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Feeding assemblages of mammals at fruiting *Dipteryx panamensis* (Papilionaceae) trees in Panama: seed predation, dispersal, and parasitism

by

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Abstract: Fruiting almendro trees, *Dipteryx panamensis,* are visited by sixteen species of mammals that eat the fruit's exocarp or seed. Seeds are susceptible to predation by granivorous rodents and peccaries. Most mammals that visit *Dipteryx* trees act as commensals, eating only the fleshy exocarp and dropping the endocarp with its enclosed seed below the parent tree. Some primates, tayras, coatis, and kinkajous occasionally disperse *Dipteryx* seeds, but only *Artibeus lituratus, Dasyprocta punctata,* and *Sciurus granatensis* disperse large numbers of seeds. Whether *D. punctata* or *S. granatensis* act as seed predators or dispersal agents depends on the behavioral context in which they handle fruits.

Plant species in tropical latitudes often produce fruits that are eaten by numerous animal species. Multi-species feeding assemblages of tropical birds or bats at fruiting trees are commonplace (Eisenman, 1961; Diamond and Terborgh, 1967; Olson and Blum, 1968; Diamond, 1973; Cruz, 1974; Howe and Primack, 1975; Downhower and Racine, 1976; and Howe, 1977 for birds; Heithaus *et al.,* 1974, Fleming *et al.,* 1977; and Bonaccorso, 1979). One advantage of having seeds dispersed by many types of animals is that dispersal agents of differing habits disperse seeds to more types of germination sites than would a single agent (Howe and Primack, 1975). Further, the plant is not dependent upon one dispersal agent that may become uncommon, become extinct, or switch food habits.

The attraction of seed dispersal agents by fruiting plants is only part of an evolved reproductive system. These same plants are under selective pressures to repel or avoid "seed predators and parasites" (Janzen, 1969). Plants may utilize toxins, urticating bristles, spines, hard exocarps or endocarps, limited seasonal fruiting, and concealment coloration to combat seed predators and parasites. If animal agents are required for seed dispersal of plants having strong defense adaptations, the dispersal agents must have counter-adaptations to overcome the

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defense. For example, a rodent's incisor teeth can counter a strong woody endocarp, and it may then eat or disperse some seeds.

This paper reports sixteen species of six mammalian orders that visit the leguminous tree, *Dipteryx panamensis,* during its fruiting. All eat the exocarp or the seeds of *Dipteryx* fruits. The interactions between each mammalian species and *Dipteryx* are identified as seed dispersal, commensalism, seed predation, and seed parasitism.

MATERIAL AND METHODS

Field observations were conducted on Barro Colorado Island (BCI), Panama Canal Zone (9° 10' N and 79° 51' W). BCI is covered with forest ranging from 60–400 years in age (Knight, 1975). This lowland area is Tropical Moist Forest of the Holdridge Life Zone system (Holdridge, 1967). A dry season occurs from late December through March. A detailed account of the climatic and biotic environment of the island may be found in Rubinoff (1974).

Field observations of mammals eating mature almendro fruits took place during January, February, and December 1973; in January, February, November, and December, 1977; and January, March and April, 1978. Diurnal mammals were observed from the ground with 7 X 35 or 8 X 40 binoculars. Fruits discarded by mammals were collected under or near the crown cover of mature *D. panamensis* trees to appraise seed damage. In many cases the species that handled a particular fruit could be determined by impressions of claws, teeth, and jaw gapes left in the fruits, or by the way the fruits were damaged (Fig. 1). Additional information on bats was provided by mist-netting and examination of the fecal matter from captives held temporarily in individual cloth bags.

PHENOLOGY AND REPRODUCTIVE CHARACTERISTICS

Dipteryx panamensis (= *Oleiocarpon panamensis* = *Coumarouna oleifera*), Papilionaceae, is a canopy tree that attains heights of 25–40 m (Holdridge, 1970). The species occurs commonly in mid-successional communities of lowland Tropical Moist and Tropical Wet Forests from Costa Rica to Colombia. On BCI flowering occurs from May to July. Immature fruits may appear in the first week of July on some trees (Smythe, 1974, and this study), and mature fruits may be on the trees from November through March (Kaufmann, 1962). In 1973 mature fruits were available from the beginning of the year through mid-March, and again in mid-December (Bonaccorso, 1979). Mature fruits were abundant in mid-December, 1976 (L. Heaney, pers. comm.), and this high level of availability continued into early February, 1977, with scattered trees producing fruits until late February. In the following season, mammals were observed feeding on mature fruits from 14 December 1977 through 4 April 1978; fruit abundance was very high from early December to mid-March.

Chapman (1938) stated that almendro trees usually fruit every year, but individuals tend to alternate between years of good and poor fruit production. Of thirteen *Dipteryx* trees that produced abundant fruit in January-February 1977, five showed markedly reduced fruit production in the following season, and three others did not fruit at all.

The almendro fruit is an elliptical drupe, 5–6 cm long by 2–3 cm wide (Fig. 1). Fresh fruit wet weights vary from 18.0 to 26.3 g. The endocarp is formed by a 4 mm thick, hard, woody shell enclosing the single large seed. A 0.5 – 0.6 cm thick pulp similar to that of a fresh almond fruit forms the outer covering or exocarp. The embryo lies to one extreme end of the long cylindrical seed. The fruit remains green in color at maturity. A large almendro tree produces a crop of fruits that may number in the tens of thousands.

MAMMALIAN CONSUMERS

Sixteen species of mammals that eat the exocarp or seeds of *D. panamensis* are listed in Table 1. We attribute the status of "dispersal agent" to a species only if it regularly transports intact seeds beyond the parental tree's crown. "Commensals" do not damage the seeds but usually do not transport the seeds beyond the crown of the parental tree. "Seed predators" damage seeds to the extent that they cannot germinate; whereas "seed parasites" partially destroy the seeds but not to the extent that they cannot germinate.

Marsupialia: The opossum, *Didelphis marsupialis,* was twice observed under fruiting *Dipteryx* trees during censuses of nocturnal mammals in January 1977. No feeding behavior was observed on these occasions, but *Didelphis* captured in traps baited with *Dipteryx* usually chewed on these fruits. This marsupial evidently does not carry food long distances and is probably not an important disperser of *Dipteryx* fruits.

Chiroptera: At least four species of phyllostomatid bats feed on *D. panamensis* fruits. *Carollia castanea, Ç. perspicillata, Artibeus jamaicensis,* and *A. lituratus* eat only the exocarp. *A. lituratus* was the only bat that regularly carried whole fruits away from *Dipteryx* trees. We netted several of these large fruit bats (mean body weight = 69.2 g); almendro fruits they were carrying in flight dropped beside them in the net. These fruits were sometimes partially eaten. *A. lituratus* removes individual fruits from trees, carries the fruit in flight, and eats the fruit at feeding roosts that may be several hundred meters distant. Individuals or small groups of bats use a given feeding roost for one or a few nights before switching to another roost (Morrison, 1980). This behavior probably reduces crowding and aggressive interactions between bats at fruiting trees and reduces exposure to owls, opossums,kinkajous, snakes and other predators that prowl at fruiting bat-attracting trees (Humphrey and Bonaccorso, 1979).

Neotropical fruit bats typically carry whole fruits from fruiting trees to feeding roosts that may be hundreds of meters away (Goodwin and Greenhall 1961, Morrison, 1979). However, *C. castanea, C. perspicillata,* and *A. jamaicensis* eat almendro fruits only within the fruiting tree, since these fruits are too large to be carried efficiently in flight by these small bats (though large individuals of *A. jamaicensis* may be able to carry very small almendro fruits). After eating the exocarp, the *Dipteryx* endocarp is dropped below the parental tree crown. We have stood under *Dipteryx* trees at night that were "raining" fruits dropped by feeding bats. Though we could not identify bat species in fruiting trees, *Dipteryx* pulp was identified in the feces of the above bat species. It is likely that other species of fruit bats on BCI also eat *Dipteryx* fruits.

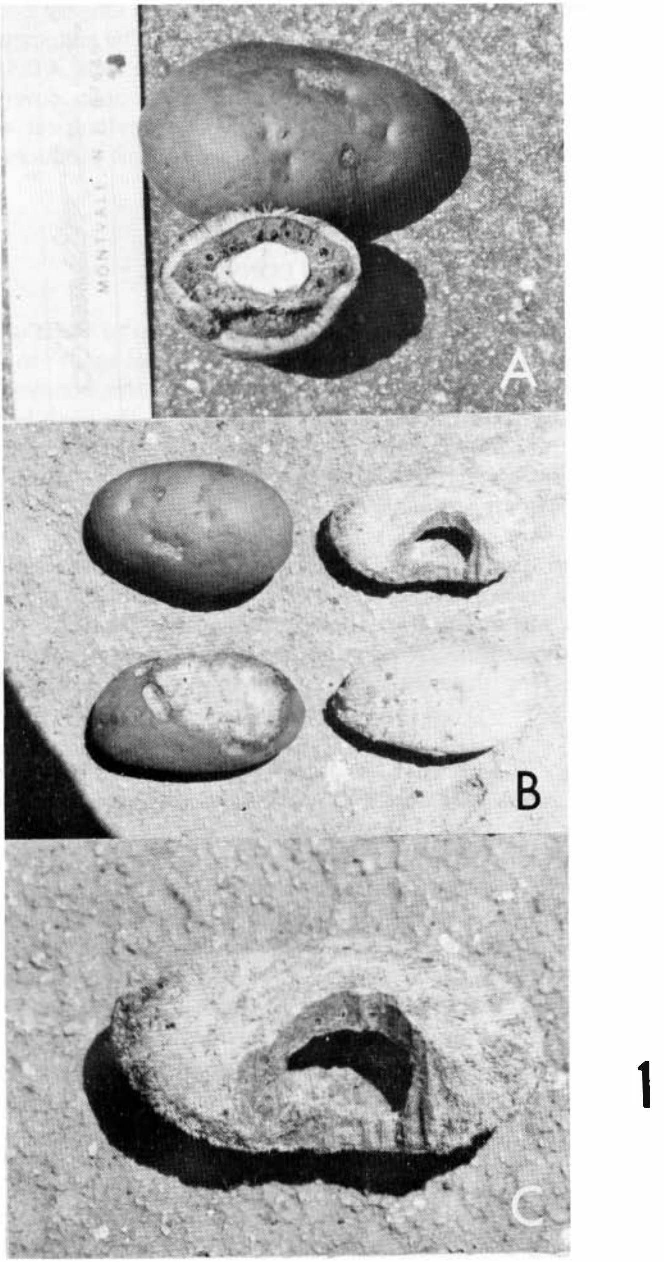

Fig.1. A. Cross section through a *D. panamensis* fruit showing seed cotyledon (inner white layer), woody endocarp (center dark layer), and fleshy exocarp (outermost layer). B. Effects of animals on fruits: top left, undamaged fruit; top right, endocarp with seed damage by *Sciurus;* bottom right, endocarp discarded by *Alouatta;* bottom left, fruit with exocarp partially eaten by *Artibeus*. C. Closeup of endocarp with cotyledon removed by *Sciurus*.

TABLE 1

Relationships between mammals and Dipteryx panamenis. *An asterisk (*) indicates a major influence, a cross (+) a minor influence*

	Fruit part eaten:		Relationship:			
Species name	Exocarp	Seed	Commensal	Dispersal	Parasite	Predator
Diadelphis marsupialis	X		*			
Carollia castanea	X		*			
Carollia perspicillata	X		*			
Artibeus jamaicensis	X		*	+(?)		
Artibeus lituratus	X			*		
Ateles geoffroyi	X		*	+		
Alouatta palliata	X		*	+		
Cebus capucinus	X		*	+		
Sciurus granatensis		X		*	*	*
Proechimys semispinosus		X		*	*	
Agouti paca	X		*			
Dasyprocta punctata	X	X		*		*
Nasua narica	X		*	+		
Potus flavus	X		*	+		
Eira barbara	X		*	+		
Tayassu tajacu		X				*

Primates: Three species of primates, *Ateles geoffroyi* (red spider monkey), *Alouatta palliata* (black howler monkey), and *Cebus capucinus* (white-face monkey), feed on the exocarp of *Dipteryx* fruits (Hladik *et al.*, 1971). The exocarp is scraped off the fruit with the teeth and the endocarp is discarded undamaged. All of the above primates act largely as commensals but occasionally disperse almendro seeds beyond the parent tree. While a troop or individual is feeding within a tree most of the endocarps are discarded directly below. Some seeds may fall up to a few meters beyond the parental crown when dropped by monkeys at the edge of the crown. When a troop moves out of an almendro tree individuals may carry fruits by hand or mouth. Spider monkeys were observed to carry *Dipteryx* fruits approximately 60 meters from the parent tree on two occasions.

Rodentia: *Sciurus granatensis* (Neotropical red-tailed squirrel), *Dasyprocta punctata* (agouti), *Agouti paca* (paca), and *Proechimys semispinosus* (spiny rat) eat the seeds of *D. panamensis.* Each may act at times as seed parasites, seed predators, or dispersal agents. Most of our field time was spent watching red-tailed squirrels and we will discuss this species at length.

Almendro fruits were the preferred food item in the diet of *Sciurus* when seasonally available (Heaney and Thorington, 1978). More than 70% of the *Sciurus* feeding sessions observed in January 1977 involved *Dipteryx* fruits. In the following season *Dipteryx* comprised more than 50% of all feeding observations from early December 1977 until mid-March, 1978, reaching 78% in late January, 1978. Squirrels frequently formed large feeding aggregations at fruit-bearing trees. One to four squirrels were seen foraging at each of the five trees checked regularly in 1973. From zero to six were seen at each of five trees censused regularly in January 1977, while from zero to ten were seen at each of eleven such trees in December-January, 1977-78. Squirrel foraging usually began shortly after 0630 (sunrise) and continued through the morning until approximately 1100 hr, with the greatest foraging activity occurring between 0730 and 0930. They were generally inactive in the late morning and early afternoon, but frequently a second, less distinct, foraging period occurred in the late afternoon, from 1530 until 1730. Squirrels generally forage for almendros on the ground in the early morning (0630–0800). Mature fruits remain firmly attached to the tree and nearly all fruits available on the ground are discarded by aerial or arboreal mammals that eat the exocarp. Only after they have eaten most of the fallen fruits do squirrels climb to the canopy to pick fruits off trees.

Squirrels on BCI ate the seeds of the almendro fruit but not the exocarp. To expose the seed, a considerable amount of time was required in scraping off the exocarp (if it was present) and gnawing through the woody endocarp. The time spent handling individual fruits varied considerably (from 4 to 26 minutes), apparently in response to the size and maturity of the fruit, the age and experience of the squirrel, and the amount of seed eaten. Mean handling times for individual fruits by mature squirrels were 8.0 min in January-February, 1973 (S.D. = 2.1, N=6); 10.7 min in December-January, 1976–77 (S.D. = 3.2, N=15, including 7 observations by L. Heaney, pers. comm.); and 7.8 min in December-January, 1977-78 (S.D.=3.2, N=31). One tree produced consistently small fruits (rarely more than 5 cm length) in December 1977; handling times at this tree were shorter (X=6.7 min, N=9) but not significantly different from those at other trees during the same season (t-test with unequal variances, $p > .10$). Handling times reported here began when the fruit was picked from the ground or tree and ended when the fruit was discarded and feeding stopped. No times were calculated if the animal ceased feeding behavior for more than 30 sec, or appeared disturbed by the observer's presence.

If the exocarp is intact, a significant fraction of the handling time is spent in scraping it from the fruit. Four feeding bouts involving whole fruits (exocarp undamaged) were observed in detail at close range. Initial scraping of the exocarp required an average of 1.0 min (S.D. = 0.4), and one squirrel spent an additional 25 sec at this task later in the bout.

The preference for almendro fruits lacking an exocarp appears to confer two advantages on *Sciurus*. First, fruits without exocarps reduce the time and energy budget devoted towards foraging. Second, by eating seeds on the ground first, squirrels minimize the number of seeds lost to competitors. Of the four mammal species that eat almendro seeds, only *Sciurus* is arboreal.

Agoutis, spiny rats, and peccaries are totally dependent on endocarps discarded by aerial or arboreal mammals that eat just the exocarp or only a portion of the seed. Squirrels frequently discard *Dipteryx* with a large part of the seed remaining. Agoutis evidently prefer such fruits, and consequently are attracted to trees where squirrels are feeding. During checks of fruiting *Dipteryx* trees in 1977 and 1978, one or more squirrels were observed at these trees on 125 occasions. Agoutis were present at trees with squirrels 52 of these times (42%), while they were seen at fruiting *Dipteryx* with no arboreal mammals present only 11 times. Each of the diurnal seed predators (squirrel, agouti, and peccary) is attracted to almendro trees where arboreal frugivores are feeding. Primates or coatis were observed in fruiting *Dipteryx* 16 times in 1977–78; on only one of these occasions were there no mammalian seed predators beneath the trees. Often several species were seen foraging on the ground together, with as many as seven squirrels and four agoutis under one spider monkey troop.

Few almendro endocarps dropped under the parental crown by nocturnal mammals remain undamaged by the end of the next morning. Of 96 fresh endocarps under two *D. panamensis* trees at 0900 hours on 9 February, 1973, 91.7% showed seed damage by squirrels (Table 2). Of those seeds that were damaged, however, 23.9% were judged capable of germination. Collections in 1977–78 show a similar pattern, but were collected later in the morning (after greater activity by squirrels and agoutis), and the embryos of most seeds were not examined. One tree (Snyder-Molino 3) suffered extremely heavy seed predation throughout its fruiting period. The other tree (Weir Trail) was very close to the laboratory clearing, and its terrestrial seed predators were frequently disturbed by humans. The final sample (22 March) was taken when squirrels and agoutis were beginning to use other fruits, particularly *Astrocaryum standleyanum.*

Many seeds severely damaged by squirrels are capable of germination because the plant embryo lies at the extreme end of the oblong endocarp. Squirrels usually gnaw at a perpendicular angle through the center point of the oblong axis of the endocarp (Fig. 1) and do not destroy the embryo. Cotyledon is extracted from the seed by scraping out bits with the upper or lower incisors. Some cotyledon remains at either end of the endocarp when it is discarded. We find that *Dipteryx* seedlings can germinate from seeds that have as much as 70% of the cotyledon scraped out of the middle of the endocarp. These seedlings appear healthy, but no data are available on comparative survivorship of seedlings germinating from damaged versus undamaged seeds.

Given the ability of damaged *Dipteryx* seeds to germinate, squirrels may act as dispersal agents if they transport the seeds beyond the parent. Heaney and Thorington (1978) report *S. granatensis* carrying nuts an average of 13.9 m from parent trees when scatter-caching food. Squirrels on BCI do not cache *Dipteryx* fruits but frequently do carry seeds a few meters beyond the parental crown. Once an almendro is taken from the ground, the squirrel carries it toward the nearest three which may be either the almendro or an adjacent tree. This behavior provides quick escape should a terrestrial predator appear, and incidentally insures that some seeds are dispersed.

The fruit may be opened and eaten on the ground beside a tree, or the squirrel may climb several meters up the tree before feeding. Several times we approached within the flight distance of feeding squirrels. They responded by quickly climbing high into the tree. Sometimes the fruit was dropped as they fled, but usually the fruit was carried in the mouth. Squirrels occasionally carried fruits well beyond the canopy of the parent tree. Four times squirrels were seen feeding on *Dipteryx* fruits between 60 and 100 m from the nearest fruiting tree. One of these individuals dropped its fruit as it climbed away from the observer, but that "dispersed" fruit had disappeared from the site 24 hours later.

The spiny rat, *Proechimys semispinosus,* is reported by Duke (1967) to feed on almendro fruits, but he did not state whether it eats the exocarp or the seed. We have seen *Proechimys* under *Dipteryx* trees at night but have not seen them feeding. *Proechimys* does eat the seeds of the palm *Astrocaryum standleyanum* (a drupe-type fruit with a woody endocarp similar to *Dipteryx*) by gnawing a hole in the endocarp much as *Sciurus* does with *Dipteryx* and *Astrocaryum.* We suspect that spiny rats probably feed on almendro fruits in a manner similar to squirrels. We score it as a probable seed parasite and occasional dispersal agent of *Dipteryx.*

The agouti gnaws squirrel-like holes in almendro endocarps. This large caviomorph rodent, with its long incisors, is able to extract nearly all the seed from the endocarp via the central hole. This species acts as seed predator of *Dipteryx,* however, it also appears to be an important agent of seed dispersal because it scatter-hoards *Dipteryx* fruits (Smythe, 1970 a & b). During the dry season agoutis eat the exocarp of fresh almendros and bury the endocarps for later use. On five occasions we observed agoutis carrying *Dipteryx* fruits in excess of 50 meters from the parent tree (at least two of these fruits were cached). Some scatter-hoards are not found again or are only partially consumed. It is likely that dispersal and germination of many *Dipteryx* seeds results.

The paca was reported by Duke (1967) to feed on *Dipteryx* fruits. We have observed pacas under fruiting *Dipteryx* trees at night, but did not observe them feeding on *Dipteryx.* Pacas typically feed on soft, fleshy fruits (Smythe, 1970b). These rodents probably eat only the exocarp of *Dipteryx* fruits fallen under parent trees, and thus we score it as a commensal of *Dipteryx.*

Carnivora: The coati, *Nasua narica,* the kinkajou, *Potos flavus,* and the tayra, *Eira barbara,* eat the exocarp of *D. panamensis* (Chapman, 1938; Kaufmann, 1962; Duke 1967; this study). Almendro fruits become a highly preferred food item of coatis when available. Coati bands and solitary males alter their daily movements from previous patterns to keep close to fruiting almendro trees (Kaufmann, 1962). Kinkajous were seen frequently in *Dipteryx* trees feeding at night. A tayra, *Eira barbara,* was seen chewing on a fallen fruit one morning in December 1977. Our observation disturbed this animal and no further notes on its feeding behavior were possible. Coatis, kinkajous, and tayras are commensals of *D. panamensis.* Occasionally they may act as seed dispersal agents when fruits are carried short distances away from a fruiting tree.

Artiodactyla: The collared peccary, *Tayassu tajacu,* is a seed predator of *Dipteryx* (Chapman, 1938; this study). The entire fruit is crushed with the molariform teeth and the seed is eaten.

DISCUSSION

Dipteryx panamensis, like many other plants dependent on animal-mediated seed dispersal, has two suites of adaptations for insuring dispersal and germination: characteristics that attract animals as potential dispersal agents, and characteristics that protect seeds from potential parasites or predators. Animal attracting features of fruiting almendro trees include: an attracting odor, edible exocarp, large fruit size, and large fruit crop. Defensive characteristics of the fruits are: a thick woody endocarp, a large seed that can supply the embryo with adequate nutrition to bring about germination when the seed is partially damaged, and an embryo located at one extreme end of the seed where small granivorous rodents usually do not attack.

Almendro fruits mature at the onset of the dry season. In Panama and Costa Rica this is the annual time when the fewest tree species present edible ripe fruits (Frankie *et al.,* 1974; Foster, 1973; Bonaccorso, 1979). The scarcity of fruiting species at the beginning of the dry season is probably a major factor contributing to the large number of mammalian species attracted to fruiting almendros. Howe (1977) finds a similar effect with 22 species of birds attracted to fruiting *Casearia corymbosa* trees in Costa Rica during the dry season.

TABLE 2

Fate of fresh fruits found under the crown canopy of four D. panamensis *trees. In 1973, samples were taken at 0900 hours, just as squirrels began to forage in the canopy. All fruits collected were dropped the previous night by nocturnal mammals. In 1977–78 samples were taken between 1030 and 1100 hrs, after extensive arboreal foraging by squirrels and terrestrial foraging by agoutis*

Date	Tree Location	Total Seeds	Uneaten Fruits	Exocarp Eaten, Endocarp Intact	Seed Damage by Rodents, Seed Capable of Germination	Seed Damage by Rodents, not Capable of Germination
9 February 1973	Armour 1	54	2	0	10	42
9 February 1973	Wheeler 6	42	0	6	11	25
Total 1973		96	2 (2.1 %)	6 (6.2 %)	21 (21.8 %)	67 (69.9 %)
13 December 1977	Snyder–Molino 3	40	0	1	5*	34 +
28 December 1977	Snyder–Molino 3	35	2	2	3*	28 +
3 January 1978	Snyder–Molino 3	52	0	0	3*	49 +
Total for tree		127	2 (1.6 %)	3 (2.4 %)	11 (8.7 %)	111 (87.4 %)
18 January 1978	Weir Trail	73	1	3	10*	54 +
22 March 1978	Weir Trail	92	4	17	9*	62 +
Total for tree		165	5 (3.0 %)	25 (15.2 %)	19 (11.5 %)	116 (70.3 %)

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* Embryo not examined; greater than 40% of seed remaining.

\+ Embryo not examined; less than 40 % of seed remaining.

Fruiting when few other trees offer competition for dispersal agents helps insure that *Dipteryx* will have many potential dispersal agents visiting it. This also makes *Dipteryx* more susceptible to attack from seed predators and parasites that are affected by the food scarcity of the dry season. However, the combined effectiveness of bats, rodents, and primates as dispersal agents and the defensive characters mentioned above provide some seeds with an escape from seed predators and parasites and a successful reproductive strategy.

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RESUMEN

En Panamá los frutos del árbol de almendro *Dipteryx panamensis* maduran al comenzar la temporada seca, época que coincide con la escasez de otros tipos de frutas comestibles. En la Isla de Barro Colorado hay 16 especies de mamíferos que se alimentan de estas frutas o de las semillas. Estos animales, por sus hábitos, pueden clasificarse en 4 categorías: parásitos, depredadores, agentes de dispersión y comensales del árbol de almendro. Los roedores y los pecaríes destruyen muchas semillas, sin embargo, el 60% de éstas germina siempre que el embrión esté intacto. Los murciélagos, los primates y algunos roedores, quienes comen solamente la fruta, son los principales agentes de dispersión.

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