LAKE SELECTION BY MADAGASCAR FISH-EAGLES

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ABSTRACT.—We investigated fish abundance and habitat characteristics at 32 lakes occupied by Madagascar Fish-Eagles (*Haliaeetus vociferoides*) and 32 randomly selected unoccupied lakes between Morondava and Boriziny in western Madagascar from May to November 1995. We measured lake and shoreline habitat characteristics and used gill nets to sample fish populations. Compared with unoccupied lakes, lakes occupied by fish-eagles were deeper and clearer, had more shoreline perch trees, and yielded gill-net catches with more fish, a higher total fish mass, and more fish species. A logistic regression model with number of shoreline perch trees and number of fish species caught in gill nets as independent variables correctly classified fish-eagle use for 76.6% of the lakes in the study. A model with number of shoreline perch trees alone was 71.9% accurate, suggesting that perch-tree availability is the most important factor limiting populations of Madagascar Fish-Eagles. The results indicate that Madagascar Fish-Eagles require bodies of water with large shoreline trees and ample populations of fish. *Received 3 August 1998, Accepted 25 January 1999.*

BIRDS CHOOSE HABITATS based on structural characteristics, food, nest-site availability, or other features that affect survival and reproduction (Cody 1985). Nest sites and food are the most important factors affecting the distribution of breeding raptors (Newton 1979). Seaeagles, including Bald Eagles (Haliaeetus leucocephalus; McEwan and Hirth 1979, Anthony and Isaacs 1989, Chandler et al. 1995), Whitetailed Eagles (H. albicilla; Love 1983, Shiraki 1994), and African Fish-Eagles (H. vocifer; Brown 1980), select large emergent trees near water for nesting, perching, and roosting. Most previous research on habitat selection by seaeagles has been at a relatively local scale, focusing on nest sites (McEwan and Hirth 1979, Anthony and Isaacs 1989, Wood et al. 1989, Shiraki 1994), perches (Stalmaster and Newman 1979, Buehler et al. 1992, Chandler et al. 1995), or roosts (Keister and Anthony 1983, Chester et al. 1990, Buehler et al. 1991). We examined habitat selection by sea-eagles at a larger scale, that of entire lakes. Because these eagles depend on fish for at least part of the year (Stalmaster 1987), aquatic habitat characteristics such as water depth and clarity are likely to be important to them.

The Madagascar Fish-Eagle (*Haliaeetus vociferoides*) nests and perches in large trees (Berkelman 1997) and forages for fish along lakes, rivers, and coastlines (Langrand and Meyburg 1989). The objectives of our study were to determine habitat characteristics of lakes used by Madagascar Fish-Eagles and to develop predictive models to identify lakes suitable for breeding fish-eagles based on shoreline characteristics, water quality, and prey abundance.

METHODS

Study area.—From 26 May to 15 November 1995, we sampled lakes in western Madagascar between the Morondava River south of Morondava (20°17'S, 44°17'E) and 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 toward the central plateaus. The study area included most of the lakes where Madagascar Fish-Eagles are known to nest (Rabarisoa et al. 1997) but excluded offshore-island nesting habitat.

The study area lies within the Western Malagasy phytogeographical region (Humbert 1954), which is characterized by annual rainfall of 1,000 to 2,000 mm, a dry season of six to eight months, monthly average temperatures $>20^{\circ}$ 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 (Donque 1972). The climax vegetation is dense tropical dry deciduous forest, but savanna grasslands maintained by burning comprise more than 80% of the vegetation of the Western Domain

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TABLE 1. Characteristics (see Methods) of 32 lakes occupied by Madagascar Fish-Eagle pairs and 32 randomly selected unoccupied lakes in western Madagascar, 1995. Values are $\bar{x} \pm SE$, with range in parentheses. *P*-values from Wilcoxon rank-sum test.

Lake type	Value	Р			
Nun	Number of perch trees				
	35.3 ± 3.5 (8 to 118) 22.4 ± 2.3 (4 to 63)	0.001			
	epth of Secchi disk (cm)				
Occupied lakes Unoccupied lakes	77.2 ± 8.6 (10 to 255) 50.0 ± 7.6 (5 to 170)	0.003			
Ma	ximum depth (m)				
Occupied lakes Unoccupied lakes	$3.0 \pm 0.3 (0.7 \text{ to } 8.2)$ $1.8 \pm 0.3 (0.2 \text{ to } 7.1)$	0.002			
Number o	f fish caught in gill nets				
Occupied lakes Unoccupied lakes	19.5 ± 3.7 (2 to 74) 7.8 ± 1.5 (0 to 36)	0.002			
Total mass of catch (kg)					
	3.5 ± 0.7 (0.1 to 13.6) 1.2 \pm 0.4 (0 to 10.4)	0.002			
Average	mass of fish caught (g)				
	164.1 ± 19.5 (35 to 575) 153.3 ± 29.0 (0 to 687)	0.173			
Number of fish species in catch					
Occupied lakes Unoccupied lakes	$3.4 \pm 0.3 (1 \text{ to } 7)$ $1.9 \pm 0.2 (0 \text{ to } 5)$	0.002			
Shore	line perimeter (km)				
Occupied lakes Unoccupied lakes	7.0 ± 1.1 (0.9 to 26.9)	0.136			
Surface area (km²)					
Occupied lakes Unoccupied lakes	$3.7 \pm 1.1 (0.1 \text{ to } 25.5) \\ 1.0 \pm 0.2 (0.1 \text{ to } 6.4)$	0.301			

(Guillaumet 1984). Most of the lakes in the study area are flood-plain lakes whose surface areas vary greatly between the rainy and dry seasons (Kiener and Richard-Vindard 1972).

Selection of lakes for study.—We spent at least 7 h of daylight at each lake that we included in the study. We considered lakes to be occupied if (1) we found at least one pair of fish-eagles nesting within 200 m from the shore (n = 18), (2) fish-eagles were known from surveys between 1991 and 1994 (Rabarisoa et al. 1997) to have nested within 200 m from the shore (n = 6), or (3) we saw a pair of adult fish-eagles foraging and vocalizing together for at least 3 h but did not find a nest (n = 8). This last category probably included lakes where a territorial pair of fish-eagles roosted but did not nest in 1995 (n = 1 confirmed), lakes where fish-eagle nesting attempts had failed earlier in the season, or lakes that nesting eagles from an adjacent lake (at which we did not find the nest) used for foraging.

Our sample of 32 lakes included all known occupied lakes within the study area except two on which boats and gill nets were forbidden by local taboo. For comparison, we randomly selected 32 unoccupied lakes from among the 496 lakes that we could identify from satellite or aerial photos of the study area. The smallest lakes from which we selected our random sample were about 10 ha in size. Because we wanted to select random unoccupied lakes that fisheagles were not likely to use for foraging, we excluded unoccupied lakes that were less than 2.5 km from an occupied fish-eagle nest. This distance was the maximum distance between occupied fish-eagle nests in 1994 at lakes Befotaka, Soamalipo, and Ankerika (Berkelman 1997), which support the highest density of breeding Madagascar Fish-Eagles (Rabarisoa et al. 1997).

Habitat measurement.-We selected habitat variables based on results of a pilot study that we conducted in the Antsalova region in 1994 (Berkelman 1997). At each lake, we recorded maximum depth, water clarity, bottom substrate, number of suitable perch trees, shoreline perimeter, and surface area. We used a weighted string to measure lake depth to the nearest 5 cm at 10 to 50 locations, starting at the approximate center of each major section of the lake and moving roughly 20 m toward the nearest point on the shore, measuring depth again, and proceeding another 20 m toward shore for another measurement only if depth was increasing. We recorded the maximum depth thus measured. The number of depth measurements that we used to determine maximum depth depended on the size, shape, and uniformity of the lake. We recorded water clarity as the maximum depth $(\pm 5 \text{ cm})$ at which we could still see a Secchi disk suspended beneath the water (Orth 1983). We recorded bottom substrate as sand, plant debris, soft mud (if we sank into the mud <10 m from shore near the nest or random tree), or firm mud (if we did not sink in the mud).

We considered trees to be suitable for perching if we estimated them to be at least 9.4 m tall, which was the height of the smallest perch tree recorded (Berkelman 1997), and if they were visible from the water from an arc $\geq 90^{\circ}$. At occupied lakes with nests (n = 24), we counted the number of suitable perch trees within 50 m of the water along a 250-m section of shoreline centered on the shoreline point nearest the nest tree (Berkelman 1997). At occupied lakes where we could not find a nest (n = 8), we counted suitable perch trees within the same-sized section of shoreline (i.e. 250×50 m) in the area where we saw the eagles most frequently. At unoccupied lakes, we counted suitable perch trees along the 250-m shoreline section that had the highest density of tall (>15 m) trees.

Fish sampling.—At each lake, we set out two monofilament gill nets for 3 h starting just before sunrise, which varied from about 0630 in June to 0500 in November. The gill nets were 0.91 m deep by 45.7 m long TABLE 2. Results of gill netting at 32 lakes occupied by resident pairs of Madagascar Fish-Eagles and 32 unoccupied lakes in western Madagascar, 1995. Data are number of lakes where each species was caught and $\bar{x} \pm SE$ of number of fish caught and total mass of catch per species.

$\begin{array}{c} \pm 259.8 \\ \pm 291.1 \\ \pm 111.1 \\ \pm 48.6 \\ \pm 178.6 \\ \pm 60.1 \\ \pm 303.3 \\ \pm 56.9 \end{array}$
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- 17 F
± 17.5 ± 8.7
_ 0.7
± 18.6
± 18.7
± 17.5
± 0
± 5.3
± 22.1
± 37.4
± 0
± 60.4
± 7.6
± 13.2
± 0
± 2.0
± 1.1
± 6.2
± 0.2 ± 0
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± 2.0
± 2.0 ± 0

Lake type	Number of lakes	Catch per lake	Mass per lake (g)
	Caran	x sp. (Carangidae)	
Occupied lakes	1	0.03 ± 0.03	3.4 ± 3.4
Unoccupied lakes	0	0 ± 0	0 ± 0
	Eleotris	s fusca (Eleotridae)	
Occupied lakes	0	0 ± 0	0 ± 0
Unoccupied lakes	1	0.03 ± 0.03	3.5 ± 3.5

TABLE 2. Continued.

and were divided into three 15.2-m panels of 2.5-, 3.8-, and 5.1-cm mesh size. We attached floats to the first net and set it out parallel to the shore on the surface in water about 0.9 m deep. We set out the second net parallel to the shore on the bottom in water about 1.8 m deep. Thus, we sampled fish from among the first and second 0.9 m of the water column. If the lake was less than 1.8 m deep, we set out the second net in the deepest water within 200 m of the first net. If the lake was less than 0.9 m deep, we set out both nets on the surface down to the maximum depth of the lake.

At occupied lakes, we placed nets adjacent to the nest site or area where we saw eagles most frequently. At unoccupied lakes, we placed nets next to the shoreline section where we counted suitable perch trees. We identified each fish to species (Arnoult 1959, Kiener 1963, Glaw and Vences 1994), measured its total length (± 1 cm) using a tape measure, and weighed it (± 1 g) with a Pesola scale. For each lake, we recorded total number of fish caught, total mass (kg) of fish caught, average fish mass (g), and number of different fish species.

Analyses.—We 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 variables using a Wilcoxon ranksum test. For bottom substrate categories, we used the chi-square test of equal proportions to determine if eagle use differed from expected use.

We developed logistic regression models to predict the probability of Madagascar Fish-Eagle lake use based on habitat characteristics and fish abundance (Hosmer and Lemeshow 1989). We constructed classification tables for each logistic regression model by using the estimated logistic probabilities for each lake to predict use or nonuse by fish-eagles (Hosmer and Lemeshow 1989:146). We considered lakes to be used if the predicted probabilities were ≥ 0.5 . Initially, we conducted a stepwise analysis. Then we substituted other variables for each of the variables selected in the stepwise analysis to determine if the other variables yielded a model that correctly classified a similar or higher proportion of the data.

RESULTS

Habitat characteristics.—Lakes occupied by fish-eagles were deeper and clearer and had

more shoreline perch trees than unoccupied lakes (Table 1). Shoreline perimeter and surface area did not differ between occupied and unoccupied lakes (P > 0.05). Bottom substrates of the 32 occupied lakes included 11 (34.4%) lakes with sand on the bottom, 16 (50%) with soft mud, 2 (6.2%) with firm mud, and 3 (9.4%) with plant debris. Bottom substrates of the 32 unoccupied lakes included 7 (21.9%) with sand on the bottom, 20 (62.5%) with soft mud, 2 (6.2%) with firm data 3 (9.4%) with firm mud, and 3 (9.4%) with firm mud, and 3 (9.4%) with firm debris. The proportion of lakes in each substrate category did not differ between occupied and unoccupied lakes ($\chi^2 = 1.34$, df = 3, P = 0.719).

Fish abundance.–We caught more fish, more species, and a higher total mass at occupied lakes than at unoccupied lakes (Table 1). The average fish mass did not differ between occupied lakes and unoccupied lakes (P > 0.05).

The introduced cichlid, Oreochromis macrochir, was the most abundant species of fish, accounting for 56.7% of the total catch at all lakes by number and 36.6% by mass. The catch of O. macrochir was higher at occupied lakes than at unoccupied lakes both in number (Wilcoxon test, S = 1,275, $n_1 = n_2 = 32$, P = 0.0015) and mass (S = 1,295, $n_1 = n_2 = 32$, P = 0.0006). The number of fish caught was higher at occupied lakes than at unoccupied lakes for 13 (76.5%) of the 17 remaining fish species caught at all lakes, and total mass of catch was higher at occupied lakes for 15 (88.2%) of the 17 remaining fish species; we did not compare these differences statistically because we caught these species at only a few lakes (Table 2).

Lake selection.—Stepwise logistic regression indicated that the probability of lake use by breeding fish-eagles was positively associated with number of shoreline perches and number of fish species caught in gill nets (Model 1; Table 3). The equation correctly classified fish-eagle use at 76.6% of 64 lakes. When we removed the number of fish species from the list of var-

		P	arameter estimat	es	
Variable	β	SE	χ ²	Р	Odds ratio
		Model	1		
Intercept	-3.81	1.07	12.79	0.0003	
No. of perches	0.06	0.02	6.39	0.012	1.07
No. of fish species	0.80	0.25	10.02	0.002	2.22
		Model	2		
Intercept	-1.67	0.65	6.73	0.010	_
No. of perches	0.06	0.02	7.71	0.006	1.06

TABLE 3. Logistic regression parameter estimates and *P*-values for classifying lake use by Madagascar Fish-Eagles in western Madagascar, 1995.

iables available for stepwise selection and analyzed the remaining variables, the resulting equation included number of shoreline perches (P = 0.005) and number of fish caught in gill nets (P = 0.018) and correctly classified fish-eagle use at 75.0% of the 64 lakes. When we removed both the number of fish species and the number of fish caught from the list of variables available for stepwise selection, the resulting equation included number of shoreline perches (P = 0.005) and total mass of fish caught in gill nets (P = 0.013) and correctly classified fish-eagle use at 76.6% of the 64 lakes.

The three fish variables (number caught, total mass of catch, and number of species) were highly correlated (Table 4). We removed the fish variables altogether from the list of variables available for stepwise selection and conducted a univariate logistic regression on the number of shoreline perches. The resulting equation (Model 2; Table 3) correctly classified fish-eagle use at 71.9% of the lakes.

DISCUSSION

Habitat characteristics.—The habitat variables that best characterized lakes occupied by Madagascar Fish-Eagles were related to prey availability. Higher water clarity of occupied lakes may reflect selection of suitable foraging locations, as Flemming and Smith (1990) observed for Ospreys (*Pandion haliaetus*) in Nova Scotia. Lakes and estuaries in Madagascar are subject to substantial soil erosion during the rainy season (Le Bourdiec 1972).

Madagascar Fish-Eagles may select deeper lakes because these lakes are more likely to persist throughout the dry season. Most of western Madagascar receives little rain from April through October. Water levels decline markedly over the course of the dry season, and some lakes dry up entirely. Fish-eagle energy demands also are likely to be highest during the dry season because eagles reproduce at this time. If fish-eagles are to reproduce successfully, they must nest near lakes that usually will persist throughout the year. Although the Wilcoxon rank-sum test indicated that water depth and water clarity were higher at occupied lakes than at unoccupied lakes, these variables were not in the logistic regression models because both of them were correlated with fish variables, and because water depth was correlated with the number of shoreline perches.

The logistic regression model that included only the number of shoreline perches correctly

TABLE 4. Spearman correlations and *P*-values for number of shoreline perches, water depth, water clarity, number of fish caught in gill nets, total mass of catch, and number of fish species caught at 64 lakes in western Madagascar, 1995.

Variable	No. of perches	Depth	Clarity	No. caught	Total mass
Depth	0.38**				
Clarity	0.16	0.77***			
No. caught	0.08	0.22	0.32**		
Total mass	0.17	0.28*	0.33**	0.86***	
No. of species	0.20	0.29*	0.23	0.84***	0.83***

*, *P* < 0.05; **, *P* < 0.01; ***, *P* < 0.001.

classified fish-eagle use for almost as high a proportion (71.9%) of the lakes as the model that included the number of shoreline perches along with number of fish species (76.6%). The number of perches also can be used to predict where fish-eagles are most likely to nest along the shore within a given body of water (Berkelman 1997). This suggests that perch-tree availability is the most important factor limiting Madagascar Fish-Eagle populations, as was the case for Bald Eagles on the northern Chesapeake Bay (Chandler et al. 1995). Haliaeetus eagles hunt mostly from perches (Brown 1980, Love 1983, Stalmaster 1987). Because much of western Madagascar's dry deciduous forest has been degraded to widely scattered trees and shrubs (Guillaumet 1984), fish-eagles may be restricted to breeding at those lakes that offer enough perch trees for foraging.

Fish populations.—Gill netting indicated that fish species diversity, numbers, and biomass are greater at lakes occupied by Madagascar Fish-Eagles than at unoccupied lakes. The logistic regression equations that included any of the fish variables along with number of shoreline perches correctly classified fish-eagle use for a similarly high proportion (\geq 75%) of lakes in the study area. We do not know which fish variable is the most important to the fish-eagles, but eagles clearly appeared to select lakes with thriving fish populations, and they may have been avoiding lakes where fish are small and scarce.

Although *Haliaeetus* eagles feed primarily on fish and other aquatic prey, Bald Eagles (Stalmaster 1987) and White-tailed Eagles (Love 1983) rely on avian and mammalian prey and carrion when fish are less available in winter. Madagascar Fish-Eagles, however, appear to rely almost exclusively on fish and occasionally on other aquatic prey such as crabs, turtles, and ducklings (Langrand and Meyburg 1989, Berkelman et al. 1999). Thus, it is not surprising that the abundance and distribution of fish affect the abundance and distribution of fish-eagles in Madagascar.

Human activity.—In our 1994 pilot study, we found no difference in the number of people living within 200 m from the shoreline between 15 lakes occupied by Madagascar Fish-Eagles and 19 unoccupied lakes in the Antsalova region (Berkelman 1997). In contrast to Bald Eagles (e.g. Fraser et al. 1985, McGarigal et al.

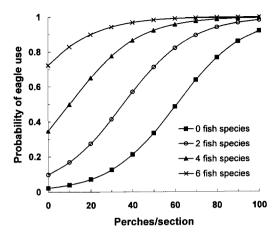


FIG. 1. Probability of lake use by breeding Madagascar Fish-Eagles as a function of number of suitable perch trees within a shoreline section $(250 \times 50$ m) centered on the nest tree, plotted for different numbers of fish species caught during 3 h of gill netting in western Madagascar, 1995. Probabilities were calculated by inserting different numbers of perch trees or fish species into the equation resulting from stepwise logistic regression analysis. Trees ≥ 9.4 m tall and visible from the water from an arc $\geq 90^\circ$ were considered suitable perch trees.

1991, Buehler et al. 1992, Chandler et al. 1995), Madagascar Fish-Eagles do not appear to avoid people when selecting nesting or perching habitat. This difference may result in part from the fact that few people in western Madagascar can afford firearms. Three of the 38 (7.9%) nests that we studied in 1994 were less than 100 m from human habitation, and fishermen and cattle herders passed beneath many of the nest trees each week (Berkelman 1997).

Conservation implications.-The probability that a lake would be occupied by Madagascar Fish-Eagles can be determined by inserting the number of perch trees along an adjacent section of shoreline (250 \times 50 m) and the number of fish species caught during 3 h of gill netting into the appropriate logistic equation. Although the probability of eagle use can be determined using the number of shoreline perch trees alone, it is useful to know the number of fish species as well, if it can be measured. For example, based on Model 1 (Table 3), a lake with 30 shoreline perches and 6 fish species would be 2.3 times more likely to be used by fish-eagles than a lake with 30 shoreline perches and only 2 fish species (Fig. 1). Based on Model 2 (Table 3), considering shoreline perch-

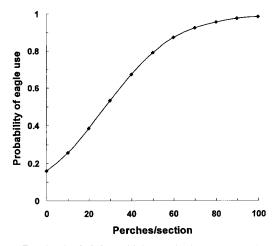


FIG. 2. Probability of lake use by breeding Madagascar Fish-Eagles as a function of number of suitable perch trees within a shoreline section (250×50 m) centered on the nest tree in western Madagascar, 1995.

es alone, we would predict a 53.3% probability that a lake with 30 perch trees along an adjacent shoreline section would be used by fisheagles.

Although Madagascar Fish-Eagles are tolerant of humans in their territories, human activities threaten their habitats and food supplies. The fish-eagle population has declined dramatically in recent decades (Langrand and Meyburg 1989), and habitat alteration has been proposed as a likely cause (Langrand and Meyburg 1989, Langrand and Goodman 1995). Forest degradation is the principal threat to the fish-eagle's terrestrial environment, and siltation of lakes and rivers and conversion of wetlands to rice paddies may reduce the suitability of aquatic habitats for foraging.

Rapidly increasing human populations are likely to further reduce habitat suitability and prey availability on lakes where fish-eagles breed. As forest degradation continues in Madagascar, the number of lakes with enough suitable perch trees will decrease, and this is likely to be a major factor contributing to the decline of the Madagascar Fish-Eagle population. Uncontrolled fishing may reduce fish populations to levels that cannot sustain breeding fish-eagles, so that more lakes will be devoid of eagles in the future. Watson and Rabarisoa (1999) documented an influx of up to 275 seasonal migrant fishermen from 1991 to 1995 and a 135% increase in the number of fishing camps and villages at lakes Befotaka, Soamalipo, and Ankerika in the Antsalova region. They observed a corresponding decrease in fish stocks and degradation of shoreline habitat as fishermen cut trees for canoes, houses, or fuel wood for smoking fish. Our lowest gill net catches generally were at the most accessible lakes where smoked fish could be transported to more densely populated areas. As the most accessible lakes are depleted of fish, exploitation of the more remote, less-accessible lakes is likely to increase.

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