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Regional Biodiversity Planning and Lemur Conservation with GIS in Western Madagascar

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Abstract: *Primary forest cover in western Madagascar declined from 12.5% in 1950 to 2.8% in 1990. Approximately 23% of remaining forest is located within reserves, but this is no guarantee of protection. Forest cover in the Andranomena Reserve in western Madagascar has been reduced by 44% since 1950. The identification of priority areas for establishment of development projects has been constrained by lack of information on the distribution, abundance, and habitat requirements of threatened species and the size, condition, and threats to survival of forest remnants. We evaluate a rapid fauna survey and habitat modeling procedure specifically designed to generate information for reserve selection and design using Geographical Information Systems (GIS). The study was conducted in the largest remnant (94,000 ha) of primary monsoon rainforest in western Madagascar, using lemurs as an indicator group. Lemur abundance and microhabitat variables were measured at 64 stratified survey sites dispersed throughout the region. These records were incorporated into a GIS with other environmental and landuse data derived from maps and satellite imagery. Statistical procedures were applied to analyze species habitats, predict and map species distributions, and estimate species population sizes throughout the study area. Patterns of slash and burn agriculture and anthropogenic disturbance were also analyzed to identify areas at low risk of cultural disturbance. A map of disturbance risk was overlaid with a map of relative lemur biodiversity to identify conservation priority areas with high biodiversity and low risk of short term disturbance. Lemur diversity was most strongly influenced by habitat clearing and human disturbance (harvesting, stock grazing, and hunting) within 8 km of villages. Lemur diversity was highest in a region of higher elevation and rainfall, distant from villages and roads. The only existing reserve in the study area was located in a region of high disturbance risk. Almost half the reserve has been degraded during the past 45 years. There is considerable scope for re-allocation of land use within the study area to include a core protected area, a buffer zone with controlled hunting and timber harvesting, and an adjacent ecotourism facility. We found that information generated by a stratified biodiversity and landuse survey at a sampling intensity of less than 0.1% was sufficient to provide an objective foundation for regional biodiversity planning.*

Planeacion de la Biodiversidad Regional y Conservación de Lemures con SIG en Madagascar Occidental

Resumen: *La cobertura de bosques primarios en el oeste de Madagascar disminuyó de 12.5% en 1950 a 2.8% en 1990. Aproximadamente un 23% del bosque remanente está localizado en reservas, pero esto no garantiza su protección. Las reservas están sujetas a caza, recolección, pastoreo y actividades de agricultura con tumba y quema. La cobertura de la reserva de Andranomena en Madagascar ha sido reducida en un 44% desde 1950. En vista de esta amenaza, los bosques tropicales estacionales deciduos de monson del oeste de Madagascar pueden ser considerados entre los ecosistemas más amenazados del planeta. La identificación de áreas prioritarias para el establecimiento de Proyectos Integrales de Conservación y Desarrolla (PICD) ha sido restringida debido a la falta de información sobre la distribución, abundancia y requerimientos de hábitat de las especies amenazadas, además del tamaño, condición y amenazas para la supervivencia del bosque remanente. Evaluamos un muestreo rápido de la fauna y procedimientos de modelado de hábitat diseñados*

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específicamente para generar información para la selección de reservas y su diseño, mediante el uso de Sistemas de Información Geográfica (SIG). El estudio fue llevado a cabo en un remanente grande de bosque primario de monson (94,000 ha), utilizando lemures como grupo indicador. La abundancia de los lemures y variables del microhábitat fueron medidas en 64 sitios estratificados de muestreo, dispersos en toda la región. Estas observaciones fueron incorporadas en el SIG con otras variables ambientales y datos de uso del suelo derivados de mapas e imágenes de satélite. Procedimientos estadísticos fueron aplicados para analizar hábitat de especies, predicciones y mapas de distribución de especies, así como para estimar tamaño poblacional de especies a lo largo del área de estudio. Patrones de agricultura con tumba y quema y perturbaciones antropocéntricas fueron también analizados para la identificación de áreas con bajo riesgo de perturbación cultural. Un mapa de distribución de riesgos se sobrepuso a un mapa de biodiversidad relativa de lemures para identificar áreas prioritarias de conservación con alta biodiversidad y bajo riego de perturbación a corto plazo. La diversidad de los lemures estuvo mas fuertemente influenciada por el clareado de hábitat y perturbación humana (cosechas, pastoreo y caza) dentro de una distancia de 8 km de las villas. La diversidad de los lemures fue mas alta en una región con mayor elevación y lluvia, distante de villas y carreteras. La única reserva existente en el área de estudio se localiza en una región con alto riesgo de perturbación. Casi la mitad de la reserva ha sido afectada durante los últimos 45 años. Existe un considerable margen para la reasignación de uso del suelo dentro del área de estudio que incluya un área protegida, una zona de amortiguamiento con caza y cosecha de madera controlada y una instalación adyacente para ecoturismo. Encontramos que la información generada por biodiversidad estratificada y análisis de uso del suelo con una intensidad de muestreo menor al 0.1% es suficiente para proveer la fundación objetiva de planes para biodiversidad regional.

Introduction

Madagascar has been assigned a global conservation priority as one of the richest and most endangered ecosystems on Earth (Mittermeier et al. 1992; Sussman et al. 1994). Large size, an equitable climate, extensive rainforest cover, and long isolation from other land masses has given rise to an exceptional level of biodiversity and endemism. Madagascar is equalled only by Australia in its proportion of unique terrestrial vertebrates and flowering plants. The flora includes an estimated 9300 identified species of which 81% are believed endemic (Phillipson 1994). Approximately 50% of plant species are known from fewer than five locations (G. Schatz pers. comm.) making them rare or poorly known using conventional criteria for assessment of conservation status. Best known amongst the fauna are 28 extant species of endemic lemurs, widely recognized as the "flagship" taxa for biodiversity conservation in Madagascar (Mittermeier et al. 1992). Fourteen lemur species have become extinct since the arrival of humans during the previous 500–2000 years (Tattersall 1982), and more than half of the surviving species are considered endangered or vulnerable (Harcourt & Thornback 1990; Mittermeier et al. 1992).

Concern for Madagascar's unique biodiversity stems from an exceptional rate of forest clearing, fragmentation, and land degradation for subsistence agriculture and fuel production. A recent assessment, using 1-km resolution satellite imagery, estimated total forest cover to be only 11% of the island area (Nelson & Horning 1993, Fig. 1). Forest clearing rates averaged 110,000 ha per annum in eastern Madagascar between 1950 and 1985 (Green & Sussman 1990) and 61,000 ha per annum in western Madagascar between 1950 and 1990 (Smith 1997). Pressure on remnant forests is being maintained by a higher than average population growth rate (doubling every 22 years; Daume 1990), a low annual per capita income (US $230), a high level of subsistence agriculture (78% of the population, Gade 1985), and weed invasion, loss of fertility, and erosion of previously cleared land. Charcoal is the principal domestic energy source in Madagascar and the equivalent of 1–3% of remaining forest cover is harvested annually, mostly from plantations in the north and east but from natural thorn scrub forest in the south and west (Pollock 1986; Suss-

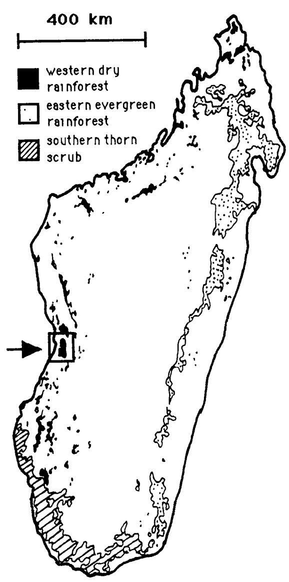

Figure 1. Remnant vegetation cover in Madagascar in 1990 (after Smith 1997) showing the distribution of western dry (monsoon) rainforest (solid black), eastern evergreen rainforest (stippled), and southern thorn scrub (hatched); and the location of the study area which encompasses the largest remnant of western dry forest (arrow).

man et al. 1994). Grazing is widespread in secondary forest and savannas, and regular uncontrolled fires started to promote fresh fodder destroy forest margins as well as preventing forest regeneration and promoting erosion. Lemurs and other vertebrates in forest remnants are directly hunted for food (Harcourt & Thornback 1990).

Efforts to conserve biodiversity in Madagascar have focused on the dedication and management of a network of nature reserves, referred to as protected areas, which covered approximately 1.05 million ha or 1.8% of the land surface in 1991 (Jenkins 1987; Smith et al. 1991). However, inclusion of remnants in nature reserves is no guarantee of biodiversity protection in Madagascar. The Malagasy Government lacks the resources for effective staffing and management of protected areas. Most reserves are understaffed and threatened by ongoing agricultural encroachment, poaching, burning, and progressive degradation. Intensive protected area management is largely confined to a limited number of Integrated Conservation and Development Projects (ICDPs). The ICDPs seek to halt forest clearing by promoting sustainable agriculture in buffer zones surrounding reserves and through financial compensation for loss of land through employment of locals as guides and guardians. The ICDPs are primarily supported by foreign aid; expenditure on ICDPs and related projects in 1990 exceeded $4.5 million (Smith et al. 1990).

The identification of priority areas for establishment of ICDPs in Madagascar has been constrained by lack of information on the size, condition, biodiversity, and conservation status of forest remnants. In recognition of the urgent need for collection, modeling and mapping of this information, the World Wide Fund for Nature (WWF-International) commissioned a feasibility study to investigate the need for a centralized Geographic Information System (GIS) based biodiversity planning service (BPS) in Madagascar (Smith et al. 1990). This study concluded that existing landscape information was inadequate for reserve planning at a regional scale and that a centralized GIS facility would need to be coupled with regional programs to collect new biological, socio-economic, and bio-physical data (Smith et al. 1990). A pilot study, to test rapid, low cost survey methods for regional biodiversity planning using GIS, was initiated in western Madagascar by WWF-I in 1991 (Smith et al. 1991).

Clearing has been most severe in the seasonally deciduous (monsoon) rainforests of western Madagascar. Western primary forest cover declined from 12.5% in 1950 to approximately 2.8% in 1990 (Smith 1997), relative to an average cover of 11% in the whole of Madagascar in 1990 (Nelson & Horning 1993). The surviving 712,000 ha of primary western forest is highly fragmented and dispersed. The largest remnant (94,000 ha) is threatened by timber harvesting and slash and burn agriculture and is not well represented in reserves. The region surrounding and including this remnant was chosen as the site for a trial evaluation of a GIS-based procedure for bioregional planning, referred to as RACE (after *RA*pid *C*onservation *E*valuation), adapted from Davis et al. (1990) and Ferrier and Smith (1990). This procedure combines rapid biological survey, multivariate habitat modeling, social impact assessment and GIS mapping and overlay procedures to identify optimum areas for location and management of reserves.

Our study presents the findings of the trial evaluation of RACE in western Madagascar, using lemurs as an indicator group. Lemurs are an ideal flagship taxa for biodiversity planning in Madagascar because they include some of the most endangered fauna on the island, their ecology is better known than that of most other vertebrate taxa, they are forest dependent, and they have a central role in development of the ecotourism industry as a means of providing alternative employment and stabilizing development in buffer zones around protected areas. Specific aims of the trial were to

- evaluate the effects of cultural disturbance (logging, clearing, and hunting) on lemur distribution and abundance in the region;
- predict and map the distribution of lemur habitats and biodiversity;
- estimate regional lemur population sizes;
- evaluate the adequacy of existing reserves for protection of representative lemur habitat;
- identify optimal locations for location and management of new reserves; and
- evaluate the effectiveness of the RACE methodology for bioregional planning.

Methods

Study Area

The survey region was located in the western zoogeographic subregion of Madagascar (Nicoll & Langrand 1989) where it encompassed the largest fragment of the remaining natural forest on the central west coast, in an area of approximately 60 by 40 km, northeast of Morondava (Fig. 1). The study area (Fig. 2) is bounded by the rivers Andranomena to the south and Tsiribihina to the north, and cleared and burnt open savannas to the east. Natural vegetation of the region is dominated by seasonally deciduous, monsoon rainforests typical of the western phytogeographic domain of Madagascar (Jenkins 1987). The study area includes approximately 94,000 ha of primary (relatively undisturbed) forest, 14,000 ha of secondary forest, 26,000 ha of degraded forest, and 5,000 ha cleared forest and non-forest (Fig. 2). Annual rainfall of 575 to 1330 mm falls predominantly in the wet season from November to March (Rakotonira 1985). There is a gradient of increasing rainfall from west to east,

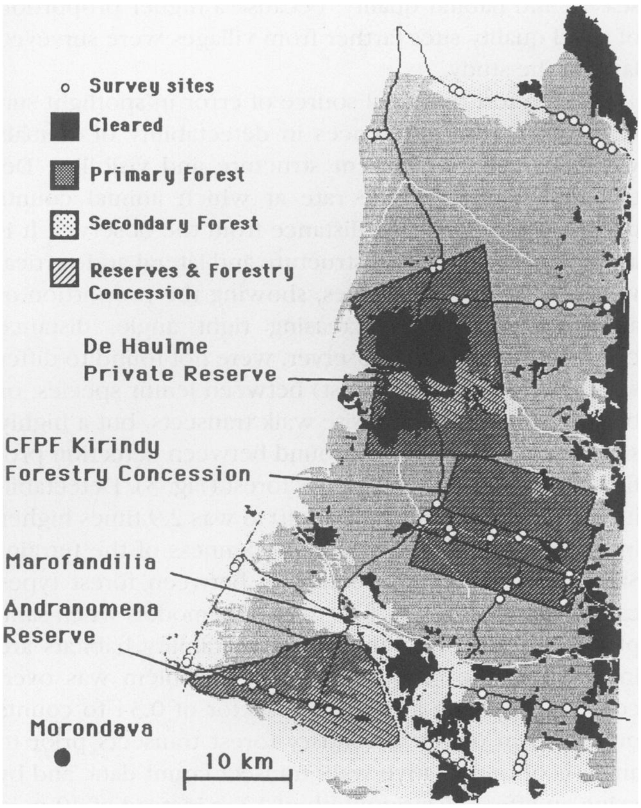

Figure 2. Map of the study area in western Madagascar showing location of survey site transects, vegetation cover, and the boundaries of reserves and a timber production concession.

which follows a gentle elevation gradient from sea level to approximately 100 m. Little or no rain falls in the dry season from April to October, during which time many animals including at least one species of lemur (*Cheirogaleus medius*) avoid food and water stress by aestivating. We conducted our study between late October and early November 1990 immediately prior to the onset of rain when temperatures averaged 17°C (min.) and 38°C (max.).

The Morondava Regional GIS Database

A 100-m resolution raster (grid based) GIS database covering the study region was established for the pilot study using ERMS (Ferrier 1988), IDRISI (Clark University), and SPANS (Tydac Technologies) GIS systems. The database included primary mapped attributes digitized from existing maps or obtained directly from satellite tapes, secondary mapped attributes derived from primary attributes within the GIS, and field survey attributes including lemur records and indices of human disturbance measured or visually estimated at 64 stratified survey sites. A new landcover (vegetation) map of the study area was prepared from a combination of sources including a 1:100000 map prepared by H. Duccenne, U. Schroff, and A. Narson from 1986/87 SPOT satellite images; an enhanced Landsat TM 1990 (bands 3,4, and 5) satellite image; air photo maps (approx 1:10,000) for the central portion of the study area; and ground truthing during the study. Mapped attributes stored in the GIS, and the sources of information for each attribute are provided in the Appendix.

Survey Design (Stratification)

Transect site locations were stratified, using a mean balance sample design (Ferrier & Smith 1990), according to the following attributes: vegetation condition (primary, secondary); proximity to water courses (within 200 m, 200 m–1 km, >1 km); latitude (within four north south bands); and longitude (within three east west bands) to give 72 unique survey strata. Each unique stratum was mapped (not all unique combinations were found to exist within the survey region) by overlay of variables stored in a GIS database on a portable computer. The resulting map was then overlayed with roads and tracks to identify potential access points and design the survey sequence which minimized time spent in travel by survey teams and maximized the number of sites that could be surveyed in the limited time available. The aim was to achieve a "balance" between a statistically ideal sampling design and the constraints imposed by limited vehicle access. Final selection of 64 sites was made after an initial vehicle reconnaissance of all major access routes. This was considered close to the minimum number of sites required to derive statistically meaningful fauna habitat models, based on prior experience in rainforests of eastern Australia (Ferrier & Smith 1990).

Fauna and Habitat Survey Methods

All vertebrate fauna (birds, mammals, reptiles) and environmental variables were measured at 64 sites over 3 weeks at a rate of three sites per team per day, using rapid standardized procedures designed to optimize the utility of the data for subsequent spatial analysis and modelling. Only the results of lemur surveys are presented.

Seven species of lemurs had previously been recorded within the survey region (Charles-Dominique & Petter 1980; Petter et al. 1971; Ganzhorn et al. 1989; Smith & Ganzhorn 1996) including two diurnal species (*Propithecus verreauxi* and *Eulemur fulvus rufus*) and five nocturnal species (*Microcebus murinus, Cheirogaleus medius, Mirza coquereli, Phaner furcifer, and Lepilemur ruficaudatus*). Investigations subsequent to this study suggest that *M. murinus* in the study area comprises two separate species, *M. murinus* and an undescribed species (J. Ganzhorn pers. comm.). For the purpose of this study these species were considered as one.

Nocturnal lemur species were surveyed by spotlight counts on 200-m walked transects at 64 survey sites ("site walk transects"). At each site a 200-m transect was flagged by pacing at right angles from access roads. Each transect commenced up to 100 m from access roads to accommodate any variation in vegetation floristics and/or structure along the road edge. At 46 of the 64 sites a second transect count was conducted along the access trail or road perpendicular to site transects, for a distance of 200 m. These "site road transects" were conducted simultaneously with "site walk transects". Surveys were conducted between 0.5 and 2 hours after sunset by one or two observers. The estimated right angle distance to each animal detected was recorded. The locations of all site transect surveys are shown in Fig. 2.

Nocturnal lemurs were also surveyed on 18 "road drive transects" of variable length (1.0–5.5 km), totaling 50.6 km, conducted during the return journey from survey sites back to basecamp. Road drive transects were conducted at approximately 5 km/hr, using hand torches and 35-watt spotlights. The location of all lemurs detected was determined by recording the distance travelled from a known starting point using vehicle odometers and a satellite navigation GPS (Global Positioning System) accurate to approximately 30 m. Observations of animals more than 40 m from the road edge, which could not be confidently identified, were not recorded. Road transects were divided into 200-m units equivalent to site transects for the purpose of data analysis. Diurnal lemurs (*P. verreauxi* and *E. fulvus*) were surveyed by three methods: recording the location of all sightings on the first occasion that roads were driven; recording all occurrences on each of the 64 site transects during the course of diurnal bird, reptile, and small mammal surveys; and spotlighting surveys for nocturnal lemurs.

Any evidence of anthropogenic activity at survey sites, including logging, grazing, hunting, burning or gathering, was visually estimated during habitat surveys and recorded to provide indices of cultural impact for correlation with lemur diversity.

Detectability of Lemurs

The number of arboreal mammals detected by spotlighting on line transects can vary significantly with weather conditions, season, time of night, vegetation structure, observer expertise, speed and mode of travel (A. Smith unpublished data). These variables were measured and compensated for, where possible, prior to habitat modelling. No significant relationships were found between species abundance and time of night or survey duration for all walk transects. There was a general trend of increasing abundance for all species with day of survey, but this effect was attributed to confounding between season and habitat quality, because a higher proportion of good quality sites farther from villages were surveyed later in the study.

The greatest potential source of error in spotlight surveys arose from differences in detectability of animals within forests of different structure and visibility. Detectability refers to the rate at which animal counts decline with increasing distance from the observer. It is a function of vegetation structure and lateral and vertical visibility. Detection profiles, showing the proportion of animals counted in increasing right angle, distance classes away from the observer, were not found to differ significantly (chi-square test) between lemur species, or between road walk and site walk transects, but a highly significant difference was found between detection profiles in primary and secondary forest (Fig. 3). Detectability out to a lateral distance of 40 m was 2.9 times higher in secondary forest due to the openness of the terrain. Such differences in detectability between forest types can introduce noise or bias to habitat models when samples from both high and low detectability habitats are included in the one analysis. This problem was overcome by applying a correction factor of 0.34 to counts out to 40 m on six secondary forest transects prior to analysis of quantitative walk transect count data, and by using an effective strip width of 12 m instead of 40 m in secondary forest for analysis of presence/absence data (see Table 1 for derivation of correction factors and effective strip widths). The mean number of lemurs per 200-m transect detected during walk counts was 4.4 times greater than numbers detected on road drive counts in similar habitat types. Lower detectability on road transects was attributed to the higher speed of travel, inability to detect animals by sound, and the reduced opportunity for effective canopy searching from a moving vehicle.

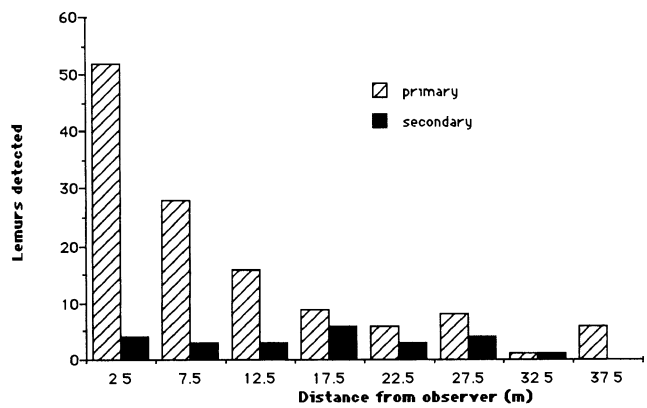

Figure 3. Detection profiles showing the number of lemurs detected at increasing right angle distance classes from transect lines in primary and secondary forests.

Table 1. Correction factors for estimating lemur density from spotlight counts out to a specified right angle distance (transect width) in primary and secondary forest.

Forest type	*Transect width (m)*	*Correction factor*	*Effective sample area (ha/100 m)*
Primary	5	1.0	0.10
	10	1.4	0.14
	20	2.0	0.20
	30	2.8	0.22
	40	3.5	0.23
Secondary	5	1.0	0.10
	10	1.0	0.20
	20	1.0	0.40
	30	1.0	0.60
	40	1.2	0.67

Statistical Analysis

Statistical associations between lemur abundance and continuous environmental variables were analyzed by correlation, regression, and stepwise multiple regression. Associations between lemur abundance and categorical environmental variables were analysed by analysis of variance and chi-square. Two variables (fire and cut stems) were excluded from quantitative linear analysis due to abnormal sample distributions. Associations between lemur frequency of occurrence and both categorical and continuous variables were determined by decision trees analysis (Knowledge Seeker 1990).

A correlation matrix was used to identify any spatial autocorrelation amongst continuous environmental variables, and Principal Components Analysis was used to group correlated variables into independent factors, or key underlying environmental gradients within the study area. The following three important factors were recognized (factor loadings are given in parentheses):

(1): a cultural disturbance gradient, showing a decrease in pig (−0.52), zebu (−0.78), root gathering (−0.57), and summed cultural impact (−0.69) with increasing distance from villages (0.68) and increasing rainfall (0.80); (2): a combined clearing (0.88) and disturbance (0.81) gradient, from primary forest to cleared savanna; and (3): a combined logging (stumps = 0.74) and hunting (0.67) gradient.

Results

Threats to Lemur Populations and Habitats

Statistically significant associations between lemur species richness, the abundance of individual lemur species, and mapped and estimated environmental variables at survey sites (including factor scores) are summarized in Table 2. These associations provide an overview of the relative importance of cultural and natural environmental variables as predictors of regional lemur abundance. The

Table 2. Significant associations between lemur abundance, natural and cultural environmental variables, and survey conditions at 64 survey sites, showing values of the correlation coefficient (r) for associations with continuous variables.

Environmental variable	Lepilemur ruficaudatus	Microcebus spp.	M. coquereli	P. furcifer	P. verreauxi	C. medius	E. fulvus	*Lemur sp. richness*
Natural site variables								
Max. rainfall		$+.24^{a}$					$-.31^{a}$	
Min. rainfall	$+.26^{a}$							$+.27^{a}$
Elevation	$+.27^{a}$							
Slope						$-.24^{a}$		
Stream		$-.32^{b}$						
Cultural (anthropogenic) site variables								
Village								$-.37^{b}$
Disturbance	$-.34^{b}$			$-.43^{c}$	$-.28^{a}$			$-.57^{c}$
Clearing (%)	$-.34^{c}$			$-.36^{b}$	$-.24^{a}$			$-.42^{c}$
Zebu Trails	$-.26^{a}$			$-.32^{b}$				$-.40^{c}$
Pig Trails	$-.27^{a}$							$-.30^{b}$
Root Digs	$-.31^{a}$							$-.26^{a}$
Cultural Impact	$-.40^{c}$	$-.36^{b}$		$-.27^{a}$				$-.41^{c}$
Factor 1 (cultural)	$-.40^{c}$							$-.45^{c}$
Factor 2 (clearing)				$-.29^{a}$				$-.38^{b}$
Survey conditions								
personnel								
temperature								
moonlight								
time of year					$+.31^{a}$		$+.28^{a}$	

$^{a}p < 0.05$
$^{b}p < 0.01$
$^{c}p < 0.001$

strongest associations are with all forms of human disturbance except selective logging activity.

Stepwise multiple regression was used to identify which additive combination of environmental variables best predicted lemur species richness and the abundance of individual lemur species in all walk transect sites and combined road and walk transect sites. All factors, independent variables, and the best predictor variable from any set of autocorrelated variables were used in model formulation (Table 3). These models clearly indicate that the cultural variables, primarily slash and burn agriculture, and root harvesting and stock grazing close to villages, are much better predictors of lemur species richness and abundance in the Morondava region than natural site variation at the macrohabitat scale. Lemur species richness and abundance generally declined with increasing cultural disturbance. The abundance of stumps, an indicator of selective logging activity, was the only cultural variable positively associated with lemur species richness.

The regression model for *P. verreauxi* (model a, Table 3) indicates that greater numbers of this species were detected later during the survey period. This effect was attributed to autocorrelation between time of survey and disturbance because the least disturbed habitats were surveyed last. When disturbance is entered into stepwise regression models before time of year (model b), time of year has no significant additive effect on *P. verreauxi* abundance.

The amount of variation in lemur abundance explained by these models is comparatively low. Unexplained variation can be attributed to inadequate survey effort (sample number or transect length), particularly for rare species, or the effects of unmeasured environmental variables not included in the analysis. We attempted to distinguish these effects by examining the relationship between survey effort and the explanatory power of linear regression models. Multiple R values for the best simple or stepwise multiple regression models for each species (from Table 3) were plotted against the mean number of lemurs per site. The existence of a significant relationship ($r = 0.82$, $p < 0.001$) suggested that the rarer species (e.g., *M. coquereli* at 0.125 animals/site) may not have been adequately sampled for development of optimal linear models.

Lemur Distribution Modeling and Mapping

Decision tree modeling permits the inclusion of all categorical and continuous variables in the one analysis and provides an output which is readily interpretable by nonstatisticians (Knowledge Seeker 1990). We used decision trees to model associations between all mapped continuous and categorical environmental variables (geology, maximum and minimum rainfall, elevation, slope, aspect, vegetation, satellite classes, landcover, disturbance, village [distance from], and stream [distance from], the frequency of occurrence [presence/absence] of individual lemur species and the mean number of lemur species in survey units. Because we used only mapped environmental variables in this analysis, we were able to include data from both road drive transects counts and site walk transects to give a total of 363 transect survey units. Mapped environmental variables at road transect sites were derived by entering the co-ordinates for each 200 m of road transect into the GIS and extracting a list of mapped attributes for each segment.

A sample decision tree model is presented for average lemur species richness in each 200-m transect (Fig. 4). This model shows that the variable disturbance was best

Table 3. Summary of multiple regression models for relationships between lemur abundance and cultural and natural environmental variables at transect survey sites.

Species	*Intercept*	*Predictor variables*	*r/multiple* R
Lepilemur ruficaudatus	1.178	−0.180 cultural impact −0.264 disturbance	0.52
Microcebus spp.	0.714	−0.086 cultural impact −0.065 stream	0.43
Phaner furcifer	0.991	−0.324 disturbance	0.44
Propithecus verreauxi (a)	0.627	+0.062 time of year −0.117 stream	0.42
P. verreauxi (b)	0.500	−0.168 disturbance	0.28
Eulemur fulvus	3.156	−0.046 maximum rain	0.31
Cheirogaleus medius	0.144	−0.057 cultural impact +0.006 slope	0.29
Mirza coquereli	NS		
Lemur species richness	0.327	−0.377 cultural impact −0.757 disturbance +0.108 stumps	0.69

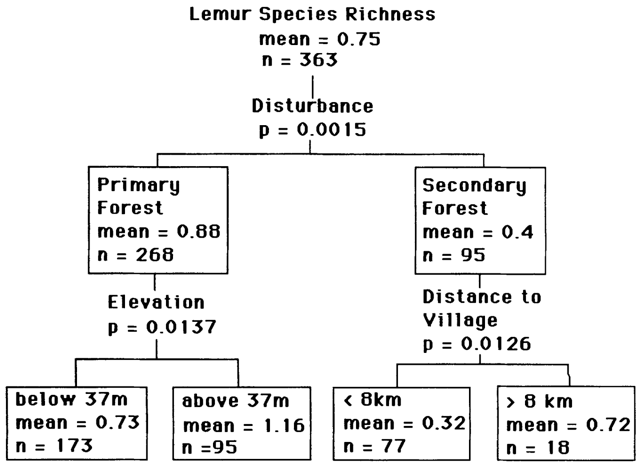

Figure 4. Decision tree model showing environmental predictors of lemur species richness on survey transects.

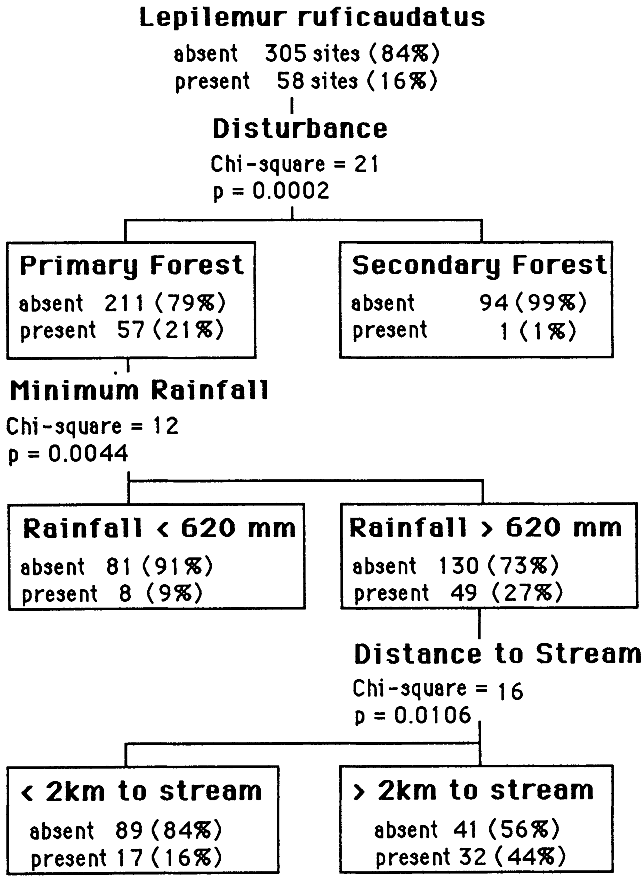

Figure 5. Decision tree model showing environmental predictors of Lepilemur ruficaudatus *frequency of occurrence on survey transects.*

able to split transects into low and high relative species richness groups. The average number of species per transect was 0.88 in primary forest and 0.40 in secondary forest. A *t*-test shows this difference to be statistically significant at a $p < 0.001$. Subsequent splits show that within areas of primary forest species richness was significantly greater above 38 m elevation and within areas of secondary forest species richness was significantly greater more than 8 km from villages.

A decision tree model is also presented for *L. ruficaudatus* (Fig. 5). This model shows that the variable disturbance was best able to split sites into groups high and low *L. ruficaudatus* frequency of occurrence (chi-square $= 21, p = 0.0002$). *L. ruficaudatus* was detected at 57 sites in primary forest and only one site in secondary forest. Six other variables (vegetation; minimum rainfall; elevation; distance away from village; maximum rainfall; and geology, in decreasing order of importance) were also significantly associated with *L. ruficaudatus* occurrence and could have been used as alternatives to disturbance in the first split. Step two in the model shows that, within primary forest, *L. ruficaudatus* occurred significantly more frequently within areas of higher minimum rainfall. The occurrence of *L. ruficaudatus* was also significantly greater in areas of higher elevation and areas with exposed sandstone substrates. Either of these variables could have been used as alternatives to minimum rainfall in the second split. The third step shows that *L. ruficaudatus* occurrence is significantly greater within high rainfall areas of primary forest greater than 2 km from streams. After the third split no further statistically significant splits were possible. This model, and alternative models derived by varying the order of entry of different variables at each split, all indicate that *L. ruficaudatus* is most frequently encountered in high rainfall, primary forest, on higher elevation sites distant from villages and streams.

Similar decision tree models were developed for each lemur species except *Microcebus* and *M. coquereli*, neither of which exhibited significant associations with mapped variables. *P. furcifer* occurred in both primary and secondary forests but was significantly more abundant in primary forest. Within secondary forest it was significantly more abundant at distances more than 4 km from villages and within primary forest it was significantly more frequent on slopes $> 1°$. All lemur species were more abundant in primary than secondary forest, and four species were only detected in primary forest (Table 4) on walk transects. Three species, *Microcebus, M. coquereli,* and *P. furcifer* were detected in secondary forest but only *Microcebus* appears to be common in secondary forest.

These associations indicate that all lemur species in the study area are responding to similar cultural disturbance gradients, but that some species, notably *Microcebus* and *M. coquereli*, are more disturbance tolerant than others. All lemur species were most abundant in primary forest, and average lemur species richness was

Table 4. Mean numbers of lemurs detected on walk transects in primary and secondary forests, showing corrected densities after allowing for differences in detectability between primary (p) and secondary (s) forest.

Species	*Succession stage*	*Abundance (counts/site)*	*Density (no./ha)*	*Significance (p)*	*Population size (± SE)*	
Lepilemur ruficaudatus	p	0.63	1.36	0.0008	128,347	(25545)
	s	0	0		0	
Microcebus spp.	p	0.26	0.56	0.1600	53,136	(13691)
	s	0.10	0.22		8447	(7141)
Mirza coquereli	p	0.12	0.26	0.0350	23,707	(10014)
	s	0.05	0.11		4093	(2264)
Phaner furcifer	p	0.70	1.52	0.0020	142,653	(22072)
	s	0.10	0.07		2700	(1916)
Propithecus verreauxi	p	0.35	0.80	0.0600	71,326	(19006)
	s	0	0		0	
*Cheirogaleus medius**	p	0.21	0.46	0.0900	42,714	(18598)
	s	0				
Eulemur fulvus	p	0.4	0.87	0.0600	80,728	(34130)
	s	0				

**Numbers are underestimated because a significant portion of the population may have been in torpor during early portion of survey*

greater in the higher rainfall, higher elevation primary forests distant from villages. This model was used to map relative lemur species richness using the overlay capabilities of the GIS (Fig. 6). This map provided the best overall indication of patterns of relative lemur species richness and abundance throughout the study area.

Estimation of Lemur Population Size

The population size of each lemur species was estimated from measures of mean lemur abundance in primary and secondary forest. Mean densities on walk transects in each disturbance stratum were multiplied by the total area of primary (94,013 ha) and secondary and degraded forest (40,065 ha), and summed to give estimated population sizes for the study region (Table 4).

Lemur densities and population sizes were also estimated from the habitat strata and distribution maps generated by decision tree models and the GIS. Mean density of *P. furcifer* was calculated for each habitat suitability class by frequency density conversion (Caughley 1977) of presence absence data on 363 transects and by multiplication by a correction factor of 2.2 to allow for the lower rate of lemur detection on road drive transects relative to site walk transects. Densities were multiplied by the area of each habitat suitability class and summed to give an estimate population size. A worked example is given in Table 5. The resulting population estimate for *P. furcifer* using presence absence data from all sites and transects was 148,000 individuals, which is close to the estimate of 145,000 derived from measures of mean abundance in primary and secondary forest at the 64 site walk transects only. Our population estimates should all be regarded as minimums because a portion of individuals are likely to have been undetected in nests or tree hollows at the time of survey. Our estimates of lemur density are either within the range of, or slightly lower than previous estimates in the region and elsewhere in Madagascar (Table 6). Lower values were expected as our estimates are averaged over large areas including suboptimal as well as optimal habitat, in contrast to localised studies which often focus on patches of high quality habitat.

Gap Analysis

A Gap Analysis (Davis et al. 1990) was carried out to determine the representation of lemur habitats and populations in reserves and protected areas within the study region. Reserved land in the region includes a small nature reserve (Reserve Speciale d'Andranomena), a timber harvesting concession (Kirindy/CFPF), and a private reserve (Analabe) largely altered by past sisal production. The remaining area consists of unallocated land in various states of naturalness and development. The adequacy of existing protected areas for lemur conservation was determined by overlaying individual lemur distribution maps on a map of land tenure and calculating the area of habitats and proportion of species populations represented in each tenure (Table 7).

Although all lemur species are expected to occur in the only existing government nature reserve (Reserve Speciale d'Andranomena), average lemur density in the reserve is low because it is located close to villages, and almost 50% of the area has been degraded to secondary forest. Most of this degradation occurred after dedication of the reserve, sometime between 1949 and 1989 (Smith 1997).

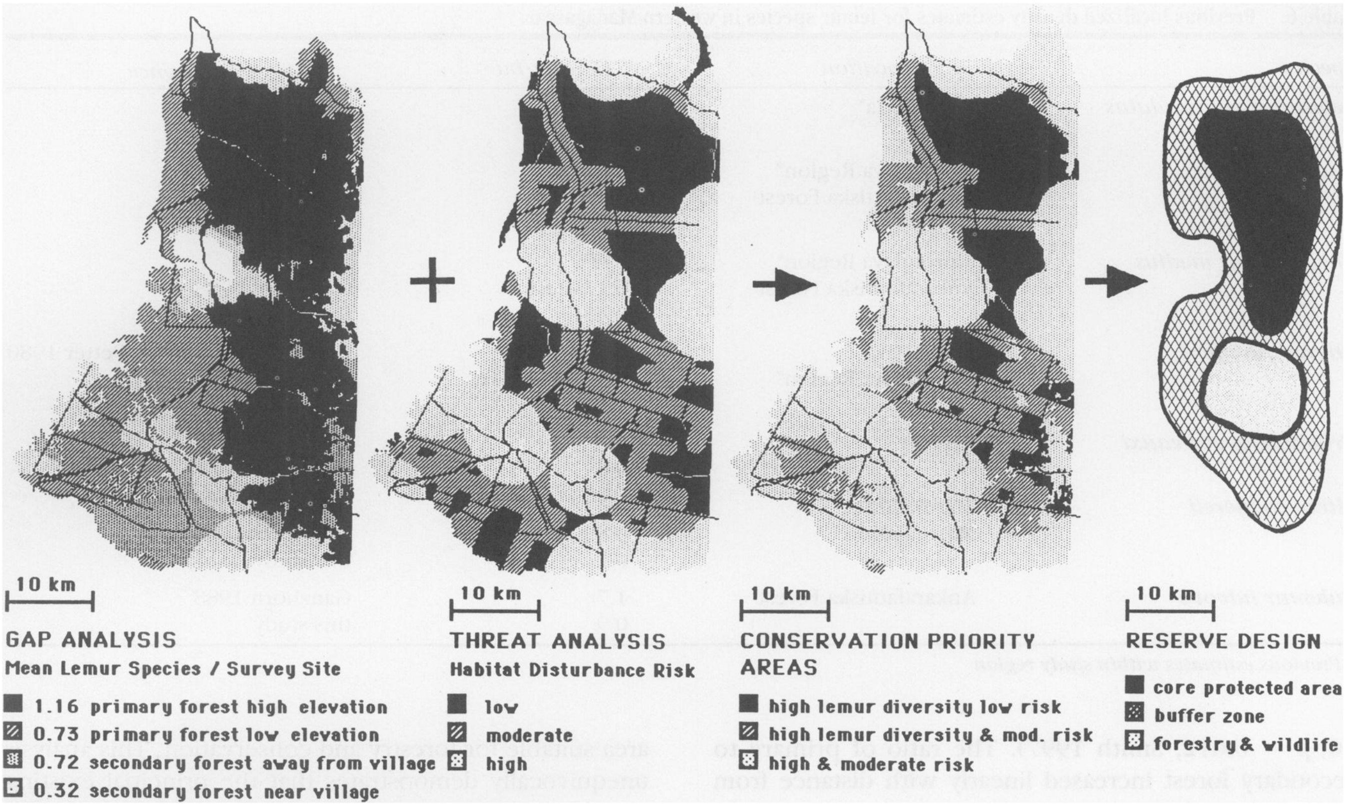

Figure 6. Illustration of the principal steps involved in location and design of new protected areas for lemur conservation in a region of western Madagascar using GIS. The maps show the overlay of relative lemur species richness (mapped by interpolation of the decision tree model in Fig. 3) and the disturbance risk (mapped by interpolation of a decision tree model referred to in the text) to produce conservation priority areas (areas of high relative lemur biodiversity at low risk of disturbance) for designing a hypothetical reserve with a core conservation area, buffer zone, and multiple use forestry and wildlife area.

Threat Analysis

Biodiversity maps alone are insufficient for identifying the most suitable locations for protected areas in developing countries because they do not necessarily consider the risk of future anthropogenic disturbance. Areas that support the highest biodiversity are often also the most suitable for development and face the greatest risk of future clearing or modification, particularly in Madagascar where regulation and enforcement of clearing legislation is difficult. We developed a second layer of primary information, a threat map, for inclusion in the reserve selection and design process. The risk of disturbance in the Morondava study area was mapped by modelling associations between the frequency of occurrence of secondary forest and mapped environmental variables in the GIS. A decision tree analysis, using a rectangular grid of sample points imposed on the study area, found distance to village to be the best predictor of secondary forest (chi-square = 20, $p = 0.0002$) and distance to trafficable roads to be an important secondary predictor in areas more than 4 km distant from villages (chi-square =

Table 5. Estimation of *P. furcifer* density and population from a map of modeled habitat suitability classes in the study area.

Habitat suitability class	*Frequency of occurrence (%)*	*Density*	*Habitat area (ha)*	*Population size*
primary forest > 1° slope	18	0.95	43,964	42,042
primary forest < 1° slope	29	1.62	50,092	81,453
secondary > 4 km from village	22	1.20	15,675	18,741
secondary < 4 km from village	4	0.19	29,257	5,597
Total Population				146,843

Table 6. Previous localized density estimates for lemur species in western Madagascar.

Species	*Location*	*Density/ha*	*Reference*
Lepilemur ruficaudatus	Marosalaza*	1.8-3.5	Petter et al. 1971
		1.36	this study
Microcebus spp.	Morondava Region*	3-4	Petter 1978
	Ankarafantiska Forest	0.42	Ganzhorn 1988
		0.44	this study
Cheirogaleus medius	Morondava Region*	3-4	Petter 1978
	Ankarafantiska Forest	0.12-0.81	Ganzhorn 1988
		0.46	this study
Phaner furcifer	Marosalaza*	0.5-0.6	Charles-Dominique & Petter 1980
	Morondava Region*	8.5 (localized)	Petter et al. 1971
		1.5	this study
Propithecus verreauxi	Berenty	1-2	O'Connor 1987
		0.8	this study
Mirza coquereli	Marosalaza*	0.3	Petter et al. 1971
	Marosalaza*	0.5	Hladik et al. 1980
		0.2	this study
Eulemur fulvous	Ankarafantiska Forest	1.7	Ganzhorn 1988
		0.9	this study

* *Previous estimates within study region*

10, $p = 0.012$, Smith 1997). The ratio of primary to secondary forest increased linearly with distance from village, from 89% secondary forest within 2 km of villages to 27% secondary forest within 2-6 km of villages and 1% secondary forest more than 6 km from villages. Using distance to village and distance to trafficable road as predictors we generated a map of disturbance risk in the study area (Fig 6). This map was overlayed with the lemur species richness map to produce a map of "conservation priority areas" (Fig. 6) which provided the foundation for development of a hypothetical reserve plan (Fig. 6). This plan includes a core conservation area essentially free of disturbance, a partially disturbed buffer zone of 4-8 km width in which regulated harvesting and hunting may be permitted, and a multiple use area suitable for forestry and conservation. This analysis unequivocally demonstrates that the principal existing reserve in the Morondava region (Andranomena) is not in the optimum location, and that further conservation effort would be better directed to the north-east.

Discussion

Threats to Lemurs in the Study Area

Lemur species richness and abundance in seasonally dry rainforest remnants north of Morondava was found to be most strongly associated with a clearing disturbance gradient (from primary forest to cleared savanna), and a cul-

Table 7. Habitat condition under different land tenures in the study area, showing the predicted total and relative population size of lemur species (population size per 1000 ha) in each tenure.

Land tenure	*Reserve Speciale d'Andranomena*	*Kirindy/CFPF*	*Analabe*	*Other*
Habitat representation in tenure				
Area (ha)	7,180	11,514	14,876	105,375
Primary Forest (ha)	3,983	11,120	8,136	70,774
Secondary Forest (ha)	1,867	161	52	10,406
Degraded Forest (ha)	1,330	233	4,367	20,200
Non-forest (ha)	0	0	2,321	2,546
Estimated species total population in tenure (1000s or 10^3)				
Lepilemur ruficaudatus	5.4	15.1	11.0	96.3
Propithecus verreauxi	3.2	8.9	6.5	56.6
Cheirogaleus medius	1.3	3.8	2.9	34.6
Phaner furcifer	10.2	14.5	11.6	109.4
Eulemur fulvus	2.4	7.3	5.7	65.4
Microcebus spp.	3.1	7.4	6.2	45.0
Mirza coquereli	1.4	3.3	2.8	20.3

tural impact gradient (the sum of all visible evidence of clearing, zebu and pig husbandry, root gathering, hunting and burning). Four lemur species (*L. ruficaudatus*, *P. verreauxi*, *C. medius*, *E. fulvus*) were largely restricted to undisturbed primary rainforests in the study area. Three species, *Microcebus*, *M. coquereli*, and *P. furcifer*, occurred in secondary forests, but at less than half their density in primary forest. The ability of these species to occupy secondary forests is consistent with their smaller size and insectivorous-omnivorous diets. Only *M. murinus* can be regarded as common in secondary forest and potentially able to survive in the absence of primary forest, although *C. medius* has been reported to occupy well established secondary forest elsewhere in Madagascar (Harcourt & Thornback 1990). We were unable to model the habitat requirements of this species conclusively as many individuals were thought to be aestivating during the earlier portion of the study.

Negative associations between lemur species richness, the abundance of individual lemur species and cultural impact can be attributed to a combination of habitat degradation and hunting. We observed use of snares and traps for harvesting arboreal mammals in the study area (set primarily for *E. fulvus*, J. Ganzhorn pers. comm.) and commonly found remains of felled trees with hollows that had been chopped open. Larger nocturnal lemurs with low reproductive rates such as *L. ruficaudatus* may be particularly vulnerable to extraction from tree hollows. Our data suggest that this activity is most prevalent in areas harvested for wood production. As evidence of hunting is difficult to obtain indirectly, it is possible that hunting impacts are more severe than indicated by our data. Hunting of ground dwelling tenrecs is reputedly severe in close proximity to a village in Kirindy Forest (Ganzhorn et al. 1990). Our data indicate that habitat clearing and degradation, particularly by zebu, declines significantly with increasing distance from villages, having a measurable impact up to a radius of approximately 8 km.

An interesting finding was the apparent lack of any significant negative association, and a contributory positive association, between logging disturbance and lemur abundance. Legal timber harvesting was occurring under the management of the CFPF (Centre de Formation Professionelle Forestiere de Morondava) in a 10,000 ha timber concession near the village of Marofandilia (Fig. 2) at the time of study. Timber harvesting is based on low intensity ($10m^3$/ha) individual tree selection and manual harvesting methods. Disturbance of non-commercial species was minimal and logging trails are regenerated after harvesting (Ganzhorn et al. 1990). The overall supply of timber is limited, and the concession area available at the time of the study (Fig. 2) was expected to be exhausted in less than a decade. This concession was doubled in size after the present study to include unlogged and undisturbed primary forest to the north of the current concession (J. Ganzhorn pers. comm.). Evidence of illegal, manual timber harvesting was apparent outside the concession along almost all trafficable roads and oil exploration tracks throughout the survey region. Although low intensity selective logging does not appear to have directly affected lemurs, road building associated with logging has increased access to the region for illegal slash burning and hunting and this effect is likely to be detrimental in the longer term. Ganzhorn et al. (1990) reached a similar conclusion in studies of timber harvesting and hunting impacts on small terrestrial mammals in the Kirindy forest.

Natural Variation in Lemur Distribution and Abundance

The study area is characterised by relatively uniform, low relief, a relatively uniform geological substrate, and a lack of permanent streams. Some vegetation zonation is apparent, based on proximity to streams, increasing rainfall and elevation, and the occurrence of sandstone outcrops. Small, apparently natural, patches of dry scrub with grassy understoreys and plant species representative of drier southern thorn scrubs were observed on elevated sandstone outcrops with shallow soils. A simplified and structurally dense low forest, with emergent baobabs (*Adansonia spp.*) and the appearance of secondary vegetation, occurred along some major streams, possibly reflecting a seral response to periodic intense flooding. The most luxuriant and diverse forests occurred in higher rainfall and elevation zones in the east. The abundance of *L. ruficaudatus* and relative lemur species richness increased along an easterly gradient of increasing elevation and rainfall, and *Microcebus* was slightly more abundant and *L. ruficaudatus* slightly less abundant, in areas close to streams. Smaller species such as *Microcebus* may find the dense, disturbed stream environment more favorable for locomotion. More subtle microhabitat preferences may have been disguised by the overriding effect of anthropogenic disturbance, and the limited range of mapped microhabitat attributes (e.g. vegetation floristics and structure) available for analysis.

Regional Conservation Planning

The human factor is an important element in conservation planning in Madagascar. Dedication of forest remnants as protected areas reduces the area available for susbsistence hunting and gathering and future slash and burn agriculture. Reserves dedicated without community support, and lacking a management infrastructure, are at risk of progressive degradation. This is clearly illustrated by changes in forest cover in the Reserve d'Andranomena, the only government nature reserve in the study area (Fig. 2). Primary forest cover in this regional nature reserve has declined by more than 44% over the past 45 years (Smith 1997). The threat of clearing can be reduced by locating conservation reserves in areas at low short term risk of clearing, surrounding reserves by buffer zone, which allows some degree of sustainable natural resource exploitation, and by establishing ICDPs or similar management programs that provide the staff and resources for reserve protection and management.

Our findings unequivocally demonstrate that the existing small nature reserve in the study area, Reserve d'Andranomena, is poorly located and at high risk of clearing and disturbance due to its proximity to roads and villages. A more suitable location for establishment of a new protected area for biodiversity conservation exists in the north east of the survey region. This area was located by overlay of relative lemur biodiversity and disturbance risk maps (Fig. 6). It is dominated by higher site quality (higher rainfall) primary forest and supports all lemur species known to occur in the region. It is also the only region in which sign of the Aye-aye was detected. The Aye-aye has not previously been reported in the region but is known to occur to the immediate north across the Tsiribihina River. Surveys of reptiles, birds and terrestrial mammals were carried out simultaneously with lemur surveys in the present study but data have yet to be analysed. On the basis of species location records we consider it likely, however, that the relative diversity of the non-lemur vertebrate species will also be greatest in the north east. A new colony of a regional endemic mammal species of particular conservation concern, *Hypogeomys antimena* (a large, rabbit-like, burrowing rodent) was located in this region during the survey.

Relationships between lemur diversity and human activity revealed in this study indicate that protected areas should be surrounded by buffer zones of up to 4–8 km in width to minimize the risk and impacts of clearing, hunting, harvesting, and zebu grazing on core conservation areas. If remnants are approximately circular in shape they need to exceed 20,000 ha in order to have a core area free of disturbance and more than 8 km from a forest edge. There are only four primary western dry forest remnants of this size left in western Madagascar (Smith 1997). The Kirindy remnant, investigated in this study, is the largest and offers the greatest scope for integrated conservation and development. Our study indicates that some level of timber harvesting may be possible in buffer zones surrounding core conservation areas provided that hunting by harvesting crews is controlled and no new roads are constructed that promote the spread of illegal hunting, harvesting, and slash and burn agriculture. A private undeveloped reserve, Analabe, comprising both highly altered and degraded forest as well as abundant primary forest in good condition, exists in the central west of the study region immediately adjacent to the main access road to the high biodiversity regions of the north east. Considerable potential exists for development of this reserve as an ecotourism facility for generation of funds necessary to improve protection and management of remaining primary forest remnants in the surrounding region. Morondava has many unique assets as a tourist destination, including abundant and visible lemur populations, spectacular baobab dominated forests, and locally abundant populations of *Cryptoprocta ferox*, a large, panther-like carnivore.

Role of GIS in Regional Biodiversity Planning

Early use of GIS for biodiversity planning focused on the use of existing biological records (from museum specimens and publications) for modeling and mapping species distribution patterns (Longmore 1986; Davis et al. 1990). Although this approach has provided some useful products for biodiversity planning at a national scale, it has been the experience in both Australia (Ferrier & Smith 1990) and Madagascar that the existing biological records are either too unreliable or too scarce for objective biodiversity planning at regional scales, unless supplemented by field survey programs to collect new records. Compilation of published lemur distribution records and museum specimen records in Madagascar (Parc de Tzimbazaza) revealed the following deficiencies with existing information (after Smith et al. 1991):

- inaccurate georeferencing (few records were located more accurately than 10 km);
- inadequate geographic representation and significant gaps in sampling distributions (records are clustered around popular and accessible reserves and research centers);
- historical changes in land use and habitat since records were made;
- a percentage (approximately 5%) of records were incorrectly recorded (at nonsense locations) due to transcription errors;
- a lack of absence (zero) records, most published surveys report only species presence, and species absence cannot be assumed unless surveys have been particularly comprehensive.

The RACE procedure was designed to overcome these limitations by rapid, systematic collection of new fauna records suitable for multivariate statistical modeling and mapping of species distribution patterns using GIS. This procedure differs from traditional approaches to biological survey in placing emphasis on the following:

- use of systematic survey techniques (independent of collector and survey conditions);
- use of many small rather than few large survey sites;
- stratification of survey sites using GIS to ensure sampling of all major environmental domains;
- extrapolating from point location records to model and map species habitats and biodiversity patterns;

- restriction of effort at each survey location to the minimum necessary to derive useful predictive models;
- modeling associations with cultural as well as natural determinants of species distribution and abundance.

Because this methodology requires a modification of traditional approaches to biological survey it was of interest to compare the products of this approach with those of previous biological studies in the study area over the previous 25 years. Key conservation products generated by this study included the following: estimates of lemur densities; estimates of lemur population sizes; maps of lemur habitat and potential distribution; maps of relative lemur diversity; identification of threats and measures of lemur sensitivity to anthropogenic disturbance; maps of disturbance risk; and a map of conservation priority areas. Previous biological studies in the study area have made significant contributions in only two of these areas, estimation of lemur densities and identification of threats to lemurs and their habitats. Our density estimates are broadly consistent with those of previous localized studies (Table 7), but provide additional measures of statistical reliability. Our evaluation of threats to lemur species is consistent with previous findings, but provides additional information on the spatial distribution of threats. The remaining products, including population estimates, maps of lemur habitat and diversity, and maps of disturbance risk and conservation priority areas, are presented for the first time in this study.

The RACE procedure has provided a more effective method of regional biodiversity planning in western Madagascar than traditional approaches to biological inventory and the use of GIS for latent processing of biological records collected in previous decades. This study has shown that information generated by a stratified survey at a sampling intensity of less than 0.1% (ha per 1000), was sufficient to exceed the conservation benefits of decades of prior research and provide information of more direct relevance to bioregional planning. Repetition of these procedures, targeting additional taxa (birds, reptiles, and plants) in other biogeographic subregions would provide an objective foundation for identifying gaps in the existing protected area network and designing a more effective conservation network for the whole of Madagascar.

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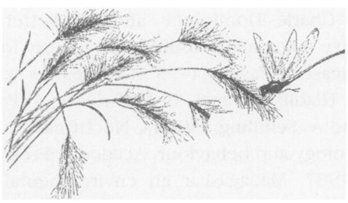

Appendix

Attributes stored in the morondava regional database and sources of information for each attribute.

Primary Mapped Landscape Attributes

Landcover (primary forest [3 types], secondary forest [4 types], cleared, savanna, sisal, rice & water);
Disturbance (land cover grouped into primary, secondary and alienated forest);
Streamlines, roads, and villages (from 1:500,000 map, FTM 1990 and Landsat TM image);
Landsat TM (unsupervised classification into 10 classes resampled to 100 m);
Geology (sandy alluvium, sandy carapace, sandstone, calcareous sandstone, after Besaire 1969);
Elevation (at 5 m intervals, interpolated from 1:100,000 topographic map);

Secondary Mapped Landscape Attributes

Slope (in 0.1 degree categories derived from elevation classes using IDRISI);
Aspect (0-360°, derived from elevation using IDRISI);
Village (distance to village in km after FTM 1990 and ground survey, interpolated in ERMS);
Stream (distance to streams in km, interpolated in ERMS);
Minimum and maximum annual rainfall (interpolated from 8 meteorological stations in the area);

Lemur Survey Records

Survey sites (the starting point for 64 survey transects of 200-m length located to +/− 30 m by GPS);
Lemur drive transects (location of 18 road transects of 1-5.5 km);
Lemur abundance (presence-absence and relative abundance of all lemur species on survey transects);
Survey Conditions (time of survey, date, temperature, personnel, moon phase, and survey technique);

Anthropogenic (Cultural) Disturbance Indicators at Survey Sites

Clearing (percentage vegetation cover estimated on a scale of 1-10);
Grazing (the sum of the number of zebu trails crossing a 200 m survey transect);
Pigs (the sum of the number of pig trails, as indicated by dung, crossing each survey transect);
Root digs (the number of potholes excavated by Malagasy to extract edible tubers and roots within a strip of approximately 20 m on either side of transects);
Logging (the number of tree stumps left by timber harvesters within a strip of approximately 20 m on either side of transects);
Cut stems (the number of stems cut to harvest poles [for hut/yard construction] and fuelwood within a strip approximately 20 m either side of site transects);
Fire (presence or absence of signs, [e.g. charcoal blackened stems]);
Cultural Impact (the sum of all anthropogenic disturbances at each site after transforming each variable to a scale of 1-10).