Chapter 4.6

Conservation of Bird Diversity in Madagascar's Southeastern Littoral Forests

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Abstract

The littoral forests of southeastern Madagascar are considered severely threatened by habitat fragmentation and degradation. Herein, the bird communities inhabiting 31 littoral forest fragments and their surrounding areas are described. Processes associated with habitat fragmentation (e.g. patch reduction and isolation) and degradation (e.g. changes in forest structure) are related to bird species abundance and help to explain bird species distribution across the littoral forest system. In total, using a standardized sampling system, 77 bird species were found inhabiting 31 littoral forest fragments. Of these, 61 species were endemic to the island or the western Indian Ocean sub-region, which consisting of Madagascar, the Comoros, and the Mascarenes. In comparison, the matrix habitats surrounding the littoral forests were depauperate of species, with the *Erica* spp. heathland containing 24 species, and the introduced *Eucalyptus* and *Melaleuca* forest patches containing 22 and 23 species, respectively. The geographic location of littoral forest patches was important in determining which bird species occurred within them, with the northern patches having similar bird communities to nearby humid forest, while the most southern patch had a bird community that resembled that of nearby spiny forest habitats. At the patch level, 31 species were found to be edge-sensitive, and nine species were affected by changes in vegetation structure at core or edge point counts. At the landscape level, 20 species were affected by patch size, and four species were affected by patch shape. No species appeared to be affected by any measure of patch isolation. If bird conservation is to become a priority within the littoral forests of southeastern Madagascar, these results indicate that large (> 200 ha) blocks of littoral forest may need to be awarded protected status, and exploitation of forest resources that results in changes in vegetation structure should be minimized, especially in smaller littoral forest fragments.

Résumé

Conservation de la diversité avienne dans les forêts littorales du sud-est de Madagascar. Les forêts littorales du sud-est de Madagascar sont considérées comme extrêmement menacées par la fragmentation et la dégradation de l'habitat. Nous décrivons ici les communautés aviennes distribuées dans 31 parcelles de forêt littorale et des habitats environnants. Les processus liés à la fragmentation de l'habitat (ex. réduction et isolement des parcelles) et la dégradation de l'habitat (ex. changement de la structure de la forêt) ont été mis en relation avec l'abondance des espèces d'oiseaux pour tenter de comprendre la distribution des espèces aviennes sur l'ensemble du système de forêt littorale. En suivant une méthode standard d'échantillonnage, nous avons inventorié 77 espèces d'oiseaux dans 31 parcelles de forêt littorale. Sur celles-ci, 61 sont des espèces endémiques de l'île ou de la région du sud-ouest de l'océan Indien qui inclut les Comores et les Mascareignes. En comparaison, les habitats marginaux limitrophes des forêts littorales étaient appauvris en espèces avec les zones de bruyères à *Erica* qui n'abritaient que 24 espèces et les zones de plantations d'arbres allogènes d'*Eucalyptus* et *Melaleuca* qui n'abritaient respectivement que 22 et 23 espèces. La localisation géographique des parcelles de forêt littorale était importante pour

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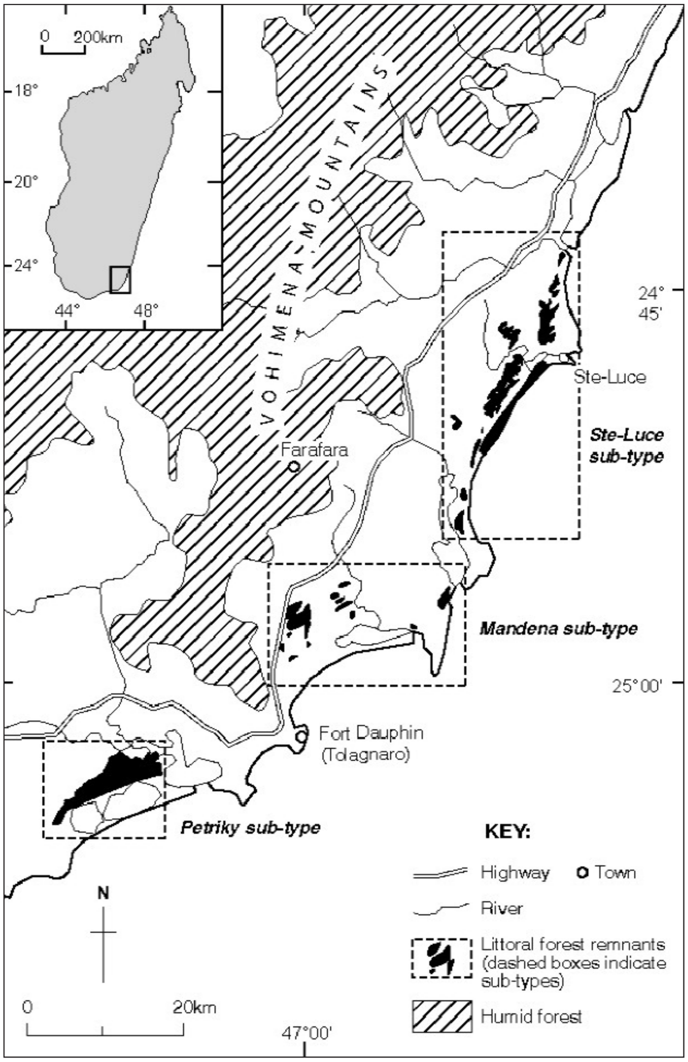

Figure 1. The location of littoral forest remnants surveyed in south-eastern Madagascar. The matrix surrounding littoral forest remnants includes marécage swamp forest, introduced *Melaleuca* forest, plantations of *Eucalyptus citriodora* and *E. robusta*, and heath-type vegetation consisting predominately of *Erica* spp. Source: Watson *et al*. (2005).

déterminer quelles espèces d'oiseaux pouvaient y être rencontrées, les parcelles du nord abritant les mêmes communautés d'oiseaux que les forêts humides proches alors que les parcelles plus au sud abritaient une communauté avienne ressemblant à celle des habitats voisins de forêt épineuse. Au niveau des parcelles, 31 espèces se sont avérées être sensibles aux effets de lisière et neuf espèces sont affectées par les changements de la structure de la végétation suivant les points d'écoute réalisés au centre et sur les lisières. Au niveau de l'environnement, 20 espèces étaient affectées par la taille de la parcelle et quatre espèces par la forme de la parcelle. Aucune espèce ne semble être affectée par une quelconque mesure de l'isolement de la parcelle. Si la protection des oiseaux devait devenir une priorité dans les forêts littorales du sud-est de Madagascar, ces résultats indiquent que de grands blocs de forêt littorale (>200 ha) devraient recevoir un statut de protection et que l'exploitation des ressources sylvicoles qui se solde par des changements dans la structure de la végétation devrait être réduite et plus particulièrement dans les plus petites parcelles de forêt littorale.

Introduction

It has been argued, from an ornithological perspective, that the region of southeastern Madagascar bounded by the Mandrare River to the west and Manantenina to the north is the most diverse on the island (Goodman *et al*. 1997). The region's size (approximately 10,000 km^2, or about 1.7% of the total land area of island) is small, but it contains a variety of forest types, coastal zones, high mountains, and areas of inland freshwater habitat. Because of this habitat variety, the region has the highest numbers of bird species of any on the island. Goodman *et al*. (1997) found 189 bird species, representing 68% of the total birds known on Madagascar. Although diverse, the region is relatively unexplored and much of the forested landscape is fragmented and degraded. Little is known of how these processes affect the region's bird communities.

Coastal littoral forests are one of the natural forest habitats of the region. These floristically distinct forests grow on a narrow band of sand and alluvium along the eastern coast of Madagascar (Lowry and Faber-Langendoen 1991, Schatz 2000). Due to their high floristic endemism, the littoral forests of southeastern Madagascar are ranked among the habitat types of highest conservation priority on the island. Even with this distinction however, there has been only one avifaunal study conducted within them prior to this study (Goodman *et al*. 1997). This study, conducted in 1989-90, was part of a larger survey of birds in southeastern Madagascar, and as a result, did not include many littoral forest fragments. Moreover, since 1989-90, the littoral forests have been subject to habitat degradation due to fire, deforestation, and other anthropogenic impacts (Ramanamanjato and Ganzhorn 2001).

In this chapter, I first describe the bird species communities that inhabit the littoral forests of southeastern Madagascar. I then present the current understandings of how processes associated with habitat fragmentation (the creation of habitat edges, the reduction and isolation of littoral forest patches, and the changing of patch shape) and habitat degradation (the loss of forest structure and complexity) affect these bird communities. It must be noted that this paper is partly a summation of results that have been previously published (Watson *et al*. 2004a, 2004b, 2005) and some additional analyses. I also provide recommendations to ensure that management plans of littoral forests take account of the conservation needs of birds.

Methods

The study area is located near Tolagnaro and includes the littoral forests of three different subregions: Mandena, Petriky, and Sainte Luce (Fig. 1). The littoral forests in these sub-regions are considered most intact on Madagascar (Dumetz 1999). These forests occur in fragments that vary in size, shape, and degree of anthropogenic impact. Dumetz (1999) found that the littoral forests of these three sites each have different plant compositions, different stand densities, and differences in vegetation structure, and are therefore distinct 'sub-types.' The matrix surrounding these forests includes *marécage* swamp forest, introduced *Melaleuca* forest, plantations of *Eucalyptus citriodora* and *E. robusta,* and heath-type vegetation consisting predominately of *Erica* spp. (Ramanamanjato and Ganzhorn 2001). Two other major forest types, humid forest and spiny forest, also occur in the study area. The humid forests occur almost exclusively on lateritic soils at the base of, and on the Anosyenne and Vohimena Mountains, while the spiny forests occur on drier, sandy soils to the west of these mountain ranges (Goodman *et al*. 1997, Ramanamanjato *et al*. 2002).

Bird surveys

The MacKinnon list census technique (MacKinnon and Phillips 1993), with 10-species species lists, was used to determine the avifauna composition of littoral forest patches in each of the three subregions. This method has been promoted as a suitable, rapid assessment technique for determining bird species communities in habitats that are relatively unknown, and when rapid assessment is necessary (see O'Dea *et al*. 2004 for a critical review of this methodology). Ten-species species lists were used for the surveying and subsequent analysis because Trainor (2002) determined that this number generated the most accurate species richness estimations in a species poor environment. Further, Herzog *et al*. (2002) recommended it as the best compromise between stable richness estimation curves and robust sample size. Fourteen littoral forest patches >

Table 1. Geographic data, species richness, and number of endemic species found at each littoral forest patch.

Patch name	Sub-type	Lat/Long	Area (ha)	Species number	Number of regional endemics	Number of island endemics
M1	Mandena	24° 45'01"S, 47° 10'55"E	126	42	15	19
M4	Mandena	24° 57'37"S, 47° 01'01"E	47	30	10	12
M5	Mandena	24° 56'49"S, 47° 06'17"E	25	25	8	9
M6	Mandena	24° 56'07"S, 47° 01'51"E	17	21	9	5
M7	Mandena	24° 56'57"S, 47° 01'33"E	13.7	15	6	4
M15	Mandena	24° 58'01"S, 47° 00'33"E	116	45	17	19
M16	Mandena	24° 59'21"S, 46° 59'51"E	73	33	14	12
M20	Mandena	24° 57'14"S, 47° 04'23"E	23	19	8	6
MA	Mandena	24° 56'36"S, 47° 01'02"E	0.8	7	2	2
MB	Mandena	24° 56'52"S, 47° 00'21"E	0.4	8	3	2
MC	Mandena	24° 56'32"S, 47° 00'52"E	0.9	11	4	3
MD	Mandena	24° 56'20"S, 47° 02'16"E	2.8	13	6	3
ME	Mandena	24° 58'01"S, 46° 59'33"E	5.9	14	6	4
MF	Mandena	24° 56'17"S, 47° 00'48"E	1.8	9	2	3
MG	Mandena	24° 58'02"S, 46° 59'09"E	4.1	16	7	3
P1	Petriky	25° 04'31"S, 46° 53'10"E	855	53	16	25
S1	Sainte Luce	24° 43'07"S, 47° 11'08"E	31	28	12	9
S7	Sainte Luce	24° 47'17"S, 47° 09'12"E	254	42	15	20
S8	Sainte Luce	24° 46'12"S, 47° 09'09"E	172	44	15	17
S9	Sainte Luce	24° 45'39"S, 47° 10'19"E	464	58	17	30
S10	Sainte Luce	24° 44'22"S, 47° 11'51"E	17	28	11	12
S11	Sainte Luce	24° 44'20"S, 47° 10'44"E	35.3	36	11	18
S17	Sainte Luce	24° 48'43"S, 47° 08'31"E	297	46	17	21
SA	Sainte Luce	24° 46'01"S, 47° 09'49"E	0.4	9	3	3
SB	Sainte Luce	24° 46'41"S, 47° 09'55"E	1.4	9	4	2
SC	Sainte Luce	24° 48'55"S, 47° 08'46"E	5.7	16	5	6
SD	Sainte Luce	24° 46'14"S, 47° 09'35"E	1	12	4	3
SE	Sainte Luce	24° 46'57"S, 47° 08'46"E	0.5	10	3	5
SF	Sainte Luce	24° 46'51"S, 47° 08'52"E	1.4	9	3	2
SG	Sainte Luce	24° 47'01"S, 47° 08'51"E	0.7	8	1	2
SH	Sainte Luce	24° 46'41"S, 47° 09'47"E	0.4	10	1	3

17 ha in size were surveyed using this technique between November and December 2001, and 31 were surveyed between October and November 2002 (Table 1). In order to determine if littoral forest bird communities differed from that of neighboring habitats, three *Eucalyptus* plantations and five *Melaleuca* forest patches immediately surrounding littoral forest fragments in Mandena were also surveyed using the MacKinnon technique. Due to the difficulty of finding discrete patches of *Erica* vegetation, which dominated the study area, an area limit of approximately 1 km^2 was used when surveying birds in the *Erica* vegetation, and all surveyed areas were separated by a distance of at least 1 km. Five surveys were conducted in this manner.

A point-count sampling strategy was employed to determine how patch and landscape characteristics affected bird community composition. A total of 90 point-count stations were placed in 30 littoral forest patches of varying sizes in the sub-types of Mandena and Sainte Luce. Point-counts were carried out during November and December 2001 and in October and November 2002. Following other similar studies (e.g., Helzer and Jelinski 1999, Saab 1999), the number of point-count stations varied depending on the area of the patch: one station in patches < 1 ha, two stations in patches of 1-10 ha, three for 10-20 ha patches, four for 20-40 ha patches, and five in patches > 40 ha.

In order to assess how forest edges influenced bird species composition, 20 littoral forest edge sites and 20 littoral forest core habitats were surveyed using point-counts in October and November 2002. All core sites were located in two large forest blocks at Sainte Luce, known as S8 and S9, and all edge sites were located on their edges (10 on each). Core habitats were defined as forest areas 300 m from the edge of the forest fragment.

For the point-counts, birds occurring within a 25-m fixed radius of each station were recorded, as it was often not possible to identify the species of an individual past this distance. Each station was located at least 100 m apart to minimize the risk of counting the same individual twice. Each station was visited twice. To reduce time-of-day effects, the order in which sites were sampled was reversed each week. For each surveying period, before conducting point-counts, the author undertook training to estimate distances to the site and to become familiar with the bird species of the study area. Ten minutes were spent at each station, and only species sighted within the point-count area were recorded as present. Calls were used to locate birds and to aid identification. Surveys were confined to the periods 0600 – 1000 hr and 1500 – 1900 hr on days without rain or strong wind.

Habitat surveys

Vegetation structure and density were visually quantified at count stations using eight categories (variables) to define the structure and numbers of trees of differing size (Table 2). Four represented vegetation vertical structure (low shrub cover, medium shrub cover, tall shrub cover, and canopy cover), and two represented vegetation density (number of small trees and number of large trees). Two other measures, percentage of litter cover and the maximum height of vegetation, were chosen to give a measure of forest habitat complexity. These eight categories were chosen to convey a wide range of vertical structure, tree density, and habitat complexity characteristics, which are associated with human degradation (Cadotte *et al*. 2002, Vallan 2002, Ingram *et al*. 2005).

Patch and landscape structure data

Eight parameters were selected that assessed the patch-based measurements and landscape mosaic: area of each patch (AR), distance to nearest large block of forest (DS), distance to the nearest patch > 100 ha (DR), distance to nearest patch (DRN), area of nearest patch (ANR), a littoral forest patch shape index (SI), patch density (PD), and edge density (ED) (Table 3). Formulas and definitions for patch density and edge density are given in Table 3. All eight patch and landscape mosaic variables were determined using ArcView GIS software from a supervised, classified Landsat TM satellite image acquired on 11 November 1999.

Analysis

A step-wise regression analysis (holding p to enter = 0.05 and p to remove = 0.1) was used to explore the relationships of species richness (dependent variable) with the patch and landscape mosaic variables recorded for each fragment in order to build the best predictive model for each richness value. The problem of analyzing patterns of species richness in fragments of differing size is that it is difficult to eliminate the effects of decreasing sampling area, which is crucial because both fragmentation and decreasing sampling area should result in decreasing species richness (Stratford and Stouffer 1999). To overcome this problem, an average was taken for species

Table 2. Description for vegetation structure measures in littoral forest point count stations within a radius of 25 m around the point count station.

Variable	Description
Number of large trees	Number of trees > 10 m in height
Number of small trees	Number of trees between 6 and 10 m in height
Maximum vegetation height	The maximum height of vegetation (m)
Canopy cover	Percentage of crown cover of trees > 10 m high
Litter cover	Percentage of leaf litter and fallen dead vegetation
Low shrub cover	Percentage of shrub cover between 0 and 0.5 m high
Medium shrub cover	Percentage of shrub cover between 0.5 and 2 m high
Tall shrub cover	Percentage of shrub cover between 2 and 6 m high

Table 3. Definition and summary statistics, with adopted transformations, for landscape structural metrics of 30 littoral forest patches in southeastern Madagascar. Landscape environmental attributes were determined from a Landsat TM satellite image acquired on 11 November 1999.

Code	Description	Units	Minimum	Maximum	Mean
Shape Index (SI)	$SI= \frac{A/P}{R/2} x100$ where R is the radius of a circle with area A and perimeter P	0-1	0.27	0.94	0.707
Edge Density (ED)	Density of littoral forest edge within 500 m of each patch's edge multiplied by 100	0-1	0.07	0.51	0.28
Patch Density (PD)	Density of littoral forest patch area within 500 m of each patch's edge	0-1	0.02	0.38	0.18
Distance to source (DS)	Distance to the nearest block of forest > 1000 ha	m	4813	17502	9965.1
Distance to large patch (DR) [1]	Distance to the nearest patch with an area > 100 ha	m	45	3968	903.2
Distance to nearest patch (DNR) [2]	Distance to the nearest patch	m	55	1600	132.5
Area of nearest patch (ANR) [1]	Area of nearest littoral forest patch	ha	0.40	464	96.2
Patch Area (AR) [1]	Total area of the patch	ha	0.30	464	57.9

[1] In transformed; [2] square-root transformed for analyses.

richness per point-count per patch. The variables 'area,' 'area of the nearest patch,' and 'distance to the nearest patch > 100 ha' were logarithmically transformed, while the parameter 'distance to nearest patch' was square-root transformed prior to analyses (Sokal and Rohlf 1981; Table 3). Since multicolinearity was found between the two independent variables 'shape' and 'area,' the variable 'shape' was removed from the step-wise, as it explained less of the variance in both analyses (Soulé *et al*. 1988).

Several procedures were used to compare bird species abundance and species richness between edge and core sites. Two analyses of variance (ANOVA) were employed to compare the total number of individuals and species richness by landscape element. These analyses allowed detection of differences among bird communities across the three landscape elements, edge, core, and matrix, and to determine whether the differences were consistent across time. Following Beier *et al*. (2002), the difference in bird species occurrence between edge and core was evaluated using paired *t*-tests based on the percentage of occurrence data from the 20 point-count stations in each habitat type. Only those species found in both of these landscape elements were analyzed.

Paired *t*-tests were used to assess the difference in the means of each habitat variable between core and edge sites. The habitat variables that were measured using percent values (i.e., maximum vegetation height, canopy cover, litter cover, low shrub cover, medium shrub cover, and tall shrub cover) were transformed using the arcsine root formula prior to the analysis to improve the normality of the data.

In order to understand how habitat degradation affected bird species distribution in different landscape elements, a logistic, step-wise regression procedure was used to examine how individual species distribution (i.e., presence/absence) corresponded with habitat variables at core and edge point-counts. Colinearity was found to exist between the habitat variables 'canopy cover' and 'height of vegetation,' when an r-value of 0.80 was used as the cut-off (Soulé *et al*. 1988, Pisces Conservation 2002). Therefore, the variable 'height of vegetation' was removed from the stepwise regression analysis as it explained less of the variance when considered independently. These statistics were calculated using SPSS software (Kinnear and Gray 2000).

Results

Bird diversity in the littoral forests

In total, this three-season study found 77 species inhabiting 31 littoral forest fragments (Appendix I). The location of littoral forest patches was an important determinant in what species occurred within them, as 14 species were found solely in the

Table 4. Results of individual logistic regression models for 63 species when related to local vegetation variables for 20 core littoral forest point counts. Bird species are classified as: edge-sensitive, edge preferring, edge-tolerant and ubiquitous following Watson *et al*. (2004a). Only bird species that had a significant relationship with habitat variables are shown. Habitat variables are defined in Table 1.

Species, by group	**Model**	**Chi square**	**d.f.**
Edge sensitive forest species			
Sarothrura insularis	4.6-5.7 (litter cover)	10.3**	1
Lophotibis cristata	3.6-4.2 (litter cover)	10.5**	1
Alectroenas madagascariensis	-2.28+2.5 (canopy cover)	9.8**	1
Ispidina madagascariensis	-3.5+2.7 (canopy cover)	8.2**	1
Newtonia archboldi	-9.6+7.27 (low shrub cover) -2.8 (litter cover)	14.3**	2
Edge-tolerant forest species			
Nesillas typica	-58.8+40.3 (low shrub cover) + 9.8 (number of small trees)	16.9**	2
Ubiquitous species			
Cisticola cherina	-1.2+2.9 (low shrub cover)	13.7**	1

** p<0.01

Sainte Luce littoral sites, and four species were found only in the Petriky forest. This difference in species composition could be a result of the more northerly location of Sainte Luce and the close proximity to the humid forests of the Vohimena Mountains. Of particular interest was the occurrence of *Newtonia archboldi* in the larger Sainte Luce forest patches, which was not found at Petriky, adjacent to the spiny forest.

An important finding was the depauperate nature of the matrix habitats surrounding littoral forest patches. The dominant matrix habitat, *Erica* heath, contained 24 species, which are all considered widespread in the region and throughout the island (Langrand 1990, Goodman *et al*. 1997, Morris and Hawkins 1998). This vegetation type did have four species (*Falco peregrinus, Charadrius pecuarius, Gallinago macrodactyla*, and *Saxicola torquata*) that were not found in littoral forest patches, but all prefer non-forested, open habitat (Langrand 1990). The three *Eucalyptus* plantations surveyed contained 22 species, and the five *Melaleuca* forest patches had 23 species, all of which were also found in littoral forest patches. The vast majority of species (n = 48) in this study were found only in littoral forest habitat.

The effect of changing habitat structure

There was variation in the vegetation density, habitat vertical structure, and habitat complexity of core and edge sampling stations in the littoral forest patches S8 and S9. On average, core habitats had significantly ($p < 0.01$) higher density of large trees, a higher maximum height of vegetation, more canopy cover, and a higher percentage of litter cover. The edge habitats had significantly ($p < 0.05$) higher amounts of low and medium shrub cover. There was as much variation in habitat variables of point-counts in the same patch as there was between point-counts in different patches. This support's Ingram *et al*.'s (2005) findings that littoral forest patches have high internal heterogeneity.

The relationship between individual bird species' presence and habitat structure were analyzed separately for core point-counts and edge point-counts. Every species found in either landscape element was analyzed independently to determine if its presence or absence within point-counts could be explained, even partially, by habitat variables. Therefore, 63 species were analyzed in core sites and 44 species in edge sites. Habitat variables significantly ($p < 0.05$) explained the distribution of seven species in core forest sampling stations, and seven species in edge sampling sites (Table 4, 5; see Watson *et al*. 2004a for further details).

Edge effects

A considerable edge effect was observed in the littoral forests in terms of both species richness, and

Table 5. Results of individual logistic regression models for 44 species when related to local vegetation variables for 20 edge littoral forest point counts. Bird species are classified as: edge-sensitive, edge-preferring, edge-tolerant, and ubiquitous following Watson *et al*. (2004a). Only bird species that had a significant relationship to habitat variables are shown. Habitat variables are defined in Table 1.

Species, by group	Model	Chi square	d.f.
Edge sensitive forest species			
Treron australis	-1.4+2.7 (canopy cover)	10.1**	1
Coracopsis nigra	29.7-25.4 (canopy cover)	12.4**	1
Newtonia brunneicauda	-114.7+104.1 (canopy cover)	20.1**	1
Vanga curvirostris	0.8+2.49 (canopy cover)	5.9*	1
Edge-tolerant forest species			
Nesillas typica	-45.6+51.6 (low shrub cover) +14.7 (number of small trees)	20.1**	2
Nectarinia notata	-2.9-5.8 (tall shrub cover)	7.1*	1
Ubiquitous species			
Cisticola cherina	-1.59+3.1 (low shrub cover)	10.3**	1

** p<0.01, * p<0.05

the total number of birds found at point-count stations. Sixty-two species were found within core littoral forest habitat, while only 44 species were found in edge habitats. Numbers of species and individuals per point-count differed between the two habitat types (repeated measures ANOVA: richness, $F_{2,57} = 41.5$, $p < 0.01$; abundance, $F_{2,57} = 38.6$, $p < 0.01$). Based on their probability of occurrence in edge and core stations in univariate tests, 31 species were identified as edge sensitive (Table 6; see Watson *et al*. 2004a for further details).

The effect of habitat fragmentation at the landscape scale

When all landscape variables measured were considered in a step-wise regression model, only patch area was a significant ($p < 0.01$) factor in explaining variation in both the total species and forest bird species richness (Fig. 2). Variance in total and forest-dependent species richness accounted for by the other variables in the step-wise regression was negligible in each case, and they were not selected in either model.

When individual landscape variables were considered in determining the probability of occurrence of individual species, patch area explained a significant ($p < 0.05$) portion of the deviance in the logistic models of 22 species (Table 6). The minimum area requirements identified from each species' incidence function varied from 15 to 150 ha (Table 6). This is most likely an underestimation of the species affected by patch area reduction, especially when considering 12 species which were removed from both individual analyses due to their rarity, and their restriction to only the very largest littoral forest patches. Of the species assessed, those with the greatest area requirements were *Lophotibis cristata, Ispidina madagascariensis, Tylas eduardi,* and *Newtonia archboldi*, with minimum area requirements of 150 ha (Table 6).

No isolation or landscape complexity measurement significantly ($p < 0.05$) explained the deviance for any species. Patch shape explained a significant ($p < 0.05$) portion of the deviance in the log/linear models of 12 species, but this was not surprising considering that the variable 'patch shape' was strongly correlated with the variable 'patch area,' and for most species this sensitivity was most likely due to 'patch area.' However, an interesting shape/area interaction for four forest-dependent species (*Coracina cinerea, Newtonia brunneicauda, Neomixis striatigula,* and *Zosterops maderaspatana*) in littoral forests patches was discovered when the species presence/absence was considered graphically against both variables (Fig. 3). As opposed to the species that were solely area-sensitive, each of these species only occurred in regular shaped patches < 100 ha, but ceased to exist in patches smaller than approximately 10 ha. This suggests that these four species are both area and shape sensitive, since

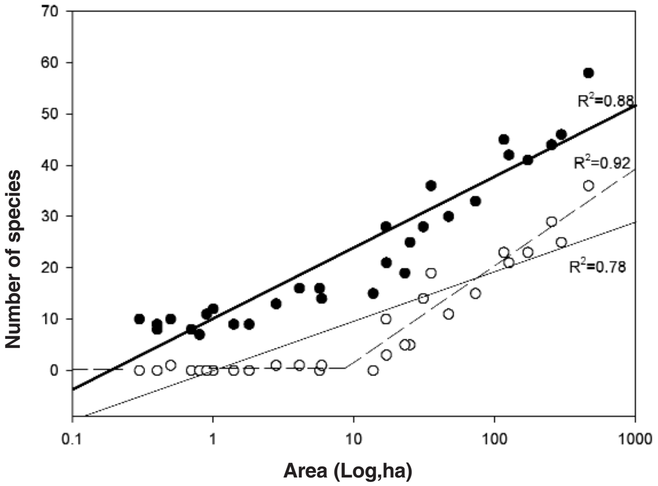

Figure 2. Bird species-area relationship in the littoral forests of southeastern Madagascar, including regressions. Two classifications of species richness were considered: total species richness (closed circles) and forest-dependent species richness (open circles). Classification of forest dependency followed Watson *et al*. (2004a). Linear regressions: unbroken lines; break-point regression: dashed line. The break-point regression procedure followed Lomolino and Wieser (2001). All regressions are significant ($p < 0.01$). Source: Watson *et al*. (2004b).

they occur in irregularly shaped patches only when they are greater than approximately 100 ha.

Discussion

An important finding of this study was the high number of bird species found inhabiting the littoral forest. Though not shown in this chapter, Watson *et al*. (2005) compared the species compositions of the largest littoral forest patches with the species compositions of nearby large humid and spiny forest blocks. When sampling effort was taken into account, Watson *et al*. (2005) found that the large littoral forest blocks had similar species richness to that of the other two forest types. This conflicts with Goodman *et al*.'s (1997) finding that the littoral forests were depauperate of birds because of their low species diversity and richness. This difference is primarily due to Watson *et al*. (2005) finding 17 species that were not previously found by Goodman *et al*. (1997) during the 1989 survey of the littoral forests (Appendix I). The increase in species number found in littoral forest patches is most likely a reflection of the larger number of patches visited in this study. In addition to higher species richness than what was previously thought, Watson *et al*. (2005) showed that the littoral forests contain an unusual bird assemblage when compared to other habitats on the island. Species not normally associated with each other due to their typical habitat affinities (e.g., *Coua gigas* and *C. caerulea*) were found occupying the same littoral forest patches.

This research shows that the littoral forests are not unique in their collection of bird species, although they do contain 57% of the island's endemic species, including three near-threatened bird species (*Accipiter henstii*, *A. madagascariensis*, and *Lophotibis cristata*; Watson *et al*. 2005, Birdlife International 2004). The forests are missing numerous forest-dependent species that are commonly found in nearby lowland humid forests (e.g., *Neodrepanis coruscans*, *Bernieria madagascariensis*, *Xanthomixis zosterops*, *Oxylabes madagascariensis*, *Mystacornis crossleyi*, *Newtonia amphichroa*, *Xenopirostris polleni*, and *Ploceus nelicourvi*) and spiny forests (e.g., *Coua cursor, Falculea palliata*, and *P. sakalava*, Goodman *et al*. 1997). The low altitude of littoral forests could explain some of these differences, as elevation has been shown to affect bird composition in many areas of the tropics (Terborgh 1971, 1977, Beehler 1982), including Madagascar (Goodman *et al*. 1997, Hawkins 1999). Other ecological factors may also be important, such as the availability of the necessary resources of particular bird species. However, these reasons may not be valid since several of these bird species were found in littoral forests on the north part of the island (Thorstom and Watson 1997). The absence of certain species in the Tolagnaro littoral forests may be a reflection of the amount of human pressure these sites have

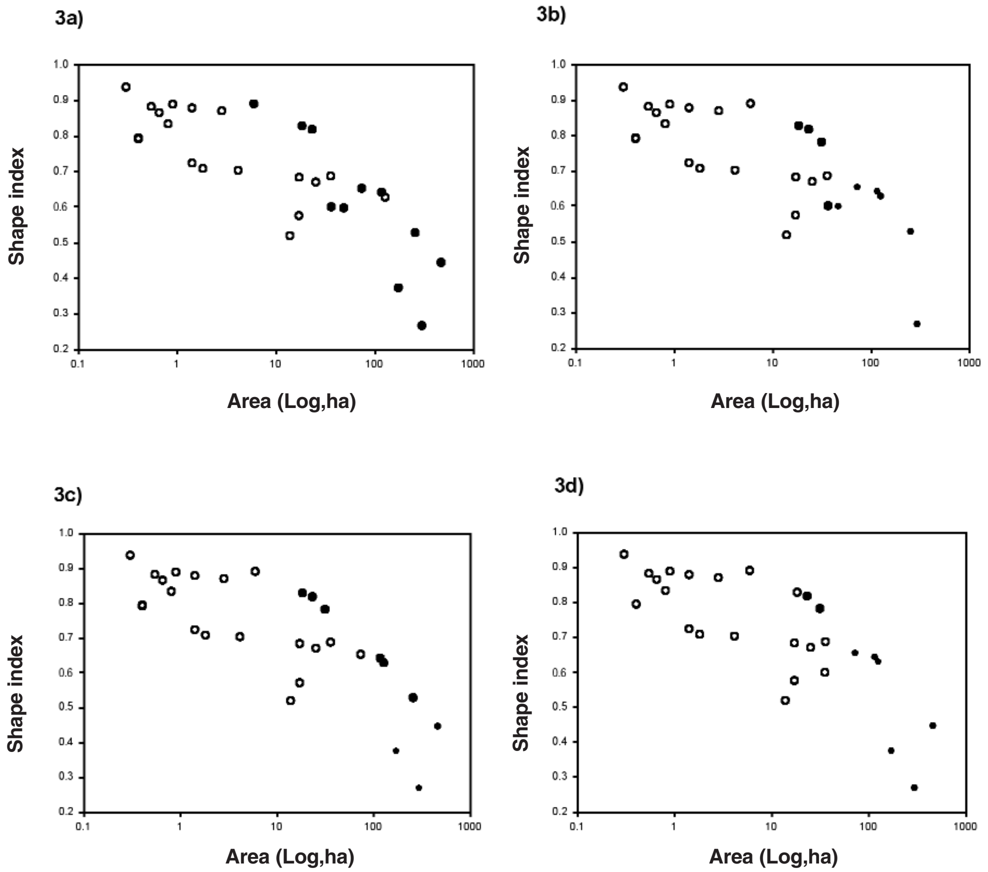

Figure 3. Presence or absence of a) *Coracina cinerea*, b) *Newtonia brunneicauda*, c) *Neomixis striatigula*, and d) *Zosterops maderaspatana* in littoral forest remnants of different size and shape indices; see Table 1 for definitions of these measurements. Closed circles indicate species presence and open circles indicate species absence within the littoral forest remnant. Source: Watson *et al*. (2004b).

endured or their long-term isolation from nearby lowland humid forest and spiny forest.

The complete lack of habitat-restricted, endemic bird species within the littoral forests could be a reflection of the relatively small amount of habitat available for species radiation. Terborgh (1992) argued that terrestrial vertebrate taxa need a minimum area of 12,000 km^2 to enter a stage of evolutionary radiation. There is no firm information available on how large the littoral forests were before human settlement, but it has been estimated to be around 4500 km^2 (Ganzhorn *et al*. 2001). If this estimation is correct, it is unlikely that the Malagasy littoral forests were large enough to allow for the radiation of highly localized vertebrate taxa at any time in their evolutionary history (Ganzhorn *et al*. 2000). As demonstrated by the high similarity of species found in littoral and spiny forests, and in littoral and humid forests, the geographic proximity of these three forest types may have also inhibited the differentiation of locally endemic bird species in the littoral forests.

The relationship between habitat structure and bird composition

There was high variability in the vertical structure of littoral forest patches. The littoral forest edge had significantly ($p < 0.01$) fewer trees, less canopy cover, less litter cover, and greater shrub cover than the core habitat. This variability between sampling stations is undoubtedly due to human use of the forest as some sampling sites were more exploited, and therefore, more degraded. A significant ($p < 0.01$) relationship was found between both bird species richness and individual abundance, and the vegetation structure at both core and edge point-count stations. Specifically, six species showed a relationship to the amount of canopy cover and three species to that of litter cover (Tables 4 and 5). It is possible that these species are affected by internal degradation of forest habitat, and in particular, the loss of the larger trees. These types of changes have been found to influence species richness and individual species abundance in other tropical studies (e.g., Beier *et al*. 2002).

The relationship between fragmentation and bird composition

At the patch level, 31 species were found to be sensitive (i.e. had significantly lower abundances), or did not occur at the edge of the littoral forest patch. This represents a large portion (68%) of the forest-dependent species found in this study (Watson *et al*. 2004a, 2004b). Other studies in tropical Africa have shown significant edge effects within forest bird communities, but not to this degree (Dale *et al*. 2000, Beier *et al*. 2002). It is unclear why the littoral forests have so many edge sensitive species. Hagan *et al*. (1996) argued that sensitivity to the edge depends on a number of factors including species' sensitivity to area effects, the duration and rate of habitat loss and fragmentation, and the proximity of the forest stand to disturbance. Further, they argue that incipient forest fragmentation may affect populations differently than later stages of fragmentation when the geometry of the landscape has reached a more stable configuration. Studies in South America support this argument showing that penetration of edge effects into bird abundance declines over a timescale of decades (Restrepo and Gomez 1998). However, in our study area, the geometry of the landscape has probably remained stable for at least 30 years (Ingram and Dawson 2005). Using the argument of Hagan *et al*. (1996), one would expect to find far fewer species affected by forest edge effects than this study encountered.

Proximal explanations for edge avoidance vary across systems and species. For instance, habitat structure and composition may be different on the edge (Lopez de Casenave *et al*. 1998, Beier *et al*. 2002), and micro-climatic changes near the patch edge can make it unsuitable for some bird species (Laurance *et al*. 1997). In the present study, it was found that the edge habitats had significantly ($p < 0.05$) more shrub cover, a less complete canopy, and less litter cover than the core habitats (see Watson *et al.* 2004a). This shift in vegetation structure and complexity is likely the result of human-induced change as local activities such as the cutting of trees were often seen occurring at the edge of forests. However, it has been shown in other tropical forests that changes to forest structure at patch edges can also be exacerbated by changes to micro-climate such as increased amounts of sunlight, higher wind speeds, and larger fluctuations in temperature and humidity (Laurance 2001). It was found that four edge-avoiding species had a significant ($p < 0.01$) portion of the variance of their distribution among edge sites explained by canopy cover (Table 5). Moreover, five species had a significant ($p < 0.01$) portion of their variance explained by canopy cover or litter cover at core sampling stations. None of the five species were encountered at any of the littoral forest edge sampling stations. Therefore, for nine species, it is possible that the cause of their edge sensitivity, at least in part, is a lack of a canopy cover and litter cover on the edge of littoral forest patches.

It should be noted, however, that there is no evidence of an edge effect due to changed forest structure for 21 edge-avoiding bird species, as they did not have their variance explained by habitat variables at either core or edge sites. One possible explanation for this is that bird species are edge sensitive because they exploit some unmeasured resource, such as food. Food supply for insectivores, for example, has been shown to vary with fragment size as a result of edge effects because invertebrates, especially surface dwellers, are prone to desiccation and may not survive well in edge habitat (Matlock 1993, Didham *et al*. 1996, Zanette *et al*. 2000). Moreover, there may be fewer fruiting and flowering trees near littoral forest patch edges, resulting in an edge effect for nectivorous and frugivorous species (Githiru *et al*.

2002, but see Lopez de Casenave *et al*. 1998). Another possible explanation is that predation, or avoidance of predation, near the edges may make a number of species 'edge sensitive' (Robinson *et al*. 1995).

At the landscape level, it was found that the size of littoral forest patches played a very important role in determining species richness. This marked relationship between species richness and patch size was not unexpected (e.g. Hagan *et al*. 1996, Beier *et al.* 2002, Santos *et al.* 2002). The most likely explanation for the littoral forest system's very strong species/area relationship is the lack of forest dependent species found in small patches. Only one forest dependent species occurred in patches < 10 ha in size, and many species needed patch areas > 15 ha (some up to 150 ha) to have a probability of occurrence greater than 50% (Appendix I). The steepness of the slope in the species/area relationship (z = 0.34) highlights the very low species richness in small patches, and suggests that species loss is occurring at a faster rate in the littoral forest than in other fragmented tropical forests (e.g., z = 0.15, Warburton 1997; z = 0.15, Stratford and Stouffer 1999; z = 0.16, Langrand and Wilmé 1997). However, since there are no baseline data on the species richness of the littoral forests before fragmentation, it is impossible to determine the extent of species loss in small patches. Other studies have found that small patches do not have sufficient resources to support a large number of species (Recher *et al*. 1987), fewer adequate breeding microhabitats (Wilcove *et al*. 1986), a higher degree of mesopredator release (Crooks and Soulé 1999), and experience more edge effects, including increased predation and parasitism (Robinson *et al.* 1995). Bird populations in small littoral forest fragments could be suffering from any one of these processes. However, the 'edge effect' hypothesis appears to be supported for some species evidenced by the patch shape/area interaction of four forest dependent species (Fig. 3). These species only occurred in patches that were more regularly shaped until the patch was greater than approximately 100 ha in size.

No measure of patch isolation or landscape complexity was related to bird species richness in littoral forest patches. There are several possible explanations for this observation. For instance, it may be that the bird species found in the study area are so mobile that they are not affected by isolation to the extent that other vertebrate taxa are, and as such, are able to immigrate (Ambuel and Temple 1983). Those species that are not as highly mobile may be able to disperse through the landscape matrix, which removes an isolation effect (Andrianarimisa *et al*. 2000, Renjifo 2001). Since the dispersal capabilities of Malagasy birds are relatively unknown, it is impossible to resolve this issue. The lack of an isolation effect in this study may not be paralleled among the other avifauna of the island because it may reflect the relatively limited range of isolation in the present study (cf. Whittaker 2000).

Conservation Recommendations

At the national level, this study has found that the bird communities inhabiting the littoral forests of the Tolagnaro region contain no species restricted to this habitat and few species of conservation significance. The three near-threatened species (*Accipiter henstii*, *A. madagascariensis*, and *Lophotibis cristata*) found in the littoral forests also occur in other forest types across Madagascar. Therefore, when comparing the littoral forests with the nearby spiny and humid forest blocks, the littoral forests should be a secondary priority in terms of bird conservation. This is because the spiny forests and humid forests of southeastern Madagascar, already recognized as conservation priorities for birds, hold many species globally threatened with extinction (Birdlife International 2004).

However, the littoral forests' comparatively low number of globally threatened and habitat-restricted bird species does not mean that they are not important from a conservation perspective. At least three factors emphasize the importance of the littoral forest ecosystem. First, the geographic location of these forest patches increases the possibility that they may enhance the connectivity of the landscape by functioning as 'stepping stones' for birds reticent to cross large expanses of hostile matrix. This could include dispersal of humid forest species in the Vohimena Mountains between the littoral forest patches of Mandena and Sainte Luce. Secondly, the littoral forests contain a bird community that is unique in the sense that it is a mixture of both spiny and humid forest bird species. Thirdly, they contain a significant portion

Table 6. Summary of the littoral forest bird species affected by landscape variables (patch area and shape) and patch variables (edge sensitivity and habitat) in littoral forest patches. Bird species shown are those that were found to have landscape or habitat variables explain a significant ($p < 0.05$) portion of their variance in step-wise regressions, and those species found to have significantly lower abundances at edge sites in paired t-tests. Minimum area requirements for all area-sensitive species were determined using incidence functions calculated from logistic regressions models. An incidence of 50% in the logistic model was used to define the minimum area. Habitat variables are found at Table 2. Landscape variables are found in Table 3. Detailed methodologies for how these species were found to be sensitive to either patch or landscape variables are found in Watson *et al*. (2004a, 2004b). The symbol Y indicates 'yes.'

Bird species	**Area sensitive?**	**Min. Area (ha)**	**Shape sensitive?**	**Relationship with habitat variable?**	**Edge-sensitive?**
Canirallus kioloides					Y
Dryolimnas cuvieri					Y
Lophotibis cristata	Y	150		Litter cover	Y
Polyboroides radiatus	Y	30			Y
Numida meleagris					
Sarothrura insularis	Y	40		Litter cover	Y
Treron australis	Y	20		Canopy cover	Y
Alectroenas madagascariensis	Y	25		Canopy cover	Y
Coracopsis nigra	Y	20		Canopy cover	Y
Coracopsis vasa					Y
Agapornis cana					Y
Cuculus rochii					Y
Coua reynaudii					Y
Coua caerulea	Y	25			Y
Coua gigas	Y	35			Y
Asio madagascariensis					Y
Ispidina madagascariensis	Y	150		Number of small trees	Y
Eurystomus glaucurus	Y	15			
Leptosomus discolor	Y	25			Y
Upupa marginata	Y	35			
Coracina cinerea	Y	50	Y		Y
Copsychus albospecularis	Y	110			Y
Nesillas typica				Low shrub cover, number of small trees	
Cisticola cherina				Low shrub cover	
Newtonia brunneicauda	Y	35	Y	Canopy cover	Y
Newtonia archboldi	Y	150		Low shrub cover, litter cover	Y
Neomixis viridis					Y
Neomixis tenella					Y
Neomixis striatigula	Y	35	Y		
Leptopterus chabert					Y
Cyanolanius madagascarinus					Y
Schetba rufa					Y
Calicalicus madagascariensis					Y
Tylas eduardi	Y	150			Y
Vanga curvirostris	Y	15		Canopy cover	Y
Terpsiphone mutata	Y	25			Y
Nectarinia notata	Y	15		Tall shrub cover	
Hartlaubius auratus					Y
Zosterops maderaspatana	Y	15	Y		Y

of the island's endemic, forest dependent bird species. As such, I argue that the littoral forests have a conservation value in their own right.

On a regional scale, this study's findings suggest that approximately 70% of forest dependent bird species will be absent from a reserve system composed solely of small patches of less than about 10-20 ha. To preserve the existing forest dependent bird community, the protection of a number of large (> 200 ha), core littoral forest areas in Mandena, Sainte Luce, and Petriky is recommended. Therefore, if the conservation goal is to conserve littoral forest bird diversity, it is argued that patches S9, S8, S17, S11, P1, and M15 be given the highest priority. These patches had the highest species richness, highest numbers of regional and island endemics, and the highest number of species found in any one sub-region. A major concern of just focusing on these patches is that large littoral forest patches are few in number and measured in hundreds, not thousands, of hectares. Some bird species may need very large fragments to survive, and they may even require groups of fragments to satisfy their habitat needs, or ensure population persistence (Pressey *et al*. 1993). Larger patches might represent core areas, but smaller patches also have a key role to play and may be especially important in this context (Fischer and Lindenmayer 2002).

I found that fragment shape, location of the edge, and the amount of habitat degradation affected the abundance of a number of forest dependent bird species. As patch size decreases, edge effects and degradation will invariably play a greater role in species distribution within the landscape. Therefore, efforts need to be made to overcome over-exploitation of smaller littoral forest patches. Since most of the very small patches (e.g., 10 ha) in this study had few species of overall conservation importance, such sites might not enter into local conservation concerns. However, it is argued that small littoral forest patches should not be ignored. Small patches have been proven to be useful stepping-stones for bird dispersal in other areas (e.g., Potter 1990, Date *et al*. 1996), butterfly dispersal (e.g., Schultz 1998), and plant dispersal (e.g., Collingham and Huntley 2000).

Even though this study indicates that patch isolation and landscape complexity are having little effect on the distribution of forest dependent birds in the littoral forest system, matrix management as part of an overall conservation strategy is encouraged. This includes both the maintenance of connectivity between littoral forest patches, and the maintenance of landscape heterogeneity within the fragmented, littoral forest landscape. Connectivity within the landscape will influence processes such as population persistence and recovery, the exchange of individuals and genes between isolates, and the occupancy of habitat patches, thereby reducing the impacts of habitat fragmentation on sensitive bird species (Lindenmayer and Franklin 2002). The maintenance of landscape heterogeneity will lead to the preservation of species diversity, since it may provide the particular environments required by habitat specialist species.

Conclusion

The littoral forests contain no bird species that are unique only to them, and their bird communities resemble a mixed assembly of species that occur in nearby humid forests and spiny forests. They are species rich when compared to their surrounding matrix habitats, however, it appears that processes associated with both habitat degradation and fragmentation affect a substantial portion of the bird species inhabiting the littoral forests, and these bird communities may be threatened. If bird conservation is to become a priority within the littoral forests of southeastern Madagascar, these results indicate that large (> 200 ha) blocks of littoral forest may need to be awarded protected status, and exploitation of forest resources which results in changes in vegetation structure should be minimized, especially in smaller littoral forest patches.

It must be noted that this research addressed only the pattern of bird distribution across the landscape and has not provided any data on 'process.' Further bird auto-ecological studies in the littoral forests to understand minimum viable populations within these fragmented landscapes are encouraged. Such data will be necessary considering the current mining program in the region. In addition to this, research should be conducted on how different bird species utilize the matrix habitats, and which habitats are the most suitable for bird species dispersing between littoral forest patches. This type of research would be directly applicable to the reforestation strategies being contemplated for the region, as it would assess both the possible effects of creating natural buffer zones around littoral forest patches, and the benefits of having corridors linking remaining forest fragments.

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References

Ambuel, B. and S.A. Temple. 1983. Area dependent changes in the bird communities and vegetation of southern Wisconsin forests. *Ecology* 64:1057-1068.

Andrianarimisa, A., L. Bachmann, J.U. Ganzhorn, S.M. Goodman and J. Tomiuk. 2000. Effects of forest fragmentation on genetic variation in endemic understory forest birds in Central Madagascar. *Journal für Ornithologie* 141:152-59.

Beehler, B. 1982. Ecological structuring of forest bird communities in Papua New Guinea. Pp. 837-861 *in*: Gressitt, J.L., ed., *Biogeography and Ecology of New Guinea*. W. Junk, The Hague, The Netherlands.

Beier, P., M.V. Drielen and B.O. Kankam. 2002. Avifaunal collapse in West African forest fragments. *Conservation Biology* 16:1097-1111.

BirdLife International. 2004. *State of the world's birds 2004: Indicators for our changing World*. BirdLife International, Cambridge, UK.

Cadotte, M.W., R. Franck, L. Reza and J. Lovett-Doust. 2002. Tree and shrub diversity and abundance in fragmented littoral forest of southeastern Madagascar. *Biodiversity and Conservation* 11:1417-1436.

Collingham, Y.C. and B. Huntley. 2000. Impacts of habitat fragmentation and patch size on migration routes. *Ecological Applications* 10:131-144.

Crooks, K.R. and M.R. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400:563-566.

Dale, S., K. Mork, R. Solvang and A.J. Plumptre. 2000. Edge effects on the understorey bird community in a logged forest in Uganda. *Conservation Biology* 14:265-276.

Date, E.M., H.F. Recher, H.A. Ford and D.A. Stewart. 1996. The conservation and ecology of rainforest pigeons in northern New South Wales. *Pacific Conservation Biology* 2:299-308.

Didham, R.K., J. Ghazoul, N.E. Stork, N.E. and A.J. Davis. 1996. Insects in fragmented forests: a functional approach. *Trends in Ecology and Evolution* 11:255-260.

Dumetz, N. 1999. High plant diversity of lowland rainforest vestiges in eastern Madagascar. *Biodiversity and Conservation* 8:273-315.

Fischer, J. and D.B. Lindenmayer. 2002. Small patches can be valuable for biodiversity conservation: two case studies on birds in southeastern Australia. *Biological Conservation* 106:129-136.

Ganzhorn, J.U., S.M. Goodman, J.-B. Ramanamanjato, D. Rakotondravony, B. Rakotosamimanana and D. Vallan. 2000. Vertebrate species in fragmented littoral forests of Madagascar. Pp. 155-164 *in*: Lourenço, W.R. and S. M. Goodman, eds., *Diversité et Endémisme à Madagascar.* Mémoires de la Société de Biogéographie, Paris.

Ganzhorn, J. B., P.P. Lowry, G.E. Schatz and S. Sommer. 2001. The biodiversity of Madagascar: one of the world's hottest hotspots on its way out. *Oryx* 35:346-348.

Githiru, M., L. Lens, A. Bennur and C.P.K.O. Ogol. 2002. Effects of site and fruit size on the composition of avian frugivore assemblages in a fragmented Afrotropical forest. *Oikos* 96:320-330.

Goodman, S. M., M. Pigeon, A.F.A. Hawkins and T.S. Schulenberg. 1997. The birds of southeastern Madagascar. *Fieldiana: Zoology*, new series, 87:1-132.

Hagan, J.M., W.M.V. Haegen and P.S. McKinley. 1996. The early development of forest fragmentation effects on birds. *Conservation Biology* 10:188-202.

Hawkins, A.F.A. 1999. Altitudinal and latitudinal distribution of east Malagasy forest bird communities. *Journal of Biogeography* 26:447-458.

Helzer, C. J. and D.E. Jelinski. 1999. The relative importance of patch area and perimeter-area ratio to grassland breeding birds. *Ecological Applications* 9:1448-1458.

Herzog, S. K., M. Kessler and T.M. Cahill. 2002. Estimating species richness of tropical bird communities from rapid assessment data. *Auk* 119:749-769.

Ingram, J.C. and T.P. Dawson T. 2005. Climate change impacts and vegetation response on the island of Madagascar. *Philosophical Transactions of the Royal Society*, London, A 363:55-59.

Ingram, J.C., R.J. Whittaker and T.P. Dawson. 2005. Tree structure and diversity in human-impacted littoral forests, Madagascar. *Environmental Management* 35:779-798.

Kinnear, P. R. and C.D. Gray. 2000. *SPSS for Windows Made Simple*. Psychology Press Ltd., Hove.

Langrand, O. 1990. *Guide to the Birds of Madagascar*. Yale University Press, New Haven.

Langrand, O. and L. Wilmé. 1997. Effects of forest fragmentation on extinction patterns of the endemic avifauna on the Central High Plateau of Madagascar. Pp. 280-305 *in*: Goodman, S.M. and B.D. Patterson, eds., *Natural Change and Human Impact in Madagascar.* Smithsonian Institution Press, Washington, D. C.

Laurance, W.F. 2001. Fragmentation and plant communities: synthesis and implications for landscape management. Pp. 97-120 *in:* Bierregaard, R.O., Jr., C. Gascon, T.E. Lovejoy and R. Mesquita, eds., *Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest*. Yale University Press, New Haven.

Laurance, W.F., S.G. Laurance, L.V. Ferreira, J.M. Rankin-de Morena, C. Gascon and T.E. Lovejoy. 1997. Biomass collapse in Amazonian forest fragments. *Science* 278:1117-1119.

Lindenmayer, D.B. and J.F. Franklin. 2002. *Conserving Forest Biodiversity: A Comprehensive Multiscale Approach*. Island Press, Washington.

Lomolino, M.V. and M.D. Wieser 2001 Towards a more general species-area relationship: diversity on all islands, great and small. *Journal of Biogeography* 28:431-446.

Lopez de Casenave, J., J. Pablo Pelotto, S.M. Caziani, M. Mermoz and J. Protomastro. 1998. Responses of avian assemblages to a natural edge in a Chaco semiarid forest in Argentina. *Auk* 115:425-435.

Lowry, P.P. and D. Faber-Langendoen, 1991. Overall flora and vegetation study. In Ilmenite Project. Social and Environmental Impact Assessment. Supporting Document no 4. Presented by QIT Madagascar Minerals S.A. (QMM S.A.) to the Madagascar National Environment Office May 2001.

Matlack, G.R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. *Biological Conservation* 66:185-194.

MacKinnon, J. and K. Phillips. 1993. *A Field Guide to the Birds of Sumatra, Java and Bali.* Oxford University Press, Oxford.

Morris, P. and F. Hawkins. 1998. *Birds of Madagascar: A Photographic Guide.* Pica Press, Robertsbridge, East Sussex.

O'Dea, N., J.E.M. Watson and R.J. Whittaker. 2004. Rapid assessment in conservation research: A critique of avifaunal assessment techniques illustrated by Ecuadorian and Madagascan case study data. *Diversity and Distributions* 10:55-63.

Pisces Conservation. 2002. *Species Diversity and Richness*. Pisces Conservation Limited, Lymington.

Potter, M. A. 1990. Movement of North Island Brown Kiwi (*Apteryx australis mantelli*) between forest remnants. *New Zealand Journal of Ecology* 14:17-24.

Pressey, R. L., C.R. Humphries, C.R. Margules, R.I. Vane-Wright and P.H. Williams. 1993. Beyond opportunism: key principles for systematic reserve selection. *Trends in Ecology & Evolution* 8:124-128.

Ramanamanjato, J.-B. and J.U. Ganzhorn. 2001. Effects of forest fragmentation, introduced *Rattus rattus* and the role of exotic tree plantations and secondary vegetation for the conservation of an endemic rodent and a small lemur in littoral forests of southeastern Madagascar. *Animal Conservation* 4:175-183.

Ramanamanjato, J.-B., P.B. McIntyre and R.A. Nussbaum. 2002. Reptile, amphibian, and lemur diversity of the Malahelo Forest, a biogeographical transition zone in south eastern Madagascar. *Biodiversity and Conservation* 11:1791-1807.

Recher, H.F., J. Shields, R.P. Kavanagh and G. Webb. 1987. Retaining remnant mature forest for nature conservation at Eden, New South Wales: a review of theory and practice. Pp. 177-194 *in:* Saunders, D.A., G.W. Arnold, A.A. Burbidge and A.J. Hopkins, eds., *Nature Conservation: The Role of Remnants of Vegetation.* Surrey Beatty and Sons, Chipping Norton.

Renjifo, L.M. 2001 Effect of natural and anthropogenic landscape metrics on the abundance of Subandean bird species. *Ecological Applications* 11:14-31.

Restrepo, C. and N. Gomez. 1998. Responses of understory birds to anthropogenic edges in a Neotropical montane forest. *Ecological Applications* 8:170-183.

Robinson, S.K., F.R. Thompson III, T.M. Donovan, D.R. Whitehead and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267:1987-1990.

Saab, V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: A hierarchical analysis. *Ecological Applications* 9:135-151.

Santos, T., J. L. Telleria and R. Carbonell. 2002. Bird conservation in fragmented Mediterranean forests of Spain: Effects of geographical location, habitat and landscape degradation. *Biological Conservation* 105:113-125.

Schatz, G.E. 2000. Endemism in the Malagasy tree fauna. Pp. 1-9 *in*: Lourenço W.R. and Goodman, S.M., eds., *Diversité et Endémisme à Madagascar*. Mémoires de la Société de Biogéographie, Paris.

Schultz, C.B. 1998. Dispersal behaviour and its implications for reserve design in a rare Oregon butterfly. Conser*vation Biology* 12:284-292.

Sokal, R. R. and F. J. Rohlf. 1981. *Biometry*. Freeman, New York.

Soulé, M. E., D. T. Bolger, A. C. Alberts, J. Wright, M. Sorice and S. Hill. 1988. Reconstructed dynamics of rapid extinctions of charparral-requiring birds in urban habitat islands. *Conservation Biology* 2:75-92.

Stratford, J.A. and P.C. Stouffer. 1999. Local extinctions of terrestrial insectivorous birds in a fragmented landscape near Manaus, Brazil. *Conservation Biology* 13:1416-1423.

Terborgh, J. 1971. Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. *Ecology* 52:23-40.

Terborgh, J. 1977. Bird species diversity on an Andean elevational gradient. *Ecology* 58:1007-1019.

Terborgh, J. 1992. *Diversity and the Tropical Rain Forest*. Scientific American Library, New York.

Thorstrom R. and R.T. Watson. 1997. Avian inventory and key species of the Masoala Peninsula, Madagascar. *Bird Conservation International* 7: 99-115.

Trainor, C.R. 2002. Status and habitat associations of birds on Lembata Island, Wallacea, Indonesia, with reference to a simple technique for avifauna survey on small islands. *Bird Conservation International* 12:365-381.

Vallan, D. 2002. Effects of anthropogenic environmental changes on amphibian diversity in the rain forests of eastern Madagascar. *Journal of Tropical Ecology* 18:725-742.

Warburton, N.H. 1997. Structure and conservation of forest avifauna in isolated rainforest remnants in tropical Australia. Pp. 190-206 *in:* Laurance, W.F. and R.O. Bierregaard, Jr. eds., *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*. University of Chicago Press, Chicago.

Watson, J.E.M., R.J. Whittaker and T.P. Dawson. 2004a. Habitat structure and proximity to forest edge affect the abundance and distribution of forest-dependent birds in tropical coastal forests of southeastern Madagascar. *Biological Conservation* 120:315-331.

Watson, J.E.M., R.J. Whittaker and T.P. Dawson. 2004b. Avifaunal responses to habitat fragmentation in the threatened littoral forests of south-eastern Madagascar. *Journal of Biogeography* 31:1791-1811.

Watson, J.E.M., R.J. Whittaker and T.P. Dawson. 2005. The importance of littoral forest remnants for indigenous bird conservation in southeastern Madagascar. *Biodiversity and Conservation* 14:523-545.

Whittaker, R.J. 2000. Scale, succession and complexity in island biogeography: are we asking the right questions? *Global Ecology and Biogeography* 9:75-87.

Wilcove, D.S., C.H. McLellen and A.P. Dobson. 1986. Habitat fragmentation in the temperate zone. Pp. 237-256 *in:* Soulé, M.E., ed., *Conservation Biology: The Science of Scarcity and Diversity.* Sinauer Associates. Sunderland.

Zannette, L., P. Doyle and S.M. Tremont. 2000. Food shortage in small fragments: evidence from an area-sensitive passerine. *Ecology* 81:1654-1666.

Appendix I. Bird species of forest habitats within the littoral forest study area. The bird species' lists for non-littoral forest habitats were lumped for all sites within each habitat class; see Table 1 for the geographic location of each littoral forest patch. X identifies bird species found in remnants of Sainte Luce (S), Mandena (M), or Petriky (P1), *Melaleuca* forest (MF), *Eucalyptus* plantations (EU), *Erica* heathland (ER), and "marécage" swamp habitats (MK); δ indicates species found in littoral forest remnants by this study but not by Goodman *et al*. (1997).

Bird species	**SA**	**SB**	**SC**	**SD**	**SE**	**SF**	**SG**	**SH**	**S1**	**S7**	**S8**	**S9**	**S10**
Little Bittern *Ixobrychus minutus*													
Black-crowned Night Heron *Nycticorax nycticorax*													
Sqaucco Heron *Ardeola ralloides*													
Purple Heron *Ardea purpurea*									x				
Grey Heron *Ardea cinerea*											x		
Madagascar Wood Rail *Canirallus kioloides δ*									x	x	x	x	
White-throated Rail *Dryolimnas cuvieri*									x	x		x	
Purple Moorhen *Porphyrio porphyrio*													
Greater Painted Snipe *Rostratula benghalensis*													
Madagascar Pratincole *Glareola ocularis*													
Kittlitz's Plover *Charadrius pecuarius*													
Madagascar Snipe *Gallinago macrodactyla*													
Madagascar Crested Ibis *Lophotibis cristata*										x		x	
White-faced Whistling Duck *Dendrocygna viduata*													
Meller's Duck *Anas melleri*													
Red-billed Teal *Anas erythrorhyncha*													
Madagascar Cuckoo-Falcon *Aviceda madagascariensis δ*													
Yellow-billed Kite *Milvus aegyptius*	x	x		x		x	x	x	x	x		x	x
Madagascar Harrier-Hawk *Polyboroides radiatus*												x	x
Madagascar Sparrowhawk *Accipter madagascariensis δ*												x	
France's Sparrowhawk *Accipter francesii*									x			x	x
Henst's Goshawk *Accipter henstii δ*													
Madagascar Buzzard *Buteo brachypterus*		x			x						x	x	x
Madagascar Kestrel *Falco newtoni*			x					x	x				
Eleonora's Falcon *Falco eleonorae*													
Sooty Falcon *Falco concolor*											x		
Peregrine Falcon *Falco peregrinus*													
Madagascar Partridge *Margaroperdix madagascarensis*										x			x
Helmeted Guineafowl *Numida meleagris*										x		x	
Madagascar Flufftail *Sarothrura insularis δ*									x	x		x	
Madagascar Buttonquail *Turnix nigricollis*			x								x		
Madagascar Turtle-Dove *Streptopelia picturata*	x	x	x	x	x	x			x	x	x	x	x
Namaqua Dove *Oena capensis*								x			x		
Madagascar Green Pigeon *Treron australis*									x	x	x	x	x
Madagascar Blue Pigeon *Alectroenas madagascariensis*										x	x	x	
Lesser Vasa Parrot *Coracopsis nigra*									x	x	x	x	x
Greater Vasa Parrot *Coracopsis vasa δ*										x	x		
Gray-headed Lovebird *Agapornis cana*										x			
Madagascar Lesser Cuckoo *Cuculus rochii δ*										x			
Red-fronted Coua *Coua reynaudii δ*										x		x	
Blue Coua *Coua caerulea*										x	x	x	x
Crested Coua *Coua cristata*													
Giant Coua *Coua gigas*									x	x	x	x	
Madagascar *Coucal Centropus toulou*	x	x	x	x	x	x	x		x	x	x	x	x
Madagascar Scops Owl *Otus rutilus*											x	x	
Madagascar Long-eared Owl *Asio madagascariensis*												x	
White-browed Owl *Ninox superciliaris*													
Madagascar Nightjar *Caprimulgus madagascariensis*												x	
Malagasy Spine-tailed Swift *Zoonavena grandidieri δ*			x	x						x	x		x
African Palm Swift *Cypsiurus parvus*			x	x				x		x	x	x	x

S11	S17	MA	MB	MC	MD	ME	MF	MG	M1	M4	M5	M6	M7	M15	M16	M20	P1	MF	EU	ER	MK
																					x
																					x
																					x
x									x												x
																					x
x	x																				x
	x								x					x	x						x
																					x
																					x
																				x	x
																				x	x
																					x
	x																				
																					x
																					x
																					x
	x								x					x							
x	x						x	x	x	x					x			x	x	x	
x	x										x			x	x		x				
x	x																				
x	x							x	x					x			x	x	x		x
x																					
x	x			x					x	x				x	x	x	x	x	x	x	
		x														x			x		
													x								
				x												x			x	x	
																			x		
x								x	x							x					
x										x	x		x			x		x	x		
x									x					x							
											x						x			x	
x	x		x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x
							x										x			x	
x	x				x			x	x	x	x			x	x	x	x	x	x		
x	x								x					x			x				
x	x								x	x				x	x	x	x				
	x																x				
	x								x					x	x		x				
	x																x		x		
x									x					x							
																	x				
x	x								x	x				x	x		x				
x	x			x	x	x		x	x	x	x	x	x	x	x	x	x		x	x	x
																		x			
																	x				
x								x	x			x		x	x		x			x	
	x				x	x	x			x		x	x	x	x		x				
	x	X		x	x	x		x	x	x	x	x		x	x	x	x	x			

Appendix I. Continued

Bird species	**SA**	**SB**	**SC**	**SD**	**SE**	**SF**	**SG**	**SH**	**S1**	**S7**	**S8**	**S9**	**S10**
Alpine Swift *Apus melba*						x	x		x		x	x	
African Black Swift *Apus barbatus*			x									x	
Malagasy Kingfisher *Alcedo vintsioides*									x	x	x	x	x
Madagascar Pygmy Kingfisher *Ispidina madagascariensis*												x	
Madagascar Bee-eater *Merops superciliosus*		x	x	x	x	x		x	x	x	x	x	x
Broad-billed Roller *Eurystomus glaucurus*									x	x	x	x	x
Cuckoo-Roller *Leptosomus discolor*												x	
Hoopoe *Upupa marginata*									x	x	x	x	
Velvet Asity *Philepitta castanea*													
Madagascar Bush Lark *Mirafra hova*	x		x	x			x	x			x	x	
Brown-throated Sand Martin *Riparia paludicola* δ				x							x		
Mascarene Martin *Phedina borbonica* δ													x
Madagascar Wagtail *Motacilla flaviventris*			x		x		x	x	x		x	x	x
Ashy Cuckoo-Shrike *Coracina cinerea*									x	x	x	x	
Madagascar Bulbul *Hypsipetes madagascariensis*	x	x	x	x	x	x	x		x	x	x	x	x
Madagascar Magpie-Robin *Copsychus albospecularis*										x		x	
Stonechat *Saxicola torquata*													
Lantz's Brush-Warbler *Nesillas lantzii*													
Madagascar Brush-Warbler *Nesillas typica*					x					x		x	
Madagascar Cisticola *Cisticola cherina*	x							x		x		x	x
Common Newtonia *Newtonia brunneicauda*					x	x			x	x	x	x	x
Archbold's Newtonia *Newtonia archboldi* δ										x	x	x	
Common Jery *Neomixis tenella*			x	x		x			x	x	x	x	x
Green Jery *Neomixis viridis* δ											x	x	
Stripe-throated Jery *Neomixis striatigula* δ									x	x	x	x	x
Madagascar Paradise Flycatcher *Terpsiphone mutata*										x	x	x	
Souminga Sunbird *Nectarinia souimanga*		x	x	x	x	x			x	x	x	x	x
Long-billed Green-Sunbird *Nectarinia notata*									x	x	x	x	x
Madagascar White-Eye *Zosterops maderaspatana*										x	x	x	
Chabert's Vanga *Leptopterus chabert* δ											x	x	
Hook-billed Vanga *Vanga curvirostris*									x	x	x	x	x
Blue Vanga *Cyanolanius madagascarinus*										x	x	x	
Rufous Vanga *Schetba rufa* δ												x	
White-headed Vanga *Leptopterus viridis*													
Tylas Vanga *Tylas eduardi* δ												x	
Crested Drongo *Dicrurus forficatus*	x	x							x	x	x	x	x
Pied Crow *Corvus albus*							x	x			x	x	
Madagascar Starling *Hartlaubius auratus*									x	x		x	x
Common Myna *Acridotheres tristis*	x		x				x	x			x	x	
Madagascar Red Fody *Foudia madagascariensis*			x	x	x					x	x	x	x
Forest Fody *Foudia omissa*											x	x	
Madagascar Manikin *Lonchura nana*	x	x	x									x	

S11	S17	MA	MB	MC	MD	ME	MF	MG	M1	M4	M5	M6	M7	M15	M16	M20	P1	MF	EU	ER	MK
x	x	X							x	x	x	x	x	x		x	x	x	x	x	x
x																			x		
	x								x		x			x	x		x	x			
														x			x				
x	x	X	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
x	x								x	x	x			x	x		x				x
	x								x								x				
										x				x	x		x	x			
			x	x	x	x	x				x	x	x	x	x	x			x	x	
	x									x	x	x	x	x					x		
x	x								x	x	x			x	x	x	x	x	x		
x	x								x					x			x				
x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
																	x				
																				x	
																	x				
x	x								x	x				x	x						
x	x	X	x	x		x	x	x	x	x	x	x	x	x	x		x	x		x	x
	x								x	x	x			x	x		x				
x	x																				
x	x				x	x		x	x	x	x	x	x	x	x	x	x	x	x		
x	x								x	x				x			x	x			
x	x								x					x	x		x				
x	x	X	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x		x
x	x								x	x	x	x		x	x	x	x				
	x					x			x	x		x		x	x	x					
x									x								x	x	x		
x	x								x	x		x		x	x	x	x	x			
														x	x						
																	x				
																	x				
x	x	X		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	x			x		x		x	x	x	x	x	x	x	x	x	x	x	x	x	x
x									x								x				
			x	x				x			x	x	x				x	x	x	x	
x	x					x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
	x													x							
		X			x				x	x	x						x			x	