrats in the study site. One regurgitated O. endrestana seed was placed in each exclusion and control plot in late June 1995. Each seed was checked after 2, 4, and 8 d, 4 mo, and 1 yr.

**Germination and seedling survival.**

The original regurgitated or defecated seed at each dispersed and nondispersed site, and each seed placed at a randomly located site, was protected by a 4 $\times$ 4 $\times$ 2 cm cage made of 3-mm galvanized wire mesh held in place by two metal stakes. Caged seeds were used to determine germination rates and insect predation rates, in the absence of mammalian seed predators. Each site was checked weekly for $\geq12$ wk and monthly.
thereafter, until June of the following year. Germination was defined as the splitting of the seed coat and spreading of the cotyledons. Typically, the radicle had emerged by the next census after germination, and a week later the stem was visible. As each seed germinated and the shoot began to grow, the cage was removed to allow normal seedling growth. The seedling location was marked with one of the stakes from the cage. Causes of seedling mortality were classified as mammal, insect, fungal pathogen, physical, or unknown. Mammals either ate the seed and left the damaged shoot behind (seed predators) or removed the entire shoot (herbivores). Some seeds that appeared to have germinated were killed by beetle larvae (Heliophilus sp., Curculionidae) developing in the seed. Insect-killed seeds frequently developed a root, but never had a shoot > 2 cm tall. Seedlings killed by fungal pathogens were characterized by a wilted and discolored shoot above ~4 cm (Augspurger 1990). Physical damage consisted of trampling by peccaries and other large mammals, or damage from falling trees, branches, or large leaves (Clark and Clark 1991). Unknown causes of mortality included cases that fit more than one category where the sequence of events could not be determined, and cases that did not clearly fall into any category. A seed was considered alive if the seed remained firm, even if the shoot had been eaten or otherwise damaged. Such seeds resprouted repeatedly (personal observation). Seeds from 1995 that had not germinated or resprouted after one year were cut open and classified as insect-killed if filled with frass, or viable if the embryo and cotyledons were not discolored or mealy in appearance.

*Germination trials.*—To determine the effect on *O. endresiana* germination of ingestion by birds and seed burial (which I initially thought would apply to seeds taken by mammals), trials were conducted in a greenhouse constructed of nylon window screen over a 12 x 6 m wooden frame on a concrete foundation set 25 cm into the ground. The roof was corrugated plastic. Seeds were planted individually in cardboard milk cartons and cut plastic bottles of various sizes. All containers were washed with hot soapy water and dried in the sun before use. Soil was collected from a nearby secondary forest and mixed 3:1 with sand.

Three seed treatments were compared: (1) naturally regurgitated seeds, collected under fruiting trees or along the trail to the study site; (2) seeds removed by hand from ripe fruits, collected under fruiting trees; and (3) entire ripe fruits, either fallen or dropped. Seeds or fruits that were misshapen, diseased, or had signs of insect infestation were not used. Each treatment had 35 seeds or fruits, placed on top of the soil. Additionally, 10 seeds were planted 5 cm deep to determine if seeds could germinate after burial by scatter hoarding rodents. Containers were watered as necessary to keep the soil moist. Seeds were planted in June 1995, and were checked weekly until early November 1995, when seeds that had not germinated were cut open and assessed for viability.

*Seedling and sapling plots.*—To determine if *O. endresiana* seedlings and saplings are more likely to recruit under or away from conspecifics, seedlings and saplings (<3 m tall) were measured and mapped in paired 10 x 10 m plots. For each of 10 trees, one plot was located near the tree, with approximately half of the plot directly under the crown. The second plot was located 10-20 m from the edge of the first plot and at least 15 m from the crown edge. No plots were located in recent (<5 yr) canopy gaps or along streams.

*Statistical analyses*

The influence of the microhabitat variables on removal of marked seeds (at day 1 [1995 only] and week 2) and on germination, and 1-yr survival of caged seeds were examined with multiple logistic regression using SAS JMP (SAS Institute 1989). For each of the binomial (live or dead) response variables, data for the two years were analyzed separately. Each model was run, first with all predictor variables, and then with and without each predictor variable to determine if the deletion of a given variable had a significant effect on the amount of variation explained. This deletion procedure was repeated until only significant predictors were retained (Trexler and Travis 1993). Models were selected manually to avoid the problems of automatic stepwise procedures (James and McCulloch 1990). The predictor variables included three measures of seed size (length, width, and mass), eight microhabitat characteristics (leaf litter, canopy cover, number of stems, and distances to nearest caged seed, herbaceous stem, woody stem, 10-cm tree, parent tree trunk, and fallen log), date of dispersal (Julian date), and tree number. Only single terms were included in the models as lack-of-fit tests indicated that the single-term models were adequate; thus, interaction terms were not required (SAS Institute 1989).

The relationships of the microhabitat variables within and among the dispersed, nondispersed, and random sites were examined with principal components analysis (PROC FACTOR) from the SAS statistical package (SAS Institute 1988). The mean loadings for the three types of sites were compared with one-way analysis of variance from Super Anova (Abacus Concepts 1989). Type III sums of squares were used to compensate for the unequal sample sizes (Shaw and Mitchell-Olens 1993). Removal rates were compared among treatments with survival analysis and Gehan–Wilcoxon tests from SAS JMP (SAS Institute 1989). The Gehan–Wilcoxon test places greater weight on early events, than later events, and was deemed appropriate for this study because most seeds were removed during the first week (Pyke and Thompson 1986).

Parametric tests were used unless the data violated the assumptions of normality and equal variance, in which case nonparametric procedures were used. Data
in the form of proportions were arcsine square root transformed before analysis. Where multiple comparisons on a data set were involved, the alpha value was adjusted according to the number of comparisons planned (Bonferroni technique, Holm [1979]). Data from the two years were very similar and were combined for analyses in which sample sizes would have been low otherwise. Throughout this paper mean values are followed by ±1 SD.

RESULTS

Seed dispersal

In 1993, 284 seeds regurgitated or defecated by birds were found (155 dispersed, 129 nondispersed), while in 1995, 234 dispersed and 171 nondispersed seeds were found. In 1993 and 1995, 95 and 100 random sites, respectively, were established. Twenty-four percent of the 1993 seeds and 28% of the 1995 seeds were found by following or observing birds (N = 184), and the rest (N = 505), by searching the ground. The total number of seeds found (689) was ~1% of the total seed crop in the 5-ha study area in both years combined.

The dispersed seeds were most common within 10 m of the crown edge (1993, 55%; 1995, 45%), but some seeds were as far as 70 m away. In rare cases (2.8%), dispersed seeds were within 5 m of an O. endresiana trunk (Fig. 1). Despite their close proximity to the parent, they were classified as dispersed, because they were not directly under the parent crown, which was a result of asymmetrical crown geometry or a tilted trunk (or both). Random sites were more evenly distributed than dispersed or nondispersed sites, but showed a peak at 20–25 m in both years (Fig. 1). Most seeds landed within 20 m of the fruiting trees, but the tail of the seed distribution curve beyond 20 m accounted for 18% of the sites in 1993 and 21% in 1995. Mean seed rain was highly variable when evaluated among trees and years (Fig. 2). In particular, note that mean seed distributions showed secondary peaks at 45–50 and 60–65 m in both years (Fig. 1). These peaks corresponded to habitual song perch sites used by bellbirds (see Results: Microhabitat characteristics) that were located 40–70 m from fruiting trees in the years this study was conducted. A map and more information on the locations of seeds are presented elsewhere (Wenny 1998).

Microhabitat characteristics

In a principal component analysis of the 1995 microhabitat characteristics, the first two components explained 63.8% of total variance; whereas, for 1993, the first two components accounted for 45.5% of total variance. The relatively low amount of variance explained is not entirely due to the inclusion of random sites (Jackson 1993), because removal of random sites increased the total variance explained by the first two components by only 2–3%. The pattern was similar in both years: the first multivariate axis (PC 1) was char-
cept for some dispersed sites that have higher values for the first component. These correspond to sites with low canopy cover, relatively far from the parent trees (Fig. 3). Seeds in the sites with values >2.0 in 1993, and >1.0 in 1995, for PC 1 were all dispersed by bellbirds into large gaps surrounding song perches. Additionally, two of the 1993 seeds were dispersed by Black Guans onto logs in another smaller gap. Bellbird-dispersed seeds, seeds dispersed by other species, and random sites had significantly different PC 1 loadings in 1993 ($F_{2,19} = 7.9, P = 0.006$) and 1995 ($F_{2,212} = 9.1, P < 0.001$). Bellbird sites had higher factor loadings than other species' sites and random sites ($P < 0.002$ in all cases), but sites of the other species and random sites did not differ ($P = 0.2$; see also Wenny and Levey 1998).

The locations of dispersed, nondispersed, and random sites differed significantly in both years with regard to canopy cover, distance to parent, and number of stems (Table 1). Dispersed seed sites had lower mean canopy cover than nondispersed or random sites in both years, while the nondispersed and random sites were similar. In 1993, dispersed and random sites had similarly high numbers of stems compared to nondispersed sites. In 1995, dispersed sites had more stems than both the other sites, while random and nondispersed sites had similar numbers of stems. The only other variable that differed among the treatments was distance to closest stem in 1995. Dispersed sites were closer to stems than nondispersed sites, while random sites did not differ from the other two treatments (Table 1).

Combining the seeds from both years, and using only seeds for which the disperser was known, the mean canopy cover at sites of seeds dispersed by bellbirds was significantly lower than of sites of seeds dispersed by all the other species (89 and 96%, respectively; Kruskal–Wallis test: $x^2 = 42.7, df = 1, P < 0.001$). Similarly, the mean distance from the closest parent tree of bellbird sites was greater than any of the other four species, (Kruskal–Wallis $x^2 = 66.06, df = 1, P < 0.001$), but the difficulty in following the birds (especially robins, which tended to fly above the canopy) biased the results in favor of bellbirds. Nevertheless, the data show that bellbirds tend not to drop many seeds near parent trees (Fig. 4). Considering that ~5.3% of the study area was in gaps, overall seed arrival in gaps (12%) occurred more often than expected by chance ($x^2 = 36.45, df = 1, P < 0.001$), whereas the expected number of random sites (4.1%) were in gaps ($x^2 = 0.557, df = 1, P > 0.05$). Furthermore, bellbirds dispersed significantly more seeds to gaps than did the other species ($x^2 = 39.3, df = 1, P < 0.001$). However, bellbirds dispersed seeds to only 2 of 29 gaps in the study area.

**Postdispersal seed predation**

More than 50% of marked seeds were removed within one week in both years (Fig. 5). In 1993, seeds at...
TABLE 1. Summary of one-way analysis of variance tests for each habitat variable, compared among sites of dispersed (D) and nondispersed (N) seeds, and randomly located sites (R) in 1993 and 1995.

<table>
<thead>
<tr>
<th>Variable</th>
<th>1993</th>
<th>1995</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>D</td>
<td>N</td>
</tr>
<tr>
<td>Leaf litter</td>
<td>2.1</td>
<td>1.9</td>
</tr>
<tr>
<td></td>
<td>(1.3)</td>
<td>(1.4)</td>
</tr>
<tr>
<td>Canopy cover (%)</td>
<td>94.3&lt;sup&gt;a&lt;/sup&gt;</td>
<td>95.6&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>(3.6)</td>
<td>(1.5)</td>
</tr>
<tr>
<td>Vegetation density</td>
<td>38.9&lt;sup&gt;a&lt;/sup&gt;</td>
<td>32.1&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>(17.3)</td>
<td>(16.2)</td>
</tr>
<tr>
<td>Closest stem (cm)</td>
<td>10.8</td>
<td>12.2</td>
</tr>
<tr>
<td></td>
<td>(5.5)</td>
<td>(6.2)</td>
</tr>
<tr>
<td>Woody stem (cm)</td>
<td>61.9</td>
<td>58.9</td>
</tr>
<tr>
<td></td>
<td>(45.7)</td>
<td>(39.7)</td>
</tr>
<tr>
<td>Closest tree (m)</td>
<td>1.50</td>
<td>1.68</td>
</tr>
<tr>
<td></td>
<td>(0.87)</td>
<td>(0.97)</td>
</tr>
<tr>
<td>Closest log (m)</td>
<td>1.47</td>
<td>1.30</td>
</tr>
<tr>
<td></td>
<td>(1.31)</td>
<td>(1.37)</td>
</tr>
</tbody>
</table>

Notes: ANOVA tests had a Bonferroni-adjusted alpha value of 0.006. Mean values are shown for each treatment for each variable. Standard deviations are in parentheses below each mean. Leaf litter was the number of leaves pierced by a metal stake thrust into the soil at the site. Canopy cover was estimated with a spherical densiometer. Vegetation density was estimated as the number of stems within a 50-cm radius of the site. The last four variables are distances to closest stem, closest woody stem (>1 m height), closest tree (>10 cm dbh), and closest log (>10 cm). Within each year and variable for which a significant difference among treatments was detected (indicated with a dagger † after the F value), results of post hoc tests (Student-Newman–Keuls tests) are indicated with a letter after the mean. Means followed by different letters are significantly different (P < 0.05).

‡ P < 0.006.

dispersed, nondispersed, and random sites were removed at similar rates, with dispersed seeds showing a nonsignificant trend for slower removal than seeds at nondispersed or random sites (Wilcoxon χ² = 5.36, df = 2, P = 0.068). In 1995, dispersed seeds were removed more slowly than those at nondispersed and random sites (Wilcoxon χ² = 9.09, df = 2, P = 0.011). Ultimately, only 2 of 923 marked seeds (one dispersed and one random site, both from 1995, and both >30 m from conspecific trees) in the entire study survived to June 1996 (and germinated), for an overall predation rate of 99.7%.

I found 75% of marked seeds after removal in 1993, and 94% in 1995. In all cases, the seed was killed, and in most cases (96%) entirely consumed. Few seeds were eaten (13%) but not moved. The general pattern was that seeds were taken a short distance (range 0–21 m, N = 761) to a site with cover, presumably where the seed could be eaten in safety. The mean transport distances of removed seeds (not counting seeds eaten but not moved) were 2.5 m (±3.8, N = 286) in 1993 and 2.1 m (±2.9, N = 475) in 1995. Approximately 50% of those removed were found on the leaf litter, but some were found in small burrows (<6 cm diameter), in or under fallen logs, or in crevices at the bases of large trees (Fig. 6). Most seeds taken to burrows, trees, and logs were clearly taken by small animals, probably rodents, because the small diameter of the opening would exclude larger species such as agoutis (Dasyprocta punctata). I found no evidence of scatter-hoarding or secondary dispersal.

Significant predictors of survival of marked seeds to 2 wk in 1993 included more open canopy cover, deeper leaf litter, and later dispersal date (Table 2 [seeds]). In 1995, single-day survival was significantly predicted by greater seed mass, earlier dispersal date, and the particular parent tree. At 2 wk, seeds farther from the parent tree, dispersed later in the season, and at certain parent trees were more likely to survive. Logistic regression models of survival past 2 wk were not significant, because so few seeds survived that long.

Distance Effect.—Seed removal from transects radiating from fruiting O. endresiana trees was slower for seeds farther from the parent trees in both 1995 and 1996. The 1995 seed removal experiment, which ran for 10 wk, showed that the effect of distance on seed
removal declined over time, and that seed predation eventually approached 100% at all distances (Fig. 7a). Only one seed (at 80 m) survived 10 wk. Removal of seeds was significantly faster for seeds ≤40 m from parents, than for seeds placed 60 or 80 m away (Wilcoxon χ² = 4.5, df = 1, P = 0.03). The 1996 experiment (Fig. 7b) showed that seed removal was significantly faster for seeds experimentally dispersed during the peak of fruiting than before the fruiting peak, but only for seeds 5 m (under the crown) from parents (χ² = 6.87, df = 1, P = 0.009), and not for seeds 40 m away (χ² = 0.21, df = 1, P = 0.64). Removal rates did not differ between seeds placed 5 and 40 m from parents at either time in the fruiting season (early, χ² = 0.65, df = 1, P = 0.42; middle, χ² = 3.17, df = 1, P = 0.20).

The 1996 sample of 44 seeds was censused at dusk (1800–1830) and dawn (0530–0600) for two consecutive days. Five seeds had been removed by the first dusk census, two of which clearly were taken by small rodents into small holes in fallen logs. By the next dawn, 27 more seeds had been removed. One seed was

![Graph showing seed removal percentages over time for different categories.](image)

**Fig. 6.** Percentage of marked seeds found in different locations after removal by animals. See text (Methods: Post-dispersal seed predation) for definitions of categories.

### Table 2. Results of logistic regressions of postdispersal survival of marked seeds and of seedlings against habitat variables.

<table>
<thead>
<tr>
<th>Response period</th>
<th>χ²</th>
<th>−2 log likelihood</th>
<th>Predictors†</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2-wk survival of seeds</td>
<td>0.311</td>
<td>54.19***</td>
<td>+ leaf litter***</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>− canopy cover</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>− dispersal date***</td>
</tr>
<tr>
<td>1-yr survival of seedlings‡</td>
<td>0.10</td>
<td>43.25***</td>
<td>− canopy cover</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>− dispersal date</td>
</tr>
<tr>
<td>1995</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1-d survival of seeds</td>
<td>0.23</td>
<td>133.3***</td>
<td>− seed mass***</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>+ dispersal date***</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>− tree number†</td>
</tr>
<tr>
<td>2-wk survival of seeds</td>
<td>0.31</td>
<td>144.5***</td>
<td>+ distance to parent***</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>− dispersal date***</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>− tree number†</td>
</tr>
<tr>
<td>1-yr survival of seedlings‡</td>
<td>0.13</td>
<td>67.52***</td>
<td>− canopy cover</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>− dispersal date***</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>− tree number†</td>
</tr>
</tbody>
</table>

Note: Only significant effects are listed.

*P < 0.05, **P < 0.01, ***P < 0.001.

† The sign in front of each predictor variable indicates positive or negative correlation with the response variable.

‡ These seeds were protected from seed predators with cages until germination. No variables significantly predicted germination success (not shown).
mo, 82% of the seeds from the “small rodents only” exclosure had been removed. Thus, although large mammals may take some seeds, small mammals (presumably rodents) will eventually find and eat most seeds.

**Germination and seedling survival**

*Ocotea endresiana* seeds began germinating ~6 wk after dispersal. The germination rate of caged seeds ranged 70–95% in both years, and did not differ among the seeds at dispersed, nondispersed, and random sites. Of the seeds that germinated in 1993 and 1995, 35 and 27%, respectively, survived one year as seedlings. Overall, 28% and 22% of seeds in 1993 and 1995, respectively, germinated and survived one year. For the 1993 caged seeds, annual mean survival for the first three years was 31% (Table 3). Seeds at four dispersed and five random sites from 1993 survived until June 1996, for an overall 3-yr survival rate of 2%. Within each stage (germination, 1-, 2-, and 3-yr survival), the three location treatments had similar survival rates except for 1-yr survival in 1993 ($F_{2,27} = 11.84, P = 0.0002$). Seeds at dispersed sites had significantly higher 1-yr survival than those at nondispersed and random sites ($P < 0.001$). Random and nondispersed sites had similar 1-yr survival ($P = 0.35$). Germination success of seeds defecated by guans did not differ from that of seeds regurgitated by the other four species ($x^2 = 0.98, df = 1, P > 0.05$).

None of the variables in the logistic regression models predicted germination success in either year. Significant predictors of 1-yr survival included lower canopy cover and later dispersal date in both 1993 and 1995 (Table 2 [seedlings]). Additionally, in 1995, 1-yr survival was heterogeneous with respect to which par-

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**Fig. 7.** (A) Removal of marked seeds experimentally dispersed 0, 20, 40, 60, and 80 m from trunks of the fruiting *Ocotea endresiana* trees, starting in June 1995 ($N = 12$ at each distance). (B) Removal of marked seeds at 5 and 40 m from parent trees in the early fruiting season (late May) and at the peak (mid-June) of the fruiting season, 1996 ($N = 24$ for each category). All seeds at 0 and 5 m were under the parental crowns.

---

**Fig. 8.** Percentage of seeds remaining in three types of exclosures after 8 d. For each treatment, $N = 38$. The “no rodent” exclosure was designed to exclude all terrestrial animals, “small rodent” exclosures excluded large animals but allowed access to small animals through 6-cm mesh, and “all rodent” plots were controls with no exclosure.
Table 3. Results of logistic regressions of postdispersal survival of seedlings predicted by habitat variables.

<table>
<thead>
<tr>
<th>Response</th>
<th>$r^2$</th>
<th>$\chi^2$</th>
<th>Predictors†</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993 1-yr survival</td>
<td>0.10</td>
<td>43.28***</td>
<td>canopy cover* + dispersal date*</td>
</tr>
<tr>
<td>1995 1-yr survival</td>
<td>0.13</td>
<td>67.52***</td>
<td>canopy cover* + dispersal date* tree number*</td>
</tr>
</tbody>
</table>

Notes: These seeds were protected from seed predators with cages until germination. Only significant effects are listed. No variables significantly predicted germination success (not shown).

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
† The sign in front of each predictor variable indicates positive or negative correlation with the response variable.

The causes of mortality of caged seeds and seedlings during the first year differed among dispersed, nondispersed, and random sites in both 1993 ($\chi^2 = 29.14$, df = 6, $P < 0.001$) and 1995 ($\chi^2 = 33.59$, df = 6, $P < 0.001$; Fig. 9). Many seedlings were killed when seed predators (presumably rodents) removed the seed and severed the connection between the shoot and root. Mammalian herbivores also killed seedlings by entirely removing the leaves and shoot. Mortality by the combination of mammalian seed predators and herbivores was significantly different among the three location treatments in 1995 ($F_{2, 35} = 4.98$, $P = 0.012$), but not in 1993 ($F_{2, 35} = 3.56$, $P = 0.044$). In 1995, mammals killed more seeds and seedlings at dispersed than at random sites ($P < 0.05$), but mortality caused by mammals at nondispersed sites did not differ from that at either dispersed or random sites ($P > 0.05$; Fig. 9). Mortality caused by beetle larvae (Heilipus sp. and at least one other unidentified species) differed among the three treatments in both years (1993, $F_{2, 35} = 4.85$, $P = 0.012$; 1995, $F_{2, 35} = 6.64$, $P = 0.003$). In both years, more nondispersed than dispersed seeds were killed by beetles ($P < 0.05$; Fig. 9). Mortality caused by fungal pathogens, physical damage (falling branches, trampling), or unknown causes did not differ among treatments or years. For the three treatments, combined levels of mortality by each cause were similar between the two years, except for insect predation, which was significantly higher in 1993 vs. 1995 ($t$ test: $t = 1.97$, df = 52, $P < 0.05$), and mortality by mammals, which was significantly higher in 1995 vs. 1993 ($t = 2.53$, df = 67, $P < 0.01$).

Mean canopy cover for seedlings that survived one year at dispersed sites (94.3% ± 3.6, $N = 86$) was significantly lower than for seedlings that died (95.2% ± 2.3, $N = 303$), whereas canopy cover did not differ with 1-yr survival for nondispersed or random sites (2-way ANOVA, $F_{2, 35} = 3.98$, $P = 0.019$). Denser canopy cover was also a significant predictor of higher mortality by fungal pathogens (logistic regression, $P = 0.0013$). Seedlings that survived one year were significantly taller at sites with less dense canopy cover (linear regression, height = 28.93 – 0.233x, $r^2 = 0.284$, $P < 0.001$). Seedlings from seeds dispersed by bellbirds were significantly taller than those at other species' sites ($t$ test = 2.37, $N = 38$, $P = 0.02$).

Germination trials.—Regurgitated seeds and seeds cleaned of pulp by hand had higher germination rates than the seeds in intact fruits ($\chi^2 = 43.94$, df = 2, $P < 0.001$). Of 30 seeds in each of the first two treatments, all but one seed germinated, and that one failed because it was infested with a beetle larva. In contrast, seeds in intact fruits tended to mold; eight germinated, and 22 appeared mealy and no longer viable after 12 wk. The eight seeds in fruits that germinated never developed a shoot outside the fruit pulp and eventually rotted. Thus, ingestion of seeds by frugivores was beneficial in terms of pulp removal, but probably did not

![Fig. 9](image_url)
otherwise affect germination. Two of the 10 buried seeds started to germinate (the seed coat appeared cracked) and seemed viable, but the other eight seeds rotted. After 4 mo, neither of the apparently germinating seeds had any sign of root development, nor had the cotyledons begun to separate. Six of 10 buried seeds had whitish mold on the seed coat. Thus, few buried seeds appear to establish as seedlings.

Seeding and sapling plots.—Seedlings and saplings were equally common in 10 × 10 m plots under (6.6 ± 1.5 individuals) and away from (4.9 ± 3.5) the parent trees (paired t test; t = 1.15, P > 0.05). Individuals in plots away from the parent trees, however, were taller (79.9 ± 14.9 cm) than those near the parent trees (47.4 ± 7.2; Mann–Whitney U test, P = 0.009).

Recruitment

Based on the experiment with marked seeds, the probability of recruitment is determined mostly by postdispersal seed predators. Assuming the experiment reflects the absolute level of seed predation, and all seeds that escape predation germinate and survive, then recruitment was 0% in 1993 and 0.4% in 1995. On the other hand, if seed removal at 2 wk (75–93%) reflects the ultimate pattern of survival (e.g., Li et al. 1996), then it is possible to calculate the influence of stage-specific mortality patterns on the relative probability of recruitment (Table 3, Fig. 10). The initial pattern of seed rain shows a strong peak near the parent trees, and secondary peaks at distances >40 m that correspond with bellbird song perches (Fig. 10a). The bellbird perches encompass a range of canopy cover values from forest–gap edge (~92%) to gap centers (~70%). Thus, seed rain is spread across a wider range of canopy conditions with increasing distance from the parent trees. Two-week seed survival is higher for seeds >10 m from fringing trees, but relatively consistent across the range of canopy cover (Fig. 10b). Germination is high for all seeds, regardless of distance from parent or canopy cover (Fig. 10c). One-year seedling survival is highest for sites >40 m from parents and <90% canopy cover (Fig. 10d). The cumulative probability of recruitment (the product of seed rain, 2-wk seed survival, germination, and 1-yr survival) shows a peak near the parent trees and shows secondary peaks corresponding to the bellbird perches (Fig. 10e). Note that the probability of a seed dispersed by birds surviving one year is <0.2% at any location.

Discussion

The results illustrate three main points: (1) bellbirds dispersed seeds in a different pattern than the other species; (2) postdispersal seed predation is highest near the parent trees, but is also high everywhere; and (3) the pattern of recruitment is bimodal with a peak near the parent tree in closed canopy forest, as well as another in gaps corresponding to bellbird perches.

Seed dispersal

Most O. endresiana seeds handled by birds land under or just beyond the crowns of parent trees. This distribution of seeds is typical for vertebrate-dispersed plants (Dirzo and Domínguez 1986, Hopkins 1988, Willson 1993, Laman 1996a). The abundance of O. endresiana adults in the study area makes dispersal beyond 80 m from any conspecific tree virtually impossible. Considering the restricted elevational range of this species, longer distance dispersal may lead to arrival in habitats unsuitable for establishment (Wheelwright 1988). Thus, while regurgitating seeds just outside the crown of a fruiting tree may seem like poor quality dispersal (McKey 1975), the sheer abundance of seeds in that region may lead to a small peak in recruitment near the parent tree (Fig. 10e), as predicted by Hubbell (1980) and Condit et al. (1992). The long tail of the seed distribution, however, is apparently important for recruitment (see Clark 1998, Clark et al. 1998), because seeds dispersed farther from the parent trees have a greater chance of arriving in a habitat where the probability of seedling survival is higher (i.e., a safe site).

Of the five species of birds that dispersed most of the seeds in this study, all but one deposited most seeds in closed canopy forest. Only male bellbirds frequently dispersed seeds to tree fall gaps. In my study site, bellbird song perches were in dead Sapum oligneron trees, bordering large tree fall gaps. Such sites are typical for bellbirds: Snow (1977) reported that bellbird song perches at lower elevations in the Monteverde area (where the forest is fragmented) are usually on dead branches in tall trees on the forest edge. In other Neotropical forests, three other species of bellbirds (Procnias spp.) exhibit similar behavior in habitual use of tall, exposed song perches, often on dead branches (Snow 1961, 1970, 1973a). Snags used by bellbirds in my site had several branches, and the birds made use of many different branches within each tree, such that seeds under them were scattered over ~25 m², including a gradient of site conditions from gap to forest understory. Male bellbirds also dispersed seeds in forest, as do the other species, but they typically spend 80–95% of the day in the vicinity of the song perch (Snow 1977) and probably disperse a similar percentage of seeds they process under song perches. Female bellbirds were rarely seen at the song perch, and then only for a few minutes.

The influence of bellbirds on the pattern of seed fall is shown by the slight increase in the number of seeds 40–65 m from the parent trees (Fig. 2). Bellbird perches in my site happened to be far (~40 m) from any fruiting O. endresiana trees. The other four bird species that disperse O. endresiana seeds occasionally perch on the edges of gaps (personal observation), although whether they do so more often than expected based on perch availability is unknown. Because birds do not
Fig. 10. (A) Mean seed rain, (B) 2-wk seed survival, (C) germination, (D) 1-yr seedling survival, and (E) cumulative probability of recruitment, as functions of canopy cover and distance from parent for both years combined, with means evaluated among 21 trees. For A–D, each bar represents the percentage of the seeds or seedlings that survived that stage in each distance/canopy cover category, averaged among trees. Categories with fewer than three seeds were not included and are blank, while categories with a flat rectangle are zero. Seed rain was determined from the original distribution of seeds naturally dispersed by birds. Two-week seed survival was estimated from the removal of marked seeds. Germination and seedling survival were estimated from the seeds caged until after germination. Recruitment (the cumulative probability of surviving every stage) is calculated as the product (A × B × C × D) for each distance/canopy cover category. For clarity, standard deviations are not shown.
regurgitate in flight, and guans apparently do not defecate in flight (personal observation), the most likely way an *O. endresiana* seed can arrive in a gap is via male bellbirds. I never observed the other four species on bellbird perches. Thus, *O. endresiana* has two types of dispersers that deposit seeds in two different, but predictable patterns: male bellbirds depositing large numbers (52%) of the seeds they disperse in and near gaps, and the other four species depositing seeds in forest, most (75%) within 25 m of parent trees, and fewer >25 m away (Wenny and Levey 1998). Additionally, on several occasions I followed quetzals and guans from one fruiting *O. endresiana* to another, where they deposited seeds before eating fruits in the second tree. Although I had no method of identifying the source tree of the seeds, it is likely that dispersal of seeds from one tree to another conspecific occurs regularly (Wheelwright 1991, Gibson and Wheelwright 1995).

The patterns of seed distribution described here may be similar for other trees in cloud forests, where these disperser species occur during the breeding season, but may be very different during the rest of the year. The five species of birds that disperse *O. endresiana* are the most important fruit consumers of canopy trees in the area (Wheelwright et al. 1984). Seeds from >20 other species of trees are dispersed by these birds, and probably have similar patterns of seedfall as *O. endresiana*, with a peak near the parent tree and a second peak at bellbird perches. However, all five dispersers (except perhaps toucanets) undertake elevational shifts that correspond with fruit availability (Wheelwright 1983, Levey and Stiles 1992, Powell and Bjork 1995, Guindon 1996) and leave the study area in late July or early August. (In 1994 they left in June, when *O. endresiana* failed to fruit). Male bellbirds may not provide such a pronounced peak in seed dispersal to song perches after the breeding season, because they seem to use many different perches in the nonbreeding season, and they tend to use subcanopy perches that are not exposed (Stiles and Skutch 1989). Thus, seed fall for the community as a whole is likely temporally, as well as spatially, heterogeneous.

The implications of seed dispersal to habitual perches deserve further study. Do habitual perches favor focal plant recruitment, or of seed predation? Seed dispersal to perches has been frequently studied in successional landscapes (Livingston 1972, McDonnell 1986, Holthuijzen et al. 1987, Guevara and Laborde 1993, McClanahan and Wolfe 1993, Robinson and Handel 1993, Vicira et al. 1994, Nepstad et al. 1996, Duncan and Chapman 1999). In these systems, directed dispersal may play a key role in the restoration of abandoned pastures, logged forests, and other degraded lands. It is possible that directed dispersal is more common in intact forests than previously expected. For example, manakins (Pipridae) and cocks-of-the-rock (*Rupicola*; Cotingidae) choose lek perches that are more sunlit than typical understory perches (Endler and Théry 1996), and such sites may provide growth advantages for seedlings. Snow (1961, 1970, 1973b) notes that other species of bellbirds (*Procnias*) preferentially select perches on dead trees or branches, or in sparsely vegetated trees. For these species, competition among males for females drives them to be as conspicuous as possible. The fortuitous outcome of this behavior may be a disproportionate effect on plant recruitment in the vicinity of their display areas (Théry and Larpin 1993). Whether habitual perches represent foci of seedling recruitment (McDonnell and Stiles 1983, McDonnell 1986) or lead to density-dependent seed and seedling mortality (Wheelwright 1988), needs to be examined in more detail.

**Seed predation**

Removal of marked seeds after dispersal in this study always resulted in predation. Although seeds were taken into burrows and logs, I never found any treatment of seeds indicative of scatter-hoarding, such as burial in the soil (Smythe 1978, Hallwachs 1986, Forget 1990, 1993), or under piles of leaf litter (Forget 1991). In addition, the failure of buried seeds to germinate and survive in the greenhouse experiment suggests that scatter-hoarding would not be advantageous for *O. endresiana* recruitment. Only two species of mammals known to scatter-hoard seeds occur in the study site: spiny pocket mice (*Heteromys desmarestianus*) and agoutis (*Dasyprocta punctata*). Both species are much less common here than at lower elevations (personal observation; K. G. Murray, personal communication). Although some species of squirrels (*Sciurus*) and deer mice (*Peromyscus*) are known to cache seeds in other regions of the world (Vander Wall 1990), information on tropical species (in this site, *S. deppei* and *P. mexicanus*) is lacking (Emmons 1990).

The main seed predators in this study were probably rodents, particularly the deer mouse *Peromyscus mexicanus*, which is by far the most common terrestrial rodent in the study area (Anderson 1982, Langtimm 1992). Based on the exclosure experiment, however, it is possible that species larger than mice (i.e., agouti, paca, peccary, wood-quail) are also important seed predators. Because removal of seeds from the open control plots was about twice that of the "small rodents only" plots, agoutis and other large mammals may have been responsible for as much as 50% of *O. endresiana* seed predation. Nevertheless, the exclosures also showed that, in the absence of agoutis, small rodents will find and eat most of the seeds, albeit over a longer time period. Additionally, the findings that most marked seeds from the removal experiment were taken at night, and that removal of seeds always resulted in predation rather than scatter-hoarding, suggest that agoutis (which are mostly diurnal and known scatter-hoarders [Smythe 1978, Hallwachs 1986], may not be taking many seeds. However, few data exist on the
extent to which agoutis eat but do not scatter-hoard, certain species (e.g., Smythe 1978).

The high degree of postdispersal seed predation reported here is not unusual (Harper 1977, Cavers 1983). Recent reviews have found 90–100% losses of seeds to predators in 22 of 62 studies (Crawley 1992, Hulme 1993). Previous studies on seed predation of Lauraceae found 96–100% predation (Wheelwright 1988, Chapman 1989, Holl and Lulow 1997). The high level of seed predation in my study site could be explained by dense vegetation and cloudy conditions, providing small rodents protection from predators (Bowers and Dooley 1993, Vásquez 1996). High predation is probably not a consequence of high rodent populations due to lack of predators, because potential predators of mice (such as owls, forest-falcons, and cats) are relatively common (personal observation). During the day, light levels in the study area are often reduced because of cloudy weather (Cavélier 1996, Chazdon et al. 1996), as well as due to dense vegetation. Indeed, on a few occasions, mice were seen during the day (especially Peromyscus and Scotinomys) and some marked seeds were removed by small rodents during the day (see Results: Postdispersal seed predation: Distance effect). In addition, local naturalists report seeing more mice on misty or rainy days and nights than during clear weather (T. Guindon, personal communication). Thus, the high levels of predation for O. endressiana could be a result of longer activity patterns by small rodents, and such levels may be typical for many large-seeded tree species in cloud forests.

Seeding survival and recruitment

Most of the seeds protected from rodents germinated. High germination rates for Lauraceae are apparently typical (Wheelwright 1985b). Some seeds that germinated were eventually killed by beetle larvae (Heilipus sp. Curculionidae) developing in the cotyledons. After the cages were removed from the growing seedlings, the seeds as well as the seedlings were susceptible to predation by mammals. It is difficult to determine the role of each species involved, but the suite of species that kill seedlings is probably larger than the suite of seed predators, and could include pacas (Agouti paca), brocket deer (Mazama americana), tapir (Tapirus bairdi), and peccaries (Tayassu tajacu), in addition to agoutis and smaller rodents.

Insects were most likely to kill nondispersed seeds or seedlings, while mammals killed all types of seeds (dispersed, nondispersed, and random). This finding is consistent with Howe (1993) and Terborgh et al. (1993), who found that insect-caused mortality was distance dependent, but mortality by mammals was not. In New Guinea, Merg (1994) found the opposite pattern: insects tended to kill dispersed seeds and mammals killed nondispersed seeds. In contrast to insects and mammals, fungal pathogens killed proportionately more O. endressiana seedlings in closed-canopy forest than in gaps. Augspurger (1984) also showed fungal pathogens of seedlings were less prevalent in gaps than forest understory, for nine species of tropical trees.

The greater height of seedlings and saplings in plots >20 m from the parent trees, compared to those in plots beneath the crowns, suggests that seedling mortality was higher closer to the parent trees. Seedling ages are not known, but this difference suggests that longer term survival several years after dispersal is higher for seedlings >20 m from the crown of parent trees than for seedlings beneath crowns. Thus, seed dispersal away from the crown of a conspecific appears to increase the chance of recruitment over the long term (Clark and Clark 1984, Li et al. 1996).

The overall pattern of recruitment with respect to distance from parent trees and canopy cover was bimodal. This pattern was caused by the combination of distance-dependent seed predation (Fig. 10b) and the influence of canopy cover on seedling survival (Fig. 10d), despite the fact that most seeds landed close to the parent trees in closed-canopy forest (Fig. 10a). This pattern is an example of spatial discordance caused by the lack of congruity among the stages leading to recruitment (Herrera et al. 1994, Jordano 1995). The occurrence of such discordance emphasizes the importance of stage-specific survival patterns on patterns of recruitment and the need for data on the sequential stages of plant reproduction rather than on only one or a few stages. Bellbirds are clearly an important part of the dispersal system of O. endressiana, as over half (52%) of the seeds they dispersed landed in a zone of higher recruitment.

Conclusion

The overall conclusion of this study is that the pattern of recruitment of O. endressiana depends on the combined effects of seed dispersers, seed predators, and seedling mortality. Selection on plant traits occurs during each stage, and selection during sequential stages may be opposed (Wheelwright and Orians 1982, Herrera 1985, 1986, Wheelwright 1988, Herrera et al. 1994). For example, high seed predation overall, and the slight preference for larger seeds by seed predators, may select for smaller seeds or larger seed crops, while seed dispersers may prefer larger fruits, which have larger seeds, but occur in smaller fruit crops (but see Howe and Vande Kerckhove 1980, 1981), Wheelwright (1991) and Mazer and Wheelwright (1993). On the other hand, seed size did not influence germination, seedling height, or seedling survival. In addition, the bimodal spatial pattern of recruitment may represent disruptive selection on seedling traits. Some trees were visited by all five species of dispersers, while the trees far from bellbird perches tended not to be visited by bellbirds. Thus, seeds dispersed to gaps beneath bellbird perches were mostly from a subset of the available trees. The extent to which such differences in dispersal and subsequent recruitment affect gene flow is poorly
understood (Gibson and Wheelwright 1995, Hamrick and Nason 1996). Further studies that compare dispersal patterns and the subsequent stages leading to recruitment at different sites, as well as over longer time periods, are especially needed.

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