Habitat Requirements and Foraging Ecology of the Madagascar Fish-Eagle

by

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(ABSTRACT)

With a population estimate of 99 pairs, the Madagascar fish-eagle (*Haliaeetus vociferoides*) is one of the rarest birds of prey in the world. I investigated the ecological requirements of the Madagascar fish-eagle in 1994 and 1995 to help determine management action to prevent its extinction. I investigated fish-eagle foraging ecology in 1996 to determine its prey preference and whether fish abundance and availability affect fish-eagle foraging rates and foraging success.

Madagascar fish-eagle nest and perch trees were taller, broader, had more unobstructed branches, and had a greater arc of accessibility than unused trees. Perch trees also were deciduous more often and had a narrower growth form than unused trees. Nest sites had more shoreline perch trees than unused sites. Lakes occupied by fish-eagles were deeper and clearer, and had more shoreline perch trees, more fish, a greater total fish weight, and more fish species than unoccupied lakes.

I developed logistic regression models to predict the probability of Madagascar fish-eagle use based on the measured habitat variables. Nest and perch tree models included tree height. The nest site model included number of shoreline perches. Lake models included number of shoreline perches and either number of fish, total fish weight, or number of fish species. These models can be used to predict fish-eagle habitat use with > 70% accuracy.

Introduced tilapia, *Oreochromis spp.* and *Tilapia spp.*, made up the majority of both the gill net (66.3%) and fish-eagle catch (64.7%) in similar proportion, which suggests that the fish-eagle is an opportunistic predator. Replacement of native fish species by exotics, thus, probably has not been detrimental to the island's fish-eagle population. Male fish-eagle foraging success was positively correlated with number of fish, total fish weight, and number of fish species, which suggests that declines in the fish population could adversely affect the fish-eagle population.

The results of this study indicate that Madagascar fish-eagles require bodies of water with large shoreline trees and an ample fish population. I recommend greater protection of aquatic habitats, monitoring and management of freshwater fish populations, and education of local people in sustainable tree harvesting practices.

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Table of Contents

List of Tables

List of Illustrations

INTRODUCTION

Madagascar Fish-eagle Status

The Madagascar fish-eagle (*Haliaeetus vociferoides*) is one of the rarest birds of prey in the world (Meyburg 1986). Reported as common along the west coast of Madagascar as recently as the 1920s (Rand 1936), the fish-eagle population has since declined and was considered to be critically endangered by the end of the 1970s (Collar and Stuart 1985). Langrand (1987) surveyed the northwest coast of Madagascar between 1978 and 1986 and located only 96 individuals, including 40 pairs and 10 single adults. Rabarisoa et al. (1997) conducted a more intensive survey between 1991 and 1995 and found at least 240 Madagascar fish-eagles, including 63 breeding pairs, 36 potential pairs, 24 single adults, and 18 immatures. They estimated the total breeding population to be 99 pairs assuming that every potential pair was breeding.

The Madagascar fish-eagle preys mostly on fish and is associated with lakes, rivers, mangrove swamps, and rocky offshore islands along Madagascar's west coast. Habitat degradation is a likely cause for its decline (Langrand 1987, Langrand and Goodman 1995). Deforestation has reduced the availability of trees for nesting and perching while conversion of wetlands for rice production and erosion-induced siltation have reduced prey abundance and availability. Persecution by humans through shooting, trapping, and destruction of nests and young is another threat even where suitable habitat remains (Langrand and Meyburg 1984).

The Madagascar fish-eagle exhibits most of the characteristics of species vulnerable to extinction (Pimm et al. 1988): narrow geographic range, small population size, low population density, large home range, large body size, and low rate of population increase. As deforestation, erosion, and wetland conversion continue in Madagascar, there is increasing urgency to determine the fish-eagle's habitat requirements and to identify areas that are critical to the survival of the species.

Habitat Degradation and Conservation in Madagascar

The flora and fauna of Madagascar are characterized by a high degree of endemism. Up to 85% of the island's plant species are endemic (Guillaumet 1984), and there are more than 400 endemic vertebrate species including all of the island’s primates, insectivores, rodents, and carnivores (Durell and Durell 1987). Madagascar has more chameleon, baobab, orchid, and palm species than has all of Africa. This endemism has resulted from the island’s long term isolation from other large landmasses. With an area of 587,044 km^2, it is the world’s fourth largest island and is believed to have separated from Africa during the Cretaceous Period between 100 and 180 million years ago (Paulian 1984).

Deforestation, erosion, and extinctions seriously threaten Madagascar’s unique and diverse flora and fauna. Prior to human settlement, natural habitats on the island included rain forests on the east coast and a patchwork of humid montane forests, dry deciduous forests, open woodlands, and grasslands in the central highlands and the west coast (Burney 1987). Although the extent of the original forest cover s is debatable, it is clear that the forests have declined dramatically since the arrival of the first human settlers from Indonesia roughly 1,500 years ago. Nelson and Horning (1993) estimated from satellite data that only 10.4% of Madagascar was forested in 1990. The primary causes of this deforestation are slash-and-burn subsistence cultivation, charcoal production for fuel, and the spread of fires to forests from adjacent grasslands that are burned to increase forage quality for cattle (Jolly and Jolly 1984). In the grasslands of the central highlands, Madagascar experiences some of the worst soil erosion in the world owing to a combination of factors including fragile soils, torrential rains, fires, and overgrazing (Wells 1995). Human activity probably has contributed to the extinction of at least 17 species over the past 1,000 years, including elephant birds, giant tortoises, giant lemurs, and a pygmy hippopotamus (Burney et al. 1987). There are species and populations currently threatened with extinction in all taxa that have been investigated (Mittermeier et al. 1987).

Concern over the plight of Madagascar’s flora and fauna has increased greatly among the international conservation community over the last decade (Kull 1996). Myers (1988) identified Madagascar's forests as one of the top 10 biodiversity conservation priorities of the world, and Mittermeier (1988) included the island among six megadiversity countries that should receive top priority for conservation. For the first decade following the country’s independence from France in 1960, the government of

Madagascar had a good conservation record with the passage of legislation to protect threatened species, limit pasture burning, and begin reforestation. Then, following a Marxist revolution between 1972 and 1975, the government began to favor rapid industrialization over environmental protection and excluded foreign researchers and conservationists. In 1980, a foreign debt crisis forced the government to seek aid from Western governments. Over the course of the 1980s, the government of Madagascar allied itself with the World Bank, the U.S. Agency for International Development, the World Wide Fund for Nature, Conservation International, and other non-governmental organizations to try to find ways to reduce environmental degradation (Jolly 1990). In 1988, Madagascar chartered an Environmental Action Plan (World Bank 1988) aimed at promoting conservation and sustainable development. This was followed by a great increase in foreign funding for conservation and a restructuring of governmental agencies responsible for the environment (Kull 1996).

Wetlands Conservation

The establishment of new protected areas is an important component of Madagascar’s Environmental Action Plan. Until now, the network of protected areas has favored the rain forests along the eastern coast because these areas hold the greatest numbers of endemic species (Nicoll and Langrand 1989). Madagascar’s wetlands also harbor a substantial number of endemic species. Many of these wetland endemics are threatened, including several species of freshwater fish (Reinthal and Stiassny 1991), the

Madagascan big-headed turtle (*Erymnochelys madagascariensis*) (Kuchling and Mittermeier 1993), the Bernier's teal (*Anas bernieri*), the Alaotra little grebe (*Tachybaptus rufolavatus*), the Madagascar pochard (*Aythya innotata*), and the Madagascar fish-eagle (Langrand and Wilmé 1993). Among the 18 avian species restricted to aquatic habitats (Langrand and Wilmé 1993), nine (50%) are classified as endangered, vulnerable, indeterminate, or insufficiently known (Collar and Stuart 1985).

The total area of Madagascar’s inland waters is roughly 500,000 ha (Davies and Burgis 1987). Much of the island’s wetlands have been converted for rice production, and the highest human population densities are near wetlands since rice is the dietary staple (Langrand and Goodman 1995). Despite these threats, Madagascar’s wetlands have received minimal protection. The nation currently has 39 protected areas, including 5 national parks, 11 strict nature reserves, and 23 special reserves, which cover 728,660 ha or 1.9% of the island’s surface area (Langrand and Goodman 1995). Only one of these areas, Tsimanampetsotsa, a 6,000 ha soda lake, is a wetland site (Langrand and Wilmé 1993).

The Madagascar fish-eagle is probably the most conspicuous and well-known of Madagascar’s endemic wetland birds. As top predators, raptors have large area requirements (Thiollay 1989). Identifying and protecting suitable fish-eagle habitat will benefit a host of other species that depend on wetland habitats in Madagascar. The Environmental Action Plan proposed increasing the number of protected areas to 50 by 1995, including some prominent wetland sites (Langrand and Goodman 1995), but this goal has not yet been achieved. This research will help to identify areas that are in greatest need of protection.

Objectives

Since 1991, The Peregrine Fund has been engaged in research intended to help prevent the extinction of the Madagascar fish-eagle and to lead to conservation of the wetland habitat shared by the eagle and other threatened and endangered species (Watson et al. 1993, Watson et al. 1996). This study was a continuation and expansion of that research and was a cooperative effort between The Peregrine Fund and the Department of Fisheries and Wildlife Sciences at Virginia Tech.

The goal of this research was to determine the ecological requirements of the Madagascar fish-eagle and to communicate this information in a manner that will facilitate its conservation. My objectives were as follows:

1) Determine characteristics of nest trees, nest sites, and perch trees used by Madagascar fish-eagles.
2) Develop predictive models to identify suitable fish-eagle nesting and perching habitat.
3) Determine habitat characteristics and prey availability of lakes used by fish-eagles.
4) Develop predictive models to identify lakes suitable for breeding fish-eagles based on shoreline characteristics, water quality, and prey availability.
5) Describe Madagascar fish-eagle diet and foraging behavior.

6) Determine fish-eagle prey preference.
7) Determine whether fish abundance and availability affect fish-eagle foraging rates and foraging success.

I will address objectives 1 and 2 in Chapter 1; objectives 3 and 4 in Chapter 2; and objectives 5, 6, and 7 in Chapter 3. The Conclusions and Management Implications section will refer to results from all three chapters.

CHAPTER 1: NEST TREE, NEST SITE, AND PERCH TREE USE

INTRODUCTION

The Madagascar fish-eagle is one of the world's most endangered raptors (Meyburg 1986). Large-scale deforestation probably has contributed to the eagle's decline (Langrand and Meyburg 1989). Nest site availability can limit the abundance and distribution of raptor populations (Newton 1979). The Madagascar fish-eagle uses tall trees near water as substrates for nests and foraging perches (Langrand and Meyburg 1989), but there have been no quantitative studies of its nesting or perching habitat.

The Madagascar fish-eagle is one of eight sea eagle species (genus *Haliaeetus*) worldwide. There is extensive information on the nesting and perching habitat requirements of its congeners the bald eagle (*H. leucocephalus*) (e. g. McEwan and Hirth 1979, Stalmaster and Newman 1979, Steenhof et al. 1980, Andrew and Mosher 1982, Anthony et al. 1982, Keister and Anthony 1983, Fraser et al. 1985a, Anthony and Isaacs 1989, Wood et al. 1989, Chester et al. 1990, Buehler et al. 1991, Fraser et al. 1991, Buehler et al. 1992, Chandler et al. 1995), the white-tailed sea eagle (*H. albicilla*) (Love 1983, Shiraki 1994), and the African fish-eagle (*H. vocifer*) (Brown 1980). The distribution and abundance of these eagles is limited in part by their need for large super-canopy trees for nesting and perching.

Knowledge of the factors limiting the Madagascar fish-eagle’s distribution and abundance is needed to determine what management action should be taken to prevent its extinction. The objectives of this study were to (1) determine characteristics of nest trees, nest sites, and perch trees used by Madagascar fish-eagles and (2) develop predictive models to identify suitable fish-eagle nesting and perching habitat.

METHODS

Study Area

I measured Madagascar fish-eagle nest and perch tree characteristics from 21 May to 14 August 1994. The study area was a roughly 3,000-km^2 area in the central portion of the west coast of Madagascar between 44°25' and 44°50'E, and 18°75' and 19°25'S (Fig. 1). This area includes the drainages of the Manambolo, Beboka, and Soahanina rivers west of the Bemaraha Plateau and east of the Mozambique Channel. I selected this area because it is known to support at least 27 resident pairs of eagles (Rabarisoa et al. 1997), as well as most of the remaining endangered Bernier's teals (*Anas bernieri*) (Safford 1993) and numerous other endemic water birds. The government of Madagascar acknowledged the importance of this area in 1988 by declaring it as one of 14 top priority areas for conservation. The greatest concentration of eagles within this area is on the three adjacent lakes Befotaka, Soamalipo, and Ankerika (19°1'S, 44°25'E), which support 10 resident pairs (Rabarisoa et al. 1997). The next nearest areas of suitable fish-eagle habitat are near Belo-sur-Tsiribihina (19°42'S, 44°33'E) to the south and Maintirano (18°05'S, 44°01'E) to the north.

The local topography consists of coastal plains and low rolling hills with elevations ranging from sea level to 126 m. Soils are shallow and sandy, and the vegetation is a patchwork of dry deciduous forest, savanna, wetlands, mangrove swamps, and rice paddies. The climate is sub-humid and tropical with a dry season from April to October and a wet season from November to March. Average annual rainfall ranges between 1,000 and 1,500 mm (Donque 1972).

Nest Tree Characteristics

I measured characteristics of 38 fish-eagle nest trees and 38 randomly selected trees to determine how characteristics of trees used by fish-eagles differed from average characteristics of large trees in the area. My sample included all nest trees within the study area known to have been used by fish-eagles from 1991 to 1994.

Most of the habitat variables that I measured were ones preferred by bald eagles (McEwan and Hirth 1979, Stalmaster and Newman 1979, Steenhof et al. 1980, Andrew and Mosher 1982, Anthony et al. 1982, Keister and Anthony 1983, Fraser et al. 1985a, Anthony and Isaacs 1989, Wood et al. 1989, Chester et al. 1990, Buehler et al. 1991, Fraser et al. 1991, Buehler et al. 1992, Chandler et al. 1995), white-tailed sea eagles (Love 1983, Shiraki 1994), or African fish-eagles (Brown 1980). I recorded the following characteristics of the nest or random trees: species, diameter-at-breast-height (dbh), height, number of unobstructed branches, arc of accessibility, growth form, and whether the tree was deciduous. I measured dbh to the nearest cm and used a clinometer to measure tree height to the nearest m. I counted branches in the tree canopy that I estimated to be > 5 cm in diameter and unobstructed for 1 m above and below. I recorded arc of accessibility as the total arc (0° to 360°) that was unobstructed by other trees for a distance of 10 m from the trunk and 3 m below the tree's crown (Buehler et al. 1992).

I classified growth form by adapting Keister and Anthony’s (1983) conifer growth form categories to fit the more widely branching growth forms typical of trees in Madagascar’s dry deciduous forests. I recorded growth form as large canopy, medium canopy, small canopy, dead top, or snag. I classified growth form as large, medium, or small canopy based on whether the lowest fork in the trunk was in the bottom third, middle third, or top third of the tree, respectively. If the top third of the crown was dead, I recorded growth form as dead top, and if the entire tree was dead and leafless I recorded it as a snag.

Nest Site Characteristics

I considered nest site characteristics to be those that related to the area surrounding each nest or random tree, rather than to the trees themselves. I measured distance to nearest water to the nearest m and estimated distance to nearest building, road, fish-eagle nest, and human disturbance to the nearest 10 m from maps and aerial photos.

Human disturbances included agricultural clearings, rice paddies, villages, tombs, and fishermen's camps. I recorded any permanent, year-round dwelling as a building but did not include temporary, seasonal shelters. There are no paved roads and very few motor vehicles in the study area, and even the most traveled roads may be traversed by less than one motor vehicle per day during the driest time of the year when roads are most passable (personal observation). The local people frequently use oxcarts to transport materials, so I recorded any route used by oxcarts as a road.

I counted the number of suitable perch trees within 50 m of the water along a 250-m shoreline transect centered at the nearest point on the shoreline to the nest tree or random tree as Chandler et al. (1995) did for bald eagles on the northern Chesapeake Bay. I considered lone trees and snags or emergent trees with stout branches high on the crown and unobstructed visibility over the water to be suitable perch trees. I recorded the length of shoreline within a 300-m radius of the tree. I used a 300-m radius because this is the approximate length of shoreline defended by nesting bald eagles (Bowman et al. 1993) and African fish-eagles (Brown 1980). Lastly, I assigned average surrounding canopy height to 5-m intervals (0-5 m, 5-10 m, etc.).

Perch Tree Characteristics

I watched each fish-eagle pair to determine which perch tree they used most frequently for foraging on the day of observation. I did not include trees immediately adjacent to the nest tree that the eagles used for guarding the nest. If the eagles were not in the area, I asked local people which tree they had seen the eagles use most frequently as a foraging perch. I measured the same characteristics for perch trees that I measured for nest trees. I did not measure site characteristics for perch trees because most of them were near enough to the nest trees that the measurements would have been similar to the measurements for the nest tree. My perch tree sample included perches of five fish-eagle pairs that defended territories but had not been known to nest.

Random Selection of Trees

To compare nest and perch trees to available large trees, I randomly selected reference trees on each lake or river. I selected trees at the same distance from the water to control for systematic differences in the frequency or size of trees at different distances from the water. To do this, I first randomly selected a shoreline reference point on the same body of water for each nest tree that I had measured. I then used this reference point to locate one nest reference tree and one perch reference tree. I measured nest and perch trees before measuring reference trees so that I could use the distances of the nest and perch trees to the water to select reference trees.

To select each nest reference tree, I measured the same perpendicular distance inland from the shoreline reference point as the distance from the nest tree to the water. I then selected the nearest tree > 20 cm in dbh as my nest reference tree. For nest trees adjacent to lakes, I selected reference trees adjacent to the same lake. For nest trees adjacent to rivers, I selected reference trees within a 1.5-km river section centered on the nest tree. I used a 1.5-km section because this distance was the mean fish-eagle inter-nest distance on lakes Befotaka, Soamalipo, and Ankerika, which hold the greatest density of breeding Madagascar fish-eagles (Rabarisoa et al. 1997).

To select perch reference trees, I first measured the shoreline distance between the point on the shoreline nearest the perch tree and the point on the shoreline nearest the nest tree of the fish-eagle pair that used that perch tree. I then located a second shoreline reference point at the same distance and orientation as the distance separating the points on the shoreline nearest the nest and perch trees. Then, just as with the nest reference tree, I measured the same perpendicular distance inland from this second shoreline reference point as the distance from the perch tree to the water. I selected the nearest tree > 20 cm in dbh as my perch reference tree. For perch trees of fish-eagle pairs that were not nesting ($n = 5$), I selected perch reference trees in the same manner that I selected nest reference trees.

Statistical Analyses

I tested the null hypothesis of no difference between trees or sites used by breeding Madagascar fish-eagles and trees or sites selected at random for each of the numerical variables using the Wilcoxon signed rank test. I paired each fish-eagle nest or perch tree with the tree that I had randomly selected on the same lake or river at the same distance from the water. I did not test for differences in distance to water because this variable was a criterion for pairing used trees with random trees. I used the Chi-square test of equal proportions to determine if fish-eagle use of categorical variables was different from expected use. Categorical variables included tree species, deciduous versus non-deciduous trees, growth form, and surrounding canopy height. If > 20% of expected values were < 5, I used the likelihood ratio Chi-square test statistic.

I developed models to predict the probability of fish-eagle use based on the measured habitat variables using stepwise logistic regression analysis (Hosmer and Lemeshow 1989). To include growth form in the analyses, I first created four variables corresponding to four of the five growth form categories. I assigned a value of one to each of these variables if a tree's growth form corresponded to that variable and zero if the tree had a different growth form. I analyzed the data for nest trees, nest sites, and perch trees first using the data from every site that I visited. These data included some sites that were probable alternate sites used in previous years by fish-eagles already in the sample, so I also analyzed the data for only the most recently used sites and conducted each analysis using this more stringent independence criterion.

RESULTS

Nest Tree Characteristics

I measured 38 nest trees, of which at least 24 were used by different fish-eagle pairs and 14 were probable alternate nests used in previous years because they were < 500 m from occupied nest trees. I also measured 38 random trees, each of which was paired with a nest tree on the same lake or river and at the same distance from the water.

I will present separate results for the complete sample (38 nest trees and 38 random trees) and for the more restricted sample (24 nest trees and 24 random trees), which included only the most recently used nest tree in each area.

In the complete sample ($n = 38$), nest trees were larger (dbh and height), had a greater arc of accessibility, and had more unobstructed branches than random trees (Table 1). Except for *Tamarindus indica*, all nest tree species were different from random tree species (Table 2). The proportion of *T. indica* among nest trees (26.3%) was not different from its proportion among random trees (34.2%) ($\chi^2 = 0.56$, df = 1, $P = 0.454$). Thirteen nest trees (34.2%) and six (15.8%) random trees were deciduous. This difference was not significant ($\chi^2 = 3.44$, df = 1, $P = 0.064$). The proportion of trees in each growth form class (Fig. 2) also was not different between nest trees and random trees ($\chi^2 = 8.26$, df = 4, $P = 0.082$). Stepwise logistic regression analysis resulted in an equation that included tree height, arc of accessibility, and number of branches (Table 3). The equation correctly classified fish-eagle nest tree use for 85.5% of 76 trees (Table 4).

In the more restricted sample ($n = 24$), nest trees were also larger (dbh and height), had a greater arc of accessibility, and had more unobstructed branches than random trees (Table 5). The proportion of *Tamarindus indica* among nest trees (29.2%) was not different from its proportion among random trees (20.8%) ($\chi^2 = 0.44$, df = 1, $P = 0.505$) (Table 2). Eight of the nest trees (33.3%) and three (12.5%) of the random trees were deciduous. This difference was not significant ($\chi^2 = 2.95$, df = 1, $P = 0.086$). There was also no difference between nest trees and random trees in the proportion of trees in each growth form class ($\chi^2 = 4.58$, df = 4, $P = 0.330$) (Fig. 3). Stepwise logistic regression analysis resulted in an equation that included tree height (Table 6) but not arc of accessibility and number of branches as for the larger sample. The equation correctly classified fish-eagle nest tree use for 83.3% of 48 trees (Table 7). I solved the equation (Table 6) and determined that trees $\geq$ 14.4 m, $\geq$ 17.3 m, and $\geq$ 20.1 m high have a 50%, 75%, and 90% probability, respectively, of being suitable fish-eagle nest trees.

Nest Site Characteristics

I analyzed site characteristics separately from tree characteristics for the same group of nest and random trees. In the complete (n = 38) sample, nest sites were farther from roads and had a greater number of suitable perch trees within an adjacent 250 m by 50 m shoreline section than random sites (Table 8). Distance to nearest human disturbance, distance to nearest building, distance to nearest fish-eagle nest, and shoreline perimeter within 300 m of the nest did not differ (Wilcoxon rank sum, $P \geq 0.05$) between nest sites and random sites. The proportion of nest sites in each 5-m canopy height interval (Fig. 4) also did not differ between nest sites and random sites ($\chi^2 = 7.26$, df = 4, $P = 0.123$). Mean distance to water from nest sites was 75.2 m (SE = 11.8, range = 5.2 to 268.3 m). This variable was not compared with random sites because it was a criterion for reference tree selection (reference trees were selected at the same distance from the water as nest trees). Stepwise logistic regression analysis resulted in an equation that included number of suitable perch trees within an adjacent 250 m by 50 m shoreline section (Table 9). The equation correctly classified fish-eagle nest site use for 63.2% of 76 sites (Table 10).

In the more restricted sample (*n* = 24), number of suitable perch trees was still greater at nest sites than at random sites (Table 11), but distance to nearest road did not significantly differ between nest sites and random sites (Wilcoxon signed rank test, P = 0.055). Distance to nearest human disturbance, distance to nearest building, distance to nearest fish-eagle nest, and shoreline perimeter within 300 m of the nest also did not differ ($P \geq 0.05$) between nest sites and random sites. The proportion of nest sites in each 5-m canopy height interval (Fig. 5) did not differ between nest sites and random sites (χ^2 = 4.93, df = 4, P = 0.295). Mean distance to water of nest trees was 70.8 m (SE = 12.6, range = 6.8 to 199.2 m). Stepwise logistic regression analysis on the smaller sample also resulted in an equation that included the number of suitable perch trees (Table 12) as for the larger sample. The equation correctly classified eagle nest site use for 72.9% of 48 sites (Table 13). I solved the equation (Table 12) and determined that sites with ≥ 23 suitable perch trees, ≥ 31 perch trees, and ≥ 38 perch trees within an adjacent 250 m by 50 m shoreline section have a 50%, 75%, and 90% probability, respectively, of being suitable fish-eagle nest sites.

Perch Tree Characteristics

I measured 38 perch trees of which at least 29 were used by different fish-eagle pairs and 9 were probable alternate sites used in previous years. As with nest trees, I will present separate results for the complete sample (38 nest trees and 38 random trees) and for the more restricted sample (29 nest trees and 29 random trees) that included only the most recently used perch trees in each area.

In the complete sample ($n = 38$), perch trees were larger (dbh and height), had a greater arc of accessibility, and had more unobstructed branches than random trees (Table 14). At least seven tree species were common to both perch trees and random trees (Table 15). The proportion of *Tamarindus indica* among perch trees (7.9%) was smaller than among random trees (34.2%) ($\chi^2 = 7.92$, df = 1, $P = 0.005$). The proportion of deciduous trees among perch trees (36.8%) was greater than among random trees (13.2%) ($\chi^2 = 5.68$, df = 1, $P = 0.017$). There was a greater proportion of perch trees in the small canopy growth form class and random trees in the large canopy growth form class (Fig. 6) ($\chi^2 = 10.75$, df = 4, $P = 0.029$). Stepwise logistic regression analysis resulted in an equation that included tree height, arc of accessibility, and the snag growth form (Table 16). The equation correctly classified eagle nest tree use for 88.2% of 76 trees (Table 17).

In the more restricted sample ($n = 29$), perch trees were also larger (dbh and height), had a greater arc of accessibility, and had more unobstructed branches than random trees (Table 18). At least six tree species were common to both perch trees and random trees (Table 15). The proportion of *Tamarindus indica* among perch trees (10.3%) was smaller than among random trees (34.5%) ($\chi^2 = 5.96$, df = 1, $P = 0.015$). The proportion of deciduous trees among perch trees (34.5%) was greater than among random trees (10.3%) ($\chi^2 = 4.86$, df = 1, $P = 0.028$). In contrast to the results for the complete sample, there was no significant difference between perch trees and random trees in the proportion of trees in each growth form class (Fig. 7) (df = 4, $\chi^2 = 8.04$, $P = 0.090$). Stepwise logistic regression analysis on the smaller sample resulted in an equation that included tree height (Table 19) but not arc of accessibility and the snag growth form as for the larger sample. The equation correctly classified eagle nest tree use for 84.5% of 58 trees (Table 20). I solved the equation (Table 19) and determined that trees ≥ 12.3 m, ≥ 13.9 m, and ≥ 15.4 m high have a 50%, 75%, and 90% probability, respectively, of being suitable fish-eagle perch trees.

DISCUSSION

Nest Tree Selection

For both the larger sample and the more restricted sample, Madagascar fish-eagles selected nest trees that were taller, had a greater dbh, had more unobstructed branches, and had a greater arc of accessibility than trees not known to have been used by fish-eagles (hereafter referred to as unused). The substantial difference between nest trees and unused trees in mean height and dbh suggests that the fish-eagle selects nest trees from among the largest trees available near water. By placing its nests in the tops of these trees, it maximizes accessibility and visibility for foraging and territorial defense. These results were consistent with those reported for bald eagles in the Pacific Northwest (Anthony et al. 1982, Anthony and Isaacs 1989) and Florida (McEwan and Hirth 1979) and white-tailed sea eagles in Japan (Shiraki 1994). These eagles also nested in large super-canopy trees near water.

The large proportion of *Tamarindus indica* among both used and unused trees in this study indicates that Madagascar fish-eagles do not necessarily prefer this tree species, but that they select the most common large tree species near water in the study area. The fish-eagles selected at least 15 other tree species besides *T. indica*, which indicates that their tree species selection is flexible.

Nest Site Selection

Among the measured variables, number of suitable perch trees along the adjacent shoreline was the most important factor determining Madagascar fish-eagle nest site selection. This result is consistent with Brown's (1980) observations of African fish-eagles on Lake Naivasha, Kenya and Chandler et al.'s (1995) research on bald eagles on the northern Chesapeake Bay, Maryland. The result for the larger sample that nest sites were farther from roads than random sites may have been spurious. The roads in the Antsalova region receive little or no vehicular traffic and at most a few oxcarts each day, mostly during the night. Mean distance to nearest road was > 1 km for both nest sites and random sites, and it is unclear why the presence of a road should make a difference to the fish-eagles at that distance with such infrequent traffic.

Perch Tree Selection

The characteristics that differed between nest trees and unused trees also distinguished perch trees, namely greater height and dbh, more unobstructed branches, and a greater arc of accessibility. These results were consistent with those reported for bald eagles in Washington (Stalmaster and Newman 1979), South Dakota (Steenhof et al.1980), and Maryland (Buehler et al. 1992). Perch trees in this study also tended to be deciduous and to have a narrower growth form than unused trees. I conducted this study during the leaf-off period for most deciduous trees, and these trees probably have greater access and provide better visibility over the water for foraging eagles.

In contrast with the nest tree results, the fish-eagles in this study appeared to avoid perching in *Tamarindus indica*, the tree species that occurred most frequently near water in the study area. Although it is a large tree species with numerous branches, most *T. indica* in the study area had a large canopy growth form and kept their leaves all year long and may have been less suitable for perching than narrower trees without leaves or snags.

Modeling Nest Tree, Nest Site, and Perch Tree Use

The models I developed can be used to identify Madagascar fish-eagle nesting and perching habitat throughout the eagle's range in western Madagascar. The nest and perch tree models developed from the more restricted samples correctly classify a slightly lower proportion of the data but have the advantage of fewer variables to measure than the models developed from the complete samples. It is sufficient to measure height alone to be able to predict a tree's suitability as either a fish-eagle nest or perch tree with > 80% accuracy. The number of suitable perch trees along a shoreline section can be used to predict its suitability as a fish-eagle nest site with > 70% accuracy.

The models suggest that the presence of tall trees close to the shoreline is the best predictor of suitable Madagascar fish-eagle habitat at the local level. The eagles often use the tallest trees available both for nesting and for foraging perches. Most of the lakes in the study area were exploited for fish, and had at least one permanent village within 0.5 km of the shore and seasonal fisherman's camps along the shoreline. Although the nest site data suggest that the Madagascar fish-eagle is not sensitive to human disturbance, the felling of tall shoreline trees by the local human population may have a negative impact on the eagles. Among the tree species used by fish-eagles for nesting or perching in this study, Zarasoa (1995) determined that local people use *Albizia lebbeck, Alleanthus greveanus, Cedrelopsis grevei*, *Colvillea racemosa*, *Cordyla madagascariensis*, *Dalbergia spp.*, *Ficus cocculifolia*, and *Tamarindus indica* for dug-out canoes, building materials, fuel wood, or medicine. People use the tallest trees available for dug-out canoes and building materials and may prevent regeneration of tall trees by harvesting smaller trees for fuel wood and medicine. Deforestation probably has already substantially reduced the amount of fish-eagle habitat available, and as the human population continues to increase, available habitat will continue to decrease unless steps are taken to conserve fish-eagle habitat.

CHAPTER 2: LAKE USE

INTRODUCTION

Considered a common species as recently as the 1920s (Rand 1936), the Madagascar fish-eagle (*Haliaeetus vociferoides*) has declined dramatically in recent decades (Langrand 1987). Habitat degradation has been proposed as a likely cause for its low population size (Langrand 1987, Langrand and Goodman 1995). The Madagascar fish-eagle nests and perches in large trees (Langrand and Meyburg 1989, Chapter 1) and forages for fish along lakes, rivers, and coastline (Langrand and Meyburg 1989), so it is likely to be affected by both terrestrial and aquatic habitat degradation. Deforestation is the principal threat to the fish-eagle’s terrestrial environment while siltation of lakes and rivers and conversion of wetlands for rice production reduce prey availability.

Aquatic habitat characteristics such as water depth and clarity are likely to influence the availability of fish for foraging fish-eagles. Numerous investigators have documented the negative effects of terrestrial habitat alteration on bald eagle (*Haliaeetus leucocephalus*) breeding habitat (McEwan and Hirth 1979, Andrew and Mosher 1982, Anthony and Isaacs 1989, Wood et al. 1989), but there has been little research on the effects of aquatic habitat degradation.

Watson et al. (1996) hypothesized that the Madagascar fish-eagle exhibits obligate siblicide based on their observations of sibling aggression and the prevalence of two-egg clutches in which only one chick survives to fledge. They are developing sibling rescue techniques as an inexpensive means to augment Madagascar fish-eagle populations. These reintroduction efforts will focus on areas of suitable unoccupied fish-eagle habitat, so it is important to be able to distinguish such areas. The objectives of this study were to (1) determine prey availability and habitat characteristics of lakes used by Madagascar fish-eagles and (2) develop predictive models to identify lakes suitable for breeding fish-eagles based on shoreline characteristics, water quality, and prey availability.

METHODS

Study Areas

From 21 May to 14 August 1994, I investigated habitat characteristics of lakes in the Antsalova region (Chapter 1) of western Madagascar (Fig. 1), where the densest breeding population of Madagascar fish-eagles occurs (Rabarisoa et al. 1997). Based on the results of this initial investigation, I decided to examine more lakes over a greater area and to sample fish populations. From 26 May to 15 November 1995, I measured habitat characteristics and sampled fish populations of lakes on the west coast of Madagascar. My study area extended from the Morondava River south of the town of Morondava (20°17'S, 44°17'E) to the Sofia River north of Boriziny (15°34'S, 47°37'E) and from the coast up to 125 km inland where the land rises towards the central plateaus (Fig. 8). The study area included most of the lakes where Madagascar fish-eagles were known to nest

(Rabarisoa 1995). The breeding range of the Madagascar fish-eagle extends beyond the northern part of the study area up to Nosy Hara near Antsiranana at the northern end of the island (12°19'S, 49°17'E). Most of the fish-eagles north of the study area nest on offshore islands (Langrand and Meyburg 1989, Watson and Rabarisoa 1995).

The entire study area lies within the Western Domain of the Western Malagasy phytogeographical region (Humbert 1954), characterized by annual rainfall between 1,000 and 2,000 mm, a 6 to 8 month dry season, monthly average temperatures > 20° C, and elevations < 800 m. The dry season lasts from April or May to October or November and decreases in duration from north to south in the study area (Donque 1972). The climax vegetation is dense tropical dry deciduous forest, but savanna grasslands maintained by pasture burning comprise > 80% of the vegetation of the Western Domain (Guillaumet 1984). Topographical features include a wide coastal plain, the Bemaraha and Ankarafantsika limestone plateaus, and interior basins. From north to south, the major rivers of the study area are the Sofia, the Mahajamba, the Betsiboka, the Mahavavy, the Andranomavo, the Sambao, the Maningoza, the Ranobe, the Manambaho, the Manomba, the Namela, the Soahanina, the Manambolo, the Tsiribihina, and the Morondava. Most of the lakes in the study area are flood-plain lakes whose surface areas vary greatly between the rainy season and the dry season (Kiener and Richard-Vindard 1972).

Lake Habitat Measurement in 1994

I considered lakes to be occupied by Madagascar fish-eagles if I observed a perched pair of eagles vocalizing together or if a nest was present that I knew that eagles had used within the past three years. In 1994, I examined all known occupied lakes in the Antsalova study area (*n* = 15). These lakes included four that had two or more nesting pairs, seven that had one nesting pair, two that had a resident pair that had nested within the past three years, and two that had a resident pair each for which I could not find a nest. For comparison, I examined every unoccupied lake in the study area with a shoreline perimeter ≥ 1.8 km (*n* = 19), the smallest shoreline perimeter of any occupied lake. I used a minimum shoreline perimeter criterion, rather than a minimum surface area, because it was easier to measure shoreline perimeter in the field. At each lake, I recorded water clarity, average depth, extent of aquatic vegetation cover, human population living within 200 m of the water, number of different fish species caught by local fishermen, distance from shoreline to nearest village, shoreline perimeter, surface area of the water, and shoreline habitat types.

I measured water depth to the nearest 5 cm using a weighted measuring string. I recorded water clarity as the maximum depth, to the nearest 5 cm, at which I could still see a Secchi disk suspended beneath the water (Orth 1983). I measured water depth and clarity at five randomly selected points at least 5 m from the shore and averaged the values for each lake.

I visually estimated the percentage of the water surface covered by aquatic vegetation and assigned each lake to one of five 20% cover intervals (0-20%, 21-40%, etc.). I asked local residents how many people lived year round within 200 m of the water and assigned each lake to a 50-inhabitant interval (0 people, 1-50 people, 51-100 people, etc.). I asked fishermen to name all the fish species they caught, and I recorded the total number of species for each lake.

I measured distance to next nearest lake to the nearest 0.1 km and used a map measurer to measure shoreline perimeter to the nearest 0.1 km on maps and aerial photos of each lake. I used a planimeter to measure surface area to the nearest 0.1 km^2. I classified shoreline habitat types as dense forest (continuous canopy), open forest (broken canopy), savanna (grasslands with scattered trees and shrubs), marsh, or rice paddy. I used a map measurer to record to the nearest 0.1 km the length of shoreline in each habitat type for each lake.

Lake Habitat Measurement in 1995

In 1995, I examined 32 lakes occupied by 42 resident Madagascar fish-eagle pairs in western Madagascar between Morondava and Boriziny. Of these lakes, one had five nesting pairs, one had four nesting pairs, three had two nesting pairs, 17 had one nesting pair, four had a resident pair that had nested within the past three years, and six had a resident pair for which I could not find a nest. For comparison, I randomly selected 32 unoccupied lakes from among the 496 lakes that I could identify from satellite or aerial photos of the study area. The smallest lakes from which I selected my random sample were about 1 ha in size. I excluded unoccupied lakes that were < 2.5 km from an occupied fish-eagle nest. This distance was the maximum inter-nest distance of occupied fish-eagle nests that I measured in 1994 at lakes Befotaka, Soamalipo, and Ankerika, which hold the greatest density of breeding Madagascar fish-eagles (Rabarisoa et al. 1997). I used this distance because I wanted to select random unoccupied lakes that fish-eagles were not likely to use regularly for foraging.

At each lake I recorded maximum depth, water clarity, bottom substrate, number of suitable perch trees, shoreline perimeter, and surface area. I measured lake depth at several spots, starting roughly at the center of each major section of the lake, and recorded the maximum depth measured. The total number of depth measurements that I used to determine maximum depth depended on the size, shape, and uniformity of the lake. I recorded bottom substrate as sand, soft mud, firm mud, or plant debris. If I sank in the mud, I classified the bottom substrate as soft mud. If I could wade into the water without sinking in the mud, I classified it as firm mud. At occupied lakes, I counted the number of suitable perch trees within 50 m of the water along a 250-m shoreline transect centered on the nearest point on the shoreline to the nest tree (Chapter 1). At lakes where I could not find a nest, I counted suitable perch trees within a 250 m by 50 m shoreline section in the area where I saw the eagles most frequently. For unoccupied lakes, I counted suitable perch trees along the 250-m shoreline section that had the highest density of tall trees, in other words where fish-eagles would most likely nest if they occupied the lake. I counted lone or emergent trees and snags with high, stout branches and unobstructed visibility as suitable perch trees.

Fish Sampling

At each lake, I set out two gill nets for three hours starting just before sunrise, which varied from about 0630 in June to 0500 in November. The gill nets had a foam core float rope and a lead core bottom rope, were 0.91 m deep by 45.7 m long, and were divided into three 15.2-m panels of 2.5, 3.8, and 5.1 cm mesh size. I attached floats to the first net and set it out parallel to the shore on the surface in water about 0.9 m deep. I set out the second net parallel to the shore on the bottom in water about 1.8 m deep. This way, I sampled fish from among the first and second 0.9 m of the water column. If the lake was < 1.8 m deep, then I set out the second net in the deepest water within a 200-m radius of the area where I had set out the first net. If the lake was < 0.9 m deep, then I set out both nets on the surface down to the maximum depth of the lake. I used a two-person inflatable kayak to set out and gather up the nets. I determined water depths using marks on the 2-m long kayak paddle.

At occupied lakes, I placed the nets adjacent to the nest site or area where I saw the eagles most frequently. At unoccupied lakes, I placed the nets next to the shoreline section where I had counted suitable perch trees. I identified each fish to species (Arnoult 1959, Kiener 1963, Glaw and Vences 1994) and weighed it to the nearest g using 500-g, 1-kg, and 2.5-kg Pesola scales. I measured total fish length to the nearest cm using a tape measure. For each lake, I calculated total number of fish caught, total weight (kg) of fish catch, average fish weight (g), and number of different species.

Statistical Analyses

I tested the null hypothesis of no difference between lakes occupied by Madagascar fish-eagles and unoccupied lakes for each of the numerical habitat and fish availability variables using the Wilcoxon rank sum test. For the categorical variables (aquatic vegetation cover, human population, and bottom substrate), I used the Chi-square test of equal proportions to determine if fish-eagle use was different from expected use. If > 20% of expected values were < 5, I used the likelihood ratio Chi-square test statistic. I developed logistic regression models (Hosmer and Lemeshow 1989) to predict the probability that Madagascar fish-eagles will occupy a lake based on habitat variables and fish availability. Initially, I conducted stepwise analyses. Then, I substituted other variables for each of the variables selected in stepwise analysis to determine whether other variables yielded a model that correctly classified a similar or higher proportion of the data. I tested the 1994 and 1995 data separately.

RESULTS

Lake Habitat Characteristics in the Antsalova Area

Lakes occupied by Madagascar fish-eagles were deeper and clearer and had more densely forested shoreline than unoccupied lakes (Table 21). Fishermen reported catching more species of fish at occupied lakes than at unoccupied lakes. Distance to nearest village, shoreline perimeter, surface area, length of open forest along shoreline, length of savanna along shoreline, length of marsh along shoreline, and length of rice paddies along shoreline did not differ ($P \geq 0.05$) between occupied lakes and unoccupied lakes. There was no difference between occupied and unoccupied lakes in percent aquatic vegetation cover ($\chi^2 = 3.60$, df = 4, $P = 0.463$) (Fig. 9) and human population ($\chi^2 = 6.07$, df = 5, $P = 0.299$) (Fig. 10).

Lake Habitat Characteristics in Western Madagascar

Lakes occupied by Madagascar fish-eagles between Morondava and Boriziny in western Madagascar were deeper and clearer and had more shoreline perch trees than unoccupied lakes (Table 22). Shoreline perimeter and surface area did not differ between occupied and unoccupied lakes ($P \geq 0.05$). Bottom substrate (Fig. 11) also did not differ between occupied and unoccupied lakes ($\chi^2 = 1.34$, df = 3, $P = 0.719$).

Fish Availability

In my gill net samples at lakes occupied by Madagascar fish-eagles ($n = 32$), I caught 623 fish of 17 species, and the total weight of the catch for all lakes was 111.1 kg. At unoccupied lakes ($n = 32$), I caught 251 fish of 12 species, and the total weight of the catch was 39.0 kg. The number of fish caught in the gill nets, total weight of the catch, and number of fish species in the catch were all greater at occupied lakes than at unoccupied lakes (Table 22). Average fish weight did not differ between occupied lakes and unoccupied lakes ($P \geq 0.05$).

The introduced cichlid *Oreochromis macrochir* was the most abundant fish, accounting for 56.7% of the total fish catch at all lakes by number and 36.6% by weight. The *O. macrochir* gill net catch was greater at occupied lakes than at unoccupied lakes both in number (Wilcoxon rank sum test: $S = 1275$, $n_1 = n_2 = 32$, $P = 0.0015$) and weight (Wilcoxon rank sum test: $S = 1295$, $n_1 = n_2 = 32$, $P = 0.0006$). The other fish species could not be statistically compared between occupied lakes and unoccupied lakes because they were not caught at a sufficient number of lakes. Number of fish caught was greater at occupied lakes than at unoccupied lakes for 14 (77.8%) of the 18 fish species caught at all lakes, and total weight of fish catch was greater at occupied lakes for 16 (88.9%) of the fish species (Table 23).

Modeling Lake Use

Stepwise logistic regression analysis on the Antsalova area data indicated that the probability of Madagascar fish-eagle occupation was positively associated with water clarity and number of fish species (Table 24). The equation correctly classified fish-eagle occupation for 70.6% of 34 lakes (Table 25).

Stepwise logistic regression analysis on the western Madagascar data indicated that the probability of Madagascar fish-eagle occupation was positively associated with number of shoreline perches and number of fish species caught in gill nets (Table 26). The equation correctly classified fish-eagle occupation for 76.6% of 64 lakes (Table 27). If I removed number of fish species from the list of variables available for stepwise selection and analyzed the remaining variables, the resulting equation included number of shoreline perches and number of fish caught in gill nets (Table 28). The equation correctly classified fish-eagle occupation for 75.0% of the lakes (Table 29). If I removed both number of fish species and number of fish caught from the list of variables available for stepwise selection and analyzed the remaining variables, the resulting equation included number of shoreline perches and total weight of fish caught in gill nets (Table 30). The equation correctly classified fish-eagle occupation for 76.6% of the lakes (Table 31).

The three fish variables number caught, total weight of catch, and number of species were all highly correlated (Table 32), so they were essentially interchangeable in the logistic regression equations. I removed the fish availability variables all together from the list of variables available for stepwise selection and conducted a univariate logistic regression on the number of shoreline perches variable. The resulting equation (Table 33) correctly classified fish-eagle occupation for 71.9% of the lakes (Table 34). I solved the equation (Table 33) and determined that lakes having 250 m by 50 m shoreline sections with ≥ 28 suitable perch trees, ≥ 46 perch trees, and ≥ 64 perch trees have a 50%, 75%, and 90% probability, respectively, of being occupied by fish-eagles.

DISCUSSION

Lake Habitat Characteristics

The habitat variables that characterized lakes occupied by Madagascar fish-eagles in this study relate to prey availability. Siltation of lakes and estuaries resulting from soil erosion during the rainy season is a major problem in Madagascar (Le Bourdiec 1972). The Madagascar fish-eagle may shift foraging locations as water clarity decreases as Flemming and Smith (1990) observed among osprey (*Pandion haliaetus*) in Nova Scotia.

Madagascar fish-eagles may select deeper lakes because these lakes are more likely to persist throughout the dry season. Most of western Madagascar receives very little rain from April through October (Donque 1972). Water levels at lakes decline markedly over the course of the dry season, and some lakes dry up entirely (personal observation). Fish-eagle energy demands are also likely to be highest during the dry season because they reproduce at this time. Clearly, if fish-eagles are to reproduce successfully, they must nest near lakes that will persist throughout the year most years.

Although occupied lakes in the Antsalova study area had more densely forested shoreline than unoccupied lakes, fish-eagles do not appear to require dense forest because two (13.3%) of the occupied lakes in this area had no densely forested shoreline. Unfortunately, I do not know whether the fish-eagles successfully reproduced at these two lakes because I was unable to collect data on nesting success. Since number of suitable perch trees on adjacent shoreline was the best predictor of fish-eagle nest site use (Chapter 1), presence of a sufficient number of large trees suitable for perching is probably more important to fish-eagles than presence of contiguous forest. Accordingly, I recorded number of suitable perch trees rather than length of densely forested shoreline when I measured lakes in 1995.

The logistic regression equation including number of shoreline perches correctly classified fish-eagle occupation for a greater proportion of the lakes in western Madagascar than any other single-variable logistic regression equation. This suggests that number of shoreline perches may be the most important factor limiting Madagascar fish-eagle populations, as is the case for bald eagles on the northern Chesapeake Bay (Chandler et al. 1995). Since there only are widely scattered trees and shrubs throughout most of western Madagascar (Guillaumet 1984), fish-eagles may be restricted to breeding at those lakes that offer enough perch trees for foraging at a number of different locations. As deforestation continues in Madagascar, the number of lakes with enough suitable perch trees is likely to decrease, and this is likely to be a major factor contributing to the decline of the Madagascar fish-eagle.

Fish Populations

The logistic regression equation based on the 1994 data on lakes in the Antsalova region suggested that the fish prey base is an important predictor of a lake's suitability for fish-eagles. Asking local fishermen what species of fish they caught may have been subject to error because they often did not distinguish among similar species or if they fished at several different lakes, they could not remember which species they caught at which lakes. To obtain a more accurate assessment of fish distribution and abundance, I decided to use gill nets to sample the fish population at occupied and unoccupied lakes over a larger area the following year. The gill net sampling results indicated that fish numbers, biomass, and species diversity were all greater at lakes occupied by Madagascar fish-eagles. The logistic regression equations including any one of these fish availability variables along with number of shoreline perches correctly classified occupation by Madagascar fish-eagles for a similarly high proportion (≥ 75%) of lakes in the study area. It is uncertain which fish availability variable is most important to the fish-eagles, but clearly the eagles appear to be selecting lakes with thriving fish populations.

With the exception of Sanford's sea eagle (*Haliaeetus sanfordi*), *Haliaeetus* eagles feed primarily on fish and other aquatic prey (Stalmaster 1987). The bald eagle (Stalmaster 1987) and white-tailed sea eagle (*H. ablicilla*) (Love 1983) may rely more on avian and mammalian prey and carrion when fish are less available in the winter. The Madagascar fish-eagle, however, appears to rely almost exclusively on fish and occasionally other aquatic prey such as crabs and turtles (Langrand and Meyburg 1989). It is not surprising, then, that the abundance and distribution of fish affects the abundance and distribution of fish-eagles in Madagascar.

Human activity

The number of people living in the area did not appear to affect Madagascar fish-eagle lake selection in this study. In contrast with the bald eagle (Fraser et al. 1985a, Buehler 1990), the Madagascar fish-eagle does not appear to be sensitive to direct human disturbance (personal observation). This difference may in part be due to the fact that very few people in western Madagascar can afford firearms, and there is a taboo against killing eagles among the Sakalava tribe, who inhabit much of the Madagascar fish-eagle's range. Three of 38 (7.9%) nests studied in 1994 (Chapter 1) were < 100 m from human habitation, and fishermen and cattle herders passed beneath many of the nest trees on a weekly basis (personal observation). Unfortunately, I only was able to visit each nest site once during a season, so I do not have data on the effect of human disturbance on nesting success.

Although Madagascar fish-eagles are less sensitive to direct human disturbance than their congeners, rapidly increasing human populations are likely to further degrade the habitat on the lakes where fish-eagles breed. Uncontrolled fishing may reduce fish populations to levels that cannot sustain breeding fish-eagles. The lowest gill net catches in this study were generally at the most accessible lakes where smoked fish could be transported to more densely populated areas. As the most accessible lakes are depleted, exploitation of the more remote, less accessible lakes is likely to increase, as is already occurring in the Antsalova region (Andrian-Harivelo 1995). Furthermore, the number of suitable perch trees on these lakes will likely decrease as fishermen cut trees for dug-out canoes, houses, or fuel wood for smoking fish. The Madagascar fish-eagle's relative insensitivity to direct human activity, thus, should not be interpreted as insensitivity to the ever-increasing effects of human activities.

CHAPTER 3: FORAGING ECOLOGY

INTRODUCTION

Presence of a thriving fish population is an important factor in determining lake use of breeding Madagascar fish-eagles (Chapter 2). Prey availability influences breeding area selection (Swenson et al. 1986), breeding density (Dzus and Gerrard 1989), reproductive success (Grubb 1995), and date of breeding onset (Hansen 1987) in bald eagles (*Haliaeetus leucocephalus*) and productivity in white-tailed sea eagles (*H. albicilla*) (Helander 1985). It also affects distribution and density of bald eagles at wintering sites (Griffin and Baskett 1985, Sabine and Klimstra 1985, Keister et al. 1987, Hunt et al. 1992a) and migratory stopovers (Fraser et al. 1985b, Bennetts and McClelland 1991).

Although prey availability is clearly important to *Haliaeetus* eagles, there has been little research aimed at quantitatively determining prey abundance and its effects on prey selection, foraging rates, and foraging success. Steenhof (1976), Mersmann (1989), and Hunt et al. (1992b) used gill nets to inventory relative fish abundance and determined that the fish species that were caught most frequently in the gill nets made up the greatest proportion of the bald eagle’s diet. Wintering bald eagles in New Mexico fed most frequently on big game carrion when it was the most abundant prey source (Grubb 1984). There is a relationship between prey abundance and foraging success of wintering bald eagles both between locations (Stalmaster and Plettner 1992) and between years (Brown 1993). Knight and Knight (1983) found a negative correlation between search time and relative prey availability of bald eagles wintering in Washington State, but Mersmann (1989) did not find a correlation between bald eagle foraging rates and gill net catch rates on the northern Chesapeake Bay.

Langrand and Meyburg (1989) and Razafindramanana (1995) have documented Madagascar fish-eagle prey captures, but there has been no previous attempt to quantitatively assess the eagle's diet. There has been a major change in Madagascar's freshwater fish fauna over the last 30 years as aquatic habitats have been degraded and introduced fish have increased at the expense of endemic species (Loiselle 1993, Reinthal et al. 1995). Changes in the freshwater fish fauna could further impact the Madagascar fish-eagle population that already has declined as a result of habitat degradation and human persecution (Langrand and Meyburg 1989).

Knowledge of fish-eagle prey preference and the effects of fish availability on foraging rates and foraging success is essential to determine the effect of fish numbers and fish species composition on the fish-eagle population. The objectives of this study were to (1) describe the diet and foraging behavior of the Madagascar fish-eagle at lakes in western Madagascar, (2) determine fish-eagle prey preference, and (3) determine whether fish-eagle foraging rates and foraging success are dependent on prey availability.

METHODS

Study Area

I investigated Madagascar fish-eagle foraging ecology from 22 May to 4 August 1996 at nine lakes in the Tsiribihina, Manambolo, and Beboka river drainages between the Bongolava escarpment and the Mozambique Channel in western Madagascar (Fig. 12). I selected lakes that I thought would offer the best conditions for viewing eagles throughout the day from among the 32 lakes with resident Madagascar fish-eagle pairs that I studied the previous year (Chapter 2). Each lake had at least one resident fish-eagle pair, and I observed extra adult or juvenile fish-eagles with five of the fish-eagle pairs that I studied (Table 35).

Foraging Behavior

A trained observer and I conducted all observations. We observed fish-eagle foraging behavior from 0600 to 1800 (daylight hours) for six or seven days at each lake. At the three lakes that had more than one resident fish-eagle pair, I randomly selected one of the pairs for observation. We watched from an inflatable kayak out in the water or from the shore using 10 x 50 binoculars and a 15 - 45 x spotting scope on a rifle mount. We focused our observations on the territorial male and followed his movements as much as possible, while also noting the behaviors of any other eagles that we could see, including juveniles and third adults that were associated with resident pairs. We distinguished adult fish-eagle sexes by the smaller size and higher pitched vocalizations of the males. We distinguished adults from juveniles by their vocalizations and by the completely white plumage on the tails and faces of the adults (Langrand and Meyburg 1989).

We recorded four categories of foraging behavior in order of increasing effort: (1) searches, (2) stoops, (3) strikes, and (4) kills. I adapted these categories from Stalmaster and Plettner's (1992) bald eagle (*Haliaeetus leucocephalus*) foraging behavior categories. When we observed a fish-eagle flying low over the water looking downward, we recorded a search. If the eagle then lowered its talons just above the water surface, we recorded a stoop. If the eagle broke the water surface, we recorded a strike, and if it emerged with a fish in its talons, we recorded a kill. For each fish-eagle pair that we observed, we recorded separate male and female foraging rates and foraging success. We also noted instances of fish-eagles scavenging dead fish from the shoreline or pirating fish from black kites (*Milvus migrans*).

We identified the fish that fish-eagles caught to species whenever possible. If we could not identify the fish while the eagle was in flight, we looked for prey remains on the ground beneath the eagle's nest or feeding perch after the eagle had eaten the fish.

Fish Sampling

I set out two gill nets for three hours at each lake starting between 0600 and 0615. I placed both nets parallel to the shore adjacent to the nest site or area where I saw the eagles perch most frequently if I did not find a nest. I set up one net on the water surface in ca. 0.9-m deep water and the other on the bottom in ca. 1.8-m deep water (Chapter 2). I identified each fish that I caught to species (Arnoult 1959, Kiener 1963, Glaw and Vences 1994) and weighed it to the nearest g using 500-g, 1-kg, and 2.5-kg Pesola scales. I measured total fish length to the nearest cm using a tape measure. I combined the data for the three days that I sampled each lake (nine hours total) and calculated total number of fish caught, total weight (kg) of fish catch, average fish weight (g), and number of different species. I did not include fish that weighed > 1.5 kg in these calculations because I estimated 1.5 kg to be the upper size limit of fish that I saw fish-eagles capture.

Statistical Analyses

I used the Chi-square test of equal proportions to determine if fish-eagle use of fish species was different from expected use based on gill net samples. After finding a significant ($P < 0.05$) overall difference, I tested the hypothesis of no difference between use and availability of each fish species, following Marcum and Loftsgaarden's (1980) technique. I used an overall confidence level of $a = 0.05$ and a confidence level of a/k, where k was the number of fish species analyzed, for each fish species, following the Bonferroni approach (Miller 1966:67). I calculated Spearman correlation coefficients between fish-eagle foraging variables and fish availability variables.

RESULTS

Foraging Behavior

We observed Madagascar fish-eagles foraging at nine lakes for a total of 669 hrs 30 min observer-time and 1030 hrs 59 min eagle-time, including 490 hrs 15 min (47.6%) male eagle-time, 526 hrs 0 min (51.0%) female eagle-time, and 14 hrs 44 min (1.4%) juvenile eagle-time. We recorded 67 occurrences of eagles obtaining fish, including 60 (89.6%) occasions when they captured fish in open water, 3 (4.4%) occasions when they scavenged dead fish from the shoreline, and 4 (6.0%) occasions when they stole fish from black kites. We also recorded 32 occurrences of eagles eating fish or delivering fish to their mate when we did not see the eagle obtain the fish. On one occasion, we observed an eagle eating a domestic duckling (*Anas sp.*). We did not see the eagle capture the duckling, but the local people claimed that the same eagle pair had killed domestic ducklings and turkey (*Meleagris sp.*) poults at the same lake on several occasions.

Of the 67 occasions when we saw eagles obtain fish, 53 (79.1%) occasions were adult male eagles, 13 (19.4%) occasions were adult females, and 1 (1.5%) occasion was a juvenile. Nine (69.2%) of 13 adult females that we saw capture fish were not nesting at the time. The other four (31.8%) were in the incubation stage of the nesting cycle. The eagle was an adult male on all 32 occasions when we saw eagles eating or delivering fish that we did not see them obtain. All four instances of piracy from kites occurred at the same lake and involved two cooperating adult male eagles associated with the same territory. In each case, eagles harassed the kite until it dropped its fish, which one of the eagles then retrieved.

Fish Availability and Foraging Success

I calculated rates for each of the four foraging behavior categories and six types of percent foraging success for male and female fish-eagles (Table 36) for comparison with fish availability variables (Table 37). Number of fish caught in gill nets was significantly ($P < 0.05$) positively correlated with male fish-eagle % strikes/search, % kills/search, and % kills/strike (Table 38). Total weight of fish catch was positively correlated with male % strikes/search, % kills/search, % kills/stoop, and % kills/strike. Number of fish species was positively correlated with male kills/hour/eagle, % strikes/search, % kills/search, % kills/stoop, and % kills/strike. Average fish weight was negatively correlated with female % kills/stoop and % kills/strike (Table 39).

The Madagascar fish-eagle search rate peaked in the early morning and peaked higher in the early afternoon with a lull in the middle of the day (Fig. 13). The kill rate exhibited a similar pattern, but the morning peak was higher (Fig.14). Foraging success, expressed as the percentage of prey searches that resulted in kills, peaked early in the day, declined steadily after 0900, and then peaked again after 1600 (Fig. 15).

Dietary Preference

Of the 99 observed occurrences of fish-eagles capturing, carrying, or eating fish, we were able to identify 68 (68.7%) either to species or to a closely related group of species (Table 40). We were unable to identify tilapia to species or to distinguish between the closely related *Oreochromis* and *Tilapia* genera. In my gill net samples, I caught 271 fish of 12 species, including four species of tilapia and eight other species. The total weight of my catch at all nine lakes was 41.1 kg.

I combined all native fish species into a single group because my catches of each native species were too low to analyze separately. These species included *Megalops cyprinoides*, *Arius madagascariensis*, *Glossogobius giuris*, *Ambassis gymnocephalus*, and *Scatophagus tetracanthus*. The proportions of fish species differed between the fish-eagle catch and the gill net catch ($\chi^2 = 41.97$, df = 4, $P = 0.001$). The 95% confidence limits for the difference between the proportion used and the proportion available suggested that fish-eagles catch *Ophicephalus striatus* in greater proportion, *Cyprinus carpio* in lesser proportion, and tilapia, *Heterotis niloticus*, and native species in equal proportion to what is available.

DISCUSSION

Foraging Behavior

Our observation that 4.4% of fish taken by Madagascar fish-eagles were scavenged was lower than scavenging rates documented for bald eagles. At least 25% of the fish that Mersmann (1989) observed and 7.7% of the fish that Brown (1993) observed bald eagles taking were scavenged. We did not see fish-eagles take floating dead fish from the surface in open water, but it is possible that some of the fish that we observed eagles catch from a distance were dead fish floating below the water surface. Black kites were abundant at all the lakes in the study, and we frequently observed kites taking small dead fish from the surface.

I am unaware of previous reports of piracy by the Madagascar fish-eagle. It is unclear why we observed four instances of piracy at one of the lakes and none at any of the other lakes. We saw numerous other fish-eating birds at all the lakes, including black kites, herons, storks, anhingas, and cormorants. The lake where we observed piracy was one of two lakes where we observed a second adult male eagle assisting the nesting pair, and when both males were present, they harassed the kites together. The nest site at this lake commanded a much wider view over the water than nest sites at any of the other lakes, so perhaps these eagles were able to spot black kites taking fish more often than the eagles at the other lakes.

Although we observed adult male eagles incubating eggs and tending nestlings, it appears that the male does most of the foraging for the pair at least during the early part of the nesting cycle. The four instances when we observed incubating females catch fish occurred near the nest when the males were not present. The most advanced nest we observed had a two- to three-week old downy chick, so we were unable to document whether female fish-eagle foraging rates increase or decrease as the young become more independent at later stages in the nesting cycle.

Fish Availability and Foraging Success

The foraging success of Madagascar fish-eagles in this study was related to prey availability. Of the foraging success variables calculated, % kills/search is perhaps most indicative of overall foraging effectiveness, and this variable for male fish-eagles was positively correlated with number of fish, total fish weight, and number of fish species. For males, kills/hour/eagle was positively correlated only with number of fish species, and the search rate was not significantly correlated with any of the fish availability variables. Fish availability appears, thus, to have a greater effect on male fish-eagle foraging success than on foraging rates.

Female foraging rates and foraging success were less correlated with fish availability, but we recorded fewer female foraging events than male foraging events. The negative correlations between average fish weight and % kills/stoop or % kills/strike may indicate that females are less likely to catch large fish than small fish after stooping or striking the water.

The early morning peak in foraging intensity that we observed also has been observed in Madagascar fish-eagles by Razafindramanana (1995) and in bald eagles (Steenhof et al. 1980, Mersmann 1989) and ospreys (*Pandion haliaetus*) (Flemming and Smith 1990). This peak may result from hunger after fasting overnight or from eagles taking advantage of greater fish availability and calmer weather during the early morning hours. Foraging intensity in this study did not peak until after 0900, possibly because frequent early morning fog prohibited earlier foraging as Razafindramanana (1995) suggested. The reasons for the early afternoon peak in foraging are less clear. Whitfield and Blaber (1978) observed a midday foraging peak in African fish-eagles (*Haliaeetus vocifer*) and suggested that they were taking advantage of thermals at this time, but the Madagascar fish-eagles that we observed foraged mostly low over the water from a perch. A more likely explanation for the early afternoon peak in foraging is that fish-eagles get hungry again after the fish that they caught early in the morning has passed. The early and late peaks in foraging success that we observed may have resulted from greater fish availability and calmer conditions at these times.

Dietary Preference

The results suggest that Madagascar fish-eagles prefer *Ophicephalus striatus* to other fish and avoid *Cyprinus carpio*. *O. striatus*, the largest of which we estimated at between 1 and 1.5 kg, were the largest fish that I saw fish-eagles capture. This species is a predatory fish that was introduced to Madagascar in 1978 (Reinthal and Stiassny 1991).

The three occasions on which we observed fish-eagles capture *O. striatus*, occurred in shallow (< 0.5 m) water near the shore, and the eagles were only able to carry the fish a short distance to land until they had eaten a substantial portion of it. On the seven occasions when we observed fish-eagles carrying *O. striatus*, which they had caught elsewhere, to the nest, the fish were already partially eaten. In field experiments, bald eagles selected large fish more often than smaller fish during the breeding season, but not during the non-breeding season (Jenkins and Jackman 1995), so Madagascar fish-eagle preference for *O. striatus* may reflect the eagle's greater energy requirements during the breeding season. The fish-eagles in the study did not exhibit any preference for *Heterotis niloticus*, another large introduced fish species, but this species was present in only three (33.3%) of the nine lakes. Fish-eagles may catch few *C. carpio* because this species feeds on the bottom of lakes and in shallow, muddy water (Scott and Crossman 1973) where it is less available and less visible for eagles to catch.

The results also may indicate biases in the fish availability data. *O. striatus*, as a visually oriented predator, may be better at avoiding entanglement in gill nets than the other fish species. All of the *C. carpio* availability data were from a single lake where I caught 33 individuals. This lake was so shallow (0.9 m) that both gill nets extended to the bottom and were, thus, more likely to catch bottom-dwelling fish such as *C. carpio*. The use and availability data for tilapia, the most abundant fish in all of the lakes, were in close concordance (64.7% of identifiable fish-eagle catch and 66.3% of gill net catch). Tilapia were introduced to Madagascar for aquaculture in the 1950s (Kiener 1963) and have since spread to most bodies of freshwater throughout the island. The predominance of tilapia in the fish-eagle’s diet in this study suggests that the Madagascar fish-eagle is an opportunistic predator that catches whatever prey species are most available. The marked change in species composition of Madagascar’s freshwater fish fauna resulting from exotic species introductions (Loiselle 1993, Reinthal et al. 1995), thus, may not have been detrimental to the island’s fish-eagle population. It is not known, however, whether the change from native fish species to predominantly introduced fish species has made it more difficult for the Madagascar fish-eagle to meet its energy requirements. The positive relationship between fish-eagle foraging success and fish availability suggests that the fish-eagle population is likely to be adversely affected by general declines in fish populations.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

My results indicate that Madagascar fish-eagles require bodies of water with large, accessible shoreline trees and an ample fish population. The trees that fish-eagles use for nesting and perching are among the tallest, most accessible shoreline trees available. They breed near lakes that have more suitable shoreline perch trees than unused lakes, and they construct their nests along sections of shoreline that have more perch trees than unused sections of shoreline. There may, however, be an upper limit to the number of tall trees that will increase the probability of fish-eagles using a particular lake. Bald eagles in the Pacific Northwest prefer to nest in forest stands that have trees of different ages and heights, rather than in dense stands of trees of similar age, such as plantations (Anthony et al. 1982).

Fish numbers, biomass, and species diversity are greater at lakes where fish-eagles breed than at lakes where they do not occur. Fish-eagle foraging success was positively associated with number of fish, total fish weight, and number of fish species caught in gill nets. The Madagascar fish-eagle appears to be an opportunistic predator. Introduced tilapia made up the majority of both the gill net catch and the observed fish-eagle catch in similar proportion. Although the introduction and establishment of exotic fish species probably has not contributed to the fish-eagle's decline, reductions in fish numbers, biomass, and species diversity may further diminish an already declining fish-eagle population.

The models presented can be used both to identify areas of unoccupied suitable fish-eagle habitat and high conservation priority areas of occupied habitat. The Peregrine Fund is developing means to augment the Madagascar fish-eagle population (Watson et al. 1996) and seeks areas of unoccupied fish-eagle habitat where young eagles may be released. The Madagascar fish-eagle is strongly territorial (Razafindramanana 1995), and adult eagles will likely chase away juveniles that are introduced into the home range of territorial adults. The models can be used to identify suitable lakes and, for larger lakes, to identify areas of suitable shoreline for releasing eagles. Although I did not measure fish-eagle habitat characteristics at rivers, mangrove swamps, or offshore islands, the criteria for fish-eagle habitat suitability, namely a sufficient number of shoreline perch trees and a sufficient fish population, may apply equally well in these areas. The bald eagle (Andrew and Mosher 1982), white-tailed sea eagle (Shiraki 1994), and African fish-eagle (Brown 1980) all have similar requirements for tall trees near water and bodies of water with an adequate, available prey base, so these habitat characteristics appear to be requirements of *Haliaeetus* eagles in general.

Lakes in the Antsalova region, especially those along the margins of the Tsimembo Forest where the densest breeding fish-eagle population is found (Rabarisoa et al. 1997), should receive the highest conservation priority. Some of my largest gill net catches were at these lakes, and the lakes are surrounded by dense dry deciduous forest that provides good perching habitat. There are large forested areas along the Tsiribihina

River east of Belo-sur-Tsiribihina (19°42'S, 44°33'E), but my gill net catches were much lower there than in the Antsalova region. I had large gill net catches at lakes in the Besalampy (16º45'S, 44º29'E) region. There is less forest cover in this region than in the Antsalova region (personal observation), but there still were sufficient numbers of perch trees along the lakeshores. Except for this study, the Besalampy region has not been censused (Rabarisoa et al. 1997). I recommend further investigation into the extent of suitable fish-eagle habitat in this region.

One area for future research is the relationship between fish-eagle habitat suitability and nesting success. Unfortunately, because I wanted to sample as many lakes as possible within one season, I only was able to visit most lakes once, and, thus, was unable to collect data on nesting success. Watson et al. (1997) believe that the Madagascar fish-eagle may have evolved delayed natal dispersal as a result of intense competition for nesting territories in an island species with limited habitat availability and a limited ability to disperse beyond the island. If the Madagascar fish-eagle exhibits strong site fidelity, it may be nesting in areas that once were suitable but have been rendered unsuitable for breeding as local habitat conditions have been degraded in recent years. Also, habitat characteristics that fish-eagles select may no longer reflect sites that can support reproduction because of human-induced habitat changes.

I recommend investigation of the effects of human-induced habitat changes on Madagascar’s wetlands, especially along the west coast where human population pressure is less intense and relatively intact wetlands remain (Langrand and Goodman 1995). As human populations increase, siltation and conversion of wetlands for rice production will increase as well. It is unclear from my study to what extent these changes threaten the Madagascar fish-eagle population. Aquatic habitat degradation may have a greater effect on species that rely on shallow water habitats, such as the Bernier's teal (*Anas bernieri*) (Green et al. 1994). All freshwater fish species depend on wetlands to some degree, and many species spawn in wetlands bordering lakes (Mitsch and Gosselink 1993). Madagascar's wetlands should receive better representation within the island's system of protected areas.

Conservation efforts aimed at preventing the extinction of the Madagascar fish-eagle should focus not only on the needs of the fish-eagle but also on the needs of other rare, sensitive, or threatened organisms that depend on wetland habitats in western Madagascar. These efforts should also consider the needs of the local human population. Because most of western Madagascar is remote, and funds and infrastructure for conservation are limited, fish-eagle management efforts will depend on the cooperation of the people who share the lakes and wetland habitats with the fish-eagle. Monitoring and management of freshwater fish populations and education of the local people in sustainable use of natural resources, including fish and large shoreline trees, are necessary to prevent further habitat degradation and fish population reductions. Management of freshwater fisheries can best be achieved by lending support to existing tribal regulations rather than imposing new regulations. The Sakalava tribe were effectively managing fish harvests at lakes in the Antsalova region until the recent mass immigration of people from other tribes, who did not respect local fishing seasons or net mesh size limits. Consequently, the fish stock and average size of fish caught in this region are rapidly diminishing (Andrian-Harivelo 1995). As Madagascar's human population continues to increase rapidly, and people migrate to western Madagascar from other parts of the island, it will become more essential for people to use the local resources without depleting them for future generations. The best habitat for Madagascar fish-eagles, clear, forested lakes with thriving fish populations, is also the best habitat for people living on these lakes. Conservation action designed to ensure the fish-eagle's survival, thus, ultimately also will ensure the survival of the human population in western Madagascar.

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TABLES

Table 1. Mean values of characteristics of Madagascar fish-eagle nest trees (n = 38) and random trees (n = 38) in the region of Antsalova, Madagascar, 1994.

Characteristic	$\bar{x}$	SE	Range	P^1
Dbh (cm)				
Nest trees	86.9	9.1	29.0 - 245.0	**0.0001**
Random trees	44.7	5.1	22.0 - 178.0	
Height (m)				
Nest trees	18.4	0.6	10.7 - 25.9	**0.0001**
Random trees	11.0	0.7	5.0 - 23.3	
# of branches				
Nest trees	5.8	0.6	1 - 17	**0.013**
Random trees	3.8	0.7	0 - 19	
Arc of accessibility (°)				
Nest trees	347.6	4.3	265 - 360	**0.0001**
Random trees	255.1	18.7	0 - 360	

[1] Wilcoxon signed rank test probability value.

Table 2. Species of nest trees and random trees in the region of Antsalova, Madagascar, 1994, including all trees measured (*n* = 38) and only the most recently used tree in each area (*n* = 24).

	n = 38		*n* = 24	
Tree species, family	Nest trees	Random trees	Nest trees	Random trees
Tamarindus indica, Cesalpinaceae	10	13	7	5
Adansonia sp., Bombaceae	5	0	2	0
Cordyla madagascariensis, Cesalpinaceae	4	0	4	0
Colvillea racemosa, Cesalpinaceae	2	0	2	0
Neobeguea mahafaliensis, Meliaceae	2	0	2	0
Acacia sp., Mimosaceae	2	0	1	0
Albizia greveana, Mimosaceae	2	0	1	0
Alleanthus greveanus, Moraceae	2	0	1	0
Unidentified mangrove, Unknown	2	1	1	1
Foetidia sp., Lecythidaceae	1	0	0	0
Strychnos madagascariensis, Loganiaceae	1	0	0	0
Cedrelopsis grevei, Meliaceae	1	0	0	0
Quivisanthe papinae, Meliaceae	1	0	0	0
Ficus baroni, Moraceae	1	0	1	0
Pandanus sp., Pandanaceae	1	0	1	0

Table 2 continued.

	n = 38		*n* = 24	
Tree species, family	Nest trees	Random trees	Nest trees	Random trees
Unidentified tree, Unknown	1	3	1	2
Dalbergia sp., Fabaceae	0	4	0	2
Poupartia sylvatica, Anacardiaceae	0	3	0	3
Terminalia sp., Combretaceae	0	2	0	2
Terminalia calcicola, Combretaceae	0	1	0	0
Stereospermum euphoriodes, Bignoniaceae	0	1	0	1
Delonix boiviniana, Cesalpinaceae	0	1	0	1
Diospyros sakalavarum, Ebenaceae	0	1	0	1
Securinega perrieri, Euphorbiaceae	0	1	0	1
Albizia lebbeck, Mimosaceae	0	1	0	1
Albizia sp., Mimosaceae	0	1	0	1
Ficus cocculifolia, Moraceae	0	1	0	1
Borassus madagascariensis, Palmaceae	0	1	0	0
Adenia microphylla, Passifloraceae	0	1	0	0
Rhopalocarpus lucidus, Rhopalocarpaceae	0	1	0	1
Hymenodictyon decarianum, Rubiaceae	0	1	0	1

Table 3. Logistic regression[1] parameter estimates for Madagascar fish-eagle nest tree use based on tree height, number of unobstructed branches, and arc of accessibility in the region of Antsalova, Madagascar, 1994.

	Parameter estimates			
Variable	Beta	SE	χ^2	*P*
Intercept	-13.30	3.50	14.42	0.0001
Tree height	0.51	0.13	16.00	0.0001
# of branches	-0.23	0.11	4.69	0.030
Arc of accessibility	0.02	0.01	6.73	0.010

[1] The logistic regression equation is:

$$\theta = 1 / (1 + \exp [-\{\beta_0 + \sum_{j=1}^{k} \beta_j x_{ij}\}]) \quad i = 1, 2, \ldots , n$$

where θ is the probability of fish-eagle use, β_0 is the beta value of the intercept, β_j is the beta value of the j dependent variables, and x_{ij}'s are the data values for the k independent variables.

Table 4. Logistic regression classification table for Madagascar fish-eagle nest tree use based on tree height, number of unobstructed branches, and arc of accessibility in the region of Antsalova, Madagascar, 1994.

	Predicted tree use		Total correct	
Observed tree use	Used	Unused	Total	%
Used	32	6	38	84.2
Unused	5	33	38	86.8
Total	37	39	76	
% correct	86.5	84.6		85.5

Table 5. Mean values of characteristics of Madagascar fish-eagle nest trees (n = 24) and random trees (n = 24), including only the most recently used tree in each area, in the region of Antsalova, Madagascar, 1994.

Characteristic	$\bar{x}$	SE	Range	P^1
Dbh (cm)				
Nest trees	87.8	11.8	29.0 - 245.0	**0.0002**
Random trees	38.4	4.2	22.0 - 114.0	
Height (m)				
Nest trees	18.7	0.8	10.7 - 25.9	**0.0001**
Random trees	10.5	0.9	5.0 - 23.3	
# of branches				
Nest trees	5.5	0.7	1 - 14	**0.021**
Random trees	3.2	0.8	0 - 19	
Arc of accessibility (°)				
Nest trees	346.7	5.4	265 - 360	**0.0009**
Random trees	260.2	25.0	0 - 360	

[1] Wilcoxon signed rank test probability value.

Table 6. Logistic regression[1] parameter estimates for Madagascar fish-eagle nest tree use based on tree height, including only the most recently used tree in each area, in the region of Antsalova, Madagascar, 1994.

	Parameter estimates			
Variable	Beta	SE	χ^2	*P*
Intercept	-5.52	1.48	13.86	0.0002
Tree height	0.38	0.10	14.57	0.0001

[1] The logistic regression equation is:

$$\theta = 1 / (1 + \exp [-\{\beta_0 + \sum_{j=1}^{k} \beta_j x_{ij}\}]) \quad i = 1, 2, \ldots , n$$

where θ is the probability of fish-eagle use, β_0 is the beta value of the intercept, β_j is the beta value of the j dependent variables, and x_{ij}'s are the data values for the k independent variables.

Table 7. Logistic regression classification table for Madagascar fish-eagle nest tree use based on tree height in the region of Antsalova, Madagascar, 1994. Only the most recently used tree in each area was included.

	Predicted tree use		Total correct	
Observed tree use	Used	Unused	Used	Unused
Used	20	4	24	83.3
Unused	4	20	24	83.3
Total	24	24	48	
% correct	83.3	83.3		83.3

Table 8. Mean values of characteristics of Madagascar fish-eagle nest sites (*n* = 38) and random sites (*n* = 38) in the region of Antsalova, Madagascar, 1994.

Characteristic	$\bar{x}$	SE	Range	P^1
Distance to disturbance (km)				
Nest sites	0.8	0.1	0 - 2.8	0.788
Random sites	0.8	0.1	0 - 2.8	
Distance to building (km)				
Nest sites	1.7	0.3	0.1 - 7.7	0.892
Random sites	1.6	0.2	0 - 5.6	
Distance to road (km)				
Nest sites	1.6	0.3	0 - 8.4	**0.018**
Random sites	1.1	0.2	0 - 5.4	
Distance to nearest nest (km)				
Nest sites	4.4	0.8	1.0 - 20.3	0.154
Random sites	4.1	0.8	0.4 - 20.1	
Shoreline within 300 m (km)				
Nest sites	0.7	0.1	0.1 - 1.6	0.601
Random sites	0.8	0.1	0.3 - 1.8	

Table 8 continued.

Characteristic	$\bar{x}$	SE	Range	P[1]
# of perch trees				
Nest sites	29.7	1.8	10 - 53	**0.0004**
Random sites	20.2	1.9	0 - 59	

[1] Wilcoxon signed rank test probability value.

Table 9. Logistic regression[1] parameter estimates for Madagascar fish-eagle nest site use based on number of suitable perch trees within an adjacent 250 by 50 m shoreline section in the region of Antsalova, Madagascar, 1994.

	Parameter estimates			
Variable	Beta	SE	χ^2	*P*
Intercept	-1.86	0.64	8.49	0.004
# of perch trees	0.08	0.02	9.67	0.002

[1] The logistic regression equation is:

$$\theta = 1 / (1 + \exp [-\{\beta_0 + \sum_{j=1}^{k} \beta_j x_{ij}\}]) \quad i = 1, 2, \ldots , n$$

where θ is the probability of fish-eagle use, β_0 is the beta value of the intercept, β_j is the beta value of the j dependent variables, and x_{ij}'s are the data values for the k independent variables.

Table 10. Logistic regression classification table for Madagascar fish-eagle nest site use based on number of suitable perch trees within an adjacent 250 by 50 m shoreline section in the region of Antsalova, Madagascar, 1994.

	Predicted site use		Total correct	
Observed site use	Used	Unused	Total	%
Used	22	16	38	57.9
Unused	12	26	38	68.4
Total	34	42	76	
% correct	64.7	61.9		63.2

Table 11. Mean values of characteristics of Madagascar fish-eagle nest sites (*n* = 24) and random sites (*n* = 24), including only the most recently used site in each area, in the region of Antsalova, Madagascar, 1994.

Characteristic	$\bar{x}$	SE	Range	P^1
Distance to disturbance (km)				
Nest sites	0.8	0.2	0 - 2.8	0.742
Random sites	0.9	0.1	0 - 2.8	
Distance to building (km)				
Nest sites	1.8	0.4	0.1 - 7.7	0.814
Random sites	1.8	0.3	0 - 5.6	
Distance to road (km)				
Nest sites	1.7	0.4	0 - 8.4	0.055
Random sites	1.3	0.3	0 - 5.4	
Distance to nearest nest (km)				
Nest sites	4.8	0.9	1.3 - 20.3	0.104
Random sites	4.3	0.9	0.4 - 20.1	
Shoreline within 300 m (km)				
Nest sites	0.8	0.1	0.2 - 1.6	0.923
Random sites	0.8	0.1	0.3 - 1.8	

Table 11 continued.

Characteristic	$\bar{x}$	SE	Range	P^1
# of perch trees				
Nest sites	30.8	2.3	10 - 53	**0.0001**
Random sites	16.6	1.9	0 - 33	

[1] Wilcoxon signed rank test probability value.

Table 12. Logistic regression[1] parameter estimates for Madagascar fish-eagle nest site use based on number of suitable perch trees within an adjacent 250 by 50 m shoreline section, including only the most recently used site in each area, in the region of Antsalova, Madagascar, 1994.

	Parameter estimates			
Variable	Beta	SE	χ^2	*P*
Intercept	-3.49	1.12	9.76	0.002
# of perch trees	0.15	0.05	10.61	0.001

[1] The logistic regression equation is:

$$\theta = 1 / (1 + \exp [-\{\beta_0 + \sum_{j=1}^{k} \beta_j x_{ij}\}]) \quad i = 1, 2, ... , n$$

where θ is the probability of fish-eagle use, β_0 is the beta value of the intercept, β_j is the beta value of the j dependent variables, and x_{ij}'s are the data values for the k independent variables.

Table 13. Logistic regression classification table for Madagascar fish-eagle nest site use based on number of suitable perch trees within an adjacent 250 by 50 m shoreline section in the region of Antsalova, Madagascar, 1994. Only the most recently used site in each area was included.

	Predicted site use		Total correct	
Observed site use	Used	Unused	Total	%
Used	17	7	24	70.8
Unused	6	18	24	75.0
Total	23	25	48	
% correct	73.9	72.0		72.9

Table 14. Mean values of characteristics of Madagascar fish-eagle perch trees (*n* = 38) and random trees (*n* = 38) in the region of Antsalova, Madagascar, 1994.

Characteristic	$\bar{x}$	SE	Range	P^1
Dbh (cm)				
Perch trees	65.3	7.2	27 - 270	**0.0001**
Random trees	36.9	3.3	21 - 120	
Height (m)				
Perch trees	16.7	0.8	9.4 - 30.3	**0.0001**
Random trees	9.8	0.4	4.9 - 15.8	
# of branches				
Perch trees	7.9	1.2	2 - 39	**0.0001**
Random trees	1.8	0.4	0 - 15	
Arc of accessibility (°)				
Perch trees	336.7	7.1	190 - 360	**0.0001**
Random trees	231.4	21.4	0 - 360	

[1] Wilcoxon signed rank test probability value.

Table 15. Species of perch trees and random trees in the region of Antsalova, Madagascar, 1994, including all trees measured ($n = 38$) and only the most recently used tree in each area ($n = 29$).

	$n = 38$		$n = 29$	
Tree species	Perch trees	Random trees	Perch trees	Random trees
Colvillea racemosa, Cesalpinaceae	6	0	5	0
Ficus cocculifolia, Moraceae	6	1	4	1
Neobeguea mahafaliensis, Meliaceae	4	0	3	0
Cordyla madagascariensis, Cesalpinaceae	3	1	2	0
Tamarindus indica, Cesalpinaceae	3	13	3	10
Albizia lebbeck, Mimosaceae	3	1	2	1
Borassus madagascariensis, Palmaceae	2	1	2	1
Unidentified, Unknown	2	2	2	1
Poupartia sylvatica, Anacardiaceae	1	0	0	0
Rhus perrieri, Anacardiaceae	1	0	0	0
Adansonia sp., Bombaceae	1	0	1	0
Cedrelopsis grevei, Meliaceae	1	1	1	1
Acacia sp., Mimosaceae	1	0	1	0
Alleanthus greveanus, Moraceae	1	0	0	0
Raphia sp, Palmaceae	1	0	1	0

Table 15 continued.

	n = 38		*n* = 29	
Tree species	Perch trees	Random trees	Perch trees	Random trees
Pandanus sp., Pandanaceae	1	1	1	1
Unidentified mangrove, Unknown	1	2	1	2
Poupartia caffra, Anacardiaceae	0	1	0	1
Terminalia calcicola, Combretaceae	0	1	0	0
Terminalia sp., Combretaceae	0	2	0	2
Securinega perrieri, Euphorbiaceae	0	5	0	4
Dalbergia sp., Fabaceae	0	1	0	0
Albizia bernieri, Mimosaceae	0	1	0	0
Pithecellobium dulce, Mimosaceae	0	1	0	1
Ziziphus mauritania, Rhamnaceae	0	1	0	1
Rhopalocarpus lucidus, Rhopalocarpaceae	0	1	0	1
Grevia sp., Tiliaceae	0	1	0	1

Table 16. Logistic regression[1] parameter estimates for Madagascar fish-eagle perch tree use based on tree height, arc of accessibility, and whether the tree was a snag in the region of Antsalova, Madagascar, 1994.

	Parameter estimates			
Variable	Beta	SE	χ^2	*P*
Intercept	-18.17	5.24	12.03	0.0005
Tree height	1.06	0.32	11.18	0.031
Arc of accessibility	0.02	0.01	6.59	0.0008
Snag	3.67	1.70	4.64	0.010

[1] The logistic regression equation is:

$$\theta = 1 / (1 + \exp [-\{\beta_0 + \sum_{j=1}^{k} \beta_j x_{ij}\}]) \qquad i = 1, 2, \ldots , n$$

where θ is the probability of fish-eagle use, β_0 is the beta value of the intercept, β_j is the beta value of the j dependent variables, and x_{ij}'s are the data values for the k independent variables.

Table 17. Logistic regression classification table for Madagascar fish-eagle perch tree use based on tree height, arc of accessibility, and whether the tree was a snag in the region of Antsalova, Madagascar, 1994.

	Predicted site use		Total correct	
Observed site use	Used	Unused	Total	%
Used	33	5	38	86.8
Unused	4	34	38	89.5
Total	37	39	76	
% correct	89.2	87.2		88.2

Table 18. Mean values of characteristics of Madagascar fish-eagle perch trees ($n = 29$) and random trees ($n = 29$), including only the most recently used tree in each area, in the region of Antsalova, Madagascar, 1994.

Characteristic	$\bar{x}$	SE	Range	P[1]
Dbh (cm)				
Perch trees	68.1	9.3	27 - 270	**0.005**
Random trees	38.0	4.2	21 - 120	
Height (m)				
Perch trees	16.8	1.0	9.4 - 30.3	**0.0001**
Random trees	9.5	0.5	4.9 - 15.8	
# of branches				
Perch trees	6.8	1.0	2 - 22	**0.0001**
Random trees	1.9	0.6	0 - 15	
Arc of accessibility (°)				
Perch trees	336.0	9.0	190 - 360	**0.001**
Random trees	249.8	25.1	0 - 360	

[1] Wilcoxon signed rank test probability value.

Table 19. Logistic regression[1] parameter estimates for Madagascar fish-eagle perch tree use based on tree height, including only the most recently used tree in each area, in the region of Antsalova, Madagascar, 1994.

	Parameter estimates			
Variable	Beta	SE	χ^2	*P*
Intercept	-8.68	2.34	13.75	0.0002
Tree height	0.71	0.19	13.53	0.0002

[1] The logistic regression equation is:

$$\theta = 1 / (1 + \exp [-\{\beta_0 + \sum_{j=1}^{k} \beta_j x_{ij}\}]) \qquad i = 1, 2, \ldots , n$$

where θ is the probability of fish-eagle use, β_0 is the beta value of the intercept, β_j is the beta value of the j dependent variables, and x_{ij}'s are the data values for the k independent variables.

Table 20. Logistic regression classification table for Madagascar fish-eagle perch tree use based on tree height in the region of Antsalova, Madagascar, 1994. Only the most recently used tree in each area was included.

	Predicted tree use		Total correct	
Observed tree use	Used	Unused	Total	%
Used	25	4	29	86.2
Unused	5	24	29	82.8
Total	30	28	58	
% correct	83.3	85.7		84.5

Table 21. Mean values of characteristics of lakes occupied by resident Madagascar fish-eagle pairs (*n* = 15) and unoccupied lakes (*n* = 19) in the region of Antsalova, Madagascar, 1994.

Characteristic	$\bar{x}$	SE	Range	P^1
Average depth, m				
Occupied lakes	2.2	0.2	1.1 - 4.2	**0.002**
Unoccupied lakes	1.4	0.2	0.6 - 4.1	
Clarity: depth of Secchi disk, cm				
Occupied lakes	78.0	10.7	36 - 180	**0.004**
Unoccupied lakes	44.7	5.5	7 - 106	
Number of fish species				
Occupied lakes	7.9	0.9	3 - 14	**0.046**
Unoccupied lakes	5.3	0.6	1 - 9	
Nearest village, km				
Occupied lakes	1.1	0.3	0 - 3.9	0.768
Unoccupied lakes	1.3	0.3	0 - 3.7	
Shoreline perimeter, km				
Occupied lakes	14.4	4.3	1.8 - 61.2	0.099
Unoccupied lakes	7.0	1.7	2.3 - 33.7	

Table 21 continued.

Characteristic	$\bar{x}$	SE	Range	P^1
Surface area, km^2				
Occupied lakes	2.7	1.1	<0.1 - 14.8	0.450
Unoccupied lakes	1.0	0.5	0.1 - 10.3	
Dense forest along shoreline, km				
Occupied lakes	8.6	3.5	0 - 47.6	**0.009**
Unoccupied lakes	1.3	0.6	0 - 10.2	
Open forest along shoreline, km				
Occupied lakes	2.3	0.8	0 - 10.2	0.972
Unoccupied lakes	2.1	0.5	0 - 7.3	
Savanna along shoreline, km				
Occupied lakes	2.0	0.9	0 - 12.1	0.686
Unoccupied lakes	2.1	1.1	0 - 19.4	
Marsh along shoreline, km				
Occupied lakes	0.6	0.2	0 - 2.7	0.885
Unoccupied lakes	0.7	0.3	0 - 5.3	

Table 21 continued.

Characteristic	$\bar{x}$	SE	Range	P^1
Rice paddies along shoreline, km				
Occupied lakes	0.7	0.4	0 - 6.5	0.142
Unoccupied lakes	0.8	0.4	0 - 7.9	

[1] Wilcoxon rank sum test probability value.

Table 22. Mean values of characteristics of lakes occupied by resident Madagascar fish-eagle pairs (*n* = 32) and randomly selected unoccupied lakes (*n* = 32) between Morondava and Boriziny in western Madagascar, 1995.

Characteristic	$\bar{x}$	SE	Range	P^1
Maximum depth, m				
Occupied lakes	3.0	0.3	0.7 - 8.2	**0.002**
Unoccupied lakes	1.8	0.3	0.2 - 7.1	
Clarity: depth of Secchi disk, cm				
Occupied lakes	77.2	8.6	10 - 255	**0.003**
Unoccupied lakes	50.0	7.6	5 - 170	
Number of perch trees				
Occupied lakes	35.3	3.5	8 - 118	**0.001**
Unoccupied lakes	22.4	2.3	4 - 63	
Number of fish caught in gill nets				
Occupied lakes	19.5	3.7	2 - 74	**0.002**
Unoccupied lakes	7.8	1.5	0 - 36	
Total weight of fish catch, kg				
Occupied lakes	3.5	0.7	0.1 - 13.6	**0.002**
Unoccupied lakes	1.2	0.4	0 - 10.4	

Table 22 continued.

Characteristic	$\bar{x}$	SE	Range	P^1
Average weight of fish caught, g				
Occupied lakes	164.1	19.5	35 - 575	0.173
Unoccupied lakes	153.3	29.0	0 - 687	
Number of fish species in catch				
Occupied lakes	3.4	0.3	1 -7	**0.002**
Unoccupied lakes	1.9	0.2	0 - 5	
Shoreline perimeter, km				
Occupied lakes	13.8	2.7	0.9 - 61.2	0.136
Unoccupied lakes	7.0	1.1	0.9 - 26.9	
Surface area, km^2				
Occupied lakes	3.7	1.1	0.1 - 25.5	0.301
Unoccupied lakes	1.0	0.2	0.1 - 6.4	

[1] Wilcoxon rank sum test probability value.

Table 23. Mean catch per lake, mean total weight of fish catch, and % of lakes sampled where fish were caught (in parentheses) for each fish species caught during three-hour gill net sampling period at lakes occupied by Madagascar fish-eagles (*n* = 32) and unoccupied lakes (*n* = 32) between Morondava and Boriziny in western Madagascar, 1995.

Fish species, family	Mean catch per lake	SE	Mean weight of catch, g	SE
Oreochromis macrochir, Cichlidae				
Occupied lakes (96.9%)	10.97	2.25	1195.5	259.8
Unoccupied lakes (68.8%)	4.56	1.30	576.2	291.1
Tilapia zilii, Cichlidae				
Occupied lakes (56.3%)	2.53	0.82	289.6	111.1
Unoccupied lakes (25.0%)	1.22	0.67	108.6	48.6
Megalops cyprinoides, Megalopidae				
Occupied lakes (53.1%)	2.22	0.66	515.7	178.6
Unoccupied lakes (21.9%)	0.31	0.11	146.7	60.1
Heterotis niloticus, Osteoglossidae				
Occupied lakes (25.0%)	1.06	0.41	798.3	303.3
Unoccupied lakes (9.4%)	0.16	0.10	93.0	56.9
Chanos chanos, Chanidae				
Occupied lakes (18.8%)	0.84	0.53	262.3	137.3
Unoccupied lakes (6.3%)	0.38	0.26	109.1	90.1

Table 23 continued.

Fish species, family	Mean catch per lake	SE	Mean weight of catch, g	SE
Cyprinus carpio, Cyprinidae				
Occupied lakes (15.6%)	0.25	0.11	123.1	53.7
Unoccupied lakes (18.8%)	0.50	0.23	90.6	42.7
Arius madagascariensis, Ariidae				
Occupied lakes (18.8%)	0.28	0.12	39.2	17.5
Unoccupied lakes (6.3%)	0.16	0.13	12.2	8.7
Valamugil robustus, Mugilidae				
Occupied lakes (9.4%)	0.25	0.16	30.3	18.6
Unoccupied lakes (3.1%)	0.16	0.16	18.7	18.7
Ambassis gymnocephalus, Ambassidae				
Occupied lakes (9.4%)	0.41	0.34	20.6	17.5
Unoccupied lakes (0%)	0	0	0	0
Glossogobius giuris, Gobiidae				
Occupied lakes (3.1%)	0.03	0.03	5.3	5.3
Unoccupied lakes (18.8%)	0.25	0.10	47.8	22.1

Table 23 continued.

Fish species, family	Mean catch per lake	SE	Mean weight of catch, g	SE
Oreochromis mossambicus, Cichlidae				
Occupied lakes (6.3%)	0.19	0.13	50.8	37.4
Unoccupied lakes (0%)	0	0	0	0
Ophicephalus striatus, Channidae				
Occupied lakes (12.5%)	0.13	0.06	114.1	60.4
Unoccupied lakes (6.3%)	0.06	0.04	10.8	7.6
Paretroplus maculatus, Cichlidae				
Occupied lakes (6.3%)	0.13	0.10	14.1	13.2
Unoccupied lakes (0%)	0	0	0	0
Scatophagus tetracanthus, Scatophagidae				
Occupied lakes (3.1%)	0.03	0.03	2.0	2.0
Unoccupied lakes (3.1%)	0.06	0.06	1.1	1.1
Terapon jarbua, Teraponidae				
Occupied lakes (3.1%)	0.09	0.09	6.2	6.2
Unoccupied lakes (0%)	0	0	0	0

Table 23 continued.

Fish species, family	Mean catch per lake	SE	Mean weight of catch, g	SE
Carassius auratus, Cyprinidae				
Occupied lakes (3.1%)	0.03	0.03	2.0	2.0
Unoccupied lakes (0%)	0	0	0	0
Caranx sp., Carangidae				
Occupied lakes (3.1%)	0.03	0.03	3.4	3.4
Unoccupied lakes (0%)	0	0	0	0
Eleotris fusca, Eleotridae				
Occupied lakes (0%)	0	0	0	0
Unoccupied lakes (3.1%)	0.03	0.03	3.5	3.5

Table 24. Logistic regression[1] parameter estimates for Madagascar fish-eagle lake use, based on water clarity and number of fish species reported by local fishermen in the region of Antsalova, Madagascar, 1994.

	Parameter estimates			
Variable	Beta	SE	χ^2	*P*
Intercept	-5.35	1.88	8.11	0.004
Water clarity	0.05	0.02	5.64	0.018
# of fish species	0.37	0.18	4.33	0.038

[1] The logistic regression equation is:

$$\theta = 1 / (1 + \exp [-\{\beta_0 + \sum_{j=1}^{k} \beta_j x_{ij}\}]) \quad i = 1, 2, \ldots , n$$

where θ is the probability of fish-eagle use, β_0 is the beta value of the intercept, β_j is the beta value of the j dependent variables, and x_{ij}'s are the data values for the k independent variables.

Table 25. Logistic regression classification table for Madagascar fish-eagle lake use, based on water clarity and number of fish species reported by local fishermen in the region of Antsalova, Madagascar, 1994.

	Predicted lake use		Total correct	
Observed lake use	Used	Unused	Total	%
Used	10	5	15	66.7
Unused	5	14	19	73.7
Total	15	19	34	
% correct	66.7	73.7		70.6

Table 26. Logistic regression[1] parameter estimates for Madagascar fish-eagle lake use, based on number of shoreline perch trees and number of fish species caught in gill nets at lakes between Morondava and Boriziny in western Madagascar, 1995.

	Parameter estimates			
Variable	Beta	SE	χ^2	*P*
Intercept	-3.81	1.07	12.79	0.0003
# of perch trees	0.06	0.02	6.39	0.012
# of fish species	0.80	0.25	10.02	0.002

[1] The logistic regression equation is:

$$\theta = 1 / (1 + \exp [-\{\beta_0 + \sum_{j=1}^{k} \beta_j x_{ij}\}]) \quad i = 1, 2, ... , n$$

where θ is the probability of fish-eagle use, β_0 is the beta value of the intercept, β_j is the beta value of the j dependent variables, and x_{ij}'s are the data values for the k independent variables.

Table 27. Logistic regression classification table for Madagascar fish-eagle lake use based on number of shoreline perch trees and number of fish species caught in gill nets between Morondava and Boriziny in western Madagascar, 1995.

	Predicted lake use		Total correct	
Observed lake use	Used	Unused	Total	%
Used	25	7	32	78.1
Unused	8	24	32	75.0
Total	33	31	64	
% correct	75.8	77.4		76.6

Table 28. Logistic regression[1] parameter estimates for Madagascar fish-eagle lake use, based on number of shoreline perch trees and number of fish caught in gill nets at lakes between Morondava and Boriziny in western Madagascar, 1995.

	Parameter estimates			
Variable	Beta	SE	χ^2	*P*
Intercept	-2.72	0.82	11.04	0.0009
# of perch trees	0.07	0.02	8.03	0.005
# of fish	0.07	0.03	5.63	0.018

[1] The logistic regression equation is:

$$\theta = 1 / (1 + \exp [-\{\beta_0 + \sum_{j=1}^{k} \beta_j x_{ij}\}]) \quad i = 1, 2, \ldots , n$$

where θ is the probability of fish-eagle use, β_0 is the beta value of the intercept, β_j is the beta value of the j dependent variables, and x_{ij}'s are the data values for the k independent variables.

Table 29. Logistic regression classification table for Madagascar fish-eagle lake use, based on number of shoreline perch trees and number of fish caught in gill nets between Morondava and Boriziny in western Madagascar, 1995.

	Predicted lake use		Total correct	
Observed lake use	Used	Unused	Total	%
Used	23	9	32	71.9
Unused	7	25	32	78.1
Total	30	34	64	
% correct	76.7	73.5		75.0

Table 30. Logistic regression[1] parameter estimates for Madagascar fish-eagle lake use, based on number of shoreline perch trees and total weight of fish caught in gill nets at lakes between Morondava and Boriziny in western Madagascar, 1995.

	Parameter estimates			
Variable	Beta	SE	χ^2	*P*
Intercept	-2.43	0.76	10.27	0.001
# of perch trees	0.06	0.02	7.73	0.005
Total fish weight	0.0003	0.0001	6.22	0.013

[1] The logistic regression equation is:

$$\theta = 1 / (1 + \exp [-\{\beta_0 + \sum_{j=1}^{k} \beta_j x_{ij}\}]) \quad i = 1, 2, ... , n$$

where θ is the probability of fish-eagle use, β_0 is the beta value of the intercept, β_j is the beta value of the j dependent variables, and x_{ij}'s are the data values for the k independent variables.

Table 31. Logistic regression classification table for Madagascar fish-eagle lake use, based on number of shoreline perch trees and total weight of fish caught in gill nets between Morondava and Boriziny in western Madagascar, 1995.

	Predicted lake use		Total correct	
Observed lake use	Used	Unused	Total	%
Used	23	9	32	71.9
Unused	6	26	32	81.3
Total	29	35	64	
% correct	79.3	74.3		76.6

Table 32. Spearman correlations and probability values for test of H_0: $\rho = 0$ for number of fish caught in gill nets, total weight of catch, and number of fish species at 64 lakes sampled between Morondava and Boriziny in western Madagascar, 1995.

Variable	Total weight	Number of species
Number caught	0.868[1] 0.0001[2]	0.839 0.0001
Total weight	- -	0.827 0.0001

[1] Spearman correlation coefficient, ρ.

[2] Probability value for H_0: $\rho = 0$.

Table 33. Logistic regression[1] parameter estimates for Madagascar fish-eagle lake use, based on number of shoreline perch trees at lakes between Morondava and Boriziny in western Madagascar, 1995.

	Parameter estimates			
Variable	Beta	SE	χ^2	*P*
Intercept	-1.67	0.65	6.73	0.010
# of perch trees	0.06	0.02	7.71	0.006

[1] The logistic regression equation is:

$$\theta = 1 / (1 + \exp [-\{\beta_0 + \sum_{j=1}^{k} \beta_j x_{ij}\}]) \quad i = 1, 2, \ldots , n$$

where θ is the probability of fish-eagle use, β_0 is the beta value of the intercept, β_j is the beta value of the j dependent variables, and x_{ij}'s are the data values for the k independent variables.

Table 34. Logistic regression classification table for Madagascar fish-eagle lake use, based on number of shoreline perch trees between Morondava and Boriziny in western Madagascar, 1995.

	Predicted lake use		Total correct	
Observed lake use	Used	Unused	Total	%
Used	23	9	32	71.9
Unused	9	23	32	71.9
Total	32	32	64	
% correct	71.9	71.9		71.9

Table 35. Lakes included in Madagascar fish-eagle foraging ecology study in western Madagascar, May-August, 1996.

Lake	River basin	Dates observed	Nesting stage	Eagles present
Ambereny	none	22 - 28 May	not nesting[1]	1 male, 1 female
Bejijo	Manambolo	30 May - 5 June	pre-incubation	1 male, 1female, 1 juvenile
Ankazomena	Tsiribihina	8 - 15 June	incubation	1 male , 1 female
Asonjo	Tsiribihina	16 - 23 June	incubation	1 male, 1 female
Ampamandrika	Tsiribihina	27 June - 3 July	pre-incubation, incubation[2]	1 male, 1 female, 1 juvenile
Befotaka	Manambolo	7 - 12, 20 July	incubation, nestling[3]	2 males, 1 female
Masama	Beboka	13 - 19 July	nestling	2 males, 1 female, 1 juvenile
Bevoay	Manambolo	22 - 28 July	nestling	1 male, 2 females
Tsiandrora	Beboka	30 July - 4 Aug.	not nesting[4]	1 male, 1 female

[1] Ambereny eagles did not nest in 1996.

[2] Incubation of eggs began on 2 July at Ampamandrika nest.

[3] First egg hatched on 10 July at Befotaka nest.

[4] Unknown whether Tsiandrora eagles had already failed a nesting attempt or did not nest in 1996.

Table 36. Mean male and female Madagascar fish-eagle foraging rates and foraging success at nine lakes in western Madagascar, May-August, 1996.

Variable	$\bar{x}$, males	SE	$\bar{x}$, females	SE
Foraging rate				
searches/hour/eagle	0.68	0.15	0.35	0.26
stoops/hour/eagle	0.24	0.05	0.13	0.10
strikes/hour/eagle	0.17	0.04	0.07	0.04
kills/hour/eagle	0.10	0.03	0.03	0.01
Foraging success				
% stoops/search	36.3	3.4	30.5	10.8
% strikes/search	28.0	4.0	28.0	10.9
% kills/search	15.9	4.0	20.5	10.5
% strikes/stoop	77.5	8.3	60.0	16.3
% kills/stoop	43.6	8.4	40.5	13.6
% kills/strike	52.4	8.9	42.0	13.3

Table 37. Mean, standard error, and range of number of fish caught, total weight of catch, average weight of fish, and number of fish species in three three-hour gill net samples at nine lakes occupied by Madagascar fish-eagles in western Madagascar, May-August, 1996.

Variable	$\bar{x}$	SE	Range
Number of fish	30.1	7.3	4 - 66
Total weight, kg	4.6	1.6	0.2 - 15.9
Average weight, g	139.0	23.7	55.3 - 269.3
Number of species	3.9	0.4	2 - 6

Table 38. Spearman correlations between male Madagascar fish-eagle foraging variables and fish availability variables at nine lakes in western Madagascar May-August, 1996.

	Number of fish caught	Total weight of catch	Average fish weight	Number of species
Searches/hour/eagle	-0.300[1]	-0.033	0.200	0.035
	0.433[2]	0.932	0.606	0.929
Stoops/hour/eagle	-0.167	0.167	0.400	0.192
	0.668	0.668	0.286	0.620
Strikes/hour/eagle	0.033	0.300	0.167	0.560
	0.932	0.433	0.668	0.117
Kills/hour/eagle	0.283	0.500	0.183	**0.778**
	0.460	0.171	0.637	**0.014**
% stoops/search	0.367	0.350	0.100	0.586
	0.332	0.356	0.798	0.097
% strikes/search	**0.683**	**0.733**	0.117	**0.813**
	0.042	**0.025**	0.765	**0.008**
% kills/search	**0.667**	**0.800**	0.233	**0.909**
	0.050	**0.010**	0.546	**0.0007**
% strikes/stoop	0.153	0.179	-0.409	0.330
	0.694	0.645	0.275	0.385
% kills/stoop	0.619	**0.762**	0.201	**0.860**
	0.075	**0.017**	0.604	**0.003**
% kills/strike	**0.686**	**0.795**	0.402	**0.843**
	0.041	**0.010**	0.284	**0.004**

[1] Spearman correlation coefficient, ρ.

[2] Probability value for H_0: $\rho = 0$.

Table 39. Spearman correlations between female Madagascar fish-eagle foraging variables and fish availability variables at nine lakes in western Madagascar, May-August, 1996.

	Number of fish caught	Total weight of catch	Average fish weight	Number of species
Searches/hour/eagle	-0.218	-0.100	-0.025	-0.140
	0.574	0.797	0.949	0.719
Stoops/hour/eagle	-0.305	-0.237	-0.051	-0.320
	0.425	0.539	0.900	0.401
Strikes/hour/eagle	-0.305	-0.237	-0.051	-0.320
	0.425	0.539	0.900	0.401
Kills/hour/eagle	-0.237	-0.170	-0.102	-0.196
	0.539	0.663	0.795	0.614
% stoops/search	-0.271	-0.356	-0.170	-0.338
	0.480	0.347	0.663	0.374
% strikes/search	-0.203	-0.356	-0.356	-0.231
	0.600	0.347	0.347	0.549
% kills/search	-0.298	-0.417	-0.409	-0.263
	0.436	0.264	0.275	0.493
% strikes/stoop	-0.298	-0.447	-0.578	-0.254
	0.436	0.228	0.103	0.509
% kills/stoop	-0.453	-0.616	**-0.684**	-0.395
	0.221	0.078	**0.042**	0.293
% kills/strike	-0.453	-0.616	**-0.684**	-0.395
	0.221	0.078	**0.042**	0.293

[1] Spearman correlation coefficient, ρ.

[2] Probability value for H_0: $\rho = 0$.

Table 40. Fish caught (number and percentage of total) and number of lakes where fish were caught (out of nine) by Madagascar fish-eagles and in gill nets in western Madagascar, May-August, 1996.

	Fish-eagle catch			Gill net catch		
Fish species, family	# of fish	% of fish	# of lakes	# of fish	% of fish	# of lakes
Exotic						
tilapia[1], Cichlidae	44	44.4	9	183	67.5	9
Heterotis niloticus, Osteoglossidae	7	7.1	3	17	6.3	3
Cyprinus carpio, Cyprinidae	2	2.0	2	33	12.2	1 (2)[2]
Ophicephalus striatus, Channidae	10	10.1	6	1	0.4	1 (6)[2]
Native						
Megalops cyprinoides, Megalopidae	2	2.0	2	18	6.6	6 (1)[2]
Arius madagascariensis, Ariidae	3	3.0	3	14	5.2	5
Glossogobius giuris, Gobiidae	0	0	0	2	0.7	1
Ambassis gymnocephalus, Ambassidae	0	0	0	2	0.7	1
Scatophagus tetracanthus, Scatophagidae	0	0	0	1	0.4	1
Unidentified	31	31.3	8	0	0	0
TOTAL	99	100		271	100	

[1] Tilapia species included in order of decreasing gill net catch: *Oreochromis macrochir*, *Tilapia zilii*, *O. mossambicus*, and *O. niloticus*.

Table 40 continued.

[2] Number in parentheses represents additional lakes where each fish species was known to be present either from 1995 gill net sampling or from fish catches of local fishermen.

FIGURES

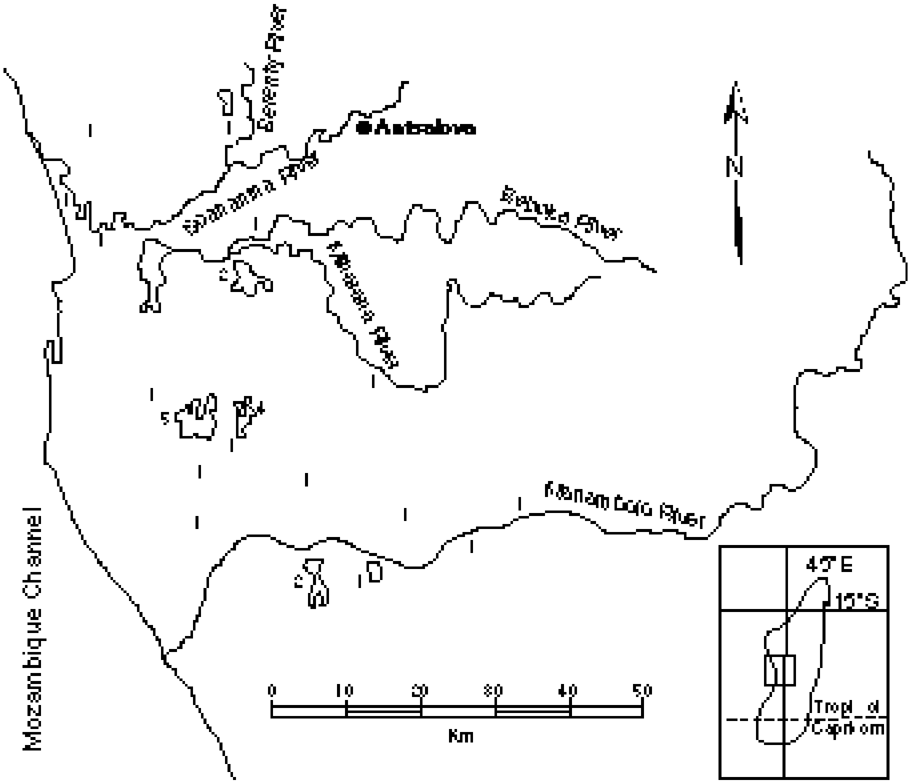

Figure 1. Study area in the Antsalova region of Madagascar, 1994. Numbers indicate locations of Madagascar fish-eagle pairs and number of pairs at each location.

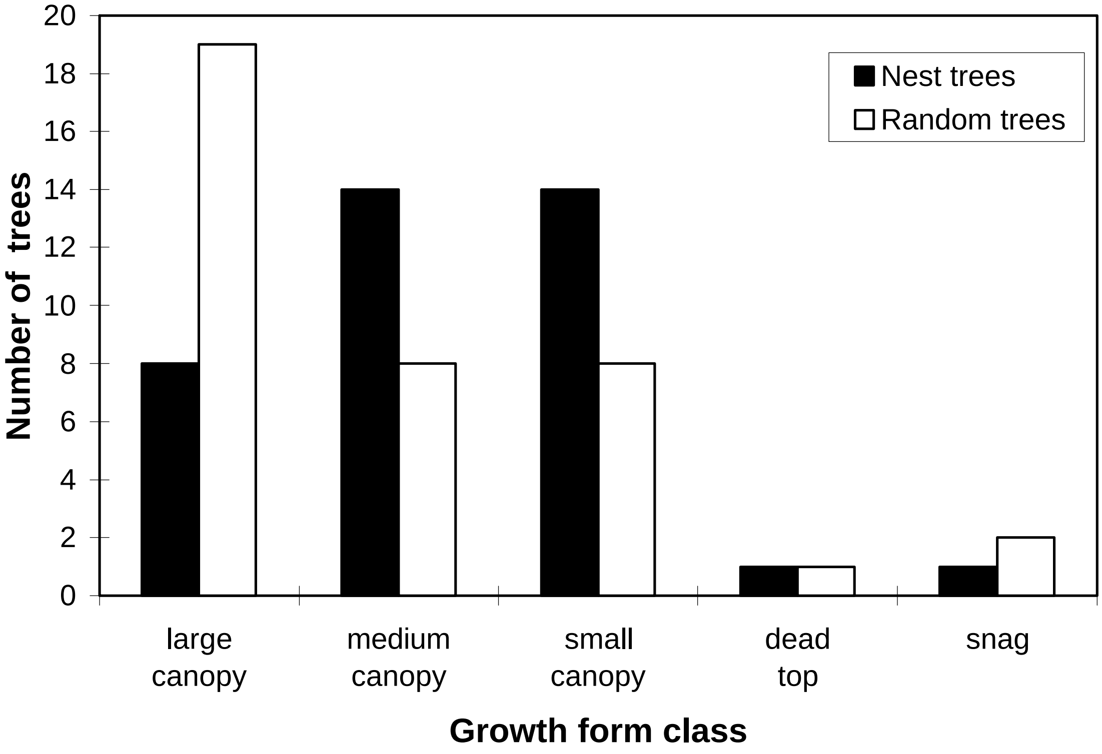

Figure 2. Number of Madagascar fish-eagle nest trees (*n* = 38) and random trees (*n* = 38) in each growth form class in the Antsalova region of Madagascar, 1994.

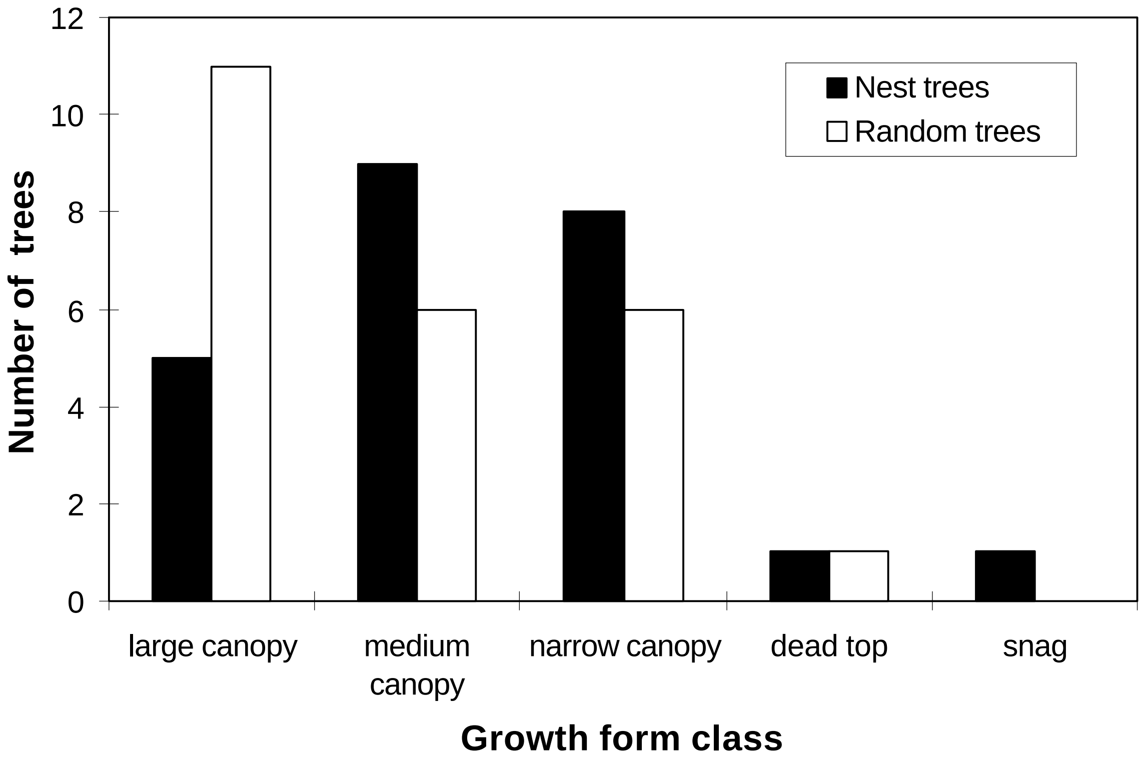

Figure 3. Number of Madagascar fish-eagle nest trees (*n* = 24) and random trees (*n* = 24) in each growth form class (including only the most recently used tree in each area) in the Antsalova region of Madagascar, 1994.

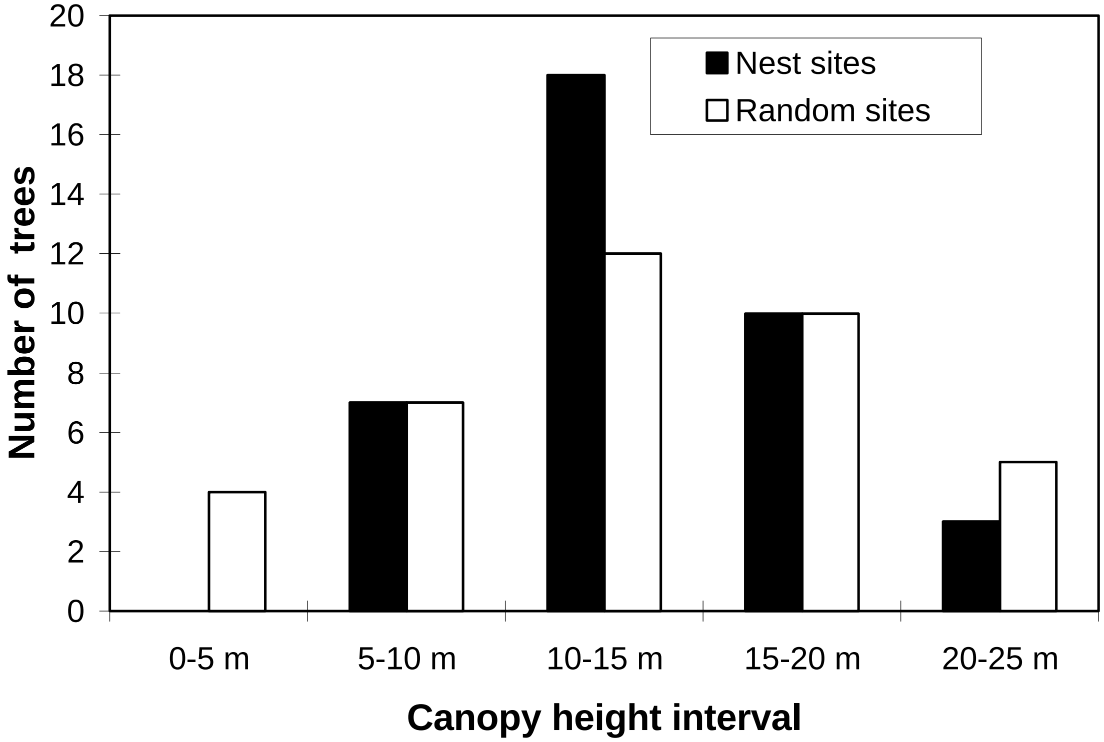

Figure 4. Number of Madagascar fish-eagle nest sites (n = 38) and random sites (n = 38) in each 5-m canopy height interval in the Antsalova region of Madagascar, 1994.

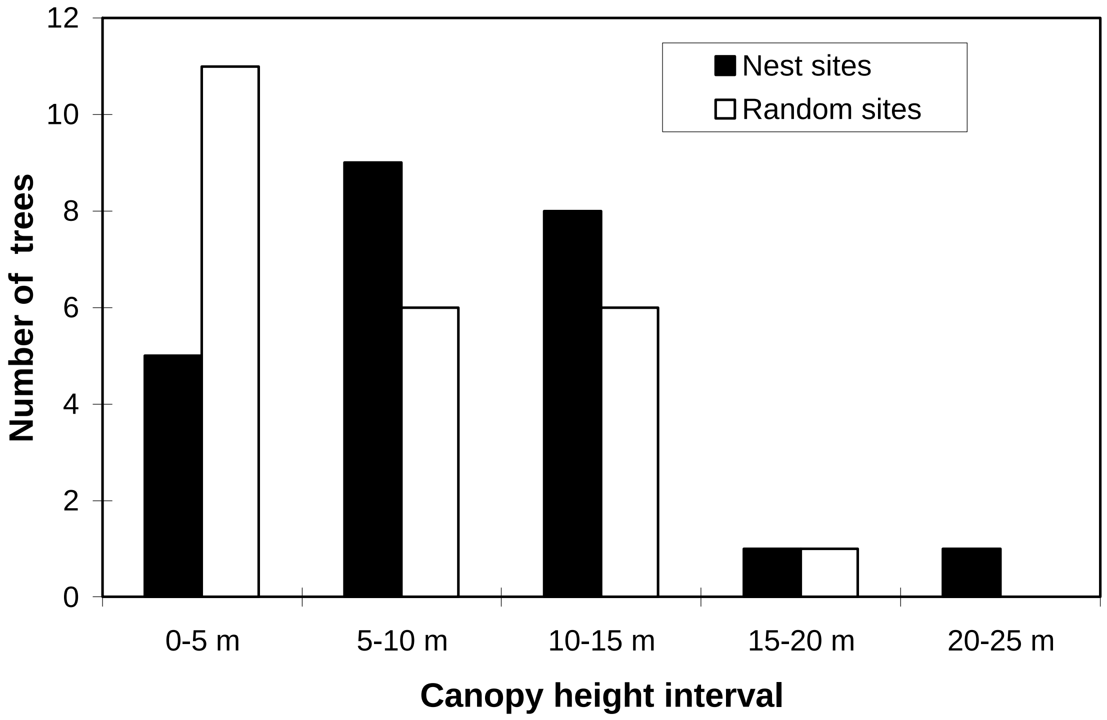

Figure 5. Number of Madagascar fish-eagle nest sites (*n* = 24) and random sites (*n* = 24) in each 5-m canopy height interval (including only the most recently used site in each area) in the Antsalova region of Madagascar, 1994.

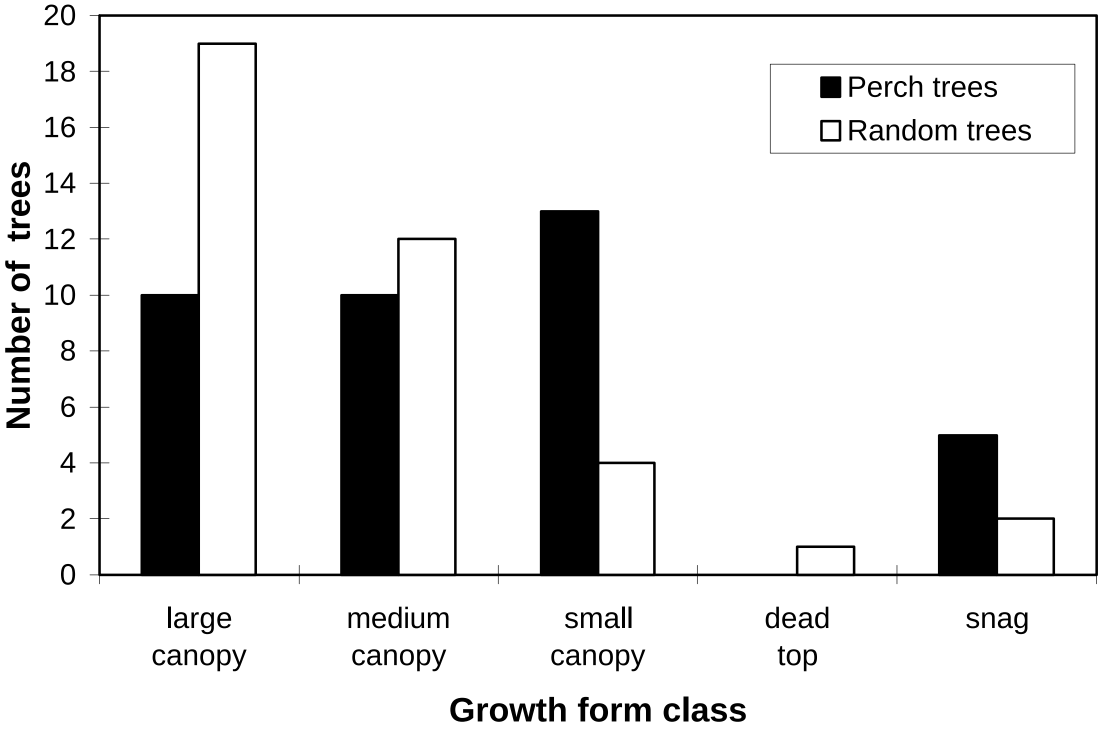

Figure 6. Number of Madagascar fish-eagle perch trees (*n* = 38) and random trees (*n* = 38) in each growth form class in the Antsalova region of Madagascar, 1994.

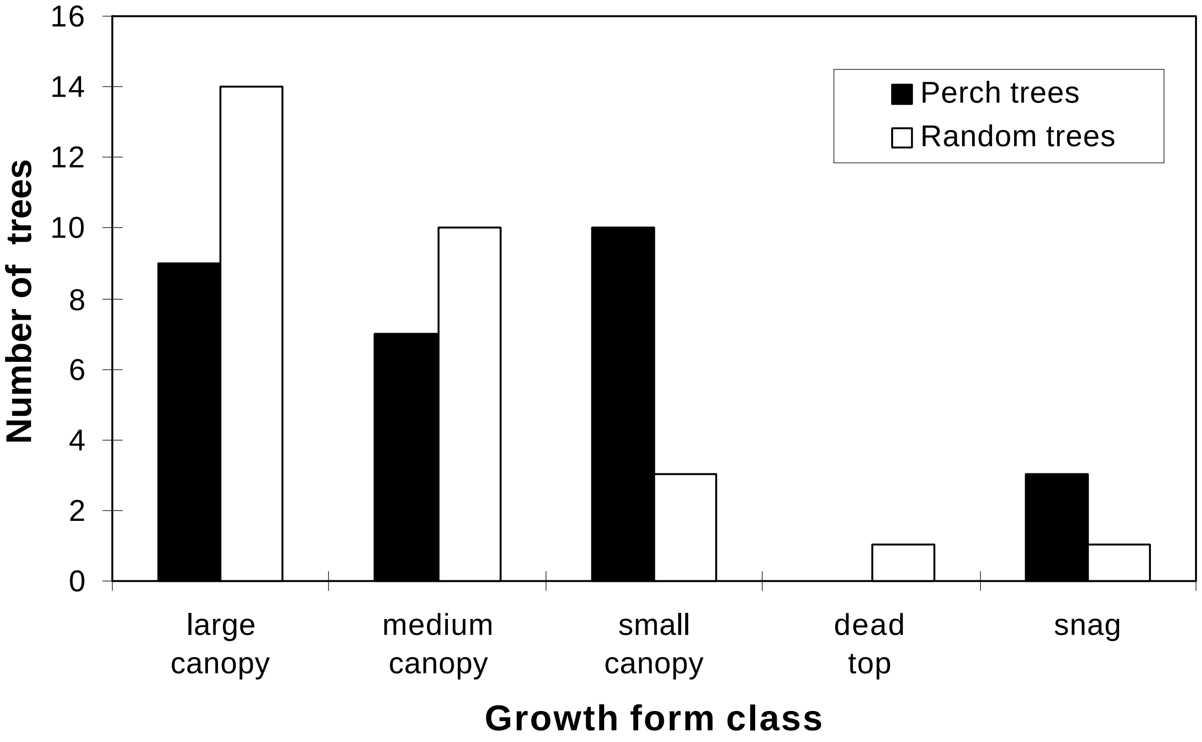

Figure 7. Number of Madagascar fish-eagle perch trees (*n* = 29) and random trees (*n* = 29) in each growth form class (including only the most recently used tree in each area) in the Antsalova region of Madagascar, 1994.

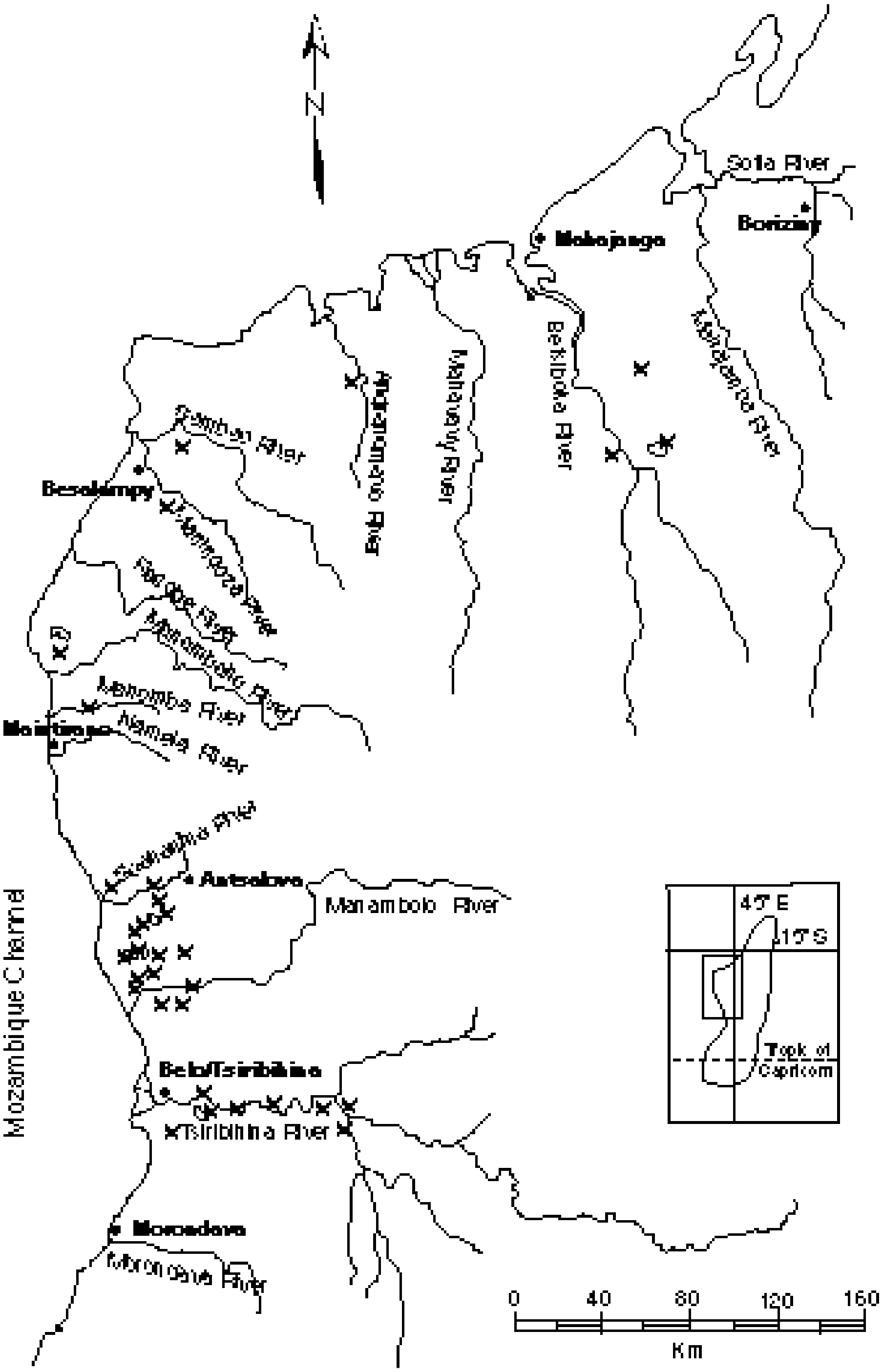

Figure 8. Study area between Morondava and Boriziny, Madagascar, 1995. Lakes occupied by Madagascar fish-eagles (*n* = 32) are marked with an “x”.

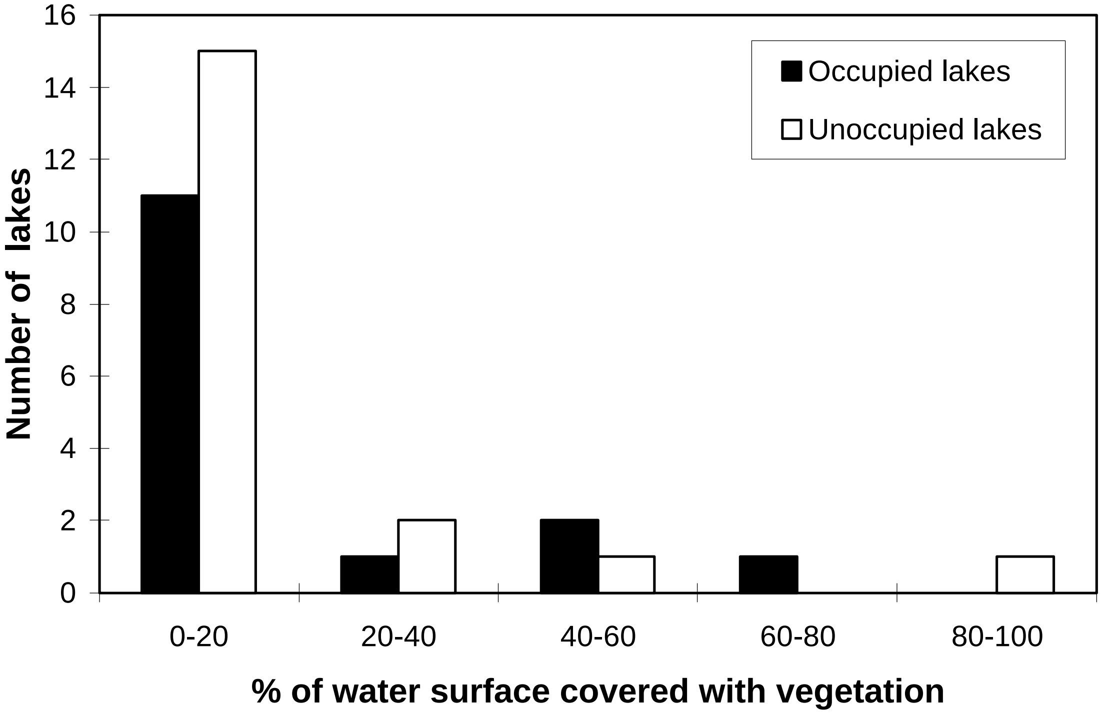

Figure 9. Percentage of water surface covered by aquatic vegetation at lakes occupied by Madagascar fish-eagles (*n* = 15) and unoccupied lakes (*n* = 19) in the Antsalova region of Madagascar, 1994.

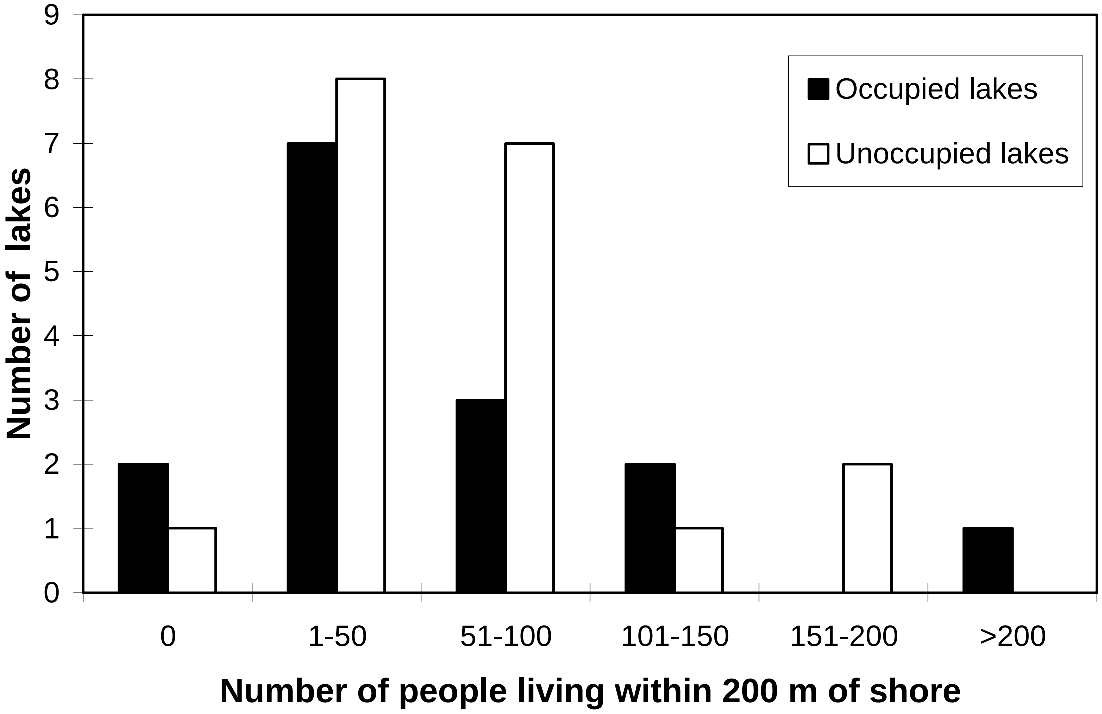

Figure 10. Number of people living within 200 m of the shore at lakes occupied by Madagascar fish-eagles (*n* = 15) and unoccupied lakes (*n* = 19) in the Antsalova region of Madagascar, 1994.

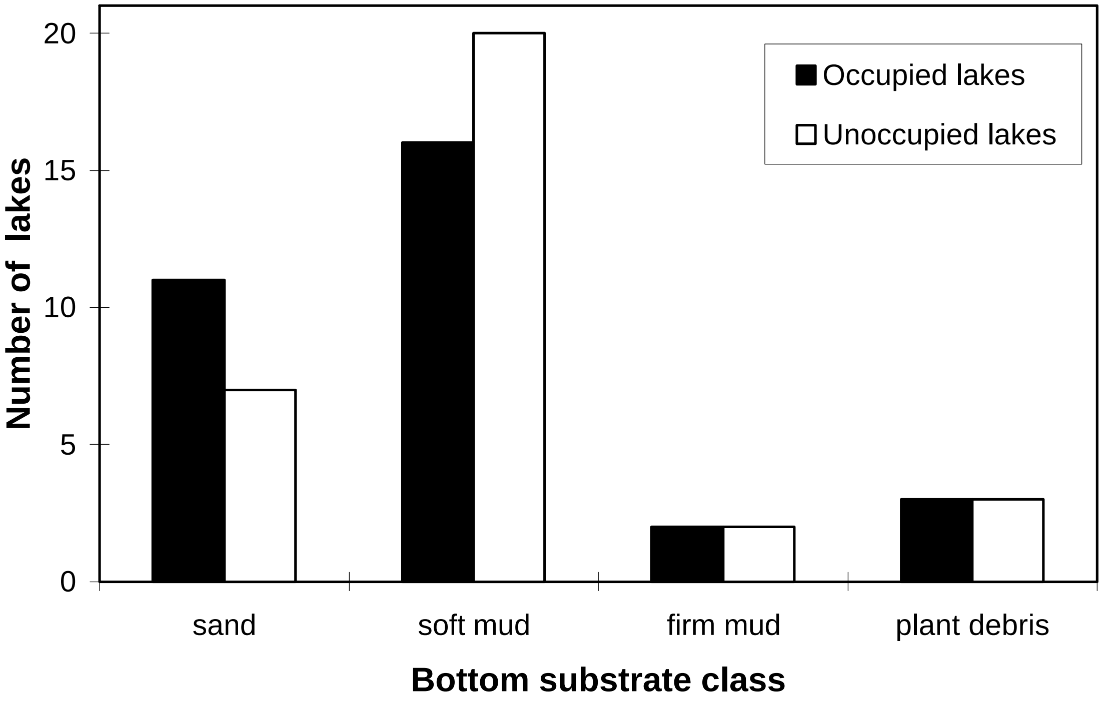

Figure 11. Bottom substrates of lakes occupied by Madagascar fish-eagles (*n* = 32) and randomly selected unoccupied lakes (*n* = 32) in western Madagascar, 1995.

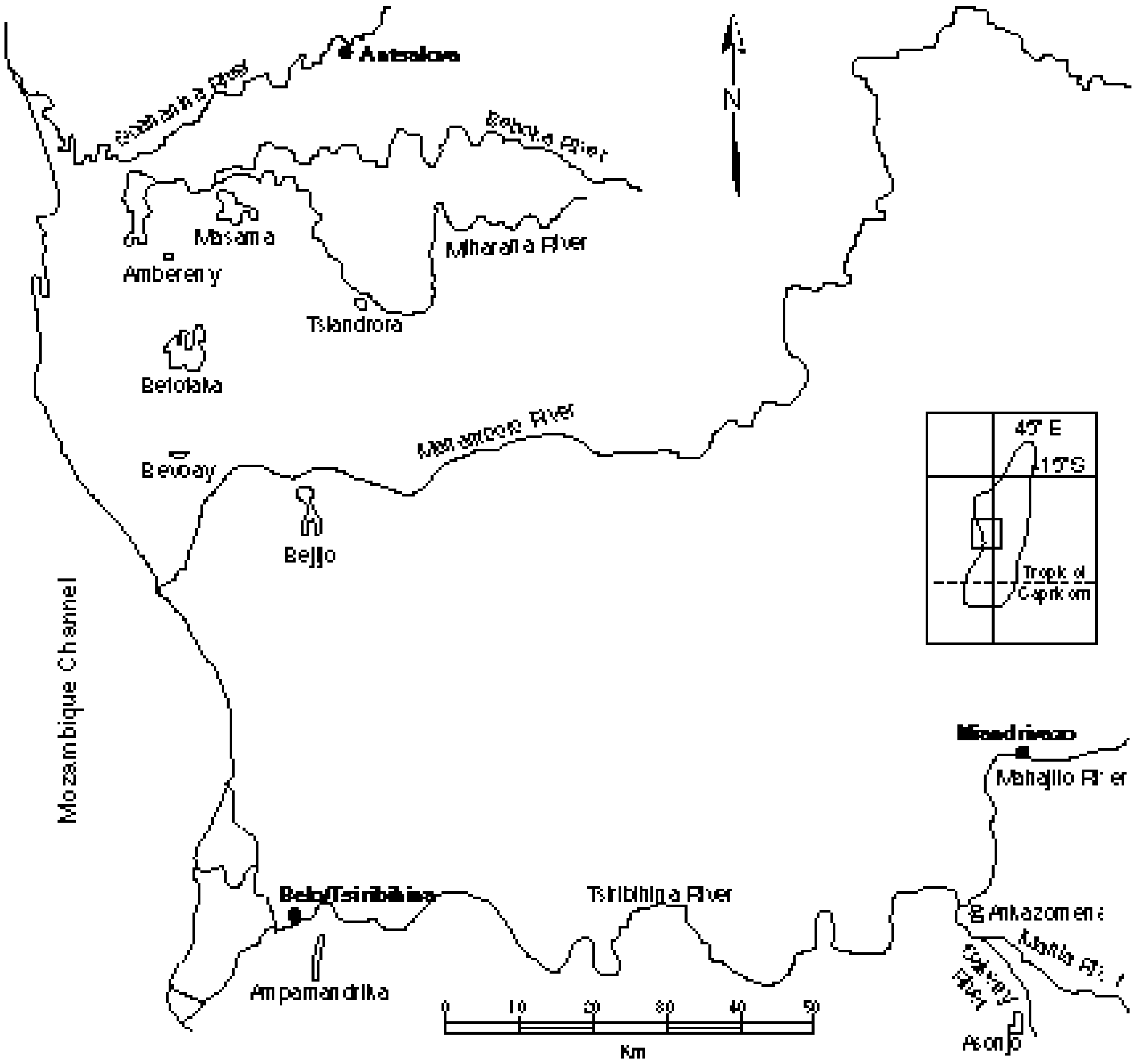

Figure 12. Study area between Morondava and Antsalova, Madagascar, 1996. Lakes included in the study (*n* = 9) are labeled.

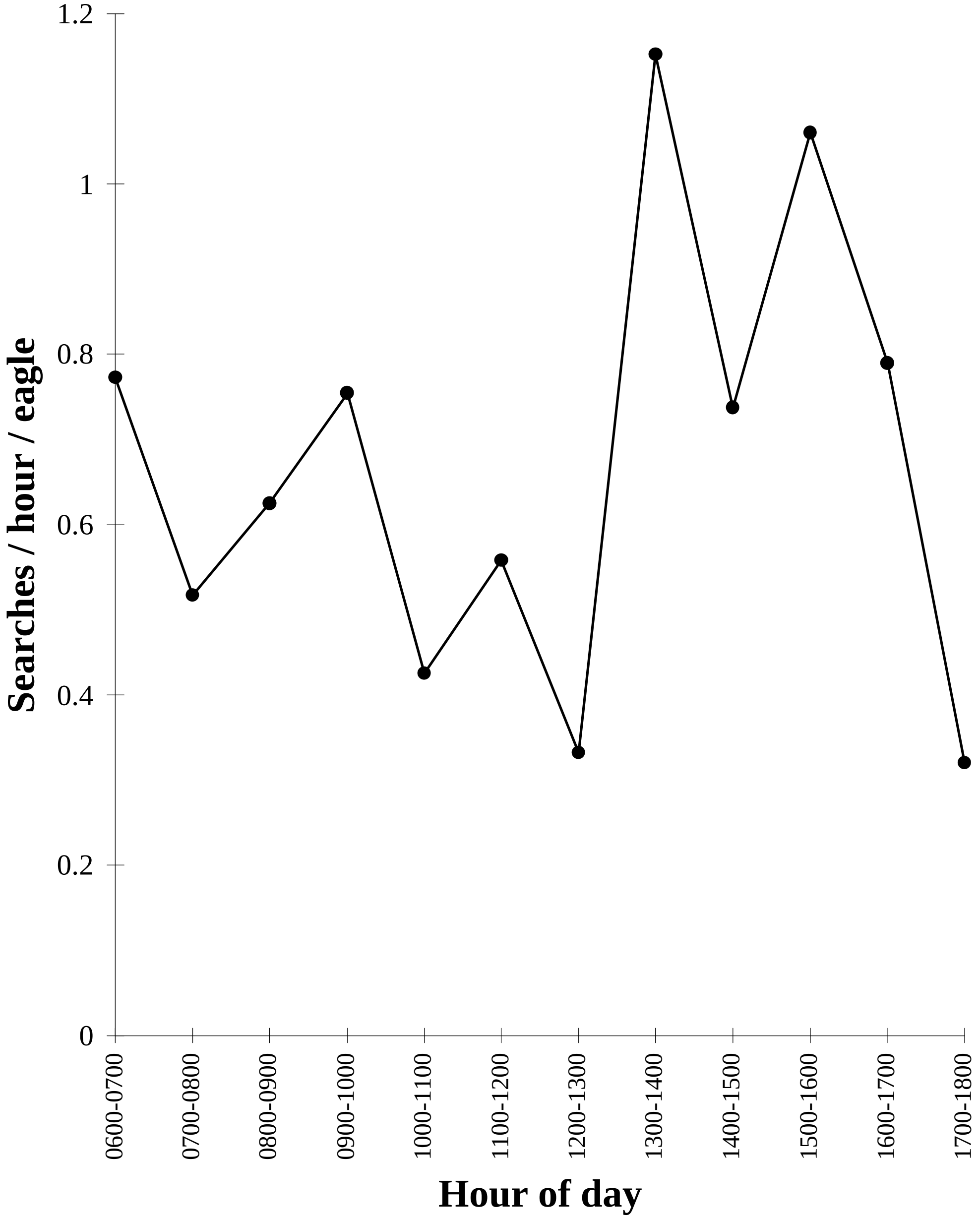

Figure 13. Madagascar fish-eagle prey searches per hour per eagle by time of day at nine lakes in western Madagascar, May-August, 1996.

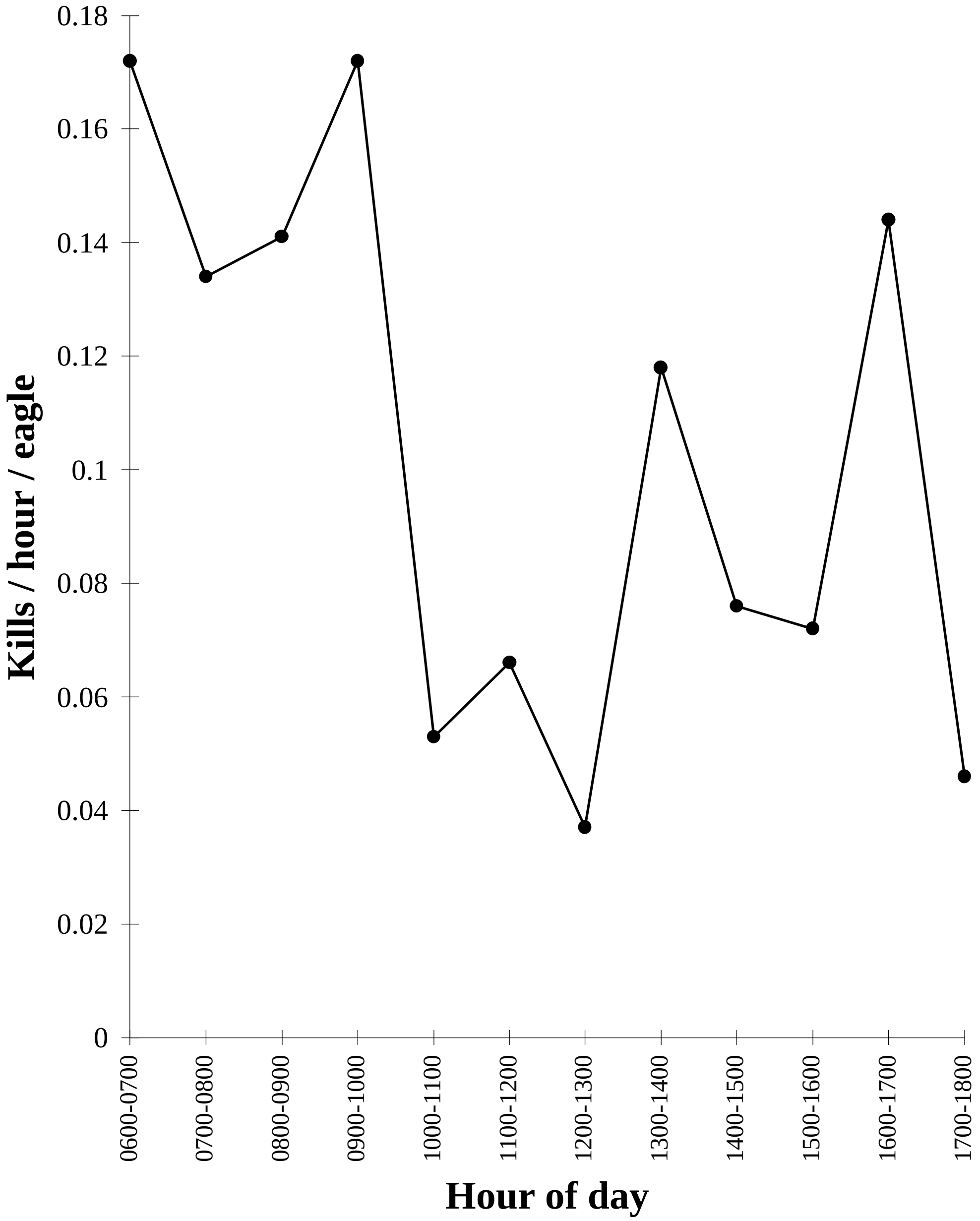

Figure 14. Madagascar fish-eagle kills per hour per eagle by time of day at nine lakes in western Madagascar, May-August, 1996.

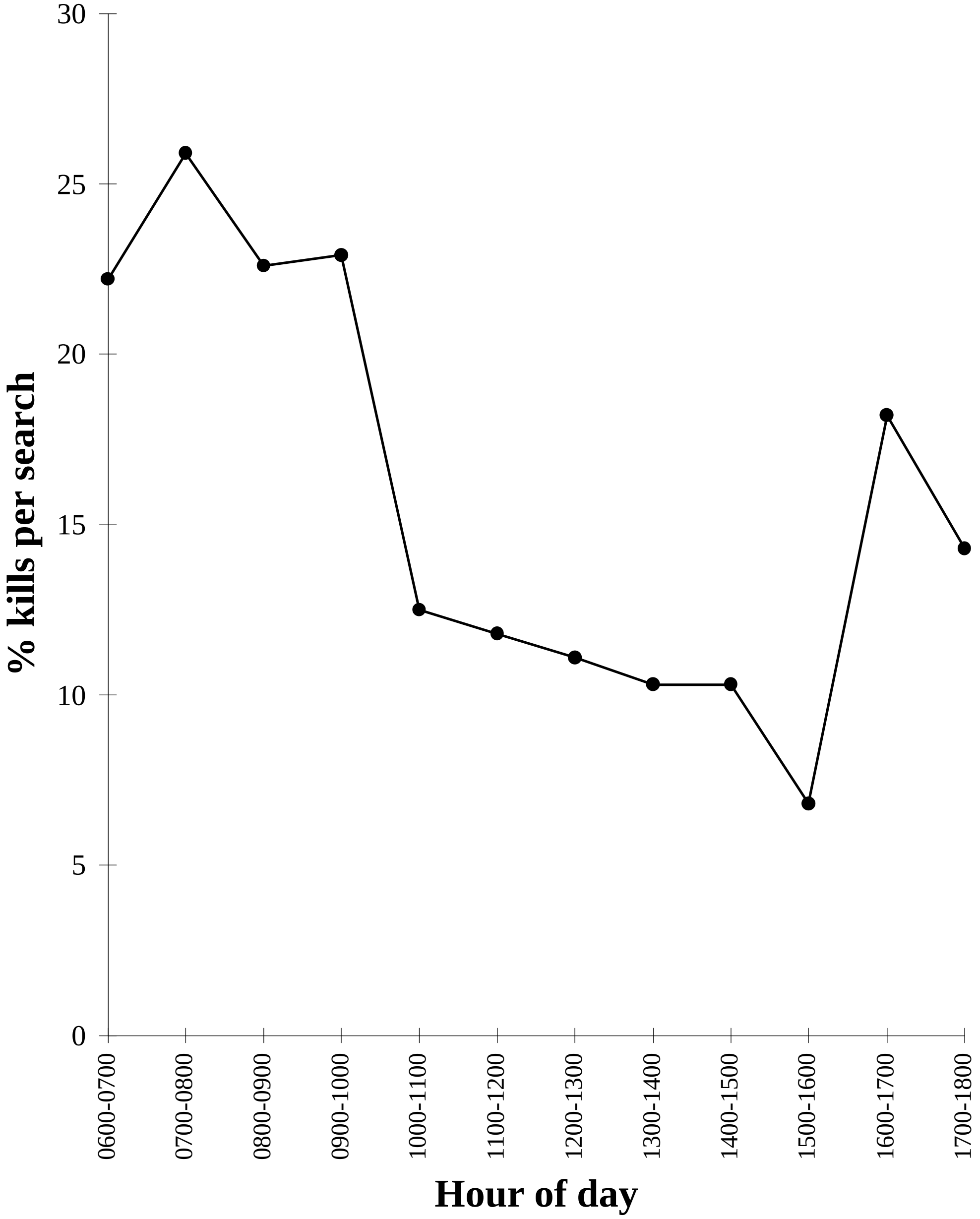

Figure 15. Percentage of Madagascar fish-eagle prey searches resulting in kills by time of day at nine lakes in western Madagascar, May-August, 1996.

VITA

James Berkelman was born on 22 March 1963 in Ithaca, New York to Mary Hobbie Berkelman and Karl Berkelman. He graduated *magna cum laude* from Cornell University in June 1986 with a B.A. in Biological Sciences. He enrolled in a Ph.D. program in zoology at Arizona State University in August 1986 but decided the following spring to gain more field experience before continuing his graduate studies. From 1987 to 1990, he worked on a variety of seasonal field positions throughout the U.S. He also hiked the Appalachian Trail in the summer of 1988. He returned to graduate school in August 1990 and received a M.S. degree in Raptor Biology from Boise State University in July 1993. His M.S. thesis title was "Ecology of the Madagascar buzzard, *Buteo brachypterus*, in the rain forest of the Masoala Peninsula." He enrolled in Virginia Polytechnic Institute and State University in August 1993 to pursue a Ph.D. in Fisheries and Wildlife Sciences under the guidance of James Fraser.