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A REVIEW OF ANIMAL-MEDIATED SEED DISPERSAL OF PALMS

SCOTT ZONA

Rancho Santa Ana Botanic Garden, 1500 North College Avenue, Claremont, California 91711

ANDREW HENDERSON

New York Botanical Garden, Bronx, New York 10458

ABSTRACT. Zoochory is a common mode of dispersal in the Arecaceae (Palmae), although little is known about how dispersal has influenced the distributions of most palms. A survey of the literature reveals that many kinds of animals feed on palm fruits and disperse palm seeds. These animals include birds, bats, non-flying mammals, reptiles, insects, and fish. Many morphological features of palm infructescences and fruits (e.g., size, accessibility, bony endocarp) have an influence on the animals which exploit palms, although the nature of this influence is poorly understood. Both obligate and opportunistic frugivores are capable of dispersing seeds. There is little evidence for obligate plant–animal mutualisms in palm seed dispersal ecology.

In spite of a considerable body of literature on seed dispersal (Guppy, 1906; Ridley, 1930; van der Pijl, 1982), the specifics of zoochory (animal-mediated seed dispersal) in regard to the palm family have been largely ignored (Uhl & Dransfield, 1987). Only Beccari (1877) addressed palm seed dispersal specifically; he concluded that few animals eat palm fruits although the fruits appear adapted to seed dispersal by animals. Dransfield (1981b) has concluded that palms, in general, have a low dispersal ability, while Janzen and Martin (1982) have considered some palms to be "anachronisms," moribund species whose coevolved agents of dispersal are now extinct. Long-distance dispersal, a possible factor in the evolution of a large number of island endemics in this family, is thought by some to be unlikely in that many palms have fruits too large for biotic long-distance dispersal (Moore & Uhl, 1973; Dransfield, 1981b; but see Carlquist, 1974).

Because seed dispersal has been so little studied, we wish to draw attention to known cases of animal-mediated seed dispersal as well as to the need for further field studies. The likelihood of animal-mediated seed dispersal is high, given the importance of palm fruits as animal food and the number of animals which forage, hoard, and consume them (Corner, 1966; Leck, 1969; Snow, 1981; Roosmalen, 1985). However, many published accounts of seed dispersal inferred from dietary observations have been unspecific or incidental; very few field studies have addressed palm seed dispersal specifically. Palm distributions are well-known (Moore, 1973a, 1973b; Dransfield, 1981b), but the role of zoochory in shaping these distributions is not fully understood. To bring attention to these palm–animal interactions, an overview is presented here of the diverse assemblages of animals which feed on palm fruits along with a brief examination of the role fruit and/or infructescence morphology may play in dispersal and subsequent distributions.

METHODS

Data for fruit consumption and seed dispersal were taken from personal observations and the literature, much of it not primarily concerned with palm seed dispersal. The data are presented in TABLE 1. The dispersal of non-native palms is omitted, as is dispersal by man and abiotic means (e.g., water dispersal of *Nypa*). The systematic arrangement of palm genera follows Uhl and Dransfield (1987), and species are arranged alphabetically within each genus. The palm nomenclature agrees with Moore (1963, 1973b), Uhl and Dransfield (1987), and recent monographs (Read, 1975; Essig, 1978; Dransfield, 1981a; Moore & Uhl, 1984; Henderson, 1987). The animal nomenclature is less standardized. Where possible, bird nomenclature agrees with the American Ornithologists' Union (1983) checklist; otherwise, the original source is followed. The arrangement of animal names for each palm taxon is not intended to suggest the animals' relative importance as dispersers. The significance of palm fruit in an animal's diet, and hence the animal's significance as a disperser, could not be determined at this level of inquiry.

The taxonomic class of each animal is indicated within TABLE 1. In those instances in which the specific identity of the disperser(s) is not known, only the class has been indicated. In cases designated with a plus sign (+), the class indi-

TABLE 1. Dispersal agents of palms. The arrangement of palm genera follows Uhl and Dransfield (1987). Disperser classes are indicated as follows: A = Aves (birds); C = Mammalia, order Chiroptera (bats); I = Insecta (insects); M = Mammalia (mammals, excluding bats); P = Pisces (fish); and R = Reptilia (reptiles). A plus sign (+) following a class designation indicates that other unspecified animal dispersers are suspected.

Taxon	Dispersal agent (class)	Reference
Coryphoideae: Corypheae		
Thrinax	*Columba leucocephala* (A)	Read, 1975
T. morrisii H. A. Wendl.	*Amazona leucocephala bahamensis* (A)	Snyder et al., 1982
	Cyclura carinata (R)	Iverson, 1979
Coccothrinax	*Artibeus lituratus palmarum* (C)	Greenhall, 1957
C. alta (Cook) Becc.	*Columba leucocephala* (A)	Wiley & Wiley, 1979
C. jamaicensis Read	*Columba leucocephala* (A)	Galeano-Garcés, 1986
Rhapidophyllum hystrix (Pursh) H. A. Wendl. & Drude)	*Ursus americanus floridanus* (M)	Maehr & Brady, 1984
	(M)	Shuey & Wunderlin, 1977
Livistona	*Ptilinopus pulchellus, P. superbus, P. iozonus, Ducula spilorrhoa* (A)	Frith et al., 1976
	Pteropus (C)	Marshall, 1985
Pritchardia	*Ciridops anna* (A)	Amadon, 1950; but see Perkins, 1903
	(A)	Guppy, 1906
Acoelorrhaphe wrightii (Griseb. & H. A. Wendl.) H. A. Wendl. ex Becc.	*Columba leucocephala* (A)	Galeano-Garcés, 1986
Serenoa repens (Bartr.) Small	*Aphelocoma coerulescens* (A)	Woolfenden & Fitzpatrick, 1984
	Ursus americanus floridanus (M)	Maehr & Brady, 1984
Washingtonia filifera (Linden) Wendl.	*Canis latrans, Urocyon cinereoargenteus* (M), *Sialia mexicana, S. currucoides, Bombycilla cedrorum* (A)	Bullock, 1980
Corypha umbraculifera L.	*Pteropus edwardsii* (C)	Petch, 1924
C. utan Lamark	(C)	Docters van Leeuwen, 1935
	(A)	Docters van Leeuwen, 1936
Sabal	*Corvus ossifragus, Mimus polyglottos, Turdus migratorius, Dendroica coronata, Dryocopus pileatus, Melanerpes carolinus* (A), *Procyon lotor, Sciurus carolinensis* (M)	Martin et al., 1951
	Cyanocorax yncas (A)	Smith, 1910
S. causiarum (Cook) Becc.	*Columba leucocephala* (A)	Wiley & Wiley, 1979
S. etonia Swingle ex Nash	*Aphelocoma coerulescens* (A), *Ursus americanus floridanus* (M)	Zona, pers. obs.
S. palmetto (Walt.) Lodd. ex Schultes	*Mimus polyglottos, Quiscalus mexicanus, Aphelocoma coerulescens, Cyanocitta cristata, Agelaius phoeniceus, Cardinalis cardinalis, Larus delawarensis* (A)	Cruickshank, 1950
	Amazona leucocephala bahamensis (A)	Snyder et al., 1982
	Ursus americanus floridanus (M)	Maehr & Brady, 1984
	(M)	Brown, 1976
S. yapa Wright ex Becc.	*Crypturellus boucardi* (A)	Lancaster, 1964
Coryphoideae: Phoeniceae		
Phoenix	*Eidolon, Rousettus* (C)	Marshall, 1985
P. dactylifera L.	*Rousettus aegyptiacus* (C)	Ridley, 1930
	Lanius excubitor (A)	Parrott, 1980; but see Cowan, 1984
P. loureirii Kunth	*Elephas maximus* (M)	Krishnan, 1972
P. paludosa Roxburgh	(C)	van der Pijl, 1957
P. pusilla Gaertner	*Osmatreron bicincta* (A)	Ridley, 1930
P. reclinata Jacq.	*Loxodonta africana* (M)	Corner, 1966
	Hapalemur griseus occidentalis (M)	Petter et al., 1977
	(C)	Schonland, 1924

TABLE 1. Continued.

Taxon	Dispersal agent (class)	Reference
Coryphoideae: Borasseae		
Borassodendron borneense Dransf.	Probably: *Pongo pygmaeus* (M)	Dransfield in Moore, 1973a
Borassus	*Eidolon, Dolosonia, Pteropus* (C)	Marshall, 1985
B. aethiopum Mart.	*Loxodonta africana capensis* (M)	Burtt, 1929
	Papio anubis (M)	Lieberman et al., 1979
Hyphaene	*Loxodonta africana* (M)	Corner, 1966
H. thebaica (L.) Mart.	(C)	van der Pijl, 1957
H. petersiana Klotzsch ex Mart.	*Papio ursinus* (M)	Hamilton et al., 1978
Calamoideae: Calameae		
Laccosperma	*Mandrillus sphinx* (M)	Lahm, 1986
Eremospatha	*Cephalophus sylvicultor, C. callipygus* (M)	Dubost, 1984
E. wendlandiana Dammer ex Becc.	*Pan troglodytes troglodytes* (M)	Hladik, 1973
	Cephalophus sylvicultor (M)	Dubost, 1984
Eugeissona tristis Griff.	(M)	Wong, 1959
Korthalsia laciniosa (Griff.) Mart.	*Anthracoceros convexus* (A)	Rubeli in Dransfield, 1981a
Salacca	(M)	Ridley, 1930
	Probably: (R)	Beccari, 1877
Daemonorops melanochaetes Blume in Shultes	*Paradoxurus hermaphroditus javanicus* (M)	Bartels, 1964
Calamus	(M)	Ridley, 1930
	Paradoxurus hermaphroditus javanicus (M)	Bartels, 1964
	Hylobates syndactylus (M)	Chivers, 1974
	Ducula spilorrhoa (A)	Crome, 1975a
	Casuarius casuarius (A)	Crome, 1976
	Ptilinopus iozonus, P. magnificus, P. superbus (A)	Frith et al., 1976
	Argusianus argus (A)	Davison, 1981
C. australis Mart.	*Casuarius casuarius* (A)	Stocker & Irvine, 1983
C. deerratus Mann & H. A. Wendl.	*Pan troglodytes troglodytes* (M)	Hladik, 1973
	Mandrillus sphinx (M)	Lahm, 1986
C. moti F. Bailey	*Casuarius casuarius* (A)	Stocker & Irvine, 1983
C. radicalis H. A. Wendl. & Drude	*Casuarius casuarius* (A)	Stocker & Irvine, 1983
C. aff. *scipionum* Loureiro	*Hylobates lar* (M)	Ellefson, 1974
Plectocomia elongata Mart. ex Blume in Schultes	*Paradoxurus hermaphroditus javanicus* (M)	Bartels, 1964
Pigafetta filaris (Griseb.) Becc.	(A, M)	Dransfield, 1976
Raphia farinifera (Gaertner) Hylander	*Gypohierax angolensis* (A)	Austen, 1953
	(M)	Otedoh, 1979
R. hookeri Mann & Wendl.	*Xerus erythropus* (M), (A, C)	Profizi, 1985
	(M)	Otedoh, 1979
R. regalis Becc.	(A)	Otedoh, 1979
R. taedigera (Mart.) Mart.	*Tapirus bairdii* (M)	Janzen, 1983b
R. vinifera Beauv.	(M)	Otedoh, 1979
Calamoideae: Lepidocaryeae		
Mauritia flexuosa L. f.	*Daptrius ater* (A)	Haverschmidt, 1962
	Cebus albifrons (M)	Defler, 1979
	Tayassu tajacu, T. pecari (M)	Kiltie, 1981b
Ceroxyloideae: Ceroxyleae		
Ceroxylon klopstockia Mart.	*Aulacorhynchus sulcatus sulcatus* (A), (M)	Braun, 1976

TABLE 1. Continued.

Taxon	Dispersal agent (class)	Reference
Ceroxyloideae: Hyophorbeae		
Hyophorbe	*Pteropus* (C)	Marshall, 1985
Chamaedorea	*Chamaepetes unicolor, Aulacorhynchus prasinus* (A)	Wheelwright et al., 1984
	Heteromys (M+)	R. Dirzo, pers. comm.
C. lanceolata (Ruiz & Pavon) Kunth	(A, M)	Foster et al., 1986
C. tepejilote Liebm. in Mart.	*Agouti paca* (M)	Gallina in Coates-Estrada & Estrada, 1986
C. poeppigiana (Mart.) Gentry	*Steatornis caripensis* (A)	Snow, 1979
Arecoideae: Caryoteae		
Arenga	*Ptilinopus magnificus, P. aurantiifrons, Ducula spilorrhoa, D. zoeae* (A)	Frith et al., 1976
	Pteropus (C)	Marshall, 1985
A. listeri Becc.	*Ducula rosacea whartoni* (A)	Powell & Covacevich, 1983
A. obtusifolia Mart.	*Paradoxurus hermaphroditus javanicus* (M)	Bartels, 1964
	Hylobates klossii (M)	Whitten, 1980
A. pinnata (Wurmb) Merrill	(C)	Docters van Leeuwen, 1935
	Paradoxurus hermaphroditus javanicus (M)	Bartels, 1964
	Sus (M)	Miller, 1964
Caryota	*Paradoxurus hermaphroditus, Viverra malaccensis* (M)	Dransfield, 1974
	Ducula zoeae, Ptilinopus magnificus (A)	Frith et al., 1976
C. cumingii Lodd. ex Mart.	*Viverra malaccensis* (M)	Ridley, 1930
C. mitis Loureiro	*Paradoxurus hermaphroditus javanicus* (M)	Bartels, 1964
C. no Becc.	*Anthracocerus coronatus convexus* (A)	Dransfield, 1974
C. rumphiana Mart.	(C)	Docters van Leeuwen, 1935
	Paradoxurus hermaphroditus javanicus (M)	Bartels, 1964
C. urens L.	*Canis aureus* (M)	Ridley, 1930
Arecoideae: Iriarteeae		
Iriartea ventricosa Mart.	*Ateles belzebuth* (M)	Klein & Klein, 1975
	Tayassu pecari (M)	Kiltie, 1981b
	(A, C, M)	Foster et al., 1986
	Cebus, Callicebus moloch, Ateles paniscus, Tayassu (M)	Terborgh, 1986
Socratea	*Steatornis caripensis* (A)	Snow, 1979
	Tayassu pecari, T. tajacu (M)	Kiltie, 1981b
	Ramphastos swainsonii (A)	Howe, 1983
S. exorrhiza (Mart.) H. A. Wendl.	*Ramphastos brevicarinatus* (A)	Van Tyne, 1929
	Artibeus jamaicensis (C)	Carvahlo, 1961
	Ateles geoffroyi (M)	Hladik & Hladik, 1969
	Heteromys desmarestianus (M)	Fleming, 1974
	Crax (A)	Gottsberger, 1978
	Cebus apella (M)	Izawa, 1979
	Alouatta palliata (M)	Milton, 1980
	Cebus capucinus (M)	Oppenheimer, 1982
	(A, M)	Foster et al., 1986
	Cebus capucinus, Ateles geoffroyi, Proechimys semispinosa (M)	Hogan, 1986
Wettinia maynensis Spruce	*Saguinus* (M)	R. Ulloa, pers. comm.

TABLE 1. Continued.

Taxon	Dispersal agent (class)	Reference
Arecoideae: Areceae		
Orania aruensis Becc.	*Casuarius* (A)	Beccari, 1877
Reinhardtia gracilis (Wendl.) Drude ex Dammer	*Heteromys* (M+)	R. Dirzo, pers. comm.
Dypsis	*Hapalemur simus* (M)	Petter et al., 1977
Euterpe	*Cotinga ridgwayi* (A)	Skutch, 1969
	Perissocephalus tricolor (A)	Snow, 1972
	Steatornis caripensis (A)	Snow, 1979
	Ateles belzebuth (M)	Klein & Klein, 1975
	Colossoma bidens, Electrophorus electricus (P)	Goulding, 1980
	Cotinga cotinga, Phoenicircus carnifex, Rupicola rupicola (A)	Snow, 1982
E. edulis Mart.	*Ramphastos tucanus, R. ariel* (A+)	Edwards in Ridley, 1930
E. langloisii Burret	*Steatornis caripensis* (A)	Snow, 1962
E. precatoria Mart.	*Cebus apella* (M)	Izawa, 1979
Prestoea	*Steatornis caripensis* (A)	B. Tannenbaum, pers. comm.
P. montana (Graham) Nicholson	*Amazona vittata* (A)	Little & Wadsworth, 1964
	Margarops fuscatus (A)	Recher & Recher, 1970
	Columba squamosa, Geotrygon montana (A)	Janzen, 1972
Oenocarpus aff. *bacaba* Mart.	*Brycon* (P)	Goulding, 1980
	Gymnoderus foetidus (A)	Novaes, 1980
O. mapora Karst.	*Cebus apella* (M)	Izawa, 1979
	Sciurus granatensis (M)	Heaney & Thorington, 1978
	Cebus capucinus (M)	Oppenheimer, 1982
Jessenia	*Tayassu tajacu, T. pecari* (M)	Kiltie, 1981b
J. bataua Burret	*Steatornis caripensis* (A)	Snow, 1979
	Pithecia monachus (M)	R. Ulloa, pers. comm.
	Cebus albifrons (M)	Defler, 1979
	Cebus apella, Ateles belzebuth (M), *Ara macao, Ramphastos tucanus, Pipile cumanensis* (A)	Izawa, 1979
Hyospathe elegans Mart.	(A, M)	Foster et al., 1986
H. weberbaueri Dammer ex Burret	(A, M)	Foster et al., 1986
Roystonea borinqueana Cook	*Columba leucocephala* (A)	Wiley & Wiley, 1979
R. oleracea (Jacq.) Cook	*Artibeus lituratus palmarum* (C)	Greenhall, 1957
	Steatornis caripensis (A)	Snow, 1962
	Thraupis palmarum (A)	Snow & Snow, 1971
R. regia (Kunth) Cook	*Myiozetetes similis* (A)	Skutch, 1960
Archontophoenix	*Ptilinopus superbus, P. magnificus* (A)	Frith et al., 1976
A. alexandrae (Mueller) H. A. Wendl. & Drude	*Ducula spilorrhoa* (A)	Crome, 1975a
	Ptilinopus superbus (A)	Crome, 1975b
	Casuarius casuarius (A)	Crome, 1976
A. cunninghamiana (Wendl.) H. A. Wendl. & Drude	*Lopholaimus antarcticus* (A)	Frith, 1957
Chambeyronia macrocarpa (Brongn.) Vieill. ex Becc.	*Ducula goliath* (A)	MacKee et al., 1985
Actinokentia divaricata (Brongn.) Dammer	(A)	Pancher in Linden, 1881
Calyptrocalyx	*Casuarius bennetti pictocollis* (A)	Pratt, 1983
Linospadix	*Casuarius casuarius* (A)	Crome, 1976
L. microcarya (Domin) Burret	*Casuarius casuarius* (A)	Stocker & Irvine, 1983
L. monostachya (Mart.) Wendl.	*Ailuroedus crassirostris, Ptilonorhynchus violaceus* (A)	Donaghey, 1981
Veitchia	(A)	Guppy, 1906

TABLE 1. Continued.

Taxon	Dispersal agent (class)	Reference
Ptychosperma aff. *macarthurii* (Wendl. ex Veitch) H. A. Wendl. ex Hook. f.	(A)	Docters van Leeuwen, 1935
Nenga gajah Dransfield	(M)	Dransfield, 1975
Pinanga coronata (Blume ex Mart.) Blume	*Paradoxurus hermaphroditus javanicus* (M)	Bartels, 1964
Areca	*Casuarius bennetti pictocollis* (A)	Pratt, 1983
Iguanura wallichiana (Mart.) Benth. & Hook. ex Becc.	*Argusianus argus* (A)	Davison, 1981
Brongniartikentia vaginata (Brongn.) Becc.	*Cyanoramphus novaezelandiae* (A)	Létocart in MacKee et al., 1985
Clinostigma savoryanum (Rehder & Wilson) Moore & Fosberg	(A)	Ono & Sugawara, 1981
Burretiokentia vieillardii (Brongn. & Griseb.) Pichi-Ser.	*Ducula goliath* (A)	MacKee et al., 1985
Oncosperma horridum (Griff.) Scheffer	(A, M)	House, 1984
O. tigillarium (Jack) Ridley	*Gracula javanica, Turtur tigrinus* (A)	Ridley, 1930
	(C)	Docters van Leeuwen, 1935
	(A)	Docters van Leeuwen, 1936
Arecoideae: Cocoeae		
Butia leiospatha (Barb.-Rod.) Becc.	(I)	Silberbauer-Gottsberger, 1973
	Rhea americana (A), *Cerdocyon thous, Chrysocyon brachyurus* (M+), (C, I, R)	Gottsberger & Silberbauer-Gottsberger, 1983
Syagrus loefgrenii Glassm.	(A, M, R, C, I)	Gottsberger & Silberbauer-Gottsberger, 1983
S. orinocoensis (Spruce) Burret	*Cebus albifrons* (M)	Defler, 1979
Allagoptera arenaria (Gomes) Kuntze	(I)	Morawetz, 1983
Attalea	(C)	van der Pijl, 1957
	Cebus albifrons (M)	Defler, 1979
	Deroptyus accipitrinus (A)	McLoughlin & Burton, 1976
A. regia (Mart.) Boer	*Echimys armatus, Philander opossum, Didelphis marsupialis* (M)	Charles-Dominique et al., 1981
Scheelea	*Cebus, Saimiri sciureus, Sciurus* (M)	Terborgh, 1986
	(A, M)	Foster et al., 1986
S. attaleoides Karst.	*Cebus apella* (M)	Izawa, 1979
S. rostrata (Oerst.) Burr.	*Sciurus variegatoides, Agouti paca, Dasyprocta punctata, Proechimys semispinosa* (M)	Bradford & Smith, 1977
S. zonensis Bailey	*Nasua narica* (M)	Kaufmann, 1962
	Cebus capucinus (M)	Hladik & Hladik, 1969
	Agouti paca, Dasyprocta punctata, Proechimys semispinosa (M)	Bradford & Smith, 1977
	Sciurus granatensis (M)	Heaney & Thorington, 1978
	Sciurus gerrardi (M)	Hogan, 1986
Orbignya martiana Barb.-Rod.	*Agouti paca, Dasyprocta punctata* (M)	Anderson, 1983
Elaeis guineensis Jacq.	*Gypohierax angolensis* (A)	Thomson & Moreau, 1957
	Tockus fasciatus, Ceratogymna elata, C. atrata, Corvus albus, Merops albicollis, Falco ardosiaceus (A)	Brooke & Jeffery, 1972
	Tockus alboterminatus, T. flavirostris, Bycanistes sharpii (A)	Dean, 1973

TABLE 1. Continued.

Taxon	Dispersal agent (class)	Reference
	Ptilostomus afer (A)	Goodwin, 1976
	Galago alleni (M)	Molez, 1976
	Papio anubis (M)	Lieberman et al., 1979
	Cricetomys gambianus, Mastomys natalensis (M)	Iwuala et al., 1980
	Pan troglodytes (M)	Wrangham & Waterman, 1983
	Eidolon (C)	Marshall, 1985
Acrocomia	(C)	Leck, 1969
	Dasyprocta, Cerdocyon thous (M+), *Rhea americana, Tinamus solitarius* (A), (R)	Gottsberger & Silberbauer-Gottsberger, 1983
A. aculeata (Jacq.) Lodd. ex Mart.	*Didelphis albiventris, Nectomys squamipes, Cebus apella, Agouti paca, Euphractus sexcinctus, Dasyprocta* (M), *Turdus* (A)	Scariot, 1987
A. vinifera Oerst.	*Sigmodon hispidus* (M)	Baker, 1983
	Probably: *Liomys salvini* (M)	Janzen, 1983a
Aiphanes	*Steatornis caripensis* (A)	Snow, 1962
Bactris	*Artibeus jamaicensis triniatus, A. lituratus palmarum* (C)	Greenhall, 1957
	Steatornis caripensis (A)	Snow, 1962
	Cebus albifrons (M)	Defler, 1979
	Colossoma bidens, Piranha preta (P)	Goulding, 1980
B. cuesa Crueger ex Griseb. & H. A. Wendl.	*Steatornis caripensis* (A)	Snow, 1962
B. gasipaes Kunth	*Ramphocelus passerinii* (A)	Skutch, 1954
	Melanerpes chrysauchen (A)	Skutch, 1969
	(C)	van der Pijl, 1957
	Heteromys desmarestianus, Hoplomys gymnurus, Dasyprocta punctata (M+)	Vandermeer, 1983
Desmoncus	*Daptrius ater* (A)	Haverschmidt, 1962
	Steatornis caripensis (A)	Snow, 1962
	Cebus capucinus (M)	Hladik & Hladik, 1969
Astrocaryum	*Ramphastos tucanus* (A)	Bourne, 1975
	(C)	Bonaccorso, 1979
	Rupicola rupicola (A)	Snow, 1982
	Cebus, Tayassu, Sciurus, Agouti (M+), *Ara* (A)	Terborgh, 1986
A. chambira Burret	*Cebus apella* (M)	Izawa, 1979
A. jauari Mart.	(P)	Gottsberger, 1978
	Colossoma macropomum, C. bidens, Brycon, Phractocephalus hemelioterus, Megaladoras irwini, Piranha preta (P)	Goulding, 1980
	Brycon cf. *melonopterus, Myleus, Metynnis, Serrasalmus, Leptorinus, Paulicea lutkeni, Rhamidia schomburgkii, Lithodoras dorsalis, Megaladoras irwini, Oxydoras niger, Semaprochilodus* (P)	Piedade, 1985
A. mexicanum Liebman in Mart.	*Sciurus aureogaster, S. deppei* (M)	Coates-Estrada & Estrada, 1986
A. polystachyum H. A. Wendl. ex Hemsl.	*Ramphastos brevicarinatus* (A)	Van Tyne, 1929
A. standleyanum Bailey	*Nasua narica* (M)	Kaufmann, 1962
	Cebus capucinus, Ateles geoffroyi (M)	Hladik & Hladik, 1969
	Dasyprocta punctata (M)	Smythe, 1970
	Sciurus granatensis (M)	Heaney & Thorington, 1978
	Tapirus bairdii (M)	Terwilliger, 1978

TABLE 1. Continued.

Taxon	Dispersal agent (class)	Reference
A. tucuma Mart.	*Deroptyus accipitrinus* (A)	McLoughlin & Burton, 1976
A. vulgare Mart.	*Deroptyus accipitrinus* (A)	McLoughlin & Burton, 1976
	Philander opossum, Caluromys philander (M)	Charles-Dominique et al., 1981
Arecoideae: Geonomeae		
Welfia georgii H. A. Wendl.	*Potos flavus, Sciurus, Cebus capucinus, Dasyprocta punctata, Heteromys desmarestianus, Hoplomys gymnurus, Proechimys semispinosa* (M), Probably: *Agouti paca, Tayassu pecari* (M), *Amazona, Ramphastos* (A)	Vandermeer et al., 1979
Geonoma	*Phainoptila melanoxantha, Catharus gracilorostris, Myadestes melanops, Chamaepetes unicolor* (A)	DeVito, 1983
	Steatornis caripensis (A)	B. Tannenbaum, pers. comm.
G. vaga Griseb. & H. A. Wendl.	*Steatornis caripensis* (A)	Snow, 1962
Phytelephantoideae		
Phytelephas	*Agouti* (M)	H. Balslev, pers. comm.
Ammandra	*Agouti* (M)	H. Balslev, pers. comm.

cation not only identifies the class of the known dispersers but also indicates that other unspecified dispersers of that class are suspected.

RESULTS

For most palms many different animals are involved in dispersal (TABLE 1). Not only are many palms visited by animals from many different classes but also a frugivorous animal may forage on more than one species of palm. Furthermore, many of the same animals which feed on palm fruit also feed on the fruit of other plants (e.g., Lauraceae, Moraceae, Burseraceae) (cf. Snow, 1981; Marshall, 1985). As a consequence of this diversity in feeding ecology, specific animal–palm obligate mutualisms are not likely to have evolved in dispersal (Wheelwright & Orians, 1982) as they have in pollination (Henderson, 1986).

The results of this survey reveal an interesting diversity of dispersers throughout the tropical and subtropical areas of Africa, Asia and Malesia, Australia and Oceania, and the Americas.

There are comparatively few palms native to Africa (Moore, 1973a, 1973b), but there are many unanswered questions about palm seed dispersal there. Burtt (1929) and Corner (1966) have reported that the African elephant is an important dispersal agent for the widespread *Phoenix reclinata, Hyphaene* sp., and *Borassus aethiopum,* although this large animal has a destructive potential which may well lessen its overall effectiveness (Krishnan, 1972). In addition, the palm nut vulture, *Gypohierax angolensis,* is well known for feeding on the fruits of *Raphia farinifera.* Shrikes (*Lanius excubitor*) are thought by Parrott (1980) and others to feed on the fruits of the date palm, *Phoenix dactylifera*; the partially eaten fruits impaled on the leaf spines of the palms bear witness to the shrike's feeding habits. Cowan (1984), however, has attributed the partially eaten impaled dates to infructescences blowing in the wind against the spines and to the pecking activities of the Spanish sparrow (*Passer hispaniolensis*). The activities of the shrike might result in limited seed dispersal, but the activities of the sparrow would not. As with other aspects of the palms of Africa, much is yet to be learned of their dispersal biology.

Much of our knowledge of dispersal in Asia and Malesia comes from observations made by Ridley (1930) and Bartels (1964). Of particular interest are the many mammals reported by Ridley and Bartels which feed on the fruits of *Arenga* and *Caryota.* The pericarps of these palm fruits contain needle-like crystals of calcium oxalate which are highly irritating to the mucous membranes of humans, yet wild dogs and palm civets consume the fruits with no apparent ill effects. The palm civet *Paradoxurus hermaphroditus javanicus* is especially important in seed dispersal. It is a skilled arborealist, quite capable of climbing even slender lianas and is not limited to feeding on fallen fruits. Bartels (1964) has observed the seeds of *Pinanga coronata, Daemonorops melanochaetes,* and *Arenga pinnata* germinating from the dung of the palm civet, which usually defecates in clearings. Bartels has speculated that the seeds of *A. pinnata* experience enhanced germination after passage through the gut of the palm civet; however, this hypothesis awaits critical testing.

Docters van Leeuwen (1936) has reported on the presence of *Corypha utan* and *Oncosperma tigillarium* on the Krakatau islets. The vegetation of these areas was totally destroyed by the 1883 volcanic eruption of Krakatau, but subsequent explorations in 1920 and 1929 revealed the presence of *O. tigillarium* and *C. utan,* respectively. Docters van Leeuwen (1936) has attributed their introduction to the activities of birds, probably fruit pigeons. Similarly, Atherton and Greeves (1985) have attributed the presence of *Calamus* on Green Island, Queensland, to dispersal from the Australian mainland by the fruit pigeon *Ducula spilorrhoa.* Indeed, the palm floras of islands, especially volcanic islands never connected to the mainland, provide the clearest evidence for long-distance dispersal.

In northeastern Queensland, the cassowary (*Casuarius casuarius*) disperses several rainforest palms (Stocker & Irvine, 1983). The cassowary feeds on a great variety of fruit including *Calamus* and *Linospadix microcarya,* and seeds collected from dung germinate satisfactorily. In Papua New Guinea, the dwarf cassowary, *Casuarius bennetti pictocollis,* feeds heavily on the fruit of *Calyptrocalyx* and is also known to feed on the fruit of an undetermined species of *Areca* (Pratt, 1983). Unlike other "bird fruit," palm fruit taken by cassowaries must be dropped when ripe or borne on low-growing palms. The fruits of the low-growing *Linospadix* are easily within reach of the flightless cassowary, but it must rely on the fallen fruits of *Calamus* and *Areca.* Although birds are not thought to take yellow fruit (Gautier-Hion et al., 1985), yellow *Calamus* fruits are taken by cassowaries. In the way it interacts with palms, the cassowary behaves more like a terrestrial mammal than a bird.

An example in which animals' foraging habits have the potential to result in long-distance dispersal is found in the fruit pigeons *Ptilinopus superbus* and *P. magnificus.* Birds collected by Frith et al. (1976) near Port Moresby in New Guinea were found to have in their crops seeds of *Archontophoenix,* a palm endemic to Australia. As *Ptilinopus* are known to feed in Australia and regurgitate seeds in a viable condition (Goodwin, 1983), *Archontophoenix* seeds taken from the New Guinea birds may well have been viable. One might conclude that the *Archontophoenix* seeds are taken in Australia and are then deposited in New Guinea, in which case the pigeons may eventually succeed in introducing *Archontophoenix* to New Guinea. Alternatively, they may already have introduced *Archontophoenix* into New Guinea, and the presence of this palm has escaped notice: Frith et al. (1976) recorded that the birds they observed were notably sedentary, appeared to forage locally, and gave no indication of nomadic foraging behavior.

In southwestern North America, Bullock (1980) and Cornett (1985) have demonstrated the viability of *Washingtonia filifera* seeds taken from coyote dung. The nomadic foraging of coyotes strongly suggests that they are important in dispersing seeds of *W. filifera,* especially in transporting seeds across unfavorable habitats, e.g., between washes in the desert. Birds also feed on the fruit, but dispersal by birds is seasonal and thought to be less effective. The coyotes depend on autogenously dropped fruit and fruit dropped by birds. Limited data suggest that autogenous fruit drop varies among individual trees. Consequently, dispersal by mammals is more likely for some seeds, and dispersal by birds is more likely for others. Palms that readily drop fruit may or may not experience enhanced reproductive success (by means of enhanced dispersal) over those with bird dispersed seeds.

In Florida, the bear *Ursus americanus* disperses *Sabal* spp., *Serenoa repens,* and *Rhapidophyllum hystrix* (Maehr & Brady, 1984; Zona, unpubl.). *Sabal etonia, Serenoa repens,* and *R. hystrix* bear their fruit at or near ground level; the fruit of *Sabal palmetto* is readily found beneath the tree. Both *S. etonia* and *R. hystrix* are restricted to specific habitats, and in central Florida bears are probably responsible for dispersing seeds of these palms not only within those habitats but also across patches of unfavorable habitat.

In northern South America, the distribution of cotingas (Cotingidae), birds which feed on *Euterpe* fruit, is nearly coincident with that of *Euterpe* (cf. Lleras et al., 1984). Work by Snow (1982) suggests that these frugivores are important agents of local dispersal for palms and other fruit trees. While birds undoubtedly are important dispersers of *Euterpe,* the fruits are also sought by fish and the electric eel, *Electrophorus electricus* (Goulding, 1980). The local peoples of Amazonia informed Goulding that the eels congregate beneath fruiting *Euterpe* trees growing in inundated areas and "shock" the trees to induce fruit drop. As it is unlikely that electrical current could induce fruit drop, Goulding has noted that this testimony by locals seems to be more folkloric than factual. The fish, including the eel, feed on fruit which drop when ripe; moreover, fishermen are able to attract fish by imitating the sound of fruit falling into water.

The frugivorous fish (Characidae, Pimelodidae, Anostomidae, Prochilodontidae, and Doradidae) of Amazonia are unique components of the guild of dispersers of the riverine and inundated forest of that region (Gottsberger, 1978; Goulding, 1980; Piedade, 1985). They can destroy seeds, as well as disperse them by cracking the endocarp and digesting the endosperm; however, thick endocarps protect some seeds from total predation. Likewise, the beetles (Coleoptera) described by Silberbauer-Gottsberger (1973), Gottsberger and Silberbauer-Gottsberger (1983), and Morawetz (1983) as seed dispersers of *Butia leiospatha, Syagrus loefgrenii,* and *Allagoptera arenaria* are likely to be mostly predatory and probably play only a minor role in dispersal. The beetles oviposit on the fruits and bury them up to 10 cm below the soil surface. It is not known what proportion of the beetle-dispersed seeds survive to germinate.

A summary of TABLE 1 is presented in TABLE 2. For each tribe, animal dispersers are tabulated by class. Unspecified dispersers are not included in TABLE 2; hence, insects, the identities of which are unspecified in TABLE 1, are not counted in TABLE 2.

TABLE 2. Number of dispersers of palms by class. Palm taxa are followed by the number of genera found in TABLE 1. Unspecified dispersers are not included; hence, class Insecta is not counted. Within each palm tribe, each animal is counted only once even though it may disperse many palms. Class abbreviations are the same as in TABLE 1.

Taxa	Class				
	A	C	M	P	R
Coryphoideae:					
Corypheae (10)	24	3	5	0	1
Phoeniceae (1)	2	3	3	0	0
Borasseae (3)	0	3	3	0	0
Calamoideae:					
Calameae (10)	8	0	9	0	0
Lepidocaryeae (1)	1	0	3	0	0
Ceroxyloideae:					
Ceroxyleae (1)	1	0	0	0	0
Hyophorbeae (2)	3	1	2	0	0
Arecoideae:					
Caryoteae (2)	6	1	5	0	0
Iriarteeae (3)	4	1	14	0	0
Areceae (24)	32	1	12	3	0
Cocoeae (12)	23	3	41	17	0
Geonomeae (2)	7	0	9	0	0
Phytelephantoideae (2)	0	0	1	0	0

DISCUSSION

An effective disperser must remove the pericarp from the seed and deposit the seed in a viable condition at a site suitable for germination and seedling establishment. Some animals, such as Indian elephants (*Elephas*) and civets (*Paradoxurus*), swallow the fruit and later defecate the seed. Many frugivorous birds (e.g., *Ducula, Steatornis caripensis*) simply swallow the whole fruit and later regurgitate the seed, which in the case of palms may be too large to pass through the intestine. The more dexterous primates and bats are able to strip the pericarp from the seed, which is then discarded.

The effectiveness of a disperser in depositing seeds in a "safe site" (Harper, 1977), one suitable for germination and seedling establishment, cannot be evaluated from dietary data. It is possible that some of the animals which feed on palm fruits are ineffective dispersal agents; however, even a low level of effective dispersal may be enough to maintain a stable distribution of the plants involved (Janzen, 1970; Hubbell, 1979).

The distinction between seed disperser and seed predator may often be fine and tenuous, if not somewhat artificial. There exists a continuum from high quality dispersal (effective dispersal) to low (predation). According to Janzen (1970), a seed predator eats the seed (or seed plus pericarp) and destroys the embryo. Alternatively, a seed predator may leave the seed undamaged but habitually deposit the seed in an unsuitable site. However, seed predators may at times act as seed dispersers ("dyszoochory" of van der Pijl, 1982). A predator may occasionally eat fruit and discard seeds (cf. Izawa, 1979), incompletely masticate seeds (cf. Goulding, 1980), or fail to recover scatter-hoarded seeds (cf. Heaney & Thorington, 1978). A seed predator, if frightened or distracted, may abandon a potential meal, thereby effecting dispersal. On the other hand, even the most efficient dispersers, such as oilbirds, occasionally deposit seeds in unsuitable habitats. Agoutis, considered to be both predator and disperser (Bradford & Smith, 1977; Vandermeer et al., 1979), can in fact play an inconsequential role in either seed predation or dispersal (Larson & Howe, 1987). Only more thorough field study can determine relative importance of the animals listed in TABLE 1 in the dispersal of palms.

For these reasons, the distinction between seed predator and seed disperser is not emphasized in this review. We prefer not to maintain the incongruous distinction between animals which are usually dispersers but are occasionally predators and those which are usually predators but occasionally disperse seeds. The resultant dispersal of seeds differs in the frequency or quantity of seed dispersed, but because quantitative data for palm seed dispersal are not available, we cannot discuss the consequences for palm population dynamics of low frequency versus high frequency seed dispersal.

For many plants, aspects of morphology such as color, size, and accessibility have been shown to influence food choice by dispersal agents and thereby presumably affect ultimate distribution (Stiles, 1982; van der Pijl, 1982; Willson & Thompson, 1982; Janson, 1983; Moermond & Denslow, 1983; Gautier-Hion et al., 1985; Wheelwright, 1985). Doubtless these attributes of palms also influence their dispersal; however, the questions of how specific morphological features of palms influence feeding activities and subsequent dispersal have only rarely been addressed. Beccari (1877) thought that several aspects of palm morphology (viz., the scales on fruits of the Calameae) actually hindered seed dispersal activities of animals, but the evidence presented here (TABLE 1) clearly does not support such a conclusion. Corner (1966) has suggested that small animals disperse small palm fruit and that large animals disperse large fruit (see Wheelwright, 1985), and Snow (1971) has stated that fruits of *Bactris* are too firmly attached to the infructescence to be taken by the frugivorous bearded bellbird (*Procnias averano*) but are accessible to the larger oilbird (*Steatornis caripensis*).

The trends in dispersal apparent from TABLE 2 likely reflect a relationship between palm morphology and disperser behavior or morphology. For example, the fruits of the Borasseae and Phytelephantoideae tend to be large, fibrous, and heavy, so, not unexpectedly, no birds are identified in TABLE 1 as dispersers of these palms. The scaly fruit and spiny infructescences of the Calamoideae may preclude bats as dispersers. The large number of fish which disperse Cocoeae is probably accounted for by the large number of Cocoeae in the Amazon basin where this unusual form of seed dispersal is most highly developed. Curiously, reptiles are identified only once in TABLE 1, whereas birds and mammals are abundantly represented.

Several important factors influencing dispersal and distribution are not evident from TABLE 1, viz., seasonal variation in seed dispersal and postdispersal predation.

The quality of dispersal may vary seasonally, independently of fruit production. For example, *Steatornis caripensis* feeds on the oil-rich fruits of several different palms. In Venezuela, the oilbird roosts in caves, and during the breeding season, thousands of seeds are deposited in the caves in what are obviously unsuitable sites for germination. However, during the rest of the year, most seeds are regurgitated as the birds forage throughout the forests thereby effecting dispersal (B. Tannenbaum, pers. comm.). The oilbird similarly disperses palms in Trinidad (Snow & Snow, 1978) and Ecuador (Snow, 1979).

Janzen (1971) has shown that *Scheelea* seeds deposited by rodents beneath the parent tree experience up to 80 percent mortality because of predation by bruchid beetle larvae; moreover, Wilson and Janzen (1972) have shown that the postdispersal distance between a seed and the parent tree does not influence the probability of bruchid predation. Bruchid predation is a "filter" between dispersal and ultimate distribution (see also Brown, 1976). Kiltie (1981a) has shown that palm seeds scatter-hoarded by squirrels may be recovered by peccaries which eat the endosperm. Additionally, there may be differences in postdispersal predation depending on dispersal agents: Bullock (1980) has noted that seeds of *Washingtonia filifera* dispersed by mammals may experience less predation by rodents than seeds dispersed by birds. These limited examples suggest that postdispersal predation ultimately influences the distribution of palms; however, biologists have only begun to examine this phenomenon.

Cotingas, cassowaries, and fruit pigeons are specialized frugivores in that they feed almost exclusively on large, highly nutritious fruits. McKey (1975) and Snow (1971, 1981) assert that a certain degree of "mutual evolution" may have occurred in both palm and frugivore as the result of frequent inclusion of palm fruits in the diets of these animals. The diversity of animals that feed on palm fruit, however, suggests that highly coevolved plant–disperser obligate mutualisms are not in operation (Vandermeer et al., 1979; Wheelwright & Orians, 1982). The high nutrient content of the fruit and the large seed size of many palms suggest dispersal by specialized frugivores (McKey, 1975; Snow, 1981), but the bony or fibrous endocarp suggests selection pressures from additional kinds of animal dispersal agents and/or postdispersal predation. Although specialized frugivores may provide a higher frequency of quality dispersal (McKey, 1975), opportunistic frugivores, those animals which take fruit only occasionally or seasonally, are also important in the dispersal of seeds and the ultimate distribution of palms. The significance of opportunistic frugivores has been demonstrated in several instances (Hladik & Hladik, 1969; Bullock, 1980; Cornett, 1985).

CONCLUSIONS

Palm fruits are important sources of food for many animals, and zoochory is common in the Palmae. The remarkable diversity in fruit morphology allows many different classes of seed dispersers to exploit palms in different ways. Without more detailed data analysis, it is difficult to identify dispersal "syndromes," but some classes of dispersal agents show a tendency to avoid certain groups of palms, i.e., bats and the Calamoideae, birds and the Borasseae. However, as more field studies are completed, trends identified in TABLE 2 may be obliterated or reversed.

Palms attract a wide variety of frugivores, both specialized and opportunistic, many of which disperse seeds, so claims that palms are poorly dispersed seem unjustified. Of the 200 known genera of palms, only 75 are listed in TABLE 1; however, as more fieldwork is completed, we expect to discover that the colorful, fleshy fruits so characteristic of most palms are indicative of their dispersal by animals.

There is no doubt that animals have influenced the distribution of palms. At this time, however, only a few examples of range extensions or long-distance dispersal (viz., *Calamus, Corypha, Oncosperma,* and perhaps *Archontophoenix*) can be directly attributed to the activities of dispersal agents. Of course, some species and even genera have very restricted distributions, but until more is known of their ecology, we can only speculate on reasons for limited distributions. Because so many palms with fleshy fruits are adapted to zoochory, small distributional ranges may be caused more by limited habitat, climate, or substrate than by a lack of dispersal agents.

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