Primate Seed Dispersal: The Fate of Dispersed Seeds[1]

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ABSTRACT

The three primate species of Santa Rosa National Park, Costa Rica (*Ateles geoffroyi, Alouatta palliata, Cebus capucinus*) have diets in which fruits are major components. All three primate species defecated seeds of many fruiting species; the majority of which (60%) germinated under experimental conditions. The sampling of seed traps placed throughout the forest indicated that, on average, 392 large seeds that passed through the stomachs of monkeys fell weekly per hectare of forest floor. However, the dispersal performed by the primates may not be the final stage of dispersal for many of these seeds. By constructing artificial dung piles containing seeds it was shown that 51.8 percent of the seeds were either removed by secondary dispersers, or killed by seed predators within 5 days of being placed in the forest. The rate of seed removal varied depending on the seed species.

Quantitative studies and theoretical discussions of seed dispersal have concentrated on dispersal of seeds by birds and bats (Snow 1965, 1971; McDiarmid *et al.* 1977; Fleming & Heithaus 1981; Fleming 1982; Heithaus 1982; Herrera 1982, 1984, 1985). However, in tropical forests, primates constitute between 25 percent and 40 percent of the frugivore biomass (Eisenberg & Thorington 1973, Eisenberg *et al.* 1979, Terborgh 1983), and they defecate large numbers of viable seeds (Hladik & Hladik 1969, Cant 1979, Estrada & Coates-Estrada 1984, 1986).

Most studies of seed dispersal report observations on which animals removed fruit from a particular fruiting tree, the removal rate, and in some instances, whether or not the injested seeds are viable when voided. Such studies only examine the very initial stage of seed dispersal and do not examine the quality of the location where the seeds are deposited. Not addressing this issue may produce misleading results (Janzen 1983). In addition, by not documenting the initial fate of seeds deposited on the forest floor, it is not possible to assess the relative importance of primary dispersers versus animals that subsequently move or kill the seeds (Estrada & Coates-Estrada 1986, Janzen 1986a).

The objective of this investigation is to describe seed dispersal associated with the three species of primates in Santa Rosa National Park, Costa Rica, and document the initial fate of the dispersed seeds under various natural and experimental conditions.

METHODS

Study site.—The study was conducted over a 3-year period for a total of 26 months (January to August 1984, January 1985 to July 1986) in Santa Rosa National Park, Costa Rica. The park is situated in the northwest corner of Costa Rica, in Guanacaste Province. The vegetation in the park is a mosaic of abandoned pastures (*Hyparrhenia rufa*), successional dry deciduous forest (containing *Spondias mombin, Luehea candida, L. speciosa, Guazuma ulmifolia, Bursera simaruba, Ficus* spp., and *Chlorophora tinctoria*), and semi-evergreen forest found mainly in the moist ravines, which contains *Hymenaea courbaril, Mastichodendron capiri,* and *Manilkara chicle* (Janzen 1986b). The home ranges of each of the three primates contained sections of both dry deciduous and semi-evergreen forests. The climate of the region is characterized by a dry season from mid December to late May; a wet season encompasses the remainder of the year. Rainfall in the park ranges between 900 mm and 2400 mm annually, almost all of which falls in the wet season.

Behavioural observations.—From each of the primates studied a group using a common section of forest was selected for study and was observed to obtain information on foraging and ranging behaviour. Behavioural data were recorded using a focal animal sampling regime which employed a 10-minute session. If the subject was lost prior to the end of the session, the session was terminated and the data discarded. In those situations where observation conditions were ideal, the rate at which food items were removed from the tree and their subsequent fate (i.e., injested, dropped, etc.) were recorded. Over the duration of the study, 394 hours of focal animal data were collected on howling monkeys, 335 hours on spider monkeys, and 171 hours on cebus monkeys. Between January and July 1986, focal animal observations were recorded only for spider monkeys.

Fecal samples.—Fecal samples were collected in one of two fashions; directly, as when an animal was seen to defecate by the observer, and from traps set out in the forest. The traps consisted of 80 cm by 98 cm tables

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covered with plastic and raised off of the forest floor by 16 cm. In 1984, 120 traps were sampled, while in 1985, 105 traps remained to be sampled. Traps were placed approximately 10 m apart adjacent to small trails or along lines out from the trails. Dung was collected early every morning from traps during the last week of every month. Although dung beetles and mice did move dung around on the traps (12% of the samples), rarely was there any indication that large seeds had been removed prior to the time the traps were sampled. The seeds in the dung were separated from the fecal matter, identified, counted, and measured. For very small seeds, such as those of *Ficus* spp. and *Muntingia calabura,* the number of seeds in the fecal sample was estimated.

To determine if the seeds defecated by the monkeys would germinate, experiments were conducted in three ways. First, seeds collected from feces were planted in dirt just under the soil and were watered at regular intervals. Secondly, seeds were placed between layers of wet paper towel and kept moist. Lastly, after the seeds were identified, they were placed back in fecal material and stored in plastic bags. Germination experiments were not continued between field seasons.

EXPERIMENTS.—Experiments were conducted to examine the initial fate of seeds that had been defecated by monkeys. The general experimental protocol involved constructing dung piles using seeds that had passed through the monkey. A dung pile was made by taking seeds and mixing them with seed-free monkey dung and placing the mixture on the forest floor in a 0.5 m^2 area cleared of leaf litter. Dung piles were placed in a line, no closer than 4 m apart. Dung containing small seeds, such as those of *Muntingia calabura, Ficus* spp., or *Visima baccifera,* were not used as sources of dung; 793 seeds of various species were set out in the forest in this fashion. Alterations of this general experimental protocol were used to examine the effect of different factors on the rate of seed removal from dung, on subsequent germination rates, and on the probability of seedling establishment.

To address the question of whether the number of seeds in a dung pile influenced the probability of seeds being removed by predators or secondary dispersers, 30 dung piles containing from 1 to 20 seeds were constructed in an area of semi-evergreen forest. Five plant species were used in this experiment; *Spondias mombin, Simaruba glauca, Mastichodendron capiri, Swartzia cubensis,* and *Ocotea veraguensis.* The upper limit of 20 seeds was set because this was the maximum number of medium sized seeds found in a single dropping.

To examine whether or not the smell of monkey dung acted as an attractant to animals that removed seeds from dung, 22 controls were established in which seeds were placed in cleared areas without dung. These were compared to 22 stations with seeds and dung. The same species of seeds were used in the controls and the experimental stations. The seeds used in the controls were washed thoroughly to assure that no fecal material remained on the seeds which could provide olfactory stimulus to the animals removing the seeds.

Finally, the effect of forest type on the rate of seed removal from primate dung was determined. Eight dung piles containing seeds of *Spondias mombin,* 12 dung piles containing seeds of *Ocotea verguensis,* 20 dung piles containing seeds of *Mastichodendron capiri,* and 20 dung piles containing seeds of *Simaruba glauca,* 5 seeds to a dung pile, were placed in three semi-evergreen forest sites and three dry deciduous forest sites.

All of these experimental dung piles were constructed between 15 April and 26 May 1985. Experimental dung piles were examined approximately once a week until 7 August 1985, after which time they were monitored during the first week of every month until the end of the study on 4 August 1986 (the seeds used in the comparisons between forest types were not monitored after 7 August 1985). Examination of a dung pile involved counting all seeds present and determining their species. The presence of seed fragments or husks were noted, and germinating seeds were counted.

The preliminary results of these experiments stimulated the development of an additional experiment in 1986. Five seeds of a species which was rapidly removed from primate dung (*Mastichodendron capiri*) and five seeds of a species for which removal was much slower (*Simaruba glauca*) were set out in 0.5 m^2 cleared area. On 28 May 1986, 20 of these stations were set out in a line in a semi-evergreen forest area and 20 were similarly established in a dry deciduous forest area. Seed species was alternated between stations. These stations were monitored approximately once a week between 28 May and 4 August 1986.

RESULTS

For all three primate species, fruit constituted a major part of their diets. Combining all years, spider monkeys spent 77.9 percent of their feeding time eating the fruit of 36 plant species and cebus monkeys spent 81.2 percent of their feeding time eating fruit of 41 plant species. Howlers were the least frugivorous, spending 28.5 percent of their feeding time eating the fruit of 19 different species. Even though all three species of monkeys ate food items from many different species of plants, only a few constituted the bulk of each species' foraging efforts. For example, the cebus monkeys spent over 50 percent of their feeding time eating fruits from only two plant species (*Sloanea terniflora, Muntingia calabura*). Similarly the spider and howling monkeys spent 50 percent of their feeding time eating food items from three plant species (*Ficus* spp.,

TABLE 1. *The major species of seeds occurring in the dung of the primates in Santa Rosa National Park, Costa Rica. Frequency of occurrence was calculated as the number of dung samples in which one or more seeds of a particular species was found, expressed as a percentage of all dung samples.*

Plant species	Primate species[a]	Frequency of occurrence	Number/ha		Coefficient of dispersion		Germinate
			84	85	84	85	
Agonandra macrocarpa	H	0.8	—	—	—	—	No
Ardisia revoluta	S, C	6.7	—	1.5	—	6.8	Yes
Bursera simaruba	H, S	1.7	0.5	—	11.0	—	Yes
Casearia arguta	S, C	2.5	—	31.6	—	26.0	Yes
Cecropia peltata	S, C	3.3	—	—	—	—	No
Coccoloba venosa	S	1.7	—	—	—	—	No
Cupanea guatemalensis	H, C	1.7	—	—	—	—	Yes
Dipterodendron costaricensis	S	2.5	1.1	6.1	2.0	5.0	Yes
Euphorbia sp.	C	3.3	—	—	—	—	Yes
Ficus sp.	H, S, C	24.2	>100	>100	—	—	Yes
Genipa americana	H, S, C	5.0	—	—	—	—	Yes
Hirtella racemosa	H, S, C	3.3	—	0.4	—	1.0	Yes
Manilkara chicle	H, S, C	5.8	21.3	—	12.9	—	Yes
Muntingia calabura	H, S, C	23.3	>100	>100	—	—	No
Ocotea veraguensis	S	5.0	—	—	—	—	Yes
Rheedia edulis	S, C	2.5	—	6.7	—	4.4	Yes
Spondias sp.	H, S	5.0	0.5	—	11.0	—	Yes
Sterculia apetala	C	1.7	—	—	—	—	No
Swartzia cubensis	S, C	1.7	—	—	—	—	Yes
Vismia baccifera	S	0.8	—	—	—	—	No
Zuelania Guidonia	H	1.7	—	—	—	—	Yes

[a] H = howler monkey (*Alouatta palliata*); S = spider monkey (*Ateles geoffroyi*), C = *cebus capucinus.*

Muntingia calabura, and *Mastichodendron capiri*) and five plant species (*Ficus* spp., *Brosimum alicastrum, Manilkara chicle, Pithecellobium saman,* and *Lonchocarpus costaricensus*) plant species, respectively. Of the fruits consumed, 53 percent had seeds that were found intact in primate dung (averaged from all collections and all monkeys; Table 1). This value is probably an underestimate of the species of seeds defecated, because many of the fruiting species are only eaten rarely, thus the probability of finding these seeds in dung was low.

There was considerable variation between years in both the types of fruits eaten and in the proportion of the diet which fruit constituted. For all three primate species, fruit constituted a greater proportion of the diets in 1984 than 1985 (differences between years: cebus 48.5%, spiders 9.4%, howlers 6.4%). The variation between years in the amount of time spent feeding on particular plant species was, in some instances, very extreme, even when the availability of the fruit did not change. For instance, in 1984 the cebus monkey group spent 8.6 percent of their total feeding time, and as much as 31.7 percent of their feeding time in one month, eating acorns (*Quercus oleoides*). In contrast, they were never observed eating acorns in 1985 or 1986, although they were available in both years. Another example concerns the use of *Dipterodendron costaricensis* fruit by all of the monkeys. The proportion of time spent eating this fruit per month changed by 270 percent for cebus monkeys, 76 percent for spider monkeys, and 100 percent for the howlers.

Seeds defecated by monkeys.—The seeds from 155 dung samples were inventoried. Of these, 35 samples were collected from the seed traps, and it was not possible to determine which primate species produced the dung. During observations, 53 samples were collected from howling, 39 spider, and 28 from cebus monkeys. All feces collected from cebus and spider monkeys contained some seeds. For howlers 15.1 percent of the samples contained only leaf material and no seeds. Seventeen known species of seeds were collected from spider monkey dung, 14 from the dung of cebus monkeys, and 12 from howling monkey dung. Seeds from 10 plant species where jointly found in the dung samples of two of the monkeys and seeds of six plant species occurred in dung collected from all three of the primates. The sizes of the seeds ranged from <1 mm (*Muntingia calabura*) to 25 mm in length (*Sterculia apetala*).

For all three primate species there was a negative relationship between the size of the seed and the frequency of occurrence of that seed species in droppings (spider $r = -0.404$, $P = 0.031$; howlers $r = -0.439$, $P = 0.020$; cebus $r = -0.492$, $P = 0.010$). Also, the frequency of

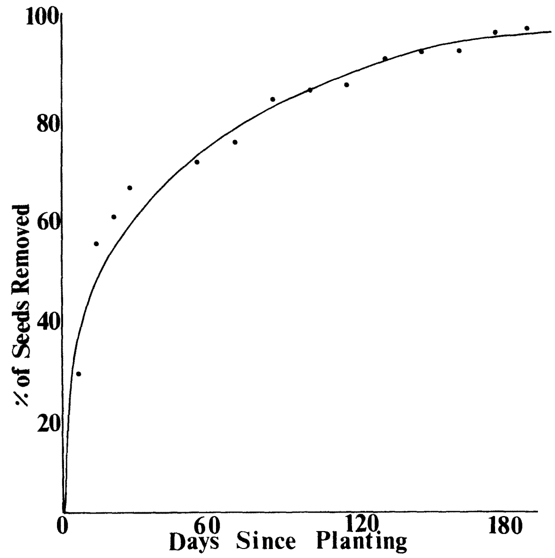

FIGURE 1. The percentage of seeds removed or killed at artifical dung piles at different times after planting in Santa Rosa National Park, Costa Rica.

occurrence of seeds in the dung was related to the length of time a plant species fruited (spiders $r = 0.867$, $P < 0.001$; howlers $r = 0.497$, $P = 0.009$; cebus $r = 0.686$, $P < 0.001$). There was no relationship between the density of adult plants and the frequency of occurrence of their seeds in primate dung (spider $r = -0.227$, $P = 0.190$; howlers $r = 0.028$, $P = 0.458$; cebus $r = -0.322$, $P = 0.104$).

The seed traps were sampled on 84 days, and there were 35 occurrences of feces on the traps. Since the trap area and the number of droppings that fell on the traps were known, it was possible to calculate that 19.8 droppings fell to the ground per hectare of forest over the 84-day period. Thus, 322 large seeds (excluding small seeds such as *Ficus* spp. and *Muntingia calabura*) passed through the stomachs of primates and fell on a hectare of forest floor per week, and a per-species basis, the number of large seeds being dispersed ranged from 32 seeds/ha/fruiting week for *Casearia arguta,* to 0.5 seed/ha/fruiting week for both *Spondias* spp. and *Bursera simaruba* (Table 1). In 1984, 22.6 droppings fell per hectare, while 1985, 17.0 droppings fell per hectare.

The spatial distribution of the traps on which monkey dung fell was very clumped. The distribution was quantitatively represented using the "Coefficient of Dispersion" (*CD,* see Sokal & Rohlf 1981 for its derivation). In 1984 the *CD* of traps receiving dung was 6.06, whereas in 1985 it was 2.59. There was great variability between plant species in the spatial distribution of the seeds falling in monkey dung (Table 1). I believe that the dung-fall pattern was probably more clumped than is represented by these values, since traps were not placed under any of the trees regularly used as sleeping sites. Under sleeping trees it was common to find large numbers of droppings in a very small area (2 m^2).

GERMINATION EXPERIMENTS.—Seeds from 26 species of plants collected from monkey dung were used in the germination experiments. Of these, 60 percent germinated in at least one of the three methods (Table 1). The three different methods used to germinate seeds differed significantly in their germination rates ($\chi^2 = 6.44$, df = 2, $P < 0.05$). This suggests that these germination experiments

TABLE 2. *A description of the initial fate of seeds placed in artificial dung piles in Santa Rosa National Park, Costa Rica.*

Plant species	No. of stations	No. of germinations	No. of seedlings	Percent remaining, day 7	Percent remaining, day 21
Agonandra macrocarpa	2	0	0	100	60
Ardisia revoluta	1	0	0	10	0
Brosimum alicastrum	2	0	0	30	0
Bursera simaruba	1	0	0	100	10
Cupanea guatemalensis	1	0	0	100	0
Dipterodendron costaricensis	2	0	0	25	0
Eugenia sp.	1	2	0	90	90
Genipa americana	1	0	0	0	0
Hirtella racemosa	2	0	0	10	0
Manilkara chicle	1	0	0	0	0
Mastichodendron capiri	4	0	0	31	2
Ocotea veraguensis	12	0	0	22	4
Simaruba glauca	5	2	1	38	59
Spondias sp.	18	0	0	65	20
Swartzia cubensis	5	1	0	6	6

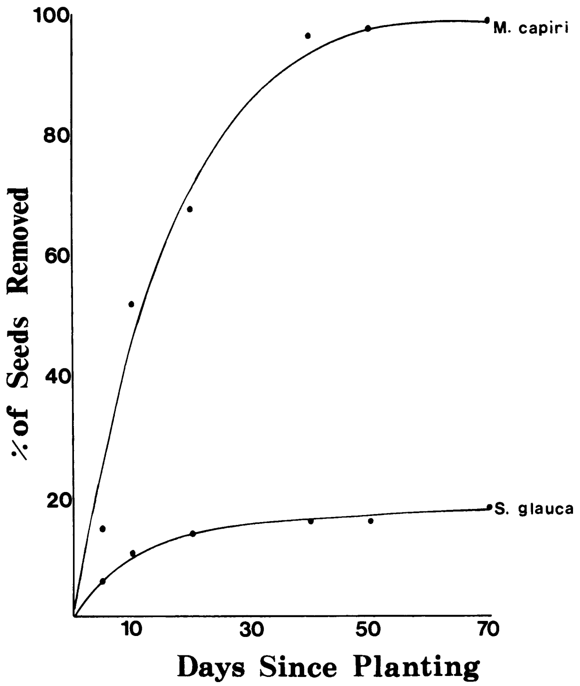

FIGURE 2. The rate of seed removal or death of *Simaruba glauca* and *Mastichodendron capiri* seeds from artifical monkey dung piles in Santa Rosa National Park, Costa Rica.

only allow one to state if germination is possible after passage through the stomach of a primate. Many dry forest trees have seeds that are capable of prolonged dormancy (Garwood 1983). Since the germination experiments were not continued between field seasons, seeds which were capable of long dormancy would have been considered incapable of germination, when in fact, they may have been viable.

DUNG PILE EXPERIMENTS.—Seeds in the experimental dung piles were rapidly removed or killed. Within 5 days of placing seeds in the forest, 51.8 percent of the seeds had either been removed or killed; 21 days after planting, 77.2 percent of the seeds had been removed or killed; and the end of the study, 97.9 percent of the seeds had been removed or killed (Fig. 1). There was a large amount of variation in removal rates depending on the species of seed at the station (Table 2). After 21 days, the removal rate varied from 100 percent (for 47% of the species examined) to 10 percent for *Eugenia* sp.. Spiny pocket mice (*Liomys salvini*) were probably responsible for the removal of the majority of the seeds (Janzen 1982). This conclusion was based on the fact that seed fragments left at the sites often had teeth marks which were characteristic of mice. Peccaries (*Tayassu tajacu*), agoutis (*Dasyprocta punctata*), and dung beetles were also seen at experimental stations.

Three different experimental treatments were used to examine factors effecting the rate of seed removal and/or the probability of germination and seedling establishment. These were the effect of the number of seeds in a dung pile, the presence or absence of fecal material, and the effect of forest type.

To examine whether or not the number of seeds placed in a dung pile influenced the proportion of the seeds removed or killed, dung piles containing between one and twenty seeds were constructed. For five species, I had sufficient seeds which had passed through monkeys to set up six stations. Twenty days after the seeds had been placed out on the forest floor, for all species except *Spondias mombin,* there was no evidence of a positive relationship between the number of seeds in the dung pile and the percentage of seeds removed or killed (Spearman Rank Correlations, *Spondias mombin* $rs = 0.533$, $P = 0.049$; *Simaruba glauca* $rs = -0.229$, $P = 0.355$; *Swartzia cubensis* $rs = -0.395$ $P = 0.255$; *Ocotea verguensis* $rs = 0.470$, $P = 0.091$; *Mastichodendron capiri* $rs = -0.274$, $P = 0.750$). This analysis was performed for *Spondias mombin* at 5, 10, 20, 60, and 90 days post-planting. By 90 days the relationship was not significant ($P = 0.217$), and at this time none of the remaining seeds had germinated.

To examine if odorous fecal material acted as an attractant to secondary dispersers or seed predators, 22 stations were established with the seeds mixed in dung, and 22 stations were set up with only seeds. A variety of species were used for comparisons, however equal numbers of each species were used with and without dung. After five days, the number of seeds removed or killed from stations without dung was 21 percent less than that from stations with dung. By three weeks, the difference had decreased to 8.0 percent. By the end of the study (approximately 17 months post-planting), the difference in the number of seeds removed from stations with and without dung was 0.06 percent.

Over a short period of time (<20 days) the rate of seed removal was higher by 22 percent at the semi-evergreen forest sites than at the dry deciduous forest locations. However, 40 days after planting there was little difference in the rate of removal between forest types.

In all of the experiments mentioned, 793 seeds from species which had been shown capable of germination after passage through the monkeys were placed out in the forest. Of these, only 11 seeds remained at the locations in which they were placed and germinated (4 *Simaruba glauca,* 4 *Mastichodendron capiri,* 2 *Eugenia* sp., 1 *Swartzia cubensis*). Only one of these 11 seeds became established and grew to a height of greater than 5 cm. No seeds were surviving when the study ended.

Initial results suggested that some seeds were being killed or removed rapidly from the experimental dung piles, whereas others were remaining in the same location for long periods. To further examine differential seed treatment by secondary dispersers and seed predators, two species were chosen to be used in further experimentation: *Mastichodendron capiri* (initial results suggested fast removal) and *Simaruba glauca* (initial results suggested slow removal). At every time period the proportion of *M. capiri* seeds that had been eaten or removed was higher than the proportion of *S. glauca* seeds eaten or removed (Fig. 2). In fact, at the end of the study, 70 days after planting, the *M. capiri* seeds had a 5.5 times greater probability of being removed or killed than the *S. glauca* seeds.

DISCUSSION

Primates constitute a major component of the frugivore biomass (Terborgh 1983), and they consume a large number of seeds with the fruits they eat, seeds that after defecation often remain viable. However, the experiments conducted here indicate that the majority of the seeds dispersed by the primates and deposited on the forest floor in their dung, are either killed by seed predators or moved by secondary dispersers.

The experiments conducted with *Simaruba glauca* and *Mastichodendron capiri* suggest that different plant species may adopt different strategies to cope with the pressures exerted by seed predators and/or secondary dispersers. *Simaruba glauca* produces a fruit that is readily eaten by primates, and once the seeds are defecated, they will likely remain in the location at which they fell. By contrast, *M. capiri* similarly produces a fruit that is readily eaten by primates, however once their seeds are defecated and fall to the forest floor they are likely to be moved by secondary dispersers or killed by seed predators. If the seeds from *M. capiri* are killed by seed predators when removed from monkey dung, the quality of the dispersal of *S. glauca* seeds by primates is likely to be relatively higher than that for *M. capiri* seeds. However, if the *M. capiri* seeds removed from the monkey's dung are secondarily dispersed, the quality of their dispersal is likely to be similar to that for *S. glauca*. These observations suggest that future investigations in the area of primate seed dispersal would benefit from the evaluation of the seed predators and secondary dispersers that are removing and killing the seed found in monkey dung.

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LITERATURE CITED

CANT, J. G. H. 1979. Dispersal of *Stemmadenia donnell-smithii* by birds and monkeys. Biotrop. (sup) 11: 122.

EISENBERG, J. F., AND R. W. THORINGTON. 1973. A preliminary analysis of a neotropical mammal fauna. Biotrop. 5: 150–161.

———, M. A. O'CONNELL, AND P. V. AUGUST. 1979. Density, productivity, and distribution of mammals in two Venezuelan habitats. *In* J. F. Eisenberg (Ed.). Vertebrate ecology in the Northern Neotropics, pp. 187–207. Smithsonian Inst. Press, Washington.

ESTRADA, A., AND R. COATES-ESTRADA. 1984. Fruit eating and seed dispersal by howling monkeys (*Alouatta palliata*) in the tropical rain forest of Los Tuxtlas, Mexico. Amer. J. Primatol. 6: 77–91.

———, AND ———. 1986. Frugivory by howling monkeys at Los Tuxtlas, Mexico: dispersal and fate of seeds. *In* A. Estrada and T. H. Fleming (Eds.). Frugivores and seed dispersal. pp. 93–104 Junk Publishers, Dordrecht.

FLEMING, T. H. 1982. Foraging strategies of plant-visiting bats. *In* T. H. Kunz (Ed.). Ecology of bats, pp. 287–325. Plenum Press, New York.

———, AND E. R. HEITHAUS. 1981. Frugivorous bats, seeds and the structure of the tropical forest. Biotrop. (sup) 13: 45–53.

GARWOOD, N. C. 1983. Seed germination in a seasonal tropical forest in Panama: a community study. Ecol. Monogr. 53: 159–181.

HEITHAUS, E. R. 1982. Coevolution between bats and plants. *In* T. H. Kunz (Ed.). Ecology of bats, pp. 327–367. Plenum Press, New York.

HERRERA, C. M. 1982. Seasonal variation in the quality of fruits and diffuse coevolution between plants and avian dispersers. Ecology 63: 773–785.

———. 1984. A study of avian frugivores, bird-dispersed plants, and their interaction in Mediterranean scrublands. Ecol. Monogr. 54: 1–23.

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

Hladik, A., and C. M. Hladik. 1969. Raports trophiques entre végétation et primates don la forêt de Barro Colorado (Panama). Terre Vie 116: 25–117.
Janzen, D. H. 1982. Removal of seeds from horse dung by tropical rodents: influence of habitat and amount of dung. Ecology 63: 1887–1900.
———. 1983. Dispersal of seeds by vertebrate guts. *In* D. J. Futuyma and M. Slatkin (Eds.). Coevolution, pp. 232–262. Sinauer Associates, Inc. Sunderland.
———. 1986a. Mice, big mammals, and seeds: it matters who defecated what where. *In* A. Estrada and T. H. Fleming (Eds.). Frugivores and seed dispersal, pp. 251–271. Junk Publishers, Dordrecht.
———. 1986b. Guanacaste National park: tropical ecological and cultural restoration. Editorial Universidad Estatal A Distancia, San Jose, Costa Rica.
McDiarmid, R. W., R. E. Ricklefs, and M. S. Foster. 1977. Dispersal of *Stemmadenia donnell-smithii* (Apocynaceae) by birds. Biotrop. 9: 9–25.
Snow, D. W. 1965. A possible selective factor in the evolution of fruiting seasons in tropical forest. Oikos 15: 274–281.
———. 1971. Evolutionary aspects of fruit-eating by birds. Ibis 113: 194–202.
Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman and Co., San Francisco.
Terborgh, J. 1983. Five new world primates: a study of comparative ecology. Princeton University Press, Princeton.

Announcement: Ecology Institute Prize in Marine Ecology

The Ecology Institute (ECI) is calling for nominations for the Ecology Institute Prize. Every year a jury composed of ECI members selects (in a rotating pattern) prize winners among marine, terrestrial or limnetic ecologists. In 1989, prize winners will be selected in the field of marine ecology.

The ECI is a non-profit, international organization with a staff of 36 ecologists—marine, terrestrial and limnetic—all of high international reputation. ECI strives to (1) further the exchange of information between marine, terrestrial and limnetic ecology; (2) provide balance between analyzing and synthesizing research; (3) draw attention to important issues resulting from ecological research; (4) assist in finding a long-term compromise between the increasingly destructive potential of modern industrial societies and the need for defining and applying measures to protect nature.

The Ecology Institute Prize is endowed with a stipend of US $5000. Taking into account the aims of ECI, as well as his or her own field of interest, the winner of the Ecology Institute Prize is requested to author a 200 to 300 printed-page book, to be published by ECI in the series "Excellence in Ecology" and to be made available worldwide at cost price. In addition to reviewing a certain field of knowledge, the book gives the authors a chance to express their personal views on important ecological issues.

Nominations are welcome from all research ecologists. They should reach the Chairperson of the ECI Jury before July 31, 1989. Eligible are all ecologists engaged in scientific research. The Jury will select the Prize Winner using the nominations received, as well as their own knowledge, and their professional judgement.

Tom Fenchel (Chairman of ECI Jury)

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