

ASSOCIATION OF MAMMALS WITH MANGROVE FORESTS: A WORLD WIDE REVIEW

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RESUMO

Associação de mamíferos com florestas de mangue: uma revisão ao redor do mundo

As florestas de mangue são relevantes para a sobrevivência de muitas espécies de vertebrados. Dentre elas estão uma variedade de mamíferos, os quais também dependem dos recursos desse sistema. Evidências paleoecológicas da presença dos mamíferos nos manguezais indicam que tal associação tem ocorrido desde os períodos geológicos mais distantes. Assim, as associações atuais poderiam ser interpretadas como um resultado de um processo evolucionário, pelo qual algumas espécies hoje existentes têm adaptado seu comportamento às condições inóspitas dos manguezais e sua fisiologia digestiva aos altos teores de tanino e sal das plantas. Muito embora muitas espécies de mamíferos ainda precisem ser registradas em florestas de mangue, elas contam menos do que 10% de todos os vertebrados já observados nesse sistema. Baseados numa revisão detalhada da literatura disponível e observações de campo, este trabalho também categoriza o *status* de residência da comunidade de mamíferos dos manguezais. O tempo gasto dentro do ecossistema, o que reflete a natureza da relação entre a espécie e o ecossistema durante o seu ciclo de vida, é o principal parâmetro para determinar seu *status* de residência.

Palavras-chave: mamíferos, florestas de mangue, status de residência, revisão.

ABSTRACT

Mangrove forests are relevant for the survival of a large assemblage of vertebrate species. Amongst these are a variety of mammals which also depend on the resources of the mangrove system. Paleoecological evidence of the presence of mammals in mangroves indicates that such association has occurred since the earlier geological periods. Thus, present day associations may be interpreted as a result of an evolutionary process by which some living

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species have adapted both their behaviour to the inhospitable conditions of the mangrove environment and their gut physiology to the high tannin and salt contents of the plants. Even though many additional mammal species remain to be recorded in mangrove forests, they amounting to less than 10% of all vertebrates observed there. Based on detailed assessment of the available literature and field observations, this report also presents a categorisation of the residence status of the mangrove mammal community. The time spent within the ecosystem, reflecting the nature of the relationship between the species and the ecosystem during the life-cycle, is the main parameter in determining its residence status.

Keywords: mammals, mangrove forests, residence status, review.

INTRODUCTION

Mangrove forests dominate around one-quarter of the world's tropical coastal zone (Chapman, 1975) providing a large variety of habitats for a diverse assemblage of species. According to Sasekumar (1974), it is the invertebrates which are considered as the principal resident fauna of mangrove forests. Consequently, the majority of previous studies on animal communities in mangroves has focused on different aspects of the natural life of the invertebrate groups (Berry, 1964; Kinne, 1964; Carpelan, 1967; Macnae, 1968; Warner, 1969; Hutchings & Recher, 1974; Rayner, 1979; Bolivar, 1984; Castro, 1986; Muller & Lana, 1986; Porto & Fonteles-Filho, 1986; Rueda, 1986; Perry, 1988; Junqueira *et al.*, 1989).

Some studies on vertebrates have in particular investigated the ecological importance of mangrove ecosystems as nursery areas for many species of fishes (Aveline, 1980; Lessa, 1986; Robertson & Duke, 1990). In addition, the fishery themselves, as a source of income and

protein for human population, have also been described. These studies have mainly concentrated either on the productivity or on the management of estuarine fish communities (Hamilton & Snedaker, 1984). Amongst other vertebrate species, e.g. birds, which often use mangrove areas as roosting or nesting sites, have also been investigated, continuing their frequent dependence on the mangrove ecosystem (Tostain, 1986; Ottenwalder *et al.*, 1990; Lefebvre *et al.*, 1992). However, mammals although a potentially significant trophic group within the mangrove community, they have been until now largely neglected. In fact, mangrove forests are relevant to the survival of a large number of mammal species. Further it can be appreciated that mammals must have developed over time a variety of physiological adaptations and behavioural strategies which have allowed them to forage on mangrove resources. It seems to be true for many species of mammals widely distributed in different geographical zones throughout the world. This report presents an extensive literature review of the mammal/mangrove

association throughout the world undertaken in order to better understand the ecological significance of different components of this association. Paleoecological evidences and a checklist of the current associated-mangrove mammal species are also presented. In addition, the residence status of the mangrove fauna is discussed in order to categorise the time spent by the current associated mammal community. Finally, the ecological relevance of the mangrove/mammal association, in particular that presented by primate species, is also discussed.

MATERIALS AND METHODS

This report was written based on information on mammal species associated with mangroves. Relevant studies have focused on the residence status of species, mainly fishes and birds, in order to quantify their role in mangrove areas (Lèfebvre *et al.*, 1992; Robertson & Duke, 1990). However, no standardised categories were found for describing the time variation that each species can spend in different activities in mangroves. Thus, an attempt to define categories of residence status is presented in order to compare all the animal groups related to the mangrove ecosystem, and particularly mammals.

The survey of the literature was principally focused on the class Mammalia to produce a checklist of species which can potentially be found in mangrove areas. The geographic zones described by Saenger *et al.* (1983) were used to show the distribution of the mammal species in mangrove forests throughout the world (Table 1). This

checklist is mainly based on records cited in the available literature world wide, as on species observed *in loco*.

The information on species cited in the literature was classified as being of two different types according to the following criteria:

1. where a species was cited by author(s) as having been directly observed in mangrove forests.

- e.g. "...the *Eonycteris spelaea* flies long distances to take the pollen of *Sonneratia*." (Berry, 1972).

- e.g. "The pig-tailed macaque is less commonly seen than the crab-eating macaque. It is less partial to the nipa-mangrove zone." (Davis, 1962).

2. where species are considered by author(s) as supposed inhabitants of mangrove areas.

- e.g. "Found at all altitudes and occurring in all vegetation types." (Stewart & Stewart, 1963).

- e.g. "...the mangrove swamps pass into the scrub jungle forest of the drier regions... it is quite likely Javan rhinos had the same habitat requirements..." (McNeely, 1977).

RESULTS

Paleoecological evidences of mammals in mangrove forests

Pure dense stands of *Nypa* palm/mangrove association flourished during the Eocene. Climatic conditions were tropical and may have been similar to those found today (Westgate & Gee, 1990). Although

many environmental changes have occurred along coastlines over time leading to the disappearance of mangrove formations in some areas, their former presence can be inferred from the frequent presence in cores of large amounts of pollen and spores of close relatives of species now living in mangrove forests. In addition, mollusc shells, and the bones of marine and estuarine fishes, and of other vertebrate species associated with mangroves, are strong indicators of previous coastal paleoenvironment. Such evidence suggests that a diverse assemblage of marine and freshwater vertebrates probably entered mangrove systems, some during dry periods when the salinity was higher and some during the wet season when salinity was lower (Westgate & Gees, 1990). Amongst these remains have been found of many terrestrial and of some freshwater species of mammal indicating their presence in association with mangroves during earlier geological periods.

A paleoecological study of a middle Eocene mangrove site carried out in south-west Texas (USA), recovered by an excavation of terrestrial and arboreal animals including at least 29 species of suite of fossil mammals which appear likely to have inhabit the brackish and freshwater areas within and adjacent to the mangrove (Westgate & Gee, 1990). This suggests that mammal species may over time have played significant roles in ecological process within or associated with mangrove ecosystem. In addition, mangrove-associated mammals seem to have

constituted an important protein resource to hunter-gatherer communities. Manatees, along with cetaceans that entered the waters of the lagoons, deer, peccaries, and other smaller mammals were all hunted by local communities at that time (Sanoja, 1989).

According to Ghosh et al. (1992), subfossil remains of the great one-horned rhinoceros have been found in southern West Bengal (India), testifying that these mammals also thrived in riverine and mangrove swamps about 3,000 years ago. The presence of mammals associated with mangroves may be interpreted as a result of an evolutionary process by which some living species still continue to acquire tolerance to the inhospitable conditions offered by this habitat.

Current mangrove-associated mammals

The species of mammal so far reported as occurring in mangrove areas are listed in Appendix 1. In general, fishes and birds have the greatest number of vertebrate species associated with mangrove forests, accounting for 52% and 38%, respectively. This indicates the importance of the mangrove forests to the diversity of these groups. By contrast, the amphibians and reptiles together represent only a small percentage, about 2%, while the mammals listed here represent around 8% of the total assemblage of vertebrate species recorded from the mangrove system (see Table 2).

Even though mammals representing only a few percent of the mangrove vertebrate species, many of the species which occur

in adjacent habitats are also liable to make some use of mangrove resources or be occasionally observed within fringe mangrove areas. An attempt was made to determine the number of species from each mammal order reported amongst mangroves within each of the six regions of the world occupied by mangroves, as previously defined by Saenger et al. (1983).

So far 111 species of mammals have been recorded as mangrove-associated in different parts of the world (see Table 3). In sum, 119 mammal species are recorded for the six regions (since the same species occurs in more than one region) giving a mean of close to 20 species per region. The regions coded as number 1 (Asia) and 6 (East Coast of Africa and the Middle East) were the geographic zones having the highest number of mammals species known to use mangroves (45 and 26, respectively - see Table 3). However, the assemblage of mammals in mangrove areas seems to have been subject to only limited research on biogeography, ecology, or even taxonomical aspects, so that further mangrove-associated mammal species seem likely to be added to the checklist here provided.

Residence status of the mangrove fauna

A rich variety of invertebrate animal life can be found in mangrove areas, but nevertheless, is mainly dominated by just a few groups which are principally represented by sipunculids, polychaetes, gastropods, and brachyurans (Sasekumar, 1974).

In addition, there is also an associated fauna occurring in different zones of the mangrove forest comprising species derived from adjacent ecosystems (Hegerls & Davie, 1977; Mandura *et al.*, 1987). It has become fairly widely accepted that these non-obligatory associated species are nevertheless an important part of the mangrove community, as well contributing to the available resource of the system.

Different periods of permanence can be observed amongst the different taxonomic groups which are regularly found in mangrove areas. Five categories of residence were identified from an attempt to categorise the patterns of residence status of species associated with the mangrove ecosystem (see Table 4). The categories were defined based on the species dependence on mangrove resources and on the time spent in the ecosystem during their life-span. From these categories a schematic model was produced in order to better visualise the relationships between categories of residence status and different adjacent ecosystems/habitats to which species may originally belong (see Figure 1).

The majority of the associated species show some type of dependence on mangrove resources which, in turn, represent one of the main factors in regulating species residence status in the system. Amphibians, for instance, are one of the most salt intolerant groups of vertebrates, but nevertheless, a species such as *Rana cancrivora* is able to spend a complete life-cycle in mangrove forests (Vannucci, 1989). Other taxonomic groups

such as reptiles (e.g. *Crocodilus porosus* - Graham, 1929) and birds (e.g. the scarlet ibis, *Eudocimus ruber* - personal observation) are found living in salt water creeks and on the edge of the swamps, where their feeding requirements are met.

Mammals can also spend long periods in mangrove forests. For example, Camels (*Camelus dromedarius* - Aleem, 1990), proboscis monkeys (*Nasalis larvatus* - Kern, 1964), and howler monkeys (*Alouatta belzebul* - personal observation) forage on leaves in mangrove areas. Even if only part of their total feeding requirements are obtained from mangrove resources, they may spend a great part of their life-cycle travelling across these forests. Although the presence of some mammals in mangrove is restricted to feeding behaviour, mangroves are also used as sleeping, roosting, and nesting sites, or simply as a suitable area for seeking shelter. The ecological relationship developed between an animal species and the ecosystem will be one of the important parameters influencing its permanence and hence its residence status. According to the available information in the literature and from personal observation, an attempt was made to determine the residence status of mammal species in mangrove areas (see Appendix 1).

The importance of mangroves to the mammal community

Hutchings & Saenger (1987) have pointed out that the majority of terrestrial vertebrate groups use mangrove areas as an

extension of their range, as a substitute habitat, or as a bridging habitat between two terrestrial ones. In addition, mangrove areas are used by many species of mammals either when seeking shelter against predators or for foraging on several resources which may be abundant during different parts of the annual cycle.

Few mammal species have shown a strong dependence on mangrove forests. The small grey false water-rat (*Xeromys myoides*) is one of the best adapted to mangrove conditions possessing well-developed skills enabling it to feed on crabs (Magnusson *et al.*, 1976). This type of adaptation seems to be an important advantage for some mammals because whilst marine invertebrates may be an abundant feeding resource, other terrestrial competitors frequently live in adjacent habitats rather than in mangrove forests.

Mangroves are ever-growing and evergreen forests. So that, mangroves may be as typically having permanent and abundant food supply whereas there may be lean seasons due to the depletion of food resources in adjacent forests. This can be exemplified by the agoutis (*Dasyprocta punctata*) and pacas (*Agouti paca*), which are not adapted to the mangrove system but can be found foraging for seeds on mangrove forest floors when the tide is out (Smythe, 1983; personal observation). Whilst the mangrove flora is largely composed of species which have leaves with high tannin and salt contents (Lacerda *et al.*, 1985; Lacerda *et al.*, 1986), some mammal species have adapted to such food

and indeed are able to thrive using mangrove resources. According to Bennet & Sebastian (1988), larger ungulates have greater needs for salt and other minerals. In this case, the key deer (*Odocoileus virginianus clavium* - Klimstra & Dooley, 1990) may be associated with mangrove areas in order to secure a suitable supply of salt and minerals. In this context it may be noted that, folivores have a specialised microflora in the foregut which can provide vitamins and break down fiber (Bauchop, 1978).

The association of primate species with mangrove forests

Primates include some of the species best known to be associated with mangroves (Kern, 1964; Kawabe & Mano, 1972; Poirrier, 1972; Macdonald, 1982; Chapman, 1987; Salter et al., 1985; Chakrabarti, 1987; Rajanathan & Bennett, 1990; Fernandes, 1991; Yeager, 1990, 1991, 1992; Fernandes & Aguiar, 1993). Many species show only short movements across the mangrove forest, principally during the drier periods. This is exemplified by bearded sakis (*Chiropotes satanas satanas*), a typical primate species from the dense rain forest, which can be seen foraging on insects at the edge of mangroves in north-eastern of Brazil (personal observation). By contrast, some other primate species are well adapted to mangrove forests and show a strong dependence on these resources. This is the case with the proboscis monkeys (*Nasalis larvatus*), a large herbivore strongly

adapted to this system. They must consume large amounts of this indigestible food, in order to obtain sufficient energy, fiber, salt, and other minerals to satisfy their intake requirements in the coastal areas (Bennett & Sebastian, 1988). It suggests that such adaptations have led these colobines to show such dependence on mangrove resources or on other comparable resources found in adjacent coastal habitats. Silvered leaf-eating monkeys (*Presbytis cristata*) seems to live under the same conditions. They forage heavily on plants such as *Rhizophora* sp. in Malaysian mangrove forests (personal observation).

Mangrove forests are also often visited by generalist primate species which use several habitats as potential patches in which to look for food. One of the most representative generalist primate species in the Old World is the long-tailed macaques (*Macaca fascicularis*). They are considered to be a regular riverine forest dwelling monkey as the proboscis monkeys (*Nasalis larvatus*) in the coastal forests (Yager, 1989). However, the long-tailed macaques show an ability to feed on resources such as the bivalve, *Anadara granosa*, that are not exploited by other primates. Long-tailed macaques forage on the edge of the mangrove forests picking up bivalves and other invertebrates from the muddy floor when the tide is out (personal observation). Another important generalist species found in mangrove areas are vervet monkeys (*Cercopithecus aetiops*), known locally as "mangrove monkeys" in southern Senegal. According to Galat & Galat-

Luong (1976) they studied a troop which spent about 80% of their time within the mangrove swamps. In addition, they spent 52% of their feeding activity hunting fiddler crabs (*Uca tangeri*) and 22% eating *Rhizophora* sp. flowers, fruits, shoots and young leaves, as well as the pith of young stilt-roots.

Otherwise, mangrove forests are usually considered as a marginal habitat for other primate species. However, these forests may provide crucial patches of habitat when their behaviour in the system is optimised due to the higher profitability of available resources. In the Neotropical region, capuchin monkeys (*Cebus apella*) are ecologically similar to long-tailed macaques or vervet monkeys. They also show an ability to search for unusual food items in various habitats, including mangrove forest. In fact, capuchin monkeys are potential predators in mangrove forest since they may feed on a variety of invertebrates including crabs, shipworms, and oysters. This may be considered an ecological advantage in colonising marginal habitat by comparison with other primate species and may be an important factor explaining their broad geographic distribution (Fernandes, 1991; Fernandes & Aguiar, 1993). In addition, capuchin monkeys may have a negative effect on mangroves due to the way they disperse the seeds of *Phoradendron* sp., a parasitic-plant found in mangrove forests. According to Terborgh (1983), capuchin monkeys forage in different habitats and in a destructive manner. This may reflect a very common

situation in which foragers adopt a foraging strategy that depletes the resources of different patches in a way that leads to the smallest consequent decline in profitability of the forest with the time.

DISCUSSION

Mammals, that come from adjacent areas, exploit mangrove resources both for long periods and for short visits over an annual cycle. In addition, many species that are looking primarily for shelter will also tend to feed on available food. This feeding activity might be also considered as being disadvantageous for mangrove resources. For example, some ungulate and rodent species may decrease tree productivity due to predation of seeds, buds, flowers, and young leaves (Klimstra & Doodley, 1990; Smythe, 1983). In addition, specialised invertebrate predators (e.g. *Xeromys myoides* - Magnusson et al., 1976) also may affect macrofauna population levels, especially of some crustacean and gastropod species. An evident example of predatory behaviour which appears to limit the macrofauna population in some mangrove areas is shown by the raccoon (*Procyon cancrivorus*) which is a skilful predator of fiddler crabs (*Uca* sp.) in the mangroves in northern Brazil (personal observation). The fact that mangroves are not usually the primary habitat for most of these terrestrial mammals does not mean that their predatory behaviour may not be one of the factors limiting mangrove development. On the other hand, it is

noteworthy that mangrove stands may also benefit from an association with vertebrates. For example, it is well known that high densities of birds on mangroves stands produce so much guano that mangrove trees grow faster there despite daily tidal flushing (Onuf et al., 1977; Simberloff, 1983). As important as birds are in this respect, mammal species also provide examples of beneficial associations with mangrove trees. The cave nectar bat (*Eonycteris spelaea*), for example, flies long distances to feed on flowers of *Sonneratia* sp. (Berry, 1972), as a result of which it acts as a critical pollinator for this particular plant species. In sum, both advantages and disadvantages can be found identified for mammals in becoming associated with mangroves. However, the overall impact of these mammals on the flora and macrofauna productivity in mangrove forests still remains to be assessed.

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Table 1. Geographic zones used by Saenger *et al.*, (1983) to describe distribution of mangrove forests.

Geographic Zones	Parts of the World
1	Asia
2	Oceania
3	West coast of the Americas
4	East Coast of the Americas
5	West Coast of Africa
6	East Coast of Africa and the Middle East

Table 2. Number of vertebrate species associated with mangrove in each of the six mangrove regions of the world (after Saenger *et al.*, 1983).

TAXONOMIC ² GROUP	REGIONS ¹						TOTAL
	1	2	3	4	5	6	
FISHES	283	156	-	212	-	114	765
AMPHIBIANS	2	-	-	2	-	-	4
REPTILES	22	3	-	3	-	-	28
BIRDS	117	244	-	138	-	-	559
MAMMALS ³	45	23	9	14	2	26	119 (111)
TOTAL	529	421	9	371	2	140	1475 (1467)

¹ 1- Asia; 2-Oceania; 3-West Coast of the Americas; 4-East Coast of the Americas; 5-West Coast of Africa; 6-East Coast of Africa and the Middle East.

² The number of fish, amphibian, reptile, and bird species (according to Saenger *et al.*, 1983) were also included in this table to provide some perspective of the richness of vertebrate species which have been recorded to mangrove areas throughout the world. However, there is no doubt that many additional species, for all those groups, remain to be recorded.

³ The number in parenthesis means the real number of mammals recorded in mangroves.

Table 3. Number of species in each order of mammal associated with mangrove throughout the world, based on available literature (see Appendix 1).

ORDER	REGIONS ¹						TOTAL ²
	1	2	3	4	5	6	
Marsupialia	-	4	-	-	-	-	4 (4)
Insectivora	1	-	-	-	-	-	1 (1)
Dermoptera	1	-	-	-	-	-	1 (1)
Chiroptera	11	4	-	-	-	-	15 (14)
Scandentia	1	-	-	-	-	-	1 (1)
Primates	8	-	2	6	1	2	19 (18)
Xenarthra	-	-	-	1	-	-	1 (1)
Rodentia	2	8	2	3	-	-	15 (13)
Cetacea	3	-	-	-	-	-	3 (3)
Carnivora	11	-	3	6	-	4	24 (21)
Proboscidea	-	-	-	-	-	1	1 (1)
Sirenia	-	-	1	1	-	1	3 (2)
Perissodactyla	2	-	1	-	-	2	5 (5)
Artiodactyla	5	2	-	2	1	16	26 (26)
TOTALS	45	18	9	19	2	26	119 (111)

¹ 1-Asia; 2-Oceania; 3-West Coast of the Americas; 4-East Coast of the Americas; 5-West Coast of Africa; 6-East Coast of Africa and the Middle East.

² Numbers in parenthesis mean the real number of mammals recorded in mangroves, according to the Appendix 1.

Table 4. Proposed categories of residence status for mangrove fauna

CATEGORY	DESCRIPTION
Permanent Resident	species which are exclusively dependent on mangrove resources throughout their life-span
Long-term Resident	species which depend on mangrove resources and spend more than a complete seasonal cycle within the system
Seasonal Resident	species which depend on mangrove resources in a single well defined season during their life-span
Partial Resident	species which, while not primarily dependent on mangrove resources, regularly make intentional short movements (days-hours) across the system
Sporadic Visitor	species which are not dependent on mangrove resources in any way, but which may occasionally benefit from foraging or sheltering within the system

Appendix 1. Checklist of mammal species previously recorded in mangrove areas throughout the world, according to a survey of available literature. **1 RS** (RESIDENT STATUS): **PR**-Permanent Resident; **LIR**-Long-term Resident; **SR**-Seasonal Resident; **PIR**-Partial Resident; **SV**-Sporadic Visitor; **2 GD** (GEOGRAPHICAL DISTRIBUTION): The numbers mean the six main geographic zones throughout the world as described in Table 1.

SPECIES	COMMON NAME	LITERATURE INFORMATION	RS ¹	GD ²	FOOD	SOURCE
MARSUPIALIA						
Peramelidae						
<i>Perameles</i> sp.	Long-nosed Bandicoot	No available information.	?	2	?	Hegerl et al., 1979
<i>Isoodon</i> sp.	Short-nosed Bandicoot	No available information.	?	2	?	Hegerl et al., 1979
Phalangeridae						
<i>Trichosurus arnhemensis</i>	Bush-tailed Possum	No available information.	?	2	?	Hegerl et al., 1979
Macropodidae						
<i>Wallabia bicolor</i>	Swamp wallaby	No available information.	?	2	?	Hegerl et al., 1979
INSECTIVORA						
Krinaceidae						
<i>Echinosorex gymnurus</i>	Moon Rat	"The moonrat is widespread but uncommon in lowland... They also extend into mangroves, especially along streams where they feed..."	PR	1	Crabs, fish, Molluscs	McNeely, 1977
DERMOPTERA						
Cynocephalidae						
<i>Cynocephalus variegatus</i>	Flying Lemur	"Found in a wide variety of forest types in high rainfall areas.... They feed on leaves..., including several mangrove species."	PR	1	Leaves and budding flowers	McNeely, 1977
CHIROPTERA						
Pteropodidae						
<i>Rousettus amplexicaudatus</i>	Rousette Fruit Bat	"This is a widespread cave-roosting fruit bat,... mangroves are a potential food source for this species,... where caves are found next mangroves."	PR	1	Molluscs	McNeely, 1977
<i>Pteropus hypomelanus</i>	Flying Fox	"This species is the insular counterpart of Lyle's flying fox roosting in mangroves on islands off of both coasts."	LIR	1	?	McNeely, 1977
<i>Pteropus lylei</i>	Flying Fox	"A colony is found in the mangroves of Ang Sila, with others in the southeast, the peninsula east coast as far south as... on the peninsular west coast."	LIR	1	?	McNeely, 1977
<i>Pteropus vampyrus</i>	Flying Fox	"Widespread in the Indo-Malayan region, it roosts in mangroves or Nipa palms... in several areas along both coasts, but ranges inland to feed."	LIR	1	?	McNeely, 1977
<i>Pteropus alecto</i>	Flying Fox	No available information.	?	1	?	Hall & Richards, 1979
<i>Pteropus conspicillatus</i>	Flying Fox	"...roost sites were located in a variety of vegetation types, including rainforest tracts or riverine rainforest, mangroves..."	LIR	2	?	Richards, 1990

<i>Pteropus poliocephalus</i>	Flying Fox	No available information.	?	1	?	Hall & Richards, 1979
<i>Cynopterus brachyotis</i>	Dog-faced Fruit Bat	"One of the commonest mammals in Thailand, it also roosts in mangroves, including on offshore islands."	LJR	1	?	McNeely, 1977
<i>Cynopterus horsfieldi</i>	Dog-faced Fruit Bat	"Confined to the far south it is often found with... sharing the same roost."	LJR	1	?	McNeely, 1977
<i>Cynopterus sphinx</i>	Dog-faced Fruit Bat	"...roosts in mangroves...a freshly killed specimen, indicating that the species may also feed in mangroves."	LJR	1	?	McNeely, 1977
<i>Eonycteris spelaea</i>	Dawn Bat	"...the <i>Eonycteris spelaea</i> flies long distances to take the pollen of <i>Sonneratia</i> ."	LJR	1	Nectar (<i>Sonneratia</i> sp.)	Berry, 1972
<i>Macroglossus minimus</i>	Long-tongued Fruit Bat	"... occurs in stands of <i>Sonneratia alba</i> in Western Australia."	LJR	2	?	Straughan, 1983
Molossidæ						
<i>Mormopterus planiceps</i>	Little Goblin Bat	"...this species was found to inhabit the mangroves of Cantaburi Province, probably attracted by the year-round availability of pollen and nectar..."	?	2	?	Hall & Richards, 1979
<i>Mormopterus loride</i>	Little Goblin Bat	No available information.	?	2	?	Hall & Richards, 1979
SCANDENTIA						
Tupaiaidæ						
<i>Tupaia glis</i>	Tree Shrew	"Found in a wide range of habitats throughout Thailand, tree shrews also occur in the drier fringes of mangrove areas, especially where there is dense secondary growth."	PJR	1	Insects, fruits, spiders, seeds, buds	McNeely, 1977
PRIMATES						
Lorisidæ						
<i>Nycticebus coucang</i>	Slow Loris	"The Slow loris is a nocturnal primate found throughout Thailand... and therefore finds a rich habitat in mangroves, where it is 'not common'..."	PJR	1	?	McNeely, 1977
Callitrichidæ						
<i>Callithrix jacchus</i>	White ear-tufted Marmoset	No available information.	?	4	?	Fernandes & Aguiar, 1993
Cebidæ						
<i>Saimiri sciureus</i>	Squirrel Monkey	" <i>Saimiri sciureus</i> foi observado forrageando numa mesma árvore (<i>Rhizophora mangle</i>) que <i>Chiropotes satanas</i> ."	PJR	4	Insects	Fernandes & Aguiar, 1993
<i>Alouatta seniculus</i>	Red Howler Monkey	No available information.	?	3	?	Scott <i>et al.</i> , 1976
<i>Alouatta belzebul</i>	Red-handed Howler Monkey	"Os guaribas, <i>A. b. belzebul</i> , podem ser considerados, potencialmente, primatas residentes dos manguezais."	PJR	4	?	Fernandes & Aguiar, 1993
<i>Chiropotes satanas</i>	Bearded Saki	" <i>Saimiri sciureus</i> foi observado forrageando numa mesma árvore (<i>Rhizophora mangle</i>) que <i>Chiropotes satanas</i> ."	SV	4	Insects	Fernandes & Aguiar, 1993

<i>Cebus capucinus</i>	Untufted Capuchin Monkey	No available information.	?	3	?	Freese, 1976
<i>Cebus apella</i>	Tufted Capuchin Monkey	"...enables them to exploit alternative resources in habitats like the mangrove swamp, where typical primates food such as fruit are relatively scarce..."	PtR	4	Oyster (<i>Crassostrea rhizophorae</i>)	Fernandes, 1991
		"...que estes primatas provavelmente desenvolvam todo um ciclo de vida neste ecossistema, e não apenas o utilizem como um ambiente marginal durante os períodos de escassez ou...refúgio contra predadores."		4	Bivalve (Teredinidae) Shrimp (Caridae) Crabs (Decapodidae) Spider (Araneae) Insects (Saturidae, Pentatomidae, Formicidae, Mantidae)	Fernandes & Aguiar, 1993
<i>Ateles geoffroyi</i>	Spider Monkey	"In an environment such as the mangrove swamp, cohesive groups may be small and approximate a family group structure."	SV	4	?	Eisenberg & Kuhen, 1966
<i>Cercopithecidae</i> <i>Cercopithecus aethiops</i>	Vervet Monkey	" <i>Cercopithecus aethiops sabaeus</i> have been known since 1906 to inhabit the mangroves of Southern Senegal, where they are called locally 'mangrove monkeys'."	LtR	5	Fiddler crab (<i>U. tangeni</i>) flowers, fruit shoots young leaves, pith of young stilt-roots	Galat & Galat-Luong, 1976
		"Mangrove swamps surrounding brackish ponds on the northeast coast, surrounded themselves by beach, pasture, and cropland..."		6	?	Sade & Hildreth, 1965
<i>Macaca fascicularis</i>	Crab-eating Macaque	"Although the macaques often spent the night in pedada trees as did the proboscis monkeys..."	PtR	1	?	Kern, 1964
		"The crab-eating macaque is one of the commonest mammals of Borneo. This monkey is common everywhere in the nipa-mangrove association in the tidal zone."		1	?	Davis, 1962
		"...and crab-eating macaque, are common and widely distributed primate through various vegetation types from the coastal swamps to the inland in Sabah..."		1	?	Kawabe & Mano, 1972
		"They are good swimmers and are perhaps the mammals which have adapted best to the mangrove habitat; they find shelter in the trees and food in the water, in exposed mud flat..."		1	Crustaceans	McNeely, 1977
<i>Macaca mullata</i>	Rhesus Monkey	"It has been observed that the monkeys and tigers are interested in honey and they do break the low-lying combs."	PtR	1	Honey (<i>Apis dorsata</i>)	Chakrabarti, 1987
<i>Macaca nemestrina</i>	Pig-tailed Macaque	"The pig-tailed macaque is less commonly seen than the crab-eating macaque. It is less partial to the nipa-mangrove zone."	PtR	1	?	Davis, 1962
		"Although usually found inland from the Crab-eating macaque, it also occurs in mangroves...it seems to be much more migratory than the previous species..."		1	?	McNeely, 1977

<i>Papio</i> sp.	Baboon	No available information.	?	6	?	Graham, 1929
<i>Presbytis melalophos</i>	Banded Langur	"They seem to replace macaques in drier areas of mangroves. The Banded langur is confined to the south and is especially common in the mangroves of Trang..."	LtR	1	Leaves, buds, fruits	McNeely, 1977
<i>Presbytis cristata</i>	Silvered Leaf Langur	"It is a common lowland form in Sarawak and so far as I have seen partial to swampy jungle beside rivers and the sea coast; it is common in the mangrove..."	LtR	1	Leaves, shoots	Banks, 1931
<i>Presbytis obscura</i>	Spectacled Langur	"In Thailand, Spectacled langur and Banded langur occur together, with Banded langur more common in the mangrove forest."	PIR	1	?	McNeely, 1977
<i>Nasalis larvatus</i>	Proboscis Monkey	"The pedada leaves are probably favored but mangrove leaves are eaten regularly."	LtR	1	Pedada leaves (<i>Sonneratia alba</i>), mangrove leaves (<i>R. apiculata</i>)	Kern, 1964
		"Travel away from the river was presumably also limited by the animals' preferred habitats (riverine and mangrove forest) being mainly along the river."		1	?	Bennett & Sebastian, 1988
		"The proboscis monkey is not strictly confined to the nipa-mangrove association. On several occasions individuals were heard in forest farther upstream..."		1	?	Davis, 1962
		"...there were many swampy deltas with well-developed mangrove and nipa-mangrove-mixed forests where the proboscis monkeys very commonly appeared."		1	?	Kawabe & Mano, 1972
XENARTHRA Myrmecophagidae <i>Cyclopes didactylus</i>	Silky Anteater	No available information.	?	4	?	Saenger et al., 1983
RODENTIA Scuridae <i>Callosciurus notatus</i>	Plantain Squirrel	"Other mammals in the area include...and plantain squirrels (<i>Callosciurus notatus</i>)."	PIR	1	?	Bennett & Reynolds, 1993
Muridae <i>Xeromys myoides</i>	False Water Rat	"Forages in <i>Avicennia marina</i> and <i>Rhizophora stylosa</i> ...appear to feed mainly on crabs."	PR	2	Crabs	Hutchings & Saenger, 1987
		"The specimens were in a nest of damp <i>Brugiera parviflora</i> leaves in a mound of black friable mud, against and interlocked within the buttress trunk."		2	?	Magnusson et al., 1976
		"The specimen was taken at low tide in a mangrove (<i>Avicennia marina</i> and <i>Rhizophora stylosa</i>) forest."		2	?	Van Dyck et al., 1979

<i>Oryzomys argentatus</i>	Rice Rat	"...it has been observed on other islands under rather saline conditions."	SV	4	?	Dunson & Lazell, 1982
<i>Rattus rattus</i>	Black Rat	"The black rat (<i>Rattus rattus</i>), a species introduced into Australia, elsewhere in its range occupies many habitats including mangrove islets lacking even brackish water..."	PR	2	?	Hutchings & Saenger, 1987
		"This is the only species of rat that Marshall (in press) found in mangroves during the course of a long-term research project on rats in Thailand."		1	?	McNeely, 1977
		"For example a dense population occurs on the Content Keys in forests of red and black (<i>Avicennia germinans</i>) mangroves."		4	?	Dunson & Lazell, 1982
<i>Rattus sordidus</i>	Rat	No available information.	?	2	?	Hegerl <i>et al.</i> , 1979
<i>Melomys</i> sp.	Mosaic-tailed Rat	No available information.	?	2	?	Hegerl <i>et al.</i> , 1979
<i>Mesembriomys</i> sp.	Tree Rat	No available information.	?	2	?	Hegerl <i>et al.</i> , 1979
<i>Conilurus</i> sp.	Rabbit Rat	No available information.	?	2	?	Hegerl <i>et al.</i> , 1979
<i>Mus musculus</i>	Mouse	No available information.	?	2	?	Hegerl <i>et al.</i> , 1979
<i>Hydromys chrysogaster</i>	Water Rat	No available information.	?	2	?	Hegerl <i>et al.</i> , 1979
Dasyproctidae <i>Dasyprocta punctata</i>	Agouti	"...both species are even found foraging for seed on mangrove forest floors when the tide is out."	SV	3	Seeds	Smythe, 1983
<i>Dasyprocta agouti</i>	Agouti	No available information.	SV	4	Seeds, propagules	Present study
<i>Agouti paca</i>	Paca	"...both species are even found foraging for seed on mangrove forest floors when the tide is out."	SV	3	Seeds	Smythe, 1983
CETACEA Platinistidae <i>Platinista</i> sp.	Susut	"Mammals of a few species have adapted well. Dolphins (<i>Platinista</i> sp.) are still a common sight in rivers of Sunderbans on the Ganga-Brahmaputra delta..."	PR	1	Fishes	Vannucci, 1989
Delphinidae <i>Orcaella brevirostris</i>	Irrawaddy River Dolphin	"Other mammals in the area include... The Irrawaddy dolphin (<i>Orcaella brevirostris</i>) has been recorded..."	SV	1	?	Bennett & Reynolds, 1992
Phocoenidae <i>Phocoena</i> sp.	Common Porpoise	No available information.	?	1	?	Chakrabarti, 1987

CARNIVORA						
Canidae						
<i>Canis</i> sp.	Jackal	No available information.	?	6	?	Graham, 1929
<i>Lycan pictus</i>	African Hunting Dog	"Found at all altitudes and occurring in all vegetation types."	SV	6	?	Stewart & Stewart, 1963
Procyonidae						
<i>Procyon lotor</i>	Raccoon	"...it became obvious that many remote islets completely lacking fresh water supported populations of... and raccoons (<i>Procyon lotor</i>)."	PIR	4	?	Dunson & Lazell, 1982
<i>Procyon cancrivorus</i>	Crab-eating Raccoon	"Other vertebrates found in the trees, particularly in the rear of swamps, are raccoons,..."	PIR	3	?	Simberloff, 1983
		No available information.	PIR	4	Crabs	Present study
Mustelidae						
<i>Lutra sumatrana</i>	River Otter	"...they are often seen on the beach near the mouth of brackish water streams... they are thus less dependent on mangroves."	PIR	1	Fishes	McNeely, 1977
<i>Aonyx chereia</i>	Small Clawed Otter	"These rather small otters are more common in fresh-water streams in mature evergreen forest than in brackish or salt water... but find a rich habitat in mangroves..."	PIR	1	Molluscs, crabs, and shell fish	McNeely, 1977
<i>Pteronura brasiliensis</i>	Otter	No available information.	PIR	4	Fishes	Present study
Viverridae						
<i>Paradoxurus hermaphroditus</i>	Palm Civet	"The common palm civet is probably the most common civet, ranging from Kashmir to the Philippines; it is found throughout Thailand..."	SV	1	?	McNeely, 1977
<i>Paguma larvata</i>	Masked Palm Civet	"The Masked palm civet is another widespread generalized civet... In mangroves, it is probably confined to true mangrove forest."	LIR	1	?	McNeely, 1977
<i>Herpestes javanicus</i>	Mongoose	"...they are primarily carnivorous and enter mangroves to seek fish and other prey..."	PIR	1	Fishes	McNeely, 1977
<i>Herpestes urva</i>	Crab-eating Mongoose	"Ranging throughout Southeast Asia north of Chumporn, the Crab-eating mongoose feeds mainly on aquatic animals..."	PIR	1	Crabs, molluscs	McNeely, 1977
Felidae						
<i>Puma concolor</i>	Mountain Lion	No available information.	?	4	?	Saenger <i>et al.</i> , 1983
<i>Felis pardalis</i>	Ocelot	No available information.	?	3,4	?	Saenger <i>et al.</i> , 1983
<i>Felis viverrina</i>	Fishing Cat	"...in Thai mangrove areas, it is found only from Samut Songkhram to Trat. It occurs in the mangroves of the Sunderbans... and in the mangroves of Java."	PIR	1	Fish, shell fish and crabs	McNeely, 1977
<i>Felis planiceps</i>	Flat-headed Cat	No available information.	?	1	?	McNeely, 1977

<i>Felis iriomotensis</i>	Iriomote Cat	SV	1	?	Vannucci, 1989
<i>Neofelis nebulosa</i>	Clouded Leopard	PtR	1	?	Davis, 1962
<i>Panthera pardus</i>	Leopard	SV	6	?	Stewart & Stewart, 1963
<i>Panthera leo</i>	Lion	SV	6	?	Stewart & Stewart, 1963
<i>Panthera onca</i>	Jaguar	PtR	3	?	Saenger <i>et al.</i> , 1983
		PtR	4	Fishes, deers, birds	Present study
<i>Panthera tigris</i>	Tiger	PtR	1	Large herbivores, fish	Vannucci, 1989
PROSBOSCIDA					
Elephantidae	African Elephant	SV	6	?	Stewart & Stewart, 1963
<i>Loxodonta africana</i>					
SIRENIA					
Dugongidae	Dugong	PtR	6	?	Aleen, 1990
<i>Dugong dugon</i>					
Trichechidae	Manatee	PtR	3	?	Ligon, 1983
<i>Trichechus manatus</i>					
PERISSODACTYLA					
Equidae	Zebra	?	6	?	Graham, 1929
<i>Equus sp.</i>					
Tapiridae	South American Tapir	SV	3	?	Janzen, 1983
<i>Tapirus bairdii</i>					
Rhinocerotidae	Javan Rhinoceros	SV	1	?	McNeely, 1977
<i>Rhinoceros sondaicus</i>					

<i>Dicerorhinus sumatrensis</i>	Sumatran Rhinoceros	"...they have been seen swimming near inlands 20 miles offshore from the Thai-Burma border area..., where mangrove are a prominent feature of the habitat."	SV	1	?	McNeely, 1977
<i>Diceros bicornis</i>	Black Rhinoceros	"From sea level to about 12,000 ft., in all vegetation types."	SV	6	?	Stewart & Stewart, 1963
ARTIODACTYLA						
Suidae						
<i>Sus scrofa</i>	Wild Boar	"Ground-dwelling animals like the wild pig <i>Sus scrofa</i> only venture into the landward edge of the mangrove and only at times of relative dryness."	PIR	1	?	Berry, 1972
		"It is found throughout Thailand, with a distinct on Terutau Island. Pigs in coastal forests feed largely on mangrove..."		1	Molluscs, crustaceans, and fishes	McNeely, 1977
<i>Potamochoerus porcus</i>	African Bush Pig	"Highland forest, tree-grassland, riverine woodland and coastal bush, from sea level to about 12,000 ft."	SV	6	?	Stewart & Stewart, 1963
Camelidae						
<i>Camelus dromedarius</i>	Camel	"The main forage for camels in northern Djibouti (mangrove with <i>Avicennia marina</i>) is very poor..."	LIR	6	Leaves (<i>A. marina</i>)	Faye <i>et al.</i> , 1992
		"Camels, during low tide, cross onto the islands close to the road to feed on the mangrove."		6	Leaves	Aleem, 1990
		"Camel grazing is an additional factor limiting the extent of mangrove development in the Red Sea."		6	Leaves	Price <i>et al.</i> , 1987
Tragulidae						
<i>Tragulus napu</i>	Greater Mouse Deer	"Greater mouse deer have been recorded only from the west coast, where they are common in the terrestrial margin in mangroves from Ranong to Satun..."	PIR	1	?	McNeely, 1977
<i>Tragulus javanicus</i>	Lesser Mouse Deer	"Lesser mouse deer, although seemingly preferring hills to swamps, occurs in all mangrove areas in Thailand, including many islands."	SV	1	?	McNeely, 1977
Cervidae						
<i>Muntiacus muntjak</i>	Barking Deer	"Barking deer are among the most adaptive of deer and it is not surprise that they also occur in mangroves, especially in the terrestrial margin."	SV	1	?	McNeely, 1977
<i>Odocoileus virginianus</i>	White-tailed Deer	"The variety of fruits and flowers important in the deer diet suggested regular and extensive use of red mangrove, black mangrove, ..."	LIR	4	Leaves, fruits (<i>R. mangle</i>), fruits of <i>Avicennia germinans</i>	Klimstra & Dooley, 1990
<i>Mazama americana</i>	Deer	No available information.	SV	4	Leaves (<i>L. racemosa</i>)	Present study
<i>Axis axis</i>	Spotted Deer	"...the spotted deer whose numbers decline as the mangroves are cut."	LIR	1	?	Vannucci, 1989

Giraffidae <i>Giraffa camelopardalis</i>	Giraffe	"Tree-grassland, desert grass-bush and scrub, and coastal forest, up to about 8,000 ft. above sea level."	SV	6	?	Stewart & Stewart, 1963
Bovidae <i>Tragelaphus imberbis</i>	Lesser Kudu	"Desert grass-bush and scrub, and coastal bush and forest, from sea level to 4,000 ft."	SV	6	?	Stewart & Stewart, 1963
<i>Tragelaphus strepsiceros</i>	Greater Kudu	No available information.	?	6	?	Graham, 1929
<i>Tragelaphus scriptus</i>	Bushbuck	"Highland forest, coastal forest and bush, riverine bush and woodland, and well-watered tree grassland."	SV	6	?	Stewart & Stewart, 1963
<i>Bubalus bubalis</i>	Asian Water Buffalo	No available information.	?	2	?	Hegerl <i>et al.</i> , 1979
<i>Syncerus caffer</i>	African Buffalo	"From sea level to over 12,000 ft., principally in highland, riverine and coastal forest..."	SV	6	?	Stewart & Stewart, 1963
<i>Bos javanicus</i>	Oxen	No available information.	?	2	?	Hegerl <i>et al.</i> , 1979
<i>Cephalophus</i> sp.	Duiker	No available information.*	?	6	?	Graham, 1929
<i>Kobus kob</i>	Buffon's Kob	"Other vegetation types that also serve as Buffon's habitat include upland forest... and exceptionally mangrove swamp forest..."	SV	5	?	Warzie, 1991
<i>Redunca redunca</i>	Reedbuck	"Highland grassland and tree-grassland between 4,000 and 7,000 ft. above sea level, and coastal bush."	SV	6	?	Stewart & Stewart, 1963
<i>Hippotragus equinus</i>	Roan Antelope	No available information.	?	6	?	Graham, 1929
<i>Hippotragus niger</i>	Sable Antelope	"Confined to coastal bush and hills near the coast with tree-grassland."	SV	6	?	Stewart & Stewart, 1963
<i>Damaliscus lunatus</i>	Topi	"Highland grassland, tree-grassland, coastal forest bush and exceptionally, desert-scrub..."	SV	6	?	Stewart & Stewart, 1963
<i>Ourebia ourebi</i>	Oribi	"Coastal bush and forest, and tree-grassland up to 8,000 ft. above sea level."	SV	6	?	Stewart & Stewart, 1963
<i>Raphicerus campestris</i>	Scienbok	"Up to 8,000 ft. above sea level in tree-grassland, coastal bush and forest, and in desert grass-bush..."	SV	6	?	Stewart & Stewart, 1963
<i>Madoqua quenitheri</i>	Dik-dik	"Desert grass-bush and scrub and coastal bush..."	SV	6	?	Stewart & Stewart, 1963
<i>Madoqua kirkii</i>	Dik-dik	"Desert grass-bush and scrub and coastal bush..."	SV	6	?	Stewart & Stewart, 1963

Figure 1. Diagram showing the residence categories and their relationships with mangrove and adjacent areas.

