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A Preliminary Estimate of *Lemur catta* Population Density Using Satellite Imagery

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2.1. Introduction

Ringtailed lemurs are found in many habitats throughout southwestern and southern Madagascar. As stated by Goodman et al. (this volume), it is the least forest-dwelling of the extant species of lemurs and lives in some of the most xerophytic forests on the island. The dry forests of the south and west are unique and are inhabited by many plants and animals found nowhere else on Earth. Although rain forests have received a great deal of research attention from conservation and development organizations, there has been less focus on dry forests, and there is some indication that these forests are among the most endangered habitats worldwide (Janzen, 1988; Kramer, 1997; Smith, 1997, Cabido and Zak, 1999; Trejo and Dirzo, 2000; Dirzo and Sussman, 2002, Sussman et al., 2003). There is great urgency to document the deforestation, to determine the rate and patterns of habitat loss, and to see how this habitat loss is affecting the unique fauna of southern and southwestern Madagascar. Given that the geographic range of ringtailed lemurs is coincidental with that of these dry forest habitats (Sussman, 1977; Sussman et al., 2003; Goodman et al., this volume), it is important to know the density of *L. catta* populations in various habitat types and how the patterns and processes of deforestation are affecting ringtailed populations currently and how they have done so in the past.

Satellite platforms, most notably the Landsat series, have benefited scientists by enabling them to observe land cover change and the patterns of land use at regional scales. Although use of the Landast platforms provides a rather narrow temporal sampling window, 1970s to present, it captures the several decades where many areas of the world have seen aggressive deforestation episodes, as is the case of dry forests in southwestern Madagascar. Cutting of forests has certainly been detectable in this study area over this breadth of time, as we observe the initial stages of major deforestation events between the early 1970s and 1985. Post-1985, accelerated deforestation has occurred resulting in large areas of contiguous forest being cut to satisfy demands for charcoal and agricultural land, both small- and large-scale (Sussman et al., 2003). Likewise, the greatest reduction in lemur habitat has occurred since 1985. In order to assess the impact that this dynamic has had on specific lemur habitats and population, the imagery acquired in 1985 was selected to represent habitat at T_0, initial habitat for this study. Additionally, image selection was influenced by resolution of the satellite platforms: 2000 (ETM) and 1985 (TM) have cell resolutions resampled to 30 m, whereas 1973 (MSS) has a cell resolution resampled to 60 m, enabling the former two to resolve objects a fraction (one-fourth) the size of the latter. At the conclusion of this analysis, an approximation of deforestation between 1985 and 2000 was calculated for our study area in an initial attempt to assess how this dynamic has affected habitat extent and predicted ringtailed populations. A future stepwise temporal analysis is planned to quantify change in specific habitat extents, conditions, locations, and lemur populations between 1950 and 2005 (using aerial photographs as well as satellite images) in an effort to reconstruct the history of deforestation during the past half-century, to predict land cover trajectories, and to identify areas for conservation efforts.

In this paper, we make a preliminary attempt to determine the population density in 1985 and the relatively current population density of *L. catta* in relationship with gradients of vegetation cover over its entire geographic range. We use a parameter of forest condition, canopy density, derived from satellite imagery, and published information on ringtailed lemur population densities to address this question. We also discuss the methodology used to make our analyses. Goodman et al. (this volume) have pointed to the fact that many of the aspects of *L. catta* life-history parameters may be exaggerated given the intensive focus of past research on gallery forest zones, the richest of ringtailed lemur habitats. We agree with this assessment and discuss how this has impinged on our analysis. In doing so, we describe the data that would be needed to improve our analysis and stress the urgent need for research to be conducted to collect these missing data.

In order to determine accurately the density of ringtailed lemur populations in space and time using remote-sensing technologies, we need to determine the existence and nature of a number of relationships. We must determine whether a relationship can be established between a quantitative measure of vegetated cover and spectral data (satellite DNs) and, if so, if this relationship will allow us to discriminate and map, with confidence, the variety of potential lemur habitats (gallery forest, dry brush and scrub forest, other xerophytic forests). Next, we must determine whether a relationship can be established between lemur densities and satellite spectral data, either directly or via a quantitative measure of vegetated land cover. It is the relationship between satellite data and lemur densities that we investigate in this paper. If these relationships can be established, an estimate of population densities of lemurs in relation to regions with different vegetation cover generally can be proposed using vegetation maps derived from the satellite images.

Given the above, in this paper we develop a methodology using reflectance spectra from Landsat images for calculating a measure of forest canopy density (FCD) and for examining the direct relationship, if any, between FCD (a measure derived from satellite reflectance data) and lemur densities. The relationships that we examine in this paper do not allow us to discriminate between habitats but do enable us to explore the extent of habitat in totality. This information enables us to map lemur habitat in its most generic form throughout southern Madagascar and estimate population using the relationships being explored between FCD and lemur densities. Although it is important to our research, and certainly a component of future research, to be able to identify lemur densities and populations in particular habitats, it is not specifically the aim of this paper. The purpose of this exercise is to explore the advantages and usefulness of incorporating a spatial and temporal mechanism for identifying and mapping, not only location but condition, of primate habitat and how it relates to densities and populations.

Thus, the synoptic view of satellite images provides spatially explicit information on potential lemur habitat, which is then used to focus on the acquisition of higher resolution, more costly field surveys in representative regions of southern forest habitat, thereby providing a robust and extensive monitoring system for *Lemur catta*. Research on the ecology of *Lemur catta* at several sites (Jolly, 1966; Budnitz and Dainis, 1975; O'Connor, 1987; Sussman, 1991; Koyama et al., 2001; Jolly et al., 2002, Gould et al., 2003, Sauther, pers. comm.) has demonstrated that ringtailed lemur density is directly related to habitat quality. However, currently available estimates of the population and distribution of *Lemur catta* are little more than guesswork. In this study, we document a research strategy for a more effective mapping. We recognize that a number of variables, other than forest condition, may affect actual lemur population densities: human activities of hunting or charcoaling, distance to village, distance to road, availability of water, soil composition, and topography. In addition, behavioral factors such as willingness of a group to range, and maximum distance, to multiple forest patches separated by nonforested land cover and the likelihood of reoccupation of a forest previously disturbed could contribute to significant disparities between actual and predicted values.

Thus, the results of this analysis represent a "best case" scenario in which we assume that all potential habitats that are adequate in extent to sustain a lemur population enjoy a lemur presence and that there are no external or behavioral factors adversely affecting lemur density in these areas. Furthermore, we stress that currently available information on ringtailed lemur densities, as mentioned above, come from a very small proportion of the habitats in which they are found.

2.2. Methods

The characterization of forest condition, as it relates to *Lemur catta* habitat, is essential to predicting lemur population in this study area. Employment of a forest canopy density measure allows us not only to identify habitat capable of sustaining a lemur population but also affords us a temporal measure of habitat condition by enabling us to detect change in the percentage of crown closure and therefore a change in area of occupation (Roy et al., 1996). This parameter of forest condition is directly related to lemur density data, and the function representing the relationship is employed to predict population densities for all potential habitats.

2.2.1. Image Pre-processing

Six footprints from the WRS2 reference system cover the study area. Landsat 5 Thematic Mapper (TM) images, acquired January thru February 1985, were selected for use in this analysis. The first step in the pre-processing sequence was to mask all cloud and cloud shadows from each TM scene. The scenes were then geo-referenced to the Laborde projection system using digital topographic base maps as the reference source. Radiometric calibration and atmospheric correction were then performed on each scene in order to relate the digital counts in satellite image data to reflectance at the surface of the earth. The entire data set was mosaiced into a single image as the final step in the initial processing sequence.

2.2.2. Computing Forest Canopy Density

Three indices, advance vegetation index (AVI), bare soil index (BI), and scaled shadow index (SSI), were generated from the TM data and employed as inputs to a forest canopy density model to (1) differentiate habitable land cover (forests) from other and (2) to give us a measure of forest condition (Figure 2.1). The black soil detection component of the processing sequence was omitted from this methodology but is available to assist in differentiating shadow from black soil, particularly burn scars (Rikimaru and Miyatake, 1997). Prior to calculating the indices, the reflectance values of each TM band are normalized over a data range with values 0–255 using the

Linear Transformation: $Y = AX + B$

$$A = (-200) / [(M_i - 2S_i) - (M_i + 2S_i)] = 50 / S_i$$
$$B = -A(M_i - 2S_i) + 20$$

where M is mean, S is standard deviation, and i is Landsat TM band number.

The model component, *advanced vegetation index* (AVI), is used to distinguish subtle differences in canopy density (Jamalabad and Abkar, 2004). After normalization of the TM bands, B_3 is subtracted from B_4 where B_4 is TM band 4 and B_3 is TM band 3. Difference values that are less than or equal to 0 are assigned an AVI value of 0. The following calculation is applied to the remaining pixels with difference values greater than 0.

Advanced Vegetation Index (AVI): $[(B_4 + 1) * (256 - B_3) * (B_4 - B_3)]^{1/3}$

where B_4 is TM band 4 and B_3 is TM band 3. (Note: AVI = 0 if $B_4 < B_3$ after normalization.)

Bare soil index (BI) is a normalized index of the difference of sums used to differentiate vegetated land cover with different background response and due to varying canopy density (Jamalabad and Abkar, 2004).

Bare Soil Index (BI): $[(B_5 + B_3) - (B_4 + B_1)] / [(B_5 + B_3) + (B_4 + B_1)] * 100 + 100$
where B_5 is TM band 5, B_4 is TM band 4, B_3 is TM band 3, and B_1 is TM band 1.

Canopies of forests vary markedly depending on age, early succession to mature, as well as species composition. Differences in canopy structure and

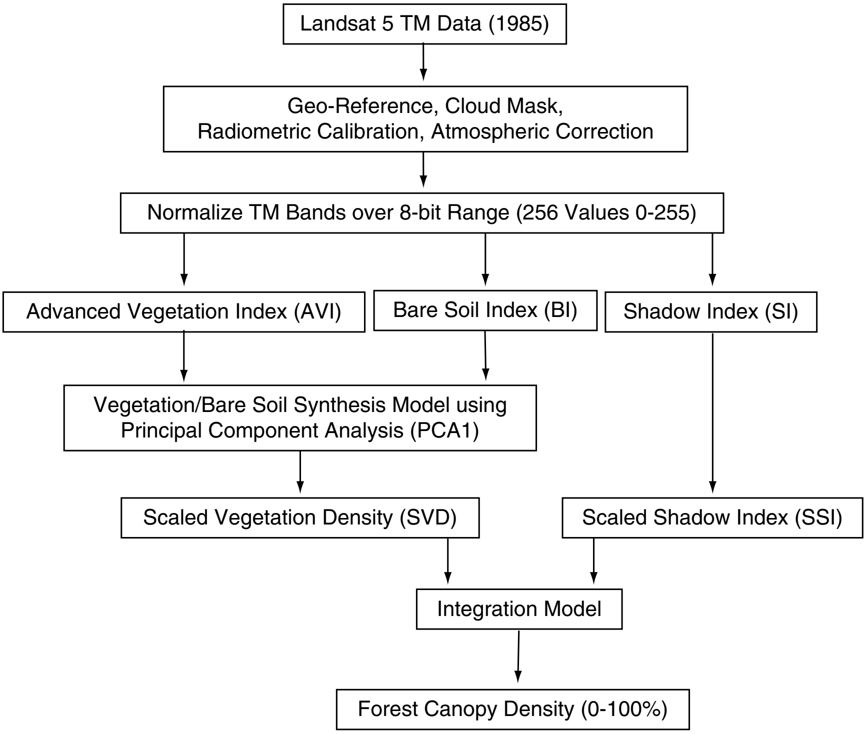

FIGURE 2.1. Forest canopy density processing flowchart.

density create differences in the amount of shadow present influencing reflectance. Scaled shadow index enhances the spectral differences between mature forests that have higher canopy shadow index values compared with that of younger forest stands (Jamalabad and Abkar 2004).

Shadow Index (SI): $[(256 - B_1)^* (256 - B_2)^* (256 - B_3)]^{1/3}$

where B_3 is TM band 3, B_2 is TM band 2, and B_1 is TM band 1.

Scaled Shadow Index (SSI): Shadow index (SI) scaled to values 0 to 100.

Vegetation Density (VDS) is produced using principal component analysis. AVI and BI (high negative correlation) are used as the model inputs.

Scaled Vegetation Density (SVD): First principal component of AVI and BI scaled to values 0 to 100.

Input parameters, SVD and SSI, share like characteristics of dimension and percentage scale units of density (Jamalabad et al., 2004) and are used to compute

Forest canopy density: $[(SVD^* SSI + 1)^{1/2}] - 1$.

Figure 2.2 was generated from these data.

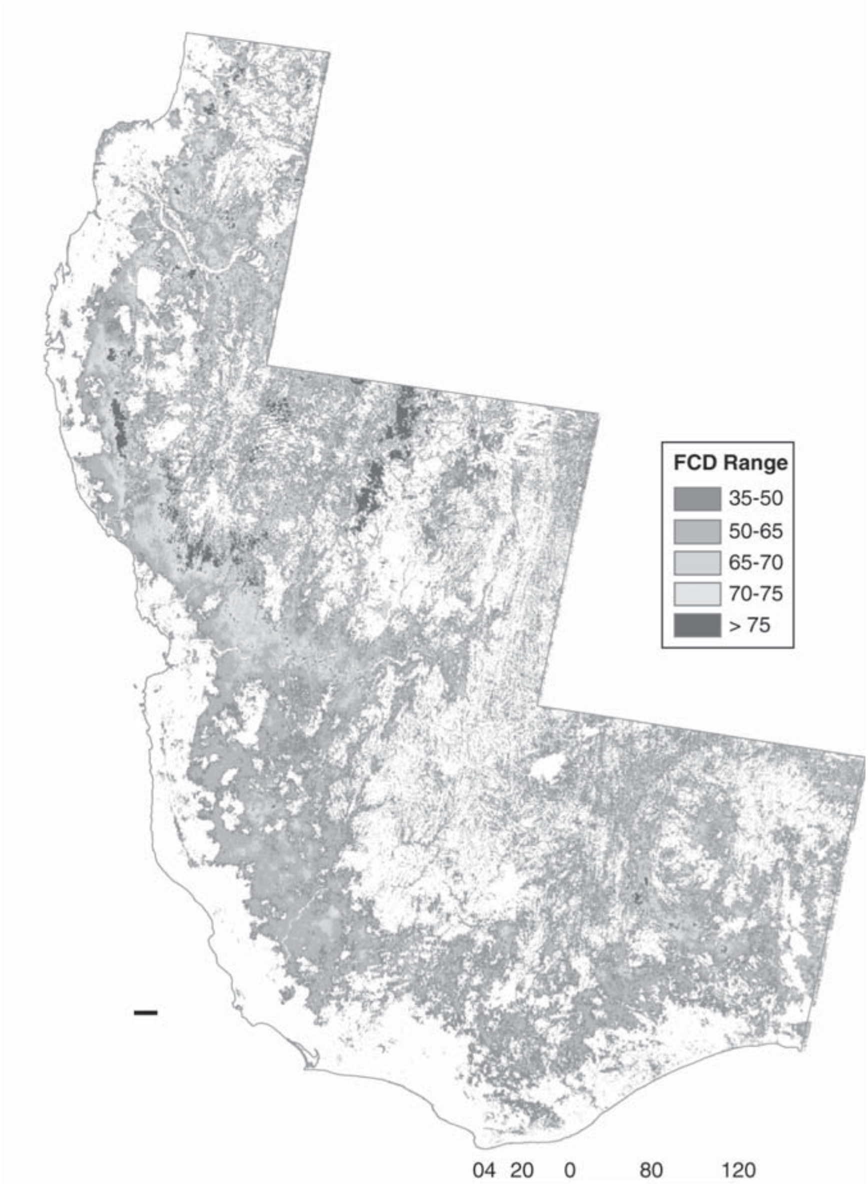

FIGURE 2.2. Stratified forest canopy density map derived from Landsat 5 Thematic Mapper images acquired January and February 1985. Pixels with forest canopy density (FCD) values less than 35 assigned a value of "0." [*See* Colour Plate I]

(This model also has the capacity to incorporate a *thermal index* (TI) to separate soil, particularly burn scars, from shadow other than that cast by trees, but this was not incorporated in this paper).

2.2.3. Linking Lemur Density to Forest Canopy Density

Mean FCD values were extracted from forest locations with known lemur densities. Using a curve-fitting software, TableCurve 2D, two relationships were examined: linear and nonlinear. A best-fitting line and a transition function, standard logistic (sigmoid), were applied to the data (Figure 2.3). Assuming that the lemur densities being employed are representative of those at the specific values of forest canopy density, the linear method underestimates lemur density at FCD values below 52% and greater than 72%, and overestimates lemur densities at FCD values greater than 53% and less than 72%. The transition function was employed to predict lemur density for the study area using FCD as the independent variable (Figure 2.4).

2.2.4. Methodology for Approximating Deforestation Between 1985 and 2000

An approximation of deforestation between 1985 and 2000 was calculated for our study area in an initial attempt to assess how this dynamic has affected habitat

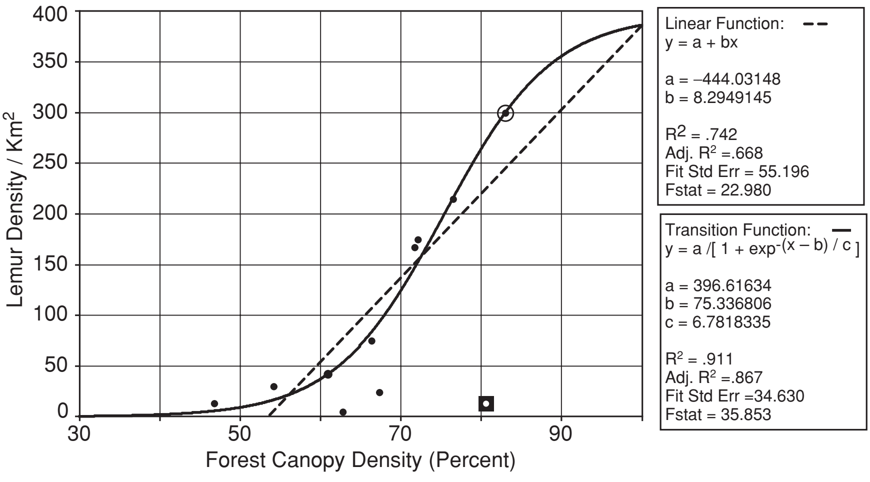

FIGURE 2.3. Plot of *Lemur catta* data with relationship functions, linear (dashed) and transition (solid). Beoloka (represented by a solid square) is an outlier and was not included as part of the data set in determining the prediction function but was added to illustrate the impact of external factors, in this instance hunting. Berenty (point with circle) is noteworthy in that the lemurs that reside within its boundaries are provisioned, likely producing the highest concentrations in this study area.

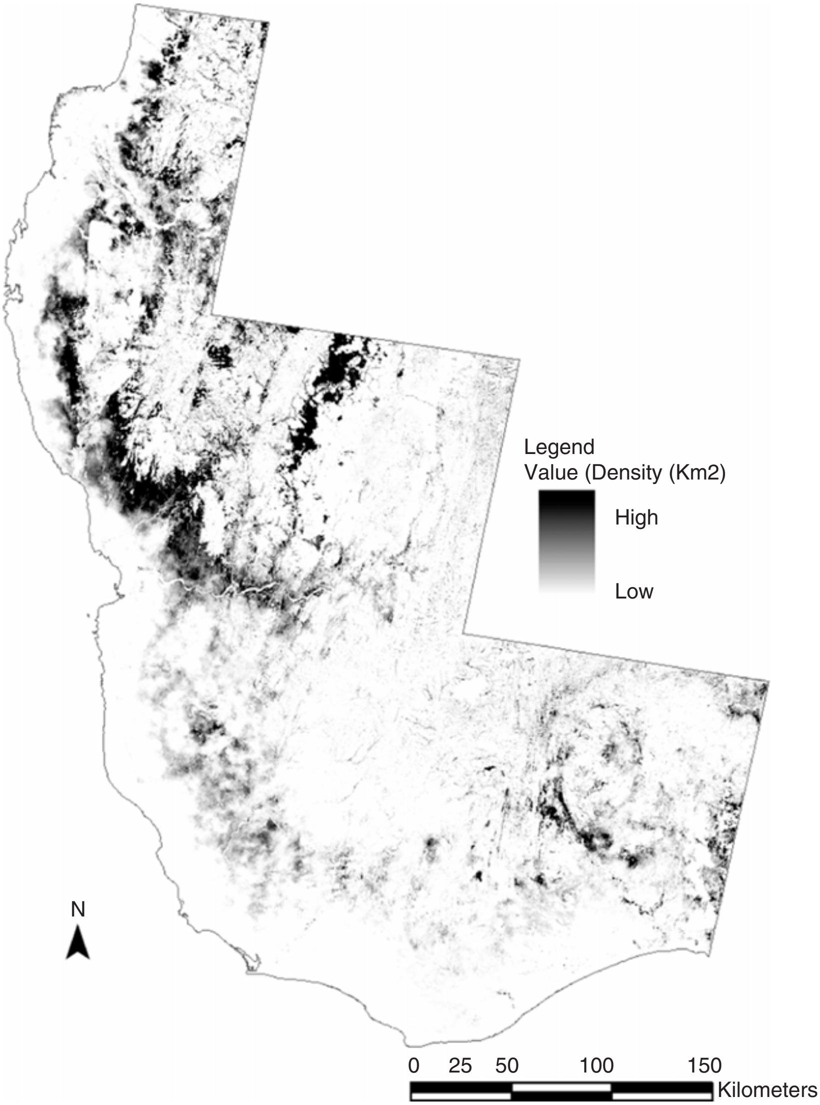

FIGURE 2.4. Lemur prediction map produced using the transition function and forest canopy density (FCD) as the independent variable.

extent and predicted populations. To identify deforested parcels, a multitemporal composite was employed. A three-layer image was constructed assigning band 3 (2000) to red, band 3 (1985) to green, and band 3 (1985) to blue. Band 3 is particularly sensitive to soil and exhibits high reflective properties in response to such. Pixels deforested between 1985 and 2000 appear red due to an increase in soil exposure; pixels reforested in that time frame appear cyan due to a decrease in soil exposure. Although a minimal amount of reforestation has taken place in this study area, the amount is negligible in comparison with that of deforestation and was not addressed in this analysis.

Deforested areas were identified in the multitemporal composite and areas of interest (AOIs) that delineated their extents used to extract spectral signatures, training samples, from the composite image. Training samples were then displayed over a frequency scatterplot, feature space image, with band 3 (2002) assigned to the Y-axis and band 3 (1985) assigned to the X-axis. An AOI delineating the cluster boundary of deforestation training samples was drawn on the feature space image. Pixels within this boundary were classified as deforested and those outside as stable. A binary image was created from the classified thematic image assigning deforested pixels a value of "0" and stable a value of "1." As a final step, the binary mask was applied to the 1985 forest canopy density map and pixels deforested between 1985 and 2000 given an FCD value of "0" (Figure 2.5). Habitat extents and ringtailed lemur numbers were recalculated for all FCD ranges.

2.2.5. Assumptions and Potential Problems

- The lemur density data were in units of km^2. Prior to calculating the lemur population for the study area, lemur densities in forests smaller in area than 1 km^2 were normalized for forest extent. Predicted lemur density represents the potential population at a particular FCD value and an area of 1 km^2. A linear relationship was assumed between lemur density and forest parcel size. The ratio of forest area to 1 km^2 was applied to lemur density when the forest patch was less than 1 km^2.
- Forest parcels were assumed to be homogeneous. No classification has been performed on the study area, and no distinction made between forest types. The mean FCD value was calculated for each forest parcel risking overestimating or underestimating FCD depending on the majority fraction and composition in a mixed forest.
- Unique relationships between FCD and lemur density may exist between forest types (gallery, dry, and xerophytic) and conditions (degraded and not). Additional data will reveal this.

2.3. Results

Lemur catta population densities are available from a number of sites (Table 2.1), and in Figure 2.3 we illustrate the relationships between lemur density and forest canopy density (FCD). As can be seen, we found an excellent curvilinear relationship between ringtailed lemur density and percent FCD ($R^2 = .91$).

In Table 2.2 (parts a and b), we give the amount of area represented by various levels of FCD over the entire geographic range in which suitable ringtailed lemur

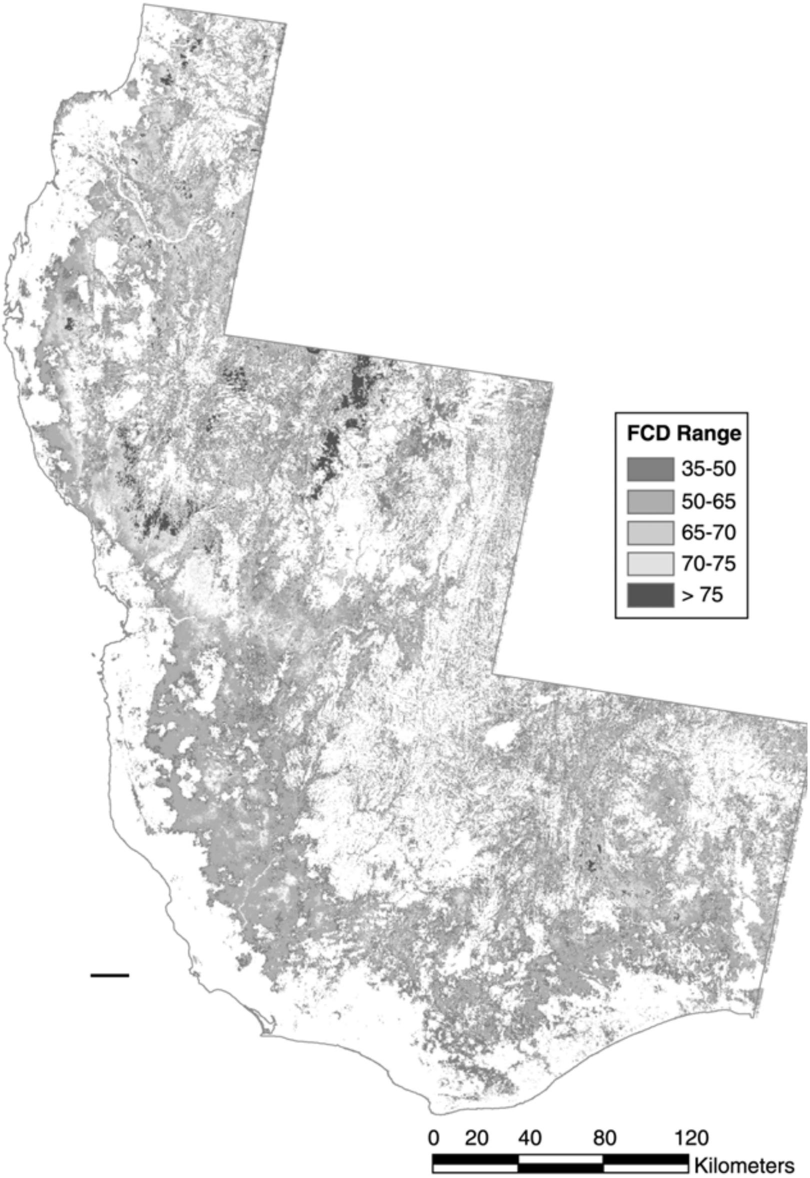

FIGURE 2.5. Stratified forest canopy density map derived from Landsat 5 Thematic Mapper images acquired January and February 1985. Pixels with forest canopy density (FCD) values less than 35 and those deforested between 1985 and 2000 assigned a value of "0." [*See* Colour Plate II]

TABLE 2.1. Known density figures and forest canopy density (FCD) for various sites.

Location	Lemur density (km^2)	FCD	References
Beza Mahafaly, Parcel 1 east	175	70.09	Sussman, 1991; Gould et al., 2003
Beza Mahafaly, Parcel 1 west	75	66.34	Sussman, 1991; Gould et al., 2003
Beza Mahafaly, Parcel 2	5	62.77	Sauther, pers. comm.
Beza Mahafaly, 1 km north	13	46.79	Sauther, pers. comm.
Beza Mahafaly, 1.5 km south	24	67.30	Sauther, pers. comm.
Beza Mahafaly, 1 km west	30	54.12	Sauther, pers. comm.
Beza Mahafaly, 1.5 km parallel to road south	42	60.87	Sauther, pers. comm.
Antserananomby	215	76.48	Sussman, 1974
Bealoka*	16	80.99	O'Conner, 1987
Berenty, Malaza west	300	83.02	Mertl-Millhollen et al., 1979; Jolly et al., 2002
Berenty, Malaza east	167	71.67	Budnitz and Dainis, 1974; Jolly et al., 2002

* Bealoka was omitted from analysis because it is a forest in which *Lemur catta* is hunted, but the forest has remained relatively intact. Therefore, the density is much lower than would be predicted for this FCD value. Also, new density figures are available form Berenty Malaza west (Jolly, this volume), but these figures are much higher than would be predicted for FCD values because some provisioning of food and water is available to these animals.

habitat is found. These areas representing each FCD range are illustrated in Figures 2.2 and 2.5. We estimate that in 1985, ringtailed lemurs occupied a total area of 27,248 km^2, representing approximately 27% of the total 100,000 km^2 area examined (Table 2, part a). The total number of ringtails at that time is estimated to have been a maximum of 933,162. By 2000, the total area occupied by the lemurs was 24,645 km^2 with a maximum of 751,251 ringtailed lemurs (Table 2, part b). Within this 15-year period, this represents a total loss of approximately 10% of suitable habitat and a 20% loss in the number of ringtailed lemurs (Table 2.3), an estimated loss of 180,000 individual lemurs. As explained in the "Methods" section, the actual numbers of ringtailed lemurs are likely overestimates because, in some forests such as Bealoka (Table 2.1), lemur densities will be lower than predicted for a particular FCD range due to hunting or other factors affecting the lemur population.

The loss of habitat varies at different ranges of FCD, and this directly relates to the relative number of ringtails affected (Table 2.2). This is related to two factors; the density of lemurs at lower FCD ranges is lower, and deforestation of lower quality forests is occurring at a much lower rate. Removal of deforested pixels between 1985 and 2000 results in an overall net loss of lemur habitat of 9.5% and a reduction in predicted lemur population of 19.5% (Table 2.3). The largest habitat extents, those at lower FCD values (35–50 and 50–65), experienced the smallest net loss, 3.9% and 9.1%, respectively, and a decrease in lemur population of 3.8% and 11.8%, respectively. Forests that are represented by the

TABLE 2.2 Area of total habitat occupied by ringtailed lemurs, percentage of total area occupied within the entire 100,000 km^2 research area, percentage of total ringtailed lemur habitat occupied, number of predicted lemurs, and average density of lemurs per FCD range for (a) 1985 and (b) 2000.

FCD Range	Area (km^2)	% Study area	% Potential habitat	No. predicted lemurs	Avg. lemur density
(a.) 1985					
35 ≤ FCD ≤ 50	11,933	11.93	43.79	36,266	3.04
50 ≤ FCD ≤ 65	10,653	10.65	39.10	301,202	28.27
65 ≤ FCD ≤ 70	2548	2.55	9.35	238,003	93.41
70 ≤ FCD ≤ 75	1540	1.54	5.65	233,939	151.91
FCD > 75	574	0.57	2.11	123,752	215.6
Totals:	27,248	27.25	100.00	933,162	
(b.) 2000					
35 ≤ FCD ≤ 50	11,472	11.47	46.55	34,898	3.04
50 ≤ FCD ≤ 65	9682	9.68	39.29	265,593	27.43
65 ≤ FCD ≤ 70	1850	1.85	7.51	171,606	92.76
70 ≤ FCD ≤ 75	1189	1.19	4.82	181,975	153.05
FCD > 75	452	0.45	1.83	97,179	215.0
Totals:	24,645	24.65	100.00	751,251	

three highest ranges of FCD (65–70, 70–75, and >75) as well as the smallest in areas all experienced at least a 20% reduction in extent up to an amount in excess of 27%. Likewise, the lemur populations in these areas declined similarly, all reduced by values greater than 20%, as high as nearly 30%.

To illustrated this point, in 1985 we estimate that 337,468 ringtails existed in an area of 22,586 km^2 with FCD of lower than 65 (Table 2.2, part a), whereas by 2000, 300,400 ringtails inhabited 21,154 km^2 in forests within this FCD range (Table 2.2, part b). This represents a 9.4% loss in habitat and a 9% reduction in the number or ringtailed lemurs. By contrast, in 1985, 357,691 ringtails occupied 2,114 km^2 in forests with 70+ FCD. In 2000, 279,154 lemurs existed in 1,641 km^2 in forests with these canopy densities. Thus, the habitat at these higher FCD ranges was lost at a rate of more than 22%, and the rate of lemur population reduction was also 22%. Although the actual area deforested during these

TABLE 2.3. The percentage of ringtailed lemur habitat loss and population reduction between 1985 and 2000 at different forest canopy density (FCD) ranges and overall.

FCD range	Habitat loss	Population reduction
35 ≤ FCD ≤ 50	3.86	3.77
50 ≤ FCD ≤ 65	9.11	11.82
65 ≤ FCD ≤ 70	27.39	27.90
70 ≤ FCD ≤ 75	22.79	22.21
FCD > 75	21.25	21.47
35 ≤ FCD ≤ 100	9.55	19.49

15 years in regions with 70+ FCD was only 437 km^2, the reduction in the lemur population in these high-density forests is inordinately high because of the high density of ringtailed lemur populations in these forests.

Although the population density is much higher for ringtails living in areas with high FCD, the total area represented by low FCD forests within the ringtailed lemur habitat is very high. Of the total area occupied by ringtailed lemurs, more than 90% is in forests ≤70 FCD. This area was occupied by 575,471 ringtailed lemurs in 1985 and 472,097 in 2000, representing 62% of the population in 1985 and 63% in 2000. In 1985 and 2000, respectively, 35% and 40% of the ringtailed lemur population lived in areas ≤65 FCD. Almost all long-term research on ringtailed lemurs has been conducted in areas with FCD ≥70 FCD (i.e., Antserananomby, Berenty, and Beza Mahafaly Parcel 1) (Table 2.1). Thus, we know very little about the ringtailed lemur populations living in low-density forests, which represent the majority of their populated area.

2.4. Discussion

In this paper, we develop a method of measuring forest canopy density (FCD) using satellite images from 1985 and 2000. This methodology enables us to identify habitat capable of sustaining ringtailed lemur populations and the condition of that habitat. Furthermore, this parameter of forest condition is directly related to lemur density data, and we employ the function representing this relationship to predict population densities for all potential habitats.

The total habitat covered in this study is 100,000 km^2, of which we estimate approximately 27,000 km^2 was occupied by ringtailed lemurs in 1985 and 24,500 km^2 in 2000. This represents a 9.5% loss in habitat during that 15-year period. During that same period, we estimate that there were 933,162 ringtailed lemurs in 1985 and 751,251 in 2000, a loss of almost 20% of the population.

Between 1985 and 2000, there was a much higher rate of deforestation in areas with higher measures of FCD, those forests with richer and denser vegetation. Habitat loss in these areas ranged between 21% and more than 27%. Furthermore, even though these areas represent less than 5% of the total area inhabited by the ringtails, because the lemur population densities are so high, the loss in the number of the ringtailed lemurs was inordinately high in these high FCD regions, reaching 21% to 28% between 1985 and 2000.

In areas with less rich vegetation (lower FCD ranges), habitat loss was less than 10% and as low as 4% in areas with very sparse vegetation, such as extremely dry brush and scrub regions. The reduction of the ringtail population in these regions was also proportionately lower, between 4% and 9% in the regions with low FCD values (35–65). However, even if this is so, a great proportion of ringtailed lemurs inhabit these dryer forest regions, and the majority of ringtail lemurs (more than 60%) live in forests able to sustain population densities lower than those at <70 FCD values. We know next to nothing about the behavior and ecology of the ringtailed lemurs living in these types of habitats.

We realize that the numbers presented here are based on a number of broad and general assumptions and estimates. We have not related specific habitat types to particular FCD levels, and different habitats with similar FCD levels may support different densities of ringtailed lemurs, though our surveys indicate that this is not generally the case (Sussman et al., 2003). Furthermore, we have ringtailed lemur population density figures from very few research sites, and these are almost exclusively from areas with FCD values above 70. As mentioned above, many areas may exist in which forest canopy density reflects a potential carrying capacity higher than actually exists due to factors affecting the ringtailed lemur population but not the forest. The forest at Bealoka is a case in point, where the lemurs are hunted but the forest remains intact (O'Conner, 1987). We also know that forest areas closer to large villages usually contain fewer lemurs than predicted by our analysis. Finally, the size, dimensions, and topography of forest parcels and the distance between these parcels may affect ringtailed lemur densities and our estimates thereof.

In order to improve the estimates that we provide in this paper, we suggest that the following data need to be collected:

1. Lemur population densities in various habitats. In higher density areas, we need to know the densities of lemurs in small forest patches and where hunting has caused population loss. In low-density areas, where more than 60% of these lemurs live, we need basic data on home range size, group size, amount of overlap of ranges, and general population density. In fact, we need to know the basic ecology and behavior of these populations.
2. We need to collect specific forest measurements (e.g., DBH, height of vegetation, canopy diameter, branching height, canopy closure, species composition, leaf area index, etc.) in different habitat types in order to better relate satellite signatures to specific habitat types.
3. We need to be able to determine how the topography, size, and dimensions of forest patches and distance between patches and to water sources and settlements affect both our FCD measures and ringtailed lemur densities.

Given the fact that forest areas with high FCD values, mainly the gallery and continuous canopy forests, are being cut at a very high rate and that these forests sustain very high densities of ringtailed and other lemurs, as well as of other endangered flora and fauna, all efforts must be made to protect what little remains of these forests. The dryer regions of the south and southwest are not being deforested at such a rapid pace. However, ringtailed lemurs and other animals and plants that are adapted to these unique xerophytic conditions are found nowhere else on Earth and are endangered. We must learn how these species, including the ringtailed lemurs, adapt to these extremely harsh conditions. Further, we must appreciate the fact that these areas and their inhabitants are also threatened by habitat modification and destruction and need to be protected.

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References

Budnitz, N., and Dainis, K. (1975). *Lemur catta*: Ecology and behavior. In: Tattersall, I., and Sussman, R. W. (eds.), *Lemur Biology*. Plenum, New York, pp. 219–236.

Cabido, M. R., and M. R. Zak. (1999). Vegetación del Norte de Córdoba. Secretaría de Agricultura, Ganadería y Recursos Renovables de Córdoba, Córdoba, Argentina.

Dirzo, R., and Sussman, R. W. (2002). Human impact and species extinction. In: Chazdon, R. L., and Whitmore, T. C. (eds.), *Foundations of Tropical Forest Biology: Classic Papers with Commentaries*. University of Chicago Press, Chicago, pp. 703–711.

Gould, L., Sussman, R. W., and Sauther, M. L. (2003). Demographic and life-history patterns in a population of ringtailed lemurs (*Lemur catta*) at Beza Mahafaly Reserve, Madagascar: A 15-year perspective. *Am. J. Phys. Anthropol.* 120:182–194.

Jamalabad, M. S., and Abkar, A. A. (2004). Forest canopy density monitoring, using satellite images. XXth ISPRS Congress, 12–23 July 2004, Istanbul, Turkey. Available at http://www.isprs.org/istanbul2004/comm7/papers/48.pdf.

Janzen, D. H. (1988). Tropical dry forests. The most endangered major tropical ecosystem. In: Wilson, E. O. (ed.), *Biodiversity*. National Academy Press, Washington, D.C., pp. 130–137.

Jolly, A. (1966). *Lemur Behavior: A Madagscar Field Study*. University of Chicago Press, Chicago.

Jolly, A., Dodson, A., Rasamimanana, H. M., Walker, J., O'Connor, S., Solberg, M., and Perel, V. (2002). Demography of *Lemur catta* at Berenty Reserve, Madagascar: Effects of troop size, habitat and rainfall. *Int. J. Primatol.* 23:325–353.

Koyama, N., Nakamichi, M., Oda, R., Miyamoto, N., and Takahata, Y. (2001). A ten-year summary of reproductive parameters for ring-tailed lemurs at Berenty, Madagascar. *Primates* 42:1–14.

Kramer, E. A. (1997). Measuring landscape changes in remnant tropical dry forests. In: Laurance, W. F., and Bierregaard, R. O., Jr. (eds.), *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*. University of Chicago Press, Chicago, pp. 400–409.

Mertl-Millhollen, A. S., Gustafson, H. L., Budnitz, N., Dainis, K., and Jolly, A. (1979). Population and territory stability of the *Lemur catta* at Berenty, Madagascar. *Folia Primatol.* 31:106–122.

O'Connor, S. M. (1987). *The Effect of Human Impact on Vegetation and the Consequences to Primates in Two Riverine Forests, Southern Madagascar*. Ph.D. thesis, Cambridge University, Cambridge.

Rikimaru, A., and Miyatake, S. (1997). Development of forest canopy density mapping and monitoring model using indices of vegetation, bare soil, and shadow. Available at http:\www.gisdevelopment.net/aars/acrs/1997/ts5/index.shtmm.

Roy, P. S., Miyatake, S., and Rikimaru, A. (1996). Biophysical spectral response modelling approach for forest density stratification. Available at http://www.gisdevelopment.net/aars/acrs/1996/ts5/index.shtml.

Smith, A. P. (1997). Deforestation, fragmentation and reserve design in Western Madagascar. In: Laurance, W. F., and Bierregaard, R. O., Jr. (eds.), *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*. University of Chicago Press, Chicago, pp. 415–441.

Sussman, R. W. (1974). Ecological distinction in two species of *Lemur*. In: Martin, R. D., Doyle, G., and Walker, A. C. (eds.), *Prosimian Biology.* Duckworth, London, pp. 75–108.

Sussman, R. W. (1977). Distribution of the Malagasy lemurs Part 2: *Lemur catta* and *Lemur fulvus* in southern and western Madagascar. *Ann. N. Y. Acad. Sci.* 293:170–184.

Sussman, R. W. (1991). Demography and social organization of free-ranging *Lemur catta* in the Beza Mahafaly Reserve, Madagascar. *Am. J. Phys. Anthropol*. 84:43–58.

Sussman, R. W., Green, G. M., Porton, I, Andrianasolondraibe, O. L., and Ratsirarson, J. (2003). A survey of the habitat of *Lemur catta* in southwestern and southern Madagascar. *Primate Conservation* 19:32–57.

Trejo, J., and Dirzo, R. (2000). Deforestation of seasonal dry forest: A national and local analysis in Mexico. *Biodiversity Conservation* 94:133–142.