Nordic Society Oikos

Distance and non-randomness of seed dispersal by the dwarf cassowary Casuarius bennetti

Andrew L. Mack

Mack, A. L. 1995. Distance and non-randomness of seed dispersal by the dwarf cassowary *Casuarius bennetti*. – Ecography 18: 286–295.

To determine the sources of dispersed seeds I inserted unique tags in fallen *Aglaia* aff. *flavida* seeds before dwarf cassowaries (*Casuarius bennetti*) ate the fruits containing the seeds. Thirty naturally-dispersed, marked seeds were re-located in cassowary droppings in a 400 ha study area. The distribution of seed dispersal distances did not differ significantly from a normal distribution with a mean dispersal distance of 388 m, SD = 196.8. Mean distance of dispersed seeds to nearest mature conspecific tree was 170 m, SD = 108.4; dispersed seeds usually landed closer to other conspecifics than their parent. The estimated distribution of all seeds (including many undispersed seeds) was leptokurtic, creating high densities near source trees (>0.035 seeds m^{-2} within 100 m of bole) that quickly tapered off (<0.002 seeds $m^{-2} > 100$ m from the bole); any density dependent effects are liable to be manifest only near parent trees.
Cassowary movement patterns and resting behavior caused non-random dispersal of seeds. Seeds were preferentially moved to level sites uphill from their source trees along routes that did not cross steep terrain. Undispersed seeds generally landed downhill from source trees. This population of *Aglaia* would probably contract downhill into smaller, fragmented populations in the absence of cassowary-mediated dispersal.

A. L. Mack, Dept of Biology, Univ. of Miami, P.O. Box 249118, Coral Gables, FL 33124, USA.

Introduction

Seed plant distribution is initially determined by dispersal of seeds, then modified by numerous biotic and abiotic factors (Janzen 1970, Harper 1977). Along with pollen flow, seed dispersal moves plant genes. Thus, how far seeds are moved has important implications for plant ecology, population biology and population genetics. However, measuring seed dispersal distances is difficult, handicapping studies of plant population biology (Silvertown 1991).

The best measurements of seed dispersal distances usually come from isolated individuals or nearest possible sources of wind-dispersed plants (Blattner and Kadereit 1991, Augspurger and Kitajima 1992, Drake 1992, Sinha and Davidar 1992 and others reviewed by Willson

1993) or ballistically dispersed plants (Rasmussen and Brodsgaard 1992, and others reviewed by Willson 1993). Studies of scatter-hoarding dispersers have reported dispersal distances (Vander Wall and Balda 1977, Sork 1984, Johnson and Adkisson 1985, Hallwachs 1986, Jensen and Nielson 1986, Stiles and Dobi 1987). However, seeds of many tropical rainforest trees are not wind-, ballistic-, or hoarder-dispersed; most are dispersed via ingestion by vertebrates (Howe and Smallwood 1982, Willson et al. 1989). Frugivorous animals might generate dispersal patterns that differ substantially from other dispersal modes.

Few studies have measured dispersal distance of seeds marked at the source prior to dispersal (Sork 1984, Jensen and Nielson 1986, Hallwachs 1986). Mapping distributions of unmarked seeds opens the possibility that dis-

persal from distant or unknown sources will not be recognized (e.g. Janzen et al. 1976, Becker and Wong 1985). Long-distance dispersal, even if infrequent, could have significant implications for population genetics (McCauley 1991, Silvertown 1991, Portnoy and Willson 1993), colonization potential, and regeneration of natural (Drake 1992, Walker and Neris 1993) and man-made disturbances (Gorchov et al. 1993). Furthermore, dispersal distance affects seed and seedling density (Peart 1985) and distance from seeds to adult conspecifics, both of which can affect seedling survivorship (e.g. Howe et al. 1985, Schupp 1988, Kitajima and Augspurger 1989, Augspurger and Kitajima 1992).

Various parameters defining the microsites where dispersed seeds land affect plant fitness (e.g. Fleming 1981, Murray 1986, Kitajima and Augspurger 1989, Schupp 1994). Mere removal from the parent tree does not necessarily increase an individual seed's probability of survival and all dispersed seeds do not share the same fate. Therefore, it is important to examine where seeds land, as well as how far they are dispersed, to understand the consequences of dispersal (Schupp and Frost 1989). In mountainous forests, ground slope is one factor that affects seedling establishment and survivorship. Seeds dispersed by animals can potentially be moved long distances uphill, whereas seeds moved only by gravity have limited potential for uphill movement. Furthermore, seedlings on level ground may be less susceptible to physical damage and mortality due to debris that slides downhill (Mack unpubl.).

In this study I marked seeds of an animal-dispersed rainforest tree prior to dispersal and located marked seeds after dispersal to unambiguously determine dispersal distance and direction in a natural system. Additionally, I examined the sites of dispersed and fallen (undispersed by cassowaries) seeds relative to ground slope. These data are discussed in light of their implications to plant population biology and conservation of plant populations where seed dispersers are extirpated.

Methods

Study area

The study was conducted at the Crater Mountain Biological Research Station (CMBRS) in southeastern Chimbu Province, 10 km east of Haia, Papua New Guinea (06°43.437 S, 145°05.576 E), on the lands of the Pawaiian people. The study area lies within a vast tract of pristine forest, 2600 km^2 of which are gazetted as the Crater Mountain Wildlife Management Area. Human disturbances are a few, widely scattered, swidden gardens mostly confined to level ground near streams. The terrain is extremely rugged, spanning 850–1300 m a.s.l. in the foothills and southern scarp of the eastern highlands of New Guinea. Forest composition is diverse, encompassing mixed evergreen hill forest and sub-montane

forest (Paijmans 1976) with no markedly dominant canopy tree species. Rainfall exceeds 650 cm yr^{-1}.

The study organisms

I examined dispersal of a canopy tree provisionally identified as *Aglaia* aff. *flavida* Merrell et Perry (Pannell 1992 and pers. comm.), hereafter called *Aglaia* (vouchers AM 256 deposited at Univ. of PNG, Missouri Botanical Gardens, and the Lae Forest Res. Inst.). This dioecious species produces a large capsular fruit (up to 18 cm diameter) containing 1–3 unattached seeds. Some fruits dehisce in the canopy and the seeds fall to the ground; other fruits fall undehisced and break open on impact. The large seeds (mean seed mass = 113.7 g ± 28.6, N = 48 from 8 trees) are c. two-thirds covered with a protein-rich (Wright and Stiles unpubl.), bright scarlet aril and one-third creamy white funicle, making a vivid bi-colored display. These diaspores are swallowed whole by cassowaries and form an important component of their diet during the fruiting season. The only other frugivore in the study area capable of dispersing such a large diaspore is the bare-backed fruit bat, *Dobsonia moluccensis* (Pteropodidae: Chiroptera), but these bats only move a few seeds for short distances (see below). Rats move a few seeds, but only short distances, they do not bury or conceal the seeds and frequently they do not kill seeds because they only remove a portion of the cotyledon (unpubl.).

The dwarf cassowary, *Casuarius bennetti*, is a large (up to 29 kg), flightless ratite inhabiting forests above 300 m in New Guinea (Beehler et al. 1986). Its diet is nearly exclusively fruits that have fallen to the forest floor or that are borne within 2 m of the ground (Pratt 1983, Stocker and Irvine 1983, Coates 1985). Fruits receive gentle treatment in the cassowary gut; seeds are voided 1.5–12 h after fruit ingestion (Mack unpubl., captive feeding trials) and are undamaged by gut passage (Stocker and Irvine 1983, Mack unpubl.). A few seeds of small-seeded species (<5 g) might be retained in cassowary guts for longer periods as happens with Emus (Davies 1978, Willson 1989). Seeds are voided in large, conspicuous droppings on the forest floor; cassowaries do not regurgitate seeds.

Seed marking

To obtain a representative sample of *Aglaia* and enable measurent of seed-to-nearest-tree distances I mapped all (64) mature individuals of *Aglaia* in a c. 260 ha study area and then chose 20 of 35 female trees (Mack 1995) from throughout the study area for seed-marking. Seeds were marked by embedding 25 or 30 mm nails beneath the seed coat. Nails for each of the 20 trees had a unique code filed in the shank. Approximately 700 seeds were marked of 3 208 seeds that were produced by these 20

trees. Marked seeds fed to two captive cassowaries did not affect the cassowaries and the tags did not dislodge.

The 20 source trees were visited at 1–3 day intervals to mark seeds throughout the June–September 1992 fruiting season. Only fresh fruits (the white funicle browns after 2 days) were marked because cassowaries reject fruits that have begun to spoil. Direct contact between the fruit and the person marking it was avoided by wrapping fruits in leaves when handling them because the olfactory capabilities of cassowaries are unknown. All efforts were made to minimize the disturbance caused by investigators at the fruiting trees. Cassowary footprints were frequently observed at source trees suggesting our activities did not deter the birds.

Measuring crop size

To determine how many diaspores were produced by each source tree I counted one, two and three-seeded capsules found beneath each tree. The number of undispersed (note: I use the term "undispersed" in this paper to indicate fallen seeds that have not been moved by cassowaries, this does not exclude "dispersal" by gravity when seeds roll downhill) seeds under each of the trees was counted at the end of the fruiting season at each tree, noting how many contained nails.

Finding marked seeds

Roughly 400 ha were systematically searched for cassowary droppings in September–November 1992 with the assistance of 15 Pawaiian men who had extensive experience hunting cassowaries. Cassowary droppings containing *Aglaia* seeds are conspicuous for at least six months and usually for over a year (Mack unpubl.). All *Aglaia* seeds found in droppings were checked for tags by inspection and cutting into seeds to expose any imbedded tags.

Source trees and their dispersed, marked seeds were mapped relative to position markers on trails in the study area and the dispersal distances calculated trigonometrically. Whether deposition sites were uphill or downhill from the source trees was readily discerned by walking between the two.

Search efforts

On a map of the study area I recorded where we searched for droppings in September–December 1992. The map had the position of each source tree and ten 100 m radius annuli drawn around each tree. As searching progressed, we attempted to fill in uncovered ground within the 1 km radii of all trees. At the conclusion of searching, I estimated the proportion of area searched in each annulus for each tree. I used this estimate to determine if our search

efforts biased the probability of locating dispersed seeds at some distances over others.

Dispersal relative to ground slope

In order to examine seed dispersal relative to ground slope, I compared ground slope (classed 1–4, level to very steep) of 65 fresh (< 3 days old) droppings with 25 randomly chosen sites. I also counted cassowary droppings and seedlings of cassowary-dispersed species (42 species) on twenty paired 25 m² quadrats. The first of each quadrat pair was established on the first level ground encountered on random compass bearings from stratified random points on trails. The second quadrat of the pair was established on the nearest non-level ground, usually < 10 m away.

Undispersed seeds and seedlings

When counting undispersed seeds under parent trees I recorded how many of the total were uphill or downhill of the bole. At nine trees I established 25 × 2 m transects running both uphill and downhill on the angle of greatest incline from the bole and counted *Aglaia* seedlings from previous cohorts in each 1 m interval of the transect. This was a conservative measure as some trees had numerous seedlings over 25 m away downhill, but not uphill.

Statistics

Statistics were calculated using the statistical package SYSTAT (Wilkinson 1990) unless otherwise noted.

Results
Search efforts

Some distances from a few source trees were searched less thoroughly than the majority of trees. The trees where potential seed shadows were less thoroughly searched also had small crops and low removal rates, so the effect of the bias was minimal. For the overall population, the last three annuli were searched with roughly 10% lower efficiency than the inner seven annuli. If we had searched these areas as thoroughly as the closer annuli, I estimated we would have found only one more tagged seed. Correcting for this bias by adding a seed to the right tail of the distribution did not significantly alter any of the statistics or conclusions. Therefore all statistics and conclusions were based on the observed distribution.
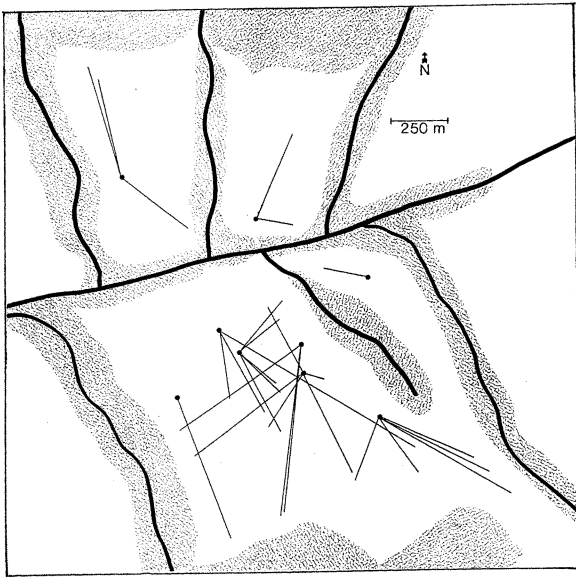
288

Fig. 1. Dispersal distance vectors of 30 *Aglaia* aff. *flavida* seeds found in 29 dwarf cassowary droppings at CMBRS. Broad lines are streams, stippled areas indicate extremely steep terrain generally impassable to cassowaries.

Extensive areas > 1000 m from source trees were searched without finding marked seeds.

Dispersal distances

Roughly 700 seeds were tagged during the fruiting season and cassowaries removed c. 300 of the tagged seeds. Thirty tagged seeds from nine source trees were found in 29 cassowary droppings (Fig. 1). The mean number of *Aglaia* seeds in these droppings was 2.4 ± 1.65, range = 1–7, N = 26). The mean (straight-line) dispersal distance was 388 m ± 196.8 (SD). The distribution of dispersal distances (Fig. 2A) did not differ from a normal distribution (Lilliefors test, p = 0.291, N = 30), but the distribution was right-skewed ($g_1 = 0.930$, p < 0.05) (Snedecor and Cochran 1989).

Dispersal by cassowaries effectively removed seeds from the proximity of conspecific mature trees but increasing dispersal distance did not necessarily result in greater distance to adult conspecifics (Fig. 3). The mean distance to nearest female *Aglaia* tree in the known population was 170 m ± 108.4, substantially less than the mean dispersal distance, 388 m. Only one dropping, which had the shortest dispersal distance, was closer to its source tree than to a different fruiting *Aglaia* tree. One seed landed < 50 m from another female conspecific (Fig. 3). The mean distance to nearest adult conspecific (including male trees) was not much less ($\bar{x} = 148.6$ m ± 114.1) because of the greater number of females than males in the population.

Total seed distribution

For the nine trees for which the dispersal distribution is shown (Fig. 2A), number of seeds removed was obtained by subtracting the count of undispersed seeds from the total number of seeds known from empty capsules under these trees. I added the number of undispersed seeds to the 0–100 m interval and allocated the dispersed seeds over the other intervals according to the measured distribution (Fig. 2A) to yield the distribution of all seeds (Fig. 2B). This distribution differs significantly from a normal distribution (Lilliefors test, p < 0.01) and is leptokurtic ($g_2 = 3.548$, p < 0.01, N = 2414) (Snedecor and Cochran 1989).

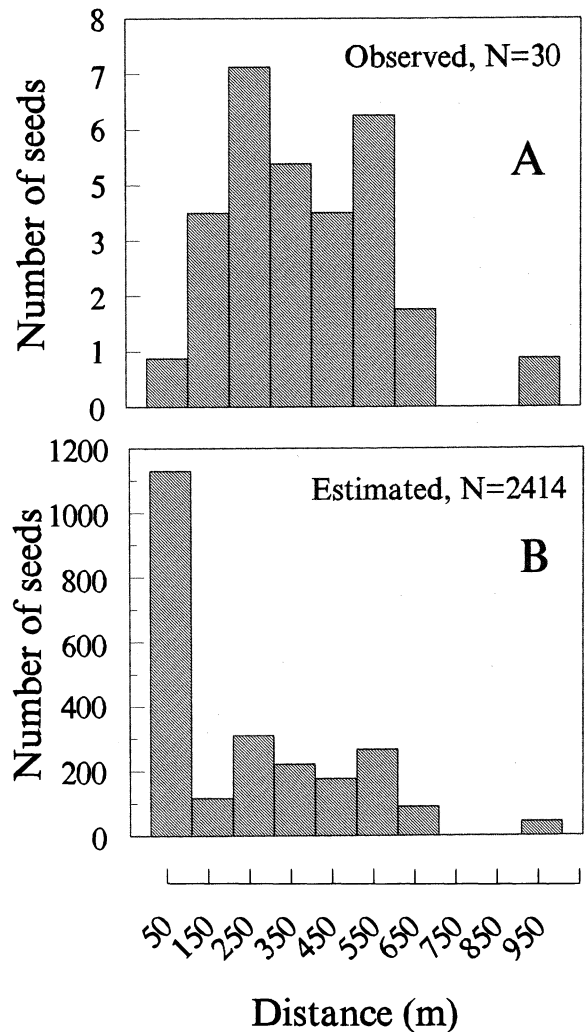The regression of estimated total number of seeds on

Fig. 2. A: Frequency histogram of dispersal distances of marked seeds (in 100 m intervals) of known origin that were taken by cassowaries and relocated in cassowary droppings. B: Estimated distribution of all seeds of nine *Aglaia* trees whose seeds formed distribution in 2A. See text for method of estimation.
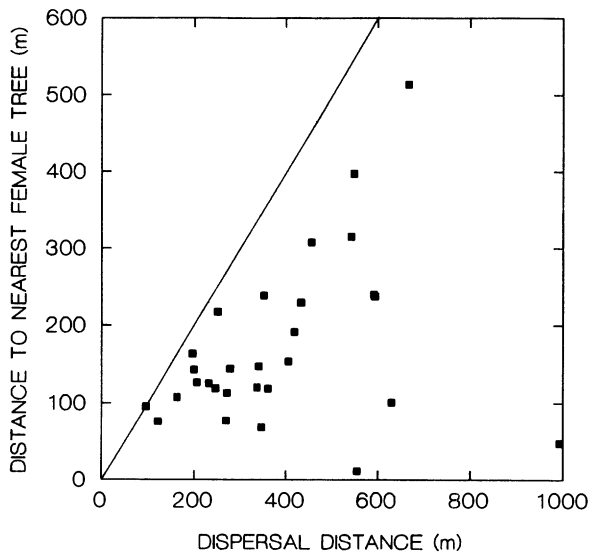
Fig. 3. Relationship between dispersal distance (n = 29 droppings) and distance to nearest mature conspecific female *Aglaia* tree. The correlation is weak ($r^2 = 0.103$, p = 0.089). The point over 500 m from the nearest tree exerts high leverage on the regression (Cook's D = 0.101). This dropping was near the edge of the study area and likely closer to a tree outside the study area. Omission of this point from the regression (n = 28) reduces the correlation coefficient to $r^2 = 0.040$ (p = 0.309). All other droppings were closer to *Aglaia* trees than the boundary of the study area. The solid line represents y = x, the result if dispersed seeds did not land closer to other fruiting trees than their source tree.

Fig. 4. A: Regression of the estimated total seed dispersal against distance (from Fig. 2B). Solid line includes two zero values (N = 10) for the 700–900 m intervals (y = −0.006x + 7.453, $r^2 = 0.549$, p = 0.014). The dotted line excludes the two zero values (n = 8) in the 700–900 m intervals (y = −0.003x + 6.610, $r^2 = 0.726$, p = 0.007). B: Estimated seed densities in 100 m annuli around source trees. (Note; y-axis represents seed density).

distance (Fig. 4A) is significant (p = 0.014). A log-linear regression model was employed because it presented a good fit to the data ($r^2 = 0.55$) and enabled direct comparison with other studies of seed dispersal with varying numbers of seeds (summarized in Willson 1993). The regression coefficient from this study (−0.006) is substantially smaller than values obtained in other studies of animal-dispersed species; slopes of this regression fell between −0.64 to −0.01 in 13 studies reported by Willson (1993).

Seed densities

The seed density-distance function was calculated by dividing the estimated number of seeds in each annulus (Fig. 2B) by the area of each annulus. This function dropped off precipitously beyond 100 m (Fig. 4B). Because of the large number of undispersed seeds, seed and seedling densities are an order of magnitude greater close to maternal trees. Dispersed and undispersed seeds both have high survivorship (Mack unpubl.).
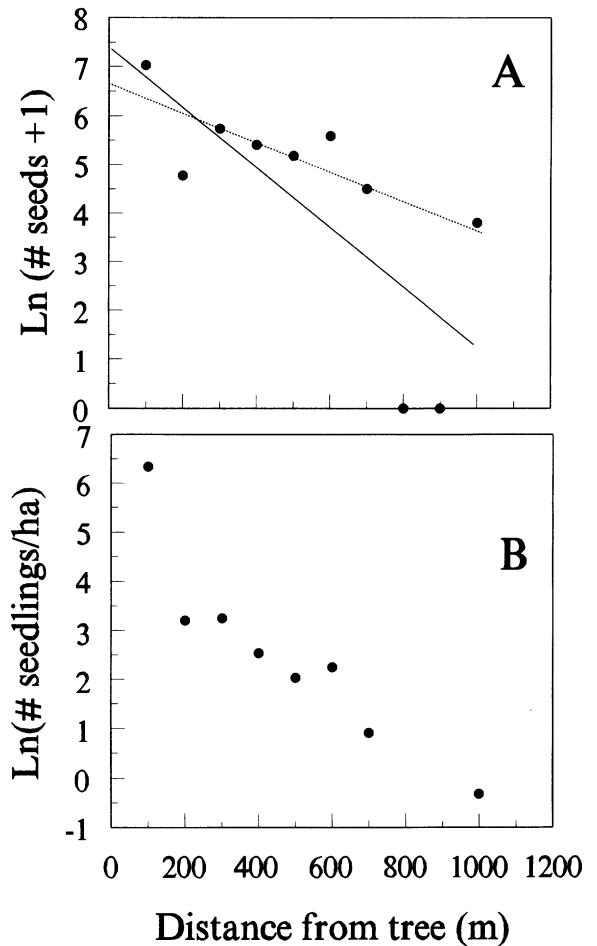
Non-randomness of dispersal: direction

Because cassowaries are large, bipedal and terrestrial, their daily movements are somewhat constrained. Cassowaries avoid the steepest terrain and probably do not often cross rivers (Fig. 1). None of the twenty-nine seed deposition sites were in very steep terrain or across a large stream from its source. Three trees (Fig. 1) had enough known dispersal events to calculate circular statistics (5, 6, and 6 vectors) (Zar 1984). Two of the three vector clusters differed from random ($U^2 = 0.2060$, 0.2319, p < 0.05); the directions of the vectors were more tightly clumped than would occur were cassowaries moving seeds in random directions.

Table 1. Seedling censuses on 10 pairs of 25 m² quadrats. One of each pair was on level ground and the other was on the nearest sloped ground. Censuses included all seedlings of woody species under 2 m tall.

	Level	Sloped	χ^2 (df = 1)
Total number of seedlings	697	605	6.50, p < 0.02
Seedlings of cassowary-dispersed species	354	220	31.28, p < 0.001
Number of *Aglaia* seedlings	4	2	0.66, n.s.
Number of cassowary droppings	27	13	4.90, p < 0.05

Non-randomness of dispersal: ground slope

Cassowaries generally disperse seeds uphill to level sites. Of the 29 droppings found, significantly more (22) were substantially uphill from their source tree than downhill (5) and 2 were roughly level ($\chi^2 = 4.57$, df = 1, p < 0.05). Significantly more seedlings of plant species known to be predominantly dispersed by cassowaries were found on level ground (Table 1), but some of these have other dispersal agents that could confound the data. More cassowary droppings were found on level quadrats than sloped quadrats (Table 1). Fresh droppings were in level sites significantly more than were random points $\chi^2 = 15.16$, df = 3, p < 0.01). Cassowaries defecate in level sites more often than would happen by chance.

Undispersed seeds (i.e. those not consumed by cassowaries) generally move downhill. Beneath 20 mature *Aglaia* trees 16% of the undispersed seeds were uphill from the tree and 84% downhill at the end of the 1992 fruiting season. At the nine trees at which I established transects, mean distance of seedlings uphill from the bole was 7.0 m (±6.3) versus 9.6 m (±5.8) downhill. More seedlings were downhill than uphill (164 vs 78).

Discussion

Following the seminal papers by Janzen (1970) and Connell (1971), many studies have examined the potential effects of seed dispersal distance on plant survivorship and demography (e.g. Hubbell 1980, Clark and Clark 1984, DeSteven and Putz 1984, Howe et al. 1985, Fleming and Williams 1990). Most studies have examined relatively short dispersal distances and found significant distance effects. For example, Howe et al. (1985) found a 44-fold increase in seed and establishing seedling survivorship among seeds moved only 45 m from the parent. Seeds in the tail of the distribution are fewer and less readily located and studied, but these can have disproportionate effects on gene flow, effective population size and colonization ability (Willson 1993, Portnoy and Willson 1993). However, distance-dependent effects might not always increase with longer dispersal distances. The mean dispersal distance for the seeds in this study was 388 m but these seeds were, on average, less than half this far from the nearest fruiting female tree (Fig. 3). Hence, if there were a selective benefit to disper-

sal by escaping distance-dependent mortality, dispersing farther would not necessarily confer any substantial advantage. These observations apply to any population of relatively abundant plants. There is an upper limit to the dispersal distance at which benefits from "escape" will increase and this limit decreases with increasing plant density.

Distribution of dispersal distances

The distance distribution curve of all seeds was leptokurtic, the usual shape of seed dispersal curves (Levin and Kerster 1974, Harper 1977, Willson 1993). This is not the same, however, as saying that seed dispersal by animals follows a leptokurtic distribution. The distribution of cassowary-dispersed seeds resembled a normal distribution rather than a leptokurtic distribution (Fig. 2). The inclusion of many undispersed seeds in the first distance interval of the total seed distribution (Fig. 2B) causes the departure from normality. In this population of *Aglaia*, most seeds are not dispersed (Mack unpubl.), but I could not find any differences (e.g. length, weight, etc.) between undispersed and dispersed seeds. The distribution of all seeds is a composite of different distributions, dispersed (in this case, by cassowaries), undispersed (in this case those that simply fell to the ground), and secondarily-dispersed.

The distinction between the distribution of all seeds versus dispersed seeds is not merely one of semantics. The seed distribution for an *Aglaia* tree probably changes with removal efficiency, becoming more platykurtic with greater removal by cassowaries and ultimately assuming a normal distribution near 100% removal. Furthermore, in many species it is important to distinguish between dispersed and undispersed seeds because they might have different survivorship probabilities independent of distance, such as deposition site characteristics (e.g. Reid 1989, Yan 1993), clumping effects (Howe 1989), or gut-treatment effects (Rick and Bowman 1961, Noble 1975, Murphy et al. 1993, but see Lieberman and Lieberman 1986).

The regression coefficient of estimated number of *Aglaia* seeds on distance is at least an order of magnitude smaller than the values obtained in other studies of vertebrate-dispersed seeds (Willson 1993). This difference suggests two, non-exclusive, considerations. First, most studies have not measured the seed distribution tails for

various logistic reasons, thus their higher regression coefficients could partially be a relict of methodological difficulties. Second, the lower regression coefficient of this study could be a result of biological differences of this system. Cassowaries are much larger than the frugivorous vertebrates cited in Willson (1993). One might expect larger frugivores to have larger home ranges and thus produce a less steep distance function. Seeds are normally retained in the guts of cassowaries for three to four hours and up to twelve hours, considerably longer than the transit time of most volant frugivores (e.g. Levey 1987, Fleming 1988, Murphy et al. 1993). Depending upon frugivore movement patterns, longer gut retention times might cause seed distributions to be more platykurtic, and the regression coefficient smaller. The markedly smaller regression coefficient of this study probably results from both methodological and biological differences.

Density of seeds and seedlings

The number of seeds was negatively correlated with distance (Fig. 4A), producing an order-of-magnitude shift in densities between dispersed and undispersed seeds (Fig. 4B). Differential survivorship in seeds and seedlings at high and low densities has been noted in other systems (Augspurger and Kelly 1984, Ellstrand and Antonovics 1985). If density-dependent mortality was significant in this or similar systems, I expect it would act as a step-function: strong among undispersed seeds and weak in dispersed seeds regardless of their dispersal distance.

Aglaia disperser assemblage

Most plants interact with a coterie of dispersal agents, making it difficult to determine the overall net effect on a plant's population biology when studying only one or a few of the potential pool of dispersers (Wheelwright and Orians 1982, Herrera 1985, 1986). Seed dispersal by cassowaries is especially germane to Aglaia because there is only one other potential Aglaia dispersal agent at CMBRS: the medium-sized bat Dobsonia moluccensis. These bats appear to have difficulty extracting the heavy diaspores of Aglaia from their capsules. The heavy, smooth diaspores must be pulled from barely-opened capsules (capsules fall before widely dehiscing). The capsules often break apart upon attempts to extract a diaspore, allowing the unattached diaspores to fall to the ground (unpubl.). Fallen, chewed seeds were occasionally found under Dobsonia feeding roosts usually < 50 m from fruiting Aglaia trees. During all searches I found only two seeds that had been moved by bats > 50 m from the nearest (presumed source) Aglaia tree. I could not obtain a precise count of dispersal events by bats. I estimated the total number of seeds moved by Dobsonia beyond 30 m for the 20 trees studied was < 150 seeds

(< 8.7% of the seeds dispersed in the sample). In the lowlands of New Guinea, Aglaia is probably effectively dispersed by larger flying foxes (Pteropus spp.), because they would be more capable of handling the large diaspores. Cassowaries are not exclusive dispersers of Aglaia on a geographic or evolutionary time scale, but at this site present Aglaia dispersion is determined more by cassowaries than any other dispersal agent.

Nonrandomness: cassowary resting sites

Places where cassowaries rest are often evident by chest and tarsus imprints on the ground and loosened feathers. The birds usually defecate 1–3 times at where they overnight and a resting bird's defecation is usually larger than those made by moving birds (unpubl.). Consequently, the majority of seeds dispersed by cassowaries are moved to places cassowaries rest or pass the night, a behavior shared with emus (Willson pers. comm.). Cassowaries rarely rest in the same place more than once within six months (Mack unpubl.). Hence, cassowaries do not generate large clumps of dispersed seeds as happens in some systems (Snow 1970, Wheelwright 1983, Dinerstein and Wemmer 1988, Dinerstein 1991); seeds are widely dispersed in small (i.e. < 10 Aglaia seeds) clumps (Fig. 1).

Cassowary droppings were found on level sites significantly more often than were randomly-selected points and were more numerous on level quadrats than on adjacent quadrats on slopes (Table 1). Dispersal biased to level sites results from cassowary preference for resting sites on level bluffs or ridgetops. Such sites are generally on drier, firmer ground and where a bird has several directions to flee if startled. Rest sites are rarely in ravines, in dense vegetation, on low-lying level (boggy) ground or on steep slopes, despite these sites being more numerous in the study area. Seeds from plants in low-lying areas or on steep slopes are more likely to be dispersed uphill because resting sites, where most defecations occur, are more numerous on ridgetops or bluffs.

Nonrandomness: movement barriers

The terrain of CMBRS, and much of New Guinea, is extremely rugged. Large bipeds cannot travel through all parts of such forest with ease (unpubl.). Despite hundreds of person-hours searching steep slopes, we rarely found cassowary droppings or footprints in these areas. The rivers in the area are generally flanked by steep to vertical topography. Cassowaries probably cross rivers infrequently for this reason, not because the rivers per se are impassable (Fig. 1). When they do cross the rivers they are limited to a small number of traversable points. Dispersal by cassowaries is disproportionately directed toward a small subset of the available habitat. Directed dispersal is especially significant if directed seeds experience better chances of survivorship than randomly dispersed seeds (Howe and Smallwood 1982).

Gene flow and population structure

The implications for plant population genetics caused by restricted disperser movements are poorly documented, perhaps because gene movement via pollen has been more widely studied. Pollination biology is poorly known in the genus *Aglaia*; small hymenoptera and diptera have been noted at *Aglaia* inflorescences (Pannell 1992). In this population of *Aglaia* evidence suggests pollination success is greatly diminished when male-female distances exceed 200 m (Mack 1995). Examples of rivers restricting movements and gene flow has been described in vertebrates (Haffer 1974, Pounds and Jackson 1981, Lamborot 1991). Therefore, barriers to cassowary movements might act as barriers to gene flow in *Aglaia*. I predict that genetic structuring of *Aglaia* populations (outside the range of *Pteropus* bats) will follow topographic boundaries that constrain cassowary movements.

Conservation implications

Uphill dispersal is significant to the population biology of *Aglaia* regardless of any possible selective benefits of level or ridgetop sites. Most undispersed *Aglaia* seeds (84%) land downhill from the mother tree. Most seedlings from undispersed seeds are downhill, and farther from the bole than seedlings uphill. Assuming that each tree in this population replaced itself by one undispersed seedling drawn randomly from its seedling pool within 25 m, in ten generations trees in the population would be, on average, 40 m downhill from their source. This value would be higher if it included seedlings > 25 m from the source tree (all downhill). In mountainous terrain, such as New Guinea, frugivores are vital for the maintenance of vertebrate-dispersed plant populations because they counteract the high probability that undispersed seeds will establish downhill of the parent.

Conservation biologists widely recognize the importance of seed dispersers in maintaining plant populations by facilitating escape from sources of mortality (Howe 1984, Bond 1994) or colonization of new areas (Primack and Miao 1992). The importance of seed dispersers for maintaining plant populations in mountainous terrain has not been emphasized, however, despite the fact that this could be a necessity for plant populations of many species worldwide. Concerns about extirpation of disperser populations in mountainous forests should include the possibility that without seed dispersers, plant populations could contract downhill, occupying ever smaller and more fragmented ranges (see Ellstrand and Elam 1993). Cassowaries are heavily hunted in New Guinea as food and for traditional cultural uses (Dwyer and Minnegal 1991, Mack unpubl.). Extirpation has already occurred due to hunting in parts of their former range (Coates 1985).

Concluding remarks

While the attributes that makes this system well-suited for studying seed dispersal (e.g. small coterie of dispersers, a large terrestrial disperser, etc.) may be uncommon in other systems, many findings are applicable to other systems. The spatial relationship of dispersed seeds to other conspecifics is a function of dispersal direction, distance and distribution of conspecifics. Density effects on seeds might be a step function, manifest at short distances from the parent in undispersed seeds and insignificant over the wide range of distances seeds are dispersed by vertebrates. The distribution of vertebrate-dispersed seeds is not a simple leptokurtic function because animals have habits and behavioral constraints that cause their seed dispersal patterns to be non-random. Such habits differ among disperser species (Reid 1989, Yan 1993) and can both place seeds in unfavorable sites (differing little from seed predation) or direct seeds to better-than-average sites for establishment. Cassowary habits directed *Aglaia* seeds uphill, to level microsites, and within topographic boundaries (defined by steep slopes); these traits could have importance for shaping *Aglaia* distributions and population genetics. The spatial and genetic structure of vertebrate-dispersed plant populations cannot be understood without knowledge of disperser behavior.

References

Augspurger, C. K. and Kelley, C. K. 1984. Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. – Oecologia 61: 211–217.

– and Kitajima, K. 1992. Experimental studies of seedling recruitment from contrasting seed distributions. – Ecology 73: 1270–1284.

Becker, P. and Wong, M. 1985. Seed dispersal, seed predation, and juvenile mortality of *Aglaia* spp. (Meliaceae) in lowland dipterocarp rainforest. – Biotropica 17: 230–237.

Beehler, B. M., Pratt, T. K. and Zimmerman, D. A. 1986. The birds of New Guinea. – Princeton Univ. Press, Princeton.

Blattner, F. and Kadereit, J. W. 1991. Patterns of seed dispersal in two species of *Papaver* L. under near-natural conditions. – Flora 185: 55–64.

Bond, W. J. 1994. Do mututlaisms matter? Assessing the impact of pollinator and disperser disruptions on plant extinction. – Phil. Trans. Roy. Soc. Lond. B 344: 83–90.

Clark, D. A. and Clark, D. B. 1984. Spacing dynamics of a tropical rainforest tree: evaluation of the Janzen-Connell model. – Am. Nat. 124: 769–788.

Coates, B. J. 1985. The birds of Papua New Guinea. Vol. 1. – Dove Publ., Aderley, Australia.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine mammals and rain forest trees. – In: den Boer, P. J. and Gradwell, G. R. (eds), Dynamics of populations. Centre for Agric. Publ. Documentation, Wageningen, pp. 298–312.

Davies, S. J. J. F. 1978. The food of emus. – Aust. J. Ecol. 3: 411–422.

De Steven, D. and Putz, F. E. 1984. Impact of mammals on early recruitment of a tropical tree, *Dipteryx panamensis*, in Panama. – Oikos 43: 207–216.

Dinerstein, E. 1991. Seed dispersal by greater one-horned rhinoceros (*Rhinoceros unicornis*) and the flora of *Rhinoceros* latrines. – Mammalia 55: 355–362.

– and Wemmer, C. 1988. Fruits *Rhinoceros* eat: dispersal of *Trewia nudiflora* (Euphobiaceae) in lowland Nepal. – Ecology 69: 1768–1774.

Drake, D. R. 1992. Seed dispersal of *Metrosideros polymorpha* (Myrtaceae): a pioneer tree of Hawaiian lava flows. – Am. J. Bot. 79: 1224–1228.

Dwyer, P. D. and Minnegal, M. 1991. Hunting in lowland, tropical rain forest: towards a model of non-agricultural subsistence. – Human Ecol. 19: 187–212.

Ellstrand, N. C. and Antonovics, J. 1985. Experimental studies of the evolutionary significance of sexual reproduction II. A test of the density-dependent selection hypothesis. – Evolution 39: 657–66?.

– and Elam, D. R. 1993. Population genetic consequences of small population size: implications for plant conservation. – Ann. Rev. Ecol. Syst. 24: 217–242.

Fleming, T. H. 1981. Fecundity, fruiting pattern, and seed dispersal in *Piper amalgo* (Piperaceae), a bat-dispersed tropical shrub. – Oecologia 51: 42–46.

– 1988. The short-tailed fruit bat: a study in plant-animal interactions. – Univ. Chicago Press, Chicago.

– and Williams, C. F. 1990. Phenology, seed dispersal, and recruitment in *Cecropia peltata* (Moraceae) in Costa Rican tropical dry forest. – J. Trop. Ecol. 6: 163–178.

Gorchov, D. L., Cornejo, F., Ascorra, C. and Jaramillo, M. 1993. The role of seed dispersal in the natural regeneration of rain forest after strip-cutting in the Peruvian Amazon. – Vegetatio 107/108: 339–349.

Haffer, J. 1974. Avian speciation in tropical South America. – Publ. Nuttall Ornithol. Club # 14. Cambridge, MA.

Hallwachs, W. 1986. Agoutis (*Dasyprocta punctata*): the inheritors of guapinol (*Hymenaea courbaril*: Leguminosae). – In: Estrada, A. and Fleming, T. H. (eds), Frugivores and seed dispersal. Dr W. Junk Publ., Dordrecht, pp. 285–304.

Harper, J. L. 1977. Population Biology of Plants. – Academic Press, New York.

Herrera, C. M. 1985. Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. – Oikos 44: 132–141.

– 1986. Vertebrate-dispersed plants: why they don't behave the way they should.– In: Estrada, A. and Fleming, T. H. (eds), Frugivores and seed dispersal. Dr W. Junk Publ., Dordrecht, pp. 5–18.

Howe, H. F. 1984. Implications of seed dispersal by animals for the management of tropical reserves. – Biol. Conserv. 30: 261–281.

– 1989. Scatter- and clump-dispersal and seedling demo-

graphy: hypothesis and implications. – Oecologia 79: 417–426.

– and Smallwood, J. 1982. Ecology of seed dispersal. – Ann. Rev. Ecol. Syst. 13: 201–228.

– , Schupp, E. W. and Westley, L. C. 1985. Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). – Ecology 66: 781–791.

Hubbell, S. P. 1980. Seed predation and the coexistence of tree species in tropical forests. – Oikos 35: 214–229.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. – Am. Nat. 104: 501–528.

– , Miller, G. A., Hackforth-Jones, J., Pond, C. M., Hopper, K. and Janos, D. P. 1976. Two Costa Rican bat-generated seed shadows of *Andira inermis* (Leguminosae). – Ecology 57: 1068–1075.

Jensen, T. S. and Nielsen, O. S. 1986. Rodents as seed dispersers in a heath-oak wood succession. – Oecologia 70: 214–221.

Johnson, W. C. and Adkisson, C. S. 1985. Dispersal of beech nuts by blue jays in fragmented landscapes. – Am. Midl. Nat. 113: 319–324.

Kitajima, K. and Augspurger, C. K. 1989. Seed and seedling ecology of a monocarpic tropical tree, *Tachigalia versicolor*. – Ecology 70: 1102–1114.

Lamborot, M. 1991. Karyotypic variation among populations of *Liolaemus monticola* (Tropiduridae) separated by riverine barriers in the Andean Range. – Copeia 1991: 1044–1059.

Levey, D. J. 1987. Seed size and fruit-handling techniques of avian frugivores. – Am. Nat. 129: 471–485.

Levin, D. A. and Kerster, H. W. 1974. Gene flow in seed plants. – Evol. Biol. 7: 139–220.

Lieberman, M. and Lieberman, D. 1986. An experimental study of seed ingestion and germination in a plant-animal assemblage in Ghana. – J. Trop. Ecol. 2: 113–126.

Mack, A. L. 1995. Seed dispersal by the dwarf cassowary, *Casuarius bennetti*, in Papua New Guinea. – Ph. D. thesis, Univ. of Miami, Dept of Biology.

McCauley, D. E. 1991. Genetic consequences of local population extinction and recolonization. – Trends Ecol. Evol. 6: 5–8.

Murphy, S. R., Reid, N., Yan, Z. and Venables, W. N. 1993. Differential passage time of mistletoe fruits through the gut of honeyeaters and flowerpeckers: effects on seedling establishment. – Oecologia 93: 171–176.

Murray, K. G. 1986. Consequences of seed dispersal for gap-dependent plants: relationships between seed shadows, germination requirements, and forest dynamic processes. – In: Estrada A. and Fleming, T. H. (eds), Frugivores and seed dispersal. Dr W. Junk Publ., Dordrecht, pp. 187–198.

Noble, J. C. 1975. The effects of Emus (*Dromaius novaehollandiae* Latham) on the distribution of the nitre bush (*Nitraria billardieri* DC.). – J. Ecol. 63: 979–984.

Paijmans, K. (ed.) 1976. New Guinea vegetation. – National Univ. Press, Canberra.

Pannell, C. M. 1992. A taxonomic monograph of the genus *Aglaia* Lour. (Meliaceae). – Kew Bull. Add. Ser. 16, HMSO, London.

Peart, D. R. 1985. The quantitative representation of seed and pollen dispersal. – Ecology 66: 1081–1083.

Portnoy, S. and Willson, M. F. 1993. Seed dispersal curves: behavior of the tail of the distribution. – Evol. Ecol. 7: 25–44.

Pounds, J. A. and Jackson, J. F. 1981. Riverine barriers to gene flow and the differentiation of fence lizard populations. – Evolution 35: 516–528.

Pratt, T. K. 1983. Diet of the dwarf cassowary, *Casuarius bennetti picticollis*, at Wau, Papua New Guinea. – Emu 82: 283–285.

Primack, R. B. and Miao, S. L. 1992. Dispersal can limit local plant distribution. – Cons. Biol. 6: 513–519.

Rasmussen, I. R. and Brodsgaard, B. 1992. Gene flow inferred from seed dispersal and pollinator behaviour compared to

DNA analysis of restriction site variation in a patchy population of *Lotus corniculatus* L. – Oecologia 89: 277–283.

Reid, N. 1989. Dispersal of mistletoes by honeyeaters and flowerpeckers: components of seed dispersal quality. – Ecology 70: 137–145.

Rick, C. M. and Bowman, R. I. 1961. Galapagos tomatoes and tortoises. – Evolution 15: 407–417.

Schupp, E. W. 1988. Seed and early seedling predation in the forest understory and in treefall gaps. – Oikos 51: 71–78.

– 1994. Quantity, quality and the effectiveness of seed dispersal by animals. – Vegetatio 107/108: 15–29.

– and Frost, E. J. 1989. Differential predation of *Welfia georgii* seeds in treefall gaps and the forest understory. – Biotropica 21: 200–203.

Silvertown, J. 1991. Dorothy's dilemma and the unification of plant population biology. – Trends Ecol. Evol. 6: 346–348.

Sinha, A. and Davidar, P. 1992. Seed dispersal ecology of a wind dispersed rain forest tree in the Western Ghats, India. – Biotropica 24: 519–526.

Snedecor, G. W. and Cochran, W. G. 1989. Statistical methods (8th ed.). – Iowa State Univ. Press, Ames.

Snow, D. W. 1970. A field study of the bearded bellbird in Trinidad. – Ibis 112: 299–329.

Sork, V. L. 1984. Examination of seed dispersal and survival in red oak, *Quercus rubra* (Fagaceae), using metal-tagged acorns. – Ecology 65: 1020–1022.

Stiles, E. W. and Dobi, E. T. 1987. Scatterhoarding of horse-chestnuts by eastern gray squirrels. – Bull. New Jersey Acad. Sci. 32: 1–3.

Stocker, G. C. and Irvine, A. K. 1983. Seed dispersal by cas-sowaries (*Casuarius casuarius*) in north Queensland's rain-forests. – Biotropica 15: 170–176.

Vander Wall, S. B. and Balda, R. P. 1977. Coadaptations of the Clark's nutcracker and the pinyon pine for efficient seed harvest and dispersal. – Ecol. Monogr. 47: 89–111.

Walker, L. R. and Neris, L. E. 1993. Post hurricane seed dynamics in Puerto Rico. – Biotropica 25: 408–418.

Wheelwright, N. T. 1983. Fruits and ecology of resplendent quetzals. – Auk 100: 286–301.

– and Orians, G. H. 1982. Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. – Am. Nat. 119: 402–413.

Wilkinson, L. 1990. SYSTAT: The system for statistics. – SYSTAT, Inc. Evanston, IL.

Willson, M. F. 1989. Gut retention times of experimental pseudoseeds by emus. – Biotropica 21: 210–213.

– 1993. Dispersal mode, seed shadows, and colonization patterns. – Frugivory and seed dispersal: ecological and evolutionary aspects. – Vegetatio 107/108: 261–280.

– , Irvine, A. K. and Walsh, N. G. 1989. Vertebrate dispersal syndromes in some Australian, and New Zealand plant communities, with geographic comparisons. – Biotropica 21: 133–147.

Yan, Z. 1993. Germination and seedling development of two mistletoes, *Amyema preissi* and *Lysiana exocarpi*: host specificity and mistletoe-host compatibility. – Aust. J. Ecol. 18: 419–429.

Zar, J. H. 1984. Biostatistical analysis. (2nd ed.). – Prentice Hall, NJ.