

RARITY OF FIGS (*FICUS*) ON MADAGASCAR AND ITS RELATIONSHIP TO A DEPAUPERATE FRUGIVORE COMMUNITY

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INTRODUCTION

In numerous tropical forests 50-90 % of tree and shrub species depend on fruit eating vertebrates to disperse their seeds (Frankie *et al.*, 1974; Alexandre, 1980; Raemaekers *et al.*, 1980; Hall & Swaine, 1981; Howe & Smallwood, 1982). In some areas, forest frugivores make up over 80 % of the mammalian and avian biomass (Terborgh, 1986a). Fleming *et al.* (1987) have pointed out that “Madagascar is strikingly depauperate in frugivorous birds,” particularly when compared to continental areas and other large tropical islands, such as Borneo and New Guinea. The extant avifauna of Madagascar is characterized by its low species diversity and high level of endemism (Langrand, 1990), and little natural history information is available on most species, particularly specific data on diet. The island’s fruit bat community (Pteropodidae) contains three species, which is few compared to many other Old World tropical islands (Heaney, 1991). Finally, the primate community shows remarkable intra — and inter — specific variability and seasonality in the consumption of different food types (leaves, fruits, nectar) without any predominantly frugivorous species (Richard, 1985).

The purpose of this paper is to present comparative data on the relationship between *Ficus* species richness and fruiting seasonality with the frugivore communities of Malagasy and other tropical Old World forests. Further, several ideas are examined on the processes that may have given rise to this depauperate guild.

WHY IS MADAGASCAR SO DEPAUPERATE IN FRUGIVORES?

In their review of tropical vertebrate frugivore communities, Fleming *et al.* (1987) proposed two processes, ecological and historical, to explain the patterns they observed. Ecological factors associated with presumed competition or at least

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dietary overlap between organisms give rise to differences in behavioral and morphological characteristics, which mold the frugivore community. Implicit within this idea is that an evolutionary trajectory is already in place for potential interactions between plants and animals in the mutual evolution of these organisms (see Howe, 1993). Since, Madagascar is depauperate in frugivores, such evolutionary pressures do not appear to manifest themselves in the extant biota, specifically in precise relationships between fruits and dispersers characteristic of tropical forests around the world. Thus, on Madagascar the importance of ecological processes has presumably not played a strong role in shaping this community.

Within the historical process, two of the factors that Fleming *et al.* (1987) propose are highly relevant to the Madagascar case: 1) history of isolation — Madagascar has been separated from Africa for 165 million years (Rabinowitz *et al.*, 1983) and India for 88 million years (Storey *et al.*, 1995), and this isolation has presumably limited colonization of plants and animals, and 2) evolutionary history of the flora — given this long history of isolation and lack of Pliocene/Pleistocene land bridges to facilitate dispersal, the pool of possible interactions between plants and animals has been limited. Madagascar is separated from the African continent by a minimum distance of approximately 400 km. It is proposed that these factors of isolation may have given rise to different evolutionary processes, both stochastic and directed, that have molded the frugivore community, particularly compared to other large tropical islands, such as Borneo. Examples of these differences within the flora include low levels of diversity and density of “keystone” plant groups (*sensu* Gilbert, 1980), such as *Ficus* or other types of fruits, which in turn gives rise to a phenological sequence in which fruiting trees are exceptionally rare during periods of the year. Further, this paucity of fruits during certain periods would limit colonization by frugivores, particularly obligate, even if they were able to disperse to the island.

The *Ficus* diversity in the forests of Madagascar is generally lower than in many other areas of the Old World tropics. In his revision of Malagasy *Ficus*, Berg (1986) recognized a total of 24 species on the island: 16 of which are apparently endemic to Madagascar and 8 occur on Madagascar, neighboring Indian Ocean Islands, and in a few cases on the African mainland. Of these 24 species, about half are known from the western edge of the central high plateau and the eastern humid forest. In contrast, *Ficus* diversity in Peninsular Malaysia, approximately one-quarter the size of Madagascar, has at least 101 *Ficus* species (Ng, 1978). The level of endemism of 67 % (16 of 24) for *Ficus* on Madagascar is lower than that of the general flora which has been estimated to be up to 85 % (Humbert, 1959; Guillaumet, 1984).

There are only a few sites in Malagasy humid forests for which the flora is reasonably well-known. In the Parc National de Ranomafana, 12 *Ficus* species have been identified (Goodman *et al.*, in press). This tally is incomplete, but reflects the approximate number of species within the park and in the eastern humid forest in general. Given the combination of relatively low species diversity, lack of extensive endemism as compared to the Malagasy flora in general, and broad extralimital distributions of about one-third of the Malagasy *Ficus* spp., it is assumed that on Madagascar this genus has not undergone the extensive speciation as other areas in the Old World and perhaps in geological terms has only recently colonized the island.

COMPARISON TO OTHER OLD WORLD SITES

There are few humid forest sites in the Old World tropics with comparative information on the diversity of *Ficus* and detailed information on the local vertebrate fauna and their food habits. The following examples were chosen for their completeness of information rather than high levels of *Ficus* diversity and local frugivory.

Kuala Lompat, Peninsular Malaysia

In a 2 km² area of humid forest 38 species of *Ficus* have been identified (Lambert, 1989a). Within the local vertebrate community 60 of 231 (26 %) birds are frugivores, 4 of 18 (22 %) bats are presumed to be frugivores, 6 of 8 (75 %) primates consume fruits, and numerous other animals such as squirrels, a civet cat, and pigs are frugivorous (Medway, 1969; Medway & Wells, 1971; Lambert, 1989a, 1990) (Table I).

TABLE I

Comparison of four Old World sites in the percentage of the bird, bat and primate fauna that consumes fruit and the number of locally occurring Ficus sp. See text for documentation.

	Ranomafana, Madagascar	Kuala Lompat, Malaysia	Negros, Philippines	Mt. Nimba, Liberia
Number <i>Ficus</i> spp.	12	38	25-30	23
Birds/frugivores (%)	110/9 (8 %) ¹	231/60 (26 %)	149/40 (27 %)	275/42 (15 %)
Bats/frugivores (%)	9/3 (33 %)	18/4 (22 %)	27/11 (41 %)	39/9 (23 %)
Primates/frugivores (%)	12/9 (75 %)	8/6 (75 %)	1/1 (100 %)	5/5 (100 %)

¹ This includes *Copsychus albospectularis*, *Pseudocossyphus sharpei*, and *Hartlaubius auratus* who are primarily non-frugivores.

Negros Island, Philippines

A wet forest area of about 300 ha near Lake Balinsasayao on this island of 13 700 km² has been well-studied. The total *Ficus* flora in the immediate region of the lake is 25-30 species (Utzurum, 1984; Heideman, pers. comm.). The local vertebrate community includes numerous frugivores: 40 of 149 (26.8 %) of birds (Delacour & Mayr, 1946; Rand, 1951; Rabor, 1977, 1986; Alcalá & Carumbana, 1980; Erickson & Heideman, 1983), 11 of 27 bats (40.7 %) (Utzurum, 1984; Heideman & Heaney, 1989; Rabor *et al.*, 1970; Heaney & Heideman, pers. comm.), and 1 of 1 primate (Utzurum, 1984) (Table I).

Mt. Nimba, eastern Liberia

23 species of *Ficus* have been recorded (Adam, 1971). The mountain's frugivore community consists of 42 of 275 (15.2 %) bird species (Colston & Curry-Lindahl, 1986), 9 of 39 (23 %) bat species (Coe, 1975; Hill, 1982; Wolton *et al.*, 1982; Brosset, 1984; Marshall, 1985), and 5 of 5 primates (Coe, 1975) (Table I).

Ranomafana National Park, Madagascar

12 species of *Ficus* have been collected in this park of about 40 000 ha (Goodman *et al.*, in press). The park's frugivore community consists of 9 of 110 (8 %) bird species, 3 of 9 (33 %) bat species, and 9 of 12 (75 %) primate species (Zack, ms.; Goodman *et al.*, in press). The insectivorous bat community of the park is poorly known and several species that presumably occur in the region have yet to be documented in the park. However, all three frugivorous bat species occurring on the island have been reported locally (Dew & Wright, in press; Goodman *et al.*, in press).

On the basis of these comparisons we conclude that the eastern humid forest of Madagascar is depauperate in *Ficus* species. In other portions of the world, Moraceae, specifically *Ficus*, has been recognized as a critical resource for most groups of frugivores, particularly obligate frugivores, during seasons when other fruits are scarce or not available (Leighton & Leighton, 1983; Terborgh, 1986b; Utzurrum, 1984). Given that the majority of figs fruit asynchronously, the reason for more-or-less continuous availability of these fruits in certain tropical forests may simply be that with greater species diversity and/or greater population size (Hubbell, 1980; Bronstein *et al.*, 1990) the fruiting periods overlap and one or another tree is in fruit. On the basis of further comparison to these four Old World tropical sites, there is a relationship, although not statistically significant, between the number of *Ficus* species and the percentage of the local avifauna that is frugivorous (Fig. 1). This pattern is not as noticeable within the Malagasy primate community which is remarkably plastic in its dietary regime (Richard & Dewar, 1991; Kappeler & Ganzhorn, 1993).

There is evidence that fruit density in Malagasy humid forests is distinctly lower than in other humid forests of the world. Fruit traps placed in the Parc National de Ranomafana (Overdorff, 1991) yielded a small fraction of the number of fruits as other sites in the New World (Foster, 1982; Terborgh, 1983) and Old World (White, 1994). Density of Moraceae trees in Malagasy humid forests tends to be low (Abraham *et al.*, 1996) and in some ways parallels the case of Makokou, Gabon, where diversity of figs is high and density is low (Gautier-Hion & Michaloud, 1989). However, at Makokou, fruits (other than *Ficus*) constituting keystone resources vary between areas and in time and food for frugivorous vertebrates is available throughout much of the year (Gautier-Hion & Michaloud, 1989). Further, fruit trees tend to be distinctly smaller in Malagasy humid forest. Ganzhorn (1988) found the average crown diameter of fruit trees at Andasibe, about 250 km north of PNR, to be between 2 and 7 m which on average is significantly smaller than the 5 to 45 m in Peruvian lowland rain forest (Terborgh, 1983).

The second aspect that we wish to contrast is the fruiting phenology of Malagasy humid forests in relation to other Old World sites. Few long-term

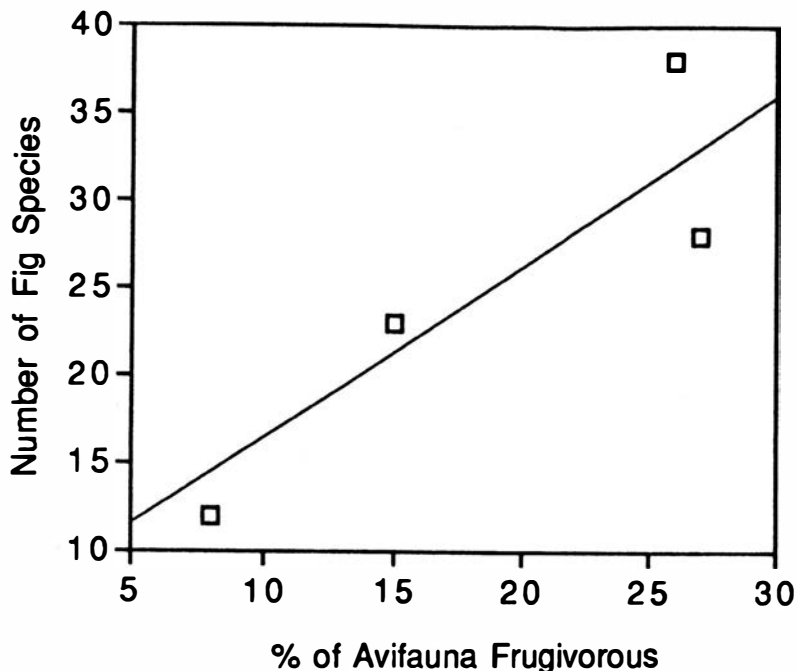


Figure 1. — Comparison of the number of fig species and percentage of the avifauna that is frugivorous at the four sites mentioned in the text ($r = 0.90$, $P = 0.1$, $DF = 3$).

phenological studies have been conducted on Madagascar and comparisons are limited. In the PNR, an area with an annual rainfall of about 2 300 mm and with 74 % of the rain falling between December and March, Overdorff (1993) studied the phenological sequence of 104 individual trees of 26 plant species known to be consumed by primates. She found the principal fruiting season to be August and February, and between March and August the number of available fruits were extremely limited. During April fruiting trees in her phenological study approached zero. Other phenological work in this park indicates that there may be considerable variation in the yearly cycles of fruit availability (Meyers & Wright, 1993). On Nosy Mangabe, an island just off the coast and 620 km north of Ranomafana, Sterling (1993) was left with the impression that fruiting followed an 18 month cycle.

At Lake Balinsasayao, Negros, Heideman (1989) during a two year phenological study found variation in the seasonal presence and abundance of fruits, but in comparison to the Ranomafana studies (Overdorff, 1993; Meyers & Wright, 1993) the Negros site did not experience extreme depressions in the availability of fruits. In a study of the forest phenology of Kuala Lompat over a 29 month period, Raemaekers *et al.* (1980) found that there was considerable variation in the number of fruiting trees on a seasonal basis, although fruits could be found in any month of the year. Further, figs were available year round in varying densities, and constituted an important primate food in periods of fruit availability. Even given the high species diversity of *Ficus* at this site, Lambert & Marshall (1991) have

concluded that birds depending on figs need to be wide-ranging or those with small home ranges have to depend on other fruits during periods of *Ficus* scarcity. Leighton & Leighton (1983) examined vertebrate responses to variability of fruit availability in the Kutai National Park, East Kalimantan, and that figs were one of the critical food resources to carry frugivores between fruiting peaks.

CONCLUSION

On the basis of comparisons between Malagasy and other Old World tropical forests, it is proposed that the depauperate frugivore community on Madagascar can be linked to three forest characteristics: 1) lower general fruit availability in terms of diversity and density, 2) seasonal reduction in fruit production, which may be similar to other tropical forests, but, 3) in Madagascar figs do not play a keystone role because of their low species diversity and extremely limited fruit production during some months of the year. At other sites figs form a critical resource for frugivores during lean periods of low fruit availability.

The few existing frugivores, several of which are actually seed predators, on the island have adapted by having broad diets (e.g. parrots and lemurs) and moving considerable distances in search of food (e.g. fruit bats and pigeons). Given the differences between Madagascar and the other tropical islands in the history of their isolation and subsequent rates of colonization (e.g. Borneo and large islands in the Philippines), it is important to distinguish between historical and ecological processes when making comparisons in the interaction between plants and animals. Further, some paradigms of plant/frugivore interaction hypothesized for other areas of the world may not have a parallel evolutionary history on Madagascar.

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SUMMARY

Several authors have recognized that Madagascar has a depauperate frugivore community, although few explanations have been offered to explain this observation. In comparison to other tropical Old World forests, Malagasy forest has a reduced diversity and density of *Ficus* (generally an important keystone group in tropical forests), relatively low fruit productivity, and an unusual phenological sequence. These factors, some of which are presumed to be related to Madagascar's long isolation from other land masses, are considered important variables to explain the island's reduced frugivore community.

RÉSUMÉ

Bien que plusieurs auteurs aient remarqué le faible nombre d'espèces frugivores présentes à Madagascar, l'interprétation de cette observation n'a jusqu'à présent fait l'objet que de quelques spéculations. Si l'on compare la forêt malgache à celles des régions tropicales de l'Ancien Monde, on y observe que le genre *Ficus* (généralement considéré comme une ressource-clé pour les frugivores des forêts tropicales) présente à la fois une faible diversité et une densité réduite. La productivité du groupe des *Ficus* y est relativement basse et sa phénologie ne correspond pas aux séquences habituellement observées par ailleurs. Ces facteurs — dont certains pourraient résulter de la longue période au cours de laquelle Madagascar a été isolée des blocs continentaux — sont considérés comme des paramètres importants pour expliquer le nombre réduit des frugivores sur cette île.

REFERENCES

- ABRAHAM, J.-P., RAKOTONIRINA, B., RANDRIANASOLO, M., GANZHORN, J.U., JEANNODA, V. & LEIGH, E.G., Jr. (1996). — Tree diversity on small plots in Madagascar: a preliminary review. *Revue d'Ecologie (Terre et la Vie)*, 51: 93-116.
- ADAM, J.-G. (1971). — Flore descriptive des Monts Nimba. *Mémoires Muséum National d'Histoire Naturelle, Paris*, sér. B, 22 : 535-905.
- ALCALA, A.C. & CARUMBANA, E.E. (1980). — Ecological observations on birds of southern Negros, Philippines. *Silliman Journal*, 27: 197-222.
- ALEXANDRE, D.Y. (1980). — Caractère saisonnier de la fructification dans une forêt hygrophile de Côte d'Ivoire. *Revue d'Ecologie (Terre et la Vie)*, 34 : 335-359.
- BERG, C.C. (1986). — The *Ficus* species (Moraceae) of Madagascar and the Comoro Islands. *Bull. Muséum Nat. Hist. Nat., Paris*, (4) 8: 17-55.
- BRONSTEIN, J.L., GOUYON, P.-H., GLIDDON, C., KJELLBERG, F. & MICHALOUD, G. (1990). — The ecological consequences of flowering asynchrony in monoecious figs: a simulation study. *Ecology*, 71: 2145-2156.
- BROSSET, A. (1984). — Chiroptères d'altitude du Mont Nimba (Guinée). Description d'une espèce nouvelle, *Hipposideros lamottei*. *Mammalia*, 48 : 545-555.
- COE, M. (1975). — Mammalian ecological studies on Mount Nimba, Liberia. *Mammalia*, 39: 523-588.
- COLSTON, P.R. & CURRY-LINDAHL, K. (1986). — *The birds of Mount Nimba, Liberia*. London, British Museum (Natural History).
- DELACOUR, J. & MAYR, E. (1946). — *Birds of the Philippines*. MacMillan Co., New York.
- DEW, J.L. & WRIGHT, P. (in press). — Frugivory and seed dispersal by primates in Madagascar's eastern rainforest. *Biotropica*.
- ERICKSON, K.R. & HEIDEMAN, P.D. (1983). — Notes on the avifauna of the Balinasayao rainforest region, Negros Oriental, Philippines. *Silliman Journal*, 30: 63-72.
- FLEMING, T.H., BREITWISCH, R. & WHITESIDES, G.H. (1987). — Patterns of tropical vertebrate frugivore diversity. *Annual Review of Ecology and Systematics*, 18: 91-109.
- FOSTER, R.B. (1982). — The seasonal rhythm of fruitfall on Barro Colorado Island, pp. 151-172 In Leigh, E. G., Rand, A. S. & Windsor, D. M. (eds.). *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Smithsonian Institution Press, Washington, D.C.
- FRANKIE, G.W., BAKER, H.G. & OPLER, P.A. (1974). — Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology*, 62: 881-919.
- GANZHORN, J.U. (1988). — Food partitioning among Malagasy primates. *Oecologia*, 75: 436-450.
- GAUTIER-HION, A. & MICHALOUD, G. 1989. — Are figs always keystone resources for tropical frugivorous vertebrates? A test in Gabon. *Ecology*, 70: 1826-1833.
- GILBERT, L.E. (1980). — Food web organization and the conservation of neotropical diversity: an evolutionary-ecological perspective, pp. 11-33 In Soulé, M.E. & Wilcox, B.A. (eds). *Conservation biology*. Sinauer Associates, Sunderland, Massachusetts.
- GOODMAN, S.M., GANZHORN, J.U., & WILMÉ, L. (In press). — Observations at a *Ficus* tree in Malagasy humid forest. *Biotropica*.

- GUILLAUMET, J.-L. (1984). — The vegetation: an extraordinary diversity, pp. 27-54 *In* Jolly, A., Oberlé, P. & Albignac, R. (eds.). *Key Environments: Madagascar*. Pergamon Press, Oxford.
- HALL, J.B. & SWAINE, M.D. (1981). — *Distribution and ecology of vascular plants in a tropical rain forest: forest vegetation in Ghana*. Junk, The Hague.
- HEANEY, L.R. (1991). — An analysis of patterns of distribution and species richness among Philippine fruit bats (Pteropodidae). *Bulletin of the American Museum of Natural History*, 206: 145-167.
- HEIDEMAN, P.D. (1989). — Temporal and spatial variation in the phenology of flowering and fruiting in a tropical rainforest. *Journal of Ecology*, 77: 1059-1079.
- HEIDEMAN, P.D. & HEANEY, L.R. (1989). — Population biology and estimates of abundance of fruit bats (Pteropodidae) in Philippine submontane rain forest. *Journal of Zoology, London*, 218: 565-586.
- HILL, J.E. (1982). — Records of bats from Mount Nimba, Liberia. *Mammalia*, 46: 116-120.
- HOWE, H.F. (1993). — Specialized and generalized dispersal systems: where does "the paradigm" stand? *Vegetatio*, 107/108: 3-13.
- HOWE, H.F. & SMALLWOOD, J. (1982). — Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, 13: 201-228.
- HUBBELL, S.P. (1979). — Tree dispersion, abundance, and diversity in a tropical dry forest. *Science*, 203: 1299-1309.
- HUMBERT, H. (1959). — Origines présumées et affinités de la flore de Madagascar. *Mémoires de l'Institut Scientifique de Madagascar (série B, Biologie Végétale)*, 9: 149-187.
- KAPPELER, P.M. & GANZHORN, J.U. (eds.). (1993). — *Lemur social systems and their ecological basis*. Plenum Press, New York.
- LAMBERT, F. (1989). — Fig-eating by birds in a Malaysian lowland rain forest. *Journal of Tropical Ecology*, 5: 401-412.
- LAMBERT, F. (1990). — Some notes on fig-eating by arboreal mammals in Malaysia. *Primates*, 31: 453-458.
- LAMBERT, F. & MARSHALL, A.G. (1991). — Keystone characteristics of bird-dispersed *Ficus* in a Malaysian lowland rain forest. *Journal of Ecology*, 79: 793-809.
- LANGRAND, O. (1990). — *Guide to the birds of Madagascar*. Yale University Press, New Haven.
- LEIGHTON, M. & LEIGHTON, D.R. (1983). — Vertebrate responses to fruiting seasonality within a Bornean rain forest, pp. 181-196 *In* Sutton, S. L., Whitmore, T. C. & Chadwick, A. C. (eds). *Tropical rain forests: ecology and management*. Blackwell Scientific Publications, Oxford.
- MARSHALL, A.G. (1985). — Old World phytophagous bats (Megachiroptera) and their food plants: a survey. *Zoological Journal of the Linnean Society*, 83: 351-369.
- MEDWAY, Lord (1969). — *The wild mammals of Malaya and offshore islands including Singapore*. Oxford University Press, Kuala Lumpur.
- MEDWAY, Lord & WELLS, D.R. (1971). — Diversity and density of birds and mammals at Kuala Lompat, Pahang. *Malaysian Nature Journal*, 24: 238-247.
- MEYERS, D.M. & WRIGHT, P.C. (1993). — Resource tracking: Food availability and *Propithecus* seasonal reproduction, pp. 179-192 *In* Kappeler, P.M. & Ganzhorn, J. U. (eds). *Lemur social systems and their ecological basis*. Plenum Press, New York.
- NG, F.S.P. (ed). (1978). — *Tree flora of Malaya*. Vol. 3. Longman, Kuala Lumpur, 339 pp.
- OVERDORFF, D.J. (1991). — *Ecological correlates to social structure in two prosimian primates: Eulemur fulvus rufus and Eulemur rubriventer in Madagascar*. Ph. D. thesis, Duke University.
- OVERDORFF, D.J. (1993). — Ecological and reproductive correlates to range use in Red-bellied Lemurs (*Eulemur rubriventer*) and Rufous Lemurs (*Eulemur fulvus rufus*), pp. 167-178 *In* Kappeler, P. M. & Ganzhorn, J. U. (eds). *Lemur social systems and their ecological basis*. Plenum Press, New York.
- RABINOWITZ, P.D., COFFIN, M.F. & FALVEY, D. (1983). — The separation of Madagascar and Africa. *Science*, 220: 67-69.
- RABOR, D.S. (1977). — *Philippine Birds & Mammals*. University of the Philippines Press, Quezon City.
- RABOR, D.S. (1986). — *Guide to Philippine Flora and Fauna, Vol. XI, Birds, Mammals*. JMC Press, Quezon City.
- RABOR, D.S., ALCALA, A.C. & GONZALES, R.B. (1970). — A list of the land vertebrates of Negros Island, Philippines. *Silliman Journal*, 17: 297-316.
- RAEMAEKERS, J.J., ALDRICH-BLAKE, F.P.G. & PAYNE, J.B. (1980). — The forest, pp. 29-61 *In* Chivers, D. J. (ed). *Malayan forest primates: ten years' study in tropical rain forest*. Plenum Press, New York.
- RAND, A.L. (1951). — Birds of Negros Island. *Fieldiana: Zoology*, 31 (48): 571-596.

- RICHARD, A.F. (1985). — *Primates in nature*. Freeman and Co., New York.
- RICHARD, A.F. & DEWAR, R.E. (1991). — Lemur ecology. *Annual Review of Ecology and Systematics*, 22: 145-175.
- STERLING, E.J. (1993). — *Behavioral ecology of the aye-aye (Daubentonia madagascariensis) on Nosy Mangabe*. Ph. D. thesis, Yale University.
- STOREY, M., MAHONEY, J.J., SAUNDERS, A.D., DUNCAN, R.A., KELLEY, S.P. & COFFIN, M.F. (1995). — Timing of hot spot-related volcanism and the breakup of Madagascar and India. *Science*, 267: 852-855.
- TERBORGH, J. (1983). — *Five New World primates: A study in comparative ecology*. Princeton University Press, Princeton.
- TERBORGH, J. (1986a). — Community aspects of frugivory in tropical forests, pp. 371-384. In Estrada, A. & Fleming, T.H. (eds), *Frugivores and seed dispersal*. Junk, Dordrecht.
- TERBORGH, J. (1986b). — Keystone plant resources in the tropical forest, pp. 330-344. In Soulé, M. (ed), *Conservation biology: the science of scarcity and diversity*. Sinauer Associates, Sunderland, Massachusetts.
- UTZURRUM, R.C.B. (1984). — *Fig fruit consumption and seed dispersal by frugivorous bats in the primary tropical rain forest of Lake Balinsasayao, Negros Oriental, Philippines*. M.S. (Biology) thesis, Silliman University, Dumaguete City.
- WHITE, L.J.T. (1994). — Patterns of fruit-fall phenology in the Lopé Reserve, Gabon. *Journal of Tropical Ecology*, 10: 289-312.
- WOLTON, R.J., ARAK, P.A., GODFRAY, H.C.J. & WILSON, R.P. (1982). — Ecological and behavioural studies of the Megachiroptera at Mount Nimba, Liberia, with notes on Microchiroptera. *Mammalia*, 46: 419-448.