

THE EFFECTS OF FOREST FRAGMENTATION ON BIRD SPECIES  
IN MADAGASCAR: A CASE STUDY FROM AMBOHITANTELY FOREST  
RESERVE ON THE CENTRAL HIGH PLATEAU

by

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**PREFACE**

The experimental work described in this dissertation was carried out in the Department of Zoology and Entomology, University of Natal, Pietermaritzburg, from October 1993 to October 1994, under the supervision of Professor Gordon L. Maclean.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others it is duly acknowledged in the text.

## 1 ABSTRACT

Considering the high rate of endemism in Madagascan organisms, which are mostly restricted to forest ecosystems, and the accelerating rate of deforestation affecting the island, it is critical to understand the effects of forest fragmentation on Malagasy biota to allow for better management of species within ecosystems. Ecological and human-induced changes have led to the disappearance of forest from vast areas of the island, including on the central High Plateau.

The Ambohitantely Special Reserve, located on the central High Plateau at 1500 m asl, was selected as the study site for research on the effects of forest fragmentation on forest-dependent bird species in Madagascar. The Ambohitantely Special Reserve covers 5600 ha of which 50% are natural forest, 35% are anthropogenic grassland savannah and 15% are exotic plantations. The forest, described as East Malagasy moist montane forest, is 2737 ha in area, of which 1487 ha are comprised of 513 forest fragments scattered around the largest block totalling 1250 ha. To investigate the effects of forest fragmentation on forest-dependent bird species, seven forest fragments were selected, ranging from 0.64 ha to 136 ha, in addition to the largest block, referred to as the control site.

The bird species composition and relative abundance in different-sized fragments were assessed in reference to the control site, by using a combination of two standardized sampling methods: mistnetting and point-counts. A total of 1804 mistnet-days were accrued, 1026 in the control site and 778 in the seven forest fragments, leading to the capture of 491 birds of 26 species. A total of 160 point-counts was made at 39 different sample plots totalling 53 h 29 min of censusing, and a record of 30 species.

A total of 72 bird species including 54 breeding forest

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species was found in the reserve, and the biogeographical affinities of the avifauna of Ambohitantely were defined with reference to 32 forest sites scattered across Madagascar.

The species composition in all fragments are fully nested subsets of the control site and the species distribution in the fragments does not represent random subsets of the control site. The analysis of the bird communities in different size fragments indicates that the occurrence of bird species reflects a regular pattern of species extinction in relation to decreasing size of forest fragment. Species composition is discussed in reference to Ambohitantely's long history of isolation that may have led to extirpation of bird species from this site. The higher bird taxa decrease in number or totally disappear as a result of their ecological specialization. Equally, they are the most affected by edge effects (e.g. *Atelornis pittoides*). The main ecological trends in disappearance or extinction of species is a decrease in the number of small-bodied insectivorous understory species and mid- and upper-stratum small-bodied insectivorous and nectarivorous species. Insectivorous species are particularly affected by forest fragmentation and three forest-dependent species found in Ambohitantely Forest are particularly sensitive to forest fragmentation: *Newtonia amphichroa*, *Calicalicus madagascariensis*, and *Cyanolanius madagascarinus*. The biological (flora species composition and forest structure) and the physical (temperature, moisture, and light) changes generated by the fragmentation of the forest have a greater impact on highly specialized foraging guilds and this explains the pattern of current bird species composition in Ambohitantely Forest.

The influence of forest fragmentation on the altitudinal migration process is debated and conservation measures such as the establishment of forest corridors are proposed to improve the protection of biota found in the Ambohitantely Special Reserve.

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## 6. LIST OF ACRONYMS

ANGAP:	Association Nationale pour la Gestion des Aires Protégées;
ASL:	above sea level;
BP:	before present;
DBH:	diameter at breast height;
DEF:	Direction des Eaux et Forêts;
DRFP:	Direction de la Recherche Forestière et Piscicole;
EAP:	Environmental Action Plan
ESSA:	Ecole Supérieure des Sciences Agronomiques d'Antananarivo;
FOFIFA:	Foibe Fihariankarena Sy Fampanandrosoana Ny Eny Ambanivohitra; Centre National de la Recherche Appliquée au Développement Rural;
FTM:	Foiben - Taosarintanin' I Madagasikara;
IGN:	Institut Géographique National;
MEF:	Ministère des Eaux et Forêts;
WWF:	World Wide Fund for Nature.

## 7. INTRODUCTION

It has long been recognized that tropical forests harbour the greatest diversity of life on earth (Raven 1980), even though they represent only 7% of the land surface (Myers 1986). Tropical forests are also well known to be the biome most rapidly affected by human expansion with an estimate of seven to nine million hectares cleared yearly (Myers 1986). This process of destruction leads to the massive extinction of species and creates new ecological conditions in which individual species populations, species composition and species density of all organisms have been altered. More and more often, remnant areas of native vegetation are surrounded by a matrix of agriculture or other anthropogenic environments (Saunders *et al.* 1991). This tendency is likely to continue, so it is important to understand how ecosystem fragmentation causes physical, chemical, and biological changes in time and space. Considering that species loss accompanies or quickly follows habitat fragmentation (Terborgh 1992), a better understanding of the effects of ecosystem fragmentation on biota is important to introduce management of natural habitats and consequently to prevent or minimize species extinction.

Madagascar, as an island, supports fewer species of plants and animals than equivalent continental areas or tropical islands of comparable size (Fig. 1). This fact of island biology is easily assessed through empirical observations. MacArthur & Wilson (1967) provide a theoretical interpretation of this fact, according to which the low diversity of island biota reflects a dynamic equilibrium between extinction and colonization rates of individual species populations. The variables considered include the size of the island, the variability of its topography, its climate, its vegetation and the proximity of the island to a potential source of colonization. The theory of MacArthur & Wilson is relevant to

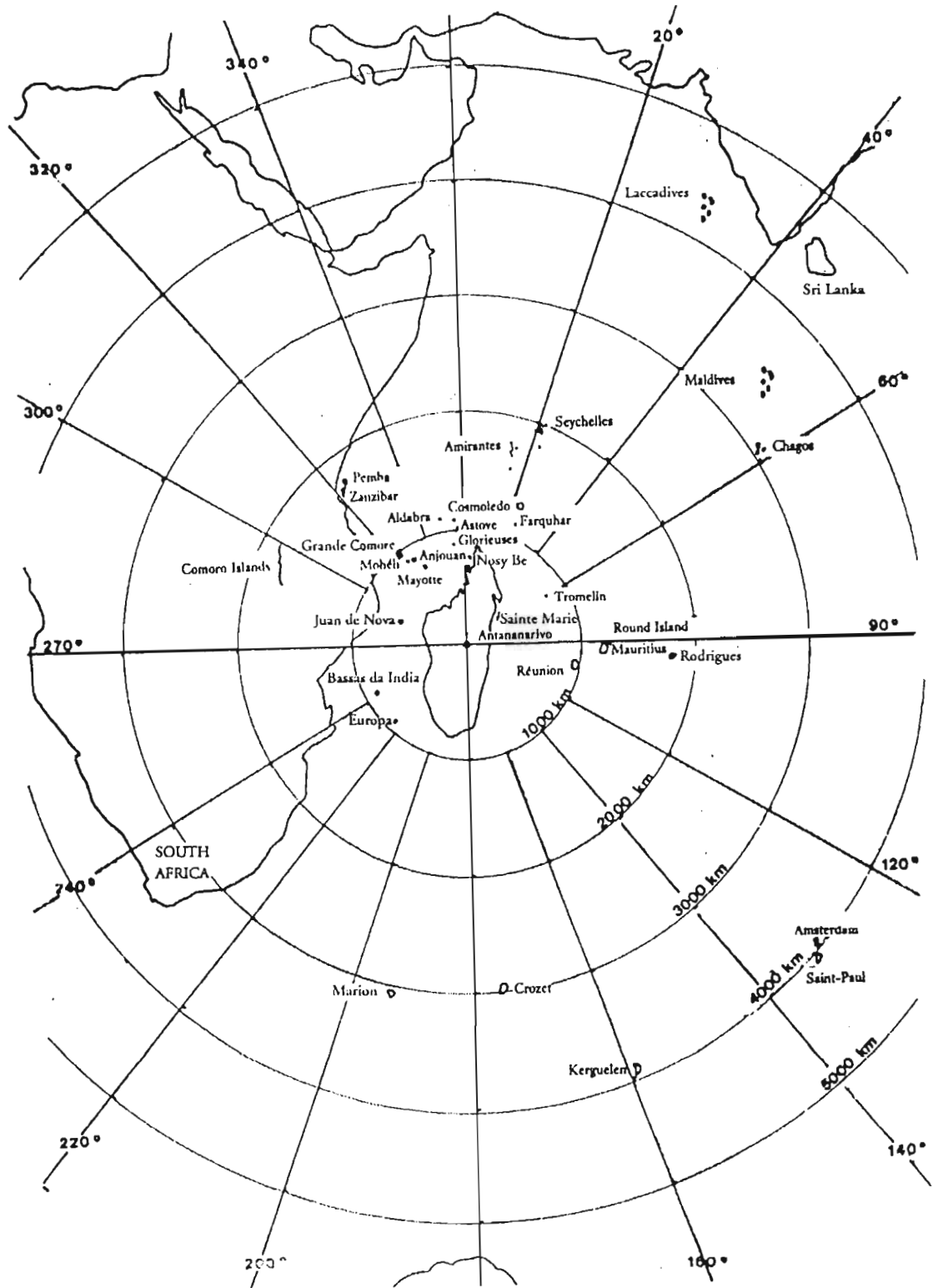


Figure 1: **MAP OF THE OCEANIC ISLANDS OF THE WESTERN INDIAN OCEAN AROUND MADAGASCAR**

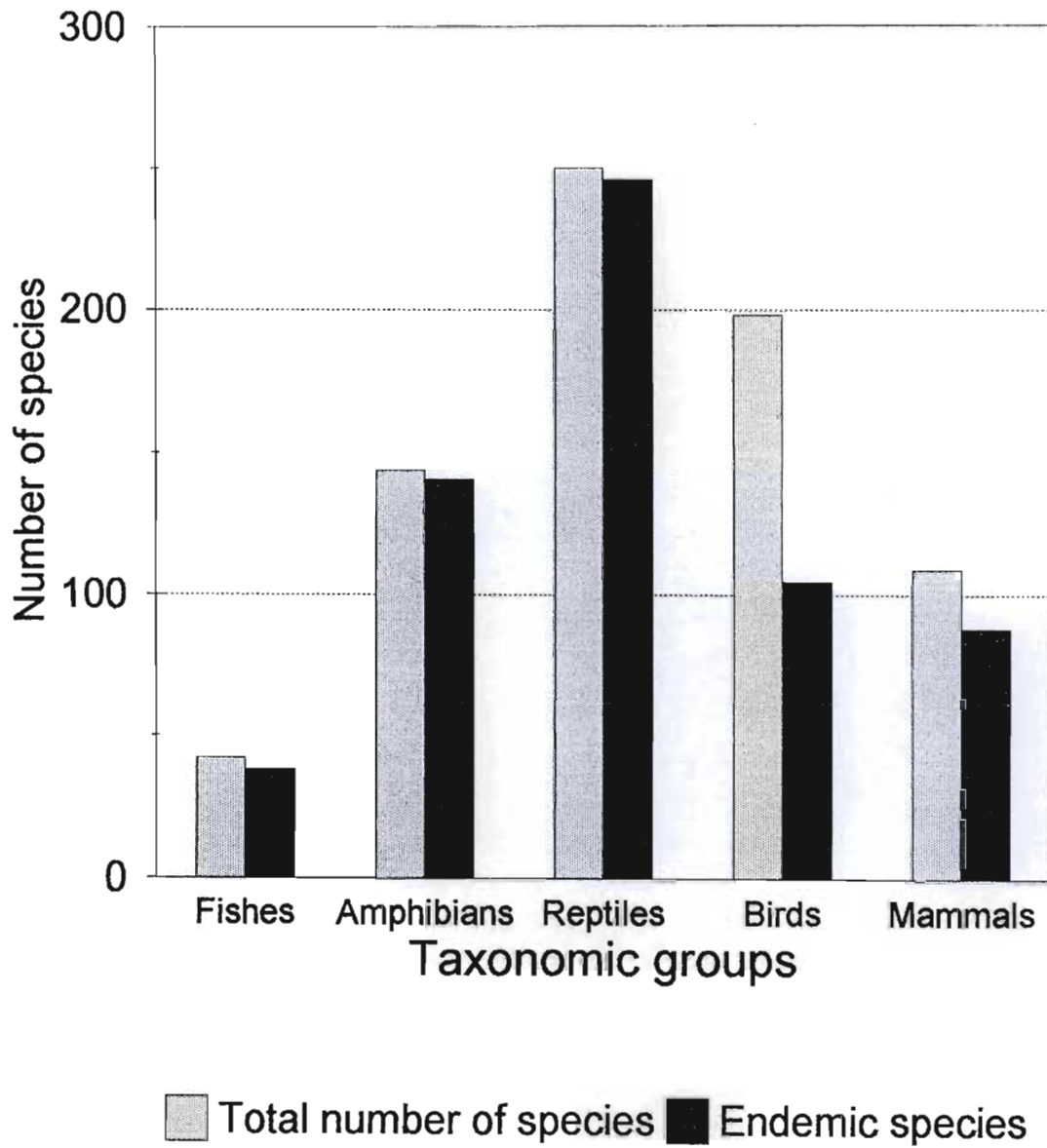
After LANGRAND (1990)



forest fragmentation, since natural habitats are often isolated and surrounded by habitat that forest-dwelling animals seldom if ever disperse across. Thus it is likely that many forest fragments in Madagascar reflect aspects of and are affected by this "island effect". Considering the high rate of endemism rate of Malagasy organisms (80% of the 10 000 vascular plants, 100% of the indigenous terrestrial mammals, 53% of the breeding bird species), mostly restricted to forest ecosystems and the high rate of deforestation (300 000 ha/year) affecting this island (Myers 1986), it is critical to understand the effects of forest fragmentation on the Malagasy biota. This will potentially allow for better management of species within such ecosystems (Fig. 2).

#### **7.1. REVIEW OF LITERATURE ON FOREST FRAGMENTATION RELATIVE TO AVIFAUNA**

About 15 years ago, the scientific community became interested in the effects of forest fragmentation on the different biota (Bierregaard *et al.* 1992). Birds, as indicator species, of worldwide distribution, diverse, especially in forest ecosystems, and fairly easily studied, have rapidly been promoted as an important group in the assessment of biological and physical effects of forest fragmentation on species survival. Loiselle & Blake (1992) described tropical bird communities as "a complex mix of stable and variable components that produce change in species composition and abundance over various spatial and temporal scales". Because of the complexity of tropical bird communities, they have been targeted in studies of forest fragmentation in tropical areas. Some seminal works were completed in the early days, mostly in the Neotropical Region (Willis 1979; Karr 1982, 1990; MacArthur *et al.* 1972; Lovejoy *et al.* 1984; Bierregaard & Lovejoy 1989; Johns 1991; Kattan 1992), but studies were also conducted in the Nearctic Region (Galli *et al.* 1976; Askins *et al.* 1987; Gibbs & Faaborg 1990; Blake 1991; Hamel *et al.* 1993),



**Figure 2: diversity and endemism of Madagascar Fauna**  
(Source: Nicoll & Langrand, 1989)

Palaearctic Region (Blondel 1985, 1991; Thiollay 1993) and Indomalayan Region (Diamond 1984; Diamond *et al.* 1987; Thiollay & Meyburg 1988). Much less attention has been paid to the same type of studies in the Afrotropical Region despite the high species richness harboured by African tropical forests which in addition are facing one of the highest rates of natural habitat destruction in the world. Dowsett-Lemaire & Dowsett's (1984) research in Malawi, Carlson's (1986) in Kenya, and more recently Blankespoor's (1991) in Liberia and Newmark's (1991) in Tanzania are notable exceptions. No similar work, however, had been undertaken hitherto on Madagascar birds.

## 7.2. ATTRITION OF FORESTS IN MADAGASCAR

Ecological change can often be a natural process, even during relatively short periods of geological time. These vicissitudes are the result of shifts in meteorological patterns or ocean levels and induce ecological changes that potentially affect biological communities. There is abundant evidence that human-induced perturbations introduce totally new variables, or at least accelerate natural processes associated with ecological change. The earliest evidence of humans on Madagascar is a human-modified hippopotamus bone which has yielded a radiocarbon date of 2000 years before the present (MacPhee & Burney 1991). This date has been the starting point for interactions between humans and the natural environment. For several decades the prevailing notion in the literature was that before human colonization, Madagascar was covered with a continuous climax forest (Perrier de la Bâthie 1921, 1936; Humbert 1927, 1949, 1955; Decary 1950; Bastian 1964) and that the disappearance of forest from vast areas of the island was the result of human habitat destruction, largely through the use of fire (Humbert 1927). Research on palynology conducted on the central high plateau documents considerable changes in floristic composition as a result of human activity. Based largely on Burney's (1987a, 1987b, 1987c, 1988) pollen studies the three most important conclusions are: "1) Over the last

ten thousand years, the highlands were never covered by a completely closed forest, but by a vegetation which ranged from grasslands to a patchy woodland even before humans arrived; 2) natural forest fires were present and were frequent on the highlands throughout the last ten thousand years; 3) changes in the environment in the direction of modern conditions seem to begin about 1300 years ago in the Itasy, and, with less precision [...]. These may have intensified 600 years ago." Palynology and radiocarbon dating of charcoal found in cores, present evidence that the central High Plateau was a mosaic composed of woodland, bushes and savannah (MacPhee *et al.* 1985).

In the general context of the central High Plateau, the specific question of the extent of the natural forest cover on the *tampoketsa* of Ankazobe (old eroded surfaces restricted to high ground in the surrounding relief) cannot be answered with certainty. However, a strong argument in favour of a much greater forest cover than the current one, is provided by soil analyses that show horizons typical of forest soils in areas that are no longer more covered with forest (Bastian 1964). This argument is supported by Humbert's (1927) statement, that considering that the interior of Madagascar is wet and warm enough to support forest, the remnant forests found today on the central High Plateau should be interpreted as vestiges of a much larger forest cover that has been largely destroyed by human activities.

Madagascar, like most forested African countries is experiencing a dramatic deforestation process. The forest is cleared mostly for subsistence swidden agriculture while in many other tropical rainforest countries the forest is mostly threatened by timber logging. In Madagascar, the tropical rainforest is mainly confined to the east and northwest of the island. The approximate original extent of closed tropical rainforest was 27 508 600 ha of which only 4 171 500 ha still

remain, which represent only 15.2% of the original area (Sayer *et al.* 1992). Green & Sussman (1990) calculated that between 1950 and 1985, 111 000 ha of rainforest were cleared annually. In 35 years time, the Malagasy rain forest will survive only on steep slopes if the destruction continues at the present rate (Green & Sussman 1990) (Fig. 3).

### 7.3. RELEVANT RESEARCH AT AMBOHITANTELY

As one of the last remnant rainforests located on the central High Plateau, various biological aspects of the forest of Ambohitantely have been studied. The *Etablissement de l'Enseignement Supérieur des Sciences d'Antananarivo* (ESSA) has promoted research on the following subjects: flora composition and distribution of the plants (angiosperms, pteridophytes), architectural analysis of arboreal tree species, and floristic and structural characteristics of forest-savannah peripheral zones (Rakotondrainibe *et al.* 1985). More recently an inventory of the vertebrates of the reserve has been completed (Séguier-Guis 1988) as well as a specific inventory of the small mammals (Stephenson *et al.* 1994).

The *Département des Eaux et Forêts* of the *Ecole Supérieure des Sciences Agronomiques d'Antananarivo* obtained in 1988 from the *Ministère des Eaux et Forêts* (MEF), the mandate to conduct research in the reserve. This has been the catalyst for a number of studies on forest ecology. Old botanical trails have been reopened, a large number of mature canopy trees has been identified and tagged and phenological surveys have been conducted regularly ever since. Permanent forest plots have been established to allow observations on the dynamics of the forest and a detailed study on typology has been produced. Mature trees of the most commercially important species have been identified and the collection of seeds has been organized (Razakarina 1993). Research on forestry applied to exotic tree species is conducted by the *Département de Recherche Forestière*

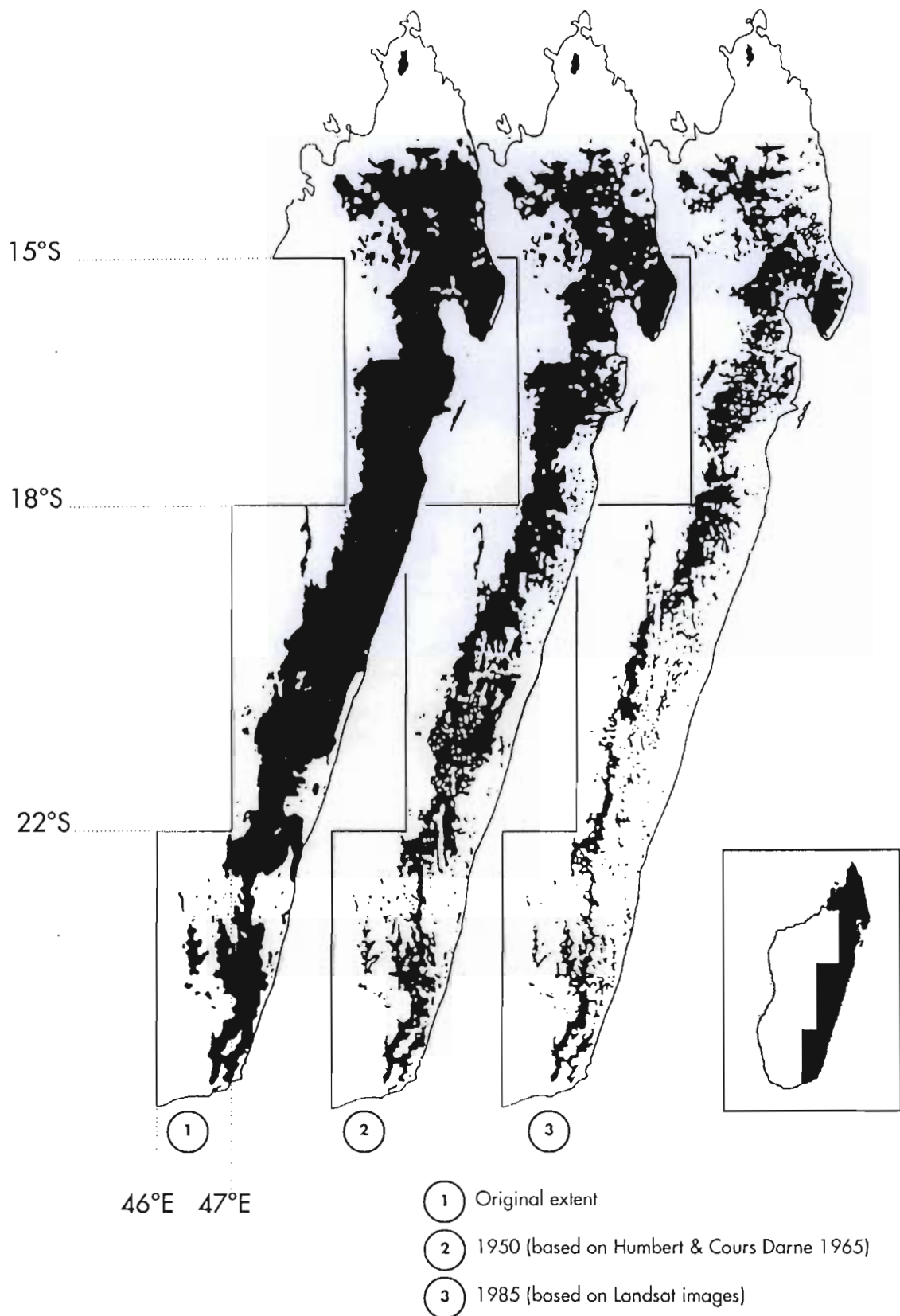


Figure 3: **DISTRIBUTION OF FOREST  
IN EASTERN REGION OF MADAGASCAR  
THROUGH TIME**

(Source : Green & Sussman 1990)



*et Piscicole* of the *Ministère des Eaux et Forêts* in collaboration with FOFIFA (*Foibe Fihariankarena Sy Fampanandrosoana Ny Eny Ambanivohitra - Centre National de la Recherche Appliquée au Développement Rural*) (Razakarina 1993). All these research efforts concentrate on a portion of the largest block of Ambohitantely Forest referred to as the *Jardin Botanique*. This plot of 22 ha was selected by Capuron in 1953 as a favourable site for the establishment of a botanical garden (Razakarina & Andriajaka 1993).

#### 7.4. AIM OF THE STUDY

The purpose of this study is the investigation on the effects of human-induced forest fragmentation on forest-dependent bird species. More specifically the following questions have been addressed: 1) What are the minimum areas of forest needed for the maintenance of certain forest-dependent bird species? 2) Do forest-dependent birds disperse across anthropogenic habitats such as grassland or exotic plantations? 3) What is the relationship between forest fragment size and species diversity?

Ambohitantely Special Reserve is well designed for the purpose of a study on forest fragmentation as it has a clear and stable (non-dynamic) pattern of fragmentation. The forest belongs to the East Malagasy regional centre of endemism (White 1983) and as such harbours an avifauna typical of this biogeographical region, the richest in terms of diversity and endemism on the island (Langrand 1990). The inventories of the avifauna have been made (Nicoll & Langrand 1988), but no in-depth research has been conducted on the birds of this forest. On the other hand, the geology, pedology, climatology, and botany of the region have been well documented (Riquier 1961; Bastian 1964; Rakontondrainibe 1989; Rajaoelison 1990; Andrianjaka 1994).

The study presented herein should be perceived as an attempt to understand more precisely the reaction of forest-dependent bird species to a fragmented forest ecosystem. The results of this study will hopefully be applied to improved management of the Malagasy biodiversity within field-conservation projects.



## 8. STUDY SITE

### 8.1. PHYSICAL FEATURES

#### 8.1.1. BRIEF DESCRIPTION

The Ambohitantely Forest situated on the southeastern side of the Ankazobe *tampoketsa* is located 130 km northwest of the capital city, Antananarivo, in the Province of Antananarivo. This forest has been legally protected for more than 40 years as part of the *Station Forestière de Manankazo* created in August 1951 (Rakotondrainibe 1989). In February 1982, the Special Reserve of Ambohitantely was created (Decree N°82.078). The total area covers 5600 ha, of which 1700 ha is still forested with natural vegetation (Nicoll & Langrand 1989). The rest comprises mostly anthropogenic savannah grassland and exotic tree plantations (*Pinus patula*, *Eucalyptus* spp.). The largest block of original forest measures 8.5 km by 1.5 km and lies between 18°09' and 18°14'S and 47°17'E. (Fig. 4).

#### 8.1.2. GEOMORPHOLOGY

The Malagasy term *tampoketsa* defines old eroded surfaces restricted to high ground in the surrounding relief. The Ankazobe *tampoketsa* is an undulating plateau located between 1662 m asl in the southeastern sector and 1550 m in the northwestern sector that originated in the late Tertiary period from a peneplain covering extensive lateritic deposits (Riquier 1951). (Fig. 5).

Most of the valleys are V-shaped and are geologically recent, although some valleys are flat-bottomed, created by the accumulation of sediments blocked by natural rocky barrages (Riquier 1951). The highest point in the reserve is at Ampasandoaka and reaches 1662 m asl (Séguier-Guis 1988). Recent rivers flow in deep valleys and follow the ancient

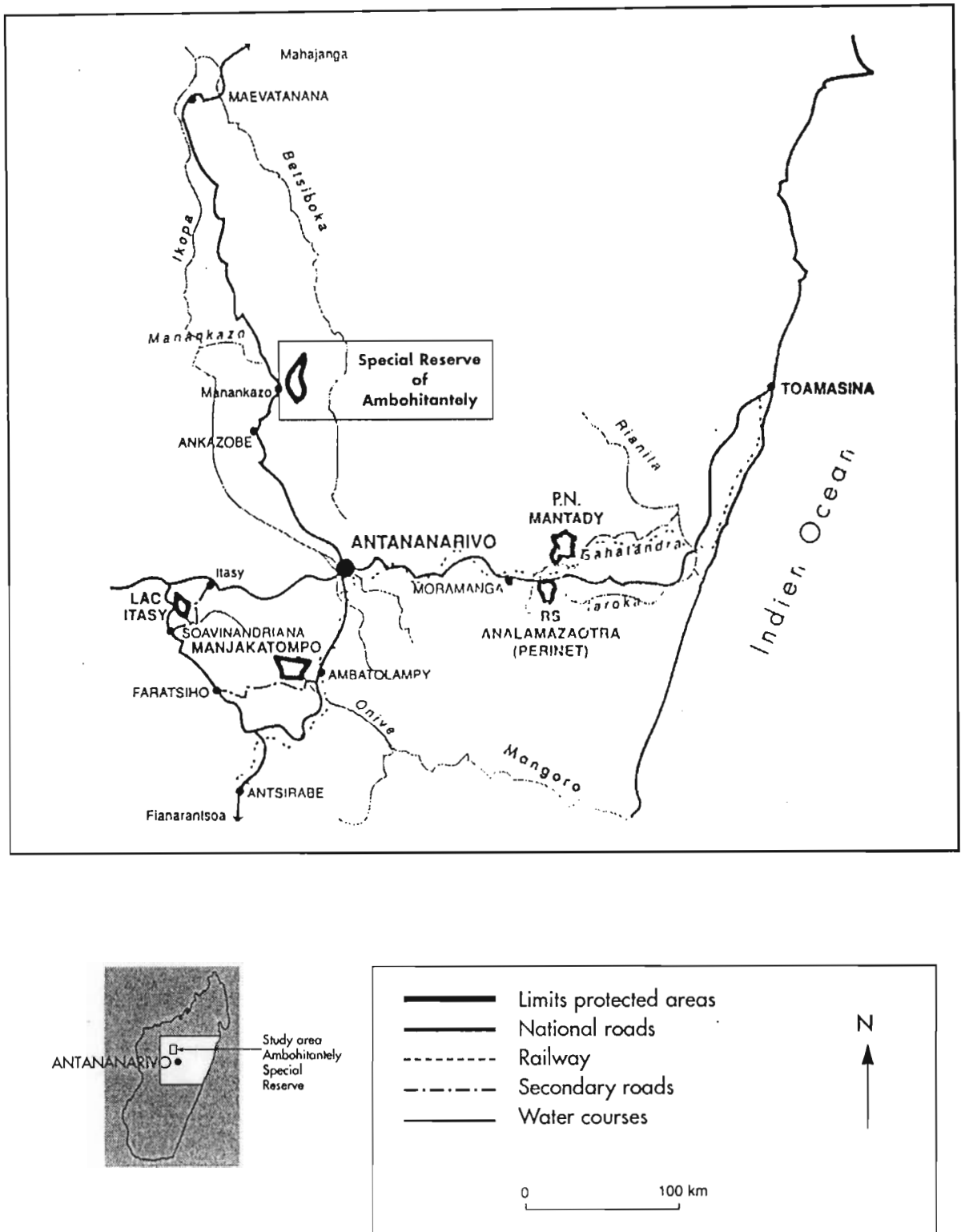


Figure 4: **LOCATION OF THE SPECIAL RESERVE OF AMBOHITANTELY IN CENTRAL EASTERN MADAGASCAR**  
Adapted from Nicoll & Langrand (1989)

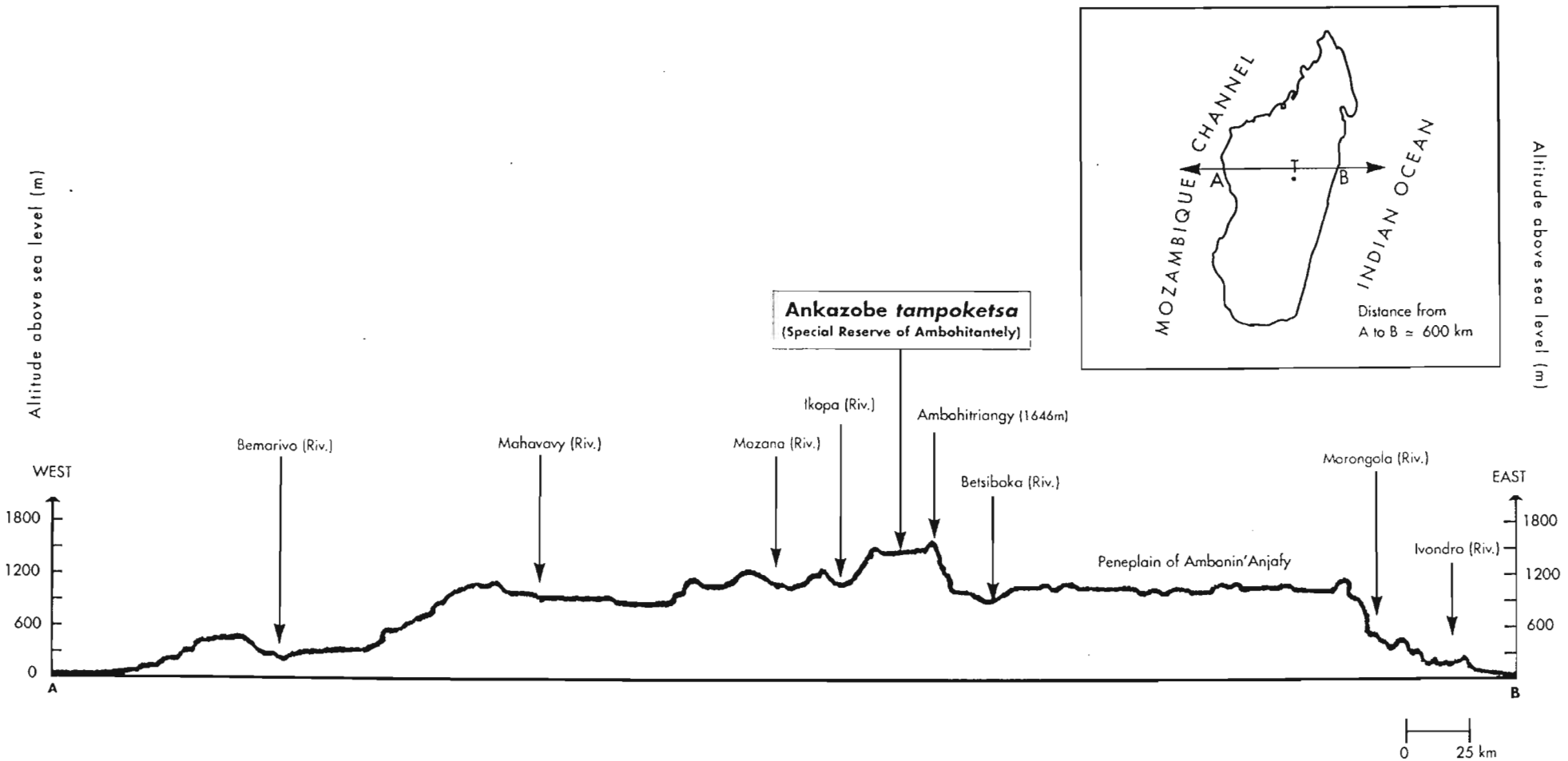


Figure 5: **SCHEMATIC EAST-WEST  
TOPOGRAPHICAL SECTION ACROSS  
THE CENTRAL PART OF MADAGASCAR**

Adapted from Bastian (1964)

hydrographic flow in a northwesterly direction. The eastern slope exposed to the trade winds is where the Ambohitantely Forest is located where it benefits from high rainfall.

#### 8.1.3. HYDROLOGY

The Ambohitantely Forest is located to a large extent in the watershed of the Ikopa River, a small area draining water into the Betsiboka River, which also flows to the West. The formation of the river system in the Special Reserve of Ambohitantely is favoured by steep slopes and good drainage in the forest blocks. Most of the streams that commence in forest fragments, bring water to the Manankazo River, a tributary of the Ikopa River (Séguier-Guis 1988). All major watercourses in the reserve are perennial.

#### 8.1.4. GEOLOGY

The geological formation of the Ankazobe *tampoketsa* is of pre-Cambrian origin and characterized by a crystalline substratum composed of gneiss with inclusions of granite and pegmatite. These rocks are covered with a lateritic surface layer except near tops of hills where the rocky substratum is exposed (Bastian 1964).

#### 8.1.5. SOILS

A dry climate with contrasting seasons led to the formation of a surface layer of red lateritic soils. The lateritic soils were formed through the repeated weathering effects of sudden desiccation and humidification that concentrate iron and aluminium compounds. In the late Tertiary, a humid period favoured the creation of a peneplain (Riquier 1951). A significant proportion of the plateau soils are composed of red laterite that cover underlying rock. However, red lateritic soils are absent in valley bottoms and are replaced in the forest by yellow ferralitic soils that show

a deep humus composition. Soils are acidic with a pH close to 5.0 in the savannah grassland and between 4.4 and 4.7 at the surface in the forest (Bastian 1964). In the valleys soils are predominantly hydromorphic.

#### 8.1.6. CLIMATE

Before 1951, climatic information for the Ambohitantely Forest was registered at the meteorological station of Ankazobe located at 1190 m asl next to an impressive rocky ridge (Bastian 1964). Since 1951, climatic data have been collected at the *Station Forestière de Manankazo*, located at 1475 m in a eucalyptus plantation. The station is 7 km from the nearest edge of the Special Reserve of Ambohitantely (Séguier-Guis 1988). Although it is useful to have access to several decades of climatic information, those originating from Ankazobe do not reflect accurately the climate of the Special Reserve of Ambohitantely because of differences existing in the location of these meteorological stations. A comparison of data collected in Ankazobe and Manankazo puts into perspective the uniqueness of the climate occurring on the Ankazobe *tampoketsa*. At the latter locality, the average temperature is lower (2°C during the coldest month), the annual rainfall is higher (+176 mm) and the total days rainfall is greater (+20 days) (Bastian 1964). Maximum and minimum average temperatures, rainfall and total days rainfall per annum registered at Manankazo are presented in Table 1.

Because of its location on the central High Plateau, the Special Reserve of Ambohitantely is affected by a cool, humid tropical climate with moderate mean temperatures (Donque 1972). The cool season (April to October) coincides with the dry season, and the warm season (October to March) with the rainy season (Donque 1972). The climatic information presented below originates from data collected at the Manankazo Station between 1965 and 1992.

Highest temperatures are recorded during the rainy season from October to March. The mean monthly maximum varies between 18.7°C (July) and 24.4°C (December). The monthly minimum mean varies between 8.0°C (August) and 14.6°C (December). The average monthly temperature varies between 13.5°C in August and 19.5°C in December.

Rainfall occurs all year round although the heaviest rains occur in summer often as thunderstorms. In winter, light rains fall mainly as a fine drizzle. Between 1965 and 1987, the average annual rainfall was 1823 mm. The maximum precipitation is 386.5 mm in January and the minimum is 13.7 mm in June (Séguier-Guis 1988). Between 1989 and 1992, an average of 187 days of rain was recorded yearly with a maximum of 24 days of rain in January and a minimum of 6 days of rain in September (Andrianjaka 1994).

The Martonne aridity index is 34.7 (Appendix 1) for Ambohitantely versus 29.8 for Périnet Analamazaotra (18°28' S - 48°28' E) located at 900 m asl (Séguier-Guis 1988). This relatively high index is the result of a foehn effect that affects this region.

Relative humidity is high all year round thanks to the frequent early-morning fogs. The driest months are September and October with 83% humidity and the most humid is May with 99%, recordings were taken at 07:00 hours (Bastian 1964).

The number of hours of sun per day on the plateau is important and decreases depending on the steepness of valley slopes. It decreases in the rainy season because of frequent thunderstorms.

The Ankazobe *tampoketsa* is a relief that displays distinctive V-shaped valleys formed to the east of the plateau at altitudes between 1500 and 1800 m asl. The scalloped valleys induce air flow that favours the formation of clouds and

Table 1:

**SUMMARY OF CLIMATIC DATA**  
**MANANKAZO (DRFP/FOFIFA) METEREEOLOGICAL STATION**  
(18°08'141 Lat.S., 47°13'971 Long.E., Alt. 1440m)

After Séguier-Guis (1988) and Andrianjaka (1994)

1965 - 1987	Jan.	Fev.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	TOTAL
Rainfall (mm)	386.5	341.7	279.7	83.2	23.2	13.7	13.8	16.6	15.8	76.6	208.1	364.2	1823.1
No. of days of rain	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Average temp. (°C)	18.4	18.4	18.2	17.5	16.1	14.1	13.6	13.5	15.3	17.3	17.9	18.3	16.5
Max. temp. (°C)	23.0	22.8	22.9	22.4	21.7	19.3	18.8	19.1	21.5	23.6	23.7	23.2	21.8
Min. temp. (°C)	13.8	14.1	13.6	12.7	10.6	8.9	8.5	8.0	9.2	11.1	12.2	13.5	11.3
Evaporation	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
1989 - 1992													
Rainfall (mm)	417.2	498.5	131.6	69.4	31.5	8.5	5.3	8.3	7.8	67.4	169.8	264.0	1662.0
No. of days of rain	24.7	23.7	23.2	14.25	13.25	11	9.25	10.25	6	10.75	17.75	23.25	187.5
Average temp. (°C)	19.3	19.2	19.2	17.9	16.6	14.2	14.3	15.2	16.7	19.0	19.0	19.5	17.5
Max. temp. (°C)	24.3	23.7	24.0	22.2	21.1	19.3	18.7	19.3	21.7	24.0	23.8	24.4	22.2
Min. temp. (°C)	14.3	14.5	12.1	13.5	12.2	10.8	9.7	11.2	12.0	13.9	13.6	14.6	12.7
Evaporation	53	36.1	43.8	51.4	44.5	51.3	54.0	60.5	80.0	84.5	58.7	50.6	668.4



consequently precipitation (Donque 1972). The Ankazobe *tampoketsa* is well known for its strong winds. The prevailing wind comes from the east. Of 2185 wind recordings, 1734 (79.4%) are accountable to the east, 171 (7.8%) to the west and 124 (5.7%) to the northwest (Bastian 1964). Winds recorded at a speed equal or exceeding 5 m/s come principally from the east (94.1%), the west accounting for only 2.2% and the northwest 3.2%. The predominantly easterly wind is a trade wind blowing mainly in winter. Much of the drizzle and dew occurring at night is brought by this wind.



## 8.2. BIOLOGICAL FEATURES

### 8.2.1. VEGETATION

#### 8.2.1.1. GENERAL DESCRIPTION

The forest of the Special Reserve of Ambohitantely is 2737 ha in area of which 1487 ha are comprised of small forest fragments scattered around the largest block of 1250 ha. These forest fragments are found mainly at the heads of valleys and at the edge of the plateau (Battistini 1972). Ambohitantely is one of the last tracts of natural forest found on the central High Plateau. The forest covers close to 50% of the area of the reserve and approximately 35% is covered by anthropogenic grassland savannah and 15% by exotic tree plantation.

#### 8.2.1.2. THE NATURAL FOREST

##### 8.2.1.2.1. PHYTOGEOGRAPHY AND PLANT DIVERSITY

The Forest of Ambohitantely is an evergreen rainforest which has close taxonomic affinities with the flora found in the eastern part of Madagascar. This forest type, which was more extensive before human colonization of the island, occurs the length of the island, from Sambava to Tolagnaro. It belongs to the East Malagasy regional centre of endemism and typifies the Central Domain of vegetation (White 1983). It is described by Perrier de la Bâthie (1921) as a moss forest with herbaceous understorey, by Koechlin *et al.* (1973) as a dense humid mountain forest and by White (1983) as East Malagasy moist montane forest. This mountain forest shows typical tropical features with a high proportion of evergreen species and only small number of deciduous species. A large proportion of trees blooms during the rainy season; flowering and

fruiting periods can be variable from year to year (Razakanirina & Andrianjaka 1993). The forest is floristically rich. For example, more than 150 species of pteridophytes have been collected (22 families, 52 genera), representing 27% of the total number of pteridophytes known from Madagascar and the Comoros Islands (Rakotondrainibe et al. 1988). Close to 900 woody plant species have been identified within the reserve (Anon. 1990).

#### 8.2.1.2.2. FOREST TYPOLOGY

Rajoelison (1990) has studied the typology of the Ambohitantely Forest and has defined four different types of forest depending on topography and soil composition. (Fig. 6).

##### RIPARIAN FOREST

This is a three-storey forest type found in valley bottoms. It is characterized by the presence of *Dyospyros gracilipes* and *Thecacoris cometra*. The canopy has an average height of 20 m with some emergent trees reaching 30 m (*Canarium madagascariense*, *Gambeya boiviniana*, and *Ocotea madagascariensis*). Large trees with a 30-40-cm diameter at breast height (dbh) are common. Some girths may reach 65 to 100 cm dbh (*Canarium madagascariense*). The deep colluvial-based soils are moist and provide nutrients. Riparian Forest is floristically the richest forest type in the reserve with 148 species of woody plants, with a dbh larger than 5 cm.

##### SLOPE FOREST

This is a forest type of two storeys and is found on slopes. It is characterized by the presence of *Podocarpus madagascariensis*. The canopy reaches an average height of 16 m and the intermediate stratum is dominated by an arboreal crawling bamboo species (*Cephalostachyum* sp.). The soils are deep and fairly rich in humus. Humidity is high with much

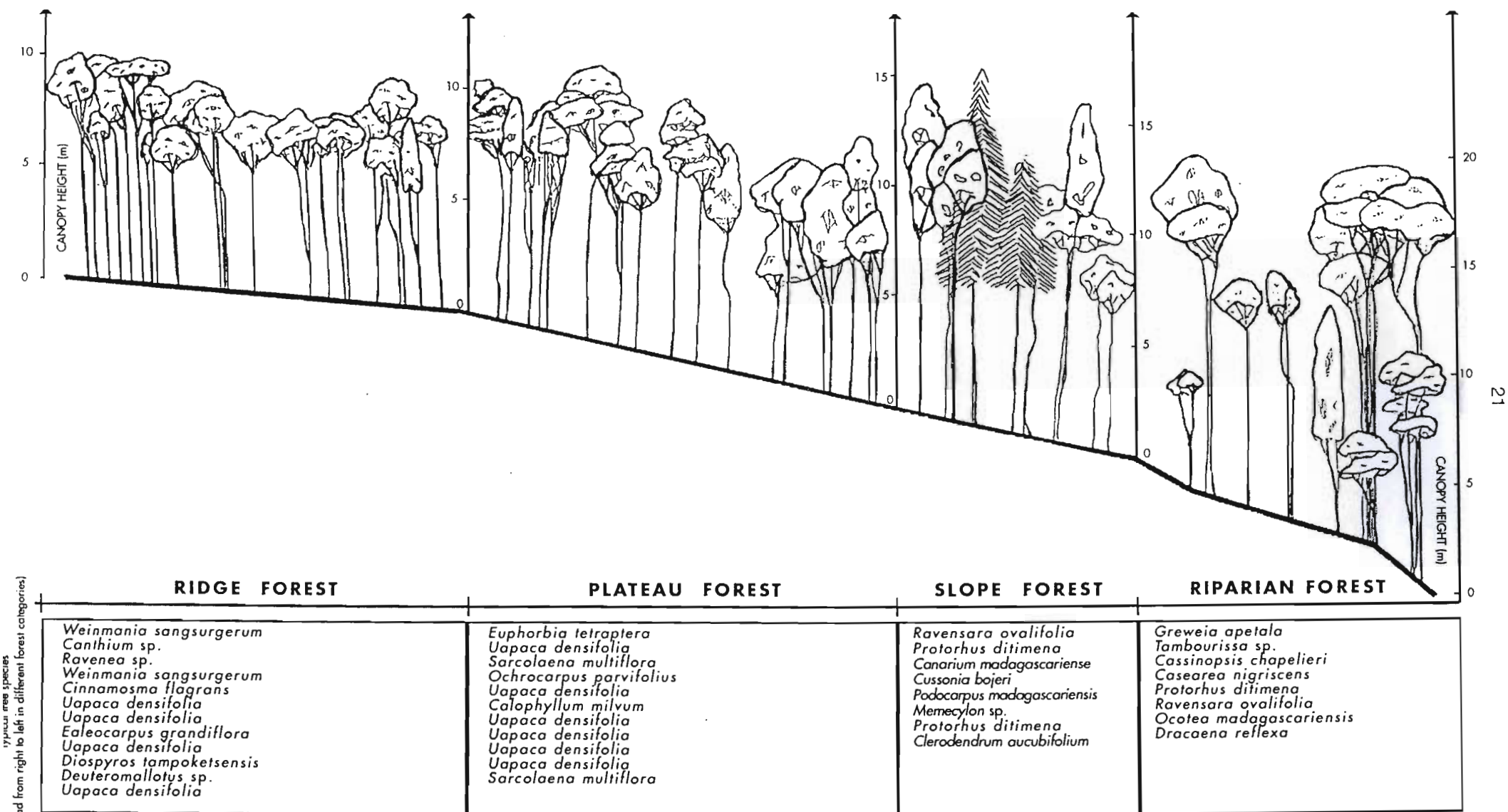


Figure 6: **STRUCTURAL PROFILE AND TYPOLOGY OF THE AMBOHITANTELY FOREST**

Adapted from Rajaoelison (1990)

precipitation at night.

#### PLATEAU FOREST

This is a forest of two storeys found on level ground and dominated by *Uapaca densifolia*, *Sarcolaena multiflora*, and *Leptolaena multiflora*. These three species occupy 53% of the area of this forest type. The canopy has an average height of 10 to 12 m. The soils are dry and compact with the rocky formations close to the surface.

#### RIDGE FOREST

This is a single-storey forest found on ridges and dominated by *Uapaca densifolia*. This single species occupies 55% of the canopy area of this forest type. The canopy has an average height of 8 m and most of the trees have a diameter at breast height of between 5 and 10 cm. Because of lower nocturnal precipitation, the soils are dry, compact, and often with exposed rocks.

#### 8.2.1.3. EDGE VEGETATION

The transition between the forest and the savannah grassland is often abrupt. The vegetation found at this ecotone is characterized by a large number of grass species and a few woody species. The edge vegetation that does not exceed 6 m in height is dominated by large ferns (*Pteridium aquilinum*), small trees (*Philippia floribunda* and *Agauria salicifolia*), and larger trees (*Weinmania rutenbergii*, *Kaliphora madagascariensis*, and *Alberta minor*). The proportion of ferns, bushes, and trees is directly related to frequency of forest-edge burning. Most recently burnt peripheral zones show a large proportion of *Pteridium aquilinum* (Radimbison & Edmond 1988).

#### 8.2.1.4. ANTHROPOGENIC GRASSLAND SAVANNAH

The grassland savannah covers about 35% of the area of the Special Reserve of Ambohitantely. This formation has an anthropogenic origin and is composed only of different grass species, some of which are indigenous(\*) (Mabberley 1989): *Aristida* sp.\*, *Loudetia stipodes*\*, *Imperata cylindrica*, *Trichopteryx drageana*\*, *Panicum* sp., and *Andropogon* sp. (Séguier-Guis 1988; pers. obs.). The limit between the savannah grassland and the forest is very abrupt. The grassland savannah is burnt almost every year by local inhabitants to provide grazing pastures for cattle.

#### 8.2.1.5. EXOTIC TREE PLANTATIONS

In 1939 the Ankazobe *tampoketsa* was considered by the colonial administration for a massive reforestation programme, but this plan was postponed because of the Second World War. In 1951, as part of a major reforestation project called "Projet Forêt Noire", the *Station Forestière de Manankazo* had been gazetted on a 15 000-ha plot and in 1953 the first plantation of exotic trees (*Eucalyptus* spp.) had been planted. Initially hardwood species were favoured (*Cedrella* spp. and *Eucalyptus* spp.), but because of poor soil quality the growth of these trees has been so slow that the production stage has yet to be implemented. In 1958 plantations on better-drained slopes with *Pinus patula* were installed and these have been successful (Bastian 1964). Since then, this species, originally from Mexico, has then been largely used in commercial forestry. Forestry activities were developed before to the creation of the Special Reserve of Ambohitantely. Today 15% of the reserve is covered with *Pinus patula* arranged in plots of varying sizes, but more extensive areas are located outside the reserve in the forest station. Some fragments of natural forest are surrounded by pine plantations but these exotic trees do not spread within the natural forest biome.

### 8.2.2. STUDY SITE

For the purpose of conducting research on the effects of the forest fragmentation on forest-dependent bird species in Madagascar, the Special Reserve of Ambohitantely was selected. It fulfilled the requirements for the study site for the following reasons.

- 1) The main forest block (control site) should be more than 1000 ha in size and "relatively" intact.
- 2) The surrounding forested islands (forest fragments) should have been connected to the control site historically.
- 3) Forested islands selected should vary in size from extremes of about 200 ha to less than one ha. The other islands should more or less evenly grade in size between these ranges.
- 4) The control site and forest fragments should be at the same elevation (about 50 m elevation difference between sites studied).
- 5) The approximate period of fragmentation of forest fragments from the control site should be known.
- 6) The avifauna should be well documented.
- 7) The number of forest-dependent species in the control site should be at least 10.

The Special Reserve of Ambohitantely harbours the largest remnant tract of original forest that now exists on the central High Plateau of Madagascar. The largest block of 1250 ha was selected as the control site. Seven fragments of different size have been selected (Figs. 7 and 8, Table 2).

### 8.2.3. FRAGMENTATION PATTERN

Bastian (1964) stated that during the late Pleistocene and Holocene, the central High Plateau was largely covered with rainforest. Some recent research on original forest cover of the central High Plateau conducted by MacPhee *et al.* (1985) and Burney (1987a; 1987b; 1987c) in the Antsirabe region offers a

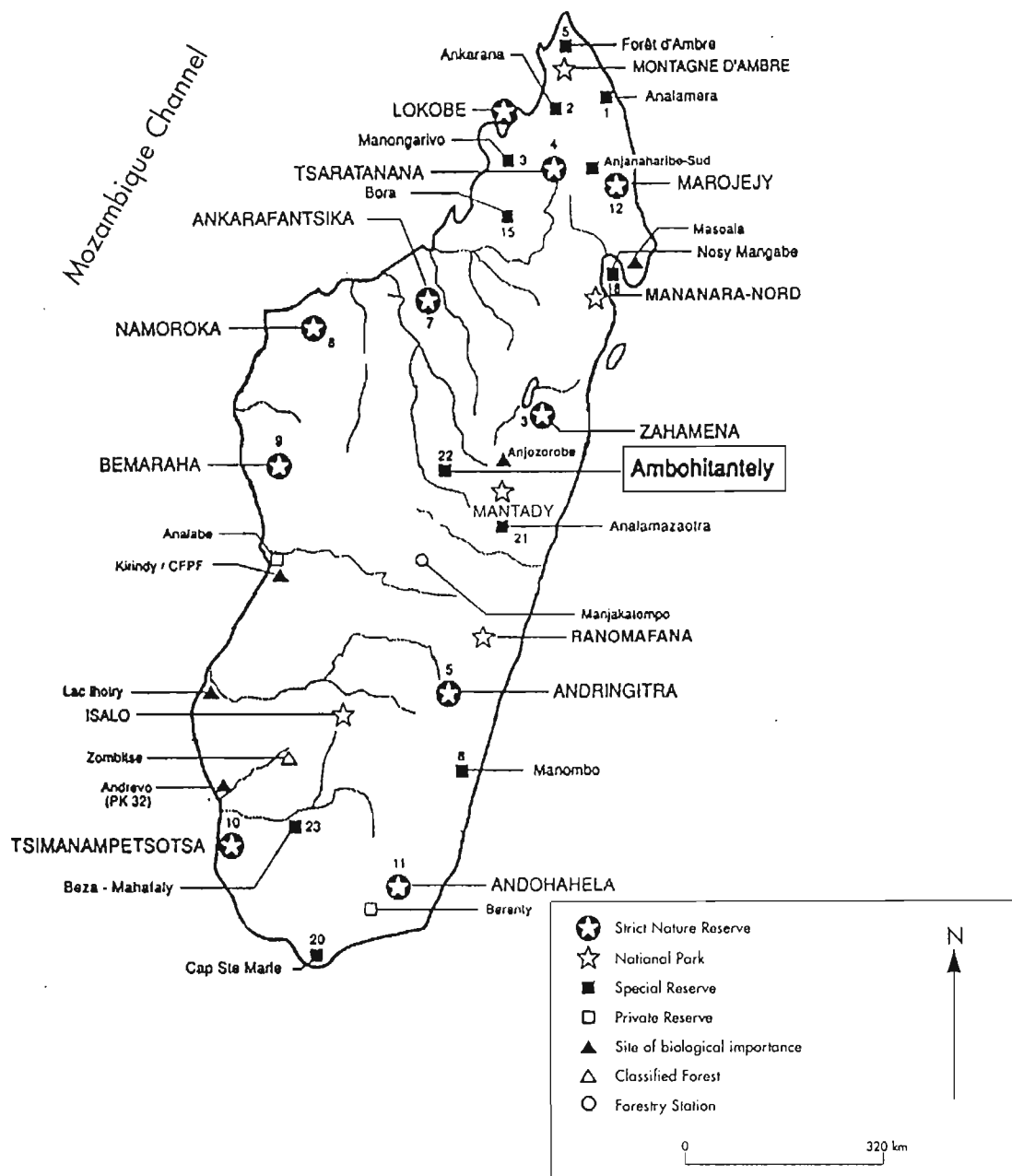
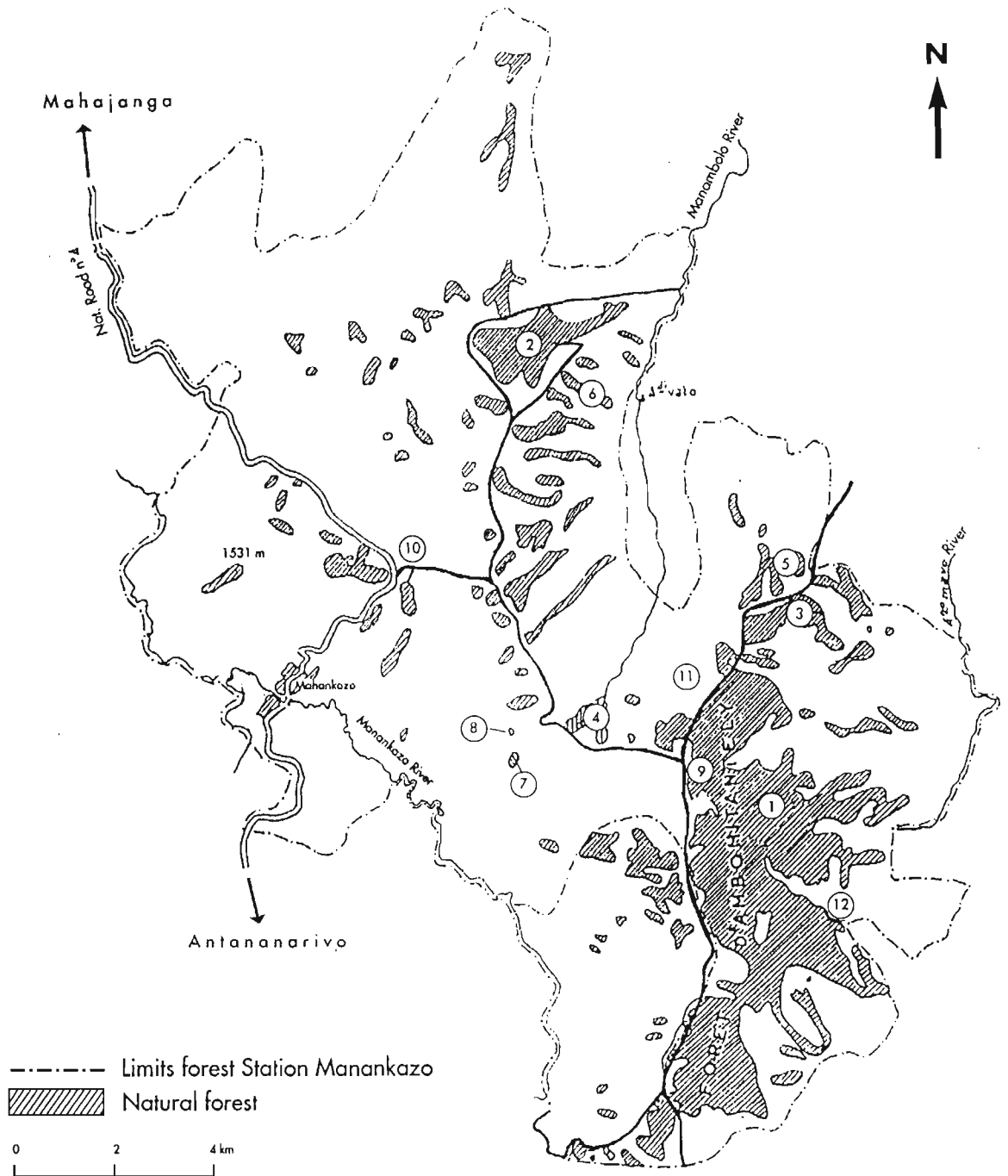


Figure 7: **LOCATION OF PROTECTED AREAS AND BIOLOGICALLY IMPORTANT SITES IN MADAGASCAR**  
(after LANGRAND 1994)





- |                          |  |
|--------------------------|--|
| ① Control site (1250 ha) | ⑦ Fragment H1 (4 ha)                               |
| ② Fragment A (136 ha)    | ⑧ Fragment H5 (0.64 ha)                            |
| ③ Fragment E (52 ha)     | ⑨ Base camp  |
| ④ Fragment H (30 ha)     | ⑩ DRFP / FOFIFA Manankazo - Meteorological Station |
| ⑤ Fragment F (28 ha)     | ⑪ Ambohitriangy 1646 m                             |
| ⑥ Fragment A12 (12 ha)   | ⑫ Ampasandoaka 1662 m                              |

Figure 8: **LOCATION MAP OF THE SPECIAL RESERVE OF AMBOHITANTELY**

Adapted from a map of Service Provincial des Eaux et Forêts (Antananarivo)



Table 2:

## SIZE AND LOCATION OF THE CONTROL SITE AND THE FOREST FRAGMENTS SELECTED

SITES	SURFACE AREA	* COORDINATES	** ALTITUDE	TRANSECTS	DISTANCE 1	DISTANCE 2
Control site	1250 ha	18°10'065 Lat S - 47°16'667 Long E 18°10'065 Lat S - 47°16'667 Long E 18°10'065 Lat S - 47°16'667 Long E 18°10'960 Lat S - 47°16'747 Long E	1420 - 1485 m 1450 - 1495 m 1460 - 1510 m 1470 - 1505 m	(A) (B) (C) (E)		
Fragment A	136 ha	18°06'368 Lat S - 47°14'913 Long E	1475 - 1525 m		5800 m	9960 m
Fragment E	52 ha	18°08'425 Lat S - 47°17'779 Long E	1370 - 1435 m		240 m	4480 m
Fragment H	30 ha	18°09'586 Lat S - 47°15'522 Long E	1375 - 1480 m		400 m	3920 m
Fragment F	28 ha	18°08'288 Lat S - 47°17'909 Long E	1395 - 1440 m		800 m	5240 m
Fragment A12	12 ha	18°06'461 Lat S - 47°15'175 Long E	1455 - 1550 m		4400 m	8640 m
Fragment H1	4 ha	18°09'463 Lat S - 47°15'062 Long E	1140 - 1450 m		1960 m	5040 m
Fragment H5	0.64 ha	18°09'465 Lat S - 47°15'311 Long E	1480 - 1490 m		2040 m	5280 m

\* Latitude and longitude measurements were made with a Geographical Positioning System (GPS) unit.

\*\* Altitude was recorded with an altimeter (accuracy 5 m).

DISTANCE 1: edge of fragment to edge of control site.

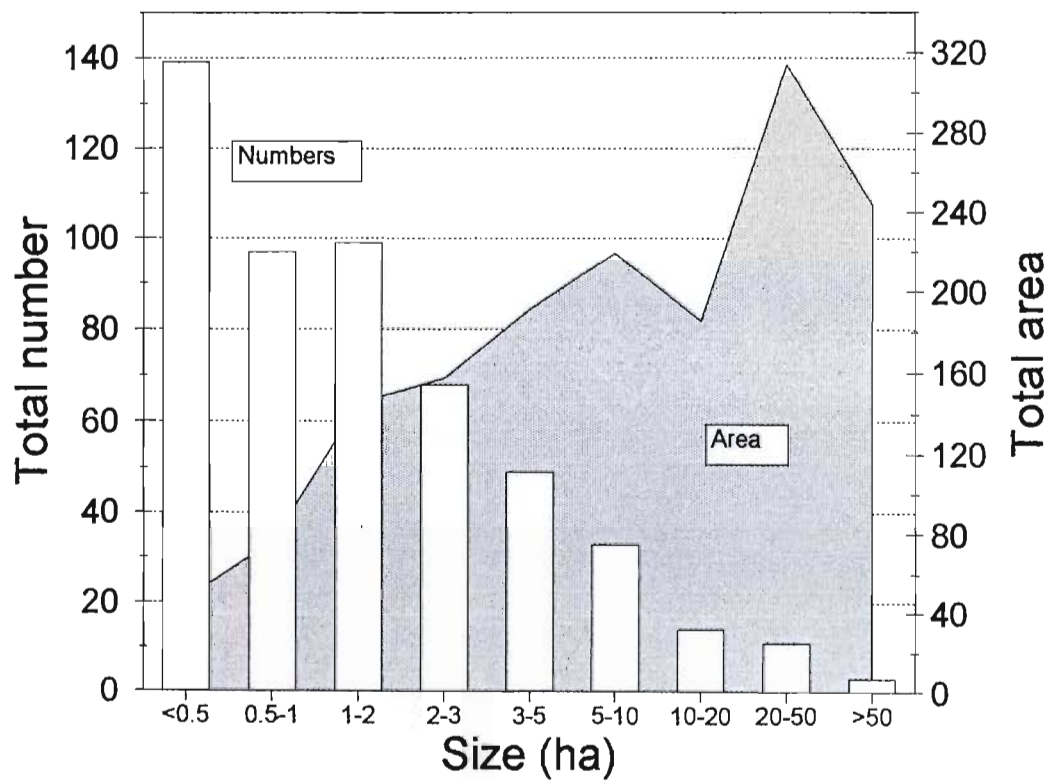
DISTANCE 2: middle of the fragment to middle of the control site.

different hypothesis. It is likely that around 7000 BP the natural vegetation of the central High Plateau was a mosaic of woodlands, bushlands and savannah, depending on the edaphic factors (MacPhee et al. 1985). However, through soil study of the Ankazobe *tampoketsa* it is possible to show that the forest largely covered the *tampoketsa* except areas where the red lateritic crust had not been broken up (Riquier 1951). The factors that have contributed to any change are likely to be natural and human (Bastian 1964). Today, the climate of Ambohitantely is drier than the one that affected this site in the late Tertiary (Riquier 1951). Ecological change associated with deforestation by humans has led to the forest-fragmentation pattern visible today. In 1897 the largest forest block of Ambohitantely measured 20 km long and today, using modern measuring instruments, 8 km in the 1980s (Séguier-Guis 1988). In 1964, Bastian estimated that the forest of Ambohitantely was composed of a block of 2000 ha and 1000 ha of fragmented parcels. About 20 years later, the largest block was estimated between 1600 ha (Ratotondrainibe et al. 1985) and 1700 ha (Nicolli & Langrand 1989). Precise mapping from aerial photos taken in 1991, proved that the natural forest of Ambohitantely is composed of a large block of 1250 ha and of 513 fragments representing 1487 ha, giving a total of 2737 ha of natural forest legally protected within the Special Reserve of Ambohitantely. Most of the fragments are small (78% less than 3 ha) and only three are larger than 50 ha (Fig. 9). They are located on slopes facing east where rainfall is higher because of prevailing trade winds, as well as along valleys.

#### 8.2.4. HISTORY OF EXPLOITATION

##### 8.2.4.1. DEFORESTATION

The main factor affecting reduction of the forest is human, but it is difficult to define the timing of events that led to the current fragmentation. The presence of tombs of "Vazimba", (considered to be ancestors of the Malagasy people),



**Figure 9: Ambohitantely Special Reserve  
Size of the 513 fragments**

found at Ampasandoaka (1662 m asl) (Bastian 1964), proves that the Ankazobe *tampoketsa* was populated for a long time. However, this region has always had a low human density, one of the lowest in Madagascar. The population density in the *fivondronana* (district) was 4.68 inhabitants/km<sup>2</sup> in the 1960s (Le Bourdieu et al. 1969), six in 1976 and nine in 1989 (Anon. 1991). For comparison, in 1969 the average density, on a national scale, was 13.5 inhabitants/km<sup>2</sup> (Le Bourdieu et al. 1969) and 17 in 1987 (Anon. 1991). Despite this historically low human density in the Ambohitantely area, the disappearance of natural forest has been rapid. The toponymy in Ambohitantely provides some arguments in favour of a formerly more extensive forest cover. Some areas, now totally or partly deforested, still have names that are witness to a forested past: e.g. Manakazo ("dense forest"), Analavory ("round forest"), Ankazomena ("red woods"), Ankafotra ("*Dombeya* sp. [Sterculiaceae] woods"), Analamafana ("hot forest") (Bastian 1964), but also Ambavahadiala ("forest entrance"), and Ankazosary ("sacred tree").

#### 8.2.4.2. LOGGING

Forest exploitation has been reported from Ambohitantely since 1897 and raw timber exceeding 2 m in diameter was recorded (Bastian 1964). The forest was selectively logged for charcoal production and wood for construction up until 1951 without proper management. No forest exploitation has been reported from Ambohitantely since this date (Rakotondrainibe 1989). The only forest exploitation sign that was noted in the course of the study was the harvesting of the large size *Pandanus* sp. leaves.

#### 8.2.4.3. GRAZING

The Ankazobe *tampoketsa* has been used for a long time as a passage area by people travelling across the country with cattle (Bastian 1964). It is likely that these people cleared

the forest to expand grazing land and it is probable that they spread fires across the savannah to maintain the grasslands. The high frequency of grassland burning prevented the forest from regenerating and caused forest shrinkage. Betsileo people who herded cattle across the Ankazobe *tampoketsa* established themselves near Ambohitantely around 1920 (Bastian 1964). Dewar & Burney (in press) report that introduction of cattle in some tropical areas (i.e. Central America, Hawaii) has had a tremendous and rapid impact on the original vegetation. These authors present the hypothesis, that introduction of cattle may have transformed the more open sectors of the mosaic of natural vegetation that occurred originally on the central High Plateau.

#### 8.2.4.4. CULTIVATION

Because of poor soils, the forest of this region was not initially cleared for cultivation.

#### 8.2.4.5. STRATEGY

Historically, wars between the minor kings of the central High Plateau were common. Clearing the forest was considered a means of facilitating military operations. Probably large portions of the central High Plateau were cleared for this purpose in the Imerina region under the reign of Radama I (1810-1828) (Bastian 1964). The toponymy in Ambohitantely provides some arguments in favour of the strategy as a cause of forest disappearance: e.g. Andriankely ("little prince"), Ampasandaoka ("where tombs were profaned") (Bastian 1964), but also Andasibe ("large campsite"), Andriamainty ("the black prince"), Didiatraoka ("where throats were cut"), Maromantsina ("sickening site"), Ankazosary ("sacred tree" [limit between two kingdoms]).

## 9. METHODS

### 9.1. REASONS FOR SELECTION OF FOREST FRAGMENTS FOR STUDY

The forest-fragmentation pattern of the Ambohitantely Special Reserve is well known and was precisely described in previous studies (Bastian 1964; Séguier-Guis 1988; Rakotondrainibe 1989; Rajoelison 1990). Although currently there is little degradation at the remaining forest, it was decided for the purpose of this study to look at the size and location of the forest tracks based upon recent aerial photographs. Séguier-Guis (1988) used aerial photographs taken in 1957 (scale 1:10 000) and in 1967 (scale 1:25 000) and Rajoelison (1990) used aerial photographs taken in 1987 (scale 1:15 000). Aerial photographs taken by the *Institut Géographique National (IGN)/Foiben - Taosarintanin' I Madagasikara (FTM)* on 3 and 21 March 1992 (scale 1:40 000) were acquired for this sole purpose and using stereoscopic pairs a precise map (scale 1:40 000) was prepared. Based on this recent set of aerial photographs, the objectives were: 1) to map the Ambohitantely Forest showing the different natural and anthropogenic vegetational formations; 2) to define precisely the size of the different fragments of natural forest and to map them; 3) to define the distance of each of these fragments of natural forest from each other and the largest natural forest block.

The resulting map (Fig. 8) shows the limits of the largest block of forest (referred to as the control site) as well as the smaller forest blocks. Furthermore the location and size of the plantations and water courses have been mapped. The size of each of these blocks (513 blocks) (Fig. 9) was defined using a pointcount grid of a 0.64 ha and the distance of each block from the nearest edge of the control site was measured (Table 2). Selection of fragments for the bird study was based on their size and their distance from the control site. The forest fragments were selected from a total of 513 fragments,

between 0.64 and 136 ha, and the largest fragment, (the only one larger than 100 ha, was selected). In addition to the control site, seven fragments were chosen. Selected fragments, when possible, had a regular shape and were located more than 500 m from the control site. Fragments clearly delineated by grassland savannah were preferred to those surrounded by secondary forest growth or exotic forest plantation.

## 9.2. DATA COLLECTION

In order to investigate the effects of forest fragmentation on forest-dependent bird species, intensive sampling is vital; thus, two methods were selected to collect data: mistnetting and point counts. Mistnetting is considered to be the best procedure for censusing understorey birds in tropical forest (Karr 1981a). Netting can be standardized to sample size, sample effort, and capture rate for a bird community; individual species can be expressed in the number of captures per net-day (Karr 1981b). This method was designed to document the effects of forest fragmentation on forest-dependent bird species occurring in the lower stratum of the forest. Point counts were used to gather data on species living in the middle and higher storeys or on species of the understorey which were unlikely to be mistnetted such as large-bodied species (i.e. *Lophotibis cristata*). This method, rarely employed in tropical forest (Karr 1981a; Thiollay 1992), has been extensively used in temperate regions, especially in Europe (Blondel et al. 1970). A combination of the two sampling techniques was used to optimize data collection on forest-dependent bird species independently of the forest storey they frequent. Transect lines of 100, 200, 400, 600 or 800 m long, depending on forest area, were cut in each of the selected fragments. These straight narrow lines of about 1 m wide were cut from the edge to the centre of the forest, thereby completely bisecting the study sites. A compass was used to ensure that east-west transect lines remained straight. Because of their large size, four transects of 400 m each were



cut in the control site and two in the largest forest fragment (Fragment A - 136 ha).

### 9.2.1. MISTNETTING

Intensive mistnetting operations (using black nylon mistnets, 12 m long, 2 m high, 4-tier, 36-mm mesh) were set up along transect lines in every study site. Mistnets were erected in a continuous linear band, starting at the edge of the forest and running for the total length (if it was a small parcel), or for a 400 or 600 m in the larger parcels. Poles were numbered, starting with number 1 at the edge of each forest. Mistnet lines ran for five consecutive days and nights at a time. The lower panel of each net was set at ground level. Mistnets were checked every 20 min to every hour depending on weather conditions and sites. Each bird captured was identified, ringed with a numbered aluminium ring, measured and released at the exact spot where it had been captured (Appendix 2). Mistnetting operations at all sites were performed intermittently between October 1993 and May 1994.

The mistnetting effort per ha varied between the different fragments:

Control site	:	0.82 mistnet-days/ha.
Fragment A 136 ha	:	1.21 mistnet-days/ha.
Fragment E 52 ha	:	2.02 mistnet-days/ha.
Fragment H 30 ha	:	3.67 mistnet-days/ha.
Fragment F 28 ha	:	4.64 mistnet-days/ha.
Fragment A12 12 ha	:	10.83 mistnet-days/ha.
Fragment H1 4 ha	:	19.50 mistnet-days/ha.
Fragment H5 0.64 ha	:	93.75 mistnet-days/ha.

### 9.2.2. POINT COUNTS

Visual and auditory censusing were conducted in all sites. Sampling plots (25 m x 25 m = 0.0625 ha) were located along



these transects every 200 m. The sampling plots in the control site were the same size as those in the forest fragments. Transects were equally divided within sampling plots, and point counts were performed at the midpoint of each transect plot. To facilitate visibility of the boundaries, flagging tape was tied to trees at each corner of each plot. A period of 4 min before the start-up of sampling was allowed to elapse so birds could settle down from any disturbance caused by the observer's arrival. Sampling periods lasted 20 min. All bird contacts, visual and auditory, within the sampling plot were registered during the 20-min census.

Point counts were made between October 1993 and December 1993 in the control site and in all other sites. This period is the best, since birds are singing and defending territories. All censuses were made from 04:45 to 10:00 hours, the earliest census being performed 15 min before sunrise. Bad weather conditions are known to affect census accuracy in the tropics, particularly wind and rain (Karr 1981), and to a lesser degree fog (pers. obs.). Censuses were not conducted when weather conditions were unsuitable for detection or identification of birds visually or auditorily. Bird-sampling effort during this study was uniform at each site and each point count was performed five times. Canopy point counts to locate forest-canopy species and wide-ranging species (i.e. *Accipiter henstii*, *Polyboroides radiatus*), were conducted in the morning, in the middle of the day, and at the end of the afternoon to determine presence-absence of bird species.

### 9.3. DATA PROCESSING

Data were organized and processed, and graphs were prepared with Quattro-Pro for Windows (6.0) and Statview (2.0).

## 10. RESULTS

### 10.1. AVIFAUNA

Three characteristics make the avifauna of Madagascar remarkable. The first is the relatively low number of species, not only in comparison with the continental areas at the same latitude, but also in comparison with bird populations on Indo-Pacific islands of approximately the same size (Langrand 1990). A total of 201 breeding species has been recorded in Madagascar (587 000 km<sup>2</sup>) (Langrand 1990). A recently discovered species new to science raises the total of the Malagasy breeding species to 202 (Goodman *et al.*(a) in prep.). This is in comparison to 420 resident species found in Borneo (730 000 km<sup>2</sup>), 340 found in Java (130 000 km<sup>2</sup>), and almost 600 recorded in New Guinea (771 900 km<sup>2</sup>). These three islands had connections during the Pleistocene with other large land masses while Madagascar has been separated from the rest of Gondwana for at least 130 million years (Coffin & Rabinowitz 1987). Thus the number of species in each island is related to the ability of birds to disperse overland rather than over water.

Recent work on subfossil birds of Madagascar indicates that there has been considerable extinction since the late Pleistocene so that the total of 202 species is below the actual number known from the island in recent geological time (Lamberton 1930; Goodman & Ravaovy 1993). The second characteristic of the Madagascan avifauna is its high level of endemism, in terms of both genera (24.6%) and species (105 spp. = 53%) (Langrand 1990). Further an additional 25 (12.5%) breeding species are endemic to the Malagasy Region, defined as Madagascar, the Comoros Islands, Aldabra Island, and the Mascarene Islands (Réunion, Mauritius, and Rodrigues). The third characteristic is that a large proportion of the resident species are forest-dwelling birds (56.9%); the proportion of forest species is even higher when only endemics are considered (80.2%) (Wilmé in press).

From a biogeographic point of view, the avifauna of Madagascar can be divided into two main groups, the birds of the Eastern Region and those of the Western Region (Langrand 1990). The Eastern Region harbours the greatest diversity of resident birds. Of the 166 nesting species known from the Eastern Region, 43 (26%) are found nowhere else on the island. These 43 species include many belonging to endemic families and subfamilies, among them one of the three Mesitornithidae, four of the five Brachypteraciidae, three of the four Philepittinae, three of the 10 Couinae, and four of the 14 Vangidae; the last family is endemic to the Malagasy Region.

The avifauna of the Ambohitantely Special Reserve shows close affinities with the Eastern Region. Seven species found at Ambohitantely occur only in the Eastern Region. These are *Sarothrura insularis*, *Alectroenas madagascariensis*, *Atelornis pittoides*, *Pseudocossyphus sharpei*, *Cryptosylvicola randrianasoloi*, *Newtonia amphichroa*, and *Foudia omissa*.

The degree of endemism of the avifauna of Ambohitantely is considerable but not as high as other rainforest sites of Madagascar. Of the 54 forest-breeding species found in the reserve, 26 (48.1%) are endemic to Madagascar, 19 (35.2%) are endemic to the Malagasy Region, and nine (16.7%) are found outside of the Malagasy Region (Table 3).

#### 10.1.1. SPECIES-AREA RELATIONSHIP APPROACH APPLIED TO THE FOREST OF AMBOHITANTELY

Madagascar, as an island, supports fewer species of plants and animals than equivalent continental areas or tropical islands of comparable size. MacArthur & Wilson (1967) provide a theoretical interpretation of this fact, in that the low diversity of island biota reflects a dynamic equilibrium between extinction and colonization rates of individual species populations. The variables considered include the size of the island, the variability of its topography, its climate, its

Table 3:

## LIST OF THE 54 BREEDING FOREST SPECIES FOUND IN AMBOHITANTELY SPECIAL RESERVE

42	<i>Lophotibis cristata</i>	Madagascar Crested Ibis
56	<i>Aviceda madagascariensis</i>	Madagascar Cuckoo-Falcon
57	<i>Machaeramphus alcinus</i>	Bat Hawk
61	<i>Polyboroides radiatus</i>	Madagascar Harrier-Hawk
63	<i>Accipiter henstii</i>	Henst's Goshawk
64	<i>Accipiter madagascariensis</i>	Madagascar Sparrowhawk
65	<i>Accipiter francesii</i>	Frances's Sparrowhawk
66	<i>Buteo brachypterus</i>	Madagascar Buzzard
68	<i>Falco zoniventris</i>	Banded Kestrel
71	<i>Falco peregrinus</i>	Peregrine Falcon
75	<i>Numida meleagris</i>	Helmeted Guineafowl
79	<i>Turnix nigricollis</i>	Madagascar Buttonquail
81	<i>Dryolimnas cuvieri</i>	White-throated Rail
85	<i>Sarothrura insularis</i>	Madagascar Flufftail
142	<i>Streptopelia picturata</i>	Madagascar Turtledove
144	<i>Treron australis</i>	Madagascar Green Pigeon
145	<i>Alectroenas madagascariensis</i>	Madagascar Blue Pigeon
147	<i>Coracopsis nigra</i>	Lesser Vasa Parrot
150	<i>Cuculus rochii</i>	Madagascar Lesser Cuckoo
161	<i>Centropus toulou</i>	Madagascar Coucal
164	<i>Otus rutilus</i>	Malagasy Scops Owl
166	<i>Asio madagascariensis</i>	Madagascar Long-eared Owl
168	<i>Caprimulgus madagascariensis</i>	Madagascar Nightjar
171	<i>Zoonavena grandidieri</i>	Malagasy Spine-tailed Swift
173	<i>Apus melba</i>	Alpine Swift
174	<i>Apus barbatus</i>	African Black Swift
176	<i>Ispidina madagascariensis</i>	Madagascar Pigmy Kingfisher
177	<i>Merops superciliosus</i>	Madagascar Bee-eater
178	<i>Eurystomus glaucurus</i>	Borad-billed Roller
181	<i>Atelornis pittoides</i>	Pitta-like Ground-Roller
184	<i>Leptosomus discolor</i>	Cuckoo-Roller
191	<i>Riparia paludicola</i>	Brown-throated Sand Martin
193	<i>Phedina borbonica</i>	Mascarene Martin
196	<i>Coracina cinerea</i>	Ashy Cuckoo-Shrike
197	<i>Phyllastrephus madagascariensis</i>	Long-billed Greenbul
202	<i>Hypsipetes madagascariensis</i>	Madagascar Bulbul
203	<i>Copsychus albospecularis</i>	Madagascar Magpie-Robin
205	<i>Pseudocossyphus sharpei</i>	Forest Rock-Thrush
209	<i>Nesillas typica</i>	Madagascar Brush-Warbler
214'	<i>Cryptosylvicola randrianasoloi</i>	Cryptic Warbler
215	<i>Newtonia amphichroa</i>	Dark Newtonia
216	<i>Newtonia brunneicauda</i>	Common Newtonia
224	<i>Terpsiphone mutata</i>	Madagascar Paradise Flycatcher
228	<i>Nectarinia souimanga</i>	Souimanga Sunbird
229	<i>Nectarinia notata</i>	Long-billed Green Sunbird
230	<i>Zosterops maderaspatana</i>	Madagascar White eye
232	<i>Calicalicus madagascariensis</i>	Red-tailed Vanga
241	<i>Cyanolanius madagascarinus</i>	Blue Vanga
245	<i>Tylas eduardi</i>	Tylas Vanga
246	<i>Dicrurus forficatus</i>	Crested Drongo
248	<i>Hartlaubius auratus</i>	Madagascar Starling
253	<i>Foudia madagascariensis</i>	Madagascar Red Fody
254	<i>Foudia omissa</i>	Forest Fody
255	<i>Lonchura nana</i>	Madagascar Mannikin

vegetation and the proximity of the island to a potential source of colonization. This approach is relevant to forest fragmentation, since natural habitats are often isolated and surrounded by habitat that impede dispersal of forest-dwelling birds. Thus it is likely that many forest fragments in Madagascar reflect aspects of, and are affected by, this "island effect".

Defining the factors that influence the distribution and the abundance of bird species on islands is of great importance to understanding the current patterns displayed by assemblages of species observed today. In order to predict how many bird species might be lost by deforestation and forest fragmentation research has focused on the species-area relationship (Simberloff 1992). The species-area relationship shows a direct linear relationship between the logarithm of the number of species and the logarithm of the area when applied to the seven forest fragments, the control site, and the Eastern Region (Fig. 10). Using the species-area approach it is possible to present an estimate of the proportion of species likely to become extinct as a result of progressive deforestation.

The power function has been used by MacArthur & Wilson (1967) to represent the species-area relationship and is still widely used (Simberloff 1992):

$$S = k A^z \quad \text{or} \quad \log S = k + z \log A$$

where,  $S$  = number of species,  $A$  = area, and  $k$  and  $z$  are constants.

The exponent  $z$  determines the slope of the curve and is the critical parameter in estimating the extinction rate (Reid & Miller 1989). From empirical studies on species-area relationship, the value of the exponent varies ( $0.15 < z < 0.35$ ) (Connor & McCoy 1979). In a variety of taxa on many different islands, the  $z$ -values ranges from 0.24 to 0.33

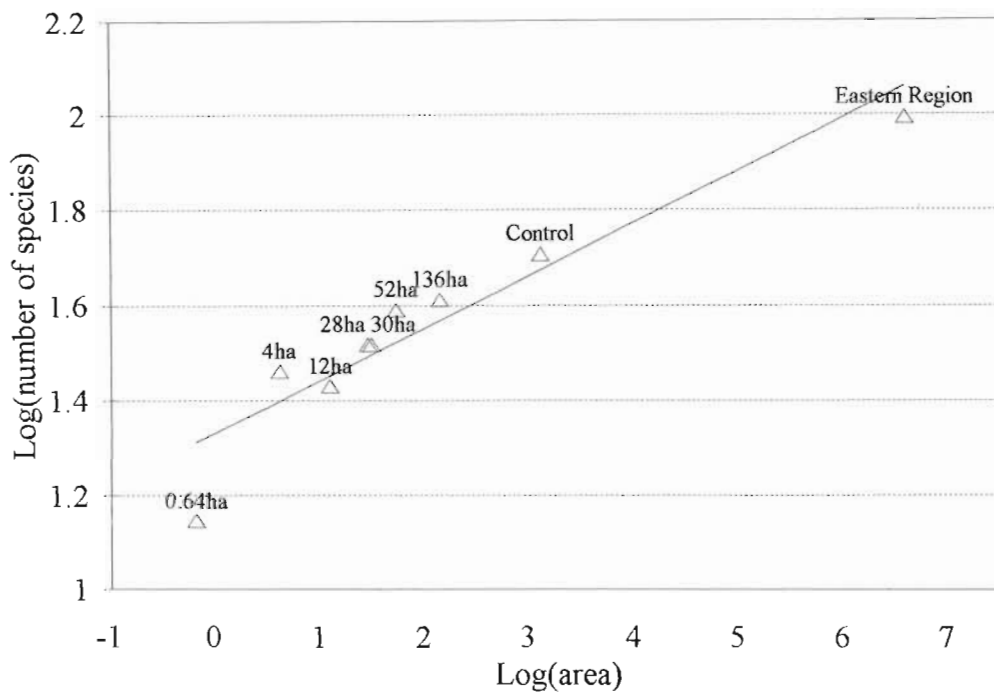


FIGURE 10: SPECIES AREA RELATIONSHIP OF SAMPLED SITES

$$\text{Log } s = 1.334 + 0.11(\text{Log } a) \quad (r^2 = 0.892)$$

(Pianka 1974) and when applied to birds of a forest oceanic island, the value of  $z$  would be expected to approach 0.25. In the specific case of Ambohitantely the exponent  $z$  is 0.16 which falls within the range proposed by Connor & McCoy (1979). The species-area relationship curve for the *Réserve Spéciale d'Ambohitantely* is as follows: (Fig. 11)

#### 10.1.2. THE BIOGEOGRAPHICAL AFFINITIES OF THE AVIFAUNA OF AMBOHITANTELY

An analysis of the occurrence of resident forest birds at 33 well studied sites (including Ambohitantely Special Reserve) on Madagascar derived from Wilmé (in press) provides information on biogeographical relationships between these forests with special reference to Ambohitantely Special Reserve. The analysis used is an index of dissimilarity and the coefficients for each site relative to Ambohitantely Special Reserve are presented in Table 4.

Equation for the dissimilarity index:

$$\text{Index} = \frac{A + B}{\Sigma A + \Sigma B},$$

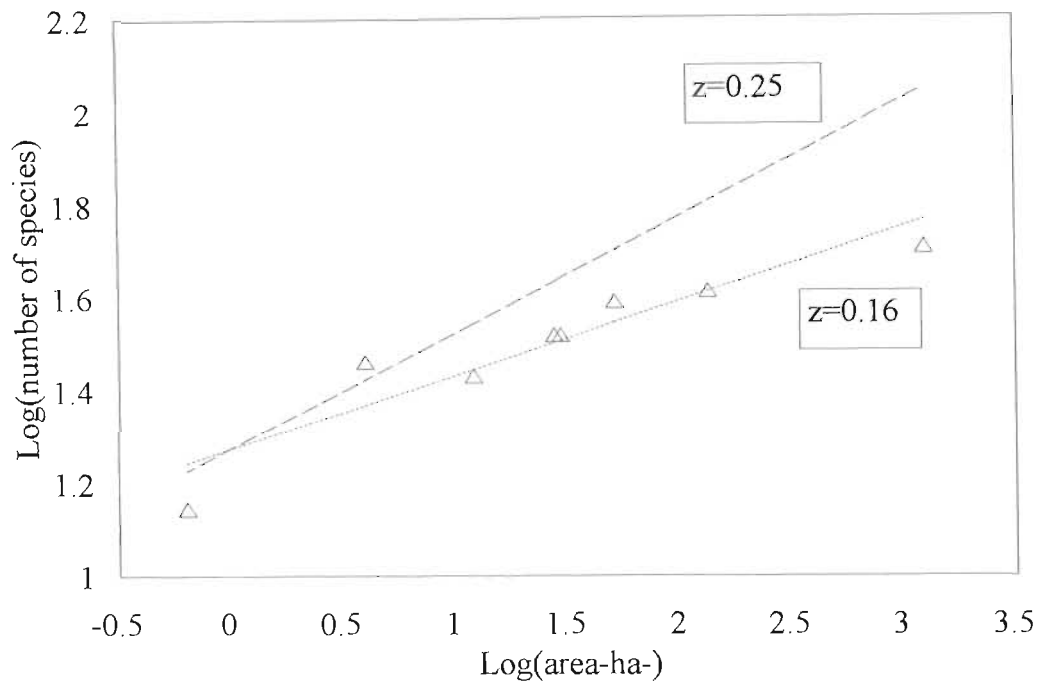
$A$  = number of species occurring only at Site A

$B$  = number of species occurring only at Site B

$\Sigma A$  = total number of species at Site A

$\Sigma B$  = total number of species at Site B

The index of dissimilarity is based on the Sorensen coefficient (Brower et al.).



**FIGURE 11: COMPARISON OF THE SPECIES-AREA REGRESSION SLOPE OF AMBOHITANTELY WITH A STANDARD VALUE OF  $z = 0.25$ .**

$$\text{Log } s = 1.273 + 0.16(\text{Log } a) \quad (r^2 = 0.878)$$



On the basis of this analysis, three main groups can be defined relative to Ambohitantely Special Reserve:

Strong affinities:    Total forest-bird index  $< 0.20$   
                              Total endemic forest-bird index  $< 0.30$   
 Moderate affinities: Total forest-bird index  $0.20 > 0.30$   
                              Total endemic forest-bird index  $0.30 > 0.43$   
 Few affinities:        Total forest-bird index  $> 0.30$   
                              Total endemic forest-bird index  $> 0.43$

The values for these categories were calculated to show the biogeographical groupings of the various sites. On the basis of values presented in Table 4, the following relationships exist between the 32 sites and Ambohitantely (sites where the species lists are presumed to be incomplete are presented in *italics*.):

Strong affinities with Ambohitantely: Montagne d'Ambre (54 forest species for Ambohitantely, 57 for Montagne d'Ambre, 48 forest species common to both sites).

Moderate affinities with Ambohitantely (in decreasing order of affinity based on forest endemic bird index): Manjakatombo, Ankarana, Andringitra, Ranomafana, Zahamena, Masoala, Andohahela (Parcel 1), Marojejy, Analamazaotra.

Few affinities with Ambohitantely (in decreasing order of affinity):    Analamera, Kirindy, Ankarafantsika, Bora, Tsaratanana, Manombo, Manongarivo, Berenty, Zombitse, Analabe, Bemaraha, Mananara, Toliara/Andrevo, Ihotry, Lokobe, Andohahela (Parcel 2), Beza-Mahafaly, Namoroka, Isalo, Tsimanampetsotsa, Nosy Mangabe, and Cap Sainte-Marie.

A location map of the sites listed above is presented in Fig. 7.

Table 4:

DISSIMILARITIES INDICES OF 32 SITES OF MADAGASCAR  
IN REFERENCE TO AMBOHITANTELY SPECIAL RESERVE

	Forest species		Passerines		Non Passerines	
	Total	Endemic	Total	Endemic	Total	Endemic
Total number of species considered	114	84	57	46	57	38
PN1 Montagne d'Ambre	0.17	0.28	0.17	0.33	0.17	0.23
PN2 Isalo	0.41	0.64	0.39	0.65	0.43	0.64
RNI 3 Zahamena	0.29	0.41	0.32	0.51	0.26	0.29
RNI 4 Tsaratanana	0.40	0.48	0.35	0.57	0.45	0.38
RNI 5 Andringitra	0.28	0.36	0.29	0.47	0.27	0.25
RNI 6 Lokobe	0.60	0.61	0.52	0.69	0.67	0.56
RNI 7 Ankarafantsika	0.28	0.47	0.30	0.58	0.27	0.38
RNI 8 Tsingy de Namoroka	0.51	0.64	0.64	0.78	0.43	0.54
RNI 9 Tsingy de Bemaraha	0.37	0.58	0.37	0.73	0.37	0.50
RNI 10 Tsimanampetsotsa	0.44	0.67	0.48	0.74	0.41	0.60
RNI 11 Andohahela (Parc. 1)	0.26	0.42	0.33	0.51	0.19	0.31
" " (Parc. 2&3)	0.40	0.64	0.48	0.74	0.34	0.56
RNI 12 Marojejy	0.27	0.42	0.35	0.53	0.19	0.30
RS Analamera	0.36	0.43	0.38	0.52	0.35	0.36
RS Ankarana	0.21	0.36	0.21	0.43	0.21	0.31
RS Manongarivo	0.32	0.49	0.30	0.52	0.33	0.46
RS Manombo	0.29	0.49	0.26	0.52	0.31	0.46
RS Bora	0.33	0.47	0.35	0.60	0.32	0.36
RS Nosy Mangabe	0.45	0.68	0.39	0.71	0.50	0.65
RS Cap Sainte Marie	0.77	0.86	0.83	0.83	0.74	0.88
RS Analamazaotra	0.27	0.42	0.34	0.52	0.21	0.30
RS Beza Mahafaly	0.41	0.64	0.51	0.74	0.34	0.56
Site Zombitse	0.30	0.53	0.28	0.52	0.31	0.54
Site Manjakatombo	0.32	0.33	0.20	0.25	0.43	0.40
Site Analabe	0.31	0.53	0.27	0.55	0.33	0.52
Site Berenty	0.30	0.53	0.35	0.67	0.27	0.42
Site Kirindy	0.30	0.44	0.33	0.52	0.27	0.38
Site Lac Ihotry	0.41	0.60	0.43	0.65	0.39	0.56
Site Mananara	0.39	0.59	0.43	0.65	0.37	0.56
Site Masoala	0.29	0.41	0.36	0.53	0.23	0.30
Site Ranomafana	0.27	0.41	0.32	0.50	0.22	0.29
Site Nord Toliara PK32	0.37	0.59	0.35	0.60	0.39	0.59

### 10.1.3. SPECIES RICHNESS

This section deals with the number of species in a given area (Ralph 1981), in this particular case the Ambohitantely Special Reserve. Information on the avifauna of this protected area was incomplete before the 1980s. Bastian (1964) mentioned vague vernacular names for only two species, a pigeon and *Foudia madagascariensis*. Séguier-Guis (1988) in the course of drawing up an inventory of the vertebrates of the Ambohitantely Special Reserve observed 30 species of birds and reported 18 others (Langrand & Wilmé in Séguier-Guis 1988). Nicoll & Langrand (1989) reported 48 species from the reserve after a two-day visit, as part of a general inventory of the biological diversity of Madagascar protected areas. A total of 72 bird species, 54 of which are considered forest species, has been documented in the reserve at the completion of the field study reported herein (Appendix 3).

The control site contains an almost complete avifauna relative to the known avifauna of the reserve. All species recorded from the forest fragments studied were also observed in the control site. Four species (*Accipiter henstii*, *Falco peregrinus*, *Numida meleagris*, and *Dryolimnas cuvieri*) were recorded only in the control site and not in the the forest fragments. Only two forest species *Machaeramphus alcinus* and *Falco zoniventris* have been recorded from Ambohitantely Forest, but were not found in the sites considered in this study. The only known record of *Falco zoniventris* in the Ambohitantely Special Reserve, is one observed at the edge of a 25-ha fragment not used in this project, adjacent to fragment A12 (12 ha).

For each site studied, a comprehensive list of forest species was tabulated using data originating from four different sources, point counts, mistnetting operations, canopy sightings, and random observations. A cumulative time curve

was calculated for each site as a function of the addition of new species per unit work-day (Fig. 12). Although not quantitative, the combination of these four datasets provides a more detailed view of the presence or absence of birds in the fragments.

In the control site a total of 37 work-days was accrued, and a total of 51 forest species was recorded in the area. The cumulative time curve begins to level off at about 13 days, at which time 43 (84 %) of the total species had been recorded.

In the forest fragments a total of 64 work-days was accrued, and a total of 47 forest species was recorded in the seven fragments. The asymptote of the cumulative curves for the different fragments varies with the size of the fragments and varies from four (fragment H5 [0.64 ha]) to 13 work-days (fragments A [136 ha] and E [52 ha]). Four main groups can be defined:

Control site and fragment A (136 ha): asymptote after 13 days;

Fragment E (52 ha): asymptote after ten days;

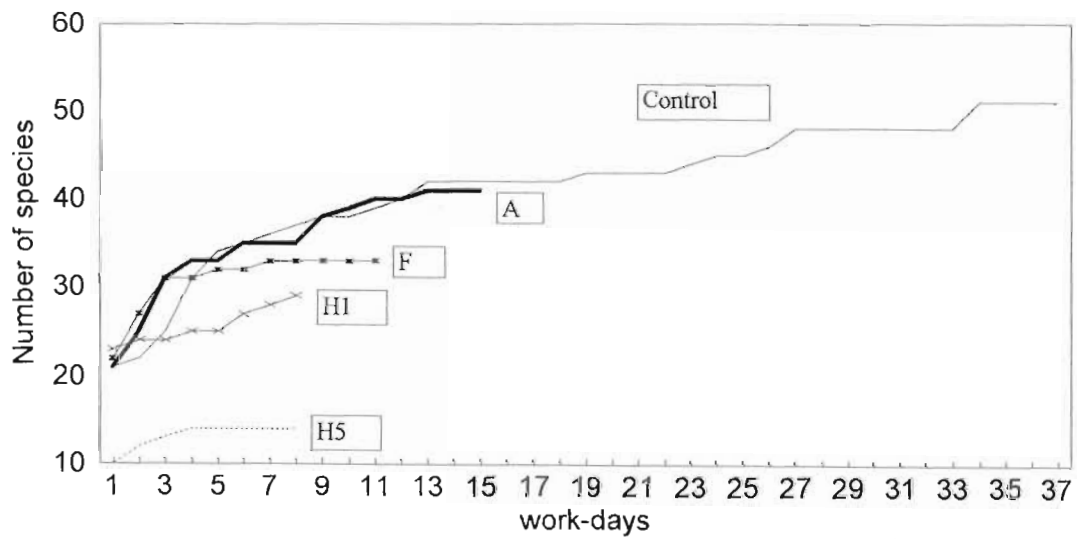
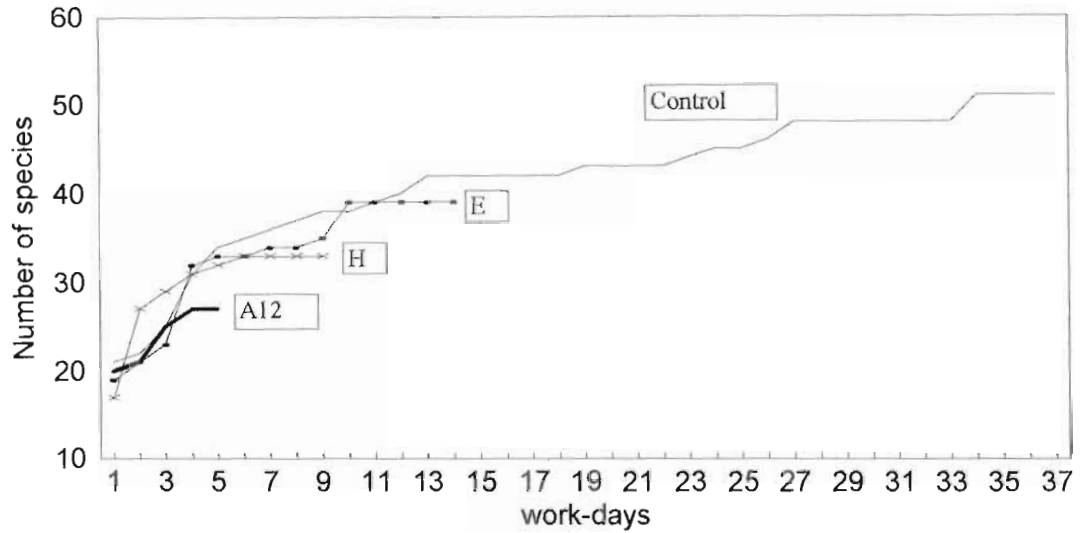
Fragments H (30 ha) and F (28 ha): asymptote after six days;

Fragments A12 (12 ha), H1 (4 ha), H5 (0.64 ha): asymptote after four days.

#### 10.1.3.1. PRESENCE-ABSENCE OF FOREST SPECIES DEPENDING ON SIZE OF FOREST FRAGMENT

Data on presence-absence of forest species depending on fragment sizes are presented in Table 5.

Species recorded only in the control site (1250 ha): *Accipiter henstii*, *Falco peregrinus*, *Numida meleagris*, and *Dryolimnas cuvieri*.



**Figure 12: Cumulative time curve for each site**  
as a function of the addition of new species per unit work-day

Species recorded in the control site and in fragments > 136 ha: *Calicalicus madagascariensis*.

Species recorded in the control site and in fragments > 52 ha: *Turnix nigricollis*, *Merops superciliosus*, and *Newtonia amphichroa*.

Species recorded in the control site and in fragments > 30 ha: *Cyanolanius madagascarinus*.

Species recorded in the control site and in fragments > 28 ha: *Otus rutilus*, *Apus barbatus*, *Atelornis pittoides*, and *Phedina borbonica*.

Species recorded in the control site and in fragments > 12 ha: *Lophotibis cristata*, *Accipiter madagascariensis*, *A. francesii*, *Zoonavena grandidieri*, *Ispidina madagascariensis*, *Leptosomus discolor*, *Phyllastrephus madagascariensis*, and *Pseudocossyphus sharpei*.

Species recorded in the control site and in fragments > 4 ha: *Aviceda madagascariensis*, *Polyboroides radiatus*, *Buteo brachypterus*, *Falco peregrinus*, *Streptopelia picturata*, *Centropus toulou*, *Asio madagascariensis*, *Caprimulgus madagascariensis*, *Apus melba*, *Eurystomus glaucurus*, *Riparia paludicola*, *Coracina cinerea*, *Newtonia brunneicauda*, *Tylas eduardi*, *Hartlaubius auratus*, *Foudia omissa*, and *Lonchura nana*.

Species recorded in the control site and in fragments > 0.64 ha: *Sarothrura insularis*, *Alectroenas madagascariensis*, *Coracopsis nigra*, *Cuculus rochii*, *Hypsipetes madagascariensis*, *Copsychus albospectularis*, *Nesillas typica*, *Cryptosylvicola randrianasoloi*, *Terpsiphone mutata*, *Nectarinia souimanga*, *N. notata*, *Zosterops maderaspatana*, *Dicrurus forficatus*, and *Foudia madagascariensis* (Plates 1-7).

Table 5:

PRESENCE - ABSENCE OF FOREST SPECIES IN CONTROL SITE AND FRAGMENTS  
First documented in the course of the study (date)

Site:	Control	A	E	H	F	A12	H1	H5
Area (ha):	1250	136	52	30	28	12	4	0.64
<i>Lophotibis cristata</i>	22/10	22/04	24/11	01/04	22/11	28/04		
<i>Aviceda madagascariensis</i>	26/10	03/12					02/12	
<i>Polyboroides radiatus</i>	24/11	31/03	24/11		24/11	25/04	29/11	
<i>Accipiter henstii</i>	29/11							
<i>Accipiter madagascariensis</i>	01/12	31/03	12/04	31/03		26/04		
<i>Accipiter francesii</i>	28/10		25/11	26/11		27/04		
<i>Buteo brachypterus</i>	21/10	02/12	18/11	25/11	22/11	25/04	29/11	
<i>Falco peregrinus</i>	14/11							
<i>Numida meleagris</i>	25/11							
<i>Turnix nigricollis</i>	13/04	29/03	03/12					
<i>Dryolimnas cuvieri</i>	02/11							
<i>Sarothrura insularis</i>	29/10	02/12	24/11	26/11	23/11	25/04	29/11	01/12
<i>Streptopelia picturata</i>	21/10	03/12	18/11		22/11	25/04	29/11	
<i>Alectroenas madagascariensis</i>	26/10	02/12	24/11	27/11	24/11	25/04		04/04
<i>Coracopsis nigra</i>	21/10	02/12	18/11	25/11	22/11	25/04	29/11	01/12
<i>Cuculus rochii</i>	21/10	02/12	18/11	25/11	22/11		29/11	01/12
<i>Centropus toulou</i>	27/10	02/12	18/11	26/11	22/11		29/11	
<i>Otus rutilus</i>	25/10	18/04	18/11	25/11	24/11			
<i>Asio madagascariensis</i>	25/10	18/04	24/11	25/11	22/11		29/11	
<i>Caprimulgus madagascariensis</i>	21/10	18/04	24/11	26/11	22/11	25/04	29/11	
<i>Zonavena grandidieri</i>	26/10	02/12				27/04		
<i>Apus melba</i>	26/10	02/12	23/11	25/11	24/11	27/04	29/11	
<i>Apus barbatus</i>	21/10	03/12	24/11	26/11	23/11			
<i>Ispidina madagascariensis</i>	03/12					28/04		
<i>Merops superciliosus</i>	21/10	19/04	19/11					
<i>Eurystomus glaucurus</i>	25/10	02/12	24/11	26/11	04/12		29/11	
<i>Atelornis pittoides</i>	27/10	28/03		26/11	22/11			
<i>Leptosomus discolor</i>	21/10	02/12	18/11	25/11	22/11	27/04		
<i>Riparia paludicola</i>	13/04	20/04	11/04	26/11	11/04		29/11	
<i>Phedina borbonica</i>	08/11				23/11			
<i>Coracina cinerea</i>	21/10	02/12	22/11	26/11	23/11		29/11	
<i>Phyllastrephus madagascariensis</i>	04/11	03/12	18/11		22/11	25/04		
<i>Hypsipetes madagascariensis</i>	21/10	02/12	18/11	25/11	22/11	25/04	29/11	01/12
<i>Copsychus albospecularis</i>	08/11	29/03	18/11	01/12	22/11		28/03	28/03
<i>Pseudocossyphus sharpei</i>	27/10	28/03	18/11	25/11	22/11	25/04		
<i>Nesillas typica</i>	21/10	02/12	18/11	25/11	22/11	25/04	29/11	01/12
<i>Cryptosylvicola randrianasoloi</i>	26/10	28/03		01/12			29/11	01/12
<i>Newtonia amphichroa</i>	21/10	28/03	11/04					
<i>Newtonia brunneicauda</i>	21/10	02/12	18/11	25/11	22/11	25/04	29/11	
<i>Terpsiphone mutata</i>	21/10	02/12	18/11	25/11	22/11	25/04	29/11	28/03
<i>Nectarinia souimanga</i>	21/10	02/12	18/11	25/11	22/11	25/04	29/11	01/12
<i>Nectarinia notata</i>	26/10	02/12	19/11	27/11	22/11	25/04	29/11	01/12
<i>Zosterops maderaspatana</i>	21/10	02/12	18/11	25/11	22/11	25/04	29/11	01/12
<i>Calicalicus madagascariensis</i>	21/10	02/12						
<i>Cyanolanius madagascarinus</i>	21/10	28/03	24/11	26/11				
<i>Tylas eduardi</i>	21/10	02/12	18/11	25/11	22/11	25/04	30/11	
<i>Dicrurus forficatus</i>	21/10	02/12	18/11	25/11	22/11	25/04	29/11	01/12
<i>Hartlaubius auratus</i>	01/11		01/12				29/11	
<i>Foudia madagascariensis</i>	21/10		12/04			25/04	29/03	31/03
<i>Foudia omissa</i>	05/11	28/03	18/11	25/11	23/11	25/04	30/03	
<i>Lonchura nana</i>	13/04						15/07	
Total	51	41	39	33	33	27	29	14

#### 10.1.4. SPECIES DIVERSITY

This is the measure of the variety of species in a community that takes into account the relative abundance of each species (Ralph 1981). Two measures of diversity are presented herein: a) point counts based on early morning sight and sound censuses using a transect method (Blondel *et al.* 1970), and b) netting results based on the capture rate of principally understorey birds (Karr 1981a).

##### 10.1.4.1. POINT COUNTS

A total of 160 point counts was made during the breeding season at 39 different sample plots, totaling 53 h 20 min of censusing. These point counts were along four different transect lines in the control site, as well as along eight transect lines in the seven different fragments. The general results for each site are summarized in Table 6.

The sampling effort at the control site was considered critical to define accurately the relative abundance of the 54 forest bird species encountered in the Ambohitantely Forest (Table 3; Fig. 13). In total 50.6% (81 of the 160) point counts were made in the control site. Point counts in fragment A (136 ha) were not satisfactorily sampled because of late opening of the trails. This delay was the result of local people being reluctant to penetrate this forest because of the proximity of some "vazimba" tombs, who are considered to be the ancestors of the Malagasy people. Because seasonality strongly affects the avifauna of Ambohitantely Special Reserve, no point counts were realized in fragment A12 (12 ha) which was the last fragment to be sampled in the season.

An overall total of 30 bird species was recorded at the selected sites during the point counts, 26 in the control site, and 20 in the fragments. Seven species have been recorded only



Table 6:

## NUMBER OF POINT COUNTS IN DIFFERENT FOREST FRAGMENTS AT AMBOHITANTELY

SITE	Number of point counts					Number of sampling plots					Total amount of time				
	TRANSECTS				Sub total	TRANSECTS				Sub total	TRANSECTS				Sub total
	A	C	D	E		A	C	D	E		A	C	D	E	
Control site	44	12	5	20	81	4	4	2	4	14	14:40	04:00	01:40	06:40	27:00
Fragment A (136 ha)	A		B		Sub total	A		B		Sub total	A		B		Sub total
	10		10		20	5		5		10	3:20		3:20		06:40
Fragment E (52 ha)	23					4					07:40				
Fragment H (30 ha)	9					3					03:00				
Fragment F (28 ha)	12					4					04:00				
Fragment A12 (12 ha)	-					-					-				
Fragment H1 (4 ha)	9					2					03:00				
Fragment H5 (0.64 ha)	6					2					02:00				
TOTAL	160					39					53:20				

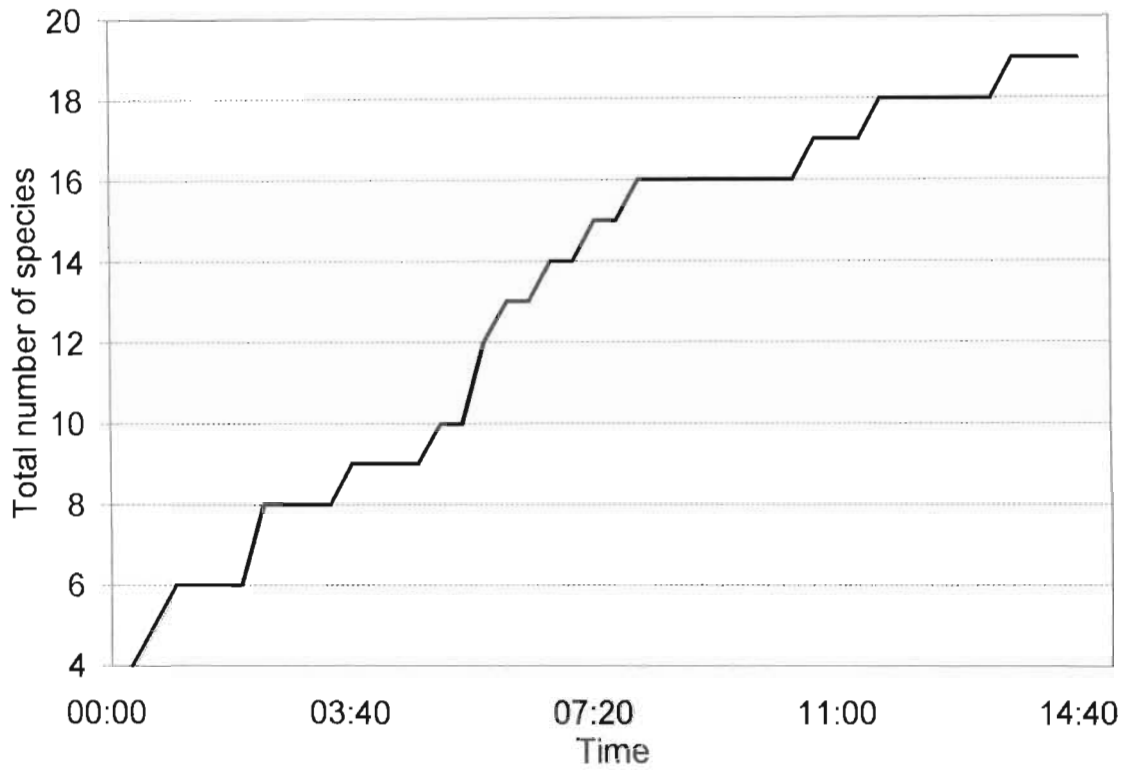
in the control site and not in the fragments, and four in the fragments and not at the control site.

An index of relative abundance was used for species sampled through the point counts (Blondel et al. 1970). For each species, a mean value per sampling hour was calculated for the control site and the different fragments at a distance of 0 m, 200 m, 400 m, 600 m from the edge.

Point-count data do not provide a clear picture of the correlation between relative abundance of species and fragment size. The general trend is that forest interior species are the most affected by forest fragmentation. Their relative abundance decreases as a function of decreasing forest fragment size (i.e. *Atelornis pittoides*, *Newtonia amphichroa*, *Calicalicus madagascariensis*, and *Cyanolanius madagascarinus*). Forest species that fly between fragments are not affected by forest fragmentation until the forest fragments are not too isolated, and their relative abundance is not correlated with fragment size (i.e. *Coracopsis nigra*, *Leptosomus discolor*, and *Tylas eduardi*). The relative abundance of edge species is somewhat positively correlated as a function of decreasing fragment size (i.e. *Hypsipetes madagascariensis*, *Nesillas typica*, *Nectarinia souimanga*, and *Zosterops maderaspatana*)

#### 10.1.4.2. MISTNETTING

A total of 1804 mistnet-days was accrued, 1026 (57%) in the control site and 778 (43%) in the seven forest fragments (Plate 8). Twenty-six different species were mistnetted, representing a total of 491 captures and 397 individuals. The extensive effort in the control site was considered critical to establish a measure of the species diversity of a site that is considered to contain a virtually complete avifauna. The control site represents 1250 ha and together the seven



**Figure 13: Cumulative time species curve**  
**Point counts in control site**  
**Transect A**

fragments 263 ha. The effort per ha is greater in the fragments (3.0 mistnet-days/ha) than in the control site (0.8 mistnet-days/ha). The mistnetting effort per ha varied between the different fragments:

Control site	:	0.82 mistnet-days/ha.
Fragment A 136 ha	:	1.21 mistnet-days/ha.
Fragment E 52 ha	:	2.02 mistnet-days/ha.
Fragment H 30 ha	:	3.67 mistnet-days/ha.
Fragment F 28 ha	:	4.64 mistnet-days/ha.
Fragment A12 12 ha	:	10.83 mistnet-days/ha.
Fragment H1 4 ha	:	19.50 mistnet-days/ha.
Fragment H5 0.64 ha	:	93.75 mistnet-days/ha.

In general, the cumulative species time curves of birds netted in the control site reach an asymptote after five mistnetting days (Table 8; Fig. 14). In a few cases up to two species were added to the total known avifauna after this period. Thus after five days of netting, there appears to be a high measure of confidence in documenting the local avifauna. Given this result, the period of five days was used in the field studies of the fragments and subsequent analyses (Table 7; Fig. 15). Twenty-six species were captured, 24 in the control site and 23 in the other fragments. Because of mistnet positioning, most of these species were understorey or mid-stratum species and very few upper-stratum species were captured; however, these species were recorded during the point counts.

Table 7a:  
Index of relative abundance based on point counts

CONTROL SITE, transects:	A	C	E	mean
Distance from edge	0	0	0	0
<i>Coracopsis nigra</i>			1.50	0.42
<i>Cuculus rochii</i>	0.30			0.17
<i>Hypsipetes madagascariensis</i>	0.60	2.50		0.75
<i>Nesillas typica</i>	0.30		1.80	0.67
<i>Cryptosylvicola randrianasoloi</i>		1.00		0.17
<i>Newtonia brunneicauda</i>	3.00			1.67
<i>Nectarinia souimanga</i>	2.85	2.00	0.60	2.08
<i>Zosterops maderaspatana</i>	1.80	1.00	1.20	1.50
<i>Dicrurus forficatus</i>				

Transect A			Transect C			Transect D		Transect E			mean		
200	400	600	200	400	600	200	400	200	400	600	200	400	600
0.35		0.38	1.00	1.00	2.50			0.60	0.30		0.44	0.20	0.66
	0.12											0.07	
1.27					2.00	0.50	1.50		0.30		0.75	0.20	0.38
				1.00						1.80		0.13	0.56
1.50			1.00		1.50	2.00				1.20	1.19		0.66
1.15	0.23	0.38						0.60	0.30	1.20	0.75	0.20	0.56
1.15	2.54	3.75	5.00	3.50	4.00	2.50		2.40		3.00	2.06	1.89	3.56
0.46	1.85	0.38	2.00	1.00	2.00	2.00		0.60	2.40	1.80	0.88	1.70	1.13
0.35		0.38	1.00							0.30	0.31		0.28

Overall mean
0.41
0.06
0.52
0.30
0.52
0.76
2.31
1.30
0.15

CONTROL SITE. Fragments:	A	C	E	mean
Distance from edge	0	0	0	0
<i>Lophotibis cristata</i>				
<i>Buteo brachypterus</i>				
<i>Streptopelia picturata</i>				
<i>Alectroenas madagascariensis</i>	0.90		0.30	0.58
<i>Apus barbatus</i>				
<i>Merops superciliosus</i>				
<i>Atelornis pittoides</i>	0.30			0.17
<i>Leptosomus discolor</i>				
<i>Phyllastrephus madagascariensis</i>				
<i>Copsychus albospectus</i>				
<i>Pseudocossyphus sharpei</i>			0.60	0.17
<i>Newtonia amphichroa</i>				
<i>Nectarinia souimanga</i>	2.85	2.00	0.60	2.08
<i>Nectarinia notata</i>		1.00		0.17
<i>Calicalicus madagascariensis</i>				
<i>Cyanolanius madagascarinus</i>				
<i>Tylas eduardi</i>	0.45			0.25
<i>Hartlaubius auratus</i>				
<i>Foudia omissa</i>				

Transect A			Transect C			Transect D		Transect E			mean		
200	400	600	200	400	600	200	400	200	400	600	200	400	600
			0.50								0.06		
										0.30			0.09
2.65			0.50								1.50		
0.12											0.06		
										1.20			0.38
0.12	0.58										0.06	0.33	
										0.30			0.07
										0.90			0.20
0.12	1.50										0.06	0.85	
0.12			1.00						0.60	1.50	0.19	0.13	0.47
1.15	2.54	3.75	5.00	3.50	4.00	2.50		2.40		3.00	2.06	1.89	3.56
						1.00					0.13		
0.46										0.60	0.25		0.19
0.46										0.30	0.25		0.09
1.15			1.00				1.50				0.75	0.13	
						0.50					0.06		

Overall mean
0.02
0.02
0.57
0.02
0.11
0.11
0.02
0.06
0.30
0.19
2.31
0.07
0.11
0.09
0.31
0.02

Index of relative abundance based on point counts

Fragment 136A, transect:	A	B	mean
Distance from edge	0	0	0
<i>Coracopsis nigra</i>		0.75	0.38
<i>Cuculus rochii</i>			
<i>Hypsipetes madagascariensis</i>			
<i>Nesillas typica</i>		0.75	0.38
<i>Cryptosylvicola randrianasoloi</i>			
<i>Newtonia brunneicauda</i>	0.75	4.50	2.63
<i>Nectarinia souimanga</i>			
<i>Zosterops maderaspatana</i>			
<i>Dicrurus forficatus</i>		0.75	0.38

A				B				mean				Overall mean
200	400	600	800	200	400	600	800	200	400	600	800	
												0.08
3.00							1.50	1.50			0.75	0.45
												0.08
	3.00		0.75	3.00			1.50	1.50	1.50		1.13	1.35
	1.50				0.75				1.13			0.23
												0.08

Fragments	136A	136B	mean
Distance from edge	0	0	0
<i>Lophotibis cristata</i>			
<i>Buteo brachypterus</i>			
<i>Streptopelia picturata</i>			
<i>Alectroenas madagascariensis</i>			
<i>Apus barbatus</i>			
<i>Merops superciliosus</i>			
<i>Atelornis pittoides</i>			
<i>Leptosomus discolor</i>			
<i>Phyllastrephus madagascariensis</i>			
<i>Copsychus albospectularis</i>			
<i>Pseudocossyphus sharpei</i>	0.75	0.75	0.75
<i>Newtonia amphichroa</i>			
<i>Nectarinia souimanga</i>			
<i>Nectarinia notata</i>			
<i>Calicalicus madagascariensis</i>			
<i>Cyanolanius madagascarinus</i>			
<i>Tylas eduardi</i>		0.75	0.38
<i>Hartlaubius auratus</i>			
<i>Foudia omissa</i>			

[illegible]



Table 7c:  
Index of relative abundance based on point counts

Overall mean	Fragments	52E					30H				28F					4H1			0.64H5		
	Distance from edge	0	200	400	600	mean	0	200	400	mean	0	200	400	600	mean	0	150	mean	0	100	mean
0.08	<i>Coracopsis nigra</i>		1.20	0.30		0.33	0.50		0.50	0.33	0.50	0.30			0.25				0.50	1.00	0.75
	<i>Cuculus rochii</i>										1.00				0.25						
0.45	<i>Hypsipetes madagascariensis</i>	2.40		1.80	0.75	1.17	1.50		1.00	0.83		1.20	1.00		0.75	0.90	1.13	1.00		0.50	0.25
0.08	<i>Nesillas typica</i>	0.60	2.70	2.40	0.75	1.50			1.00	0.33		0.60	1.00		0.50	0.60		0.33		1.00	0.50
	<i>Cryptosylvicola randrianasoloi</i>																		1.00	1.00	1.00
1.35	<i>Newtonia brunneicauda</i>	1.80	1.80	3.30	1.88	2.15					2.00	0.60			0.75		1.50	0.67			
0.23	<i>Nectarinia souimanga</i>	3.60	1.20	1.50	2.06	2.09	1.50	1.00		0.83	2.50	2.70	2.50	3.00	2.63	1.20	0.75	1.00	2.00	2.50	2.25
	<i>Zosterops maderaspatana</i>	1.80	1.20	2.40	1.13	1.57	4.00	1.00	1.00	2.00		2.10	2.00	4.50	1.75	0.30	1.50	0.83		1.00	0.50
0.08	<i>Dicrurus forficatus</i>		1.20		0.38	0.39			1.50	0.50	1.00	0.30			0.38	0.30	0.38	0.33	1.00	1.00	1.00

Overall mean	Fragments	52E					30H				28F					4H1			0.64H5		
	Distance from edge	0	200	400	600	mean	0	200	400	mean	0	200	400	600	mean	0	150	mean	0	100	mean
	<i>Lophotibis cristata</i>																				
	<i>Buteo brachypterus</i>								0.50	0.17											
	<i>Streptopelia picturata</i>			0.30	0.19	0.13															
	<i>Alectroenas madagascariensis</i>																				
	<i>Apus barbatus</i>											0.30			0.13						
	<i>Merops superciliosus</i>																				
	<i>Atelornis pittoides</i>																				
	<i>Leptosomus discolor</i>												1.00		0.25						
	<i>Phyllastrephus madagascariensis</i>			0.60		0.13					0.50	1.20			0.63						
	<i>Copsychus albospectus</i>				0.19	0.07															
0.15	<i>Pseudocossyphus sharpei</i>	0.60				0.13		2.00		0.67											
	<i>Newtonia amphichroa</i>																				
0.23	<i>Nectarinia souimanga</i>	3.60	1.20	1.50	2.06	2.09	1.50	1.00		0.83	2.50	2.70	2.50	3.00	2.63	1.20	0.75	1.00	2.00	2.50	2.25
	<i>Nectarinia notata</i>	0.60	0.60		0.56	0.46						0.60			0.25	0.30		0.17			
	<i>Calicalicus madagascariensis</i>																				
	<i>Cyanolanius madagascarinus</i>																				
0.08	<i>Tylas eduardi</i>			1.80	1.13	0.78			1.00	0.33		0.60		3.00	0.50						
	<i>Hartlaubius auratus</i>																				
	<i>Foudia omissa</i>	1.20	0.60		0.38	0.52					1.50				0.38						

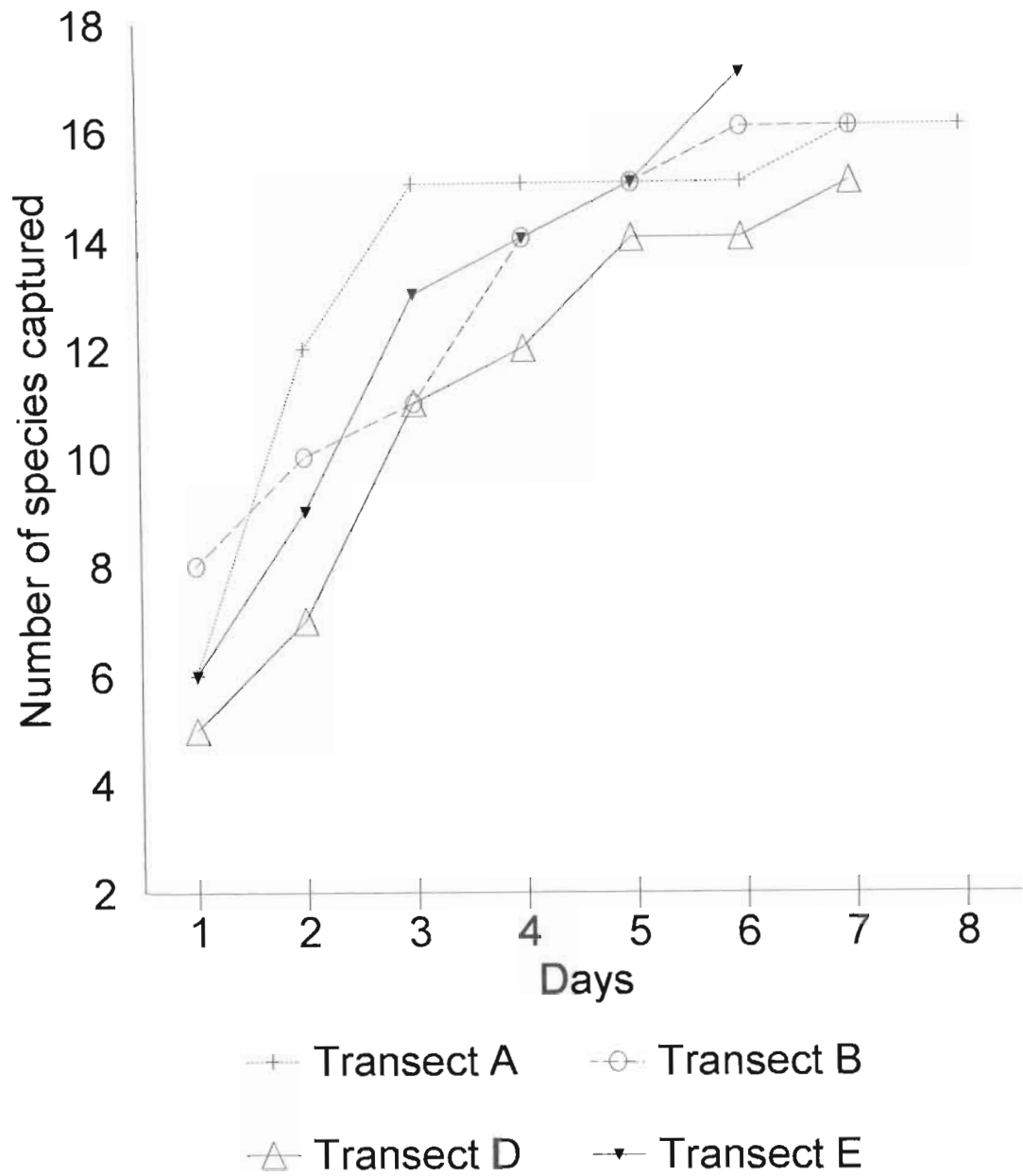
Table 8:

## SUMMARY OF MISTNETTING OPERATIONS IN THE AMBOHITANTELY SPECIAL RESERVE

(Column "D5" gives results based on the five first days of mistnetting; second column "D+"  
gives results based on total number of days of mistnetting if number of days exceeds five)

Count	Control site (1250ha)										Frag A	Frag E	Frag H	Frag F	A 12	Frag H1	Frag H5		Subtotal		Total		
	A		B		D		E		Subtotal		(136ha)	(52ha)	(30ha)	(28ha)	(12ha)	(4ha)		(0.64ha)		Fragments			
	D5	D+	D5	D+	D5	D+	D5	D+	D5	D+	D5	D5	D5	D5	D5	D5	D+	D5	D+	D5	D+	D5	D+
Number of days of mistnetting	5	8	5	7	5	7	5	6	20	28	5	5	5	5	5	5	6	5	6	35	37	55	65
Nb of mistnets	33	33	33	33	33	33	50	50	149	149	33	21	22	26	32	13	13	10	10	157	157	306	306
Number of captures	59	77	53	56	41	52	38	47	191	232	57	58	15	41	54	20	23	10	11	255	259	446	491
Number of individuals	44	53	40	42	35	41	33	40	152	176	52	49	12	33	43	20	23	9	9	218	221	370	397
Number of species	15	16	14	16	14	15	15	17	23	24	14	12	5	11	17	7	7	5	5	23	23	26	26
Number of mistnet-days	165	264	165	231	165	231	250	300	745	1026	165	105	110	130	130	65	78	50	60	755	778	1500	1804
Number of individuals captured per day	8.80	6.63	8.00	6.00	7.00	5.86	6.60	6.67	7.60	6.29	10.40	9.80	2.40	6.60	8.60	4.00	3.83	1.80	1.50	6.23	5.97	6.73	6.11
Number of individuals captured per mistnet-day	0.27	0.20	0.24	0.18	0.21	0.18	0.13	0.13	0.20	0.17	0.32	0.47	0.11	0.25	0.33	0.31	0.29	0.18	0.15	0.29	0.28	0.25	0.22





**Figure 14: Cumulative species time curves in control site**

#### 10.1.5. POTENTIALLY BREEDING SPECIES

Among the 72 species recorded within the Ambohitantely Special Reserve, 69 (95.8%) are breeding and only three (4.2%) are non-breeding. *Falco eleonora*, *F. concolor*, and *Actitis hypoleucos* are the only species occurring in Ambohitantely that breed in the Palaearctic and Afrotropical Regions and visit Madagascar during the boreal winter.

#### 10.1.6. COMPOSITION

The avifauna found in the Ambohitantely Special Reserve can be divided into two major ecological groups: forest birds and non-forest birds (Wilmé in press). Among the 72 species recorded in the reserve, 56 (77.7%) are classified as forest species and 16 (22.2%) are non-forest species (Wilmé in press).

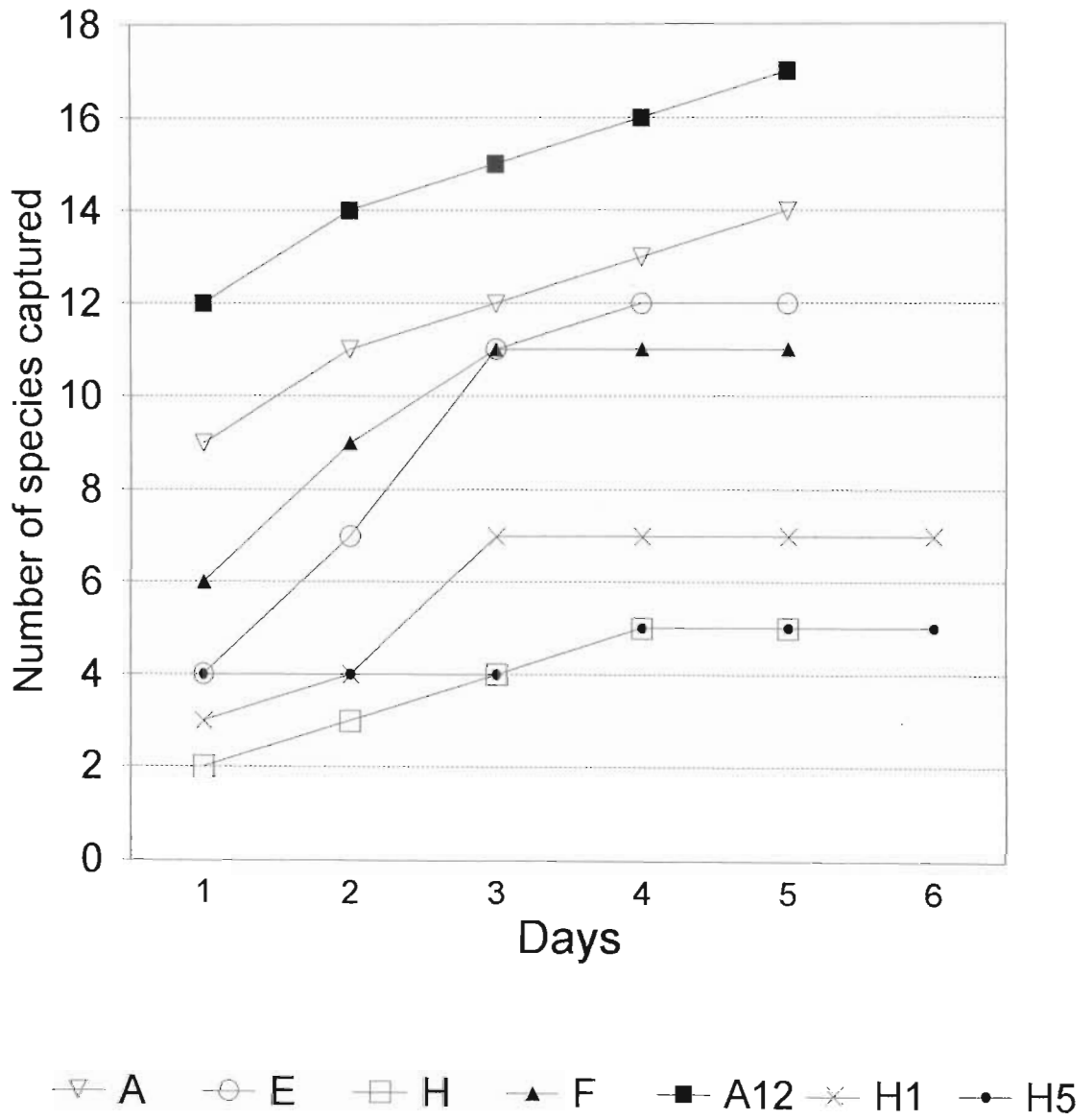
The 16 non-forest species are divided into two sub-categories: seven (43.8%) are aquatic and nine (56.2%) occur in savannah and/or exotic-tree plantations.

The seven aquatic species are:

*Scopus umbretta*  
*Anas melleri*  
*Circus maillardi*  
*Glareola ocularis*  
*Actitis hypoleucos*  
*Corythornis vintsioides*  
*Motacilla flaviventris*

and the nine savannah and exotic-plantation species are:

*Milvus migrans*  
*Falco newtoni*



**Figure 15: Cumulative species time curves  
Fragments**

*Margaroperdix madagascarensis*

*Tyto alba*

*Upupa epops*

*Mirafra hova*

*Saxicola torquata*

*Cisticola cherina*

*Corvus albus*

The present study was principally focused on the forest birds; non-forest species that were occasionally observed in the forest have been excluded from the analysis. This is the case for two species, *Motacilla flaviventris* and *Corvus albus*.

Among the 56 species that frequent the forest of Ambohitantely, two non-breeding species have been excluded from the analysis, *Falco eleonora* and *F. concolor* (Table 3).

#### 10.1.6.1. FOREST SPECIES

Following the classification by Wilmé (in press), 54 species have been identified as forest-dwelling (Table 3). Some of these species are also found in anthropogenic habitats. Six species are known to occur in a variety of habitats including forest, savannah grassland, and exotic-tree plantations: *Numida meleagris*, *Turnix nigricollis*, *Caprimulgus madagascariensis*, *Merops superciliosus*, *Foudia madagascariensis*, and *Lonchura nana*. Fourteen species have been found both in natural forest and in exotic-tree plantations, or in natural forest and in savannah grassland: *Machaeramphus alcinus*, *Falco peregrinus*, *Sarothrura insularis*, *Cuculus rochii*, *Apus melba*, *A. barbatus*, *Riparia paludicola*, *Phedina borbonica*, *Hypsipetes madagascariensis*, *Nesillas typica*, *Nectarinia souimanga*, *N. notata*, *Zosterops maderaspatana*, and *Dicrurus forficatus*. Thirty-four species have been found exclusively in the natural forest: *Lophotibis cristata*, *Aviceda madagascariensis*, *Polyboroides radiatus*, *Accipiter henstii*, *A. madagascariensis*,

*A. francesii*, *Buteo brachypterus*, *Falco zoniventris*, *Dryolimnas cuvieri*, *Streptopelia picturata*, *Treron australis*, *Alectroenas madagascariensis*, *Coracopsis nigra*, *Centropus toulou*, *Otus rutilus*, *Asio madagascariensis*, *Zoonavena grandidieri*, *Ispidina madagascariensis*, *Eurystomus glaucurus*, *Atelornis pittoides*, *Leptosomus discolor*, *Coracina cinerea*, *Phyllastrephus madagascariensis*, *Copsychus albospectularis*, *Pseudocossyphus sharpei*, *Cryptosylvicola randrianasoloi*, *Newtonia amphichroa*, *N. brunneicauda*, *Terpsiphone mutata*, *Calicalicus madagascariensis*, *Cyanolanius madagascarinus*, *Tylas eduardi*, *Hartlaubius auratus*, and *Foudia omissa*. These thirty-four species together with the 20 occurring in forest and/or anthropogenic habitats are those considered in this study.

#### 10.1.6.1.1. CUMULATIVE SPECIES TIME CURVES

Cumulative species time curves for all study sites within the reserve were generated for the point counts and mistnetting operation (Fig. 12).

A total of 54 forest-bird species was recorded during 53 h 20 min point-count sampling and 1804 mistnet-days, and on the basis of cumulative curves our knowledge of the bird species at these sites approaches completeness.

The cumulative species time curves for the control site and the seven fragments, based on mistnetting operations and point-counts, indicate that the total of species for each site is probably complete. Fifty-one forest species were recorded in the control site, 41 in fragment A 136 ha, 39 in fragment E (52 ha), 33 in fragment H (30 ha), 33 in fragment F (28 ha), 27 in fragment A12 (12 ha), 29 in fragment H1 (4 ha) and 14 in fragment H5 (0.64 ha).

A regression analysis of species diversity versus the log. function of the total area of each site reveals that these two variables are significantly correlated ( $r^2 = 0.95$ ;  $P < 1.0000$

E-4) (Fig. 16).

#### 10.1.6.1.2. EDGE EFFECTS ON FOREST BIRDS

The edge effect on forest species found in the control site and the seven fragments was investigated, based on mistnetting operations and point-count sampling. Three main groups of species can be defined:

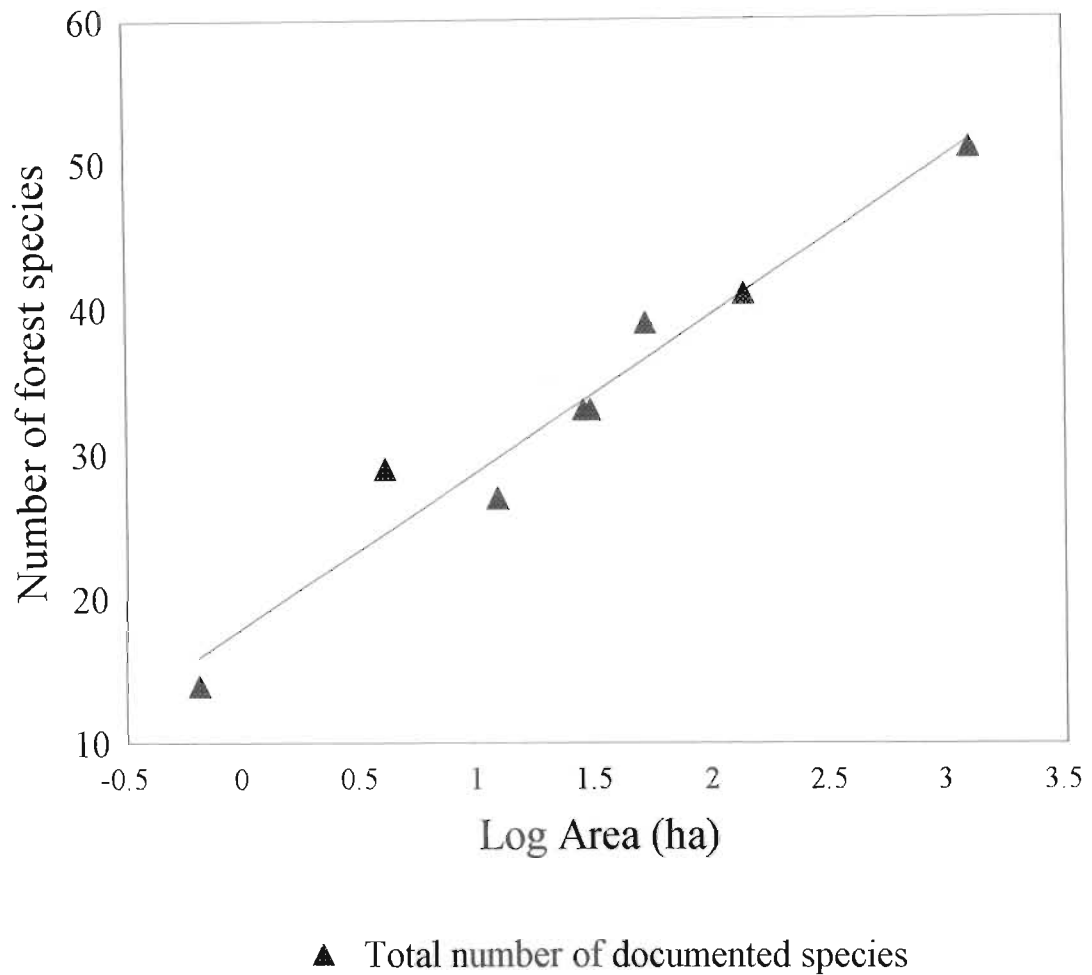
Forest-interior species: *Accipiter madagascariensis*, *Streptopelia picturata*, *Otus rutilus*, *Ispidina madagascariensis*, *Atelornis pittoides*, *Phyllastrephus madagascariensis*, *Terpsiphone mutata*, *Newtonia amphichroa*, *Calicalicus madagascariensis*, *Cyanolanius madagascarinus*, *Foudia omissa*.

Edge species: *Sarothrura insularis*, *Cuculus rochii*, *Caprimulgus madagascariensis*, *Eurystomus glaucurus*, *Riparia paludicola*, *Phedina borbonica*, *Nesillas typica*, *Copsychus albospectularis*, *Foudia madagascariensis*, *Lonchura nana*.

Ubiquitous species: *Accipiter francesii*, *Alectroenas madagascariensis*, *Coracopsis nigra*, *Asio madagascariensis*, *Leptosomus discolor*, *Coracina cinerea*, *Hypsipetes madagascariensis*, *Pseudocossyphus sharpei*, *Cryptosylvicola randrianasoloi*, *Newtonia brunneicauda*, *Nectarinia souimanga*, *N. notata*, *Zosterops maderaspatana*, *Tylas eduardi*, *Dicrurus forficatus*, *Hartlaubius auratus*.

#### 10.1.6.2. FEEDING HABITS

The feeding habits of the 54 forest-dwelling species have been defined following Wilmé's (in press) categorization. Seven (13%) are terrestrial feeders (*Lophotibis cristata*, *Numida meleagris*, *Turnix nigricollis*, *Dryolimnas cuvieri*, *Sarothrura insularis*, *Streptopelia picturata*, and *Atelornis*



**Figure16: Species-area relationship for eight forest sites**  
Straight line shows the relation  $S = 18.00 + 10.83(\text{Log Area})$  ( $r^2=.95$ )

*pittoides*), ten (18.5%) are aerial feeders (*Machaeramphus alcinus*, *Falco peregrinus*, *Caprimulgus madagascariensis*, *Zoonavena grandidieri*, *Apus melba*, *A. barbatus*, *Merops superciliosus*, *Eurystomus glaucurus*, *Riparia paludicola*, and *Phedina borbonica*.), and the remaining 37 (68.5%) are arboreal feeders.

The food items are divided into three categories, "Plant food" including nectar, fruit and seeds, "Invertebrates," and "Vertebrates". Seventeen species feed on vegetation (7-13% strictly) , 42 on invertebrates (30-55.5% strictly) and 17 on vertebrates (5-9.26% strictly).

The location of captures for selected species and forest fragments are shown in Figs 18-45. Table 12 shows the biogeographical and ecological parameters of the resident birds of Ambohitantely Special Reserve.

#### 10.1.6.3. DISTRIBUTION OF BIRD SPECIES IN THE DIFFERENT FOREST FRAGMENTS BASED ON MISTNETTING RESULTS

It is important to define to what extent the avifauna represents nested subsets (Patterson & Atmar 1986) in the different forest fragments that were sampled. For this purpose a data matrix of species occurrences by forest fragment has been prepared (Table 9).

This data matrix (Table 9) reflects clear nested subsets in the occurrence of bird species in forest fragments. All species found in the different forest fragments are also found in the control site. Generally, nested avifauna suggests that extinction proceeds in a predictable fashion and is a deterministic process. The non-random nature of extinction may lead the bird species composition of forest fragments to converge over time, with the survival of generalist forest species and the extinction of the specialized forest species.



Table 9  
Proportional distribution of bird species in forest fragments

Species	Nb of ind. captured	Size and names of fragments							Control site
		.64ha H05	4ha H1	12ha A12	28ha F	30ha H	52ha E	136ha A	
<i>Zosterops maderaspatana</i>	25		0.087	0.095	0.063		0.102		0.142
<i>Nectarinia souimanga</i>	18			0.095			0.020	0.038	0.102
<i>Newtonia brunneicauda</i>	16			0.143			0.224	0.115	0.091
<i>Hypsipetes madagascariensis</i>	15	0.444	0.130	0.024	0.313	0.167	0.388	0.096	0.085
<i>Terpsiphone mutata</i>	13	0.111	0.130	0.095	0.188	0.333	0.061	0.173	0.074
<i>Nesillas typica</i>	11	0.222	0.130	0.095	0.031	0.083	0.061		0.063
<i>Pseudocossyphus sharpei</i>	11			0.048	0.063	0.333	0.020	0.135	0.063
<i>Foudia omissa</i>	10		0.043	0.095	0.031			0.038	0.057
<i>Newtonia amphichroa</i>	10						0.041		0.057
<i>Phyllastrephus madagascariensis</i>	7			0.048	0.219			0.135	0.040
<i>Dicrurus forficatus</i>	6			0.048					0.034
<i>Accipiter francesii</i>	6			0.024					0.034
<i>Atelornis pittoides</i>	5								0.028
<i>Copsychus albospecularis</i>	4	0.111	0.087		0.031			0.115	0.023
<i>Streptopelia picturata</i>	4			0.024			0.041	0.019	0.023
<i>Otus rutilus</i>	4				0.031			0.019	0.023
<i>Leptosomus discolor</i>	4							0.019	0.023
<i>Accipiter madagascariensis</i>	2			0.024		0.083	0.020	0.019	0.011
<i>Foudia madagascariensis</i>	1	0.111	0.391	0.071	0.031		0.020		0.006
<i>Tylas eduardi</i>	1			0.048				0.058	0.006
<i>Ispidina madagascariensis</i>	1			0.024					0.006
<i>Cyanolanius madagascarinus</i>	1							0.019	0.006
<i>Nectarinia notata</i>	1								0.006

This pattern is visible from the result of the data matrix.

To confirm the tendency of generalists being proportionally more common in the smaller forest fragments and specialized being more common in larger forest fragments, I compared the percentage of generalist with the fragment size (Fig. 17). This figure confirms that generalists are proportionally much more common (95-100%) in small fragments ( $\leq 4$  ha). It also shows that generalists maintain their proportion to an average level (55-70%) in all other forest blocks ( $\geq 12$  ha  $\geq 1250$  ha).

#### 10.1.6.4. RANDOM VERSUS NON-RANDOM DISTRIBUTION OF BIRD SPECIES IN FOREST FRAGMENTS BASED ON MISTNETTING RESULTS

After analyzing and interpreting the data on the distribution of forest-dependent bird species in forest fragments of the Réserve Spéciale d'Ambohitantely, it is essential to ask the following question: is the distribution of the different bird species in forest fragments a random or a non-random subset of the control site? To answer this question, I proposed the null hypothesis that there is no difference in the distribution of bird species found in the fragments. The alternative hypothesis is that there is a difference in the distribution of birds species found in the fragments.

Using the data on the birds captured in the control site and in the seven fragments ( $n = 395$ ) through mistnetting operations, I conducted a  $\chi^2$  analysis to test the null hypothesis.

Based on the results of the  $\chi^2$  analysis it is possible to say that the distribution of birds species found in the control site and in the forest fragments is non random ( $P < 0.01$ ;  $P < 0.001$ ) (Table 10).

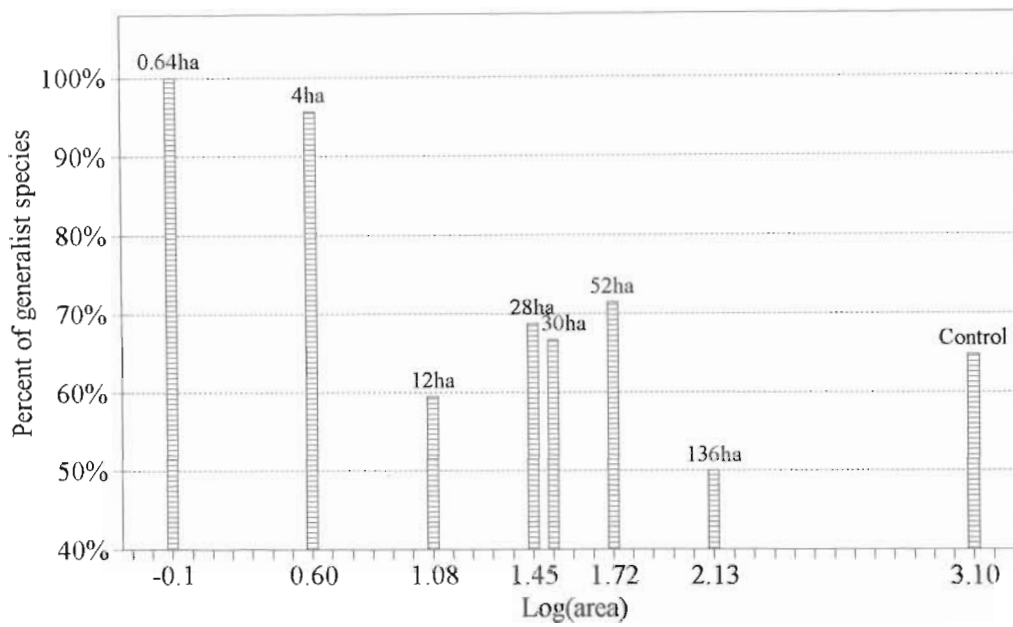
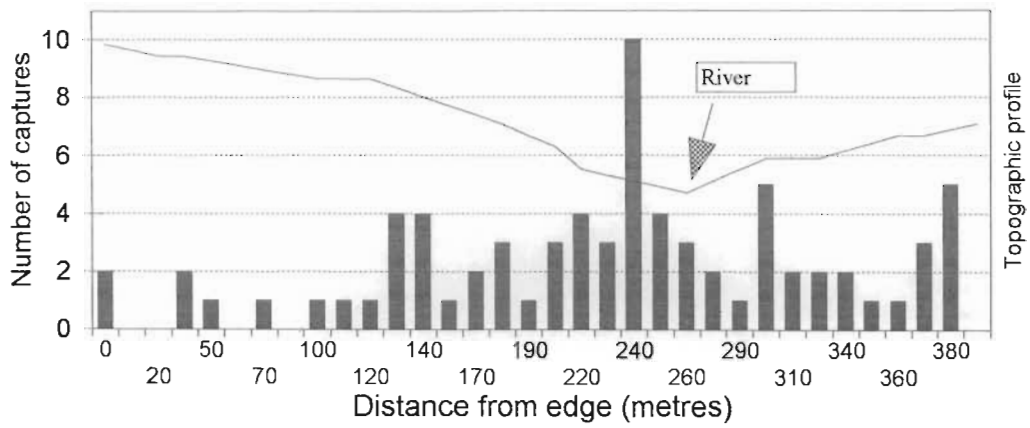


Figure 17  
Proportion of generalist species as a  
function of forest fragment size

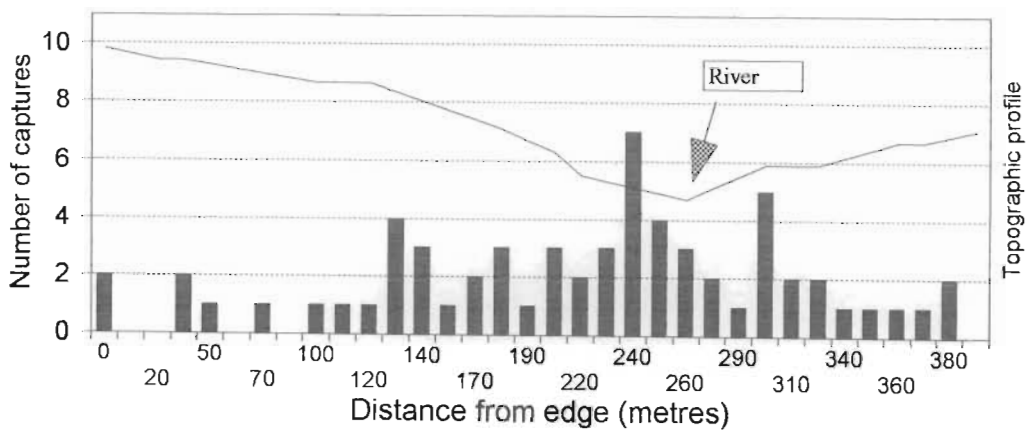
Table 10  
Significance table of  $\chi^2$

	.64ha H05	4ha H1	12ha A12	28ha F	30ha H	52ha E	136ha A
$\chi^2$	44.92	622.62	61.29	70.58	39.96	84.57	91.76
Level of significance*	0.01	0.001	0.001	0.001	0.001	0.001	0.001

\* Critical  $\chi^2$  value 22 df:  $p < 0.01 = 40.29$   
 $p < 0.001 = 48.2$

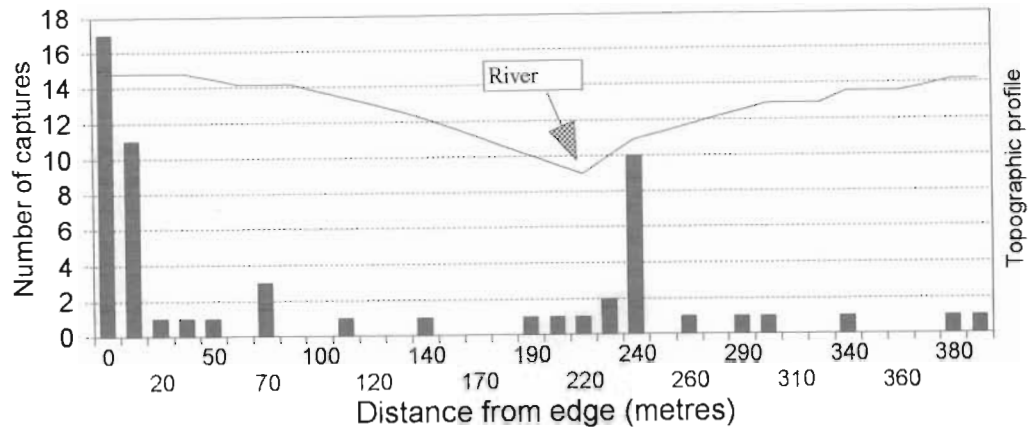


Location of captures

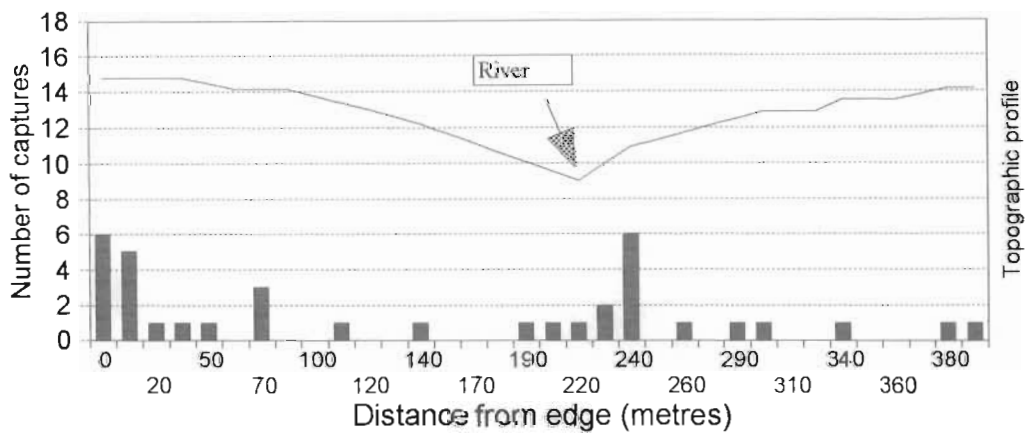


Location of species

**Figure 18: Control site,  
transect line A**

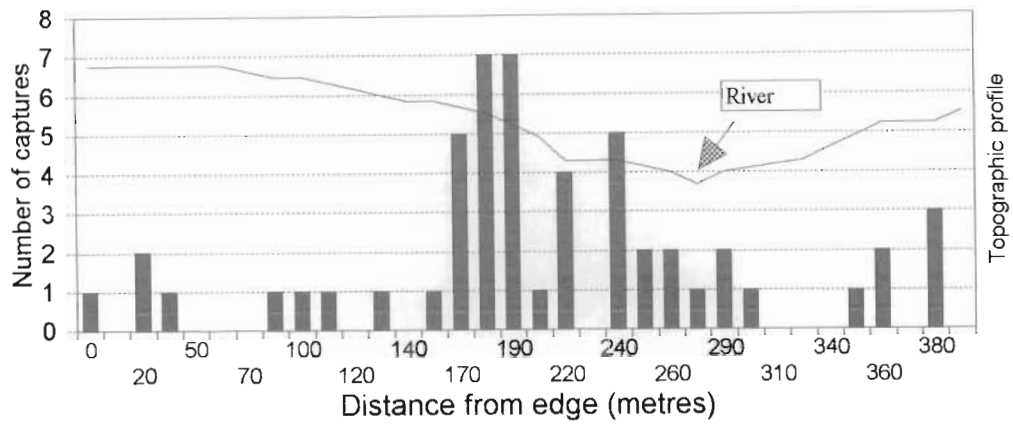


Location of captures

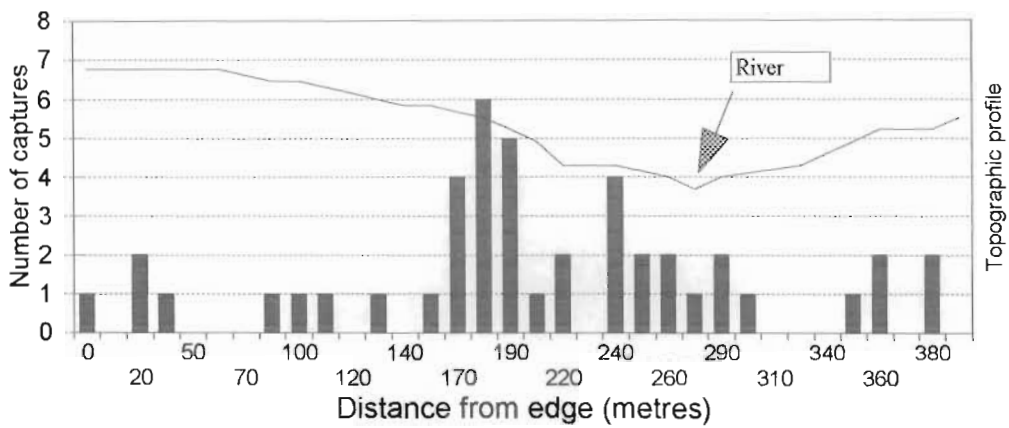


Location of species

**Figure 19: Control site,  
transect line B**



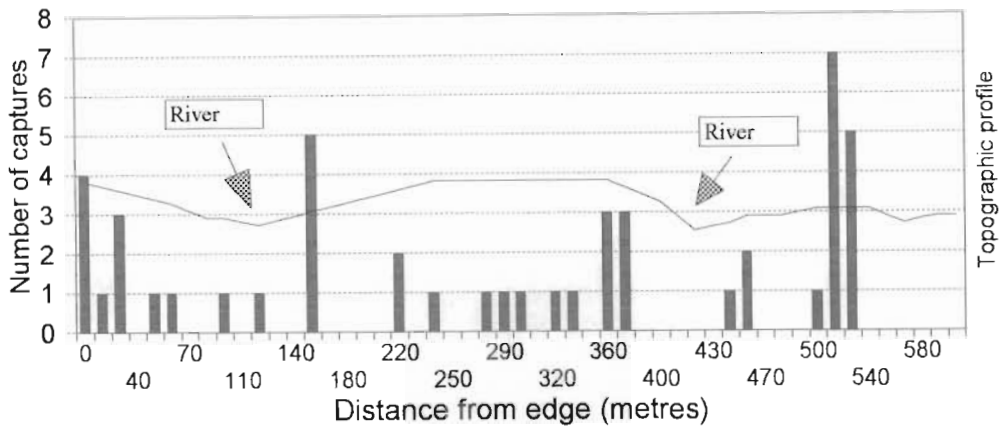
Location of captures



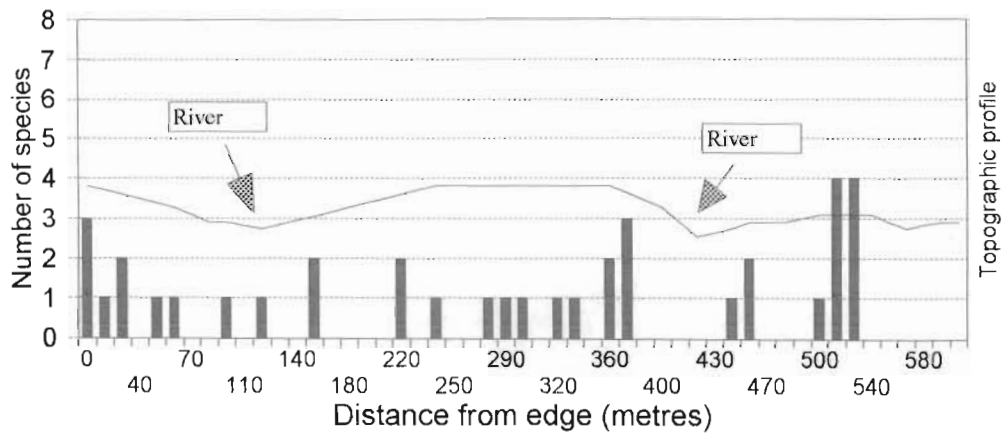
Location of species

**Figure 20: Control site,  
transect line D**





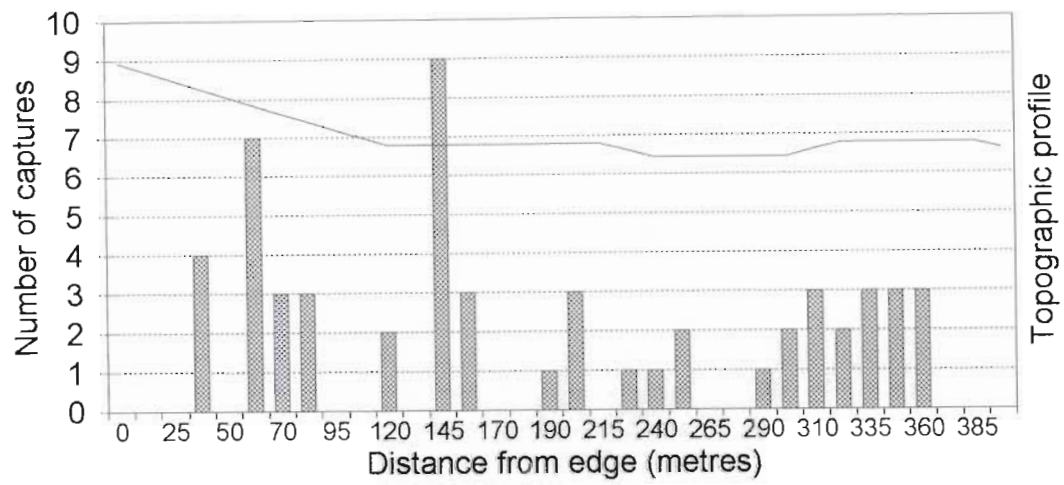
Location of captures



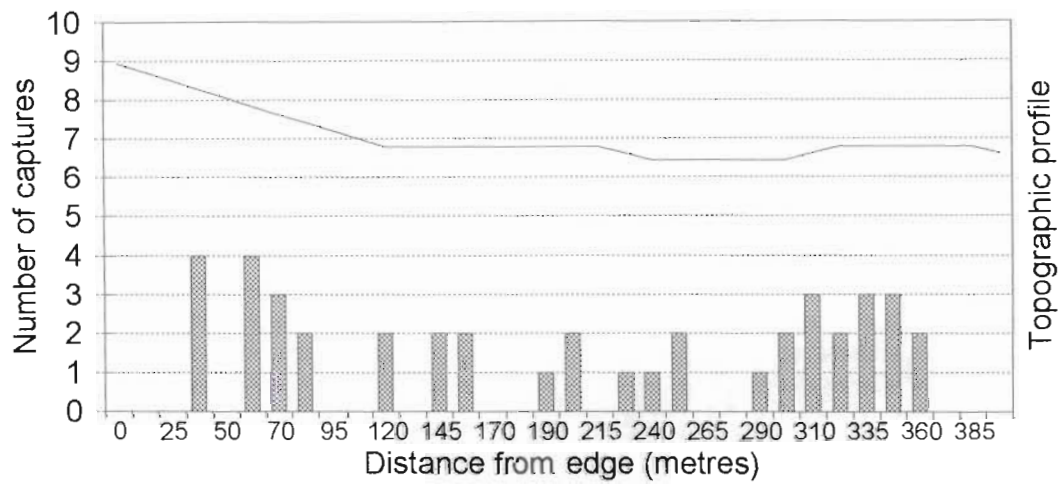
Location of species

**Figure 21: Control site,  
transect line E**



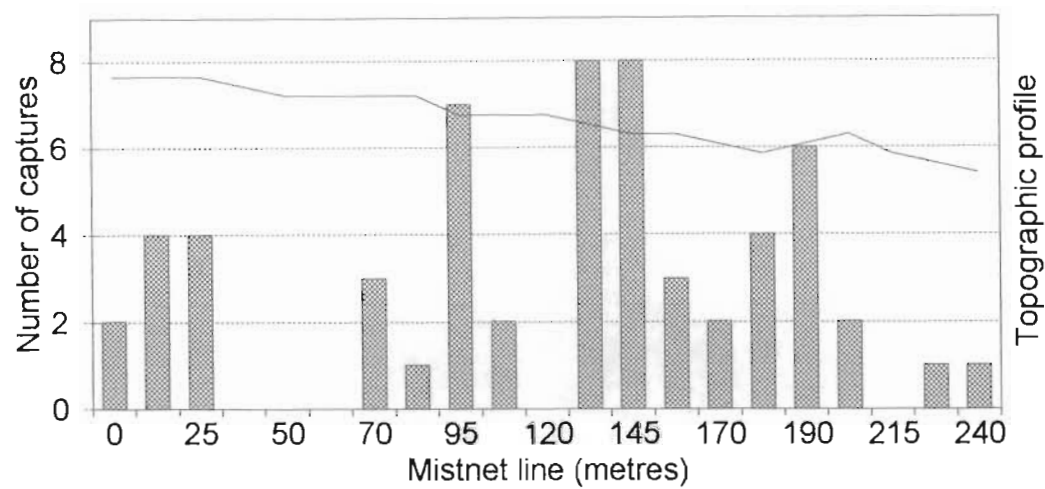


## Location of captures

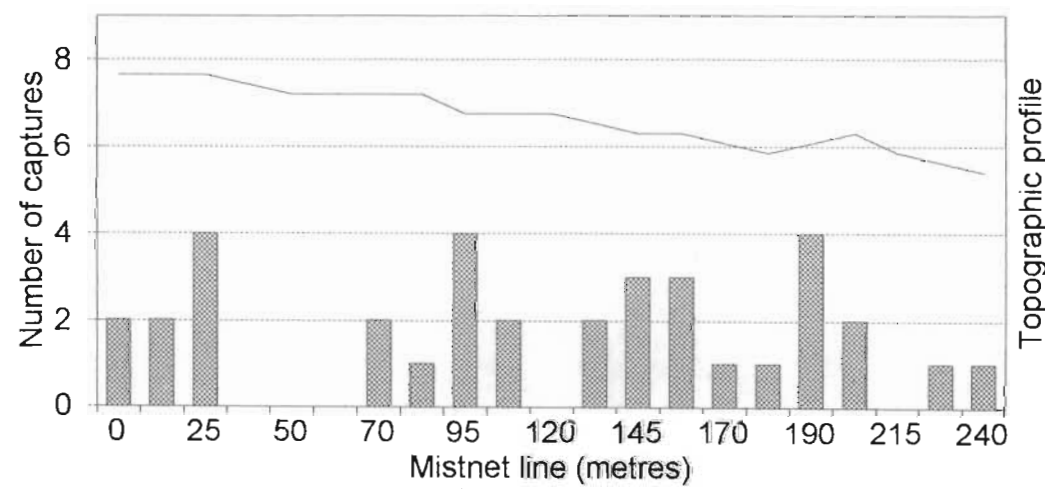


## Location of species

Figure 22: Fragment A

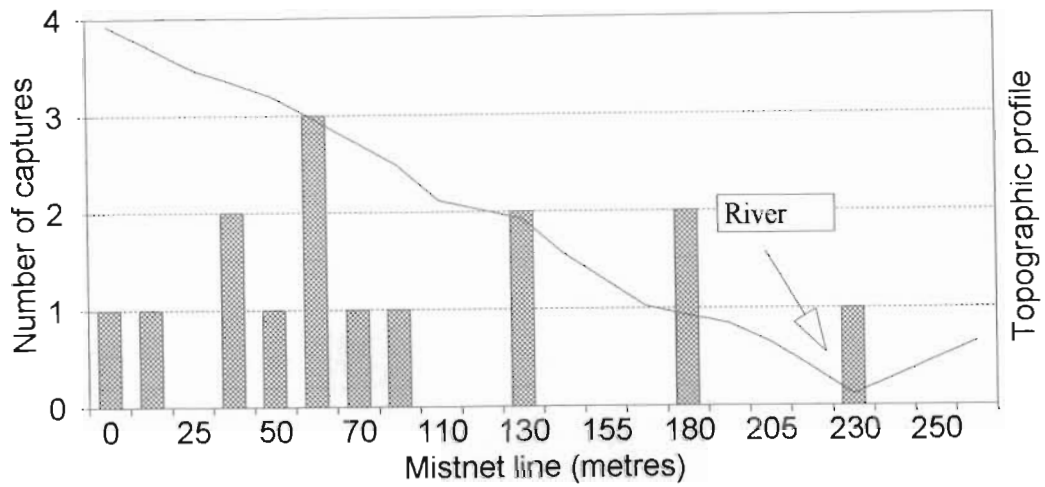


Location of captures

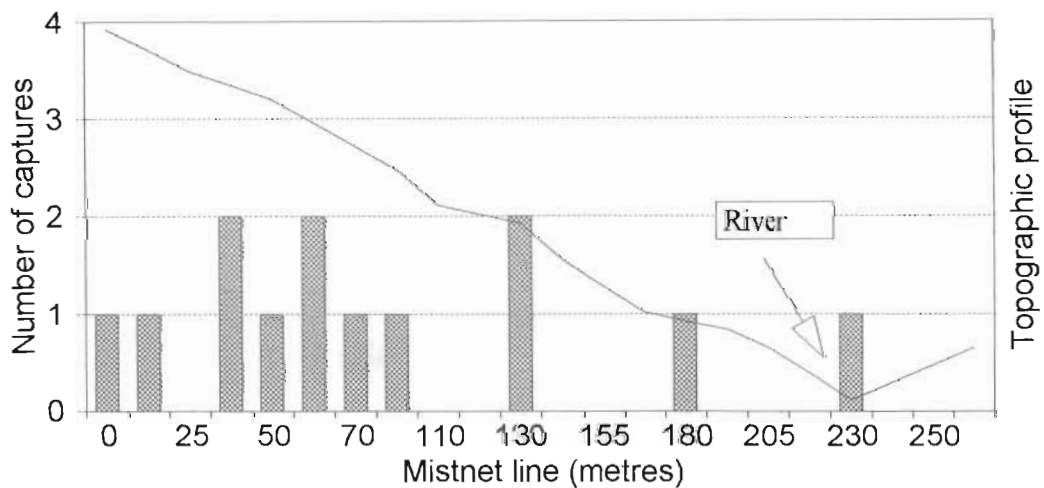


Location of species

Figure 23: Fragment E  
(mistnet line from edge to edge)

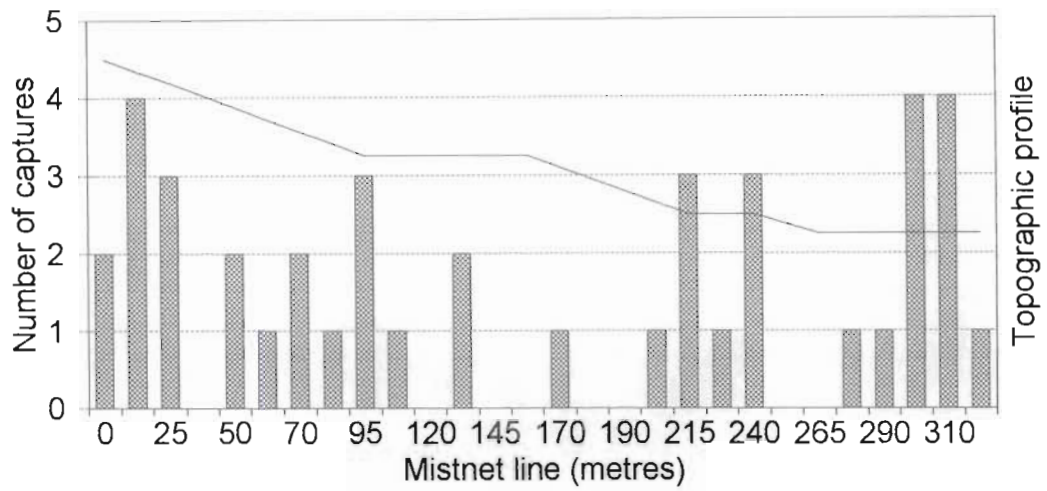


Location of captures

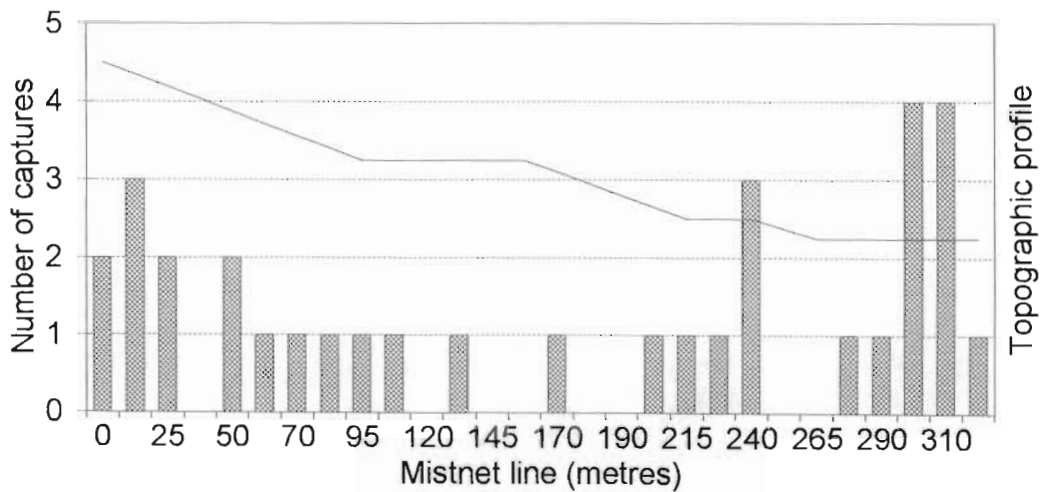


Location of species

Figure 24: Fragment H  
(mistnet line from edge to edge)

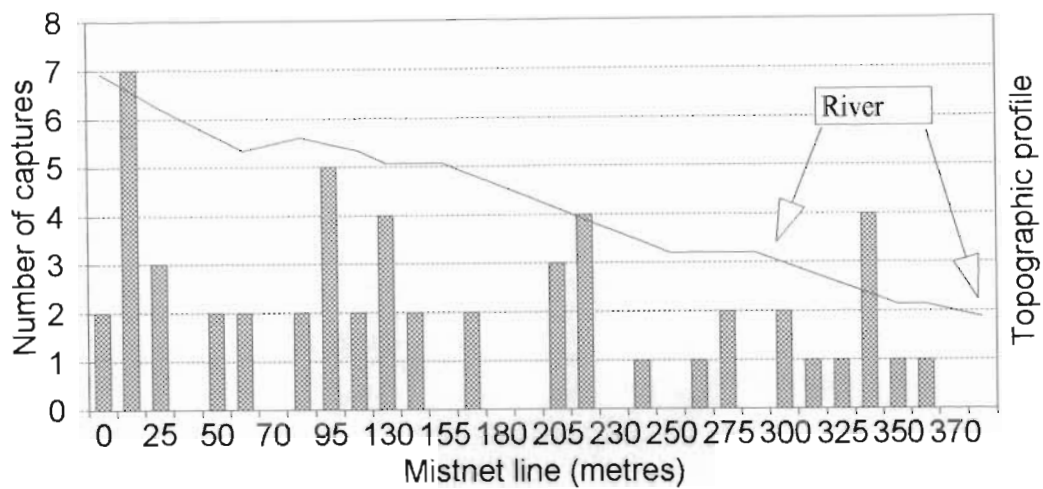


## Location of captures

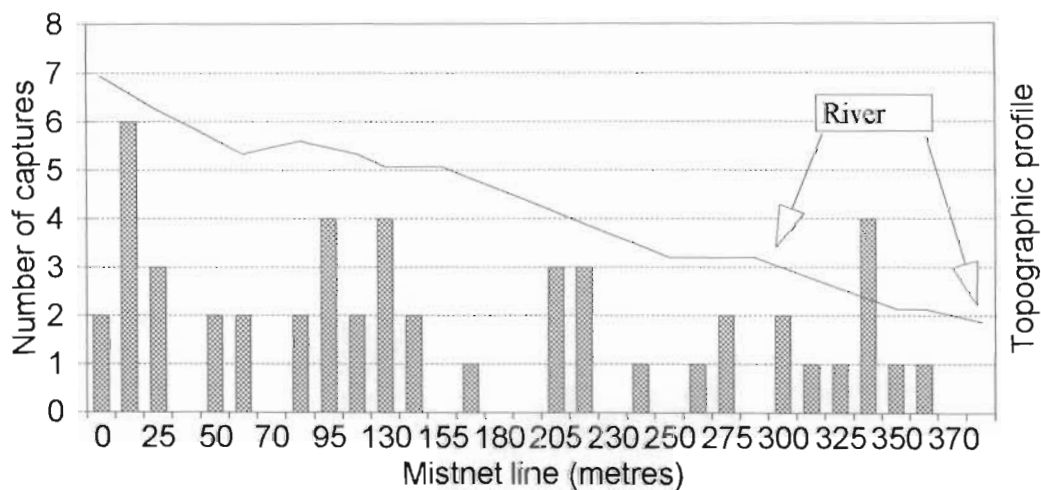


## Location of species

**Figure 25: Fragment F**  
(mistnet line from edge to edge)

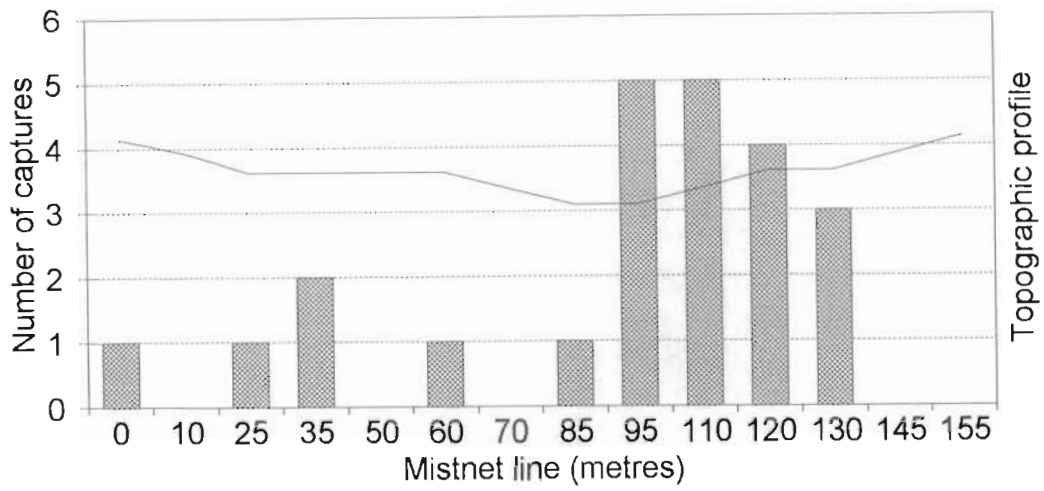


Location of captures

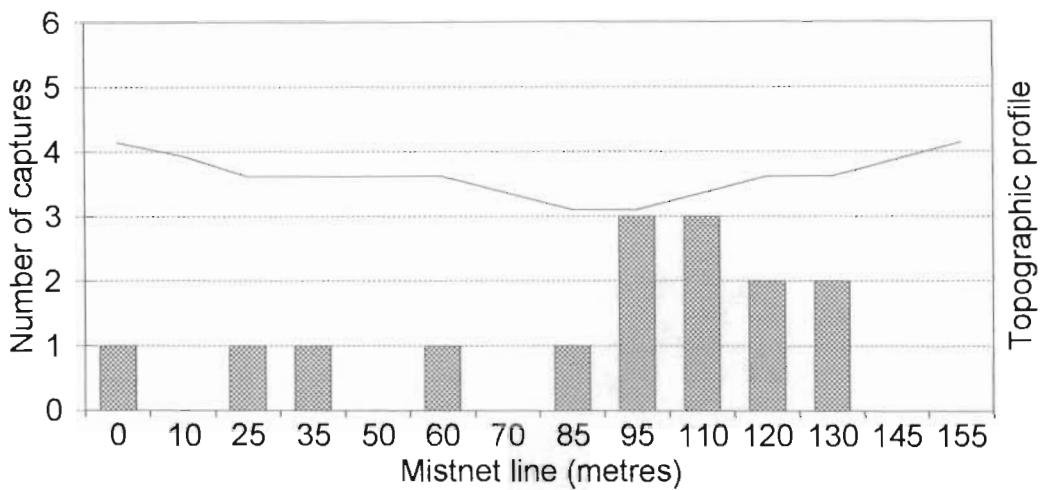


Location of species

Figure 26: Fragment A12  
(mistnet line from edge to edge)

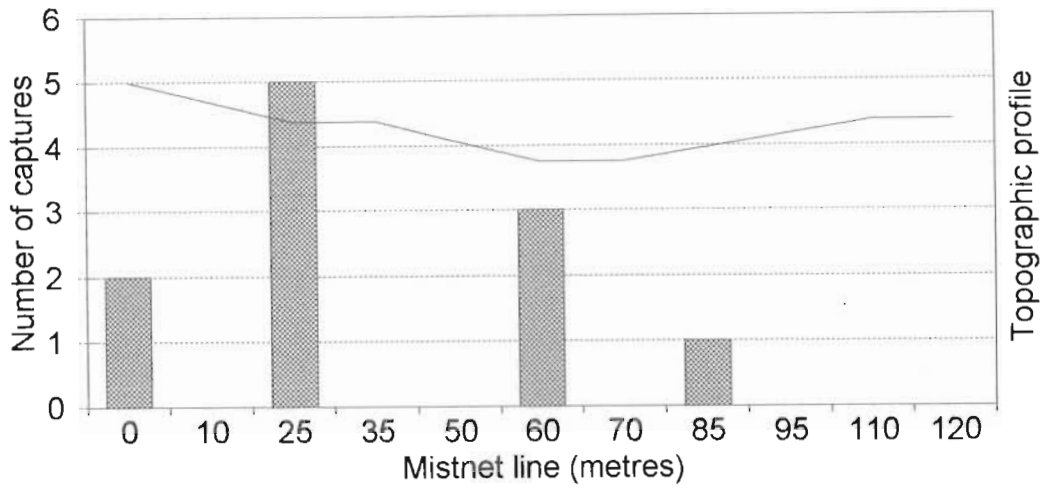


## Location of captures

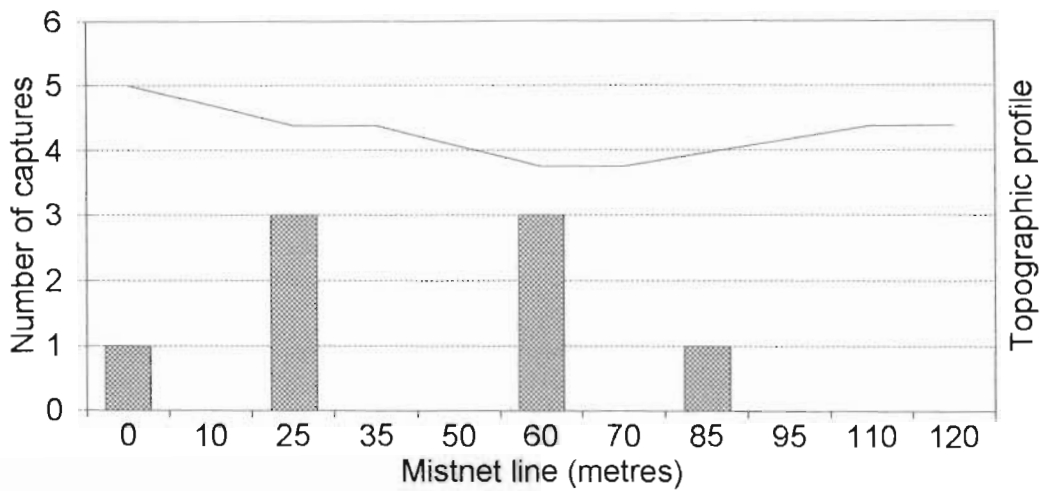


## Location of species

**Figure 27: Fragment H1**  
(mistnet line from edge to edge)



## Location of captures



## Location of species

**Figure 28: Fragment H5**  
(mistnet line from edge to edge)



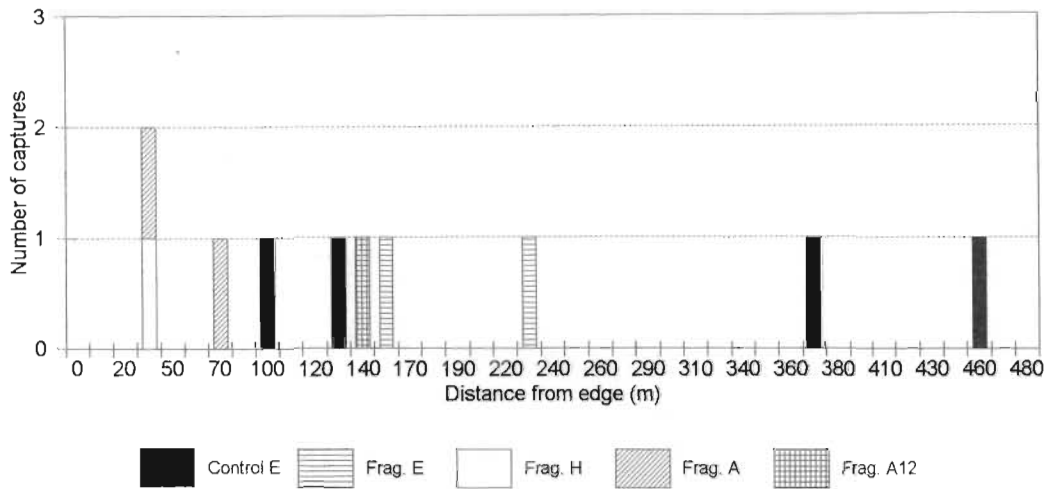


Figure 29: Location of capture  
*Accipiter madagascariensis*

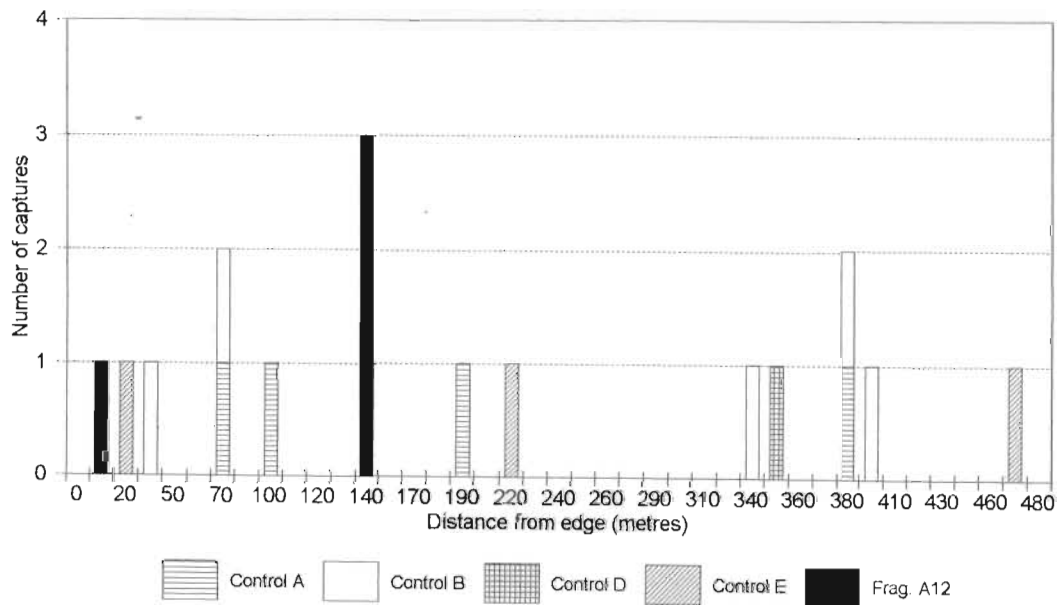


Figure 30: Location of capture  
*Accipiter francesii*



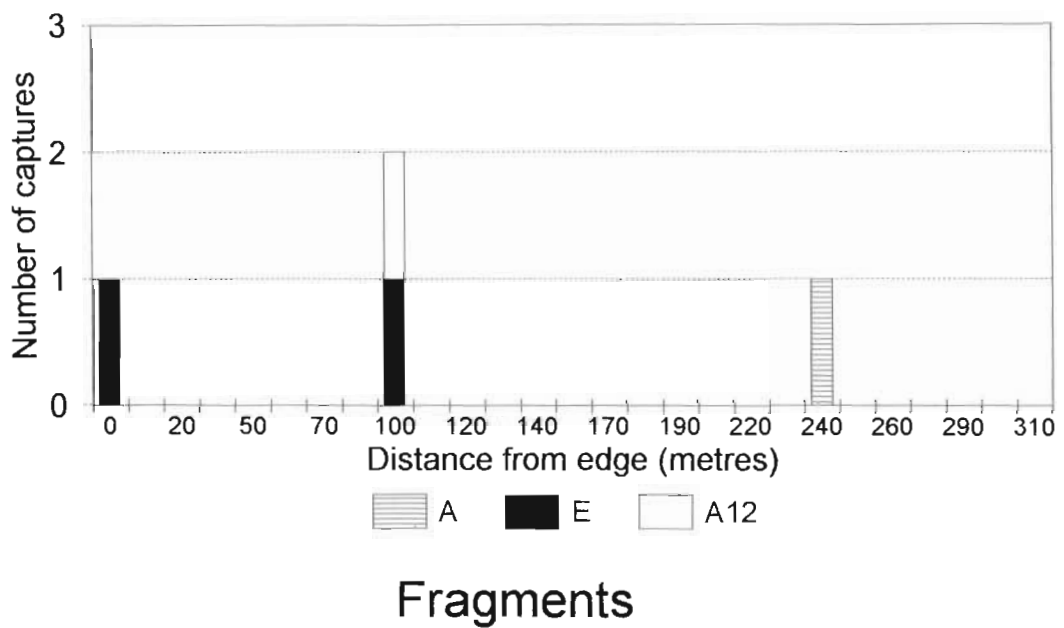
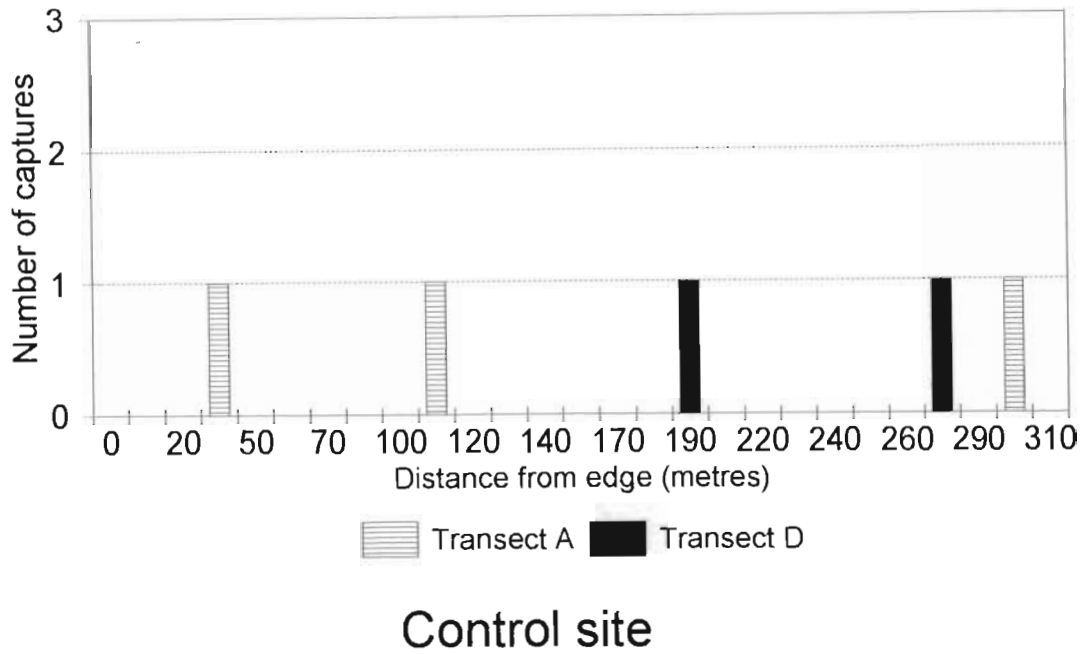


Figure 31: Location of capture  
*Streptopelia picturata*

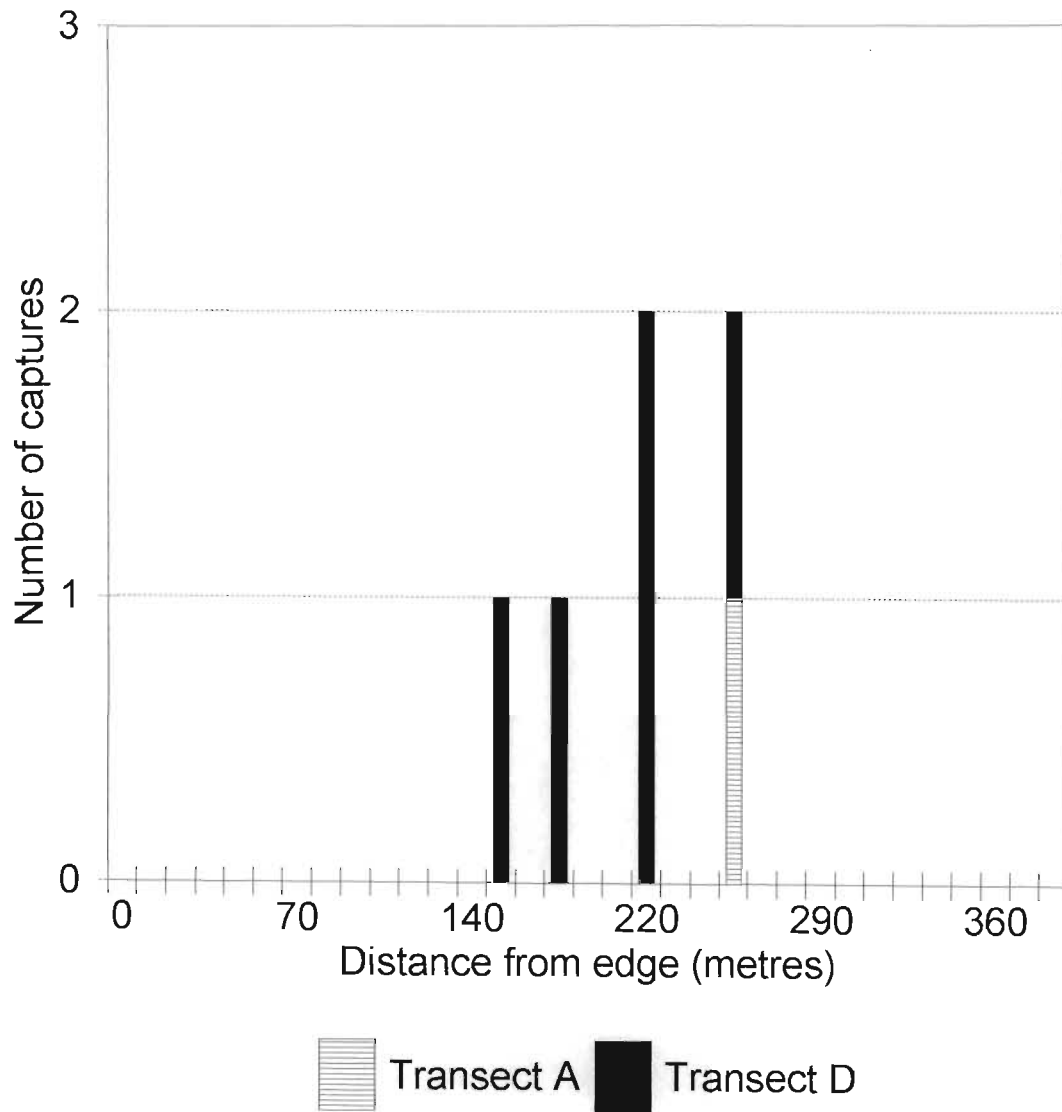
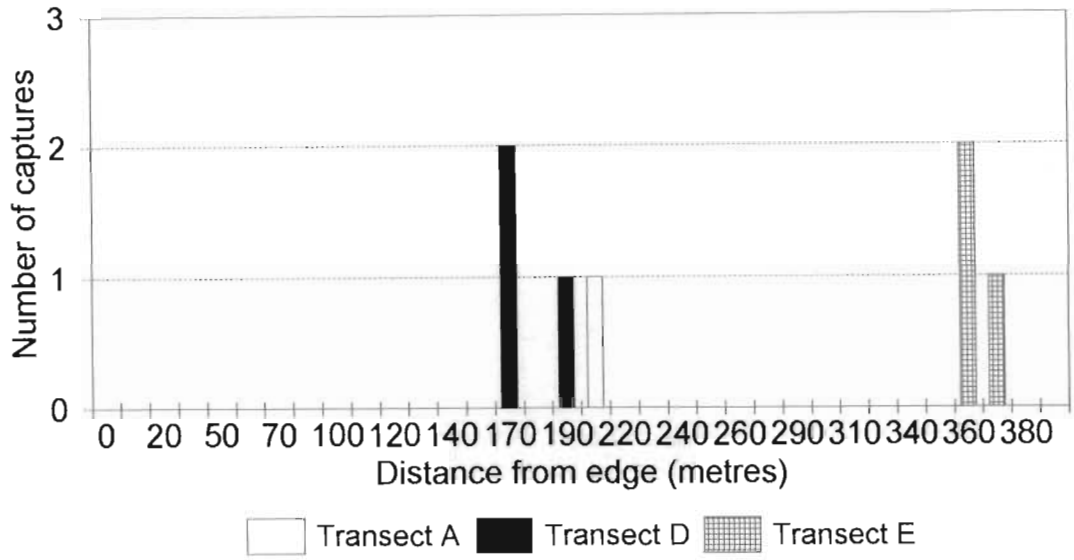
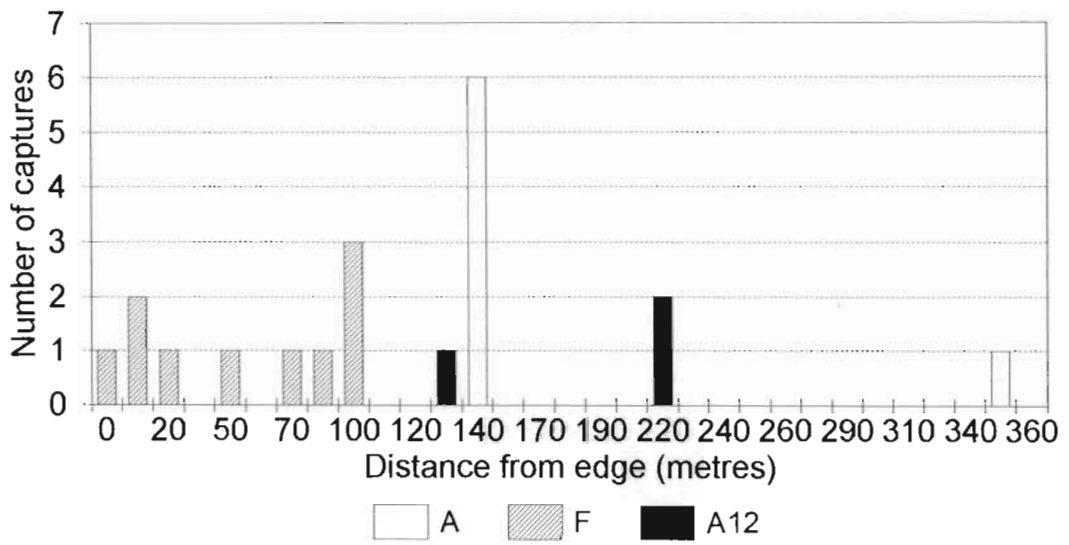


Figure 32: Location of capture  
in control site  
*Atelornis pittoides*

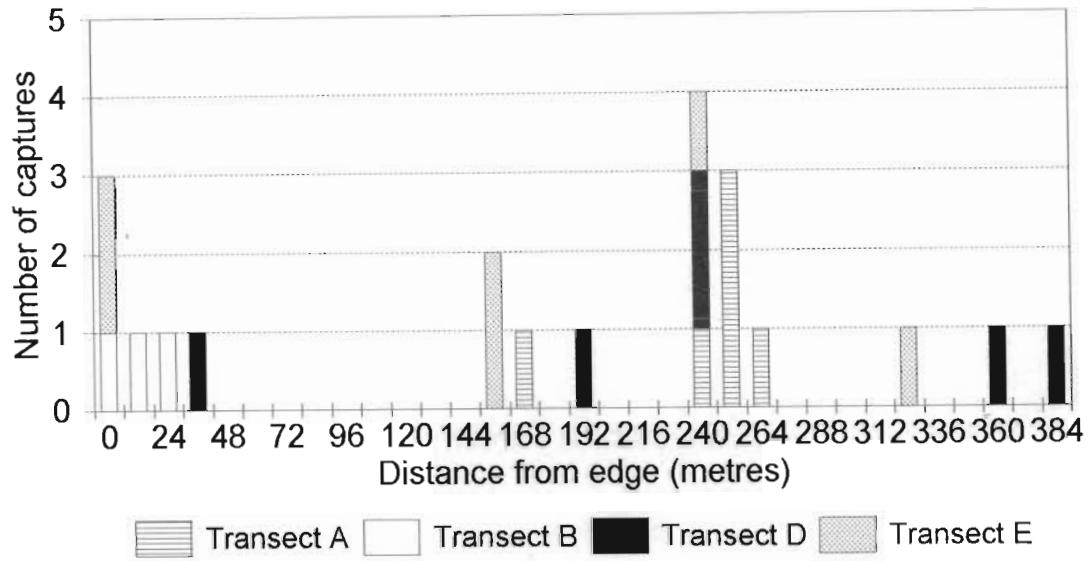


### Control site

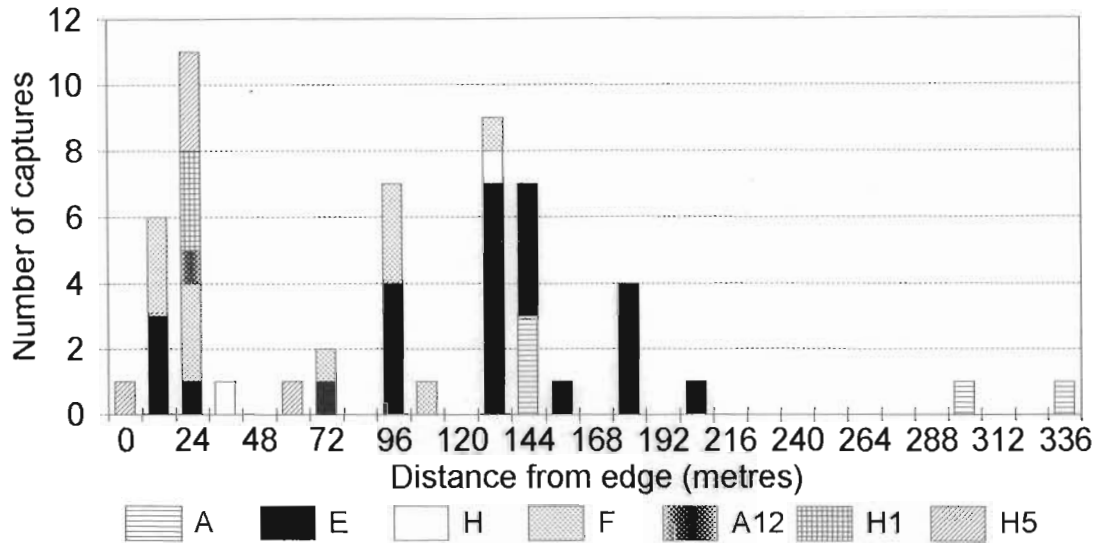


### Fragments

Figure 33: Location of capture  
*Phyllastrephus madagascariensis*



### Control site



### Fragments

Figure 34: Location of capture  
*Hypsipetes madagascariensis*

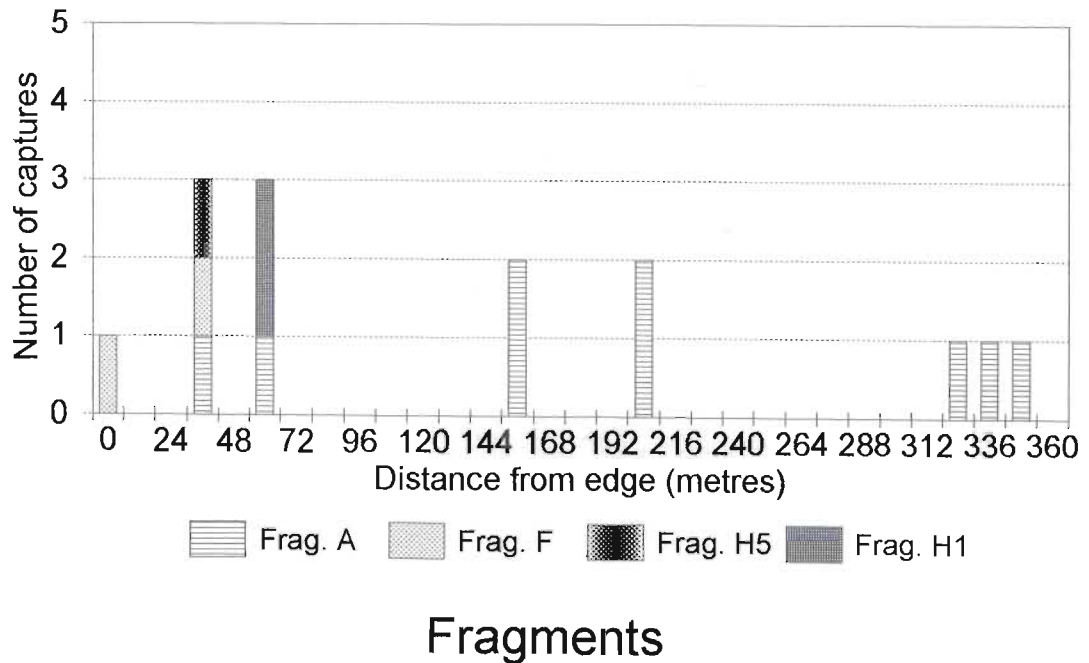
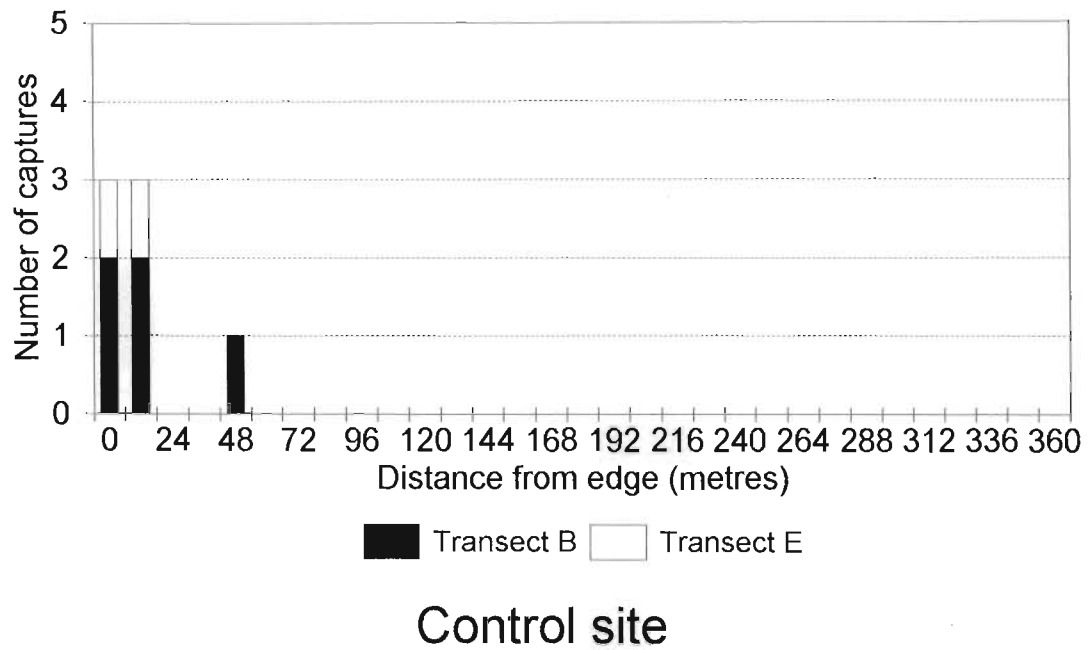
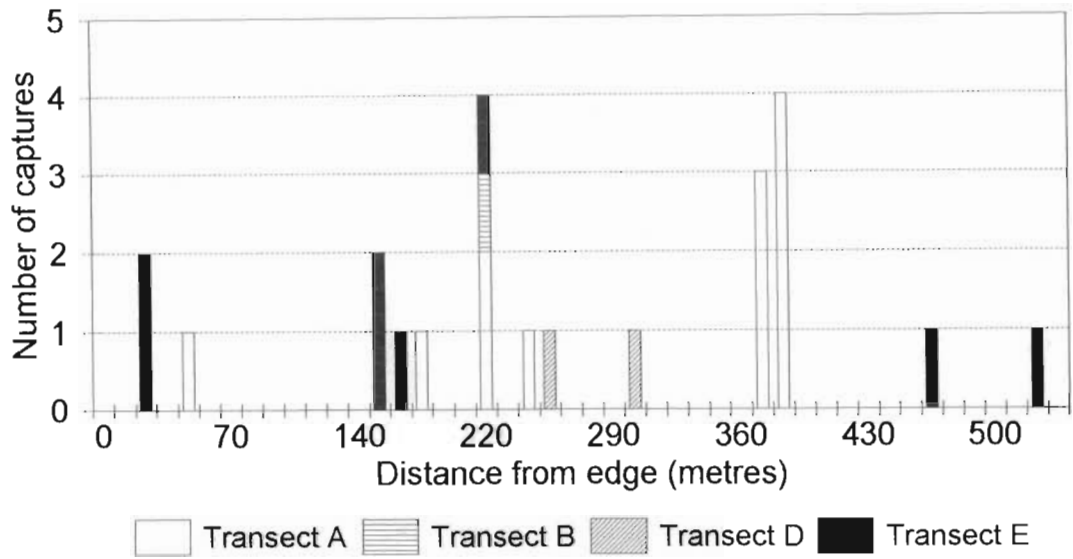
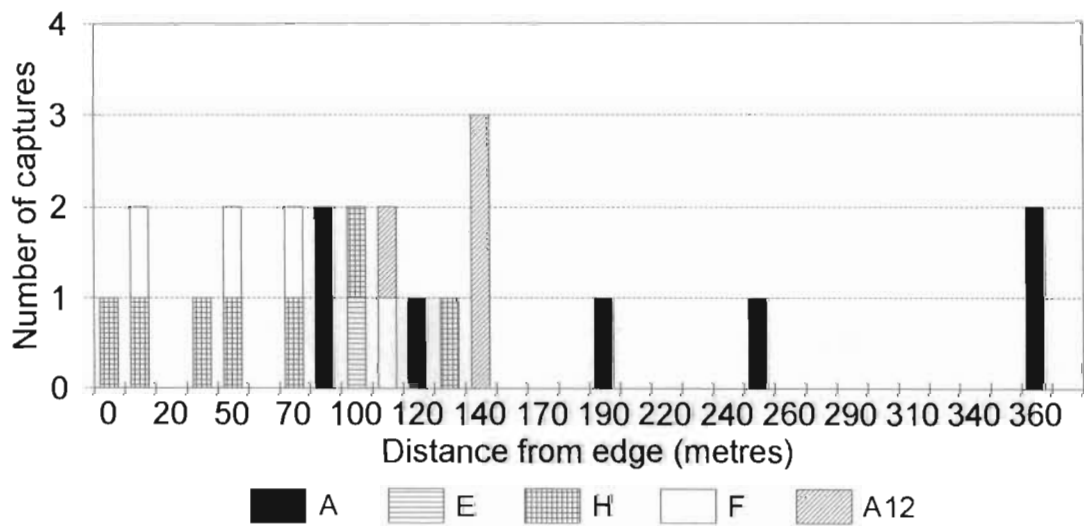


Figure 35: Location of capture  
*Copsychus albospecularis*

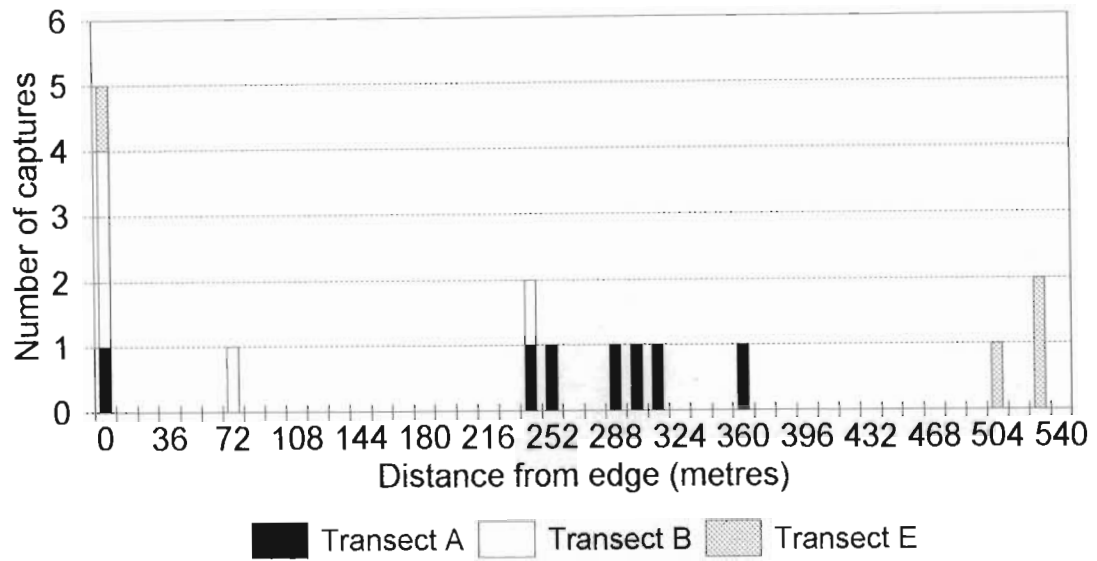


Control site

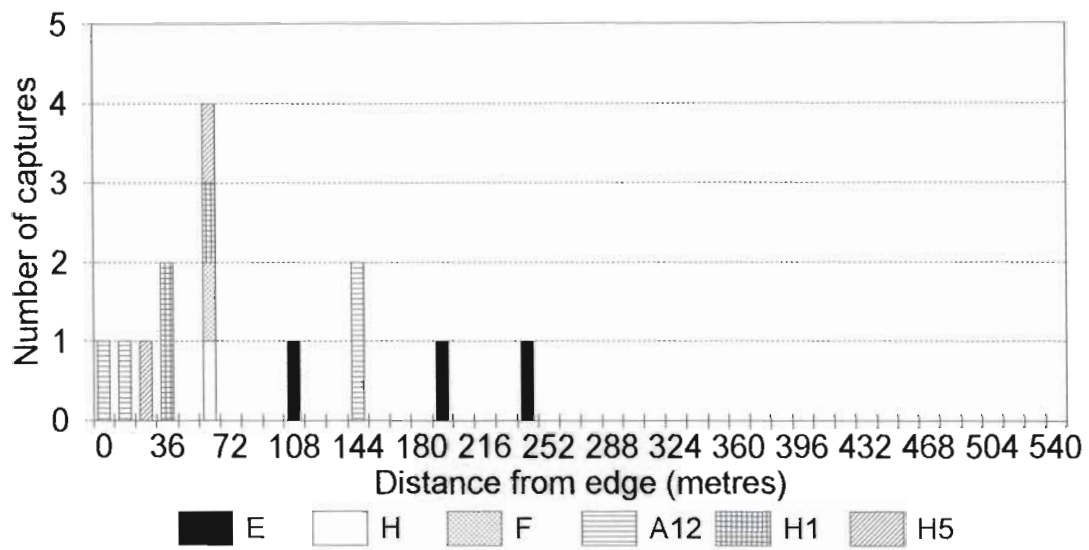


Fragments

Figure 36: Location of capture  
*Pseudocossyphus sharpei*

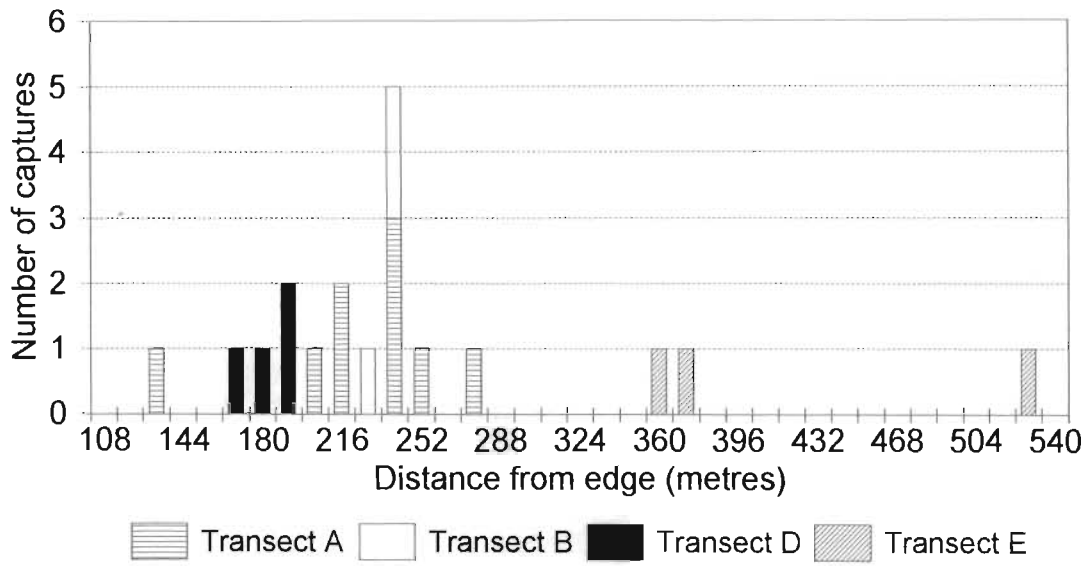


### Control site

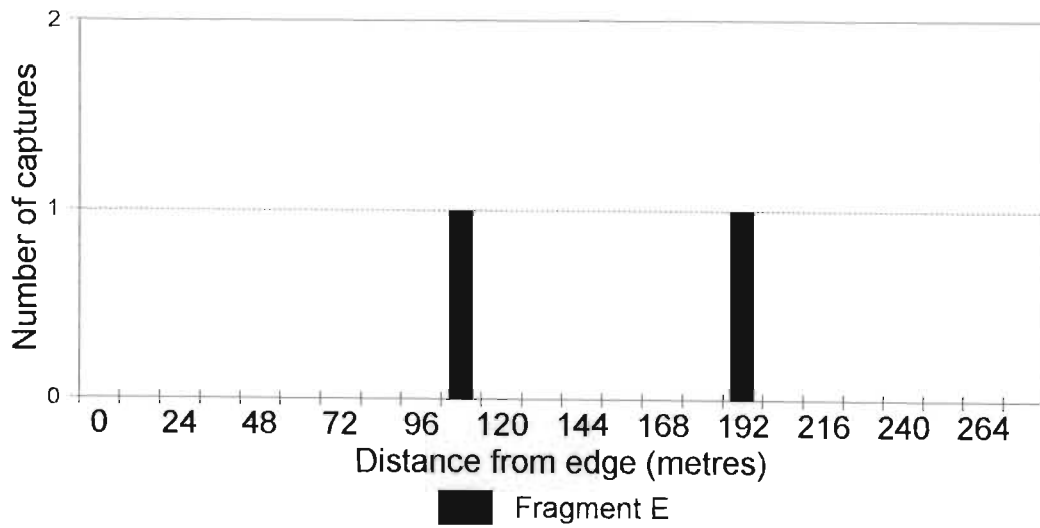


### Fragments

Figure 37: Location of capture  
*Nesillas typica*



### Control site



### Fragments

Figure 38: Location of capture  
*Newtonia amphichroa*



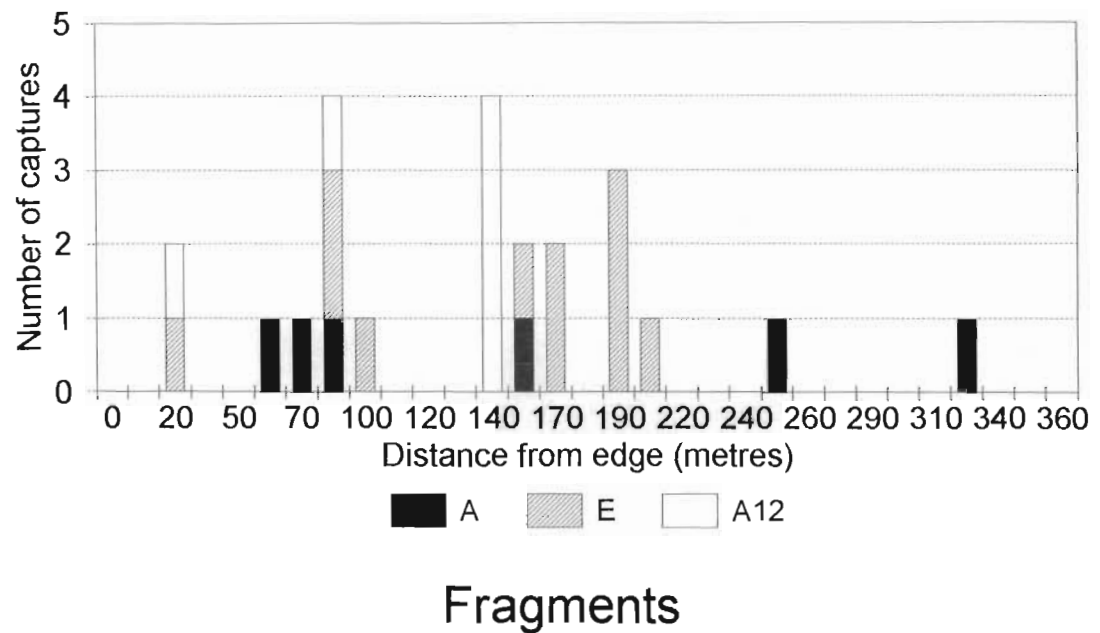
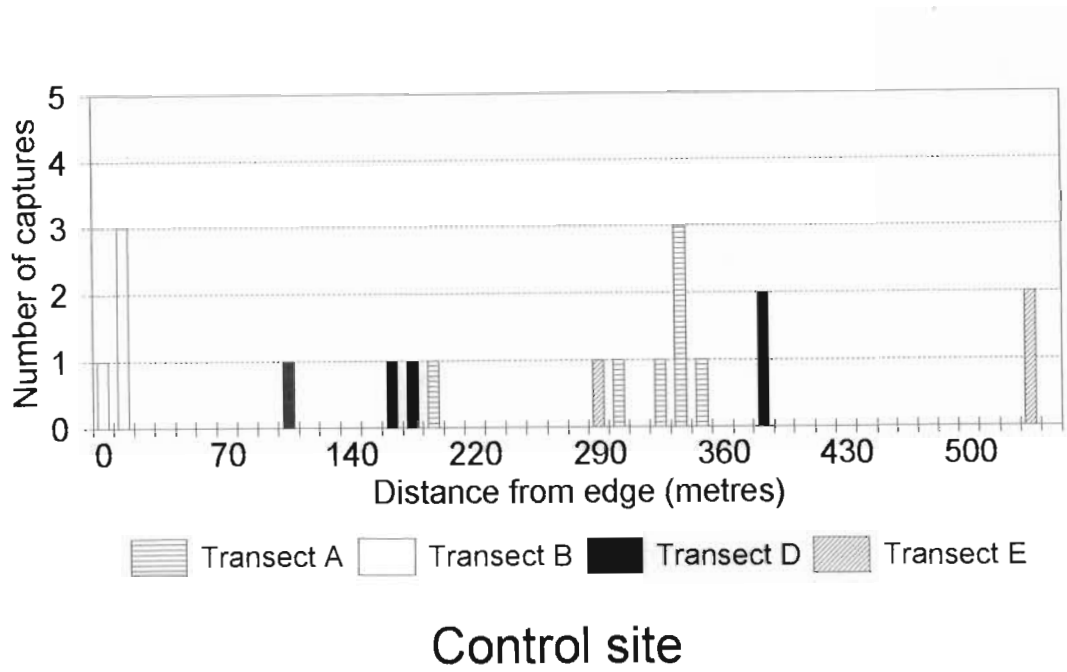
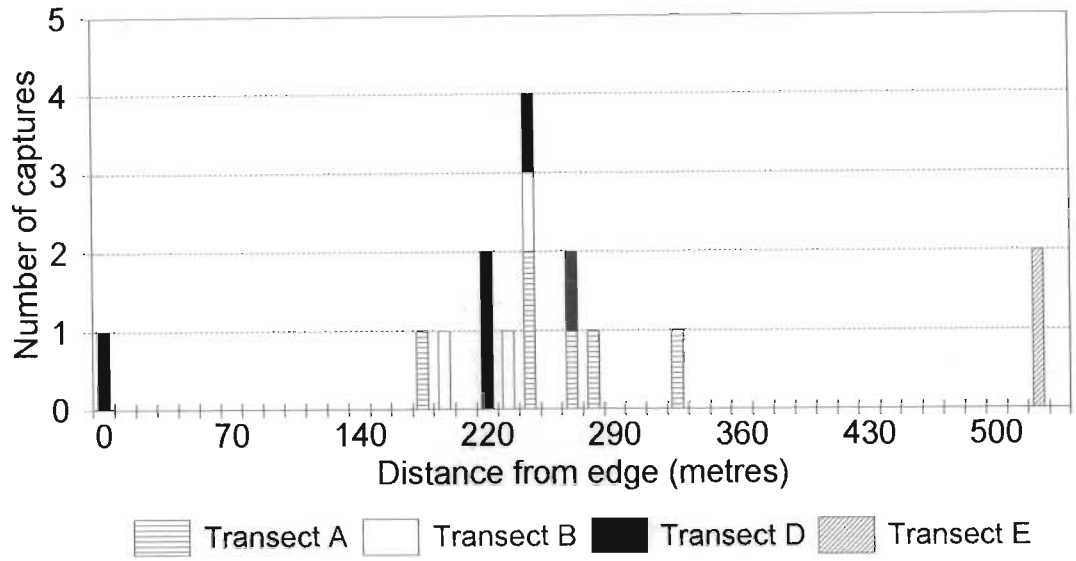
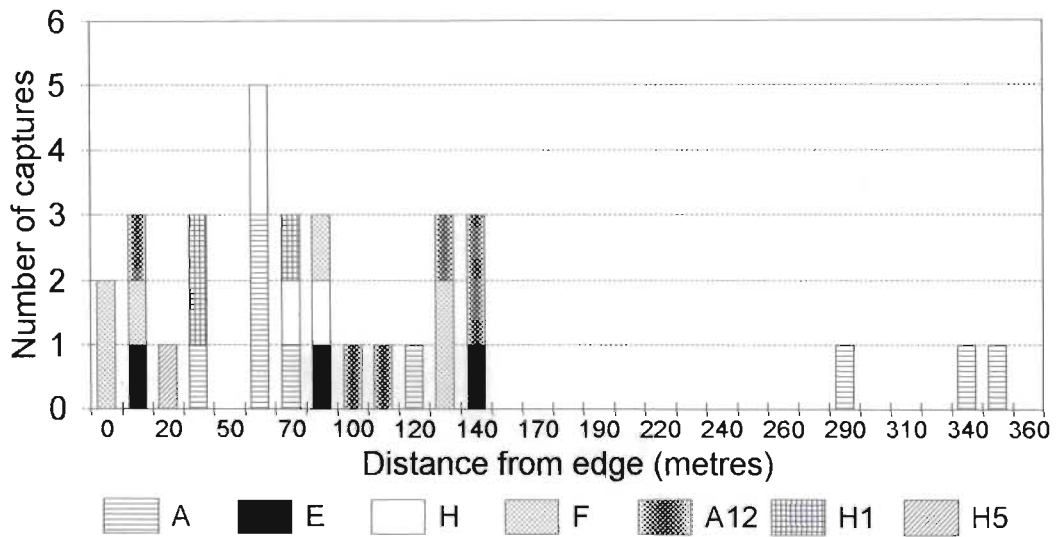


Figure 39: Location of capture  
*Newtonia brunneicauda*

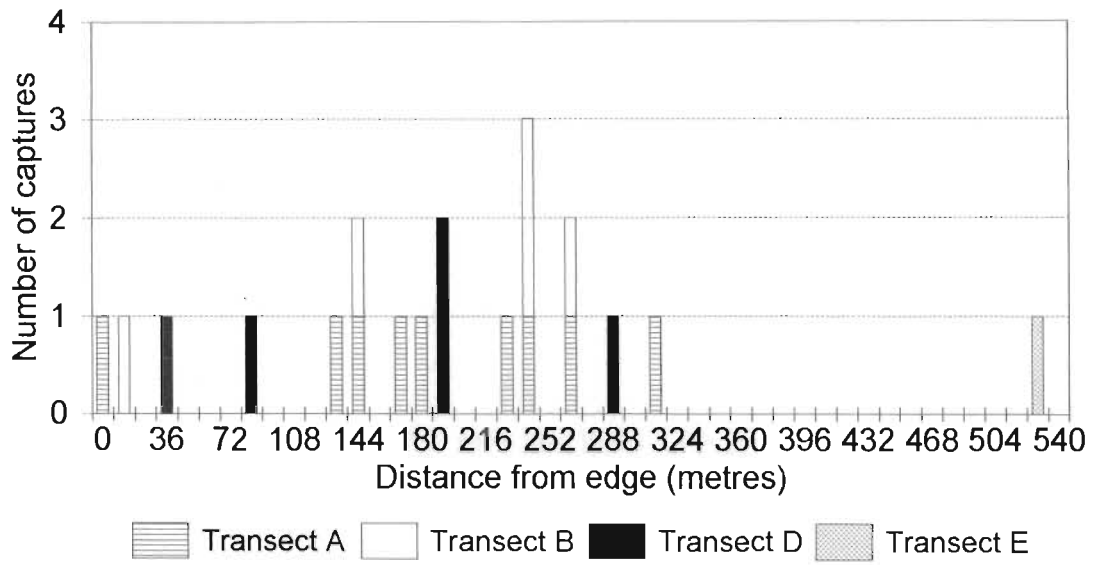


### Control site

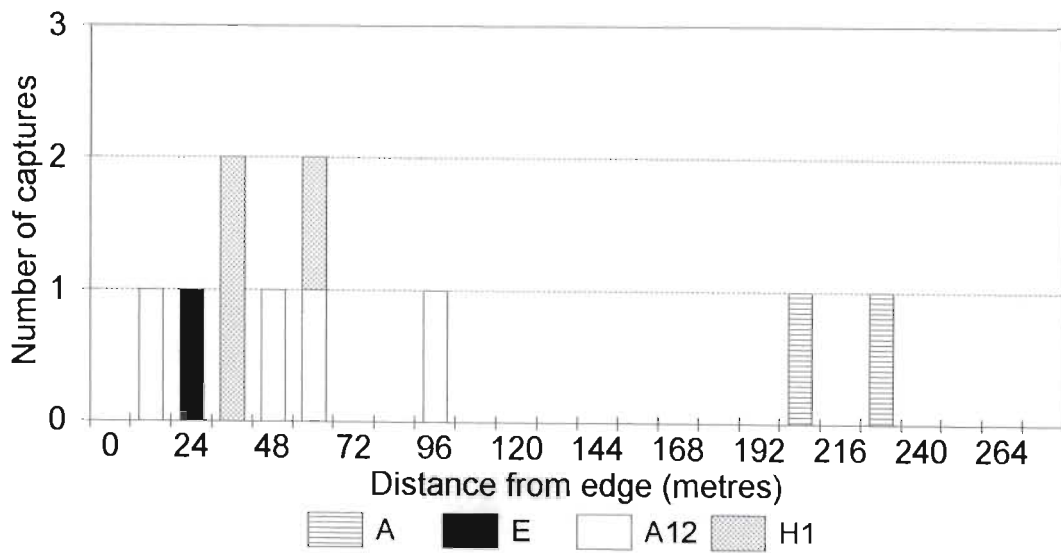


### Fragments

Figure 40: Location of capture  
*Terpsiphone mutata*

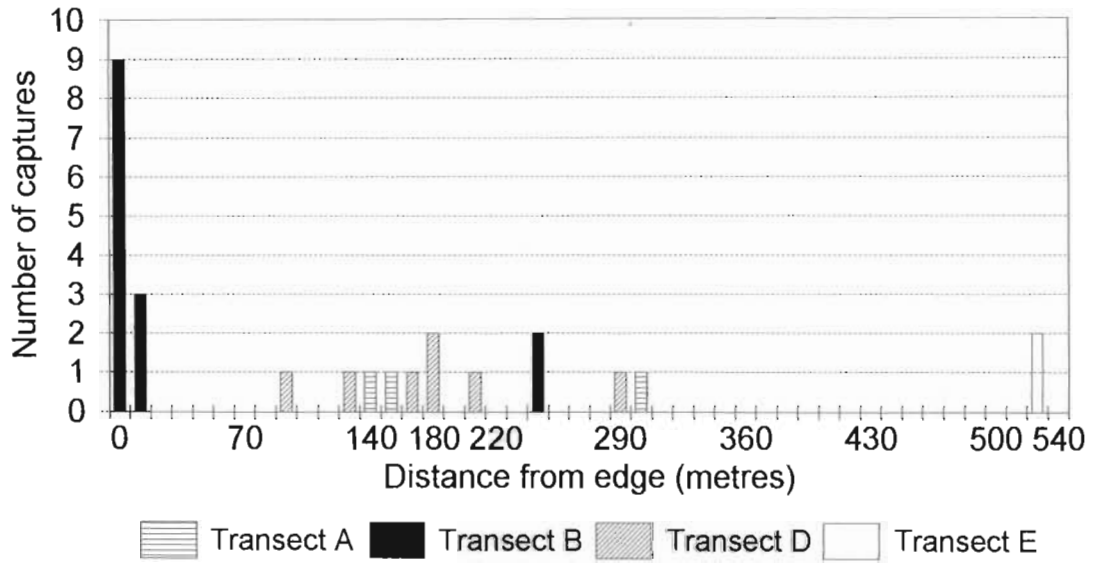


### Control site

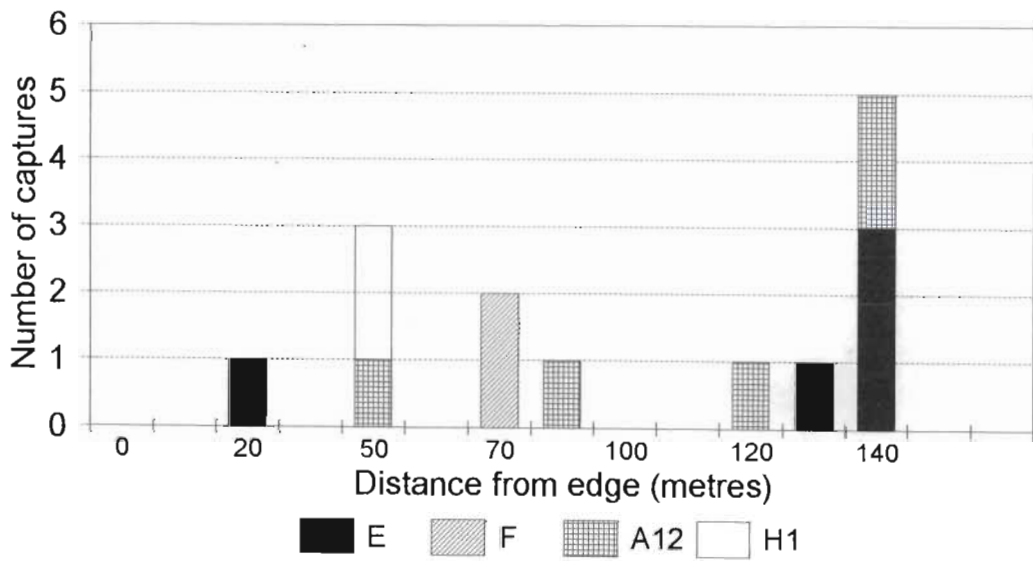


### Fragments

Figure 41: Location of capture  
*Nectarinia souimanga*



### Control site



### Fragments

Figure 42: Location of capture  
*Zosterops maderaspatana*

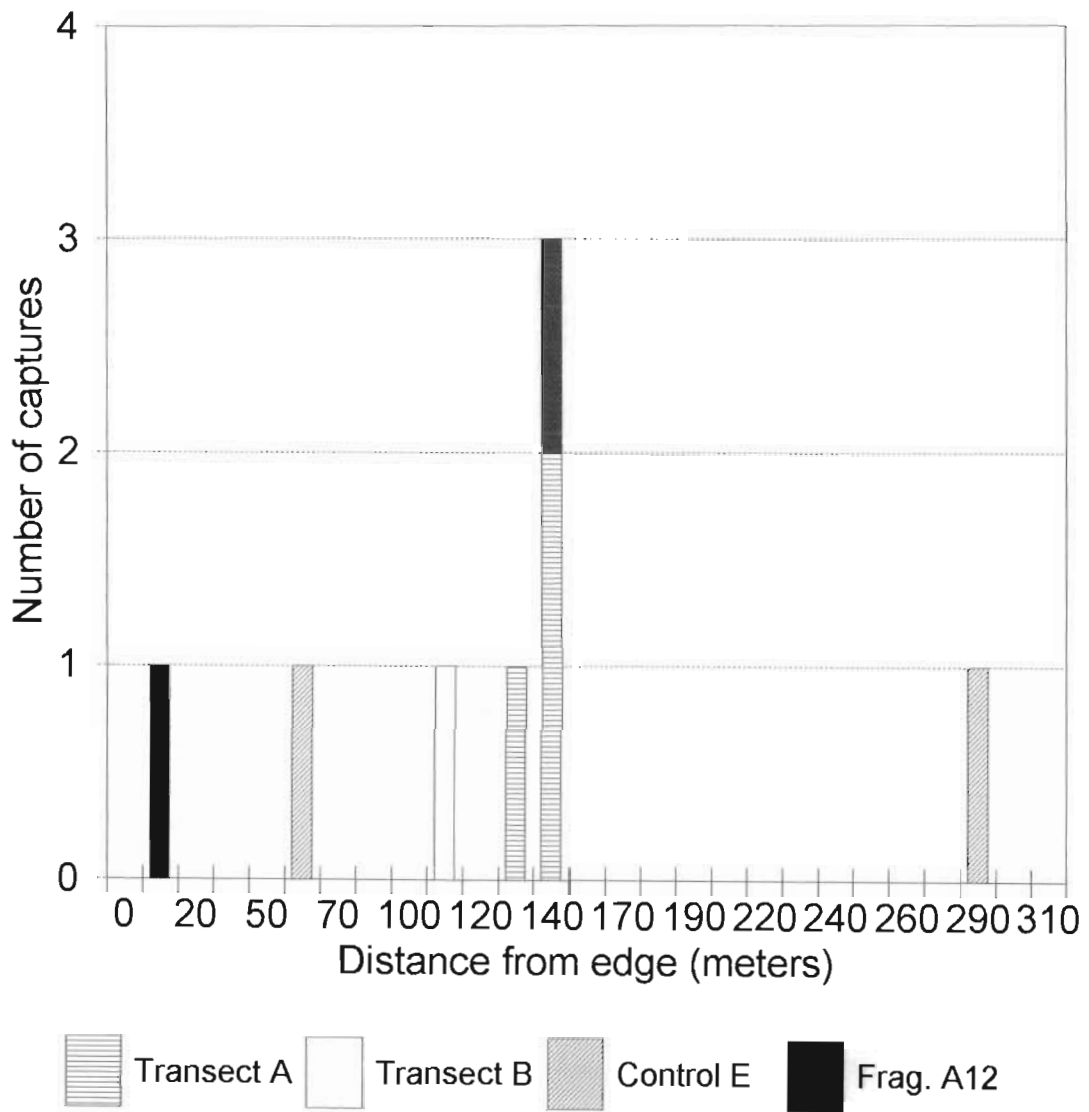


Figure 43: Location of capture  
*Dicrurus forficatus*

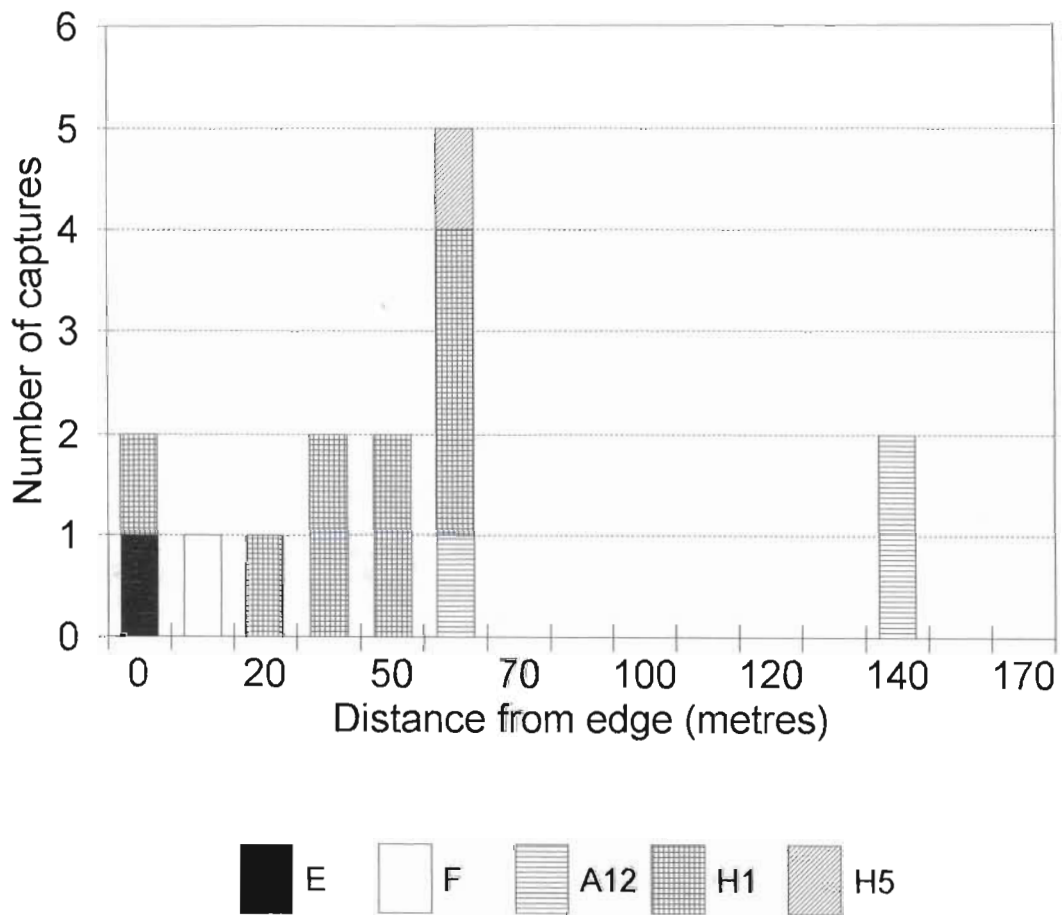
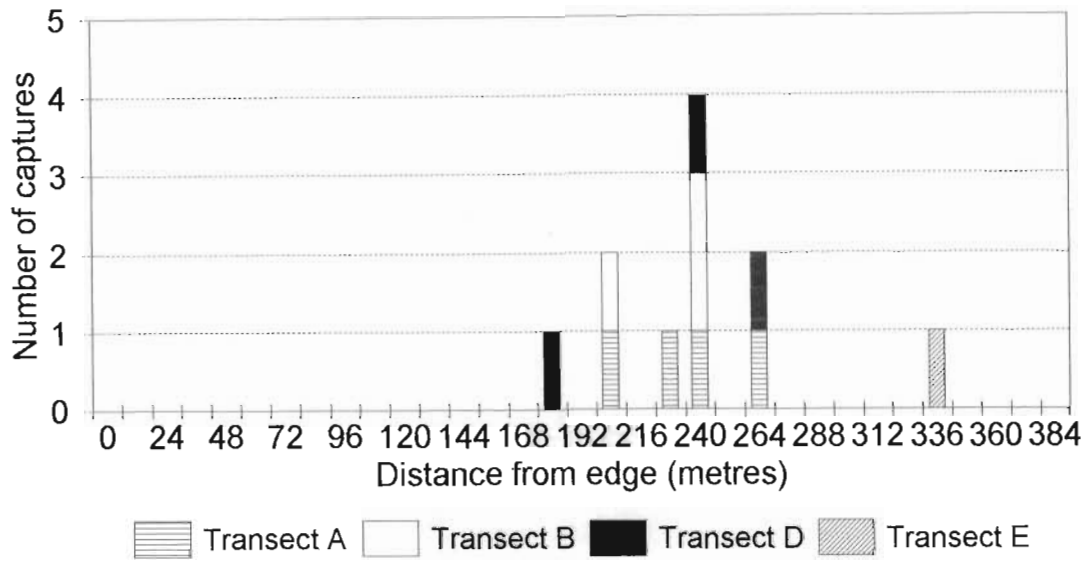
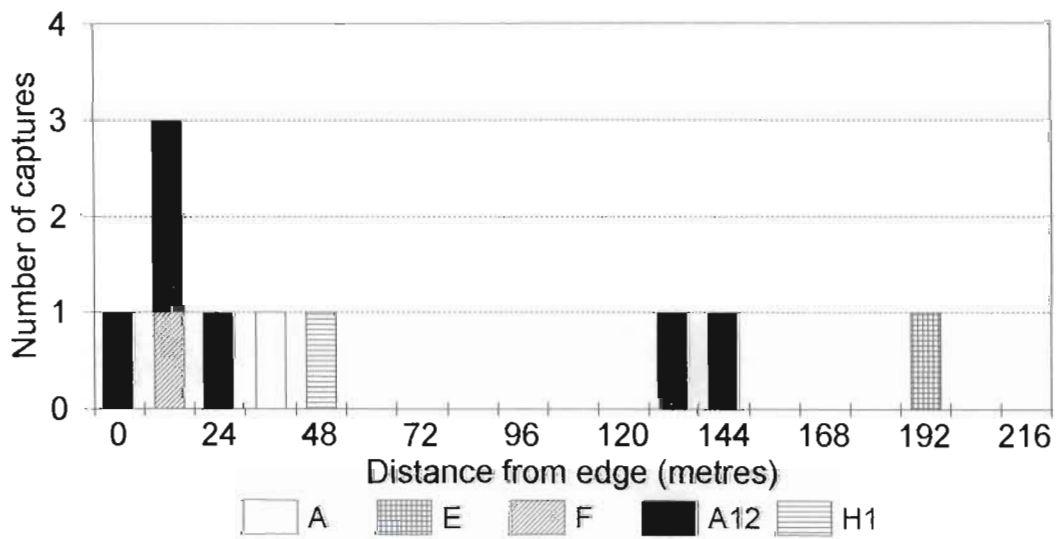


Figure 44: Location of capture  
in fragments  
*Foudia madagascariensis*



### Control site



### Fragments

Figure 45: Location of capture  
*Foudia omissa*

**Table 11:**  
**Location of occasional captures**

Species	Date	Time	Site	Edge	Shell	Sex	Age	Ring#
<i>Buteo brachypterus</i>	04/12	07:20	CE	530	2		Ad	4801
<i>Alectroenas madagascariensis</i>	25/04	15:50	A12	140	3		Ad.	4518
<i>Otus rutilus</i>	11/11	07:23	CA	300	3		Ad	47BLA
	17/11	06:10	CD	360	3		Ad	4584
	18/11	20:52	CD	240	3		Ad	4504
	25/11	06:50	CB	290	2		Ad	4506
	11/04	18:05	F	0	2		Ad	4510
	22/04	07:30	A	310	4		Ad	4516
<i>Ispidina madagascariensis</i>	03/12	07:15	CE	300	3		Ad	93
	28/04	07:14	A12	140	3		Ad	246
<i>Leptosomus discolor</i>	03/11	07:30	CA	130	2	M	Ad	7
	03/11	07:36	CA	130	2	F	Ad	8
	16/11	16:50	CD	40	3	M	Ad	4501
	27/11	07:40	CB	70	4	M	Ad	4601
	20/04	09:15	A	310	2	M	Imm	4602
<i>Coracina cinerea</i>	13/04	11:49	F	0	2	F	Ad	1052
<i>Nectarinia notata</i>	24/11	13:40	CB	0	2	F	Ad	69
<i>Cyanolanius madagascarinus</i>	25/11	07:00	CB	300	2	F	Ad	
	21/04	12:12	A	300	1		Imm	1069
<i>Tylas eduardi</i>	18/04	10:50	A	60	2	M	Imm	1062
	18/04	10:53	A	60	4	F	Imm	1061
	21/04	12:02	A	310	3	M	Imm	1070
	25/04	12:02	A12	140	2	M	Imm	1074
	25/04	12:04	A12	140	3	F	Imm	1073
	02/12	08:29	CE	60	2	M	Juv	1018



Table 12a:

## BIOGEOGRAPHICAL AND ECOLOGICAL PARAMETERS OF THE RESIDENT FOREST BIRDS OF THE AMBOHITANTELY SPECIAL RESERVE

Ref.	Breeding forest species of Ambohitantely Special Reserve	Endemism			Passerine		Habitat				Feeding habits			Arboreal nesting	Food item		
		Yes	Region	No	No	Yes	Forest	Savannah	Tree plantation	Total	Terrestrial	Arboreal	Aerial		Vegetarian	Invertebrates	Vertebrates
42	<i>Lophotibis cristata</i>	1			1		1			1	1			1		1	1
56	<i>Aviceda madagascariensis</i>	1			1		1			1		1		1		1	1
57	<i>Machaeramphus alcinus</i>			1	1		1		1	2			1	1		1	1
61	<i>Polyboroides radiatus</i>	1			1		1			1		1		1			1
63	<i>Accipiter henstii</i>	1			1		1			1		1		1			1
64	<i>Accipiter madagascariensis</i>	1			1		1			1		1		1		1	1
65	<i>Accipiter francesii</i>		1		1		1			1		1		1		1	1
66	<i>Buteo brachypterus</i>	1			1		1			1		1		1			1
68	<i>Falco zoniventris</i>	1			1		1			1		1		1		1	1
71	<i>Falco peregrinus</i>			1	1		1	1		2			1				1
75	<i>Numida meleagris</i>			1	1		1	1	1	3	1				1		
79	<i>Turnix nigricollis</i>	1			1		1	1	1	3	1				1	1	
81	<i>Dryolimnas cuvieri</i>		1		1		1			1	1					1	1
85	<i>Sarothrura insularis</i>	1			1		1	1		2	1				1	1	
142	<i>Streptopelia picturata</i>		1		1		1			1	1			1	1		
144	<i>Treron australis</i>		1		1		1			1		1		1	1		
145	<i>Alectroenas madagascariensis</i>	1			1		1			1		1		1	1		
147	<i>Coracopsis nigra</i>		1		1		1			1		1		1	1		
150	<i>Cuculus rochii</i>	1			1		1		1	2		1		1		1	
161	<i>Centropus toulou</i>		1		1		1			1		1		1		1	1
164	<i>Otus rutilus</i>		1		1		1			1		1		1		1	
166	<i>Asio madagascariensis</i>	1			1		1			1		1		1			1
168	<i>Caprimulgus madagascariensis</i>		1		1		1	1	1	3			1			1	
171	<i>Zoonavena grandidieri</i>		1		1		1			1			1	1		1	
173	<i>Apus melba</i>			1	1		1	1		2			1			1	
174	<i>Apus barbatus</i>			1	1		1	1		2			1			1	1
176	<i>Ispidina madagascariensis</i>	1			1		1			1		1				1	
177	<i>Merops superciliosus</i>			1	1		1	1	1	3			1			1	

Table 12b:

## BIOGEOGRAPHICAL AND ECOLOGICAL PARAMETERS OF THE RESIDENT FOREST BIRDS OF THE AMBOHITANTELY SPECIAL RESERVE

Ref.	Breeding forest species of Ambohitantely Special Reserve	Endemism			Passerine		Habitat				Feeding habits			Arboreal nesting	Food item		
		Yes	Region	No	No	Yes	Forest	Savannah	Tree plantation	Total	Terrestrial	Arboreal	Aerial		Vegetarian	Invertebrates	Vertebrates
178	<i>Eurystomus glaucurus</i>			1	1		1			1			1	1		1	
181	<i>Atelornis pittoides</i>	1			1		1			1	1					1	1
184	<i>Leptosomus discolor</i>		1		1		1			1		1		1		1	1
191	<i>Riparia paludicola</i>			1		1	1	1		2			1			1	
193	<i>Phedina borbonica</i>		1			1	1	1		2			1			1	
196	<i>Coracina cinerea</i>		1			1	1			1		1		1		1	
197	<i>Phyllastrephus madagascariensis</i>	1				1	1			1		1		1		1	
202	<i>Hypsipetes madagascariensis</i>			1		1	1		1	2		1		1	1	1	
203	<i>Copsychus albospectularis</i>	1				1	1			1		1		1		1	
205	<i>Pseudocossyphus sharpei</i>	1				1	1			1		1		1	1	1	
209	<i>Nesillas typica</i>		1			1	1		1	2		1		1		1	
215	<i>Cryptosylvicola randrianasoloi</i>	1				1	1			1		1		1		1	
215	<i>Newtonia amphichroa</i>	1				1	1			1		1		1		1	
216	<i>Newtonia brunneicauda</i>	1				1	1			1		1		1		1	
224	<i>Terpsiphone mutata</i>		1			1	1			1		1		1		1	
228	<i>Nectarinia souimanga</i>		1			1	1		1	2		1		1	1	1	
229	<i>Nectarinia notata</i>		1			1	1		1	2		1		1	1	1	
230	<i>Zosterops maderaspatana</i>		1			1	1		1	2		1		1	1	1	
232	<i>Calicalicus madagascariensis</i>	1				1	1			1		1		1		1	1
241	<i>Cyanolanius madagascarinus</i>		1			1	1			1		1		1	1	1	
245	<i>Tylas eduardi</i>	1				1	1			1		1		1		1	
246	<i>Dicrurus forficatus</i>		1			1	1		1	2		1		1		1	
248	<i>Hartlaubius auratus</i>	1				1	1			1		1		1	1		
253	<i>Foudia madagascariensis</i>	1				1	1	1	1	3		1		1	1	1	
254	<i>Foudia omissa</i>	1				1	1			1		1		1	1	1	
255	<i>Lonchura nana</i>	1				1	1	1	1	3		1			1		
	TOTALS (55 species)	26	19	9	31	23	54	12	14		7	37	10	40	17	42	17

## 11. DISCUSSION

The analysis of bird communities in fragments of different size described in this study, indicates that the occurrence of bird species is not random, but instead reflects a clearly predictable pattern. This regular pattern of species extinction in relation to forest-fragment size has been described for temperate forest (Blake 1991) as well as for tropical forest (Newmark 1991). A general pattern has emerged from the study of the bird communities of isolated forest fragments: with isolation and decreasing size of fragments, many species drop out, particularly those with specialized diets or large territories. Small fragments are typically dominated by generalist forest species that are able to breed and forage in a great variety of habitats (Blake & Karr 1984; Blake 1991).

Bird communities of the fragments of Ambohitantely Forest form "nested subsets" (Patterson 1987), in which all species found in the smallest forest fragments are also found in larger forest patches (Blake 1991).

### 11.1. SPECIES-AREA RELATIONSHIP

Using the species-area relationship is a worthwhile exercise to obtain an estimate of the number of species that may become extinct from the *Réserve Spéciale d'Ambohitantely* as a result of deforestation, despite some factors that may biased the results such as habitat heterogeneity among the different fragments sampled.

The exponent  $z$  generally applied to oceanic island is 0.25. In the specific case of Ambohitantely the exponent  $z$  is 0.16 which falls within the range proposed by Connor & McCoy (1979).

In a non-isolated forest fragment of 1000 ha situated at 750 m altitude, the number of forest species is 82 which is 83% ( $n = 114$ ) of the forest species found in the Eastern Region (Wilmé in press). In the case of Amber Mountain (23 000 ha) which has been isolated for a long time, 53 forest species have

been recorded. The species richness is higher than would be expected in Ambohitantely Forest. This pattern may be the result of history of isolation. When compared to Amber Mountain one could say that the higher species number might result from a more recent isolation of Ambohitantely compared to Amber Mountain.

### 11.2. BIOGEOGRAPHICAL AFFINITIES

Historically scientists have defined the biogeographical regions of Madagascar based on the distribution of the principal vegetation formations. The recent increase in vertebrate field studies, particularly in previously poorly known portions of the island, indicates that for several areas this phytogeographical classification does not always apply to vertebrate distribution. For example, it has been assumed that the Eastern and Western Regions have limited affinity with each other and few contact zones. Concrete evidence of these former connections are observed in a number of different sites and involve species that were previously considered as "typical" western species or "typical" eastern species. This is the case for *Mesitornis variegata* known from four localities of the Western Region of Madagascar (Langrand 1990) and which was discovered in the lowland rainforest of Ambatovaky, in the Eastern Region, living in sympatry with *Mesitornis unicolor* (Thompson & Evans 1991); it is also the case of *Coua gigas* largely distributed in the Western Region in the sub-arid thorn scrub and in the deciduous dry forest (Langrand 1990), which was found in lowland rainforest north of Tolagnaro, in the Eastern Region (Goodman et al.(b) in prep). *Canirallus kioloides* has a broad distribution in the Eastern Region, including the Sambirano Domain (Langrand 1990). Recently the presence of this species was documented in the Strict Nature Reserve of Bemaraha, Western Region (T. Mutschler, in litt.). The occurrence of *Coua caerulea*, a species previously thought to be restricted to the Eastern Region, in the Western Region such as the Special Reserve of Bora and the Special Reserve of Ankarana (Langrand 1990), further supports a forest connection between these two regions.

The biogeographical relationships of Ambohitantely's forest-dwelling avifauna supports arguments in favour of a connection between the eastern and the western parts of Madagascar. Ambohitantely has the strongest affinities with Montagne d'Ambre (0.17), and also, but to a lesser extent, with several eastern sites located at mid- or high-altitude (Manjakatampo, Andringitra). The affinity of Ambohitantely Special Reserve with Montagne d'Ambre is interpreted as reflecting a former forest connection between the northern part of the central High Plateau and the northern portion of the island. Subsequent forest degradation has isolated these two sites, and both either retain the set of birds found across this former connection or both have lost species in parallel fashion. These two sites have several topographical and physical characteristics in common. The Ambohitantely forest falls between 1350-1600 m asl, is 2737 ha, and is approximately 80 km from closest extensive rainforest area (Anjozorobe) compared to Montagne d'Ambre which is located between 850 and 1475 m asl (Nicoll & Langrand 1989), is about 23 000 ha, and is approximately 125 km from extensive rain forest area (Tsaratanana). Further, both Montagne d'Ambre and Ambohitantely Special Reserve are evergreen forest, the former distinctly wetter than the latter.

Today, Ambohitantely and Montagne d'Ambre are disconnected from the principal blocks of Eastern and Western Region forest. On the basis of the high dissimilarity index between Ambohitantely Special Reserve and sites in the Western Region forest, it is assumed that any connection between these areas was severed in the distant past. The forest of Montagne d'Ambre was disconnected from a Western Region forest block, the dry deciduous forest of Ankarana, not more than 50 years ago. Ankarana contains bird species typical of the Western Region of Madagascar. Several species typical of the Western Region occur within or at the edge of Montagne d'Ambre (e.g. *Haliaeetus vociferoides*, *Oena capensis*, and *Ploceus sakalava*).

To show the affinities of Ambohitantely avifauna to the Eastern Region it is possible to look at forest species found in both the Eastern and Western Regions, and with subspecies



typical of each region. This differentiation is a result of the genetic isolation of these two regions through some vicariant events related to a reduction of forest cover on the central High Plateau. The factors that led to this change are a combination of natural and human-induced. Eighteen species fall into this category, among which eight (44.4%) are represented in Ambohitantely by their eastern subspecies.

### 11.3. COMPOSITION OF PRE-FRAGMENTATION AVIFAUNA

Does the present bird community of Ambohitantely Forest reflect the one that prevailed in prehistoric times? And if not, has the species composition gone through major changes as a result of physical isolation and fragmentation?

Major ecological changes have affected Madagascar over the course of the past few millennia (see section 7.2.). Some of these changes occurred during the early Holocene before humans arrived, and have led to extinction of many vertebrates, including birds. The human-induced factors, in combination with natural factors, probably accelerated the rate of animal extinction leading, for example, to the disappearance of a complete family of birds, the elephant birds (Aepyornithidae) (Dewar 1984). The combined impacts of natural and human-induced changes have been documented for aquatic bird species through identification of sub-fossil bones (Rakotozafy 1993; Langrand & Goodman in press). Three aquatic species are known to have become extinct (*Centronis majori*, *Alopochen sirabensis*, and *Hovacrex roberti*) and a few others have undergone significant contractions of their original Holocene range (*Anas bernieri*, *A. melleri*, and *Haliaeetus vociferoides*). Information is available on landbird species of dry areas, because conditions for bone preservation are more favourable in deciduous dry forest or in spiny bush than in rainforest habitat. In addition to several species of elephant birds (Lamberton 1934), five other species are known to have gone extinct: *Coua primavea* (Milne Edwards & Grandidier 1895), *C. berthae* (Goodman & Ravoavy 1993), *Stephanoaetus mahery* (Goodman 1994), and *Aquila* spp. (Goodman & Rakotozafy in press).

Around 7000 BP, the forest of the central High Plateau was a mosaic of woodlands, bushlands and savannah according to edaphic factors (MacPhee et al. 1985). On the basis of the soil composition of Ambohitantely, it is assumed that the forest covered a large proportion of the Ankazobe *tampoketsa* (Riquier 1951). Consequent upon the size restriction and the biological isolation of Ambohitantely Forest, it is probable that the avifauna of this site suffered from a decline in species number and species densities as a result of an excess of extinctions over immigrations.

When a pre-fragmentation species list for a forest study is not available, which is the case for Ambohitantely Forest, there are two alternative ways to assess the pre-fragmentation avifauna: "to equate it with the pre-fragmentation fauna of a larger region including the patch; or, to equate it with the fauna of a much larger forest in the vicinity today" (Diamond 1984 pp 210-211). The Ambohitantely Forest is isolated and there are no forests that could really be considered located at its vicinity. The closest forest is at Anjozorobe 90 km from Ambohitantely. No biological inventory has been made at Anjozorobe and thus the avifauna of this forest is incompletely known. In the absence of a comprehensive species list for Anjozorobe I decided to relate the pre-fragmentation avifauna of Ambohitantely Forest to those of Andringitra and Marojejy, located at 430 km and 480 km respectively from Ambohitantely Forest. Andringitra and Marojejy have a portion located at an equivalent altitude as Ambohitantely, and because their avifauna has been extremely well documented (Safford & Duckworth 1990; Goodman & Putnam in prep.). Analamazaotra Forest is closer to Ambohitantely but is located at a lower altitude (900 versus 1500 m asl, respectively).

A comparison of the species composition of these ornithologically well documented rainforest sites located in the Central Domain provides some insight into the local species extinction that may have taken place in the Ambohitantely Forest. The following species are likely to have occurred in Ambohitantely Forest in pre-fragmentation times: *Mesitornis unicolor*, *Canirallus kioloides*, *Coua reynaudii*, *C. caerulea*,

*Atelornis crossleyi*, *Philepitta castanea*, *Neodrepanis coruscans*, *N. hypoxantha*, *Phyllastrephus zosterops*, *P. cinereiceps*, *Dromaeocercus brunneus*, *Neomixis tenella*, *N. viridis*, *N. striatigula*, *Hartertula flavoviridis*, *Pseudobias wardi*, *Oxylabes madagascariensis*, *Crossleyia xanthophrys*, *Mystacornis crossleyi*, *Schetba rufa*, *Vanga curvirostris*, *Leptopterus viridis*, *L. chabert*, and *Ploceus nelicourvi*.

The upper altitudinal distribution of these 24 species in Marojejy, Andringitra, and across Madagascar is presented in Table 13.

The differences between pre- and post-fragmentation avifaunal compositions of Ambohitantely Special Reserve, require some explanations and comments. The causes for the decline in species numbers in post-fragmentation avifauna composition relevant to habitat have been described by Whitcomb et al. (1991) and are the following:

a) the quantity of habitat: a bird species population requires enough habitat to support an adequate number of individuals needed for the maintenance of a longterm viable population;

b) the isolation of habitat: the extinction rate increases and the immigration rate decreases as a result of habitat isolation;

c) the quality of habitat: the biological and physical characteristics of the forest have changed as a result of the fragmentation, e.g. food resources and nesting sites;

d) the heterogeneity of habitat: some forest micro-habitats, critical for highly specialized species, disappear through the effects of fragmentation;

Although changes in size and quality of forest habitat are critical in determining the species composition of a site, it is equally important to consider the disturbances affecting the migration strategy as a major cause of decline of species numbers in Ambohitantely.



Table 13:

**UPPER ALTITUDINAL LIMIT OF 24 BIRD SPECIES  
IN MAROJEJY, ANDRINGITRA, AND ACROSS MADAGASCAR**

Species	Marojejy (1 & 7)	Andringitra (2)	Upper limit
<i>Mesitornis unicolor</i>	700 m	1 625 m	1 625 m (2)
<i>Canirallus kioloides</i>	1 300 m	800 m	1 450 m (3)
<i>Coua reynaudii</i>	1 900 m	1 625 m	2 500 m (4)
<i>C. caerulea</i>	1 900 m	1 625 m	1 900 m (1)
<i>Atelornis crossleyi</i>	1 300 m	1 625 m	1 800 m (5)
<i>Philepitta castanea</i>	1 500 m	1 625 m	1 800 m (5)
<i>Neodrepanis coruscans</i>	1 450 m	800 m	1 800 m (5)
<i>N. hypoxantha</i>	1 700 m	1 625 m	2 000 m (3)
<i>Phyllastrephus zosterops</i>	1 300 m	1 210 m	1 800 m (3)
<i>P. cinereiceps</i>	1 500 m	1 625 m	2 000 m (6)
<i>Dromaeocercus brunneus</i>	2 000 m	1 625 m	2 000 m (7)
<i>Neomis tenella</i>	1 700 m	1 210 m	1 800 m (3)
<i>N. viridis</i>	1 500 m	1 625 m	2 050 m (3)
<i>N. striatigula</i>	1 300 m	1 625 m	1 800 m (5)
<i>Hartertula flavoviridis</i>	1 300 m	1 625 m	2 300 m (3)
<i>Pseudobias wardi</i>	1 700 m	1 210 m	1 800 m (3)
<i>Oxylabes madagascariensis</i>	1 300 m	1 625 m	1 800 m (5)
<i>Crossleyia xanthophrys</i>	1 300 m	1 625 m	2 300 m (4)
<i>Mystacornis crossleyi</i>	1 300 m	1 625 m	1 800 m (5)
<i>Schetba rufa</i>	800 m	1 210 m	1 800 m (5)
<i>Vanga curvirostris</i>	1 300 m	1 625 m	1 800 m (3)
<i>Leptopterus viridis</i>	1 300 m	1 625 m	2 000 m (6)
<i>L. chabert</i>	800 m	1 210 m	1 800 m (3)
<i>Ploceus nelicourvi</i>	2 100 m	1 625 m	2 100 m (1)

- (1): after Safford & Duckworth (1990);  
 (2): after Goodman & Putnam (in prep);  
 (3): after Langrand (1990);  
 (4): after Albignac (1970);  
 (5): after Rand (1936);  
 (6): after Milon (1951);  
 (7): after Evans *et al.* (1992).

Altitudinal migration: in sites such as Andringitra, Marojejy, and Andohahela, the forest extends from 600 m to 2000 m asl and encompasses a diverse array of vegetation forms, from lowland forest to high-mountain forest. The altitudinal migration of the Malagasy avifauna has not been yet studied and it is impossible to know what portion of the species move through the forest on this manner. It is also possible that some species have both resident and migratory populations along the altitudinal gradient as is the case in other tropical rainforest areas (Loiselle & Blake 1992).

Before presenting the hypothesis that altitudinal migration of forest bird species is a critical aspect in the dynamics of this system, it is important to determine if there is evidence of recent natural rainforest below the Ankazobe *tampoketsa*? If there was, the 24 bird species listed above are likely to have disappeared from Ambohitantely Forest. If not, these 24 species probably never occurred in Ambohitantely Forest.

Ambohitantely is located in a geological unit (granite and migmatite) that runs from the central High Plateau in the direction of the east coast through the Mangoro Valley. More important is the soil composition in assessing the possibility of forest cover. The *tampoketsa* of Ankazobe is covered with yellow and red lateritic soils that follow the upper valleys of the Betsiboka and Ikopa Rivers towards the East. These yellow and red lateritic soils continue down to the east coast along the Mangoro and Onive Rivers. These are all soil types associated with rainforest cover.

On the basis of pollen samples MacPhee *et al.* (1985), have proposed that the central High Plateau was once a mosaic of large forest patches, savannah grassland and bushlands. The existing forest of Ambohitantely is one of the highest forested areas on that portion of the Madagascar central High Plateau. Even if a conservative view is adopted concerning the extent of the original forest cover on the central High Plateau, it is likely that a continuous rainforest that ran from the eastern side of the *tampoketsa* of Ankazobe down to the foothills of the

Angavo Cliff (between 600 and 900 m asl). There is evidence that the former altitudinal forest gradient of this forest tract would have been more-or-less equivalent to Andringitra and Marojejy. This belt of forest would have provided a continuous corridor for seasonal altitudinal migrations of forest dwelling species. Thus, it is concluded that the 24 bird species listed in Table 13, were probably present in the area when Ambohitantely Forest was previously connected with lower-altitude forest and may have been extirpated as a result of the isolation of Ambohitantely Forest.

Considering the harsh climatic conditions prevailing in winter in Ambohitantely Forest, it is likely that altitudinal migration was a strategy used by an array of bird species when it was contiguous with lower-altitude forest sites to avoid the changes in resource abundance occurring in high-altitude forest. Two feeding guilds, the frugivorous and the nectarivorous, are known to be the most common altitudinal migrants in Central America (Loiselle & Blake 1992). Five species belonging to this feeding guild occur at relatively high altitudes at Marojejy and Andringitra (Table 13), but are absent from Ambohitantely (*Coua reynaudii*, *C. caerulea*, *Philepitta castanea*, *Neodrepanis coruscans*, and *N. hypoxantha*). It is hypothesized that the extinction of these forest-dependent species from Ambohitantely after fragmentation is a response to the destruction of forest corridors needed to perform seasonal altitudinal migrations.

Further evidence of the effects of isolation on the composition of the avifauna is provided by Manjakatampo Forest. This site located in altitude on the central High Plateau shows a similar pattern of isolation as Ambohitantely. None of these 24 species listed as likely to occur in high-altitude central High Plateau forest are found in Manjakatampo Forest.

The general trends in species disappearing are presented below:

a) a decrease in the number of large-bodied insectivorous terrestrial species (e.g. *Mesitornis unicolor*, *Canirallus kioloides*, and *Atelornis crossleyi*);

b) a decrease in the number of small-bodied insectivorous understorey (bark-gleaning and foliage-gleaning) species (e.g. *Phyllastrephus zosterops*, *P. cinereiceps*, *Hartertula flavoviridis*, *Oxylabes madagascariensis*, *Crossleyia xanthophrys*, *Mystacornis crossleyi*, and *Ploceus nelicourvi*);

c) a decrease in the number of insectivorous/frugivorous mid- and upper-stratum species (e.g. *Coua reynaudii*, *C. caerulea*, and *Philepitta castanea*);

d) a decrease in the number of mid- and upper-stratum small-bodied insectivorous and nectarivorous species (e.g. *Neodrepanis coruscans*, *N. hypoxantha*, *Neomixis tenella*, *N. viridis*, *N. striatigula*, *Pseudobias wardi*, *Leptopterus chabert*);

e) a decrease in the number of medium-bodied mid- and upper-stratum small-predator species (e.g. *Schetba rufa*, *Vanga curvirostris* and *Leptopterus viridis*);

The reasons why the 24 species listed above are likely to have disappeared from Ambohitantely are discussed below.

One endemic family (Mesitornithidae) and two Malagasy endemic sub-families (Couinae and Philepittinae) of birds are absent from the reserve, although they are generally well represented in rainforest areas.

*Mesitornis unicolor* is an uncommon forest-dependent species across its whole range, from Marojejy to Andohahela (Langrand 1990). It is a terrestrial forest-dwelling bird that favours mid-altitude forest. As a result of its high-altitude location, the ecological conditions of Ambohitantely are at the upper limits for this species to maintain viable populations.

*Canirallus kioloides* is a terrestrial, lowland, mid-altitude, common forest-dependent species. Because of high-altitude, the ecological conditions of Ambohitantely are probably not suitable for the establishment of this species.

*Atelornis crossleyi* is an uncommon terrestrial forest-dependent species across its whole range from Marojejy to Andringitra (Langrand 1990). As an insectivorous species, it

may be affected by a decrease in arthropod abundance related to desiccation of understorey and leaf litter caused by an increase in wind penetrance as a result of forest fragmentation. This species nests in ground burrows. The penetration and the proliferation of *Rattus*, favoured by the fragmentation of the forest, may have had an impact on *A. crossleyi* through predation on the eggs and nestlings.

*Coua reynaudii*, *C. caerulea*, *Philepitta castanea*, *Neodrepanis coruscans*, and *N. hypoxantha*: the Couinae are represented by six species in the rainforest and the Philepittinae by four species in a similar biome. The absence of these two subfamilies of forest-dependent species, some of them ecologically specialized (Philepittinae) is an argument in favour of a long history of isolation. In some similar forest isolates, these two subfamilies are scarce or absent. For example, at Montagne d'Ambre only one species of Couinae (*Coua cristata*), mostly found in the lower-altitude portions of the forest, and no Philepittinae are recorded (Langrand & Lenormand 1985) and at Manjakatombo no Couinae nor Philepittinae are recorded (Nicoll & Langrand 1989). At sites in a similar type of forest, but connected with larger forest blocks, these two sub-families are well represented. Four species of Couinae (*Coua cristata*, *C. caerulea*, *C. serriana*, and *C. reynaudii*) and three species of Philepittinae (*Philepitta castanea*, *Neodrepanis coruscans*, and *N. hypoxantha*) are found in Analamazaotra Special Reserve (Nicoll & Langrand 1989) and in Marojejy Strict Nature Reserve (Safford & Duckworth 1990). The list for Andringitra Strict Nature Reserve is similar, except that *Coua serriana* and *C. cristata* are not known from the reserve (Goodman & Putnam in prep.).

The fragmentation of forest into smaller and isolated patches affects species distribution (Blake & Karr 1984) and local extinctions are positively correlated with body size. Thus it is not surprising that Couinae (*Coua reynaudii* and *C. caerulea*) have become extinct in the Ambohitantely Special Reserve. There are some other possible causes of local extinctions for the two coua species; this subfamily is prone



to extinction. Two species, *Coua primavea* and *C. berthae*, are only known as sub-fossils (Milne Edwards & Grandidier 1895; Goodman & Ravoavy 1993). Both were ground-dwelling birds and the cause of their extinction is unclear (Goodman & Ravoavy 1993). The recent extinction of a third species of coua, *Coua delalandei*, from Ile Sainte-Marie is the consequence of the degradation of original forest habitat, trapping and hunting, and proliferation of rats (Langrand 1990). Even today, couas are still hunted on a broad scale by local people along the trails that penetrate the forest (Goodman 1993; Goodman & Putnam in prep.). *Coua caerulea* is a common species at low altitude, where it can be seen in secondary forest and in forest fragments (Langrand 1990; Goodman 1993). At middle- or upper-altitudes its habitat requirements are stricter, and it is rarely seen in secondary forest. The combination of more specific habitat requirements, lower population density, and hunting are possible reasons for the extinction of *Coua caerulea* from the Ambohitantely Forest.

The present absence of Philepittinae from Ambohitantely can be explained by isolation of the forest block and the inability of this group to perform seasonal altitudinal migration. *Philepitta castanea* feeds extensively on fruits of Rubiaceae, a plant family represented by 61 species and 21 genera in the Ambohitantely Special Reserve (Anon. 1990). It is more difficult to explain the absence of *Neodrepanis hypoxantha* which is adapted to high-altitude rainforest (Langrand 1990). As a general rule, insectivorous and nectarivorous birds benefit from fragmentation which generates abundance of flowering plants along the edge (Johns 1991). As typical edge species and nectarivores, *Nectarinia souimanga* and *N. notata* are benefiting from the effects of forest fragmentation and are still common at Ambohitantely. As forest-interior species, *Neodrepanis coruscans* and *N. hypoxantha* do not utilize plants at the ecotone. *Philepitta castanea*, *Neodrepanis coruscans*, and *N. hypoxantha* are common in Andringitra, Marojejy, and Andohahela at altitudes ranging between 1300 m and 1800 m. This constitutes an argument in favour of their presence in Ambohitantely in pre-fragmentation time. However, these species have been observed at the same

sites and in some additional localities at lower altitudes, between 750 m and 1000 m asl, (Analamazaotra Special Reserve, Ranomafana National Park) in winter. This may explain their absence from Ambohitantely as these highly specialized species may require lower altitude forest during the winter. The range of *Neodrepanis coruscans* is generally lower than the existing forest of Ambohitantely and never may have occurred in this forest. *Neodrepanis hypoxantha* may have needed the elevation gradient for migration and may have become extinct in Ambohitantely. In addition, *Neodrepanis coruscans* and *N. hypoxantha* have been seen feeding largely on *Bakerella* (Loranthaceae) in Ranomafana (Langrand & Sinclair 1994) and Andringitra (Goodman & Putnam in prep.) as well as on *Aframomum* (Zingiberaceae) in Marojejy (Evans & Duckworth 1990). These two plant taxa are not recorded from Ambohitantely Special Reserve (Anon. 1990) and this may explain the absence of *Neodrepanis* spp. from Ambohitantely Forest in itself.

*Phyllastrephus zosterops*, *P. cinereiceps*, *Hartertula flavoviridis*, *Oxylabes madagascariensis*, *Crossleyia xanthophrys*, *Mystacornis crossleyi*, and *Ploceus nelicourvi*: the small-bodied insectivorous understorey species are particularly sensitive to habitat disturbance as the abundance of their food resources depends on percentage of ground cover (Johns 1991). The biological (floral species composition and forest structure) and the physical (temperature, moisture, and light) changes generated by the fragmentation of the forest have a strong impact on this highly specialized foraging guild.

*Neomixis tenella*, *N. viridis*, *N. striatigula*, and *Leptopterus chabert*: mid- and upper-stratum insectivores common throughout their distribution range (Langrand 1990). Some of these species are well adapted to secondary forest (*Neomixis tenella* and *Leptopterus chabert*), thus their disappearance from Ambohitantely Forest is probably related to the decrease in food abundance during the winter, associated with their inability to migrate to lower-altitude forest.

*Schetba rufa*, *Vanga curvirostris*, and *Leptopterus viridis*: mid- and upper-stratum predators on small animals, particularly

reptiles, highly specialized, common throughout their range. The absence of these three species from Ambohitantely Forest is probably related to the scarcity during the winter months of small reptiles. These forest-dependent birds may also be competing with small forest raptors, such as *Accipiter francesii* and *A. madagascariensis* which are common forest species that fly between fragments.

#### 11.4. ISLAND BIOGEOGRAPHY THEORY APPLIED TO AMBOHITANTELY

Island biogeography or equilibrium theory (*sensu* MacArthur & Wilson 1967) provides a means to assess the effects on bird populations of forest fragmentation on the central high plateau of Madagascar. As a result of their dispersal ability, birds are an excellent group to study such dynamics. For natural populations on islands in other areas of the world, this theory has provided insight into the dynamics of local colonization and extinction. However, one of the critical problems in using this method to extrapolate local extinctions in forest islands of the region, is that no large forest block remains that allow an assessment of the original intact community. The human-induced fragmentation of the region has had a profound influence on local extinctions. The extent of these habitat changes have almost certainly kept ahead of any equilibrium between extinction and colonization rates. Further, it is now abundantly clear that even though the avifauna of the island is depauperate with respect to continental areas of similar size, that numerous Holocene bird extinctions have reduced significantly the natural avifauna occurring on the central high plateau. Thus, the combination of these factors greatly limits any interpretation of the natural population dynamics of extinction/colonization that equilibrium theory might provide.

To a large extent the species of birds that continue to exist in fragmented forests such as Ambohitantely, are those that have broad niches or in other ways are not so strongly affected by the magnitude of recent ecological vicissitudes in the region. Thus, when examining the dynamics of the forest fragmentation at Ambohitantely, most of the species are "the survivors". Having said this, there are still clear patterns



that emerge with respect to the effects of forest fragmentation which can be interpreted using island biogeography theory.

One of the most powerful and clear points that has emerged from the initial hypothesis of MacArthur and Wilson (1967) is the relationship between species and area. Across a remarkable diversity of organisms there is a close correlation between the size of an island, defined in numerous ways, and the total number of species (Begon *et al.* 1986). Whether this relationship is direct, for example as a result of increased habitat diversity as a function of forest size, or indirect, for example a change in abiotic variables associated with canopy height or exposure is unknown (Saunders *et al.* 1991). Even though the current species assemblage of the central high plateau is depauperate in comparison to the natural avifauna of pre-human perturbations, the relationship between species and area remains (see p. 40).

Another key aspect of equilibrium theory is the dynamic process of extinction and colonization, specifically the importance of immigration of colonizing species to replace those have gone extinct. In the case of humid forests on Madagascar, most of the forest-dependent species have broad distributions across the complete eastern humid forest and to a large extent the source pool for immigration approaches zero. This is the result of the rarity of wet-forest birds colonizing from Africa (no clear cases in the past 100 years) and birds occurring in other areas of the island, specifically dry habitats, would probably be unable to colonize humid forest. Thus the case of Ambohitantely provides a lop-sided interpretation of equilibrium theory, only local extinctions and basically no means of immigration for species previously not represented in the local species pool.

The community structure of the rainforest avifauna is at first glance unsaturated, that is not all the niches are filled. This appears to be the case in Malagasy forest, for example, the depauperate number of obligate frugivores in comparison to other tropical areas of similar size. However, phenological patterns of forest availability on the island are very seasonally restricted (Goodman *et al.* submitted) and the obligate frugivore niche on Madagascar is better termed

"unavailable" rather than "unsaturated". It is presumed that if strict frugivores were able to migrate to Madagascar, for example from East Africa, they would almost certainly not be able to colonize the island.

Thus in summary, the evolution of the Malagasy biota of Madagascar has had a unique history and extrapolation to previous axioms associated with community structure, particularly in other tropical areas, in many cases do not apply. This is in part the result of its geographical isolation from the nearest source area (about 400 km from the eastern coast of Africa) and long geological isolation (about 130 million years since the break up of Gondwanaland [Coffin & Rabinowitz 1987]). Both biotic and abiotic factors have given rise to an unusual ecosystem that may preclude the use of classical theories in interpreting community structure, for example equilibrium theory.

#### 11.5. COMPOSITION OF POST-FRAGMENTATION AVIFAUNA

The fragmentation of Ambohitantely forest has had an effect on species composition, depending on forest-parcel size. However these changes followed significant natural ecological change over the previous millennia. This disconnection has presumably affected a range of forest-dependent species that had annual or seasonal altitudinal migrations from Ambohitantely to lower-elevation forest sites. This is probably true for a number a strictly insectivorous and frugivorous forest-dependent species, for which elevational movements are critical to secure food resources, particularly during the winter.

The post-fragmentation avifaunal composition reached an equilibrium after a wave of species extinction that was the consequence of the isolation of Ambohitantely Forest. The relationship between fragment size and species composition provides a picture of the general pattern of local extinction. The number of bird species is positively correlated with the size of the forest fragments.

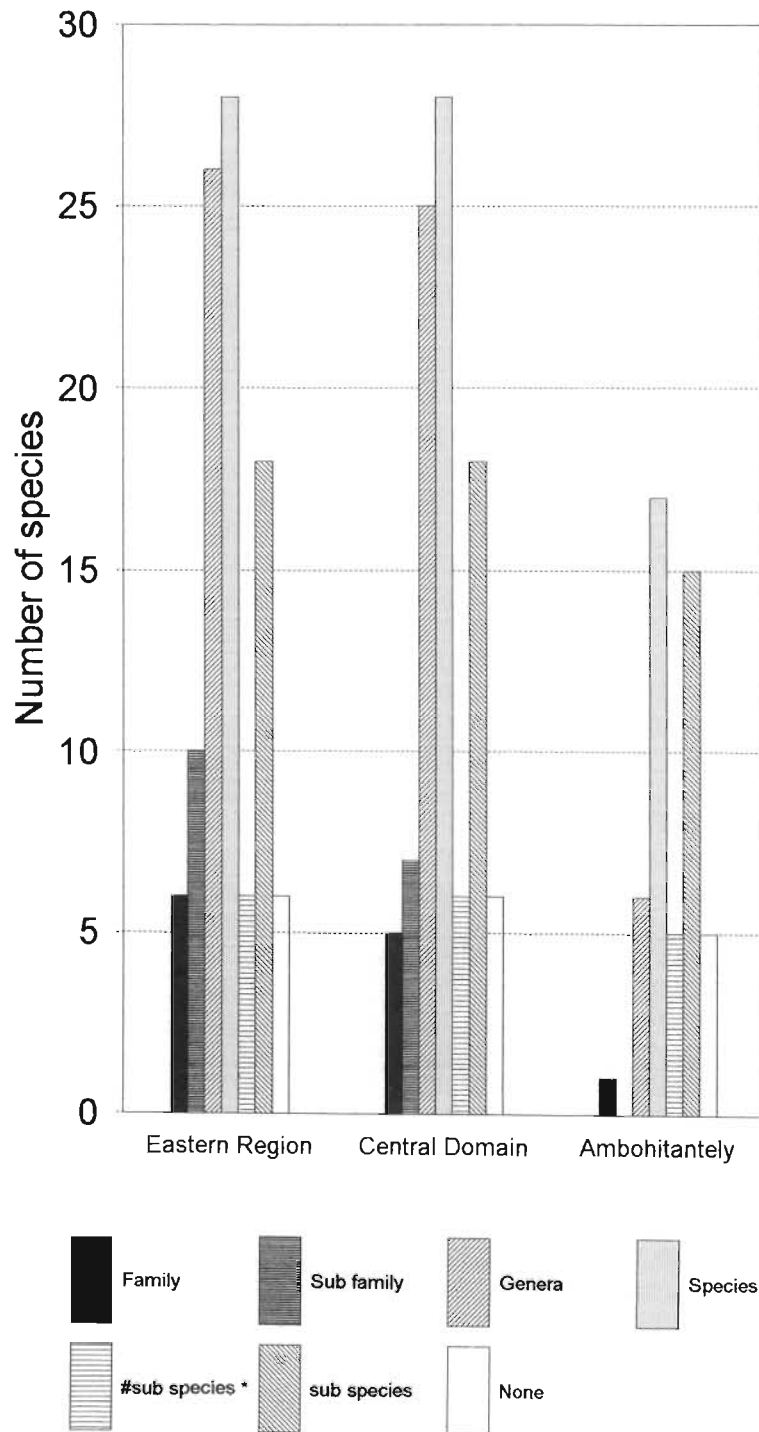
The level of endemism of the bird taxa found in Ambohitantely Forest reflects a general trend in the composition of the avifauna. When the avifauna of Ambohitantely is compared with that of the Eastern Region, or more specifically with that of the Central Domain, the following pattern emerges: the higher taxonomic levels (i.e. families, subfamilies, and genera) decrease in number or totally disappear; only one endemic family is represented in Ambohitantely Forest instead of the typical three in the Eastern Region and the Central Domain; none of the two endemic subfamilies occurring in the Eastern Region are represented in Ambohitantely Forest; and only about 25 % of the endemic genera distributed in the Eastern Region are represented in Ambohitantely Forest (Fig. 46 & Fig. 47).

The endemic higher taxa are considered to be the most ecologically specialized and apparently less adaptable, and thus are the most affected by forest fragmentation. The forest birds that remain at Ambohitantely share some general ecological characteristics (general diet, broad elevational range) and are presumably adaptable to some level of change, and as such remain.

#### 11.5.1. DISTRIBUTION OF BIRD SPECIES IN THE DIFFERENT FOREST FRAGMENTS BASED ON MISTNETTING RESULTS

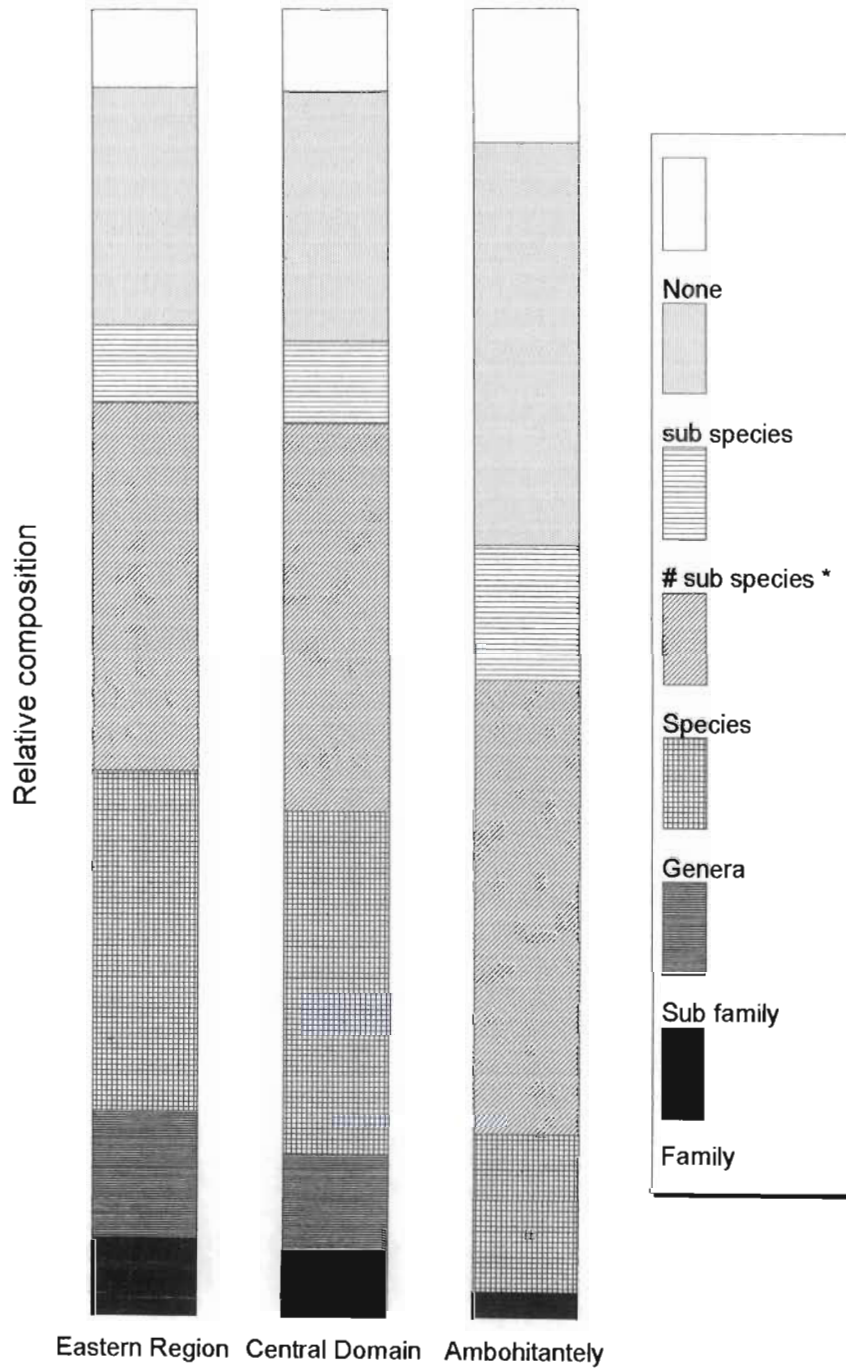
The matrix on proportional distribution of bird species in the forest fragments presented in Table 10 and in Figure 17 (Significance table of  $\chi^2$ ), shows some clear trends.

The occurrence of bird species in forest fragments reflects clear nested subsets. The three conditions which appear necessary for nested community structure [(a) common biogeographical history, (b) similar contemporary environments and (c) hierarchical sets of ecological relationships among species (Patterson & Brown 1991)] are to a large extent applicable to the forest of the *Réserve Spéciale d'Ambohitantely*. The bird species community of the different forest fragments is assembled from a common species pool and all forest fragments have experienced a similar biogeographic history with its related effects (extinction/colonization) on



\* species present east and west (endemic or not) with subspecific differentiation

**Figure 46: Endemism of forest species in three areas as related to taxonomic levels**



\* species present east and west (endemic or not) with subspecific differentiation

**Figure 47: Relative composition of forest bird endemism in three areas as related to taxonomic levels**



a common species pool, and finally all forest fragments face similar contemporary ecological conditions.

A number of species defined as forest generalists possess good dispersal abilities and as a result are becoming proportionally more common in small forest fragments than in large forest fragments (*Hypsipetes madagascariensis*, *Terpsiphone madagascariensis*, *Copsychus albospectus*, *Nesillas typica*). This category is favoured because it shows a greater adaptability to changes.

Edge species benefit from the effects of the fragmentation of the forest and become more common in small fragments as the edge length is proportionally more important in small fragments than in large fragments. This is the case for *Foudia madagascariensis*.

A number of species defined as forest-specialized species become progressively rarer in small forest fragments as a result of their limited dispersal ability. Most of these species are ground-dwelling forest species (*Atelornis pittoides*), understory species (*Newtonia amphichroa*), and to some extent midstorey and forest canopy species (*Tylas eduardi*, *Cyanolanius madagascarinus*). These species become extinct in the smallest fragments possibly as the result of genetic depression (inbreeding) when the size of the fragments is not able to maintain a viable population of these species. The factors that cause the drop in the size of the population can be biological (increase in predation, increase in nest predation, decrease in availability of food, increase in brood parasitism, increase in interspecific competition) and/or physical (change in forest structure, modification of the climate. In order to determine with certainty which factors lead to extinction in forest fragments it is necessary to select particular species for study.

The group of specialized species shows some major critical steps in the increasing rarity of forest-dependent birds:

- between the control site and the 136-ha fragment one species drops out (*Atelornis pittoides*);
- between the 136-ha fragment and the 50-ha fragment one species drops out (*Cyanolanius madagascarinus*);
- between the 50-ha fragment and the 30-ha fragment one species drops out (*Newtonia amphichroa*);
- and finally between 12-ha and 4-ha fragments two species drop out (*Phyllastrephus madagascariensis*, *Tylas eduardi*).

If *Foudia omissa* is excepted, one can say that forest-dependent bird species do not frequent forest fragments of 4 ha or less in area.

Based on these findings, some conclusions can be presented which may be important for management decision making as optimal design of a reserve is dependent on the composition of the assemblages and their species richness (Patterson 1990).

1. The patterns in the species composition of the different forest fragments match with those displayed by insular communities which have a tendency to constitute nested subsets of one another (Patterson 1990; Patterson & Brown 1991). The species compositions in all fragments are fully nested subsets of the control site;

2. Species distribution in the fragments does not represent random subsets of the control site;

3. There is an apparent increase in the percentage of generalist species in the two smallest fragments;

4. Although the species composition differs significantly between the control site and the other fragments (Table 10), the proportion of generalist species appears to be similar in fragments of 12 ha or more in area;

5. The forest-dependent (specialized) species are the most affected by forest fragmentation (i.e. *Atelornis pittoides*).

6. The fragment A12 (12 ha) harbours a high species richness of birds proportional to its size when compared to all other fragment sampled. This is mostly the result of the shape of the A12 fragment which is a narrow forest band established along a watercourse. The scarcity of fragments in the class size 10-12 ha did not permit the choice of a different fragment from A12 in this class size. Based on mistnetting results in other fragments sampled, it is evident that forests along watercourse harbour a higher species richness and a higher number of individuals than fragments far away from rivers.

#### Conclusion on conservation objectives:

Considering that the avifauna found in the forest fragments of the *Réserve Spéciale d'Ambohitantely* forms nested subsets and considering the non-randomness of the distribution of the bird species in the control site compared to the forest fragments, the larger fragments can more effectively fulfil biological conservation objectives. As a result, all forest fragments of 12 ha or larger should be considered as priority sites for long-term biological conservation objectives. For the unique purpose of preservation of the avifauna, fragments of 4 ha or less need not be targeted for priority protection unless they can be used as corridors between larger fragments.

Forest fragments in which watercourses run should be targeted as priorities if protection of species richness is the main objective.

#### 11.5.2. RESPONSES OF DIFFERENT FORAGING GUILDS TO FOREST FRAGMENTATION

Forest fragmentation limits the pattern of food availability and constricts the habitat space occupied by an array of similar species (Johns 1991).

##### Frugivores

In Madagascar, the ecological niche of large canopy fruiteaters is largely filled by the lemurs, and in the case of



Ambohitantely by *Eulemur f. fulvus*. Among birds in general the few large fruit canopy feeders are *Treron australis* and *Coracopsis vasa*. These two species are rare above 1000 m asl (Langrand 1990) which would explain their absence from Ambohitantely. *Alectroenas madagascariensis* and *Coracopsis nigra* are common frugivores in all forest fragments at Ambohitantely and they fly readily between fragments. Both species exploit the disturbed forest successfully, especially the pioneer edge species, and use a variety of forest levels and food resources opportunistically.

#### Ground seed-eaters

This group is represented in Ambohitantely Forest by species that are mostly forest-edge species (*Numida meleagris*, *Turnix nigricollis*, and *Sarothrura insularis*) and by forest-interior species (*Streptopelia picturata*). Fragmentation has had a favourable impact on the forest-edge species as it increases the amount of edge habitat. *Streptopelia picturata* is successful in exploiting forest fragments of a size < 4 ha that it reaches by flying across anthropogenic savannah. It avoids forest edge and is not found in fragments > 4 ha where forest cover is probably too dense to allow ground feeding.

#### Insectivores

Understorey insectivores are particularly prone to forest fragmentation and forest degradation, especially at the edge where the understorey is heavily disturbed. More generalist species such as those able to incorporate fruit into their diet have been more successful and have not become extinct. *Phyllastrephus madagascariensis* is one of the few understorey insectivores found in fragments  $\geq 12$  ha. This forest-dependent species is more of a generalist than the other Malagasy *Phyllastrephus* species. It is the only forest-dependent bird species left on Ile Sainte-Marie on which only a few natural rainforest fragments remain (Goodman 1993). It looks for food from ground level to mid-stratum, gleaning insects in the leaf litter but also along the trunks and large branches. This forest-interior species is affected by the edge effect induced by the fragmentation of the forest. The tangled vegetation

found at the edge does not constitute a favourable habitat for this species.

*Nesillas typica* is the species found in the thick edge vegetation. This insectivorous species is found in fragments  $\geq 0.64$  ha and is able to move between fragments. *N. typica* is typically a forest-edge species, occurring also in higher density along river course where the vegetation is dense.

*Newtonia amphichroa* is a forest-dependent species that is found only in fragments  $\geq 52$  ha. It is a forest-interior species that frequents thick understorey of the riparian forest type. It is not known to cross anthropogenic grassland and seems to be dependent on good quality riparian forest structure. Proportionately the riparian forest type is limited in medium and small fragments and this reduction of habitat may constitute the limiting factor for the maintenance of *N. amphichroa* in fragments  $\geq 52$  ha.

Mid- and upper-stratum insectivores (*Cuculus rochii*, *Coracina cinerea*, *Cryptosylvicola randrianasoloi*, *Newtonia brunneicauda*, *Terpsiphone mutata*, *Calicalicus madagascariensis*, *Cyanolanius madagascarinus*, *Tylas eduardi*, *Dicrurus forficatus*, and *Foudia omissa*) are common in the control site but their occurrence in fragments varies between species. *Cuculus rochii*, a nest parasite targeting *Cisticola cherina* and *Saxicola torquata*, both savannah grassland species, is found in fragments  $\geq 0.64$  ha. It is more common along the forest edge, and is a species capable of long-distance movements, migrating to Africa during the austral winter. *Cuculus rochii* reacts favourably to forest fragmentation.

The nine other species are typically forest-dependent, three of which, *Coracina cinerea*, *Tylas eduardi*, and *Dicrurus forficatus*, have been seen flying across anthropogenic savannah grassland and are found commonly in fragments  $\geq 4$  ha, or  $\geq 0.64$  ha (*Dicrurus forficatus*).

The case of *Calicalicus madagascariensis* and *Cyanolanius madagascarinus* is different. These two forest-dependent

species are sensitive to forest fragmentation. *Calicalicus madagascariensis* is found in fragments  $\geq 136$  ha and *Cyanolanius madagascarinus* occurs in fragments  $\geq 30$  ha. They are not known to cross anthropogenic savannah grassland and seem to be dependent on good-quality forest structure with a solid canopy. Further they seem to prefer riparian forest, particularly areas with large trees. Proportionately the riparian forest type is limited in medium and small fragments and this reduction of habitat may constitute the limiting factor for the maintenance of these two species.

*Cryptosylvicola randrianasoloi* and *Newtonia brunneicauda* are respectively found in fragments  $\geq 0.64$  ha and 4 ha. These two forest-dependent species are found at the edge as well as in the interior of the forest and they are well adapted to fragmentation and they are likely to fly between fragments. In addition to adaptation to forest fragmentation, *Cryptosylvicola randrianasoloi* shows adaptation to plantation as it was seen in several occasions in eucalyptus trees at the edge of the fragment H5 (0.64 ha).

*Foudia omissa* is a forest-dependent species found in fragments  $\geq 4$  ha. This forest-interior species frequents the riparian forest type and is more common in large fragments. Forest fragmentation favours *F. madagascariensis* which is a typical edge species. The hybridization of *Foudia omissa* with *F. madagascariensis* is not scientifically proved, but is likely to occur. Forest fragmentation through the increase of the ecotone, favours the expansion of *F. madagascariensis* and encourages this edge species to penetrate into fragments. This process of invasion of *F. madagascariensis* into fragments may lead to the disappearance of *F. omissa* by hybridization.

#### Frugivores/insectivores

*Hypsipetes madagascariensis*, *Copsychus albospectularis*, *Pseudocossyphus sharpei*, and *Hartlaubius auratus* have a diet of fruit and insects. The proportion between these two food items is likely to change according to the species, sites, and seasons considered.

*Hypsipetes madagascariensis* is the commonest forest species, found in fragments  $\geq 0.64$  ha, and adapts well to forest fragmentation. It exploits the disturbed forest of the ecotone successfully, especially the pioneer edge species, and uses a variety of forest levels and food resources opportunistically. This ubiquitous species found in the forest interior as well as at the forest edge, and readily flies between fragments.

*Copsychus albospecularis* is an uncommon forest species in Ambohitantely Forest where it is found in fragments  $\geq 0.64$  ha. It frequents the understorey of the forest and exploits food resources (fruit and insects) at the forest edge. This species flies between fragments.

*Pseudocossyphus sharpei* is a common forest-dependent species found in fragments  $\geq 12$  ha. This forest-interior species that feeds on fruit and insects occupies the four types of forest found in Ambohitantely Forest. There is no evidence that this species moves between fragments.

*Hartlaubius auratus* is an uncommon forest-dependent species found in fragments  $\geq 4$  ha. This canopy species feeds mostly on fruit and occasionally on insects. As a tree-hollow nester, *H. auratus* is competing for nesting sites with other species such as *Coracopsis nigra*, *Otus rutilus*, *Eurystomus glaucurus*, and *Leptosomus discolor*. Big trees providing potential nesting sites for these species are more abundant in large fragments as they frequently die in small fragments through the action of wind and desiccation. The scarcity of nesting site may be the reason for the scarcity of *Hartlaubius auratus*. *Acridotheres tristis*, an exotic species initially introduced on the east coast of Madagascar 100 years ago reached the central High Plateau ten years ago. This species has been observed 50 km east of the Ankazobe *tampoketsa* in 1994. If *A. tristis* reaches the region of Ambohitantely, which is likely to happen in the coming years, *Hartlaubius auratus* will certainly suffer from the competition imposed by *Acridotheres tristis*, a tree-hollow nester, extremely well adapted to secondary forest and to anthropogenic habitats.

*Hartlaubius auratus* flies between fragments. No observations of *H. auratus* have been made in winter at Ambohitantely. This species probably makes a seasonal altitudinal migration.

#### Nectarivores/Insectivores

Three species present in Ambohitantey belong to this tropical guild: *Nectarinia souimanga*, *N. notata*, and *Zosterops maderaspatana*.

*Nectarinia souimanga*, *N. notata*, and *Zosterops maderaspatana* are forest species found in fragments  $\geq 0.64$  ha. These three species occupy the understorey (*Nectarinia souimanga* and *Zosterops maderaspatana*), the mid-, and the upper-stratum of the forest where they feed on nectar and insects. The three species are highly adaptable to anthropogenic habitats, and as such are commonly encountered at the edge of the forest and they readily fly between fragments. Forest fragmentation, in favouring the growth of forest edge pioneer tree species, provides food resources for *Nectarinia souimanga*, *N. notata*, and *Zosterops maderaspatana*.

#### Predators on small vertebrates and invertebrates

Species feeding on small vertebrates are included in this guild. The availability of the small vertebrates found in Ambohitantely Forest, specifically reptiles and amphibians, is correlated with seasonal climatic conditions. Only bird species with diverse diets, such as small birds and large invertebrates, remain in the Ambohitantely Forest.

*Lophotibis cristata* is found in fragments  $\geq 12$  ha, which is surprisingly small for such a large-bodied species. It is likely that the presence of riparian forest constitutes the vital factor for the maintenance of this species in small fragments. Movements of *L. cristata* between fragments have not been documented, but they are likely to occur, especially at night. The riparian forest provides an array of prey and is less affected by seasonality than other forest types.

*Ispidina madagascariensis* is a rare forest-dependent species found in fragments  $\geq 12$  ha. This mid-stratum forest-dwelling species that feeds on small reptiles and amphibians



seems to prefer the riparian forest. Its rarity is probably related to the decrease in the number of potential prey animals during the winter.

*Atelornis pittoides* is a terrestrial forest-dwelling species found in fragments  $\geq 28$  ha. There is no evidence that this species moves between fragments. Its absence from fragments  $< 28$  ha is probably related to the decrease in food abundance (arthropods and small vertebrates) as a result of desiccation of the understorey and the leaf litter caused by an increase in wind penetration. This species nests in a burrow in the ground. The proliferation of *Rattus rattus*, favoured by the fragmentation of the forest, may have a negative impact on populations of *Atelornis pittoides* through predation of eggs and nestlings.

*Leptosomus discolor* is found in fragments  $\geq 12$  ha. This forest-dependent species exploits the different levels of the forest, from the understorey to the canopy where it feeds on small vertebrates (reptiles, amphibians). It breeds in tree hollows and has the same breeding requirements as *Otus rutilus* and *Eurystomus glaucurus*. *Leptosomus discolor* flies readily between fragments and is certainly capable of long-distance movements.

In general, Malagasy forest raptors are not suffering from forest fragmentation or forest degradation (Langrand 1990). With the exception of *Eutriorchis astur*, all other rainforest raptors have been found in secondary forest, where they appear more common than in pristine forest. *Aviceda madagascariensis*, *Polyboroides radiatus*, *Accipiter madagascariensis*, *A. francesii*, and *Buteo brachypterus* are forest species that have been found in fragments  $\geq 12$  ha, and for several in fragments  $\geq 4$  ha, and have been observed flying between fragments. The diet is not specialized and varies from large invertebrates (millipedes, insects) to small vertebrates (birds, reptiles, amphibians) (*Aviceda madagascariensis*, *Accipiter madagascariensis*). *Accipiter francesii* feeds on large invertebrates to medium to large vertebrates, while *Polyboroides radiatus* and *Buteo brachypterus* feed on mammals,

birds, reptiles, amphibians. *Accipiter henstii* is the only raptor seemingly restricted to the control site, although it has been seen flying across anthropogenic savannah grassland. Unlike *Polyboroides radiatus* and *Buteo brachypterus*, *Accipiter henstii* does not fly above the forest canopy to search for prey, but rather hunts below the canopy. This technique is possible only in large forest blocks. Further fragmentation of the control site would presumably result in the local extinction of *Accipiter henstii* from Ambohitantely.

Recent findings have shown that at least three species of large raptors on the island have gone extinct in the past few thousand years (Goodman 1994, Goodman & Rakotozafy 1995). These species may have had specialized diets, and if this is the case the remaining extant species are "the survivors" and presumably have broader niches or are adaptable in some manner to recent ecological changes.

*Otus rutilus* and *Asio madagascariensis* are found respectively in fragments  $\geq 28$  ha and  $\geq 4$  ha. The restriction of *Otus rutilus* to large fragments (136 ha, 52 ha, 30 ha, 28 ha) is a response to its habitat preference. Large trees of the riparian forest, which provide nesting sites, are more common in large fragments. For *Otus rutilus*, the thick vegetation along the forest edge probably makes hunting difficult. *Asio madagascariensis* follows the distribution pattern in forest fragments of the diurnal raptors. Its occurrence in all fragments  $\geq 4$  ha is the result of its flexible diet composed of small mammals, including introduced species (*Rattus*), birds, reptiles and amphibians. Further, this owl is not dependent on tree hollows for nesting sites and is able to fly between fragments. The distribution of this species may be actually favoured by forest fragmentation as it relates to the proliferation of introduced rodents in disturbed habitat. An analysis of pellet remains of *A. madagascariensis* indicates that its diet in Ambohitantely is largely composed of *Rattus*. This introduced rodent represents 89 % of the minimum number of individuals and 73.5 % of total biomass of samples analyzed. In comparison, at Bezavona Forest near Tolagnaro, *Rattus* represents between 35.6 % and 43.9% of total biomass of the diet of *A. madagascariensis* (Goodman et al. 1991) and rats represent 72 % of the total biomass of vertebrates identified



from *A. madagascariensis* food remains at Beza-Mahafaly (Goodman et al. 1993). Since no native rodents are known to occur in the reserve (Stephenson et al. 1994) and *Rattus* is such a prominent proportion of its diet, perhaps *Asio* has only recently colonized the area or, more likely, has a highly adaptable feeding regime.

#### Aerial feeders

This trophic guild is composed of two distinct groups, the non-forest-breeding aerial feeders (*Caprimulgus madagascariensis*, *Apus melba*, *A. barbatus*, *Merops superciliosus*, *Riparia paludicola*, and *Phedina borbonica*) and the forest-breeding aerial feeders (*Zoonavena grandidieri* and *Eurystomus glaucurus*). The non-forest-breeding aerial feeders do not follow a specific pattern regarding their distribution in relation to fragment size. They favour fragments  $\geq 4$  ha where food resources seems to be abundant and are distinctly less common or not present in fragments  $\geq 0.64$  ha. *Caprimulgus madagascariensis*, *Riparia paludicola*, and *Phedina borbonica* feed principally at the forest edge.

*Zoonavena grandidieri* is present in the 136-ha fragment and marginally in the adjacent 12-ha fragment. This species feeds on types of small insects that are presumably not present above small forest fragments. The breeding habits of *Z. grandidieri* are poorly documented, but apparently it is dependent on the forest for breeding (Langrand 1990). The only African congener, *Z. thomensis*, breeds in tree hollows and among buttress-roots (Fry et al. 1988). *Z. grandidieri* is likely to be dependent on large trees for breeding and big trees are more common in large fragments as they are less vulnerable to desiccation and wind breaking.

*Eurystomus glaucurus* breeds in tree hollows, has the same breeding requirements as *Otus rutilus* and *Leptosomus discolor*, and feeds in all fragments  $\geq 4$  ha. *Eurystomus glaucurus* is clearly capable of long-distance movements, as it migrates to Africa during the austral winter.

#### 11.6. EDGE EFFECT

The edge-effect principle refers to the increased number of species encountered where two major habitat types intergrade (Leopold 1933), or to the high diversity of plants and animals associated with edges and ecotones (Harris 1988). In forest fragmentation studies, the edge effect refers to an array of "changes affecting a previously undisturbed ecosystem by an abrupt creation of a sharp edge at the forest margin" (Lovejoy et al. 1986). By extension, it describes the minimum distance at which a given species can be seen from the forest edge.

In Ambohitantely Forest, the edge effect benefits a number of species and is negative for a few others. The edge provides a greater variety of food resources and attracts certain species of birds, such as *Hypsipetes madagascariensis*, *Nectarinia souimanga*, and *Zosterops maderaspatana*. Disturbances, both ecological and climatical associated with the creation of an edge have a negative impact on a number of forest-interior species. This is the case for *Atelornis pittoides*, *Coracina cinerea*, *Phyllastrephus madagascariensis*, *Cryptosylvicola randrianasoloi*, *Newtonia amphichroa*, *Calicalicus madagascariensis*, *Cyanolanius madagascarinus*. Knowledge about edge effect on forest-dependent species is essential to determine the minimum width of corridors necessary to allow bird species to move between forest fragments.

Does edge effect vary for a given species depending on fragment size? Based on results of the mistnetting, edge effects follow five different trends:

a) species that occur in all or almost all fragments are usually not affected by the edge effect. They occur equally near the edge and in the forest interior. As there is greater diversity of food resources associated with the edge of the fragments than inside the fragments, these species are more frequently observed at the edge of the forest in the smaller fragments. This is the case of *Hypsipetes madagascariensis*, *Newtonia brunneicauda*, *Nectarinia souimanga*, and *Zosterops maderaspatana*. *Accipiter* spp. that feed principally on small

birds have a similar pattern of distribution since there is an increase in prey abundance near the edge.

*Accipiter madagascariensis*: 50 % of the individuals captured were at a distance  $\leq 96$  m from the edge in the fragments, versus 25 % in the control site. *A. francesii*: 100 % of individuals captured were at a distance  $\leq 144$  m from the edge in the fragments, versus 38 % in the control site.

b) species that occur only in the largest fragments are proportionally captured more frequently near the edge in small fragments. This is the case for *Phyllastrephus madagascariensis*, *Pseudocossyphus sharpei*, *Newtonia amphichroa*, and *Foudia omissa*. The smaller the fragment, the closer to the edge the species is observed:

*Phyllastrephus madagascariensis*: 100% of individuals captured were at a distance  $\leq 168$  m from the edge in the control site, versus 15% in the fragments and 30% of individuals captured were at a distance  $\leq 72$  m in the fragments, versus 0% in the control site.

*Pseudocossyphus sharpei*: 87% of individuals captured were at a distance  $\leq 156$  m from the edge in the control site, versus 17% in the fragments and 35% of individuals captured were at a distance  $\leq 72$  m from the edge in the fragments, versus 13% in the control site;

*Foudia omissa*: 100% of individuals captured were at a distance  $\leq 180$  m from the edge in the control site, versus 10% in the fragments and 70% of individuals captured were at a distance  $\leq 48$  m from the edge in the fragments, versus 0% in the control site.

c) Typical edge species (i.e. *Copsychus albospectularis*, *Nesillas typica*, and *Foudia madagascariensis*) are found almost exclusively in the ecotone or along streams where the understorey vegetation is dense. Edge species penetrate deeper inside the forest in smaller fragments. This is a result of change in the vegetational structure that is affecting more the small fragments than the large one.

d) Some species do not show a clear edge-effect pattern. These species occupy a specific microhabitat and the edge effect does not influence their distribution as long as the microhabitat where they live is not affected. This is the case for species principally restricted to the riparian forest such as *Terpsiphone mutata*.

e) Some species show a clear edge effect pattern in the control site, but are rare enough in the fragments that comparisons are difficult to make. These species are *Atelornis pittoides* (100% of captures made at a distance  $\leq 142$  m from the edge), *Newtonia amphichroa* (95% of captures made at a distance  $\leq 156$  m from the edge).

With the results of the point counts, edge effects follow the same trends described based on the results of mistnetting:

a) Species that occur in all or almost all fragments are usually not affected by the edge effect: *Alectroenas madagascariensis*, *Coracopsis nigra*, *Cuculus rochii*, *Hypsipetes madagascariensis*, *Newtonia brunneicauda*, *Nectarinia souimanga*, *Zosterops maderaspatana*, and *Dicrurus forficatus*;

b) species that occur only in the largest fragments are proportionally recorded more frequently near the edge in small fragments: *Phyllastrephus madagascariensis*, *Pseudocossyphus sharpei*, *Newtonia amphichroa*, and *Foudia omissa*;

c) Typical edge species: *Copsychus albospectularis* and *Nesillas typica*;

d) Clear edge-effect pattern: *Cryptosylvicola randrianasoloi*, and *Tylas eduardi*;

e) Some species (*Atelornis pittoides*, *Newtonia amphichroa*, *Calicalicus madagascariensis*, and *Cyanolanius madagascarinus*) show a clear edge-effect pattern in the control site, but are so rare in the fragments that comparisons are difficult to make.



Which species constitute the limiting factor in terms of edge effect? On the basis of mistnetting and point counts, *Atelornis pittoides* is the species most affected by the edge effect. This endemic species that still exists at Ambohitantely is one the most prone to local extinction through the effect of forest fragmentation. As an example, *Atelornis pittoides* is absent from Manjakatombo Forest which is a site located on the central high plateau, smaller than Ambohitantely (150 ha versus 1250 ha for the largest fragment). *Atelornis pittoides* is the only species belonging to an endemic family present in Ambohitantely, and is the most tolerant of the ground-roller species and this is presumably why a population remains at Ambohitantely. It is considered one of the species most affected by forest fragmentation (present in fragments  $\geq$  28 ha), and constitutes one of the species most affected by the edge effect (156 m from the edge in the control site). These arguments designate *Atelornis pittoides* as the limiting species for establishment of corridors between fragments.

The edge effect is affecting more significantly the higher endemic taxa (endemic family or genus) such as *Atelornis pittoides*, *Pseudocossyphus sharpei*, and *Newtonia amphichroa* than the lower endemic taxa (endemic species) or the non-endemic taxa such as *Nectarinia souimanga*, *Zosterops maderaspatana*, and *Hypsipetes madagascariensis*. This difference is related to the high degree of habitat specialization that has been evolved by the Malagasy endemic forest-dependent species that show limited tolerance to modified habitat. *Atelornis pittoides* is tolerant to forest fragmentation up to a certain point. At Manjakatombo, that point has been passed, leading to the local extinction of this species. The species that remain at Ambohitantely are adaptable to disturbance at some level and that is the reason why they remain in the area. But once disturbance gets to a certain point, they disappear.

#### 11.7. SPECIES DIVERSITY

The index of relative abundance measured through the point counts for the control site and for the forest fragments shows

that for most of the forest-dependent species there is a negative correlation between size of fragment and relative abundance.

#### **11.8. CONSERVATION MANAGEMENT MEASURES TO OPTIMIZE BIRD PRESERVATION OF AMBOHITANTELY**

The world is increasingly dominated by man. The original biomes are now being destroyed, modified and fragmented at a rate that is leading to a critical situation for a large number of animal and plant species (Myers 1993). Therefore the continued existence of many species depends on the protection of areas that form islands of natural habitats within man-made environments (Blake & Karr 1984). This is the reason why it is important to create and manage parks and reserves properly.

The Ambohitantely Special Reserve has been gazetted in order to preserve the last forest tract of the central High Plateau. The final objective of its creation was clearly for the protection of biodiversity. This is an important consideration, since a number of parks and reserves are created for other purposes such as landscape or watershed protection. In general, the initial motivation that led to the creation of a protected area has a direct influence on its management.

Ambohitantely Special Reserve is a small reserve in the Malagasy context as it covers a total of 5600 ha, 1700 ha of which are natural forest (Nicolli & Langrand 1989). The reserve is composed of a single block of 1250 ha and of 513 forest fragments, most of which are isolated from one another (Plates 9-14). It is largely agreed that the size and design of reserves can help to reduce local extinctions (Diamond 1975). Since it is clear that the reduction and isolation of forest leads to a decline in species number and species densities (Karr 1982), it is critical to consider management of forest fragments together with the control site.

The only large tract of original forest remaining on the central High Plateau is in the Ambohitantely Special Reserve.

Most importantly little of this forest type remains in the reserve, and it is critical to include all remaining natural forest fragments in the reserve management plan. Close to 150 species of pteridophytes (Rakotondrainibe et al. 1988), and 900 species of woody plants have been identified in the reserve (Anon. 1990). Further, 17 native species of mammals, 72 species of birds, 20 species of reptiles, and 15 species of amphibians (Séguier-Guis 1988; this study) have been recorded in Ambohitantely Special Reserve. Tropical forests are very complex ecologically, and species interactions play a crucial role in the maintenance of biodiversity.

Despite the arguments presented by Simberloff & Abele (1976), it is generally agreed that larger reserves provide better preservation to more species than a series of small reserves (Blake & Karr 1984), because the former hold more species at equilibrium and have a lower extinction rate (Diamond 1975). In the case of Ambohitantely Special Reserve, only a few fragments are located outside of the reserve boundaries. Therefore, the surface of the reserve cannot be expanded greatly. There are four possibilities for improvement of the conservation potential of this protected area: a) limitation of impact of bush fires on the natural forest, b) expansion of natural forest cover through tree planting, c) establishment of forest corridors between forest fragments of the Ambohitantely Forest and d) establishment of inter-forest corridors between the Ambohitantely Forest and other forest blocks.

#### 11.8.1. FIRE CONTROL

The high frequency of grassland burning prevents forest regeneration and promotes forest shrinkage. It is doubtful that grassland fires could be stopped or even reduced on the central High Plateau. This destructive practice has been used for several centuries and despite the efforts developed by the early monarchies and thereafter by the colonial administration and the Malagasy governments, no effective solution has been found. In the case of Ambohitantely, where human population density is low, reinforcement of the existing legislation to



stop fires is possible. However, it might be more realistic to consider stopping the effects of fires on the forests rather than preventing grassland fires. From a logistical and economic point of view this could only be done by establishing fire-breaks around the reserve. Special attention should be given to the eastern edge of forests, as this is the prevailing direction for most winds spreading fires. Fire-breaks should have strict specifications in terms of width, as the grass is tall and the wind generally strong. The maintenance of these fire-breaks could be done by the forest guards in charge of the reserve's management.

The development of native pioneer species along the forest edge would allow forest to reestablish naturally and to increase forest size relative to grassland, if the action of fire is reduced or stopped. The natural process of forest regeneration could be favoured by planting forest-edge species that are recognized as forest pioneer species such as *Weinmannia rutenbergii* (Cunoniaceae), *Agauria salicifolia* (Ericaceae), *Alberta minor* (Rubiaceae) (Radimbison & Roger Edmond 1986), and *Harungana madagascariensis* (Guttiferae) (Rajoelison et al. 1992).

#### 11.8.2. TREE PLANTING

A large proportion of the reserve area is covered with anthropogenic grassland. In order to increase the size of the forest of Ambohitantely Special Reserve it would be possible to envision planting local tree species. The use of such tree species for reafforestation is not well developed in Madagascar. However, some forestry tests (germination and planting) have been made in rainforest with *Canarium madagascariense* (Burseraceae) and *Afzelia bijuga* (Leguminosae) and in deciduous dry forest with *Commiphora* spp. (Burseraceae) and *Colvillea racemosa* (Leguminosae). When considering technical and ecological limitations, six tree species could be considered for reafforesting Ambohitantely Special Reserve: *Gambeya boiviniana* (Sapotaceae), *Canarium madagascariense*, *Ocotea laevis* (Lauraceae), *Ocotea madagascariensis* (Lauraceae), *Calophyllum milvum* (Guttiferae), and *Podocarpus*

*madagascariensis* (Podocarpaceae) (Rajoelison et al. 1992). The first four species are heliophilous and could be considered for reafforestation at the edge of the forest blocks, in natural (landslides) or human-made forest clearings, and in the valleys along river courses as they are predominant in the riparian forest of Ambohitantely. *Calophyllum milvum* and *Podocarpus madagascariensis* are sciophilous species and as such should be used for replanting in degraded forest where some shading trees are still present. These six species mature to large trees. They are an important source of food in the trophic chain and provide nesting sites for a number of bird species, particularly for tree-hollow nesters such as *Leptosomus discolor*, *Eurystomus glaucurus*, and *Coracopsis nigra*.

#### 11.8.3. FOREST-FRAGMENT CORRIDOR

Tree planting should have two main objectives: a) expanding the size of the natural forest of Ambohitantely and b) creating forest corridors between forest fragments. The definition of forest corridors used here is that of Newmark (1993), namely "natural habitat that permits the movement of organism between ecological isolates". Especially in the case of sedentary species with restricted habitat preferences, corridors between fragments may dramatically increase dispersal rates over what would otherwise be negligible values (Diamond 1975). The creation of forest corridors is an essential aspect of the management of Ambohitantely Special Reserve. Many forest fragments are too small to contain longterm viable populations for some bird species. Establishing forest corridors may reduce loss of forest species, that would happen as a result of forest fragmentation, in allowing birds to expand their feeding and breeding habitat and in promoting gene flow between previously isolated populations. Further corridors might provide an increase in habitat heterogeneity, for example across elevational gradients or an increase in available microhabitats, and in doing so increased available habitat diversity.

In recent years, the use of corridors has come under scrutiny and some proponents conclude they have serious

negative effects (Noss 1987, Simberloff & Cox 1987, Newmark 1993). One potential problem is the introduction of diseases or parasites to populations that have been previously isolated. Further, corridors might encourage the spread of noxious or exotic plants and animals. Planted corridors are by definition secondary, even when native species are used, and these may provide routes of dispersal for forest edge species to colonize relatively intact forest. In doing so, particularly in small forest fragments, these forest edge species might come in contact with and displace forest dependent species. The exact opposite of what was originally intended by putting the corridor in place. However, there is little definitive evidence to show that these theoretical factors manifest themselves when corridors are used to connect fragmented habitat. Further, the remaining forested areas of Ambohitantely are so fragmented that corridors are the only logical step in providing the means to increase total forest area and routes for forest-dependent birds to disperse.

In the case of Ambohitantely, the corridors should be designed with the emphasis on the species most prone to extinction (Newmark 1993), which are (1) the largest species, (2) the rarest species, (3) the forest-interior species, and (4) the species needing large territories. The following species would therefore benefit from establishment of forest corridors between fragments: *Lophotibis cristata* (1, 3), *Ispidina madagascariensis* (2, 3, 4), *Atelornis pittoides* (3), *Phyllastrephus madagascariensis* (3), *Pseudocossyphus sharpei* (3), *Newtonia amphichroa* (3), *Calicalicus madagascariensis* (3, 4), *Cyanolanius madagascarinus* (4), and *Foudia omissa* (3).

The forest corridors should be wide enough to avoid adverse edge effects on the targeted species. Many tropical bird species are known to avoid forest edge where ecological and climatic conditions (temperature, light, humidity) are different from what they are in the forest interior (Willis 1979). Among the nine targeted species listed above, considered as forest-dependent species, *Atelornis pittoides*, *Phyllastrephus madagascariensis*, *Newtonia amphichroa*, *Calicalicus madagascariensis*, and *Foudia omissa* are the most

affected by the edge effect and have rarely been recorded closer than 100 m to the edge in the control. The minimum width of the corridors is in most cases determined empirically in considering the ecology and life history of the target species, although computer simulations could be used to provide general guidelines for designing forest corridors (Newmark 1993). In Ambohitantely the distance from the forest edge at which the forest-dependent bird species were found, should be used to calculate the minimum width of forest corridors between forest fragments. The riparian type of forest found in Ambohitantely is a habitat that supports a high diversity and density of forest birds, especially forest-interior species. In addition, it offers breeding and foraging sites for large forest birds, especially the hollow-nesting species which are dependent on large trees for breeding sites. Proper management of riparian forest would also maintain perennial water sources and quality, and would reduce local land erosion.

The only feasible means to improve the potential of Ambohitantely Special Reserve to conserve the local biodiversity, in particular its avifauna, is to establish forest corridors between the existing forest fragments. Connections between large fragments (20-55 ha) should be given higher priority than between the smaller ones. The design of forest corridors should be made by a specialist wildlife manager, familiar with the practical and theoretical aspects of this field, for the purpose of optimizing survival of local biodiversity. The technical aspects of selecting tree species, establishment of tree nurseries, tree growing, tree planting should be devoted to the *Ecole des Sciences Supérieures Agronomiques d'Antananarivo* (ESSA) who, through its *Département Eaux et Forêts* has considerable experience in forestry. ESSA has been working for several years on forestry and ecological aspect of the Ambohitantely forest and as such would be the best choice for implementing, monitoring, and evaluating the establishment of forest corridors in Ambohitantely Special Reserve.



#### 11.8.4. INTER-RESERVE CORRIDORS

Although it does not seem realistic to consider establishing forest corridors between the Ambohitantely Special Reserve and adjacent forests considering the geographical isolation of Ambohitantely Special Reserve, it is important to propose some technical solutions that would envision this possibility. These solutions could be applied in the future if the economic situation of the country improves and if the interest of the Malagasy Government in proper management of the biodiversity of Madagascar continues.

Technical feasibility is only one aspect to be addressed to link the different forest fragments of Ambohitantely. The second aspect is political feasibility. Through the Environmental Action Plan (EAP) designed in the late 1980s and implemented since 1989, the Malagasy Government has given in principle high priority to the sustainable management of the natural resources. The "biodiversity" component of the EAP is dealing with protected areas and natural forest management to improve protection and sustainable use of endemic biota and natural habitats of Madagascar. The establishment of a forest corridor to link Ambohitantely Special Reserve to the eastern forest block is of paramount importance for the longterm biological viability of this reserve. Unfortunately, this proposal has little chance of success, since this would subtract grazing and cultivating land from local human populations. Considering the technical and political constraints, a successful design of this forest corridor cannot be done without the assistance of a Geographic Information System (GIS) which would allow conservationists and developers to present their vision of a regional landscape in which the biological and the socio-economical situations would be taken into consideration. This would help to define the current constraints in the establishment of the forest corridor and would allow the design of effective measures for its future protection. However, planning concrete actions with the assistance of a GIS can be successful only if a recent and complete database is available. For the purpose of planning the design of a forest corridor to connect Ambohitantely Forest

and Anjozorobe Forest, such a national database, should include human population densities, land-use pattern, river network, topography, soil-type distribution, forest distribution, and climate (rainfall and temperatures). Such a database is currently not available for Madagascar.

Recently established forest corridors would be a major attraction to local people who are still largely dependent on forest products for house construction and food. Thus if this plan were implemented, there would be a critical need to manage and protect the corridor to keep it untouched, which is unlikely considering the weakness of the governmental institutions in charge of forest protection.

The nearest natural forest (Anjozorobe) is located 80 km east of Ambohitantely and separated by anthropogenic grassland extensively used for cattle grazing. The establishment of a corridor between Ambohitantely and Anjozorobe constitutes the first option. This option is valid from the biological point of view only if a link remains between Anjozorobe Forest and the eastern forest block. Thus it would allow movements and genetic exchange between the two sites and would permit species of Ambohitantely Forest to migrate to lower-altitude sites during winter. Wintering sites located at an altitude between 750 and 900 m asl would constitute an optimal compromise for the possible longterm establishment of breeding species such as *Coua caerulea*, *C. cristata*, *C. reynaudii*, *Philepitta castanea*, *Neodrepanis coruscans*, *N. hypoxantha*, *Phyllastrephus zosterops*, *P. cinereiceps*, *P. zosterops*, and *Ploceus nelicourvi* in Ambohitantely.

Since the avifauna of Ambohitantely before it was isolated cannot be documented, the reintroduction of bird species should not be considered. If subfossil deposits of birds are found in the area, this view should be reevaluated.

After the forest corridor is established, a strict monitoring of the avifauna of Ambohitantely should be considered to document the trends in colonization and bird movements between Ambohitantely and Anjozorobe Forests. The avifauna of Anjozorobe Forest should be properly inventoried

and a few targeted forest-dependent species found at both sites should be studied to document bird movements between the two sites. These species should be representative of the different forest strata and individuals should be ringed to allow individual identification through observation (colour rings) or capture (numbered metal rings). The last option remains the most reliable technique to document movements of individual birds between sites, but relies on capture-recapture which is more difficult to implement. The selected species should be forest-dependent, common or fairly common to have a reasonable probability of being mistnetted and should be representative of the lower-, mid- and upper-stratum of the forest. The proposed selection of species takes into consideration these criteria:

Lower-stratum: *Newtonia amphichroa* and *Pseudocossyphus sharpei*;

Mid-stratum: *Phyllastrephus madagascariensis* and *Newtonia brunneicauda*;

Upper-stratum: *Calicalicus madagascariensis* and *Cyanolanius madagascarinus*.

Theoretically it is clear why it is important to establish a corridor between Ambohitantely Forest and Anjozorobe Forest. However, the feasibility of such a project is unrealistic considering the extreme difficulties faced by the national economy, the population growth rate, the technical capacity of local institutions to design, implement, and maintain such a corridor, and the degree of priority that this project would be given by the Malagasy Government. It is more realistic to concentrate on Ambohitantely Special Reserve in order to optimize the management of this protected area, for the benefit of its local biodiversity.

Some important results have been obtained through this study. For example, on the basis of distance to forest edge and minimum fragment size for numerous forest-dependent bird species, some clear and simple recommendations can be proposed possibly to stabilize the populations of Ambohitantely Special Reserve. The creation of corridors between the largest



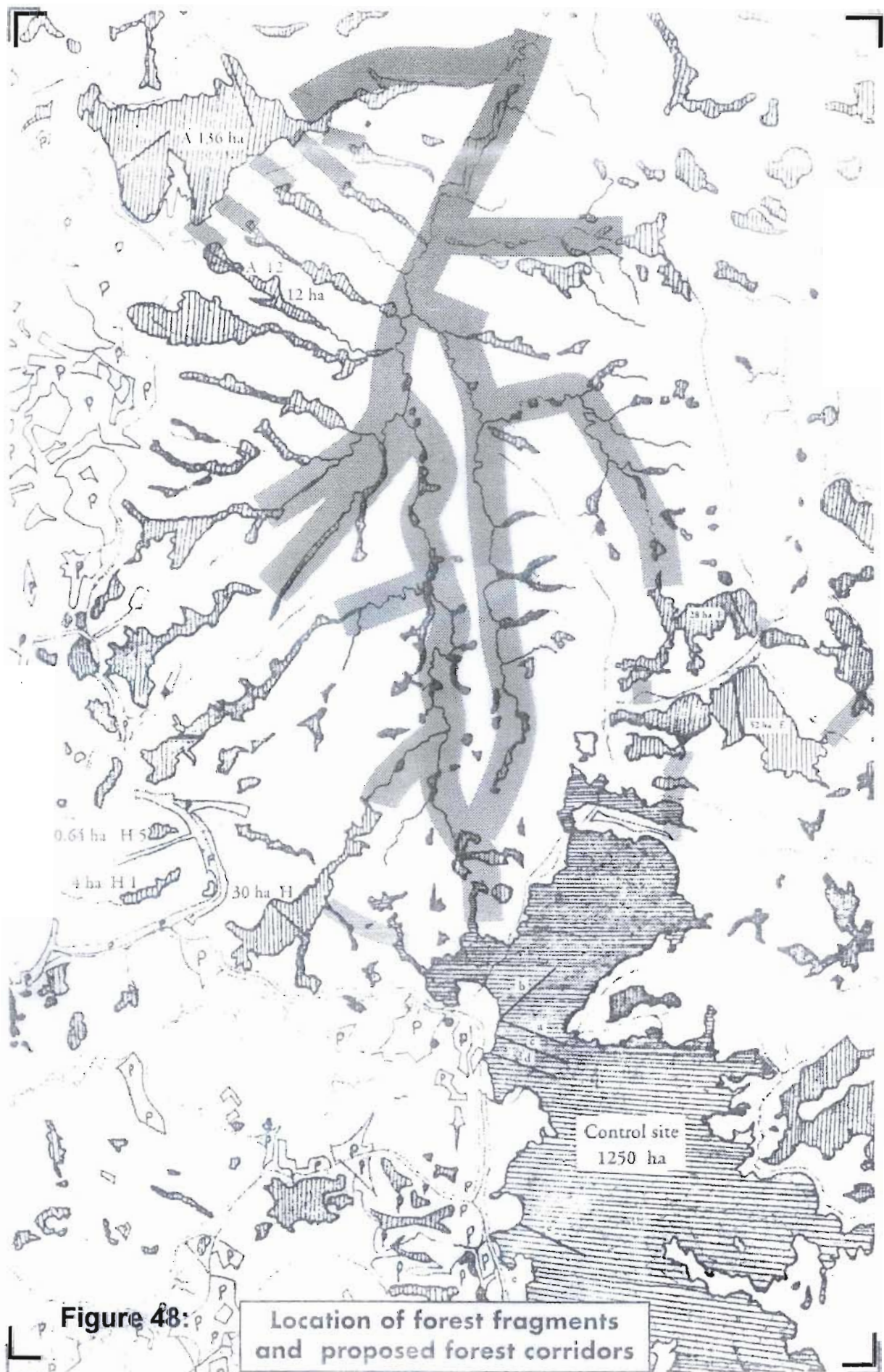
fragments located northwest of the control site would constitute an important test to assess the effectiveness of forest corridors in the dispersal of bird species. Further, such a project would provide the basis, or at least the start, of understanding the processes of reestablishing natural forest and how plants and animals utilize such corridors and colonize fragments.

The proposed actions for establishment of forest corridor between fragments of the Ambohitantely Special Reserve are described below and are depicted on the map of the reserve (Fig. 48).

Two management activities appear to be essential to preserve the long-term biodiversity of Ambohitantely Forest. The first is to maintain the control site as an intact unit and protect it against further fragmentation. A fairly large portion ( $\approx 200$  ha), located in the southern part of the control site is already almost disconnected from the rest of the forest block. Only a narrow natural forest corridor maintains the connection between the southern portion and the rest of the control site. The width of this existing corridor should be expanded through tree planting. At the same time, it would be an excellent occasion to measure the success rate in tree planting and it would be a unique opportunity to monitor bird movements through this corridor. The information gathered would be used to refine a strategy for the establishment of corridors in the rest of the reserve. The second is to create connections between the control site and fragments located to the northwest of the control site. There are three reasons why these fragments have been selected. a) The fragments are located in a large valley and belong to the same water catchment. The priority for planted forest corridors should be along streams. Thus, trees would be less vulnerable to the action of fire and wind and would benefit from deep rich soils. In addition, the forest tree species that have been targeted for possible reafforestation are riparian. b) This forest type was identified to harbour the greatest diversity of bird species and the highest density of birds. c) The most vulnerable bird species in Ambohitantely are principally







distributed in the riparian forest (i.e. *Newtonia amphichroa*, *Calicalicus madagascariensis*, and *Cyanolanius madagascarinus*).

The proposed establishment of forest corridors would allow the reconnection of 46 forest fragments (1 fragment larger than 100 ha; 1 fragment smaller than 60 ha and larger than 50 ha; 1 fragment smaller than 50 ha and larger than 30 ha; 8 fragments smaller than 30 ha and larger than 12 ha; 10 fragments smaller than 12 ha and larger than 5 ha; 25 fragments smaller than 5 ha) totalling 462 ha, and hopefully would constitute a way to enhance migration between these fragments. A 100-m-wide corridor established between these fragments would cover 283 ha. Together with the existing control site, the largest parcel would reach a total of 1995 ha, which would constitute an increase of 63% of the total area of the largest forest block.

The management activities are proposed to improve the value of Ambohitantely Forest as a biological refuge. However, the Ambohitantely Forest has already suffered from species extinction as a result of its long history of isolation. The natural recolonization of species through stochastic dispersal is certainly not possible without a forest connection between Ambohitantely and the eastern forest block. Even if it were technically feasible, there is no chance that such a forest corridor could be established. In fact, considering the overall rate of deforestation on Madagascar, the situation of Ambohitantely Forest may worsen. The closest natural forest from Ambohitantely, Anjozorobe Forest, is severely affected by deforestation. If this destruction trend is not reversed, in two or three decades Anjozorobe Forest will have disappeared or will be extensively reduced.

Ambohitantely Special Reserve is a small and fragmented reserve and as such may be considered worthless by some conservationists. However, it is the last remaining tract of forest on the central High Plateau forest and as such is important for conserving local endemics. In this context, its preservation is important at the very least for archival reasons. The longterm survival of the forests of Madagascar depends on the attitude of the Malagasy government and of the

Malagasy people. The main conservation goal of the Malagasy Government should be to promote vast natural refugia that are of paramount importance for the future of Malagasy biota. In the context of a national effort to promote the preservation of Madagascar biological richness, Ambohitantely Forest could become a pilot project where the feasibility of natural forest management for the preservation of endemic biota could be tested. Further, the proximity of this reserve from the capital city, Antananarivo, would also allow on-site training for national students and researchers.

Burkey (1989) said "It is imperative that we all take active part in safeguarding the species for whose demise we will otherwise be responsible." As human population dramatically expands around the world, including Madagascar, our responsibility to share and deal with this problem increases, but at the same time our ability to truly face the issue decreases.



## Plate 1



(Above) *Ispidina madagascariensis*: This rare, sexually monomorphic mid-stratum forest-dependent species was captured twice only (control site and fragment A12 [12 ha]), and never observed during this study.

(Below) *Pseudocossyphus sharpei* (female): A common, understorey forest-dependent species found in the control site and in fragments larger than 12 ha.



## Plate 2



(Above) *Copsychus albospectus* (male): An uncommon, mid-stratum forest species found in the control site and all forest fragments but the fragment A12 (12 ha).

(Below) *Otus rutilus* (red form): A common, nocturnal forest species showing no sexual dimorphism in plumage colouration was found in the control site and in fragments larger than 28 ha.





## Plate 3



(Above) *Alectroenas madagascariensis*: A common, upper stratum forest-dependent species showing no sexual difference in plumage colouration that was found in control site and in all the fragments but fragment H1 (4 ha).

(Below) *Accipiter madagascariensis* (immature male): An uncommon, forest species found in the control site and in fragment A (136 ha).



## Plate 4



(Above) *Newtonia brunneicauda*: A common, forest-dependent species not sexually dimorphic that was found in the control site and in all fragments larger than 4 ha (above).

(Below) *Newtonia amphichroa*: An uncommon, understorey forest-dependent species showing no sexual dimorphism in plumage colouration that was found in the control site and in fragments A (136 ha) and E (52 ha), where it frequents ripicolous forest where large trees and moist dense understorey are common features.





## Plate 5



(Above) *Cyanolanius madagascarinus* (immature): An uncommon, mid- to upper-stratum forest-dependent species showing no sexual dimorphism, which was found in the control site and in fragments larger than 30 ha.

(Below) *Tylas eduardi* (immature male): A common mid- and upper-stratum forest-dependent species found in the control site and all the fragments larger than 4 ha.



## Plate 6



(Above) *Leptosomus discolor* male and (Below) female: common, mid- and upper-stratum forest-dependent species found in the control site and in fragments larger than 12 ha.





## Plate 7



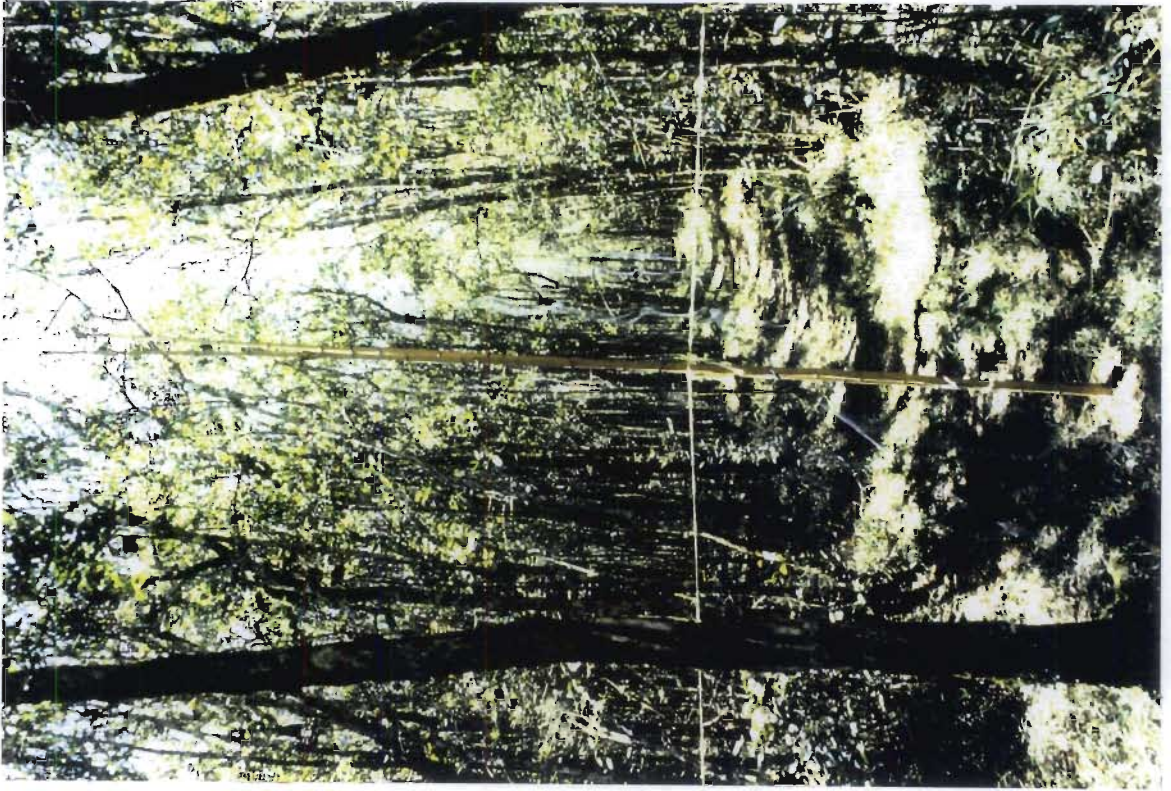
(Above) Standard morphometric measurements were recorded for each of the 500 birds captured before they were released at the original capture point.

(Below) *Atelornis pittoides*: An uncommon, terrestrial forest-dependent species showing no plumage dimorphism, belonging to the endemic family Brachypteraciidae, and found in the control site and in fragments larger than 28 ha.





## Plate 8



(Above) Mistnet line erected in plateau-type forest at 1460 m asl in the control site. This type of forest is dominated by *Uapaca densifolia* and reaches 8 m in height on average.

(Below) Riparian forest in the control site at 1420 m asl. Large trees average 30 to 40 cm diameter at breast height, sometimes reaching 65 to 100 cm dbh.





## Plate 9



(Above) Ambohitantely Forest (portion at 1640 m asl) benefits from eastern facing slope which receives higher rainfall because of dominant easterly trade winds. Severe erosion occurs on hills where forest has been cleared. (Below) Natural forest corridors (at 1400 m asl) that run through deep valleys maintain physical continuity between forest fragments and allow forest-dependent bird species to move between areas.





## Plate 10



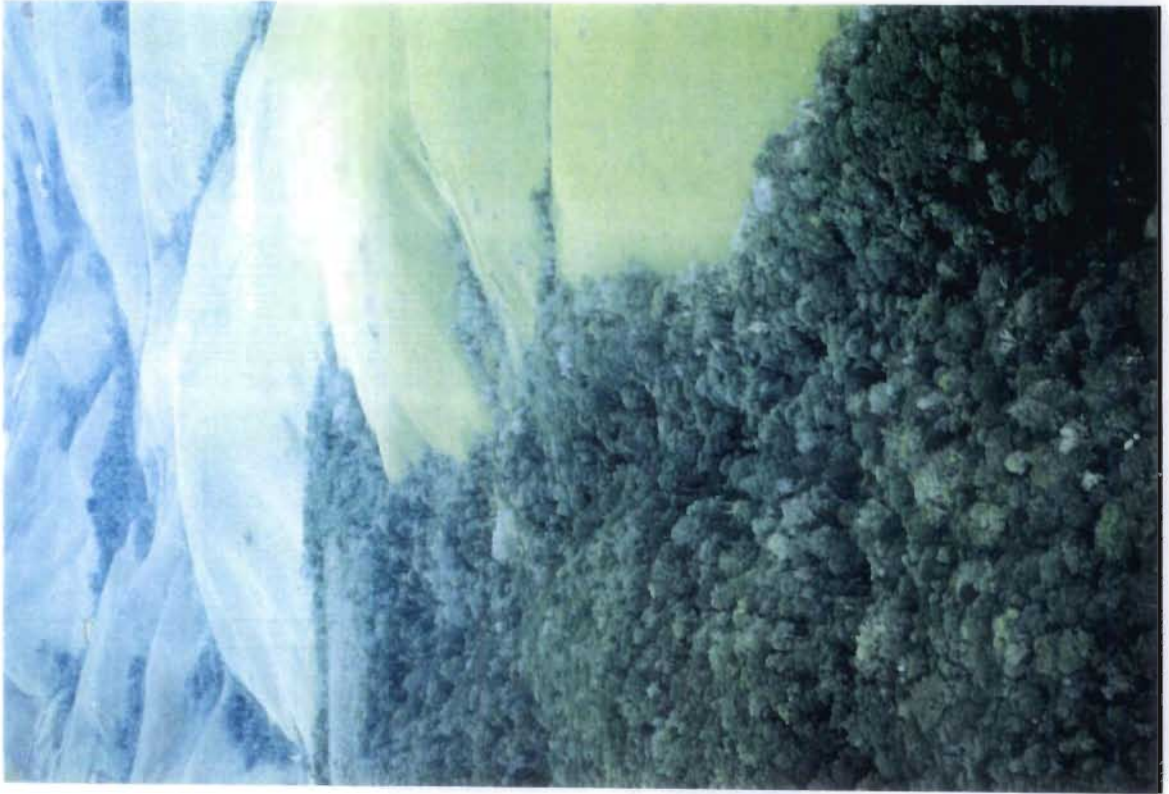
(Above) Swidden agriculture, is the major source of deforestation in Madagascar, although it is less of a problem in the Ambohitantely Forest where soil fertility is poor and human population density low. (Photo taken in Anjanaharibe).

(Below) The field camp located at 1560 m asl at the edge of fragment A (136 ha) which accommodated three people: one researcher, an assistant researcher, and a camp assistant.





## Plate 11



(Above) The transition between the forest and the human induced savannah grassland is abrupt. In the control site (portion visible located at about 1500 m asl), the structure of the canopy of the forest is continuous with few breaks and rare emergent trees. (Below) Swidden cultivation (Analamazaotra, east central Madagascar) on steep slopes leads to heavy soil erosion which affects the quality of river systems.





## Plate 12



(Above) Uncontrolled fires which spread across the savannah grassland frequently damage portions of the forest (fragment F located at 1450 m asl), leading to a significant reduction in fragment size. The damage is particularly noticeable on the forest edge, where trees rarely recovered from burning. (Below) In the forest, landslides occur naturally during the rainy season, because of pliable soil structure and heavy rains.





## Plate 13



(Above) Control site (1250 ha)(portion visible located at 1460 m asl), fragment E (52 ha)(on the right) and F (28 ha)(on the left) are separated respectively from the control site by only 240 m (E) and 800 m (F). (Below) Fragment E, located at an average elevation of 1400 m asl, is the second largest fragment studied. The bird species composition is almost identical to the control site's.



## Plate 14



(Above) Fragment H (30 ha), located at an average elevation of 1425 m asl, is the third largest fragment studied, and one edge is distant from the control site of 400 m. (Below) Sampling within the control site (1250 ha) (portion visible located at 1525 m asl) was conducted along four different transect lines (three of 400 m and one of 600 m) selected to include most of the micro-habitats found in the Ambohitantely Forest.





## 12. REFERENCES

- ALBIGNAC, R. 1970. Mammifères et oiseaux du massif du Tsaratanana. *Mémoire ORSTOM* 37:223-229.
- ANDRIANJAKA, M. 1994. Phénologie et germination des espèces de la forêt d'Ambohitantely (Hauts-Plateaux Malgaches). *Mémoire D.E.A., Option Ecologie. E.S.S.A.-Forêts, Université d'Antananarivo. Antananarivo.*
- ANON. 1990. Listes des espèces autochtones avec code E.S.S.A.-Forêts. Antananarivo.
- ANON. 1991. *Régions et développement, programmes régionaux et projets locaux. Faritany : Antananarivo, études régionales.* République Démocratique de Madagascar, Ministère de l'Economie et du Plan et Programme des Nations Unies pour le Développement, Projet PNUD/OPS MAG/89/018. Dirasset (Ed.), Tunis.
- BASTIAN, G. 1964. La forêt d'Ambohitantely, Madagascar. *Revue de Géographie, Madagascar* 5:1-42.
- BATTISTINI, R. 1963. Les Tampoketsa de la région centrale de Madagascar d'après Hottin. *Revue de Géographie, Madagascar* 2:95-101.
- BATTISTINI, R. 1972. Madagascar Relief and Main Types of Landscape. Pp. 1-25. In: *Biogeography and Ecology of Madagascar*, RICHARD-VINDARD, G. & BATTISTINI, R. (Eds). *Monographiae Biologicae*, Vol. 21. Junk, B. V. (Publ.). The Hague.
- BEGON M., HARPER, J. L. & TOWNSEND, C. R. 1986. *Ecology: Individuals, Populations and Communities.* Blackwell Scientific Publications. Oxford. 876 pp.
- BIERREGAARD, R. O. & LOVEJOY, T. E. 1989. Effects of Forest Fragmentation on Amazonian understory bird communities. *Acta Amazonica* 19:215-241.
- BIERREGAARD, R. O., LOVEJOY, T. E., KAPOV, V., DOS SANTOS, A. A. & HUTCHINGS, R. W. 1992. The biological dynamics of tropical rainforest fragments: A prospective comparison of fragments and continuous forest. *Bioscience* 11:859-866.
- BLAKE, J. G. 1991. Nested subsets and the distribution of birds in isolated woodlots. *Conservation Biology* 1:58-66.

- BLAKE, J. G. & KARR, J. R. 1984. Species Composition of Bird Communities and the Conservation Benefit of Large versus Small Forests. *Biological Conservation* 30:173-187.
- BLANKESPOOR, G. W. 1991. Slash-and-Burn Shifting Agriculture and Bird Communities in Liberia, West Africa. *Biological Conservation* 57:41-71.
- BLONDEL, J. 1985. Habitat Selection in Island versus Mainland Birds. Pp. 477-516. In: *Habitat Selection In Birds*, CODY, M. L. (Ed), Academic Press, Orlando.
- BLONDEL, J. 1991. Birds in biological isolates. Pp. 45-72. In: *Bird Population Studies, Relevance to conservation and management*. PERRINS, C. M., LEBRETON, J.-D & HIRONS, G. J. M. Oxford University Press, Oxford.
- BLONDEL, J., FERRY, C. & FROCHOT, B. 1970. La méthode des indices ponctuels d'abondance (I.P.A.) ou des relevés d'avifaune par "Stations d'écoute". *Alauda* 1:55-71.
- BROWER, J. E., ZAR, J. H. & VON ENDE, C. E. 1990. *Field and laboratory methods for general ecology*. Third Ed. Brown Publishers, Dubuque.
- BURKEY, T. V. 1988. Extinction in nature reserves: the effects of fragmentation and the importance of migration between reserve fragments. *Oikos* 55:75-81.
- BURNEY, D. A. 1987a. Late Holocene vegetational change in central Madagascar. *Quaternary Research* 28:130-143.
- BURNEY, D. A. 1987b. Late Quaternary stratigraphic charcoal records from Madagascar. *Quaternary Research* 28:274-280.
- BURNEY, D. A. 1987c. Pre-settlement vegetation changes at Lake Tritrivakely, Madagascar. *Palaeoecology of Africa* 18:357-381.
- BURNEY, D. A. 1988. Modern pollen spectra from Madagascar. *Palaeogeography, Palaeoclimatology, Palaeoecology* 66:63-75.
- CARLSON, A. 1986. A Comparison of Birds Inhabiting Pine Plantation and Indigenous Forest Patches in a Tropical Mountain Area. *Biological Conservation* 35:195-204.
- COFFIN, M. F. & RABINOWITZ P. D. 1987. Reconstruction of Madagascar and Africa: Evidence from the Davie fracture zone and western Somali basin. *J. Geophys. Res.* 92(B9):9385-9406.

- CONNOR, E. F. & MCCOY, E. D. 1979. The statistics and biology of the species-area relationship. *American Naturalist* 113:791-833.
- DECARY, R. 1950. La faune malgache, son rôle dans les croyances et les usages indigènes. Payot (Ed.), Paris.
- DEWAR, R. E. 1984. Recent extinctions in Madagascar: the loss of the subfossil fauna. Pp. 574-593. MARTIN, P. S. & KLEIN, R. G. (Eds): *Quaternary Extinctions*, University of Arizona Press, Tucson.
- DIAMOND, J. M. 1975. The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation* 7:129-146.
- DIAMOND, J. M. 1984. "Normal" extinctions of isolated populations. Pp 192-246. In *Extinctions*, NITECKI, M. H. (Ed). The University of Chicago Press. Chicago.
- DIAMOND, J. M., BISHOP, D. K. & VAN BALEN, S. 1987. Bird survival in an isolated Javan woodland : island or mirror? *Conservation Biology* 2:132-142.
- DONQUE, G. 1972. The climatology of Madagascar. Pp. 87-144. In: *Biogeography and Ecology of Madagascar*, RICHARD-VINDARD, G. & BATTISTINI, R. (Eds). *Monographiae Biologicae*, Vol. 21. Junk, B. V. (Publ). The Hague.
- DOWSETT-LEMAIRE, F. & DOWSETT, R. J. 1984. The effects of forest size on montane bird populations. Pp. 237-248. *Proceedings of the Fifth Pan-African Ornithological Congress*, LEDGER, J. (Ed), Johannesburg.
- EVANS, M. I., DUCKWORTH, J. W., HAWKINS, A. F. A., SAFFORD, R. J., SHELDON, B. C. & WILKINSON, R. J. 1992. Key bird species of Marojejy Strict Nature Reserve, Madagascar. *Bird Cons. Int.* 2:201-220.
- FRY, H.G., KEITH, S. & URBAN E. K. 1988. *The birds of Africa* Vol. III. p 99 . Academic Press, London.
- GALLI, A. E., LECK, C. F. & FORMAN, R. T. T. 1976. Avian distribution patterns in forest islands of different sizes in Central New Jersey. *The Auk* 93:356-364.
- GIBBS, J. P. & FAABORG, J. 1990. Estimating the viability of Ovenbird and Kentucky Warbler populations in forest fragments. *Conservation Biology* 2:193-196.
- GOODMAN, S. M. 1993. A reconnaissance of Ile Sainte Marie, Madagascar: the status of the forest, avifauna, lemurs and

- fruit bats. *Biological Conservation* 65:205-212.
- GOODMAN, S. M. 1994. Description of a new species of subfossil eagle from Madagascar: *Stephanoaetus* (Aves: Falconiformes) from deposits of Ampasambazimba. *Proc. Biol. Soc. Wash.* 107(3):421-426.
- GOODMAN, S. M. & RAVOAVY. 1993. Identification of bird subfossils from cave surface deposits at Anjohibe, Madagascar, with description of a new giant *Coua* (Cuculidae: Couinae). *Proc. Biol. Soc. Wash.* 106:24-33.
- GOODMAN, S. M., CREIGHTON, G. K. & RAXWORTHY, C. J. 1991. The food habits of the Madagascar Long-eared Owl *Asio madagascariensis* in southeastern Madagascar. *Bonn zool. Beitr.* 42:21-26.
- GOODMAN, S. M., LANGRAND, O. & RAXWORTHY, C. J. 1993. Food habits of the Madagascar Long-eared Owl *Asio madagascariensis* in two habitats southern Madagascar. *Ostrich* 64:79-85.
- GOODMAN, S. M. & RAKOTOZAFY L. M. A. 1995. Evidence for the existence of two species of *Aquila* on Madagascar during the quaternary. *Geobios.*
- GOODMAN, S. M. & PUTNAM, M. In prep. The birds of the eastern slopes of RNI d'Andringitra. In: *A faunal and floral inventory of the RNI d'Andringitra*. GOODMAN, S. M. (Ed). *Fieldiana*.
- GOODMAN, S.M., GANZHORN, J.U. & WILME, L. In prep. Observations at a *Ficus* tree in Malagasy humid forest: Why are there so few frugivores on Madagascar?.
- GOODMAN, S. M., LANGRAND, O. & WHITNEY, B. (a). In prep. A new genus and species of passerine from the eastern rainforest of Madagascar. *Ibis*.
- GOODMAN, S. M., PIDGEON, M. & SCHULENBERG, T. S. (b). In prep. Birds of southeastern Madagascar. *Fieldiana*.
- GREEN, G. M. & SUSSMAN, R. W. 1990. Deforestation history of the eastern rain forests of Madagascar from satellite images. *Science* 248:212-215.
- HAMEL, P. B., SMITH, W. P. & WAHL, J. W. 1993. Wintering bird populations of fragmented forest habitat in the Central Basin, Tennessee. *Biological Conservation* 66:107-115.
- HARRIS, L. D. 1988. Edge effects and conservation of biotic diversity. *Conservation Biology* 4:330-332.



- HUMBERT, H. 1927. Destruction d'une flore insulaire par le feu: principaux aspects de la végétation de Madagascar. *Mémoires de l'Académie Malgache* 5:1-80.
- HUMBERT, H. 1949. La dégradation des sols à Madagascar. *Mémoires de l'Institut des Sciences de Madagascar* 1:33-52.
- HUMBERT, H. 1955. Les territoires phytogéographiques de Madagascar: leur cartographie. *Ann. Biol.* 31:439-448.
- JOHNS, A. D. 1991. Responses of Amazonian rain forest birds to habitat modification. *Journal of Tropical Ecology* 7:417-437.
- KARR, J. R. 1981a. Surveying birds in the tropics. *Studies in Avian Biology* 6:548-553.
- KARR, J. R. 1981b. Surveying birds with mist nets. *Studies in Avian Biology* 6:62-67.
- KARR, J. R. 1982. Population variability and extinction in the avifauna of a tropical land bridge island. *Ecology* 6:1975-1978.
- KARR, J. R. 1990. Avian survival rates and the extinction process on Barro Colorado Island, Panama. *Conservation Biology* 4:391-397.
- KATTAN, G. H. 1992. Rarity and vulnerability: The birds of the Cordillera Central of Colombia. *Conservation Biology* 1:64-70.
- LAMBERTON, C. 1930. Contribution à l'étude anatomique des Aepyornis. *Bull. Acad. Malgache* 13:151-174.
- LAMBERTON, C. 1934. Contribution à la connaissance de la faune de Madagascar. Lémuriens et Ratites, *Mémoire de l'Académie Malgache* 17:1-168.
- LANGRAND, O. 1990. Guide to the birds of Madagascar. Yale University Press, New Haven and London. 364 pp.
- LANGRAND, O. & LENORMAND, B. 1985. Présentation sommaire du Parc National de la Montagne d'Ambre. Pp. 260-264. In: *L'équilibre des écosystèmes forestiers à Madagascar: Actes d'un séminaire international*. RAKOTOVAO, L., BARRE, V. & SAYER, J. (Eds.). I.U.C.N., Gland & Cambridge.
- LANGRAND, O. & SINCLAIR, J. C. 1994. Additions and supplements to the Madagascar avifauna. *Ostrich* 3:(in press).

- LANGRAND, O. & GOODMAN, S. M. (in press). Monitoring Madagascar's ecosystems: a look at the past, present, and future of its wetlands. Second International Conference on Science and the Management of Protected Areas (1994), Halifax.
- LANGRAND, O., NICOLL, M. E. & POST J. 1988. Synthèse sur le maintien de la biodiversité. Pp. 1-23. In: *Madagascar Plan d'Action Environnemental*, Vol. 2 *Synthèses spécifiques et recommandations*. Banque Mondiale, Washington.
- LE BOURDIEC, F., BATTISTINI, R. & LE BOURDIEC, P. 1969. *Atlas de Madagascar*. Bureau pour le Développement de la Production Agricole. 60 Planches. Tananarive.
- LEOPOLD, A. 1933. *Game Management*. Charles Scriber and Sons. New York 481 pp.
- LOISELLE, B. A. & BLAKE, J. G. 1992. Population variation in a tropical bird community. *BioScience* 11:838-845.
- LOVEJOY, T. E., RANKIN, J. M., BIERREGAARD, R. O., BROWN, K. S., EMMONS, L. H. & VAN DER VOORT, M. E. 1984. Ecosystem decay of Amazon forest remnants. Pp. 296-325. In: *Extinctions*, Nitecki, M. H. (Ed) The University of Chicago Press. Chicago & London.
- LOVEJOY, T. E., BIERREGAARD, R. O., RYLANDS, A. B., MALCOLM J. R., QUINTELA, C. E., HARPER, L. H., BROWN, K. S., POWELL, A. H., POWELL, G. V. N., SCHUBART, H. O. R. & HAYS, M. B. 1986. Edge and other effects of isolation on Amazon forest fragments. Pp 257-285. In: *Conservation Biology, the Science of Scarcity and Diversity*. SOULE, M. E. (Ed.). Sunderland.
- MABBERLEY, D. J. 1989. *The plant book, a portable dictionary of the higher plants*. Cambridge University Press. Cambridge. 706 pp.
- MACARTHUR, R. H., DIAMOND, J. M. & KARR, J. R. 1972. Density compensation in island faunas. *Ecology, all forms of life in relation to environment* 2:330-342.
- MACARTHUR, R. H. & WILSON, E. O. 1967. *The theory of island biogeography*. Princeton University Press. Princeton.
- MACPHEE, R. D. E., BURNEY, D. A. & WELLS, N. A. 1985. Early Holocene chronology and environment of Ampasambazimba, a Malagasy subfossil lemur site. *International Journal of Primatology* 6(5):461-487.



- MACPHEE, R. D. E. & 1986. Environment, extinction, and Holocene vertebrate localities in southern Madagascar. *National Geographic Research* 2:441-455.
- MACPHEE, R. D. E. & BURNEY D. A. 1991. Dating of modified femora of extinct dwarf *Hippopotamus* from southern Madagascar: Implication for constraining human colonization and vertebrate extinction events. *Journal of Archaeological Science* 18:695-706.
- MILNE EDWARDS, A. & GRANDIDIER, A. 1895. Sur des ossements d'oiseaux provenant des terrains récents de Madagascar. *Bull. Mus. Nat. d'Hist. Naturelle*.
- MILON, P. 1951. Etude d'une petite collection d'oiseaux du Tsaratanana. *Naturaliste Malgache* 3:167-183.
- MYERS, N. 1986. Tropical deforestation and a mega-extinction spasm. Pp. 394-409. In: *Conservation Biology: the Science of Scarcity and Diversity*. SOULE, M. E. (Ed). Sunderland.
- MYERS, N. 1993. Questions of mass extinction. *Biodiversity and Conservation* 1:2-17.
- NEWMARK, W. D. 1991. Tropical Forest Fragmentation and the Local Extinction of Understorey Birds in the Eastern Usambara Mountains, Tanzania. *Conservation Biology* 1:67-78.
- NEWMARK, W. D. 1993. The Role and Design of Wildlife Corridors with Examples from Tanzania. *Ambio* 8:500-504.
- NICOLL, M. E. & LANGRAND, O. 1989. Madagascar : *Revue de la conservation et des aires protégées*. World Wildlife Fund. Gland. XVII + 374 pp.
- PATTERSON, B. D. 1987. The principle of nested subsets and its implications for biological conservation. *Conservation Biology* 1:323-324.
- NOSS, R. F. 1987. Corridors in real landscapes: a reply to Simberloff and Cox. *Conservation Biology* 2:159-164.
- PATTERSON, B. D. 1990. On the temporal development of nested subset patterns of species composition. *Oikos* 59:330-342.
- PATTERSON, B. D. & ATMAR, W. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biological Journal of the Linnean Society* 28:65-82.
- PATTERSON, B. D. & BROWN, J. H. 1991. Regionally nested patterns of species composition in granivorous rodent assemblages. *Journal of Biogeography* 18:395-402.

- PERRIER DE LA BATHIE, H. 1921. La végétation malgache. *Annales du Musée Colonial de Marseille* 9:1-266.
- PERRIER DE LA BATHIE, H. 1936. Biogéographie des plantes de Madagascar. Société d'Éditions Géographiques, Maritimes et Coloniales, Paris.
- RADIMBISON, M. A. & ROGER, E. 1986. Approche sur l'étude du dynamisme des lisières de la forêt d'Ambohitantely. *Recherches pour le Développement, Série Sciences Biologiques* 4:217-226.
- RAJOELISON, G. 1990. Analyse sylvicole d'une forêt naturelle des Hauts-Plateaux malgaches. Cas du Jardin Botanique d'Ambohitantely (Tampoketsa d'Ankazobe). Mémoire de D.E.A./E.S.S.Sciences, Université d'Antananarivo.
- RAJOELISON, G., BLASER, J. & CHOLLET, M. 1992. Comportement sylvicole de quelques essences d'intérêt économique dans la forêt dense humide de montagne d'Ambohitantely (Tampoketsa d'Ankazobe). *Akon'ny Ala* 9:2-17.
- RAKOTONDRAINIBE, F. 1989. Contribution à la connaissance de la flore ptéridologique de Madagascar, étude floristique, biologique, phytogéographique et écologique des fougères de la forêt d'Ambohitantely (forêt tropicale d'altitude). Thèse de Docteur en Science, Université des Sciences et Techniques de Lille, Flandres, Artois.
- RAKOTONDRAINIBE, F., JEANNODA, V. H. & RADIMBISON, M. A. 1988. La forêt d'Ambohitantely, résultats d'études préliminaires. Pp. 144-154. In: *L'équilibre des écosystèmes forestiers à Madagascar: Actes d'un séminaire international*. RAKOTOVAO, L., BARRE, V. & SAYER, J. (Eds). I.U.C.N., Gland & Cambridge.
- RAKOTOZAFY, L. M. A. 1993. Etude sur des Anatidae subfossiles et leur paléoenvironnement dans les Hauts-Plateaux malgaches. Mémoire de D.E.A., Option Paléontologie des Vertébrés. Université d'Antananarivo, Madagascar.
- RALPH, J. C. 1981. Terminology used in estimating numbers of birds. Appendix I. *Studies in Avian Biology* 6:577-578.
- RAND, A. L. 1936. The distribution and habits of Madagascar birds. *Bull. Amer. Mus. Nat. Hist.* 72:143-499.
- RAVEN, P. H. 1980. Research Priorities in Tropical Biology. National Research Council, Washington.

- RAZAKANIRINA, D. 1993. Le Jardin Botanique de la Réserve Spéciale d'Ambohitantely. *Akon'ny Ala*, 11:50-52.
- RAZAKANIRINA, D. & ANDRIANJAKA, M. 1993. Les résultats des observations phénologiques dans la forêt d'Ambohitantely. *Akon'ny Ala* 11:19-31.
- REID, W. V. & MILLER, K. R. 1989. *Keeping options alive: the scientific basis for conservation biology*. World Resources Institute, Washington.
- RIQUIER, J. 1951. Les sols du tampoketsa d'Ankazobe. *Mémoire de l'Institut Scientifique de Madagascar* 1:113-126.
- SAFFORD, R. J. & DUCKWORTH, J. W. 1990. A wildlife survey of Marojejy Nature Reserve, Madagascar. Report of the Cambridge Madagascar Rainforest Expedition 1988. International Council for Bird preservation Study Report N°40, 172 pp.
- SAUNDERS, D. A., HOBBS, R. J. & MARGULES, C. R. 1991. Biological consequences of ecosystem fragmentation: A review. *Conservation Biology* 5:18-32.
- SAYER, J. A., HARCOURT, C. S. & COLLINS, N. M. 1992. The Conservation Atlas of Tropical Forest. Africa. I.U.C.N., Gland.
- SEGUIER-GUIS, M. 1988. Contribution à l'inventaire des vertébrés de la forêt d'Ambohitantely (Tampoketsa d'Ankazobe), Mémoire de D.E.A. de Sciences Biologiques Appliquées, option Ecologie, Université de Madagascar.
- SIMBERLOFF, D. S. 1992. Do species-area curves predict extinction in fragmented forest? *In: Tropical deforestation and species extinction*. WHITMORE, T. C. & SAYER, J. A. (Eds). Chapman & Hall, London.
- SIMBERLOFF, D. S. & ABELE, L. G. 1975. Island biogeography theory and conservation practise. *Science* 191:285-286.
- SIMBERLOFF, D. S. & COX, J. 1987. Consequences and costs of conservation corridors. *Conservation Biology* 1:63-71.
- STEPHENSON, P. J., RANDRIAMAHAZO, H., RAKOTOARISON, N. & RACEY, P. A. 1994. Conservation of mammalian species diversity in Ambohitantely Special Reserve, Madagascar. *Biological Conservation* 69:213-218.
- THIOLLAY, J. M. 1992. Influence of selective logging on bird species diversity in a Guianan rain forest. *Conservation Biology* 1:47-63.

- THIOLLAY, J. M. 1993. Response of a raptor community to shrinking area and degradation of tropical rain forest in the south western Ghâts (India). *Ecography* 16:97-110.
- THIOLLAY, J. M. & MEYBURG, B. U. 1988. Forest fragmentation and the conservation of raptors: a survey on the island of Java. *Biological Conservation* 44:229-250.
- THOMPSON, P. & EVANS M. I. 1991. *A survey of Ambatovaky Special Reserve Madagascar*. Madagascar Environmental Research Group, London.
- WHITE, F. 1983. The vegetation of Africa. A descriptive memoir to accompany the UNESCO/AETFAT/UNSO Vegetation Map of Africa. *Natural Resources Research* 20, 356 pp. UNESCO, Paris.
- WILLIS, E. O. 1979. The composition of avian communities in luminescent woodlots in southern Brazil. *Papéis Avulsos de Zoologia* 33:1-25.
- WILMÉ, L. In press. Composition and characteristics of bird communities in Madagascar. *Biogeographica*.

## Appendix 1: CALCULATION OF MARTONNE ARIDITY INDEX

$$I = (A1 + A2) / 2$$

$$A1 = P1 / (T1 + 10)$$

$$A2 = P2 / (T2 + 10)$$

P1= mean of annual rainfall

T1= mean of annual temperature

P2= rainfall of the driest month

T2= temperature of the driest month

$$A1 = 1823 / (16.5 + 10)$$

$$A2 = 13.7 / (14.1 + 10)$$

$$I = 34.7$$



## APPENDIX 2:

MIST NETTING FORM / FOREST FRAGMENTATION STUDY / OLIVIER LANGRAND  
AMBOHITANTELY SPECIAL RESERVE

[illegible]

# TAXONOMIST LIST OF SCIENTIFIC, FRENCH, ENGLISH AND GERMAN NAMES

## OF BIRD SPECIES FOUND IN THE

### SPECIAL RESERVE OF AMBOHITANTELY, MADAGASCAR

Olivier Langrand  
WWF BP 738 Antananarivo (101) Madagascar



Legend  
FOR : Forest  
PLA : Tree plantation  
WET : Wetland  
SAV : Savannah grassland

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Sp nb	Ref. GUIDE	Habitat	Obs.	Scientific	French	English	German
1	37	WET		<i>Scopus umbretta</i>	Ombrette	Hamerkop	Hammerkopf
2	42 *	FOR		<i>Lophotibis cristata</i>	Ibis huppé de Madagascar	Madagascar Crested Ibis	Schopfibis
3	51 *	WET		<i>Anas melleri</i>	Canard de Meller	Meller's Duck	Madagaskarente
4	56 *	FOR		<i>Aviceda madagascariensis</i>	Baza malgache	Madagascar Cuckoo-Falcon	Lemurenweihe
5	57	FOR		<i>Machaeramphus alcinus</i>	Milan des Chauves-Souris	Bat Hawk	Fledermausaar
6	58	FOR/PLA		<i>Milvus migrans</i>	Milan noir	Black Kite	Schwarzmilan
7	61 *	FOR		<i>Polyboroides radiatus</i>	Polyboroide rayé	Madagascar Harrier-Hawk	Höhlenweihe
8	62 (*)	SAV		<i>Circus maillardi</i>	Busard de Maillard	Réunion Harrier	Réunionweihe
9	63 *	FOR		<i>Accipiter henstii</i>	Autour de Henst	Henst's Goshawk	Madagaskarhabicht
10	64 *	FOR		<i>Accipiter madagascariensis</i>	Epervier de Madagascar	Madagascar Sparrowhawk	Madagaskarsperber
11	65 (*)	FOR		<i>Accipiter francesii</i>	Epervier de Frances	Frances's Sparrowhawk	Echsenhabicht
12	66 *	FOR		<i>Buteo brachypterus</i>	Buse de Madagascar	Madagascar Buzzard	Madagaskar-Bussard
13	67 (*)	SAV		<i>Falco newtoni</i>	Faucon de Newton	Madagascar Kestrel	Malegassenturmfalke
14	68 *	FOR		<i>Falco zoniventris</i>	Faucon à ventre rayé	Banded Kestrel	Bindenfalke
15	69 nb	FOR		<i>Falco eleonorae</i>	Faucon d'Eléonore	Eleonora's Falcon	Eleonorenfalke
16	70 nb	FOR		<i>Falco concolor</i>	Faucon concolore	Sooty Falcon	Schieferfalke
17	71	FOR/SAV		<i>Falco peregrinus</i>	Faucon pèlerin	Peregrine Falcon	Wanderfalke
18	72 *	SAV		<i>Margaroperdix madagascarensis</i>	Caille de Madagascar	Madagascar Partridge	Perlwachtel
19	75	FOR/PLA		<i>Numida mitrata</i>	Pintade mitrée	Helmeted Guineafowl	Helmpertlhuhn

## SPECIAL RESERVE OF AMBOHITANTELY, MADAGASCAR

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Sp nb	Ref. GUIDE	Habitat	Obs	Scientific	French	English	German
20	79 *	FOR/PLA/SAV		<i>Turnix nigricollis</i>	Turnix de Madagascar	Madagascar Buttonquail	Schwarzkügel-Laufhühnchen
21	81 (*)	WET		<i>Dryolimnas cuvieri</i>	Râle de Cuvier	White-throated Rail	Cuvier-Ralle
22	85	SAV		<i>Sarothrura insularis</i>	Râle insulaire	Madagascar Flufftail	Hovaralle
23	96 *	WET		<i>Glaucopis ocellata</i>	Glaréole malgache	Madagascar Pratincole	Madagaskarbrachschwalbe
24	114 nb	WET		<i>Actitis hypoleucos</i>	Chevalier guignette	Common Sandpiper	Flussuferläufer
25	142 (*)	FOR/PLA		<i>Streptopelia picturata</i>	Tourterelle peinte	Malagasy Turtledove	Madagaskarturteltaub
26	144 (*)	FOR		<i>Treron australis</i>	Pigeon vert de Madagascar	Madagascar Green Pigeon	Madagaskar-Grüntaube
27	145 *	FOR		<i>Alectroenas madagascariensis</i>	Pigeon bleu de Madagascar	Madagascar Blue Pigeon	Madagaskar-Blautaube
28	147 (*)	FOR		<i>Coracopsis nigra</i>	Petit Perroquet noir	Lesser Vasa Parrot	Rabenpapagei
29	150 *	FOR/PLA		<i>Cuculus rochii</i>	Coucou de Madagascar	Madagascar Lesser Cuckoo	Madagaskar-Gackelkuckuck
30	161 (*)	FOR/PLA		<i>Centropus toulou</i>	Coucal malgache	Madagascar Coucal	Tulukuckuck
31	163	SAV/PLA		<i>Tyto alba</i>	Chouette effraie	Common Barn Owl	Schleiereule
32	164 (*)	FOR		<i>Otus rutilus</i>	Petit duc de Madagascar	Malagasy Scops-Owl	Inseleule
33	166 *	FOR		<i>Asio madagascariensis</i>	Hibou de Madagascar	Madagascar Long-eared Owl	Streifenohreule
34	168 (*)	SAV/PLA		<i>Caprimulgus madagascariensis</i>	Engoulevent de Madagascar	Madagascar Nightjar	Madagaskar-Nachtschwalbe
35	171 (*)	FOR		<i>Zoonavena grandidieri</i>	Martinet de Grandidier	Malagasy Spine-tailed Swift	Malagassensegler
36	173	FOR/SAV		<i>Apus melba</i>	Martinet à ventre blanc	Alpine Swift	Alpensegler
37	174	FOR/SAV		<i>Apus barbatus</i>	Martinet noir africain	African Black Swift	Kapsegler
38	175 (*)	WET		<i>Corythornis vintsioides</i>	Martin-pêcheur malachite	Malagasy Kingfisher	Schwarzschnabel-Zwergfischer
39	176 *	FOR		<i>Ispidina madagascariensis</i>	Martin-chasseur malgache	Madagascar Pigmy Kingfisher	Madagaskar-Zwergfischer

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Sp nb	Ref. GUIDE	Habitat	Obs.	Scientific	French	English	German
40	177	FOR/PLA		<i>Merops superciliosus</i>	Guêpier de Madagascar	Madagascar Bee-eater	Blauwangenspin
41	178	FOR		<i>Eurystomus glaucurus</i>	Rollier malgache	Broad-billed Roller	Zimtröller
42	181 *	FOR		<i>Atelornis pittoides</i>	Rollier terrestre pittoïde	Pitta-like Ground-Roller	Blaukopferdracke
43	184 (*)	FOR		<i>Leptosomus discolor</i>	Courol	Cuckoo-Roller	Kurol
44	185	PLA/SAV		<i>Upupa epops</i>	Huppe fasciée	Hoopoe	Wiedehopf
45	190 *	SAV		<i>Mirafrapa hova</i>	Alouette malgache	Madagascar Bush Lark	Hovalerche
46	191	FOR/SAV		<i>Riparia paludicola</i>	Hirondelle paludicole	Brown-throated Sand Martin	Braunkehl-Uferschwalbe
47	193 (*)	FOR/SAV		<i>Phedina borbonica</i>	Hirondelle des Mascareignes	Mascarene Martin	Maskarenen-Schwalbe
48	195 *	PLA/WET		<i>Motacilla flaviventris</i>	Bergeronnette malgache	Madagascar Wagtail	Madagaskarstelze
49	196 (*)	FOR		<i>Coracina cinerea</i>	Echenilleur malgache	Ashy Cuckoo-Shrike	Madagaskarraupenfänger
50	197 *	FOR		<i>Phyllastrephus madagascariensis</i>	Bulbul de Madagascar	Long-billed Greenbul	Gmelinbülbul
51	202	FOR/PLA		<i>Hypsipetes madagascariensis</i>	Bulbul noir	Madagascar Bulbul	Madagaskarfluchtvogel
52	203 *	FOR		<i>Copsychus albospectus</i>	Dyal malgache	Madagascar Magpie-Robin	Malegassendajal
53	204	SAV		<i>Saxicola torquata</i>	Traquet pâtre	Stonechat	Schwarzkehlchen
54	205 *	FOR		<i>Pseudocossyphus sharpei</i>	Merle de roche de forêt	Forest Rock-Thrush	Laubrötel
55	209 (*)	FOR		<i>Nesillas typica</i>	Fauvette de Madagascar	Madagascar Brush-Warbler	Madagaskarbuschsänger
56	*	FOR		<i>Cryptosylvicola randrianasoloi</i>	Fauvette de Georges	Georges' Warbler	Georges-Baumsänger
57	211 (*)	SAV		<i>Cisticola cherina</i>	Cisticole de Madagascar	Madagascar Cisticola	Madagaskarcistensänger
58	215 *	FOR		<i>Newtonia amphichroa</i>	Newtonie sombre	Dark Newtonia	Olivbauch-Newtonie
59	216 *	FOR		<i>Newtonia brunneicauda</i>	Newtonie commune	Common Newtonia	Rostbauch-Newtonie

## SPECIAL RESERVE OF AMBOHITANTELY, MADAGASCAR

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Sp nb	Ref. GUIDE	Habitat	Obs.	Scientific	French	English	German
60	224 (*)	FOR/PLA		<i>Terpsiphone mutata</i>	Gobe-mouche de paradis de Madagascar	Madagascar Paradise Flycatcher	Rotbrust-Paradiesschnäppe
61	228 (*)	FOR/PLA		<i>Nectarinia souimanga</i>	Souimanga malgache	Souimanga Sunbird	Malegassennektarvogel
62	229 (*)	FOR/PLA		<i>Nectarinia notata</i>	Souimanga angaladian	Long-billed Green Sunbird	Stahlnektarvogel
63	230 (*)	FOR/PLA		<i>Zosterops maderaspatana</i>	Zosterops malgache	Madagascar White-Eye	Madagaskarbrillenvogel
64	232 *	FOR		<i>Calicalicus madagascariensis</i>	Vanga à queue rousse	Red-tailed Vanga	Rotschwanzvanga
65	241 *	FOR		<i>Cyanolanius madagascarinus</i>	Artamie azurée	Blue Vanga	Blauvanga
66	245 *	FOR		<i>Tylas eduardi</i>	Tylas	Tylas Vanga	Bülbülvanga
67	246 (*)	FOR/PLA		<i>Dicrurus forficatus</i>	Drongo malgache	Crested Drongo	Gabeldrongo
68	247	SAV/PLA		<i>Corvus albus</i>	Corbeau pie	Pied Crow	Schildrabe
69	248 *	FOR		<i>Hartlaubius auratus</i>	Etourneau de Madagascar	Madagascar Starling	Madagaskarstar
70	253 *	FOR/PLA		<i>Foudia madagascariensis</i>	Foudi de Madagascar	Madagascar Red Fody	Madagaskarweber
71	254 *	FOR		<i>Foudia omissa</i>	Foudi de forêt	Forest Fody	Tamataveweber
72	255 *	FOR/PLA		<i>Lonchura nana</i>	Mannikin de Madagascar	Madagascar Mannikin	Zwergelsterchen

## Summary :

72 species recorded in the Special Reserve of Ambohitantely  
 31 endemic to Madagascar \* : 43 %  
 22 endemic to Malagasy region (\*) : 30,5 %  
 3 non breeding species <sup>nb</sup> : 4,2 %  
 69 breeding species : 95,8 %

Ref. GUIDE : Langrand, O. 1990. Guide to the Birds of Madagascar. Yale University Press. New Haven & London.