# Implications of Seed Dispersal by Animals for Tropical Reserve Management

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## ABSTRACT

*Many tropical trees bear fruits adapted for consumption by animals, and many tropical animals depend on fruits for food for at least part of the year. The purpose of this paper is to discuss the potential importance of: (1) uneven species abundance distributions; (2) the imperative of local seed dispersal for plant recruitment; and (3) seasonality of fruit production for managing small tropical reserves. Some mutualistic seed-dispersal systems are 'pivotal' for forest communities. Although most species of trees produce when other fruits are readily available in the forest, others (e.g.* Casearia corymbosa *in Costa Rican rainforest and* Virola sebifera *in Panamanian rainforest) bear fruits during annual periods of fruit scarcity, and consequently maintain species of fruit-eating birds and mammals which are critical for the dispersal and ultimate recruitment of many tree species at other times of the year. The question of relative abundance presents particular problems when 'pivotal' plant species are rare or confined to special habitats. This paper conside ecological relationships which accelerate species loss from habitat islands over and above 'random' loss of ecologically independent species predicted from biogeographic theory, and suggests management methods that can reduce such excessive loss.*

# INTRODUCTION

Human needs for living space, agricultural land, and firewood in tropical regions create imperatives for government and private agencies concerned with selecting and maintaining habitat remnants. Refuges may

261

to designed to maintain particular 'focal' endangered species, or to protect entire communities. Either kind of reserve is likely to become a habitat island, and will consequently lose species through chance (MacArthur & Wilson, 1967). The process will be especially rapid in small reserves harbouring small populations of animals and plants (Wilson & Willis, 1975). The most mathematically tractable predictions assume no interactions between species (Wright & Hubbell, 1983). Such theory is directly applicable to animals with generalized feeding habitats, to plants that do not require animals for pollination or dispersal, and to plants that are pollinated and dispersed by a wide variety of animals. But in tropical forests 'all species are not equal'. Interactions occur. Futuyma (1973) asserts that ecological links in such forests make them particularly vulnerable to human perturbation. Local extinction of a fruit-eating bird, bat, or primate might, for instance, reduce recruitment of fruiting trees dependent upon it for reproduction, and consequently increase the chance of local extinction of the focal trees, of other animals that eat their fruits, and ultimately of other trees dispersed by members of the initial assemblage (Howe, 1976). The general consequence would be a widening circle of extinctions, precipitated by the disappearance of one 'pivotal' species (Howe, 1977). This paper develops the biological assumptions behind such a prediction, reviews relevant evidence from neotropical forests, and makes qualitative recommendations for selection and maintenance of tropical reserves.


## FRAMEWORK

The following discussion assumes that: (1) the species in any major taxon are unequally represented in any community; (2) many tropical animals depend partly or entirely on fruit for food, and many tropical plants require fruit-eating animals for seed dissemination and ultimately for seedling recruitment; and (3) fruiting phenologies in most tropical forests are seasonal. Each affects community integrity.

### Species abundances

Preston (1948, 1962; also Hairston, 1969) first developed the concept of the 'canonical lognormal' distribution of species abundances. In any community, the members of a major taxonomic unit such as 'birds' or
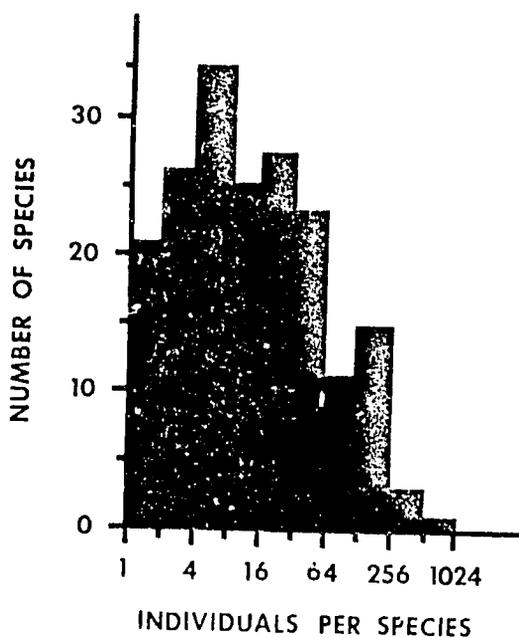
Fig. 1.   Relative abundances of 186 tree species 20 cm or more in diameter at breast height in 50 ha of rainforest on Barro Colorado Island, Panama. This exceptionally good sample (7614 individuals) shows a typical lognormal distribution, indicating that most species are present in low abundances while some are very common. Adapted from Hubbell & Foster (1983).

'angiosperms' are distributed unequally. Some species are common, some are less common, and many are rare. Complete data sets are unusual, but Hubbell (1979) has found this to be true for tree and shrub species in a dry seasonal Costa Rican forest as well as for tree species in a Panamanian rainforest (Fig. 1; Hubbell & Foster, 1983). Estimates of bird species abundances on Barro Colorado Island, Panama show unequal abundances for both the total avifauna and for fruit-eating species (Fig. 2; see Willis, 1980). The relative paucity of rare bird species may be due to differential extinction of small populations on the island or inadequate sampling of those species. Even so, 18 of 62 species of fruit-eating birds are represented by fewer than 64 individuals (Fig. 2). The preservation of a community requires the preservation of species present in substantially different numbers.

The elementary observation of unequal species abundances has consequences for conservation. Populations oscillate over time, and the chance that any given population will oscillate to extinction is inversely related
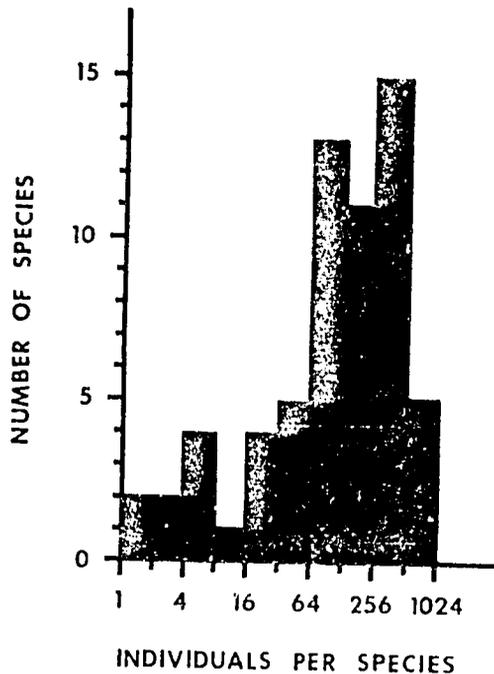
Henry F. Howe



Fig. 2.   Relative abundances of fruit-eating birds on Barro Colorado Island, Panama. This atypical distribution shows fewer rare species than expected, although 18 of 62 are represented by fewer than 64 individuals. Estimates are from Willis (1980).

to its size (MacArthur & Wilson, 1967; see Wright & Hubbell, 1983). Many local extinctions do not dramatically affect the general aspect of a community. It is neither surprising nor distressing that three pairs of the barred woodcreeper *Dendrocolaptes certhia* have disappeared from Barro Colorado Island since the building of the Panama Canal (Willis, 1974). But disappearance of approximately the same number of pumas *Felis concolor*, a large predator, might have been much more important if it released populations of rodents that eat tree seeds and seedlings (Terborgh & Winter, 1980; see Paine, 1966). Such unequal importances of rare species have not yet been demonstrated, but the point remains that the ecological consequences of local extermination of different rare species may be appreciably different. In general, the importance of a species to a community is not necessarily related to its abundance, even though its likelihood of extinction *is* inversely related to abundance.

## Animal-mediated dispersal

Many tropical animals depend partly or entirely on fruit for food for at least part of each year, and many tropical trees and shrubs bear fruits adapted for animal consumption. In neotropical forests, 50–90 % of the canopy trees bear fruits adapted for animal dispersal, while close to 100 % of the shrubs and sub-canopy trees produce fleshy fruits (Howe & Smallwood, 1982). Paleotropical forests have smaller but still substantial proportions of animal-dispersed species in each category (35–48 % and 70–80 %; respectively, Howe & Smallwood, 1982), implying a widespread advantage to local seed dissemination by animals. Analogous figures for animals are difficult to interpret because categories are not as discrete as they are for the fruits themselves; fruits constitute varying proportions in the diets of many neotropical bird species (Orians, 1969; Karr, 1971), and the birds may either disperse seeds, destroy them outright, or simply fail to disperse them (McKey, 1975; Howe & Estabrook, 1977). In the well-studied Barro Colorado forest we find a typical 78 % of 291 canopy trees and 87 % of 131 sub-canopy trees produce fleshy fruits adapted for animal consumption (Howe & Smallwood, 1982; also Foster, 1982a), while 38 % of 164 resident birds species eat fruits (see Willis, 1980). Of the total bird count, 24 % species are in such groups as toucans (Ramphastidae) and cotingas (Cotingidae), largely or entirely dependent on fruits for food and likely to be dispersal agents, while others such as parrots (Psittacidae) digest seeds and are consequently not dispersal agents. Additionally, North American migrants eat fruits and disperse seeds (see Leck, 1972; Howe & De Steven, 1979; Greenberg, 1981). Although less known, mammals such as bats (Morrison, 1978) and monkeys (Howe, 1980; Milton, 1980) are clearly dispersal agents in the Barro Colorado forest, while others such as agoutis and pacas (Dasyproctidae) have more questionable roles (Howe, 1980; 1981). In short, the taxonomic compositions of the Barro Colorado and other forest communities imply pervasive importance of fruit as food and indicate that many bird and mammal species are likely to be important dispersal agents of a variety of tree species.

In what sense are plants 'dependent' on animals for seed dissemination? Local seed dispersal might either be an escape from density-dependent seed mortality near the parent tree (Janzen, 1970) or a means of 'colonizing' ephemeral light gaps caused by either large-scale clearing or small-scale treefalls and branchfalls (see Howe & Smallwood, 1982).

Citation of the first hypothesis has far outstripped field corroboration, although in neotropical forests it is now clear that disproportionate mortality of seeds or seedlings does occur near the parent trees in *Casearia* (Howe & Primack, 1975), *Andira* (Janzen *et al.*, 1976), *Bursera* (Clark & Clark, 1981), *Platypodes* (Augspurger, 1983), and *Virola* (Howe *et al.*, in prep). The latter example is *Virola surinamensis*, a myristicaceous tree with fruits dispersed by toucans in Central and South America. A quantitative field experiment shows that an immediate advantage to dispersal away from the crown exists because the probability of infestation by *Conotrachelus* weevils (Curculionidae) is four times higher for seeds close to the tree than for those 25 or more metres away from the crown. Other local advantages to dispersal exist, however. Hartshorn (1978) has suggested that at least 75 % of the trees in one Costa Rican rainforest require light gaps, even if small and ephemeral, for recruitment. Howe & Smallwood (1982) point to an inexorable advantage to parent trees which, through animals or other means, broadcast seeds so widely that they maximize the chance that their offspring will occupy such randomly-occurring gaps. If the parental crown represents one 'tree space' suitable for an offspring, only one such potential space exists under the parent, should it fall, while an infinity of potential gaps exist away from the parent. Even if mortality of seeds or seedlings is density-independent, there will be an inevitable advantage to dissemination away from the crown. For either or both reasons, animal-mediated dispersal is certain to be critical for the demographic recruitment of many or most tropical tree species.

## Seasonality

All studies of tropical fruiting phenologies report seasonality. Extreme seasonality is the rule in forests with distinct wet and dry seasons in Australia (Crome, 1975), Brazil (Jackson, 1981), Costa Rica (Frankie *et al.*, 1974), Malaya (Medway, 1972), and Panama (Foster, 1982*a*), and substantial fruiting seasonality even occurs in very wet (annual precipitation of 4000–6000 mm) neotropical forests with weak dry seasons (Frankie *et al.*, 1974). Fruiting seasonality is less pronounced, but noticeable, in wet forests showing virtually no monthly variation in rainfall, as has been reported in one Colombian forest (Hilty, 1980). It is likely that food resources for fruit-eating animals are not as constant as was once thought (Leigh & Windsor, 1982). Food may be far more

limiting in some seasons than in others, and consequently trees bearing fruits during lean times will play a greater role in maintaining entire communities of fruit-eating animals than those bearing fruit during peak production of the entire forest (Howe, 1977).

Does *enough* seasonality exist to cause food limitation? Direct evidence of food limitation is scarce in extremely diverse forests in which the food habits of frugivores are poorly known. But the extremes of fruit production in any given forest introduce the potential for seasonal famine. In well-studied Central American forests, most trees produce seeds that fall, and germinate, at the beginning of a long wet season (Garwood, 1982). Only a few produce fruits with dormant seeds that must wait several months for the beginning of the next wet season (Garwood, 1982). The consequences for phenologies are notable. In a dry deciduous Costa Rican forest, the total number of trees with mature fruits falls from 41 at the peak in May to 8 during the depths of the late wet season in October and November. In an evergreen wet forest in the same country, the extremes are 33 species at the September peak and 12 at the late wet season low in early December (Frankie *et al.*, 1974). In a seasonal rainforest in Central Panama, 48 and 50 trees drop fruits during dual October and May peaks, but only 12 bear fruits during the early December depression immediately before the beginning of the severe four-month dry season (Foster, 1982*a*). Elimination of any or most of these 12 crops for even a few weeks in a critical habitat patch could precipitate rapid local extinctions of frugivores. Even extensive forests suffer mass starvation of fruit-eating birds and mammals when anomalous weather conditions lead to widespread failures in fruit crops (Foster, 1982*b*); small reserves will be even more fragile.

## Focal dispersal systems

Recent studies of tropical 'dispersal systems', defined here as plant species and the animal visitors that disperse or destroy fruits, offer enough precision to allow at least qualitative management decisions. Earlier work was of limited utility because it usually failed to distinguish animals that dispersed seeds from those that did not, and it usually sampled bird visitation for only 1–14 days out of seasons that lasted 4–32 weeks (e.g. Diamond & Terborgh, 1967; Land, 1963; Howe & Primack, 1975; McDiarmid *et al.*, 1977). It is now clear that grossly inadequate sampling is at best useless and at worst misleading: feeding assemblages change as a

season progresses, and visitation need not imply seed dispersal. A manager needs to know which visitors enhance seed dispersal and which preclude it, and further needs to have some idea of community-wide patterns of production and use. Examples of recent work in Central American forests are edifying because they illustrate that some tree species are likely to be 'pivotal' to the frugivore community, while others are not. The following natural history summaries bring important issues into focus.

First, two systems (*Casearia* in rainforest and *Virola sebifera*) generally fit the description of a pivotal or keystone species. Both trees bear fruit during annual fruit scarcity, both bear rich fruits that apparently supply much of the diet for visitors to the trees, and both support frugivorous birds which are clearly important dispersal agents for many trees during other seasons of the year.

(1) *Casearia corymbosa* H.B.K. (= *nitida*) (Flacourtiaceae) occurs from Mexico to Colombia (Croat, 1978). In Costa Rica it is a canopy tree in rainforests of the Caribbean slope and a shrub or small tree in the seasonal deciduous forests of the Pacific Lowlands (Frankie *et al.*, 1974). Dispersal biology varies dramatically from one habitat to the other (Howe & Vande Kerckhove, 1979).

The rainforest *Casearia* provides the first, and as yet the best, evidence of 'pivotal' fruit-bearing trees in tropical forest (Howe, 1977). At Finca La Selva in eastern Costa Rica the species is largely restricted to flood-plains. Each tree produces 600–40 000 (mean = 13 000) fruits from December through early February. Conspicuous red-brown capsules open during the morning to expose a brilliant red aril. The elliptical seeds, approximately 10 mm long by 8 mm wide, are covered with an oily red aril 1 mm thick. The aril and seed weigh less than 0·6 g. December corresponds with the annual low of fruit production in this forest, with only 12 trees (some not animal-dispersed) producing fruits among those censused by Frankie *et al.* (1974). Twenty-two species of birds of remarkably diverse taxonomic affinities consume the arils during a 10 week season (see Table 1); several birds have little else to eat in December. Of these, two *Amazona* parrots simply strip off the arils and drop the seeds under the crown and 19 species swallow the seed and aril and regurgitate the seed intact, but leave the vast majority in the intermediate vicinity of the crown (e.g. within 10 m) where seed and seedling mortality is high (Howe & Primack, 1975; Howe, 1977). One cotinga (*Tityra semifasciata*) visits consistently throughout the season, feeds at a high

8

## TABLE 1
Six Most Frequently Seen Resident Birds at Some Fruiting Trees of Primary Central American Rainforest
(The table illustrates overlap in use of fruits of medium to large size; consult references for other visitors)

| Bird species | Tree species | | | |
|---|---|---|---|---|
| | Casearia corymbosa[a] | Tetragastris panamensis[b] | Virola sebifera[c] | Virola surinamensis[d] |
| *Amazona autumnalis* | X | X | ... | ... |
| *Amazona farinosa* | X | X | .... | --- |
| *Penelope purpurascens* | | X | ---- | --- |
| *Baryphthengus martii* | . | - | --- | X |
| *Trogon massena* | --- | | X | X |
| *Ramphastos swainsonii* | X | rare | X | X |
| *Ramphastos sulfuratus* | X | X | X | X |
| *Pteroglossus torquatus* | X | X | X | X |
| *Tityra semifasciata* | X | X | X | X |
| *Querula purpurata* | rare | X | X | X |
| *Myiozetetes similis* | X | X | --- | --- |
| *Myiozetetes granadensis* | X | | .. | --- |

Code: 'X' among 6 most-frequently seen; ' ' not recorded; 'rare' recorded but not common.
[a] The seed plus aril weigh ~0·6 g (Howe, 1977).
[b] Primarily monkey-dispersed. The seed plus aril weigh ~2·0 g (Howe, 1980).
[c] The seed plus aril weighs 0·9 g (Howe, 1981).
[d] The seed plus aril ranges from 3·8 to 4·8 g (Howe & Vande Kerckhove, 1981).

rate without dropping seeds, and habitually removes seeds from the immediate vicinity of the tree. It appears to be a 'reliable' dispersal agent in the sense of McKey (1975) and Howe & Estabrook (1977). If La Selva were isolated from other forests, local extinction of *Casearia* would almost certainly force local extinction of the *Tityra*, which has little else to eat in December at this site. Local extinction of the bird would appear to be a severe constraint on *Casearia* recruitment. But the key insight from this system is that *Casearia* apparently maintains many other frugivorous birds through a seasonal period of dearth. Toucans (*Ramphastos*), for instance, often simply occupy individual trees and feed on the fruits without consistently dispersing them early in the season. By January other preferred trees are in fruit (e.g. *Protium* spp. and *Virola koschnyii*) and

toucans are no longer common visitors at *Casearia*. But extinction of *Casearia* would certainly directly affect the survival of toucans in times of dearth, and would indirectly depress recruitment of plants dispersed by these wide-ranging birds throughout the rest of the year. This is clearly a 'pivotal'(Howe, 1977) or 'keystone' (Gilbert, 1980) plant in the La Selva forest.

*Casearia corymbosa* also occurs in second growth dry forest, where different birds visit the plant (Howe & Vande Kerckhove, 1979). The tree bears fruit during September and October in Santa Rosa National Park during the low point of fruit production in that deciduous forest, but it is visited there primarily by migrants from South America (*Vireo flavoviridis*) or North America (several species). The crops are small, and the fruit is only common for a short (1–2 week) time. At this site the tree might be important for one migrant (the *Vireo*), but it certainly is not critical for the entire frugivore community. The example underscores both the point that 'coevolution' between birds and fruiting trees is usually rather general (Snow, 1981), and that the overall significance of a plant species must be determined in the locality targeted for management. At La Selva there is every reason to ensure that riverbottom habitats for *Casearia corymbosa* be included in a reserve; at Santa Rosa special measures for inclusion are unnecessary.

(2) *Virola sebifera* Aubl. (Myristicaceae) occurs from Nicaragua to Brazil (Croat, 1978). On Barro Colorado Island the species bears fruit from September through February, with a dramatic November peak during the annual low of fruit production in the forest (Howe, 1981). The typical nutmeg capsule dehisces early in the morning to expose an elliptical 14 × 10 mm seed enveloped in a brilliant red laciniate aril. The entire diaspore weighs 0·9 g. Despite heavy insect infestations, individuals succeed in maturing 5 to 2163 fruits in a season (mean = 594). A small but efficient assemblage depletes each day's crop shortly after dawn, stripping the trees bare by mid-morning. Regular visitors include two toucans (*Ramphastos swainsonii* and *R. sulfuratus*) and a cotinga (*Tityra semifasciata*), while other birds (*Baryphthengus martii*, *Pteroglossus torquatus*, and *Trogon massena*) take the fruits near heavy second growth, but not of those trees in the primary forest (see Table 1). All regurgitate viable seeds away from the parent plants. Although toxins in the arils may exclude a wide variety of birds and mammals (see Howe, 1981; Howe & Vande Kerckhove, 1981), this plant does provide a critical food resource to the two large toucans and the *Tityra* during an otherwise scarce time in

the annual cycle of this forest (see Foster, 1982a). Furthermore, the small size of the regular assemblages indicates dependence on these birds by the tree; few seedlings survive to the sapling stage under the crowns, despite the fact that dozens to hundreds of seeds fall there. Considering the widespread importance of these toucans and the tityra in the dispersal of other fruits, *Virola sebifera* appears to be 'pivotal' to this community. But it does not affect as many birds as *Casearia corymbosa* in eastern Costa Rica, and it is both widespread and abundant in the Barro Colorado forest.

Secondly, five trees (*Guarea glabra, Lindackeria laurina, Miconia argentea, Tetragastris panamensis,* and *Virola surinamensis*) produce fruits much used by some Panamanian birds and mammals, but for various reasons do not appear 'pivotal' to the forest community. All bear fruit when many other trees are in fruit. Two (*Lindackeria* and *Miconia*) provide critical food resources for migrant warblers from North America, but the transient status of these birds suggest that they are not important 'mobile links' (Gilbert, 1980) for other trees in the forest. *Guarea* is visited by many birds, none of which alone appears critical for its reproduction. *Tetragastris* bears substantial crops only occasionally; heavy use by monkeys is entirely facultative. *Virola surinamensis* is a preferred food of large toucans, but it is so fecund that only a very few trees could support many of these mobile birds. It is unlikely to be limiting, unless widely scattered or completely absent.

(3) *Guarea glabra* Vahl (Meliaceae) is an understorey tree in Central and South America (Croat, 1978). It bears fruit from March through late April on Barro Colorado Island, Panama, and is in fact one of the tree species in fruit at the end of the dry season and beginning of the wet season when most species bear fruits in this forest (Foster, 1982a). Arillate seeds average $10.0 \times 6.3$ mm, and weigh ~0.5 g. Visitors include 12 species of resident birds, but most fruits are actually taken by 7 species of North American migrants (Howe & De Steven, 1979). There is little consistency in visitation from one individual tree to another, and little reason to believe that it is critical for the survival of any resident or migrant species. *Guarea* is not 'pivotal' to the community on Barro Colorado Island, nor is its reproduction dependent on any particular bird.

(4) *Lindackeria laurina* Presl. (Flacourtiaceae) is an understorey-to-overstorey tree from Mexico to northern South America (Croat, 1978). Berries are eaten by a variety of resident and migrant birds during the fruiting season from December through early January, which corresponds to the low point of fruit production in the Barro Colorado Forest

(Foster, 1982*a*). Berries average 0·08 g of pulp and 0·02 g of seed (Greenberg, 1981). Greenberg (1981) has found that this species may in fact be critical for migrant wood warblers (*Dendroica castanea* and *D. pennsylvanica*), which are found at the species far out of proportion to its abundance in the forest. Another parulid (*Vermivora peregrina*) is also a common visitor. Interestingly, an unnamed *Casearia* was simultaneously an important food source for these warblers. *Lindackeria* and this *Casearia* may be critical for some migrants, but not 'pivotal' in the sense that they support many additional birds which serve as important dispersal agents of other plants in the forest.

(5) *Miconia argentea* (Sw.) DC (Melastomataceae) occurs from southern Mexico to Panama (Croat, 1978). The tree produces small (0·1 g) berries from late February through June on Barro Colorado Island, and is also visited heavily by migrating warblers (*Dendroica* and *Vermivora*) (Greenberg, 1981). As with *Lindackeria*, there is little reason to believe that the plant is dependent on any particular bird species, or that it is 'pivotal' to the frugivore fruiting tree community. It could be especially important to two or three North American migrants at this site, but these birds are not present in numbers at many other trees in the Barro Colorado forest.

(6) *Tetragastris panamensis* (Engl.) O. Kuntze (Burseraceae) occurs from Honduras through northern South America (Croat, 1978). The population on Barro Colorado Island fruits erratically, with heavy crops every 5 or 10 years and moderate or non-existent crops at other times (R. Foster, pers. comm.; H. Howe, pers. obs.). An intensive study during a season of heavy fruit production indicated opportunistic use by 22 species of birds and mammals (Howe, 1980; see Table 1). Fruits are usually compound capsules, with 1 6 seeds imbedded in sugary white arils. Dehiscence occurs day and night, exposing a dangling diaspore much sought after by monkeys (*Allouatta, Cebus, Ateles*), and other mammals (*Nasua, Potos*). The seeds and arils together averaged 18·1 × 14·4 mm, and weighed ∼2 g. Crops ranged from 165 to 99 000 (mean = 22 951) arillate seeds, and were produced from February through May and June. Use by the three common fruit-eating monkeys closely approximated the relative abundance of the monkeys on the island: 97 "ₒ of all fruits eaten by animals were taken by very common howler monkeys *Allouatta palliata*, with lesser proportions by others. This occurred despite the fact that *Allouatta* was not known to eat this fruit during other years of intensive observation in this same forest (Milton, 1980). The generalized

nature of the fruiting display, erratic fruit production, and the wide and opportunistic array of birds and mammals using this tree clearly indicate that this is not a 'pivotal' plant annually relied upon by frugivorous animals.

(7) *Virola surinamensis* (Rol.) Warb. (Myristicaceae) is a canopy tree of rainforests from Costa Rica to Brazil (Croat, 1978). On Barro Colorado Island, the species is less common than *Virola sebifera* but still widespread in primary forest. Fruits are similar to those of its congener, but considerably larger, the seed and arils together averaging 19·7 × 16·3 mm long and 4·8 g in weight. A three-year study shows that during a given year crops range from 428 to 31 006 (median = 8579), with a dramatic peak in production occurring in July or August for a season that lasts from April through September (Howe, 1983). The same birds that commonly visit *V. sebifera* eat the fruits of its larger congener, except that the tityra is too small to swallow the seeds and a much larger guan *Penelope purpurascens* consumes a substantial fraction of the crop. The birds use the tree heavily, but individual crops are so large that few are depleted except in the worst years; even then plants with small fruits are selectively visited and depleted while crops of large seeds are largely left uneaten. Complete extirpation of this tree probably would affect populations of one toucan (*R. swainsonii*), but crops are large enough that even a few individual plants could provide fruits for these mobile animals. In addition, many other fruiting plants are available for most of the *Virola surinamensis* season. It would be difficult to argue that this tree is 'pivotal' to the Barro Colorado community in the same sense as its congener *V. sebifera*, even though the birds are clearly critical for *V. surinamensis* recruitment (Howe *et al.*, in prep.).

## Other evidence

Studies of the frugivorous animals themselves usually do not provide the kinds of information necessary to distinguish 'pivotal' from other dispersal systems. For instance, 40 % of the howler monkey diet on Barro Colorado Island is fruit (Milton, 1980). A study as careful as this one would be of assistance in preserving monkey populations themselves. But it does not indicate how important the focal animal is for the plants, nor even the identity of other visitors to the plants, in enough detail to permit predictions. Snow (1962*a*, *b*) shows that manakins (*Manacus manacus* and *Pipra erythrocephala*) fed on 66 and 48 species of fruiting plants in

Trinidad, respectively. Some of these plants are found in abundance near courting areas, suggesting that the birds influence plant recruitment there. But it is beyond the scope of ornithological studies to determine whether courting leks are the best, or only, places to which the birds carry seeds. Neither can such work usually determine the relative importance of other animals for the destruction or dispersal of these same food plants. In one famous instance, a study of oilbirds *Steatornis caripensis* showed that the birds indirectly cause the mortality of hundreds of thousands of seeds by depositing them in caves where establishment is virtually impossible (Snow, 1962c). But this bypasses the possible positive effects of oilbird foraging on dispersal. Even the best natural histories of focal frugivores yield only incidental information about their potential influence on plant reproduction.

Some exceptional approaches to the study of focal animals deserve emphasis because they provide relevant information. Crome (1975), for instance, documented annual patterns of fruit use by the large fruit-pigeon guild in seasonal tropical forests of northern Australia. Systematic censuses showed subsequential use of alternate food resources, and coincidentally indicated which birds were resident in an area and which roamed widely in search of important food trees. Such a community-wide study of birds similarly yielded the critical insights concerning fruit use by wood warblers in Panama (Greenberg, 1981). Secondly, Beehler's (1983) study of paradise birds in Papua New Guinea provides a new standard for frugivore autecology. Beehler discovered that monogamous species tended to specialize on figs, which were eaten by many other birds. Polygamous birds of paradise ate fruits with a narrow visitor range; two trees (*Chesocheton weinlandii* and *Gastonia spectabilis*) were visited *only* by birds of paradise. In this case the role of pivotal species may be reversed; a small taxon of birds may, like pivotal trees, be necessary for the persistence of some tree species. The same may eventually prove to be true of some neotropical birds such as toucans and tityras.

## CONCLUSIONS

Even rather preliminary data indicate that fruit-bearing trees are limiting resources in some reserves. These limited resources must be interpreted against the backdrop of uneven species distributions, habitat diversity, the necessity of local dispersal, and the fact of seasonality.

First, some pivotal fruit trees are uncommon, while others are abundant. Different challenges are evident with different sorts of pivotal dispersal systems. The example of *Casearia corymbosa* at La Selva is instructive because the tree is largely restricted to riparian habitat, where only 20 fruiting individuals were counted in 1976. Perhaps 40 adults, including males, occur in the reserve. A scarce 'pivotal' species with restricted habitat requirements such as this one is particularly susceptible to ecological catastrophe; one can only be grateful that as many individuals were included in the alluvial habitats of the La Selva reserve as there were. One general message is that Preston's (1962) uneven species distributions will continue to haunt us when plants critical for maintaining wider diversity in the community are especially vulnerable to extinction. A second general message is that it is imperative to include a variety of habitats in any reserve; habitat complexity and habitat diversity count (Foster, 1980). Quite a different situation is presented by *Virola sebifera*, which bears fruit needed by toucans and a tityra during November and December, at the low point of fruit production in the Barro Colorado. But the plant is abundant. At least 2000 individuals exist in the Barro Colorado forest (S. P. Hubbell, pers. comm.), implying that it is – for the foreseeable future – immune from either genetic degradation through inbreeding or ecological catastrophe. Furthermore, the species bears fruit every year. This species is pivotal, but neither in danger nor prone to fruiting failure. The rare pivotal species demand more diligence.

Second, the ecological connectedness of tropical animals and plants suggests that the impact of one local extinction may range well beyond the particular plant and animal species in a given dispersal 'system'. Local extinction of *Gastonia* or *Chesocheton* in New Guinea might or might not influence the abundances of birds of paradise (see Beehler, 1983). It certainly seems likely that a local extinction of *Casearia corymbosa* in eastern Costa Rica would stress local populations of tityras, toucans, and fruit-eating flycatchers. If they in turn faced extinction or severely reduced population sizes, the local recruitment of other species of trees that bear fruits at other times of the year would be threatened (Howe, 1976, 1977). The trees discussed here are largely dispersed by a small set of birds (Table 1); many other trees of similar sort are probably largely or partially dependent on the same birds in these forests. It is reasonable to imagine a scenario of a widening circle of extinctions of mutually inter-dependent plants and animals (Futuyma, 1973; May, 1973; Howe, 1976; Gilbert, 1980). Such a domino effect would clearly accelerate the loss of species

beyond that assumed by random extinctions of ecologically independent species (e.g. Diamond, 1975; Wilson & Willis, 1975; Wright & Hubbell, 1983). To the degree that reserves are isolated from other forests which serve as sources of immigrants, such rapid losses of ecologically interdependent species will be permanent, to an even larger extent than predicted by the simplest interpretation of biogeographic theory. The relict forests may be diverse by many standards, but they will lack the richness of ecological interaction just now becoming evident to tropical ecologists.

## RECOMMENDATIONS

Enough relevant natural history is known that recommendations are both possible and necessary. On one level, general procedures should be adopted for assessing the suitability for including areas within reserves. On another, successional management may be necessary where relatively uniform stands fail to include 'pivotal' fruiting plants that are restricted to specific habitats. Both kinds of predictions will develop as the field itself develops.

First, a preliminary impact study of a prospective park should include both a phenology census and a systematic census of animal use of different fruits. The purpose of the phenology census is to document fruiting seasonality within the forest order to discern annual periods of fruit scarcity, and to provide a count of potentially important fruiting plants. The bird and mammal census, which can be done simultaneously, can give a rough assessment of relative use of different food plants by different fruit-eating animals (Crome, 1975). The best general system for phenological study is probably a walk, performed at least once per month for a year, through a diversity of habitats. A large (e.g. 400–500) but random selection of trees gives some notion of the total activity of the forest, while also providing a rough estimate of relative species abundances (Leigh & Windsor, 1982). These phenological censuses should also allow the biologist to notice trees, which may be quite rare, that attract a disproportionate number or variety of fruit-eating animals (e.g. *Cascaria*; see Howe, 1977). The censuses must include all major habitat types which could conceivably be included in a park; the habitat mosaic which is conspicuous in many tropical forests will very likely include habitat types required by 'pivotal' plants (see Foster, 1980). The best method for censusing birds is a replicated randomly-timed route including several to many individual plants of a species (Howe & Vande

Kerekhove, 1981). But any systematic census yields more reliable information than casual observation (Howe, 1980). Where time is limited, morning censuses yield the most information about bird activities (see Howe, 1981; Howe & Vande Kerekhove, 1981). The number and activity of birds and mammals (e.g. monkeys) in each tree species should be noted, thereby giving a rough estimate of the relative importance of each. Census data can be supplemented with extended watches at particularly promising trees, the point being to discover which animals actually disperse seeds and which kill them outright or leave them under the crowns. If systematic phenology and animal censuses are impossible, local residents or foresters may be able to suggest key tree species on which to focus, although reliance on such information is quite likely to miss inconspicuous frugivory, such as early morning visits at *Virola sebifera* (Howe, 1981). Overall, monthly censuses will be the best sources of baseline information upon which to base judgements of inclusion or exclusion of land in reserves.

If it proves impossible to save sufficient numbers of individuals of pivotal species within habitat patches easily included in a reserve, active management may be necessary. Many animal-dispersed fruits are of second growth plants (Richards, 1952), and many fruit-eating birds and mammals are mobile enough to seek out food where it exists (e.g. Crome, 1975; Howe, 1981). One remedy is active maintenance of areas of second growth that maintain a consistent supply of fruit through the year. In the neotropics, 5–10 ha blocks of early and late successional trees and shrubs would maintain small populations of fruit-bearing trees. If critical pivotal species can be recognized, of course, plantings may be both possible and necessary. In either case the details will have to be determined for each forest community, the goal being to maintain birds or primates that would otherwise be exterminated during normal periods of fruit scarcity in the forest.

Both the general discussion and this preliminary attempt to formulate recommendations underscore the practical difficulties and the profound ignorance that underlies preservation of diverse tropical forests. A conservationist will always be faced with unequal species abundances, and consequently with the imperative of managing uncommon or rare species. Further, we rarely know, at this point, which of the rare species are actually important for the preservation of wider components of the plant and frugivore communities. Hopefully this paper will give concerned conservationists both the perspective necessary to recognize such problems and a key to the means of tackling them.

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